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Anuran Habitat Associations in the Northern Chihuahuan Desert, USA

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ABSTRACT.—Understanding amphibian habitat associations allows us to assess the impacts of environmental change on amphibian populations. We studied the habitat associations of five anurans in the Chihuahuan Desert of southern New Mexico, USA. We used amphibian call surveys at 36 ephemeral water bodies and recorded an index of abundance for each species. We used GIS to identify vegetation communities (e.g., creosote bush, grassland, mesquite) within a buffer zone around each water site. We used ordinal logistic regression, Akaike's information criterion (AIC_c), and canonical correspondence analysis to elucidate relationships between an index of anuran abundance and habitat variables. Creosote bush, mesquite, and grasses dominate the landscape in our study region. We detected *Anaxyrus debilis* (Green Toad) and *Spea multiplicata* (New Mexico Spadefoot Toad) most frequently (>70% of water bodies observed). *Anaxyrus cognatus* (Great Plains Toad), *Scaphiopus couchii* (Couch's Spadefoot Toad), and *Spea bombifrons* (Plains Spadefoot Toad) were detected at about half of water bodies studied. *Anaxyrus cognatus*, *Spea bombifrons*, and *Sp. multiplicata* tended to co-occur at breeding sites. *Anaxyrus cognatus* and *Sp. bombifrons* were more common in mesquite habitat. Succulent desert scrub, though not common, seemed to affect *Sc. couchii* positively and *A. debilis* negatively. *Spea multiplicata* was more generalistic and did not show strong habitat associations. We did not find evidence that shrub encroachment has had negative impacts on the amphibian community in our study system and may even have had positive effects on anurans, especially *A. cognatus* and *Sp. bombifrons*.

Global amphibian population declines caused by anthropogenic factors like habitat degradation, invasive species, and climate change (Green, 1997; Gallant et al., 2007; Lacoul et al., 2011) have led to amphibians being used as indicator species for environmental change (Allentoft and O'Brien, 2010). Desert amphibians might be particularly vulnerable to population declines because of the ephemeral nature of their breeding sites and precipitation, which is predicted to become more variable (Sheppard et al., 2002; Lenart et al., 2007; Archer and Predick, 2008). Desert amphibians are only active during a short period of time each year and are largely nocturnal (Creusere and Whitford, 1976). Thus, little is known about them and they are seldom used as a response variable to ecosystem change. Right after rain, desert anurans come out of their burrows, call, and then mate in newly filled puddles and ponds (Chan and Zamudio, 2009; Griffis-Kyle et al., 2011). Explosive breeding in desert anurans is typically completed within a few days after rain (Degenhardt et al., 1996; Griffis-Kyle et al., 2011) and often lasts only a single night (Woodward, 1984; Sullivan, 1989).

Many arid and semiarid grasslands, as found in the southwest of the United States (New Mexico, Arizona, Texas), have been converted to shrublands because of shrub encroachment (Van Auken, 2000; Reynolds and Stafford Smith, 2002). The northern Chihuahuan Desert in southern New Mexico has seen significant increases in honey mesquite (*Prosopis glandulosa*) and creosote bush (*Larrea tridentata*) replacing native black grama grass (*Bouteloua eriopoda*) over the last century (Buffington and Herbel, 1965; Brown and Archer, 1999). Habitat dominated by mesquite in this part of the Chihuahuan Desert was less than 25% in the 1930s but increased and stabilized at 43% by the 1970s (Goslee et al., 2003). The increasing abundance of woody shrubs in desert grasslands has led to loss of herbaceous forage and increased soil erosion (Glover and Musick, 1990) as well as a decrease in vegetation cover (Turnbull et al., 2010) and plant diversity (Baez and Collins, 2008). Shrubland interactions between soil and vegetation result in water and nutrients accumulating under shrubs while

leaving the larger interspaces barren (Huxman et al., 2005; Peters et al., 2010).

Shrub encroachment also affects desert fauna. For example, increased shrub cover is linked to increased rates of nest predation of desert birds (Mason et al., 2005) and decreased occurrence of the White-sided Jackrabbit, *Lepus callotis* (Desmond, 2004), causing a reorganization of the ecosystem. However, terrestrial habitat associations of desert amphibians are poorly understood (but see Dayton and Fitzgerald, 2006) and, thus, we can only speculate how this change in habitat has impacted anurans in the Chihuahuan Desert. Information on how anurans are associated with various habitats is critical for understanding how habitat changes might impact amphibian communities and potentially contribute to amphibian declines (Alford and Richards, 1999; Stuart et al., 2004).

The purpose of this study was to examine relationships between Chihuahuan Desert anurans and terrestrial habitat. We will infer how past change in the Chihuahuan Desert (from grassland to shrubland) might have impacted the anuran community in that area or how future habitat change might affect certain anuran species. Anurans in the Chihuahuan Desert are classified as "grassland" or "shrubland" species (Degenhardt et al., 1996), but more-subtle differences in habitat preference have not fully been explored. We examined how the Great Plains Toad (*Anaxyrus cognatus*), Green Toad (*Anaxyrus debilis*), Couch's Spadefoot Toad (*Scaphiopus couchii*), Plains Spadefoot (*Spea bombifrons*), and New Mexico Spadefoot Toad (*Spea multiplicata*) related to six habitat classifications (creosote bush, grassland, mesquite, desert pavement, playa, and succulent desert scrub) in the area around the breeding sites. We hypothesized that the composition of the terrestrial habitat will influence species composition and abundance at breeding pools.

MATERIALS AND METHODS

Study Area and Species.—We surveyed several areas in Doña Ana County, southern New Mexico for amphibian breeding choruses. All areas were close to Las Cruces, a town with approximately 100,000 inhabitants. Survey areas included land

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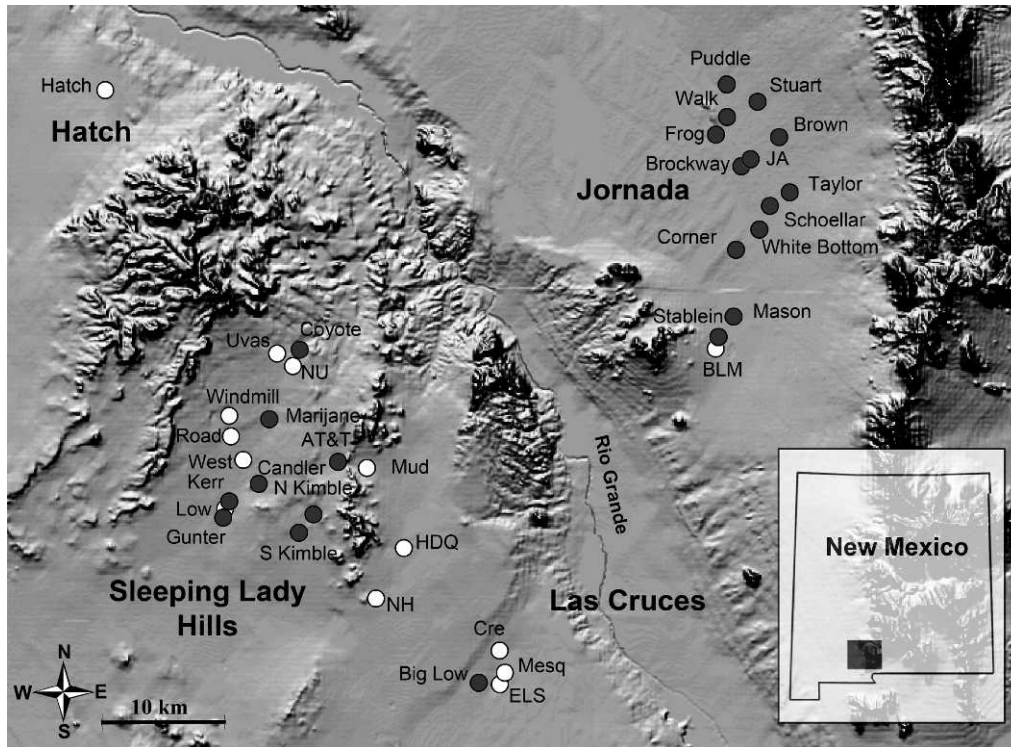


FIG. 1. Map of study area. Sampling sites where toads were calling are marked as circles. White circles are natural ephemeral playa lakes and gray circles are earthen stock tanks (built for livestock). Las Cruces is a city and Jornada, Sleeping Lady Hills, and Hatch refer to our three regional field locations.

managed by the Jornada Long Term Ecological Research Site north-east of Las Cruces (Jornada), Bureau of Land Management (BLM) rangeland in and south of the Sleeping Lady Hills (north-west and west of Las Cruces), and areas close to Hatch, New Mexico ($32^{\circ}9' - 32^{\circ}39'N$, $106^{\circ}38' - 107^{\circ}9'W$; Fig. 1). We refer to our three survey areas of Jornada, Sleeping Lady Hills, and Hatch as “regional field locations” hereafter. Rainfall was higher than average during our study (average cumulative yearly rainfall for all rain gauges at the Jornada Long Term Ecological Center was 41.1 cm for 2006 compared to the yearly average of 24.8 cm).

We located potential anuran breeding sites using the BLM’s GIS database 7.5-minute topographic maps and by querying the Southwest Regional Gap Analysis Project (SWReGAP) habitat layer for playa lake habitats in ArcGIS 9.1. Sites fell into two distinct categories; natural playa lakes, often with some degree of modification to hold water for a longer period of time (14 sites), and cattle tanks constructed to collect and hold water for livestock (earthen stock tanks, 22 sites). There was no difference in number of toads occurring or total strength of calling between playas and stock tanks (t -test; $P > 0.25$), so breeding sites were pooled and analyzed together.

We selected 36 breeding sites according to accessibility (some dirt roads become impossible to navigate during monsoon season) and whether or not they filled with water (only the ones with water were included and ranged from 1.4–2.5 m maximum water depth). Hydroperiod of breeding sites is extremely variable and ranges from a few days to several months depending on rain patterns. Desert anurans may call from larger ponds, roadside ditches, or drying mud puddles (Degenhardt et al., 1996; Griffis-Kyle, pers. obs.).

After monsoon rains, five anurans can be detected in the lowlands of our study region including two species of *Anaxyrus*

(*A. cognatus* and *A. debilis*) and three Spadefoot Toads (*Scaphiopus couchii*, *Sp. bombifrons*, and *Sp. multiplicata*). They can remain dormant in burrows for several years when rainfall is insufficient. Mating occurs opportunistically after summer rain events at high densities during short time-periods at night (Degenhardt et al., 1996). *Anaxyrus cognatus* is the largest anuran in the study region and females can reach up to 112 mm snout-vent length (SVL). Males start calling from breeding sites shortly after sunset and larval period ranges from 18 to 49 days (Degenhardt et al., 1996). With an average female SVL of 36.5 mm, *A. debilis* is the smallest anuran in the study region (Degenhardt et al., 1996). Though records are sparse, larval development is presumably around 25 days (Degenhardt et al., 1996). *Scaphiopus couchii* adults are, on average, larger than the other two Spadefoots, reaching up to 90 mm SVL. Among North American anurans, these tadpoles are the most rapid in their development. Eggs hatch within 15 h at temperatures of $30^{\circ}C$ and metamorphosis occurs in as few as 8 day at an SVL of only 15–20 mm (Justus et al., 1977; Newman, 1988; Degenhardt et al., 1996). *Spea bombifrons* eggs can hatch within 20 h (Justus et al., 1977) and time to metamorphosis can be as short as 13 days (King, 1960), wherein the larger carnivorous morph develops faster than the smaller omnivorous morph (Pfennig et al., 1991). *Spea multiplicata* undergo metamorphosis in approximately 3 weeks (Degenhardt et al., 1996).

Call Surveys.—Study participants were trained in early 2006 to recognize the mating calls of southern New Mexico anuran species. Participants had to first learn the calls from recordings and identify pictures in the laboratory before conducting surveys in the field. Amphibian call surveys began with the onset of heavy monsoon rains 29 June 2006 and the last survey was conducted on 6 August, after which rains subsided. Rain in the Chihuahuan Desert is patchy, and it is critical to survey

newly filled ponds the first night after the rain when detection is highest (Woodward, 1984; Harings, 2012). Every night we used weather maps that predicted local rainfall and focused our surveys on those regional field locations to look for newly filled ponds.

We searched for new breeding sites and started surveys after 2200 h and continued as late as 0400 h the next morning (the sun sets between 2010 and 2025 h in July). We calculated “minutes after dark” when our survey was conducted by assigning complete darkness to 2100 h. We then ran regression analyses (linear, logarithmic, and 2nd-order polynomial) between minutes after dark and call intensity of each anuran species. No difference in the intensity of calls was noticed based on time of night within our time period when surveys were conducted ($r^2 < 0.09$; $P > 0.07$ in all cases). We used the amphibian call index used by the United States Geological Survey (USGS) in the North American Amphibian Monitoring Program (NAAMP) (USGS, 2005) whereby an index of 0 indicates no individuals calling, 1 is a few individuals calling, 2 is overlapping calls, and 3 indicates a full chorus. At each location we stood approximately 50 m from the water body and waited for 3 min before beginning the 3-min survey and recording amphibian call indices for each species calling.

Nightly routes included all potential breeding sites for any particular regional field location (Jornada, Sleeping Lady Hills, and Hatch). In most cases precipitation occurred exclusively in one or another area, allowing us to survey each regional field location at almost every precipitation event. Half the sites were revisited once or twice within 5 nights of water accumulation, and the highest call indices for each species during that time period were used for analyses. Occupancy modeling suggested that our method had a 75% chance of detecting the species on a given visit at sites where it occurred (Harings, 2012).

Vegetation Classifications.—We used Feature Analyst 4.1 (Visual Learning Systems, Inc., 2006) to classify Visible and Near-Infrared (VNIR) data—imagery (15-m spatial resolution) from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER). Feature Analyst (FA) uses both spatial context and spectral variables in an object-based classification process. The user supplies initial training data to the software which then applies a machine learning algorithm to classify remaining data. Unlike other classification approaches, FA is user intensive and output can be further refined in an iterative manner, where the user identifies incorrectly classified objects and may add more training data (Visual Learning Systems, Inc., 2006). This method compares favorably with the results from other classification technologies (Vanderzanden and Morrison, 2002). The images were cropped to the boundaries of the three regional field locations and areas classified into twelve habitat categories. The categories were subsequently combined to form six cover classifications based on structure. The combined classifications were creosote bush, grassland, desert pavement, mesquite, playa, and succulent desert scrub.

We followed the descriptions from NatureServe (2004) for all habitat classifications. The habitat type “creosote bush” is defined as “Chihuahuan creosote bush, mixed desert, and thorn scrub,” mainly represented by creosote bush (*Larrea tridentate*) (NatureServe, 2004). “Grassland” habitat consists of “Apacherian–Chihuahuan piedmont semi-desert grassland and steppe,” the “inter-mountain basins semi-desert shrub steppe,” “Chihuahuan–Sonoran desert bottomland and swale grassland,” and “Chihuahuan sandy plains semi-desert grassland” represented

TABLE 1. Models used in the ordinal logistic regression evaluated with information-theory criteria (AIC_c).

Models
playa
mesquite
creosote bush
succulent desert scrub
grassland
desert pavement
mesquite + creosote bush
mesquite + succulent desert scrub
creosote bush + succulent desert scrub
mesquite + creosote bush + succulent desert scrub

by various grass and dwarf-shrub species. “Desert pavement” is largely unvegetated areas which can be populated by ephemeral herbaceous species after precipitation events. “Mesquite” consists of “Apacherian–Chihuahuan mesquite upland shrub” dominated by honey mesquite *Prosopis glandulos* and velvet mesquite *Prosopis velutina* with typically barren spaces between shrubs. “Playa” is “open water” or “North American arid west emergent marsh.” “Succulent desert scrub” habitat is defined by “Chihuahuan succulent desert scrub” such as agave (*Agave lechuguilla*) and banana yucca (*Yucca baccata*) as well as “inter-mountain basins and Chihuahuan mixed salt desert scrub” represented by saltbushes (*Atriplex* spp.) (NatureServe, 2004).

The classification maps were then queried by creating a 712-m buffer around each potential breeding site, and the area for habitat types within each buffer was tabulated. Buffer zones were defined from a central point within the playa or tank with a 712-m radius. We used 712-m buffer zones based on the average distance plus 1 standard deviation (712 m) traveled by the Great Plains Toad individuals from a release point to overwintering grounds (Ewert, 1969). Our assumption was that anurans migrate to the closest pond and that the buffer zone represents the habitat they chose in which to burrow and spend the rest of the year. Travel data was not available for other smaller species in the study. We calculated percentage habitat for the six classes in the buffer zone for each water body.

Because the buffer zones of some sites overlapped, we used a cluster analysis to identify sites with similar buffer zone habitat ratios. We eliminated three water bodies (Low, Brockway, ELS; see Fig. 1) that had overlapping buffer zones from the analysis and where the normative average distance between their buffer zones’ habitat ratios was < 0.20 . This reduced our data to 33 breeding sites.

Statistical Analysis.—We calculated associations among habitat types as well as associations among species using Spearman’s rank correlation coefficients (SPSS version 20). We used information theory and ordinal logistic regressions with model-averaged parameter estimates (Venables and Ripley, 2002; Mazerolle, 2012; R Development Core Team, 2012) to assess the relationships between habitat categories surrounding the breeding sites and call indices at the breeding sites as well as anuran species richness (number of anuran species occurring at a breeding site). We analyzed 10 models created to assess terrestrial habitat from the NatureServe (2004) classifications (Table 1). We excluded the variables of pavement and playa from higher-order models because very few data points ($< 30\%$) actually had areas of pavement or additional playa within the 712-m radius. Grassland was negatively correlated with

TABLE 2. Average percentages of habitat categories with standard deviation (SD) and range combined in the 712-m buffer zones of 36 ephemeral water bodies.

	Creosote bush	Grassland	Mesquite	Desert pavement	Playa	Succulent desert scrub
Average \pm 1 SD (%)	35.66 \pm 21.5	32.73 \pm 26.9	28.43 \pm 33.1	1.36 \pm 2.9	0.36 \pm 0.9	1.46 \pm 2.1
Range (%)	1.5–71.8	0.9–80.3	0–94.8	0–13.6	0–4.9	0–7.5

TABLE 3. Percentage of the 36 ephemeral water bodies (playas and stock tanks) visited where anuran calls were heard and average call index.

	<i>A. cognatus</i>	<i>A. debilis</i>	<i>Sc. couchii</i>	<i>Sp. bombifrons</i>	<i>Sp. multiplicata</i>
Detection	53%	81%	53%	47%	72%
Mean call index	2.37	2.52	1.89	1.94	2.42

mesquite (Spearman rank correlation = -0.71) and was also removed from higher-order models to reduce multicollinearity.

We also used canonical correspondence analysis (CCA) to relate species richness and individual toad calling indices to habitat. CCA relates patterns in community composition to variations in the environment and is a robust, nonlinear, constrained ordination method (ter Braak and Šmilauer, 1998). The order in which habitat explanatory variables were included was determined by stepwise forward selection (999 Monte Carlo permutations).

RESULTS

In the 712-m buffer zone around the breeding sites, the variability of habitat classes was large. On average the percentage of creosote bush, grassland, and mesquite classes was fairly large while the percentage of desert pavement, playa, and succulent desert scrub was small (Table 2). Areas with large amounts of mesquite cover tended to have little coverage of grass, creosote bush, and desert pavement and vice versa (in all cases Spearman's rank correlations >0.56 , $P < 0.001$).

Anaxyrus debilis was the most frequently detected toad and occurred in 29 of 36 breeding sites, followed by *Sp. multiplicata* which was found in 26 locations. *Anaxyrus cognatus* and *Sc. couchii* were present in 19 water bodies and *Sp. bombifrons* was present in 17 tanks or playas (Table 3). When present, *A. cognatus*, *A. debilis*, and *Sp. multiplicata* were typically abundant as estimated by average call index. *Sp. bombifrons* and *Sc. couchii* tended to be present in low numbers at the breeding sites

(Table 3). Additionally, *A. cognatus*, *Sp. multiplicata*, and *Sp. bombifrons* tended to co-occur with each other (in all cases Spearman's rank correlations >0.45 , $P < 0.004$).

Using ordinal logistic regression and evaluating models with AIC_c , we found all species and overall anuran species richness associated with mesquite in at least one of the models, with a delta AIC_c less than 2 (Table 4). When examining model average parameter estimates and unconditional confidence intervals (CI), *A. cognatus*, *Sp. bombifrons*, and anuran species richness were positively affiliated with mesquite and *A. cognatus* was negatively associated with grassland. *Anaxyrus debilis* and *Sp. bombifrons* were both negatively associated with succulent desert scrub (Table 5). All CIs on parameter estimates for *Sc. couchii* and *Sp. multiplicata* included or overlapped zero (Table 5).

The canonical correspondence analysis explained 89.2% of the variation in the species–environment relationships with the first two axes and 100% of the variation by the fourth axis (eigenvalues axis 1 = 0.069, axis 2 = 0.057, axis 3 = 0.012, axis 4 = 0.003). Concurrent with the ordinal logistic regression and information-theory analyses, canonical correspondence analysis revealed that mesquite ($P = 0.002$) and succulent desert scrub ($P = 0.033$) explained 10% of the variation in individual species abundances (Fig. 2). *Anaxyrus cognatus* and *Sp. bombifrons* were associated with abundant cover of mesquite and were less common when grass dominated the landscape (Fig. 2). *Scaphiopus couchii* associated positively with succulent desert scrub and negatively with creosote bush while *A. debilis* was

TABLE 4. Results from AIC_c analysis of ordinal logistic regression for those models with a delta $AIC_c < 2.0$. Parenthetical signs following variable names indicate the direction effect; LL = log likelihood.

Species	Model	ΔAIC_c	Model weight	–LL
<i>A. cognatus</i>	mesquite (+)	0.0	0.47	32.1
	mesquite (+) + creosote	1.3	0.24	31.6
<i>A. debilis</i>	succulent (–)	0.0	0.40	34.3
	mesquite + succulent (–)	1.4	0.19	33.9
<i>Sc. couchii</i>	creosote + succulent	0.0	0.37	36.8
	mesquite + creosote + succulent	1.8	0.15	36.6
<i>Sp. bombifrons</i>	mesquite (+) + succulent (–)	0.0	0.62	33.8
	mesquite (+) + creosote + succulent (–)	1.5	0.30	33.5
<i>Sp. multiplicata</i>	mesquite	0.0	0.21	37.5
	grassland	0.2	0.19	37.6
	mesquite + succulent	1.1	0.12	36.9
	playa	1.7	0.09	38.3
	mesquite + creosote	1.9	0.08	37.3
Species richness	mesquite (+)	0.0	0.37	50.4
	mesquite (+) + succulent	0.7	0.26	49.7

TABLE 5. Model-averaged parameter estimates and unconditional confidence intervals (CI) in parentheses on the estimates for candidate models. For numbers in bold, CIs do not overlap zero.

	Creosote bush	Grassland	Mesquite	Desert pavement	Playa	Succulent desert scrub
<i>A. cognatus</i>	0.02 (-0.02, 0.06)	-0.05 (-0.08, -0.02)	0.05 (0.02, 0.08)	-0.2 (-0.5, 0.07)	-0.3 (-1.1, 0.5)	0.01 (-0.4, 0.4)
<i>A. debilis</i>	0.01 (-0.03, 0.05)	0 (-0.02, 0.02)	0.01 (-0.01, 0.04)	0.01 (-0.2, 0.2)	-0.3 (-0.9, 0.2)	-0.4 (-0.8, -0.06)
<i>Sc. couchii</i>	-0.04 (-0.07, 0)	-0.01 (-0.04, 0.01)	0.02 (-0.01, 0.04)	-0.2 (-0.4, 0.1)	-0.5 (-1.4, 0.5)	0.4 (-0.02, 0.7)
<i>Sp. bombifrons</i>	0.02 (-0.03, 0.06)	-0.03 (-0.05, 0)	0.04 (0.01, 0.07)	0.1 (-0.1, 0.3)	-0.6 (-1.6, 0.5)	-0.5 (-1.0, -0.1)
<i>Sp. multiplicata</i>	0 (-0.04, 0.04)	-0.02 (-0.04, 0.01)	0.02 (-0.01, 0.04)	0.02 (-0.2, 0.3)	-0.2 (-0.8, 0.3)	-0.1 (-0.5, 0.2)
Species richness	0.02 (-0.04, 0.04)	-0.02 (-0.05, 0)	0.03 (0.01, 0.05)	-0.07 (-0.3, 0.1)	-0.3 (-0.9, 0.3)	-0.2 (-0.5, 0.1)

negatively influenced by succulent desert scrub (Fig. 2). *Spea multiplicata* is located close to the middle of the graph and thus not strongly influenced by the surrounding habitat (Fig. 2).

DISCUSSION

Overall our results suggest that shrubs, in particular mesquite, are likely an important habitat component for desert anurans, as the abundance index of all species were associated positively with mesquite, especially for *A. cognatus* and *Sp. bombifrons* and overall anuran species richness. Several factors may account for this pattern including mesquite's ability to provide shelter, modify surface moisture and temperature, and the abundance of food resources within this habitat. High numbers of small mammal burrows are associated with mesquite mounds and the roots of mesquite function to prevent collapse of such burrows (Roberts and Packard, 1973), potentially benefiting anurans. And while the Spadefoots are all capable of digging their own burrows (Degenhardt et al., 1996), Wright and Wright (1949) described a *Sc. couchii* individual withdraw into a packrat burrow and Hammerson (1982) reported *Sp. bombifrons* taking advantage of gopher (Geomysidae) and ground squirrel (Sciuridae) burrows. In arid environments, shrubs may increase soil surface moisture through hydraulic lift of water from deeper soil levels (Richards and Caldwell, 1987), providing more humidity in the burrows which is likely beneficial to amphibians. However, as vegetation type and soil composition are often tightly linked (Yang and Lowe, 1956; Monger and Bestelmeyer, 2006), we cannot rule out the possibility that the mesquite association with anuran presence at breeding sites is instead because of differences in soil type.

Succulent desert scrub was the second habitat variable that significantly entered our ordination and was also identified by our information-theoretic approach. *Anaxyrus debilis* and *Sp. bombifrons* were associated negatively with this habitat component (Table 4) as others have found (Dayton et al., 2004). Succulent desert scrub was a very small proportion of the landscape (<8% of the landcover) and the associations that we identified with these species are probably indirect. It is more likely that amphibians are responding to a common landscape attribute such as soils or predators associated with succulent desert scrub.

We found that *A. cognatus*, *Sp. multiplicata*, and *Sp. bombifrons* were often associated with each other. This result is in contrast to the findings of Dayton and Fitzgerald (2001), where only a single desert anuran was found breeding in 88% of the water bodies assessed, and *Sc. couchii* was suggested to be the superior competitor. In our study, 86% (31 breeding sites) were occupied by more than one species, and we did not find any evidence for competition for breeding sites among desert anurans (no significant negative correlations between any of the anurans). The breeding sites surveyed by Dayton and Fitzgerald (2001) in south-central Texas where "[p]ools often dry before metamorphosis occurs (Newman, 1994; GHD, unpubl. data)" may have shorter hydroperiods than did our sites.

Other work suggests that desert amphibian populations respond to breeding sites at scales much larger than traditionally expected in more mesic environments, potentially diluting habitat effects directly around breeding sites (Bradford et al., 2003; Griffis-Kyle et al., 2011). Consequently, desert amphibians may move relatively large distances (several kilometers) to access breeding sites with available water. Additionally, anurans might migrate among water bodies during one season. Krupa (1994) observed groups of male Great Plains Toads in Oklahoma

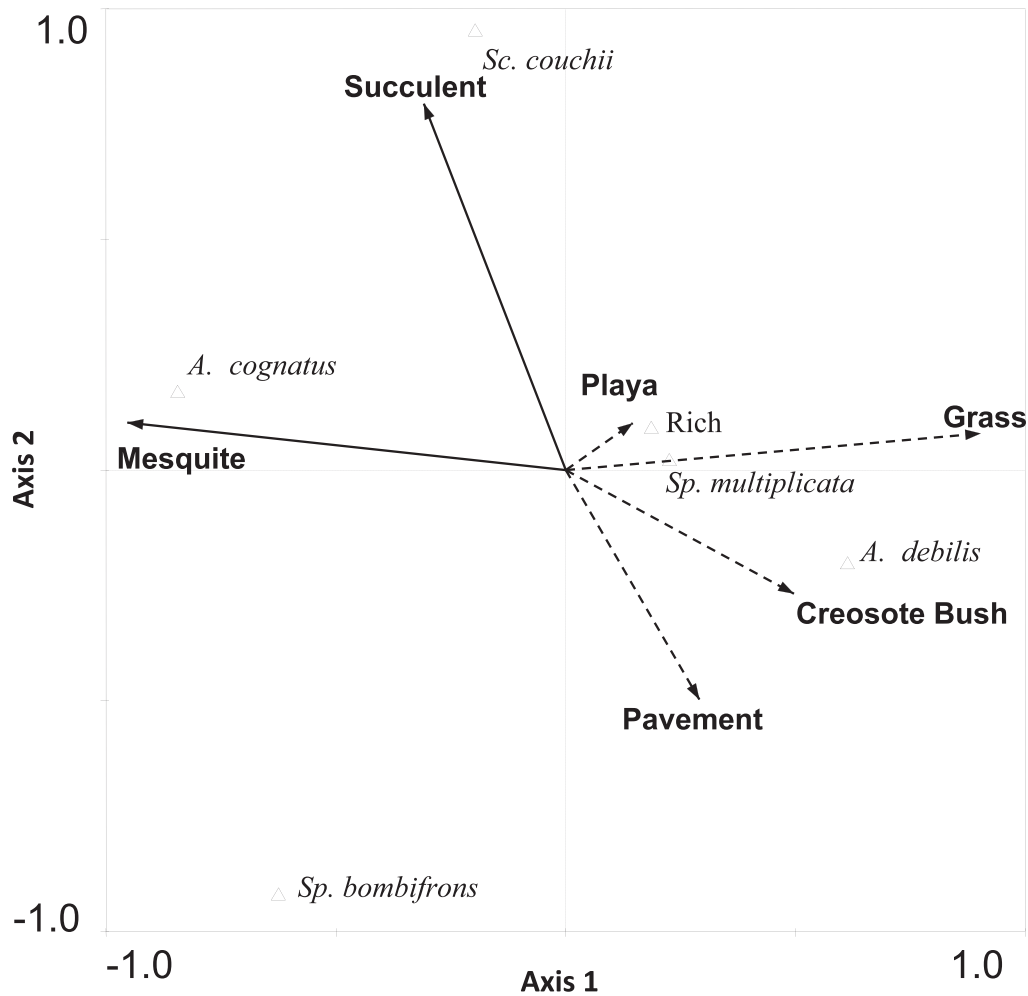


FIG. 2. Canonical correspondence analysis relating toad call indices to habitat parameters ($N = 33$). Species (triangles) that are located in the same direction as a habitat variable (arrows) correspond positively, species located in the opposite direction correspond negatively. A right angle between species and habitat direction means no correspondence. The longer the arrow, the higher the observed variability of that parameter in the field. Solid arrows show habitat parameters that significantly influenced species occurrence ($P < 0.05$). The further the species are from the center point, the stronger the correspondence. "Rich" stands for anuran species richness.

moving between breeding sites of close proximity and calling in these different locations on subsequent nights. Despite a high fidelity to their native birth place, observed in several anuran species (Berven and Grudzien, 1990; Gulve, 1994), it is possible that desert amphibians are more opportunistic (Jungels et al., 2010; Griffis-Kyle et al., 2011) and are not as philopatric as amphibians in more-mesic environments. Other factors not addressed in this study can have a profound influence on amphibian occurrence, factors such as physical and chemical properties of breeding sites, weather patterns, presence of predators, and availability of resources.

Our results compare well with a study conducted by Dayton et al. (2004) at Big Bend National Park, Texas, USA. Despite different methodologies and, in part, different species, both studies identified mesquite as a major positive factor for desert anurans. Both studies suggest a negative influence of succulent desert scrub habitat on amphibians.

In summary, we conclude that at least some desert anurans are found associated with shrub-dominated systems. This is interesting given the demonstrated negative consequences of shrub encroachment (especially mesquite) in the Chihuahuan Desert ecological communities. Our work suggests that, at least in this northern Chihuahuan Desert system, shrub encroach-

ment has likely not harmed the amphibian community and may have positive effects, especially for *A. cognatus* and *Sp. bombifrons*. Thus, future change in mesquite abundance would likely impact desert anurans.

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APPENDIX 1

Raw data of call indices of anurans (see Fig. 2 legend for species abbreviations) at various breeding sites (compare to Fig. 1).

Tank	A. <i>cognatus</i>	A. <i>debilis</i>	Sp. <i>multiplicata</i>	Sp. <i>bombifrons</i>	Sc. <i>couchii</i>
AT&T	0	2	2	0	1
Big Low	3	3	2	1	3
BLM	3	3	3	1	2
Brockway	2	3	2	0	0
Brown	0	0	0	0	0
Candler	1	3	3	3	0
Corner	0	1	0	0	2
Coyote	0	0	0	0	1
Cre	3	2	0	1	2
Mud	0	3	2	0	2
ELS	3	0	3	2	3
Frog	3	0	3	2	0
Gunter	0	3	3	2	0
Hatch	3	3	3	3	0
HDQ	3	3	3	2	2
JA	1	2	2	0	1
Kerr	0	2	2	1	0
Low	0	0	2	1	2
Marijane	0	3	2	0	0
Mason	3	3	3	0	0
N Kimble	0	3	0	0	0
Uvas	1	3	2	1	3
Mesq	3	0	2	0	3
NH	2	3	3	3	3
Puddle	3	3	2	3	0
NU	0	2	0	0	0
Road	2	2	2	0	1
S Kimble	0	3	0	0	0
Schoellar	1	2	2	0	0
Stablein	0	0	3	1	0
Stuart	0	1	1	0	0
Taylor	3	3	3	3	2
Windmill	0	3	0	0	0
Walk	2	3	3	3	1
West	0	2	0	0	1
White Bottom	3	0	0	0	0