

# THE DEVELOPMENT AND EVOLUTION OF EXAGGERATED MORPHOLOGIES IN INSECTS

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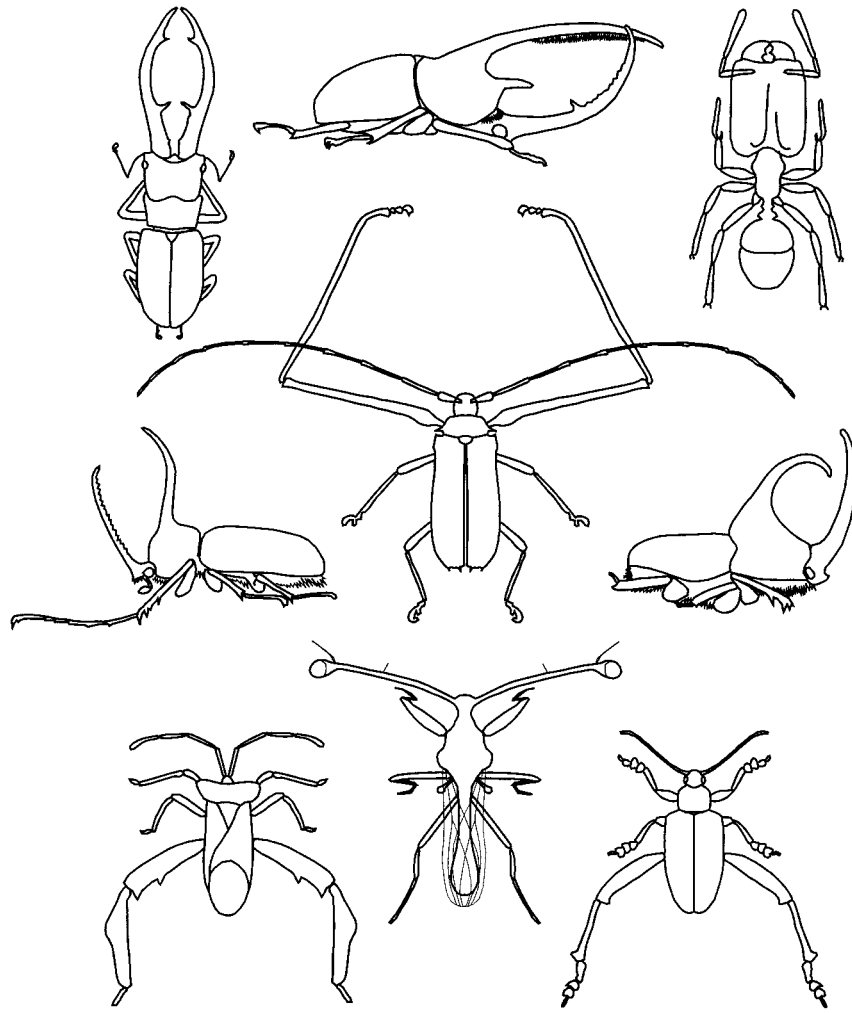
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■ **Abstract** We discuss a framework for studying the evolution of morphology in insects, based on the concepts of “phenotypic plasticity” and “reaction norms.” We illustrate this approach with the evolution of some of the most extreme morphologies in insects: exaggerated, sexually selected male ornaments and weapons, and elaborate social insect soldier castes. Most of these traits scale with body size, and these scaling relationships are often nonlinear. We argue that scaling relationships are best viewed as reaction norms, and that the evolution of exaggerated morphological traits results from genetic changes in the slope and/or shape of these scaling relationships. After reviewing literature on sexually selected and caste-specific structures, we suggest two possible routes to the evolution of exaggerated trait dimensions: (*a*) the evolution of steeper scaling relationship slopes and (*b*) the evolution of sigmoid or discontinuous scaling relationship shapes. We discuss evolutionary implications of these two routes to exaggeration and suggest why so many of the most exaggerated insect structures scale nonlinearly with body size. Finally, we review literature on insect development to provide a comprehensive picture of how scaling relationships arise and to suggest how they may be modified through evolution.

## INTRODUCTION

Insects take shape to the extreme: eyes on the ends of long stalks, forelegs longer than twice the body length, long, serrated mandibles—again, sometimes reaching lengths greater than the rest of the body, and countless knobs, spurs, and horns extending from all parts of the head and thorax (4, 41, 124, 174). In some cases, the sizes of these traits can be so extreme that they yield some of the most bizarre-looking organisms in the animal world (Figure 1).

Species with extraordinary morphologies are also characterized by extreme variation in morphology, so that not all individuals express the trait to the same extent (9, 102, 105, 124). Often, the exaggerated traits are expressed in only one sex, as, for example, in the case of the huge head and mandibles of soldier ant



**Figure 1** Examples of exaggerated morphologies in insects. *Left to right, top row*: mandibles in *Cyclommatus imperator* (Coleoptera: Lucanidae); head and thoracic horns in *Dynastes neptunus* (Coleoptera: Scarabaeidae); head width in *Pheidole tepicana* (Hymenoptera: Formicidae); *Middle row*: head and thoracic horns in *Golofa porteri* (Coleoptera: Scarabaeidae); forelegs in *Acrocinus longimanus* (Coleoptera: Cerambycidae); head and thoracic horns in *Enema pan* (Coleoptera: Scarabaeidae); *Bottom row*: hind legs in *Acanthocephala declivis* (Hemiptera: Coreidae); eyestalks in *Cyrtodiopsis whitei* (Diptera: Diopsidae); hind legs in *Sagra papuana*. (Coleoptera: Chrysomelidae).

castes (all females; e.g. 238), or the enlarged legs or horns in beetles (generally, all males; e.g. 4, 65). In addition, trait size often scales with body size, so that in a population individuals range from small, relatively normally proportioned animals, to very large animals with grossly enlarged structures.<sup>1</sup>

Most measurable aspects of the insect body covary with body size (e.g. large flies have larger wings than small flies). When measurements are collected for large numbers of individuals of similar age or at the same life stage, it is possible to characterize the precise relationship between the dimensions of each trait and individual variations in overall body size (“static allometry;” 28, 32, 118). The slopes of these scaling relationships vary almost as much as the shapes of the traits themselves, from no slope (size-invariant trait expression) to very steep slopes (traits become disproportionately larger with increasing body size), and even in a few cases, to negative slopes (traits become proportionately smaller with increasing body size). A large number of scaling relationships depart from linearity, with discontinuous and sigmoid patterns surprisingly widespread. What can the study of scaling relationships tell us, and what, if anything, can we learn from the variations in slope and shape of these scaling relationships?

Here we survey the range of variation that occurs in insect scaling relationships, with particular emphasis on exaggerated morphological traits. We provide a framework for viewing and studying the evolution of exaggerated traits and their scaling relationships that builds on recent developments in the fields of reaction norms and phenotypic plasticity.<sup>2</sup> While this view is not entirely new, it is seldom made explicit for the study of trait allometry. We make this framework explicit because it incorporates a more accurate appreciation for how exaggerated traits are inherited and because it offers new and informative avenues for future research. We summarize this review with six points: (*a*) the decades-old view of allometries as constraints to evolution is inaccurate and misleading; (*b*) scaling relationships may be considered a special type of reaction norm, whereby the expression of specific traits is influenced by growth in overall body size, and growth in body size (at least in insects) is influenced by the environment; (*c*)

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<sup>1</sup>We use the term scaling instead of allometry as recommended by Schmidt-Nielsen (189) and LaBarbera (123). For this paper, “scaling relationships” refers to the covariation of trait magnitude with overall body size, with no assumptions as to the slope or shape of the relationship.

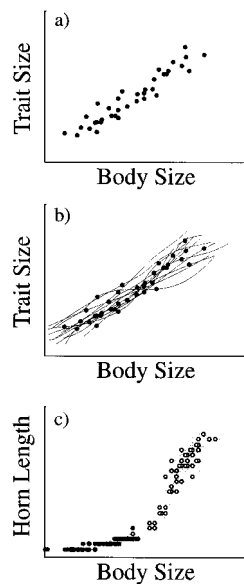
<sup>2</sup>We use the term reaction norm to refer to the range of possible morphologies that individuals with the same genotype would express were they reared across a range of different environments or growth conditions (after 15, 188). Each individual insect that a researcher captures and measures will have one morphology—one body size and one horn, foreleg, or mandible size. Yet that same individual, had it been reared in a different environment, would have matured at a different body size, with a correspondingly altered horn, foreleg, or mandible. The reaction norm encompasses the entire range of morphologies that are possible endpoints for that genetic individual. This can also be viewed as the range of morphologies that would be produced either by close relatives (e.g. siblings) or by subsequent generations of one lineage, were they reared in different growth environments.

components of the developmental mechanism producing scaling are heritable, and scaling relationships can and do themselves evolve; (d) rich insight may be gained from comparative studies of the shapes or slopes of scaling relationships and how these relate to physical and social selective environments; (e) we use this approach to suggest why many exaggerated morphological traits exhibit discontinuous, or nonlinear scaling relationships; (f) we draw on what is currently known about how the development of some of these traits is regulated, and suggest implications of these mechanisms for the evolution of extreme shapes in insects.

## SIZE-DEPENDENT EXPRESSION OF MORPHOLOGICAL TRAITS

Scaling relationships depict the size-dependent expression of body parts (32, 102, 123, 189). Large individuals tend to have larger wings, legs, or eyes than smaller individuals have (Figure 2a). But what makes an individual insect large or small? In most insects growth in body size is influenced by the larval environment (e.g.

**Figure 2** “Reaction-norm” view of scaling relationships. (a) The dimensions of most morphological traits covary with body size. The slopes or shapes of these scaling relationships are generally measured from static samples of individuals (“static allometry;” 32). (b) Static samples can obscure the fact that genotypes may have the potential to generate a range of different trait sizes, depending on how large each individual expressing the genotype grows to be. For example, an individual insect reared on a favorable diet will have a large body size and a large trait size. Yet that same individual, had it been reared in a poor growth environment, would have matured at a smaller body size, with a correspondingly smaller trait magnitude. The “reaction norm” view of the scaling relationship considers the breadth of possible endpoints for each genotype. In this case, the morphology actually produced by a specific individual depends on the shape of that individual’s genotype-specific reaction norm (genotypes are indicated by *thin lines*), and on how large that individual grows to be (*filled circles*). (c) Evidence that scaling relationships can be considered reaction norms comes from controlled breeding experiments that compare the morphologies of close relatives reared across a range of nutrient conditions. For example, *Onthophagus acuminatus* males reared with large amounts of food grew to large body sizes and produced long horns (*open circles*), whereas sibling males reared on smaller food amounts remained small, and these males produced shorter horn lengths (*closed circles*; from 59).



12, 26, 103, 104, 231). Fluctuations in nutrient availability, temperature, and humidity all affect larval growth, as does the intensity of larval competition and larval population density. Through their effects on larval growth, these environmental factors all influence how large a larva grows to be, and hence partially determine the final adult size of that animal. Often sequential offspring from the same parents encounter different environmental conditions and mature at different body sizes despite the fact that they are genetically similar. This is perhaps most obvious in insects with parthenogenetic generations, such as aphids, where genetic clones vary extensively in body size. Yet even in these clones, morphological traits scale with variations in body size (e.g. 201, 202).

The scaling relationship, then, must reflect allocation to a trait across a range of possible final body sizes (53, 60, 61, 187, 223, 224). The body size actually attained, and thus the dimension of trait produced, depends on the environment that each larva encounters, as well as inherited factors. More specifically, the dimensions of each trait will depend on an interaction between the genotype of each individual, and the environmental factors influencing that larva's final adult body size (Figure 2*b*). Scaling relationships may thus be considered a special type of reaction norm (15, 187, 188), with each genotype capable of expressing a range of trait sizes (59, 60, 61, 187). Just as genotypes can produce a range of different phenotypes in response to variations in the physical environment (e.g. plant shape responding to variation in light availability; 49, 190), they can also produce different phenotypes in response to a range of final adult body sizes. In this case, the shape of the reaction norm determines the types of morphologies produced at each possible body size, and these relationships may be simple (linear), or more complex (e.g. threshold traits).

Despite this realization, the "reaction norm" view of phenotypes has seldom been applied to the study of insect allometry. One reason for this discrepancy may be that reaction norm studies and scaling relationship studies often use different types of data. The reaction norm concept arose from studies on plants where seeds of similar genotype could be planted across an array of physical environmental conditions (15, 127, 186, 187, 188). When relatives were planted in different environments it became clear that a genotype grown in one environment produced a different phenotype than that same genotype would produce in a second environment (15, 49, 186, 187, 188, 190). Furthermore, it became obvious that to understand the evolution of these characters it was necessary to consider not just the plastic phenotypes, but also the genotype-specific reaction norms that gave rise to the phenotypes (76, 77, 127, 183, 184, 186, 187, 199, 221, 223).

In contrast, studies of relative growth or scaling in insects generally do not involve rearing related individuals across a range of growth conditions. Instead, these studies often use collections of individuals sampled from wild populations or museums (Figure 2*a*). From these static samples it is less obvious that each genotype is capable of producing a range of different forms (Figure 2*b*), and it becomes easy to study the phenotypes (e.g. the exaggerated traits) and to overlook the underlying reaction norms that generated the phenotypes.

There is good evidence that the size-dependent expression of morphological structures in insects is sensitive to the growth environment (i.e. that scaling relationships can be equated with reaction norms). Body size in insects is strongly affected by the physical and social environment (e.g. 12, 26, 104, 231), and genotypes must therefore be capable of producing a range of different trait forms depending on how large any individual grows to be. The best evidence is provided by controlled laboratory experiments where relatives (or clones) are reared under a range of growth conditions. From these experiments it is possible to characterize the shapes of the reaction norms for specific genotypes or families. Several recent studies have deliberately manipulated environmental variables relevant to growth in insects, and these clearly demonstrate that single genotypes can generate the full range of possible trait dimensions (59, 100, 219). For example, manipulations of the amount of food available to growing larvae determined the final body sizes attained by male *Onthophagus acuminatus* and *O. taurus* (Coleoptera: Scarabaeidae), and these experimentally induced variations in body size were accompanied by corresponding variations in male horn length (Figure 2c; 59, 100). Because these diet manipulations were administered within beetle families, it was possible to illustrate that each family had the potential to generate the full range of possible horn lengths. Furthermore, in all cases where these reaction norms have been studied so far, the shapes of these relationships match closely with the general scaling relationship for the population (e.g. Figure 2c; 59, 100, 219).

Consequently, we suggest that a useful framework for viewing and studying scaling relationships is to recognize that the shape of the static relationship is a reflection of underlying patterns of allocation to traits by genotypes across a range of body sizes. This means that studies of morphological traits in insects must consider not just the traits themselves (e.g. the horns or mandibles) but also the underlying reaction norms that relate expression of the trait to variations in body size. It is evolutionary modifications to these scaling relationships that ultimately yield exaggerated or bizarre morphological structures in insects. It is also important to remember that these scaling relationships are not the same as growth trajectories (i.e. ontogenetic and static allometries are not the same thing; 32). It is very clear now—especially in holometabolous insects—that traits do not grow along the trajectory that we define as a static allometry (153, 200). Instead, the scaling relationship reflects the range of possible endpoints—final shapes—that would be generated by genotypes at each possible adult body size.

## SCALING RELATIONSHIPS CAN AND DO EVOLVE

Scaling relationships result from developmental processes that regulate the growth of body parts (153, 200). The final dimensions of any morphological trait will be determined by patterns of gene expression, by patterns of cell growth and division, by the actions of hormones, and by the growth of other tissues (reviewed in 200). All of these processes can be influenced by the internal and external environments

that growing tissues encounter, and in some cases this can result in condition sensitivity of final trait size. For example, the nutritional environment encountered by a larva will determine the rate at which that animal acquires nutrients essential for growth. Acquisition of nutrients by a larva can translate into protein and fat stores, as well as circulating levels of nutrients, and these can determine how large both the animal and the different body parts grow to be. The usual result: animals encountering favorable nutritional environments end up larger and with larger traits than individuals encountering less favorable diets. Similarly, larval exposure to environmental factors such as crowding, photoperiod, or temperature can influence levels of hormones, and these can also affect both overall growth and the growth of specific tissues.

Although these mechanisms may permit the growth of body parts to be sensitive to changes in the environment and to variations in overall body size, this characteristic does not indicate that these mechanisms are “non-genetic.” Inherited differences in the expression or interaction of the various components of these mechanisms can cause different individuals to be sensitive to the environment in slightly different ways. For example, different individuals within a population may vary genetically in *how* they respond to changes in the growth environment, such that for any given final body size, some genotypes produce slightly larger or smaller traits than other genotypes (Figure 2*b*). Whenever differences among individuals result from genetic variations in components of the mechanisms that regulate trait growth, then these mechanisms may themselves evolve.

This condition is exactly analogous to the regulation of reaction norms in other animals or plants, where genotypes vary in the shape or position of their respective reaction norms: that is, genotypes differ in how they respond to the environment (e.g. 91, 161, 211). In these situations, the reaction norms may themselves evolve, and selection experiments clearly indicate that reaction norms are often capable of very rapid responses to selection (15*a*, 48, 97, 117, 182, 185, 214–216).

Scaling relationships for morphological traits in insects should therefore be capable of adaptive evolution (see 125, 187, 219, 242). Evidence that this is indeed the case comes from two sources: comparative studies measuring differences in the scaling relationships among related taxa, and artificial selection experiments that select directly on scaling relationships within populations.

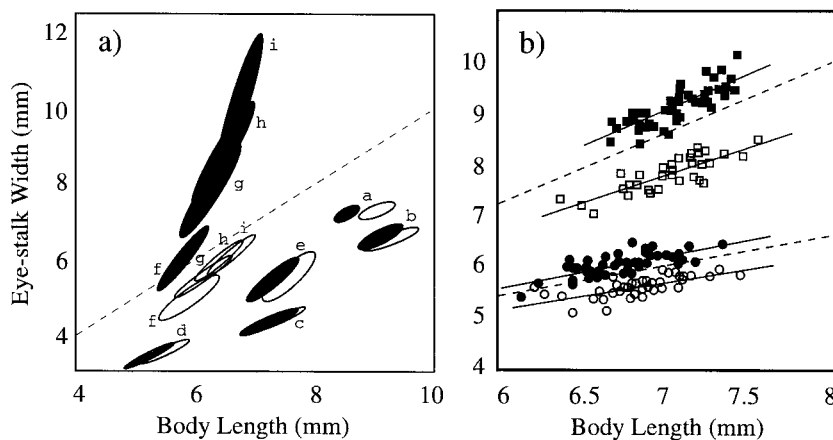
## Comparative Studies

The recognition that different taxa display scaling relationships with different slopes or shapes is not new. Huxley, Rensch, Gould, and others all used scaling relationships as a convenient way to compare populations or species (86–88, 95, 102, 173, 196, 197). Ironically, many of these same authors invoked the scaling relationship as evidence of restricted (immutable) patterns of growth, and considered these relationships to be evidence that the evolution of populations was constrained—even though they recognized that closely related taxa differed in

aspects of their scaling relationships (e.g. taxa differed in the slopes of scaling relationships when measured on log-log plots; 88, 95, 102, 164, 167, 173, 196, 197). Many studies have shown that the scaling relationships of closely related taxa can differ significantly (e.g. Figure 3a; 23, 61, 86, 114, 116, 119, 158, 178, 189, 194, 234, 238). Although such comparative studies do not necessarily indicate that the trait allometries of *extant* populations are capable of evolving, they certainly demonstrate that such changes have occurred extensively in the past. A better way to reveal whether the size-dependent expression of morphological traits in current populations can evolve is by artificial selection experiments.

### Artificial Selection Experiments

At least three recent studies have attempted to artificially select for changes in trait scaling relationships. In the first case, Weber (219) selected for several different changes in the wing morphology of flies (*Drosophila melanogaster*). In these experiments, he did not select on wing length, or wing width per se, but selected instead on the relative sizes of specific wing parts. He applied selection



**Figure 3** Evidence that scaling relationships evolve. (a) Comparative studies illustrating changes that have already occurred [example: bivariate distributions between eyestalk width and body length for nine Malaysian species of Diopsidae. Separate ellipses are shown for the males (black) and females (open) of each species; a: *Diopsis indica*; b: *Eurydiopsis subnotata*; c: *Cyrtodiopsis quinqueguttata*; d: *Maglabops quadriguttata*; e: *M. sexguttata*; f: *M. rubicunda*; g: *C. dalmanni*; h: *C. whitei*; i: *Teleopsis discrepans* (modified from 23)]; (b) Artificial selection experiments altering scaling relationships directly (example: scaling relationships for eyestalk width in *Cyrtodiopsis dalmanni* were subjected to artificial selection for either increased relative male eyestalk width, *closed squares*, or decreased relative male eyestalk width, *open squares*. Tenth generation individuals are shown. Shifts in the male scaling relationship were accompanied by correlated but smaller shifts in the female scaling relationship (*circles*; modified from 233).



to the scaling relationships between five different sets of landmarks on the wings. These experiments produced rapid visible changes in the dimensions of parts of the fly wings and resulted in significant shifts in the scaling relationships among these traits (219). Weber argued that all subdimensions of the wing exhibit locally acting additive genetic variation and that the heritability of the allometry was as large as the heritability of wing size itself (219).

A second study involves the stalk-eyed flies (Diptera: Diopsidae). A number of species in this family exhibit striking sexual dimorphism, with males producing eyes that are perched at the ends of long eyestalks (23, 174, 193, 234). In some individuals, the distance between the eyes can be more than twice the body length. Both males and females have eyestalks, but in dimorphic species the slope of the male eyestalk/body-size scaling relationship is much steeper than the relationship for females (23, 234). Comparisons among related taxa revealed marked differences in the slopes of the eyestalk scaling relationships, ranging from sexually monomorphic taxa, like *Cyrtodiopsis quinqueguttata*, where both males and females have the same low slope of eyestalk-to-body size relationship, to other taxa, such as *Cyrtodiopsis whitei*, where the males have eyestalk scaling relationships that are much steeper than those of females (Figure 3a; 23, 234). These interspecific comparisons suggest that eyestalk scaling relationships have evolved extensively in the past. The most convincing evidence for scaling relationship evolution was provided by an artificial selection experiment in one of the species. In the sexually dimorphic species *Cyrtodiopsis dalmanni*, Wilkinson artificially selected on male eyestalk allometry, by directly selecting on the ratio of eyestalk length to overall body length (233). In each of two genetically independent lines he selected males with disproportionately long eyestalks (males with high eyestalk-width/body-length ratios), and in two additional lines he selected for males with relatively short eyestalks (small eyestalk-width/body-length ratios). *Cyrtodiopsis dalmanni* populations responded rapidly and significantly to selection, so that after 10 generations the scaling relationships of the two types of treatment lines were completely nonoverlapping (Figure 3b; 233). The scaling relationship between eyestalk length and body size had changed dramatically in response to artificial selection (see also 235a).

A third example involves horns in male beetles. Males in many beetle taxa produce elongated extensions of the cuticle called horns (4, 41, 51–53, 55, 174). In *Onthophagus acuminatus*, males, but not females, produce a pair of cephalic horns (59, 60). Male horn length increases with overall body size, and this scaling relationship is not linear (discussed further below). The horn-length/body-size scaling relationship in this and related species is sigmoidal in shape and results in a bimodal horn-length frequency distribution: males with long horns are common, as are males with only rudimentary horns, but males with intermediate horn lengths are relatively rare (59). One of us (61) used an artificial selection design to select directly on the horn-length/body-size scaling relationship. By selecting on the relative length of male horns (i.e. selecting males with unusually long or unusually short horns for their respective body sizes), significant shifts in this

scaling relationship were produced after only seven generations. Again, this indicates that populations of this species contain heritable variation for the relationship between horn length and body size.

### Scaling Relationships as Traits

As noted above, scaling relationships have been considered a form of constraint on evolutionary change—a reflection of underlying immutable properties of a developmental system that restrict evolutionary changes to the direction specified by the scaling relationship. Increasingly, however, this view is being called into question as both inaccurate and misleading. The studies mentioned in this section indicate that scaling relationships vary heritably within populations, that they have evolved extensively in the past, and that they are still capable of evolving rapidly if the selective environment is changed.

These findings have important implications for the study of insect scaling relationships. If we stop viewing scaling relationships as immutable properties of development, and instead consider them to be manifestations of condition-sensitive mechanisms of trait expression that have been molded by a history of natural and sexual selection, then we can begin to explore not just *how* traits covary with body size, but *why* they covary with body size. More specifically, we can begin to examine the slopes or shapes of scaling relationships in different taxa and ask why these relationships have the shapes that they have. Again, to draw on the literature from the study of reaction norms, we can ask why the reaction norms that relate the expression of a trait to variations in the growth environment have the precise shapes that they have. Why are some slopes steeper than others? Why do some traits exhibit discontinuous or sigmoidal scaling relationships and others exhibit linear relationships? We suggest that in many cases, the shape of trait-scaling relationships will contain valuable information regarding the underlying developmental mechanisms that give rise to the scaling relationship, as well as the natural forces of selection on each trait and how those forces of selection vary with differences in body size. This is especially evident for scaling relationships of exaggerated, disproportionately large morphological traits like eyestalks and horns. With this as a framework, we explore the range of variation present in insect scaling relationships, with particular emphasis on exaggerated structures.

### SURVEY OF SCALING RELATIONSHIPS OF EXAGGERATED MORPHOLOGICAL TRAITS

We reviewed literature on bivariate scaling relationships for morphological traits and body size. For exaggerated traits, we recorded the trait involved, the sex expressing the exaggerated form of the trait, and the shape of the scaling relationship (linear, curved, sigmoid, or discontinuous). Because in most cases we

did not have access to the raw data, we were unable to use the quantitative methods of Happell (92) or Eberhard & Gutierrez (58) to describe scaling relationship shape. Instead, scaling relationships were characterized qualitatively by visual examination of the bivariate relationships.

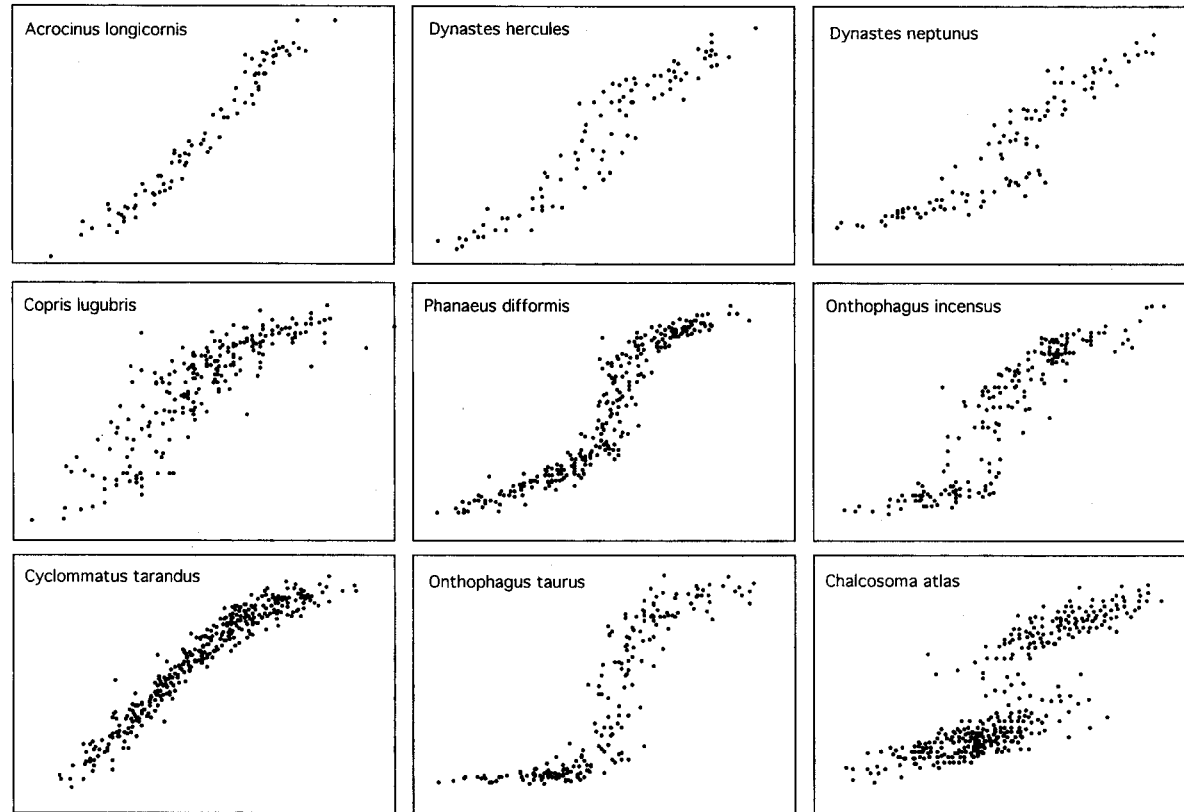
To facilitate visual comparison of variations in the shapes of scaling relationships, we selected a subset of nine of the studies and digitized the points from the published figures (Figure 4). Digitization was necessary because the overall sizes of the insects and traits varied considerably, and published figures differed in the use of logarithmic and linear scales in one or both axes. Digitization of published scaling relationships allowed us to standardize the body size and trait values around the mean of each species, and to perform the same transformations on all of the data. For this comparison we selected taxa where linear measures of body size were compared with linear measures of trait dimension. All body size and trait values were mean standardized, and all data were examined on both log and untransformed scales (for studies where log values were plotted, we converted these to antilogs after digitization).

Most scaling relationships for morphological traits in insects are linear. However, when we considered the subset of morphological traits that reach unusual proportions—the exaggerated ornaments or weapons of males, or the distended heads of soldier castes in ants—the shapes of scaling relationships were quite diverse (Table 1). Scaling relationships for exaggerated traits were either linear, curved, sigmoid, or composed of completely discontinuous segments (Table 1; see Figure 4 for examples). When we considered the most extreme traits, a comparison across taxa revealed two types of scaling relationship shapes, suggesting that there are two basic ways of achieving grossly enlarged morphological structures: linear relationships with very steep slopes, or sigmoid/broken relationships incorporating a threshold (Figure 5).

## Steep Allometry Slopes

Populations may produce ever larger traits by evolving ever steeper scaling relationships, so that with increases in body size, genotypes produce disproportionately larger increases in trait magnitude (Figure 5*b*). Some of the most extreme morphologies are produced this way, including the antlers and eyestalks of Tephritid and Diopsid flies, forceps in many species of earwig, and the enlarged legs of bugs, weevils, and harlequin beetles (Table 1).

With the exception of ant castes, exaggerated traits tend to be expressed primarily in males, and in all cases where behavior has been explored, the exaggerated traits play a role in competition over access to reproduction (sexual selection). Male eyestalks in Diopsid flies, for instance, are characters on which direct female choice of mates is based (23, 24, 128, 235). Enlarged male legs are used for male-male combat over access to females in bugs (*Coreidae*: 56, 75, 134–136), weevils (*Macromerus bicinctus*: 218), and harlequin beetles (*Acrocinus longimanus*: 241). Fly antlers (*Phytalmia* spp.: 45, 234) and eyestalks (160a) and



**Figure 4** Examples of nine scaling relationships for exaggerated morphological traits. Scaling relationships for these traits were linear, curved, sigmoid, or completely broken. All figures included linear measures of both trait magnitude (*Y-axis*) and body size (*X-axis*). Values were digitized from published graphs and mean-standardized to facilitate shape comparisons. See Table 1 for trait descriptions and references.

**TABLE 1** Scaling relationships for exaggerated traits in insects

| Order                    | Family        | Genus and Species               | Exaggerated Trait | Sex-expressing trait | Scaling-relationship shape | Reference              |
|--------------------------|---------------|---------------------------------|-------------------|----------------------|----------------------------|------------------------|
| Dermaptera               | Chelisochidae | <i>Adiathetus tenebrator</i>    | forceps           | males                | linear                     | J Tomkins, pers. comm. |
|                          |               | <i>Chelosoches morio</i>        | forceps           | males                | linear                     | J Tomkins, pers. comm. |
|                          |               | <i>Eunkrates varegatum</i>      | forceps           | males                | linear                     | J Tomkins, pers. comm. |
|                          |               | <i>Proreus ludekingi</i>        | forceps           | males                | discontinuous              | 206                    |
|                          | Forficulidae  | <i>Anechura harmandi</i>        | forceps           | males                | linear                     | 204                    |
|                          |               | <i>Doru taeniatum</i>           | forceps           | males                | linear                     | 58                     |
|                          |               | <i>Eluanon bipartitus</i>       | forceps           | males                | discontinuous              | 206                    |
|                          |               | <i>Forficula auricularia</i>    | forceps           | males                | sigmoid                    | 9, 43, 170, 206, 207   |
|                          |               | <i>Metrasura ruficeps</i>       | forceps           | males                | linear                     | 58                     |
|                          |               | <i>Oreasiobias stolickzae</i>   | forceps           | males                | discontinuous              | 206                    |
|                          |               | <i>Timomenus aeris</i>          | forceps           | males                | discontinuous              | 206                    |
|                          | Labiidae      | <i>Chaetospania thoracia</i>    | forceps           | males                | linear                     | J Tomkins, pers. comm. |
|                          |               | <i>Paralabella dorsalis</i>     | forceps           | males                | linear                     | 58                     |
|                          |               | <i>Spongovostox assiniensis</i> | forceps           | males                | discontinuous              | 206                    |
|                          |               | <i>Vostox punctipennis</i>      | forceps           | males                | linear                     | J Tomkins, pers. comm. |
|                          | Labiduridae   | <i>Forcipula gariazzi</i>       | forceps           | males                | linear                     | J Tomkins, pers. comm. |
|                          |               | <i>Forcipula quadrispinosa</i>  | forceps           | males                | sigmoid                    | J Tomkins, pers. comm. |
| <i>Labidura truncata</i> |               | forceps                         | males             | discontinuous        | 9, 43, 170, 206, 207       |                        |
| Hemiptera                | Coreidae      | <i>Acanthocephala declivis</i>  | hind femur        | males                | linear                     | 56                     |
|                          |               | <i>Leptoglossus australis</i>   | hind femur        | males                | linear                     | 136                    |
| Homoptera                | Hormaphidae   | <i>Pseudoregma alexanderi</i>   | fore femur        | females              | discontinuous              | 201                    |
| Coleoptera               | Cerambycidae  | <i>Acrocinus longimanuss</i>    | forelegs          | males                | linear                     | 241                    |

TABLE 1 (continued) Scaling relationships for exaggerated traits in insects

| Order      | Family        | Genus and Species                | Exaggerated Trait | Sex-expressing trait | Scaling-relationship shape | Reference   |
|------------|---------------|----------------------------------|-------------------|----------------------|----------------------------|-------------|
| Coleoptera | Cerambycidae  | <i>Dendrobias mandibularis</i>   | mandibles         | males                | sigmoid                    | 82          |
|            | Curculionidae | <i>Rhinostomus barbirostris</i>  | beak/rostra       | males                | linear                     | 54, 58      |
|            |               | <i>Centrinaspis sp.</i>          | ventral spine     | males                | linear                     | 58          |
|            |               | <i>Geraeus sp.</i>               | ventral spine     | males                | sigmoid                    | 57          |
|            |               | <i>Macromerus bicinctus</i>      | forelegs          | males                | linear?                    | 218         |
|            | Endomychidae  | <i>Stenotarsus rotundus</i>      | hind trochanter   | males                | linear                     | 144         |
|            | Lucanidae     | <i>Cyclommatus bicolor</i>       | mandibles         | males                | linear                     | 116         |
|            |               | <i>Cyclommatus elaphus</i>       | mandibles         | males                | linear                     | 116         |
|            |               | <i>Cyclommatus lunifer</i>       | mandibles         | males                | curved                     | 101, 116    |
|            |               | <i>Cyclommatus tarandus</i>      | mandibles         | males                | curved                     | 50, 58, 101 |
|            |               | <i>Hexarthris davisoni</i>       | mandibles         | males                | linear                     | 158         |
|            |               | <i>Lamprima alophinae</i>        | mandibles         | males                | linear                     | 158         |
|            |               | <i>Lucanus cervus</i>            | mandibles         | males                | curved                     | 31, 58, 101 |
|            |               | <i>Lucanus elephas</i>           | mandibles         | males                | linear                     | 158         |
|            |               | <i>Neolucanus cinglatus</i>      | mandibles         | males                | linear                     | 116         |
|            |               | <i>Neolucanus nitidus</i>        | mandibles         | males                | linear                     | 116         |
|            |               | <i>Neolucanus perarmatus</i>     | mandibles         | males                | linear                     | 116         |
|            |               | <i>Odontolabis cuvera</i>        | mandibles         | males                | sigmoid                    | 158         |
|            |               | <i>Odontolabis imperialis</i>    | mandibles         | males                | sigmoid                    | 116         |
|            |               | <i>Odontolabis micros</i>        | mandibles         | males                | discontinuous              | 116         |
|            |               | <i>Odontolabis siva</i>          | mandibles         | males                | discontinuous              | 116, 158    |
|            |               | <i>Prosopocoelus serricornis</i> | mandibles         | males                | linear                     | 158         |

|               |                                |                         |       |               |                      |
|---------------|--------------------------------|-------------------------|-------|---------------|----------------------|
|               | <i>Psalidoremus inclinatus</i> | mandibles               | males | curved        | 158                  |
|               | <i>Serrognathus platymelus</i> | mandibles               | males | linear        | 158                  |
|               | <i>Xylotrupes gideon</i>       | mandibles               | males | sigmoid       | 9, 101, 58           |
| Melolonthidae | <i>Inca clathra</i>            | clypeal horn            | males | linear        | 142                  |
| Scarabaeidae  | <i>Ageopsis nigricollis</i>    | head and thoracic horns | males | sigmoid       | 55                   |
|               | <i>Allomyrina dichotoma</i>    | head horn               | males | linear        | 103, 198             |
|               | <i>Chalcosoma atlas</i>        | head and thoracic horns | males | discontinuous | 114                  |
|               | <i>Chalcosoma caucasus</i>     | head and thoracic horns | males | discontinuous | 114                  |
|               | <i>Copris lugubris</i>         | head horn               | males | curved        | 58                   |
|               | <i>Coprophanaeus ensifer</i>   | head horn               | both  | linear        | 159                  |
|               | <i>Drepanoceros kirbyi</i>     | thoracic horn           | males | sigmoid       | R Knell, pers. comm. |
|               | <i>Dynastes centaurus</i>      | thoracic horn           | males | sigmoid       | 58                   |
|               | <i>Dynastes hercules</i>       | head and thoracic horn  | males | sigmoid       | 114                  |
|               | <i>Dynastes hyllus</i>         | thoracic horn           | males | linear        | 143                  |
|               | <i>Dynastes neptunus</i>       | head and thoracic horns | males | sigmoid       | 114                  |
|               | <i>Megasoma elephas</i>        | head horn               | males | curved        | 58                   |
|               | <i>Onthophagus acuminatus</i>  | head horns              | males | sigmoid       | 59, 61               |
|               | <i>Onthophagus australis</i>   | head horns              | males | sigmoid       | J Hunt, pers. comm.  |
|               | <i>Onthophagus batesi</i>      | head horns              | males | sigmoid       | D Emlen, unpublished |
|               | <i>Onthophagus binodis</i>     | thoracic horn           | males | curved        | 35, 195              |
|               | <i>Onthophagus ferox</i>       | head and thoracic horns | males | linear        | 35                   |
|               | <i>Onthophagus fuliginosus</i> | head horns              | males | curved        | J Hunt, pers. comm.  |
|               | <i>Onthophagus gazella</i>     | head horns              | males | sigmoid       | J Hunt, pers. comm.  |
|               | <i>Onthophagus haagi</i>       | head horns              | males | sigmoid       | J Hunt, pers. comm.  |
|               | <i>Onthophagus hecate</i>      | thoracic horn           | males | curved        | D Emlen, unpublished |
|               | <i>Onthophagus incensus</i>    | head horns              | males | sigmoid       | 58                   |

TABLE 1 (continued) Scaling relationships for exaggerated traits in insects

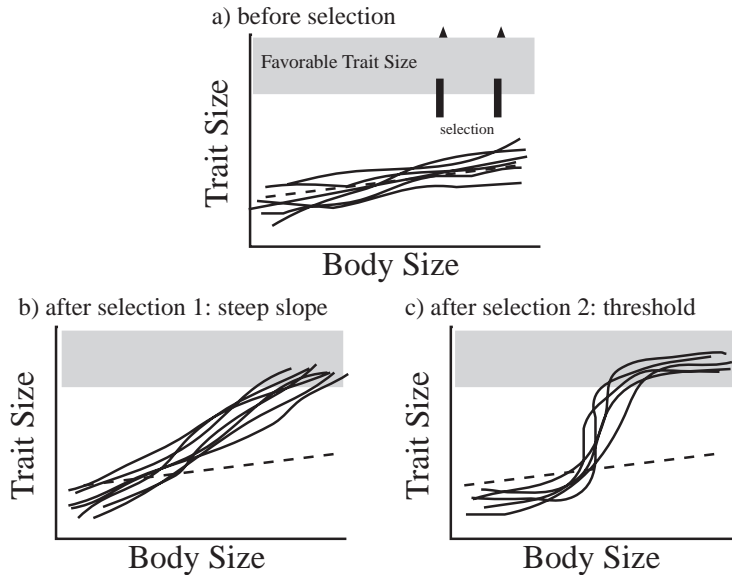
| Order                         | Family                      | Genus and Species                | Exaggerated Trait | Sex-expressing trait         | Scaling-relationship shape | Reference              |        |
|-------------------------------|-----------------------------|----------------------------------|-------------------|------------------------------|----------------------------|------------------------|--------|
| Coleoptera                    | Scarabaeidae                | <i>Onthophagus marginicollis</i> | head horns        | males                        | sigmoid                    | D Emlen, unpublished   |        |
|                               |                             | <i>Onthophagus striatulus</i>    | head horns        | males                        | sigmoid                    | D Emlen, unpublished   |        |
|                               |                             | <i>Onthophagus taurus</i>        | head horns        | males                        | sigmoid                    | 63, 100, 137, 138, 195 |        |
|                               |                             | <i>Onthophagus vermiculatus</i>  | head horns        | males                        | sigmoid                    | J Hunt, pers. comm.    |        |
|                               |                             | <i>Phanaeus difformis</i>        | head horn         | males                        | sigmoid                    | 171                    |        |
|                               |                             | <i>Podischnus agenor</i>         | head horn         | males                        | sigmoid                    | 53                     |        |
|                               |                             | <i>Xylorectes lobicollis</i>     | head horn         | males                        | linear                     | 58                     |        |
|                               |                             | <i>Leistotrophus versicolor</i>  | mandibles         | males                        | linear                     | 70                     |        |
|                               |                             | <i>Bolitotherus cornutus</i>     | thoracic horns    | males                        | linear                     | 20, 21                 |        |
|                               |                             | Diptera                          | Diopsidae         | <i>Cyrtodiopsis dalmanni</i> | eyestalk                   | males                  | linear |
| <i>Cyrtodiopsis whitei</i>    | eyestalk                    |                                  |                   | males                        | linear                     | 23, 234                |        |
| <i>Diasemopsis dubia</i>      | eyestalk                    |                                  |                   | males                        | linear                     | 234                    |        |
| <i>Diasemopsis fasciata</i>   | eyestalk                    |                                  |                   | males                        | linear                     | 234                    |        |
| <i>Diasemopsis sylvatica</i>  | eyestalk                    |                                  |                   | males                        | linear                     | 234                    |        |
| <i>Teleopsis boettcheri</i>   | eyestalk                    |                                  |                   | males                        | linear                     | 193                    |        |
| <i>Teleopsis breviscopium</i> | eyestalk                    |                                  |                   | males                        | linear                     | 234                    |        |
| <i>Teleopsis rubicunda</i>    | eyestalk                    |                                  |                   | males                        | linear                     | 234                    |        |
| Tephritidae                   | <i>Phytalmia alcicornis</i> |                                  |                   | antler                       | males                      | linear                 | 234    |
|                               | <i>Phytalmia mouldsi</i>    |                                  |                   | antler                       | males                      | linear                 | 234    |
| Hymenoptera                   | Andrenidae                  | <i>Perdita portalis</i>          | large head        | males                        | discontinuous              | 38, 39                 |        |
|                               |                             | <i>Perdita texana</i>            | large head        | males                        | linear                     | 39, 40                 |        |
|                               | Formicidae                  | <i>Anomma nigricanus</i>         | wide head         | females                      | curved                     | 99, 238                |        |



|                                   |           |         |               |            |
|-----------------------------------|-----------|---------|---------------|------------|
| <i>Atta colombica</i>             | wide head | females | curved        | 69         |
| <i>Atta texana</i>                | wide head | females | curved        | 238        |
| <i>Camponotus castaneus</i>       | wide head | females | linear        | 237        |
| <i>Camponotus floridanus</i>      | wide head | females | sigmoid       | 238        |
| <i>Camponotus maculatus</i>       | wide head | females | discontinuous | 7          |
| <i>Camponotus novaeboracensis</i> | wide head | females | linear        | 78         |
| <i>Camponotus rufipes</i>         | wide head | females | curved        | 44         |
| <i>Cephalotes atratus</i>         | wide head | females | linear        | 37         |
| <i>Daceton armigerum</i>          | wide head | females | linear        | 140        |
| <i>Dorylus spp.</i>               | wide head | females | curved        | 84, 85, 98 |
| <i>Eciton hamatum</i>             | wide head | females | discontinuous | 69         |
| <i>Formica exsecta</i>            | wide head | males   | discontinuous | 71         |
| <i>Formica obscuripes</i>         | wide head | females | linear        | 238        |
| <i>Lasius flavus</i>              | wide head | females | linear        | 72         |
| <i>Lasius fuliginosus</i>         | wide head | females | linear        | 238        |
| <i>Lepthothorax longispinosus</i> | wide head | females | linear        | 94, 98     |
| <i>Megaponera foetens</i>         | wide head | females | linear        | 212        |
| <i>Messor capensis</i>            | wide head | females | linear        | 213        |
| <i>Messor spp.</i>                | wide head | females | linear        | 80, 98     |
| <i>Myrmecia brevinoda</i>         | wide head | females | linear        | 96         |
| <i>Myrmecia froggatti</i>         | wide head | females | linear        | 106        |
| <i>Neivamyrmex nigrescens</i>     | wide head | females | linear        | 238        |
| <i>Oecophylla leakeyi</i>         | wide head | females | sigmoid       | 238, 239   |
| <i>Oecophylla smaragdina</i>      | wide head | females | broken        | 237        |
| <i>Paraponera clavata</i>         | wide head | females | linear        | 16         |
| <i>Pheidole bicarinata</i>        | wide head | females | discontinuous | 227, 228   |

**TABLE 1** (continued) Scaling relationships for exaggerated traits in insects

| <b>Order</b> | <b>Family</b> | <b>Genus and Species</b>        | <b>Exaggerated Trait</b> | <b>Sex-expressing trait</b> | <b>Scaling-relationship shape</b> | <b>Reference</b>     |
|--------------|---------------|---------------------------------|--------------------------|-----------------------------|-----------------------------------|----------------------|
| Hymenoptera  | Formicidae    | <i>Pheidole rhea</i>            | wide head                | females                     | sigmoid                           | 238                  |
|              |               | <i>Pheidologeton diversus</i>   | wide head                | females                     | discontinuous                     | 139                  |
|              |               | <i>Ropalidia ignobilis</i>      | wide head                | females                     | discontinuous                     | 222                  |
|              |               | <i>Solenopsis germinata</i>     | wide head                | females                     | linear                            | 225                  |
|              |               | <i>Solenopsis invicta</i>       | wide head                | females                     | linear                            | 225                  |
|              | Vespidae      | <i>Pseudopolybia difficilis</i> | large head               | females                     | discontinuous                     | 107                  |
|              |               | <i>Synagris cornuta</i>         | mandibular tusks         | males                       | discontinuous                     | Longair, pers. comm. |



**Figure 5** Alternative routes to the evolution of exaggerated traits. (a) Populations subjected to selection for enlarged trait dimensions (e.g. sexual selection for a large male weapon) can evolve the capacity to generate extreme forms in one of two ways: (b) genotypes that allocate disproportionately rapidly to the trait may be favored, so that populations evolve steep, positive linear scaling relationships, or (c) genotypes capable of facultatively expressing the trait may be favored, resulting in populations with sigmoid or broken scaling relationships. It is also possible that steep scaling relationships evolve first, and facultative expression evolves later (b  $\rightarrow$  c). Reasons why this might occur are discussed in the text. An additional possibility not considered here would be a shift in the intercept of a linear scaling relationship.

earwig forceps (*Forficula* spp.: 18, 141, 170) are also used in aggressive encounters between males.

Given that many of these are sexually selected traits, their steep linear scaling relationships are not surprising. Theoretical models of sexual selection predict the evolution of steep positive scaling relationship slopes (89, 165, 166, 194). Sexual selection is generally manifest whenever disproportionate access to reproduction is gained by a small, nonrandom subset of males (2, 13, 30, 41). Often this means that males with the best genetic constitution, or more importantly, males whose genotypes interact the most favorably with surrounding conditions, have the highest relative fitnesses. In insects, these individuals are generally the largest individuals (examples in 30, 205), as body size can reflect both the genotype and the interaction between that genotype and the physical and social environment (e.g. competitively superior larvae gain disproportionate access to limiting nutritive resources, and emerge at larger body sizes). Sexual selection

that favors large body size can operate either through females that prefer to mate with only the largest males, or through male-male competition, with only the largest males able to secure access to females or to resources utilized by females (2, 205).

In either situation (direct female choice of males, or male-male competition), individuals must assess the relative size of other individuals in the population. Morphological structures that scale with body size contain information regarding the overall body size of each individual, and traits that exhibit steep positive scaling relationships are typically the most effective indicators of body size because they amplify subtle differences in body size among individuals. In these traits, each incremental increase in overall body size is magnified into a disproportionately larger increase in trait dimension, with the result that individual variations in the size of these traits offer greater resolution to underlying variations in body size than a direct assessment of size itself would provide. For this reason, exaggerated morphological traits are predicted to be unusually effective criteria for either female choice of mates, or similarly, for male assessment of rival males (2, 89, 165, 166). If this is indeed the case, then we might expect the intensity of sexual selection present in each species to be correlated with the steepness of the slope of the scaling relationship, with stronger sexual selection leading to steeper slopes (194). Simmons & Tomkins (194) found exactly this pattern when they compared the slopes for 42 species of earwigs (Dermaptera): taxa with the most intense sexual selection showed significantly steeper allometry slopes than taxa with weaker sexual selection.

One interesting outcome of the present survey is the realization that many of the most extreme morphological characters do not show steep linear scaling relationships. In fact, many of these taxa exhibit sigmoid or discontinuous scaling relationships, suggesting the operation of threshold mechanisms during development.

## Threshold Traits

Horns in most species of rhinoceros beetle (Scarabaeidae: Dynastinae), mandibles in many of the stag beetles (Scarabaeidae: Lucanidae), mandibles in Cerambycidae, tusks in wasps (Hymenoptera: Vespidae), forceps in several earwig species (Dermaptera), and head widths in ants with the most pronounced castes (Hymenoptera: Formicidae), all exhibited broken or sigmoid scaling relationships (Table 1). In fact, both the literature and our survey of taxa suggest that sigmoid and discontinuous scaling relationships have arisen repeatedly within the insects. Within the Hymenoptera, for example, sigmoid or discontinuous scaling relationships have arisen independently in at least seven ant genera (98, 157), and separately at least once each within the bees and wasps (Table 1). Likewise, sigmoid and discontinuous scaling relationships have arisen many times within the Coleoptera: at least once each in the Cerambycidae, Curculionidae, and Lucanidae,

and multiple times within the Scarabaeidae (Note: These are conservative estimates based on the taxa included in Table 1, and the assumption of parsimony).

Despite the large number of independent origins, the evolution of sigmoid or discontinuous scaling relationships is consistently associated with the expression of the most exaggerated morphological structures. It is the most elaborate castes in ants, with the most extreme head morphologies, that incorporate complex scaling relationships (98, 237, 238). Similarly, it is the most elaborate of the horned beetles—the rhinoceros beetles with the largest or most dramatic horns, and the stag beetles with the most distended mandibles—that exhibit nonlinear scaling relationships. Why is the expression of enlarged or exaggerated morphological structures so often associated with sigmoid or discontinuous scaling relationships?

Trait exaggeration can arise through either sigmoid, discontinuous, or linear scaling relationships (all can produce disproportionately large structures in individuals with the largest body sizes; Figure 5c). But several properties distinguish sigmoid and discontinuous relationships from linear scaling relationships. First, the switch between minimal and exaggerated trait expression often occurs abruptly, over a small range of body sizes (the “critical” or threshold body size). As a result few individuals with intermediate shapes are produced. Second, because this switch occurs abruptly, the exaggerated traits are facultatively expressed: Individuals larger than a threshold body size produce one morphology, whereas individuals smaller than this size produce a different morphology. Because only large individuals express the trait, this results in co-occurrence within populations of two relatively discrete morphs (polyphenisms). Both of these factors have important implications for the evolution of exaggerated morphologies in insects, and we discuss each factor in detail in the next section.

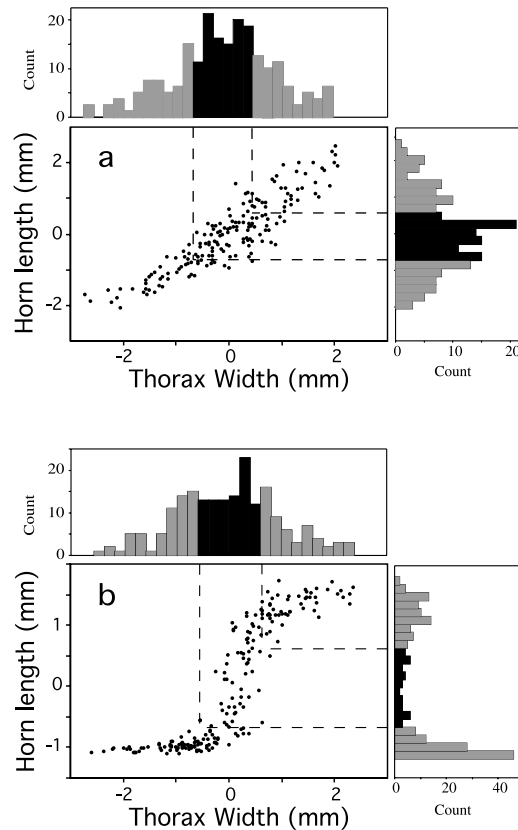
## WHY ARE SO MANY EXAGGERATED TRAITS FACULTATIVELY EXPRESSED?

The incorporation of thresholds into the development of morphological traits has several consequences that may facilitate the evolution of the most bizarre, or exaggerated morphologies; (a) they minimize the production of animals with intermediate forms; (b) they permit the morphologies of large and small individuals within a sex to evolve independently—at least with respect to the trait of interest—allowing a genotype to simultaneously specialize for more than one task or situation; (c) they uncouple the phenotypes of males and females so that only one sex produces the enlarged trait. These three properties of thresholds all reduce the “cost” to a genotype for producing an exaggerated morphological trait and may facilitate the evolution of such structures.

### Thresholds Minimize Production of Intermediate Forms

The morphologies generated at intermediate body sizes differ for the two basic scaling relationship types (linear versus sigmoid/discontinuous; Figure 6). A linear scaling relationship produces the trait in all individuals, including those with

**Figure 6** The production of intermediate morphologies by linear versus sigmoidal scaling relationships. Histograms show frequencies of body sizes (*top margin*), and horn lengths (*right margin*). (*a*) Genotypes with linear scaling relationships express the trait in all individuals, and consequently these genotypes generate large numbers of individuals with intermediate trait dimensions (*black bars*). (*b*) Genotypes with broken or sigmoidal scaling relationships switch abruptly from minimal to complete trait production and consequently produce fewer individuals with intermediate forms.



intermediate sizes (Figure 6*a*). Sigmoid or broken scaling relationships, in contrast, switch between minimal and complete trait expression over a narrow range of body sizes. As a result, few individuals emerge with intermediate morphologies (Figure 6*b*). Why should this matter, if both linear and sigmoid scaling relationship types result in large individuals that have the selected dramatic morphology?

To address this question it is necessary to adopt the framework we put forward in this review: that scaling relationships reflect the allocation by a genotype to a trait across the range of possible body sizes. The scaling relationship becomes the focal trait. In this context, comparing the relative reproductive success of males with different ornament sizes (e.g. horned versus hornless males) is less relevant than comparing the average success of genotypes that vary in *how* they allocate to the ornament. Do genotypes with linear patterns of allocation to the ornament do better or worse, on average, than alternative genotypes that facultatively express the ornament only in the largest individuals (e.g. sigmoid/discontinuous scaling)? Viewed this way, the consequences of the shape of the

scaling relationship become clear. In both situations, genotypes encounter a range of growth environments, and consequently both types of genotypes are expressed in individuals of all possible body sizes. Linear and sigmoid genotypes do basically the same thing at the body size extremes: in both types of scaling, large ornaments are expressed in the largest individuals, and rudimentary ornaments are expressed in the smallest individuals. But these two types of scaling differ substantially in the morphologies they generate when they are expressed in individuals with intermediate body sizes. Genotypes with linear relationships produce intermediate morphologies when expressed in individuals of average body sizes, whereas genotypes with sigmoid or broken relationships do not (Figure 6).

The relative success of each genotype will be the sum of the reproductive contributions of all individuals of that genotype. Two factors are important here: First, in most insect populations body sizes are normally distributed, so the majority of individuals that express each genotype will be of average body size (the largest individuals are actually relatively rare). Second, intermediates often do poorly. In many cases, individuals with either of the extreme morphologies perform better than individuals with intermediate morphologies. In the case of sexually selected traits, intermediate males incur the cost of producing and maintaining an ornament or weapon, but are not successful at outcompeting larger males, and so derive no reproductive benefit from this morphology. Likewise, their unwieldy shapes often make them less effective at adopting the alternative behavioral tactics often employed by smaller males (small males frequently avoid aggressive encounters and sneak access to females: reviewed in 2). Similarly, in non-sexually selected traits (e.g. soldier head morphologies in ants), intermediate shapes may perform less well at size-specific colony tasks.

We suggest that whenever intermediate morphologies perform poorly compared to either of the extremes, genotypes encoding sigmoid or discontinuous scaling relationships will outperform genotypes with linear relationships. In these situations, genotypes that generate a majority of intermediate forms will have lower average fitnesses than genotypes that switch abruptly between minimal and complete trait expression. This is what we refer to as the “cost” of producing intermediates, and we suggest that genotypes with sigmoid or broken scaling relationships may minimize the costs associated with the exaggerated production of morphological traits. Evolution of such traits may be more likely in taxa with the capacity to facultatively express the trait, perhaps explaining why so many sexually selected traits exhibit sigmoid or broken scaling relationships (61).

### Thresholds Uncouple the Phenotypes of Large and Small Individuals

Genotypes with linear scaling relationships produce one basic morphology. The relative dimensions of the horn, tusk, or femur may vary with body size, but all individuals express the trait. In these genotypes, the only way to generate an extreme morphology in the largest individuals is to also express that trait in all

of the intermediate and smaller individuals (Figures 5*b*, 6*a*). Thus the morphologies of large and small individuals will not be independent, and the potential for these size classes to diverge morphologically will be limited.

Threshold mechanisms permit genotypes to switch abruptly between minimal and complete trait expression (Figures 5*c*, 6*b*). Alternative morphologies regulated by thresholds often result from the expression of alternative, partially non-overlapping sets of genes (see section on How Threshold Traits Work; and 66, 199, 223, 224), and in these animals the evolution of large and small morphologies can be at least partially independent (223, 224). This means that small individuals can dispense with the investment of producing and bearing the same traits as large individuals, “uncoupling” the phenotype produced by the two size classes.

These differences in scaling relationship shape are relevant to the evolution of exaggerated morphologies because large and small individuals often do very different things, and the enlarged trait may be beneficial in only one of these contexts. For example, large and small males often differ substantially in their competitive status, affecting their ability to garner access to critical resources or females (90, 205). In a variety of taxa, small, competitively inferior males adopt alternative behaviors that bypass direct competition with larger males (1, 6, 47, 205). These alternative reproductive tactics can cause large and small individuals to experience very different physical and social environments, and this may favor different morphologies of large and small males. For example, ornaments or weapons that contribute substantially to the reproductive success of the largest males may be useless or detrimental to smaller males. What this means is that selection is often heterogeneous: The best morphologies for large males differ from the best morphologies for smaller males. Whenever large and small individuals encounter divergent selective situations, incorporation of a threshold into trait development may be favored because it permits the shape of these size classes to evolve relatively independently.

For example, in horned beetles, large and small males often employ separate behavioral tactics to encounter and mate with females (36, 53, 60, 62, 83, 137, 137*a*, 171, 198). Large males generally use their horns in battles with other males over access to females (34, 51–55, 59, 60, 62, 137, 137*a*, 160, 171, 198), and long horns have been shown to improve male competitive ability in several of these taxa (60, 62, 137, 137*a*, 171). Relatively small males in many of the same species adopt nonaggressive alternative behaviors like dispersing (53) or sneaking (60, 62, 137, 137*a*, 171) to encounter females. Horns may directly impede performance of the alternative behavior (e.g. in *Onthophagus acuminatus* and *O. taurus* small males may be better at sneaking into tunnels containing females if they do not produce horns; 60, 62, 137, 137*a*), and horns may be costly to produce. Horn growth requires resources that could otherwise be used for different traits (151), and horn growth slows development time, increasing the risk of larval mortality (100). Because horns are not utilized in the sneaking or dispersing alternative behaviors, their production may be prohibitively costly for small males.



Because large and small males appear to experience disruptive selection for horns (large males do best with long horns, small males do best without horns), the mating system in these beetles may have favored genotypes capable of uncoupling the phenotypes produced by large and small individuals, so that neither size class has an inappropriate horn morphology. Although similar heterogeneous selection may be present in most or all taxa expressing a costly, exaggerated male ornament, only species with sigmoid or discontinuous scaling relationships uncouple the morphologies of large and small males. Nonaggressive, alternative reproductive behaviors of small males have been described for cerambycid beetles (*Dendrobias mandibularis*, 82, 83), rhinoceros beetles (e.g. *Podischnus agenor*, 53), dung beetles (*Onthophagus acuminatus*, 60, 62; *O. taurus*, 137, 137a; *Phanaeus difformis*, 171), and bees (*Perdita portalis*, 38), and all of these insects exhibit sigmoid or discontinuous scaling relationships.

These conditions are not exclusive to sexually selected ornaments or weapons in males. In ants, large and small females may perform very different colony tasks, and these tasks can select for divergent morphologies. Soldiers may be more effective at colony defense if they have enlarged heads with biting mandibles and extensive jaw musculature, while these same traits would be a hindrance to smaller colony workers. Many of the ants with the most specialized caste behaviors also exhibit sigmoid or discontinuous scaling relationships (“triphase allometry” of 98, 238), with the result that exaggerated head structures are produced only in the largest females.

In all of these cases, the developmental capacity to uncouple the morphologies of large and small individuals paves the way for subsequent morphological divergence because it permits these forms to become increasingly specialized for their respective behaviors, tasks, or situations. Interestingly, this capacity to uncouple ornament expression between large and small individuals *within* a sex appears to apply *between* the sexes as well.

### Thresholds Uncouple the Phenotypes of Males and Females

Species with linear scaling relationships generally show correlations between the sexes, such that the exaggerated trait is expressed to some extent in both males and females (e.g. 233, 241). Selection favoring sexual dimorphism appears to reduce this correlation so that males show steeper scaling relationship slopes than females, but these correlations persist nevertheless. For example, in harlequin beetles, males have dramatically enlarged forelegs and a steep linear scaling relationship, but females have elongated forelegs as well (241). Similar conditions apply for eyestalks in the Diopsidae. Males often have much steeper scaling relationships than females, but both sexes produce eyestalks. In this case, the genetic correlation is especially clear: when Wilkinson artificially selected on the scaling relationship for the male trait, he observed a correlated response in the scaling relationships of the females (Figure 3b; 233). What this means is that sexual selection favoring enlargements of a male trait will also affect the mor-

phology of the females. Because females generally do not use these ornaments or weapons (1, 2, 30), and because these traits are often costly to produce and to bear (reviewed in 2), this viability selection on female morphology may hinder extreme enlargement of male traits.

In species with sigmoid or discontinuous scaling relationships, in contrast, the ability to facultatively produce the trait within a sex appears to transfer to the other sex as well. In most of the horned beetles, for example, large males produce elongated horns, whereas both small males and females do not. In these cases, the horns are truly absent from females. This suggests that the capacity to facultatively express an exaggerated trait permits a genotype to produce the trait only in a subset of situations (e.g. when the individual expressing the genotype is male, and grows large), and to completely dispense with the trait in other circumstances. Facultative trait expression has important consequences for the evolution of sexually selected ornaments or weapons (which includes all of the taxa in Table 1 except for the ants), because these traits are generally favored only in males, and only in the largest males. Genotypes that express the trait in either small males or females incur fitness costs because these individuals produce and bear the ornament but derive no benefits in return. Consequently, taxa with sigmoid or broken scaling relationships may be more likely to evolve exaggerated secondary sexual weapons or ornaments in response to sexual selection.

In summary, scaling relationships dictate the size-dependent expression of secondary sexual and other traits. The shapes of these relationships vary, and in many cases, differences in the shape of the scaling relationships have important consequences for the evolution of exaggerated or extreme morphologies. Linear and sigmoid scaling relationships differ substantially in how and when they express enlarged morphological structures, and this difference can influence the “cost” incurred by a genotype for producing the structure. Enlarged ornaments or weapons may be unusually expensive to generate and maintain, and often only the largest individuals profit by utilizing the structure. In these situations, smaller individuals may benefit by not producing the exaggerated trait, but this is impossible with linear scaling relationships. We suggest that the developmental capacity to minimize the production of intermediate shapes, the capacity to uncouple the phenotypes of large and small individuals, and the capacity to uncouple the phenotypes of males and females all may predispose traits to evolutionary enlargement and may help to explain why so many of the most bizarre and exaggerated structures exhibit sigmoid or discontinuous scaling relationships.

## CONNECTING GENOTYPE TO PHENOTYPE: HOW MIGHT SCALING RELATIONSHIPS CHANGE IN SHAPE?

This review focuses on the evolution of scaling relationships. By considering exaggerated traits like eyestalks or horns to be the result of evolutionary changes in scaling relationship slope or shape, we hope to provide a realistic view of the

evolution of insect morphology. Doing so entails re-aligning our perspective of trait evolution to consider the scaling relationship itself. One potential problem with this view is that it explicitly incorporates aspects of mechanism: it is the developmental mechanisms regulating the expression of traits that ultimately generate the shape of the scaling relationship, and evolutionary modifications to the scaling relationship must therefore result from genetic changes to the underlying regulatory mechanisms. While this view may be attractive to some (because it attempts to span the gulf between genotype and phenotype), it can also constitute a limitation. By placing emphasis on the scaling relationship, we reveal our ignorance of the underlying mechanisms. After all, what does a change in the shape of a scaling relationship really mean? How can such changes arise, and can we assume that all such changes are possible?

Insects are perhaps unique in that their development has been so well characterized that we can begin to appreciate how scaling relationships are generated, and from this information we can glimpse how they may evolve. Here we briefly describe the developmental processes regulating the expression of morphological traits in insects. We start by describing how the general scaling of body parts occurs (i.e. how a linear scaling relationship is generated). We then consider the special situation with threshold traits and discuss how polyphenisms in insects are regulated. Finally, we use this information to suggest how linear scaling relationships may have been modified during the course of evolution to generate sigmoid or discontinuous scaling relationships.

## Background: Separation of Larval and Adult Tissues

We focus our discussion on the development of holometabolous (completely metamorphic) insects because the regulation of growth is best understood in these animals (primarily from work on *Drosophila melanogaster* and *Manduca sexta*) and because most of the taxa known to exhibit extreme or exaggerated morphologies are holometabolous (Table 1). Postembryonic development in insects has been recently reviewed (8, 79, 149), so we briefly describe only those aspects relevant to this review.

In holometabolous insects, larvae bear little physical resemblance to the adults. Animals proceed through several larval stages before molting into a pupa and then subsequently into the adult insect. Although the pupal stage is typically credited with the metamorphic transformation from larva to adult, many of the adult morphological structures are produced *before* the pupal stage, while the animals are still larvae. Cells that will form the adult structures (e.g. eyes, wings, legs, genitalia) are set aside very early in development, during embryogenesis (33, 73, 122, 155, 191). These “imaginal” cells (imago means adult) remain distinct from the larval cells throughout development. In many insects, as these clusters of imaginal cells divide, they fold into the body cavity of the larva, forming isolated pockets of adult cells called “imaginal disks” (33, 73). Once they have invaginated away from the body wall, the imaginal disks can grow

without affecting the exterior shape or structure of the larva. At the very end of the larval period, when animals are ready to molt into pupae, these imaginal disks evert and join to form the morphological structures of the pupal cuticle. When animals shed their larval cuticle and expand to fill this new pupal cuticle, they now have all the morphological structures characteristic to the adults (pupae have visible legs, compound eyes, wing buds, genitalia, etc).

Two features of this mechanism are relevant to the generation of trait-scaling relationships. First, the adult structures form as discrete pockets of imaginal cells. For example, there are separate imaginal disks for left and right wings and for forewings and hindwings. Likewise, there are imaginal disks for each of the legs, for the genitalia, for the eyes and antennae, and there are distinct pockets of imaginal cells that form cuticular protrusions such as horns. This means that the adult structures develop from independent clusters of cells that may be regulated at least partially autonomously (22, 33, 236).

Second, these imaginal structures (i.e. the adult traits) do not grow at the same time and rate as the larvae. Imaginal disks undergo much of their growth very late in the larval period—after the animals have stopped feeding, and after all growth in overall body size has ceased (122, 133, 151, 153). In hemimetabolous insects, too, growth of appendages is independent of body growth and can be adjusted late in development (11, 68, 131, 132). Consequently, the relative growth of adult traits is not simply a result of tissues growing gradually at rates proportional to overall growth in body size. This also means that scaling relationships are not reflections of the underlying growth trajectories of traits (i.e. small animals with small traits do not simply stop the growth process earlier than larger animals). Instead, the scaling of body parts must result from some centralized system of coordination, where growth in the imaginal traits is modified depending on the body size each animal attains (200). Hormones are one way this “size” information may be communicated to the growing traits.

## Background: Hormones and the Regulation of Tissue Growth

Many developmental events in insects are regulated by hormones. Circulating hormones coordinate the timing of physiological events, such as molting or metamorphosis, so that all of the tissues undergo these changes in synchrony (reviewed in 149). Hormones also regulate the fates of specific tissues, by signalling which of several possible phenotypic outcomes are expressed (as in the polyphenisms discussed below). Finally, hormones couple developmental events with the outside world. The secretion of the primary hormones (ecdysteroids and juvenile hormones) is controlled by the central nervous system (149), meaning that it is possible for these hormonal signals to become part of a transduction pathway between an environmental stimulus (perceived and integrated by the nervous system) and a developmental response (controlled by the hormone). In

other words, the endocrine control of development makes it possible for certain aspects of development to become sensitive to specific environmental variables.

Cells respond to hormones only during brief periods of the life cycle. Developing tissues become sensitive to the presence or levels of specific hormones during discrete "critical" or sensitive periods, and these periods vary for different hormones, and for different stages in larval development (149). Perhaps the most important feature of hormone-sensitive periods is that they appear to be tissue- and character-specific. Thus in *Manduca* there are distinct juvenile hormone (JH) sensitive periods for pupal commitment of the imaginal disks and the larval epidermis (149, 175). Moreover, in the epidermis there are separate JH-sensitive periods for pupal commitment and for pigmentation (149, 209). In *Onthophagus*, the JH-sensitive period for horn induction affects only a small portion of the head epidermis (63), and in the alate/apterous polyphenism of aphids, JH can suppress the development of wings without affecting the normal development and metamorphosis of other body parts (93).

The simplest explanation for the tissue specificity and relatively narrow time windows of hormone sensitivity is that not all tissues express receptors for a given hormone, and those that express receptors do so for only brief periods of time. Recent advances in the molecular studies of hormone receptor expression support this view. Riddiford and her colleagues have shown that different tissues in *Manduca* have very different patterns of expression for various ecdysteroid receptors (74, 108). Ecdysteroid receptors in the imaginal disks fluctuate with a different temporal pattern from those in the epidermis. In addition, *within* tissues the temporal pattern of ecdysteroid receptor expression is complex, with many distinct peaks of expression occurring throughout larval and pupal development. Furthermore, different types of ecdysteroid receptor have different patterns of fluctuation (74, 108), and these different isoforms of the ecdysteroid receptor appear to control different downstream response pathways (27, 208). This arrangement suggests that the response of a tissue to a hormone signal may be altered by altering the expression of receptors.

It appears, then, that tissue responses to hormones show great temporal and spatial precision. Superimposed on these fluctuations in hormone receptor expression is the pattern of hormone secretion. Both ecdysteroid and JH secretion patterns exhibit great fluctuations in the course of larval and pupal development (175–177), and at least some of these peaks of hormone secretion coincide with times at which certain developmental events are most sensitive to the hormone (149, 150). The overall picture that emerges is that of a dialogue between the endocrine system and the responsive tissues: The amount and type of hormone receptors expressed in each tissue controls when, where, and how that tissue responds to a hormone.

The hormone, in turn, is a means of providing a centrally controlled synchronizing signal. At some points in development a given hormone may only affect one tissue, while at another time it may control the synchronized development of many. Because the ability to respond to a hormone can be regulated and varied

at the tissue level, hormone-mediated developmental control is essentially modular. Therefore, the hormone-responsiveness of a given tissue (e.g. an exaggerated trait) could, in principle, evolve independently of that of other tissues, and this leads us to the mechanisms regulating the scaling of body parts.

### Mechanisms of Scaling in Insects: The Linear Allometry

The question of how body parts scale with variations in body size can now be examined at a mechanistic level. Larvae feed and gain weight during much of the larval period (the feeding period). At the end of the feeding period, they purge their guts and begin the behavioral and physiological processes associated with the onset of metamorphosis, and it is at this time, after increases in overall body size have ceased, that the imaginal structures undergo their most prolific growth (151, 153). Some of these larvae will have encountered favorable growth conditions, and these animals will terminate growth at very large body sizes. Others will have encountered less favorable conditions, and these animals enter metamorphosis at much smaller body sizes. The mechanisms of scaling concern how the final sizes of each of the various adult traits becomes matched with the final body size of each individual larva (i.e. how a genotype generates a linear allometry; these mechanisms are reviewed in 200). How do large animals end up with larger wings and legs and eyes than smaller animals?

Somehow, the growth of the adult traits must be modified to scale with the actual size of each developing animal. This suggests that information pertaining to the actual body size of an individual (or some close correlate, e.g. growth conditions) is communicated to all of the growing tissues. Although few researchers have looked for such a signal, there is accumulating evidence that these signals exist (reviewed in 200). For example, several studies indicate that the final sizes of imaginal disks can be modified by growth factors and hormones (14, 19, 25, 42, 67, 112, 130, 168). However, for a growth factor or a hormone to modify the growth of an imaginal structure *relative to body size*, the levels or period of activity of that factor or hormone must contain information about the final body size of that animal—thus developing insects must assess their own body size. In fact, many developmental events in insects are triggered by internal assessments of body size (110, 145, 146, 154). Even insects that develop in isolation from other larvae are able to assess whether they are large or small, and their development is regulated accordingly. In some cases, these size-detection mechanisms are known, as in Hemiptera, where stretch receptor neurons respond to distensions in the abdominal wall (3, 10, 29, 147, 148, 230). In other cases the precise mechanisms remain elusive (149).

In summary, it appears that sometime late in the larval period, after all intake of resources has ceased, imaginal tissues become sensitive to the presence and level of a hormone or growth factor that modifies their growth (200). It is likely that quantitative variation in the levels of this factor communicate size information to the growing tissues, and by responding to this signal, tissues grow to

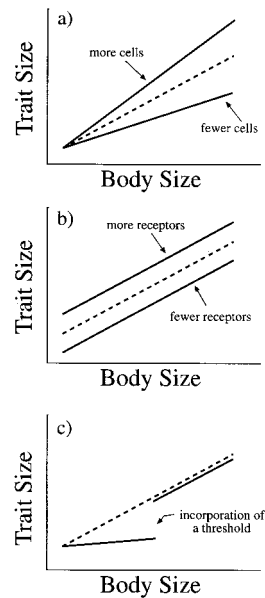
dimensions appropriate for the actual body size of each animal. Although the specific factors that regulate scaling relationships have not yet been identified, and several additional aspects of these mechanisms remain to be explored, the existing picture provides an adequate framework to consider how scaling relationships arise, and, more importantly, to consider how they may change over time. The relative size of body parts will result from intrinsic properties of each developing trait (i.e. the number of cells and their rate of proliferation), as well as how those cells respond to the body size information (determined by numbers or densities of receptors expressed and/or the timing of receptor expression). Modifications to any of these components could lead to changes in how large tissues become relative to body size. Because these changes in mechanism have predictable consequences for the shape of scaling relationships, they reveal possible avenues by which exaggerated morphologies may have evolved. Here we consider two of the many possible routes to scaling relationship evolution: variations in the number of starting cells, and variations in the sensitivity of those cells to the hormone.

### Changing the Slope or Intercept of a Linear Scaling Relationship

All of the imaginal disks undergo some proliferation during the earlier larval stages, but the extent of this early growth depends on the identity of the imaginal disk. Different disks grow at different rates (e.g. forelegs may grow faster than hind legs), and the same disks may grow at different rates in different genotypes (forelegs may grow faster in one genotype than in another). One possible way this variation may arise concerns the starting conditions of the imaginal disk. Variation in the number of cells present at the onset of exponential growth may lead to large differences in the absolute rates of growth of those traits at the end of larval life, because if all cells are dividing, initial differences in cell numbers will be magnified with subsequent cell proliferation (153). This suggests one mechanism for scaling-relationship evolution: Changes in the slope of a scaling relationship could arise through genetic changes in these starting conditions (e.g. changes in cell number within an imaginal disk). Large numbers of starting cells would produce fast trait growth and a steep scaling relationship and vice versa (Figure 7a). Consequently, differences in the number of dividing cells provide one possible explanation for how different parts of an organism could scale with body size in different ways. This mechanism could also explain how the same trait scales differently in males and females, as well as how the unusually steep scaling relationships of exaggerated insect ornaments or weapons arise.

Evolutionary changes in the relative growth of imaginal disks may also occur by modifying the expression of hormone receptors. Changing the number or density of receptors may change the way that imaginal structures “read” body size information from the hormone signal (200). Increased receptor density may cause genotypes to be more sensitive to the hormone signal and thus to begin or cease

**Figure 7** Suggested mechanisms for scaling relationship evolution. Adult structures in holometabolous insects derive from isolated, semiautonomous pockets of cells (imaginal disks) which undergo most of their growth during a concentrated period at the very end of the larval stage. This growth appears to be regulated by size-dependent variations in circulating levels of a hormone or growth factor. (a) Changes in the starting conditions (e.g. the number of simultaneously dividing cells present at the beginning of the concentrated period of trait growth) may lead to changes in the relative rates of tissue growth. In genotypes whose traits contain large numbers of cells at the outset of exponential growth, the exaggerated traits may grow at faster rates (and have steeper scaling relationship slopes) than traits in genotypes with fewer cells. (b) Changes in how long each trait grows may affect the relative size of the trait. Genotypes expressing large numbers of receptors for the hormone or growth factor in the exaggerated trait may be more sensitive to this factor, and subsequently may commence or terminate trait growth at slightly different times than genotypes with fewer receptors. This would change the total length of time the trait grows and could shift the relative size of the trait (i.e. shift the intercept of the scaling relationship). (c) Incorporation of a threshold may “uncouple” the relative growth of tissues in large and small individuals. By bringing trait expression under the regulatory control of a new hormonal stimulus, it may be possible to express the trait only in a subset of individuals (e.g. only in individuals with sufficiently high concentrations of hormones present). This can lead to sudden changes from minimal, to extensive (but still size-dependent) trait expression, and could generate sigmoid, or discontinuous scaling relationship shapes.



trait growth at slightly different times. In this manner the length of the total period of trait growth can be affected and cause traits to grow to relatively larger or smaller sizes. Such a mechanism could explain evolutionary changes in the intercept of a scaling relationship, as genotypes now express trait dimensions that previously had been appropriate for individuals with a different body size (Figure 7b).

Combined, these results suggest how linear scaling relationships may arise, and we have used this information to suggest how these linear relationships may change in either slope or intercept (see also 200). We now consider how these basic, linear scaling relationships might be modified to incorporate a threshold.



## How Threshold Traits Work

The facultative expression of traits (polyphenism) requires a stimulus that is experienced by some members of a population and not by others. Often this stimulus comes from the external environment in the form of temperature, photoperiod, pheromone, or nutrient, but as we show in the following section, some facultative characters are allometric consequences of body size, and the stimulus in such cases is generated entirely internally.

All polyphenisms whose development has been studied in some detail appear to be controlled by hormones, and these fall into three classes: ecdysteroids, juvenile hormones, and an as yet poorly characterized set of neurosecretory hormones (149, 150). Hormones alter the fate of threshold traits by inducing the expression of specific genes (66, 149, 224). The general picture that has emerged from these studies is that the polyphenic traits are sensitive to the presence and level of hormones, that an environmental factor somehow alters the temporal pattern of hormone secretion, and that this change in the timing of hormone secretion reprograms the developmental trajectory of the polyphenic trait. The color polyphenism of *Precis coenia*, for instance, is controlled during a critical period of sensitivity to ecdysteroids that lasts from 28 to 48 hours after pupation (181). Presumably, the ecdysteroid receptors are expressed in the presumptive wings for this brief period, causing them to be sensitive to levels of hormone during that time. The control of polyphenic development lies in a shift in the timing of ecdysteroid secretion that depends on the photoperiod experienced by the larva. Under long-day conditions (summer) secretion of ecdysteroids begins about 18 hours after pupation, whereas under short-day conditions (spring) it does not begin until about 48 hours after pupation (after the critical period has ended). Hence, long-day pupae experience elevated ecdysteroids during the sensitive period and short-day pupae do not. The result is that different pigmentation patterns develop in spring and summer animals.

A number of insect polyphenisms are regulated by levels of juvenile hormone (JH). As with the ecdysteroid example, these polyphenic traits are sensitive to JH only during specific critical periods (63, 64, 93, 93a, 121, 163, 203, 228, 240, 243–245). Where they have been studied at the molecular level, the JH-sensitive periods appear to coincide with periods of ecdysteroid secretion (149, 150, 152), and levels of JH may affect patterns of gene expression indirectly by interacting with the ecdysone (149, 150, 152). Ecdysteroids initiate a series of molecular and cellular events by altering patterns of gene expression, and the presence or absence of JH during this process can affect which genes will be expressed. For instance, during metamorphosis in *D. melanogaster* and *M. sexta*, transcripts of the *Broad-complex* genes (which code for transcription factors) appear in epidermal cells within six hours of exposure to ecdysteroids in the absence of JH but not in the presence of JH (111, 177). By contrast, ecdysteroid-induced transcription of the *E-75A* gene (which also codes for a transcription factor) is enhanced in the presence of JH (177, 192). All of these genes encode transcription factors

and are therefore involved in the regulation of further downstream genes. Although many of the details remain to be elucidated, these studies indicate that the levels of hormone (e.g. JH) present during critical periods of sensitivity can alter patterns of gene expression, and this mechanism can induce changes within the developing animals (e.g. switch the fate of a developing organ).

The picture that emerges is that developmental thresholds, like linear scaling relationships, result from tissue-specific responses to hormones. In both cases, tissues become sensitive to hormones by expressing receptors to the hormone, and in both cases these receptors appear to be present only during brief periods. However, scaling (graded) and threshold responses to the hormone differ in one key respect: In graded responses the hormone is present in all individuals, and variations in the levels of the hormone translate into graded differences in the dimensions of trait produced. In threshold traits, by contrast, adequate levels of the hormone are present only in a subset of the individuals. In this case, sufficient levels of hormone “reprogram” the fate of developing tissues, with the result that some individuals produce a phenotype very different from the phenotype that other individuals produce (149, 226).

### Scenario for the Evolution of Sigmoid or Discontinuous Scaling Relationships

We are now in a position to speculate how linear scaling relationships may have been modified to generate sigmoid or discontinuous scaling relationships. Because the developmental system is modular, it is possible to obtain novel patterns of trait expression by deploying old, previously existing mechanisms in new contexts. Indeed, there is now excellent evidence for such redeployment at the molecular level in the evolution of eyespots in butterflies (220).

Sigmoid or discontinuous scaling relationships can be considered polyphenisms where facultative expression of the trait depends on body size (large individuals do one thing, small individuals do another). Where studied, these size-dependent polyphenisms work in the same basic ways as the polyphenisms described in the previous section: They involve hormones, the tissues are sensitive to the hormone only during brief periods, and exposure to sufficient levels of hormones appears to result in altered patterns of gene expression and subsequent reprogramming of the growth rates of specific tissues (63, 169, 172, 180, 210, 226, 240). Thus size-dependent polyphenisms may be built from the same hormone-response pathways already utilized in other tissues and in other developmental contexts. Coupling the regulatory mechanisms for an existing exaggerated trait with a different type of hormone receptor, or with receptors expressed at different developmental periods, may have permitted the expression of that structure to become sensitive to a novel environmental stimulus: in this case, the attainment of a critical body size. But how could developmental events be coupled with growth in body size?

For most studied polyphenisms, hormones couple the expression of morphology with environmental stimuli that are external to the developing animal. Photoperiod, crowding, temperature, and diet each affect the expression of some polyphenic traits. However, as discussed already, insects can also respond to stimuli that occur within each developing animal, including the growth or body size of that animal. A number of developmental events in insects are regulated by assessments of body size, and for some of these, the responses incorporate a threshold. For example, the onset of molting and metamorphosis occurs only after larvae attain a specific critical body size in *M. sexta* (145, 154), and *Trichoplusia ni* (110). These developmental events also are regulated by hormones, except that in this case the levels of hormone are associated with individual variations in growth and body size, rather than variations in photoperiod or temperature.

Whenever the levels of a hormone are influenced by growth or by body size, the potential exists to bring the size-dependent expression of traits under hormonal control. Juvenile hormone meets these criteria: Levels of JH are known to be sensitive to both diet conditions and larval growth (5, 42a, 46, 81, 109, 126, 156, 172, 210), and levels of JH appear to communicate size information to growing tissues (63, 200, 229). Thus size-dependent polyphenism could arise simply by incorporating a threshold response to JH into the development of the trait. In fact, this is exactly what appears to have occurred in every studied example of size-dependent threshold traits. JH regulates the size-dependent expression of the horn length polyphenism in dung beetles (*Onthophagus taurus*; 63), as well as size-dependent caste polyphenism in ants (*Myrmica rubra*, *Pheidole bicarinata*, *Pheidole pallidula*, and *Solenopsis invicta*; 17, 162, 179, 228, 229), honeybees (*Apis mellifera*, 169, 217, 240), bumblebees (*Bombus terrestris* and *Bombus hypnorum*, 180), wasps (*Polistes gallicus*, 180), and termites (*Kaloterms flavicollis*, *Macrotermes michaelseni*, and *Reticulitermes santonensis*, 125a, 129, 155a).

Combined, these patterns suggest an avenue for the evolution of sigmoid and discontinuous scaling. Ancestrally, the trait would be expressed in all individuals (genotypes have linear scaling relationships). In the derived situation, trait expression becomes facultative (i.e. trait expression is brought under the control of a new hormonal stimulus). Because the hormone communicates body size information, it is now possible to couple trait expression with the attainment of a specific body size (e.g. by only expressing the trait when sufficient levels of hormone are present). Genotypes regulating trait expression in this fashion do not produce the trait in small individuals. Because this developmental reprogramming results from hormone-mediated changes in patterns of gene expression, the resulting phenotypes of large and small individuals would be at least partially uncoupled and free to evolve at least partially independently.

In conclusion, we suggest that the evolution of complex scaling relationships may entail the incorporation of a threshold into the development of the trait (Figure 7c). The modular nature of polyphenic development suggests that this evolutionary transformation need not be a difficult one. In fact, simple changes

in the timing or levels of hormone-receptor expression may be adequate to bring the development of a trait under hormonal control.

## A FINAL CAVEAT: TRAITS INTERACT WITH EACH OTHER

One outcome of the study of exaggerated traits is the realization that traits interact with one another during development (120, 151, 153). These interactions cause correlations among traits, meaning that variation in one trait is coupled to variation in another trait. For example, male beetles expressing long horns also have disproportionately small eyes (151) or wings (113, 115), and ants with the largest head widths also have proportionately smaller legs (69).

The best evidence that morphological structures interact comes from perturbation experiments, where the growth of one trait is altered experimentally during development, and resultant changes in nontarget traits are monitored. In the buckeye butterfly *Precis coenia*, surgical removal of a hindwing imaginal disk prior to the period of rapid growth results in overgrowth of the adjoining forewings (151). Removal of one hindwing disk causes forewings to be disproportionately larger than they otherwise would be, and removal of both hindwings cause the forewings to be larger still (151). These experiments also affected the symmetry of the animal: when the left hindwing disk was removed, both forewings grew larger than they should have, but the forewing on the left side of the animal grew larger than the forewing on the opposite side (120). In the beetle *O. taurus* experimental reductions in the relative length of male horns were accompanied by increases in the relative sizes of male eyes (151), and this same interaction was manifest as a negative genetic correlation between horns and eyes in an artificial selection experiment in *O. acuminatus* (151).

Interactions among growing morphological traits mean that the scaling relationships of these traits will not be independent. This is particularly relevant to taxa with nonlinear scaling relationships because reprogramming of the growth of one tissue (e.g. through attainment of a threshold body size) may lead to nonlinear scaling of other tissues (153).

We advocate exploring the evolutionary significance of scaling relationship shapes. Yet we must end with a note of caution. Sigmoid or discontinuous scaling relationships make obvious targets for this type of study, and several important consequences of such scaling relationships may affect the evolution of insect morphology. However, this approach assumes that the nonlinearity in trait expression evolved in response to selection on the trait in question. If the nonlinearity arises as an indirect consequence of selection on another trait, then the observed relationship could be unrelated to selection on the focal trait. In these situations, investigators may be misled. Consequently, we suggest a multivariate approach (e.g. 118), by which scaling relationships are simultaneously examined for a num-

ber of traits. Nonlinear scaling relationships in very small traits, or traits adjacent to much larger structures also showing nonlinear scaling, may be particularly suspect and should be treated with caution.

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