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Costs and the Diversification of Exaggerated Animal Structures

Douglas J. Emlen

Sexual selection can favor production of extravagant ornaments and weapons in the contest for access to the opposite sex. Existing explanations for the diversity of sexually selected structures focus on reproductive benefits conferred by particular ornament or weapon morphologies. Here, I show that costs of weapon production also may drive patterns of weapon evolution. In beetles, production of horns reduces the size of neighboring morphological structures (antennae, eyes, or wings, depending on the location of the horns), and these tradeoffs reveal unexpected functional associations between ecology and horn morphology. This study illustrates a critical but overlooked role of costs in sexual selection and has implications for understanding the evolution of animal morphology.

From the tail coverts of peacocks to the antlers of elk and the horns of beetles, competition for access to mates (sexual selection) is credited with the evolution of nature's most extreme animal forms (*1*, *2*). Sexually selected structures are impressive for their variability as well as their size. Closely related species frequently produce very different types of ornaments or weapons, suggesting rapid evolutionary diversification of these structures. Yet, the question of why species differ in the form and not just the size of the structures they produce remains unanswered for most sexually selected traits. Proposed mechanisms for this structural diversity have focused on the reproductive benefits of particular ornament or weapon morphologies (*1*–*9*). Here, I suggest a mechanism for the diversification of exaggerated animal structures that focuses on the costs, rather than the benefits, of producing these traits. I illustrate the utility of this approach with a comparative study of beetle horns.

Thousands of beetle species produce horns (*10*, *11*). Beetle horns reach gigantic proportions and occur in diverse shapes and locations. One dung beetle genus alone (*Onthophagus*; Coleoptera: Scarabaeidae) contains more than 2000 described species, with hundreds of different types of horns that can arise from the front, middle, or back of the head, or from the front of the thorax (*12*–*15*). Yet, despite this diversity, most beetle horns function in the same basic way. In dung beetles, for example, male horns are used to block entrances to underground tunnels containing females (*16*–*20*). Regardless of whether they extend from the front of the head, the back of the head, or the thorax, horns help males keep rivals out of a tunnel, and larger horns are more effective than smaller horns (*18*–*20*). Thus, the reproductive benefits of horn production may explain why horns are large, but they cannot explain why beetle horns occur in so many different forms and in so many varied locations on the animals. Consideration of the functional costs of producing horns may help explain why they vary in form.

Production of a morphological structure often comes at a cost to the development of other morphological traits because of competition between traits for limited resources. Indeed, large structures can stunt the growth of other organs (*21*–*24*), and this is true of beetle horns. There is a tradeoff between beetle horns and eyes, an adjoining trait (*20*, *23*, *25*); experiments perturbing male horn expression revealed a negative genetic correlation between horn size and eye area (*20*, *23*). However, I show here that the functional cost of horn expression varies depending on the location of the horn because different horn locations influence different morphological traits.

I examined morphological tradeoffs from horn production for three species of beetle that differ in the location of their horns (Fig. 1). Samples of beetles were collected from wild populations and were measured for horn size as well as antenna, eye, and wing size. Relative trait sizes were calculated as residuals from regressions of trait size on a measure of overall body size (prothorax width), and tradeoffs were measured as negative phenotypic correlations between relative trait sizes.

In all three species, tradeoffs were present in the sex that expressed enlarged horns (Fig. 2), and the strength of the tradeoff decayed with physical distance from the horns (i.e., horns reduced the relative size of nearby structures more than that of distant structures) (Fig. 3). Animals with horns at the front of the head had proportionately smaller antennae; animals with horns at the base of the head had proportionately smaller eyes; and animals with horns on the thorax had proportionately smaller wings. Physically adjacent traits were between 20 and 28% smaller in individuals with enlarged horns than in conspecific individuals without horns (*26*). Thus, the functional cost of horn expression (reduced and/or impaired olfaction, vision, or flight) depends on the location of horns produced, which differs from species to species.

This variation in the functional cost of horn production may interact with the ecology of beetles to influence the evolution of horn location. Beetles in the genus *Onthophagus* inhabit varied physical environments, ranging from tropical wet forest to desert, and they feed on dung from antelope, elephants, rabbits, kangaroos, emus, tapirs, horses, and monkeys, to name just a few. Once they locate dung, female beetles excavate brood chambers in the soil beneath the dung, and males use their horns to guard the tunnels leading to these underground chambers (*16*–*19*, *27*). Although horns appear to function in guarding tunnels in all species, the physical and social situations beetles encounter before getting to the tunnel vary extensively among species. Beetles in all environments are likely to need to smell, see, and fly. However, the relative importance of these functions may vary depending on the characteristics of each species' environment; as a result, some horn types may be more costly to produce than others.

One example involves the timing of flight activity of beetles. Nocturnal species of dung beetle have larger eyes than diurnal species, and are better at seeing in low-light conditions (*28*); horns at the base of the head, because they lead to reductions in the size of the eyes, may be more costly to nocturnal species than to diurnal ones. Thus, if the

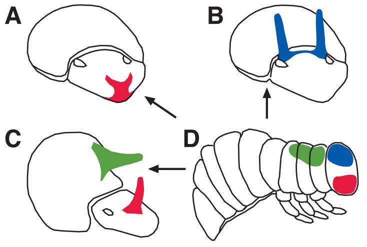

Fig. 1. Physical locations of beetle horns. (**A**) Males of *O. sharpi* produce a horn that extends from the front of the head. (**B**) Males of an unidentified *Onthophagus* species sampled from lowland forests of Ecuador produce a pair of horns that extend from the base of the head. (**C**) Females of *O. sagittarius* produce two horns, one extending from the thorax and the other from the center of the head. (**D**) Horns in different locations develop adjacent to different structures. Horns at the center or front of the head (red) develop closest to growing antennae, horns at the base of the head (blue) develop nearest to eyes, and horns on the thorax (green) develop nearest to wings.

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functional costs of horn production have influenced the evolutionary diversification of horns, then nocturnal species will be less likely than diurnal species to have horns at the base of their head. Horns in other physical locations (e.g., on the front of the head or the thorax) are not expected to be influenced by the diurnal or nocturnal activity of beetles because these horns do not reduce eye area as strongly (Fig. 3).

I used published accounts of morphology and behavior to test these predictions about the associations between the timing of flight activity and patterns of interspecific variation in horn morphology. Each of 161 Onthophagine beetle species (74 nocturnal, 87 diurnal) (*29*) was scored as having either large horns, or reduced or nonexistent horns, at the base of the head, the front of the head, or on the thorax. Nocturnal species were significantly less likely to have large horns at the base of their head than diurnal species (Fig. 4). In contrast, and as predicted, the presence of horns at the front of the head or on the thorax in these same species was independent of whether they were diurnal or nocturnal (Fig. 4). These results suggest that costs of horn production have indeed interacted with the ecology of species to influence the evolutionary diversification of horn morphology.

Similar predictions can be generated for other aspects of beetle ecology. Species using dung that is sparsely or widely distributed may rely more heavily on efficient flight capabilities than species that use dung sources that are densely or uniformly distributed. Thoracic horns, which reduce relative wing size, may be prohibitively costly in these taxa. Likewise, ecological factors influencing the dispersal of dung odors may affect the relative profitability of horns at the front of the head, because these horns lead to reductions in antenna size. Although data are lacking to test these additional hypotheses, they illustrate the potential for this approach to help explain the evolution of exaggerated structures in animals. In each instance, predicted associations between horn morphology and ecology depend on the costs of producing the trait rather than on the reproductive benefits of the trait itself, providing fresh insight to old problems regarding the diversity of sexually selected structures.

How generalizable is this approach? The idea that different ornament or weapon morphologies generate different functional costs may help explain the evolution of a variety of exaggerated structures. The specific costs demonstrated in this study (i.e., reduced size of nearby structures) should exist when two conditions are met: (i) the enlarged structures are produced coincident with the rest of the adult morphology (i.e., during ontogeny, when they may influence other growing structures) and (ii) resources are limiting for at least part of this period. Insects with complete metamorphosis meet these criteria because exaggerated structures are produced before the adult stage and because growth of the adult traits (including the exaggerated structures) occurs during a period of resource limitation—after larvae have ceased feeding and at a time when stored resources must be distributed among growing adult traits (*21*, *23*). Thus, beetle horns grow when resources are limiting and when horn growth could affect the growth of other simultaneously growing adult structures. Similar tradeoffs are likely for the multitude of exaggerated insect structures, most of which occur in species with complete metamorphosis (*30*) and in which these two conditions are met. In contrast, structures such as cervid antlers and avian tail plumes may not be expected to generate size-reductions of neighboring traits because these traits are produced after the adult morphology is established (they are shed and regrown repeatedly during the adult period). Whether other functional costs vary with these exaggerated animal structures remains to be investigated.

This study reveals a mechanism for the evolutionary diversification of sexually selected

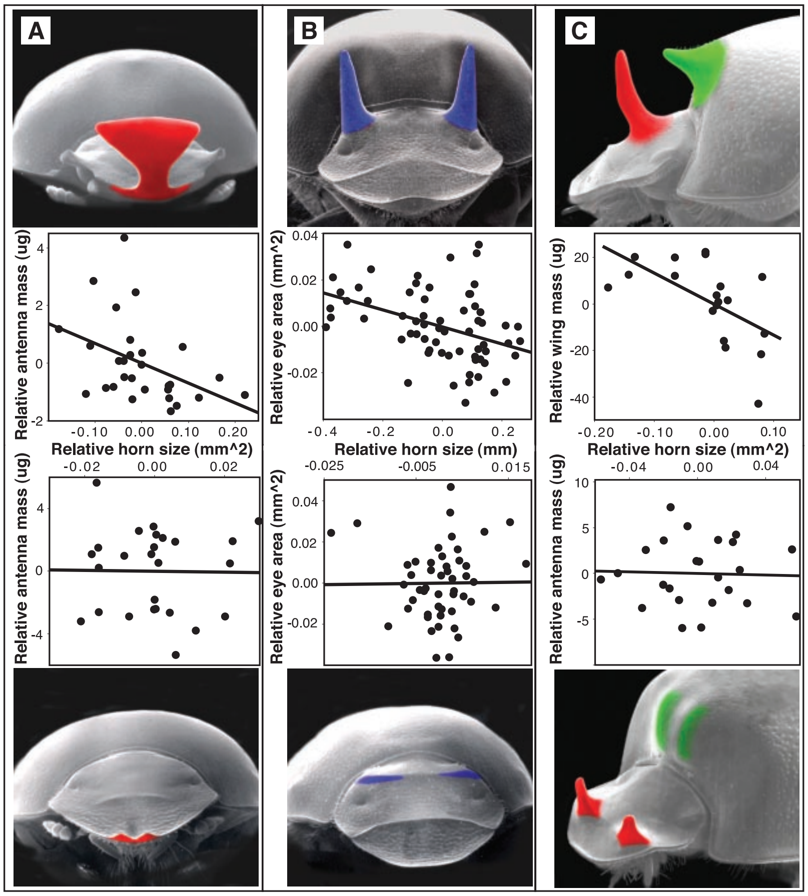


Fig. 2. Functional costs of beetle horns. In each species, the relative size of horns was negatively correlated with the relative size of the nearest neighboring structure (antennae, eyes, or wings), and these developmental tradeoffs were present only in the sex-expressing enlarged horns. (**A**) *O. sharpi* males (top) produce a horn at the front of the face (red), and males with the longest horns relative to their body size had proportionately smaller antennae (measured as a negative phenotypic correlation between relative horn area and relative antenna mass). Female *O. sharpi* (bottom) do not produce enlarged horns and do not have negative correlations with antenna size. (**B**) In an unidentified *Onthophagus* species from Ecuador, males (top) produce a pair of horns extending from the base of the head (blue), and the relative length of male horns was negatively correlated with the relative area of eyes. Females of this species (bottom) do not produce enlarged horns and show no evidence for tradeoffs with eyes. In both of these species, "horn" size in females was estimated as the area of the comparable region of head cuticle (shown in red, or blue, as appropriate). (**C**) In *O. sagittarius*, females produce two horns (top), one extending from the thorax (green), and a second from the center of the head (red), and relative female horn length was negatively correlated with the relative mass of both wings and antennae (horns versus wings shown). Males of *O. sagittarius* produce only minimal horns extending from the front of the face (bottom), and these small horns are not negatively correlated with antennae (the closest neighboring trait). This third species provides the most convincing evidence for developmental tradeoffs associated with horn expression because females rather than males produce the enlarged horns, and females also show location-specific patterns of negative phenotypic correlation with adjoining structures.

Fig. 3. Functional costs of beetle horns depend on the physical location of the developing horns. Horn production is associated with reductions in the sizes of nearby structures (shown as negative phenotypic correlations between relative horn size and the relative size of antennae, eyes, or wings), so that horns at the center or front of the head (red) reduce the size of antennae, horns at the base of the head (blue) reduce the size of eyes, and horns on the thorax (green) reduce the size of wings. For each species, the sex with enlarged horns is shown in the top panel, and the sex without horns is shown below (species as in Figs. 1 and 2). Asterisk indicates significance ($P < 0.05$) after Bonferroni correction for multiple comparisons.

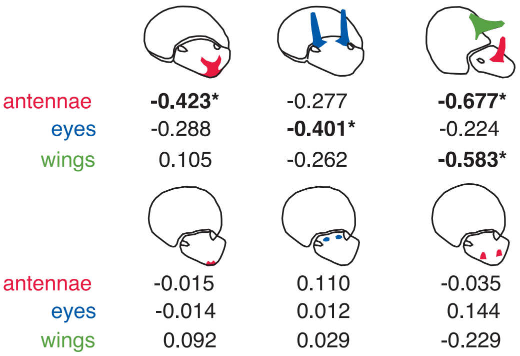
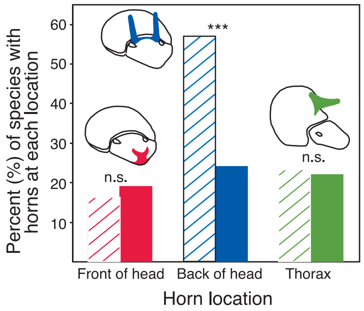


Fig. 4. Association between horn morphology and ecology. Each of 161 onthophagine species (74 nocturnal, 87 diurnal) (*29*) was scored as having either enlarged horns or reduced or no horns at the front of the head (red), the base of the head (blue), or on the thorax (green). Nocturnal species (solid bars) were significantly less likely to have horns at the base of their heads than diurnal species (dashed bars) (18 nocturnal species had horns at the base of the head, 56 did not; 50 diurnal species had horns at the base of the head, 37 did not; two by two contingency test for independence of head-horn presence and diel activity: $\chi^2 = 16.531$, $P < 0.001$). Horns at the front of the head and horns on the thorax were not associated with timing of flight activity in these beetle species (14 nocturnal species had horns at the front of the head, 60 did not; 14 diurnal species had horns at the front of the head, 73 did not; $\chi^2 = 0.222$, $P > 0.5$; 16 nocturnal species had horns on the thorax, 58 did not; 20 diurnal species had horns on the thorax, 67 did not; $\chi^2 = 0.043$; $P > 0.75$). These results suggest that functional costs of horn production interact with the ecology of species to shape the evolutionary diversification of beetle horns.



structures that focuses on the costs of trait production. Exaggerated sexually selected ornaments or weapons may cost animals in a variety of ways, such as impaired locomotion (*31–33*), increased risk of predation (*34*), reduced viability or survival (*35*), impaired immune response (*36*), and stunted growth of nearby organs (*20–23*). Costs of exaggerated animal structures need not be the same for all versions of the structure, and selection to minimize costs might favor new forms or locations for the exaggerated traits. Thus, functional costs of producing enlarged structures may affect the outcome of sexual selection and lead to predictable, although previously unanticipated, associations between morphology and ecology.

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25. The mechanism of inhibition among neighboring morphological traits is not yet known and may involve competition for hormones (*37*, *38*), growth factors (*39*), nutrients (*23*, *24*, *40–42*), or some other as-yet-unidentified cell signal [reviewed in (*43*)].
26. The extent by which reductions in antenna, eye, or wing size impair olfactory, visual, or flight capacities, respectively, has not been quantified and warrants further study. In this study, horns reduced antenna mass by as much as 25% (*O. sharpi*), eye area by as much as 20% (*Onthophagus* spp. from Ecuador), and wing weight by as much as 28% (*O. sagittarius*). Interestingly, wing area was not negatively correlated with horn size, suggesting that animals compensate for horn growth by producing proportionally thinner wings, rather than smaller-area wings [but see (*22*)].
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29. I included all Onthophagine taxa for which I was able to collect both diel activity information and descriptions of morphology. Diel activities for *Onthophagus* species were taken from (*14*, *15*, and *44*), as well as personal observations, and descriptions of beetle morphology are from (*12–15*). Nocturnal species included: *altidorsus*, *apiciosus*, *beiranus*, *bimarginatus*, *bituberculatus*, *blackwoodensis*, *capella*, *carbonarius*, *corniculiger*, *cornifrons*, *curvifrons*, *declivis*, *denudatus*, *depilis*, *deplanatus*, *depressus*, *dicranocerus*, *ebenus*, *ferox*, *flavoapicalis*, *flexicornis*, *fuscatus*, *fuscidorsis*, *gandju*, *gazella*, *glabratus*, *hecate*, *interstitialis*, *juvencus*, *lacustris*, *lamelliger*, *lamgalio*, *laminatus*, *laminosus*, *latigibber*, *leanus*, *leroyi*, *liberianus*, *mamillatus*, *mirabilis*, *mjobergi*, *mocquerysi*, *mucronifer*, *mulgravei*, *naevius*, *neostenocerus*, *nodulifer*, *orthocerus*, *parvus*, *pentacanthus*, *plebejus*, *pleurogonus*, *picatus*, *picipennis*, *pronus*, *pugionatus*, *pugnax*, *queenslandicus*, *reticulatus*, *rufostillans*, *sanguinolentus*, *semivirescens*, *sharpi*, *sloanei*, *stellio*, *strictestriatus*, *tenuistriatus*, *tripartitus*, *variegatus*, *verticalis*, *vinctus*, *vultuosus*, *wombalano*, *yiryoront*; Diurnal species included: *aciculatus*, *acuminatus*, *aeruginosis*, *alcyonides*, *androgynus*, *atridorsis*, *atronitidus*, *auriceps*, *auritus*, *australis*, *bambra*, *batesi*, *bidentifrons*, *bicarinaticeps*, *bidens*, *bunamin*, *clypeatus*, *consentaneus*, *coscineus*, *cribellum*, *cribripennis*, *crinitus*, *cuniculus*, *cupreus*, *cyanochlorus*, *densipillis*, *denticulatus*, *dicranius*, *discolor*, *dives*, *dunningi*, *evanidus*, *fabricii*, *feai*, *fimetarius*, *furcaticeps*, *granulatus*, *gravoti*, *haagi*, *haemotopus*, *hilaris*, *imbellis*, *incanus*, *incensus*, *iphis*, *laeviceps*, *lebasi*, *lioides*, *longipilis*, *marginicollis*, *mucronatus*, *mutatus*, *nigriventris*, *nuchicornis*, *nurubuan*, *nyctopus*, *obtusicornis*, *ocelliger*, *pallidipennis*, *paluma*, *praecellens*, *pullus*, *quadripustulatus*, *quadrituber*, *rubrimaculatus*, *rufonotatus*, *sagittarius*, *sanguineus*, *semiviridus*, *signatus*, *stigmosus*, *stockwelli*, *striatulus*, *subaeneus*, *subsulcatus*, *sydneyensis*, *taurus*, *tersidorsis*, *tersipennis*, *vanellus*, *vermiculatus*, *villosus*, *walteri*, *xanthomerus*, *yeyeko*, *unk* spp. from Ecudaor.
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