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GROWTH MODELS OF COMPLEX ALLOMETRIES IN HOLOMETABOLOUS INSECTS

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Abstract.—Allometries among body parts of adult holometabolous insects differ from allometries among body parts of many other animals because adult structures (many of which are derived from imaginal disks) do not grow synchronously with the body. Imaginal structures grow little during larval life but experience most of their growth during the prepupal and pupal period, after food intake and somatic growth have ceased. Growth of imaginal tissues thus occurs in a closed system at the expense of nutrients accumulated during larval life. In a closed system, growing imaginal tissues compete for available nutrients, and the growth trajectory and final size of one tissue (or disk) are influenced by the growth of others. We use the Gompertz growth equation and a model of growth in a closed system in which imaginal disks compete for nutrients to model the growth of imaginal disks and the resulting allometric relations among them. By incorporating known features of ant caste development, such as reprogramming of the critical size for metamorphosis in major workers (soldiers) and reprogramming of developmental parameters in individuals larger than a critical size, we show that the nonlinear and discontinuous allometries of ants with polymorphic castes result from normal developmental processes during the metamorphosis of holometabolous insects. The imaginal disk competition model predicts that when one disk is reprogrammed, others will show a compensatory response. Such correlated developmental responses may play a role in the evolution of body proportions in ants, rhinoceros beetles, and other insects.

Changes in the relative growth of tissues, organs, appendages, and other body parts are the basis for much of the morphological evolution observed at taxonomic levels below the phylum and class (Gould 1966; Alberch et al. 1979). This observation has found its most elegant expression in the Cartesian transformations whereby D'Arcy Thompson attempted to map complex morphological differences between species as large-scale differences in growth gradients (Thompson 1942; Bookstein 1978), and its most generally useful one in the analyses of allometry that allowed Huxley to deduce that many changes in form are simple mechanical consequences of differences in the intrinsic growth rates of body parts (Huxley [1932] 1972).

Differences in the relative growth of body parts can account for much intraspecific variation of form, as well as for the diversity of form we observe between taxa. Differences in the growth rates among body parts are referred to as *allometric growth*. It is common practice to study allometric growth on the basis of bivariate plots of the dimensions of two body parts or the dimension of a body

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part against body size. After logarithmic transformation of the measures (and an appropriate transformation of each measure to bring both to the same dimensionality), simple allometric growth is characterized by a straight-line relationship among the two variates. A broad diversity of morphological and functional variation has been shown to fit such simple linear allometric relationships (Cock 1966; Gould 1966; Huxley 1972; Schmidt-Nielsen 1984).

Allometric relationships in holometabolous insects present a special problem that arises from the fact that the appendages of the adult develop from structures that do not grow at the same time as the larval body. Imaginal disks for appendages, head structures, and portions of the thorax grow very slowly during most of larval life and then undergo a brief period of explosive growth just before metamorphosis (Williams 1980). The growth of most imaginal structures is concentrated in the prepupal and pupal periods and usually occurs at a time when food intake (and therefore body growth) has ceased. This fact and the difficulty it poses in interpreting patterns of relative growth in holometabolous insects have long been recognized (Huxley 1931, 1972; Wilson 1953) but have received little attention in models of growth and allometry. It is clear, however, that the patterns of growth that generate many adult features in holometabolous insects produce allometric relations that are fundamentally different from those observed in animals whose body parts grow continuously and synchronously as the body grows.

The peculiar way in which adult Holometabola are built has two consequences for allometry. First, where allometric relations among body parts exist, they cannot be interpreted as straightforward results of relative growth. This is particularly true when the dimensions of adult appendages are compared to overall body size, since the two grow at different times during development and under very different endocrine and nutritive conditions. Second, some of the unusual allometric relations found in insects, such as the curvilinear and discontinuous allometries found in worker castes of ants (Wilson 1953; Feener et al. 1988; Wheeler 1991) and beetles (Huxley 1931, 1972; Emlen 1994; Kawano 1995), might be explained in part by interactions among imaginal tissues during metamorphosis.

In this article, we explore the process of allometry in holometabolous insects by comparing patterns of allometry found in ants to patterns produced by two models of growth. The first model applies the Gompertz equation to the growth of individual imaginal disks during the prepupal and pupal period. When the Gompertz equation is used to model the growth of imaginal disks, it can generate linear and curvilinear allometries similar to those observed in many ants. In the second model, imaginal disks grow at the expense of nutrients stored in the prepupal stage and disks compete for limiting nutrients. We compare allometries produced by the second model, which is based on more realistic assumptions about imaginal growth in holometabolous insects, to those produced by the Gompertz model. Under some conditions, both models yield qualitatively similar allometry curves, but the disk competition model is biologically more realistic and produces a greater diversity of realistic allometry curves. Most importantly, the disk competition model makes certain predictions not made by the Gompertz model, which are confirmed by observations on the allometries of ants and scarab beetles. Although the disk competition model is based on known developmental

and physiological processes in ants, the principles should be applicable to holometabolous insects in general.

GROWTH RATIOS, GROWTH-PARTITION COEFFICIENTS, AND GROWTH IN CLOSED SYSTEMS

Huxley (1972) considered two types of growth relations that can lead to allometry. The first, differential growth ratios, obtains when two structures grow simultaneously (such as carapace width and interocular distance in crustaceans, or brain volume and body weight in vertebrates). In most such cases, the bivariate allometry curve also traces a portion of the growth history of both structures. The second, growth-partition coefficients, obtains when one structure grows while the other is static (such as yearly antler growth in deer). In such cases, the new structure develops in proportion to the current body size of the animal, and the allometry curve simply describes this static relationship.

Allometry in holometabolous insects corresponds to neither of these alternatives. Unlike deer, which continue to feed while they regenerate antlers, holometabolous prepupae and pupae are essentially closed systems during the period of imaginal disk growth and development. While the imaginal structures grow, the animal does not feed, so that imaginal disk growth actually occurs at the expense of overall body size. If nutrients are limiting, then it is also possible that one disk may grow at the expense of another.

ALLOMETRY OF HOLOMETABOLOUS APPENDAGES

To model allometry in holometabolous insects, we first modeled growth of imaginal disks. Disks may differ in their initial size, their rate of growth, or the duration of their developmental period. The allometry relation consists of the final dimension of the imaginal structure produced by the disk plotted against a second structure for a set of individuals. The second structure can be another disk or a measure of body size. Figure 1 illustrates two ways in which such an allometric relation can be obtained.

THE THREE DEVELOPMENTAL MECHANISMS OF CASTE

The most unusual allometric relations among body parts are found among the various morphological castes of ants (Wilson 1953). Understanding the developmental causes of caste differentiation in ants has proven to be essential for understanding these allometric relations and leads to a model for nonlinear and complex allometries that may apply to the holometabolous insects in general. The diversity of physical caste systems in worker ants can be classified into four major categories, based on the form of log-log plots of two body parts and their size frequency distribution (Wilson 1953, 1971; Oster and Wilson 1978). Ant allometries can be linear, curvilinear (it is often ambiguous whether curvilinear allometries are made up of two intersecting linear allometries or are indeed smoothly curvilinear), triphasic (with three intersecting lines or a sigmoid curve), or completely dimorphic (made up of two discontinuous and displaced lines). It has been shown

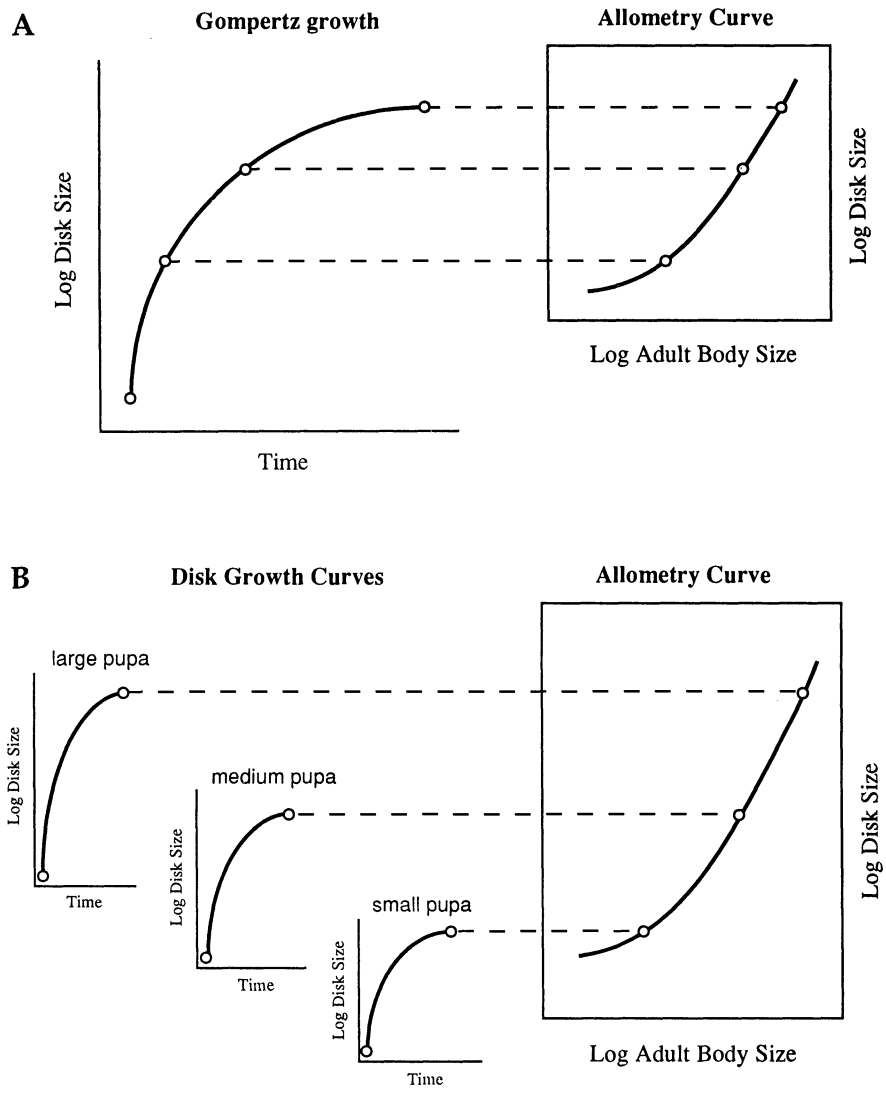

FIG. 1.—Two mechanisms for obtaining allometric relationships among body parts in holometabolous insects. *A*, Allometry is the result of differences in the duration of the growth period of imaginal disks (or other adult body parts) that are following identical growth trajectories. This model assumes that in large pupae, disks grow for longer periods of time than in small pupae. The Gompertz model discussed in the text produces allometries by this mechanism. *B*, Allometry is the result of differences in growth rates of disks in individuals of different sizes. Disks in larger pupae grow more rapidly, while the duration of growth is the same in pupae of all sizes. The disk competition model described in the text produces allometries by this mechanism.

(Wheeler 1991) that these four major categories and their variants can be produced by variation in only three developmental processes. First, there is variation in the values of the *growth parameters* of body parts, such as the relative growth rates of those parts, their initial sizes, and any internal or external constraints on their growth that might exist. Second, variation occurs in the setting of the *critical size,* which is defined as the size at which a developing larva takes the first physiological steps to initiate metamorphosis (Nijhout 1981, 1994). This leads to variation in absolute size. Third, *reprogramming* of the critical size and the growth parameters can take place during development, in response to environmental and endocrine cues. Reprogramming is believed to play an important role in the determination of size range, multimodality, and dimorphism in worker caste systems (Wheeler 1991). It has also been documented as one of the principal causes of worker polymorphism in *Pheidole bicarinata* (Wheeler and Nijhout 1983). Reprogramming of developmental parameters occurs when developmental hormones such as the juvenile hormone are secreted (or disappear) during certain critical periods in the molting cycle. Empirical and experimental data have demonstrated the significance of each of these three components in the development of insect polymorphisms in general and in caste determination in particular (Nijhout and Wheeler 1982; Wheeler 1991; Nijhout 1994). These developmental features are essential components in the models we present below.

RESULTS

Allometry and the Gompertz Function

An appropriate equation describing the growth of organisms is the Gompertz function. This function describes a sigmoid pattern of growth and has been shown to fit observed data in a broad range of organisms and over a wide range of absolute sizes (Laird 1965; Wilbur and Collins 1973; Ricklefs 1979). The Gompertz function describes a growth rate that declines as mass grows:

$$dS/dt = ASe^{-\alpha t}, \tag{1}$$

where S is size, A is the exponential growth rate, and α is the exponential damping of A (Laird 1965; Edelstein-Keshet 1988; Jolicoeur 1989). The exponential growth rate is generally assumed to be the consequence of a constant frequency of cell division (Katz 1980) or of a growth rate that is proportional to size. The physiological basis of the damping factor is more obscure, even though the phenomenon is well documented. Damping may result from an increasing limitation of nutrients as tissues get larger, which, in turn, could be due to a decreasing surface-to-volume ratio or an inability of the rate of supply of nutrient to keep up with ever-increasing growth requirements of the cells and tissues. A Gompertz growth trajectory eventually reaches an asymptote with a value of $A/\alpha + \ln(S_0)$, where S_0 indicates initial size.

Bivariate plots of the sizes of two structures generated by different relative values of the constants in the Gompertz equation yield allometric patterns observed in many systems (Laird 1965; Wheeler 1991). To obtain an allometric

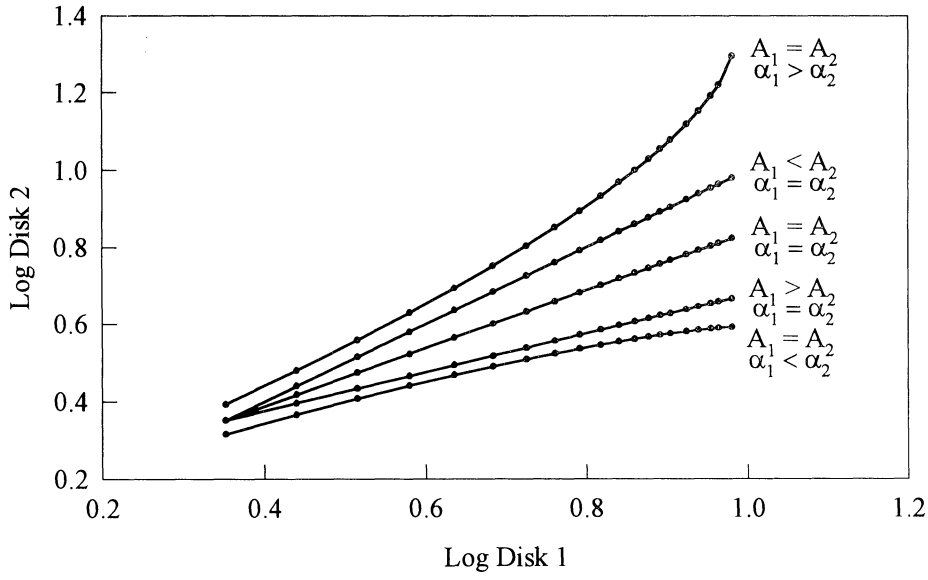

FIG. 2.—Disk-disk allometry based on Gompertz growth, illustrating the effects of inter-disk differences in A (growth rate) and α (damping coefficient) on the shape of the allometry.

relationship, it is necessary to vary absolute body size, which, with the Gompertz equation, is done by varying the time allowed for growth. A bivariate logarithmic plot of the size of two body parts, measured at a series of times along their growth trajectory, will give the allometric relation between those body parts.

Figure 2 illustrates the forms of the bivariate allometry plots based on this assumption, for body parts that differ in initial size (S_0), growth rate (A), or damping factor (α). Changes in initial disk size (S_0) affect only the intercept of the allometry curve, not its slope. Changes in initial growth rate (A) affect the slope of the curve and determine the traditional allometric coefficient. In general, the slope of the allometry curve is A_y/A_x. When the damping factor (α) of the two body parts is not the same, the allometric relation between them becomes curvilinear. If the body part plotted on the ordinate has a higher damping factor than the reference body part, the slope of the plotted curve will decrease with increasing overall size. Conversely, a lower damping factor will produce a curve with increasing slope.

Reprogramming with the Gompertz Function

Nonlinearity and internal discontinuity are common features of bivariate plots of size variation in worker castes in ants (Wilson 1952; Wheeler 1991) and dimorphic males in beetles (Emlen 1994; Kawano 1995). We have found that a number of these "unusual" allometry patterns found in ants can be simulated by a model that combines the Gompertz equation with reprogramming of the variables of growth (A, α). Figure 3*A* shows the diversity of allometries that can be generated

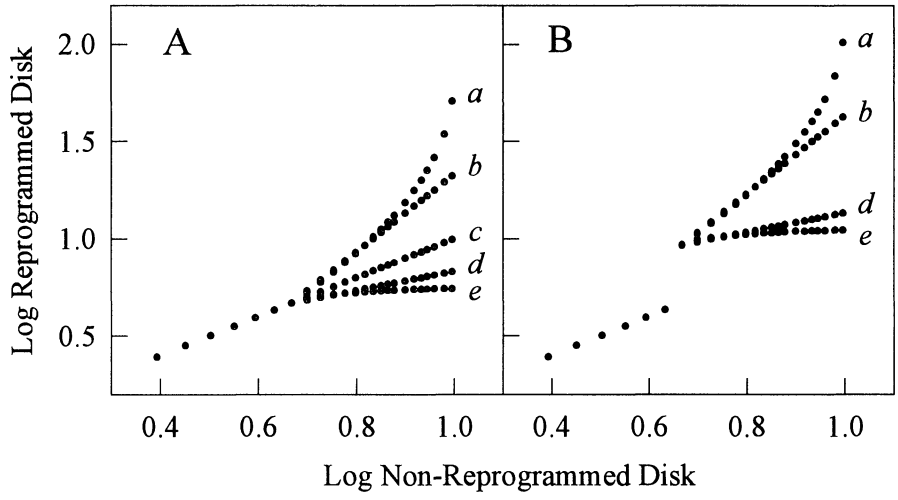

FIG. 3.—Allometry based on Gompertz growth with reprogramming. *A*, The effect of reprogramming A or α in the middle of the growth period. *B*, In addition to reprogramming A or α, the critical size is also reprogrammed, which leads to a discontinuity in the allometry plot. Key to labels: *a*, α reprogrammed downward; *b*, A reprogrammed upward; *c*, no reprogramming; *d*, A reprogrammed downward; *e*, α reprogrammed upward.

by reprogramming these growth parameters during development. Reprogramming the growth rate alters the slope of the allometric curve, while reprogramming the damping factor alters the shape of the allometry curve. In addition, when critical size is also reprogrammed, the second portion of the plot is displaced, producing a spatially discontinuous allometry curve (fig. 3*B*) of the type common in many ants (illustrations in Wilson 1953; Wheeler 1991).

Gompertz growth, particularly when combined with reprogramming, can clearly produce a broad variety of complex allometries among imaginal structures that resemble those found in many species of ants. But there are several reasons that Gompertz growth does not provide a fully adequate biological model for the growth of imaginal disks. First, the Gompertz function does not contain an independent variable for body size: variation in body size can be modeled only by variation in the length of the growth period. Although this approach can accurately model reprogramming of the critical size for metamorphosis, it is not a realistic model for imaginal disk growth insofar as the duration of the prepupal and pupal periods of large individuals do not differ significantly from those of small individuals in a population. Second, although α provides a means for damping growth, this parameter does not correspond to an identifiable physiological function (though it could be made to do so by appropriate modification). Third, the Gompertz equation does not provide a way to model explicitly the closed environment of the prepupa and thus does not allow us to examine the possible interactions between disks growing in a common environment or the possible effects of limitation of stored nutrients.

An Imaginal Disk-Interaction Model

Here, we develop a model of growth based on competition among body parts that generates allometry plots more diverse than those generated by the Gompertz equation and in which all parameters have an unambiguous and empirically testable biological meaning. Typically holometabolous larvae build up large stores of lipids, carbohydrates, and storage proteins during the growth period to meet the demand of pupal development and adult reproduction (Wigglesworth 1965). During the prepupal period, food intake ceases, and the level of stored nutrients drops precipitously over the subsequent course of pupal development as these stores are used in metabolism and the construction of imaginal structures.

The imaginal disks that will make up the head and appendages of the adult insect undergo most of their growth during the prepupal period, after feeding has stopped. The prepupa must allocate a finite supply of reserves that have been accumulated during larval life (in the form of fat body, hemolymph proteins, and other tissues) to fashion the adult body form. The dimensions of all body parts of the adult are determined during the prepupal stage and must necessarily be influenced by the amount of "building material" available within the closed system.

The growth of imaginal structures can be modeled as the growth of an assemblage of entities competing for a fixed and perhaps limited nutrient resource that was accumulated during the larval stage. Different imaginal structures may differ in their efficiency of resource utilization, which will influence their relative growth rates. Perhaps most importantly, the gradual depletion of nutrient reserves provides a built-in damping factor for growth and sets an upper limit to the size of each imaginal structure. We believe that this view of a pupa, as a closed miniature ecosystem with limiting resources and competing consumers of those resources, provides a useful and ultimately correct model in which the relative growth of imaginal structures can be studied.

We assume a system composed of a body containing two independent imaginal disks, each of which grows at a rate proportional to its current size and to the concentration of nutrients according to

$$dS_1/dt = k_1 S_1^P N$$

and

$$dS_2/dt = k_2 S_2^P N, \tag{2}$$

where S is the size of the disk, N is the concentration of nutrient, and k_1 and k_2 are reaction constants that describe the intrinsic rate of growth and the efficiency of nutrient utilization. The exponent P is a coefficient whose value can be used to model a structural constraints on growth. For instance, if S is mass and growth is proportional to surface area, then a spherical structure can be modeled by setting P to a value of 2/3. In all but one of the figures below, $P = 1$. The nutrient N is assumed to be present continuously as a mass parameter that is depleted by the growing disks at the rate

$$dN/dt = -(k_1 S_1^P + k_2 S_2^P) N. \tag{3}$$

Disk size S and nutrient quantity N are assumed to be expressed in the same units of mass, so the model essentially transforms nutrient mass into disk mass. This model can be readily expanded to include more than two competing imaginal structures. Variation in body size can be modeled by variation in N. For the purposes of the present article, we assumed that one-third of the body mass at the time that prepupal development starts is composed of available nutrients. We also assume that the developmental period during which disk growth occurs is the same for all individuals, irrespective of body size, because in most species of insects that have been studied the duration of the pupal stage is the same for individuals of different body sizes. Alternatives to both assumptions can be readily modeled (and the model could be extended to include hemimetabolous insects if N is allowed to grow with time). The model produces damped growth of imaginal disks; each disk eventually reaches a plateau when nutrient is exhausted.

Figure 4 illustrates the allometric relationships between body size and disk size for different values of the initial size (S) and growth constant (k) of a single disk. The shapes of the allometry plots in figure 4 thus allow examination of the effects of the relative dimensions of parameter values in the model. Each point in these graphs represents the end point of the growth trajectory of an imaginal disk given a different value of N and thus body size (cf. fig. 1*B*). The allometries in figure 4 span a range of body sizes of two orders of magnitude in mass. Insofar as real intraspecific allometries generally span one order of magnitude or less, these curves represent extended allometries of broader range than are likely to be found in nature. Species whose body size is small relative to the sizes of their disks will have allometries that resemble the left-hand portions of the curves in figure 4, while those with body sizes that are large relative to their disks will have allometries that resemble the right-hand portions of those curves. The shape of the allometry is also affected by the duration of the growth period. In the cases illustrated, the disks did not grow long enough to exhaust the available nutrient, as is indeed the case in life. When disks in all body sizes exhaust their nutrient, the disk–body size allometry becomes linear. Thus, different values for initial disk size, specific growth rates of disks, and relative amount of nutrient can produce disk–body size allometries that are linear, concave, convex, or sigmoid. In general, relatively large initial disk sizes and relatively small intrinsic growth rates produce allometries that are concave (increasing slope with increasing body size), while larger body sizes (and relatively smaller disk sizes) and higher growth rates produce allometries that are more nearly linear or convex (decreasing slope with increasing body size). The shape of disk-disk allometries is determined entirely by the exponent P. If P is equal to one, the disk-disk allometries are linear; whereas if P is greater or less than one, these allometries are curvilinear (fig. 5).

Reprogramming the Critical Size

In the ant *Pheidole bicarinata,* larvae destined to become soldiers are reprogrammed to grow to a linear size about 1.6–1.8 times that of larvae destined to become workers before they begin metamorphosis (Wheeler and Nijhout 1983). Thus, the imaginal disks of a soldier grow within a body that is four to six times the mass of that of a worker. If only the critical size for metamorphosis is repro-

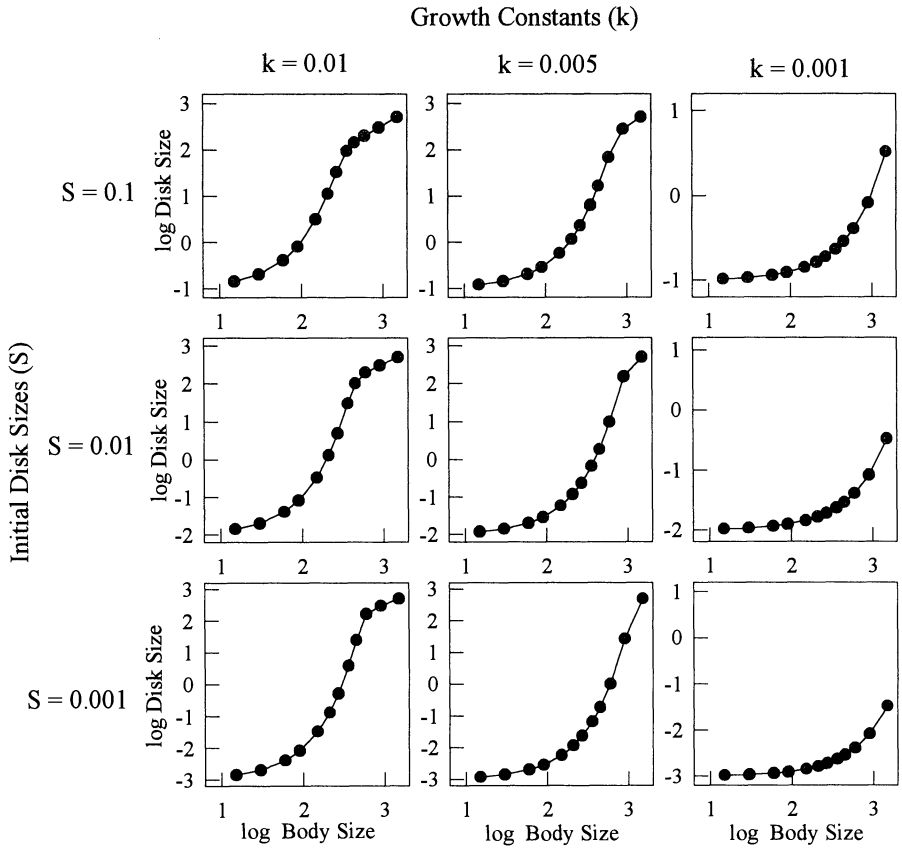

FIG. 4.—Allometries derived from competition model with a single disk, illustrating effects of systematic variation in S and k on the shape of the allometry curve. Each point represents the end point of a growth trajectory of an individual disk (cf. fig. 1*B*).

grammed, then body size–disk allometries of workers and soldiers should occupy different regions of a single continuous curve. Thus, the curves in figure 4 can also be interpreted as representing allometries of dimorphic ants, with the smaller worker caste occupying the left portion of each curve and the larger soldier caste occupying the right portion. In many ants that have a dimorphic worker/soldier caste, the two castes clearly occupy different portions of a nonlinear but smoothly continuous allometry curve (Wilson 1953; Diniz-Filho et al. 1994). In many cases, however, the allometric curves of soldiers and workers are not smoothly continuous but either intersect at an angle or lie parallel to one another (Wilson 1953; Wheeler 1991). We show below that reprogramming of growth parameters at a critical size leads to just such allometric relationships.

Reprogramming the Growth Parameters

When one disk is reprogrammed to grow at a higher rate in pupae whose body size is above a critical size, a discontinuity in the allometry plot is produced.

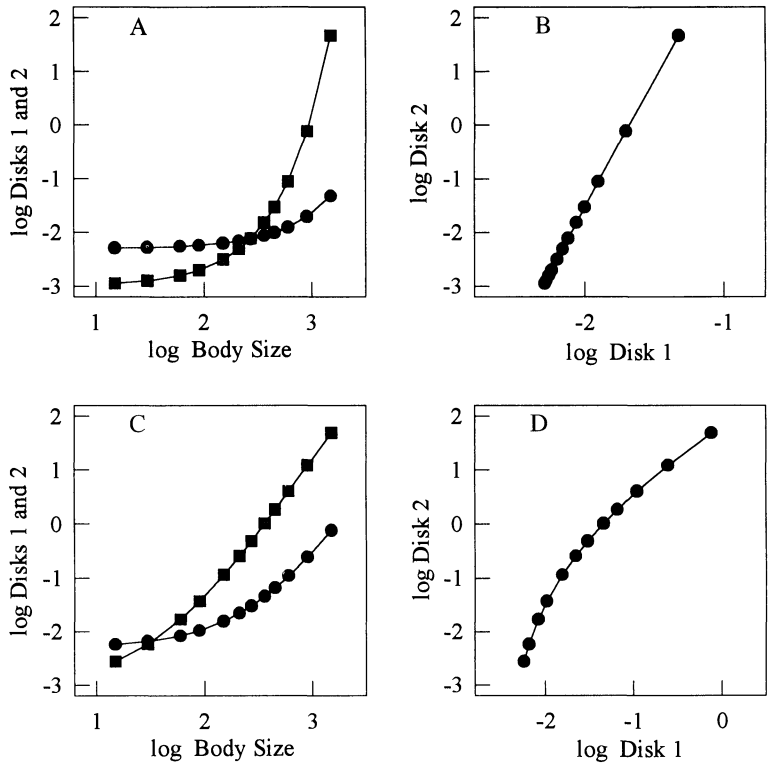

FIG. 5.—Allometries derived from the competition model with two disks, illustrating the effect of altering the exponent P in equations (1) and (2). The top panels show body size–disk (A) and disk-disk (B) allometries, when $P = 1$. The bottom panels show body size–disk (C) and disk-disk (D) allometries when $P = 2/3$. In both cases, $S_1 = 0.005$, $S_2 = 0.001$, $k_1 = 0.001$, and $k_2 = 0.005$.

These complex or broken allometries closely resemble the allometry relations observed in a great diversity of polymorphic ants (Wilson 1953; Baroni Urbani 1976; Wheeler and Nijhout 1983; Feener et al. 1988; Wheeler 1991; Diniz-Filho et al. 1994). Figure 6 illustrates the allometry of two disks that have identical growth constants in animals with small body sizes while one of the disks is reprogrammed to grow at several times (or at a fraction of) the rate of the other disk in animals of larger body sizes.

When only one disk is reprogrammed, its rate of nutrient use changes. Because all disks share the same nutrient pool, such a reprogramming event affects other disks as well. As a consequence, the growth rate of disks that are not reprogrammed also changes as less (or more) nutrient is now available to them. This compensatory response of nonreprogrammed disks results in a discontinuity in the allometry plot of all disks that share the nutrient pool, even if not all are reprogrammed.

Reprogramming and the compensatory response of nonreprogrammed disks

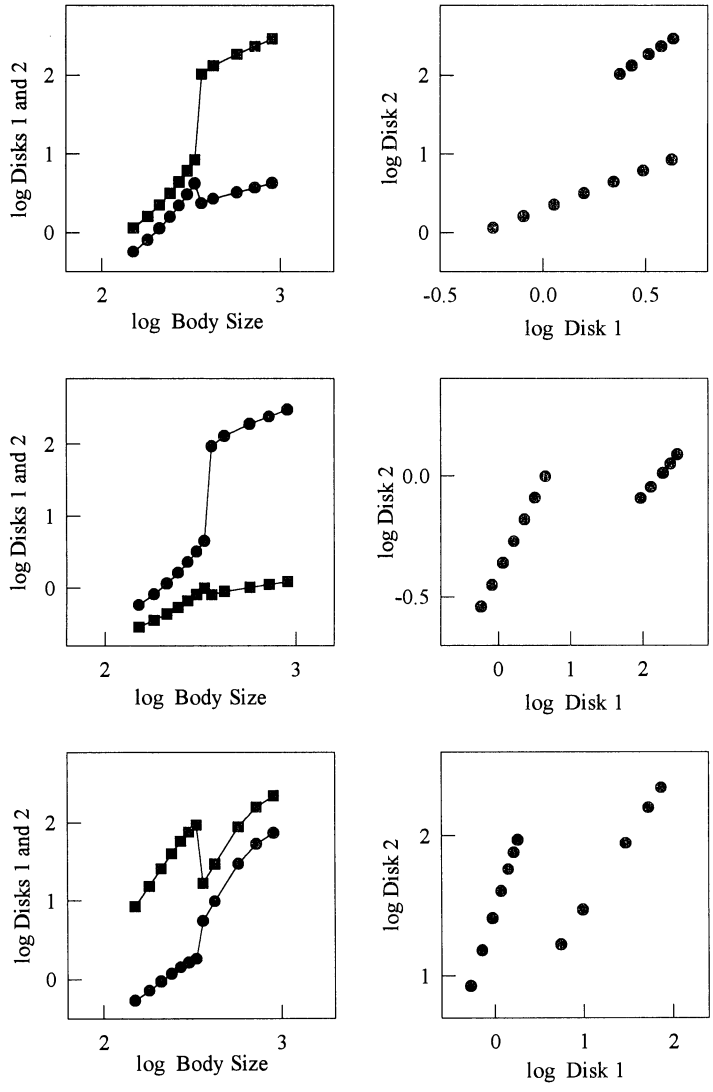

FIG. 6.—Allometries derived from competition model with two disks, illustrating the effect of reprogramming k on disk–body size (*left panels*) and disk-disk (*right panels*) allometry. *Top two panels,* reprogramming growth coefficient of disk 2 upward: $S_1 = 0.1$, $S_2 = 0.3$, $k_1 = 0.005$, and $k_2 = 0.005$ before and 0.01 after reprogramming. *Center two panels,* reprogramming growth coefficient of disk 1 upward: $S_1 = 0.3$, $S_2 = 0.1$, $k_1 = 0.005$ before and 0.01 after reprogramming, $k_2 = 0.004$. *Bottom two panels,* reprogramming growth coefficient of disk 2 downward: $S_1 = 0.1$, $S_2 = 0.3$, $k_2 = 0.01$ before and 0.005 after reprogramming, $k_1 = 0.005$. *Circles,* disk 1; *squares,* disk 2.

lead to particularly complex disk-disk allometries. It is easy to obtain broken allometries with a partial overlap between the allometric curves of reprogrammed and nonreprogrammed individuals, as well as with wide separations between the allometric curves of reprogrammed and nonreprogrammed individuals (fig. 6). If, in addition to reprogramming a growth parameter, the critical size is reprogrammed upward, then the reprogrammed portion of the allometry is shifted to the right, and the gap between soldier and worker allometries becomes larger.

DISCUSSION

The relationship between growth equations, such as the Gompertz model, and allometry has been explored previously by Laird (1965) and Jolicoeur (1989), though these authors restricted their studies to systems in which all parts grow simultaneously with the body. In holometabolous insects, by contrast, the imaginal structures begin to grow after all somatic growth has stopped and the total mass of the system no longer changes (it declines somewhat, in fact, because of metabolic losses; this decline was not modeled in the present study). This characteristic makes the allometric relationships among body parts of adult holometabolous insects fundamentally different from classical growth allometries. Allometric relations between body parts and the whole body are complicated by the fact that the parts grow at the expense of the body, not in parallel with it.

Throughout the preceding account, we have used the term *imaginal disk* to refer to structures that compete for nutrients during development. In reality, of course, all adult structures that grow during prepupal and pupal development use the same resources and should thus be in competition with one another. Accordingly, other imaginal structures that are not derived from imaginal disks or that represent portions of a disk-derived structure (such as head width, scape length, or femur length in ants or horn length in scarabeid beetles) should be expected to participate in allometric relationships of the type described by our competition model.

The existence of nonlinear allometries, sudden changes in slope, and gaps in the allometric curve, has long been recognized (Cock 1966; Reeve and Huxley 1972; Forbes and Lopez 1989; Jolicoeur 1989). Previous attempts to analyze nonlinear allometries have relied largely on curve-fitting methods such as polynomial regression and moving regression analysis (Baroni Urbani 1976; Feener et al. 1988; Forbes and Lopez 1989). While curvilinear regression methods can accurately describe the shapes of complex allometric curves, the parameters of the resulting model (in the case of polynomial regression, the terms of the polynomial) seldom correspond to meaningful biological variables (Sokal and Rohlf 1981). Curve-fitting methods and multivariate statistical analyses such as those of Diniz-Filho et al. (1994) are useful if we wish to describe and categorize the shapes of curves. Ultimately, however, we would like to understand the underlying causes of nonlinear allometries. We would also like to understand the biological basis of the differences in the allometry curves of different species and different organ systems within a species. To do that, we must have a reasonably accurate model for the processes that actually produce the allometry curves.

We have shown that a great diversity of nonlinear and discontinuous allometries in the ants are the simple result of normal developmental processes in holometabolous insects. The key to understanding the causes of complex allometries lies in the observation that the growth of imaginal structures largely occurs after the larval insect has grown to its maximal size and has stopped feeding. Imaginal structures thus grow in a closed system using nutrients accumulated during larval life and thus compete with each other when those nutrients are limiting. The allometric relations between adult structures reflect the outcome of this competition.

We examined the characteristics of two growth models of body parts: the Gompertz equation, which models damped growth, and a competition model that treats the growth of imaginal structures explicitly as occurring in a closed system with a limited amount of nutrient. Both growth models yield complex nonlinear allometries that closely resemble those of polymorphic ants. The usefulness of the Gompertz model is limited, however, by the facts that the damping coefficient is an artificial parameter and that body size cannot be modeled independently of development time. Thus, the Gompertz equation cannot be used to model all three of the aspects of development (growth parameters, critical size for metamorphosis, and reprogramming) whose variation is the root cause of morphological variation in caste determination in ants (Wheeler 1991). The competition model, by contrast, describes duration of growth, body size, initial size of disks, and growth parameters as independent variables. Damped growth in this model is not an artificial variable but arises as an emergent property of nutrient depletion in a closed system.

The competition model can be used to deduce the specific aspects of growth and development responsible for producing allometries of particular shapes (figs. 4–6). If disk-disk allometries are not linear, then the exponent P in equations (2) and (3) is greater or less than one. The shape of disk–body size allometries is determined by the relative dimensions of the nutrient pool, the initial disk sizes, and their intrinsic growth rates. It is worth noting at this point that to interpret the shape of an insect allometry curve correctly, it is essential to know exactly what is being plotted. For instance, it is commonplace in studies of insect allometry to use a linear measure of a body part such a femur length or width of thorax (rather than total weight) as a proxy for body size. If the body part in question is derived from an imaginal disk (a femur for instance), then the plot is essentially a disk-disk allometry. If a structure such as the thorax is used, then it is necessary to consider that its size is also affected by the growth of imaginal disks because the pupa is a closed system, and excessive growth of disk-derived structures must necessarily go at the expense of the remainder of the body. The dimension of a nondisk structure may not be a simple function of body mass (if a linear measure is taken, it will scale as the cube root of body mass minus disk mass) and may therefore yield allometric curves different from the ones we have modeled.

Reprogramming of the critical size for metamorphosis or reprogramming of the growth constants in individuals larger than a critical body size causes a discontinuity in the allometry. If only critical size is reprogrammed, the allometries of soldier and worker ants lie on different regions of a smoothly continuous curve,

as in *Oecophylla smaragdina* (Wilson 1953). When soldier and worker allometries do not fuse smoothly (i.e., when they intersect at an angle or lie parallel to one another, as in *Pheidole bicarinata* and *Camponotus festinatus*; Wheeler and Nijhout 1983; Wheeler 1991), the growth constant of one or both must have been reprogrammed.

When reprogramming of a growth constant takes place, the competition model predicts that disks that are *not* reprogrammed should have a compensatory response to the increased (or decreased) growth rate of the reprogrammed disk. The Gompertz model makes no such prediction. Because its parameters correspond to real developmental and physiological variables, the disk competition model has the virtue of being testable by experiment and observation. Compensatory growth, for instance, could be demonstrated experimentally by showing that surgical removal of one disk at the beginning of the prepupal period caused the remaining ones to grow larger.

Compensatory growth can also be inferred from the shapes of allometry curves. The data reported by Feener at al. (1988) on curvilinear allometries in *Atta colombica* and *Eciton hamatum* suggest that some structures indeed compensate for excessive growth of others. In both species, the allometric relationship between head width and body size has an increasing slope with body size (i.e., is concave), and this increase in slope is more severe in *Eciton* than in *Atta*. In contrast, the allometry of leg length with body size has a decreasing slope in both species, with a more severe decrease in *Eciton* than in *Atta*. Allometry of thorax length with body size has a decreasing slope in *Eciton,* whereas it is linear in *Atta*. Thus, in both species, some parts of the adult body are proportionally smaller than one would expect and are inversely correlated with the degree of hypertrophy of the head.

In at least two species of dung beetles (Scarabeidae), there is a negative correlation between horn length and relative head width (Rensch 1960; D. Emlen, personal communication), which suggests that large horns develop at the expense of other structures in the head. Recent studies of four species of tropical rhinoceros beetles (Scarabeidae) have demonstrated that in horned males, a positive allometry in horn length is associated with a negative allometry in wing length. Large males have disproportionately large horns and small wings, and small males have comparatively small horns and large wings (Kawano 1995).

If size compensation of imaginal structures produces maladapted phenotypes, then compensatory responses constitute a form of developmental constraint on the evolution of castes in ants and of body proportions in other holometabolous insects. Presumably the degree of correlation among different imaginal structures can be modified through selection so that some structures come to show a greater (or lesser) compensatory response than others. Of course, the compensatory response could, under certain circumstances, actually constitute a preadaptation for the evolution of other functional specializations. In addition to the allometric relationship noted above, Feener et al. (1988) show that in *Atta,* but not in *Eciton,* the relative leg length decreases with increasing body size. Feener et al. (1988) have interpreted these differences in relative leg length in large-bodied individuals as ecological adaptations to the specialized foraging behaviors of each species.

If the size of the leg is determined at least in part by its compensatory response to increased head size, then the model we have presented opens the way for an integrated view of the development and evolution of head size, leg length, and foraging strategies in ants. In rhinoceros beetles, small hornless males are known to disperse farther than large horned males (Eberhard 1980, 1982), which suggests the possibility that the differences in the relative size of the wings of horned and hornless males, which arose as an accidental consequence of horn development, may have provided a preadaptation for the evolution of differences in the dispersal behavior of the two morphs.

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