

A test of the reproductive cost hypothesis for sexual size dimorphism in Yarrow's spiny lizard *Sceloporus jarrovi*

R. M. COX

Graduate Program in Ecology and Evolution, Rutgers University, New Brunswick, NJ 08901, USA

Summary

1. Trade-offs between reproduction and growth are central assumptions of life-history theory, but their implications for sexual size dimorphism (SSD) are poorly understood.
2. Adult male Yarrow's spiny lizards *Sceloporus jarrovi* average 10% larger than adult females. In a low-altitude (1700 m) population, this SSD develops because males grow more quickly than females during the first year of life, particularly during the first female reproductive season. This study tests the hypothesis that SSD develops because female growth is constrained by energetic costs of reproduction.
3. To test for a growth cost of reproduction, I compared growth rates of free-living females that differed, either naturally or experimentally, in reproductive status. Females that naturally delayed reproduction until their second year grew more quickly than females that reproduced as yearlings, and ovariectomized yearlings grew more quickly and to larger sizes than reproductive controls.
4. To determine whether SSD develops in the absence of this inferred reproductive cost, I also studied a high-altitude (2500 m) population in which all females delay reproduction until their second year. Sex differences in growth trajectories were similar to those observed at low altitude, such that males averaged 10% larger than females even prior to female reproduction.
5. Although female growth may be constrained by reproduction, multiple lines of evidence indicate that this cost is insufficient to explain the full magnitude of SSD in *S. jarrovi*. First, differences in growth of reproductive and nonreproductive females are not observed until the final month of gestation, by which time SSD is already well developed. Second, the growth benefit accruing from experimental inhibition of reproduction accounts for only 32% of the natural sex difference in body size. Finally, SSD develops well in advance of female reproduction in a high-altitude population with delayed maturation.

Key-words: body size, cost of reproduction, growth rate, ovariectomy, trade-off

Journal of Animal Ecology (2006) **75**, 1361–1369

doi: 10.1111/j.1365-2656.2006.01160.x

Introduction

Many species exhibit sex differences in adult body size, and this widespread phenomenon of sexual size dimorphism (SSD) has generally been attributed to differences in the selective forces acting on male vs. female body size (reviewed in Andersson 1994). However, most of the interspecific variance in lizard SSD is left unexplained by primary adaptive hypotheses invoking sexual selection for large male size and fecundity selection

for large female size (Cox, Skelly & John-Alder 2003). One shortcoming of this traditional adaptive paradigm lies in its failure to integrate proximate energetic constraints on male and female growth within its ultimate theoretical framework for SSD. Adult body size is the result of a complex ontogenetic growth process, and life-history ecologists have long recognized that growth may be traded off against reproduction. Given the many fundamental sex differences in reproductive investment, growth may often be differentially constrained in males vs. females. However, this 'reproductive cost hypothesis' (Schultz 1993) for SSD remains largely unexplored.

Reproduction can incur a growth cost by reducing energy acquisition and/or by increasing energy allocation to reproductive functions at the expense of growth. For

example, reproductive females may decrease foraging because the burden of a clutch or litter compromises their ability to escape predators (Cooper *et al.* 1990; Sinervo, Hedges & Adolph 1991), or because eggs or embryos limit the abdominal space available for food items (Weeks 1996; Weiss 2001). Reproduction also demands energy allocation to eggs or embryos, as well as metabolic costs associated with offspring production and the maintenance of a clutch or litter (Beuchat & Vleck 1990; Demarco & Guillette 1992; Angilletta & Sears 2000). Such reductions in energy acquisition or increases in energy expenditure may constrain energy allocation to growth (Schwarzkopf 1993; Landwer 1994), but the implications of such constraints with respect to SSD remain largely unexplored.

Much of the evidence for growth costs of reproduction comes from negative correlations between natural variation in growth and some measure of reproductive investment (Reznick 1985; Partridge & Harvey 1988; Schwarzkopf 1994). However, strictly correlative approaches suffer several important limitations. For example, individuals in relatively good physiological condition or living in optimal habitat patches may be able to both grow quickly and reproduce, whereas those in relatively poor condition or suboptimal habitat may be unable to do either (e.g. Brown & Weatherhead 2004). This confounding variance in condition or habitat could obscure any actual growth cost of reproduction (Partridge & Harvey 1988; Landwer 1994). Further, growth rate typically decreases with body size in lizards, whereas reproductive investment often increases with body size. These contrasting allometries could produce a spurious negative correlation between reproduction and growth even in the absence of an actual trade-off. One way to overcome these limitations is to manipulate reproductive investment in individuals that are matched for size and randomized with respect to other potentially confounding factors (e.g. Landwer 1994).

The present study combines both correlative and experimental approaches to test the hypothesis that reproductive investment constrains female growth and thus gives rise to male-larger SSD in the lizard *Sceloporus jarrovii*. Previous studies have shown that SSD develops in this species because yearling males grow more quickly than females, particularly during vitellogenesis in the autumn and gestation the following spring (Cox 2005). Reproduction incurs a demonstrable energetic cost in *S. jarrovii* (Tinkle & Hadley 1973; Beuchat & Vleck 1990; Demarco & Guillette 1992), but it is not known whether this cost actually constrains female growth. If reproduction incurs a growth cost, then (1) females that reproduce as yearlings should grow more slowly during the reproductive season than nonreproductive females that delay reproduction, and (2) yearlings prevented from reproducing via surgical ovariectomy should grow more quickly than intact, reproductive controls. Support for these predictions would indicate a growth cost of reproduction, but this evidence alone would not directly address the causation of SSD. Thus, the present study also compares two populations of *S. jarrovii* that

differ dramatically in the timing of female maturation: most females reproduce as yearlings at low altitude, whereas all females delay reproduction until their second year at high altitude (Ballinger 1979). If SSD develops because female growth is constrained by reproduction, then sex differences in growth and the development of SSD should be delayed at high altitude.

Materials and methods

STUDY SPECIES AND SITES

Yarrow's spiny lizard *Sceloporus jarrovii* Cope is a viviparous species in which adult males average 10% larger (longer in snout–vent length, SVL) than adult females (Fitch 1978; Ruby & Dunham 1984; Cox 2005). The reproductive cycle of this species is well described (Goldberg 1971; Ballinger 1973, 1979; Tinkle & Hadley 1973; Ballinger & Nietfeldt 1989), and can be summarized as follows: vitellogenesis typically begins in late September or October, mating occurs in October and November, and ovulation and fertilization occur in November. From December through February, activity is largely constrained by cold winter temperatures, and little embryonic development occurs until March. Embryonic development is rapid during April and May, and parturition occurs in late May or June. Females are nonreproductive from July to September, during which time they accumulate lipid reserves to support future reproduction (Ballinger 1973; Congdon 1977).

Sceloporus jarrovii was studied for three consecutive years (2002–04) at two sites in the Chiricahua Mountains, Coronado National Forest, Cochise Co., Arizona (USA). The first site (low altitude) is located along a 2-km section of streambed in the North Fork of Cave Creek Canyon, about 1–3 km north-west of the American Museum of Natural History's Southwestern Research Station (31°53–54'N, 109°13'W, altitude 1700 m). The second site (high altitude) is located along an exposed ridgeline and talus slope about 1 km south-east of Buena Vista Peak (31°54–55'N, 109°16'W, altitude 2500 m). Although these sites are separated by less than 6 km in linear distance, they differ by about 800 m in altitude, which profoundly impacts the life history of *S. jarrovii*. At the low-altitude site, most females reproduce as yearlings, although the percentage that do so varies among years (mean 75%, range 41–84%, Ballinger 1979). However, because thermal constraints impose a shorter growing season and a later birth date, all females delay reproduction until their second season at the high-altitude site (Ballinger 1979).

INDIVIDUAL VARIATION IN REPRODUCTION

Standard mark–recapture methods were used to compare the growth rate of low-altitude females that reproduced as yearlings (REP) vs. those that naturally delayed reproduction until their second year (NON). Upon initial capture, each animal received a toe clip for

permanent identification. At each capture, SVL was measured to the nearest 1 mm with a ruler and body mass was measured to the nearest 0.1 g with a Pesola® scale. Reproductive status was determined by abdominal palpation. Individual growth rates were calculated by dividing change in SVL by elapsed time. Body size (SVL) and growth rate were compared using ANOVA with reproductive status (REP or NON) and year (2002 or 2003) as categorical effects. To determine whether differences in growth rate were related to differences in size, ANCOVA was performed with reproductive status and year as categorical effects and initial SVL as a covariate. For the subset of females that were measured at every census, repeated measures ANOVA was used with reproductive status as a between-subjects effect, time as a within-subjects effect, and a reproductive status \times time interaction term. Effects of reproductive status and the reproductive status \times time interaction were assessed using multivariate Wilks' Lambda tests.

EXPERIMENTAL MANIPULATION OF REPRODUCTION

To test experimentally for a trade-off between growth and reproduction, low-altitude yearling females were prevented from reproducing via surgical ovariectomy. In early September of 2003, prior to the onset of vitellogenesis, 65 yearling females were captured, measured for SVL and body mass, and assigned to one of two, size-matched treatment groups: ovariectomy (OVX) and intact control (CON). Animals were anaesthetized with an intramuscular injection of ketamine (Vetus Animal Health, 130 mg per kg body mass). OVX females were bilaterally ovariectomized by ligating each oviduct, ablating each ovary, and then cauterizing each ligated oviduct. CON females received sham surgeries in which the ovaries were manipulated but left intact. Incisions were closed with Nexaband® surgical glue (Veterinary Products Laboratories). Surgeries were performed within 2 days of capture and animals were released at their location of capture within 3 days of surgery. All animals appeared healthy and vigorous upon release, and survival from surgery to release was high (62 of 65, 95%; $n = 31$ per treatment). Females were recaptured at four time points in 2004: April (6.5 months post-treatment), May (7 months), June (8 months, just prior to parturition), and August (11.5 months). Linear growth rates (mm day^{-1}) were calculated between successive captures by dividing change in SVL by elapsed time. Statistical comparisons of OVX and CON are analogous to those for REP and NON (see above), with the exception that year effects were not included because all data were collected in the same reproductive season.

ALTITUDINAL VARIATION IN REPRODUCTION

To evaluate the influence of female reproduction on SSD at the population level, sexual divergence in growth

and body size was compared between low altitude (early female maturation) and high altitude (delayed female maturation). Two complementary methods were used to analyse growth at each site. First, linear growth rates were calculated over each separate recapture interval by dividing change in SVL by elapsed time. Male and female SVL and growth rate were then compared over each recapture interval using ANOVA with sex and year as categorical effects (significant sex \times year interactions were never observed). Experiment-wise error rates were adjusted for multiple comparisons within each population. This method is advantageous because it allows for seasonal variation in growth and permits direct inferences about age-specific sex differences in absolute growth rate. However, underlying differences in age and body size complicate direct comparisons of linear growth rates between populations.

As a complementary approach, nonlinear growth models were used to estimate asymptotic size (A) and the characteristic growth parameter (k) for males and females at each site. This method is advantageous because parameter estimates are directly comparable between sexes and populations, but limited because k is modelled as invariant through time (see Dunham 1978a). Parameter estimates were derived from the interval forms of three common growth models (Von Bertalanffy, logistic-by-length, and logistic-by-weight) using a Marquardt nonlinear least-squares regression procedure (Dunham 1978b). For each model, estimates of A and k were considered statistically different when their associated 95% planar support confidence intervals did not overlap (Dunham 1978a). A single growth measurement was randomly chosen for each animal to ensure statistical independence among data points. Growth trajectories were plotted by estimating size at birth (L_0) from the smallest measured neonate (28 mm for both sexes at both sites). Absolute time was converted to 'growth days' by subtracting out periods of winter dormancy on the basis of Ballinger's (1979) estimates of the active seasons at low altitude (early April to mid-November, 220 days) and high altitude (late April to mid-October, 170 days). Date of birth was assumed to be 1 June at low altitude (median date on which neonates were first observed) and 15 June at high altitude (parturition is delayed several weeks relative to low altitude; Ballinger 1979).

Results

INDIVIDUAL VARIATION IN REPRODUCTION

Reproductive status was determined for 76 yearling females from the 2002 and 2003 cohorts, of which 61 (80%) reproduced as yearlings. In September, prior to the onset of vitellogenesis, females that reproduced as yearlings (REP) averaged 5.5 mm longer in SVL than females that did not reproduce as yearlings (NON) ($F_{2,36} = 17.20$; $P < 0.001$; Fig. 1a). Over the autumn mating season and subsequent winter, REP and NON

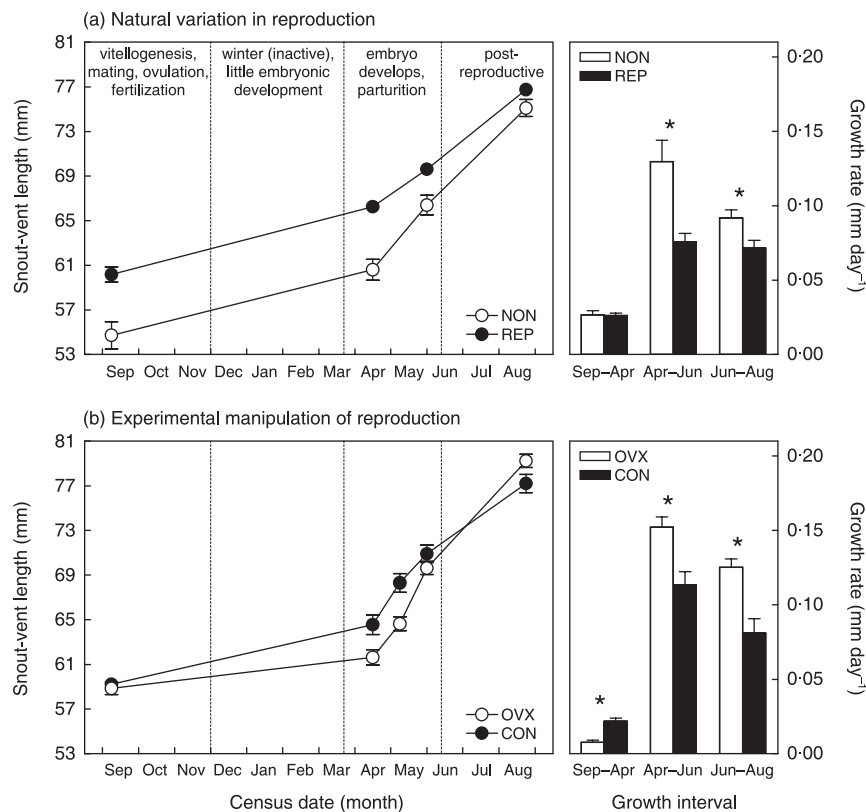


Fig. 1. (a) Mean (± 1 SE) snout-vent length (left) and growth rate (right) of reproductive (REP) and naturally nonreproductive (NON) yearling *Sceloporus jarrovi* females in the low altitude population. Data are combined for the 2002 and 2003 cohorts. (b) Mean (± 1 SE) snout-vent length (left) and growth rate (right) of ovariectomized (OVX) and reproductive control (CON) yearling females. Asterisks indicate significant ($P < 0.01$) growth differences.

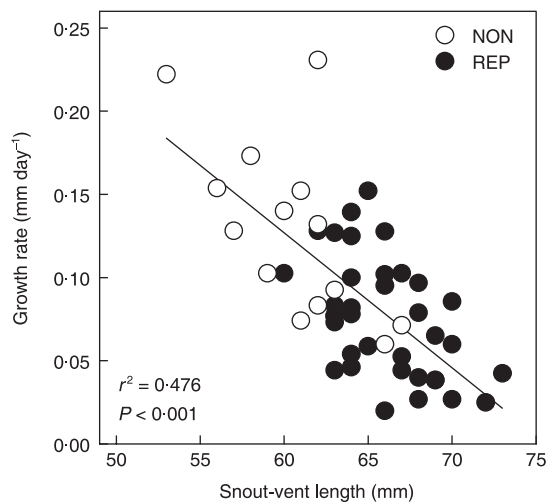


Fig. 2. Growth rate as a function of snout-vent length (SVL) for reproductive (REP) and nonreproductive (NON) yearling *Sceloporus jarrovi* females during gestation (April–June).

$P = 0.016$; Fig. 1a). As a result, REP were only slightly (1.7 mm) larger than NON by late August ($F_{2,23} = 3.01$; $P = 0.096$). Repeated-measures ANOVA revealed that growth rate was strongly influenced by reproductive status ($F_{1,14} = 8.12$; $P = 0.013$), time ($F_{2,13} = 98.48$; $P < 0.001$), and their interaction ($F_{2,13} = 5.60$; $P = 0.018$), indicating that growth costs of reproduction were only evident during late gestation and following parturition (Fig. 1a).

Although NON grew more quickly than REP during gestation, growth rate over this interval was negatively correlated with body size (Fig. 2). Consequently, the effect of reproductive status on growth rate disappeared when initial SVL was included as a covariate ($F_{3,46} = 1.10$; $P = 0.300$). Similar results were obtained when initial SVL was included as a covariate in the analysis of post-partum growth rate ($F_{3,22} = 0.60$; $P = 0.446$), and in the repeated measures model for growth across all seasons ($F_{3,13} = 1.05$; $P = 0.304$).

EXPERIMENTAL MANIPULATION OF REPRODUCTION

Two intact control (CON) females that did not reproduce as yearlings were omitted from subsequent analyses. Survival did not differ between CON and ovariectomized (OVX) females over any portion of the experiment (Table 1). Opposite the predictions of the reproductive

grew at similar rates ($F_{2,35} = 0.02$; $P = 0.893$; Fig. 1a), such that they still differed in SVL the following April ($F_{2,71} = 37.39$; $P < 0.001$; Fig. 1a). As predicted by the reproductive cost hypothesis, NON grew more quickly than REP during spring gestation ($F_{2,47} = 16.90$; $P = 0.002$; Fig. 2a), and this growth difference persisted for several months following parturition ($F_{2,23} = 6.73$;

Table 1. Survival of experimental *Sceloporus jarrovi* groups from treatment in September 2003 to the end of the experiment in August 2004

Census Dates	Months post-treatment	Captured (<i>n</i>)		Survival (%)	
		OVX	CON*	OVX	CON*
5–11 September	0	31	29	–	–
13–23 April	6.5	16	15	52	52
3–6 May	7.0	15	13	48	45
2–7 June	8.0	14	11	45	38
22–28 August	11.5	8	8	26	28

*Two nonreproductive CON were omitted from calculations.

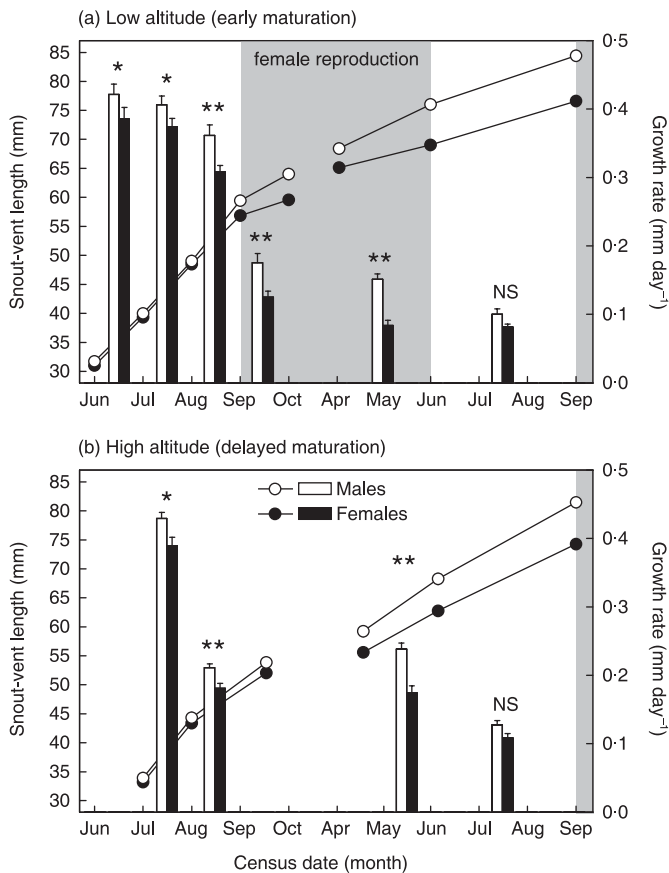


Fig. 3. Mean snout–vent length (circles) and growth rate (± 1 SE, bars) for males and females at (a) low altitude (1700 m) and (b) high altitude (2500 m). Shaded areas indicate the timing of reproduction, beginning with vitellogenesis (September) and ending with parturition (June). Asterisks indicate significant sex differences in growth rate (**P* < 0.05; ***P* < 0.008, adjusted for multiple comparisons). Sex differences in growth and SVL occur well in advance of female maturation in the high-altitude population.

cost hypothesis, CON grew more quickly than OVX over the autumn mating season and subsequent winter ($F_{1,29} = 33.75$; $P < 0.001$; Fig. 1b). Thus, upon recapture in April, CON averaged 3 mm larger than OVX for any given initial SVL ($F_{2,29} = 36.67$; $P < 0.001$). However, as predicted by the reproductive cost hypothesis, OVX grew more quickly than CON during gestation ($F_{1,29} = 12.58$; $P = 0.002$; Fig. 1b), particularly during the final month before parturition ($F_{1,22} = 20.02$; $P < 0.001$). The mean growth rate of OVX females during gesta-

tion (0.152 mm day⁻¹; Fig. 1b) was nearly identical to that of intact yearling males (0.151 mm day⁻¹; Fig. 3a), suggesting that OVX restores female growth to the rate of males.

Following parturition, OVX continued to grow more quickly than CON ($F_{1,15} = 14.31$; $P = 0.002$; Fig. 1b), such that OVX were 2.5 mm larger than CON for any given initial SVL upon recapture in August ($F_{2,14} = 11.10$; $P = 0.005$). Over this time, the mean growth rate of OVX females (0.125 mm day⁻¹; Fig. 1b) was slightly greater than that of intact yearling males (0.100 mm day⁻¹; Fig. 3a). Repeated measures ANOVA revealed that growth rate was strongly influenced by treatment ($F_{1,14} = 29.74$; $P < 0.001$), time ($F_{2,13} = 206.35$; $P < 0.001$), and their interaction ($F_{2,13} = 20.66$; $P < 0.001$), indicating that growth costs of reproduction were only evident during late gestation and following parturition (Fig. 1b).

ALTITUDINAL VARIATION IN REPRODUCTION

At low altitude, SSD developed within the first year of life because of an underlying sex difference in growth rate. Although males grew more quickly than females at all intervals within the first year of life, this sex difference in growth was most pronounced during the first autumn ($F_{1,61} = 10.39$; $P = 0.002$; Fig. 3a, August–September) and subsequent spring ($F_{2,86} = 37.70$; $P < 0.001$; Fig. 3a, April–June). As a result, males averaged 7.0 mm (10%) larger than females by the end of the first reproductive season (age 12 months; Fig. 3a, June).

Despite delayed female maturation in the high-altitude population, sex differences in growth and the development of SSD were similar to patterns observed at the low-altitude site (Fig. 3). At both sites, sex differences in SVL were highly significant ($P < 0.001$) as early as September (age 3–4 months), fully 1 year prior to maturation for high-altitude females. High-altitude males grew more quickly than females at all points during the first year of life, and this sex difference in growth was most pronounced during the first autumn ($F_{1,30} = 11.08$; $P = 0.002$; Fig. 3b, August–September) and subsequent spring ($F_{2,60} = 22.84$; $P < 0.001$; Fig. 3b, April–June). As a result, high-altitude males averaged 5.5 mm (9%) larger than females at 12 months of age (Fig. 3b, June). By the time that high-altitude females attained sexual maturity in their second autumn (age 15 month), males already averaged 7.2 mm (10%) longer in SVL (Fig. 3b, September).

At both low and high altitudes, males attained significantly larger asymptotic sizes (*A*) than females under each nonlinear growth model (Table 2, Fig. 4). By contrast, males and females exhibited similar characteristic growth parameters (*k*) within each population (Table 2). The fact that males attained larger *A* with similar values for *k* implies that males must have greater absolute growth rates (mm day⁻¹) than females for each population (Dunham 1978a). Overall, both sexes exhibited larger values for *A* and smaller values for *k* at high

Table 2. Summary of estimates for asymptotic size (A) and the characteristic growth parameter (k) of *Sceloporus jarrovii* males and females at each site using interval equations for the Von Bertalanffy (VB), logistic-by-length (LL), and logistic-by-weight (LW) growth models. Differences in parameter estimates were considered significant if there was no overlap in associated 95% planar support confidence intervals (95% CI). See Fig. 4 for graphical presentation of growth trajectories

Site	Model	Sex	n	R^2	A	95% CI	k	95% CI
Low altitude (1700 m)	VB	♀	193	0.998	82.13	± 2.02	0.00780	± 0.00079
		♂	149	0.999	92.49	± 2.15	0.00757	± 0.00077
	LL	♀	193	0.997	78.68	± 2.09	0.01446	± 0.00159
		♂	149	0.998	86.52	± 1.99	0.01597	± 0.00152
	LW	♀	193	0.996	77.26	± 2.30	0.02200	± 0.00302
		♂	149	0.997	84.23	± 2.33	0.02567	± 0.00316
High altitude (2500 m)	VB	♀	86	0.999	82.99	± 1.83	0.00731	± 0.00091
		♂	90	0.999	97.35	± 3.61	0.00612	± 0.00085
	LL	♀	86	0.999	81.28	± 1.66	0.01209	± 0.00166
		♂	90	0.998	92.31	± 2.62	0.01174	± 0.00136
	LW	♀	86	0.998	80.99	± 1.71	0.01665	± 0.00231
		♂	90	0.998	90.66	± 2.35	0.01751	± 0.00178

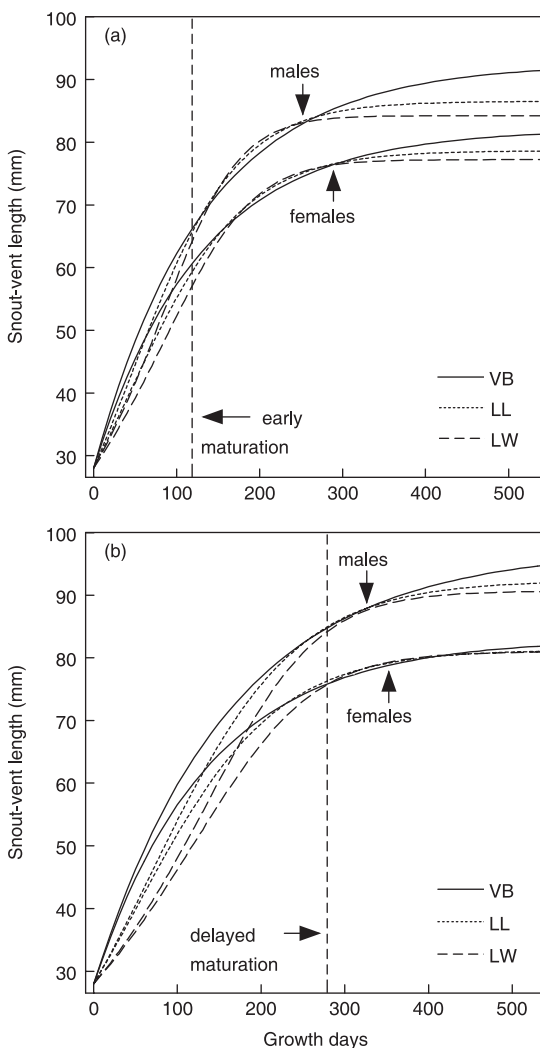


Fig. 4. Growth trajectories for *Sceloporus jarrovii* males and females at (a) low altitude (1700 m) and (b) high altitude (2500 m), derived from three models: Von Bertalanffy (VB), logistic-by-length (LL), and logistic-by-weight (LW). See Table 2 for parameter estimates. Dashed lines indicate the onset of female reproduction. The development of SSD occurs well in advance of female maturation in the high-altitude population.

relative to low altitude (Table 2). Consequently, the magnitude of sexual dimorphism in asymptotic size was actually greater at high (range 12–18% among models) than at low altitude (9–13%; Table 2). By the time of delayed female maturation at high altitude ($c.$ 280 growth days), all three models predicted a large sex difference in SVL of about 8.5–9.0 mm (11–12%; Fig. 4).

Discussion

GROWTH COST OF REPRODUCTION

Trade-offs between growth and reproduction are central assumptions of life-history theory (Stearns 1992), and are often inferred from negative correlations between reproductive status and growth (reviewed in Reznick 1985). Such trade-offs have been observed in a variety of organisms with indeterminate growth, including isopods (e.g. Lawlor 1976), amphibians (e.g. Yurewicz & Wilbur 2004), fishes (e.g. Reznick 1983), snakes (e.g. Brown & Weatherhead 1997) and lizards (e.g. Schwarzkopf 1993). However, other studies have found no evidence for such a relationship (e.g. Smith 1997; Lardner & Loman 2003). In the present study, *Sceloporus jarrovii* females that delayed reproduction until their second year grew more quickly than females that reproduced as yearlings. However, the evidence for this growth cost of reproduction disappeared when body size was included as a covariate. Thus, nonreproductive females may grow more quickly than reproductive females simply on account of their smaller size, and these data cannot be definitively interpreted as evidence for growth cost of reproduction. This calls attention to the limitations of purely correlative methods for measuring reproductive trade-offs (Reznick 1985; Bell & Koufopanou 1986; Partridge & Harvey 1988; Landwer 1994).

Phenotypic manipulations of reproductive investment can overcome the limitations of correlative studies and provide direct experimental evidence for growth costs of reproduction. For example, Landwer (1994) used

surgical yolk removal to terminate follicular growth and reduce the clutch size of tree lizards *Urosaurus ornatus*. In response to this 50% reduction in reproductive effort, manipulated females grew to larger sizes than controls. In the present study, ovariectomized females grew more quickly than reproductive controls during the final month of pregnancy and for several months following parturition. As a result, ovariectomized females averaged 2.5 mm larger than controls by about 1 year post-treatment. On the basis of published relationships between female body size and litter size (Ballinger 1973, 1979), this translates into an expected cost to future reproduction of 0.8 young per litter. More relevant to the purposes of this paper, this 2.5 mm growth cost accounts for 32% of the 7.9 mm sex difference in SVL observed at this time.

Energy budgets were not measured in this study, so it cannot be determined whether the reduced growth of reproductive females is a consequence of reduced energy acquisition, increased energy expenditure, or both. However, the timing of the observed growth cost (during the late stages of gestation) suggests several aspects of reproduction as likely mechanisms for this cost. *Sceloporus jarrovi* is lecithotrophic (i.e. nutrients that support embryonic development are present in the yolk at ovulation), so energetic costs of nutrient provisioning occur during vitellogenesis, not pregnancy (Tinkle & Hadley 1973; Demarco & Guillette 1992). Although production costs of egg provisioning comprise a substantial portion of reproductive effort in *S. jarrovi* (Tinkle & Hadley 1975; Congdon 1977), the present study found no evidence for a resultant trade-off with growth during vitellogenesis. However, *S. jarrovi* females do incur a metabolic cost of pregnancy during the late stages of gestation, when growth costs were observed (Beuchat & Vleck 1990; Demarco & Guillette 1992; Demarco 1993). Pregnant females also maintain lower body temperatures than nonreproductive females (Beuchat 1986; Mathies & Andrews 1997), which could further constrain growth. Finally, females may reduce foraging while pregnant, as observed in sympatric *S. virgatus* (Weiss 2001) and other lizards (Shine 1980). Thus, decreased energy acquisition, reduced body temperature, and increased metabolic expenditure are potential mechanisms for the reduction in growth observed among pregnant *S. jarrovi* females.

Interestingly, growth differences between reproductive and nonreproductive females persisted even after parturition. Similar results have been reported for the lizard *Urosaurus ornatus*, in which the size benefits of an experimental reduction in reproductive effort were still evident at 1–2 years after reproduction (Landwer 1994). These results suggest that reproduction leaves females energetically compromised and unable to support maximal growth thereafter. Postpartum females may also experience greater metabolic maintenance costs than nonreproductive females, as suggested by several previous studies of *S. jarrovi* (Beuchat & Vleck 1990; Demarco & Guillette 1992).

Contrary to the reproductive cost hypothesis, CON grew significantly faster than OVX females during the autumn and winter. One possibility is that ovariectomy inhibited growth by removing a source of hormones involved in growth regulation. For example, ovariectomy can inhibit mammalian growth by decreasing circulating oestrogen levels (reviewed in Ford & Klindt 1989). While it is unknown whether ovarian hormones affect growth in this species, sex steroids have been implicated in the regulation of female aggression (Woodley & Moore 1999), and may influence other behaviours related to growth (e.g. activity, foraging, thermoregulation). However, the close agreement between experimental and correlative results supports the interpretation that reproduction constrains female growth in *S. jarrovi*.

IMPLICATIONS FOR SEXUAL SIZE DIMORPHISM

Reproduction likely constrains female growth in *S. jarrovi*, but can this trade-off explain why males average 10% larger than females? The results of the present study indicate that this cost of reproduction cannot explain SSD. At low altitude, sex differences in growth are pronounced during vitellogenesis and gestation. SSD increases dramatically over this period, such that males average 7.9 mm (10%) larger than females by the end of the first reproductive season. This suggests that female growth is constrained by energetic costs of reproduction. However, the present study found no evidence for a growth cost of reproduction until the final month of gestation, by which time SSD is already well developed. Further, on the basis of the 2.5 mm difference in final size between OVX and CON females, the overall growth cost of reproduction accounts for only 32% of the observed difference in adult SVL. Thus, growth costs of female reproduction may explain some, but certainly not all, of the natural sex difference in body size in the low-altitude population.

If growth costs of reproduction contribute to SSD, then the development sex differences in size and growth should be delayed at high altitude, where all females delay reproduction until their second year. The results of the present study do not support this prediction: the development of SSD is similar at both high and low altitudes. In fact, by the time that high-altitude females begin vitellogenesis, males are already 7.2 mm (10%) larger in SVL. A comparison of asymptotic growth trajectories at high altitude reinforces this conclusion: by the time females begin vitellogenesis, the predicted sex difference in body size is already 8.5–9.0 mm (11–12%). Further, SSD in asymptotic size is actually greater at high than low altitude (Table 2). Thus, although female growth may be constrained by energetic costs of reproduction, SSD clearly develops in the absence of such costs. While these results do not support the hypothesis that female reproductive investment has a direct, proximate effect on SSD, they also cannot discount the possibility that female growth has been

genetically constrained as a result of past selection for such a trade-off. Thus, high-altitude females may be genetically predisposed to shunt energy allocation away from growth as a result of past selection for early reproduction, even if local environmental conditions preclude reproduction as a yearling.

Previous investigators have suggested that growth costs of female reproduction may explain why males are the larger sex in lizards (Sugg, Fitzgerald & Snell 1995), snakes (Beaupre, Duvall & O'Leile 1998) and salamanders (Bruce 1993). Conversely, growth costs of male reproduction may explain female-larger SSD in some lizards (Cox, Skelly & John-Alder 2005), anurans (Woolbright 1983, 1989) and fishes (Schultz 1993). Rigorous tests of this 'reproductive cost hypothesis' (Schultz 1993) for SSD are generally lacking, but the present study does not support the hypothesis that male-larger SSD develops because of a trade-off between reproduction and growth in *S. jarrovi* females. However, related studies of the effect of testosterone on male growth suggest that associated energetic costs of male reproductive investment may constrain growth in female-larger *Sceloporus* species, but not in *S. jarrovi* (Cox & John-Alder, 2005; Cox *et al.* 2005). Thus, focus on growth costs of male reproductive investment may provide a profitable extension of the reproductive cost hypothesis in this group. Although the present study has focused primarily on female growth, it is clear that a complete understanding of SSD requires knowledge of the selective forces and proximate energetic constraints acting on both male and female size.

Acknowledgements

Wade Sherbrooke, Dawn Wilson, and the staff of the American Museum of Natural History's Southwestern Research Station (SWRS) provided logistical support and laboratory facilities. George Middendorf suggested the high-altitude study site, and Henry John-Alder and Diana Hews gave helpful advice and criticism. The Arizona Game and Fish Department granted collecting permits (SP 696192, 751920 and 553889) and the United States Forest Service provided land use permits within Coronado National Forest. The Rutgers University Animal Care and Facilities Committee reviewed and approved all experimental procedures (protocol 01-019). This project was funded by the American Museum of Natural History (Theodore Roosevelt Memorial Fund and SWRS Student Support Fund), the Graduate School-New Brunswick at Rutgers University (Pre-Dissertation Travel Award), the Society for Integrative and Comparative Biology (Grant-In-Aid of Research), and a National Science Foundation grant to Henry John-Alder (IBN 0135167).

References

Andersson, M. (1994) *Sexual Selection*. Princeton University Press, Princeton, NJ.
 Angilletta, M.J. Jr & Sears, M.W. (2000) The metabolic cost of

reproduction in an oviparous lizard. *Functional Ecology*, **14**, 39–45.
 Ballinger, R.E. (1973) Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). *Ecology*, **54**, 269–283.
 Ballinger, R.E. (1979) Intraspecific variation in demography and life history of the lizard, *Sceloporus jarrovi*, along an altitudinal gradient in southeastern Arizona. *Ecology*, **60**, 901–909.
 Ballinger, R.E. & Nietfeldt, J.W. (1989) Ontogenetic stages of reproductive maturity in the viviparous lizard, *Sceloporus jarrovi*. *Journal of Herpetology*, **23**, 282–292.
 Beaupre, S.J., Duvall, D. & O'Leile, J. (1998) Ontogenetic variation in growth and sexual size dimorphism in a central Arizona population of the western diamondback rattlesnake (*Crotalus atrox*). *Copeia*, **1998**, 40–47.
 Bell, G. & Koufopanou, V. (1986) The cost of reproduction. *Oxford Surveys in Evolutionary Biology* (eds R. Dawkins & M. Ridley), Vol. 3, pp. 83–131. Oxford University Press, Oxford.
 Beuchat, C.A. (1986) Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia*, **1986**, 971–979.
 Beuchat, C.A. & Vleck, D. (1990) Metabolic consequences of viviparity in a lizard, *Sceloporus jarrovi*. *Physiological Zoology*, **63**, 555–570.
 Brown, G.P. & Weatherhead, P.J. (1997) Effects of reproduction on survival and growth of female northern water snakes, *Nerodia sipedon*. *Canadian Journal of Zoology*, **75**, 424–432.
 Brown, G.P. & Weatherhead, P.J. (2004) Sexual abstinence and the cost of reproduction in adult male water snakes, *Nerodia sipedon*. *Oikos*, **104**, 269–276.
 Bruce, R.C. (1993) Sexual size dimorphism in desmognathine salamanders. *Copeia*, **1993**, 313–318.
 Congdon, J.D. (1977) *Energetics of the montane lizard Sceloporus jarrovi: a measurement of reproductive effort*. PhD Thesis, Arizona State University, Tempe, AZ.
 Cooper, W.E. Jr, Vitt, L.J., Hedges, R. & Huey, R.B. (1990) Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. *Behavioral Ecology and Sociobiology*, **27**, 153–157.
 Cox, R.M. (2005) *Integrating proximate and ultimate causes of sexual size dimorphism in lizards*. PhD Thesis, Rutgers University, New Brunswick, NJ.
 Cox, R.M. & John-Alder, H.B. (2005) Testosterone has opposite effects on male growth in lizards (*Sceloporus* spp.) with opposite patterns of sexual size dimorphism. *Journal of Experimental Biology*, **208**, 4679–4687.
 Cox, R.M., Skelly, S.L. & John-Alder, H.B. (2003) A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, **57**, 1653–1669.
 Cox, R.M., Skelly, S.L. & John-Alder, H.B. (2005) Testosterone inhibits growth in juvenile male eastern fence lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. *Physiological and Biochemical Zoology*, **78**, 531–545.
 Demarco, V. (1993) Metabolic rates of female viviparous lizards (*Sceloporus jarrovi*) throughout the reproductive cycle: do pregnant females adhere to standard allometry? *Physiological Zoology*, **66**, 166–180.
 Demarco, V. & Guillelte, L.J. Jr (1992) Physiological cost of pregnancy in a viviparous lizard (*Sceloporus jarrovi*). *Journal of Experimental Zoology*, **262**, 383–390.
 Dunham, A.E. (1978a) Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology*, **59**, 770–778.
 Dunham, A.E. (1978b) *Marquardt, Non-Linear Least-Squares Regression Growth Analysis Program*. University of Pennsylvania, Philadelphia, PA.
 Fitch, H.S. (1978) Sexual size differences in the genus *Sceloporus*. *University of Kansas Science Bulletin*, **51**, 441–461.

- Ford, J.J. & Klindt, J. (1989) Sexual differentiation and the growth process. *Animal Growth Regulation* (eds D.R. Campion, G.J. Hausman & R.J. Martin), pp. 317–336. Plenum Press, New York.
- Goldberg, S.R. (1971) Reproductive cycle of the ovoviparous iguanid lizard *Sceloporus jarrovi* Cope. *Herpetologica*, **27**, 123–131.
- Landwer, A. (1994) Manipulation of egg production reveals costs of reproduction in the tree lizard (*Urosaurus ornatus*). *Oecologia*, **100**, 243–249.
- Lardner, B. & Loman, J. (2003) Growth or reproduction? Resource allocation by female frogs *Rana temporaria*. *Oecologia*, **137**, 541–546.
- Lawlor, L.R. (1976) Molting, growth and reproductive strategies in the terrestrial isopod, *Armadillidium vulgare*. *Ecology*, **57**, 1179–1194.
- Mathies, T. & Andrews, R.M. (1997) Influence of pregnancy on the thermal biology of the lizard, *Sceloporus jarrovi*: why do pregnant females exhibit low body temperatures? *Functional Ecology*, **11**, 498–507.
- Partridge, L. & Harvey, P.H. (1988) The ecological context of life history evolution. *Science*, **241**, 1449–1455.
- Reznick, D. (1983) The structure of guppy life histories: the tradeoff between growth and reproduction. *Ecology*, **64**, 862–873.
- Reznick, D. (1985) Costs of reproduction: an evaluation of the empirical evidence. *Oikos*, **44**, 257–267.
- Ruby, D.E. & Dunham, A.E. (1984) A population analysis of the ovoviparous lizard *Sceloporus jarrovi* in the Pinaleño mountains of southeastern Arizona. *Herpetologica*, **40**, 425–436.
- Schultz, E.T. (1993) Sexual size dimorphism at birth in *Micrometrus minimus* (Embiotocidae): a prenatal cost of reproduction. *Copeia*, **1993**, 456–463.
- Schwarzkopf, L. (1993) Costs of reproduction in water skinks. *Ecology*, **74**, 1970–1981.
- Schwarzkopf, L. (1994) Measuring trade-offs: a review of studies of costs of reproduction in lizards. *Lizard Ecology: Historical and Experimental Perspectives* (eds L.J. Vitt & E.R. Pianka), pp. 7–29. Princeton University Press, Princeton, NJ.
- Shine, R. (1980) 'Costs' of reproduction in reptiles. *Oecologia*, **46**, 92–100.
- Sinervo, B., Hedges, R. & Adolph, S.C. (1991) Decreased sprint speed as a cost of reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *Journal of Experimental Biology*, **155**, 323–366.
- Smith, G.R. (1997) Growth of reproducing and non-reproducing female lizards (*Sceloporus virgatus*). *Journal of Herpetology*, **31**, 576–578.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Sugg, D.W., Fitzgerald, L.A. & Snell, H.L. (1995) Growth rate, timing of reproduction, and size dimorphism in the southwestern earless lizard (*Cophosaurus texanus scitulus*). *Southwestern Naturalist*, **40**, 193–202.
- Tinkle, D.W. & Hadley, N.F. (1973) Reproductive effort and winter activity in the viviparous montane lizard *Sceloporus jarrovi*. *Copeia*, **1973**, 272–277.
- Tinkle, D.W. & Hadley, N.F. (1975) Lizard reproductive effort: caloric estimates and comments on its evolution. *Ecology*, **56**, 427–434.
- Weeks, S.C. (1996) The hidden cost of reproduction: reduced food intake caused by spatial constraints in the body cavity. *Oikos*, **75**, 345–349.
- Weiss, S.L. (2001) The effect of reproduction on food intake of a sit-and-wait foraging lizard, *Sceloporus virgatus*. *Herpetologica*, **57**, 138–146.
- Woodley, S.K. & Moore, M.C. (1999) Ovarian hormones influence territorial aggression in free-living female mountain spiny lizards. *Hormones and Behavior*, **35**, 205–214.
- Woolbright, L.L. (1983) Sexual selection and size dimorphism in anuran Amphibia. *American Naturalist*, **121**, 110–119.
- Woolbright, L.L. (1989) Sexual dimorphism in *Eleutherodactylus coqui*: selection pressures and growth rates. *Herpetologica*, **45**, 68–74.
- Yurewicz, K.L. & Wilbur, H.M. (2004) Resource availability and costs of reproduction in the salamander *Plethodon cinereus*. *Copeia*, **2004**, 28–36.

Received 3 April 2006; accepted 24 July 2006