Journal of Herpetology, Vol. 35, No. 2, pp. 232–238, 2001

Growth of the Original Tail in *Anolis grahami*: Isometry of the Whole Is a Product of Regional Differences

PHILIP J. BERGMANN AND ANTHONY P. RUSSELL[1]

Vertebrate Morphology Research Group, Department of Biological Sciences, University of Calgary,
2500 University Drive N.W., Calgary, Alberta T2N 1N4, Canada

ABSTRACT.—**The original tail of lizards is a segmental structure, each segment containing a vertebra. We examine how the growth of the original tail of *Anolis grahami* is characterized as a single structure and as a structure composed of discrete segments. It is hypothesized that the tail grows isometrically both in its entirety and regionally. The results reveal that the entire tail grows isometrically with reference to SVL but that this isometric growth pattern results from differential growth in successive regions of the tail. Segmentally the tail grows faster proximally than distally and incorporates a middle transitional region. These findings may have implications for the various patterns of tail growth in squamates with different functional roles of the tail.**

The squamate tail is a primitively autotomic structure (Hoffstetter and Gasc, 1969), and caudal autotomy is characteristic of many groups of lizards. The mechanism of tail breakage and the process of regeneration have been the focus of a wide array of investigations (Bryant and Bellairs, 1967; Cox, 1969; Arnold, 1994; Zani, 1996; for a review, see Bellairs and Bryant, 1985). Many studies have examined growth of the regenerate and have shown how it comes to resemble the original in size and form (Bryant and Bellairs, 1967; Cox, 1969; Baranowitz et al., 1977). However, despite obvious structural differences between the regenerate and the original, growth of the latter has not been well studied. To establish a basis by which the growth of the original tail can be compared in taxa exhibiting a wide variety of caudal specializations, we have examined caudal allometry in a lizard (*Anolis grahami*) with a "normally" shaped tail that is subject to autotomy.

Because the original tail is segmented, containing discrete, serially repeating, and easily measured units (the vertebrae), it lends itself to investigation by way of these as well as by measurement of the entire tail. Considering the tail of *A. grahami* as a whole, the null hypothesis has been adopted because it is the simplest case: (1) It grows isometrically relative to snout–vent length (SVL), thus maintaining a constant proportion throughout growth. Considering the individual vertebrae, we hypothesised that, in concordance with the first hypothesis, (2) all caudal vertebrae grow isometrically within their series.

Because *A. grahami* is a lizard with an "actively functional" tail (one which is important in balancing the lizard during locomotion; Vitt et al., 1977; Bauer and Russell, 1994), an alternate hypothesis can be formulated: that the proximal segments of the tail exhibit positive allometry and the distal segments negative allometry. This would allow for rapid growth of proximal nonsegmental caudal muscles (i.e., the m. caudifemoralis longus) and minimize tissue devoted to distal segments, which are more likely to be lost at autotomy. To test these hypotheses, we have employed geometric mean regression (GMR) and principal components analysis (PCA) on cross-sectional data from animals taken from the same field location over a short time span, thereby controlling for geographic and temporal variation.

MATERIALS AND METHODS

Specimen and Data Collection.—A series of *A. grahami* was collected by hand or by using a rubber band to dislodge them from their perches, in June 1978 and May and June 1979 by one of us (APR), south of Mandeville, near Marlborough Airstrip (77°28′E, 18°03′N), Jamaica. On the day of collection, each animal was weighed (to the nearest 0.1 g), sexed, and had its SVL measured (to the nearest 0.1 mm) prior to fixation and preservation. These specimens now reside in the personal collection of APR. *Anolis grahami* is a trunk-crown ecomorph exhibiting sexual size dimorphism, with males attaining a much larger size (Williams, 1983; Powell and Russell, 1992). Growth is determinate in *Anolis* (Stamps and Andrews, 1992), and the tail of *A. grahami* is autotomic.

In the laboratory, 30 individuals with original tails had their sex reconfirmed and SVL, head length (HL), and total tail length (TTL; from posterior edge of cloaca to the tail tip) measured to the nearest 0.1 mm using a digital caliper

---

[1] Corresponding Author. E-mail: arussell@ucalgary.ca.

(each dimension measured three times and the mean value recorded). This sample of specimens was then radiographed using a Hewlett-Packard Faxitron model 43805N radiology unit and Polaroid® Type 55 black-and-white positive/negative film. Radiographs were taken with the specimens lying in direct contact with the film, rendering a 1:1 ratio of original to image size (Myers, 1998).

The following counts and measurements were recorded from the radiographs (Fig. 1): number of presacral, sacral, and postsacral (caudal) vertebrae; number of nonautotomic and autotomic caudal vertebrae; number of caudal vertebrae traversed by the m. caudifemoralis longus and the m. retractor penis magnus [determined after the methods of Russell and Bauer (1992) and Blob (1998)]; the distance from the cloaca to the distal tip of each of these muscles; the length of the nonautotomic and autotomic portions of the tail; the length of the sacrum (two vertebrae); and the length of each individual caudal vertebra. Intergirdle distance was calculated by subtracting HL from SVL. All variables were log-transformed prior to analysis to better approximate normality and linearity.

Statistical Methods.—SYSTAT© versions 5.05 and 7.0 were used for all statistical analyses (Wilkinson, 1990, 1997). Sexual differences in morphometric tail variables were tested using analysis of variance. The assumption of normality of the residual terms was examined using the Kolmogorov-Smirnov test and homoscedasticity of the residuals was investigated with the F_{max}-test. The assumption of independence of the error terms is untestable, so residuals were plotted against estimated values and the resulting plot inspected for the desired random scatter. When one or more of the assumptions were unfulfilled, the Kruskal-Wallis (nonparametric) test was used instead.

Scaling of the original tail as a single unit was modeled using geometric mean regression (GMR; Clarke, 1980; Seim and Saether, 1983; Ricker, 1984). GMR is best used when both variates have error associated with them (Gould, 1966). Testing the slope of the GMR for isometry was carried out as per Ricker (1984).

Scaling of individual components of the tail was examined by running a Principal Components Analysis (PCA) on log-transformed lengths of pairs of vertebrae (see below for reasons). PCA is an exploratory method that reduces large datasets to identify which aspects may be biologically meaningful (Anderson, 1963; Shea, 1985). As a single sample from a single population with multiple measurements per individual was used (Pimentel, 1979), and as growth and size allometry in an ontogenetic series (Shea, 1985) were investigated, PCA was deemed appropriate. All measurements (caudal vertebral lengths) were single dimensional, linear, continuous, and with the same scale, so the R-technique and covariance matrix model were used (Pimentel, 1979).

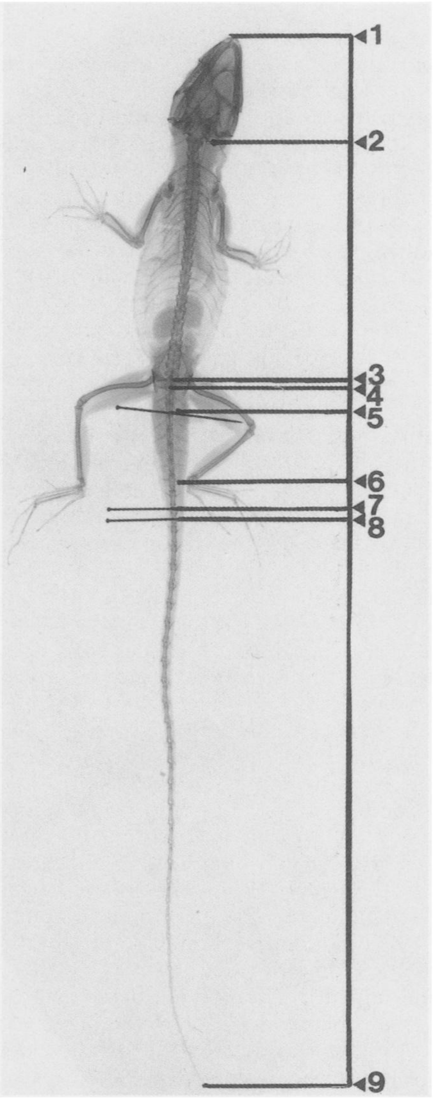

FIG. 1. Dorsal radiograph of an adult male *Anolis grahami* indicating the measurements taken in this study. Snout–vent length (1–5); head length (1–2); total tail length (5–9); Intergirdle length (2–5); cloaca to distalmost origin of m. retractor penis magnus (5–7); cloaca to distalmost origin of m. caudifemoralis longus (5–8); length of nonautotomic portion of the tail (4–6); Length of sacrum (3–4). Pins, in anterior to posterior sequence, are placed at the cloaca, the distalmost point of origin of the m. retractor penis magnus, and the distalmost point of origin of the m. caudifemoralis longus. Individual caudal vertebral lengths were measured between successive points of articulation.

The PCA method assumes a multivariate normal distribution (mnd), that the sample is random, and that the data are linear (Pimentel, 1979). Log-transformation linearizes the data and helps to approximate the mnd (Pimentel, 1979). Although it is difficult to take a truly random biological sample, the assumption of randomness is safe because of the general repeatability of biological studies (Pimentel, 1979). A multivariate normal distribution, although not practically testable, is a conservative assumption (Pimentel, 1979).

The mean vertebral count for the entire sample of individuals with original tails was 39.5 (SD = 0.937, range 38–42), and the mode was 39. Using the modal number would have resulted in a subsample of only 15 individuals. Thus, all specimens were retained for the analysis, with vertebrae 39–42 being excluded from examination. In this way, vertebral number was standardized at 38, with comparisons being run for these first 38 vertebrae, which we have regarded as iterative homologues (Haszprunar, 1991; Roth, 1994). For these analyses, lengths of each adjacent pair of caudal vertebrae were combined (the sacrum is already two vertebrae), decreasing the number of variables (p) to 20. This permitted the sample size ($N = 30$) to exceed the number of variables or measurements ($p > N$; Pimentel, 1979).

Component loadings of principal components were standardized by dividing by the square root of the eigenvalue to give allometric loadings (Pimentel, 1979). The squared (standardized) allometric loadings sum to one (Shea, 1985) and are proportional to growth (Pimentel, 1979). Allometric component correlations were determined by multiplying the allometric loadings by the square root of the eigenvalue and dividing the product by the standard deviation of each variable (Pimentel, 1979). Variance explained by each component for each variable was calculated by multiplying the squared allometric loading by the eigenvalue and dividing the product by variance of the given variable, S_{ai}^2 sensu Pimentel (1979). The contribution of each individual to each component was also determined according to Pimentel (1979).

Sexes were also compared with respect to each principal component by ANOVA or Kruskal-Wallis tests on the specimen component scores for that component, as appropriate (Pimentel, 1979; Adams, 1998). Allometric component correlations were tested for significance by computing the corresponding Pearson's correlation coefficients (Pimentel, 1979; Tissot, 1988). The first principal component (PC-1), generally interpreted as representing changes in shape that are size dependent (Pimentel, 1979; McKinney and McNamara, 1991), was tested for isometry, using ($p^{-1/2}$) as a value for isometry and Anderson's (1963) χ^2 statistic to determine whether the growth of the tail is isometric along its whole length (Jolicoeur, 1963a,b; Mosimann, 1970; Pimentel, 1979). Finally, PC-2 and PC-3, representing size-independent changes in shape (Pimentel, 1979; McKinney and McNamara, 1991), were tested for sphericity using Bartlett's test to determine whether these two PCs were equal or whether they could be interpreted as independent (Pimentel, 1979).

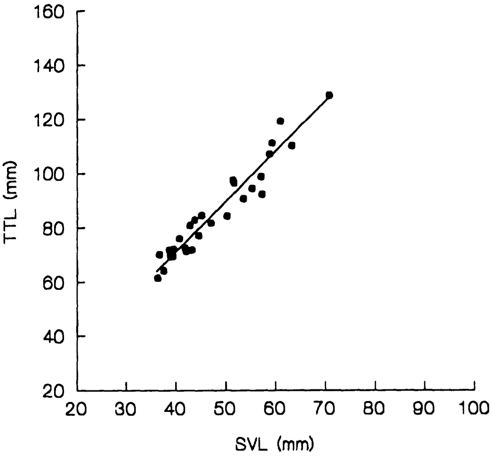

FIG. 2. GMR model of original tail length relative to SVL for *Anolis grahami*. The GMR line superimposed on original tail lengths, showing close fit of the data to the line.

RESULTS

Analysis of Sexual Dimorphism.—Sexual size dimorphism is present in *A. grahami*. SVL is significantly greater in males than in females (ANOVA: $df_{error} = 101$, $F = 99.472$, $P < 0.001$), necessitating evaluation of the features of interest with effects of size removed (relative sexual dimorphism). GMRs were conducted on length variables [TTL, nonautotomic length, autotomic length, and m. caudifemoralis longus (nonsegmental muscle) length]. Their residuals were then compared between sexes using ANOVAs or Kruskal-Wallis tests, thereby eliminating effects of sexual size dimorphism. No relative sexual differences were evident, males simply being larger versions of females. This justified the pooling of the sexes for subsequent analysis.

Scaling of the Tail and Its Segments.—The pooled GMR line relating SVL and TTL yielded the allometric model: $TTL = 1.638\ SVL^{1.024}$ ($r = 0.967$; coefficient: SE = 0.080; exponent: SE = 0.048). This model fits the data well (Fig. 2) and can be used to predict original tail length for a particular SVL that would have been present in individuals that have autotomized or regenerated tails. Our test fails to refute the hypothesis

(1) that the tail as a whole grows isometrically relative to SVL [df = 28, $T_{12} = 0.477$, $P > 0.5$, as per Ricker (1984)].

Inspection of factor scores for each individual for PC-1, PC-2, and PC-3 indicate no special or otherwise outlying individuals. For the PCA carried out on $\log_{10}$-transformed paired vertebral lengths, component loadings, allometric loadings, deviation of allometric loading 1 from the value of isometry, allometric component correlations, and variance explained by each component for each variable (vertebral pair) are presented in Table 1. This PCA assumed no sexual dimorphism (see above), and this was confirmed for all three principal components by comparing factor scores for all individuals with the Kruskal-Wallis test (PC-1: $N = 29$, $U = 105.0$, $P > 0.9$; PC-2: $N = 29$, $U = 113.0$, $P > 0.6$; PC-3: $N = 29$, $U = 73.0$, $P > 0.15$).

The first three principal components explained 95.25% (89.95 + 3.88 + 1.42) of the variance present in the length of the tail. The first principal component (PC-1) is a general component that can be interpreted as explaining variance resulting from changes in size (growth) or shape that is dependent upon size (Pimentel, 1979; McKinney and McNamara, 1991). PC-1 demonstrated allometry when compared to a theoretical isometric vector (df = 19, $\chi^2 = 123.984$, $P \ll 0.001$). This appears to contradict the results from the SVL-TTL regression model described above. However, although the tail grows isometrically relative to SVL, all regions of the tail do not grow at the same rate (allometry occurs between different regions of the tail). Comparing the isometric value ($p^{-1/2} = 0.2236$) to the allometric loadings for PC-1 suggests that the vertebrae at the proximal end of the tail (and the sacrum) grow more quickly (positive allometry), whereas those at the distal end grow more slowly (negative allometry; Table 1). The vertebrae in the middle of the tail constitute a transitional region that fluctuates around (generally within 0.01) the isometric value (Table 1). High and significant ($P < 0.001$) allometric component correlations and inspection of variance explained by PC-1 (Table 1) indicates that PC-1 alone explains a great deal of the variance in tail length. These findings lead us to reject our hypothesis (2) that all segments of the tail grow in the same way.

The second and third principal components were found to be unequal (not spherical; df = 189, $\chi^2 = 1941.841$, $P \ll 0.05$) and, therefore, to represent different portions of the total variance. The second principal component (PC-2) is bipolar, representing variance resulting from shape not associated with growth or size (Mosimann, 1970; Pimentel, 1979; McKinney and McNamara, 1991). Its allometric loadings are positive proximally and negative distally, suggesting relative decrease in some tail characteristic at its distal end. As one proceeds to the very distal extremity of the tail, PC-2 decreases quite dramatically (Table 1). Significance of the allometric component correlations of the last two vertebral pairs for PC-2, as well as the variance explained by PC-2 for each variable (Table 1), indicate that PC-2 mainly explains a difference in the distal end of the tail relative to the more proximal regions.

The third principal component (PC-3) is another bipolar component that explains a small amount (1.42%) of the variance in tail length not associated with growth or size (a shape component). It divides the tail into three regions (proximal, middle, and distal) based on polarity changes from positive allometric loadings to negative and then to positive again (Table 1). Allometric component correlation values and variance of each variable explained by PC-3 suggest that several variables (lv^a, lv^j, lv^k, and lv^s) contribute significantly to PC-3 (Table 1).

Discussion

In the case of *A. grahami*, no sexual differences (size effects removed) were found between males and females. Thus, males are essentially hypermorphic females, corroborating sexual comparisons for this species with regard to locomotor parameters (Powell and Russell, 1992).

With regard to the entire tail (Fig. 2), it is apparent that it grows isometrically relative to the body (SVL), as in *Pachydactylus capensis capensis* (Bates, 1989). However, isometry in *A. grahami* is more complicated than it at first appears, and it is now possible to consider tail growth in two different ways—in relation to SVL (in which case isometry is displayed) and with regard to the relative growth of individual caudal segments (in which case it is not). Comparing the PC-1 vector to a theoretical (isometric) vector suggests allometry, indicating that the tail's shape is not independent of its size (Pimentel, 1979) and that relative to the overall pattern of growth (Shea, 1985), different regions of the tail grow at different rates. Simply, the proximal end of the tail grows fastest (positive allometry), a large central portion grows isometrically (relative to the value of isometry), and the distal end grows more slowly (negative allometry; Table 1). The observed fluctuation and lack of clarity in scaling of the central transitional region of the tail may become clearer with a larger sample size and further study. It may well be currently obscured by the pairing of vertebrae into variables, reducing the resolution of our analysis.

The regionalization of the tail by PC-2 (Table 1) into a proximal and a distal half can be considered as a response to a genetic or environ-

TABLE 1. Summary of results for Principal Components Analysis conducted on log-transformed caudal vertebral lengths for *Anolis grahami*. (lsac = log(sacral length), lv = log(vertebral pair length), CLoad—Component loadings, ALoad—Allometric loadings, Deviation—difference between Aload-1 and the value of isometry (0.2236, not relevant for PC-2 and PC-3), ACorr—Allometric component correlations, Var—Variance explained for each variable. See text.)

Variable	CLoad-1	CLoad-2	CLoad-3	ALoad-1	Deviation	ALoad-2	ALoad-3	ACorr-1	ACorr-2	ACorr-3	Var-1	Var-2	Var-3
lsac	0.0919	0.0064	0.0005	0.2583	0.0347	0.0870	0.0106	0.9421	0.0659	0.0049	0.9951	0.0049	0.0000
lv^{a}	0.0832	0.0200	0.0329	0.2340	0.0104	0.2708	0.7352	0.8952	0.2153	0.3536	0.8238	0.0477	0.1286
lv^{b}	0.0797	0.0118	0.0087	0.2240	0.0004	0.1603	0.1954	0.9405	0.1398	0.1031	0.9670	0.0214	0.0116
lv^{c}	0.0774	0.0139	0.0047	0.2175	−0.0061	0.1881	0.1059	0.9448	0.1698	0.0578	0.9652	0.0312	0.0036
lv^{d}	0.0802	0.0075	0.0061	0.2256	0.0020	0.1016	0.1367	0.9713	0.0909	0.0740	0.9856	0.0086	0.0057
lv^{e}	0.0774	0.0122	−0.0041	0.2175	−0.0061	0.1650	−0.0917	0.9693	0.1528	−0.0514	0.9731	0.0242	0.0027
lv^{f}	0.0811	0.0125	0.0006	0.2282	0.0046	0.1684	0.0144	0.9666	0.1483	0.0077	0.9769	0.0230	0.0001
lv^{g}	0.0822	0.0081	−0.0093	0.2312	0.0076	0.1096	−0.2077	0.9674	0.0953	−0.1093	0.9780	0.0095	0.0125
lv^{h}	0.0795	0.0102	−0.0039	0.2236	0.0000	0.1383	−0.0878	0.9657	0.1242	−0.0477	0.9814	0.0162	0.0024
lv^{i}	0.0806	0.0105	−0.0069	0.2266	0.0030	0.1415	−0.1543	0.9672	0.1255	−0.0828	0.9764	0.0164	0.0072
lv^{j}	0.0842	0.0063	−0.0138	0.2367	0.0131	0.0848	−0.3080	0.9771	0.0728	−0.1598	0.9687	0.0054	0.0259
lv^{k}	0.0860	0.0020	−0.0134	0.2417	0.0181	0.0267	−0.2990	0.9710	0.0223	−0.1510	0.9759	0.0005	0.0236
lv^{l}	0.0788	−0.0020	−0.0102	0.2217	−0.0019	−0.0276	−0.2283	0.9712	−0.0251	−0.1257	0.9829	0.0007	0.0165
lv^{m}	0.0791	−0.0028	−0.0019	0.2223	−0.0013	−0.0375	−0.0425	0.9860	−0.0346	−0.0237	0.9982	0.0012	0.0006
lv^{n}	0.0804	−0.0080	−0.0036	0.2261	0.0025	−0.1084	−0.0811	0.9780	−0.0975	−0.0441	0.9882	0.0098	0.0020
lv^{o}	0.0822	−0.0122	−0.0022	0.2310	0.0074	−0.1651	−0.0492	0.9767	−0.1451	−0.0261	0.9777	0.0216	0.0007
lv^{p}	0.0818	−0.0155	0.0038	0.2301	0.0065	−0.2092	0.0855	0.9672	−0.1827	0.0452	0.9635	0.0344	0.0021
lv^{q}	0.0727	−0.0232	0.0039	0.2045	−0.0191	−0.3134	0.0867	0.9346	−0.2977	0.0498	0.9056	0.0919	0.0026
lv^{r}	0.0642	−0.0337	0.0018	0.1805	−0.0431	−0.4561	0.0398	0.8547	−0.4490	0.0237	0.7833	0.2161	0.0006
lv^{s}	0.0627	−0.0432	0.0094	0.1763	−0.0473	−0.5846	0.2107	0.7827	−0.5395	0.1176	0.6677	0.3172	0.0151
Eigenvalue	0.1265	0.0055	0.0020										

mental causal stimulus (Pimentel, 1979). A steady drop in PC-2 allometric loadings suggests a process that changes directionally along the length of the tail. If the vertebrae in the tail are shaped and constrained, as other bones are, by their immediate environment (forces and tensions from muscles; Currey, 1984), then different caudal vertebrae will be under slightly different sets of constraints. Specifically, it can be hypothesized that vertebrae at the distal end of the tail are loaded differently from more proximal ones. This hypothesis arises from the suggestion that the former are not encroached upon by the nonsegmental muscles of the body (the m. caudifemoralis longus in both sexes, and the m. retractor penis magnus in males).

At its proximal end, the tail is more stationary, loaded more severely at both ends (the body at one extreme and the remainder of the tail at the other), and influenced by the nonsegmental muscles of the tail base (see above). Russell and Bauer (1992) suggested that a larger (by mass) m. caudifemoralis longus would yield a greater power output and that, in lizards tending toward faster locomotion, the m. caudifemoralis longus is larger. As the lizard grows, this muscle requires more space, and so may influence the proximal vertebrae to grow more quickly. Furthermore, if the lizard loses a portion of its tail, there is always a greater probability of losing the distalmost vertebrae than more proximal ones, and the proximalmost of these (the first 6–7 caudal vertebrae in *A. grahami*) are never lost. The distalmost segments will always be more prone to loss, and thus it may be disadvantageous to invest substantial resources in the distal vertebrae. These ideas require testing and can be approached by examining the growth rate of the m. caudifemoralis longus through ontogeny and the pattern of growth of the distal tail segments relative to more proximal ones in taxa that possess nonautotomic tails, where there is no risk of loss of the distal segments. Under this conceptual framework, one would hypothesize that m. caudifemoralis longus grows more quickly than the rest of the body and that distal vertebrae in lizards that lack capacity for autotomy would grow more quickly than in lizards that are capable of autotomy.

PC-3 allometric loadings regionalize the tail into three parts. The proximal section correlates quite well with the nonautotomous vertebrae (variables lv^a-lv^d, Table 1), of which *A. grahami* has six to seven. The distal section imperfectly correlates with the negative allometric growth region. This pattern may support the alternative hypotheses concerning the roles of the nonsegmental musculature in the base of the tail and imposition of autotomy on the distal end of the tail. This, however, requires further investigation to see whether it is a more general phenomenon and has biological meaning (Pimentel, 1979).

In the model presented here, vertebrae (or pairs of vertebrae) were used. These are meaningful units as they are discrete rather than arbitrary. Comparisons across species to investigate patterns of original tail growth are possible by applying this approach along with the assessment of growth of the tail as an entire unit. Specifically, similar allometric patterns should be tested for in other taxa with "actively" functional tails as well as those with "passively" functional tails (Vitt et al., 1977; Bauer and Russell, 1994) on the one hand and nonautotomic tails on the other. In this way, correlation between differential allometry and caudal autotomy can be evaluated.

Acknowledgments.—We would like to thank L. Powell for his willing (and integral) donation of time in statistical and theoretical advice and discussion and for reviewing numerous earlier drafts. We thank K. Bergmann, who helped with the recording of data, making this process more expedient. Two anonymous reviewers helped us to improve the manuscript considerably. Financial support was provided by way of an NSERC Research Grant to APR.

LITERATURE CITED

ADAMS, R. A. 1998. Evolutionary implications of developmental and functional integration in bat wings. J. Zool. Lond. 246:165–174.

ANDERSON, T. W. 1963. Asymptotic theory for principal component analysis. Ann. Math. Stat. 34:122–148.

ARNOLD, E. N. 1994. Investigating the evolutionary effects of one feature on another: does muscle spread suppress caudal autotomy in lizards? J. Zool. Lond. 232:505–523.

BARANOWITZ, S. A., S. N. SALTHE, AND P. F. A. MADERSON. 1977. The use of the Gompertz Curve in an analysis of the dynamics of lizard tail regeneration. J. Theor. Biol. 65:267–279.

BATES, M. F. 1989. Tail-break frequency, tail size and extent of caudal autotomy in the cape thick-toed gecko, *Pachydactylus capensis capensis* (Sauria: Gekkonidae). Navors. Nasionale Mus. Blomfontein 6: 223–242.

BAUER, A. M., AND A. P. RUSSELL. 1994. Is autotomy frequency reduced in geckos with "actively functional" tails? Herpetol. Nat. Hist. 2:1–15.

BELLAIRS, A. D'A., AND S. V. BRYANT. 1985. Autotomy and regeneration in reptiles. *In* C. Gans and F. Billet (eds.), Biology of the Reptilia. Vol. 15. Development B, pp. 301–410. John Wiley and Sons, New York.

BLOB, R. W. 1998. Evaluation of vent position from lizard skeletons for estimation of snout–vent length and body mass. Copeia 1998:792–801.

BRYANT, S. V., AND A. D'A. BELLAIRS. 1967. Tail regeneration in the lizards *Anguis fragilis* and *Lacerta dugesii*. Zool. J. Linn. Soc. 46:297–305.

CLARKE, M. R. B. 1980. The reduced major axis of a bivariate sample. Biometrika 67:441–446.

COX, P. G. 1969. Some aspects of tail regeneration in the lizard, *Anolis carolinensis*. I. A description based on histology and autoradiography. J. Exp. Zool. 171:127–150.

CURREY, J. 1984. The Mechanical Adaptations of Bones. Princeton Univ. Press, Princeton, NJ.

GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biol. Rev. Camb. Philos. Soc. 41: 587–640.

HASZPRUNAR, G. 1991. The types of homology and their significance for evolutionary biology and phylogenetics. J. Evol. Biol. 5:13–24.

HOFFSTETTER, R., AND J.-P. GASC. 1969. Vertebrae and ribs of modern reptiles. *In* C. Gans, A. d'A. Bellairs, and T. S. Parsons (eds.), Biology of the Reptilia. I: Morphology A, pp. 201–310. Academic Press, London.

JOLICOEUR, P. 1963a. The degree of generality of robustness in *Martes americana*. Growth 27:1–27.

———. 1963b. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

MCKINNEY, M. L., AND K. J. MCNAMARA. 1991. Heterochrony: The Evolution of Ontogeny. Plenum Press, New York.

MOSIMANN, J. E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. J. Am. Stat. Assoc. 65:930–945.

MYERS, M. F. 1998. Morphometry of the limb skeleton of *Anolis garmani*: practical and theoretical implications. Unpubl. master's thesis. Univ. of Calgary, Calgary, Alberta, Canada.

PIMENTEL, R. A. 1979. Morphometrics: The Multivariate Analysis of Biological Data. Kendall/Hunt Publishering Co., Dubuque, IA.

POWELL, G. L., AND A. P. RUSSELL. 1992. Locomotor correlates of ecomorph designation in *Anolis*: an examination of three sympatric species from Jamaica. Can. J. Zool. 70:725–739.

RICKER, W. E. 1984. Computation and uses of central trend lines. Can. J. Zool. 62:1897–1905.

ROTH, V. L. 1994. Within and between organisms: replicators, lineages and homologues. *In* B. K. Hall (ed.), Homology: The Hierarchical Basis of Modern Biology. Academic Press, San Diego, CA.

RUSSELL, A. P., AND A. M. BAUER. 1992. The *m. caudifemoralis longus* and its relationship to caudal autotomy and locomotion in lizards (Reptilia: Sauria). J. Zool., Lond. 227:127–143.

SEIM, E., AND B.-E. SAETHER. 1983. On rethinking allometry: Which regression model to use? J. Theor. Biol. 104:161–168.

SHEA, B. T. 1985. Bivariate and multivariate growth allometry: statistical and biological considerations. J. Zool. Lond. 206:367–390.

STAMPS, J. A., AND R. M. ANDREWS. 1992. Estimating asymptotic size using the largest individuals per sample. Oecologia 92:503–512.

TISSOT, B. N. 1988. Multivariate analysis. *In* M. L. McKinney (ed.), Heterochrony in Evolution, pp. 35–51. Plenum Press, New York.

VITT, L. J., J. D. CONGDON, AND N. A. DICKSON. 1977. Adaptive strategies and energetics of tail autotomy in lizards. Ecology 58:326–337.

WILKINSON, L. 1990. SYSTAT: The System for Statistics. SYSTAT, Inc., Evanston, IL.

———. 1997. SYSTAT. SYSTAT, Inc., Chicago.

WILLIAMS, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations in *Anolis*. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology: Studies of a Model Organism, pp. 326–370. Harvard Univ. Press, Cambridge, MA.

ZANI, P. A. 1996. Patterns of caudal-autotomy evolution in lizards. J. Zool. Lond. 240:1201–220.

Accepted: 26 June 2000.