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ONTOGENETIC SCALING AND SIZE CORRECTION IN THE COMPARATIVE STUDY OF PRIMATE ADAPTATIONS

ABSTRACT: The identification and removal of allometric effects is generally deemed desirable in the comparative analysis of form and adaptation. Debates continue regarding the most appropriate and effective allometric "criteria of subtraction" in such analyses. Here I argue that utilization of ontogenetic scaling (Gould, 1975; Shea, 1981) within an explicitly phylogenetic context provides a powerful and biologically-justifiable criterion for identifying both (1) the shared, correlated effects of size change on morphological features and proportions; and (2) the derived dissociations of ancestral allometries which indicate novel shape transformation requiring additional explanation. These novel shape divergences may result from biomechanical scaling, or they may be associated with non-allometric, extrinsic factors such as ecological shifts, etc. Thus, a hierarchical procedure beginning with analysis of ontogenetic allometries in groups of related species can be very useful in comparative studies of adaptation. I review examples of both intersexual and interspecific comparisons in primate evolution where ontogenetic scaling has been used effectively as a criterion of subtraction to identify derived proportions resulting from dissociations of shared patterns of allometric growth covariance. This approach emphasizes the necessity of integrating studies of ontogeny with traditional interspecific adult analyses in the investigation of adaptation, phylogeny reconstruction and the role of historical factors or constraints in evolutionary transformations.

KEY WORDS: Allometry - Ontogenetic scaling - Dissociation - Adaptation - Comparative studies

INTRODUCTION

Morphological or shape differences among groups provide a vital focus for investigations of adaptation, phylogenetic relationships, and paleobiological reconstruction in the fields of biological anthropology and evolutionary biology. A key element in the effective execution of these various investigations involves recognition and analysis of the influence of allometry, which can be described as the study of how variation in overall or local size causally influences differences in shape or morphology among organisms (Thompson, 1917; Huxley, 1932; Gould, 1966; McMahon and Bonner 1983; Schmidt-Nielsen, 1984). Due to both the frequency of size change during evolution and the pervasive effects of these shifts on the form, physiology and ecology of organisms, it has literally become a truism in biology that one should attempt to distinguish allometric shape differences from those unrelated to size differences when undertaking com-

parisons among groups (Gould, 1966, 1975; Harvey and Pagel, 1991). This perspective is no less prevalent in the realm of biological anthropology. Pilbeam and Gould (1974, p. 400) pointed this out in their classic Science paper, which did much to introduce the fields of paleoanthropology and biological anthropology to issues of allometry and relative growth, when they stressed that because "...many lineages display phyletic size increase ...[and] allometric changes almost always accompany increase in body size ... we cannot judge adaptation until we separate such changes into those required by increasing size and those serving as special adaptations to changing environments". More recently, Martin (1989, p. 100) reiterated this perspective when he noted that "Given a comparison between any two species of different body sizes, it is necessary to ask the question: 'To what extent do these two species differ merely because they differ in body size and to what extent do they differ because of some fundamental difference in biological organisation'."

In this paper, I wish to re-evaluate our current understanding of this use of allometry as a "criterion of subtraction" (Gould, 1966, 1975) in assessing adaptation in comparative biology. I will consider both theoretical and methodological issues which arise in the application of such allometric correction, and I will discuss past and more recent proposals for the most appropriate approaches to size correction. My primary conclusion is that the comparative study of patterns of growth allometry (relative growth) in an explicitly phylogenetic context does indeed provide us with the best available, most biologically-justifiable, means of controlling for the influence of size variation when assessing shape differences in comparative studies of adaptation and phylogeny reconstruction. I draw examples from both intraspecific (sexual dimorphism) and interspecific morphological comparisons among primates in order to illustrate these points.

SIZE CORRECTION AND CRITERIA OF SUBTRACTION

Once it is agreed that correction for the effects of size differences will yield a clearer understanding of other (e.g., non-size related adaptive or phylogenetic) influences on form, the primary issue becomes one of how to accomplish this goal. It is fair to say that the majority of studies over the past several decades have followed a common approach to this problem. This approach is exemplified in the case of brain/body scaling, one of the first allometric relationships recognized. *Figure 1* illustrates Jerison's (1969, 1973) scatterplot of brain and body weights for selected vertebrates, depicted against a backdrop of the entire sample (dashed polygons), and with empirical linesof-best-fit determined for "higher" and "lower" vertebrates (heavy lines). The empirical regression for brain vs. body weight in the higher vertebrates (mammals plus birds) determined by Jerison (1969) was:

$$E = .07 P^{2/3}$$
 (1)

Here E equals brain weight, P represents body weight, .07 is the y-intercept for the regression line, and the value of 2/3 is the allometry or scaling coefficient.

This example is characteristic of the majority of sizecorrection approaches in several key ways. First of all, the baseline against which individual species are compared is determined empirically as the (least-squares regression) line of best-fit, based on the accumulated sample at hand. Jerison's well-known Encephalization Quotient (E.Q.) represents a "size-corrected" comparison of *observed* brain size relative to *expected* brain size, calculated as follows for the extant mammal portion of the entire sample:





(2)

$$EQ_i = E_i$$

0.12 P.^{2/3}

Jerison's residualized E.Q. values (or some minor variation of this) provided the basis for many comparative studies of relative brain size and various ecological or behavioral features (see references in Harvey and Pagel, 1991). Moreover, this general approach to size correction has been very widely used and there are literally hundreds of examples which could be cited in the literature of comparative biology over the past several decades. An excellent example from the realm of biological anthropology is Kay's (1981) analysis of relative enamel thickness in living and fossil primates. He used residuals from a plot of enamel thickness (at the M_2 oblique cristid) against tooth size (M_2 length) to demonstrate an association between relatively thick enamel and a diet of hard seeds, nuts or fruits.

There are at least three potential problems with utilizing this traditional approach to the identification of allometric influences and subsequent size correction via their removal. The first problem involves the statistical fitting of the baseline relationship. It is well known that alternative models to the traditional least-squares fit exist, and in fact are preferable in certain cases. There is a large literature on this important issue in allometric studies (e.g., Rayner, 1985; Riska, 1991), and it primarily relates to the most appropriate estimation of the functional relationship between x and y, usually in relation to the testing of a particular slope value (e.g., metabolic vs. geometric scaling in relative tooth size – see Pilbeam and Gould, 1974). The main significance in the present context, however, is to emphasize that as the slope of the line changes, so will the value and perhaps even the sign of the residuals. Furthermore, no matter which regression model is used, slopes and therefore residualized values will also change as the basic sample changes, as for example when additional species are added, or when one person chooses a catarrhine-wide sample for comparison while another chooses just the hominoids. These implications of line-fit and sampling choice are often depicted as simply statistical issues, but in fact they are fundamentally biological ones as well, since our preference for a particular regression model should ultimately be based on biological factors (see Riska, 1991, for discussion), and the decision to utilize one comparative sample as opposed to another also involves decisions (or assumptions) of biological content.

A second problem with the traditional approach to size correction can be summarized by the well-worn adage that "correlation doesn't necessarily imply causation." Specifically, the fact that proportions change or correlate with size does not necessarily mean that such variance is truly allometric in nature. A number of workers have raised this admonition, but Fleagle's (1985) discussion of limb proportions and body size in catarrhine primates is particularly informative. In regard to Biegert and Maurer's (1972) or Jungers' (1977, 1978, 1979, 1985) claims that increasing intermembral indices in various primate groups were allometric, Fleagle (1985) stresses that we must also carefully consider the alternative explanation of spurious correlation. For example, the apparent allometric trend in catarrhines may simply reflect the fact that hominoids are larger on average than cercopithecoids, combined with the fact that they move differently, emphasizing climbing and arm-swinging (Figure 2). The frequently-noted allometric trend of increased sexual dimorphism at larger size in cross-primate comparisons may be a similar example, since anthropoids are more dimorphic than non-anthropoids, and also on average larger (though Leigh, 1992, demonstrates the validity of the size/dimorphism correlation on the more restricted level of the superfamily Cercopithecoidea). My own allometric approaches (e.g, Shea, 1981, 1983a, 1984, 1985) to African ape morphological variance also provide an instructive example. Literally every difference between the chimpanzee and the gorilla is correlated with their disparity in overall size; the fundamental biological question posed by allometry is which of these correlations are causally linked to their size differences?

The third problem with the traditional approach of interspecific residualization is in a sense a combination of the previous two problems. Stated simply, residuals should optimally be determined relative to a theoretically-derived line, not relative to an empirical best-fit to the sample at hand. This has long been recognized in principle by allometricians (e.g., Gould, 1966; Jerison, 1973), and it has been particularly stressed by Smith (1984) among primatologists. The reason more studies have not followed this procedure is a biological one, i.e., our understanding of the theoretical scaling principles in the system under consideration is usually not developed enough to permit deductive predictions about specific slope values and criteria of functional equivalence. This type of understanding can only be attained after detailed theoretical work, substantial empirical comparisons, and careful experimental testing of assumptions. And when such work is carried out, the biological situation is often complex in surprising ways, as for example the finding that similarity in peak strain levels across a wide range of mammalian body sizes is maintained not by regular changes in bony morphology, but rather by postural adjustments (Biewener, 1990). In the absence of such a well-developed matrix of theory, empirical comparison and experimental testing, the procedure of choice in comparative biology has been to go with the empirical line of best-fit for the determination of residuals. While risks can be ameliorated somewhat by broad sampling, strong correlations and careful consideration of adaptive diversity, this approach is still in principle flawed and reduces to a "hope" that the true allometric signal is strong enough in the sample at hand to be picked up via the empirical fit. The reason for this inherent flaw is simple - if we do not understand a priori the effect of size change on a particular variable, how can we possibly control for, or extract, this effect?

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FIGURE 2 (from Fleagle, 1985). A schematic allometric plot of any scaling variable against body weight in primates. For this discussion, assume the y variable represents a limb bone length or proportion index. Changing proportions with increasing body size are clearly seen, but the locomotor (and other) specializations of the various species bring into question whether such shifts are truly allometric or merely correlated with size (and other changes).

ONTOGENETIC AND BIOMECHANICAL SCALING

The preceding emphasis on biologically-justifiable criteria of subtraction leads to a multi-level approach to the recognition and control of causal allometric influences. The scheme I propose here is essentially similar to that which I have previously discussed (e.g., Shea, 1981, 1983a, 1984), and it builds directly on Gould's (1966, p. 588) discussion of "size-related" and "size-required" allometry. I distinguish two types of allometric influences on morphological (shape) differences among groups - biomechanical scaling and ontogenetic scaling. In the case of biomechanical scaling, interspecific shape differences are produced in order to maintain the functional equivalence of a particular physiological parameter or ability. Whether such scaling parameters are initially arrived at inductively or deductively, they provide the appropriate interspecific criterion of subtraction. A theoretical example would be McMahon's (1975) model of "elastic similarity", which predicted specific allometric coefficients of limb width (.375) and length (.25) scaling relative to body mass across species in order to maintain comparable resistance to buckling of support structures under their own weight.

The second type of allometric influence on intergroup shape differences is referred to as ontogenetic scaling (*sensu* Gould, 1975, p. 278). Here intergroup differences may be allometric due to the extrapolation or truncation of inherited patterns of ontogenetic allometry (or relative growth – Huxley, 1932) in descendants of larger and

smaller terminal sizes. The scaling exponents in this case are not theoretically derived a priori (although this is conceivable for well-understood functional shifts during ontogeny), but rather the appropriate criteria of subtraction are determined by the ancestral patterns of allometric covariance during growth. Huxley (1932) provides many examples, and a schematic representation of the predicted pathway in a comparison of chimpanzees and gorillas is noted in Figure 3 from my own work. A particularly informative example from outside the primates is provided by the work of Lauder, Reilly and Ashley, who used ontogenetic scaling as a criterion of subtraction to look at the musculoskeletal proportion changes accompanying the marked functional and habitat shifts during metamorphosis from aquatic larvae to terrestrial adults in tiger salamanders (Ambystoma tigrinum). They found that the locomotor hindlimb muscles followed allometric expectations (i.e., were ontogenetically scaled) across metamorphosis, while the cranium and masticatory musculature exhibited marked dissociations related to the transformation to tongue-based terrestrial feeding (Ashley et al., 1991; Lauder and Reilly, 1990; Reilly and Lauder, 1990). This use of ontogenetic scaling as a criterion of subtraction in analyzing morphological and functional/ecological transformations across different stages of ontogeny within a single species can be productively analogized to the examination of different species in the realm of comparative biology.

Perhaps the major problems which emerge in utilizing ontogenetic scaling as an interspecific criterion of subOntogenetic Scaling and Size Correction in the Comparative Study of Primate Adaptations



FIGURE 3. A schematic representation of the hypothesis of ontogenetic scaling. The axes could represent single dimensions, or some multivariate description of local or global size and feature shape. Illustrated here are (dental) age group means for ontogenetic sequences of the African apes. Ontogenetic scaling predicts that the species will follow a common trajectory of ontogenetic allometry, terminating at varying body sizes.

traction are the identification of the relevant baseline or primitive ontogenetic allometry, and the assumption that must be made regarding the comparability of phenotypic and underlying genetic patterns of covariance and correlation. This latter issue refers to the fact that it is the genetic correlation and not the phenotypic one which will determine the correlated change in the y variable when selection acts on the x variable or overall size (Lande, 1979). In fact, Cheverud (1988) has shown that where genetic correlations are adequately determined, there is a high correlation between the patterns of phenotypic and genetic covariance, making extrapolation from phenotypic patterns quite justifiable in practice.

From the perspective of the "biology of size change", then, biomechanical scaling addresses the question of "how would we 'bioengineer' novel organisms of different sizes according to particular stated biomechanical principles and similarity criteria?", while ontogenetic scaling addresses the question of "how would we 'grow' our novel organisms to larger or smaller sizes based on inherited patterns of developmental covariance?" In confronting an observed pattern of morphological variance among groups, I have suggested a sequential approach to identifying and extracting the allometric "signals", so that we might better meet the goals stated at the beginning of this paper. This sequence is summarized in Table 1. First, interspecific shape differences which result from ontogenetic scaling should be identified; these differences are classified as allometric in the sense of relative (differential) growth.

Second, remaining interspecific shape differences which can be accounted for by biomechanical scaling are identified, and these are interpreted as allometric in the sense of bioengineering and functional equivalence. Finally, residual interspecific shape differences which cannot be accounted for by ontogenetic and/or biomechanical scaling are identified as "non-allometric", regardless of whether or not they are correlated with size. If we are unable to execute either component of the allometric analysis, as for example when we do not have ontogenetic data or do not know the appropriate criteria of similarity and functional equivalence, we must acknowledge that our interspecific morphological differences have not been completely size-corrected and may still contain hidden allometric influences. This hierarchical approach emphasizes that proper recognition of allometric and nonallometric transformations is essentially a biological rather than merely a statistical undertaking.

ALLOMETRY AND ADAPTATION

The nature of allometric phenomena in relation to the process or state of adaptation is one of the most misunderstood aspects of comparative morphology. This is undoubtedly due in part to the fact that adaptation as a concept continues to be debated and reinterpreted (e.g., Williams, 1966; Gould and Lewontin, 1979; Lewontin, 1978; Bock, 1980; Gould and Vrba, 1982; Arnold, 1983;

Coddington, 1988; Reeve and Sherman, 1993). Here I follow Coddington (1988), Baum and Larson (1991) and others in rejecting broad definitions of adaptation which roughly equate it with function and current utility (e.g., Bock, 1980). Rather, adaptation should encompass a historical component, so that identification of an adaptation requires that it be a novel (apomorphic) feature produced directly by natural selection via improved performance (in specified functions, behaviors, etc.) and increased fitness (see Baum and Larson, 1991; Coddington, 1988; Gould and Vrba, 1982; Arnold, 1983). This definition can be productively incorporated into studies in comparative biology, though it requires a phylogenetic framework in order to identify when features are novel or derived. The definition further stipulates that we should not classify as adaptations those novel morphologies which develop due to genetic correlations with other features that are in fact the object of selection (see Gould and Lewontin, 1979; Price and Langen, 1992; Strauss, 1984; Sinervo, 1993;

Shea and Bailey, 1996).1 This perspective and the definition of ontogenetic and biomechanical scaling allows us to accurately translate allometric differences among groups into a framework of adaptive vs. non-adaptive change (see Table 1). Allometric shape differences between groups which can be accounted for via ontogenetic scaling of the inherited ancestral pattern of covariance with local or global size are classified as non-adaptive, sensu Huxley (1932) and Gould and Lewontin (1979). Allometric shape differences between groups which reflect fundamental dissociations in the ancestral pattern of covariance, but which have been selected to maintain functional equivalence at different body size (i.e., are biomechanically scaled), are clearly most appropriately viewed as adaptations. Non-allometric shape differences which have been selected in response to external

NOTE:

An interesting logical extension of this approach is the conclusion of Price et al. (1984) that no change in a particular feature's morphology should in fact be viewed as an adaptation in cases where the underlying genetic correlations would have predicted a correlated shift accompanying change in the other variable. Because beak length and depth have been shown to be genetically (and phenotypically) corre-lated within species, Price et al. (1984) concluded that there must have been strong selection against beak depth in order to maintain a constant value of that feature in a comparison of shorter-beaked medium ground finches (Geospiza fortis) with longer-beaked cactus finches (G. scandens).

TABLE 1. Hierarchical approach to assessing and controlling allometric influences in the comparative study of morphological variation. The sequence of analysis runs from top to bottom and includes information on level of allometric or non-allometric influence, the type of data and statistical testing required for assessment, additional special assumptions or testing which are relevant, and whether concordance with a particular level provides comparative evidence of primary adaptation or (non-adaptive) correlated change. See text for additional discussion.

| Type of intergroup adu shape transformation | lt Data Required | Statistical testing ¹ | Ontogenetic allometries | Additional Primar requirements independer | y evidence of at adaptation? |
|--|---|--|----------------------------|---|---------------------------------|
| Ontogenetic scaling | Growth data for clade of species | No slope and/or position differences between species | Concordant | Testing or assumptions regarding genetic correlations | No |
| Biomechanical scaling | Adult means for broad size range of diverse species ² | No significant deviation from predicted slope values for adults | Discordant ³ | Specified criteria of functional equivalence (theoretically justified, experimentally tested) ⁴ | Yes ⁵ |
| Non-allometric change | Both growth data and adult means for relevant species ⁶ | Significant deviation from both ontogenetic and biomechanical scaling | Discordant | Demonstrable (or assumed links among variance in morphology, function and fitness ^{7,8} | Yes |

NOTES:

Bivariate analyses are assumed here (particularly for hypotheses of biomechanical scaling, which usually predict a specific slope value for a bivariate relationship), but multivariate procedures could be substituted in certain situations.

Ontogenetic allometries could be incorporated into investigations of biomechanical scaling, but the most significant component on this level is normally a broad size range of adaptively diverse species which provide an adequate sampling and test of purported relationships. Strictly speaking, however, we could effectively test a single species relative to theoretically-derived predictions.

³ Normally inferred because size ranges are too extensive to permit ontogenetic scaling without maladaptive consequences (Gould, 1966; McMahon, 1975) McMahon, 1975).

Criteria of functional equivalence will vary depending on the biomechanical issue involved; since a given variable may be subject to multiple criteria simultaneously, observed scaling patterns could reflect compromises in response to these multiple inputs.

Selection acts to modify ancestral ontogeny and produce novel proportions, but the context is the need to maintain functional equivalence at new sizes, not a response to other extrinsic factors new sizes, not a response to other extrinsic factors.

Comparative ontogenetic allometric data may not be required to establish a plausible adaptive link with extrinsic factors, but they are required to eliminate ontogenetic scaling as a more parsimonious explanation for proportion changes in light of new terminal sizes (e.g., Shea and Bailey, 1996. Bailey, 1996.

⁷ Elimination of ontogenetic and biomechanical scaling as responsible for novel proportions opens the possibility of adaptive links with extrinsic (e.g., environmental) factors in comparative studies, but optimally the proportions opens the possibility of adaptive links with extrinsic (e.g., environmental) factors in comparative studies, but optimally these associations would be further tested through more direct analyses (e.g., Arnold, 1983), since novel proportions may also double analyses (e.g., Arnold, 1983), since novel proportions may also develop as a result of drift or correlated response to selection on some other variable besides size (e.g., Lande, 1979; Price and Langen, 1992).

In comparative studies it is also assumed (rather than demonstrated) that the changes in morphology observed here or via biomechanical scaling result from heritable variation being shifted by selection (i.e., and the changes in morphology observed here or via biomechanical scaling result from heritable variation being shifted by selection (i.e., not a result of environmental variations).

factors of course get classified as adaptations. The gist of this scheme is that one type of allometric change can clearly be non-adaptive, while the other type is unquestionably adaptive according to any reasonable definition. Additionally, the keys to the implementation of this scheme are the construction of a phylogenetic framework of ontogenetic allometries, plus the biological knowledge requisite for the recognition of biomechanical scaling. It is important to note in passing that patterns of biomechanical scaling almost always reflect dissociations of the underlying ontogenetic allometries, probably because the size range observed during ontogeny is not great enough to elicit most of the size-required shifts (McMahon, 1975). and also because marked extensions of inherited patterns of covariance will often lead to maladaptive proportions, and thus selection is required to reconfigure these ancestral patterns to new and suitable morphological ranges (Gould, 1966). I have discussed elsewhere in more detail the relationship between different types of allometry and adaptation in comparative studies (Shea, 1981, 1983a, 1985, 1988; Shea and Bailey, in press).

No comparative study can elucidate adaptation in the way that a direct analysis incorporating lab and field investigation of morphology, performance and fitness can (e.g., Arnold, 1983; Bock, 1980). Comparative analyses can only demonstrate a correlation between novel morphological features and reconstructed selective forces in a well-established phylogenetic framework. What I am advocating here is simply the use of patterns of ontogenetic allometry in a comparative phylogenetic framework as the appropriate criterion of subtraction for identifying truly novel morphological transformations which are not interpretable as correlated allometric changes due to ontogenetic scaling. I now turn to discussion of various examples from primate morphology and biological anthropology to illustrate the usefulness of this approach in comparative studies of sexual dimorphism and interspecific adaptation.

INTERSEXUAL DIFFERENCES

Studies of sexual dimorphism nicely illustrate how an ontogenetic allometric approach can identify intergroup morphological differences which are allometrically related to overall size differences, and further distinguish these from group shape differences which are independently associated with sex. In this case, the distinction is fundamental to an understanding of the actions and results of sexual selection on both overall body size and specific individual morphological features.

A considerable amount of ontogenetic allometric work has now accumulated on sexual dimorphism in various macaque species. In the first such application of this approach to cranial dimorphism in *Macaca mulatta*, Cochard (1985) demonstrated that the majority of intersexual shape differences (such as degree of prognathism, relative facial and mandibular lengths, relative facial height, facial angles, and cranial base proportions) resulted from ontogenetic scaling, and thus could be viewed as correlated by-products of the overall body size differences between the sexes (*Figure 4*). This approach also clearly revealed several key differences in male and female shape which resulted from allometric dissociations, notably bizygomatic breadth (*Figure 4*, upper right panel) and relative canine size, which Cochard (1985) interpreted as reflecting hypertrophy of the muscles (anterior temporalis) and teeth associated with male intraspecific competition (and interspecific agonistic interactions).

A subsequent study (Cheverud and Richtsmeier, 1986) using finite element scaling analysis (FESA) of three-dimensional coordinate landmark transformations during growth corroborated Cochard's (1985) findings for those areas of the skull measured in common in rhesus macaques. Richtsmeier and Cheverud (1989) undertook a comparable study of sexual dimorphism using FESA on 150 skulls of crab-eating (Macaca fascicularis) macaques. They concluded that "the male face is an allometrically scaled up version of the adult female face" (p. 439); they did not specify morphological features in which the two sexes did not share similar patterns of ontogenetic allometry. Ravosa (1991) undertook a bivariate allometric investigation of sexual dimorphism in skull morphology in both crab-eating macaques (Macaca fascicularis) and proboscis monkeys (Nasalis larvatus). In both species, bicanine breadth clearly emerged as the only variable among 30 linear dimensions which differed between the sexes in the pattern of growth allometry. This intersexual difference stands out in exception to the pervasive pattern of shape differences associated with ontogenetic scaling, and Ravosa (1991) suggests that this bicanine divergence reflects the disproportionately enlarged canines of the male. A more recent study by Richtsmeier et al. (1993) of sexual dimorphism and craniofacial growth in Macaca fascicularis using euclidean distance matrix analysis (EDMA) appears to yield results somewhat contrary to those offered in earlier analyses by Richtsmeier and Cheverud (1989) and Ravosa (1991), but differences in the way that "relative" growth is assessed and comparisons against age rather than regional or overall size make direct comparisons of these various studies problematic.

An investigation of intersexual morphological differences in one of the most sexually dimorphic of the primates, *Papio cynocephalus* baboons, was completed by Leigh and Cheverud (1991). This study provides the most explicit link between the FESA methodology and traditional perspectives of ontogenetic allometry and scaling, utilizing plots of landmark-local size (or shape) changes relative to global (average) size change as the appropriate criteria of subtraction. Only one slope or intercept value differed significantly in the ontogenetic allometric comparisons; this landmark was nasal (inferior internasal junction), which differed in the y-intercept value. The authors suggest that the intersexual difference could very likely have arisen from mixed-sex sampling, measurement error, or even pre- or post-mortem damage. Whether arising from any these factors or a true growth difference, the point for our purposes is to stress that Leigh and Cheverud (1991) were able to isolate, from the myriad and extensive shape differences found between adult male and female baboons, the one landmark or region where the local size differences could not be explained as simply an allometric correlate.

Studies of sexual dimorphism in the skulls of New World monkeys have also successfully utilized the ontogenetic allometric criterion of subtraction. Ravosa and Ross (1994) undertook such a study in red (*Alouatta seniculus*) and mantled (*Alouatta palliata*) howler monkeys. They were able to identify outer orbital breadth as a dimension which differed significantly in non-allometric fashion between the sexes of *A. seniculus*, and interorbital breadth, orbital height, symphyseal width, and lever arm length for the medial pterygoid muscle as dimensions which differed in *A. palliata*. The authors did not offer any specific scenarios as to why the sexes differed fundamentally, as opposed to merely allometrically, in these particular dimensions.

Masterson (1995) has completed studies of ontogenetic allometry and sexual dimorphism in the skulls of Cebus apella, C. albifrons, C. capucinus and C. nigrivittatus. His results published to this point (Masterson, 1994) indicate that bizygomatic breadth in C. albifrons exhibits an allometric dissociation in males vs. females, as was the case in several of the cercopithecoid studies reviewed above. In C. apella, there are several non-allometric differences, including palatal width at the canine, and others that may be suggestive of intersexual dietary differences (Masterson, 1994). Cole's (1992) study of relative growth in the masticatory apparatus of males and females in both C. albifrons and C. apella revealed a number of dimensions for which these cebids demonstrated sexual differentiation of allometric growth trajectories. For example, dimensions of the mandibular symphysis indicated that the "initial shape" or position of the growth trajectories differed significantly between the sexes. Cole (1992) did not offer specific functional explanations for these morphometric differences between the sexes, but rather concentrated on interspecific contrasts (see below).

Leutenegger and Masterson (1989) examined cranial sexual dimorphism in the orangutan from the perspective of ontogenetic allometry and scaling. They were able to identify a set of 10 dimensions (of 20 total) where the growth allometries were dissociated; these dimensions included palate width at the canine, bizygomatic breadth, several skull widths, and basion-to-prosthion length. In all cases, males exhibited higher slope values than females, but it must also be stressed that the females generally had lower correlation coefficients, which means that the slopes would have converged considerably if reduced major axis or major axis slopes were compared. Nevertheless, here again we see the pattern where dimensions reflecting canine size and jaw adductors differentiate the males from females in more than just an allometric fashion.

Many other examples of growth allometry and sexual

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dimorphism could also be cited. I have concentrated on how ontogenetic scaling can be effectively used as a criterion of subtraction to control for the ontogenetic "allometric signal" resulting from shared patterns of differential growth, and thereby clearly discern the "nonallometric signal". In the preceding examples, this latter signal relates to non-allometric differences between the sexes which may then specifically inform us about function in the presumed context of sexual selection. I now turn to some representative examples of interspecific morphological differences whose adaptive basis has been elucidated through the use of ontogenetic scaling as a criterion of subtraction.

INTERSPECIFIC DIFFERENCES

A number of the very earliest investigations of allometry in primates focused on comparing patterns of relative growth among closely-related species (e.g., Lumer, 1939-Lumer and Schultz, 1941, 1947; Giles, 1956). While these studies were very successful at dissecting interspecific adult shape differences into components related to ontogenetic scaling and allometric dissociation, respectively, they almost studiously avoided relating the latter divergences to possible functional factors that might reflect adaptive differences between the species. In contrast, the excellent study by Jungers and Fleagle (1980) reveals how ontogenetic allometric data can be productively used in comparative studies of adaptation. They linked dissociations of the postcranial allometric trajectories to key differences in body mass distribution, locomotor behavior and foraging strategies distinguishing Cebus apella from C. albifrons. I related allometric dissociations in postcranial skeletal anatomy among the three species of African apes to adaptations for the maintenance of functional equivalence (biomechanical scaling) or, alternatively, divergent locomotor behaviors (Shea, 1981). This paper and several others (e.g., Buschang, 1982; Shea, 1984; Jungers and Susman, 1984; Jungers and Hartmann, 1986; Jungers and Cole, 1992) have expanded on Lumer's (1939) early work to more explicitly discuss differences in allometric growth patterns in relation to specific locomotor functions and adaptations in the hominoid radiation.

A postcranial study nicely identifying both adaptation and phylogenetic proximity is Gomez's (1992) investigation of limb growth allometries in five lorisid species (Nycticebus coucang, the slow loris, Nycticebus pygmaeus, the pygmy slow loris, Loris tardigradus, the slender lotis, Perodicticus potto, the potto, and Arctocebus calabarensis the golden potto). Gomez found that L. tardigradus was clearly differentiated from the other taxa in bivariate and multivariate analyses of limb allometry (see Figure 5); she attributed the relatively longer limbs of the slender loris to greater walking speeds and the increased propensity for bridging behaviors during locomotion. Gomez (1992) also argued that these changes were likely derived in L. tardigradus, since the other three taxa share many of FIGURE 4 (from Cochard, 1985). Ontogenetic allometries for facial area, facial prognathism, bizygomatic breadth and mandibular length in male (solid line) and female (dashed line) rhesus macaques. The intersexual scaling difference for bizygomatic breadth is clearly revealed against a general pattern of ontogenetic scaling in the other cases. Adult shape differences resulting from such allometric dissociations are different in nature than those simply linked to terminal size differences.



the growth allometries examined. The likely adaptive and phylogenetic significance of limb proportions in these lorisids could not have been similarly elucidated through traditional analyses focusing on adult shape differences or interspecific allometric patterns, since the ontogenetic analyses revealed that many adult shape differences also characterized a comparison of the pygmy slow loris and slow loris, and the potto relative to both of these slow lorises. These latter allometric correlates of ontogenetic scaling are not as clear indicators of either adaptive specialization or phylogenetic relationships as are the novel divergences.

Inouye (1992) has used ontogenetic allometry to demonstrate that the metacarpals and phalanges of gorillas differ from those of chimpanzees in relative length, but not relative breadth, thus focusing attention on novel transformations in contrast to those which follow common allometric patterns. She presented several functional scenarios to account for the adaptive dissociations in the allometric patterns between the genera (Inouye, 1992, 1994). Similarly, Falsetti and Cole (1992) demonstrated that adult differences in intermembral and brachial indices distinguishing the saddle-back tamarin (Saguinus fuscicollis) from the cotton-top tamarin (Saguinus oedipus) and the common marmoset (Callithrix jacchus) were produced by allometric dissociations (see Figure 6). They linked the derived proportions of S. fuscicollis to its propensity for increased leaping and vertical climbing as compared to related species. In another study, Ravosa et al.

(1993) compared ontogenetic allometric sequences of postcranial dimensions of Milne-Edwards's diademed sifaka (*Propithecus diadema edwarsi*) and the goldencrowned sifaka (*Propithecus tattersalli*) to predominantly adult data for two subspecies of the western sifaka (Coquerel's sifaka: *P. verreauxi coquereli*; and Verreaux's sifaka: *P. verreauxi verreauxi*). Differences among the adults in postcranial proportions were almost all a result of ontogenetic scaling, but shortened relative foot length in the western sifaka (*P. verreauxi*) clearly emerged as a non-allometric differentiating feature, which Ravosa et al. (1993) suggest may be functionally linked to variation in the diameter of vertical supports preferentially utilized by the various species.

Two of the studies discussed previously in terms of sexual dimorphism also provide an important perspective on interspecific differentiation. Ravosa and Ross (1994) found that one-fourth of their bivariate comparisons departed from the pattern of ontogenetic scaling found for the majority of their cranial dimensions. Those allometric dissociations distinguishing *Aloutatta palliata* from *A. seniculus* included symphysis width (*Figure 7*), bizygomatic breadth, mandibular corpus width, and several dimensions of the zygoma and circumorbital regions. *A. palliata* exhibited upward transpositions relative to *A. seniculus* for these dimensions, and Ravosa and Ross (1994, p. 293) linked these divergences to the the fact that the mantled howler has a diet characterized by a higher percentage of tough, mature leaves, presumably selecting



Log trunk height (mm)

for "structures which resist masticatory stresses and ...[the] ...forces produced by relatively larger jaw muscles and a tougher diet".

Cole's (1992) comparative analysis of growth allometry in Cebus apella vs. C. albifrons has expanded upon the observations of Kinzey (1974) and others (e.g., Bouvier, 1986; Daegling, 1992) which suggested that the tufted capuchin (C. apella) exhibits a more robust masticatory apparatus as an adaptation to a diet specialized toward hard-object feeding. Cole (1992) demonstrated that C. apella deviates from the ontogenetic trajectories of C. albifrons for numerous dimensions, particularly those associated with mandibular robusticity and symphyseal area. Cole (1992, p. 253) concluded that his use of ontogenetic scaling as a criterion of subtraction had effectively identified a "pattern ...consistent with the expectation of a need for increased resistance to parasagittal bending and twisting stresses in the corpus, increased resistance to wishboning stresses in the symphysis and greater resistance to shear stresses in both the corpus and symphysis" in the hard-chewing C. apella.

A contrast of ontogenetic allometric patterns between representative members of the colobine (*Nasalis larvatus*) and cercopithecine (*Macaca fascicularis*) radiations was reported by Ravosa (1991). This study demonstrated pervasive departures from ontogenetic scaling, reflecting a fundamental reorganization of the masticatory apparatus and other aspects of skull form. Ravosa linked these differences to the functional requirements of increased gape in cercopithecine species and increased masticatory efficiency for repetitive and powerful loading in the colobine species. The allometric dissociations are clearly highlighted against the backdrop of some degree of ontogenetic scaling (Ravosa, 1991) and other shared structural relations (Ravosa and Shea, 1994; Ross and Ravosa, 1993).

APPLICATIONS TO FOSSIL TAXA

We are frequently confronted in comparative morphology with the claim that a particular shape difference distinguishing a fossil morph from its extant relatives is of some functional and adaptive significance. Analyzing such a claim using the perspective advocated here is somewhat problematic, since we normally have but a single or a few fragmentary fossils, certainly not an adequate sample to reliably reconstruct patterns of growth allometry. This concern is ameliorated somewhat if we have adequate samples of the extant relatives. The following are selected examples where the ontogenetic criterion of subtraction has been productively used to assess the morphological distinctiveness of a particular fossil form.

In a study of craniodental scaling in Malagasy lemurs. Ravosa (1992) showed that for several dimensions the large-bodied subfossil lemur species *Pachylemur insignis* fell above the value predicted by the ontogenetic allometries observed within its extant sister taxon, *Varecia*. These variables relate to facial shortening combined with relative enlargement of the mandibular corpus and symphysis (see *Figure 8*), and the divergences contrast with a general finding of ontogenetic scaling. Ravosa (1992) suggested that these allometric dissociations sup ported both the generic separation of the two taxa and a dietary reconstruction of obdurate or fibrous food items for the fossil *Pachylemur insignis*.

An example where the ontogenetic criterion of sub-

-og leg length (mm)

FIGURE 6 (from Falsetti and Cole, 1992). A comparative ontogenetic plot of radius length against geometric mean size in saddle-back tamarins, (*Saguinus fuscicollis* – open squares), cotton-top tamarins (*Saguinus oedipus* – closed circles), and common marmosets (*Callithrix jacchus* – open circles). The specialized, nonallometric elongation of forelimb length in the saddle-back tamarin is demonstrated in this analysis.



traction provides a different perspective than the traditional reconstruction of function or behavior in a fossil form is provided by debates over whether early hominids exhibit morphological evidence of knuckle-walking behavior or a knuckle-walking ancestry (e.g., Tuttle, 1967; Susman, 1979). Susman and Stern (1991, p. 123) summarize a widely-held position when they state that "the lack of evidence of knuckle-walking in both early hominids and modern humans suggests humans did not have a knuckle-walking ancestor." The bony evidence referred to here would be the "classic" morphological indicators of knuckle-walking behavior, notably the prominent dorsal metacarpal ridges (e.g., Tuttle, 1967; Susman, 1979). In a morphometric and allometric sense, this is equivalent to predicting that early hominids would significantly diverge from any pattern of variation or covariation exhibited by knuckle-walking great apes of various ages and sizes. However, recent work by Inouye (1994) on ontogenetic and interspecific allometric patterning in the morphological features linked to knuckle-walking has revealed that both the presence and degree of development of the dorsal metacarpal ridges is significantly influenced by overall size. Therefore, the allometric perspective indicates that we cannot rule out a knuckle-walking habitus when such ridges are miniscule or absent in fossil species, as long as these extinct hominoids also happen to be of small body size (see Shea and Inouye, 1993). The absence of dorsal metacarpal ridges in extinct and/or modern humans provides no clear "litmus test" for whether the common ancestor of African apes and humans was a knuckle-walker or had such bony features.

A similar situation is presented by the claim that the orientation of the glenoid fossa in "Lucy" (AL 288-1) is divergent from the allometric predictions for a human of her body size, thus clearly indicating significant degrees of arboreal climbing in the reconstructed locomotor repertoire of Australopithecus afarensis (Susman et al., 1984). This position was championed by Susman et al. (1984), based on their analysis and predictions from a sample of adult intraspecific static allometry. In fact, Inouye and Shea (1993; in press) have recently shown that Lucy's glenoid orientation falls comfortably within the confidence intervals on the predicted value when an ontogenetic allometric criterion of subtraction is generated from a large sample of modern humans (see Figure 9). This brings into question the reconstructed locomotor behavior, at least within the constraints of our current understanding of the degree and bases of variation in the bar-glenoid angle and its allometric covariation with size.

The preceding examples are not intended as the "last word" in these ongoing debates and fossil reconstructions. They are, rather, illustrative of the ways in which an ontogenetic criterion of subtraction can be used alongside more traditional analyses in order to recognize novel morphologies and reconstruct adaptations in extinct forms.

GENETIC AND DEVELOPMENTAL BASES OF ONTOGENETIC SCALING

Space is too limited to permit a full consideration or review of this important topic, but a few quick points should be made regarding the genetic and developmental control of ontogenetic scaling. When we use this as a criterion of subtraction in a controlled phylogenetic context, we inevitably raise issues of what types of changes underlie allometric dissociations (e.g., vertical transpositions, slope divergences) and allometric truncations and extensions. Also, are suites of features which exhibit comparable allometric patterning in fact controlled by common genes

and gene products? We are a long way from definitive answers to these questions, but preliminary data derived from human and non-human models of growth control and disturbances at least suggest that coordinated allometric transformations resulting from ontogenetic scaling are underlain by shifts in systemic hormonal controls such as growth hormone (GH), insulin-like growth factors (IGF's), and growth hormone binding proteins (GH-BP). I have reviewed elsewhere work on transgenic and mutant mice, various other mammalian models, as well as human pygmy populations, which in fact support this view (e.g., Shea et al., 1987, 1990; Shea, 1988, 1992b, 1993; Shea and Bailey, 1996). It seems reasonable that the types of allometric dissociations emphasized in the present paper as indicative of derived adaptations would be underlied by more local, region-specific controls (Katz, 1980; Bryant and Simpson, 1984; Shea, 1992b). Only additional work investigating ontogenetic allometry in organisms where genetic and developmental changes are known will further clarify this issue.

ONTOGENETIC SCALING AND BRAIN: BODY ALLOMETRY

A return to our earlier example of interspecific patterns of brain:body allometry permits a synthesis of the major points of this paper. Although Jerison's (1969, 1973) empirical size-correction and derivation of the residual E.Q. produced results which generally corresponded well with alternative estimates of "behavioral complexity", he also noted a frequent pattern of "artifically" elevated (in "phyletic dwarfs") or depressed (in "phyletic giants") values of the E.Q. in cases of apparent selection for rapid size change within clades (Jerison, 1973, p. 345; see Gould, 1975, and Shea, 1983b, 1992a, for relevant discussion). This pattern in fact makes sense if rapid body size evolution is mediated predominantly by postnatal growth, when brain:body allometry exhibits a markedly lower slope than the typical broad interspecific value of 0.66 to 0.75 or higher. I utilized observed patterns of neonatal/maternal weight scaling to make precisely this argument for primates such as the highly-encephalized talapoin monkey and the under-encephalized gorilla (Shea, 1983b). More recently, evidence from quantitative genetics (e.g., Lande, 1979) and the hormonal control of growth (Riska and Atchley, 1985; Shea et al., 1987; Shea and Gomez, 1988 Shea, 1992b) has strengthened this perspective. Postnatal growth is predominantly controlled by IGF-1, which appears to have less direct effects on overall brain growth in utero and postnatally, so that size change mediated through such systemic hormonal shifts would be expected to yield little correlated change in brain size. Therefore, forms truncated in overall size would end up with high relative brain sizes, and forms enlarged in overall size would end up with low relative brain sizes, when compared to predictions derived from the broad, interspecific scaling patterns. Once we utilize a size-correction procedure approximating ontogenetic scaling (of postnatal brain:body



FIGURE 7 (from Ravosa and Ross, 1994). The dissociation (bottom) of the growth allometry of symphysis width (and several other masticatory features) in mantled howlers (*Alouatta palliata*) may be related to its relatively larger jaw muscles and a diet of tougher food items. Most of the shape differences between adults of this species and red howlers (*A. seniculus*) result from ontogenetic scaling (top) rather than derived dissociations.

allometries) relative to the specified ancestral taxa that gave rise to these phyletic dwarfs and giants, respectively, our descendant taxa are no longer characterized by large residual values which are seemingly aberrant, based on other behavioral criteria. Rather, they approximate the relative brain size values expected in taxa which have undergone rapid size shifts from an ancestral condition (Shea, 1983b; Shea and Gomez, 1988; Shea, 1992b).

CONCLUSIONS

The research reviewed here supports the contention that the criterion of subtraction based on "ontogenetic scaling" provides an effective and powerful approach to controlling for one important type of allometric influence on between-group morphological differences. When comparative studies of growth allometry are carried out in a phylogenetically-controlled context, ontogenetic scaling as a null hypothesis of proportion changes allows us to readily identify those adult shape differences which result from novel (derived) "repatterning" of the inherited traFIGURE 8 (from Ravosa, 1992). Scaling of mandibular corpus height (at M2) against basicranial length in an ontogenetic series of ruffed lemurs (Varecia variegata – closed circles). Specimens of Pachylemur insignis, the extinct sister species of V. variegata, are shown as open squares. The deviation of P. insignis from the ruffed lemur's observed and extrapolated trajectory for this and other variables indicates a reorganization of skull proportions in the extinct form.



jectories of allometric growth covariance. These truly novel features (and their developmental bases) can then be effectively incorporated into comparative studies of adaptation (e.g., Gould and Vrba, 1982; Coddington, 1988; Baum and Larson, 1991), as the work reviewed here indicates. Students and other researchers initiating their research programs in functional and adaptive morphology should seriously consider incorporating these comparative ontogenetic allometric approaches into their research design.

It is also important to stress here that direct examination of the nature and degree of the shape variance resulting from ontogenetic scaling provides key insights into the role of "historical factors" (e.g., Lauder, 1981; Shea, 1985) and "loose constraints" (e.g., Maynard Smith et al., 1985; Levinton, 1986; Gould, 1989) in directing patterns of correlated (allometric) change when selection acts on overall size or other features. Due to the focus of this paper on the identification and interpretation of (derived) allometric dissociations, I have not emphasized here studies targeted at elucidating the (primitive) common vector of ontogenetic scaling. Much of my own previous work in primate evolution has focused differentially on this allometric patterning (e.g., Shea, 1981, 1983a, 1984, 1985, 1992a,b); some recent work has shown how the strength of allometric trajectories in a general context of ontogenetic scaling can determine degrees and ranges of morphological diversity between sexes and among species (Profant and Shea, 1994; in press; Profant, 1995). While many other such examples can be cited, here I want to stress that when we utilize a morphometric model like that advocated in this paper, we have a very powerful way to tease apart and measure the relative strengths of the shape influences associated with both (1) inherited patterns of allometric growth covariance and (2) derived dissociations likely associated with novel adaptive shifts. Most of the papers reviewed here in fact simultaneously focus on both of these

components, rather than exclude one to the benefit of the other. Our total understanding of evolutionary morphology would advance considerably if more comparative investigations were structured so as to utilize this multi-level, allometric and non-allometric, model of shape analysis in the species and clades of interest.

Finally, I must return to a point made at the beginning. While ontogenetic scaling provides a very effective means



Humans + Lucy

FIGURE 9. Least-squares regression line and 95% prediction intervals for a plot of glenoid orientation vs. size in an ontogenetic series of modern humans (squares). The position of Lucy (AL 288-1) is indicated by the cross in the filled circle. See text for discussion.

of controlling for one type of causal allometric influence, we must keep in mind that an entirely different framework is required to effectively control for the influences of biomechanical scaling (Gould, 1966; Shea, 1981, 1984). We have to assume that some (unknown) percentage of the intergroup shape variance remaining subsequent to control via ontogenetic scaling is in fact still causally allometric, since dissociations of growth allometries may occur in order to produce functional equivalence in new size ranges. If our understanding of the biomechanical relationships and relevant principles of similitude is not sufficient to effectively incorporate biomechanical scaling into our program of assessment and control of allometry, then we must acknowledge that our residual intergroup shape variance is likely not fully cleansed of allometric influences. An alternative approach becoming popular is to simply "size-adjust" using isometric criteria of subtraction across interspecific adult series (e.g., Jungers and Cole, 1992; Falsetti et al., 1993; Jungers et al., 1995); this is a sort of "minimalist" approach which avoids the necessity of collecting ontogenetic data, on the one hand, and determining valid biomechanical criteria of functional equivalence, on the other. Another of its advantages is that it does not attribute truly causal allometric status to what may in fact be spurious size/shape correlations (cf. Jungers and Cole, 1992, p. 95); its disadvantage is that it effects no true "size-correction" whatsoever, since allometric phenomena, resulting from ontogenetic and/or biomechanical scaling, are not explicated, and isometric scaling itself is merely a geometric tool that turns out to be of questionable relevance from a biological perspective (see, Shea, in prep. for more detailed discussion of these points). Our ultimate goal should be to advance our understanding of both growth controls and biomechanics sufficiently to where we can reliably dissect intergroup morphological variance into components reflecting (1) non-adaptive correlated by-products of allometric growth covariance (i.e., ontogenetic scaling); (2) adaptive allometric shifts required to maintain functional equivalence (i.e., biomechanical scaling); and (3) adaptive shifts causally unrelated to size differentiation and linked to changes in selective forces, ecological factors and other extrinsic influences.

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