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GROWING APART TOGETHER: THE DEVELOPMENT OF CONTRASTING SEXUAL SIZE DIMORPHISMS IN SYMPATRIC *SCELOPORUS* LIZARDS

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ABSTRACT: Comparative biologists often conceptualize sexual size dimorphism (SSD) as a static characteristic of adult populations, but recent work has emphasized that SSD reflects a developmental process in which males and females “grow apart” in body size. This ontogenetic perspective requires knowledge of (1) the demographic factors that give rise to SSD (e.g., differential survival, migration, or growth) and (2) the ontogenetic timing of these sexual differences (e.g., juvenile, maturational, or adult divergence). Together, such data help formulate testable hypotheses concerning proximate physiological mechanisms responsible for the development of SSD. To illustrate this approach, we present a case study of two sympatric lizard congeners with opposite patterns of SSD (*Sceloporus virgatus*: female-larger; *S. jarrovi*: male-larger). Using mark-recapture data, we show that (1) sex differences in survival and migration cannot account for SSD, and (2) both nonlinear growth models and age-specific linear growth rates identify sexually dimorphic growth as the cause of SSD in each species. SSD develops in *S. virgatus* because females grow more quickly than males, particularly during the spring mating season. By contrast, SSD develops in *S. jarrovi* because males grow more quickly than females throughout the first year of life, particularly in association with vitellogenesis and gestation in females. Thus, opposite developmental patterns of SSD in these species may reflect underlying differences in energetic trade-offs between reproduction and growth.

Key words: Asymptotic size; Body size; Growth model; Growth rate; Survivorship

SINCE the pioneering work of Darwin (1871), evolutionary biologists have devoted considerable attention to the selective forces responsible for sex differences in body size, or sexual size dimorphism (SSD). However, recent work has sought to integrate this knowledge of ultimate causation with an understanding of the proximate developmental mechanisms that regulate sex differences in growth and body size (e.g., Badyaev, 2002; Duvall and Beaupre, 1998; Watkins, 1996). As an example of such an approach, we have recently begun to develop *Sceloporus* lizards as a model comparative system for integrative studies of the ontogenesis, physiological regulation, genetic basis, environmental plasticity, and adaptive significance of SSD (Cox, 2006; Cox and John-Alder, 2005; Cox et al., 2005; Cox et al., 2006; Haenel and John-Alder, 2002). Lizards have historically served as important models for SSD (Cox et al., 2007; Cox et al., 2003), and *Sceloporus* lizards in

particular are well suited to such studies because they exhibit multiple evolutionary shifts in the direction of SSD (John-Alder and Cox, 2007). For example, in the present study, we compare two related *Sceloporus* species that differ in the direction of SSD: females average 10% larger than males in *S. virgatus*, while males average 10% larger than females in *S. jarrovi*. These congeners are also sympatric, providing a unique opportunity to compare the development of contrasting patterns of SSD in a common environmental context.

In a recent review, Badyaev (2002) emphasized the importance of adopting an ontogenetic perspective in which SSD is viewed as a developmental process of “growing apart”. This requires the careful description of growth trajectories for each sex in the natural environment, which is essential for at least two reasons. First, sex differences in the body size of sampled individuals can reflect a variety of underlying causes, including sex differences in size at birth, pre- or post-maturational growth trajectories, survival, emigration and recruitment, behavioral exclusion of small individuals, or some combination of these factors (Haenel and John-Alder, 2002; Stamps, 1993; Watkins,

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1996). To understand both how and why SSD arises, it is essential to determine which of these factors contribute to SSD within a population.

Second, a careful description of the ontogenesis of SSD is necessary to identify the critical developmental periods in which males and females diverge in size, thereby suggesting testable hypotheses for how and why SSD occurs. For example, a detailed demographic study of the lizard *Sceloporus undulatus* concluded that female-larger SSD develops because of a sharp sexual divergence in the growth rate of juveniles during a discrete ontogenetic period (Haenel and John-Alder, 2002). Subsequent studies linked this ontogenetic period to maturational increases in plasma testosterone levels and associated activity patterns in males, and then proceeded to use an experimental approach to verify an inhibitory effect of testosterone on the growth of males (Cox et al., 2005).

In the present study, we provide a similar ontogenetic characterization of SSD in two sympatric congeners with opposite patterns of SSD. Our data clearly show that SSD develops in each species because of sex differences in postnatal growth trajectories, rather than differences in survival or migration. Further, we identify the critical ontogenetic periods when growth diverges between males and females and illustrate how these data have informed subsequent experiments addressing the proximate physiological mechanisms that give rise to SSD in each species (Cox, 2006; Cox and John-Alder, 2005). We propose that SSD develops in *S. virgatus* in part because the growth of males is constrained by energetic costs associated with reproduction, such as reduced feeding and increased metabolic expenditure. Opposite patterns of SSD in *S. virgatus* and *S. jarrovi* may thus reflect underlying differences in such energetic constraints on the growth of males.

MATERIALS AND METHODS

Study Species and Sampling Methods

Sceloporus virgatus Smith (striped plateau lizard) and *S. jarrovi* Cope (Yarrow's spiny lizard) are sympatric in the Chiricahua Mountains of southeastern Arizona (USA). Although these species belong to divergent

clades within the speciose genus *Sceloporus* (Wiens and Reeder, 1997), they are ecologically similar in a number of ways. Both species are primarily saxicolous, employ sit-and-wait foraging tactics, share common prey and predators, attain sexual maturity as yearlings, reproduce only once annually, and exhibit polygynous mating systems characterized by males that engage in aggressive intrasexual competition for breeding females (reviewed by Degenhardt et al., 1996). These species also differ in several important regards. *Sceloporus virgatus* is small (maximum SVL = 71 mm), mates in the spring, and lays a single clutch of eggs (oviparity) in the summer. By contrast, *S. jarrovi* is relatively large (maximum SVL = 97 mm), mates in the fall, and gives birth to live young (viviparity) in late spring. Of central importance to this study, *S. virgatus* females average 10% larger than males, whereas *S. jarrovi* males average 10% larger than females (Fitch, 1978; Ruby and Dunham, 1984).

We studied both *S. virgatus* and *S. jarrovi* along a single 1-km section of streambed in Cave Creek Canyon (North Fork) located 1–2 km northwest of the American Museum of Natural History's Southwestern Research Station in the Coronado National Forest, Cochise Co., Arizona (31° 53–54' N, 109° 13' W, elevation 1660–1710 m). Previous authors have summarized the important biotic and biophysical features of this habitat (Ballinger, 1979; Vinegar, 1975b). Over three consecutive years (May 2002 through October 2004), we periodically searched the entire site and captured all visible animals of each species by noose. Sampling censuses typically lasted 7–10 d (about 50 person-hours of search effort) and were conducted at intervals ranging from 1–3 mo within each active season (April–October).

We gave each animal a unique toe clip for permanent identification. At each capture, we measured snout–vent length (SVL) to the nearest 1 mm with a ruler and body mass to the nearest 0.1 g with a Pesola® spring scale. We determined sex by the presence (males) or absence (females) of enlarged post-anal scales. We determined year of birth (i.e., cohort) based on SVL and mass at initial capture. Both species breed synchronously and only

once per year, so individuals from the same cohort differ at most by several weeks of age. We were able to determine cohort from body size for all *S. virgatus* individuals first captured before the age of 9 mo post-hatching (June) and all *S. jarrovi* individuals captured before an age of 12 mo (June). After these ages, we found within-sex overlap in the size distribution of animals from different cohorts. Thus, if our initial capture of an individual occurred after these time points, we considered its age uncertain and omitted such animals from most analyses (see below).

Body Size and Growth

Length is the preferred metric for measuring growth in lizards because body mass typically fluctuates with variation in stomach contents, fat storage, and reproductive status (Andrews, 1982; Dunham, 1978a; Haenel and John-Alder, 2002). Accordingly, our analyses of size and growth focus on SVL. For illustrative purposes, we express sex differences in SVL using the Lovich and Gibbons (1992) index of SSD, calculated as follows:

$$\text{SSD} = \left(\frac{\text{mean SVL of larger sex}}{\text{mean SVL of smaller sex}} \right) - 1$$

To indicate the direction of SSD, we assigned this index a positive value when females were the larger sex and a negative value when males were the larger sex.

We used two different approaches to compare body size and growth. First, we derived growth trajectories for males and females of each species by fitting asymptotic growth curves to our recapture data. We used the interval forms of three common models (Von Bertalanffy, logistic-by-length, and logistic-by-weight) to estimate two parameters for each sex: asymptotic size (A) and characteristic growth rate (k). We randomly selected a single growth interval per animal to ensure independence among data points and fitted growth trajectories using a Marquardt nonlinear least-squares regression procedure (Dunham, 1978b). For each model, we calculated 95% support plane confidence intervals for A and k and considered sex differences to be significant when these confidence intervals did not overlap (Dun-

ham, 1978a). For illustrative purposes, we plotted our fitted growth trajectories against size data for animals of known age. We estimated size at birth (L_0) based on the smallest measured animal of each sex (24 mm for both sexes of *S. virgatus*, 29 mm for both sexes of *S. jarrovi*). To align size data with growth trajectories, we estimated cumulative age by assuming that all animals were born on the first day on which neonates were observed for a given cohort. We then estimated the number of days spent growing (growth days) by subtracting periods of winter dormancy from our estimates of cumulative age. Periods of winter dormancy were approximated from data in Ballinger (1979) as well as our own observations of each species. Our estimates of winter dormancy are solely for graphical convenience to align our size data with growth trajectories and do not affect our statistical comparisons or parameter estimates.

Asymptotic growth models are useful because they yield parameter estimates that are directly comparable between sexes, populations, and species, but they assume that these parameters are invariant with respect to time. Thus, stationary growth models are poorly suited to analyses of seasonal variation in growth (Dunham, 1978a). As a complementary approach, we also compared linear growth rates of males and females of known age over discrete time intervals. We calculated linear growth rates by dividing change in SVL by elapsed time (mm/d). Recapture intervals ranged from 1–3 mo within each active season (April–October). For each interval, we compared growth rate between males and females using ANOVA with sex, cohort, and their interaction as categorical effects. To investigate the development of SSD, we compared SVL of males and females at the beginning and end of each interval using ANOVA with sex and cohort as categorical effects with interaction.

Survival and Recapture Probabilities

We used the program MARK (version 4.2, White and Burnham, 1999) to estimate the probability of survival (Φ) and recapture (p) from our mark-recapture data. We estimated Φ and p separately for yearlings versus older animals over three successive intervals within

each season: spring (Apr–Jun), summer (Jun–Sep), and winter (Sep–Apr). In all models, we allowed Φ and p to vary over these six age classes. We generated four alternative candidate models by variably including or excluding sex effects on Φ and p . We assessed goodness-of-fit for the fully parameterized model (i.e., both Φ and p estimated separately by sex) by using a bootstrapping procedure (1000 iterations) to estimate the variance inflation factor for *S. virgatus* ($\hat{c} = 1.492$) and *S. jarrovi* ($\hat{c} = 1.459$). In both species, this \hat{c} value was significantly ($P < 0.001$) lower than simulated values, indicating that our recapture data fit our a priori model (Cooch and White, 1999). We used these \hat{c} values to calculate quasi-likelihood adjusted Akaike's information criteria (QAIC) for each candidate model. The QAIC score corrects for variance overdispersion (as indicated when $\hat{c} > 1$) by dividing the model likelihood estimate by \hat{c} , thereby diminishing the contribution of model likelihood and increasing the penalty for additional parameters as \hat{c} increases (Cooch and White, 1999). We tested for significant sex differences in Φ and p by comparing QAIC for models with and without sex effects on each parameter. Cooch and White (1999) provide a detailed description of this procedure.

Size-specific Survival and Migration

Even if age-specific survival is identical in both sexes, it is possible that sex differences in size-specific survival or migration could differentially affect the size distributions of males and females of the same age. At each census, we separated animals into (1) those that were recaptured in any subsequent census (survivors that remained on site), and (2) those that were never recaptured (assumed to have either died or emigrated). For each interval, we used logistic regression to determine the effects of sex, initial SVL, cohort, and their interactions on this binomial survival outcome. We inferred sex differences in the size-dependence of survival on the basis of significant sex*SVL interactions. We conducted analogous ANOVA analyses to investigate the effect of immigration on the size distributions of males and females. At each census, we separated animals into (1) those captured in previous censuses (residents), and

(2) those with no prior record of capture (assumed to be recent immigrants, exclusive of neonates). For each census, we used ANOVA with SVL as the dependent variable and immigration status, sex, and year of birth as categorical effects with full interaction. We inferred sex differences in the size-dependence of immigration on the basis of significant sex*immigration interactions.

Body Condition and Growth

To estimate energy balance during the mating season, we compared the relationship between body mass and SVL in yearling males and females captured at both the beginning and the end of the mating season. For each species, we regressed \log_{10} body mass against \log_{10} SVL, with separate regressions performed for each sex. Within each sex, we estimated a single regression line from a dataset including two sets of size measurements for each individual: one measurement from the beginning of the mating season, and one from the end of the mating season. Residuals were obtained from this pooled regression line and a single value was calculated for each animal by subtracting the residual of its initial measurement from the residual of its own final measurement. The resultant values facilitate a direct statistical test for change in the relationship between mass and SVL. If mass and length increase isometrically (i.e., parallel to the regression line), these values should average zero. If change in mass is disproportionate to change in length, these values should be positive (body condition improves) or negative (body condition declines). Therefore, these values were examined using a two-tailed t -test with a null hypothesis that change in body condition over the mating season would equal zero. We emphasize that changes in the relationship between body mass and length provide only a crude approximation of changes in energy balance, so inferences with respect to the underlying energetics of males and females should be made with caution.

RESULTS

Over three successive years (May 2002–October 2004), we made a total of 1391 captures of 777 individuals of *Sceloporus*

TABLE 1.—Parameter estimates for asymptotic size (A) and the characteristic growth parameter (k) of males and females under the Von Bertalanffy (VB), logistic-by-length (LL), and logistic-by-weight (LW) growth models. Sex differences in parameter estimates were considered significant if there was no overlap in associated 95% planar support confidence intervals (95% CI).

Species	Model	Sex	n	R^2	$A \pm 95\% \text{ CI}$	$k \pm 95\% \text{ CI}$
<i>S. virgatus</i>	VB	♀	156	0.999	67.40 \pm 1.50	0.00994 \pm 0.00119
		♂	112	0.999	61.76 \pm 1.25	0.00875 \pm 0.00125
	LL	♀	156	0.999	64.35 \pm 0.93	0.01752 \pm 0.00143
		♂	112	0.999	59.52 \pm 0.96	0.01512 \pm 0.00222
	LW	♀	156	0.999	63.24 \pm 0.90	0.02485 \pm 0.00203
		♂	112	0.999	58.81 \pm 1.00	0.02046 \pm 0.00393
<i>S. jarrovi</i>	VB	♀	193	0.998	82.13 \pm 2.02	0.00780 \pm 0.00079
		♂	149	0.999	92.49 \pm 2.15	0.00757 \pm 0.00077
	LL	♀	193	0.997	78.68 \pm 2.09	0.01446 \pm 0.00159
		♂	149	0.998	86.52 \pm 1.99	0.01597 \pm 0.00152
	LW	♀	193	0.996	77.26 \pm 2.30	0.02200 \pm 0.00302
		♂	149	0.997	84.23 \pm 2.33	0.02567 \pm 0.00316

virgatus (389 males, 388 females), and 1847 captures of 753 individuals of *S. jarrovi* (336 males, 417 females). Of these animals, we reliably determined age for 683 individuals of *S. virgatus* (339 males, 344 females) and 718 individuals of *S. jarrovi* (320 males, 398 females).

Asymptotic Growth Models

Table 1 reports parameter estimates and associated 95% support plane confidence intervals for asymptotic size (A) and the characteristic growth parameter (k) for males and females of each species. Overall, the Von Bertalanffy model provided the best fit to our recapture data (Table 1; Fig. 1), although both the logistic-by-length and logistic-by-weight models performed nearly as well ($r^2 \geq 0.997$; Table 1). Under all three models, females grew to significantly larger asymptotic sizes than males in *S. virgatus*, whereas males grew to significantly larger asymptotic sizes than females in *S. jarrovi* (Table 1; Fig. 1). Sex differences in k were not evident in either species under any of the three models, although the larger sex of each species tended to exhibit slightly higher k values under the logistic-by-length and logistic-by-weight models (Table 1).

Size and Growth Over Discrete Intervals

Males and females of *S. virgatus* hatched in early September at similar size (SSD = 0.007; $F_{3,110} = 0.00$; $P = 0.995$; Fig. 2a). Neonatal males and females grew at similar rates during

their first fall ($F_{1,38} = 0.02$; $P = 0.901$; Fig. 2a), such that SSD was still absent in late October (SSD = 0.022; $F_{1,83} = 1.85$; $P = 0.178$; Fig. 2a). Although *S. virgatus* exhibits female-larger adult SSD, yearling males were slightly but consistently larger than females upon emergence the following April (SSD = -0.026; $F_{3,343} = 6.76$; $P = 0.010$; Fig. 2a). However, over the ensuing spring mating season, mean growth rate of yearling females was nearly twice that of yearling males ($F_{5,163} = 73.28$; $P < 0.001$; Fig. 2a), such that females were significantly larger than males by early June (SSD = 0.028; $F_{5,308} = 11.62$; $P < 0.001$; Fig. 2a). Females also tended to grow more quickly than males over the subsequent summer ($F_{3,52} = 3.91$; $P = 0.052$; Fig. 2a). By late August (1 yr post-hatching), sex differences in SVL were pronounced (SSD = 0.084; $F_{5,90} = 104.59$; $P < 0.001$; Fig. 2a). Growth was negligible in both sexes over the second winter, but growth rate of females exceeded that of males during the second spring mating season ($F_{3,36} = 8.17$; $P = 0.007$; Fig. 2a), such that SSD was pronounced at the end of the second mating season (SSD = 0.081; $F_{3,66} = 108.89$; $P < 0.001$; Fig. 2a).

Neonatal males of *S. jarrovi* were slightly larger than females when all measurements from within a month of birth were pooled (SSD = -0.027; $F_{5,206} = 8.41$; $P = 0.004$; Fig. 2b), but SSD was not evident when we considered only those animals measured within 7 d of birth (SSD = -0.011; $F_{3,56} = 0.22$; $P = 0.644$). Males grew more quickly

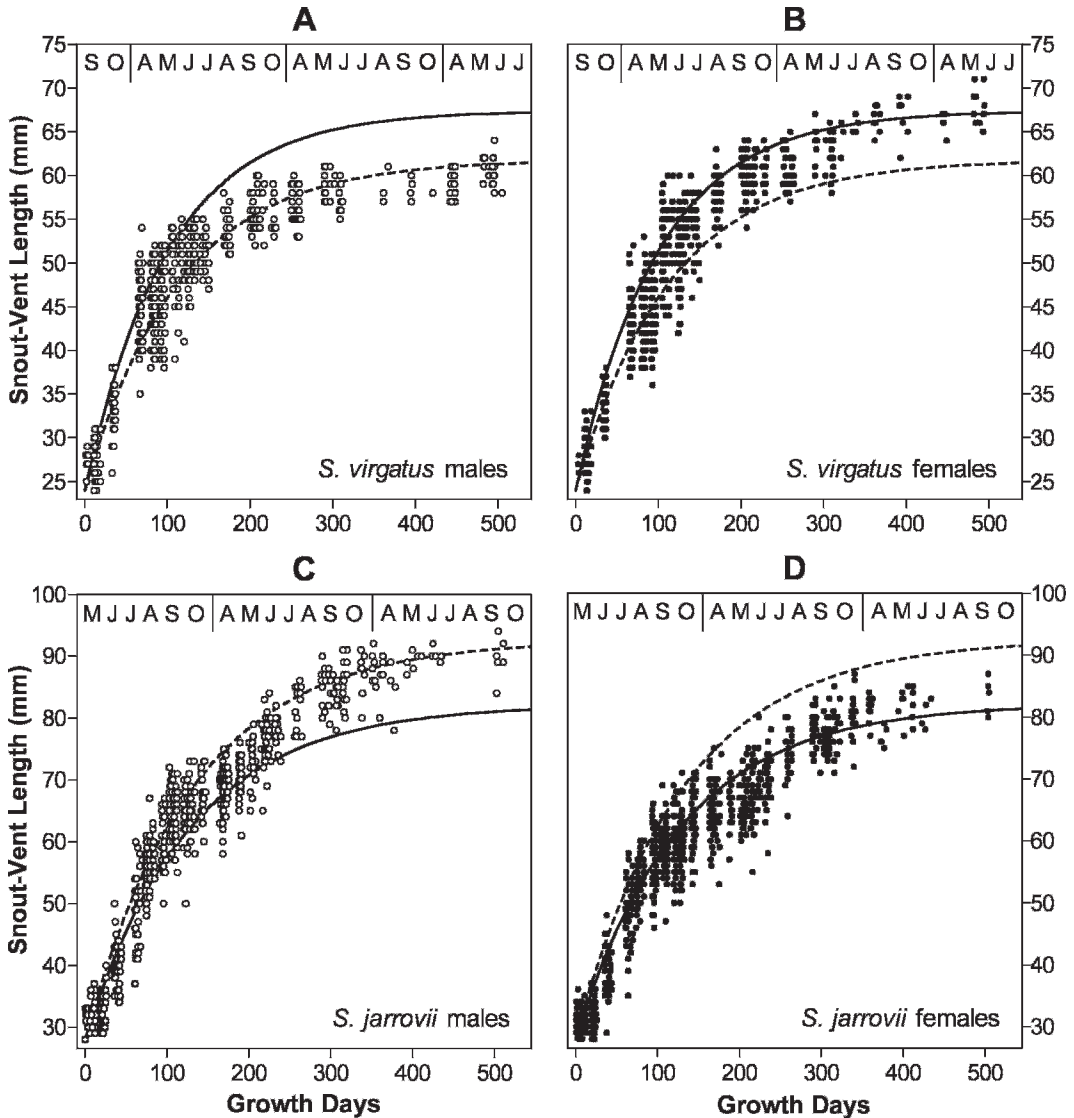


FIG. 1.—Snout-vent length (SVL) versus time spent growing (growth days) for males (open symbols) and females (filled symbols) in *Sceloporus virgatus* (top panels) and *S. jarrovii* (bottom panels). Growth trajectories for males (dashed lines) and females (solid lines) are superimposed over these data, as derived from the Von Bertalanffy growth model. Growth trajectories of both sexes are plotted in each panel to facilitate comparison. Time is expressed in months at the top of each panel.

than females over the ensuing summer months ($F_{5,69} = 14.50$; $P < 0.001$; Fig. 2b) and were substantially larger than females by late August (SSD = -0.055 ; $F_{5,373} = 67.50$; $P < 0.001$; Fig. 2b). Growth rate of males continued to exceed that of females during the first fall mating season ($F_{3,121} = 20.28$; $P < 0.001$; Fig. 2b), such that sex differences in

SVL were pronounced by late October (SSD = -0.081 ; $F_{3,168} = 62.43$; $P < 0.001$; Fig. 2b). Upon emergence the following spring, yearling males continued to grow more quickly than females ($F_{3,90} = 24.44$; $P < 0.001$; Fig. 2b), at which time most (80%) yearling females were pregnant. By early June (ca. 1 yr of age), SSD reached maximal values and

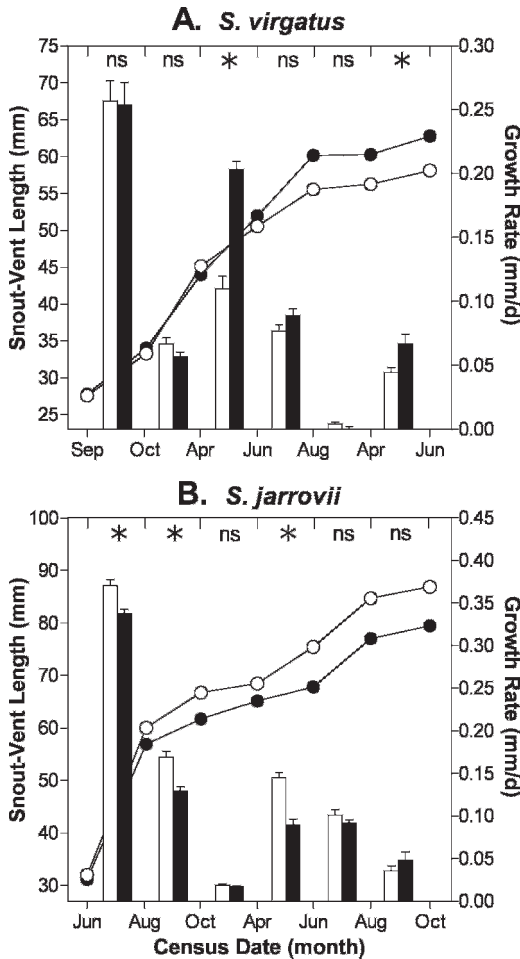


FIG. 2.—Mean (± 1 SE) growth rate (bars) and snout-vent length (circles) for males (open symbols) and females (filled symbols) of *Sceloporus virgatus* (A) and *S. jarrovii* (B) of known age over several intervals during the active season. Data are pooled across cohorts. Asterisks indicate significant ($P < 0.01$) sex differences in growth rate based on ANCOVA with sex and cohort as categorical variables with interaction.

changed relatively little thereafter (SSD = -0.113 ; $F_{3,36} = 107.10$; $P < 0.001$; Fig. 2b). Growth did not differ between males and females during the second summer ($F_{5,60} = 1.36$; $P = 0.249$; Fig. 2b) or the second fall mating season ($F_{1,17} = 0.75$; $P = 0.401$; Fig. 2b).

Survival and Recapture Probabilities

In both *S. virgatus* and *S. jarrovii*, models assigning males and females equivalent prob-

abilities of survival (Φ) and recapture (p) received the greatest support in maximum likelihood analyses (Table 2). On the basis of QAIC scores and associated likelihood estimates, these simplified models were 6.4 (*S. virgatus*) and 3.2 (*S. jarrovii*) times more likely than models that estimated Φ separately for each sex. Although these analyses suggest that sex differences in Φ are minor, females of both species exhibited slightly greater cumulative survivorship than males over the first year of life (Fig. 3).

Size-specific Mortality and Emigration

During the first spring mating season, survival of *S. virgatus* yearlings was related to the sex*SVL interaction (Wald $\chi^2 = 6.58$; $P = 0.010$; $n = 280$). Males that remained on site were larger (mean ± 1 SE = 46.06 ± 0.64 mm; $n = 31$) than males that died or emigrated (44.42 ± 0.45 mm; $n = 71$), while females that remained on site were slightly smaller (43.51 ± 0.039 mm; $n = 87$) than females that died or emigrated (44.53 ± 0.37 mm; $n = 91$). During the second mating season, new immigrants onto the site were smaller (58.50 ± 0.58 mm; $n = 12$) than animals captured previously (60.64 ± 0.41 mm; $n = 55$; $F_{11,252} = 19.23$; $P < 0.001$). However, this immigration effect on SVL was similar in males and females (sex*immigration interaction: $F_{11,252} = 0.03$; $P = 0.857$). Size was not related to survival, immigration, or the interaction of either measure with sex over any other interval in *S. virgatus*.

In *S. jarrovii*, size at birth was positively associated with survival over the subsequent summer (Wald $\chi^2 = 7.19$; $P = 0.007$; $n = 206$). Animals that remained on site were smaller (31.11 ± 0.45 mm; $n = 81$) than those that died or emigrated (31.81 ± 0.45 mm; $n = 125$; $F_{11,205} = 6.41$; $P = 0.012$), but this size-dependence of survival occurred in both sexes (sex*SVL interaction: Wald $\chi^2 = 0.30$; $P = 0.598$). During the three months following birth, new immigrants onto the site were smaller (58.17 ± 0.41 mm; $n = 195$) than animals captured previously as neonates (59.52 ± 0.53 mm; $n = 69$; $F_{11,252} = 19.23$; $P < 0.001$), but this immigration effect on SVL did not differ between sexes (sex*immigration interaction: $F_{11,252} = 0.03$; $P = 0.857$).

TABLE 2.—MARK maximum likelihood comparison of four candidate models estimating survival (Φ) and recapture (p) probabilities as a function of age (six age classes, see Fig. 3) and sex. Models are ranked in descending likelihood on the basis of quasi-likelihood adjusted Akaike's information criterion (QAIC) and associated model weights. In both species, models without sex effects on Φ and p received the greatest support (i.e., lowest QAIC, highest weight and likelihood).

Species	Model			QAIC	Δ QAIC	Weight	Likelihood
	Parameters	Φ	p				
<i>S. virgatus</i>	12	age	age	1044.87	0.00	0.843	1.000
	18	age*sex	age	1048.57	3.70	0.132	0.157
	18	age	age*sex	1052.88	8.01	0.015	0.018
	24	age*sex	age*sex	1053.97	9.10	0.009	0.011
<i>S. jarrovi</i>	12	age	age	1050.20	0.00	0.676	1.000
	18	age*sex	age	1052.51	2.31	0.213	0.315
	18	age	age*sex	1054.31	4.11	0.086	0.128
	24	age*sex	age*sex	1056.79	6.59	0.025	0.037

Size was not related to survival, immigration, or the interaction of either measure with sex over any other interval in *S. jarrovi*.

Body Condition and Growth

Body condition of yearling *S. virgatus* males declined over the course of the spring mating season ($t = 4.13$; $P < 0.001$; Fig. 4). In contrast, body condition remained constant over this period in yearling females ($t = 0.26$; $P = 0.797$; Fig. 4). Change in body condition was positively correlated with growth rate in yearling *S. virgatus* males ($r^2 = 0.155$; $P = 0.032$). Individual males that declined more in body condition also grew less in length. Change in body condition was not correlated with growth rate in *S. virgatus* females ($r^2 = 0.007$; $P = 0.462$).

Body condition remained constant over the fall breeding season in yearling *S. jarrovi* males ($t = 0.32$; $P = 0.750$) and increased in yearling females ($t = 7.03$; $P < 0.001$; Fig. 4). Change in body condition was not correlated with growth rate in yearling males ($r^2 = 0.001$; $P = 0.855$). However, change in body condition was negatively correlated with growth rate in yearling females ($r^2 = 0.053$; $P = 0.036$). Individual females that increased in body condition also grew relatively less in length.

DISCUSSION

Demography and Ontogeny of SSD

In natural populations, sex differences in the body size of sampled individuals may reflect differential survival of males and

females (Rutherford, 2004; Watkins, 1996). For example, even though male *Ctenotus* skinks grow more quickly than females, adult SSD is biased toward larger females on account of their higher rate of survival to larger sizes (James, 1991). In the present study, we avoided this confound by restricting our comparisons of size and growth to males and females of the same age. Further, our likelihood analyses revealed that survival probabilities were generally similar in males and females of both species. Although yearling females exhibited slightly higher cumulative survivorship than yearling males, this pattern was evident in both species (Fig. 3), regardless of the direction of SSD. Thus, any hypothesized relationship between survival and SSD would be incapable of parsimoniously explaining SSD in both species without invoking additional factors.

Even in the absence of sex bias in overall survival, SSD can be influenced by sex differences in size-specific survival or migration. For example, small yearling males of *S. virgatus* were more likely to die or emigrate during the spring breeding season than were large yearling males, while survival was independent of size in females. However, this bias should actually favor the expression of male-larger SSD, and we found no evidence for an opposing bias that could explain the observed pattern of female-larger SSD. We conclude that the development of SSD in *S. virgatus* and *S. jarrovi* is clearly driven by sex differences in growth, rather than differential survival and migration. This conclusion is strengthened by the agreement between our

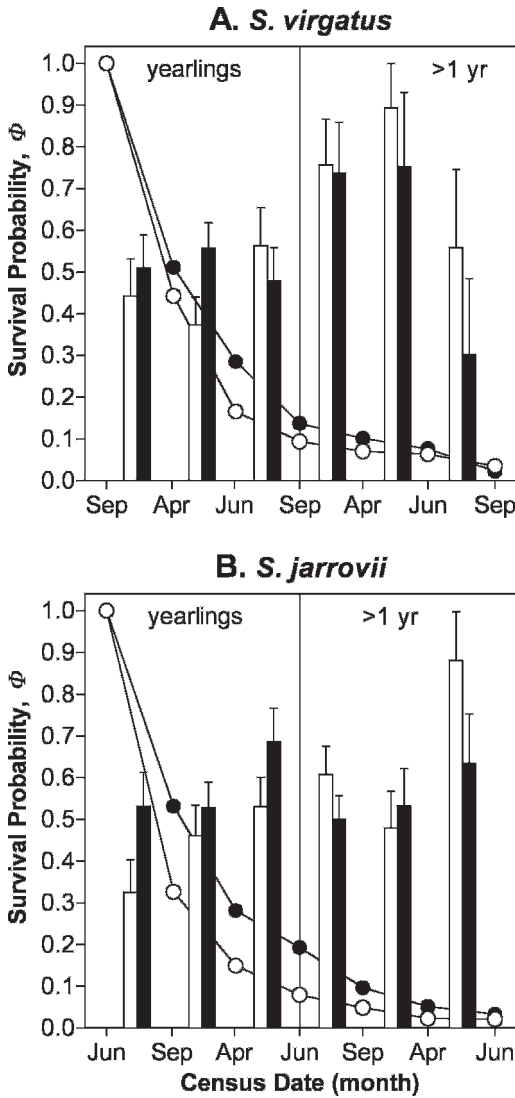


FIG. 3.—Mean (± 1 SE) survival probability (Φ) for males (open bars) and females (filled bars) of *Sceloporus virgatus* (A) and *S. jarrovii* (B) over three intervals: spring (Apr–Jun), summer (Jun–Sep), and winter (Sep–Apr). Survival probability over each interval was estimated separately for yearlings versus older animals, resulting in six age-specific estimates of Φ for each sex. Estimates of Φ were obtained using MARK analysis with recapture probability (p) modeled as equivalent in both sexes but variable across age classes. Symbols connected by lines represent cumulative survivorship (i.e., the product of successive Φ estimates) for males (open symbols) and females (filled symbols).

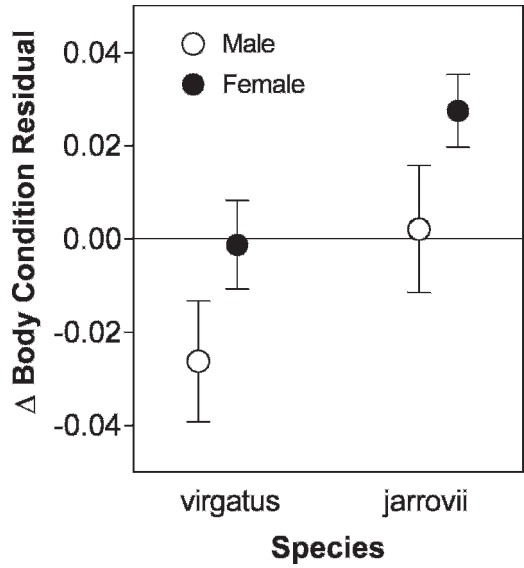


FIG. 4.—Mean ($\pm 95\%$ confidence interval) change in body condition residuals during the mating season for yearling males and females of *Sceloporus virgatus* and *S. jarrovii*. Values with confidence intervals including zero (solid line) indicate that animals maintained isometry between body mass and snout–vent length during the breeding season.

asymptotic growth models (Fig. 1) and linear growth rates calculated over discrete recapture intervals (Fig. 2). The fact that the larger sex of each species grew to a greater asymptotic size with the same (or slightly greater) characteristic growth parameter implies that the larger sex of each species must have a greater absolute growth rate (Dunham, 1978a), and this is confirmed by our direct comparisons of linear growth rates (Fig. 2).

While previous studies have documented sex differences in growth for both *S. virgatus* (Rose, 1981; Smith, 1996) and *S. jarrovii* (Ruby and Dunham, 1984; Smith and Ballinger, 1994), ours is the first to resolve the early ontogeny of sexual growth divergence in these species. This finding represents a critical step toward developing hypotheses for how and why males and females “grow apart” (Badyaev, 2002). Our results indicate subtle differences in the ontogenetic timing of sexual growth divergence in each species. Male-larger SSD develops in *S. jarrovii* because males grow consistently faster than females throughout the first year of life, whereas female-larger SSD develops in *S. virgatus*

because of a dramatic sex difference in growth that is primarily restricted to the mating season (Fig. 2). In the following sections, we illustrate how these ontogenetic data have informed subsequent experimental tests of the proximate developmental mechanisms mediating growth divergence and SSD in each species.

Male Growth and Reproductive Investment

The association between sexual growth divergence and the onset of the first mating season for yearling *S. virgatus* males suggests that their growth may be energetically constrained by reproductive investment. During the mating season, *S. virgatus* males have longer daily activity periods, engage in more aggressive interactions, move greater distances, and maintain larger home ranges than females (Merker and Nagy, 1984; Rose, 1981; Smith, 1985; Vinegar, 1975a). This incurs costs in the form of increased metabolic expenditure and decreased energy acquisition (Merker and Nagy, 1984; Weiss, 2001), such that yearling males decline in body condition during the mating season (Fig. 4). By contrast, yearling females maintain isometry between mass and length, which indicates that a decline in body condition is not obligated by environmental conditions such as food availability. We interpret this as evidence for a sex difference in energetic costs experienced during the mating season. Further, change in body condition is positively correlated with growth rate in yearling males of *S. virgatus*, suggesting that individuals that incur greater energetic costs also grow more slowly.

In contrast to *S. virgatus*, body condition does not decline during the mating season in yearling males of *S. jarrovii* (Fig. 4b). This result suggests that yearling males of *S. jarrovii* do not experience a comparable energetic trade-off during the mating season, but the reasons for this difference are unclear. Yearling males of *S. virgatus* may invest a relatively larger fraction of their time and energy budgets into reproduction, or the environmental potential for an energetic trade-off with growth may be greater for *S. virgatus* in the spring (when prey densities are low) than for *S. jarrovii* in the fall (following peaks in prey density driven by summer

monsoons) (Smith, 1996; Smith and Ballinger, 1994).

Maturation changes in the behavior, growth, and energy allocation of males are mediated by increases in circulating testosterone, which peaks during the mating season in yearling males of each species (Cox and John-Alder, 2005). If testosterone and its associated energetic costs influence the growth of males and the development of SSD (see Cox et al., 2005), then the ontogenesis of sexual growth divergence predicts that these species should differ in their response to testosterone manipulation at this developmental stage (John-Alder and Cox, 2007). Experimental manipulations have verified this prediction: castration promotes and testosterone inhibits growth in yearling males of *S. virgatus*, while castration inhibits and testosterone restores growth in yearling males of *S. jarrovii* (Abell, 1998; Cox and John-Alder, 2005; John-Alder and Cox, 2007). The inhibitory effect of testosterone on growth in *S. virgatus* is similar to that observed in *S. undulatus*, a congener with female-larger SSD. In this species, testosterone increases daily activity period, movement, and home-range area (Cox et al., 2005), all factors that the present study identifies as potential causes of SSD in *S. virgatus*. Although testosterone has similar effects on the time and energy budgets of *S. jarrovii* males (Marler and Moore, 1989; Marler et al., 1995), testosterone does not inhibit growth in this species (Cox and John-Alder, 2005). While the underlying reasons for this difference between species are unclear, it is noteworthy that both our experimental testosterone manipulations and our descriptions of growth and body condition during the breeding season converge on the inference that species differences in energetic costs of testosterone and associated reproductive investment may help explain the diversity of SSD in *Sceloporus*.

Energetic constraints on the growth of males likely influence SSD in other vertebrate taxa, particularly those in which growth continues into adulthood and reproductive investment entails a substantial energetic cost for males. Female-larger SSD develops in *Eleutherodactylus coqui* frogs because males stop growing upon maturation, coincident

with the onset of reproductive behaviors (i.e., vocalization to attract mates) that incur an impressive metabolic cost in hyliid frogs (e.g., Taigen and Wells, 1985; Wells and Taigen, 1989; Woolbright and Stewart, 1987). However, captive males grow quickly and attain large sizes characteristic of females, suggesting that the removal of reproductive costs in captivity may consequently remove the proximate energetic basis for SSD (Woolbright, 1989). Female-larger SSD is present at birth in the dwarf surferperch, *Micrometrus minimus*, apparently due to sex differences in the ontogenetic timing of maturation. Females do not reproduce until nearly one year after birth, but males are born sexually mature due to rapid prenatal testicular growth that is traded off against somatic growth (Schultz, 1993). These studies, together with our own, illustrate the importance of documenting the ontogenesis of SSD and exploring concomitant differences in physiology and energetics when attempting to explain growth divergence between the sexes.

Female Growth and Reproductive Investment

The opposite patterns of SSD exhibited by *S. virgatus* and *S. jarrovi* may be explained in part by differences in energetic constraints on the growth of males, but a complete explanation for SSD must also consider factors influencing the size of females. Thus, another possibility is that energetic costs of reproduction may differentially constrain the growth of females in each species. For example, sexual growth divergence in *S. jarrovi* is maximal during the first fall (vitellogenesis) and subsequent spring (gestation), when most yearling females are reproductive. This ontogenetic correlation suggests that growth of females may be constrained by reproductive investment, and subsequent experimental manipulations of reproductive investment via ovariectomy have demonstrated a trade-off between growth and reproduction (Cox, 2006). However, the ontogenetic timing of this inferred growth cost (late gestation) occurs well after the development of SSD has begun, and the ontogenesis of SSD is similar in a high-elevation population in which all females delay reproduction until their second year (Cox, 2006). Together, these

ontogenetic data argue that, although reproduction may constrain energy allocation to growth, this cost of reproduction in females cannot explain the development of male-larger SSD in *S. jarrovi*. Further, empirical measures of the energy content of eggs or embryos (Tinkle and Hadley, 1975) and the metabolic costs accruing to gravid or pregnant females (Angilletta and Sears, 2000; Beuchat and Vleck, 1990; Demarco and Guillette, 1992) indicate that such costs are actually greater in female-larger *S. virgatus* and *S. undulatus* than in male-larger *S. jarrovi*. Thus, focus on energetic consequences of reproductive investment of females does not seem likely to resolve patterns of SSD in *Sceloporus*.

Synthesis and Conclusions

In the present study, we have shown that opposite patterns of SSD develop in two sympatric congeners because of underlying sex differences in postnatal growth trajectories, rather than differential survival or migration. We have also characterized the important ontogenetic stages during which males and females of these species “grow apart” (Badyaev, 2002). The close ontogenetic association between sexual growth divergence and the onset of reproductive maturity in *S. virgatus* males suggests that energetic costs of reproductive investment may constrain their growth. Our estimates of change in body condition over the mating season also indicate that any such energetic constraints are less severe in yearling *S. jarrovi* males. These ontogenetic data have informed subsequent manipulations of plasma testosterone levels during appropriate developmental stages, and the combined results of three such experiments indicate that the development of contrasting SSD is mediated in part by species differences in the effect of testosterone (and its associated energetic costs) on growth of males (Cox and John-Alder, 2005; Cox et al., 2005; John-Alder and Cox, 2007). In analogous fashion, reproductive investment may constrain the growth of females, as suggested by the ontogenetic association between maturation of females and the development of SSD in *S. jarrovi*. While subsequent experiments have provided direct evidence for

a trade-off between growth and reproduction, both the timing and the magnitude of this trade-off suggest that it cannot explain male-larger SSD in this species (Cox, 2006). These examples illustrate the crucial role of ontogenetic studies in identifying key developmental periods and formulating experimentally testable hypotheses for the proximate causation of SSD.

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