

On the Relationship between Ontogenetic and Static Allometry

Christophe Pélabon,^{1,*} Geir H. Bolstad,¹ Camilla K. Egset,¹ James M. Cheverud,² Mihaela Pavlicev,³ and Gunilla Rosenqvist¹

1. Centre for Conservation Biology, Department of Biology, University of Science and Technology (NTNU), 7491 Trondheim, Norway; 2. Department of Anatomy and Neurobiology, Washington University School of Medicine, St. Louis, Missouri 63110; 3. Konrad Lorenz Institute for Evolution and Cognition Research, Adolf Lorenz Gasse 2 14, A-3422 Alternberg, Austria

Submitted January 2, 2012; Accepted September 21, 2012; Electronically published January 11, 2013

Online enhancement: appendix tables.

ABSTRACT: Ontogenetic and static allometries describe how a character changes in size when the size of the organism changes during ontogeny and among individuals measured at the same developmental stage, respectively. Understanding the relationship between these two types of allometry is crucial to understanding the evolution of allometry and, more generally, the evolution of shape. However, the effects of ontogenetic allometry on static allometry remain largely unexplored. Here, we first show analytically how individual variation in ontogenetic allometry and body size affect static allometry. Using two longitudinal data sets on ontogenetic and static allometry, we then estimate variances and covariances for the different parameters of the ontogenetic allometry defined in our model and assess their relative contribution to the static allometric slope. The mean ontogenetic allometry is the main parameter that determines the static allometric slope, while the covariance between the ontogenetic allometric slope and body size generates most of the discrepancies between ontogenetic and static allometry. These results suggest that the apparent evolutionary stasis of the static allometric slope is not generated by internal (developmental) constraints but more likely results from external constraints imposed by selection.

Keywords: shape, size, growth, constraints, *Poecilia reticulata*, *Mus musculus*, caudal fin, tail size.

Introduction

Whether microevolutionary processes can explain patterns of macroevolution remains a major question in evolutionary biology (Eldredge et al. 2005; Futuyma 2010; Uyeda et al. 2011). In this context, the study of morphological allometry, which can be broadly defined as how specific organs vary in size when body size changes (Mosimann 1970), is particularly relevant. Indeed, patterns of allometry can be observed at different taxonomic levels, offering a unique opportunity to study how processes acting at the individual level affect or constrain patterns of

population and species differentiation. Depending on the level at which they are estimated, three types of allometry can be distinguished (Cock 1966; Gould 1966; Cheverud 1982; Lande 1985). Ontogenetic allometry is estimated at the individual or population level during development, static allometry is estimated on individuals from the same population measured at the same developmental stage, and evolutionary allometry is estimated across populations or species. Although each type of allometry can be studied separately, ontogenetic, static, and evolutionary allometry can and should be considered as different outcomes of a single biological process, namely, growth. It remains uncertain, however, whether ontogenetic allometry constrains patterns of static and evolutionary allometry or whether these allometric relationships at higher taxonomic levels result from adaptive evolution. To answer this question, it is particularly important to understand the relationship between ontogenetic and static allometry.

Huxley (1932 [1993]) showed that when the growth of two traits x and y is regulated by a common growth parameter, the relative change in size of the two traits can be explained by a power relationship, $y = ax^b$ (see also Savageau 1979). On a logarithmic scale, this relationship becomes linear: $\log(y) = \log(a) + b \times \log(x)$, with an intercept $\log(a)$ and a slope b that correspond to the ratios between the specific components of the growth rates of y and x , respectively. Huxley (1932 [1993]) acknowledged that similar power relationships could be observed across individuals of different size measured at the same developmental stage (i.e., static allometry) but recognized that the two patterns were not necessarily generated by similar processes, because static allometry will depend not only on the relative growth of the two traits but also on the total amount of growth achieved (see also Cock 1966; Gould 1966; Cheverud 1982). Several authors further suggested that the amount of individual variation in ontogenetic allometry will affect the relationship between ontogenetic and static allometry. They generally concluded

* Corresponding author; e-mail: christophe.pelabon@ntnu.no.

that no specific relationship should be expected between the two types of allometry (Cock 1966; Cheverud 1982; Lande 1985; Strauss 1993).

To our knowledge, the relationship between ontogenetic and static allometry has never been formalized, despite the fact that changes in static and evolutionary allometry must be generated to a large extent by changes in ontogenetic allometry. Furthermore, among the few studies that empirically tested the relationship between ontogenetic and static allometry, some concluded that the two types of allometry were closely related (Leamy and Bradley 1982; Klingenberg and Zimmermann 1992; Klingenberg 1996), while others concluded the opposite (Cheverud 1982). This contradiction apparently stems from the fact that positive correlation between ontogenetic and static allometry has been considered indicative of their close relationship (e.g., Leamy and Bradley 1982), despite the fact that two entities can be strongly correlated but still different. In addition, for logistic reasons (e.g., measurements requiring the organism to be sacrificed), ontogenetic allometry has often been estimated from transversal data (e.g., Cheverud 1982; Emerson and Voris 1992), therefore preventing the estimation of individual heterogeneity. These considerations underscore the necessity of a better understanding of the relationship between ontogenetic and static allometry, both theoretically and empirically.

Building on Huxley's allometric model, we first show analytically how individual variation and covariation in the different parameters defining ontogenetic allometry affect static allometry. Using two longitudinal data sets, on guppies (*Poecilia reticulata*) and mice (*Mus musculus*), we then test whether ontogenetic and static allometries differ. By estimating variances and covariances in ontogenetic allometric parameters, we further assess the relative contributions of these variance components to the difference between ontogenetic and static allometry.

The Model

Huxley (1932 [1993]) showed that a trait's size (Z) is related to body size (M) by an allometric relation, if both the trait size and the body size depend on some common growth parameter G , such that $dM/dt = \alpha MG$ and $dZ/dt = \beta ZG$, where α and β are specific constants for body size and trait size, respectively, and t is the time during growth. This implies that $dZ/Z = \beta dM/\alpha M$. Integrating on both sides gives $Z/Z_0 = (M/M_0)^{\beta/\alpha}$, where Z_0 and M_0 are the initial values of Z and M , respectively. On a logarithmic scale, this relationship becomes linear: $z = a + bm$, where $z = \log(Z)$, $m = \log(M)$, $a = \log(Z_0/M_0^{\beta/\alpha})$, and $b = \beta/\alpha$. Later, Savageau (1979) generalized the allometric model by showing that whenever two or more variables are connected in a dynamic syn-

ergistic system controlled by one variable, the relation between variables will follow an allometric relationship (see also Lande 1985).

Linear Ontogenetic Allometry

From the same model, the static allometric slope can be estimated by the linear regression of trait size on body size for individuals measured at a developmental stage t . In this case, the slope of the static allometry $b_{\text{static}} = \sigma(m_p, z_t)/\sigma^2(m_t)$, where $\sigma(m_p, z_t)$ and $\sigma^2(m_t)$ are the covariance between m and z and the variance of m at stage t , respectively. Assuming a linear ontogenetic relationship between z and m , we can substitute the value of z_t in the equation of the static allometric slope by the ontogenetic allometric equation $z_t = a + bm_t + e_t$, where e_t is an error term (on a logarithmic scale). The static allometric slope is then given by

$$b_{\text{static}} = \frac{\sigma(m_p, a + bm_t + e_t)}{\sigma^2(m_t)}. \quad (1)$$

Following Bohrstedt and Goldberger (1969), we can express the different covariance terms to obtain

$$b_{\text{static}} = \bar{b} + \frac{\sigma(m_p, a) + \bar{m}_t \sigma(m_p, b)}{\sigma^2(m_t)} + \frac{E[(m_t - \bar{m}_t)^2(b - \bar{b})]}{\sigma^2(m_t)} + \frac{\sigma(m_p, e_t)}{\sigma^2(m_t)}, \quad (2)$$

where a bar or E denotes expectation. From equation (2), we note that the static allometric slope is determined by four additive terms that can be interpreted as follows. The first term on the right-hand side, \bar{b} , is the ontogenetic allometric slope averaged across individuals, that is, the mean ontogenetic allometry of the population. The second term, $(\sigma(m_p, a) + \bar{m}_t \sigma(m_p, b))/\sigma^2(m_t)$, is the covariance of m_t with the ontogenetic allometric slope b and the intercept a , estimated among individuals. Note that the two components of this second term, that is, $\sigma(m_p, a)/\sigma^2(m_t)$ and $\bar{m}_t \sigma(m_p, b)/\sigma^2(m_t)$, are not independent, because it is always possible to find a scale where $\bar{m}_t = 0$ and therefore all the contribution of this term is due to variation in the intercept a . However, the sum of the two components is scale independent. The third term, $E[(m_t - \bar{m}_t)^2(b - \bar{b})]/\sigma^2(m_t)$, is nonzero if there is asymmetry in the bivariate distribution of m_t and b . With an approximate normal multivariate distribution, we expect this term to be small. The last term, $\sigma(m_p, e_t)/\sigma^2(m_t)$, represents the contribution of systematic change of the residual deviance from the ontogenetic allometry with m . This last term will increasingly affect the static allometric slope when deviation from the assumption of linear ontogenetic allometry increases. As-

suming no covariance between m and e , and that m and b are symmetrically distributed (i.e., $E((m_t - \bar{m}_t)^2(b - \bar{b})) = 0$), the static allometric slope is given by

$$b_{\text{static}} = \bar{b} + \frac{\sigma(m_p, a) + \bar{m}_t \sigma(m_p, b)}{\sigma^2(m_t)}. \quad (3)$$

Therefore, not only the average slope of the ontogenetic allometry but also the covariation between the parameters of the ontogenetic allometry (slope and intercept) and body size at stage t will influence the static allometric slope (fig. 1A, 1B). This implies that the ontogenetic and static allometric slopes will be equal (i.e., $b_{\text{static}} = \bar{b}$) only when the sum of the second, third, and fourth terms in equation (2) equals 0. In addition, because the covariance between m_t and b in the second term is multiplied by the average body size \bar{m}_t , the effect of this covariance on the static allometric slope will increase during growth, and we expect the difference in slope between ontogenetic and static allometry to change systematically whenever this covariance term is nonzero.

Similarly, the static allometric intercept is given by $a_{\text{static}} = \bar{z}_t - \bar{m}_t(\sigma(m_p, z_t)/\sigma^2(m_t))$ and can be written as a function of the ontogenetic allometry. However, because of the lack of biological significance of the static allometric intercept (which strongly depends on the unit of the X-axis), it is more relevant to investigate the effect of the ontogenetic allometry on the elevation of the static allometry, that is, on the average value of the trait, \bar{z}_t , at the population mean body size \bar{m}_t (see Egset et al. 2011). At the developmental stage t , the elevation will be

$$\bar{z}_t = \bar{a} + E(bm_t) = \bar{a} + \bar{b}\bar{m}_t + \sigma(b, m_t). \quad (4)$$

This shows that in addition to its effect on the static allometric slope, the covariance between the ontogenetic slope and body size achieved at stage t will affect the mean trait value of the population (i.e., the elevation), a positive covariance increasing the mean trait while a negative covariance will decrease it (fig. 1C).

Quadratic Ontogenetic Allometry

Ontogenetic allometries are not necessarily linear, however, and a progressive decrease or increase in the growth rate of the trait relative to the growth rate of the body should generate concave (negative second derivative) or convex ontogenetic allometries, respectively. We extend our model to the effects of nonlinear ontogenetic allometry on the static allometric slope. In the simplest case, nonlinear ontogenetic allometry can be described by a quadratic function: $z = a + b_1m + b_2m^2 + e$. The static allometric slope is then defined as

$$b_{\text{static}} = \frac{\sigma(m_p, z_t)}{\sigma^2(m_t)} = \frac{\sigma(m_p, a + b_1m_t + b_2m_t^2 + e_t)}{\sigma^2(m_t)}, \quad (5)$$

which gives

$$b_{\text{static}} = \frac{\sigma(m_p, a) + \sigma(m_p, b_1m_t) + \sigma(m_p, b_2m_t^2) + \sigma(m_p, e_t)}{\sigma^2(m_t)}. \quad (6)$$

The terms for $\sigma(m_p, b_1m_t)$ are the same as for linear ontogenetic allometry, while

$$\begin{aligned} \sigma(m_p, b_2m_t^2) &= \bar{b}_2\sigma(m_p, m_t^2) + E(m_t^2)\sigma(m_p, b_2) \\ &\quad + E[(m_t - \bar{m}_t)(m_t^2 - E(m_t^2))(b_2 - \bar{b}_2)], \end{aligned}$$

where $\bar{b}_2\sigma(m_p, m_t^2) = 2\bar{b}_2\bar{m}_t\sigma^2(m_t) + \bar{b}_2E[(m_t - \bar{m}_t)^3]$. Assuming that all underlying variables are multivariate normally distributed, we can write

$$\begin{aligned} b_{\text{static}} &= \bar{b}_1 + 2\bar{b}_2\bar{m}_t \\ &\quad + \frac{\sigma(m_p, a) + \bar{m}_t\sigma(m_p, b_1) + E(m_t^2)\sigma(m_p, b_2)}{\sigma^2(m_t)} \\ &\quad + \frac{\sigma(m_p, e_t)}{\sigma^2(m_t)}. \end{aligned} \quad (7)$$

Assuming no correlation between the error e_t and the size m_p , the fourth term equals 0, leaving the static allometric slope determined by the first three terms. If the body size achieved at stage t , m_p , is uncorrelated with the parameters from the ontogenetic allometry (a , b_1 , and b_2), then the third term equals 0. In this specific case, the static allometric slope will be similar to the slope of the tangent to the ontogenetic allometry at the point m_p , because the first and second terms in equation (7) correspond to the derivative of the quadratic function for the parameters mean (fig. 1D). If, however, covariation occurs between m_t and the parameters of the ontogenetic allometry, then various patterns can be generated, and the relationship between the ontogenetic and static allometric slopes becomes difficult to predict because the effects of the different correlations may cancel or reinforce each other.

The difference in slope between static allometry and the tangent of the ontogenetic allometry (i.e., the contribution of the third and fourth terms in eq. [7]) can be tested statistically with hierarchical random regression models (contextual models). Contextual models are multiple regressions that include predictor variables at several levels (e.g., individuals, populations, and species; Blalock 1984; Raudenbush and Bryk 2002; and see Heisler and Damuth 1987; van de Pol and Wright 2009; Bolstad et al. 2010, 2012; Egset et al. 2011 for some biological applications).

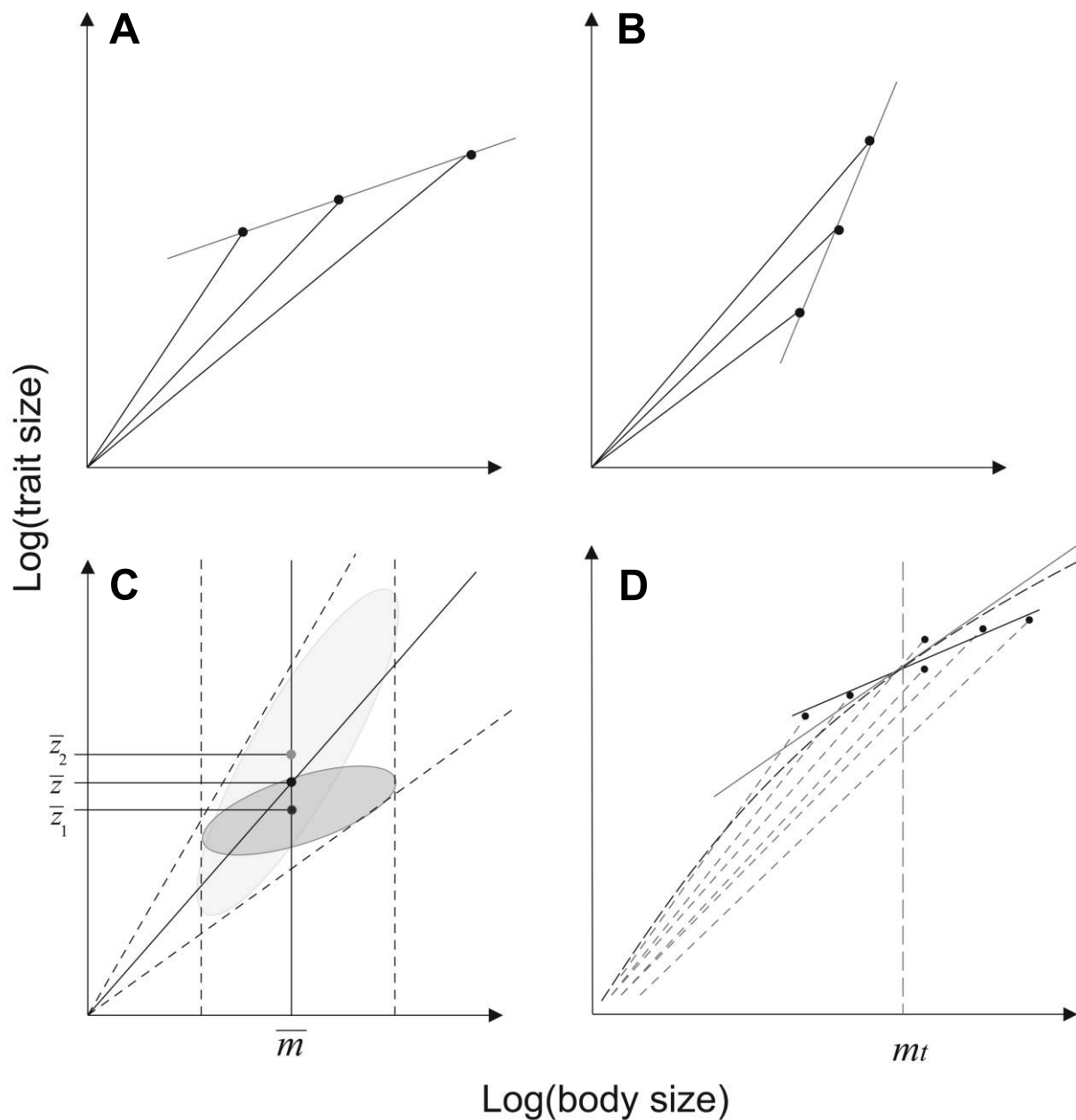


Figure 1: Effects of the variation and covariation in ontogenetic allometric slope and body size on the static allometric slope (A, B) and on the population mean trait size (C). In A, the negative covariance ($\sigma(m, b) < 0$) generates a static allometry (solid gray line) shallower than the average ontogenetic allometry, while in B the positive covariance ($\sigma(m, b) > 0$) generates a static allometry steeper than the average ontogenetic allometry. Shallower and steeper static allometries will also affect the trait mean \bar{z} at similar mean body size \bar{m} , as illustrated in C. Shallower static allometry reduces the trait mean (\bar{z}_1), and steeper allometry increases it (\bar{z}_2). In D, we represent schematically the relationship between ontogenetic and static allometry when ontogenetic allometry is quadratic (curved dash line) at the population level. Adult individuals are represented by black dots, and the static allometry (at adult stage) is represented by a solid black line. The dark gray solid line represents the tangent to the ontogenetic allometry at the population mean for the adult individuals. Finally, the light gray dashed lines represent the mean ontogenetic allometric slope (i.e., the average proportional increase in trait size relative to body size). In this example, the static allometry in adults does not follow the trajectory of the ontogenetic allometry, since it is shallower than the tangent to the ontogenetic allometry. The discrepancy between ontogenetic and static allometry is generated by a negative covariation between the steepness of the individual mean ontogenetic allometry and the body size achieved by adults.

To compare ontogenetic and static allometry, the predictor variables will consist of the individual body size at each ontogenetic stage as well as the individual body size at the stage at which static allometry is estimated. Interpretation of the model parameters depends on the zero point of the predictor variables at the various levels (Kreft et al. 1995; Enders and Tofghi 2007). To test for the difference in slope between static allometry and the tangent of the ontogenetic allometry, it is necessary to center both predictor variables on the population mean body size at the developmental stage at which static allometry is measured. The size measurement for each ontogenetic stage may include higher-order terms (quadratic, cubic, and onward) in addition to the linear term. Similarly, the random factors at the individual level may include linear, quadratic, and cubic (and onward) terms in addition to the intercept. Note, however, that the random factors should not be assumed to be independent and that the model complexity rapidly increases when additional terms are added, because the covariance between the terms should be estimated.

Generalization for Complex Ontogenetic Allometry

Nonlinearity in ontogenetic allometry does not necessarily follow simple quadratic patterns, and complex allometries are commonly observed (Knell 2009; Nijhout 2011). We argue that independently of the complexity of the ontogenetic allometric function generated by nonsimultaneous growth of the different parts of the body, static allometry will be primarily affected by the individual mean ontogenetic allometric slope (fig. 1D) and the covariance between this mean slope and the size achieved when static allometry is estimated. We define the mean ontogenetic allometric slope as the relative growth rate of the trait compared to the relative growth rate of the body during a given interval of time, independently of the exact time at which the growth of each part occurred during this interval.

This allows us to derive a general model linking ontogenetic and static allometry for any ontogenetic allometric function f that links the growth of z to the growth of m as $z = f(m)$. We define the individual mean ontogenetic allometric slope at a specific developmental stage t as the change in z relative to the change in m : $b_t^* = (f(m_t) - f(m_0))/(m_t - m_0)$, where m_t is the body size at stage t , m_0 the initial body size, and the asterisk denotes the parameter for the individual mean ontogenetic allometry. The intercept of this mean ontogenetic allometry is given by $a_t^* = f(m_t) - b_t^* m_t$. In this case, the static allometric slope will be

$$b_{\text{static}} = b_t^* + \frac{\sigma(m_t, a_t^*) + \bar{m}_t \sigma(m_t, b_t^*)}{\sigma^2(m_t)} + \frac{E[(m_t - \bar{m}_t)^2 (b_t^* - \bar{b}_t^*)]}{\sigma^2(m_t)} + \frac{\sigma(m_t, e_t)}{\sigma^2(m_t)}, \quad (8)$$

where $e_t = m_t - f(m_t)$. This expression is similar to equation (2), and the third term will equal 0 if m and b^* present normal multivariate distributions. If the individual ontogenetic allometry is linear, then equation (8) is equivalent to equation (2). These two parameters will become increasingly different when the nonlinearity of the ontogenetic allometry increases.

This study focuses on the relationship between ontogenetic and static allometry. However, the models developed are easily extended to map the relationship between ontogenetic and evolutionary allometry by having the (co)variances in the equations describing among-populations rather than within-population heterogeneity in the ontogenetic parameters. In addition, equation (2) can be used to study the relationship between static and evolutionary allometry.

Material and Methods

In order to assess the relative importance of the different variance components that generate discrepancies between ontogenetic and static allometry, we analyze two different data sets. The first data set comprises data on ontogenetic allometry of the caudal fin length collected on female guppies (*Poecilia reticulata*) from three different populations maintained in captivity. The second data set comprises data on ontogenetic allometry of head length and tail length of mice (*Mus musculus*) bred in captivity (Cheverud et al. 1983; Cheverud and Leamy 1985). These organisms differ in their growth pattern, fish having indeterminate growth while the growth of mice ceases after ~12 weeks.

Study Populations and Data Collection

Guppy. The guppy is a freshwater fish native to Trinidad and the northeastern part of South America. The species presents a pronounced sexual dimorphism, including an enlarged caudal fin in males (Endler and Houde 1995; Houde 1997). In females, caudal fin size most likely affects swimming performance (Karino et al. 2006), which may in turn affect their ability to escape predators and harassing males.

Fish used in the study were descendants of wild-caught fish collected from three populations on Trinidad. Two of the lab populations were founded in early 1998 with ~500 individuals each, sampled from two localities in the Quare River. The first locality, referred to as Quare (10°39'N,

61°12'W), was a high-predation site, where guppies coexisted with the predator pike cichlid (*Crenicichla alta*). The other locality, Campo (10°41'N, 61°13'W), was situated upstream from the first locality and experienced low predation, only killifish (*Rivulus hartii*) being present at this site. After transportation to the lab (Trondheim, Norway), the Quare population was maintained with always more than 200 individuals. Fish from the Campo population suffered from an outbreak of fish tuberculosis shortly after their arrival in the lab. Almost 90% of the population died during the outbreak. After this event, however, the population grew rapidly and reached a large population size (>200 individuals) maintained since 1999. The third population was founded in 1992 with 400 individuals sampled from a low-predation site in the Paria River (10°45'N, 61°16'W). This population was first maintained at J. Endler's lab (Santa Barbara, CA) under large population size (>200 individuals). In late 1994, 400 individuals were transported to Trondheim to establish a new population maintained with always more than 200 individuals. All stock populations were kept under standardized conditions in 200–500-L aquariums with a 12L : 12D cycle and a water temperature of $24^{\circ} \pm 2^{\circ}\text{C}$. Fish were fed daily, alternating commercial dried flakes and newly hatched brine shrimp (*Artemia nauplii*).

In September 2008, ~30 females, as young as possible, were collected from each of the three lab populations within a period of 3 days. Individual ontogenetic allometries were obtained for 24, 29, and 28 females from the Campo, Paria, and Quare populations, respectively. The exact age of these fish was not known, but their size when first measured suggests that they were not older than 1 week when sampled. Furthermore, age variation may affect static allometry but does not affect patterns of ontogenetic allometry (Strauss 1987; Klingenberg 1998). The pedigree of these individuals was also unknown, and related individuals (full-sib or half-sib) could have been included in the samples. When sampled, each fish was photographed (day 0) and then stored individually in a 1-L aquarium. Aquariums were placed in a single room, at randomly assigned places on shelves. Fish were then photographed every second week until 84 days (range 83–86 days) after sampling, providing seven successive measurements (fig. 2). Fish were photographed in a standardized setup with a digital camera (Canon E 300D, Canon, Tokyo), two mounted lights on each side, and a moistened white plastic background with a millimeter scale. Before being photographed, fish were immobilized in cool water (8° – 10°C). After photographing, fish were immediately placed in a small aquarium at 22° – 24°C , where they rapidly recovered, before being returned to their storage aquarium. From each picture, standard length (from the tip of the upper jaw to the base of the caudal fin) and caudal fin length

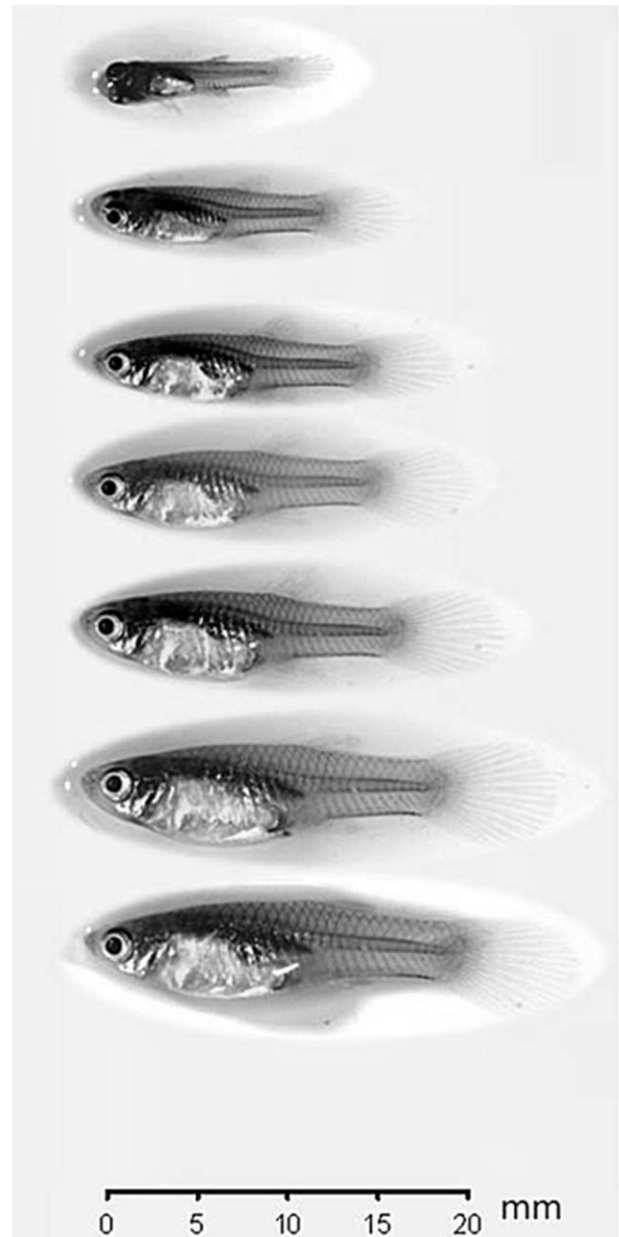


Figure 2: Successive pictures of a female guppy. The first picture was taken less than a week after birth, the last picture being taken 84 days later.

were measured using Adobe Photoshop CS3 Extended, version 10.0.1 (Adobe Systems, San Jose, CA).

Mouse. The murine data were collected by J. M. Cheverud and L. J. Leamy from a population developed by W. R. Atchley and J. J. Rutledge at the University of Wisconsin–Madison in the early 1980s. They were presented in a series of papers on the quantitative genetics of growth (Cheverud

et al. 1983; Leamy and Cheverud 1984; Cheverud and Leamy 1985). However, allometry was not analyzed in these studies. Offspring from random-bred ICR (Institute of Cancer Research) mice were obtained from 60 full-sib families. Litters were standardized at birth to eight pups, four males and four females. Offspring were removed from their mothers at 21 days of age and randomly assigned to single-sex cages containing four mice. Mice were measured, on average, every week. In order to minimize age variation on estimates of static allometry, the data were divided into nine age categories (developmental stages) in our analysis: (1) 16 and 17 days; (2) 19 and 20 days; (3) 23 and 24 days; (4) 26 days; (5) 30–32 days; (6) 44–46 days; (7) 51–53 days; (8) 58–60 days; and (9) 65–67 and 69 days. Five live-body traits were measured with a caliper: head length, head breadth, ear length, trunk length, and tail length. However, two of these traits showed poor repeatability (ear length and head breadth; table 3 in Cheverud et al. 1983). We therefore chose to analyze the allometric relationship between trunk length, as a measure of body size, and head length and tail length. Note that although the growth in terms of body mass was not completed by 66 days of age (Riska et al. 1984), skeletal growth as measured by the trunk length was achieved at this age (not shown). In total, 125 males and 122 females were included in the data set.

Length measurements do not represent good estimates of size, and parameters such as centroid size may be more appropriate to conduct such a study. In the guppy data set, we also conducted the analysis on body area and caudal fin area (more equivalent to centroid size) and obtained similar results (not presented here). Therefore, we believe that the results presented here are robust and relatively independent from the size measurement used. For the guppy, we decided to present the data on body length and caudal fin length because these traits are less subject to measurement errors and allow comparison with the allometry estimated for the same traits in male guppies from natural populations (Egset et al. 2011). Furthermore, in fish, swimming performances seem to depend more strongly on the length of the caudal fin than on the area, because of its effect on the rigidity of the fin (Langerhans 2008; see Egset et al. 2011 for further discussion).

Statistics

All allometric relationships were estimated on log-transformed data. In both data sets, the different traits have the same dimension and unit (centimeters) and were therefore not transformed further.

Ontogenetic Allometry and Individual Heterogeneity. Preliminary analyses (not shown) indicated that populations

(guppy) and sexes (mouse) differed in their ontogenetic allometry. Therefore, analyses were conducted separately for the different populations and for the two sexes. To describe patterns of ontogenetic allometry, we fitted mixed-effects models with body size (log standard length or log trunk length) as the predictor variable and individual as a random factor. In all models, we assumed non-linearity of the ontogenetic allometry by including up to fourth-order terms for the body size variable. We did not include higher-order terms to avoid overparameterization of our models. We tested individual heterogeneity in ontogenetic allometry by comparing models with different structure for the random effect, using restricted maximum likelihood (REML). We then tested for nonlinearity in ontogenetic allometry by comparing models including or not including high-order terms, using maximum likelihood. Parameter estimates were finally obtained for the best-fit model via REML.

Comparing Ontogenetic and Static Allometry in Adults. In the absence of covariance between the parameters of the ontogenetic allometry and body size, static allometry should follow the pattern of ontogenetic allometry (eq. [7]). In this particular case, at each specific point during ontogeny, the static allometric slope should equal the slope of the tangent to the ontogenetic allometry (fig. 1D), the static allometry corresponding to a linear approximation of the ontogenetic allometry at this specific point. Ontogenetic allometry and the final static allometry, that is, the allometry measured at the last stage (84 days of age in guppies, 66 days of age in mice), were compared using contextual models where body size measured at each ontogenetic stage and at the last measurement only were entered as predictor variables, both centered on the mean body size at the last measurement. In these models, the effect of the latter predictor variable gives the contrast between ontogenetic and static allometry at the last measurement. The random effects in these models were the same as those in the models testing for individual heterogeneity in ontogenetic allometry. The discrepancy between ontogenetic and static allometry revealed by these models implies that static allometry does not follow the pattern of ontogenetic allometry, probably because of nonzero covariation between body size and parameters of the ontogenetic allometry (see eq. [7]). Because predictor variables are mean centered (intercept at the population mean), the linear term in each model of the ontogenetic allometry can be directly interpreted as the slope of the tangent to the ontogenetic allometry at the population mean.

Estimates of the Covariance between a, b, and m. Ontogenetic allometries were mostly nonlinear and presented different shapes in the different traits, populations, and

Table 1: Mean \pm SE standard length and caudal fin length of female guppies in the three populations at the first (day 0) and last (day 84) measurements

Population	Standard length (mm)		Caudal fin length (mm)	
	Day 0	Day 84	Day 0	Day 84
Quare ($n = 28$)	8.82 \pm .14	20.31 \pm .23	2.84 \pm .049	6.24 \pm .071
Paria ($n = 29$)	8.94 \pm .13	17.36 \pm .23	2.77 \pm .055	5.51 \pm .069
Campo ($n = 24$)	8.35 \pm .20	19.32 \pm .32	2.60 \pm .049	5.97 \pm .093
Population differences:				
$F_{2,78}$	3.80	34.85	4.18	24.13
P	<.027	<.001	<.019	<.001

Note: Tests for population differences (ANOVA) are provided in the last two rows.

sexes (see “Results”). To estimate the underlying variables from the variance components that affect the static allometric slope, we used the generalization of our model for nonlinear allometry (eq. [8]), where we considered the individual mean ontogenetic allometry between the first and last measurements. To do so, we fitted a separate generalized additive model for each trait and each individual and used these models to estimate the value for the trait z at the first and last body size measurements, in order to calculate the individual mean ontogenetic allometry (parameters a^* and b^* in eq. [8]). We did not estimate these parameters from mixed-effects models with individual as a random factor, because point estimates of random effects in mixed-effects models have a downward-biased variance, compared to the true effects (Hadfield et al. 2010). Uncertainty of the covariance terms was estimated by means of nonparametric bootstrapping with 1,000 bootstrap replicates at the level of the individual fish or mouse. All the statistical analyses were performed in R, version 2.10.0 (R Development Core Team 2011), using the packages lme4 (Bates et al. 2011) and mgcv (Wood 2004).

Change in Static Allometry during Ontogeny. Because the static allometric slope partly depends on the product of the covariance between m_i and b and the average body size \bar{m}_i (eq. [3]), a systematic change in the static allometric slope is expected during ontogeny whenever a nonzero covariance between m_i and b occurs. We tested for such a change by fitting mixed-effects models on ontogenetic allometry data where the fixed effects were body size and the interaction between body size and age at ontogenetic stage, which gives the change in the static allometric slope with age. The predictor variable (log standard length or log trunk length) was centered on its mean for each ontogenetic stage. Ontogenetic stage was also entered as random factor in order to allow for change in intercept.

Choice of the Regression Model and Measurement Error. Major-axis or reduced-major-axis regression models have

often been used in place of ordinary least squares regression to estimate allometric parameters. However, these two models provide estimates of the allometric slope that have no specific link with our parameter of interest. Indeed, our model assumes that the allometric slope corresponds to σ_{xy}/σ_x^2 . Because the estimated slope in the major-axis regression is given by $b = (1/2\sigma_{xy})\{\sigma_y^2 - \sigma_x^2 + [(\sigma_y^2 - \sigma_x^2)^2 + 4\sigma_{xy}]^{1/2}\}$, while in the reduced major axis it is given by $b = (\sigma_y^2/\sigma_x^2)^{1/2}$, neither of these two models provides estimates of the allometric slope relevant for our analysis. We therefore conducted all our analyses using ordinary least squares regression.

Estimates of the allometric slope using ordinary least squares regressions are susceptible to measurement and biological errors in the predictor variable. Furthermore, if the magnitude of the measurement error changes during ontogeny, it may generate a change in static allometry measured at different ontogenetic stages that can be mistaken for the effect of a nonzero covariance between ontogenetic allometry and body size (eq. [3]). For the guppy data, the various estimates of the repeatability (ratio between among-individual and total variance) for the body size measurement showed that this repeatability is high (between 0.98 and 0.99; Egset et al. 2011, 2012). Therefore, the downward bias of the static allometric slope due to measurement error should be on the order of 1%–2% (Hansen and Bartoszek 2012) and should not strongly affect differences between ontogenetic and static allometry as well as the changes in static allometry during ontogeny. For the mouse data, the repeatability of the trunk length was relatively high (0.9 on average) but tended to decrease in the measurements done at an older age (table 3 in Cheverud et al. 1983). This could generate a downward bias of the static allometric slope of $\sim 10\%$ during ontogeny. Because the opposite pattern was observed (see “Results”), we conclude that changes in static allometry during ontogeny were not generated by differences in measurement error at different ages.

Results

Ontogenetic Allometry

Guppy. Females from the three guppy populations differed in their initial standard length and in the standard length achieved 84 days after sampling (table 1). Females from the Paria population, which were the largest at the first measurement, were, on average, the smallest at the last measurement 84 days later.

The best models to describe ontogenetic allometry differed among populations. In the Campo and Quare populations, ontogenetic allometry was nonlinear. The best model for the Campo population included a quadratic term, whereas the best model for the Quare population included both a quadratic and a cubic term (fig. 3; table A1, available online). In both populations, we found evidence of individual heterogeneity for the different parameters (table A1). In the Paria population, ontogenetic allometry was linear on average, but we found evidence of individual heterogeneity, some individuals showing nonlinear ontogenetic allometry (fig. 3; table A1).

Mouse. Ontogenetic allometry in head length and tail length were both nonlinear. For the ontogenetic allometry in head length, the best models for males and females included both quadratic and cubic terms (fig. 4; table A2, available online). Similarly, the best model for the ontogenetic allometry in tail length included a cubic and a quadratic term for the females but also a fourth-order term for the males (fig. 4; table A2). For the ontogenetic allometry in head length, the best models included random (individual) variation in the intercept, while for tail length the best model included random variation in the linear, quadratic, and cubic terms.

Head length displayed a negative ontogenetic allometry

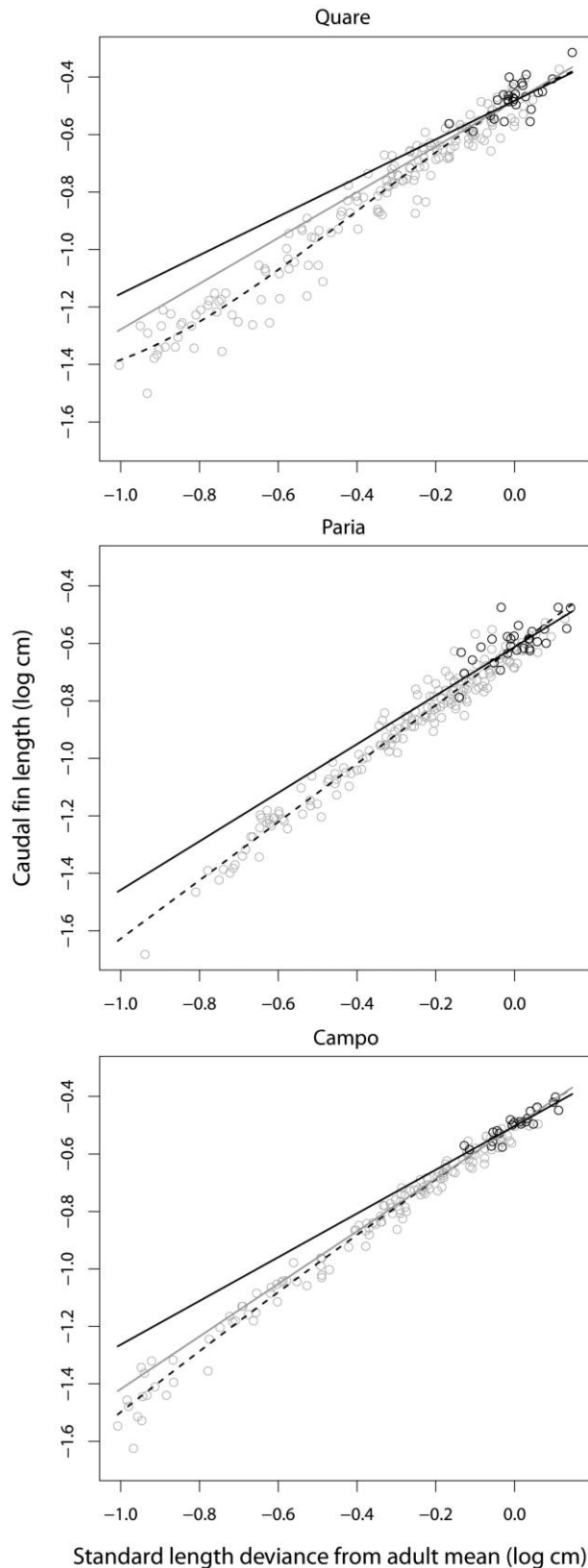


Figure 3: Ontogenetic and adult static allometry between caudal fin length and body length in females from three guppy populations (dashed line: mean ontogenetic allometry; gray line: tangent to the mean ontogenetic allometry at adult stage; black line: adult static allometry). The parameter estimates (\pm SE) for the mean ontogenetic allometry in each population are $y = (-0.482 \pm 0.009) + (0.796 \pm 0.072)x - (0.609 \pm 0.217)x^2 - (0.503 \pm 0.170)x^3$ in Quare, $y = (-0.612 \pm 0.009) + (1.015 \pm 0.016)x$ in Paria, and $y = (-0.503 \pm 0.005) + (0.915 \pm 0.023)x - (0.080 \pm 0.030)x^2$ in Campo. Static allometric slopes at the last measurement are reported in table 2. Differences between the static allometric slopes and the slopes of the tangent to the ontogenetic allometry at the last measurement are -0.124 ± 0.130 in Quare, -0.170 ± 0.072 in Paria, and -0.154 ± 0.059 in Campo. (The slopes of the tangents to the ontogenetic allometries are 0.958, 1.044, and 0.954 for Quare, Paria, and Campo, respectively.) The adult means for standard length are 0.71 log cm for Quare, 0.55 log cm for Paria, and 0.67 log cm for Campo.

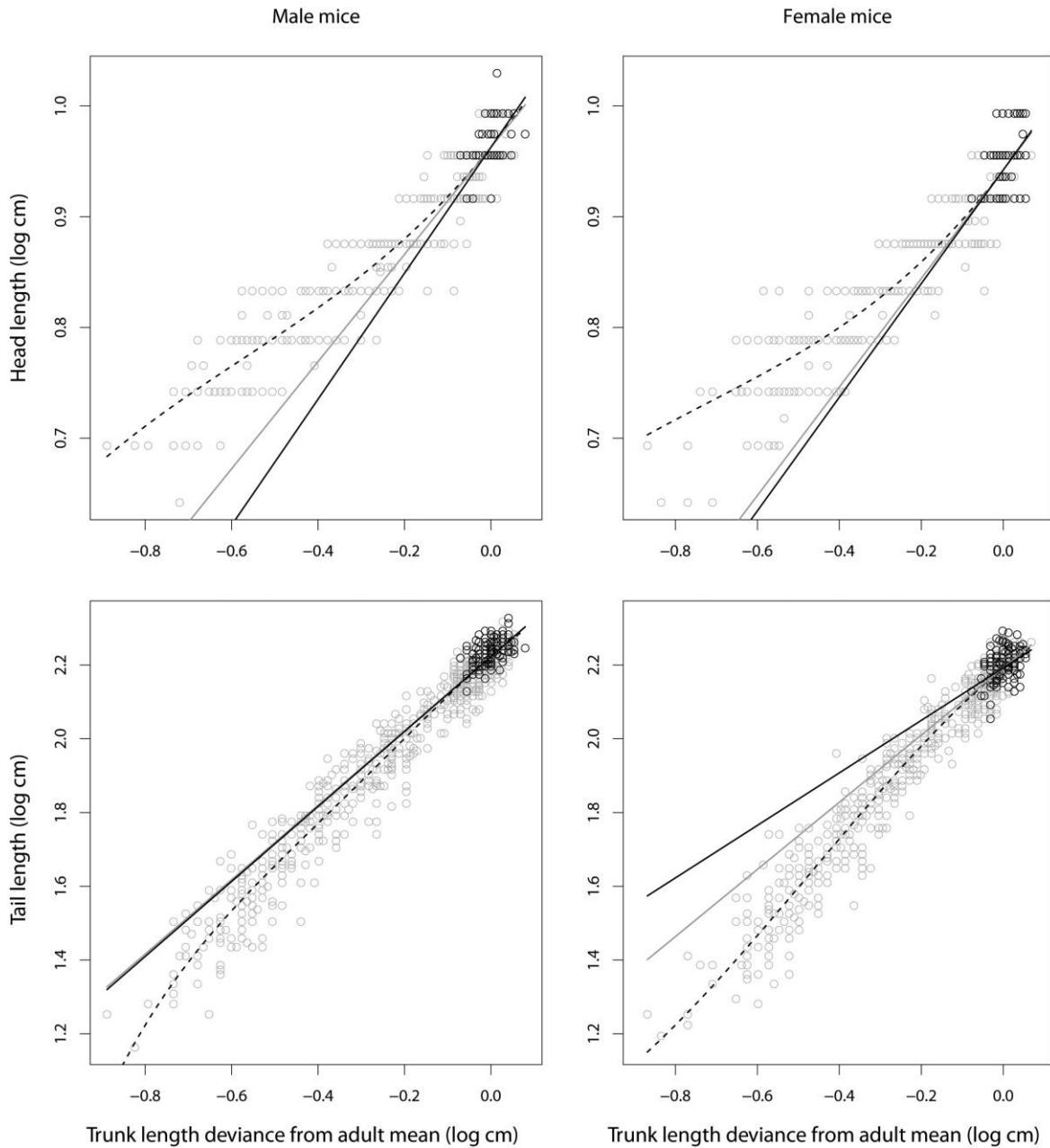


Figure 4: Ontogenetic and adult static allometry between head length or tail length and trunk length in male and female mice (dashed line: mean ontogenetic allometry; gray line: tangent to the mean ontogenetic allometry at adult stage; black line: adult static allometry). Parameter estimates (\pm SE) for the mean ontogenetic allometry in each trait and each sex: $y = (0.963 \pm 0.001) + (0.474 \pm 0.019)x + (0.395 \pm 0.073)x^2 + (0.230 \pm 0.074)x^3$ for head length in males, $y = (0.942 \pm 0.001) + (0.490 \pm 0.020)x + (0.412 \pm 0.081)x^2 + (0.189 \pm 0.085)x^3$ for head length in females, $y = (2.223 \pm 0.003) + (1.007 \pm 0.050)x - (0.877 \pm 0.332)x^2 - (2.127 \pm 0.771)x^3 - (1.757 \pm 0.753)x^4$ for tail length in males, and $y = (2.192 \pm 0.003) + (0.911 \pm 0.039)x - (0.869 \pm 0.183)x^2 - (0.617 \pm 0.211)x^3$ for tail length in females. Static allometric slopes in adults are reported in table 3. Differences between the static allometric slopes and the slopes of the tangents to the ontogenetic allometry in adults (last measurement): 0.085 ± 0.037 for head length in males, 0.023 ± 0.044 for head length in females, 0.008 ± 0.095 for tail length in males, and -0.199 ± 0.109 for tail length in females. (The slopes of the tangents to the ontogenetic allometries are 0.478, 0.482, 1.073, and 0.912 for these four trait-sex combination, respectively.) The adult means for trunk length of mice are 1.97 log cm for males and 1.91 log cm for females.

(slope < 1), as expected from the low growth rate of the brain after birth (Deacon 1990). However, this allometry became steeper at later stages (fig. 4). Ontogenetic allometry in tail length was positive (slope > 1) but became slightly shallower at later stages (fig. 4).

Differences between Ontogenetic and Static Allometry in Adults

Guppy. Static allometry between caudal fin length and body length measured at the last ontogenetic stage (84 days) in the female guppies from the three populations was always shallower than the tangent of the ontogenetic allometry at this stage (fig. 3), although the difference in slope was not statistically significant in the Quare population.

Mouse. Static allometry between head length and trunk length measured at 66 days of age tended to be steeper than the tangent of the ontogenetic allometry in males, while the two lines were very similar in females (fig. 4). In tail length, static allometry measured at 66 days of age followed the same slope as the tangent of the ontogenetic allometry in males, while it was shallower in females (fig. 4).

Overall, these results show that, in several cases, static allometry in adult individuals (here estimated at the last measurement) differs from the trajectory defined by the ontogenetic allometry.

Relationship between Ontogenetic and Static Allometry

In order to understand what generates the differences between static and ontogenetic allometric slopes, we estimated the different parameters of the individual ontogenetic allometry that influenced the static allometric slope. Because ontogenetic allometries were mostly nonlinear, we used the general model describing the relationship between the mean ontogenetic allometry and static allometry (eq. [8]).

Guppy. The different components contributing to the static allometric slope for the three populations are reported in table 2. The static allometric slope is mainly determined by the average slope of the population mean ontogenetic allometry and the covariance between m and the individual parameters of the mean ontogenetic allometry, a^* and b^* . The minor contribution of the third term (the third moment) suggests that the standard length and the slope of the mean ontogenetic allometry are multivariate symmetrically distributed. In the two populations where static allometry is shallower than the ontogenetic allometry, the difference in slope is generated by the neg-

ative covariance between body size and the slope of the mean ontogenetic allometry, $\sigma(m, b^*)$.

As predicted by our model, the multiplication of the covariance term $\sigma(m, b^*)$ by the mean body length (eq. [8]) generates a systematic decrease in static allometry during the ontogeny in each of the three populations (fig. 5). At the first measurement, static allometry is close to isometry (slope = 1) in each population. At the last measurement, 84 days later, static allometry does not differ between populations (interaction effect in the ANCOVA: $F_{2,75} = 1.71$; $P = .19$; population effect: $F_{2,75} = 0.14$; $P = .87$) and presents a slope shallower than the one observed at the first measurement (average slope: 0.764 ± 0.047 ; table 2).

Mouse. Estimates of the different components determining the static allometry of head length and tail length in male and female mice are reported in table 3. As for the guppy data, the contribution of the third moment (deviation from multivariate normal distribution) remains limited and never statistically different from 0. Furthermore, static allometries shallower than the mean ontogenetic allometry observed for tail length in both sexes are generated by the negative covariance between body size and the ontogenetic allometric slope (note that the 95% confidence interval of $\sigma(m, b^*)$ overlaps 0 in males). We note, however, that the R^2 values of the static allometry in this data set are rather low. This may be due to the strong decrease in trait variation in later ontogenetic stages (fig. 6).

As expected from these results, static allometry between head length and trunk length remained constant during ontogeny in both sexes, despite the strong nonlinearity of the ontogenetic allometry (fig. 6). However, this nonlinearity generates strong changes in the static allometric intercept during ontogeny (fig. 6). In contrast, static allometry between tail length and trunk length decreased during ontogeny (fig. 6), as expected from the negative covariance between the slope of the mean ontogenetic allometry and body length.

Discussion

Building on Huxley's (1932 [1993]) model of relative growth, we showed that the static allometric slope is determined by four additive components. The first component is, of course, the average slope of the ontogenetic allometry. This confirms that changes in ontogenetic allometric slope directly affect the static allometric slope, therefore generating positive correlation between the two types of allometry (Leamy and Bradley 1982; Klingenberg and Zimmermann 1992; Klingenberg 1996). However, our model also shows that, even if ontogenetic allometry is

Table 2: Estimates of the additive components of the static allometric slope b_{static} in the last age class for the three guppy populations and of the different terms of these components

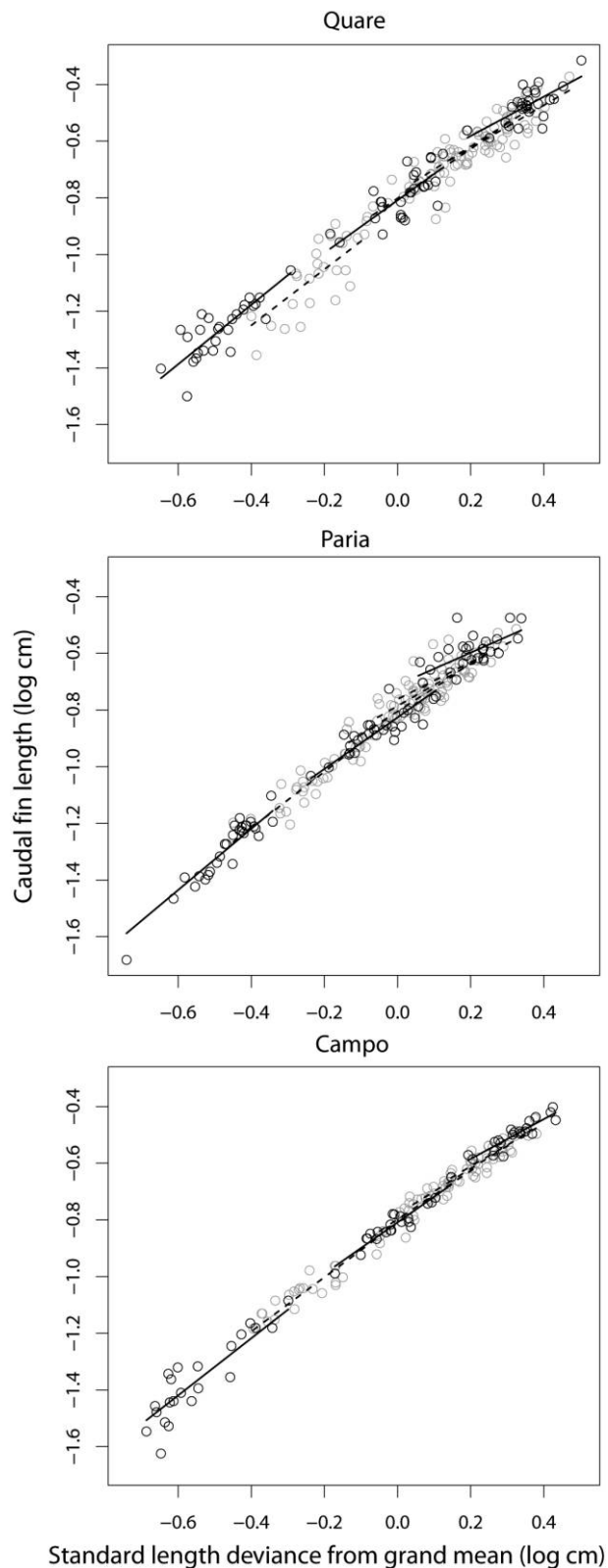
	Quare	Paria	Campo
A. Additive components:			
\bar{b}_t	.950 (.927, .972)	1.032 (1.002, 1.063)	.992 (.965, 1.021)
$\frac{\sigma(m_t, a) + \bar{m}_t \sigma(m_t, b)}{\sigma^2(m_t)}$	-.268 (-.539, -.030)	-.369 (-.621, -.134)	-.261 (-.421, -.031)
$\frac{E[(m_t - \bar{m}_t)^2(b_t - \bar{b}_t)]}{\sigma^2(m_t)}$.0150 (-.0165, .0419)	.0154 (-.0163, .0497)	.0242 (-.0163, .0550)
$\sigma(m_t, e_t) / \sigma^2(m_t)$.017 (-.153, .104)	-.046 (-.132, .019)	-.029 (-.085, .012)
Sum	.714 (.420, .958)	.632 (.332, .894)	.727 (.590, .900)
Least squares estimate	.714 (.421, .958)	.633 (.332, .894)	.728 (.592, .900)
R^2 of least squares estimate	.502	.475	.834
B. Terms:			
\bar{b}_t	.950 (.927, .972)	1.032 (1.002, 1.063)	.992 (.965, 1.021)
$\sigma(m, a) (\ln \text{ cm})^2$	-6.72×10^{-4} (-1.69×10^{-3} , 3.02×10^{-4})	-5.05×10^{-4} (-1.62×10^{-3} , 5.41×10^{-4})	-2.69×10^{-4} (-9.82×10^{-4} , 1.32×10^{-3})
$\bar{m}_t (\ln \text{ cm})$.708 (.684, .730)	.546 (.518, .573)	.672 (.647, .697)
$\sigma(m, b) (\ln \text{ cm})$	-4.28×10^{-4} (-1.50×10^{-3} , 6.16×10^{-4})	-3.04×10^{-3} (-4.94×10^{-3} , -1.15×10^{-3})	-1.99×10^{-3} (-4.03×10^{-3} , -1.06×10^{-4})
$\sigma^2(m) (\ln \text{ cm})^2$	3.64×10^{-3} (1.41×10^{-3} , 6.35×10^{-3})	5.87×10^{-3} (3.02×10^{-3} , 8.43×10^{-3})	4.10×10^{-3} (1.90×10^{-3} , 6.19×10^{-3})
$E[(m_t - \bar{m}_t)^2(b_t - \bar{b}_t)] (\ln \text{ cm})^2$	5.46×10^{-5} (-4.38×10^{-5} , 1.76×10^{-4})	9.04×10^{-5} (-9.04×10^{-5} , 2.83×10^{-4})	9.93×10^{-5} (-3.77×10^{-5} , 2.54×10^{-4})
$\sigma(m, e) (\ln \text{ cm})$	6.27×10^{-5} (-3.76×10^{-4} , 3.97×10^{-4})	-2.69×10^{-4} (-6.11×10^{-4} , 1.14×10^{-4})	-1.20×10^{-4} (-2.73×10^{-4} , 5.67×10^{-5})

Note: Values in parentheses represent 95% confidence intervals. The “sum” row corresponds to the sum of the different components, that is, the calculated slope of the static allometry at 84 days of age, while the “least squares estimate” row presents the slope estimated from the least squares regression.

linear, static allometry can be affected by the covariance between the parameters of the ontogenetic allometry and the length of growth vector, that is, the body size achieved when static allometry is measured, as suggested by Cock (1966) and others (Gould 1966, 1971; Cheverud 1982; Lande 1985). Negative (or positive) covariance between body size and either the slope or the intercept of the ontogenetic allometry will generate static allometry shallower (or steeper) than the ontogenetic allometry, given that these parameters are multivariate symmetrically distributed. Therefore, even if ontogenetic and static allometric slopes are correlated, they are not necessarily similar, and static allometry rarely equals ontogenetic allometry. Finally, our model shows that static allometry may change during ontogeny according to the sign and strength of the covariance between the ontogenetic allometric slope and body size.

Using longitudinal data on the growth of the caudal fin and body length in female guppies from three populations and on the growth of the head, tail, and trunk in mice, we described patterns of ontogenetic and static allometry

and estimated the variances and covariances in the different parameters from the ontogenetic allometries, in order to understand the causes of discrepancy between ontogenetic and static allometric slopes. With the exception of one guppy population, ontogenetic allometries were nonlinear and showed individual heterogeneity. Static allometries differed from the average ontogenetic allometry, sometimes markedly, but these differences were not generated by the nonlinearity of the ontogenetic allometries, because the static allometric slopes differed from the tangent to the ontogenetic allometries. Instead, we showed that the discrepancy between the two types of allometry resulted primarily from nonzero covariance between body size and the slope of the mean ontogenetic allometry (b^*). For caudal fin length (guppy) and tail length (mouse), individuals showing steeper ontogenetic allometry also showed lower growth in body size, therefore generating a negative covariance between the slope of the mean ontogenetic allometry and body size. This resulted in static allometries systematically shallower than the ontogenetic allometries. Furthermore, differences between static and



ontogenetic allometry were magnified during ontogeny, static allometries becoming gradually shallower. Interestingly, in the case of the caudal fin length, females from the three guppy populations eventually showed similar patterns of static allometry (i.e., slope and intercept not statistically different), despite differences in their ontogenetic allometry.

Covariance between body size and ontogenetic allometric slope therefore appeared as the key factor generating differences between ontogenetic and static allometry, while the contribution of the skewness in the bivariate distribution of these parameters and the contribution of the residual deviance from the ontogenetic allometry were negligible. Furthermore, while the covariance between the ontogenetic allometric intercept and body size could generate similar differences between static and ontogenetic allometry, this covariance did not contribute markedly to the discrepancies between ontogenetic and static allometries.

Comparative analyses of static allometry among populations or species suggest that most of the variation concerns the allometric intercept, while the allometric slope is less variable across taxa (Bonduriansky 2007). In the guppy, a comparison of static allometries of the caudal fin length in males among 21 natural populations from different drainages and exposed to different predation intensities revealed no effect of these ecological variables on the allometric slope, while the allometric intercept differed between geographic areas (Egset et al. 2011). In addition, the static allometric slopes observed in these populations were similar to the one observed in females in our study ($\beta = 0.79 \pm 0.05$), despite the fact that caudal fin size in males is under sexual selection (Bischoff et al. 1985; Endler and Houde 1995). Similar results were obtained in a comparative study on the allometry between eye span and body size in the stalk-eyed fly *Cyrtodiopsis dalmanni*, where the allometric slope remained relatively constant despite marked variation in body size and relative eye span (Voje and Hansen 2012).

The low variability of the static allometric slope has

Figure 5: Changes in static allometry between caudal fin length and body length during ontogeny in female guppies from three populations. Measurements and static allometries are reported with black circles and solid lines at measurements 1, 3, and 7 and with gray circles and dashed lines for the other measurement sessions. Estimates for the static allometric slope at the first measurement (\pm SE) are 1.048 ± 0.078 in Quare, 1.080 ± 0.073 in Paria, and 1.008 ± 0.071 in Campo. Estimates for the systematic change in the static allometric slope during ontogeny (interaction effect between age and \ln standard length; \pm SE) are $-0.0042 \pm 0.0017 \text{ day}^{-1}$ in Quare, $-0.0061 \pm 0.0015 \text{ day}^{-1}$ in Paria, and $-0.0036 \pm 0.0017 \text{ day}^{-1}$ in Campo. The grand mean for the standard length is 0.35 log cm.

Table 3: Estimates of the additive components of the static allometric slope b_{static} in the last age class for head length and tail length in male and female mice and of the different terms of these components

	Head length, males	Head length, females	Tail length, males	Tail length, females
A. Additive components:				
\bar{b}_i	.333 (.327, .341)	.327 (.318, .336)	1.155 (1.138, 1.173)	1.195 (1.173, 1.218)
$\frac{\sigma(m_i, a_i) + \bar{m}_i a(m_i, b_i)}{\sigma^2(m_i)}$.159 (.085, .241)	.103 (.004, .200)	-.134 (-.349, .098)	-.292 (-.507, -.086)
$\frac{E[(m_i - \bar{m}_i)^2(b_i - \bar{b}_i)]}{\sigma^2(m_i)}$	-.0024 (-.0140, .0095)	-.0007 (-.0086, .0081)	.0186 (-.0101, .0463)	-.0144 (-.0350, .0081)
$\sigma(m_i, e_i)/\sigma^2(m_i)$	-.083 (-.162, -.003)	-.114 (-.224, -.006)	-.343 (-.482, -.190)	-.372 (-.494, -.261)
Sum	.407 (.318, .510)	.315 (.162, .455)	.698 (.465, .953)	.517 (.263, .757)
Least squares slope	.394 (.293, .503)	.310 (.158, .449)	.630 (.438, .860)	.509 (.236, .757)
R^2 of least squares estimate	.304	.161	.261	.113
B. Terms:				
\bar{b}_i	.333 (.327, .341)	.327 (.318, .336)	1.155 (1.138, 1.173)	1.195 (1.173, 1.218)
$\sigma(m, a)$ (ln cm) ²	2.13×10^{-4} (-1.90×10^{-4} , 6.21×10^{-4})	3.83×10^{-4} (-1.03×10^{-4} , 8.24×10^{-4})	3.82×10^{-4} (-7.97×10^{-4} , 1.59×10^{-3})	1.52×10^{-3} (3.74×10^{-4} , 2.55×10^{-3})
\bar{m}_i (ln cm)	1.987 (1.982, 1.992)	1.933 (1.928, 1.937)	1.987 (1.981, 1.992)	1.933 (1.928, 1.938)
$\sigma(m, b)$ (ln cm)	-4.14×10^{-5} (-2.54×10^{-4} , 1.65×10^{-4})	-1.58×10^{-4} (-3.85×10^{-4} , 1.05×10^{-4})	-2.48×10^{-4} (-8.18×10^{-4} , 2.93×10^{-4})	-8.98×10^{-4} (-1.41×10^{-3} , -3.13×10^{-4})
$\sigma^2(m)$ (ln cm) ²	8.20×10^{-4} (6.32×10^{-4} , 1.01×10^{-3})	7.46×10^{-4} (5.77×10^{-4} , 9.00×10^{-4})	8.20×10^{-4} (6.42×10^{-4} , 1.02×10^{-3})	7.46×10^{-4} (5.84×10^{-4} , 8.98×10^{-4})
$E[(m_i - \bar{m}_i)^2(b_i - \bar{b}_i)]$ (ln cm)	-1.94×10^{-6} (-1.24×10^{-5} , 7.80×10^{-6})	-5.35×10^{-7} (-6.25×10^{-6} , 5.76×10^{-6})	1.53×10^{-5} (-7.37×10^{-6} , 4.05×10^{-5})	-1.07×10^{-5} (-2.69×10^{-5} , 5.69×10^{-6})
$\sigma(m, e)$ (ln cm)	-6.80×10^{-5} (-1.35×10^{-4} , 2.27×10^{-6})	-8.50×10^{-5} (-1.67×10^{-4} , -4.17×10^{-6})	-2.81×10^{-4} (-4.13×10^{-4} , -1.42×10^{-4})	-2.77×10^{-4} (-3.76×10^{-4} , -1.79×10^{-4})

Note: Values in parentheses represent 95% confidence intervals. The "sum" row corresponds to the sum of the different components, that is, the calculated slope of the static allometry at 66 days of age, while the "least squares estimate" row presents the slope estimated from the least square regression. CI = confidence interval.

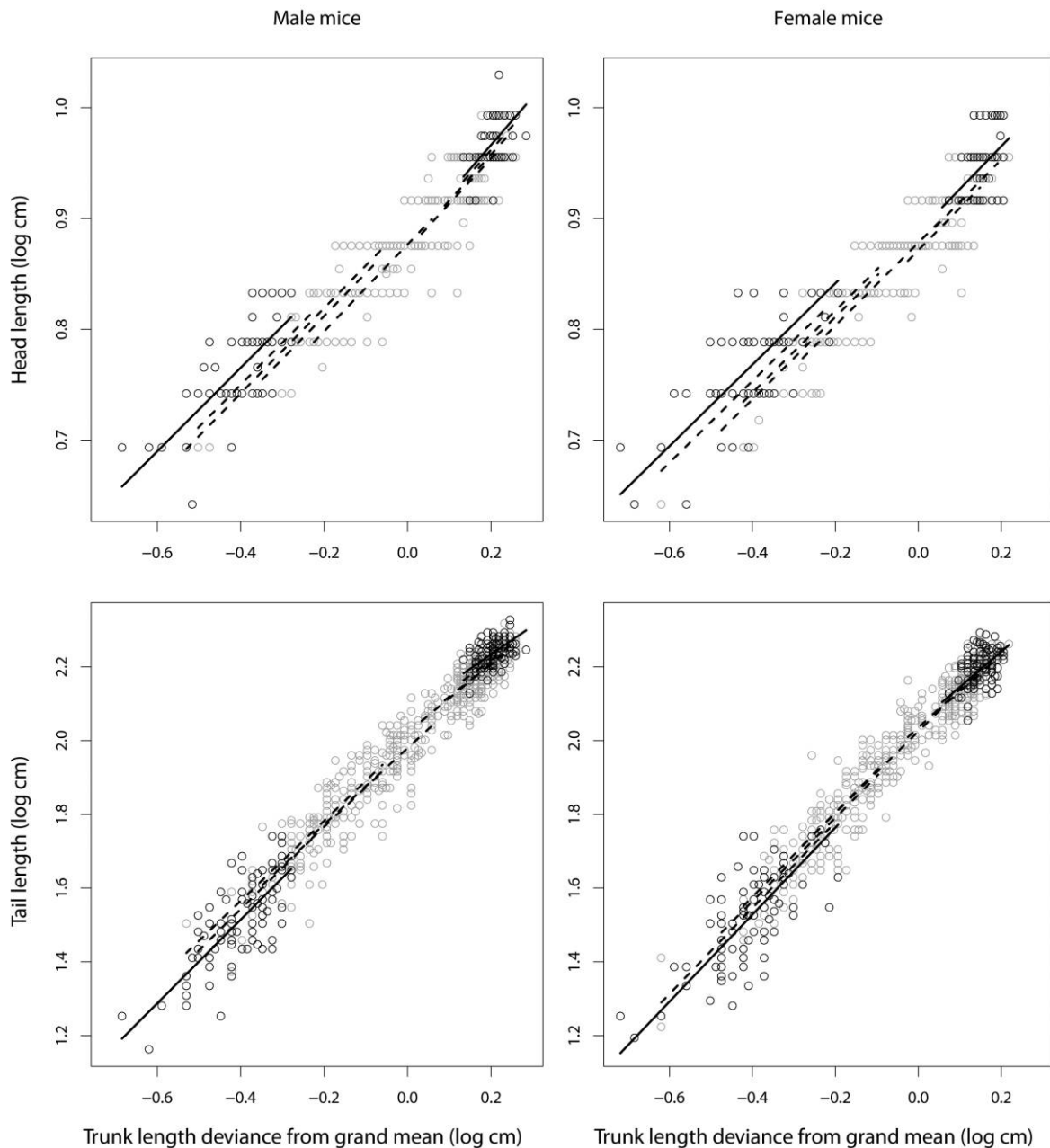


Figure 6: Changes in static allometry between the head length or tail length and trunk length during ontogeny in male and female mice. Measurements and static allometries are reported with black circles and solid lines for the first and last measurements and with gray circles and dashed lines for the intermediate measuring sessions. Estimates for the static allometric slope at the first measurement (\pm SE) are 0.359 ± 0.035 for head length in males, 0.360 ± 0.034 for head length in females, 1.257 ± 0.085 for tail length in males, and 1.269 ± 0.083 for tail length in females. Estimates for the systematic change in the static allometric slope during ontogeny (\pm SE) are $0.0011 \pm 0.0011 \text{ day}^{-1}$ for head length in males, $0.0004 \pm 0.0011 \text{ day}^{-1}$ for the head length in females, $-0.0072 \pm 0.0027 \text{ day}^{-1}$ for tail length in males, and $-0.0053 \pm 0.0026 \text{ day}^{-1}$ for tail length in females. The grand mean for trunk length is 1.78 log cm.

often been interpreted as resulting from the difficulties selection has in changing patterns of proportional growth among traits (Maynard Smith et al. 1985; Huxley 1932 [1993]). This hypothesis seems supported by the experi-

ment from Egset et al. (2012), who selected independently on the slope and intercept of the static allometry of the caudal fin area in male guppies. After three episodes of selection, they showed that the allometric intercept was

highly evolvable, while the allometric slope apparently harbored very little genetic variation. These observations suggest that the evolutionary potential of the static allometric slope is possibly constrained by the ontogenetic allometry, that is, by internal (developmental) constraints. Our results challenge this interpretation. Indeed, if covariances between parameters of the ontogenetic allometry and body size are different from 0, any selection on size should generate changes in the static allometric slope. Conversely, a constant static allometric slope in populations or species that differ in size necessarily requires evolution of the growth patterns and ontogenetic allometry to maintain the consistency of the static allometric slope.

These considerations lead to two predictions. First, because selection on variance and covariance is expected to be less efficient than selection on the mean (Hansen 2006; Pélabon et al. 2010), we may expect that directional selection on size generates changes in static allometry during early episodes of selection (i.e., when covariance between body size and the parameters of the ontogenetic allometry are unchanged). Very few artificial-selection experiments on body size have analyzed the effects of such a selection on static allometry. In a recent experiment, however, Tobler and Nijhout (2010) selected females of the moth *Manduca sexta* for increase or decrease in body mass and analyzed the static allometry between body mass and wing mass after 10 generations. Static allometry did not differ in the strain selected for smaller body mass but became shallower in the strain selected for an increased body mass, as expected if the covariance between body size and the ontogenetic allometric slope was negative. Although this study provides only partial support for our prediction, it nicely illustrates how one can further test the validity of our model.

Second, the consistency of the static allometric slope in populations of varying size suggests that underlying parameters such as growth rate and ontogenetic allometric slope should be evolvable. In this study, we found individual heterogeneity in nearly all data sets, suggesting that ontogenetic allometry is variable and most likely harbors genetic variation. Similarly, body size is well known as an evolvable character in both guppies (Reynold and Gross 1992) and mice (Falconer 1973). Therefore, proportional growth seems variable and unlikely to constrain the evolution of allometry.

If the relative invariance in static allometric slope is not generated by internal constraints, then external constraints, that is, selection, should generate such consistency. This implies that in order to understand the apparent stasis of the static allometric slope across populations or species, we should focus more on adaptive surfaces and patterns of selection than on possible internal developmental mechanisms. It should be kept in mind,

however, that patterns of both ontogenetic allometry and static allometry can be adaptive and that the nonlinearity often observed in ontogenetic allometry may reflect such an adaptation. For example, the shallow allometry observed in head length in mice follows the pattern of allometry in brain size after birth in mammals (Deacon 1990). Most of the growth in brain size occurs before birth in mammals, and in mice the brain reaches its adult size at about 2–3 weeks of age, while the face and trunk continue to lengthen. These different growth patterns are reflected in changes in the genetic and hormonal basis of body growth at different ages (Riska et al. 1984; Cheverud et al. 1996; Vaughn et al. 1999; Cheverud 2005) and possibly result from selection on size at birth. Tail length, on the other hand, grows faster during the postweaning period. Maintaining temperature is an important factor in maximizing body growth in the early postnatal growth period. Mice are born relatively undeveloped and spend their first week or two sequestered in a nest built by their mother, who lies over her pups to provide protection, heat, and milk. The tail lengthens primarily after weaning, when it can serve as a radiator for dispersing heat. Therefore, the steep ontogenetic allometry in tail length observed in this study may result from selection acting on this trait via its thermoregulatory function.

We provided here a simple model to explore the link between ontogenetic and static allometry. We showed that static allometry is rarely similar to ontogenetic allometry and that the difference between the two is most likely affected by the covariance between the size measurement and the ontogenetic allometric slope. It remains unclear what mechanisms generate such a negative correlation in our data. Because steeper ontogenetic allometry will produce larger traits relative to the body size, one can suggest that a trade-off between growing body parts (Klingenberg and Nijhout 1998) could generate such a negative correlation between the ontogenetic allometric slope and body size (e.g., Bonduriansky and Day 2003). A better understanding of the selection acting on these traits both during growth and at the adult stage is therefore necessary to further understand the links between ontogenetic and static allometry.

Acknowledgments

We thank T. F. Hansen, K. L. Voje, and three anonymous reviewers for their comments on earlier versions of this article. The Research Council of Norway supported this project (projects 166869/V40 and 196434/V40). The Norwegian Animal Research Authority gave consent to this research.

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