COMMON CHUCKWALLAS (*SAUROMALUS ATER*) IN URBAN PRESERVES: DO FOOD PLANTS OR CREVICE RETREATS INFLUENCE ABUNDANCE?

BRIAN K. SULLIVAN[1] AND RACHEL E. WILLIAMS[2]

[1]*Division of Mathematical and Natural Sciences, Arizona State University, PO Box 37100, Phoenix, Arizona 85069, USA,
email:bsullivan@asu.edu*
[2]*Applied Biological Sciences, Arizona State University, Mesa, Arizona, USA*

ABSTRACT.—Understanding anthropogenic effects on key habitat features for reptile populations is critical to ongoing conservation efforts in urban regions. We surveyed habitat features associated with populations of the Common Chuckwalla (*Sauromalus ater*) in preserves of the Phoenix Mountains and adjacent areas near the Phoenix Metropolitan region during spring and fall, 2009. Extending prior work with fecal count indices, we assessed current population levels as indicated by fecal counts in relation to variation in abundance of preferred food plants and availability of rock crevice refuges. Our results revealed an association between fecal counts and presence of six favored food plants, but not number of crevices or overall plant density. These six plant species, previously established to influence female selection of male territories, were uncorrelated with plant density. A secondary analysis indicated that overall plant diversity was strongly correlated with fecal counts. Our survey results suggest that Common Chuckwalla populations are stable in these island preserves, and that the presence of particular plant foods may be critical to their persistence.

Key Words.—Common Chuckwalla; crevices; indirect survey; plants; preserves; reptile conservation; *Sauromalus ater*; urbanization

INTRODUCTION

Understanding the relationships between key environmental variables and abundance of vertebrate species, especially in natural areas isolated within urban landscapes, is increasingly important to conservation (Sullivan et al., in press). The notion that individual ecological factors are essential to population viability is widely held among wildlife biologists, and derives in part from investigations in which singular factors such as critical nesting sites or keystone predators have been identified as central to the persistence of endangered or threatened organisms. Less is known about the responses of reptiles to anthropogenic effects on habitat structure within remnant communities (see reviews in MacNally and Brown 2001; Garden et al. 2007; Sullivan and Sullivan 2008; Sullivan et al., in press). Only recently have we gained insights into both community (e.g., Koenig et al. 2001; Garden et al. 2007) and species level responses of reptiles to anthropogenic habitat alteration associated with urbanization (e.g., Sullivan 2000; Sullivan et al. 2004a; Kwiatkowski et al. 2008).

Although conservation biologists have long debated whether a single large or several small preserves are ideal for managing particular species, it is increasingly recognized that for squamate reptiles, habitat structure within preserves, independent of preserve size, is vital to population viability of a number of taxa. Garden et al. (2007) found that reptile communities in the Brisbane area (Australia) were influenced to a greater extent by habitat structure rather than floristic composition of available preserves (see also Koenig et al. 2001). Davidson et al. (2008) documented that ground dwelling lizards of the Chihuahuan Desert were two to four times as abundant in grasslands differing solely with respect to presence or absence of burrows of native rodents, apparently because burrows represent important avenues of escape from predators. Habitat alteration influencing refuges from predators, such as the loss of rocky microhabitats in forest communities, has been shown to negatively affect lizard communities in lacertids (Amo et al. 2007a), and even overall physiological condition in one species in particular (Amo et al. 2007b; but see French et al. 2008).

A little appreciated aspect of anthropogenic effects on reptiles in urban landscapes is habitat alteration due to collecting of animals for the pet trade. Goode et al. (2005) documented a reduction in rock dwelling lizards at one site in the Sonoran Desert, which they attributed to the influence of habitat destruction by collectors. As they noted, even if the individuals collected are few in number, destruction of critical refuge sites such as rock crevices that regenerate over geological time, might be far more significant. Habitat change leading to higher levels of predation has been suggested to cause declines in lizards (Lettink et al. 2010).

Hypotheses under test.—It is well documented that habitat loss and alteration resulting from anthropogenic activities have profoundly affected vertebrates of the

Sonoran Desert of the southwestern United States (reviewed by Sullivan et al., in press). The Common Chuckwalla (*Sauromalus ater*) is a large, herbivorous lizard inhabiting the Sonoran Desert, as well as parts of California, Nevada and Utah, and has been the subject of a number of behavioral studies (Fig. 1; for review of literature, see Kwiatkowski and Sullivan 2002a, b and Sullivan and Sullivan 2008). Sullivan and Flowers (1998) documented that Common Chuckwallas are present in all preserves of the Phoenix Mountains with rocky outcrops and that larger preserves generally have higher densities of this lizard even though other large squamates (e.g., *Dipsosaurs dorsalis, Gambelia wislizenii*) are absent or declining. Kwiatkowski and Sullivan (2002b) found that female Common Chuckwallas selected male territories in part on the basis of plant species important as food resources. They also suggested that variation in underlying geological formations might influence abundance of these rock dwelling lizards, especially in the light of their anti-predatory behavior, consisting of taking refuge in a narrow rock crevice and inflating (Smith 1946; Lappin et al. 2006). Results of Goode et al. (2005) confirmed this suggestion since Common Chuckwallas were one of the rock-dwelling lizards they found in lower numbers in areas of a Phoenix Preserve in which crevices had been damaged and rendered unusable by these lizards as a result of anthropogenic activities.

We therefore tested the hypothesis that rock crevice refuges from predators used by Common Chuckwallas correlate with population levels in remnant habitats of the Phoenix Mountain Preserve system. Specifically, using fecal counts as an index of relative abundance, we assessed the relationship between crevice density and population size of Common Chuckwallas, building on prior analysis at one of the Phoenix Preserve sites indicating activities associated with the pet trade reduce crevice numbers and consequently, abundance of Common Chuckwallas (Goode et al. 2005). Because previous investigations also established that particular plant species, used as food by these herbivorous lizards, are important in selection of male territories by females (Kwiatkowski and Sullivan 2002a, b), we also examined the association of plant density with fecal counts. Hence, as an alternative hypothesis to the importance of rock crevices, we hypothesized that preferred plant foods of the Common Chuckwalla are a stronger predictor of population size, based on the work of Kwiatkowski and Sullivan (2002b) regarding plants commonly consumed by these lizards.

METHODS

Study populations.—Although Common Chuckwallas are large and long-lived, they are typically wary and thus, difficult to census (Sullivan and Flowers 1998;

FIGURE 1. Male (upper) and female Common Chuckwallas (*Sauromalus ater*) from the Phoenix Mountains, Phoenix, Arizona (Photographed by Brian K. Sullivan).

Sullivan et al. 2004b). Like those produced by many medium to large sized vertebrate herbivores, however, Common Chuckwalla feces are distinctive and easily recognized, and typically deposited in obvious and exposed locations allowing for indirect survey methods (Sullivan and Flowers 1998). In the spring and fall of 2009, we surveyed eight sites previously scored for fecal counts in 1995 and 2008 (Sullivan and Flowers 1998; Sullivan and Sullivan 2008) to test our competing hypotheses as to whether density of key plant species or abundance of crevice refuges influence population size of Common Chuckwallas.

All sites were located in the Sonoran Desert Upland Community (Brown 1982), dominated by Saguaro Cactus (*Carnegiea gigantea*), Creosote Bush (*Larrea tridentata*), Ocotillo (*Fouquieria splendens*), Foothill Palo Verde (*Parkinsonia microphyllum*), Brittlebush (*Encelia farinosa*) and Triangle-leaf Bursage (*Ambrosia deltoidea*). Additional plant species important as food resources for Common Chuckwallas, based on prior studies establishing plant preferences (Kwiatkowski and Sullivan 2002a, b), were present in far lesser numbers (Table 1).

Each site was a series of rocky outcrops associated with mountain preserves set aside almost fifty years ago prior to dramatic expansion of the metropolitan area, which effectively surrounded the preserves so that they now represent rocky islands in a sea of suburban development. Geologically, sites consisted of metamorphosed sedimentary rock (primarily schist and gneiss; Fig. 2) at some locations, and basaltic boulder fields at others (Fig. 2). Survey sites comprised six ridges or outcrops in the Phoenix Mountains: Lookout Mountain (LM); Piestewa Peak (PP); North Mountain 1, 2, and 3 (i.e., three sites separated by at least one km, NM1, NM2, and NM3); Shadow Mountain (ShM); one

TABLE 1. Plant species found in the Phoenix Mountain Preserve sites surveyed during Fall, 2009. The first six plants are "favored plant food species" (ranked 1-6 based on preference as food plant) as determined by Kwiatkowski and Sullivan (2002b).

Common Name	Scientific Name
Foothills Palo Verde (1)	*Parkinsonia microphyllum*
Globemallow (2)	*Sphaeralcea ambigua*
America Threefold-	*Trixis californica-*
-Golden Eye (3)	*-Viguiera deltoidea*
Ocotillo (4)	*Fouquieria splendens*
Desert Lavender (5)	*Hyptis emoryi*
Wolfberry (6)	*Lycium* spp.
Triangle-leaf Bursage	*Ambrosia deltoidea*
Brittlebush	*Encelia farinosa*
Creosote Bush	*Larrea tridentata*
Pincushion Cactus	*Mammillaria* spp.
Cholla	*Opuntia* spp.
Mormon Tea	*Ephedra* spp.
Barrel Cactus	*Ferocactus wislizeni*
Saguaro	*Carnegiea gigantean*

site in the Hedgpeth Hills (HH, 20 km west of the Phoenix Mountains); and one site in the South Mountains (SM, 30 km south of the Phoenix Mountains). Elevations ranged from 400 to 600 m; details on each of these sites, including precise locations, are provided in Appendix 1.

Survey methods.—We used fecal counts as an indirect indicator of population size, following the methodology of Sullivan and Flowers (1998). They documented a highly significant correlation between total fecal dropping counts and total numbers of Common Chuckwallas across the eight survey sites described above. In brief, this consisted of assigning a "count" for each basking site (i.e., a portion of a rock outcrop) of an approximately circular area (diameter = 1 m) sampled throughout a roughly one to two hectare area of Common Chuckwalla habitat at each of the eight original sites within the mountain preserves. We tallied counts by a single observer over a one hour period; counts obtained in 2008 (Sullivan and Sullivan 2008) were averaged with those from 1995 (given they were highly correlated) and used in the present study as an estimate of relative population size to assess the
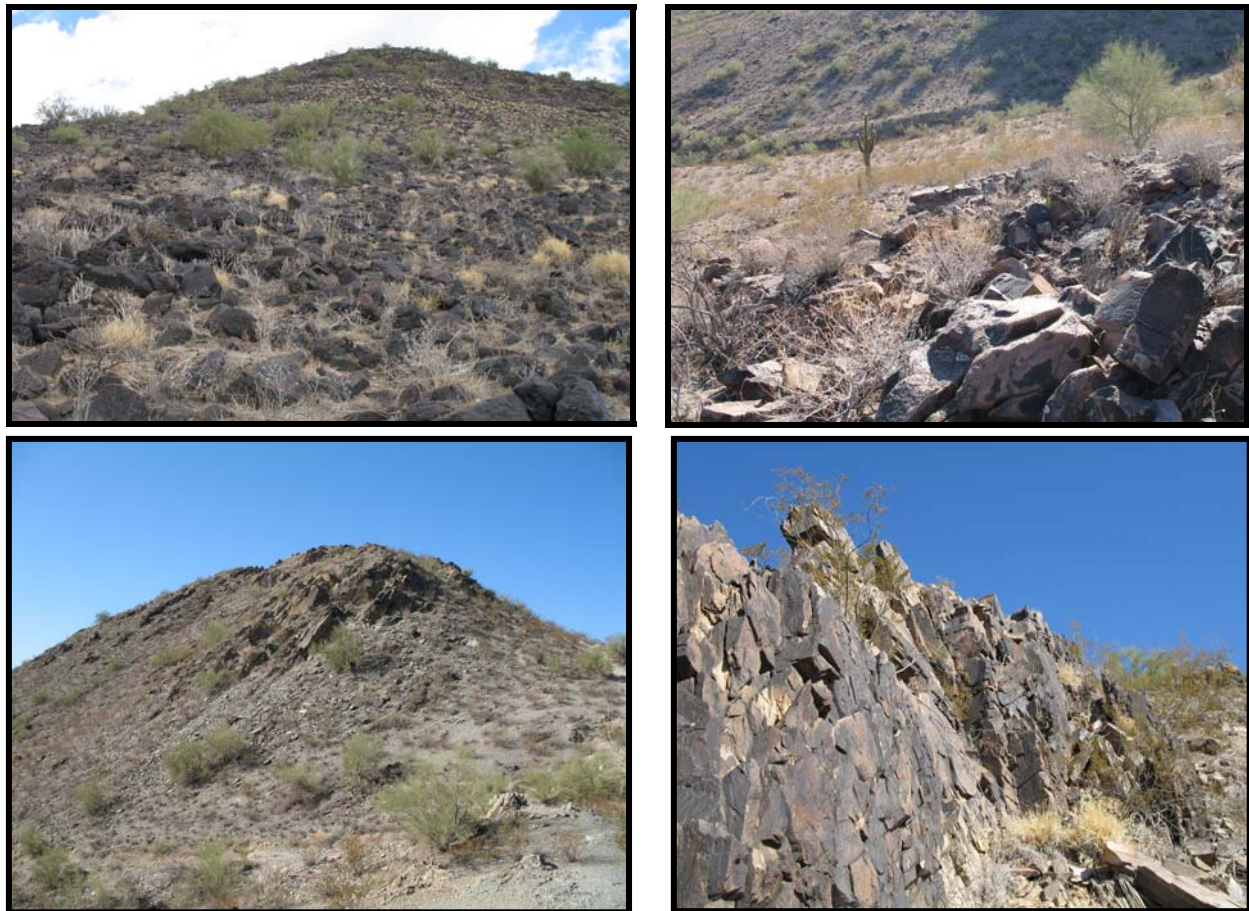

FIGURE 2. Geological formations of survey sites in the Phoenix metropolitan area. Basaltic boulder fields with few crevices typified both the Hedgpeth Hills (upper left) and Lookout Mountain (upper right) sites, correlated with low fecal counts. Metamorphosed sedimentary rock (schist) with abundant crevices, characterized both the Shadow Mountain (lower left) and Piestewa Peak (lower right) sites, correlated with high fecal counts (Photographed by Brian K. Sullivan).

relationship between plants and crevices, and abundance. The consistency in counts documented each year (see Sullivan and Sullivan 2008), regardless of whether observations were conducted during winter rains, dry fall periods, or after torrential summer storms, indicates that fecal counts are relatively invariant for a site in spite of seasonal differences in wind, rain, and temperature.

We used belt transects (1 m X 10 m) to assess crevice numbers, and plant diversity and abundance. Transect placement within each of the eight original study sites was based on presence of fecal droppings at a rock outcrop. We selected these transect placement points by entering each of the original eight study sites from downslope, and initiating a search for fecal droppings. The first outcrop with fecal droppings was used for the first set of transects. The fecal droppings served as the anchor for four (one in each cardinal direction) 1 m wide X 10 m long belt transects (40m^2 per transect survey site). After scoring each transect line for plants and crevices, we moved 10 m up slope from the initial transect site in a randomly selected line (one of three possible cardinal directions: e.g., NW, N or NE), and began searching until a second fecal dropping site was found. We scored the second set of transects, and then we selected a third transect site in a similar fashion to complete the transect surveys for plants and crevices. Because the original fecal count surveys had been time-based, we covered larger areas in low density sites or where rocky outcrops were farther apart. Thus, for smaller survey areas, or those with difficult access (e.g., steep cliff faces at Shadow Mountain), we used two sets of transects for plants and crevices (8 X 1 m X 10 m = 80 m^2 total survey area for two transect sites); for remaining sites (N = 6), we used three sets of transects (12 X 1 m X 10 m = 120 m^2). We conducted all surveys for plants and crevices in 2009 over a 12-week period from September to December.

At each transect survey site, we counted all large ("trunk" base > 10 mm) perennial plants along transects, with special attention to species known to represent preferred food sources of the Common Chuckwalla (Table 1; Kwiatkowski and Sullivan 2002b). We scored crevices as any space between two rocks deep enough

and wide enough to harbor a Common Chuckwalla of any size; however, if crevice width exceeded more than three body heights of a large Common Chuckwalla (i.e., approximately 75 mm), we excluded it unless it was very deep (> 250 mm) or narrowing in the interior, or both. Large gaps between rocks are rarely used by Common Chuckwallas taking refuge as they can be easily removed by predators given their inability to inflate and wedge themselves between the relatively widely separated rock surfaces (Lappin et al. 2006).

To assess the relationship between plant resources and population levels, we first calculated overall plant density on an area basis. We also determined the density of "favored plants" available along transects (i.e., near basking sites) by calculating "favored plant density" as the sum of the densities of the six plants most commonly consumed by Phoenix area Common Chuckwallas (Table 1).

Statistical methodology followed Hollander and Wolfe (1973) and Zar (1999); SPSS (version 16.0, SPSS for Windows, Rel. 16.0.2., 15 November 2007, Chicago: SPSS Inc.) was used for all calculations. We used a stepwise multiple linear regression to estimate the influence of three independent variables on average fecal count: crevice density (crevices per m^2), overall plant density (plants per m^2), and favored plant density (combined density of six plants favored by Common Chuckwallas as food [Table 1]; favored plants per m^2). Strictly speaking, assumptions of independence were violated for two of the independent variables (*a priori*, plant density and favored plant density would be expected to covary): examination of correlations among independent variables was undertaken to assess this potential violation. We calculated Spearman's rho correlations to assess relationships among independent variables, and in relation to fecal counts. For all tests, (α = 0.05)

RESULTS

Transects revealed striking differences in numbers of crevices and plants available across the eight sites (Tables 1 and 2). The sites dominated by basaltic

TABLE 2. Results of surveys at eight sites in the Phoenix Mountains, Hedgpeth Hills, and South Mountains. Densities (m^2) represent averages of 8–12 transects from each site for crevices, plants, and favored food plants. Plant diversity represents total species count, based on transects alone, for each site. Sites are Hedgpeth Hills (HH), Lookout Mountain (LM); North Mountain 1, 2, and 3 (NM1, NM2, and NM3); Piestewa Peak (PP); Shadow Mountain (ShM); South Mountains (SM).

Site	Fecal Count	Crevice Density	Plant Density	Favored Plant Density	Plant Diversity
HH	11	0.067	0.450	0	3
LM	8	0.067	0.650	0.025	5
NM1	4	0.075	0.733	0.017	5
NM2	8	0.067	0.517	0.017	5
NM3	23	0.400	0.775	0.088	5
PP	26	0.617	0.358	0.016	10
ShM	24	0.638	0.513	0.139	8
SM	42	0.208	0.992	0.116	12

FIGURE 3. Trails at both the Shadow Mountain (top) and the Lookout Mountain (bottom) sites run along ridge tops resulting in degradation of crevices and loss of favored food plants for Common Chuckwallas (Photographed by Brian K. Sullivan).

FIGURE 4. South Mountains survey site showing presence of three plants favored by Common Chuckwallas (upper panel; Wolfberry, Foothills Palo Verde and Ocotillo), and large expanse of granodiorite rock with abundant crevices (lower panel; Photographed by Brian K. Sullivan).

boulder fields (e.g., Lookout Mountain, Hedgpeth Hills) had the lowest crevice densities, while sites with metamorphosed sedimentary rock (i.e., Piestewa Peak and Shadow Mountain) had considerably higher crevice densities (Table 2). Trails along ridge tops were associated with significantly reduced crevice numbers at both basaltic and metamorphosed rock sites (Fig. 3).

Plant diversity was relatively low, ranging from a low of three species (five at a number of sites) to more than twelve species at the South Mountains (Table 2). Plant density was variable, and often influenced by large numbers of common plants (Brittlebush, Triangle-leaf Bursage) rarely consumed by Common Chuckwallas (Kwiatkowski and Sullivan 2002b). Favored plant density was high at the South Mountains site (Fig. 4), as predicted by Kwiatkowski and Sullivan (2002b), but even higher at the Shadow Mountain site, a survey area with relatively high fecal counts as well (Table 2).

Fecal count data from 1995 and 2008 were highly correlated ($r_s = 0.92$, df = 6, $P = 0.001$, N = 8 sites; Sullivan and Sullivan 2008); hence, total counts for those two years were averaged and used as the

dependent variable (proxy for population size) in a multiple regression. With respect to assumptions of normality, skewness, and kurtosis statistics were all non-significant (± 2 SE encompassed zero), and visual inspection of P–P and Q–Q plots substantiated approximately normal distributions for all independent variables and the dependent variable.

The hypothesis that abundance of crevice refuges correlates with Common Chuckwalla population size was not supported: crevice density was not significantly predictive of population size (Table 2). By contrast, the hypothesis that favored plant density (i.e., those plants favored in consumption by Common Chuckwallas) is associated with Common Chuckwalla population size was supported: favored plant density was the only significant (Fig. 5; $F_{1,6} = 6.20$, $R^2 = 51\%$, $P = 0.04$) independent variable entered in the stepwise regression analysis. Residuals were normally distributed, and in conjunction with prior assessment of normal distributions for all variables, indicated MLR was appropriate for this data set. Additionally, plant density
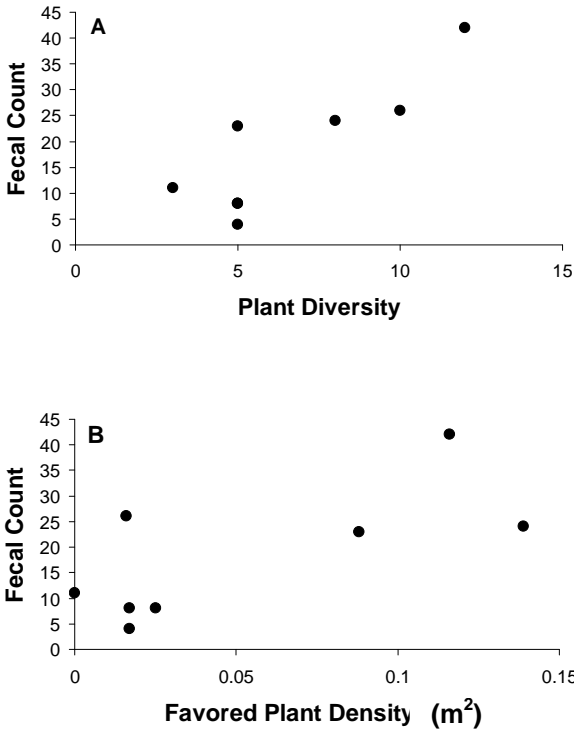
FIGURE 5. Scatter plot of fecal counts against overall plant diversity (A) and against favored plant density (B) for the survey sites.

FIGURE 6. Common Chuckwallas in a crevice at the Piestewa Peak site. Note extensive layering of parent rock material (metamorphosed sedimentary rock) predisposed to formation of crevices (Photographed by Rachel E. Williams).

and favored plant density were not correlated ($r_s = 0.58$, $P = 0.14$, N = 8), obviating concerns of multi-colinearity in the MLR.

Having concluded that favored plant density is a better predictor of population size than crevice density, we examined the influence of overall plant diversity at sites in relation to Common Chuckwalla population size. Although alteration of a MLR model *a posteriori* (i.e.,

after inspection of results obtained) is frowned upon by most, we note that a second MLR using the original target variables (crevice density, plant density, favored plant density) plus overall plant diversity (simple counts for sites; Table 2), provided a highly significant regression in which only overall plant diversity was entered (Fig. 5; $F_{1,6} = 17.33$, $R^2 = 74\%$, $P = 0.006$). Thus, these *post hoc* results suggest that overall plant diversity, no doubt indicative of sites containing the favored plants as well as other potential food plants, is the single most important variable of those we measured in predicting Common Chuckwalla abundance.

DISCUSSION

Alteration of natural landscapes due to urbanization is one of the most critical issues facing conservation biologists today. The Sonoran Desert of southwestern North America has been extensively developed over the past five decades, especially in the Phoenix Metropolitan area (Knowles-Yanez, K., C. Moritz, J. Fry, C.L. Redman, M. Bucchin, and P.H. McCartney. 1999. Historic Land Use: Phase I Report on Generalized Land Use. Central Arizona-Phoenix Long-Term Ecological Research (CAPLTER), Arizona State University, Tempe; Faeth et al. 2005; Sullivan et al., in press). Although other lizard species (e.g., *Dipsosaurus dorsalis, Gambelia wislizenii, Phyrnosoma solare*) appear to have been extirpated from preserves of the Phoenix Mountains (Sullivan and Flowers 1998), the Common Chuckwalla is still found in all preserves regardless of size. Our results document that this large lizard is persisting in even the smallest preserves that have been set aside within a sea of urbanization, and that their preferred food plants more so than crevice refuges may be critical to their continued presence. No doubt additional factors (e.g., abundance of non-native predators, variation in plant quality in relation to soil substrate, and level of recreational use by the local population) influence abundance of Common Chuckwallas in these preserves as well.

A number of studies suggest that squamates are negatively impacted by habitat alteration, even when preserves of natural habitat are set aside. For example, the lacertid lizard, *Psammodromus algirus*, is apparently more attuned to variation in habitat quality (aspects allowing for thermoregulation, foraging opportunities) than preserve size (Santos et al. 2008). Hence, it may decline as a result of human activity in even large preserves if specific components of habitat quality are degraded. Martin and Lopez (2002) also found that Mediterranean lizard communities were sensitive to habitat alteration associated with anthropogenic changes; lizard assemblages were negatively impacted by a reduction in ground cover. Goode et al. (2005) similarly suggested that destruction of crevice refuges might lead

to the decline of Common Chuckwallas in Phoenix area preserves. Surprisingly, our results could not confirm this hypothesis as crevices were not highly correlated with abundance of Common Chuckwallas in the preserves we surveyed. Nonetheless, it is important to note that our surveys did not directly test the impact of crevice reduction on population size in Common Chuckwallas.

MacNally and Brown (2001) and Sarre et al. (1995) found that lizards with specialized niches were more likely to decline with increasing fragmentation and urbanization. Similarly, Kitchener et al. (1980) found that diversity of habitats within preserves was associated with lizard diversity; presumably, increased habitat variation provides for a larger number of specialized forms to persist. Habitat structure rather than vegetational composition was also important for reptile species in yet another Australian study (Garden et al. 2007). All of these investigations (Kitchener et al. 1980; Sarre et al. 1995; MacNally and Brown 2001; Martin and Lopez 2002; Santos et al. 2008) suggest that microhabitat requirements are critical to the persistence of squamates in preserves. Our results offer long-term data to support this assertion: though the Common Chuckwalla might be classified as an extreme specialist with respect to habitat preference (Lappin et al. 2006), it continues to inhabit the Phoenix Mountains, due in part to the continued presence of critical food plant resources.

Common Chuckwallas may persist in even small preserves given the availability of appropriate microhabitats including both rock outcrops with sufficient crevices for refuges and plant species preferred as food. This may be a common occurrence for saxicolous squamates (Fischer et al. 2005): in some settings rocky areas may be the least likely area of a preserve to be affected by human activity. It may be that the more restricted microhabitat preferences of Common Chuckwallas allow them to persist while other large lizards of the Sonoran Desert inhabiting open areas have apparently declined (Sullivan and Flowers 1998) in these same preserves, perhaps in part due to a reduction in prey preferred by some of these species (e.g., native ants for horned lizards). The steep, rocky slopes of the Phoenix Mountains are often the last to be impacted by human recreational activities. If rock outcrops remain undisturbed, especially given the propensity of favored plants such as *Lycium* spp. and *Trixis* spp. to grow among rocks, Common Chuckwallas may have a better chance than more generalized lizards occupying open areas and lacking a unique escape behavior (Lappin et al. 2006) used in rocky microhabitats (Fig. 6). Unfortunately, trails are increasingly formed in new areas, especially along ridge tops, leading to degradation of rocks and a corresponding loss of vegetation. Crevices quickly deteriorate and fill with rubble, rendering them useless for the lizards as escape sites

(pers. obs.), and plants no longer grow among such degraded rock outcrops.

Why are Common Chuckwallas so common in the South Mountains?—The South Mountains have an extremely high density population of Common Chuckwallas, twenty times the estimated population size of Lookout Mountain (Sullivan and Flowers 1998). Our results reveal that diversity and abundance of food plants are in part associated with this large population estimate. Although crevice density was intermediate at the South Mountains relative to the other survey sites, it is the case that the South Mountains exhibit large rocky outcrops over a much larger area than all of the other preserves in the Phoenix area we surveyed. The large population size for the South Mountains no doubt derives from a combination of geological (extensive rocky areas with crevices) and ecological factors (density and diversity of available plant food species). The significance of the unique color pattern exhibited by Common Chuckwallas in the South Mountains (bright orange tail in males), though important in mate choice, remains enigmatic in regard to population size.

Additional study will be necessary to fully understand the factors influencing population size of Common Chuckwallas in the South Mountains and other Phoenix area preserves, especially as the preserves are increasingly affected by anthropogenic activities (hiking, biking, horseback riding). Monitoring also will be necessary to evaluate other possible impacts (e.g., lack of gene flow due to absence of corridors in the face of high density housing) of the structure of the Phoenix Mountain Preserves on these lizards. The large size of the South Mountain Preserve (larger than all the other sites we surveyed combined) will presumably buffer this population to greater extent than is possible for some of the smaller preserves we examined. As noted by Hawlena and Bouskila (2006), maintenance of intact habitat fragments with connectivity (corridors) is ideal, but not always obtainable for conservation of squamates in arid environments.

LITERATURE CITED

Amo, L., P. Lopez, and J. Martin. 2007a. Natural oak forest vs. ancient pine plantations: lizard microhabitat

use may explain the effects of ancient reforestations on distribution and conservation of Iberian lizards. Biodiversity and Conservation 16:3409–3422.

Amo, L., P. Lopez, and J. Martin. 2007b. Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards. Canadian Journal of Zoology 85:743–751.

Brown, D.E. (Ed.). 1982. Biotic Communities of the American Southwest, United States and Mexico. University of Arizona Press, Tucson, Arizona, USA.

Davidson, A.D., D.C. Lightfoot, and J.L. McIntrye. 2008. Engineering rodents create key habitat for lizards. Journal of Arid Environments 72:2142–2149.

Faeth, S.H., P.S. Warren, E. Shochat, and W. Marussich. 2005. Trophic dynamics in urban communities. Bioscience 55:399–407.

Fischer, J., D.B. Lindenmayer, S. Barry, and E. Flowers. 2005. Lizard distribution patterns in the Turmut fragmentation "Natural Experiment" in south-eastern Australia. Biological Conservation 123:301–315.

French, S.S., H.B. Fokidis, and M.C. Moore. 2008. Variation in stress and innate immunity in the Tree Lizard (*Urosaurus ornatus*) across an urban-rural gradient. Journal of Comparative Physiology B 178:997–1005.

Garden, J.G., C.A. McAlpine, H.P. Possingham, and D.N. Jones. 2007. Habitat structure is more important than vegetation composition for local-level management of native terrestrial reptile and small mammal species living in urban remnants: A case study from Brisbane. Austral Ecology 32:669–685.

Goode, M.J., W.C. Horrace, M.J. Sredl, and J.M. Howland. 2005. Habitat destruction by collectors associated with decreased abundance of rock-dwelling lizards. Biological Conservation 125:47–54.

Hawlena, D., and A. Bouskila. 2006. Land management practices for combating desertification cause species replacement of desert lizards. Journal of Applied Ecology 43:701–709.

Hollander, M., and D.A. Wolfe. 1973. Nonparametric Statistical Methods. John Wiley and Sons, New York, New York, USA.

Kitchner, D.J., A. Chapman, J. Dell, and B.G. Muir. 1980. Lizard assemblage and reserve size and structure in the western Australian wheatbelt—some implications for conservation. Biological Conservation 17:25–62.

Koenig, J., R. Shine, and G. Shea. 2001. The ecology of an Australian reptile icon: how do Blue-tongued Lizards (*Tiliqua scincoides*) survive in suburbia? Wildlife Research 28:215–227.

Kwiatkowski, M.A., and B.K. Sullivan. 2002a. Geographic variation in sexual selection among populations of an iguanid lizard, *Sauromalus obesus* (= *ater*). Evolution 56:2039–2051.

Kwiatkowski, M.A., and B.K. Sullivan. 2002b. Mating system structure and population density in a polygynous lizard, *Sauromalus obesus* (= *ater*). Behavioral Ecology 13:201–208.

Kwiatkowski, M.A., G.W. Schuett, R.A. Repp, E.M. Nowak, and B.K. Sullivan. 2008. Does urbanization influence the spatial ecology of Gila Monsters in the Sonoran Desert? Journal of Zoology 276:350–357.

Lappin, K.R., P.S. Hamilton, and B.K. Sullivan. 2006. Bite-force performance and head shape in a sexually dimorphic crevice dwelling lizard, the Common Chuckwalla (*Sauromalus ater* [=*obesus*]). Biological Journal of the Linnean Society 88:215–222.

Lettink, M., G. Norbury, A. Cree, P.J. Seddon, R.P. Duncan, and C.J. Schwarz. 2010. Removal of introduced predators, but not artificial refuge supplementation, increases skink survival in coastal duneland. Biological Conservation 143:72–77.

MacNally, R., and G.W. Brown. 2001. Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: predictions, compositional change and faunal nestedness. Oecologia 128:116–125.

Martin, J., and P. Lopez. 2002. The effect of Mediterranean dehesa management on lizard distribution and conservation. Biological Conservation 108:213–219.

Santos, T., J.A. Diaz, J. Perez-Tris, R. Carbonell, and J.L. Telleria. 2008. Habitat quality predicts the distribution of a lizard in fragmented woodlands better than habitat fragmentation. Animal Conservation 11:46–56.

Sarre, S., G.T. Smith, and J.A. Meyers. 1995. Persistence of two species of gecko (*Oedura reticulata* and *Gehyra variegata*) in remnant habitat. Biological Conservation 71:25–33.

Smith, H.M. 1946. Handbook of Lizards: Lizards of the United States and of Canada. Comstock Publishing Company, Ithaca, New York, USA.

Sullivan, B.K. 2000. Long-term shifts in snake populations: a California site revisited. Biological Conservation 94:321–325.

Sullivan, B.K., and M. Flowers. 1998. Large iguanid lizards of urban mountain preserves in northern Phoenix, Arizona. Herpetological Natural History 6:13–22.

Sullivan, B.K., and K.O. Sullivan. 2008. Common Chuckwalla (*Sauromalus ater*) populations in the Phoenix Metropolitan area: stability in urban preserves. Herpetological Conservation and Biology 3:149–154.

Sullivan, B.K., M.A. Kwiatkowski, and G.W. Schuett. 2004a. Translocation of urban Gila Monsters: a problematic conservation tool. Biological Conservation 117:235–242.

Sullivan, B.K., M.A. Kwiatkowski, and P.S. Hamilton. 2004b. Growth in Sonoran Desert populations of the Common Chuckwalla (*Sauromalus obesus*). Western North American Naturalist 64:137–140.

Sullivan, B.K., D.R. van Haverbeke, and C. Chambers. In press. Wildlife and Anthropogenic Changes in the Arid Southwest. *In* Design with the Desert. Malloy, R. (Ed.). University of Arizona Press, Tucson, Arizona, USA.

Zar, J.H. 1999. Biostatistical Analysis. 4th Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

ERRATUM CORRECTED 3 MAY 2010: Page 107 the words preferred and overall were transposed in Figure 5.

BRIAN K. SULLIVAN is a Professor of Evolutionary Biology and Herpetology at Arizona State University. His research interests are focused on the evolutionary biology of vertebrates, including behavior, ecology, conservation, and systematics of amphibians and reptiles of arid regions, especially the southwestern United States. He has published over 100 articles, book reviews, technical reports, and book chapters. (Photographed by Robert Bowker)

RACHEL E. WILLIAMS conducted the research reported herein while attending the Polytechnic campus of Arizona State University, but has since graduated with a Bachelors degree in Wildlife and Restoration Ecology. While attending Arizona State she participated in a variety of wildlife nutrition studies on large ungulates and was a member of the Range Plant Identification Team. She has varied interests and has worked with a variety of threatened and endangered species throughout Arizona including the Mexican Gray Wolf (*Canis lupus baileyi*), the Chiricahua Leopard Frog (*Rana chiricahuensis*), the Razorback Sucker (*Xyrauchen texanus*), and the Southwestern Willow Flycatcher (*Empidonax traillii extimus*). She is currently working as a Wildlife Technician for Vernadero Group Incorporated in Phoenix, Arizona.

APPENDIX 1. Precise locations of survey sites. All measurements are UTM (12S; NAD CONUS 1927). Hedgpeth Hills (=HH): sample 1: 391967 E, 3726116 N; sample 2: 382031 E, 3726254 N; sample 3: 391985 E, 3726264 N; Lookout Mountain (= LO): sample 1: 402309 E, 3720868 N; sample 2: 402277 E, 3720999 N; sample 3: 402184 E, 3721068 N; North Mountain # 1 (= NM#1): sample 1: 399502 E, 3718275 N; sample 2: 399516 E, 3718225 N; sample 3: 399496 E, 3718164 N; North Mountain # 2 (= NM#2): sample 1: 400717 E, 3718125 N; sample 2: 400747 E, 3718145 N; sample 3: 400766 E, 3718118 N; North Mountain # 3 (= NM#3): sample 1: 398622 E, 3717426 N; sample 2: 398582 E, 3717470 N; Piestewa Peak (= PP): sample 1: 406220 E, 3710672 N; sample 2: 406238 E, 3710704 N; sample 3: 406244 E, 3710715 N; Shadow Mountain (= ShM): sample 1: 404574 E, 3719056 N; sample 2: 404564 E, 3719082 N; South Mountain (= SM): sample 1: 402731 E, 3689600 N; sample 2: 402723 E, 3689321 N; sample 3: 402649 E, 3689375 N.