

# Mechanisms causing variation in sexual size dimorphism in three sympatric, congeneric lizards

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**Abstract.** Sexual differences in adult body size (sexual size dimorphism, or SSD) ultimately can be favored by selection because larger males are more likely to be successful competitors for females, because larger females bear larger clutches, or because intersexual size differences reduce resource competition. Natural selection during juvenile development can influence sexual dimorphism of adults, and selection on adults and juveniles may differ. Studies that address the relative contributions of adult body shape dimorphism *and* sexually dimorphic patterns of growth and maturity are particularly useful in understanding the evolution of size dimorphism, yet they are rare. We investigated three sympatric, congeneric lizard species with different degrees and directions of adult sexual dimorphism and compared their growth patterns, survival probabilities, and intersexual trophic niche differences. Different mechanisms, even within these closely related, sympatric species, acted on juvenile lizards to produce species differences in adult SSD. Both degree and direction of dimorphism resulted from differences between the sexes in either the duration of growth or the rate of growth, but not from differences in rates of survival or selection on juvenile growth rate. Species- and sex-specific trade-offs in the allocation of energy to growth and reproduction, as well as differential timing of maturation, thus caused the growth patterns of the sexes to diverge, producing SSD. The differences that we observed in the direction of SSD among these species is consistent with their different social systems, suggesting that differential selection on adult body size has been responsible for the observed species-specific differences in juvenile growth rates and maturational timing.

**Key words:** *body size; Carlia rostralis; Carlia rubrigularis; Carlia storri; growth; head size; lizards; northeastern Australia; prey size; sexual maturity; sexual size dimorphism; survival.*

## INTRODUCTION

Males and females often differ in body size. Sexual size dimorphism (or SSD) most likely evolves in response to three processes: (1) sexual selection to increase male size, thereby increasing mating success of males competing for females (e.g., Darwin 1871), (2) natural selection to increase female size, thereby allowing a larger instantaneous reproductive investment (e.g., Olsson 1993), and (3) natural selection for sexual size differences that reduce intersexual competition for food (e.g., Camilleri and Shine 1990, Butler et al. 2000). Studying patterns of sexual dimorphism provides an opportunity to examine the actions of sexual and natural selection on organisms (Fairbairn 1997).

The majority of work on SSD examines patterns of sexual selection in adults (e.g., Schulte-Hostedde and Millar 2000, Karubian and Swaddle 2001, Olsson et al.

2002). Sexual dimorphism is, however, strongly influenced by the interaction of the ontogeny of sexual dimorphism and selection on juvenile morphology. Hence, observations of the evolutionary history and functional significance of adult size differences provide little insight into the underlying, proximate causes of SSD (Cox and John-Alder 2007). Understanding the proximate mechanisms by which sex-specific patterns in growth are achieved is an important aspect of understanding how their eventual endpoint—adult SSD—is achieved. For instance, survival may be gender biased, so that one sex lives longer than the other, and thereby grows to a larger size. Alternatively, variation in adult sexual dimorphism could be influenced by evolutionary forces acting on juvenile development, which may be very different from those acting on adults (Clutton-Brock et al. 1985, Badyaev et al. 2001). Differences in SSD may arise from differences in developmental pathways that would go unnoticed if only adult body size were considered. For example, the sexes can differ markedly in the shape of their growth curves, overall rates of growth, duration of growth, and age at maturity; all factors that can themselves be subject to selection (Clutton-Brock et al. 1985, Badyaev 2002). As

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sexual differences in growth patterns can evolve rapidly (e.g., Stearns 1983), knowledge of sex-specific growth trajectories, patterns of maturation, and the probability of survival is crucial for understanding and interpreting the developmental basis of sexual dimorphism, and ultimately for understanding the evolutionary significance of differences among taxa (Badyaev 2002, Cox and John-Alder 2007).

Lizards are frequently used as models for the study of SSD; there are many examples of dimorphism among lizards, with considerable variation in its direction and magnitude. Although there is evidence that sexual selection, fecundity selection, and the avoidance of intersexual competition have influenced patterns of SSD in lizards, the possible causes of variation in body size are numerous and have multiple evolutionary origins, so that distinguishing their relative importance remains a major challenge (Wikelski and Trillmich 1997). Although we may discuss the functional significance of size differences between the sexes due to selection on adults, such differences must emerge proximally as the outcomes of different growth trajectories, maturation patterns, or survival rates between the sexes. Understanding and identifying the development of body size differences will facilitate the development of clearer hypotheses for how sexual size dimorphism has evolved, because selection during growth can be the most important determinant of adult SSD (Badyaev 2002). Long-term mark-recapture studies are essential for providing this information on animals in nature.

Males are larger than females in many lizard families (Fitch 1981), but in the family Scincidae there is no consistent pattern of dimorphism (Vitt and Cooper 1985, James 1991, Olsson et al. 2002, Schwarzkopf 2005). In this study, we used multiyear monitoring of three sympatric, congeneric scincid lizards, which varied in their patterns of SSD, to examine the proximate mechanisms leading to adult SSD. We describe sex-specific patterns of growth and evaluate the relative contributions of sexual differences in growth rate, growth duration, and the age when growth asymptotes to SSD in each species. We also test for the influence of sex-biased survival, selection on growth rate, and trophic niche partitioning on adult SSD, and use this knowledge to formulate hypotheses on selection on adult body size.

## METHODS

### *Study species*

*Carlia* spp. are small (<10 g), insectivorous, scincid lizards that forage actively in the leaf litter and on low vegetation during the day (Manicom et al. 2008) and are widespread and abundant in northeastern Australia (Wilson 2005). We studied *Carlia rostralis*, *C. rubrigularis*, and *C. storri*. These species occur at high densities: in an average year of the study, 14.2 individual *C. rostralis*, 7.1 individual *C. rubrigularis*, and 5.8 individ-

ual *C. storri* occur per 100 m<sup>2</sup> at the study site (Manicom 2010). *Carlia* breed during the summer wet season (Clerke and Alford 1993, Manicom 2010). The three species vary in length of breeding season: *C. rostralis* and *C. rubrigularis* start breeding in August (late dry season) and *C. storri* in November (start of wet season, Manicom 2010). Females produce invariant clutches of two eggs and may lay up to three clutches in a season (James and Shine 1988, Goodman 2006). Adult *C. rostralis* and *C. rubrigularis* are sexually dichromatic, with males exhibiting striking throat coloration, which is exaggerated during the breeding season (red in *C. rubrigularis* and black in *C. rostralis*), whereas females of these two species have pale pink (*C. rubrigularis*) or white (*C. rostralis*) throats. Both sexes of *C. storri* are monochromatic light brown.

### *Study area*

A 5-ha study site was established on Hinchinbrook Island (Hinchinbrook Island National Park, Queensland, Australia, 18°24' S, 146°17' E) in May 2003. The study site consists of open woodland interspersed with closed vine forest. The area experiences a seasonally monsoonal climate with mild, relatively dry conditions May to October, and hot, humid, and rainy weather from November to April. We established 21 14.14 × 14.14 m (200-m<sup>2</sup>) plots within the 5-ha area for intensive sampling as we will outline. The plots were haphazardly distributed such that sampling intensity was roughly even across the full area of the study site.

### *General methods*

We visited the site for 25 days at approximately 90-day intervals, on 13 occasions from May 2003 to May 2007. We could not access the site between December and April due to inclement tropical conditions. During each visit, the sampling plots were searched over consecutive days until no new individuals (not previously captured on that visit) were captured by hand and in funnel traps (Fitch 1951). We measured snout-to-vent length (SVL) using a ruler ( $\pm 0.5$  mm), mass using a Pesola spring balance ( $\pm 0.1$  g), and head length (HL, from the tip of the snout to the anterior edge of the ear opening), jaw width (JW, across the widest part of the jaw), and interlimb length (ILL, from the posterior point of insertion of the forelimb to the anterior point of insertion of the hindlimb), using digital calipers ( $\pm 0.1$  mm). Head length and interlimb length were measured only on the right side of the body. The presence of an intact or broken tail was recorded, and lizards were permanently and individually marked by toe clip (Schmidt and Schwarzkopf 2010). At each capture, the sex of lizards was determined by manual eversion of hemipenes. Sex could not be determined reliably for juveniles, unless they were recaptured at a later occasion as an adult or subadult. Lizards were returned to the site of capture after measurement.

### *Minimum size at maturity*

During the study, 49 subadult and adult *C. rostralis* (25 females, 24 males), 54 subadult and adult *C. rubrigularis* (27 females, 27 males) and 49 subadult and adult *C. storri* (24 females, 25 males) captured near, but outside the study area, were dissected for analysis of diet and reproductive condition. Minimum size at sexual maturity was determined for females as the SVL of the smallest female containing vitellogenic follicles or oviducal eggs, and for males as the SVL of the smallest male with enlarged testes (Dunham et al. 1988).

### *Sexual dimorphism*

Morphological data on subadult and adult lizards were used to examine body size and shape dimorphism. We used analysis of variance (ANOVA) to evaluate the effects of species, sex, and their interaction on body size (SVL,  $\log_{10}$ -transformed). We examined body shape dimorphism within species using analyses of covariance (ANCOVA) on each morphological character with sex as the factor and SVL as the covariate. SVL and other morphometric variables were  $\log_{10}$ -transformed to meet the assumptions of least-squares regression and ANCOVA. A significant main effect of SVL indicated an overall correlation between a measured character and SVL, a significant main effect of sex indicated that values of the character differed between males and females of the same SVL, and a significant SVL  $\times$  sex interaction indicated that the slope of the regression of character size on SVL differed between the sexes.

### *Effects of gender and species on growth rates*

We used a modeling approach to examine influences on the growth rates of individuals that had intact tails (because tail regeneration may divert energy from somatic growth; Ballinger and Tinkle 1979). Individual lizards were represented only once in growth analyses. Very few suitable individuals (11 *C. rostralis*, 4 *C. rubrigularis*, and 16 *C. storri*) were captured only as juveniles (i.e., were not recaptured as a subadult or adult and therefore could not be sexed). Because sex significantly affected growth rate (see *Results*), we could not compare the growth rates of this small sample of individuals with those of individuals captured as both juveniles and as adults. Data on individuals captured only as juveniles were therefore excluded from further analyses. By doing this, we ensured that models were used to examine influences, including sex and species identity, on growth patterns over a relatively great proportion of the growth of each individual.

We constructed a set of generalized linear models using the `glm` function in R (R Development Core Team 2012) with an identity link function, and used  $AIC_c$  (corrected Akaike Information Criterion) to select a subset including models with  $\Delta AIC_c < 3$ ; these were averaged to obtain a final predictive model (Burnham

and Anderson 2002). The response that we included in the initial model set was the mean change in SVL (mm/d) between the initial captures of individuals as juveniles and their final captures as adults.

Factor variables included in the initial model set were species identity and sex, plus their interaction. The covariate was mean SVL, in mm ( $(\text{length at initial capture} + \text{length at final capture})/2$ ). The model set also included the interactions of the covariate with each of the factors and with the interaction between the factors. We selected a final model set with  $\Delta AIC_c < 3$  and produced a final averaged model. We examined this model to interpret how growth influenced these species, and also used it to generate predicted changes in SVL. Residuals from these predictions were used in an analysis in Program MARK to determine whether differences in relative growth rate among individuals significantly affected estimated rates of survival (see *Modeling survival and recapture probability as a function of individual growth rate*). Because our final averaged model included the effects of both species identity and sex, indicating that growth depended upon both factors, the residuals were standardized to Z scores ( $Z = (X - \text{mean of } X)/\text{SD of } X$ ) by species and sex before use in that analysis.

### *Estimation of standard growth curves and age at minimum size for sexual maturity*

In a review of body size growth in reptiles, Andrews (1982) concluded that the logistic-by-weight model was most appropriate for small, short-lived lizards, and this model fit growth data best for a number of small Bahamian species (Schoener and Schoener 1978). We fitted lizard body length measurements from mark-recapture data to the logistic-by-weight growth model using standard methods. The data for individuals with intact tails that were used in our initial growth modeling were analyzed separately by species and sex. We used the nonlinear least squares function `nls` in R (R Development Core Team 2012) to estimate the parameters  $a$  (asymptotic body length), and  $k$  (intrinsic growth rate) and the body size at age 0 ( $b$ , derived from hatchling size). We did not collect eggs from the study site to measure body size at hatching; we therefore estimated length at time zero ( $L_0$ ) using the size of the smallest captured lizard of each species (25.0, 22.0, and 20.5 mm for *C. rostralis*, *C. rubrigularis*, and *C. storri*, respectively). These individuals had probably hatched just before capture, because their body sizes were similar to the mean body size of captive hatchlings (25.38 mm [ $n = 3$ ], 23.12 mm [ $n = 35$ ], and 20.04 mm [ $n = 23$ ] for *C. rostralis*, *C. rubrigularis*, and *C. storri*, respectively, measured in another study; Goodman 2006; B. Goodman, *unpublished data*). We used the fitted growth curves with our data on minimum size at sexual maturity to estimate mean age at the minimum size for maturity for each species and sex.

### *Selection on growth rate and sex-specific survival*

We defined selection as the covariance between the growth rate and apparent survival of an individual, using survival as an estimate of lizard fitness (Brodie et al. 1995). Residuals from growth rates predicted using the final ANCOVA model (see *Effects of gender and species on growth rates*) were used as covariates in Program MARK (version 5.1; White and Burnham 1999) to examine whether the relative growth rates of individuals affected their survival probabilities. We tested for directional selection (linear selection for higher or lower individual growth rate, by incorporating individual residual growth rate in covariate models), and stabilizing or disruptive selection (selection against extreme or intermediate individual growth rate, respectively, by incorporating individual residual growth rate and the square of growth rate in covariate models).

The data set that we used to build our models included only individuals initially captured as juveniles and later captured as adults. We did not include growth data from individuals captured only as adults in these models, because all species exhibited asymptotic growth; many individuals initially captured as adults grew little or none regardless of the span of time from first to final capture; their inclusion in selection models would have obscured possible differences in rate of change in size during active growth. Individual lizards were represented only once in analyses.

We used the Cormack-Jolly-Seber (CJS) method (Cormack 1989) in Program MARK to test for heterogeneity in apparent survival ( $\phi$ ) and recapture ( $p$ ) probabilities between males and females of the three *Carlia* species from mark–recapture data. We constructed a candidate set of survival and recapture models to answer the following questions: (1) Is there support for an interaction of sex and relative growth rate on variation in survival for each species, indicating differential selective forces acting on growth rate between the sexes? And, (2) if there is no strong support for such an interaction, then is there evidence supporting a difference between the sexes in survival or recapture probability for each species? In the absence of a difference between the sexes of each species, (3) is there any evidence of a relationship between survival and growth rate for each species, and do apparent survival and recapture rates differ among the species?

We compared models using the logit-link function and we assessed model fit with a bootstrap goodness-of-fit (GOF) test with 1000 iterations of the model with the most parameters. We objectively evaluated our models using quasi-likelihood corrected Akaike's information criterion (QAIC<sub>c</sub> – AIC adjusted for overdispersion by calculating a variance inflation factor from the GOF statistics). For each model, we calculated  $\Delta$ QAIC<sub>c</sub>, the difference between the QAIC<sub>c</sub> for that model and the smallest QAIC<sub>c</sub> among the set of models fitted. Models with  $\Delta$ QAIC<sub>c</sub> < 3 were given the greatest support (Burnham and Anderson 2002). Models were also

weighted so that the likelihood of each model could be compared relative to the other models considered. We initially tested the effects of time, species, and the combination of species  $\times$  sex (and their interactions) independently on survival and recapture probability of *Carlia*, along with constant (no effect) models. Using this approach, a well-supported model that included sex as a factor would provide evidence for sex-specific differences in survival or recapture rate (Burnham and Anderson 2002).

Preliminary survival analyses revealed a strong effect of time on both survival and recapture rates of *Carlia* ( $\phi$  [time]  $p$  [time]: AIC<sub>c</sub> weight = 0.99; compared with the second model in the candidate set,  $\phi$  [species]  $p$  [constant]:  $\Delta$ QAIC<sub>c</sub> = 16.77, AIC<sub>c</sub> weight = 0.0002). Because time accounts for seasonal differences in survival and recapture probability (sampling trips coincided with early dry, late dry, and early wet seasons over four years), we expect time to strongly influence lizard survival in the tropics. To test for sex-specific survival without overwhelming seasonal effect, we removed time variation from the candidate set of models, comparing only models incorporating species and sex, and their interaction, with constant (no effect) models on survival and recapture probability. We incorporated the individual covariates growth rate, and growth rate<sup>2</sup>, into models accounting for species and species  $\times$  sex differences in survival, to test for differential selection on growth rate. Model fit of the candidate set was assessed from the most parameterized model without covariates ( $\phi$  [species  $\times$  sex]  $p$  [species  $\times$  sex]; GOF test,  $P = 0.026$ ), and the variance inflation factor ( $\hat{c} = 1.129$ ) was adjusted to calculate QAIC<sub>c</sub>.

An estimate of the maximum age attained by each lizard, in days, was calculated using the logistic growth equations for males and females of each species (see *Estimation of standard growth curves*) to estimate age at first capture, and added to days to final capture (Caughley 1977). This analysis was only performed on lizards captured first as juveniles, in order to accurately estimate age at first capture (because adult lizard body size is asymptotic; see *Results*). Species and sex differences were compared using ANOVA Type II tests, with significant effects further analyzed with Fisher's LSD test (Hochberg and Tamhane 1987).

### *Prey size dimorphism*

Size measurements (total length and width to the nearest 0.1 mm using digital calipers) were taken from every arthropod prey item found in the stomachs of subadult and adult lizards (see number of dissected lizards in *Minimum size at maturity*; see also Manicom and Schwarzkopf 2011). The median prey dimensions of male and female lizards relative to lizard body length were compared for each species using ANCOVA, with median prey length as the variable, sex as the factor, and SVL as the covariate.

### Analysis

Except where otherwise stated, all statistical analyses were performed using the statistical packages SPSS version 16.0 (2007; SPSS, Chicago, Illinois, USA), and R (R Development Core Team 2012). When multiple measurements existed for an individual, only the measurements made at the last capture were included in analyses. Significance level was set at  $\alpha = 0.05$ .

### RESULTS

#### Minimum size at maturity

As determined by dissection of individuals collected outside the study area, minimum snout–vent length (SVL) at maturity was 46.0 mm for males and 51.0 mm for females of *C. rostralis*; 38.0 mm for males and 44.0 mm for females of *C. rubrigularis*; and 36.0 mm for males and 41.0 mm for females of *C. storri*.

#### Sexual dimorphism

Morphological data were collected from 368 *C. rostralis* (176 male, 192 female), 274 *C. rubrigularis* (147 male, 127 female), and 185 *C. storri* (94 male, 91 female) individuals. We found significant sexual size dimorphism in two of the three species. All effects (species, sex, and their interaction on SVL) were highly significant (ANOVA: for species,  $F_{2,821} = 201.75$ ,  $P < 0.0001$ ; for sex,  $F_{1,821} = 67.16$ ,  $P < 0.0001$ ; for species  $\times$  sex,  $F_{2,821} = 18.12$ ,  $P < 0.0001$ ; Fig. 1). In *C. rostralis*, adult males were longer (mean SVL = 57.7 mm, range 43.0–69.0 mm) than adult females (mean SVL = 53.2 mm, range 39.0–63.0 mm; Fig. 1). *Carlia storri* showed the reverse pattern, with adult females reaching larger body sizes (mean SVL = 43.0 mm, range 34.0–48.0 mm) than adult males (mean SVL = 41.5 mm, range 30.0–46.0 mm; Fig. 1). *Carlia rubrigularis* males and females did not differ significantly in body length (mean SVL: males = 46.2 mm, range 34.0–53.0 mm; females = 45.9 mm; range 33.0–54.0 mm; Fig. 1).

Male head dimensions were relatively larger than those of females in all species. Head length and jaw width increased more rapidly with body length for males than for females in *C. rostralis* (ANCOVA, slopes of regressions: for head length,  $F_{1,367} = 5.95$ ,  $P = 0.02$ ; for jaw width,  $F_{1,367} = 6.98$ ,  $P < 0.01$ ; Fig. 2). In *C. rubrigularis*, male head dimensions were longer and wider than female head dimensions at a given SVL (ANCOVA, intercept of regressions: for head length,  $F_{1,273} = 69.66$ ,  $P < 0.01$ ; for jaw width,  $F_{1,273} = 11.42$ ,  $P < 0.01$ ; Fig. 2). In *C. storri*, head length of males increased faster and jaw width was broader at a given body length than that of females (ANCOVA, slopes, for head length,  $F_{1,184} = 21.61$ ,  $P < 0.01$ ; intercept, for jaw width,  $F_{1,184} = 32.00$ ,  $P < 0.01$ ; Fig. 2). The difference in relative head dimensions between the sexes differed significantly among species (ANCOVA head length: for species  $\times$  sex  $\times$  snout-to-vent length (SVL),  $F_{2,826} = 8.21$ ,  $P < 0.001$ ; for jaw width, species  $\times$  sex  $\times$  SVL,  $F_{2,826} =$

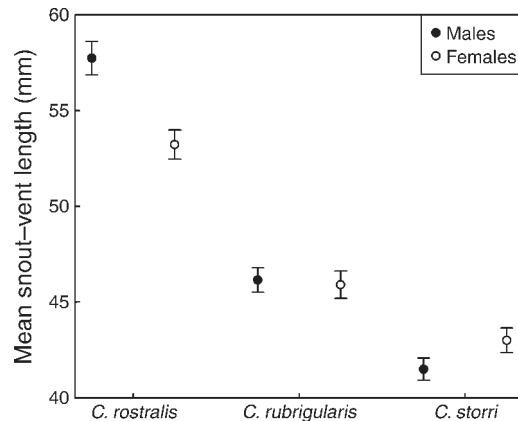


FIG. 1. Mean snout–vent length (SVL) and 95% confidence intervals of adult male and female sympatric Australian lizards *Carlia rostralis*, *C. rubrigularis*, and *C. storri*.

5.57,  $P < 0.01$ ). Difference in head size between males and females was greatest for *C. storri* and smallest between male and female *C. rostralis* (relative to SVL). Within males, head length of all three species increased at a similar rate with increasing body length (SVL), but jaw width increased with SVL at a different rate in the three species (fastest for *C. rostralis* males, slowest for *C. storri* males with increasing SVL; ANCOVA: for head length,  $F_{2,416} = 1.93$ ,  $P = 0.15$ ; for jaw width,  $F_{2,416} = 4.04$ ,  $P = 0.02$ ).

At the same SVL, female *C. rostralis* and *C. rubrigularis* had a greater interlimb length than males (ANCOVA, intercepts of regressions: for *C. rostralis*,  $F_{1,366} = 5.35$ ,  $P = 0.02$ ; for *C. rubrigularis*,  $F_{1,273} = 20.76$ ,  $P < 0.01$ ; Fig. 2), but the slopes of the relationship between interlimb length and SVL did not differ significantly between the sexes in either species, indicating that, during most of post-hatchling growth, female interlimb length did not increase faster with SVL than that of males for either species. For *C. storri*, although females had longer absolute interlimb length due to their larger asymptotic size, there was no significant difference between male and female interlimb length at the same SVL, or between the slopes of the relationship of interlimb length with SVL for either sex (ANCOVA: intercept,  $F_{1,184} = 2.25$ ,  $P = 0.14$ ; slopes,  $F_{1,184} = 0.64$ ,  $P < 0.43$ ; Fig. 2). Within females, interlimb length of all three species was similar at a given SVL and increased at a similar rate with increasing SVL (ANCOVA: species,  $F_{2,406} = 0.39$ ,  $P > 0.5$ ; slopes,  $F_{2,406} = 2.1$ ,  $P > 0.1$ ). The difference in interlimb length between males and females was relatively greater in *C. rubrigularis* than in the other two species, but not quite significantly so (ANCOVA: species  $\times$  sex  $\times$  body size,  $F_{2,825} = 2.35$ ,  $P = 0.09$ ).

#### Growth rate and age–size growth curves

The data used to build our models included 433 individuals (87 male and 99 female *C. rostralis*, 71 male

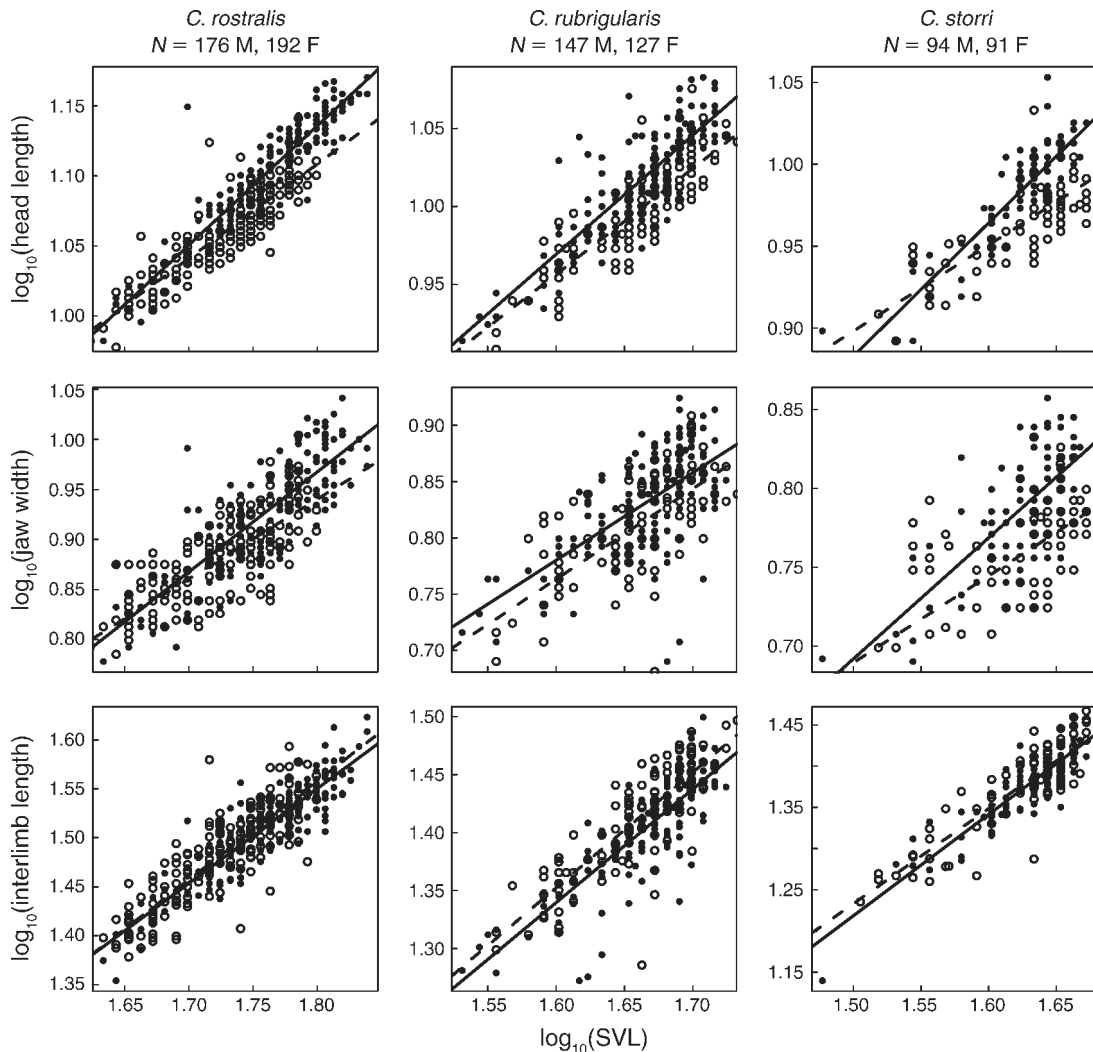


FIG. 2. Morphological traits (log-transformed, all originally measured in mm) on log-transformed snout-vent length, SVL (originally measured in mm), with lines of best fit from regression analysis for male (M, solid symbols, solid lines) and female (F, open symbols, dashed lines) adult *Carlia* lizards;  $P < 0.001$  for all regression models. Sample sizes of males and females are given above the panels. Regressions for *C. rostralis* are: head length, male  $y = 0.85x - 0.39$  ( $R^2 = 0.88$ ), female  $y = 0.67x - 0.10$  ( $R^2 = 0.67$ ); jaw width, male  $y = 1.00x - 0.83$  ( $R^2 = 0.67$ ), female  $y = 0.80x - 0.50$  ( $R^2 = 0.54$ ); interlimb length, male  $y = 0.97x - 0.20$  ( $R^2 = 0.82$ ), female  $y = 1.02x - 0.28$  ( $R^2 = 0.76$ ). Regressions for *C. rubrigularis* are: head length, male  $y = 0.76x - 0.25$  ( $R^2 = 0.71$ ), female  $y = 0.68x - 0.13$  ( $R^2 = 0.74$ ); jaw width, male  $y = 0.78x - 0.47$  ( $R^2 = 0.41$ ), female  $y = 0.81x - 0.52$  ( $R^2 = 0.41$ ); interlimb length, male  $y = 0.98x - 0.23$  ( $R^2 = 0.69$ ), female  $y = 0.99x - 0.25$  ( $R^2 = 0.72$ ). For *C. storri*: head length, male  $y = 0.81x - 0.34$  ( $R^2 = 0.79$ ), female  $y = 0.53x - 0.11$  ( $R^2 = 0.63$ ); jaw width, male  $y = 0.77x - 0.46$  ( $R^2 = 0.47$ ), female  $y = 0.55x - 0.14$  ( $R^2 = 0.22$ ); for interlimb length, male  $y = 1.23x - 0.63$  ( $R^2 = 0.80$ ), female  $y = 1.16x - 0.51$  ( $R^2 = 0.78$ ).

and 76 female *C. rubrigularis*, and 49 male and 51 female *C. storri*). Time intervals between capture and recapture of individual skins ranged from 42 to 1196 days; intervals between captures were  $275 \pm 16.1$  days (mean  $\pm$  SE) for *C. rostralis*,  $288 \pm 19.9$  days for *C. rubrigularis*, and  $245 \pm 20.0$  days for *C. storri*. Of the 19 models in our candidate set, only three had  $\Delta AIC_c$  values  $< 3$ ; the total Akaike weight of those models was 0.957. The model created by averaging those three models appears in Table 1. Initial SVL, days between captures, species, and sex all affected growth (the change in SVL between captures). The reference species and sex

in the model set were *C. rostralis* and males, respectively. Examination of the parameters shows that growth rate was affected by body size, species, sex, and interactions involving these parameters. The model suggests that, all else being equal, individuals with greater mean sizes grew more rapidly than those with lesser mean sizes. This result might appear contradictory, given that all three species clearly did attain maximum body sizes at which growth ceased; however, it reflects the fact that although proportional growth rate slows with increasing size, during some stages of growth absolute growth rate of larger individuals is greater than that of smaller ones.

TABLE 1. Model created by averaging three models with  $\Delta\text{AIC}_c < 3.0$  from the candidate set of 19 models relating individual growth rate (mm/d) to mean snout–vent length (SVL), species, sex, and their interactions for three sympatric Australian lizards (*Carlia* spp.).

Parameter	Estimate	Z	P	Importance
Intercept	0.2044	15.962	<0.0001	
Mean SVL	0.003082	12.435	<0.0001	1
Sex = female	0.05971	3.917	<0.0001	1
Species = <i>C. rubrigularis</i>	−0.03770	3.076	0.0021	1
Species = <i>C. storri</i>	−0.05569	5.437	<0.0001	1
Mean SVL × sex = female	−0.001360	4.324	<0.0001	1
Sex = female × species = <i>C. rubrigularis</i>	0.006798	1.157	0.2474	0.18
Sex = female × species = <i>C. storri</i>	0.002738	0.374	0.7085	0.18
Mean SVL × species = <i>C. rubrigularis</i>	0.0004951	1.137	0.2555	0.16
Mean SVL × species = <i>C. storri</i>	0.0000876	0.159	0.8736	0.16

*Notes:* Parameters are not adjusted for shrinkage; adjusted parameters can be obtained by multiplying estimates by importance scores, which are the proportion of the total Akaike weight (0.957) of the averaged models accounted for by models containing each parameter. Although the *P* values for some parameters are not significant, they were retained because they appeared in the best-fitting model set. The reference species and sex in the model set were *C. rostralis* and males, respectively; therefore no parameters explicitly referencing them appear in the model.

Across species, the model suggests that females tended to grow more rapidly than males, and that *C. rostralis* grew faster than *C. rubrigularis*, whereas *C. storri* grew more slowly than either of the other species. The effects of species and sex were complicated by the presence of interactions; growth decreased more rapidly as mean SVL increased in females than it did in males, and this effect was slightly greater in the reference species, *C. rostralis*, than in either *C. rubrigularis* or *C. storri*, which had positive interaction coefficients for females, but with low importance and thus little influence in the final model. The positive coefficients for the interactions of mean SVL and species for *C. rubrigularis* and *C. storri* indicate that the mean rate of change in SVL per day decreased slightly more slowly in larger individuals of these species than it did in larger individuals of *C. rostralis*; however, the values of these coefficients are small and their importances are low, indicating that these effects are weak.

We summarized the patterns of growth over time of each sex of each species using the logistic-by-weight growth models presented in Table 2 and Fig. 3. Table 2 presents the parameters estimated using nonlinear least squares for asymptotic size (*a*), characteristic growth rate (*k*), and the body size at age 0 (*b*, derived from hatchling size) for males and females of each species, based on the logistic-by-weight growth model. Asymptotic sizes predicted by the logistic-by-weight model parallel mean body sizes of adults of each sex and species (Fig. 1).

In all three species, juvenile growth was rapid, slowing as individuals approached asymptotic adult size (Fig. 3). Males reached sexual maturity at a smaller body size than females in all three species. In all three species, female body growth slowed after reaching sexual maturity (Fig. 3). Based on the logistic-by-weight model, males of both *C. rostralis* and *C. storri* attained sexual maturity two to three months before females (Fig. 3). Age at minimum size at sexual maturity estimated from the fitted growth models for *C. rostralis* was 255 d (~8.5

months) for males and 301 d (~10 months) for females (Fig. 3). For *C. storri*, sexual maturity was reached at age 270 d (~9 months) for males and 336 d (~11 months) for females (Fig. 3). In both species, the sexes differed in duration of growth; in *C. rostralis* the growth rates of females decreased earlier than those of males, resulting in male-biased SSD, and in *C. storri* the growth rates of males decreased earlier than those of females, causing female-biased SSD. In contrast, age at sexual maturity for *C. rubrigularis* was similar for both sexes (265 d for males and 271 d for females, ~9 months; Fig. 3). However, body size at maturity for male and female *C. rubrigularis* differed by 6.0 mm due to the fast growth of young females, which were fully grown at least 12 months younger than males (Fig. 3). The initially fast growth of young female *C. rubrigularis* slowed after maturation was reached, whereas male *C. rubrigularis* continued to grow after maturation, resulting in an asymptotic body size similar to that of females.

#### *Selection on growth rate and sex-specific survival*

The data used to construct the models describing selection on growth rate, and survival and recapture probability, included the capture histories of 114 individuals (19 male and 36 female *C. rostralis*, 15 male and 19 female *C. rubrigularis*, and 11 male and 14 female *C. storri*) initially captured as juveniles and later captured as adults (i.e., actively growing lizards). There was little support for selection acting on growth rate: survival models incorporating individual residual growth were poorly supported by the data (Table 3; top model including growth rate covariate:  $\phi$  [species]; constrained by GR) *p* [species];  $\Delta\text{QAIC}_c = 5.06$ , model weight = 0.04). There was even less support for differences between the sexes of each species in selection on growth rate (top model including an interaction of sex and the growth rate covariate:  $\phi$  [species × sex]; constrained by GR) *p* [species];  $\Delta\text{QAIC}_c = 17.47$ , model weight < 0.001; Table 3).

TABLE 2. Growth parameters ( $\pm$ SE):  $a$  (asymptotic SVL in mm),  $k$  (intrinsic growth rate), and  $b$  (body size at age 0) for the logistic-by-weight model for the three *Carlia* species.

Species	Sex	$N$	$a$	$k$	$b$
<i>C. rostralis</i>	male	99	62.215 ( $\pm$ 0.512)	0.009 ( $\pm$ 0.0005)	14.412 ( $\pm$ 0.381)
	female	87	58.759 ( $\pm$ 0.375)	0.010 ( $\pm$ 0.0005)	11.983 ( $\pm$ 0.249)
<i>C. rubrigularis</i>	male	51	49.232 ( $\pm$ 0.449)	0.008 ( $\pm$ 0.0007)	10.207 ( $\pm$ 0.310)
	female	49	49.437 ( $\pm$ 0.386)	0.012 ( $\pm$ 0.0008)	10.347 ( $\pm$ 0.266)
<i>C. storri</i>	male	76	43.442 ( $\pm$ 0.577)	0.009 ( $\pm$ 0.0012)	8.516 ( $\pm$ 0.379)
	female	71	45.426 ( $\pm$ 0.364)	0.010 ( $\pm$ 0.0007)	9.881 ( $\pm$ 0.262)

Note: The logistic-by-weight model is lizard body length =  $[a^3/(1 + be^{-kt})]^{1/3}$ , where  $b = [a^3/L_0^3] - 1$ ;  $L_0$  is estimated length at time zero (Schoener and Schoener 1978).

Species differences in survival and recapture probability were greater than differences between the sexes of each species (Table 3). The most parsimonious model using the CJS method for *Carlia* was species-dependent survival and recapture rate ( $\phi$  [species]  $p$  [species]; model weight = 0.47; Table 3). Estimates of monthly survival, from parameter estimates for this top model, were greater for *C. rostralis* and *C. rubrigularis* than for *C. storri* (*C. rostralis*, 0.84 [ $\pm$  95% CI 0.06]; *C. rubrigularis*, 0.86 [ $\pm$  95% CI 0.07]; and *C. storri*, 0.71 [ $\pm$  95% CI 0.11]). Models incorporating sex differences in survival and recapture probability had little support ( $\Delta$ QAIC<sub>c</sub> > 5.47, model weight < 0.03; Table 3).

Maximum age of lizards was  $465 \pm 166$  d (mean  $\pm$  SD) and  $438 \pm 181$  d for *C. rostralis* males and females,  $492 \pm 161$  d and  $483 \pm 249$  d for *C. rubrigularis* males and females, and  $363 \pm 121$  d and  $329 \pm 133$  d for *C. storri* males and females, respectively. This estimate of age of lizards revealed that *C. rostralis* and *C. rubrigularis* lived longer than *C. storri* (ANOVA Type II sum of squares,  $F = 4.77$ ,  $P < 0.05$ ; Fisher's LSD test,  $P < 0.05$ ), but that males and females of each species did not differ in maximum age (ANOVA Type II sum of squares,  $F = 0.45$ ,  $P > 0.5$ ).

#### Prey size dimorphism

In all three species, there was wide variation in the prey size consumed by individuals. Males and females consumed prey of similar sizes in all three species. In *C. storri*, there was a significant relationship between head size and prey size, but this relationship did not differ significantly between the sexes (Table 4).

#### DISCUSSION

In this study, three sympatric species of lizards in the genus *Carlia* had strongly contrasting patterns of adult sexual size dimorphism (SSD). *Carlia rostralis* was the largest species, had the fastest growth, and had male-biased size dimorphism. *Carlia rubrigularis* was intermediate in size and females grew more rapidly than males, but for a shorter period, resulting in similar adult body size for the two sexes. *Carlia storri*, the smallest species, grew more slowly than the other species and had female-biased size dimorphism. Despite this variation in sexual size dimorphism, all three species were broadly similar in terms of sexual shape dimorphism: males had

larger head dimensions and females had longer interlimb lengths. Head size differences could have ecological causes related to food acquisition (e.g., Cox et al. 2008), but both the male and female patterns of dimorphism were consistent with sexual and fecundity selection, respectively. Size of prey items did not differ significantly between the sexes for any species and therefore natural selection due to trophic partitioning is not likely to be driving sexual dimorphism in these species. If survival probability were sex biased, then one sex might live longer than the other and grow to a larger size, so that body size dimorphism could reflect differential survival rates between sexes rather than differences in body size per se (James 1991, Johnston 2011). However, for *Carlia*, SSD was not due to higher mortality of one sex; we found no significant effect of sex on survival probability, or maximum age, in any of the three species. If differential selective forces between the sexes were acting on juvenile growth rate, this would indicate that factors directly affecting juveniles were responsible for

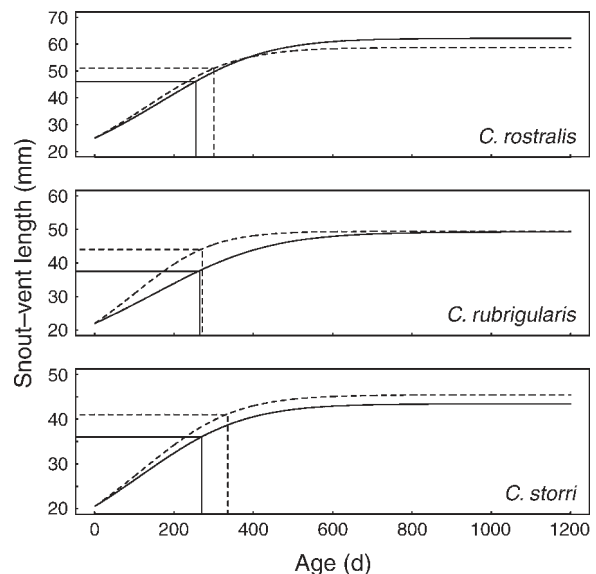


FIG. 3. Growth trajectories of male and female *Carlia* lizards: *C. rostralis*, *C. rubrigularis*, and *C. storri* from the logistic-by-weight model, with minimum size and age at sexual maturity for each sex. Solid lines indicate males and dashed lines indicate females.



TABLE 3. Summary of maximum likelihood comparison of mark–recapture models, estimating survival ( $\phi$ ) and recapture ( $p$ ) probability as a function of species, a combination of species and sex, or constant ( $\bullet$ ) for the three *Carlia* species.

Survival	Recapture	Covariate	$n$	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	Model weight	QDeviance
<b>Species</b>	<b>species</b>	<b>none</b>	<b>6</b>	<b>631.20</b>	<b>0.00</b>	<b>0.47</b>	<b>618.94</b>
$\bullet$	<b>species</b>	<b>none</b>	<b>4</b>	<b>632.28</b>	<b>1.08</b>	<b>0.27</b>	<b>624.16</b>
$\bullet$	$\bullet$	none	2	634.48	3.29	0.09	630.45
Species	$\bullet$	none	4	635.63	4.43	0.05	627.51
Species	species	GR	9	636.26	5.06	0.04	617.69
Species	species $\times$ sex	none	9	636.66	5.47	0.03	618.10
Species $\times$ sex	species	none	9	637.42	6.22	0.02	618.90
$\bullet$	species $\times$ sex	none	7	637.74	6.54	0.02	623.40
Species	species	GR and GR <sup>2</sup>	12	641.37	10.18	0.003	616.40
Species $\times$ sex	$\bullet$	none	7	641.75	10.55	0.002	627.40
Species	$\bullet$	GR	8	642.76	11.55	0.001	626.31
Species $\times$ sex	species $\times$ sex	none	12	642.91	11.71	0.001	617.93
Species	$\bullet$	GR and GR <sup>2</sup>	10	645.58	14.38	<0.001	624.89
Species $\times$ sex	species	GR	15	648.67	17.47	<0.001	617.14

Notes: Survival models were also constrained to be functions of the covariate residual growth rate (GR), or GR and the square of residual growth rate (GR<sup>2</sup>). The Akaike weight of each model is used as a measure of the relative likelihood of the best model compared with the other candidate models. Models with the greatest support are in boldface. Shown are the number of model parameters ( $n$ ), quasi-likelihood adjusted Akaike’s Information Criterion (QAIC<sub>c</sub>), the difference between the QAIC<sub>c</sub> for each model and the smallest QAIC<sub>c</sub> among the set of models fitted ( $\Delta$ QAIC<sub>c</sub>), AIC<sub>c</sub> weights, and deviance for candidate models describing survival ( $\phi$ ) and recapture ( $p$ ) of lizards at monthly intervals.

SSD. We found no evidence of directional or stabilizing selection on juvenile growth, suggesting that sexual differences in adult body size instead may be due to sexual selection acting on adult body size. We conclude that size differences between adult *Carlia* males and females occurred as a result of sexual differences in growth, and not differential trophic niches or differential likelihood of survival.

*Body shape dimorphism*

Selection may act differentially on various morphological traits of each sex, causing dimorphism in trait size. Additionally, selection can mold sexual dimorphism in shape independent of size (Losos et al. 2003, Schwarzkopf 2005). Regardless of variation in body length dimorphism, males of all three species had relatively larger heads and females had longer interlimb lengths, suggesting that some benefits of body shape dimorphism are independent of the direction of SSD. Trophic resource partitioning could select for head size differences between the sexes (Slatkin 1984), or could also result secondarily from sexually selected dimorphism. In either case, the larger sex should be able to

capture and consume larger and harder-bodied prey (Vitt and Cooper 1985, Cox et al. 2003). Estimates of the intensity of trophic competition between males and females were lacking, but in all three species in this study, the size and type (taxonomic groups) of prey consumed did not differ significantly between male and female lizards (Table 4; see Manicom and Schwarzkopf 2011). Thus, it is unlikely that avoidance of dietary overlap selects for larger head size in males; even though male lizards in our study had relatively larger heads, they did not use this size difference to exploit larger prey. It also appears that, although we found overall differences in body size between the sexes in two of the three species, variability in prey size was sufficiently large to obscure any effect that this may have on the size of prey consumed. Typically, studies showing differences in prey size consumption involve lizards with considerably larger degrees of sexual dimorphism than in these *Carlia* species (e.g., Schoener 1967, Schoener and Gorman 1968).

Lizards fight using their jaws (Carpenter and Ferguson 1977), and male aggression by biting has been documented in both *C. rostralis* and *C. rubrigularis*

TABLE 4. Summary of mean median length of arthropod prey from diet analysis of male and female *Carlia* species with ANCOVA, showing the influence of jaw width and sex on prey size; there were no significant interactions.

Species	Sex	$N$	Median prey length, mean $\pm$ SD (mm)	Jaw width			Sex		
				$F$	df	$P$	$F$	df	$P$
<i>C. rostralis</i>	male	23	7.55 ( $\pm$ 3.6)	0.85	1	0.4	1.9	1	0.2
	female	26	6.72 ( $\pm$ 3.7)						
<i>C. rubrigularis</i>	male	26	5.62 ( $\pm$ 3.8)	0.09	1	0.8	1.11	1	0.3
	female	22	5.02 ( $\pm$ 2.2)						
<i>C. storri</i>	male	21	4.56 ( $\pm$ 3.4)	14.6	1	0	3.1	1	0.08
	female	19	3.51 ( $\pm$ 1.8)						



PLATE 1. Copulating pair of *Carlia rubrigularis* lizards. The male grasps the female with a bite to her flank. Photo credit: C. Manicom.

(Whittier and Martin 1992, Torr 1994). A large and robust head increases the strength of jaws, increasing fighting ability and giving males an advantage over other males in contests for territory and access to females, and thus increased mating success (Trivers 1976, Vitt and Cooper 1985, Gvozdik and van Damme 2003). Further, many lizards use their jaws during copulation (Carpenter and Ferguson 1977). Male *Carlia* initiate copulation by grasping the female with a bite to her flank, often needing to subdue struggling females with a firm grip, which may need to be readjusted and maintained for 2–3 minutes for insemination to take place (C. Manicom, *personal observation*; Langkilde and Schwarzkopf 2003; see Plate 1). Large-headed male lizards often have greater mating success (Vitt and Cooper 1985, Gvozdik and van Damme 2003). Gular nuptial coloration is an important sexual signal in contest competition and determination of mate preference (Andersson 1994). For lizards with gular nuptial coloration, larger heads provide a greater area of color to display and therefore increased mating success (Vitt and Cooper 1985, Anderholm et al. 2004). Both *C. rostralis* and *C. rubrigularis* males exhibit striking gular coloration (black and red, respectively) during the breeding season; this could contribute to selection for the relatively larger heads of males of these two species. Taken together, the evidence suggests that there is selection for larger head size in males of all three species, independent of body size. Males with relatively larger heads may have greater success in territory acquisition and/or mating in all three species, and there also may be selection for larger color

patches in species with color. For *C. rostralis* and *C. storri*, head size differences between the sexes resulted from differential growth, but for *C. rubrigularis*, males and females differed in head size from birth. These alternate patterns in development are commonly found in studies of lizard shape dimorphism (Braña 1996, Olsson et al. 2002, Schwarzkopf 2005); however, the importance of ontogenetic timing of the onset of this dimorphism is not known (Shine 1989).

Female *C. rostralis* and *C. rubrigularis* have longer relative interlimb lengths (length of body between fore and hind limbs) than males of the same body length, and adult *C. storri* females have long absolute interlimb lengths due to their larger asymptotic size. Selection for increased clutch size in females is a common cause of body shape dimorphism in lizards, and females with longer bodies can carry more offspring (Olsson et al. 2002, Schwarzkopf 2005; reviewed by Cox et al. 2007). Larger-bodied female lizards typically produce larger clutches, but *Carlia* produce fixed clutch sizes of two eggs (James and Shine 1988, Goodman 2006). With clutch size fixed, females can only adjust egg size and frequency of reproduction. Egg size is frequently positively related to offspring fitness in lizards (Doughty 1997); hence, selection for increased egg size, rather than increased clutch size, could influence female abdomen size in *Carlia* (Goodman et al. 2009). Abdomen volume can limit egg volume (Goodman et al. 2009), and if females produce eggs of maximal size, then egg size correlates with maternal abdomen size in invariant-clutch producers. Mean egg volume and maternal body

size (SVL) are significantly correlated in *C. rubrigularis* (Goodman 2006), but not in the other two species (B. Goodman, *unpublished data*) or in five other species of *Carlia*, although in other scincid genera there were positive correlations between egg volume and SVL (James and Shine 1988). When interspecific correlations are significant, but intraspecific correlations are not, it suggests there is selection for larger eggs, coupled with a body size constraint within species (Fischer et al. 2002), processes likely to be operating in *Carlia* lizards.

*How do observed patterns in dimorphism develop?*

*Size dimorphism due to growth and age at maturity*

Body size dimorphism was caused by growth trajectories that differed between males and females. The sexes often differ in their energy allocation to body growth because they differ in the amount of time, resources, and energy assigned to reproduction (Dunham et al. 1989, Anderson and Vitt 1990). Reproduction can consume resources in both sexes in many ways: to support maturation (i.e., changes in morphology or physiology related to reproduction), to support mating behavior, or to compete for resources needed for reproduction (Schwarzkopf and Shine 1992, Stamps et al. 1998). Additionally, in male lizards, increased activity caused by increased plasma testosterone levels at maturity, and frequent aggressive interactions and greater movement associated with reproduction, can inhibit growth (Cox et al. 2005). For reproductive female lizards, resources may be allocated to provision eggs, both before and after fertilization, and females may reduce activity, and therefore food intake, to reduce their vulnerability to predators during this time (e.g., Schwarzkopf 1996). Female *Carlia* grew faster than males, but in all species, female growth slowed more upon reaching sexual maturity (Fig. 3). *Carlia* species always produce two eggs, so selection for increased reproductive allocation could act on egg size or the frequency of reproduction. Egg size, however, is fairly strongly constrained in *Carlia* (Goodman 2006). Producing frequent clutches of eggs during the breeding season, thus allocating large quantities of resources to egg production and mating activity when sexually mature, may occur at the expense of body growth for females (e.g., Schwarzkopf 1993).

In *Carlia*, there was no evidence that the energy costs of male reproduction affected male growth rate, because achieving sexual maturity did not slow the growth of males of any species. In *C. rostralis*, size dimorphism occurred because the sexes differed in duration of growth: the sexes experienced similar growth rates before reaching maturity. However, females reached asymptotic body length soon after sexual maturity, whereas male *C. rostralis* continued to grow after attaining minimum size for sexual maturity (at ~9 months) well into the second year of life, resulting in a substantially greater body size than for females. In *C. rubrigularis*, female growth was initially considerably faster than that of males but also slowed when females

became sexually mature. *Carlia rubrigularis* females reached sexual maturity relatively early by growing rapidly as juveniles. Females differed significantly from males, in that their growth rate decreased faster with increasing body length, probably due to the allocation of resources to reproduction rather than growth, until females and males were similar asymptotic sizes. The energy constraints of reproduction were further evident in the slowed growth of female *C. storri* at maturation; however, female *C. storri* delayed sexual maturity to ~11 months. The relatively slower growth rate of *C. storri*, combined with a restricted breeding season for this species (November to January, compared to August to January for *C. rostralis* and *C. rubrigularis*; Manicom 2010), means that most *C. storri* females attained sexual maturity only after one full breeding season had passed. Thus, females of this species were larger when breeding for the first time, compared to species with a longer breeding season. Larger relative body size at first mating may be a strategy used by *C. storri* females to increase survival and ensure high reproductive potential (Stearns 1992).

*Integrating ontogenetic pattern to suggest possible selective origins of dimorphism*

The close association between sexual growth divergence and the onset of reproductive maturity in *C. rostralis* females suggests that energy costs of reproductive investment may constrain their growth. The growth of females of all three species was similarly affected, probably by energy allocation to reproduction, and yet the three species had different patterns of SSD, suggesting that constrained female growth due to reproductive investment is unlikely to be the sole selective force acting on SSD in these three species. Development of sexual size dimorphism in the three species was caused, proximately at least, by juvenile growth processes that varied among the species: in *C. rostralis* the sexes differed in duration of growth, in *C. rubrigularis* the sexes differed in rate of growth, and in *C. storri* the sexes differed somewhat in growth rate and duration, and female sexual maturity was delayed. There was no evidence for selection on juvenile growth rate in any species, which suggests that SSD may be a result of selection on adult sexual traits. We used survival as a measure of fitness, but sex differences in juvenile growth rate instead may be driven by other traits (Brodie et al. 1995), such as increased reproductive success with early maturation. Importantly, differences in rates of survival between the sexes were not responsible for the patterns that we observed.

The ontogenetic stages at which sexual divergence in body size occurred allow us to suggest hypotheses for the ultimate causes of sexual dimorphism in these species. We propose that different patterns of SSD in *Carlia* spp. may reflect underlying differences in population size, species' social systems, and their use of space and resources. For instance, selective pressures

giving large males the ability to repel competitors and defend high-quality resources are believed to be more important than female choice in determining male size in many lizards (e.g., Schoener and Schoener 1980; reviewed in Olsson and Madsen 1998). These interactions ensure that large, dominant males have increased access to females and therefore greater reproductive success (Vitt and Cooper 1985, Anderson and Vitt 1990). *Carlia rostralis* males are highly aggressive (Whittier and Martin 1992), and male-biased SSD is generally more pronounced in lizards with male aggression and territoriality than in species lacking these behaviors (Stamps 1983, Cox et al. 2003). *Carlia rostralis* occur at high densities at the study site relative to *C. rubrigularis* and *C. storri* (14 *C. rostralis* individuals/100 m<sup>2</sup>; Manicom 2010). High density is likely to lead to a high encounter rate with conspecifics, so that male *C. rostralis* may need to compete for access to females by attacking other males and defending good-quality territory (e.g., Calsbeek and Smith 2007). In this system, selection should favor large males with large heads because they have advantages in male–male competition, territory defense, display of breeding color, copulation success, and, therefore, reproductive success.

Sexual selection may also select for small males, for instance in populations where densities are low and females are widely dispersed, so that male mating success depends on the number of females encountered rather than on competitive advantages over other males (Zamudio 1998). In this type of system, selection favors small males that reach sexual maturity at an earlier age than females, are highly mobile, and can spend time and energy searching for mates instead of food (Trivers 1976). Population densities of *C. storri* are low relative to the other two *Carlia* species at the study site (6 individuals/100 m<sup>2</sup>; Manicom 2010), and it is likely that individual male *C. storri* that can devote a large proportion of time and energy to finding a mate, rather than to food acquisition and growth, when females are highly dispersed, will achieve greater reproductive success. *Carlia storri* males do not appear to require large body size, yet their relative head proportions are larger than those of females at the same body size. Because *C. storri* are widely dispersed, we expect encounter rates between individuals to be low, male territory defense to be counterproductive, and male combat to be rare. *C. storri* do not display breeding coloration. This suggests that there is strong selection on the head dimensions of male *C. storri* for successful copulation and increased mating success in these lizards.

If *C. rostralis*, the largest of the sympatric species, has male-biased dimorphism due to high density and the need for male–male competition, and *C. storri*, the smallest species, has female-biased dimorphism due to low density and the need for males to be small and mobile to find mates, why then is *C. rubrigularis*, with intermediate size and density, sexually similar in overall body size? If adult body size alone were considered, we

would assume that selection pressures on body size were similar for male and female *C. rubrigularis*. Instead, young female *C. rubrigularis* grow rapidly and mature early and achieve the same adult body size as male conspecifics. Male *C. rubrigularis* are aggressive (Torr 1994) and display gular nuptial color, and therefore probably compete for females and resources. The relatively larger heads of male *C. rubrigularis* compared to those of conspecific females may assist in male–male competition, successful copulation, and may increase the area of breeding color on display, and yet in this species, sexual selection has not produced larger overall body size of males. Although very little is known about the use and benefit of nuptial coloration in *Carlia* lizards, it is likely that the area of bright color on display is important in dominance interactions, and that a larger color patch leads to increased mating success, as in other lizard species (Anderholm et al. 2004). It is possible that, in *C. rubrigularis*, size of color patch on display is more important than overall body size in competitive interactions and subsequent mating success (as in side-blotched lizards, *Uta stansburiana*; Calsbeek and Sinervo 2002). Alternatively, *C. rubrigularis* may be the only study species in which females also experience selection for large body size (Stuart-Smith et al. 2007). We predict that female *C. rubrigularis* may also need to compete for and defend resources, or compete with other females for reproductive opportunities (a similar pattern was observed in *Anolis sagrei* females; Schoener and Schoener 1980). Body size similar to that of males may be an advantage driving selection for fast growth in young females. We observed exclusive space use by *C. rubrigularis* females, indicating that they probably engage in site defense (L. Schwarzkopf, unpublished data). Competitive interactions of female lizards are rarely documented (Woodley and Moore 1999), but can be important selective forces on female body size (Calsbeek and Smith 2007).

The occurrence of nuptial coloration in some male *Carlia* and its influence on *Carlia* social systems and mating success needs further study. The molecular phylogeny of *Carlia* shows rapid differentiation of 30 species early in the evolution of the genus (Dolman and Hugall 2008). Speculatively, if the evolution of sexual dimorphism in this genus were driven by the evolution of social systems and the use of nuptial coloration, these factors may have led to the rapid speciation of this genus (as in the extreme case of cichlid fish; Seehausen and van Alphen 1999, and see Hochberg et al. 2003).

### Conclusion

Sympatric *Carlia* exhibit differential juvenile growth and differential timing in the cessation of growth for the sexes, and thereby achieve various directions of adult SSD. Differential mortality of the sexes, differential selection on juvenile growth rate, and differential food intake apparently do not contribute to SSD in these species. Inference from our knowledge of other aspects

of the biology of these species, such as population density and social system, suggests that various sorts of selection on adults for enhanced reproductive success may have shaped sexual dimorphism in these three species. Our study illustrates how knowledge of growth rate and juvenile-to-adult survival can identify developmental causes of differences in size between the sexes and aid devising testable hypotheses for the proximate causes of SSD.

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