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EVOLUTIONARY, ECOLOGICAL, AND MORPHOLOGICAL DISTINCTIVENESS OF AN ENDEMIC ARIZONA LIZARD, PAI STRIPED WHIPTAIL (*ASPIDOSCELIS PAI*)

JAMES M. WALKER[1]***, BRIAN K. SULLIVAN***[2,4]***, KEITH O. SULLIVAN***[2]***,***
MARLIS R. DOUGLAS[1,3]***, AND MICHAEL E. DOUGLAS***[1,3]

[1]*Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas 72701, USA*
[2]*School of Mathematical and Natural Sciences, P.O. Box 37100, Arizona State University, Phoenix, Arizona 85069, USA*
[3]*Illinois Natural History Survey, University of Illinois, Champaign, Illinois 61820, USA*
[4]*Corresponding author, e-mail: bsullivan@asu.edu*

***Abstract.*—The distribution of Pai Striped Whiptail (*Aspidoscelis pai*) includes much of north-central Arizona in its hypothetical geographic range. However, during a systematic survey across the northern third of the state in 2000–2010, we found it at relatively few sites, and primarily in Plains and Great Basin grassland biomes at elevations between 1600 and 2000 m. Evidence of habitat disturbance was typically apparent (i. e., road corridors, livestock grazing, livestock trails, and/or relocation of rocks). Based on 40 specimens from four areas in Coconino and Gila counties, including 11 gravid females to 72 mm snout-vent length (SVL) with a mean clutch size of 3.2 (range: 2–4) and several males to 71 mm SVL, we found no support for reports of maximum SVL in either sex of 78–85 mm. Whereas the original description of *A. pai* was based on data for five characters in one sample, we present data on 10 characters in four samples. We compared *A. pai* with its Arizona close relative, *A. arizonae*, which is restricted to parts of Cochise and Graham counties. Although it is an oversimplification to state that *A. pai* is a six–striped species, because an indistinct vertebral stripe is often present, we agree that *A. pai* and *A. arizonae* are distinct historical entities based on significant differences in six meristic characters and distinctive color patterns throughout ontogenetic development.**

***RESUMEN.*—Mapas que muestran la distribución del Huico Rayado de Pai (*Aspidoscelis pai*) incluyen gran parte del centro-norte de Arizona en su distribución geográfica hipotética. Sin embargo, durante un estudio sistemático para documentar su presencia en el tercio norte de este estado en el año 2003, lo encontramos en relativamente pocos sitios, principalmente en los biomas de pastizales de las Llanuras y de la Gran Cuenca a altitudes entre 1,600 y 2,000 m sobre el nivel del mar. Generalmente, encontramos evidencias de perturbación del hábitat en estos sitios, los efectos sobre las especies fueron desde positivos (creación de hábitats favorables por aclaramiento, preparación de terreno y apertura de caminos) hasta negativos (degradación por sobrepastoreo severo y presencia de plantas invasoras). Sobre la base de 40 especímenes recolectados en cuatro áreas en los condados Coconino y Gila, que incluyeron 11 hembras grávidas de hasta 72 mm de LHC (tamaño de camada 2-4, $\bar{x}$ = 3.2) y varios machos de hasta 71 mm de LHC, no encontramos evidencia para reportar que hembras y machos crecen hasta 78 y 85 mm de LHC, respectivamente. Considerando que la descripción original de *A. pai* se basó en datos de cinco caracteres de una sola muestra, nosotros presentamos datos sobre el doble de caracteres en cuatro muestras. Comparamos *A. pai* con su especie hermana endémica a Arizona, *A. arizonae*, la cual está limitada a partes de los condados Cochise y Graham. Aunque ésta es una sobre-simplificación se puede decir que *A. pai* es una especie de seis rayas, ya que una indistinta raya vertebral está frecuentemente presente, estamos de acuerdo en que *A. pai* y *A. arizonae* son entidades históricas distintas basándonos sobre diferencias significativas en los promedios de seis características merísticas y en distintivos patrones de coloración a través del desarrollo ontogenético.**

Key Words.—Aspidoscelis arizonae; Pai Striped Whiptail; grassland; Arizona endemic lizard; mtDNA; meristics

INTRODUCTION

The northwesternmost distributional and altitudinal limits for members of the gonochoristic *Aspidoscelis inornata* (Little Striped Whiptail) complex of Mexico and the United States are in diverse habitats including grassland, chaparral, woodland, and forest landscapes in Arizona at elevations between 1600 and 2000 m (Stevens 1983; Wright and Lowe 1993). These upper elevation and disjunct populations in Coconino, Gila, and Mohave counties were included in a new subspecies, *Cnemidophorus inornatus pai* = *Aspidoscelis inornata pai* (Reeder et al. 2002), briefly described by Wright and Lowe (1993). Lizards allocated to this taxon have also been reported from additional disjunct populations in Apache and Navajo counties in eastern Arizona by Persons and Wright (1999), though the characters upon which this allocation was based have not been summarized in the literature. At present, the taxonomic status of Pai Striped Whiptail is in need of additional study with reference to its relationship to *A. arizonae* (Arizona Striped Whiptail) and *A. inornata llanuras*

(Plains Striped Whiptail). Although we follow the SSAR checklist in the use of the name *A. pai* (de Queiroz and Reeder 2012) in this report, whether it should be treated as a subspecies (sensu Wright and Lowe 1993; Walker et al. 2009) or a species (sensu Collins 1997; Crother et al. 2000) is a question that we will subsequently discuss elsewhere with reference to molecular data. However, we provide estimates of dissimilarity among Pai, Arizona, and Plains striped whiptails, using as our gauge mitochondrial (mt) DNA sequence divergences.

In this report, we use descriptions of habitat occupancy of *A. pai* to clarify its ecological status in Arizona as was done more completely for *A. arizonae* by Sullivan et al. (2005). We also present newly obtained morphological data to help clarify variation in the species, both with reference to previously studied characters of scutellation and color pattern (Wright and Lowe 1993) and those reported on for the first time herein. In addition, Stevens (1983) conducted a study of reproduction and life history in upper elevation populations in Gila County, which presently would be taxonomically included in *A. pai*; however, the methods used to assess snout-vent length (SVL) for lizards has resulted in data incongruent with those reported for other populations of the *A. inornata* complex (e.g., Christiansen 1971; Walker et al. 2009). We attempt to reconcile inconsistencies pertaining to SVL, sexual dimorphism, and clutch size in *A. pai* (Stevens 1983) with additional analyses using 40 specimens obtained from 2000 through 2010.

MATERIALS AND METHODS

Field studies.—Sites were sampled on three to eight occasions during May, June, July or August, 2000–2010, with at least one visit to each site following summer rainfall events to document activity in relation to recent precipitation. At all sites, one to three individuals with considerable experience conducting lizard surveys in Arizona, walked 20 m abreast over 1–3 ha for a minimum of one person hour and a maximum of three person hours per site per visit. Site visits were usually conducted under mild conditions (air temperatures 20 ± 3 °C) during morning activity periods (0900–1130) of the lizards on days with little wind. We recorded descriptive behavioral observations on *A. pai* pertaining to effects of changes in weather conditions on activity, responses of lizards to human presence, and their use of habitat components.

We collected individuals of *A. pai* (n = 40) and *A. arizonae* (n = 30; Tables 1–3), two of the smallest species of *Aspidoscelis* in the United States, from six areas of Arizona between 2000 and 2010 under authority of permits provided by the Arizona Game and Fish Department. Physical features of habitat and components of the vegetational assemblage were also evaluated to obtain cues about new areas to search for *A. pai*, and we photographed panoramic habitat scenes inhabited by the species (Fig. 1). We assessed grazing across sites in a relative fashion, and considered heavy if most grasses were closely cropped, cattle droppings were visible throughout the site, and other indirect signs (e.g., hoof prints, well-worn trails to water bodies, etc.)

TABLE 1. Samples of *Aspidoscelis pai* from three northern sites within ca. 100 km of one another in Coconino County, Arizona, USA including the Grand Canyon area (GCA), Babbitt Ranch area (BRA), and Twin Arrows area (TAA) and two southern sites in Gila County, Arizona, including Mazatzal Mountains area (MMA) and Pigeon Springs area (PSA), and samples of *Aspidoscelis arizonae* from southern sites in Graham County, Arizona, including Bonita area (BA), and Cochise County, including Willcox area (WA).

Taxon	n	County, Area (Code) GPS	Preserved Specimens Examined Brian K. Sullivan (BKS) and Arizona State University (ASU)
A. pai	11	Coconino County: Grand Canyon area (GCA) 35.95782ºN, 111.78201ºW	BKS 1891–1895, 1925–1930
A. pai	5	Coconino County: Babbitt Ranch area (BRA) 35.61844ºN, 111.52843ºW	BKS 1412, 1414–1415, 1856–1857
A. pai	17	Coconino County: Twin Arrows area (TAA) 35.14858ºN, 111.24764ºW	BKS 1323–1324, 1416–1418, 2008–20015, 1386–1389
A. pai	7	Gila County: Mazatzal Mountains area (MMA) 35.73116ºN, 111.34477ºW	BKS 1879 (2)–1884
A. pai	49	Gila County: Pigeon Springs area (PSA) 33.71265ºN, 111.33437ºW	Specimens Numbered Between ASU 17344 and 17533
A. arizonae	6	Graham County: Bonita area (BA) 32.51405ºN, 109.97340ºW	BKS 1200–1202, 1255–1256, 1261
A. arizonae	24	Cochise County: Willcox area (WA) 32.23208ºN, 109.82540ºW	BKS 1168, 1173–1174, 1176, 1196–1199, 1222, 1228–1229, 1248, 1253, 1263–1265, 1267–1268, 1296–1299, 1303–1304

TABLE 2. Summary of meristic characters (see text for definitions of character abbreviations) for samples of *Aspidoscelis pai* (*A. p.;* PS = pooled sample) from three areas in Coconino County (GCA = Grand Canyon area; TAA = Twin Arrows area; BRA = Babbitt Ranch area) and one area in Gila County (MMA = Mazatzal Mountains area), Arizona, USA compared with samples of *Aspidoscelis arizonae* (*A. a.*; PS = pooled sample) from one area in Graham County (BA = Bonita area) and one area in Cochise County (WA = Willcox area), Arizona. Data are mean ± standard error (first row) and range and sample size (n; second row). In comparisons of pooled sample means ± standard error, only those followed by an asterisk were significantly different (P ≤ 0.05).

Character	*A. p.* PS ♀♂	*A. p.* MMA ♀♂	*A. p.* GCA ♀♂	*A. p.* TAA ♀♂	*A. p.* BRA ♀♂	*A. a.* PS ♀♂	*A. a.* BA ♀♂	*A. a.* WA ♀♂
GAB	69.3 ± 0.74* 60–80 (40)	72.6 ± 2.18 66–80 (7)	71.0 ± 0.74 67–76 (11)	67.6 ± 1.12 60–76 (17)	66.4 ± 1.72 60–70 (5)	65.5 ± 0.97* 51–73 (30)	65.2 ± 1.56 61–71 (6)	65.6 ± 1.16 51–73 (24)
OR	153.7 ± 2.29 128–190 (40)	166.6 ± 4.41 152–182 (7)	151.5 ± 1.69 144–162 (11)	150.5 ± 4.07 128–190 (17)	151.0 ± 7.41 134–178 (5)	158.5 ± 1.60 141–184 (30)	161.8 ± 3.32 153–172 (6)	157.7 ± 1.81 141–184 (24)
PV	6.7 ± 0.18* 4–9 (40)	6.0 ± 0.31 5–7 (7)	7.2 ± 0.30 6–9 (11)	6.7 ± 0.33 4–9 (17)	6.6 ± 0.40 6–8 (5)	9.2 ± 0.24* 6–12 (30)	9.2 ± 0.75 6–11 (6)	9.2 ± 0.75 7–12 (24)
PV/GAB	9.9 ± 0.24* 6.9–12.7 (40)	8.3 ± 0.45 6.9–10.4 (7)	10.1 ± 0.41 8.3–12.3 (11)	10.3 ± 0.38 7.6–12.7 (17)	9.9 ± 0.52 8.8–11.8 (5)	14.0 ± 0.34* 9.8–16.7 (30)	14.0 ± 0.91 9.8–15.5 (6)	14.0 ± 0.37 10.3–16.7 (24)
FP	31.0 ± 0.41 26–37 (40)	32.6 ± 1.13 27–37 (7)	32.0 ± 0.43 29–34 (11)	29.5 ± 0.57 26–35 (17)	31.6 ± 1.12 28–34 (5)	31.4 ± 0.42 25–35 (30)	32.0 ± 0.52 30–33 (6)	31.3 ± 0.51 25–35 (24)
SDL	30.8 ± 0.30* 28–37 (40)	33.4 ± 0.92 29–37 (7)	30.5 ± 0.41 29–32 (11)	30.2 ± 0.25 28–32 (17)	29.8 ± 0.49 29–31 (5)	28.2 ± 0.29* 25–31 (30)	28.3 ± 0.56 27–31 (6)	28.2 ± 0.35 25–31 (24)
COS	9.7 ± 0.59 6–27 (40)	11.6 ± 1.46 8–19 (7)	9.0 ± 0.65 7–14 (11)	9.6 ± 1.15 6–27 (17)	8.8 ± 0.58 7–10 (5)	10.1 ± 0.39 8–16 (30)	11.2 ± 0.91 8–14 (6)	9.9 ± 0.42 8–16 (24)
LSG	27.2 ± 0.91* 17–43 (40)	30.0 ± 2.76 22–43 (7)	26.2 ± 1.54 20–37 (11)	28.1 ± 1.30 21–39 (17)	22.2 ± 1.66 17–27 (5)	23.1 ± 0.85* 15–33 (30)	23.7 ± 1.38 20–27 (6)	23.0 ± 1.01 15–33 (24)
MS	12.0 ± 0.25* 9–15 (40)	12.7 ± 0.57 11–15 (7)	12.3 ± 0.41 10–14 (11)	11.6 ± 0.45 9–14 (17)	12.0 ± 0.32 11–13 (5)	13.8 ± 0.22* 11–17 (30)	13.8 ± 0.48 12–15 (6)	13.8 ± 0.25 11–17 (24)
ILS	30.6 ± 1.68 15–62 (40)	24.6 ± 2.20 18–32 (7)	34.5 ± 2.49 23–49 (11)	32.5 ± 3.13 19–62 (17)	23.4 ± 2.20 15–28 (5)	24.3 ± 1.10 21–42 (30)	26.7 ± 2.40 21–37 (6)	23.7 ± 1.23 15–42 (24)

were abundant.

For various analyses, we grouped specimens of *A. pai* into three northern sites within ca. 100 km of one another in Coconino County, including Grand Canyon area southeast of Grand Canyon National Park, Babbitt Ranch area north of Flagstaff, and Twin Arrows area east of Flagstaff (Table 1). The southern sample was obtained from Gila County on the east slope of the Mazatzal Mountains (Table 1). We collected two samples of *A. arizonae*, the other member of the *A. inornata* complex in Arizona (Wright and Lowe 1993; Sullivan et al. 2005), from near Bonita in Graham County and near Willcox in Cochise County (Table 1), and we compared them with *A. pai*. We also examined *A. pai* (= *Cnemidophorus inornatus*) from Gila County that were used in an upper elevation, reproductive study (Stevens 1983), and which bear Arizona State University (ASU) Museum Numbers (Table 1).

Size, color pattern, scutellation, meristic characters, and mtDNA.—Prior to preservation, the tip of the tail was removed from numerous lizards for DNA extraction. Individuals not released after clipping the tail were fixed in 10% formalin and stored in 70% ethanol. Snout–vent length (SVL) reported herein for *A. pai* are to the nearest 1.0 mm using straight, though not stretched, specimens from ethanol storage. Stevens (1983) measured SVL in *A. pai* (= *C. inornatus*) prior to preservation and the straightening (i.e., stretching) of lax specimens for SVL measurement greatly exaggerates this datum (Walker et al. 1994). Consequently, SVL reported for *A. pai* by Stevens (1983) are artifacts of methodology and are thus incongruent with data reported for other taxa in the *A. inornata* complex (e.g., Christiansen 1971; Wright and Lowe 1993; Walker et al. 2009).

Descriptions of dorsal color pattern in *A. pai* (i.e., terminology applied to the longitudinal pale colored

TABLE 3. The number of granular scales separating the paravertebral stripes in the two Arizona members of the *Aspidoscelis inornata* complex, *A. pai* (n = 40 from Coconino and Gila counties) and *A. arizonae* (n = 30 from Cochise and Graham counties).

Taxon	5	6	7	8	9	10	11	12	Tally
A. pai	4	13	13	6	4	0	0	0	In *A. pai* >8 in 4 of 40 = 10.0%
A. arizonae	0	1	1	9	5	10	3	1	In *A. arizonae* <9 in 11 of 30 = 36.7%

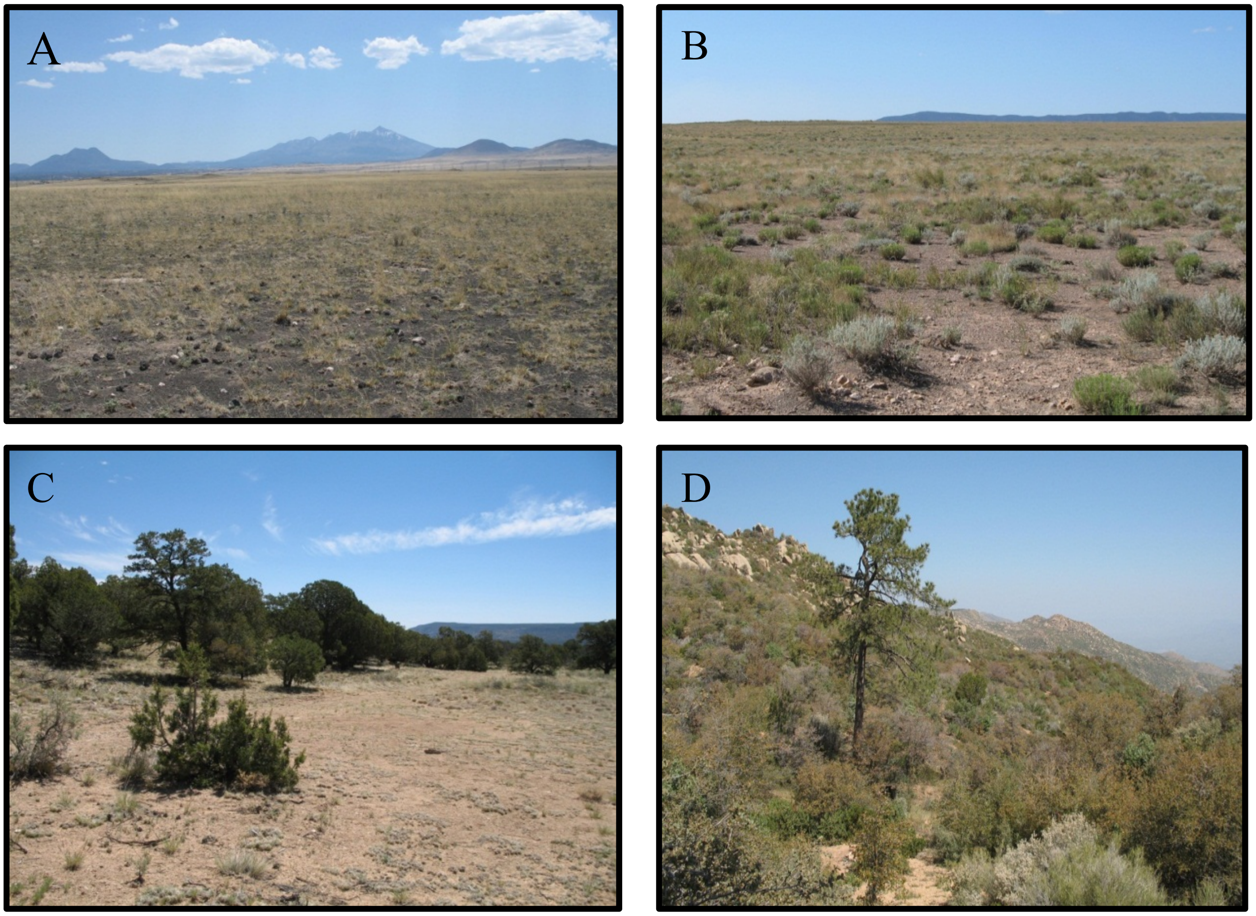

FIGURE 1. Habitats where *Aspidoscelis pai* was found during this study. A) Babbitt Ranch area, west side of state route 89, 45 km north of Flagstaff, Coconino County, Arizona, USA. B) Twin Arrows area, 60 km southeast of Babbitt Ranch, south side of interstate 40, 35 km east of Flagstaff, Coconino County, Arizona. C) Grand Canyon area, state Route 64, southeast of Grand Canyon National Park, 37 km west of state route 89, 112 km northwest of Flagstaff, Coconino Coounty, Arizona. D) Mazatzal Mountains area, El Oso Road, 12 km west of state route 188, Mazatzal Mountains, Gila County, Arizona. (Photographed by Brian K. Sullivan).

stripes and the intervening dark fields) are based on Burt (1931), Duellman and Zweifel (1962), and Walker et al. (2009). In *A. pai,* diagnostic characters in the original description by Wright and Lowe (1993) included the number of distinct stripes and coloration (= hue) of the fields and six primary stripes that are fixed in position, and hue of the ventral surfaces of the body (Fig. 2). We recorded relative size of mesoptychial scales along the edge of the posterior gular fold, relative size of the postantebrachial scales on the posterior surfaces of forearms, and anterior extent of the circumorbital scale series in each voucher of *A. pai* (see Burt 1931; Duellman and Zweifel 1962; Walker et al. 2009). Meristic characters and a ratio we analyzed in samples of *A. pai* and *A. arizonae* included counts of granular scales around midbody from the lateral longitudinal row of ventral scales on the left side of the body to these scales on the right side of the body (GAB), scales in a relatively straight line between the occipital scales of the head and the first row of caudal scales (OR), scales between the paravertebral stripes at midbody (PV), ratio of number of granular scales between paravertebral stripes to those around midbody (PV/GAB), femoral pores of both sides summed (FP), subdigital lamellae of the longest toe of the left pes (SDL), circumorbital scales of both sides summed (COS), lateral supraocular granules of both sides summed (LSG), enlarged scales in the first or second row bordering the gular fold (MS), interlabial scales of both sides summed (ILS), and supraocular scales of both sides summed (SO).

We extracted genomic DNA with Puregene DNA Purification or Qiagen DNeasy kits. We amplified mtDNA ATP8 and ATP6 genes (as per Douglas et al. 2006), sequenced the mtDNA using BigDye (ver.3.1) chemistry (Applied Biosystems, Inc. [ABI], Forest City, California), and analyzed the sequences on an ABI Prism 3100 Genetic Analyzer. We aligned the sequences manually using Sequencher (Gene Codes, Ann Arbor

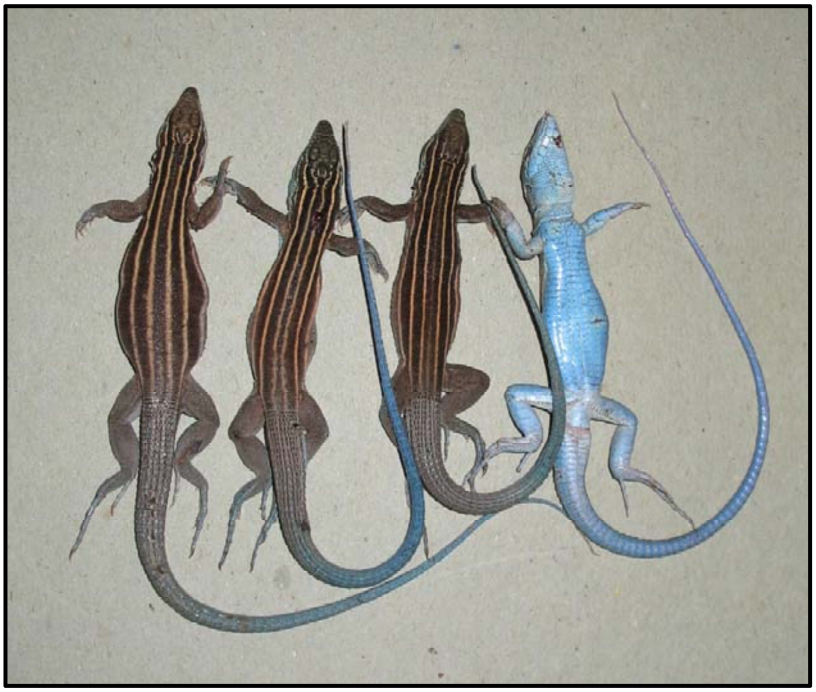

FIGURE 2. Ventral and dorsal colors and patterns of adult males and females of *Aspidoscelis pai* collected from Twin Arrows area, Coconino Co., Arizona, USA, 14 June 2009. (Photographed by Brian K. Sullivan).

MI). To derive estimates of sequence divergences among haplotypes, we combined both mtDNA genes based on 1,000 bootstrapped replications (MEGA5; Tamura et al. 2011).

Statistical analysis.—We used JMP software (Version 9; SAS Institute, Inc., Cary, North Carolina, 1987–2007) to generate a mean ± 1 standard error and range for each character and ratio analyzed. We compared means (α = 0.05) using Tukey posthoc tests in JMP to preserve alpha for multiple means.

RESULTS

Habitats.—The Babbitt Ranch area in Coconino County is a tract of Plains and Great Basin grassland (Brown et al. 2007) that has long been heavily grazed, thus promoting an open, exposed, and barren landscape with virtually no shrubs (Fig. 1). Small rocks are present along the roadway and other disturbed areas (e.g., powerlines, roads to cattle tanks placed regularly throughout the landscape, etc.). The vegetational structure is an open mixture of introduced and native grasses, including Blue Grama (*Bouteloua gracilis*) and Red Brome (*Bromus rubens*), with few shrubs other than invasive forms in the arid Southwest, including Golden Rabbit Bush (*Chrysothamnus nauseosus*), Russian Thistle (*Salsola iberica*), and Broom Snakeweed (*Gutierrezia sarothrae*). The soil structure is well drained gravelly loam, alluvium material derived from basalt pyroclastic rock (note dark color in Fig. 1A). In 2004–2005, a single lizard was observed during each of the two hours of searching per day. In 2006–2007, greater numbers were observed, but never more than five in the 2–4 ha tract searched thoroughly by 2–3 individuals. Both Long–nosed Leopard Lizard (*Gambela wislizenii*) and Eastern Collared Lizard (*Crotaphytus collaris*) were present, the latter in large numbers along the small rocks near the roadways. Other commonly observed lizards included Plateau Fence Lizard (*Sceloporus tristichus*) and Common Lesser Earless Lizard (*Holbrookia maculata*). Triploid parthenogenetic Plateau Striped Whiptail (*Aspidoscelis velox*) was also observed, but was only rarely encountered in the area inhabited by *A. pai*.

The Twin Arrows area in Coconino County, just under 60 km to the southeast of the Babbitt Ranch area, consists of a narrow band of Plains and Great Basin Grassland (Fig. 1B) bounded by Great Basin Woodland to the west (higher elevations) and Great Basin Desert Scrub to the east (lower elevations). It is heavily grazed and relatively open, but with more shrubs than the Babbitt Ranch area including Great Basin Sagebrush (*Artemisia tridentata*), Four-wing Saltbush (*Atriplex* *canescens*), Littleleaf Globemallow (*Sphaeralcea parvifolia*), and One-seed Juniper (*Juniperus monosperma*). The higher density of shrubs at this site is unsurprising, particularly given the proximity of the Twin Arrows area to the eastern edge of Great Basin Woodland (ca. 1 km east of the ecotone between grassland and the woodland). There is a mix of introduced and native grasses (e.g., Blue Grama) interspersed with the same invasive shrub species and noted at Babbitt Ranch (e.g., Russian Thistle, Rabbit Bush, and Broom Snakeweed). The substrate consists of well-drained sandy loam. Also present are eolian sands from limestone/sandstone erosion that contributes a soil color lighter than that found in the Babbitt Ranch area. *Aspidoscelis pai* was observed during all visits (n = 6) to the site from 2003–2009, even when none were observed at the Babbitt Ranch area. The only other lizards regularly observed in syntopy with Pai Striped Whiptail in the Twin Arrows area were *S. tristichus* and *H. maculata*, although *A. velox* was seen nearby and on site in some years. Like Babbitt Ranch, Twin Arrows supports *A. pai, H. maculata*, and *S. tristichus*, three saurians that consistently co-occur in northern Arizona Plains and Great Basin Grassland habitats.

The Grand Canyon area, inhabited by *A. pai* southeast of the canyon in Coconino County, consists of a mosaic of Great Basin Woodland and Great Basin Desertscrub (Fig. 1C). Areas most often inhabited by lizards were open ecotones with few trees between the two biomes, and open areas with white well-drained sandy soil. Lizards were absent in flats uniformly dominated by sagebrush, and roadcuts and grading have seemingly increased available (disturbed) habitat. If one searched within pure woodland or pure sagebrush flats, lizards were absent. During three visits in 2007–2008, up to five *A. pai* were observed daily, ranking between Babbitt Ranch and Twin Arrows in predictability (relative) density of the species. *Crotaphytus, Holbrookia*, and *Sceloporus* were also observed in the Grand Canyon Area.

The Mazatzal Mountains area in Gila County is inhabited by a disjunct population of *A. pai*. This site, when compared with the Babbitt Ranch site, exemplifies the diversity of landscape patches suitable for occupancy by the species. It is primarily chaparral dominated by Scrub Oak (*Quercus turbinella*) and Manzanita (*Arctostaphylos pungens*), with some granitic boulders, and with mixed oak/pine woodland nearby (Fig. 1D). No lizards were observed in forest habitat per se at higher elevations; they were primarily observed along roadways, and in relatively open portions of chaparral apart from closed canopies. Some individuals of the gonochoristic Tiger Whiptail (*A. tigris*) and triploid parthenogenetic Gila Spotted Whiptail (*A. flagellicauda*) were observed in nearby formations, but only *S. tristichus* was actually syntopic with *A. pai*. During a total of three visits (in 2007 and 2008), 10 *A. pai* were observed/collected over a period of two hours. However, none were observed in late April, presumably owing to the lower temperature regimen at higher elevations outside of the May to September activity period.

Body size and clutch size.—We assessed whether females and males attain a maximum SVL of 78 and 85 mm, respectively (Stevens 1983), by gathering SVL data for 40 preserved *A. pai* specimens. Gravid females (n = 11) had a mean SVL of 65.3 ± 1.08 mm (61–72 mm), of which only two exceeded 70 mm. Clutch size was 3.18 ± 0.18 (2–4), and was not correlated with SVL (r = 0.27, *P* = 0.436). The largest male had a SVL of 71 mm, thus indicating sexual dimorphism in SVL is not apparent. We noted the relatively small SVL and large clutches (i.e., 3–4) in *A. pai* resulted in intriguing and variable arrangements of either yolked follicles (to ca. 10 mm in diameter) in ovaries or eggs (to ca. 8.5 x 14.5 mm) in oviducts, with displacement of organs in each female to accommodate the developing clutch.

Color pattern.—The dorsal color pattern of *A. pai* includes three pairs of yellow primary stripes, so designated because they are fixed components (Fig. 2) invariably present from hatchling through adulthood. Dorsal granular scales aligned along the margins of the stripes are partially the light color of the stripes and dark color of the fields. The relatively straight, unbroken, primary stripes include the laterals (beneath eyes to the femora), dorsolaterals (superciliary scales to base of tail), and paravertebrals (parietal scales to base of tail). Also fixed in position in the dorsal pattern are the intervening brown–black to black fields between the stripes (Fig. 2). Included are the lower laterals (between the ventral scales and lateral stripes), upper laterals (between the lateral and dorsolateral stripes), dorsolaterals between the dorsolateral and paravertebral stripes), and the vertebral field (between the paravertebral stripes) which is variable in width (Fig. 2). Spots of any size (discrete rounded light colored areas) never develop in the dorsal pattern of *A. pai*, which is the basis for the appellation "striped-unspotted species" (= Pai Striped Whiptail). The base of the tail lacks distinct stripes (i.e., stripes only faintly visible) and the hind limbs are more or less uniformly patterned (Fig. 2). The tail is blue-gray, becoming blue distially. In adults, the ventral body surfaces are blue, being darker in males (Fig. 2). The blue color of *A. pai*, in life, is often a deeper, almost indigo to violet relative to the sky or gray blue seen in *A. arizonae*, or the blue green shade observed in asexual forms (*A. velox* and *A. uniparens*).

The critical diagnostic characters given by Wright and Lowe (1993) for *A. pai* included the narrow spacing of the paravertebral stripes, as expressed by the PV count

(6.2 ± 0.24, 4–9, n = 29), PV/GAB ratio (9.3 ± 0.34, 6.4–12.3, n = 29), and absence of a vertebral (= middorsal) stripe. Our data (PV, 6.7 ± 0.18, 4–9, n = 40; PV/GAB, 9.9 ± 0.24, 6.9–12.7, n = 40) also revealed a narrow spacing of the paravertebral stripes and a low ratio value. Although mean PV for *A. pai* and *A. arizonae* are significantly different (Table 2), ranges overlap to an extent that they are not diagnostic per se (Table 3). Only four of 40 (10 %) specimens in *A. pai* have a PV separation of more than eight scales; however, 11 of 30 (36.7%) *A. arizonae* had a PV separation of less than nine.

The reference by Wright and Lowe (1993) to *A. pai* as a six-striped entity (mean = 6.07 stripes; range 6.00–6.50 stripes) was apparently based on a decision not to count a weakly expressed vertebral stripe. Among our specimens, lack of a vertebral stripe was noted for 17 of 40 (42.5%) lizards. In 22 (55%) specimens, a faint to moderately distinct vertebral stripe was present; however, there is a distinct vertebral in only one lizard (female of 57 mm SVL). Evidence of a geographic pattern of variation is seen in the Mazatzal Mountains area from which all specimens (n = 7) lack a vertebral stripe, compared with the Twin Arrows area from which 13 of 17 lizards (76.5%) have a thin, weakly expressed vertebral. Consequently, it is correct to say that *A. pai* has a vertebral stripe in > 50% of specimens, though it is typically only faintly visible.

We also examined 49 specimens from the Pigeon Springs area of Gila County (just south of our samples from El Oso Road) randomly selected from among the specimens of *A. pai* (= *C. inornatus*) used by Stevens (1983). Of these, 47 lizards (96%) are truly six striped, one (2%) has an indistinct vertebral stripe, and one (2%) has a distinct vertebral stripe most of the length of the vertebral field. Also, two specimens have irregularly margined paravertebral stripes on the neck and four have joined paravertebrals on the neck, to mark variations not seen in specimens from the Mazatzal Mountains area. Thus, *A. pai* is a six-striped entity (Wright and Lowe 1993) only in the Mazatzal Mountains and Pigeon Springs areas, Gila County (54 of 56 = 96.4%). However, 22 of 33 (66.7%) from Babbitt Ranch, Twin Arrows, and southeast of the Grand Canyon, Coconino County, have a thin faint to moderately distinct vertebral stripe and one female of 57 mm SVL has a distinct vertebral stripe.

Scutellation, meristic characters, and mtDNA sequence divergence.—Most individuals of *A. pai* (n = 31, 77.5%) have short bilateral circumorbital series in which the anteriormost scale of each series lies against a third supraocular suture. However, one specimen has a complete circumorbital series on the right side of the head, and a series on the left that lacks two scales being complete, for the highest combined COS count (27) among 40 specimens. The specimen also has the highest ILS value (62) in the pooled sample. All specimens of *A. pai* have slightly enlarged postantebrachial scales, compared with the more uniformly granular scales of *A. tigris*, and the moderately enlarged scales of *A. velox*. The mesoptychial scales bordering the gular fold are larger in *A. pai* than the scales in *A. arizonae*, which is reflected in a significant difference in the pooled samples means for the MS character (Table 2).

We analyzed nine meristic characters and a ratio in four samples of *A. pai* and two samples of *A. arizonae* (Table 1), of which the OR, SDL, COS, LSG, MS, ILS, and SO are reported for the first time for each species. For each, there is broad overlap in ranges of variation (Table 1) such that no single one or combination thereof can be used to distinguish individual specimens of these species, though they are distinguishable based on color pattern. Nevertheless, the fact that the pooled samples *A. pai* and *A. arizonae* resulted in six of 10 significantly different mean characters is support for their recognition as separate historical entities with different evolutionarily trajectories.

Among the characters studied, the SO was the least variable, with 4L/4R supraocular scales in 39 of 40 *A. pai*. The lone exception, a male of 48 mm SVL, from the Mazatzal Mountains area, has 4L/5R SO, in addition to having very high counts for four characters (i.e., 78 GAB, 182 OR, 37 SDL, and 14 MS). Also subject to relatively little variation are PV (4–9), which is a measure of the separation of the paravertebral stripes that are consistently positioned in all specimens and FP (26–37), of which there are numerous L/R combinations including 42.5% (17 of 40) with equal numbers. Characters subject to higher levels of variation are: GAB (60–80); OR (128–190); LSG (17–43), and ILS (15–62). Percentage mtDNA sequence divergence ranged from 2.06% (± 0.44) between haplotypes of *A. pai*/ *A. arizonzae* to 3.86% (± 0.63) between *A. i. llanuras*/*A. arizonzae*, with *A. i. llanuras/ A. pai* diverging at 2.64% (± 0.49).

DISCUSSION

The composite geographic range of the *Aspidoscelis inornata* (Little Striped Whiptail) complex comprises a diverse array of ecotones, plains, and desert habitats in the states of Arizona, New Mexico, and Texas in the United States, and Chihuahua, Coahuila, Durango, Nuevo León, San Luis Potosi, Tamaulipas, and Zacatecas in Mexico (Wright and Lowe 1993; Farr et al. 2009; Walker et al. 2009). We have studied members of the complex in each of the states listed for both countries except Tamaulipas and Zacatecas. In many areas of both countries the principal distinguishing features of the complex are small body size (72 mm maximum SVL) and striped unspotted dorsal patterns, the only exception

TABLE 4. Comparison of data (mean ± 1 standard error, range of variation, and sample size, n) for "diagnostic characters" provided by Wright and Lowe (1993) with data generated from different specimens used in this study; note close agreement in results. Character are counts of granular scales around midbody (GAB), scales between the paravertebral stripes at midbody (PV), and femoral pores of both sides summed (FP).

Character	Wright and Lowe 1993	This Study
GAB	67.0 ± 0.66 (60–76, n = 29)	69.3 ± 0.74 (60–80, n = 40)
PV	6.2 ± 0.24 (4–9, n = 29)	6.7 ± 0.18 (4–9, n = 40)
PV/GAB	9.3 ± 0.34 (6.4–12.3, n = 29)	9.9 ± 0.24 (6.9–12.7, n = 40)
FP	30.9 ± 0.34 (28–34, n = 28)	31.0 ± 0.41 (26–37, n = 40)

being the inornate dorsal pattern of *A. inornata inornata* in Nuevo León (Walker et al. 2009). However, maximum SVLs of 78 and 85 mm have been reported (Stevens 1983) for what is now recognized as *A. pai* (Collins 1997; de Quieroz and Reeder 2012) in Gila County, Arizona. This assessment was based on 185 specimens that includes ASU 17338–17538 (n = 201), within which we found specimens of *A. flagellicauda* (e.g., ASU 17490, 17494, 17500). The ASU sample represents poorly preserved and mangled lizards that were formalin hardened in a stretched and/or distorted state, and from which we randomly selected 49 specimens of *A. pai*. We obtained several SVL measurements of 75–77 mm, which we attributed to artifacts of preservation (see Walker et al. 1988). Therefore, the assertions pertaining to maximum SVL in *A. pai* (per Stevens 1983) are indeed doubtful. We instead accept the SVL data obtained from the present samples of *A. pai* summarized herein as representative for the species. Wright and Lowe (1993) also reported a maximum SVL of 72 mm for the species, the same as our number, based on study of > 1,800 specimens of the *A. inornata* complex from the United States and Mexico.

Wright and Lowe (1993) presented data for five characters in their Table 1 for populations in the *A. inornata* complex allocated among 10 subspecies. Our data for four of these characters used to diagnose *A. pai* (Table 4; GAB, PV. PV/GAB, and FP) are in close agreement with these authors. However, our analysis of variation in the species used additional characters as a standard for future research on the *A. inornata* complex. Although the data summarized for characters in Tables 1–3 do not distinguish *A. pai* from all members of the *A. inornata* complex, they are useful in distinguishing it from other congeners (e.g., *A. uniparens* and *A. velox* in Arizona). While these data suggest evolutionarily distinct entities and separate trajectories, the extent of mtDNA sequence divergences and meristic/color pattern differences in *A. i. llanuras/A. arizonae* will be discussed elsewhere.

The distribution of *A. pai* emerges as a composite of disjunct populations in parts of five counties in Arizona. Wright and Lowe (1993) provided a range map for *A. pai* that spans a considerable portion of north-central Arizona. However, we found it at relatively few sites across the northern third of the state in 2000–2010, and primarily in Plains and Great Basin grassland biomes as described herein. Surveys for whiptails across northern Arizona were conducted in all major biotic communities, from Mohave County near Kingman (Semi-desert Grassland), east across all areas south of the Grand Canyon (Great Basin Woodland, Montane Conifer Forest), through the Painted Desert (Great Basin Desertscrub and Great Basin Woodland), to the border with New Mexico. Most sites surveyed in these areas were occupied by *A. velox* (grassland and woodland) or *A. tigris* (desertscrub), and only rarely by *A. pai* (specifically, the sites described herein). Given its patchy distribution in Arizona, the habitats occupied by *A. pai* are surprisingly varied, though in general, they are in less arid grassland formations or heterogeneous mosaics between woodland and desertscrub communities (e.g., Grand Canyon Area). This distribution is consistent with the notion that this whiptail was once more widely distributed, and has contracted dramatically due to recent ecological changes, such as over-grazing or climate change.

With respect to daily activity, much like *A. arizonae* (Sullivan et al. 2005), *A. pai* is primarily active during early morning hours on calm days from late April through early September (May through August in the Mazatzal Mountains). It is an active forager that may move several meters during its daily activity period. Unlike the notoriously wary Tiger Whiptail (*A. tigris*), *A. pai* is especially approachable, often taking refuge beneath the branches of small shrubs, or within bunch grasses, only to re-emerge within a few moments to continue foraging or basking, in a manner similar to *A. arizonae*. Activity was invariably higher following rainfall events. As noted by Sullivan et al. (2005) for *A. arizonae*, additional study will be necessary to evaluate the stability of these disjunct and widely separated populations of *A. pai*.

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APPENDIX 1. Preserved Specimens Examined

Aspidoscelis pai (n = 89)

Arizona: Coconino County: **(GCA = Grand Canyon Area, n = 11)** SR 64, 23 mi W of State Road (= SR) 89, UTM (datum = NAD 1927) 12S 429735E, 3979417N [31 May 2007 (BKS 1891–1895, n = 5); 1 June 2008 (BKS 1925–1928, n = 4)]; SR 64, 23 mi W of SR 89 (west side),12S 429287E, 3979072N [2 June 2008 (BKS 1929–1930, n = 2)].

Arizona: Coconino County: **(BRA = Babbitt Ranch Area, n = 5),** SR 89, 29 mi N of I–40, Babbitt Ranch, 12S 452177E, 3941544N [6 July 2004 (BKS 1412, n = 1)]; SR 89, 29 mi N of I–40, Babbitt Ranch, 12S 452163E, 3941426N [17 July 2004 (BKS 1414–1415, n = 2)]; 28 mi N of Flagstaff, Babbitt Ranch [14 May 2007 (BKS 1856–1857, n = 2)].

Arizona: Coconino County: **(TAA = Twin Arrows Area, n = 17)** Twin Arrows on I–40, 12S 477590E, 3889477N [6 August 2003 (BKS 1323, n = 1), 7 August 2003 (BKS 1324, n = 1); 14 June 2009 (BKS 2008–2015, n = 8)]; Twin Arrows, just S of I–40, 12S 477443E, 3889389N [17 July 2003 (BKS 1416–1418, n = 3)]; Twin Arrows, just S of I–40, 12S 477596E, 3889431N [22 May 2004 (BKS 1386–1389, n = 4)]..

Arizona: Gila County: **(MMA = Mazatzal Mountains Area, n = 7)** El Oso Road, 7.5–8.2 mi W of SR 188, 12S 469157E, 3732108N [24 May 2007 (BKS 1879 (2)–1884, n = 7)].

Arizona: Gila County**: (PSA = Pigeon Springs Area, n = 49)**; Pigeon Springs (33º42’45”N, 111º 20’0”W) to Little Pine Flat, 2–18 km NNW of Four Peaks Mountain reset (1600–2000 m elev.) (Arizona State University 17344–17345, 17358, 17366, 17369, 17374–17377. 17379, 17386, 17388, 17391, 17393, 17396, 17399, 17401, 17403, 17406, 17408, 17410, 17415–17416, 17418, 17421, 17424, 17430, 17432, 17438, 17443, 17451, 17456, 17458–17459, 17464, 17466–17467, 17477, 17487, 17503, 17507, 17509, 17511, 17514–17516, 17518, 17529, 17533, n = 49).

.*Aspidoscelis arizonae* (n = 30)

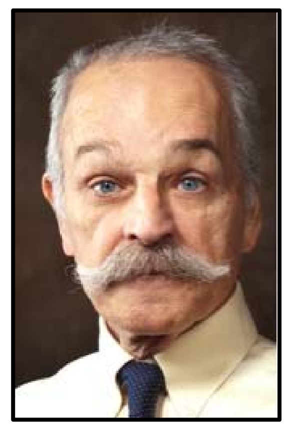
Arizona: Graham County: **(BA = Bonita Area, n = 6)** Fort Grant Road, 23 mi N of Willcox, 12S 596466E, 3597736E [17 July 2000 (BKS 1200–1202, n = 3); 24 May 2003 (BKS 1255–1256, n = 2)]; 3.8 mi S Bonita, 12S 595953N, 3600345E [25 May 2003 (BKS 1261, n = 1)].

Arizona: Cochise County: **(WA = Willcox Area, n = 24)** Blue Sky Road N of SR 186, SE of Willcox [13 May 2000 (BKS 1168, n = 1)]; Twin Lakes, 12S 610547E, 3566454N [13 June 2000 (BKS 1173, n = 1); [25 June 2002 (BKS 1222, n = 1)]; Exit 336, immediately N of I–40 [13 June 2000 (BKS 1174, n = 1); 6 July 2003 (BKS 1298, n = 1)]; Exit 186, 3.8 mi SE of Willcox [14 June 2000 (BKS 1176, n = 1)]; Twin Lakes, 2 mi SW of Willcox [18 July 2000 (BKS 1196–1199, n = 4); 21 May 2003 (BKS 1263–1265, 1267–1268, N = 5)]; 0.5 mi N of Exit 340 off I–40, N of Stout’s, 12S 609115E, 3572144N [27 June 2002 (BKS 1228–1229, n = 2)]; Twin Windmills, S of Exit 336 on I–10, 12S 606032E, 3564493N [24 May 2003 (BKS 1248, n = 1); 16 June 2003 (BKS 1291, n = 1); 6 July 2003 (BKS 1296–1297, N = 2)]; Ash Creek Road, 12S 593681E, 3593729N (BKS 1253, n = 1)]; Railroad Road West, 12S 607565E, 3564043N [7 July 2003 (BKS 1303–1304, n = 2)].

JAMES M. WALKER is a Professor of Biological Sciences at the University of Arkansas, Fayetteville, Arkansas. Since earning his B.S. and M.S. degrees from Louisiana Tech University, and Ph.D. from the University of Colorado, he has taught and conducted research at the University of Arkansas (1965–present). He has collaborated with many scientists, on publications pertaining to the biology and systematics of whiptail lizards (genera *Aspidoscelis* and *Cnemidophorus*: Family Teiidae). His graduate students have completed theses and dissertations on a variety of amphibian and reptile subjects. (Photographed by Douglas D. Rhoads)

BRIAN K. SULLIVAN is a Professor of Evolutionary Biology and Herpetology at Arizona State University. He is currently investigating Desert Tortoises (*Gopherus morafkai*) and other herpetofauna in islands of Sonoran Desert habitat isolated by a sea of urbanization near Phoenix, Arizona. He has published over 100 articles, book reviews, technical reports, and book chapters. (Photographed by Gillian Rice)

KEITH O. SULLIVAN is a life science major at Arizona State University. His research interests are focused on the ecology, behavior, and conservation of amphibians and reptiles, especially of the Sonoran Desert. He has published articles on Common Chuckwallas (*Sauromalus ater*) and gartersnakes, and is currently working with horned lizards and Desert Tortoises (*Gopherus morafkai*) in central and southwestern Arizona. (Photographed by Brian Sullivan)



MARLIS R. DOUGLAS (left) and **MICHAEL E. DOUGLAS** (right) share a common interest in the western North American deserts, a unique landscape where '. . . every creature has a sting and every plant a thorn.' Their research transects multiple disciplines and embraces cutting-edge technologies so as to recognize, define, conserve, and restore the endemic and isolated desert biodiversity. They strive to combine theory with application, for this offers a more succinct approach to biodiversity conservation. Both jointly run the Conservation Genetics and Molecular Ecology Laboratories at University of Arkansas (Fayetteville) and the Illinois Natural History Survey (University of Illinois-Urbana/Champaign). (Photographer unknown)