THE EVOLUTION OF STATIC ALLOMETRY IN SEXUALLY SELECTED TRAITS

RUSSELL BONDURIANSKY[1,2] AND TROY DAY[3,4]
[1]*Department of Zoology, University of Toronto, Toronto, Ontario M5S 3G5, Canada*
[2]*E-mail: russell.bonduriansky@utoronto.ca*
[3]*Departments of Mathematics and Biology, Jeffery Hall, Queen's University, Kingston, Ontario K7L 3N6, Canada*
[4]*E-mail: tday@mast.queensu.ca*

Abstract.—Although it has been the subject of verbal theory since Darwin, the evolution of morphological trait allometries remains poorly understood, especially in the context of sexual selection. Here we present an allocation trade-off model that predicts the optimal pattern of allometry under different selective regimes. We derive a general solution that has a simple and intuitive interpretation and use it to investigate several examples of fitness functions. Verbal arguments have suggested cost or benefit scenarios under which sexual selection on signal or weapon traits may favor larger individuals with disproportionately larger traits (i.e., positive allometry). However, our results suggest that this is necessarily true only under a precisely specified set of conditions: positive allometry will evolve when the marginal fitness gains from an increase in relative trait size are greater for large individuals than for small ones. Thus, the optimal allometric pattern depends on the precise nature of net selection, and simple examples readily yield isometry, positive or negative allometry, or polymorphisms corresponding to sigmoidal scaling. The variety of allometric patterns predicted by our model is consistent with the diversity of patterns observed in empirical studies on the allometries of sexually selected traits. More generally, our findings highlight the difficulty of inferring complex underlying processes from simple emergent patterns.

Key words.—Allometry, display traits, evolution, exaggerated traits, morphology, sexual selection, signaling, weapons.

An organism's shape is defined by the sizes of its body parts (traits) in relation to the size of the whole (body size), with the scaling pattern relating trait size to body size known as the trait allometry. Although a great deal of work has been devoted to the mathematical analysis of observed allometric patterns (e.g., Brody 1945; Gould 1966; Sprent 1972; Eberhard and Gutiérrez 1991) and the effects of biomechanical constraints (e.g., McMahon 1975; Pennycuick 1992; Ravosa et al. 2000), much less is known about how allometry is shaped by selection. This last question is of particular interest in the context of sexually selected traits, which sometimes exhibit spectacular elaboration and enlargement (e.g., Darwin 1871; Gould 1974; Simmons and Tomkins 1996; Emlen and Nijhout 2000). In this paper, we use a resource allocation trade-off model to investigate how the form of selection acting on a trait and body size affects the evolution of static allometry, trait scaling with body size among conspecific individuals at the same developmental stage (Cock 1966). The model yields some intuitively appealing predictions as well as counterintuitive insights that challenge the validity or generality of verbal theories.

Allometries are usually modeled using the allometric equation (Brody 1945), $Y = aX^b$. When log-transformed, this becomes the linear equation $\log(Y) = \log(a) + b\log(X)$, where b is the allometric slope. Although, in practice, any pattern of linear or nonlinear scaling can arise, depending on the species, trait, and index of body size used, allometries are often classified using a simple system. Isometry occurs when $b = 1$, so that the ratio of trait to body size remains constant across the range of body sizes. In contrast, negative (hypo-) allometry occurs when $b < 1$, so that larger individuals have relatively smaller traits, whereas positive (hyper-) allometry occurs when $b > 1$, so that larger individuals have relatively larger traits. Whereas the above definitions are used in this paper, we note that some authors (e.g., Enders et al. 1998) define allometries by the linear scaling slope on nonlog-transformed axes, thus constraining relative trait size to a constant value (equal to the linear slope) across the range of body sizes.

Most traits in most organisms appear to be negatively allometric (Eberhard 2002), while perfect isometry can be regarded as a special case (Gould 1966). However, the relatively small subset of traits exhibiting positive allometry includes many exaggerated or bizarre structures. Many such traits are employed in combat and/or courtship and, thus, appear to be shaped by sexual selection (Darwin 1871). For example, in a variety of dung beetles (Scarabaeidae), males possess large horns used as weapons in male-male combat for access to females (see Emlen and Nijhout 2000) and, in some birds, males possess enlarged tails or crests used as signals in courtship displays to females (see Andersson 1994).

Sexual selection is generally thought to favor the evolution of positive trait allometries (Petrie 1988, 1992; Green 1992; Simmons and Tomkins 1996; Tomkins and Simmons 1996; Emlen and Nijhout 2000) and, conversely, positive allometries have been interpreted as evidence of sexual selection (Green 2000). Several mechanisms have been proposed to account for this relationship. It has been suggested that positive allometry may evolve when larger trait size confers a direct advantage in sexual competition, resulting in stronger directional selection on trait size than on body size (e.g., Green 1992), or when the relative costs of trait expression are lower for larger individuals (Petrie 1992). Larger individuals may pay lower costs or derive greater benefits per unit increase in relative trait size if body size reflects condition (Petrie 1992). In addition, it has been suggested that positive allometry of linear dimensions or surface areas would be favored in traits used as honest advertisements of body size, because this would amplify apparent differences

between individuals in body mass, thus facilitating mutual assessment of competitive ability (Wallace 1987; see also Gould 1974). We evaluated these arguments using an analytical model that predicts the optimal allometries of traits subject to a resource allocation trade-off during development and varying regimes of sexual and viability selection at the adult stage.

THE MODEL

Because sexually selected traits are likely to reduce survivorship or foraging efficiency (Zahavi 1975; Petrie 1992), net selection on such traits will be a product of sexual selection (i.e., effects on mating rate) and viability selection (i.e., effects on survivorship). Moreover, energy and material allocated to one trait is not available for other traits (Nijhout and Emlen 1998). We construct a continuous-time allocation trade-off model to investigate how much an organism should allocate to a trait, z, and how much it should allocate to further growth in body size, m, to maximize its fitness. We assume that trait and body size are both measured in the same units of mass, and that the total amount of energy, E, that the organism has at its disposal at any given time during development is a power function of its current mass, $E = am^b$, where a and b are positive parameters. The growth rate parameter, b, is within the range $0 < b < 1$ (see Day and Taylor 1997; Brown et al. 2000), so that growth decelerates as body size increases, but large individuals always have more energy than smaller ones. This simulates the biology of an organism with determinate growth of body size and trait size (i.e., where adult body and trait size are fixed), such as an insect.

Starting with an initial body size m_0 and an initial trait size z_0 (assumed to be negligible) the organism faces a trade-off in how it allocates its available energy. Devoting energy to an increase in body size at any given time will yield a greater pool of available energy in the future, but it is typically advantageous to devote some energy to growth of the trait as well, because fitness as an adult is influenced by both body size and trait size.

Mathematically, this process is described as follows:

$$\frac{dm}{dt} = u(t)am^b \tag{1}$$

where $m(0) = m_0$ and

$$\frac{dz}{dt} = [1 - u(t)]kam^b \tag{2}$$

where $z(0) \approx 0$; t is time, $u(t)$ is the proportion of the total energy allocated to further growth at developmental time, t (with $0 \leq u(t) \leq 1$), and k is a parameter that scales the efficiency with which resources are converted into trait growth relative to that of body size. Equations (1) and (2) describe development over a fixed period of length T, resulting in a body size $m(T)$ and trait size $z(T)$. We assume that the organism's fitness is a function of adult body and trait size only, $\phi(m, z)$. However, we assume that smaller adult body size is never favored by selection: relaxing this assumption would require an extension of our model to include development time as an additional parameter. These assumptions are not particularly restrictive from a biological

standpoint, and are represented formally by supposing that one of the following two sets of inequalities always holds: $\partial\phi/\partial z \neq 0$, $\partial\phi/\partial m \geq 0$ or $\partial\phi/\partial z = 0$, $\partial\phi/\partial m > 0$. We caution, however, that alternative assumptions are likely to yield different results.

We assume that individuals vary in initial body size, m_0, and use an energy allocation strategy, $u(t)$, over their period of development, that maximizes their fitness given their initial body size. This strategy—the proportion of total resources allocated to trait growth—will typically differ between individuals with different initial body sizes, resulting in variation in adult body and trait sizes. We can then plot an adult's relative trait size, defined by

$$R = z(T)/m(T), \tag{3}$$

against its body size, $m(T)$. Such a plot corresponds to the allometric equation divided by X, yielding $Y/X = aX^{b-1}$. Thus, isometry ($b = 1$) is indicated by a horizontal line. A slope that is positive ($b > 1$) or negative ($b < 1$) indicates positive or negative allometry respectively, because the relative trait size increases or decreases as body size increases. Our aim is to predict this slope for different forms of the fitness function, $\phi(m, z)$.

Although we allow for the possibility that an individual might adopt any (potentially very complex) pattern of energy allocation during development, Appendix 1 demonstrates that the optimal allocation strategy is always one whereby all energy is devoted to growth in body size up until some switching time, α, after which point all energy is devoted to growth of the trait until the end of development (Fig. 1A). This prediction is interesting in itself: it is analogous to the so-called bang-bang resource allocation principles that have long been known in life-history theory (for a review, see Perrin and Sibly 1993). Intuitively, this occurs because the marginal returns from investment in body growth and trait growth are unequal, so that a switch occurs at the point in development where returns from investment in trait size exceed those from investment in body size. The dependence of adult trait size on body size is illustrated by the maximization of trait size at an intermediate switching point (Fig. 1B). Such an ontogeny is comparable to the larval development of holometabolous insects like *Drosophila*, where early larval instars exhibit mainly vegetative growth but late instars invest mainly in the growth of adult organ precursors (see Britton and Edgar 1998). Similarly, in organisms with less clearly defined ontogenetic stages (e.g., mammals), secondary sexual traits typically begin to develop in the later stages of ontogeny.

RESULTS

General Solution

Appendix 2 shows that the direction of allometry resulting from the optimal developmental program is given by the sign of

$$\frac{dR}{dm} \propto \frac{\partial}{\partial m}\left[\frac{\phi_z(m, Rm)}{\phi_m(m, Rm)}\right], \tag{4}$$

where $\phi_z(m, Rm)$ and $\phi_m(m, Rm)$ are derivatives of fitness with respect to trait size and body size respectively, evaluated
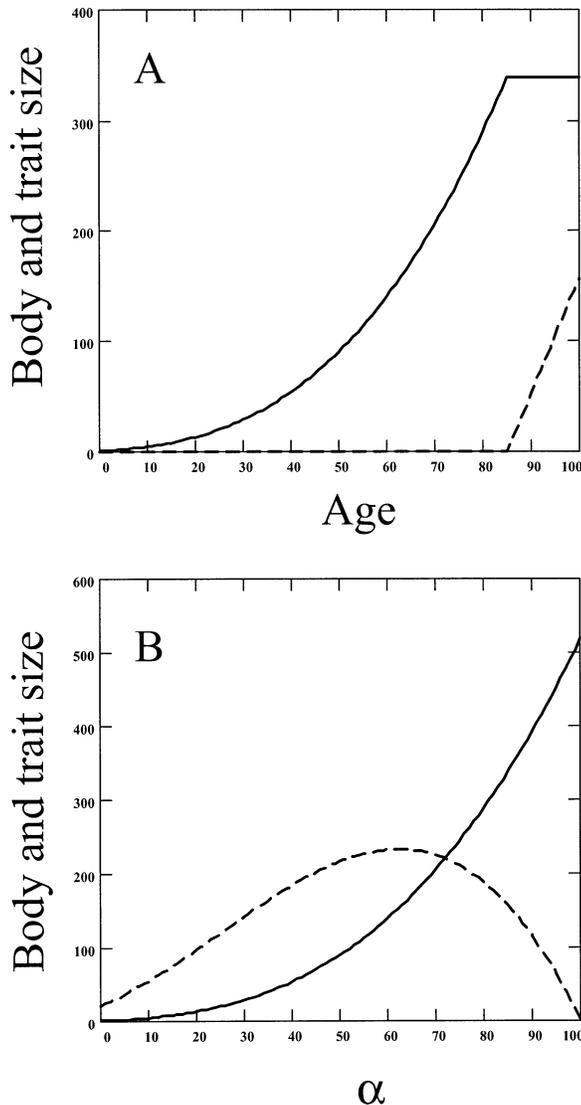
Fig. 1. (A) Change with age of body size (solid line) and trait size (dashed line) for a hypothetical organism, based on a discreet-time simulation with α = 85 of 100 ontogenetic time steps. (B) The relation of body size (solid line) and trait size (dashed line) to the timing of the ontogenetic switch-point (α), where allocation to body growth ceases and allocation to trait growth begins (see text for further explanation).
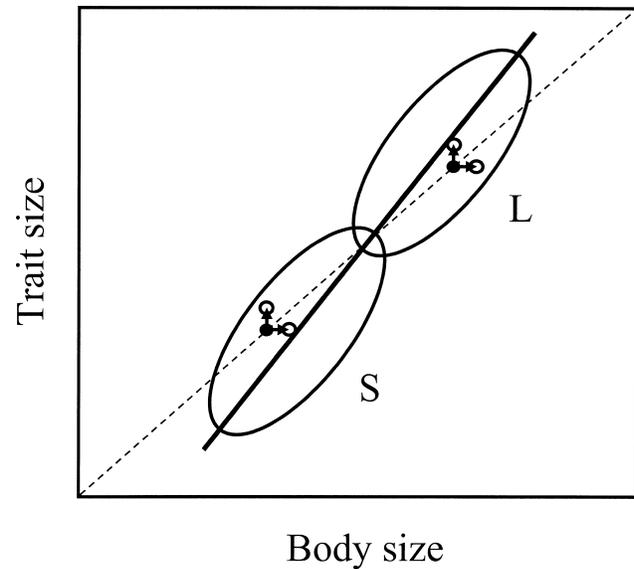

Fig. 2. A hypothetical experiment on an organism with a positive trait allometry (solid line), in which the body size and trait size of one strain (represented by the ellipse marked S) is decreased, while those of another strain (ellipse marked L) are increased, in such a way that relative trait size is constant and equal in reference individuals (closed circles) in each strain, which fall on the line of isometry (dashed line). Then, in each group, the advantage of an increase in trait size (vertical arrows) is compared to the advantage of an increase in body size (horizontal arrows), using test individuals (open circles) selected in relation to the reference individuals. This gives θ_S and θ_L, the relative advantage of increased trait size for the small and large individuals (see text for explanation).

the relative advantage of an increase in trait size (θ) changes as body size increases, while maintaining a constant proportional relationship, R.

It is easiest to interpret expression (4) by imagining a hypothetical, idealized experiment (Fig. 2). The first treatment experimentally increases adult body and trait size while keeping the relative trait size, R, constant (large treatment, denoted by L in Fig. 2). The second treatment decreases adult body and trait size, also keeping R constant (small treatment, denoted by S in Fig. 2). Next, suppose that we measure the relative advantage of an increase in trait size for the large (θ_L) and small (θ_S) treatments, respectively. Our theory predicts that the species should exhibit positive static allometry if $\theta_L > \theta_S$, whereas it should exhibit negative static allometry if $\theta_L < \theta_S$. Isometry is predicted if $\theta_L = \theta_S$.

These predictions are intuitively appealing, suggesting that positive allometry is expected whenever the relative advantage of an increase in trait size is greater for larger individuals. However, this result has utility beyond this verbal cost-benefit reasoning. First, although cost-benefit reasoning must always be true given that the costs and benefits are appropriately defined, our model illustrates precisely what is meant by the costs and the benefits. Second, this result can actually yield some rather counterintuitive predictions (see below).

Examples: Selection and Allometry

For illustration, we choose some specific fitness functions and explore the predicted pattern of allometry. Because very

at $z = Rm$. If expression (4) is zero, the result is isometry, whereas a positive or negative slope represents positive or negative allometry, respectively. Note that expression (4) is valid only when $\phi_m \neq 0$. Otherwise, the more general results of Appendix 2 can be used to determine the pattern of allometry.

Expression (4) has a simple interpretation. The quantity in brackets (which, for simplicity we will denote by θ) is the advantage of a unit increase in trait size relative to that of body size, because the derivatives in the numerator and denominator represent the marginal returns from a unit increase in trait and body size, respectively. Thus, we will refer to this ratio, θ, as the relative advantage of an increase in trait size. The sign of expression (4) (i.e., $\partial\theta/\partial m$) indicates how

TABLE 1. Examples of selection on trait and body size, corresponding fitness functions, and resulting patterns of allometric scaling, illustrating the application of the general solution (expression 4) to our ontogenetic allocation trade-off model (see Results for further explanation). Note that the allometries in the right column are contingent on the specific fitness function form (middle column), and will not necessarily result from every possible function that fits the verbal description in the left column.

Selective regime	Fitness function	Result
1. Directional selection on trait size (e.g., a courtship signal trait)	$\phi(m, z) = g(z)$	isometry
2. Selection on the ratio of trait to body size, favoring any particular ratio or the greatest relative trait size possible	$\phi(m, z) = g(z/m)$	isometry
3. Directional sexual selection on trait size, with stabilizing viability selection on the ratio of trait to body size (e.g., a trait with both sexual and viability-related functions)	$\phi(m, z) = z \times g(z/m)$	isometry
4. Directional selection on trait size and body size; however, trait size is subject to stronger selection ($p > 1$)	$\phi(m, z) = z^p \times m$	isometry
5. Directional sexual selection on trait size, where viability increases with body size with diminishing returns (e.g., a trait with sexual functions but without direct viability costs)	$\phi(m, z) = z \times \dfrac{m}{c + m}$	positive allometry
6. Directional sexual selection on trait size, with viability increasing with body size but decreasing with trait size (e.g., a trait with sexual functions and direct viability costs)	$\phi(m, z) = z \times \dfrac{m}{c + m}$	negative allometry
7. Stabilizing selection on trait size and directional selection on body size	$\phi(m, z) = (z + c)(1 - z)m$	polymorphism

little is known about the actual forms of fitness functions under different selective regimes, we use a variety of possibilities (summarized in Table 1).

Example 1.—To begin with, we ask whether directional selection on trait size is sufficient to produce positive allometry. Suppose that fitness depends on trait size alone: $\phi(m, z) = g(z)$, where $g(z)$ is any increasing function of z (e.g., linear, exponential). This represents (in the most simplified form) a system where sexual competition is severe and success depends on the expression of a secondary sexual trait. Because fitness is independent of body size, we use equation (A13) in Appendix 2, which shows that $R^* = k/b$. Thus, the optimal relative trait size is constant across all body sizes, indicating that isometry will evolve.

Example 2.—Alternatively, fitness may depend on the ratio of trait size to body size. For example, in traits used in intrasexual combat (e.g., antlers), weapon effectiveness might be maximized at a particular ratio of trait to body size, rather than the largest trait size possible (see Kitchener 2000). Under this situation, intuition suggests that a pattern of isometry should evolve, and our model confirms this prediction. Less intuitively, however, our model also suggests that any form of selection on the trait to body size ratio results in isometry, even if selection favors the largest possible relative trait size. For example, with the fitness function $\phi(m, z) = g(z/m)$, where $g(\cdot)$ can be any function of its argument,

$$\theta = \frac{g'(R)\dfrac{1}{m}}{g'(R)\dfrac{-z}{m^2}} = -\frac{m}{z} = \frac{-1}{R}. \qquad (5)$$

The relative advantage of an increase in trait size is the same for all body sizes, indicating isometry.

Example 3.—More realistically, secondary sexual traits are likely to be subject to viability selection, in combination with sexual selection. Suppose that fitness is the product of survival until the mating period, which is a function of the trait to body size ratio, $g(z/m)$, and mating success, which is proportional to trait size, z. Thus, fitness is given by $\phi(m, z) =$ $z \times g(z/m)$. This represents an organism with a trait that is under directional sexual selection but also serves some viability-related functions, so that survival is maximized at a particular ratio of trait to body size (e.g., a bird's tail, used in flight, or a beetle's mandibles, used in feeding). It can be verified using expression (4) that the expected result is isometry.

Example 4.—Green (1992, p. 170) argued that "positive allometry will result if the net benefit of larger characters increases faster than the net benefit of larger bodies." The simplest way to represent this situation is to suppose that survivorship increases linearly with body size, while mating success increases as trait size raised to a higher power: $\phi(m, z) = z^p \times m$, where $p > 1$. This fitness function yields $\theta = p/R$. Because the relative advantage of an increase in trait size is independent of body size, isometry will evolve.

Example 5.—Now consider a fitness function like that in example 4, but where the probability of survival to the mating period is an increasing function of body size with diminishing returns: $\phi(m, z) = z \times m/(c + m)$, where c is a positive parameter. Here, the secondary sexual trait is under directional sexual selection, but it neither has viability-related functions nor imposes direct viability costs. In this case,

$$\theta = \frac{c + m}{cR}. \qquad (6)$$

Because the relative advantage of an increase in trait size is an increasing function of body size, positive allometry is predicted.

Example 6.—Petrie (1992) suggested that positive allometry would evolve if the viability costs for a given trait size were smaller for larger individuals. Consider a situation where mating success is proportional to trait size, z, but survival is a decreasing function of trait size and an increasing function of body size: $\phi(m, z) = z \times m/(c + z)$, where c is a positive parameter. This can represent an organism with a display trait that has direct viability costs that decrease with body size, but no viability-related functions (e.g., a bird's crest or dung beetle's horn). This yields
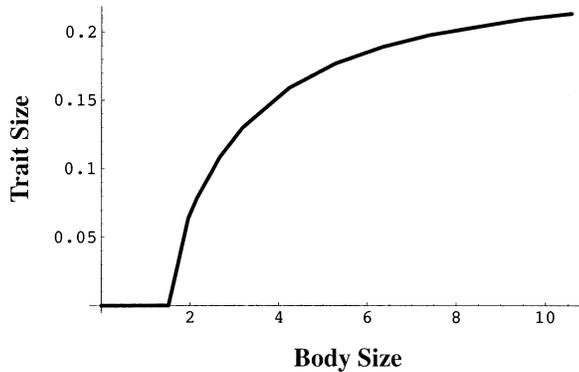
FIG. 3. An example of a sigmoidal pattern of allometry. Fitness is given by $\phi(m, z) = (z + c)(1 - z)m$, with parameter values $a = 0.01$, $b = 0.75$, $k = 0.75$, $T = 15$, $c = 0.5$. Variation on adult size was generated by varying initial body size from $w_0 = 0.1$ to $w_0 = 10$, and the curve was generated assuming that individuals use the optimal developmental program for their initial size.

$$\theta = \frac{c}{R[(Rm) + c]}. \qquad (7)$$

Because θ decreases as body size increases, this function yields negative allometry.

Example 7.—Finally, consider the fitness function $\phi(m, z) = (z + c)(1 - z)m$, where c is a positive parameter. In this case, larger body size is always favored, but there is an intermediate trait value at $z = (1 - c)/2$ that yields the highest fitness. This can represent a trait that is subject to net stabilizing selection, perhaps through a balance of conflicting sexual selection vectors (e.g., Moore and Moore 1999; Bonduriansky and Rowe 2003) or conflicting sexual and viability selection (e.g., Wilkinson 1987). Here, numerical solutions reveal that the optimal switching time during development is on the boundary $\alpha^* = T$ (i.e., no growth in trait) for individuals that start out below a critical initial body size. Thus, the smallest adults of this population will produce no trait at all, while those that start out above this threshold size will devote some energy to trait production. The overall pattern resembles a sigmoidal relationship between trait and body size, with negative allometry among large individuals (Fig. 3).

DISCUSSION

We investigated the effect of selection regime on trait allometry using an allocation trade-off model. The general, analytical solution in expression (4) revealed that the optimal static allometry is determined by the relative advantage of an increase in trait size (i.e., θ) across different sized individuals whose relative trait size (R) is the same.

Our model suggests that selection favors isometry whenever fitness is an increasing function of trait size alone (example 1). The reason for this somewhat counterintuitive result is that, although larger traits are always favored, a larger body size enhances an individual's ability to produce a larger trait size because larger-bodied individuals have more energy at their disposal. Thus, it is beneficial to invest in body growth as well, and the optimal relative investment in each (see Fig. 1B) is equal for all body sizes, resulting in isometric scaling.

If fitness depends on a combination of trait size and body size, we found that positive or negative deviations from isometry may be favored, depending on the specifics of the selective regime. Several authors have predicted that positive allometry will evolve in response to particular combinations of costs or benefits. Our model suggests that these verbal arguments can be valid under specific selective conditions, but not as general rules. Rather, we found that positive allometry will only evolve if the combined effect of sexual and viability selection on trait size and body size results in a greater relative advantage of increased trait size in larger individuals. Although this result seems similar to previous verbal formulations (e.g., Green 1992), the critical sensitivity of allometric patterns to the selection regime requires that selective conditions be specified very precisely. This highlights the value of a formal, mathematical approach to problems of this nature. For example, Green (1992) suggested that positive allometry will evolve whenever the intensity of directional selection on trait size exceeds the intensity of directional selection on body size. Our results suggest that this is true for some fitness functions (example 5), but not others (example 4). Similarly, Petrie (1992) suggested that sexually selected traits will evolve positive allometry if a given trait size imposes greater viability costs for smaller individuals than for larger ones. We found that positive allometry need not necessarily result from this type of cost (example 6). Wallace (1987) suggested that traits used as advertisements of body size (especially in intrasexual displays) will evolve exaggerated linear dimensions or surface areas because such exaggeration will amplify the apparent variation among individuals in body mass, thus reducing the probability of assessment error (see also Gould 1974). However, an honest-advertisement trait of this type may also be selected to retain a constant relative width or depth as body size increases, to prevent increased trait fragility (but cf. Aparicio et al. 2003), in which case such a trait must be positively allometric in units of mass. Our results suggest that selection on absolute or relative trait size per se is not sufficient to produce a positively allometric trait (examples 1, 2). Simmons and Tomkins (1996, p. 97) reaffirmed these arguments, stating that ''positive allometry should arise where the costs and/or benefits of signaling are size dependent.'' However, we found that not all fitness functions that fit this formulation will produce positive allometry (examples 3–6). Our model thus suggests that the evolution of positive allometry requires a narrower set of selective conditions than previously assumed. Our results also point to the general conclusion that complex underlying dynamics such as selection regimes cannot be inferred reliably from simple emergent patterns like allometric slopes.

A relationship between positive allometry and reliable signaling was suggested by Alatalo et al. (1988), Petrie (1992), and Simmons and Tomkins (1996). Likewise, our results indicate that the general requirement for positive allometry is analogous to the general requirement for reliable signaling—that higher-quality individuals receive greater marginal returns from greater signaling effort (Getty 1998). Stable signaling systems are not indicative of any particular relation between signaler quality and the viability costs or mating success gains associated with signaling, but only of the net effect of the combination of these variables on the marginal

returns (Getty 1998, 2002). Similarly, our model suggests that positive allometry can result from any combination of cost and benefit functions that yields a positive result in expression (4).

As suggested above (examples 2, 7), some morphological traits may be subject to stabilizing sexual selection: for example, combat success may be maximized with a particular relative weapon size (Clutton-Brock 1982; Kitchener 2000; but see Preston et al. 2001, 2003), multiple mechanisms of sexual selection may exert conflicting selection on a trait (Moore and Moore 1999; Bondurianski and Rowe 2003), or sexual and viability selection may balance (e.g., Wilkinson 1987). Our model suggests that selection on the trait size to body size ratio per se produces isometric scaling (example 2), while more complex functions that yield net stabilizing selection on trait size (example 7) may produce other allometric patterns. Thus, although isometric scaling may be common in weapon traits, it would not be valid to infer that an isometric secondary sexual trait must function as a weapon.

Interestingly, some simple fitness functions readily yield polymorphic patterns, where trait expression is favored only in individuals exceeding some threshold body size (Fig. 3). These patterns resemble the sigmoidal trait scaling observed in many species of horned beetles and earwigs (e.g., Eberhard 1982; Eberhard and Gutiérrez 1991; Emlen and Nijhout 2000). Our results thus suggest that sigmoidal trait scaling can result from the same types of fitness functions as continuous scaling patterns. Moreover, whereas sigmoidal scaling is generally thought to arise as a result of disruptive selection on trait size (Tomkins and Simmons 1996; Moczek and Emlen 1999), our results suggest that such patterns may also result from stabilizing selection on trait size (example 7).

It has been suggested that all sexually selected traits should be positively allometric (see Green 1992, 2000). Although our model challenges this idea from its first principles, we also feel that our results are also more consistent with the observed diversity of allometric patterns. A preliminary survey of the literature reveals examples of sexually selected traits that exhibit isometry, positive allometry, or negative allometry (e.g., Gould 1974; Alatalo et al. 1988; Simmons and Tomkins 1996; Tomkins and Simmons 1996; Sneddon et al. 1997; Enders et al. 1998; Knell et al. 1999). For example, Simmons and Tomkins (1996) examined the allometries of forceps length in 42 species of earwigs and found significant positive allometries in 11 species, a significant negative allometry in one species, and patterns that did not differ significantly from isometry in the remaining 30 species (although 12 of these had major axis slopes > 2). However, forceps length (a sexually selected trait) did exhibit significantly higher allometric slopes than elytra length (a nonsexually selected trait), a pattern that supports the idea that sexual selection may elevate allometric slopes. Eberhard (2002) investigated the allometries of several male traits used in sexual competition in two drosophilid species and found that all of these traits exhibited either isometric or negatively allometric scaling. Such a diversity of allometric patterns is consistent with our model. Note, however, that we are not arguing that positive allometry is rare, but only that it requires an adequate theoretical explanation. If a systematic survey of the evidence were to reveal that a large proportion of sexually selected traits are positively allometric, further research (including possible extensions to the model presented here) would be required to account for this pattern in nature.

Two other lines of empirical evidence are relevant to our model. First, several studies have applied artificial selection to trait allometries, including wing length in *Drosophila melanogaster* (Weber 1990), eye-stalk width in a diopsid fly (Wilkinson 1993), and horn length in a dung beetle (Emlen 1996). These studies showed that static allometries can respond to selection. More importantly, such studies could represent direct tests of our model: if the precise form of selection acting on the target trait were known, it would be possible to relate the fitness function to the evolutionary response. Unfortunately, net fitness functions are difficult to estimate even in the laboratory, and are not available in any of the above cases. Second, interspecific comparisons have shown that, in species of earwigs with larger pincers (a sexually selected trait), males tend to have steeper pincer size allometries (Simmons and Tomkins 1996). Likewise, male tail length was found to be positively allometric in several species of birds with sexually dimorphic tails, but near isometric in several species with sexually monomorphic tails (Alatalo et al. 1988). These patterns suggest that trait allometry may increase with sexual selection intensity, although the nature of the selective mechanisms involved remains to be determined.

Our analysis is based on several simplifying assumptions. First, we assume that the developing organism can switch its resource allocation instantaneously from body growth to trait growth. Although such a strategy is almost certainly unrealistic biologically because of physiological constraints, numerical simulations suggest that constraining the model to a gradual shift in resource allocation does not alter our qualitative results. Second, we have modeled an organism with only two traits (i.e., body size and one sexually selected trait). Real organisms possess many traits linked by complex resource allocation trade-offs, where the allometry of each trait is likely to be affected by the allometry of every other trait. Third, we assume that the evolution of relative trait size is not constrained by genetic correlation with body size (see Lande 1980). Fourth, for simplicity, we have assumed that an organism's condition (i.e., the amount of resources it has to allocate during ontogeny, as well as its adult viability and mating success) can be expressed adequately as body size (i.e., mass). Although body size may covary with condition in many organisms (Blanckenhorn 2000), it is not likely to capture all aspects of condition (see Rowe and Houle 1996; Ditchkoff et al. 2001). Additional factors, such as variation in metabolic efficiency, immunocompetence, or ability to perform behavioral tasks, may also affect selection on relative trait size. Fifth, we have assumed that selection acts independently of the distribution of phenotypes in the population (i.e., there is no frequency dependence). In reality, an individual's optimal strategy may depend on the strategies adopted by its rivals. Finally, we have assumed that each individual has a single, fixed level of allocation to the sexually selected trait, whereas some models suggest that selection may favor changes in allocation with age (e.g., Kokko 1997; Proulx et al. 2002). The potential effects of these additional factors can be clarified through further elaboration of our general model.

Our general theory may be tested by estimating the ratio of fitness payoffs of an increase in trait size to that of body size (θ) for small and large individuals. Note, however, that the individuals compared must have the same relative trait size (R). It may be possible to perform such an experiment using an organism (such as an insect) whose body size can be manipulated by varying its diet. One can thus create strains of large- and small-bodied individuals (see Fig. 2), then select reference individuals with equal relative trait sizes from each strain (closed circles in Fig. 2), along with test individuals that have slightly greater relative trait size or body size (open circles in Fig. 2). By comparing the fitness of these test individuals to that of the reference individuals within the large- and small-bodied strains, it should be possible to estimate the advantage of increased trait size, relative to that of increased body size (i.e., θ) within each strain. For a species with a positively allometric trait (i.e., where relative trait size increases with body size), our model predicts that θ will be greater in the large-bodied strain than in the small-bodied strain. The reverse is predicted for a species with a negatively allometric trait. The above approach seems preferable to simply using intrapopulation variation in body size and shape, because intrapopulation variation is likely to reflect variation in genetic quality (a confounding variable), whereas variation in body size across populations reared at different food levels need not correlate with genetic quality. Unfortunately, neither approach entirely eliminates confounding environmental variables, such as variation in phenotypic aspects of condition.

In summary, we found that the allometric pattern favored by selection (e.g., isometry, positive or negative allometry, sigmoidal scaling) depends critically on the precise form of the function relating fitness to body size and trait size. Our model suggests that no particular pattern of fitness costs or payoffs is invariably sufficient to produce positive allometry. Rather, the optimal allometry depends on the net fitness function. Our results are consistent with the observed diversity of allometric patterns.

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Corresponding Editor: S. Pitnick

APPENDIX 1

The optimal allocation strategy, $u(t)$, can be determined using Pontryagin's Maximum Principle from the theory of optimal control (Leitmann 1966, 1981; Flemming and Rishel 1975; Knowles 1981).

Formally, we seek a piecewise continuous control function $u(t)$, such that $\phi(m, z)$ is maximized, subject to differential equations (1) and (2). The first step is to define the so-called Hamiltonian, which in this case is

$$H(u, \lambda_m, \lambda_z) = \lambda_m u a m^b + \lambda_z(1 - u)kam^b. \quad (A1)$$

The optimal control, $u^*(t)$, must then maximize $H(u, \lambda_m, \lambda_z)$ as a function of u, where λ_m and λ_z are given by the solutions to the system of differential equations (1) and (2), along with

$$\frac{d\lambda_m}{dt} = -\frac{\partial H}{\partial m}, \quad \text{and} \quad (A2a)$$

$$\lambda_m(T) = \frac{\partial \phi}{\partial m}\bigg|_{t=T}, \quad (A2b)$$

$$\frac{d\lambda_z}{dt} = -\frac{\partial H}{\partial z}, \quad \text{and} \quad (A3a)$$

$$\lambda_z(T) = \frac{\partial \phi}{\partial z}\bigg|_{t=T}, \quad (A3b)$$

where the optimal control, u^*, is used in equations (1), (2), (A2), and (A3). Equations (A2) and (A3) evaluate to

$$\frac{d\lambda_m}{dt} = -abm^{b-1}\{u^*\lambda_m + (1 - u^*)k\lambda_z\}, \quad (A4a)$$

$$\lambda_m(T) = \frac{\partial \phi}{\partial m}\bigg|_{t=T}, \quad (A4b)$$

$$\frac{d\lambda_z}{dt} = 0, \quad \text{and} \quad (A5a)$$

$$\lambda_z(T) = \frac{\partial \phi}{\partial z}\bigg|_{t=T}. \quad (A5b)$$

The quantities λ_m and λ_z represent the marginal returns of a unit investment in body size and trait size respectively. Notice that λ_z remains constant over the period of development (and equal to $\partial \phi/\partial z$).

We now characterize the optimal control as follows. Because $u^*(t)$ must maximize H, we have

$$\lambda_m > k\lambda_z \Rightarrow u^*(t) = 1, \quad (A6)$$

$$\lambda_m < k\lambda_z \Rightarrow u^*(t) = 0, \quad \text{and} \quad (A7)$$

$$\lambda_m = k\lambda_z \Rightarrow \text{undetermined}. \quad (A8)$$

Conditions (A6–A8) state that, if the marginal return of an investment in body growth exceeds an investment in trait growth (accounting for differences in the energy conversion efficiency), then all resources should be devoted to body growth and vice versa. The third possibility, that the marginal return from each is equal over some period of development (termed a singular control), might allow for a mixed allocation strategy to be optimal. However, we can prove (by contradiction) that (A8) can never hold over an interval of time and therefore that mixed allocation strategies are never optimal. In particular, suppose that a singular control did occur. Then we have

$$\lambda_m = k\lambda_z = k\frac{\partial \phi}{\partial z}\bigg|_{t=T}, \quad (A9)$$

and we must also have that $d\lambda_m/dt = 0$ over this time interval because λ_z is constant (by eq. A5). But equation (A4) shows that, in this case, the dynamics of λ_m satisfy

$$\frac{d\lambda_m}{dt} = -abm^{b-1}k\frac{\partial \phi}{\partial z}\bigg|_{t=T}. \quad (A10)$$

Therefore, we can have $d\lambda_m/dt = 0$ if and only if $(\partial \phi/\partial z)|_{t=T} = 0$, in which case we must also have $\lambda_m = 0$ over the time interval in question. But we have assumed that either $\partial \phi/\partial z \neq 0$, $\partial \phi/\partial m \geq 0$

or $\partial\phi/\partial z = 0$, $\partial\phi/\partial m > 0$, and therefore we know that, in general, equations (A4a,b) reduce to

$$\frac{d\lambda_m}{dt} = -abm^{b-1}u^*\lambda_m \quad \text{and} \quad \text{(A11a)}$$

$$\lambda_m(T) = \frac{\partial\phi}{\partial m}\bigg|_{t=T} > 0 \quad \text{(A11b)}$$

for all time. Equations (A11a,b) imply that $\lambda_m > 0$ for all time, and this contradicts the requirement that $\lambda_m = 0$. Thus, a singular control (i.e., condition A8) can occur for at most an instant in time; there cannot be a period of mixed allocation.

We can further characterize the optimal allocation strategy by considering the two other possible cases for $(\partial\phi/\partial z)|_{t=T}$.

Case 1.—Suppose that $\partial\phi/\partial z < 0$. In this case the Hamiltonian reduces to $H = \lambda_m uam^b - n(1 - u)kam^b$, where $n > 0$. Now by assumption we have $\lambda_m = \partial\phi/\partial m \geq 0$ in this case at the end of development, and therefore a consideration of the Hamiltonian reveals that we must also have $u^*(t) = 1$ for some time interval $t \in [t_{crit}, T]$ near the end of development (because λ_m is continuous). But a consideration of equation (A4) in this case reveals that λ_m must be nondecreasing backward in time. As a result, $\lambda_m \geq 0$ throughout all of development and therefore again (A6) is satisfied throughout development, implying that $u^* = 1$ throughout the entire period of development.

Case 2.—Suppose that $\partial\phi/\partial z > 0$. In this case, either (A6), (A7), or (A8) holds at the end of development. If (A6) holds, then $u^* = 1$ at this point, and an argument similar to that above reveals that (A6) must therefore hold throughout all of development. If (A7) holds, then $u^* = 0$ for some time interval $t \in [t_{crit}, T]$ near the end of development (because λ_m is continuous). In this case, equation (A4) reveals that λ_m increases backward in time, and therefore either (A7) remains in effect during all of development (in which case $u^* = 0$ throughout development) or else there is a time at which (A8) is satisfied. At this point, the above considerations reveal that λ_m must continue to increase backward in time; thus the allocation strategy switches to $u^* = 1$ prior to this point. Moreover, because λ_m still increases backward in time, the optimal control in this case is a period of pure growth in body size followed by a period of pure growth in the trait. Finally, if (A8) holds at the end of development, arguments similar to those above demonstrate that the optimal strategy has $u^* = 1$ (i.e., pure growth in body size) for all of development.

The above results can thus be summarized as follows: the optimal developmental program is one in which the organism devotes all available energy to body growth up until time α, and then devotes all available energy to trait growth, where $0 \leq \alpha \leq T$. Thus, the mathematical problem is reduced to one of determining the optimal switching time, α^*.

APPENDIX 2

Fitness, $\phi(m, z)$, is a function of the two variables m and z. However, because we are ultimately interested in how $R = z/m$ varies across different adult body sizes, it is more straightforward to treat fitness as a function of m and R instead; that is, an individual with body size m and relative trait size R has fitness $\phi(m, Rm)$. Recall that we are seeking the optimal switching time, where both R and m change as this switching time is varied. Because R is strictly decreasing in α (this can be checked using the equations for $z[\alpha]$ and $m[\alpha]$), we can simplify matters by treating R as the decision variable and treating m as a function of R. In this case, assuming an intermediate switching time and thus an intermediate value of R is optimal, this value of R must satisfy the first order condition

$$\frac{\partial\phi}{\partial m}\frac{dm}{dR} + \frac{\partial\phi}{\partial z}\left(m + R\frac{dm}{dR}\right) = 0. \quad \text{(A12)}$$

Noting that $dm/dR = (dm/d\alpha)/(dR/d\alpha)$, one can show using equations (1), (2), and (3) that $m + R(dm/dR) = (bR - k)(dm/dR)$. Therefore, (A12) is equivalent to

$$\frac{dm}{dR}\left[\frac{\partial\phi}{\partial m} + \frac{\partial\phi}{\partial z}(bR - k)\right] = 0. \quad \text{(A13)}$$

Writing the parenthetical term of (A13) as $G(R, m)$, we have that $G(R, m) = 0$ at the optimal R. Now we can increase adult body size, m, by increasing m_0 to see how the optimal R changes across increasing adult body sizes. To do so, we implicitly differentiate G with respect to m_0,

$$\frac{\partial G}{\partial R}\frac{dR}{dm_0} + \frac{\partial G}{\partial m}\frac{dm}{dm_0} = 0. \quad \text{(A14)}$$

Because we are dealing with a fitness maximum, we know that $\partial G/\partial R > 0$ from the left side of (A13) (because $dm/dR < 0$), and therefore we have

$$\frac{dR}{dm} \propto \frac{\partial G}{\partial m}. \quad \text{(A15)}$$

The derivative, dR/dm, on the left side of (A15) is the change in R with an increase in adult body size, m, that results from an increase in m_0. In light of the definition of G, and the fact that $bR - \varepsilon = -\phi_m(m, Rm)/\phi_z(m, Rm)$ at the optimal R (from eq. A13), expression (A15) simplifies to expression (4) of the text.