

Exaggerated Trait Growth in Insects

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Abstract

Animal structures occasionally attain extreme proportions, eclipsing in size the surrounding body parts. We review insect examples of exaggerated traits, such as the mandibles of stag beetles (Lucanidae), the claspers of praying mantids (Mantidae), the elongated hindlimbs of grasshoppers (Orthoptera: Caelifera), and the giant heads of soldier ants (Formicidae) and termites (Isoptera). Developmentally, disproportionate growth can arise through trait-specific modifications to the activity of at least four pathways: the sex determination pathway, the appendage patterning pathway, the insulin/IGF signaling pathway, and the juvenile hormone/ecdyteroid pathway. Although most exaggerated traits have not been studied mechanistically, it is already apparent that distinct developmental mechanisms underlie the evolution of the different types of exaggerated traits. We suggest this reflects the nature of selection in each instance, revealing an exciting link between mechanism, form, and function. We use this information to make explicit predictions for the types of regulatory pathways likely to underlie each type of exaggerated trait.

INTRODUCTION

Body parts typically scale proportionally with body size, but in some organisms, one or a few traits grow disproportionately large, becoming defining features of the species. Exaggerated morphologies, such as elongated appendages or large outgrowths, have fascinated biologists for many reasons. They push the bounds of what we know is possible in nature, and raise numerous questions about how such traits can develop and evolve. What habitats or social situations provide sufficiently strong selection to favor extreme trait size? How does one trait become uncoupled from the rest of the body so that it grows more rapidly, or for a longer period, than surrounding structures? And what can an understanding of extreme development tell us about the regulation of growth in general?

Here we review recent advances in our understanding of the evolution and development of exaggerated structures, emphasizing insect models. We explore three contexts favoring exaggerated traits: sexual selection (**Figure 1a–d**), locomotion/predation/feeding (**Figure 1e–h**), and coloniality (**Figure 1i–l**). Although extreme appendages can result from each context, the nature of selective forces results in different trait properties. For example, whereas ornaments and weapons of sexual selection exhibit heightened nutrition-sensitive expression and display enhanced among-individual variability (**Figure 2**), properties that make these traits conspicuous and reliable signals of male quality, feeding, locomotor, and colony defense structures do not. For the first time, we can begin to relate the details of developmental mechanism to ecological context, connecting growth, form, and function. Although most studies are preliminary, the patterns revealed are clear and suggest that the mechanistic routes are not the same for all exaggerated traits. We use this information to make explicit predictions for the types of regulatory mechanisms likely to underlie each type of exaggerated trait.

THREE REASONS WHY TRAITS GET REALLY BIG

Reproductive Competition

One widespread driver of extreme trait size is competition for mates (sexual selection). In many species, rival males battle over access to territories or resources utilized by females. In other species, females actively choose mates on the basis of the relative size of an ornamental structure. Multiple studies involving diverse species demonstrate greater reproductive success for males with the most exaggerated weapon or ornamental feature, resulting in intense directional selection (reviewed in 2, 3, 46, 47, 85). As tusks, horns, or displays become bigger within this social context, so too does the standard against which a male must contend, favoring further increases that can eventually result in weapons or ornaments of extreme proportion (36, 186). Indeed, understanding the causes and consequences of trait exaggeration in the context of sexual selection has been a fertile area for evolutionary theory (14, 119, 157).

Male competition has driven the evolution of a diversity of exaggerated structures in insects. Examples include mandibles in stag beetles (76, 117, 140), rove beetles (55, 68), flour beetles (137, 138), wetas (88, 94), and dobsonflies (166) (Lucanidae, Staphylinidae, Tenebrionidae, Orthoptera: Anostomatidae, and Corydalidae, respectively); forelegs in harlequin beetles (196), rhinoceros beetles (42), and weevils (185) (*Acrocinus longimanus*, Dynastinae, and Curculionidae, respectively); hindlegs in leaf-footed bugs (43, 58, 126, 127) and frog-legged leaf beetles (86) (Coreidae and *Sagra* spp., respectively); and abdominal cerci in earwigs (Forficulidae) (129, 163). Male competition has also led to the evolution of enlarged heads in ants (72), snouts in bees (34, 101), “necks” in flies (17, 145, 190), and eyestalks in weevils (84, 143) (*Cardiocondyla* spp., Andrenidae and Halictidae, Diopsidae, and Brentidae, respectively); novel protrusions including tusks and antlers in flies

(41, 130, 188), wasps (110), and wetas (62) (Tephritidae, *Synagris* spp., and *Motuweta* spp., respectively); and horns in weevils (44), fungus beetles (27), dor beetles (77), flower beetles (74, 105), dung beetles (49, 79, 142, 148), and rhinoceros beetles (33, 42, 54, 75, 149) (Baridinae, *Bolitotherus cornutus*, Geotrupinae, Cetoniinae, Scarabaeinae, and Dynastinae, respectively) (**Figure 2**).

Female choice for exaggerated structures is less well studied in insects than in other animals. Nevertheless, female earwigs (*Forficula auricularia*) prefer males with longer forceps (174), female bees (*Crabro cribrellifer*) prefer males with the most elaborate foretibial plates (111), and female stalk-eyed flies prefer males with the longest eyestalks (17, 18, 189, 190). Females may use other exaggerated traits, such as the massive sex combs on the legs of *Drosophila prolongata* males, to determine postcopulatory utilization of sperm (7, 96).

Feeding, Prey-Capture, and Locomotor Traits

In contrast with sexual selection, which can produce consistent directional selection for larger traits, natural selection on exaggerated traits is typically stabilizing. Although large weapons may enhance prey handling, they might also impede movement, reducing capture rates. As a result, exaggerated predator weapons tend to evolve when the constraints of weapon size on locomotion are relaxed, such as hunters that creep up on unsuspecting prey or ambush predators that wait for prey to come to them (47). Praying mantises (Mantidae), for example, have enlarged raptorial forelegs used to snatch prey (112). Capture success is determined by clasper speed, not rate of locomotion. Longer forelegs move through the air faster than shorter ones and create a larger kill zone (56, 112, 116), providing a selective advantage for elongation even though the forelegs are cumbersome during walking or flight. Similar forelegs have evolved in the mantispids (Neuroptera) (100) and the shore fly genus *Ochthera* (Diptera) (120). Other exaggerated raptorial appendages include the enlarged mandibles of larval antlions (Neuroptera) (66, 102) and the snap-jaw labium of dragonfly nymphs (*Aeshna* spp.) (169). Feeding specialization has also resulted in the evolution of elongated mouthparts, such as the extreme sucking proboscis of some flies (e.g., *Moegistorhynchus longirostris*) (146), hawk moths (Sphingidae) (184), and soapberry bugs (*Jadera* spp.) (22), and the long snouts of some weevils (*Curculio* spp.) (12, 173).

In other cases, selection for jumping, swimming, or digging has led to disproportionately large appendages. Lengthened limbs can enhance leverage, reducing the force needed to jump long distances. Many insects combine this elongation with a ballistic release mechanism that uses elastic energy stored in the exoskeleton to enhance limb momentum (10, 20, 67). Enlarged hindlegs facilitate jumping in crickets, grasshoppers (19, 20), flea beetles (Alticinae) (59, 60), and predatory pouncing in backswimmers (Notonectidae) (63). Similarly, water striders (Gerridae) have enlarged midlegs that function like oars (78), and mole crickets use fossorial legs for digging (180).

Social Insect Soldiers

Like ambush predators, social insects also experience selection for extreme fighting structures, most often in the context of colony defense. These colonial insects also faced trade-offs with enhancing weapon size, including basic functions such as being able to handle food. However, the evolution of a division of labor, with nestmates performing tasks related to reproduction and colony maintenance, freed a caste of soldiers to evolve exaggerated traits that could be employed in defending the colony (193). Specialized colony defenders are found in two families of aphids (Pemphigidae, Hormaphididae) (165), several genera of ants (73), and all termites (38, 45, 147) (**Figure 1i-l**). We focus on the last group, as termite soldiers have a number of physiological modifications that distinguish them from the more utilitarian workers.





Figure 1

Examples of the diversity of structure and function of exaggerated traits in insects. Sexually selected, condition-dependent male traits: (a) forked head horns of the rhinoceros beetle *Trypoxylus dichotomus* (used with permission from Shutterstock), (b) the elongated eyespan of the stalk-eyed fly *Teleopsis dalmanni* (photo credit: Gerald Wilkinson), (c) the long, protruding thoracic horn of the dung beetle *Onthophagus nigriventris* (photo credit: Douglas J. Emlen), and (d) the elongated mandibles of the stag beetle *Lucanus cervus* (© Henrik Larsson; reproduced with permission from Shutterstock). Traits used in prey capture: raptorial forelegs of (e) the mantispid *Mantispa asphavexelte* (photo credit: H. Dumas) and (f) the mantid *Archimantis latistyla* (photo credit: Tibor Duliskovich). Traits used in locomotion: (g) elongated midlegs of the backswimmer *Notonecta glauca* (photo credit: E. van Herk) and (h) enlarged jumping hindlegs of the clown cricket *Zeromastax* spp. (photo credit: Hugo Quintero). Defensive traits evolved in social insects: (i) soldier termite with an extended rostrum (nasus) (*Tenuirostritermes* sp.), enlarged soldier ant head and mandibles of (j) *Pheidole rosae* and (k) *Pheidole tepicana* (photos © Alex Wild; reproduced with permission), and (l) enlarged head and mandibles of soldier termite (*Prorbiotermes* spp.) (© Sydeen; reproduced with permission from Shutterstock).

Termite soldiers often develop larger bodies and limbs and a more sclerotized cuticle than workers do. However, the most pronounced soldier-specific traits are associated with the head, commonly involving an elongation of the apical portion of the mandible (98, 106), often with a loss of dentition (38), to create weapons that can penetrate an opponent's cuticle (147). In some species the soldiers' mandibles are more elastic and store energy as they are distorted into a locked position. When the mandibles release, they can stun adjacent opponents (38, 158).

Soldiers in other species exhibit substantial thickening of the head cuticle to form a cylindrical protrusion of the rostrum. These phragmotic plugs can be positioned to block the entrances to nest galleries (147), and the width of the soldier head, unlike that of the worker's, often matches that of the surrounding tunnels (38). In some species this trait is combined with enlarged mandibles, whereas in others the mandibles are almost nonfunctional (156).

A third defensive head modification delivers chemical agents. Some termite soldiers have hypertrophied frontal glands that synthesize and store chemical weapons that can act as glues, irritants,



Figure 2

Exaggerated traits that function as signals in the context of sexual selection are always unusually variable in their expression from male to male. Rhinoceros beetle horns (*Dynastes hercules*) vary in length more dramatically than their legs, wings, or overall body size. Hypervariability results from developmental mechanisms that couple trait growth with nutrition, stress, parasites, and/or physiological condition. In insects, this appears to involve heightened sensitivity of exaggerated tissues to either insulin-like signaling or juvenile hormone signaling. Illustrations by David J. Tuss.

toxins, or a combination of all three (147). Many compounds target ants (38), the primary invertebrate predators of termites (73). Some species simply exude the chemicals and transfer them to enemies through contact; others forcibly eject the frontal gland contents with a contraction of modified mandibular muscles, spraying opponents from a safe distance (193). Affording even greater self-protection, some termites have evolved soldiers with an extended rostrum (nasus) (38), elevating the release point away from the head.

Termite soldiers are often so specialized for defense that they are no longer capable of making other contributions to their colony. Mandibular modifications can make it impossible for them to care for immature nestmates, construct or repair tunnels and galleries, or perform other basic colony tasks carried out by less specialized workers. Many soldiers are even dependent on nestmates for food because they cannot provision themselves (45).

MECHANISMS OF EXAGGERATED GROWTH

Sexually Dimorphic Exaggerated Traits

Many exaggerated traits are expressed by only a single sex, either because they arose through reproductive competition that led to divergent expression or because they are wholly sex specific. Sex-specific expression of exaggerated traits in horned beetles and stag beetles appears to be regulated, at least in part, by the sex determination pathway gene *doublesex* (*dsx*; 65, 80, 90). *dsx*

is a member of the highly conserved DNA binding motif gene family (*Dmrt*), major effectors of sexual differentiation across diverse animal taxa (97, 118). Male- and female-specific splice variants of *dsx* act as transcriptional regulators that modulate tissue-specific sexual differentiation during development (8, 21, 61, 191).

Specifically, *dsx* controls sex-specific trait growth by binding *cis*-regulatory regions of downstream target genes (114, 162, 192). Both general and tissue-specific expression modifications of *dsx* can contribute to sexual dimorphism in trait size (90, 109, 153, 168) by controlling downstream patterning genes responsible for trait development, as observed for primary sexual traits such as genital structures and gonads (5, 24, 87, 153) and secondary traits such as the male-specific sex combs of some *Drosophila* flies (6, 168).

The function of *dsx* has been studied in four beetle species with highly developed weapons: *Onthophagus taurus*, *O. sagittarius*, *Trypoxylus dichotomus*, and *Cyclommatus metallifer* (65, 80, 90). Knockdown by RNAi revealed *dsx* regulated growth of sexually dimorphic traits, including exaggerated horns and mandibles (65, 80, 90). *dsx* appears to act upstream of other growth-regulating processes in species with sexually dimorphic traits. For example, knockdown of *dsx* in stag beetles reduces juvenile hormone (JH) sensitivity in the developing mandible tissue of males, reducing the size of the structure, whereas in females the tissue becomes more sensitive to JH (65). These results suggest that the mechanism of sexual dimorphism in weapon expression is not a simple on-or-off growth switch, but rather regulation of sex-specific trait expression. Actual growth of these traits, and of other, constitutively expressed exaggerated traits, requires locally acting mechanisms that lead to heightened proliferation within a particular tissue (161; **Figure 3**). That is, once growth is permitted, mechanisms capable of affecting the development of individual body parts must stimulate the excessive growth. Each of the following mechanisms can produce this effect, causing particular body parts to grow to extreme proportions.

The Role of Homeotic Genes and Appendage Patterning Genes in Exaggerated Trait Growth

Insect appendage primordia are patterned by a largely self-contained cascade of gene networks. Interactions among these patterning gene products, many of which diffuse between cells as locally acting morphogens, delineate anterior-posterior, dorsal-ventral, and proximal-distal compartments within the field of cells that will form the structure. These gene products also coordinate growth, determining the shape, size, and function of the final structure (reviewed in 93; **Figure 3**). For this reason, appendage patterning genes have been the focus of numerous evo-devo studies of insect diversity (4, 144). Because shifts in expression of developmental patterning genes can drive major structural changes, these genes are obvious candidates for the evolution of extreme traits.

Regulation of exaggerated growth of legs by developmental patterning genes has been shown in many insect species such as water striders (89, 150), grasshoppers (83, 115), crickets (Gryllidae) (115, 135), cockroaches (Blattidae) (115), and mantids (Mantidae) (115). For these species, structure elongation is stimulated, at least in part, by changes in expression of the homeotic genes *Ultrabithorax* (*Ubx*; 89, 150) and *abdominal-A* (*abd-A*; 115) and the growth-promoting morphogen *decapentaplegic* (*dpp*; 83, 135).

A comparative study of 11 insect species (115) showed that expression of *Ultrabithorax* and *abdominal-A* (*UbdA*, collectively) in the developing hindlimbs correlated with species differences in hindleg size. In the butterfly *Precis coenia*, the bumble bee *Bombus*, the flour beetle *Tribolium castaneum*, the lacewing *Chrysoperla*, the firebrat *Thermobia*, and the collembolan *Folsomia*, the absence of *UbdA* expression was associated with uniform leg morphology among the three pairs of legs, consistent with *UbdA* genes uncoupling growth regulation of hindlegs from other appendages,

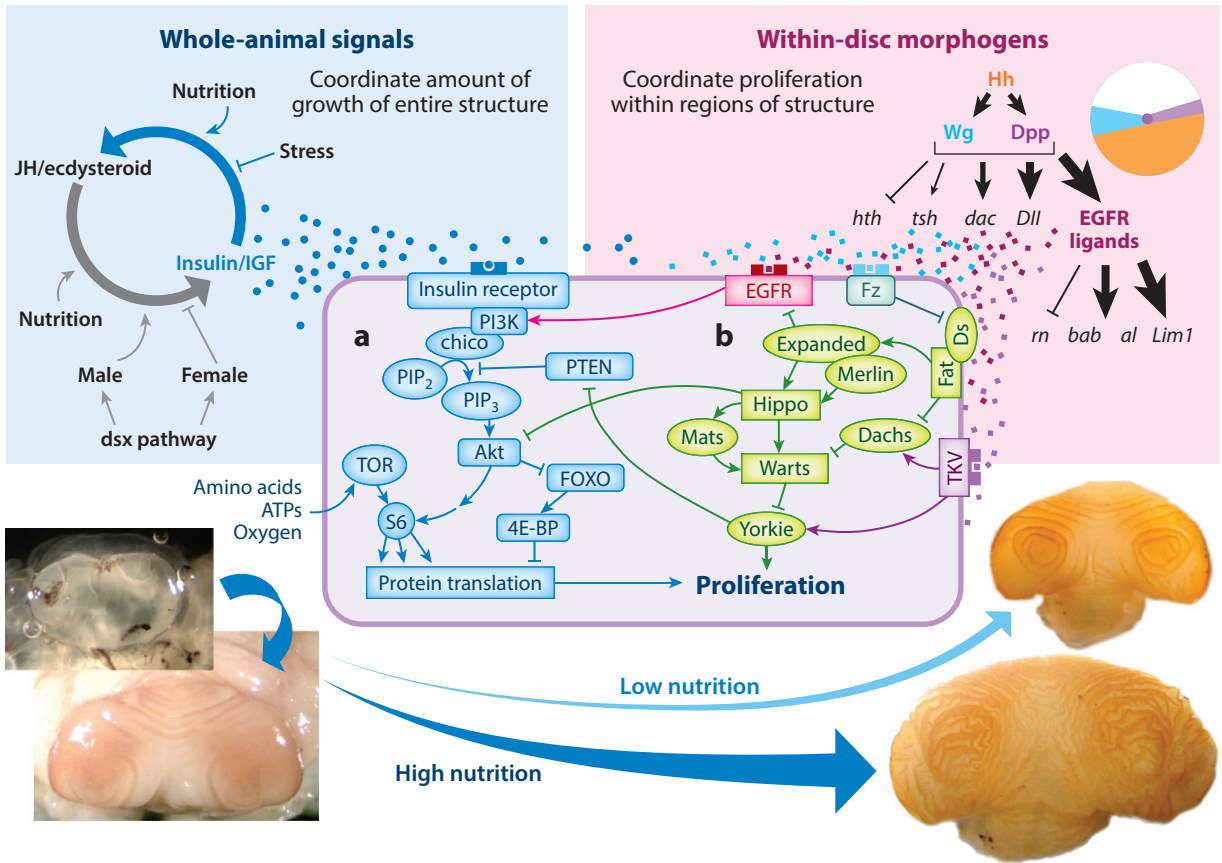


Figure 3

Pathways known to be involved with regulation of exaggerated trait growth. Within developing insect appendages (including rhinoceros beetle horns, as our example here), a patchwork of partially overlapping gradients of morphogen signals specifies the shape and approximate final size of the structure (patterning pathway, *top right*). Overall amounts of growth are modulated (*a*) in response to several whole-animal-circulating signals [e.g., insulin-like peptides, juvenile hormone (JH)] whose levels are sensitive to the nutritional state of the animal, and (*b*) by the Fat/Hippo pathway. Amounts of growth are also regulated by the sex-determination pathway (*dsx*). Pathway interactions from References 93, 121, 134, 182, 195, and 197. Other abbreviations: Akt, protein kinase B; *al*, *aristalless*; *bab*, *bric-a-brac*; *dac*, *dachsbund*; *Dll*, *Distalless*; *Dpp*, *Decapentaplegic*; *Ds*, *Dachsous*; *EGFR*, epidermal growth factor receptor; 4E-BP, 4E-binding protein; FOXO, forkhead box O; *Fz*, *frizzled*; *Hh*, *Hedgehog*; *hth*, *homothorax*; *Mats*, *Mob as tumor suppressor*; *PI3K*, phosphatidylinositol-4,5-bisphosphate 3-kinase; *PIP2*, phosphatidyl inositol bisphosphate; *PIP3*, phosphatidylinositol (3,4,5)-triphosphate; *PTEN*, phosphatase and tensin homolog; *rn*, *rotund*; *S6*, *S6 kinase*; *TKV*, *thick veins*; *TOR*, *target of rapamycin*; *tsb*, *teashirt*; *Wg*, *Wingless*.

stimulating enlargement of these legs directly, or both (115). The spatial and temporal pattern of expression of *UbdA* in the developing hindlimbs of the cockroach *Periplaneta*, the praying mantid *Tenodera*, the crickets *Gryllus* and *Acheta*, and the grasshopper *Schistocerca* coincided with disproportionate growth of the adult hindlegs (11, 115).

Ubx regulates the development and growth of the exaggerated midlegs in water striders (89, 150). Water striders are semiaquatic bugs that as a group possess a remarkable diversity of leg lengths and shapes among species and between sexes. Water striders use their first pair of legs for prey handling, the second as oars for locomotion, and the third as rudders (78, 176). Changes in *Ubx* expression in the water strider are postulated to regulate leg length. In *Gerris buenoi*, *Ubx*

overexpression in the second pair of legs produced exaggerated growth, whereas a loss of *Ubx* expression in the first and third pairs of legs reduced growth (89, 150).

These homeotic genes likely act in concert with other effectors to determine appendage growth. In *Drosophila*, primordial haltere cells that lack *Ubx* proliferate, resulting in larger organ size, compared with cells expressing *Ubx* normally (32). However, expression of *Ubx* appears to affect the growth of the haltere by its action on the TGF- β homolog *dpp* (32). *dpp* is a morphogen that coordinates patterning and growth in animal cells during development (151) and appears to contribute to exaggerated growth of the hindlegs in both the grasshopper *Schistocerca americana* (83) and the cricket *Gryllus bimaculatus* (135). In *Drosophila* flies, *Ubx* reduces both *dpp* production and mobility through enhanced expression of the *dpp* receptor, *thick veins* (32). This finding strongly suggests that interactions between upstream genes, such as *Ubx*, and downstream regulators of cell growth and proliferation, such as *dpp*, ultimately specify the final size and shape of a structure.

Although details vary by species, all exaggerated traits examined thus far are formed via this same homeotic gene and appendage patterning network. Interactions among these genes specify the identity of each structure and likely coordinate, to some extent, their final relative sizes. The studies mentioned above suggest that altered activity of *Ubx/UbdA* and *dpp* can contribute directly to the evolution of disproportionate growth in at least some insect structures, including beetle horns (183). However, growth of tissues in insects and other animals is usually modulated by signaling from additional physiological pathways, and these mechanisms, too, can lead to exaggerations.

Some Exaggerated Traits Exhibit Heightened Sensitivity to Insulin/IGF Signaling

The insulin/insulin-like signaling (ILS) pathway is a well-studied, highly conserved physiological pathway that transduces the nutritional status of an individual to its cells and functions in metabolism, aging, reproduction, and growth (25, 26, 194). We (181) have reviewed in detail the ILS pathway with regard to its role in the growth of condition-dependent sexually selected exaggerated traits, and Koyama et al. (99) have reviewed ILS and target of rapamycin (TOR) signaling in the regulation of nutrition-dependent, developmentally plastic, organ-specific responses in insects. Here we summarize these findings and discuss additional case studies.

The ILS pathway likely contributes to exaggerated growth in a diversity of vertebrate and invertebrate structures. For example, insulin-like growth factor 1 (IGF1) levels are positively correlated with both body and antler size in deer, and IGF *in vitro* stimulates antler cell growth (9, 40, 167). Within invertebrates, particularly arthropods, numerous members of the ILS pathway, from ligands (insulin-like peptides, ILPs) and receptors (InR) to downstream effectors (FOXO), control condition-dependent exaggerated trait growth in the enlarged chelae of male crabs and shrimp (178, 179), the enlarged head and mandibles of termite soldiers (71), and the horns of beetles (53, 103).

A key characteristic of the ILS pathway is that it integrates physiological condition and metabolism with growth in a condition-dependent manner. Well-fed and unstressed individuals have increased levels of IGFs/insulin/ILPs relative to poorly fed, diseased, or stressed individuals, resulting in differential growth (16, 39, 170). How these signals are interpreted within an individual is critical to the evolution of exaggerated trait growth. For example, downstream signaling cascades of the ILS pathway act in tissue- and cell-specific manners (25, 26, 35), such that the nutrition- and condition-dependent plasticity of a trait is determined by its relative sensitivity to ILS signaling (53, 170, 194). In fruit flies and rhinoceros beetles, male genitalia are insensitive to the ILS pathway and grow to a specific size regardless of the animal's physiological condition. In contrast, wings, which are moderately sensitive to ILS signaling, grow larger in large, well-fed

individuals than in smaller, poorly fed individuals (53, 170). In the Asian rhinoceros beetle, *Trypoxylus dichotomus*, the male head horn is more sensitive to signaling through the ILS pathway than other traits are, resulting in unusually rapid growth in the largest, best-fed males to produce extreme weapons (53).

ILS signaling also contributes to exaggerated growth in the heads of termite soldiers, although the soldiers live in a nutritionally stable environment. In this case, the ILS pathway appears to act as an intermediary between the environmental and hormonal milieus that control soldier-specific trait growth. Several genes in this pathway are upregulated in mandibular epithelial tissues of the damp-wood termite, *Hodotermopsis sjostedti*, and disruption by RNAi can prevent mandibular elongation (71). Although the ILS pathway is normally responsive to nutritional signals, it appears to have evolved a sensitivity to colony signals in termites and contributes to socially mediated caste differentiation in honey bees (1, 30, 37, 131, 187) and ants (108, 113, 139). Activation of the ILS pathway can stimulate cell growth and protein synthesis (69, 155), and it modulates circulating JH, possibly by triggering the release of neuropeptides that influence JH production (177). As this example suggests, ILS signaling and TOR signaling (99) control production of morphogenic hormones that influence body size and shape.

Hormonal Regulation of Exaggerated Trait Growth

Hormones regulate growth, proliferation, metamorphosis, and myriad other developmental and physiological functions in insects. The two most important effector hormones are JH and ecdysteroid, which, through downstream actions, regulate growth, molting, metamorphosis, and reproduction (132). Not surprisingly, these hormones appear to regulate growth in at least some exaggerated insect structures.

JH has diverse functions during insect development (82, 132). Its classic roles are to ensure a stationary molt when titers are high (82, 132, 152) and to regulate developmental switches between alternative phenotypes (70, 133). But JH can also stimulate cell proliferation (82, 132, 152) and link trait growth with nutrition (48, 175, 122). Perturbations to JH affect the size of a number of exaggerated insect traits including eyestalks of stalk-eyed flies (57), mandibles of stag beetles (64) and flour beetles (136), and horns of dung beetles (51, 128, 159).

As with ILS signaling, tissue-specific responses to JH render some traits more sensitive than others. Coordinated expression of suites of functionally related traits may result from shared responses to JH. For example, in the broad-horned flour beetle, *Gnatocerus cornutus*, application of a JH analog (JHA) stimulates growth not just of enlarged mandibles but also of the head and prothorax, which mechanically support the enlarged mandibles (136). However, the same JHA application produced smaller elytra and wings and had no effect on legs (136), demonstrating differential trait sensitivity to JH. Varied interpretation of JH signaling at the tissue and cellular levels may result from varied expression of the JH receptor (23, 95, 107) or from tissue-specific coupling to other signaling cascades such as the *dsx* and ILS pathways (48, 65, 99, 160, 164).

Weapon-specific sensitivity to JH signaling is seen in the dung beetle *Onthophagus taurus* and the stag beetle *Cyclommatus metallifer*, in which JHA stimulated weapon growth in males but not females (50, 64). In addition, JH titer did not differ between the sexes during the JH-sensitive period (64), suggesting sexual dimorphism in weapon size is influenced by differential responsiveness to JH. Although sex-specific hormone action is widespread in insects, these data do suggest that the JH signaling pathway is a plausible mechanism for the evolution of exaggerated traits.

Termite soldiers exhibit tissue-specific modulation of exaggerated growth by JH signaling. This caste is produced by changes during successive molts, moving away from the utilitarian

phenotype typical of the worker caste toward species-specific soldier traits. The switch from worker to soldier development appears to be triggered by social cues mediated by increases in circulating JH (reviewed in 15, 125). As with beetle mandibles, termite tissues appear to differ in their response to JH in ways that result in coordinated expression of suites of functionally related traits. For example, in *Hospitalitermes medioflavus*, soldiers have an enlarged head with a long nasus and regressed mandibles. The nasus originates from the equivalent of an imaginal disc that forms under the cuticle of the head capsule (124). JH stimulates nasus elongation and simultaneously promotes selective apoptosis of mandibular tissue. Together these divergent tissue responses produce a functional soldier morphology (172).

JH does not appear to act alone, however. In termites, molts are directed by an interaction between JH and ecdysteroid. The specific modulatory role of ecdysteroids is unknown, but they appear to enhance mandible development and cuticle deposition in soldiers of *Macrotermes michaelsoni* (141) and may contribute to the elongation of the tissue that forms the nasus (123). Ecdysteroids are also hypothesized to play a role in the programmed cell death leading to mandible regression (172).

LINKING MECHANISM WITH FUNCTION

Ecological forces selecting for extreme trait development vary considerably, and as a result, different underlying regulatory mechanisms may have been favored. Thus, whereas some genes and pathways may be responsible for exaggerated features in one species, they may not influence similar traits in another. In particular, we argue that mechanisms of exaggeration of sexually selected structures are likely to have co-opted pathways very different from those regulating the expression of prey-capture or locomotor traits. Although sexual selection may lead to extreme trait size in a species, such that traits like eyestalks or tusks or horns are larger in sexually selected species than in related species lacking intense sexual selection, not all individuals within the sexually selected species carry full-sized versions of the structure. In fact, one of the hallmarks of intense sexual selection is that only a few individuals wield a highly exaggerated structure. Additionally, the growth of these sexually selected traits is influenced more strongly by exogenous stressors than is the growth of other body parts—they exhibit heightened condition sensitivity (13, 31, 53, 92). Thus, only the dominant, best-conditioned individuals produce full-sized versions of the trait, whereas the remainder have modest or rudimentary versions (**Figure 2**). Even subtle differences in state translate into conspicuous differences in the final dimensions of the ornament or weapon.

Heightened condition-sensitive expression and hypervariability between individuals are precisely the properties that make these traits reliable and informative signals of quality in the context of female choice of mates or male assessment of rival males (14, 81, 85, 91, 119, 154, 157). Thus, an understanding of the nature of sexual selection helps explain critical properties shared by exaggerated male ornaments and weapons, and these properties in turn provide clues to the most likely underlying mechanisms of growth. For example, although patterning genes no doubt contribute to the regulation of growth in all insect structures, changes in the activity of these genes are not likely to be the primary route to extreme growth in sexually selected structures. Instead, we predict that changes in tissue sensitivity to whole-animal signals of nutritional state or quality will allow evolutionary increases in the sizes of sexually selected traits. The extreme traits derived from these changes to sensitivity would be favored because they are reliable signals of overall male quality. Both ILS and JH act as whole-animal signals, communicating nutrition and physiological condition to developing tissues, and increased regional sensitivity to either or both signals could result in the evolution of traits that are extreme in both size and variability. For example, rhinoceros beetle horns are sensitive to ILS (53) but not to JH, stag beetle mandibles are sensitive to JH but not to

ILS (64), and dung beetle horns are sensitive to both ILS and JH (50, 52, 103). These findings suggest that each beetle lineage arrived at weapon exaggeration through a different nutrition-sensitive mechanism.

Unlike weapons and ornaments of sexual selection, exaggerated claspers, proboscises, jumping legs, and ovipositors (104) are not used as intraspecific signals. These traits are exaggerated in individuals of all body sizes. Heightened condition-sensitive growth and hypervariability in expression would not be beneficial to these traits as they are for sexually selected signals. Indeed, excessive plasticity or variability may detract from their performance. Although the field of research is nascent, we have seen already that the exaggerated growth of hindlegs in crickets and grasshoppers, and elongated midlegs in water striders, results primarily from altered expression of appendage patterning genes, a constitutive mechanism likely to generate extreme trait sizes in all individuals regardless of sex or body condition (83, 89, 115, 135, 150). Although growth of these traits may be sensitive to nutrition signals such as JH and/or IGF, as indeed are the majority of body parts in insects, we do not expect to see heightened sensitivity in these exaggerated structures relative to other body parts.

The weapons of soldier insects also do not function as intraspecific signals, and they are not likely to benefit from extreme variability in size from one soldier to the next. Thus, at first glance, it would seem that the evolution of exaggerated soldier morphologies should also most likely result from constitutive mechanisms such as appendage patterning, rather than from changes in tissue sensitivity to circulating nutrition-sensitive signals. However, social insects develop under extraordinary circumstances. Developing soldiers are fed by workers within the colony, providing a highly predictable nutritional environment. In these unusually stable developmental environments, an increase in sensitivity to nutrition within the weapon tissue may be an ideal route to the evolution of trait exaggeration, generating extreme trait sizes in all soldiers without the hypervariability observed in other insects. Interestingly, it now appears that weapons of termite soldiers, at least, are sensitive to both JH and ILS signaling (28, 29, 71, 171).

CONCLUSIONS

Exaggerated structures function in a variety of ecological contexts, and these contexts, in turn, favor very different properties of expression: extreme plasticity and among-individual variability in some cases, for example, but canalization and minimal variability in others. Linking ecological contexts such as sexual signaling, prey capture, locomotion, and colony defense with specific types of underlying developmental mechanisms promises to reveal much more than the alleles and genes responsible for morphological evolution; it promises insight into why particular types of pathways underlie the evolution of each type of structure—why, for example, mutations in genes affecting tissue-level responses to whole-animal signals of nutrition or condition might underlie the evolution of exaggerated size in ornaments and weapons of sexual selection, whereas mutations in genes acting in within-tissue patterning mechanisms underlie the evolution of extreme size in locomotor or prey-capture traits.

Despite their compelling biology and fantastic diversity, very few species with exaggerated morphological structures have been studied at the genetic or physiological level. However, we suggest that this field is poised to make significant contributions to our understanding of how selection shapes the evolution of animal form.

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