

The Evolution of Animal Weapons

Douglas J. Emlen

Division of Biological Sciences, The University of Montana, Missoula, Montana 59812;
email: Doug.Emlen@mso.umt.edu

Annu. Rev. Ecol. Syst. 2008. 39:387–413

First published online as a Review in Advance on
September 2, 2008

The *Annual Review of Ecology, Evolution, and
Systematics* is online at ecolsys.annualreviews.org

This article's doi:
[10.1146/annurev.ecolsys.39.110707.173502](https://doi.org/10.1146/annurev.ecolsys.39.110707.173502)

Copyright © 2008 by Annual Reviews.
All rights reserved

1543-592X/08/1201-0387\$20.00

Key Words

animal diversity, sexual selection, male competition, horns, antlers, tusks

Abstract

Males in many species invest substantially in structures that are used in combat with rivals over access to females. These weapons can attain extreme proportions and have diversified in form repeatedly. I review empirical literature on the function and evolution of sexually selected weapons to clarify important unanswered questions for future research. Despite their many shapes and sizes, and the multitude of habitats within which they function, animal weapons share many properties: They evolve when males are able to defend spatially restricted critical resources, they are typically the most variable morphological structures of these species, and this variation honestly reflects among-individual differences in body size or quality. What is not clear is how, or why, these weapons diverge in form. The potential for male competition to drive rapid divergence in weapon morphology remains one of the most exciting and understudied topics in sexual selection research today.

INTRODUCTION

Sexual selection is credited with the evolution of nature's most extravagant structures, and these include showy male adornments that are attractive to females (ornaments) and an arsenal of outgrowths that function in male-male combat (weapons) (Darwin 1871). Both types of structures arise as a result of selection generated by competition over access to reproduction (Darwin 1871; West-Eberhard 1979, 1983), but the underlying mechanisms of sexual selection, female mate choice and male-male competition, differ in interesting ways that are likely to affect the evolution of these two categories of traits.

Early reviews of sexually selected traits tended to give equal weight to both ornaments and weapons (Darwin 1871, Davitashvili 1961, Richards 1927, Shine 1989), but modern considerations have focused primarily on ornaments (Andersson 1994, Andersson & Iwasa 1996). This is especially apparent for theoretical treatments of sexual selection, and genetic models for the evolution of sexually selected structures are almost entirely built around the mechanism of female mate choice (Andersson 1987, Mead & Arnold 2004; S.M. Shuster and D.J. Emlen, in preparation). Consequently, we lack an explicit theoretical framework for considering weapon evolution, and there has been no attempt to systematically review the diversity of animal weapons.

Here, I review the empirical literature on the evolution of enlarged male weapons of sexual selection. In the past few decades a great deal has been learned. Most of the relevant animal clades now include species that have been studied rigorously in the field, and for which we now have an appreciation for the biological contexts and functions of male weapons. Several of these same clades have working phylogenetic hypotheses that have permitted comparative tests of alternative scenarios of weapon evolution.

The purposes of this review are to illuminate the stunning breadth of taxa in which weapons have arisen and to highlight the myriad forms in which these structures have existed. I use this broad taxonomic review to identify common themes—critical aspects of the natural histories and ecologies of species that frequently accompany the evolution of exaggerated weapons and to identify important unanswered questions for future research. The central conclusion from this study is that animal weapons have diverged as dramatically and as rapidly as ornaments, despite the fact that these structures often experience no discernable female mate choice. This observation alone provides ample raw material for a reappraisal of our understanding of the mechanisms by which sexual selection generates nature's most spectacular forms.

THE MAJOR RADIATIONS OF ANIMAL WEAPONS¹

Arthropods: Trilobites and Crustacea

Trilobites were among the dominant invertebrates in Paleozoic seas (~543–251 Mya), and they exhibited a bewildering array of exoskeletal morphologies. Ordovician trilobites included numerous species with long spines that could exceed the length of the body and that either trailed backward and from their sides or projected dorsally and forward (**Figure 1a**) [see the **Supplemental Literature Cited** for numbered references (follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>): 73, 88, 107, 150, 264]. Some of these projections, no doubt, served to protect these animals from predators (9, 84, 89, 191, 244), but many of these spines—especially the long anterior projections—were evidently used in intraspecific male

¹For this section, numbered references are provided in the **Supplemental Literature Cited**. Follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>.



Figure 1

Weapons in arthropods I. Weapons are shown in black. (a) Trilobites. All trilobite species are extinct. 1, *Zlichovaspis rugosa*; 2, *Walliserops trifurcatus*; 3, *Bulbaspis mirabilis*; 4, *Lonchodomas volbortbi*; 5, *Cyrbaspis* sp.; 6, *Kingaspis* sp.; 7, *Ceratarges* sp.; 8, *Psychopyge elegans*; 9, *Dicranurus monstrosus*; 10, *Dicranurus monstrosus* (front view); 11, *Morocconites malladoides*. (b) Amphipods and isopods. 1, *Erichthonius difformis*; 2, *Deutella venenosa*; 3, *Bregmotypta* sp.; 4, *Geocerceis* sp.; 5, *Jassa herdmani*; 6, *Caprella verrucosa*; 7, *Microdeutopus gryllotalpa* (gnathopod only); 8, *Cymodopsis impudica*; 9, *Cilicaca tasmanensis*; 10, *Ceratocephalus grayanus*; 11, *Caprella mutica*; 12, *E. punctatus*; 13, *Platynympha* sp.; 14, *Cymodopsis impudica*; 15, *Isocladus armatus*; 16, *Paracassidina cervina*; 17, *Paracerceis* sp. (c) Decapods. 1, *Callinassa californiensis*; 2, *Macrobrachium* sp.; 3, *Callinassa gigas*; 4, *Eunephrops bairdii*; 5, *Myra fugax*; 6, *Callappa calappa*; 7, *Neoglypheca inopinata*; 8, *Uca pugnax*; 9, *Platylambrus granulata*; 10, *Homarus gammarus*; 11, *Pseudocarcinus gigas*; 12, *Callinassa australiensis*.

combat (e.g., the family Raphiophoridae; 62, 150). These structures were highly sexually dimorphic, unusually diverse in shape and location (across species), unusually variable in size (within a species), and did not become enlarged in males until the end of development (35, 150): all typical characteristics of sexually selected weapons. What critical resources these males defended is unknown, though many species apparently aggregated into groups (203, 245, 246) and excavated burrows (83, 90, 247). These are surprisingly common features of taxa with enlarged male weapons (see below).

Within the Crustacea, weapons have arisen in many groups, including amphipods, isopods, stomatopods, and especially the decapods. Amphipod weapons include enlarged claws (gnathopods), and several genera of isopods produce rigid cuticular extensions (“bosses”) that extend from their anterior or posterior ends, or elongated movable appendages (uropods) (**Figure 1b**). In both groups these structures are sexually dimorphic (41, 47, 48, 129, 137, 159, 205) and used to guard females (22, 64, 141, 231, 250, 257) or burrows or cavities used by females (21, 41, 47, 232–235). Stomatopods (mantis shrimp) are highly aggressive and defend burrows or cavities in rock or coral, and many species have enlarged raptorial appendages that they use to smash both prey and rival individuals (32, 39). Stomatopod weapons can inflict lethal blows (32, 202a) and individuals with the largest body and weapon sizes win (31).

The most diverse and extreme crustacean weapons are the enlarged, often highly sexually dimorphic chelipeds of many decapods (shrimp, crayfish, and crabs) (**Figure 1c**). Chelipeds are often used by males in contests over females, or over food or burrows used by females (11, 37, 38, 52, 130, 151, 160, 162, 173, 220), and they can be used either as weapons or as visual displays in agonistic encounters (123, 220, 242, 271).

Male fiddler crabs (*Uca*) produce the most dramatic weapons ever recorded (claws comprising 50% of total body weight; 37, 53, 162), and males in the most highly armed species use these claws in contests over burrows along the tidal margins of beaches (38, 39, 138). Females use male claws and associated visual displays (e.g., waving) to assess males (206), and claws in many species likely function as both weapons and ornaments (18). In most crustaceans studied, males with the largest weapons win contests over resources or females most frequently (38, 160, 240, 242).

Arthropods: Arachnids and Insects

Males with weapons have been studied in mites (213), spiders (93), amblypygids (261–263), and pseudoscorpions (274), as well as in most of the principal orders of insects. In males of some Australian thrips (Thysanoptera), distended forelegs and spines are used in lethal contests over oviposition sites used by females (55), and male New Zealand stone and tree wetas (Orthoptera) use their enlarged mandibles in fights over harems of females (99, 131, 146, 147, 152, 189).

Features that are enlarged in males and are used as weapons include the cerci (“forceps”) in many earwigs (Dermaptera) (**Figure 2a**) (63, 188, 212, 236), and the hind femora or tibiae of leaf-footed bugs (Hemiptera: Coreidae) (**Figure 2b**) (71, 92, 180, 182). In many coreid species, males use hind legs in visual displays during agonistic encounters (181, 184; C.W. Miller, personal communication). When competitions escalate, males turn end-to-end, wrap their hind legs around each other’s abdomens, and squeeze in intense bursts (71, 183).

Among the few enlarged sexually selected weapons in the Hymenoptera, the most extreme are the long, sometimes branched facial outgrowths in African tusked wasps (*Synagris*) (**Figure 2c**), which are used as visual signals and weapons in fights over mud burrows constructed by females on the undersides of leaves (17, 165). Specialized fighter males occur in some andrenid (57, 58) and halictid (157, 158) bees, many fig and parasitic wasps (1, 16, 51, 54, 91), and a few ants (e.g., *Cardiocondyla*) (109, 110, 248), whose males fight to the death over emerging female brood mates

in their natal nests. All of these species are unusual within their respective clades in having two discrete male types: typical dispersing males and fighter males who lack wings but have expanded heads and large mandibles.

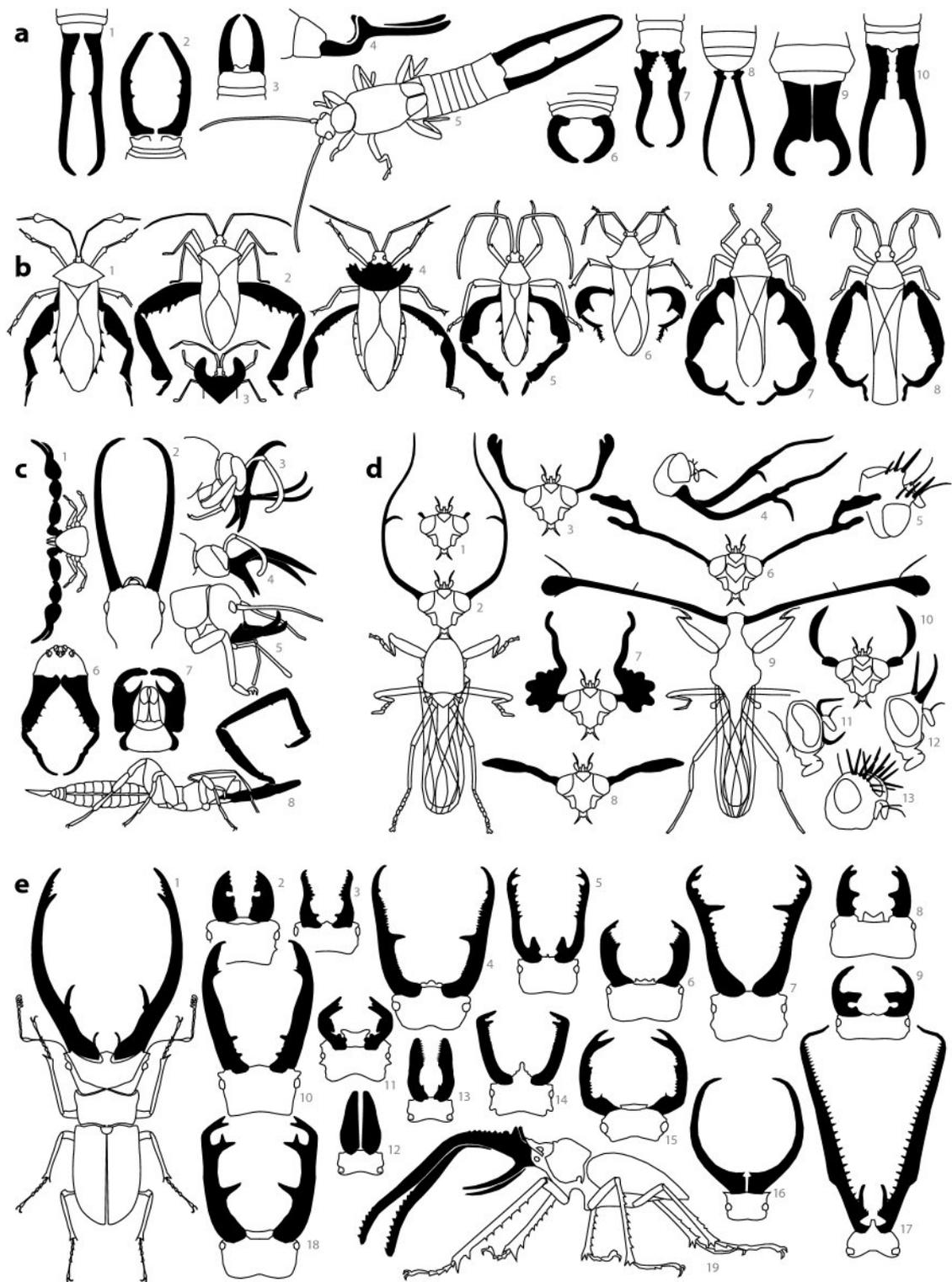
Long “antlers” that extend from the cheeks, which can be curved, branched, or palmate, have evolved in at least five families of flies (Diptera), and eyestalks have arisen in eight (**Figure 2d**) (103, 177, 227, 265). The males of all species of *Phytalmia* (Tephritidae) possess antlers, which are the most divergent morphological traits between these species (177, 178, 265). In the four species studied, males defend oviposition microsites on the surfaces of decaying wood (65, 190) and use their antlers as visual signals and in escalated fights that proceed through species-specific sequences of stereotyped interactions (e.g., rearing up on hind legs with locked antlers; 65, 265). In the mostly paleotropical Diopsidae, both sexes have eyestalks, but disproportionately long male eyestalks have arisen at least four times (10). In *Cyrtodiopsis whitei*, females coalesce at night on rootlets hanging from the banks of small streams. Males with the largest body sizes and widest eyestalks are best able to guard these nightly aggregations (28, 201) and sire the greatest number of offspring (30, 166). Defendable aggregations of females occur in most of the studied species with extreme sexually dimorphic eyestalks, but in none of the four studied monomorphic species (28, 265). In addition, females of sexually dimorphic (but not monomorphic) diopsids use eyestalks as a basis for mate choice (28, 29, 266, 269), and they derive an unusual genetic benefit from this preference: In addition to being in the best overall condition (60), males with the longest eyestalks appear to possess a suppressor to an X-linked meiotic drive element that can avoid producing extremely female-biased offspring sex ratios (139, 268).

Considering the astonishing diversity of beetles (with over 120 families and more than 330,000 species; 125), it is not surprising that exaggerated male weapons have arisen in many lineages. The champions of weaponry are the scarabs (superfamily Scarabaeoidea) (8, 59), which include approximately 14 recognizable families with an estimated 35,000 extant species worldwide that feed as larvae on microbially enriched humus, rotting wood, animal remains, fungi, plant roots, and herbivore dung (25, 102, 224).

Almost all species of Lucanidae (stag beetles) (**Figure 2e**) have enlarged mandibles in males (119, 126, 128, 143, 144, 192, 221, 229, 251). A recent molecular phylogeny suggested that ancestral lucanids had weakly developed mandibles with minimal sexual dimorphism, that exaggerated male mandibles arose at least twice, and that male mandible size was subsequently reduced at least once (119). Males in the most dimorphic species fight over access to feeding sites visited by females (sap flows on tree trunks) (108, 119, 127, 175, 192, 229), whereas males of species with weakly developed mandibles generally wait for females at oviposition sites such as the insides of hollow trees or underneath logs and decayed wood (6, 7, 119, 192). This association suggests that highly localized and defendable resources (e.g., sap flows), possibly combined with unrestricted terrain for fighting (the exposed sides of trees), may provide opportunity for males to derive fight-performance advantages from elaborate mandibular weapons, a hypothesis supported by the reduction of male mandibles in *Perisognathus angularis*, which appears to have shifted contest locations from sap sites to the insides of hollow trees (119).

The weapons most typical of scarabs are horns, which are rigid, hollow outgrowths of the body wall, often with teeth, branches, and/or dense rows of setae (8, 67). Scarab horns are generally (but not always) confined to males, and these horns can reach truly extraordinary proportions. Although almost every scarab family or subfamily has at least a few species with horns (78), the vast majority of horned species are confined to four clades, considered to represent independent origins of these weapons (8, 59; but see 78): the Geotrupidae, Cetoniinae, Scarabaeinae, and Dynastinae.

Very little is known about the function of geotrupid and cetoniid horns. Most geotrupids have head or thorax horns in males (and in some cases also in females; 121, 122) (**Figure 3a**), and



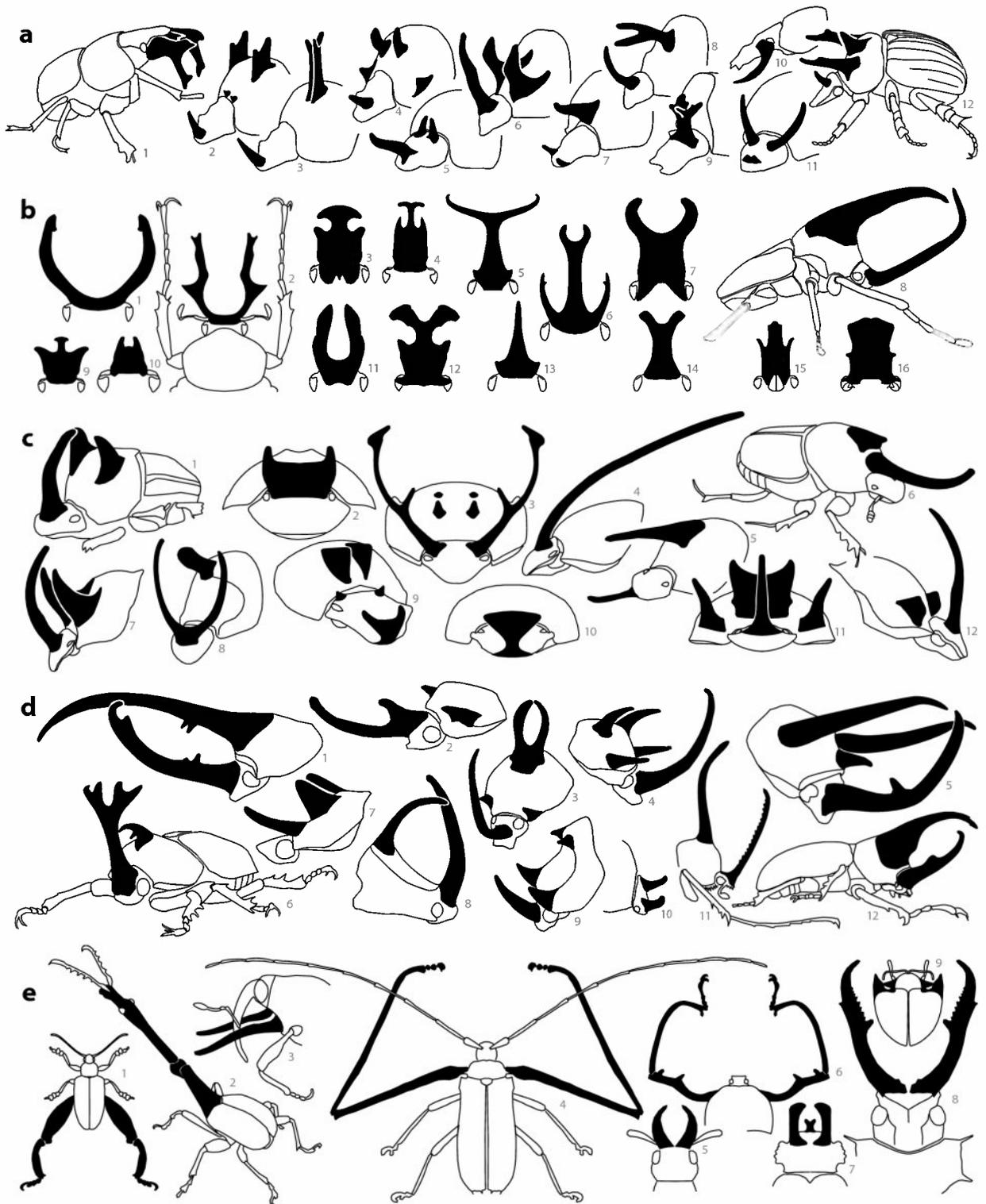
one clade in the Cetoniinae is exceptional in having enormous, often branched, cephalic male horns (**Figure 3b**) (115, 155, 161). There is evidence from a few species that males guard localized resources where females are present [e.g., tunnels (Geotrupidae) or branches (Cetoniinae); 115, 120, 200].

The Scarabaeinae, or “dung beetles,” today comprise more than 230 genera and 5000 species (104, 106). Although these beetles may have specialized originally on dinosaur dung, they diversified with the mammal radiation (36, 61). Some species have now also colonized dung from other vertebrates and invertebrates, as well as carrion, fungi, and rotting fruit (106). Thousands of scarabaeine dung beetles produce horns, and these horns appear to have been gained and lost repeatedly within this clade (79, 80). Horns of extant species occur on at least five different body regions and display a remarkable diversity of shapes and sizes (**Figure 3c**). In all horned dung beetle species studied to date, males use horns inside burrows, in contests over reproductive access to females. Both body size and horn length confer significant performance advantages to fighting males (76, 185, 198, 204, 215), and this can translate into fertilization success (124). In most species, fighting dung beetles brace themselves inside tunnels and use their horns to block passage of rival males into the tunnel, as well as to twist, pry, or otherwise dislodge opponents—all functions of horns that appear to derive in part from the confined nature of the tunnels, and suggesting that the location of contests in restricted spaces may have favored the enlargement of male weapons (67, 77, 79, 80). In a recent test of this idea, Emlen & Philips (80) showed that across a phylogeny of 45 genera of dung beetles, gains of enlarged horns in males were confined to lineages that also employed tunneling behavior, and two lineages that subsequently lost male horns also had abandoned tunneling behavior (these males fight above ground while rolling balls of dung away from the source). Interestingly, females of a number of dung beetle species also produce horns, which in some species are used in female–female contests inside burrows (215; D. Emlen and J. Marangelo, unpublished data).

The most famous of the horned beetles are the rhinoceros, Hercules, and elephant beetles (Dynastinae) (**Figure 3d**), comprising over 1500 primarily tropical species (69, 70, 81, 154, 216). Although rhinoceros beetles have been prized by collectors for centuries, the long larval developmental periods (often 2 or 3 years), relatively brief adult lifespans, and nocturnal habits of many species have made rigorous field studies of their behavior difficult, but males of a few species are known to fight over burrows, sap flows, and other localized resources attended by females (56, 66, 67, 69, 116, 238, 241; A. King, unpublished results). In *Trypoxylus dichotomus*, male fighting and mating success are positively correlated with body and horn size (116).

Figure 2

Weapons in arthropods II. (a) Dermoptera. 1, *Neolobophora ruficeps*; 2, *Ancistrogaster championi*; 3, *Labia championi*; 4, *Opisthocosmia americana* (side view); 5, *Forficula* sp.; 6, *L. arcuata*; 7, *O. americana*; 8, *A. variegatus*; 9, *F. macrobasis*; 10, *F. tomis*. (b) Corecidae (Hemiptera). 1, *Thasus acutangulus*; 2, *Acanthocephala declivis*; 3, *Capaneus* sp. 1 (head and thorax only); 4, *Capaneus* sp. 2; 5, *Pternistria* sp.; 6, *Anoplocnemis curvipes*; 7, *Espazaniella reclusa*; 8, *Romoniella perfecta*. (c) Miscellany. 1, pseudoscorpion (*Dinocheirus arizonensis*); 2, dobsonfly (*Corydalus cornutus*); 3, 4, tusked wasps (*Synagris fulva*, *S. cornuta*); 5, tusked weta (*Anisoura nicobarica*); 6, spider (*Linyphia triangularis*); 7, thrips (*Macrophthalmothrips kiesteri*); 8, whipscorpion (*Rowlandius longipalpus*). (d) Diptera. 1, *Sessilina nigrilinea*; 2, *Phytalmia alicornis*; 3, *P. robertsi*; 4, *P. alicornis* (side view); 5, *Paramyiolia nigricornis*; 6, *Phytalmia antilocapra*; 7, *P. mouldsi*; 8, *P. cervicornis*; 9, *Cyrtodiopsis dalmanni*; 10, *Giraffomyia* sp.; 11, *Wawu queenslandensis*; 12, *Paramyiolia rhino*; 13, *Strauzia intermedia*. (e) Stag beetles (Scarabaeoidea: Lucanidae). 1, *Cyclommatus elaphus*; 2, *Odontolabis latipennis*; 3, *Prosopocoilus serricornis*; 4, *Hexarthrius mandibularis*; 5, *P. bison*; 6, *Dorcus titanus*; 7, *P. giraffa*; 8, *D. alcidis*; 9, *Aegus punctipennis*; 10, *Cyclommatus giraffa*; 11, *Mesotopus tarandus*; 12, *Colophon primosi*; 13, *P. sericeus*; 14, *Weinreichius perroti*; 15, *Rbaetulus speciosus*; 16, *Sphaenognathus feistharneli*; 17, *Chiasognathus grantii*; 18, *O. femoralis*; 19, *Chiasognathus grantii* (side view).



In beetles other than scarabs, mandibular weapons have arisen at least twice in the Staphylinidae (87, 105) and occur also in some Cerambycidae, Ciidae, and Tenebrionidae (**Figure 3e**). In all of these cases, males guard mating sites on localized resources or in galleries inside fungi or rotting wood (67, 100, 145).

Male baradine weevils, with projecting, ventral, paired horns, fight over females' drilling oviposition holes in the stems of oil palms (72). Males in several brentid weevils have elongated snouts that are used to guard ovipositing females (140, 179). In the chrysomelid genus *Acromis*, males have lateral elytral and pronotal projections, which they use as forceps to grasp and remove rival males from hostplant vines (34, 272; P. Trillo, personal communication), and males of the chrysomelid *Doryphora* sp. have a ventral horn which is used to pry rival males from females (68). In the forked fungus beetle *Bolitotherus cornutus* (Tenebrionidae), males with the longest thoracic horns win disproportionate access to females (49, 50), and females appear to prefer males with long horns (24). The forelegs of male harlequin beetles (*Acrocinus longimanus*; Cerambycidae) (**Figure 3e**) are among the most extreme weapon forms in any insect (with a reach that can exceed 30 cm in width and be three times the male's body length) and are used in grappling contests over sap oozes on fig trees where females feed, mate, and lay eggs (275).

Vertebrates: Fish, Amphibians, and Reptiles

Jawless fish (Galeaspida) and sharks each radiated in the Devonian (~400 Mya) and included many species with odd projections that may have functioned as weapons (**Figure 4a**) (45, 164, 167, 168). Unicornfish, swordfish, paddlefish, and sawfish all produce bizarre structures that look like weapons (**Figure 4a**), but the functions of these structures are not well understood. Sawfish "saws" are relatively longer in males (252), and unicornfish protuberances are used as visual signals in male contests (5) and appear to have been gained multiple times (20). Spawning salmonid males have a large hump on their backs and greatly enlarged jaws used in battles over access to spawning sites and females, and in these fish body and weapon sizes predict both fighting performance and reproductive success (86, 94, 211).

Most amphibians, past and present, lack conspicuous male weapons. Diplocaulids (Carboniferous, ~350–300 Mya) had broad flattened heads with laterally projecting "horns" (**Figure 4b**) (193), and in the Southeast Asian voiceless frogs enlarged male heads, spines, and tusks, have arisen multiple times (75). In these unusual frogs, males are relatively larger than females and defend burrows in the soil (74, 75, 142, 228, 254).

Figure 3

Weapons in arthropods III. Coleoptera. (a) Dor beetles (Geotrupidae). 1, *Lethrus apterus*; 2, *Athyreus nitidus*; 3, *A. tridens*; 4, *Blackbolbus brittoni*; 5, *B. lunatus*; 6, *Blackburnium angulicorne*; 7, *Bolborbathium hollowayi*; 8, *Enoplotrupes sharpi*; 9, *B. coronatum*; 10, *Lethrus borealis*; 11, *Blackbolbus boplocephalus*; 12, *Typhaeus typhoeus*. (b) Flower beetles (Cetoniinae). 1, *Cyphonocephalus olivaceus*; 2, *Dicranocephalus bourgoini*; 3, *Eudicella quadrimaculata*; 4, *Ichnestoma rostrata*; 5, *Megalorrhina harrisi*; 6, *Mecynorrhina polyphemus*; 7, *Compsoccephalus dmitriewi*; 8, *Theodosia viridiaurata*; 9, *Taurhina polycrus*; 10, *Gnatocera trivittata*; 11, *Anisorrhina algoensis*; 12, *Goliathus albosignatus*; 13, *M. torquata*; 14, *M. passerinii*; 15, *T. longiceps*; 16, *T. splendens*. (c) Dung beetles (Scarabaeinae). 1, *Oxysternon conspiciatum*; 2, *Ontophagus capella*; 3, *Proagoderus rangifer*; 4, *O. raffrayi*; 5, *O. dunningi*; 6, *O. nigriventris*; 7, *P. lanista*; 8, *O. mouboti*; 9, *O. praecellens*; 10, *O. sharpi*; 11, *O. pentacanthus*; 12, *P. tersidorsis*. (d) Rhinoceros beetles (Dynastinae). 1, *Dynastes bercules*; 2, *Megasoma elephas*; 3, *Eupatorus birmanicus*; 4, *E. gracilicornis*; 5, *Chalcosoma caucasicus*; 6, *Allomyrina (Trypoxylus) dichotoma*; 7, *Strategus antaeus*; 8, *Enema pan*; 9, *Dipelicus cantori*; 10, *Phileurus truncatus*; 11, *Golofo porteri*; 12, *Xylotrupes gideon*. (e) Miscellaneous. 1, frog-legged leaf beetle (*Sagra buqueti*; Chrysomelidae); 2, giraffe weevil (*Lasiorhynchus barbicornis*; Curculionidae); 3, baradine weevil (*Parisoschoenus expositus*; Curculionidae); 4, harlequin beetle (*Acrocinus longimanus*; Cerambycidae); 5, rove beetle (*Oxyporus rufus*; Staphylinidae); 6, euchirid beetle (*Euchirus longimanus*; Scarabaeidae); 7, forked fungus beetle (*Bolitotherus cornutus*; Tenebrionidae); 8, *Macrodonia cervicornis* (Cerambycidae); 9, tortoise beetle (*Acromis sparsa*; Chrysomelidae).



Reptiles underwent several major radiations into both terrestrial and marine ecosystems beginning in the Triassic (~245–205 Mya) and peaking in diversity during the Jurassic (~205–145 Mya). Dinosaurs comprised a truly astonishing collection of forms, impressive both for the absolute sizes that some species attained, and for the odd collection of spines, plates, claws, crests, and frills that adorned their bodies (**Figure 4b**). Davitshavilli (62) was probably the first to propose that many of these elaborate structures were the result of sexual selection, and similar conclusions have since been reached by Molnar (186), Spassov (243), Farlow & Dodson (82) and Sampson (222).

Distinguishing weapons from ornaments is especially difficult for extinct taxa, but it is noteworthy that several dinosaur structures are now thought to have transitioned from weapons into ornaments. Early ceratopsids (e.g., *Protoceratops*) had short horns on their snouts and small frills on their heads, but both structures were enlarged and elaborated in later lineages, resulting in considerable diversity in horn and frill form (**Figure 4b**) (82, 222). Although the major horns almost certainly functioned as weapons (82, 222), the frills, and the many small horns adorning frill margins, are more likely to have functioned as visual signals (S. Sampson, personal communication). Similarly, hadrosaurs started with small cranial projections (e.g., *Kritosaurus*) that probably functioned as weapons (118), but these became increasingly large and structurally complex, and later forms are now thought to have functioned as both visual and auditory displays to either mates or rival males (118, 260). Although less well resolved at present, male combat functions have also been proposed for theropod cranial projections (187), ankylosaur tail clubs (223), and even sauropod necks (226).

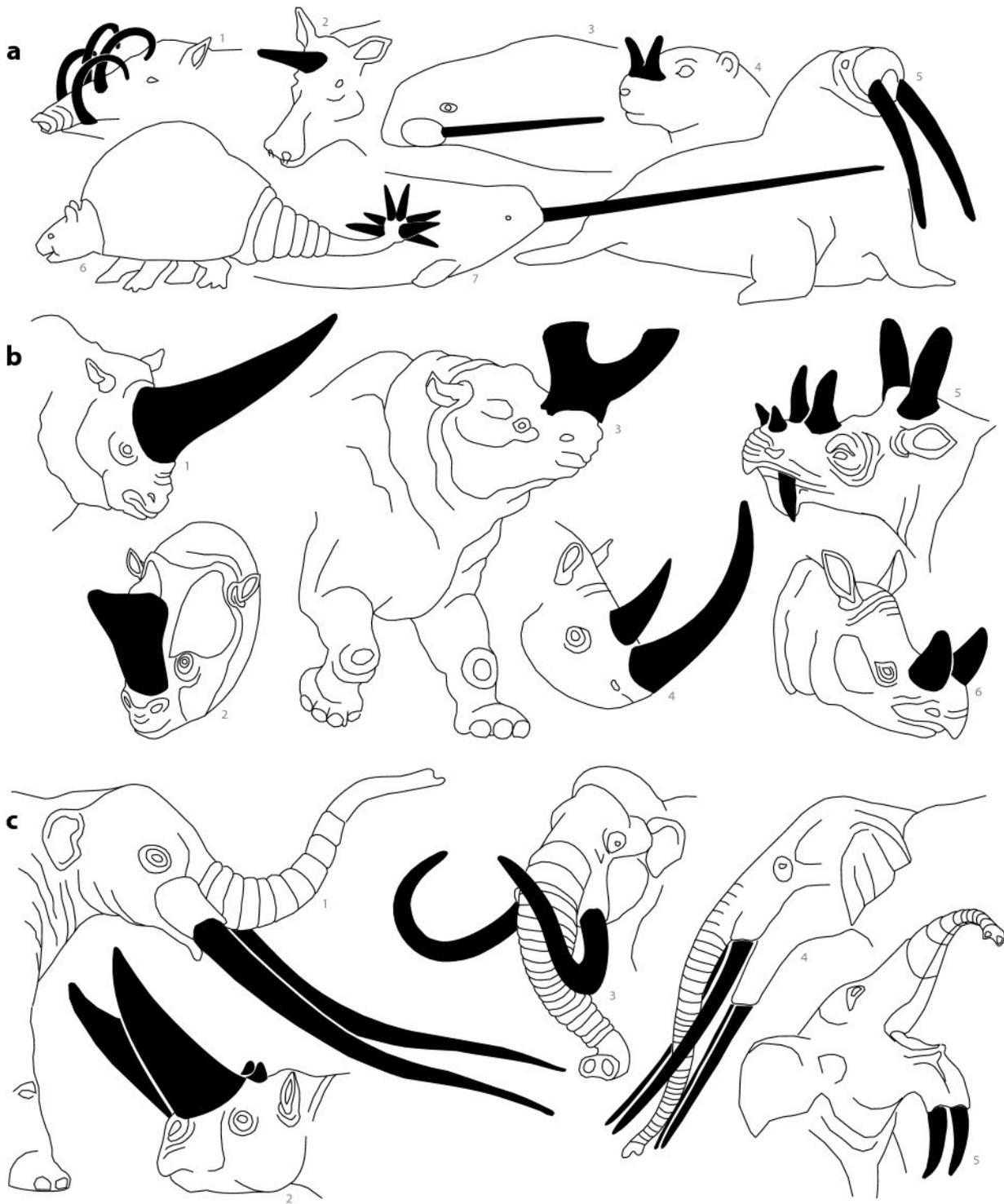
Visual displays (e.g., dewlaps, head bobbing) and male competition are pervasive and well studied in extant reptiles (4, 153, 194, 195, 197, 249, 258), but very few species produce enlarged weapons, and empirical studies of the functions of these weapons are sparse. A few species of “proboscis anoles” and several agamids produce rostral horns (172, 219, 225, 270), and many species of African chameleon produce rostral projections, ranging from broad, flat scale-colored lobes, to as many as four long pointed horns (**Figure 4c**) (19, 217, 253). What little is known about these lizards suggests that horns are used as visual signals and as weapons in agonistic male contests on tree branches (202, 214).

Vertebrates: Mammals

Although a few nonungulate lineages of mammals had impressive male weapons [e.g., the rodent *Ceratogaulus* (117), the walrus (239), and the giant armadillo *Doedicurus* (2)] (**Figure 5a**), the vast majority of sexually selected weapons arose within the hoofed mammals, or ungulates (95, 96, 133, 210, 256). In general, both the Eocene (~55–34 Mya) and the Miocene (~24–5 Mya) saw multiple

Figure 4

Weapons in vertebrates I. (a) Fish. 1, *Polyodon spathula*; 2, *Xiphias gladius*; 3, *Pristis pectinata*; 4, *Pristiophorus cirratus*; 5, *Pituriaspis doylei**; 6, *Sanhaspis* sp.* (headshield only); 7, *Naso annulatus*; 8, *Akmonistion (Stetbocanthus) zangerli**; 9, *Machiaraspis* sp.*; 10, *Lungmensbanaspis* sp.* (headshield only); 11, *Oncorhynchus nerka*; 12, *Hybodus* sp.*; 13, *Falcatus* sp.*; 14, *Protosphyraena* sp.* (Asterisks denote extinct species.) (b) Dinosaurs and other extinct reptiles, amphibians. 1, *Ceratopsaurus nasicornis*; 2, *Allosaurus fragilis*; 3, *Stygimoloch spinifer*; 4, *Elginia mirabilis*; 5, *Dicynodon* sp.; 6, *Diplocaulis* sp. (Amphibia: Nectridea); 7, *Cryolophosaurus ellioti*; 8, *Carnotaurus sastrei*; 9, *Ankylosaurus magniventris*; 10, *Therizinosaurus cheloniformis* (forelimb only); 11, *Dromaeosaurus albertensis* (hindlimb only); 12, *Hypognathus fenneri*; 13, *Stegosaurus longispinus* (tail); 14, *Dilophosaurus wetherilli*; 15, *Tsintaosaurus spinorhinus*; 16, *Corythosaurus casuaricus*; 17, *Lambeosaurus lambei*; 18, *Parasaurolophus walkeri*; 19, *Desmatosuchus haplocerus*; 20, *Styracosaurus albertensis*; 21, *Centrosaurus apertus*; 22, *Pachyrhinosaurus canadensis*; 23, *Einosaurus procurvornis*; 24, *Albertaceratops nesmoi*; 25, *Cbasmosaurus mariscalensis*. (c) Chameleons and agamids. 1, *Ceratophora tennentii*; 2, *Calumma nasuta*; 3, *Chamaeleo (Trioceros) montium*; 4, *Bradypodion tavetanum*; 5, *Harpesaurus beccarii*; 6, *C. quadricornis*; 7, *C. jacksonii*.



independent and spectacular radiations in weapon form within the ungulates (210). Because so many of these clades have well-defined fossil records of both extinct taxa and transitional sequences of morphology, it is clear that enlarged male weapons arose and diversified independently within each of the groups (33, 95, 96, 132–134, 163, 210), an observation also supported by the diverse forms and physical locations of the structures themselves (27, 210).

Within the odd-toed ungulates (Perissodactyla), the brontotheres diversified during the Eocene. Brontotheres had large, often forked, bony horns on their noses (113, 133, 170), and in some species these clearly were sexually dimorphic (210). The rhinos (Rhinocerotidae) arose from this clade during the mid-Eocene and radiated during the Miocene. Most early rhinos were hornless, but keratinized horns arose several times (209, 210) and included the side-by-side nasal horns of *Diceratherium* and the two-meter-long forehead horn of *Elasmotherium* (Figure 5b).

Weapons arose several times within the tethytheres, originally in the arsinotheres (Eocene animals with giant pairs of horns on their noses), and later in the proboscideans, which peaked in diversity during the late Miocene (~10 Mya) (Figure 5c). Early proboscideans such as *Stegotetrabelodon* had tusks arising from both their upper and lower jaws; later forms included *Deinotherium*, with tusks arising from the lower jaw, the bizarre shovel-tusked *Platybelodon*, and the extremely long-tusked *Anancus*, as well as mastodons and modern elephants (196, 210, 230).

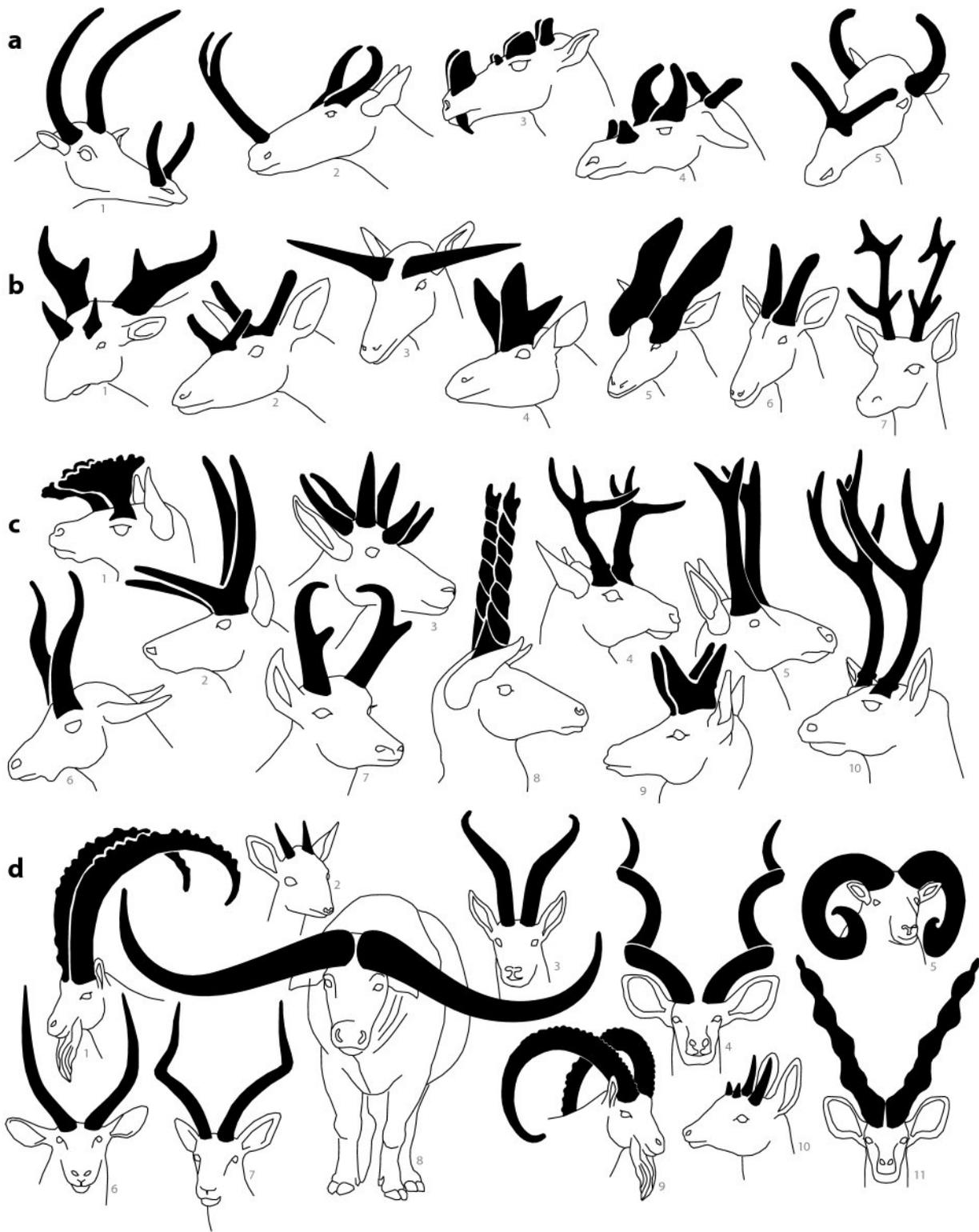
Within the even-toed ungulates (Artiodactyla), weapon radiations occurred in the pigs, giraffids, antilocaprids, cervids, and bovids, as well as in the extinct protoceratids, palaeomerycids, and hoplitomerycids. Pig-like modes of life apparently evolved several times (210), and both the entelodonts, and later the suoids, included species with impressive canines and extreme bony jaw protuberances (Figure 5a) (112, 133, 273). The earliest protoceratids (Tylopoda) were hornless, but many later species had diverse—even bizarre—head outgrowths (Figure 6a) (132, 133, 208). Both the entelodonts and the protoceratids were largely extinct by the end of the Miocene (210).

The giraffids date back to the early Miocene (~18 Mya), and by the middle of the Miocene they had diversified into at least eight forms with elaborate weapons called “ossicones” (Figure 6b) (40). Most of these taxa had died off by the Pliocene (5 Mya), and only the giraffes and okapi survive today. Interestingly, one recent study suggested that the long necks of modern giraffes may function together with the ossicones in male combat over access to females, as this species exhibits pronounced male aggression with frequent injuries to fighting males, as well as sexual dimorphism in neck and ossicone length (237) [a similar argument was also recently proposed for the sexually dimorphic necks of sauropod dinosaurs (226)].

The pronghorns (Antilocapridae) diversified during the Miocene in the Americas and were represented by an impressive variety of species and weapon forms as recently as two million years ago (Figure 6c) (133, 210, 259). In the earlier antilocaprids only the males produced the horns, but all of the more derived species had horns in both sexes (though these were relatively longer in males) (133). All but our current pronghorn (*Antilocapra americana*) went extinct by the end of the last Ice Age.

Figure 5

Weapons in vertebrates II. (a) Miscellaneous mammals. 1, babirusa (*Babirusa babirusa*); 2, horned pig (*Kubanochoerus gigas**); 3, walrus-like dolphin (*Odobenocetops* sp.*); 4, horned rodent (*Epigaulus* sp.*); 5, walrus (*Odobenus rosmarus*); 6, glyptodont (*Doedicurus* sp.*); 7, narwhal (*Monodon monoceros*). (b) Thunder beasts and rhinoceroses. 1, *Elasmotherium sibiricum**; 2, *Embolotherium andrewsi**; 3, *Brontops robustus**; 4, woolly rhino (*Coelodonta antiquitatis**); 5, *Uintatherium anceps** [Uintatheres may be more appropriately placed within the rodent/rabbit lineage (Lucas 1998.)]; 6, *B. brachycephalus**. (c) Proboscidea. 1, *Anancus arvernensis**; 2, *Arsinotherium**; 3, woolly mammoth (*Mammuthus primigenius**); 4, *Stegotetrabelodon syrticus**; 5, *Deinotherium giganteum**. (Asterisks denote extinct species.)



The true deer (Cervidae) are unique among the ungulates in bearing antlers. Antlers are rigid bony outgrowths that are shed and regrown each year, and in all of the 47 extant species except the reindeer (*Rangifer tarandus*), these weapons are confined to males (26, 27, 97, 101, 163, 210). Early deer had enlarged tusks in males (as in present-day Chinese water deer, *Hydropotes inermis*). Tusks were subsequently complemented by the addition of cranial structures (as in modern muntjac, *Muntiacus muntjak*) and eventually replaced by these cranial weapons (96, 97, 163). Early deer lineages displayed a remarkable diversity of horn (antler) locations and numbers (**Figure 7**) (133, 210). All extant deer produce a single pair of antlers at the base of the head. However, the forms of these antlers have radiated impressively and include extinct giants such as the Irish elk (*Megaloceros giganteus*), the Gallic moose (*Cervalces latifrons*), and the “brush-antlered” deer with twelve tines on each antler (*Eucladoceros sedgwicki*; **Figure 7**).

The Bovidae (antelope, cattle, sheep, goats) are the most diverse family of living ungulates, with approximately 140 extant species on four continents and more than 300 fossil species (98). The bovids underwent several rapid radiation events: an initial radiation in the early Miocene that led to the major tribes and then at least one (and possibly several) subsequent radiations associated with major changes in vegetation and climate (e.g., the emergence of savannah) (3, 98, 111, 176). Several bovid lineages independently colonized the new savannah habitats, and as a result, many morphological adaptations (including enlarged male weapons) are thought to have arisen independently in each of the bovid tribes (3), contributing to the diversity among lineages we see today.

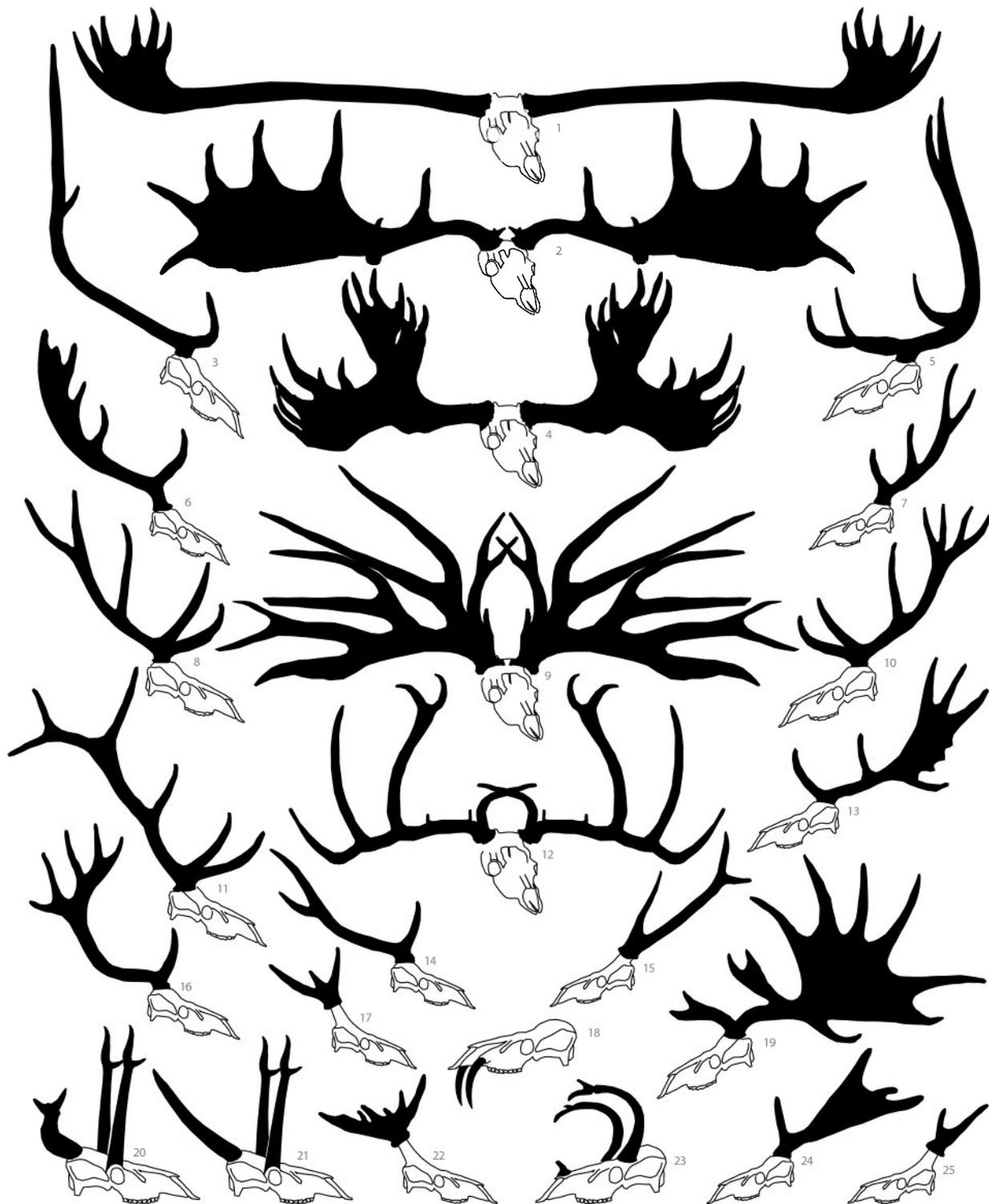
The earliest fossil bovids (*Eotragus*) had short, straight postorbital horns on their heads and were sexually dimorphic (98, 133, 136). Horn morphologies peaked in diversity in the Pleistocene (98) and today include species with thick, curled horns (e.g., bighorn sheep), twisted and spiraling horns (e.g., greater kudu), and long, straight horns (e.g., oryx (**Figure 6d**); many species also have horns in females (136, 148, 199, 218).

The ungulates are without question the best-studied animals with weapons, and countless field studies on their behavior, life history, and reproductive biology have documented weapon use as both visual signals assessed by rival males and weapons in escalated fights (13–15, 42, 114, 174, 255). Males with the largest weapons are generally the largest and best-conditioned males (42, 44, 46, 85, 255), are almost always the most likely to maintain access to females (14, 15, 43, 44, 114), and usually achieve the highest fertilization success (46, 156, 171, 207).

The ungulates are also noteworthy in that numerous researchers have tackled the question of why weapon forms are diverse. Modern considerations of this topic have converged on two basic and complementary evolutionary scenarios. The first explicitly considers the habitats and substrates in which the male fights occur (e.g., dense forests, open grasslands, cliffs), with emphasis on the details of the fights themselves, to test whether evolutionary changes in the nature of male fights (e.g., from lunging and stabbing, to stabbing and blocking, to sparring and pushing) might have led to changes in the particular forms of the weapons (e.g., additions of branches or

Figure 6

Weapons in vertebrates III. (a) Protoceratidae (Tylopoda). 1, *Kyptoceras**; 2, *Synthetoceras**; 3, *Protoceras**; 4, *Paratoceras**; 5, *Syndyoceras**. (b) Giraffidae. 1, *Sivatberium**; 2, *Giraffokeryx**; 3, *Canthuneryx**; 4, *Bramatherium**; 5, *Prolibytherium**; 6, *Samotherium**; 7, *Climacoceras**. (c) Antilocapridae. 1, *Merriamoceros**; 2, *Tetrameryx**; 3, *Hexameryx simpsoni**; 4, *Paramoceros**; 5, *Paracosoryx**; 6, *Osbornoceros osborni**; 7, *Antilocapra americana*; 8, *Ilingoceros**; 9, *Plioceros**; 10, *Ramoceros**. (d) Bovidae. 1, Spanish ibex (*Capra pyrenaica*); 2, dik-dik (*Madoqua kirkii*); 3, Grant's gazelle (*Gazella granti*); 4, kudu (*Tragelaphus strepsiceros*); 5, bighorn sheep (*Ovis canadensis*); 6, waterbuck (*Kobus ellipsiprymnus*); 7, impala (*Aepyceros melampus*); 8, long-horned African buffalo (*Peloroavis antiquus*)*; 9, Asiatic ibex (*Capra ibex*); 10, chowsingha (*Tetracerus quadricornis*); 11, markhor (*Capra falconeri*). (Asterisks denote extinct species.)



tines, inward or outward curls). This approach has been applied to weapon radiations in both the cervids and bovids (12, 95–97, 149, 163, 169), and in general these comparative (though often not phylogenetic) studies have concluded that habitat-specific changes in male fighting styles, resulting in part from evolutionary increases in overall body size, are likely to have contributed to the evolution of increasingly large and elaborate male weapons.

The second approach also focuses on the ecological contexts in which fights take place, including especially the habitats (forest, grassland, etc.), but emphasizes the distribution and defensibility of food resources (selective foragers on forbs, grazers on abundant fibrous vegetation) and the mating systems that are favored in these ecological situations (territorial and largely solitary pairs, resource-defense and harem-defense polygyny). This approach has been applied to both cervids and bovids (133, 135, 148, 199), and using reconstructions of paleoenvironments and dentition of fossil taxa, it has also been applied to extinct ruminants (132, 133) and ceratopsid dinosaurs (186, 222). The general conclusions are that the evolutionary transitions in ungulates from forests to open grasslands and savannah were accompanied by increased group sizes, as well as increased potential for males to guard access to multiple females. This led to increases in the intensity of sexual selection and favored the evolution of increasingly large and elaborate male weapons.

Only very recently have phylogenetic comparative methods been used to test directly for evolutionary associations between these aspects of ecology and behavior and specific changes in ungulate weapon morphology. Caro et al. (33) found compelling support for relationships between mating system (e.g., monogamy versus polygyny), group size (intensity of sexual selection), fighting style (stabbing, wrestling), and major changes in weapon size and shape in both bovids and cervids. Similarly, in his study of bovids, Bro-Jorgensen (23) found that the intensity of sexual selection predicted weapon size.

SYNTHESIS: THE NATURE OF ANIMAL WEAPONS

Weapons Evolve in Animals with Resource-Defense or Female-Defense Mating Systems

In almost all of the animals studied, weapons were used to defend critical resources that directly or indirectly translated into mating opportunities. Despite a truly breathtaking range of habitats and lifestyles, all of the resources in question were limiting in either space or time, and they were localized in ways that rendered them economically defendable. By displacing rival males, the winners of these contests are predicted to garner disproportionate access to fertilizations, and these reproductive benefits, if they are high enough, can outweigh even substantial costs of producing and bearing a weapon (Grafen 1990, Nur & Hasson 1984, Parker 1983, Zeh & Zeh 1988). Thus, we predict weapons will be favored whenever the benefits of their expression outweigh the costs, and in an ecological context this occurs whenever critical resources are confined in such a way that one or a few males are able to defend them (Emlen & Oring 1977).

Figure 7

Weapons in vertebrates IV. Cervidae and Dromomerycidae. 1, *Cervalces latifrons**; 2, *Megaloceros giganteus**; 3, *Axis axis*; 4, *Cervalces scotti**; 5, *Cervus elaphus affinis*; 6, *Aoglochia* sp.; 7, *Cervus* sp.*; 8, *C. elaphus acoronatus**; 9, *Eucladoceros sedgwicki**; 10, *C. elaphus hippelaphus**; 11, *C. elaphus canadensis*; 12, *E. senezensis**; 13, *Dama dama**; 14, *Axis* sp.*; 15, *Rusa unicolor*; 16, *Rucervus* sp.; 17, *Dicrocerus* sp.*; 18, *Hydropotes inermis*; 19, *Megaceros giganteus**; 20, *Procranioceras** (Dromomerycidae); 21, *Cranioceras** (Dromomerycidae); 22, *Stephanocemas**; 23, *Sinclairiomeryx** (Dromomerycidae); 24, *Cervavitus* sp.*; 25, *Eustyllocerus**. (Asterisks denote extinct species.)

In a surprising diversity of taxa, these critical resources were burrows or tunnels where females lay eggs, and the especially defensible nature of burrows may have played an important role in favoring the evolutionary enlargement of weapons in these cases. Most of the beetles with weapons (Daguerre 1931; Eberhard 1979, 1987; Emlen & Philips 2006) and many of the amphipods (Clark 1997; Conlan 1989, 1991), isopods (Shuster 1989), decapods (Christy & Salmon 1984, Jennions & Backwell 1996, Knowlton & Keller 1982), tusked wasps (Longair 2004), big-headed bees (Kukuk & Schwartz 1988), and tusked frogs (Emerson 1992) guard entrances to burrows containing females [even horned rodents may have guarded burrows (Hopkins 2005)]. In other cases, feeding or egg-laying sites are confined in ways that permit them to be guarded by males, as occurs along branches and new shoots of plants guarded by coreid bugs (Miyatake 2002), rhinoceros and cerambycid beetles (Eberhard 1978, Goldsmith 1987), and chameleons (Parcher 1974); sap oozes on tree trunks guarded by many rhinoceros beetles (Hongo 2007) and stag beetles (Hosoya & Araya 2005); and bracts of fungi guarded by tenebrionid and staphylinid beetles (Conner 1988, Hanley 2001). In still other cases, males guard access to females directly, as in stalk-eyed flies (Burkhardt & de la Motte 1987, Lorch et al. 1993, Wilkinson & Dodson 1997), amphipods (Ward 1988), crabs (Jormalainen 1998), and many ungulates (Coltman et al. 2001).

All of these taxa exploit some type of critical resource that is patchily distributed and required by females, and males compete for exclusive access to these locations. Although the actual intensities of selection on male weapons have only been quantified for a few species (Coltman et al. 2001, Conner 1988, Hongo 2007, Hunt & Simmons 2001, Kruuk et al. 2002, Preston et al. 2003, Shuster & Wade 1991, Wellborn 2000, Zeh & Zeh 1992), it appears that the ecology and behavior of these animals generally result in intense and consistent directional sexual selection for increased competitive abilities in males. These situations could easily lead to the rapid evolution of extreme trait sizes (Andersson 1994; West-Eberhard 1979, 1983) and may help explain the prolific occurrence of extreme weapon proportions across taxa.

Weapons Honestly Indicate Differences in Individual Condition or Quality

Fisher (1930) first pointed out that it would not pay for small males to cheat by producing a mismatched weapon, because these males would be challenged repeatedly by rivals and quickly discovered as charlatans. More recent theoretical models reach the same conclusion: Not all males in a population should benefit from producing the largest possible weapon sizes. Specifically, males in the best physical condition—often those with the best nutritional histories, best genetic qualities, and/or the largest body sizes—are predicted to invest relatively more into weapons than poorer-condition, smaller males (Bonduriansky & Day 2003, Grafen 1990, Kodric-Brown et al. 2006, Nur & Hasson 1984, Zeh & Zeh 1988).

Many of the animal weapons reviewed here have been studied in this regard. All exaggerated male weapons vary prolifically among individuals within populations, and nearly always, these weapons are the most variable structures in these species. Furthermore, allocation to weapon growth is exquisitely sensitive to individual condition and to aspects of the environment that affect condition, such as nutrition (Kruuk et al. 2002, Kukuk 1996, Kurdziel & Knowles 2002, Smith & Palmer 1994, Tömkins 1999), and parasites (Folstad et al. 1996, Ezenwa & Jolles 2008). Consequently, enlarged or exaggerated animal weapons almost always amplify and honestly indicate among-individual differences in size, condition, or quality [e.g., fiddler crab claws (Levinton & Allen 2005, Pope 2000) and deer antlers (Kruuk et al. 2002, Vanpe et al. 2007)].

Weapons Function as Assessment Signals as Well as Armaments in Combat

Game theory models of male combat predict that males will benefit if they are able to assess the potential of rival males and avoid dangerous contests with unbeatable opponents. These models make two specific predictions, both of which have been substantiated repeatedly in taxa with pronounced weapons. First, weapons should function as signals that are used by males to resolve contests, and second, contests should be most likely to escalate when opponents are similar in body or weapon size (Enquist & Leimar 1983, Maynard Smith 1974, Parker 1974). Crab and shrimp claws, fish horns, coreid femora, and the antlers of flies and deer have been found to function as visual or tactile signals in male contests, and in all of these animals fights are most likely to escalate into true battles only when rival individuals are similar in size (Arai & Sato 2007, Barrette & Vandal 1990, Hoem et al. 2007, Hughes 1996, Jennions & Backwell 1996, Miyatake 1993, Panhuis & Wilkinson 1999, Rubenstein & Hazlett 1974, Sneddon et al. 1997, Wilkinson & Dodson 1997).

Interestingly, this basic process may account for one of the recurring patterns of weapon evolution. The most elaborate weapons rarely inflict real damage to opponents, but these structures are very effective at revealing even subtle differences among males in their size, status, or physical condition [e.g., rhinoceros beetle horns (Eberhard 1979), fiddler crab claws (Levinton & Allen 2005), and harlequin beetle forelegs (Zeh et al. 1992)]. In contrast, many animals with unimpressive or even inconspicuous weapons regularly inflict serious damage in male contests [e.g., many wasps (Abe et al. 2003, Bean & Cook 2001, Danforth 1991) and spiders (Leimar et al. 1991)], and this pattern suggests a causal mechanism for the enlargement and elaboration of weapons: Weapons of increased size or complexity may be favored because they more readily incorporate an assessment component to their function.

For a few clades it is now possible to reconstruct some of the historical sequences of weapon evolution, and the same basic pattern is evident in the cervids and bovids (Geist 1966, 1998; Lincoln 1994; Lundrigan 1996), ceratopsids (Farlow & Dodson 1975, Sampson 1997), and hadrosaurs (Hopson 1975). Weapons begin as relatively small and very dangerous traits (e.g., short, sharp horns, fangs, tusks). Later versions tend to be much larger, more complex, and in particular, more likely to serve as indicators of status assessed by rival males. The recurrence of this basic transitional sequence implicates the evolution of assessment behavior as a mechanism driving the diversification of weapon, form a hypothesis that will need to be tested directly in future research. If true, then we would predict a positive relationship across taxa within a clade between the degree of elaboration or exaggeration of weapons and the extent to which male contests are resolved by assessment prior to escalated combat (or a negative correlation with the relative frequency of lethal or dangerous male combat).

Some Weapons Also Function in Female Choice

Berglund et al. (1996) suggested that if weapons convey such useful information to rival males, females should also benefit from this information. Although by no means universal, it does appear that many male weapons are used by females as a basis for mate choice. Female preferences for males with large weapons have been observed in earwigs (Moore & Wilson 1992, Tomkins & Simmons 1998), stalk-eyed flies (Burkhardt & de la Motte 1988, Wilkinson et al. 1998), and fiddler crabs (Pope 2000).

That female choice may also be shaping weapon evolution raises several exciting possibilities. Models of ornaments suggest that female choice can dramatically accelerate the rate of evolution of ornament size or complexity (reviewed in Andersson 1994, Mead & Arnold 2004), but this has

never been explicitly tested in the case of weapons (but see A.J. Moore & J.B. Wolf, in preparation; S.M. Shuster & D.J. Emlen, in preparation). One obvious direction for future empirical research would be to compare the relative rates of evolution of weapons that are, and are not, also used as a basis for female mate choice, and to test whether traits of dual function (sensu Berglund et al. 1996) evolve more rapidly and/or reach more extreme sizes than do pure weapons.

Some Females Bear Weapons as Well

The spiny horns of “horned lizards” (*Pbrynosoma*) and “thorny devils” (*Moloch horridus*) are produced by both males and females, and horns in these species are thought to function primarily as a defense against predators (Young et al. 2004). In many beetles, some decapods, and many of the armed dinosaurs, fish, and ungulates, the females also produce weapons. In virtually every case these female weapons are similar to, but smaller than, the corresponding structures of males. In the few studied examples, females use horns in fights with conspecific females, generally over food resources or to protect young (e.g., Berger & Cunningham 1994, Knowlton & Keller 1982, Ezenwa & Jolles 2008). Two comparative studies explicitly tested for a role of sexual selection in the evolution of female weapons and concluded that these structures most likely had been shaped by natural, rather than sexual selection (Bro-Jorgensen 2007, Caro et al. 2003). Although several reviews have focused on this topic (Kiltie 1985, Packer 1983, Roberts 1996), a great many taxa with female weapons have yet to be studied, and basic questions still linger. For example, under what circumstances do female weapons evolve? Do weapons arise in both sexes due to natural selection (e.g., as a defense against predators) and then subsequently become co-opted as signals in males? Or do these weapons arise initially in males, and only in specific circumstances become co-opted by females? To what extent can/does the evolution of female weapons occur independently from the evolution of male weapons?

WHY ARE ANIMAL WEAPONS DIVERSE?

Animal weapons clearly are capable of rapid diversification in form, and most clades with exaggerated male fighting structures are characterized by extraordinary among-species variation in weapon morphology. Here, the biology is less well understood, and with only a very few exceptions, compelling arguments for why male weapons should differ in form are lacking. In almost all cases, the details of the shape or structure of the weapons, and in particular, the differences in these details from one species to the next, have not been adequately explored.

Nonetheless, several mechanisms have been proposed to account for weapon diversity. One, already mentioned, is that weapons gradually change their function from pure armaments to structures that increasingly perform display or other assessment behaviors [in addition to serving in combat (Mechanism 1)]. These assessment functions could then favor any of numerous possible elaborations to weapon form, provided that these new versions enhance the ability of individuals to readily communicate their status or condition to opponents (or to mates), and provided the new versions could still be used in fights when necessary. There are many ways to make a weapon more conspicuous, and subsequent adornments can take a variety of forms. Thus, in principle, this process can occur along independent trajectories in each lineage, and it has the potential to generate among-species divergence in weapon morphology (West-Eberhard 1983).

A corollary of this could also shape the directions of weapon evolution (Mechanism 2). Non-lethal assessment can take many forms. Certainly, visually conspicuous structures facilitate this process. But so, too, do ritualized or stereotyped contest behaviors. In many taxa, males lock their weapons into highly repeatable positions, and thus entwined, engage in protracted pushing or

wrestling matches. With weapons locked into position, males are able to effectively assess the strength and condition of rivals without significant risk of physical harm. This type of combat has been proposed for many ungulates (Geist 1966, 1998; Lincoln 1994), ceratopsids (Farlow & Dodson 1975, Sampson 1997, Spassov 1979), and several beetles (Eberhard 1979), and in all of these taxa males have grooves or forks in either their weapons or the contact regions of their bodies that “fit” the weapons of rival males. Baradine weevils actually have deep invaginations into their chest cavity that fit the paired horns of opponent males, and effective battles require the horns to be inserted into these pockets (Eberhard et al. 2000). Thus, the evolution of ritualized pushing or wrestling may select for particular features or shapes of weapons. For this process to generate divergence in weapon form, it would have to favor different locking mechanisms in different lineages, and it is not clear why this should occur (indeed, this form of fighting has been proposed to generate stabilizing, rather than diversifying, selection; Andersson 1994). Nevertheless, this aspect of combat behavior may help explain some of the details of weapon morphology in specific lineages, and in principle, it could contribute to the evolutionary diversification of weapon form.

Additional mechanisms have been proposed that also involve the particulars of the male contests. In one case, divergent lineages of animals, by expanding into new and different habitats, may end up fighting under very different conditions, and these changes in the physical contexts of male contests may drive the evolution of habitat-specific modifications to weapon form (Mechanism 3). We have already seen how this logic has been applied to diversity in ungulate weapons (Caro et al. 2003, Geist 1966, Lincoln 1994, Lundrigan 1996), and similar processes may help explain variation in insect weapons [e.g., stag and rhinoceros beetles that fight in the open on tree trunks or branches have longer and spindlier legs and more awkward horns than species that fight inside burrows or under logs (Eberhard 1979, Hosoya & Araya 2005)], but these ideas have yet to be tested directly.

However, it is clear that this mechanism does not explain weapon diversity in all cases, because it is possible for taxa to radiate into diverse habitats without significantly altering the physical contexts of their male contests. This is particularly relevant for the many animals that defend burrows. One recent phylogenetic study of dung beetles found surprisingly little association between aspects of the habitat or ecology of species and the types of weapons they produced (Emlen et al. 2005), and this appears to reflect the fact that male fights nearly always occurred in the same setting (inside burrows), regardless of where the beetles lived (e.g., desert, savannah, tropical wet forest) or what types of dung resources they utilized. Consequently, habitat-specific variation in fighting styles may help explain the evolutionary diversification of weapon morphologies in clades of animals that fight in varied physical contexts (as appears to be the case for ungulates and possibly the dynastine and lucanid beetles), but these explanations are predicted to be less useful for taxa that consistently fight over similar resources (e.g., burrows).

It is also possible that the nature of the fights themselves may confer a performance advantage to novelty per se (Mechanism 4) (Darwin 1871, West-Eberhard 1983). If adornments to a weapon (e.g., new forks, tines, or twists) gave their bearers an edge, then male competition could prove to be a potent driver of weapon divergence. This idea is especially attractive given that it is compatible with arms races and that it can lead to “arbitrary” directions of weapon evolution. This mechanism could well account for the seemingly inexplicable differences in weapon form that we observe across taxa. However, it is not at all clear why novelties should confer performance advantages in contests, and to my knowledge, this mechanism has yet to be rigorously tested for any clade.

In some cases, the directions of weapon evolution may be driven by selection to minimize the costs of producing and wielding these structures (Mechanism 5) (Emlen 2001). Whenever alternative weapon forms differ in the nature of the costs they incur (e.g., in flying insects, mandible

or horn shapes may affect the center of gravity, wing loading, rotational inertia, and the streamlining of these animals as they fly), then the potential exists for selection to favor some weapon forms over others in different environments. In one study of dung beetles, among-species patterns of weapon diversity were best explained by considering pleiotropic consequences (trade-offs) of horns for adjacent morphological structures (e.g., eyes, antennae, wings), and at least some of the historical transformations in horn morphology in these beetles may have been brought about to minimize these different costs of horns in specific habitats (Emlen et al. 2005).

Finally, it may be that the volatility of sexual selection in general, and its intrinsic potential for rapid character evolution, is sufficient to generate diversity in weapon form, irrespective of the particular habitats or fighting styles (Mechanism 6). Because performance in male competition is always measured relative to the milieu of rival males present at any place and time, sexual selection may be especially sensitive to chance events (West-Eberhard 1983). Even brief population bottlenecks, or founder events, if they alter the mixture of male phenotypes, may be sufficient to tip the subsequent evolution of that population in a new direction. Most likely, this volatility of intense selection, combined with any mechanism resulting in speciation, would be enough to initiate divergence in weapon form, and these processes may combine easily with any of the above mechanisms to drive related lineages of animals along very different trajectories of weapon evolution: all increasing in size and complexity, but in different directions (West-Eberhard 1983). This logic has been incorporated into recent theoretical models for the evolution of ornament diversity and speciation (i.e., for female choice; Higashi et al. 1999, Panhuis et al. 2001, Pomiankowski & Iwasa 1998, Ritchie 2007, Schluter & Price 1993), but it has yet to be considered for weapons.

It is noteworthy that many of the clades in this review are thought to be specious for reasons that have nothing to do with sexual selection or the weapons themselves. For example, the major radiations of ungulates coincided with dramatic changes in climate, the appearance of new and open habitats (grasslands, savannas), and cyclic expansion and contraction of habitats (e.g., from the advancing and retreating ice sheets of the successive ice ages)—all potential drivers of speciation (Gentry 1990, Hernandez-Fernandez & Vrba 2005). Similarly, dramatic habitat fluctuations are thought to have driven pulses of diversification in dinosaurs (e.g., the repeated expansion and retraction of the Cretaceous Western Interior Seaway in North America; Horner et al. 1992, Sampson 1997). In this case, explosions of rapidly diverging animal lineages may be the backdrop against which the most impressive radiations in weapons evolved, and the diversity of weapons may simply be an inevitable outcome of a volatile agent of rapid change superimposed on splitting lineages.

At the time of this publication, comparative phylogenetic tests of alternative hypotheses for the diversity of weapon form are almost nonexistent, and even these are merely first attempts at resolving these questions. Theoretical treatments of weapon divergence have yet to be attempted, and as a result we know surprisingly little about how or why animal weapons should exhibit such stunning variations in form.

In summary, exaggerated male weapons of sexual selection have arisen many, many times and have radiated spectacularly in form. Without question, the diversity of these structures easily rivals that of their better-studied counterparts, the ornaments of female mate choice. Many of these armed species have now been studied rigorously in the field, and from these studies it appears that existing theory does an admirable job of characterizing the biology of male-male competitions, with explicit predictions for the ecological contexts of fights, the intensity and duration of fights, the investment patterns by individual males into the armaments of fights, and the assessment of these weapons by both rival males and females, all of which receive robust empirical support from diverse taxa. What is less well understood is how the mechanism of male-male competition compares to that of female choice, particularly with respect to the relative rates of character

evolution, and to the intrinsic potential for divergence in trait form. Indeed, the most glaring void in our understanding of weapon evolution concerns the mechanisms generating diversity in weapon form. The potential for male competition to drive rapid divergence in weapon morphology remains one of the most exciting and understudied topics in sexual selection research today.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I thank the National Science Foundation (IOS-0642409) for funding and Kerry Bright, John Christy, William Eberhard, Ben Ewen-Campen, Vanessa Ezenwa, Douglas Futuyma, Anne Greene, Ashley King, Christine Janis, Annika Kinsner, Roselyn Lowe-Webb, Tara Maginnis, Christine W. Miller, Josephine Pemberton, J. Mark Rowland, Scott Sampson, and especially Steve Shuster for help with the ideas and manuscript.

LITERATURE CITED

- Abe J, Kamimura Y, Kondo N, Shimada M. 2003. Extremely female-biased sex ratio and lethal male-male combat in a parasitoid wasp, *Melittobia australica* (Eulophidae). *Behav. Ecol.* 14:34–39
- Andersson M. 1987. Genetic models of sexual selection: some aims, assumptions and tests. In *Sexual Selection: Testing the Alternatives*, ed. JW Bradbury, MB Andersson, pp. 41–53. Chicago: Wiley
- Andersson M. 1994. *Sexual Selection*. Princeton: Princeton Univ. Press
- Andersson M, Iwasa Y. 1996. Sexual selection. *Trends Ecol. Evol.* 11:53–58
- Arai H, Sato T. 2007. Prominent ornaments and rapid color change: use of horns as a social and reproductive signal in unicornfish (Acanthuridae: Naso). *Ichthyolog. Res.* 54:49–54
- Barrette C, Vandal D. 1986. Social rank dominance: antler size and access to food in snow-bound wild woodland caribou. *Behaviour* 97:118–46
- Bean D, Cook JM. 2001. Male mating tactics and lethal combat in the nonpollinating fig wasp *Sycoscapter australis*. *Anim. Behav.* 62:535–42
- Berger J, Cunningham C. 1994. Phenotypic alterations, evolutionarily significant structures, and rhino conservation. *Conserv. Biol.* 8:833–40
- Berglund A, Bisazza A, Pilastro A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol. J. Linn. Soc.* 58:385–99
- Bonduriansky R, Day T. 2003. The evolution of static allometry in sexually selected traits. *Evolution* 57:2450–58
- Bro-Jorgensen J. 2007. The intensity of sexual selection predicts weapon size in male bovids. *Evolution* 61:1316–26
- Burkhardt D, de la Motte I. 1987. Physiological, behavioural, and morphometric data elucidate the evolutive significance of stalked eyes in Diopsidae (Diptera). *Entomol. Gener.* 12:221–33
- Burkhardt D, de la Motte I. 1988. Big ‘antlers’ are favoured: female choice in stalk-eyed flies (Diptera, Insecta), field collected harems and laboratory experiments. *J. Comp. Physiol. A Sensory Neural Behav. Physiol.* 162:649–52
- Caro TM, Graham CM, Stoner CJ, Flores MM. 2003. Correlates of horn and antler shape in bovids and cervids. *Behav. Ecol. Sociobiol.* 55:32–41
- Christy JH, Salmon M. 1984. Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*). *Biol. Rev.* 59:483–509
- Clark RA. 1997. Dimorphic males display alternative reproductive strategies in the marine amphipod *Jassa marmorata* Holmes (Corophioidea: Ischyroceridae). *Ethology* 103:531–53

- Coltman DW, Festa-Bianchet M, Jorgenson JT, Strobeck C. 2001. Age-dependent sexual selection in bighorn rams. *Proc. R. Soc. B Biol. Sci.* 269:165–72
- Conlan KE. 1989. Delayed reproduction and adult dimorphism in males of the amphipod genus *Jassa* (Corophioidea: Ischyroceridae): an explanation for systematic confusion. *J. Crustacean Biol.* 9:601–25
- Conlan KE. 1991. Precopulatory mating behavior and sexual dimorphism in the amphipod Crustacea. *Hydrobiologia* 223:255–82
- Conner J. 1988. Field measurements of natural and sexual selection in the fungus beetle *Bolitotherus cornutus*. *Evolution* 42:736–49
- Daguerra JB. 1931. Costumbres nupicales del *Diloboderus abderus* Sturm. *Rev. Soc. Entomologia Argent.* 3:253–56
- Danforth BN. 1991. The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). *Behav. Ecol. Sociobiol.* 29:235–47
- Darwin C. 1871. *The Descent of Man*. London: William Clowes and Sons
- Davitashvili L. 1961. *The Theory of Sexual Selection*. Moscow: Izo-vo Acad. Nauk USSR. 538 pp.
- Eberhard WG. 1978. Fighting behavior of male *Golofa porteri* beetles (Scarabaeidae: Dynastinae). *Psyche* 83:292–98
- Eberhard WG. 1979. The function of horns in *Podischnus agenor* (Dynastinae) and other beetles. In *Sexual Selection and Reproductive Competition in Insects*, ed. MS Blum, NA Blum, pp. 231–59. New York: Academic
- Eberhard WG. 1987. Use of horns in fights by the dimorphic males of *Ageopsis nigricollis* Coleoptera Scarabaeidae Dynastinae. *J. Kansas Entomol. Soc.* 60:504–9
- Eberhard WG, Garcia CJM, Lobo J. 2000. Size-specific defensive structures in a horned weevil confirm a classic battle plan: avoid fights with larger opponents. *Proc. R. Soc. London Ser. B Biol. Sci.* 267:1129–34
- Emerson SB. 1992. Courtship and nest-building behavior of a Bornean frog, *Rana blythi*. *Copeia* 1992:1123–27
- Emlen DJ. 2001. Costs and the diversification of exaggerated animal structures. *Science* 291:1534–36
- Emlen DJ, Marangelo J, Ball B, Cunningham CW. 2005. Diversity in the weapons of sexual selection: Horn evolution in the beetle genus *Ontobopagus* (Coleoptera: Scarabaeidae). *Evolution* 59:1060–84
- Emlen DJ, Philips TK. 2006. Phylogenetic evidence for an association between tunneling behavior and the evolution of horns in dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae). *Coleopterists Soc. Monogr.* 5:47–56
- Emlen ST, Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–23
- Enquist M, Leimar O. 1983. Evolution of fighting behavior decision rules and assessment of relative strength. *J. Theor. Biol.* 102:387–410
- Ezenwa VO, Jolles AE. 2008. Horns honestly advertise parasite infection in male and female African buffalo. *Anim. Behav.* In Press
- Farlow JO, Dodson P. 1975. The behavioral significance of frill and horn morphology in ceratopsian dinosaurs. *Evolution* 29:353–61
- Fisher RA. 1930. *The Genetical Theory of Natural Selection*. Oxford United Kingdom: Oxford University Press
- Folstad I, Arneberg P, Karter AJ. 1996. Antlers and parasites. *Oecologia* 105:556–58
- Geist V. 1966. The evolution of horn-like organs. *Behavior* 27:175–214
- Geist V. 1998. *Deer of the World*. Mechanicsburg, PA: Stackpole Books
- Goldsmith SK. 1987. Male dimorphism in *Dendrobias mandibularis* Aubinet-Serville (Coleoptera: Cerambycidae). *J. Kansas Entomol. Soc.* 58:534–38
- Grafen A. 1990. Biological signals as handicaps. *J. Theor. Biol.* 144:517–46
- Hanley RS. 2001. Mandibular allometry and male dimorphism in a group of obligately mycophagous beetles (Insecta: Coleoptera: Staphylinidae: Oxyporinae). *Biol. J. Linn. Soc.* 72:451–59
- Hernandez-Fernandez M, Viba ES. 2005. A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. *Biol. Rev.* 80:269–302
- Higashi M, Takimoto G, Yamamura N. 1999. Sympatric speciation by sexual selection. *Nature* 402:523–26
- Hoem SA, Melis C, Linnell JDC, Andersen R. 2007. Fighting behaviour in territorial male roe deer *Capreolus capreolus*: the effects of antler size and residence. *Eur. J. Wildlife Res.* 53:1–8
- Hongo Y. 2007. Evolution of male dimorphic allometry in a population of the Japanese horned beetle *Trypoxylus dichotomus septentrionalis*. *Behav. Ecol. Sociobiol.* 62:245–53
- Hopkins SSB. 2005. The evolution of fossoriality and the adaptive role of horns in the Mylagaulidae (Mammalia: Rodentia). *Proc. R. Soc. B Biol. Sci.* 272:1705–13

- Hopson JA. 1975. The evolution of cranial display structures in hadrosaurian dinosaurs. *Paleobiology* 1:21–43
- Horner JR, Varricchio DJ, Goodwin MB. 1992. Marine transgressions and the evolution of Cretaceous dinosaurs. *Nature* 358:59–61
- Hosoya T, Araya K. 2005. Phylogeny of Japanese stag beetles (Coleoptera: Lucanidae) inferred from 16S mtDNA gene sequences, with reference to the evolution of sexual dimorphism of mandibles. *Zool. Sci.* 22:1305–18
- Hughes M. 1996. Size assessment via a visual signal in snapping shrimp. *Behav. Ecol. Sociobiol.* 38:51–7
- Hunt J, Simmons LW. 2001. Status-dependent selection in the dimorphic beetle *Onthophagus taurus*. *Proc. R. Soc. London Biol. Sci.* 268:2409–14
- Jennions MD, Backwell PRY. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol. J. Linn. Soc.* 57:293–306
- Jormalainen V. 1998. Precopulatory mate guarding in crustaceans: male competitive strategy and intersexual conflict. *Q. Rev. Biol.* 73:275–304
- Kiltie RA. 1985. Evolution and function of horns and horn-like organs in female ungulates. *Biol. J. Linn. Soc.* 24:299–320
- Knowlton N, Keller BD. 1982. Symmetric fights as a measure of escalation potential in a symbiotic, territorial snapping shrimp. *Behav. Ecol. Sociobiol.* 10:289–92
- Kodric-Brown A, Sibly RM, Brown JH. 2006. The allometry of ornaments and weapons. *Proc. Natl. Acad. Sci. USA* 103:8733–38
- Kruuk LEB, Slate J, Pemberton JM, Brotherstone S, Guinness F, Clutton-Brock T. 2002. Antler size in red deer: heritability and selection but no evolution. *Evolution* 56:1683–95
- Kukuk PF. 1996. Male dimorphism in *Lasioglossum (Chilalictus) hemichalceum*: the role of larval nutrition. *J. Kansas Entomol. Soc.* 69:147–57
- Kukuk PF, Schwartz M. 1988. Macrocephalic male bees as functional reproductives and probable guards. *Pan-Pac. Entomol.* 64:131–37
- Kurdzial JP, Knowles LL. 2002. The mechanisms of morph determination in the amphipod *Jassa*: implications for the evolution of alternative male phenotypes. *Proc. R. Soc. London B Biol. Sci.* 269:1749–54
- Leimar O, Austad S, Enquist M. 1991. A test of the sequential assessment game: fighting in the bowl and doily spider *Frontinella pyramitela*. *Evolution* 45:862–74
- Levinton JS, Allen BJ. 2005. The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure. *Funct. Ecol.* 19:159–65
- Lincoln GA. 1994. Teeth, horns and antlers: the weapons of sex. In *The Differences Between the Sexes*, ed. RV Short, E Balaban, pp. 131–58. Cambridge: Cambridge Univ. Press
- Longair RW. 2004. Tusked males, male dimorphism and nesting behavior in a subsocial afro-tropical wasp, *Synagris cornuta*, and weapons and dimorphism in the genus (Hymenoptera: Vespidae: Eumeninae). *J. Kansas Entomol. Soc.* 77:528–57
- Lorch P, Wilkinson GS, Reillo PR. 1993. Copulation duration and sperm precedence in the Malaysian stalk-eyed fly, *Cyrtodopsis whitei* (Diptera: Diopsidae). *Behav. Ecol. Sociobiol.* 32:303–11
- Lucas SG. 1998. Dinocerata. In *Evolution of Tertiary Mammals of North America. Volume 1: Carnivores, Ungulates and Ungulate-like Mammals*, ed. CM Janis, KS Scott, LL Jacobs. Cambridge: Cambridge Univ. Press.
- Lundrigan B. 1996. Morphology of horns and fighting behavior in the family Bovidae. *J. Mammal.* 77:462–75
- Maynard Smith J. 1974. The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* 47:209–21
- Mead LS, Arnold SJ. 2004. Quantitative genetic models of sexual selection. *Trends Ecol. Evol.* 19:264–71
- Miyatake T. 1993. Male-male aggressive behavior is changed by body size difference in the leaf-footed plant bug, *Leptoglossus australis*, Fabricius (Heteroptera: Coreidae). *J. Ethol.* 11:63–65
- Miyatake T. 2002. Multi-male mating aggregation in *Notobitus meleagris* (Hemiptera: Coreidae). *Ecol. Popul. Biol.* 95:340–44
- Moore AJ, Wilson P. 1992. The evolution of sexually dimorphic earwig forceps: social interactions among adults of the toothed earwig, *Vostox apicedentatus*. *Behav. Ecol.* 4:40–48
- Nur N, Hasson O. 1984. Phenotypic plasticity and the handicap principle. *J. Theor. Biol.* 110:275–98
- Packer C. 1983. Sexual dimorphism: the horns of African antelopes. *Science (Wash. DC)* 221:1191–93
- Panhuis TM, Butlin R, Zuk M, Tregenza T. 2001. Sexual selection and speciation. *Trends Ecol. Evol.* 16:364–71

- Panhuis TM, Wilkinson GS. 1999. Exaggerated male eye span influences contest outcome in stalk-eyed flies (Diopsidae). *Behav. Ecol. Sociobiol.* 46:221–27
- Parcher SR. 1974. Observations on the natural histories of six Malagasy Chamaeleontidae. *Z. fuer Tierpsychol.* 34:500–23
- Parker GA. 1974. Assessment strategy and evolution of fighting behaviour. *J. Theor. Biol.* 47:223–43
- Parker GA. 1983. Arms races in evolution an evolutionarily stable strategy to the opponent independent costs game. *J. Theor. Biol.* 101:619–48
- Pomiankowski A, Iwasa Y. 1998. Runaway ornament diversity caused by Fisherian sexual selection. *Proc. Natl. Acad. Sci. USA* 95:5106–11
- Pope DS. 2000. Testing function of fiddler crab claw waving by manipulating social context. *Behav. Ecol. Sociobiol.* 47:432–37
- Preston BT, Stevenson IR, Pemberton JM, Coltman DW, Wilson K. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. *Proc. R. Soc. London Ser. B* 270:633–40
- Richards OW. 1927. Sexual selection and allied problems in the insects. *Biol. Rev.* 2:298–364
- Ritchie MG. 2007. Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.* 38:79–102
- Roberts SC. 1996. The evolution of hornedness in female ruminants. *Behaviour* 133:399–442
- Rubenstein DI, Hazlett BA. 1974. Examination of the agonistic behavior of the crayfish *Orconectes virilis* by character analysis. *Behaviour* 50:193–216
- Sampson SD. 1997. Dinosaur combat and courtship. In *The Complete Dinosaur*, ed. JO Farlow, MK Brett-Surman, pp. 383–93. Bloomington: Indiana Univ. Press
- Shine R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* 64:419–61
- Shluter D, Price T. 1993. Honesty, perception and population divergence in sexually selected traits. *Proc. Biol. Sci.* 253:117–122
- Shuster SM. 1989. Male alternative reproductive strategies in a marine isopod crustacean (*Paracerceis sculpta*): the use of genetic markers to measure differences in fertilization success among alpha, beta and gamma-males. *Evolution* 43:1683–98
- Shuster SM, Wade MJ. 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350:608–10
- Smith LD, Palmer AR. 1994. Effects of manipulated diet on size and performance of Brachyuran crab claws. *Science* 264:710–12
- Sneddon LU, Huntingford FA, Taylor AC. 1997. Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenas* (L.). *Behav. Ecol. Sociobiol.* 41:237–42
- Spassov NB. 1979. Sexual selection and the evolution of horn-like structures of ceratopsian dinosaurs. *Paleontol. Stratigr. Lithol.* 11:37–48
- Tomkins JL. 1999. Environmental and genetic determinants of the male forceps length dimorphism in the European earwig *Forficula auricularia* L. *Behav. Ecol. Sociobiol.* 47:1–8
- Tomkins JL, Simmons LW. 1998. Female choice and manipulations of forceps size and symmetry in the earwig *Forficula auricularia* L. *Anim. Behav.* 56:347–56
- Vanpe C, Gaillard JM, Kjellander P, Mysterud A, Magnien P, et al. 2007. Antler size provides an honest signal of male phenotypic quality in roe deer. *Am. Nat.* 169:481–93
- Ward PI. 1988. Sexual selection, natural selection, and body size in *Gammarus pulex* (Amphipoda). *Am. Nat.* 131:348–59
- Wellborn GA. 2000. Selection on a sexually dimorphic trait in ecotypes within the *Hyaella azteca* species complex (Amphipoda: Hyallellidae). *Am. Midl. Nat.* 143:212–225
- West-Eberhard MJ. 1979. Sexual selection, social competition, and evolution. *Proc. Am. Philos. Soc.* 123:222–34
- West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* 58:155–83
- Wilkinson GS, Dodson GN. 1997. Function and evolution of antlers and eye stalks in flies. In *Mating Systems in Insects and Arachnids*, ed. JC Choe, BJ Crespi, pp. 310–28. Cambridge: Cambridge Univ. Press
- Wilkinson GS, Kahler H, Baker RH. 1998. Evolution of female mating preferences in stalk-eyed flies. *Behav. Ecol.* 9:525–33

- Young KV, Brodie ED, Brodie ED. 2004. How the horned lizard got its horns. *Science* 304:65–65
- Zeh DW, Zeh JA. 1988. Condition-dependent sex ornaments and field tests of sexual-selection theory. *Am. Nat.* 132:454–59
- Zeh DW, Zeh JA. 1992. Dispersal-generated sexual selection in a beetle-riding pseudoscorpion. *Behav. Ecol. Sociobiol.* 30:135–42
- Zeh DW, Zeh JA, Tavakilian G. 1992. Sexual selection and sexual dimorphism in the Harlequin beetle *Acrocis longimanus*. *Biotropica* 24:86–96



Contents

Top Predators as Conservation Tools: Ecological Rationale, Assumptions, and Efficacy <i>Fabrizio Sergio, Tim Caro, Danielle Brown, Barbara Clucas, Jennifer Hunter, James Ketchum, Katherine McHugh, and Fernando Hiraldo</i>	1
Revisiting the Impact of Inversions in Evolution: From Population Genetic Markers to Drivers of Adaptive Shifts and Speciation? <i>Ary A. Hoffmann and Loren H. Rieseberg</i>	21
Radial Symmetry, the Anterior/Posterior Axis, and Echinoderm Hox Genes <i>Rich Mooi and Bruno David</i>	43
The Great American Schism: Divergence of Marine Organisms After the Rise of the Central American Isthmus <i>H.A. Lessios</i>	63
The Ecological Performance of Protected Areas <i>Kevin J. Gaston, Sarah F. Jackson, Lisette Cantú-Salazar, and Gabriela Cruz-Piñón</i>	93
Morphological Integration and Developmental Modularity <i>Christian Peter Klingenberg</i>	115
Herbivory from Individuals to Ecosystems <i>Oswald J. Schmitz</i>	133
Stoichiometry and Nutrition of Plant Growth in Natural Communities <i>Göran I. Ågren</i>	153
Plague Minnow or Mosquito Fish? A Review of the Biology and Impacts of Introduced <i>Gambusia</i> Species <i>Graham H. Pyke</i>	171
The Impact of Natural Selection on the Genome: Emerging Patterns in <i>Drosophila</i> and <i>Arabidopsis</i> <i>Stephen I. Wright and Peter Andolfatto</i>	193

Sanctions, Cooperation, and the Stability of Plant-Rhizosphere Mutualisms <i>E. Toby Kiers and R. Ford Denison</i>	215
Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences <i>Fernando Valladares and Ülo Niinemets</i>	237
The Impacts of Fisheries on Marine Ecosystems and the Transition to Ecosystem-Based Management <i>Larry B. Crowder, Elliott L. Hazen, Naomi Avissar, Rhema Bjorkland, Catherine Latanich, and Matthew B. Ogburn</i>	259
The Performance of the Endangered Species Act <i>Mark W. Schwartz</i>	279
Phylogenetic Approaches to the Study of Extinction <i>Andy Purvis</i>	301
Adaptation to Marginal Habitats <i>Tadeusz J. Karwecki</i>	321
Conspecific Brood Parasitism in Birds: A Life-History Perspective <i>Bruce E. Lyon and John McA. Eadie</i>	343
Stratocladistics: Integrating Temporal Data and Character Data in Phylogenetic Inference <i>Daniel C. Fisher</i>	365
The Evolution of Animal Weapons <i>Douglas J. Emlen</i>	387
Unpacking β : Within-Host Dynamics and the Evolutionary Ecology of Pathogen Transmission <i>Michael F. Antolin</i>	415
Evolutionary Ecology of Figs and Their Associates: Recent Progress and Outstanding Puzzles <i>Edward Allen Herre, K. Charlotte Jandér, and Carlos Alberto Machado</i>	439
The Earliest Land Plants <i>Patricia G. Gensel</i>	459
Spatial Dynamics of Foodwebs <i>Priyanga Amarasekare</i>	479
Species Selection: Theory and Data <i>David Jablonski</i>	501

New Answers for Old Questions: The Evolutionary Quantitative Genetics of Wild Animal Populations <i>Loeske E.B. Kruuk, Jon Slate, and Alastair J. Wilson</i>	525
Wake Up and Smell the Roses: The Ecology and Evolution of Floral Scent <i>Robert A. Raguso</i>	549
Ever Since Owen: Changing Perspectives on the Early Evolution of Tetrapods <i>Michael I. Coates, Marcello Ruta, and Matt Friedman</i>	571
Pandora's Box Contained Bait: The Global Problem of Introduced Earthworms <i>Paul F. Hendrix, Mac A. Callabam, Jr., John M. Drake, Ching-Yu Huang, Sam W. James, Bruce A. Snyder, and Weixin Zhang</i>	593
Trait-Based Community Ecology of Phytoplankton <i>Elena Litchman and Christopher A. Klausmeier</i>	615
What Limits Trees in C ₄ Grasslands and Savannas? <i>William J. Bond</i>	641

Indexes

Cumulative Index of Contributing Authors, Volumes 35–39	661
Cumulative Index of Chapter Titles, Volumes 35–39	665

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://ecolsys.annualreviews.org/errata.shtml>