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GROWTH IN SONORAN DESERT POPULATIONS OF THE COMMON CHUCKWALLA (*SAUROMALUS OBESUS*)

Brian K. Sullivan[1], Matthew A. Kwiatkowski[1], and Paul S. Hamilton[2]

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The common chuckwalla, *Sauromalus obesus* (= *ater;* Hollingsworth 1998), is a large, herbivorous lizard found throughout the Sonoran and Mojave Deserts of the southwestern United States and northwestern Mexico (Hollingsworth 1998). Throughout their range chuckwallas are limited to rocky outcrops typically associated with isolated mountain ranges, probably because of their unique antipredator behavior whereby they retreat into rock crevices and inflate their bodies to prevent removal by predators (Berry 1974, Hollingsworth 1998). Population subdivision resulting from their patchy distribution might be expected to lead to genetic (Lamb et al. 1992) or morphological (Hamilton 1995) variation. Although dietary (Johnson 1965, Nagy 1973) and life history (Abts 1987) investigations have been conducted for chuckwalla populations in California, Arizona populations remain little known (but see Prieto and Sorenson 1977, Prieto and Ryan 1978).

Chuckwalla populations vary considerably in body size (Case 1976, Tracy 1999) and growth rates (Johnson 1965, Berry 1974, Abts 1987). Additionally, a recent study documented substantial variation in density among populations of chuckwallas in central Arizona (Kwiatkowski and Sullivan 2002). Populations in the Sonoran Desert near Phoenix, Arizona, range from densities typically found in the Mojave Desert of California (i.e., 7–23 individuals · ha^{-1}) to the lowest (3 individuals · ha^{-1}) and highest (65 individuals · ha^{-1}) densities yet recorded (Sullivan and Flowers 1998). Contrary to a hypothesis of Berry (1974), changes in population density were not associated with changes in male behavior; males in high-density populations did not form dominance hierarchies; rather, males were territorial regardless of density. However, it is unclear whether these density differences are associated with variation in other life history characters. We report on variation in growth rates of males and females of 2 populations in the Phoenix area that vary dramatically in density.

We established study sites for 2 populations of *Sauromalus* near Phoenix, Arizona, in the north central Sonoran Desert. The South Mountains ("South") study site (2.0 ha) was immediately south of Phoenix in the west central portion of the city park surrounding the South Mountains (33°20′26″N, 112°02′48″W), and the Lookout Mountain ("Lookout") study site (10.4 ha) was in the southwestern section of the Lookout Mountain Preserve in the Phoenix Mountains of northern Phoenix (33°37′22″N, 112°03′12″W), Maricopa County, Arizona.

Because plant productivity is thought to influence growth in chuckwallas (Berry 1974, Case 1976), rainfall data for the 2 sites were obtained from weather recording stations (Arizona Meteorological Network) at Laveen (South) and north Phoenix (Lookout) for 1994–1999. Each weather station is within 10 km of the respective study site.

All chuckwallas encountered on study sites were uniquely and permanently marked by toe-clips. If more than 1 toe had to be removed, no more than 1 toe per limb was clipped. No chuckwalla had more than 3 toes clipped and only 2 had more than 2 toes clipped. Individuals were also marked with paint on the tip of the tail to facilitate identification without capture. Most animals were initially marked in 1995 and 1996 and were recaptured to determine growth in 1997–1999.

[1]Department of Life Sciences, Arizona State University West, Box 37100, Phoenix, AZ 85069.
[2]Department of Biology, Arizona State University–Tempe, Tempe, AZ 85287.

Snout-vent length (SVL) and tail length (mm) were measured by pressing the lizard flat against a metal or plastic rule. Growth was calculated as follows: recapture SVL—initial SVL / years between captures. Because some processing required off-site activity (e.g., attachment of radio tags; Kwiatkowski and Sullivan 2002), some lizards were removed from the site on the day of capture. All such individuals were released at capture site within 24 hours.

Nineteen individuals were recaptured during a total of 38 occasions at the Lookout site, while 15 individuals were recaptured on 20 occasions at the South site; on average, 2.5 years elapsed between captures (Fig. 1). Because juveniles exhibit high growth rates (Johnson 1965, Berry 1974), and because some samples had juveniles while others did not, only sexually mature individuals (initial SVL >135 mm; Johnson 1965, Hamilton 1995) were used for between-population comparisons (e.g., males of South versus males of Lookout). All individuals (i.e., juveniles and adults) were used for analysis of within-population sample parameters (e.g., asymptotic growth with South males), and nonparametric tests were used, given the small sample sizes and non-normality of growth data.

Sample sizes were small, but growth of females from South (n = 4; 1.7 mm · yr^{-1}; range = 0–8 mm · yr^{-1}) and Lookout (n = 10; 1.4 mm · yr^{-1}; range = 0–9.7 mm · yr^{-1}) was similar, as was that for males of Lookout (n = 8; 1.4 mm · yr^{-1}; range = 0–3.5 mm · yr^{-1}). However, males of South had significantly (Mann-Whitney U = 12.5, P = 0.04, n = 16) higher growth (n = 8; 5.4 mm · yr^{-1}; range = 0–25 mm · yr^{-1}) than Lookout males. For the individuals evaluated for growth, maximum SVL for Lookout males was 194 mm and for females was 173 mm; maximum SVL for South males was 209 mm and for females was 154 mm.

Interestingly, in spite of the higher growth rates of South males over the course of the surveys (1995–1999), rainfall was generally higher at the Lookout site compared with the South site (Table 1). This pattern is not unexpected given the more northern location of Lookout, but it is counter to the higher growth exhibited by South males. Unfortunately, small sample sizes precluded an analysis of individual growth in relation to rainfall. Although the regions received somewhat unequal rainfall, plant density was higher in the South site relative to the Lookout site over the course of this study (Kwiatkowski and Sullivan 2002).

TABLE 1. Rainfall (mm) by year and season (W = October–April, S = May–September) for the 2 study sites. Lookout = 19th Ave. and Greenway Road; South = Laveen.

Year	Season	Lookout	South
1995	W	167	135
	S	34	26
1996	W	80	69
	S	105	49
1997	W	33	33
	S	33	64
1998	W	190	152
	S	76	49
1999	W	85	52
	S	84	123

Our results indicate that growth of male chuckwallas of the South Mountains exceeded that of males from the Lookout site in the nearby Phoenix Mountains. The higher growth of males at the South site may be the result of an interaction between resource availability and energetic costs of defending territories. Despite higher rainfall at Lookout, food resources were considerably higher at the South site over the course of this study, and males had home ranges 6 times smaller than home ranges of males at the Lookout site (Kwiatkowski and Sullivan 2002). Because males at both sites were territorial (Kwiatkowski and Sullivan 2002) and patrolled their territories to defend against intruders, males at Lookout may have expended considerably more energy in territory defense. However, if growth was dependent on plant resources and energy expenditure in territory defense alone, then females from the South site, which also have small home ranges relative to females at the Lookout site, should have exhibited higher growth rates. Females from South did exhibit a higher growth rate (Fig. 1), but small sample sizes precluded statistical analysis.

Berry (1974) found that male chuckwallas grow faster than females; for size classes of 170–220 mm SVL, females averaged 0.21 mm · yr^{-1} while males averaged 4.41 mm · yr^{-1}. For the Phoenix area populations that we studied, males exceeded females in growth, but

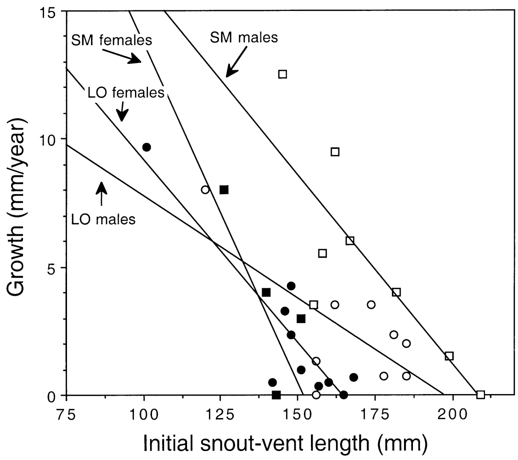

Fig. 1. Amount of growth by initial snout-vent length in chuckwallas for the Lookout (LO) and South Mountains (SM) populations. Lookout males = open circles; Lookout females = filled circles; South males = open squares; South females = filled squares.

this was primarily the result of dramatically higher growth of South males.

Much attention has been paid to the development of growth models to explain lizard growth trajectories (Sugg et al. 1995). These models can be used to address hypotheses concerning proximate and ultimate factors influencing body size, size at maturity, and the asymptotic size (at which point further growth is negligible) reached by each sex (Stamps and Krishnan 1997). While the data presented here do not lend themselves to such a longitudinal analysis of growth, some inferences can be drawn about 1 growth-model parameter: asymptotic growth. Stamps and Andrews (1992) found that in anoles, size of the largest-bodied individual in a given population is an accurate estimate of the asymptotic size reached in that population. By regressing the average growth of animals on size class (Fig. 1), one can estimate asymptotic size as the size at which growth reaches zero (i.e., where the regression line intersects with the x-axis). Our growth data show that asymptotic size of males is greater than females in each population, and there is less sexual dimorphism in asymptotic size in Lookout than in South lizards. Estimated in this fashion, asymptotic sizes of each sex and population are concordant with maximum sizes reached in each population and sex, suggesting that the size of the largest individual may serve as a proxy for asymptotic size in populations in which no longitudinal growth data are available.

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