Growth, Activity, and Survivorship from Three Sympatric Parthenogenic Whiptails (Family Teiidae)

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ABSTRACT.—We surveyed whiptail lizard populations for seven summers (2000–2006) in riparian forests along the Rio Grande in central New Mexico. We captured 5,382 individuals from three parthenogenic species (*Aspidoscelis exsanguis, Aspidoscelis neomexicana,* and *Aspidoscelis uniparens*) including 129 hatchlings (young-of-the-year) that were later recaptured as adults. Growth data were fit to a logistic growth model and compared using a likelihood ratio test. Comparisons of growth rates showed that *A. exsanguis* grew faster than both *A. neomexicana* and *A. uniparens* and attained a larger snout-vent length (SVL). Comparisons of capture rates showed that species had similar activity patterns during the summer. Captures of adults peaked in mid-June and decreased in August. Hatchlings became active at the end of July and captures peaked in September. Some individuals were captured several seasons indicating that lizards lived for at least 3–4 yr. Our study shows both similarities and differences in life-history characteristics for three closely related and coexisting whiptail species.

Whiptails (genus Aspidoscelis) are some of the most apparent lizards in the southwestern United States but are lesser known in terms of understanding their seasonal activity, growth rates, and longevity. Growth and activity are fundamental in life-history studies, and whiptail lizards provide a model system to study the demographics of coexisting populations. Studies on whiptails in this region have described their reproductive modes (Wright and Lowe, 1968; Dessauer and Cole, 1986; Reeder et al., 2002), life-history characteristics (Pianka, 1970; Congdon et al., 1978; Vitt and Breitenbach, 1993; Taylor and Caraveo, 2003), and habitat associations (Cuellar, 1979; Price et al., 1993; Bateman et al., 2008a). However, little has been published on body growth rates, longevity, and activity patterns of these lizards. Although markrecapture methods can yield reliable data on growth from specific time intervals (Halliday and Verrell, 1988; Paulissen, 1999-2000), few attempts have modeled growth rates, seasonal activity patterns, and longevity for whiptails in a field setting (but see Carpenter, 1959).

New Mexico is inhabited by 15 species of *Aspidoscelis* lizards (Stuart, 2005), eight of which are parthenogenic species. As part of a study designed to evaluate the effects of removing nonnative plants and fuels on wildlife, we monitored herpetofauna for seven years in central New Mexico (Bateman et al., 2008a,b). During our study, whiptail lizards composed the majority of captures. This provided an opportunity to follow individual lizards of parthenogenic *Aspidoscelis exsanguis, Aspidoscelis neomexicana,* and *Aspidoscelis uniparens* over time and record their rates of growth from hatchling to adult, longevity, and seasonal activity patterns in a field setting.

Given that these lizards experienced generally the same climatic regimes and, thus, similar resource availability during the study, and that body-size differences exist among these species (Degenhardt et al., 1996), we tested the hypothesis that adult body size differences result from differences in growth rates among species rather than differences in longevity or survivorship. We can falsify our hypothesis if growth rates are similar among species or if smaller species have lower life expectancies or lower adult survivorship compared to larger species. In addition, we present information on seasonal activity patterns for adult and young-of-the-year (YOY).

METHODS AND MATERIALS

Study Site.—We conducted our study in the riparian forests along the Rio Grande in semiarid central New Mexico. The riparian forests contain a mixture of native Rio Grande cottonwood (*Populus deltoides wislizenii*), nonnative saltcedar (*Tamarix chinensis* and *Tamarix ramosissima*), and nonnative Russian olive (*Elaeagnus angustifolia*) trees. We captured lizards from June to September at 12 20-ha sites spanning 140 km of riparian forest from Albuquerque (35.0004°N– 106.4104°W) to Bosque del Apache National Wildlife Refuge (33°47′59N–106°52′59W).

Field Measurements.—We captured lizards during the summers of 2000–2006 using trap arrays with pitfall and funnel traps set along drift fences. Trapping methods and array design are described elsewhere (Bateman et al., 2008a). Traps were open continuously from June through mid-September and checked three days per week. Animals that died during the study were deposited in the Museum of Southwestern Biology (Appendix 1).

We identified lizards to species using field guides (Degenhardt et al., 1996) and followed current nomenclature (Crother, 2008). At each capture we measured snout–vent (SVL) and tail lengths with a

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linear ruler (millimeters) and mass (grams) with a Pesola spring scale. At first capture, we assigned each lizard a unique toe clip. We identified YOY based on body size, presence of an umbilical scar, and tail coloration.

Growth Comparisons.—We used SVL rather than mass to estimate growth to eliminate confusion potentially caused by changes in stomach contents, fat bodies, reproductive status, and hydration (Dunham, 1978). We calculated growth rate by organizing numbers of captures and SVL into monthly intervals during summer censuses. SVL was averaged monthly for each individual because we found that best represented the precision of our measuring techniques. We used growing seasons (April through November) as time intervals on a continuous basis. Because lizards are inactive during the winter and presumed not to grow, we excluded winter months (December through March; sensu Haenel and John-Alder, 2002).

Because data from individuals of known size, but not age, yield size-specific growth rates and not agespecific growth rates (Halliday and Verrell, 1988), we used data from individuals first marked as YOY and later recaptured. When an individual was not captured in successive seasons, we used unique characteristics (i.e., particular toes clipped, measurements, and tail regeneration status) to distinguish individuals for inclusion in analyses. We excluded questionable records (i.e., inconsistent unique characteristics) from analyses.

To address potential treatment effects from the larger study design (described elsewhere, Bateman et al., 2008a), we evaluated growth relationships of each species in treated and untreated sites using a composite likelihood ratio test across species. To relate SVL to age (months of growth), we used a logistic growth model (equation 1). The growth equation,

size =
$$a/[1 + \exp(b - c \cdot \operatorname{age})],$$
 (1)

was defined as a = asymptote of maximum size (SVL), and b and c describe the shape of the logistic curve (Ratkowsky, 1989). No log transformation was necessary because parameters a, b, and c were estimated from empirical data using a nonlinear regression procedure (Ratkowsky, 1989). We used the NLMIXED nonlinear mixed model procedure (SAS vers. 9.1, SAS Institute Inc., Cary, North Carolina, 2004) for estimation with individual animals specified as analysis subjects to account for multiple remeasurements of some animals.

To compare growth rates, we tested the null hypothesis that growth relationships did not vary among species. An initial growth model was constructed by pooling size and age of all three species and estimating a single a, b, and c (equation 1); then subsequent models were constructed by estimating a, b, and c for each species and for combinations of species. We selected the most parsimonious model to explain lizard growth based on likelihood ratio test and goodness-of-fit comparisons among candidate models (Mood et al., 1974).

Seasonal Activity.—We plotted activity as weekly rate of captures from 2000 through 2006. We defined rate of

TABLE 1. Comparison of standard error of estimate (SEE) for power, von Bertalanffy, and logistic growth models for three whiptail lizard species from the Rio Grande, New Mexico, 2000–2006 for the growing season (April through November). Models estimated parameters a, b, and c of equation 1 for each species. The logistic models best fit the data and have the lowest SSE values.

| Model | A. exsanguis | A. neomexicana | A. uniparens |
|-----------------|--------------|----------------|--------------|
| Power | 7.53 | 5.29 | 4.75 |
| von Bertalanffy | 9.55 | 8.32 | 9.53 |
| Logistic | 6.19 | 4.69 | 4.09 |

captures as the number of lizards captured in each site per 100 trap days and trap days were averaged within sites. Individuals captured more than one time during the week were recounted at each encounter. We assigned the Julian number of each week to observations using WEEKNUM procedure (Excel, Microsoft Corporation, Redmond, Washington, 2003). We classified lizards as YOY or adult (juveniles captured in spring were classified as adults).

Longevity.—We estimated individual lifespan by calculating the longest temporal interval over which lizards first marked as YOY were recaptured. We only used records from lizards continually present in summer censuses.

Results

Field Captures.—During seven summers from 2000 to 2006, we captured 5,382 individual whiptail lizards and included data from 129 individuals in these analyses. We captured 56 individuals of *A. exsanguis* on 153 occasions, 61 individuals of *A. neomexicana* on 193 occasions, and 12 individuals of *A. uniparens* on 34 occasions.

Comparing Models of Growth.—Because of too few observations in control sites, we compared growth models in only experimental sites before and after treatment. Lizard growth before treatment did not significantly differ from growth after treatment (pooled period log likelihood = 2,210.0, separate period log likelihood = 2,201.2; likelihood ratio test statistic = 8.8, df = 9, and P = 0.46), suggesting that experimental treatments from the nonnative plant removal project had no effect on lizard growth. Therefore, we combined all captures from sites before and after treatment.

We compared power, von Bertalanffy, and logistic models of growth. The logistic model was chosen to represent growth over other models based on goodness-of-fit statistics (Table 1). The specific logistic growth model that estimated separate *a* parameter (maximum SVL) for each species and common *b* and *c* parameters (shapes of growth curve) for *A. neomexicana* and *A. uniparens* was chosen to represent whiptail growth (model 2; Table 2). Estimating common *a*, *b*, and *c* parameters for *A. neomexicana* and *A. uniparens* for *A. neomexicana* and *A. uniparens* for *A. neomexicana* and *A. uniparens* significantly degraded the fit (model 3; Table 2), and defining separate parameters for each species was not significantly better than the simpler model (model 1; Table 2). The growth curve for *A.*

TABLE 2. Comparison of three models (logistic growth, equation 1) of whiptail growth. Model 1 estimates separate *a*, *b*, and *c* parameters for each species. Model 2 estimates common *b* and *c* parameters for *Aspidoscelis neomexicana* and *Aspidoscelis uniparens*. Model 3 estimates common *a*, *b*, and *c* parameters for *A. neomexicana* and *A. uniparens*. Model 2 is more parsimonious and does not significantly differ from model 1.

| Model | -2 log likelihood | χ^2 (df) | Р |
|-------|-------------------|---------------|---------|
| 1 | 2,273.9 | | |
| 2 | 2,276.6 | 2.7 (2) | 0.259 |
| 3 | 2,310.6 | 34.0 (1) | < 0.001 |

neomexicana and A. uniparens was similar, but A. neomexicana attained a larger maximum size (Fig. 1).

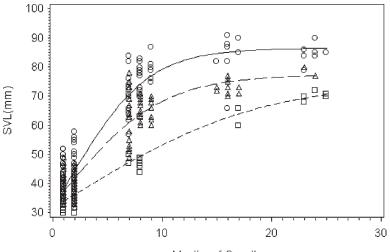
Activity Patterns.—Adult and YOY whiptails exhibited different patterns of activity during summer censuses and this pattern was similar among species (Fig. 2). Captures of adult whiptails peaked in mid-June and began to decline toward the end of July. Hatchlings first appeared in traps in mid-July, and captures peaked the beginning of September. Capture rates differed among species, *A. neomexicana* had the highest capture rate of adults, and *A. exsanguis* had the highest capture rate of hatchlings (Fig. 2).

Longevity.—It was difficult to estimate longevity because most individuals we captured were first encountered as adults of unknown age. Also, the fate of lizards was unknown at the conclusion of the study; therefore, we excluded these records from comparative analyses. However, we did find that individual whiptails could live at least four years. Recapture histories from lizards of known age showed that YOY were rarely recaptured as adults (Table 3). On average, less than 1% of young were captured into their third year.

DISCUSSION

Growth curves for *A. neomexicana* and *A. uniparens* were similar, whereas *A. exsanguis* grew at a faster rate to attain a larger maximum SVL. It is interesting to note that all three species reached their adult sizes at approximately the same time, even though differences existed in growth rates and ultimate body size. Parthenogenic whiptails exhibited the same nonlinear growth pattern reported for other vertebrates, where growth rates are highest for young animals (Charnov and Berrigan, 1991; Charnov et al., 1993). Growth slowed as individuals matured. Although the reproductive status of individuals was unknown, this slowed body growth was likely caused by shifts in energy allocation from growth to reproduction (Case, 1978).

We observed similar seasonal activity patterns in adult and hatchling whiptails compared to previous reports for whiptails and other species of lizards (Milstead, 1957; Carpenter, 1959; Routman and Hulse, 1984; Paulissen, 1999–2000). Although we could not directly test the hypothesis that the interaction between thermal requirements and body size limit activity in these lizards as they age, we provided data demonstrating that activity of adults was curtailed at the end of the summer, when temperatures and time



Months of Growth

FIG. 1. Growth of three whiptail species along the Rio Grande in New Mexico. Months represent time spent growing (April through November), not actual ages. For example, month 1 is August and month 7 is June the following year. Size (SVL) of lizards is known from uniquely marked individuals recaptured in the field from 2000–2006. Individual lizards occur more than once in figure. Lines are fit using a logistic growth model (equation 1). Growth curves of the three species have a different asymptote (mean SVL \pm SE), *Aspidoscelis exsanguis* (circle, solid line; 86.5 \pm 1.7 mm), *Aspidoscelis neomexicana* (triangle, dashed line; 77.3 \pm 1.7 mm), and *Aspidoscelis uniparens* (square, dotted line; 75.5 \pm 4.0 mm). *Aspidoscelis neomexicana* and *A. uniparens* have similar-shaped growth curves, whereas *A. exsanguis* grows at a faster rate.

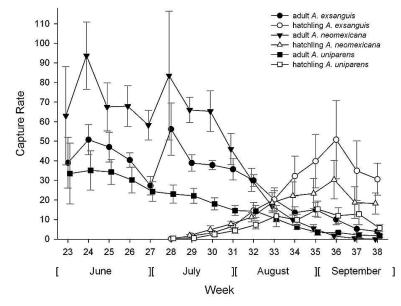


FIG. 2. Seasonal activity for three species of adult and hatchling whiptail species, *Aspidoscelis exsanguis*, *Aspidoscelis neomexicana*, and *Aspidoscelis uniparens* from June to September, 2000–2006, along the Rio Grande in New Mexico. Capture rates are mean numbers (\pm SE) of lizards captured per site per 100 trap days per year, and months are represented as week number in a given year. Individual lizards occur more than once in figure.

necessary to meet energetic requirements were reduced. Whiptail lizards are efficient foragers, but daily energy expenditure is high because of their active foraging lifestyle (Anderson and Karasov, 1981; Ethridge and Wit, 1993). Perhaps, the smaller body size of young whiptail lizards have provided them greater heating efficiency allowing them to be active longer during cooler periods compared to adults (Cowles, 1941), enabling them to acquire energy later in the summer.

Captures of hatchling *A. exsanguis* were more numerous than hatchlings of other species; however, *A. exsanguis* was outnumbered by *A. neomexicana* as adults. It is possible *A. exsanguis* produce more offspring than *A. neomexicana*, because of larger clutch sizes or a larger portion of females reproducing. Schall (1978) reported the average clutch size of *A. exsanguis* as 2.96 eggs, and Christiansen (1971) reported the average clutch size of *A. neomexicana* as 2 eggs, adding that some *A. neomexicana* laid second clutches. A second possibility could be that hatchling *A. neomexicana* have better overwinter survival compared to *A. exsanguis*. Taylor and Caraveo (2003) reported *A.* exsanguis reproduce at smaller body sizes compared to other sympatric parthenogenetic species (i.e., *Aspidoscelis sonorae* and *Aspidoscelis flagellicauda*). Our growth analyses showed that *A. exsanguis* grew faster to attain a larger body size compared to the other species. Perhaps *A. exsanguis* reach sexual maturity sooner and reproduce earlier than other whiptails in our study. Clutch size is often correlated with female body size in lizards (Vitt and Congdon, 1978); therefore, *A. exsanguis*, the larger species, may have larger clutches compared to *A. neonexicana*.

The three species of parthenogenic whiptails we studied share a common parental species (*Aspidoscelis inornata*; Cullum, 1998; Reeder et al., 2002) and are genetically more similar to each other compared to bisexual species. Our study shows that *A. exsanguis*, *A. neomexicana*, and *A. uniparens* are morphologically different in body size, and perhaps this could allow their coexistence. The size of insect prey often correlates with lizard body size (Schoener, 1967). Our comparisons of seasonal capture rates found that patterns of activity were similar, whereas overwinter survival, clutch sizes, or age at first reproduction may

TABLE 3. Age-related capture frequencies of whiptails captured along the Rio Grande in New Mexico. Most hatchling lizards were not recaptured as adults; however, some lizards were recaptured up to three years after hatching. Numbers represent individually marked lizards and are not repeated in the table.

| Species | Hatched | 1st year | 2nd year | 3rd year | Total |
|----------------|---------|----------|----------|----------|-------|
| A. exsanguis | 995 | 18 | 5 | 4 | 1,022 |
| A. neomexicana | 671 | 18 | 10 | 2 | 701 |
| A. uniparens | 402 | 4 | 2 | 1 | 409 |
| Percent | 97.0% | 1.9% | 0.8% | 0.3% | |

differ among the species. Several potential drivers could explain the patterns we observed, and we recommend these topics for future study.

Our results establish important baseline data for growth rates, longevity, and activity patterns of three whiptail species. By reaching adult size at about the same time, the model for whiptail life history could be described as one of reproducing in the spring, eggs hatching in late summer, maturing early, and reaching a growth asymptote at an age about 13–15 months. Our data provide a foundation of whiptail life history from which comparisons of populations could be made. These data offer future comparisons of whiptail morphometrics among different regions.

Acknowledgments.--We thank the Middle Rio Grande Conservancy District, Bosque del Apache National Wildlife Refuge, and Albuquerque Open Space for permitting access to study sites, conducting treatments, and many other forms of assistance during this project. We are grateful to R. King (USDA Forest Service, Rocky Mountain Research Station [RMRS]) for statistical help. We thank D. Hawksworth (RMRS) and numerous RMRS field assistants for collecting and processing herpetofaunal data, especially L. W. Gorum and H. MacCurdy. We thank T. Giermakowski (Museum of Southwestern Biology) for preparing specimens. We also thank C. Painter (New Mexico Department of Fish and Game) and D. Burkett (Mevatec Corporation) for their initial assistance on study design and techniques. We thank two anonymous reviewers and B. Sullivan of Arizona State University West for helpful comments on this manuscript. The University of New Mexico Animal Care and Use Committee approved field techniques (protocol 20415). This study was funded by the U.S. Department of Agriculture Forest Service-RMRS Middle Rio Grande Ecosystem Management Unit, Joint Fire Sciences Program, National Fire Plan, State and Private Forestry New Mexico, Collaborative Forest Restoration Program, and U.S. Fish and Wildlife Service Bosque Improvement Initiative. Additional support to HLB was provided by University of New Mexico (UNM) Graduate Research Development grants, UNM Grove grants, and a National Fish and Wildlife Foundation grant.

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Accepted: 2 July 2009.

Appendix 1

Specimens collected from 2000–2006 of whiptail species, *Aspidoscelis exsanguis, Aspidoscelis neomexicana*, and *Aspidoscelis uniparens* were deposited in the Museum of Southwestern Biology (MSB), at the University of New Mexico, Albuquerque.

| Species | MSB catalog number | | |
|----------------|--|--|--|
| A. exsanguis | 62853–62860, 62911, 62933, 62935, 62939–62940, 74102, 74104, 74108–74110, 74112, 74115–74116, 74121, 74184, 74190, 74202–74204, 74206–74207, 74213, 74215, 74229, 74236–74237, 74240, 74244, 74254–74267 | | |
| A. neomexicana | 62861–62869, 62934, 62936–62937, 74107, 74113, 74117, 74122, 74185, 74205, 74209, 74216, 74227, 74230, 74232–74234, 74242–74243, 74245–74253 | | |
| A. uniparens | 62870–62876, 62938, 66796, 74106, 74111, 74120, 74182, 74208, 74217–74218, 74228, 74231, 74235, 74238–74239 | | |