available at www.sciencedirect.com

SCIENCE DIRECT®

journal homepage: www.elsevier.com/locate/biocon

Habitat suitability models for desert amphibians

Gage H. Dayton[*,1], *Lee A. Fitzgerald*

Section of Ecology and Evolutionary Biology, Department of Wildlife and Fisheries Sciences, Texas A&M University, Tamus 2258, College Station, TX 77843-2258, United States

A R T I C L E I N F O

Article history:
Received 2 June 2005
Received in revised form
3 March 2006
Accepted 8 March 2006
Available online 27 April 2006

Keywords:
Anuran
Habitat
Model
Desert
Conservation

A B S T R A C T

A fundamental step in conserving biodiversity is identification of quality habitat needed to sustain populations of target species. We used coarse scale environmental features (soil water holding capacity, soil texture, slope, elevation, and proximity to drainage channels) to predict habitat suitability for four species of desert amphibians in Big Bend National Park, USA: *Scaphiopus couchii*, *Bufo debilis*, *Bufo punctatus*, and *Gastrophryne olivacea*. Habitat suitability models were evaluated using data from 7 years of breeding site surveys. Overall our models provide quantitative measures of reliability for where species are likely to occur; however, results varied among species. Suitable habitat for *B. punctatus* and *G. olivacea* extended over greater proportions of the study area and encompassed a wider variety of habitats compared to suitable habitat for *S. couchii* and *B. debilis*. Our models performed better at predicting where *S. couchii* and *B. debilis* were likely to occur compared to *B. punctatus* and *G. olivacea*. The variation in the predicted suitable habitat among these species, as well as the agreement between model output and breeding site use, elucidates the fact that developing single species habitat suitability models may be a more appropriate approach than trying to develop multi-species models. Our study provides the first habitat suitability models for desert amphibians and provides important information for conservation biologists and land managers concerned with preserving amphibian diversity in xeric landscapes.

1. Introduction

The distribution of organisms is linked to habitat, hence identifying spatial relationships between organisms and environmental features is important for understanding autecology of species (Cowles, 1899; Grinnell, 1917). Moreover, understanding the environmental features that predict species occurrence is important for planning successful conservation efforts (Pereira and Itami, 1991; Akcakaya and Atwood, 1997; Gibson et al., 2004). Habitat suitability models have used species–environmental correlations to predict the distribution of species across complex landscapes (Verner et al., 1986; Guisan and Zimmermann, 2000; Manly et al., 2002). Extrapolating from species–habitat relationships at the local scale, to develop predictive models of habitat suitability at the landscape scale, helps elucidate factors that influence species persistence across multiple spatial scales (Pereira and Itami, 1991; Burnside et al., 2002; Root et al., 2003).

Landscape-level habitat suitability models have proven especially useful for predicting quality habitat for organisms that are endangered, rare, or have a patchy distribution over space or time (Wu and Smeins, 2000; Gibson et al., 2004). Many amphibian species, for example, are patchily distributed due to their tight association with wetlands, particularly in arid

* *Corresponding author*: Tel.: +1 (831) 771 4428/11 979 820 1859; fax: +1 11 979 845 4096.
E-mail addresses: gdayton@mlml.calstate.edu, gdayton@tamu.edu (G.H. Dayton).
[1] Present address: Habitat Restoration Laboratory, Moss Landing Marine Laboratories, Moss Landing, CA 95039, United States.
0006-3207/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2006.03.012

regions where suitable habitat is relatively sparse or fragmented (Dayton et al., 2004; Gray et al., 2004b). Although the presence of water and the suitability of the aquatic environment are often critical components of amphibian habitat, many amphibians are also dependent on specific terrestrial habitat components that provide refugia or foraging habitat for adults. Thus, when identifying habitat suitability for many amphibians it is essential to consider both terrestrial and aquatic habitat requirements (Pope et al., 2000; Hazell, 2003; Porej et al., 2004). Adult frogs that burrow into the soil, for example, are less likely to persist in rocky areas regardless of whether aquatic habitats are present. Alternatively, if suitable aquatic environments are absent, the presence of suitable terrestrial habitat for adults is unlikely to influence presence of the species in that area. As a result of this co-dependence of aquatic and terrestrial habitat features, many amphibians often occur in metapopulations because they rely upon multiple habitat types that do not always co-occur synoptically (Ray et al., 2002; Greenberg and Tanner, 2005). This pattern is especially prevalent in landscapes where terrestrial habitat between breeding sites is unsuitable (Marsh and Trenham, 2001).

Disruption or alteration of suitable habitat is well known to lead to increased isolation (spatially and genetically) among populations (Ficetola and Bernardi, 2004; Banks et al., 2005), and is believed to be one of the causes implicated in recent declines in amphibian populations throughout the world (Blaustein and Kiesecker, 2002; Brook et al., 2003). Although significant research and monitoring efforts over the past three decades have focused on factors influencing species assemblages and conservation issues of many amphibians (Heyer et al., 1994; Lips et al., 2004; Hermann et al., 2005), factors that influence distributions, abundance, and persistence of amphibians in desert environments are relatively understudied (Woodward and Mitchell, 1991).

In the present study our objectives were two-fold. Our first objective was to create predictive habitat suitability models for four amphibian species found in the Chihuahuan Desert: *Scaphiopus couchii* Baird, 1854 (Couch's Spadefoot Toad), *Bufo debilis* Girard, 1854 (Western Green Toad), *Bufo punctatus* Baird and Girard, 1854 (Red-spotted Toad), and *Gastrophryne olivacea* Hallowell, 1857 (Plains Narrow-mouthed Toad). Models were created using environmental data in a geographical information system (GIS). Our second objective was to evaluate the accuracy of the models to predict suitable habitat for these species. Model output was evaluated using data from 7 years of field surveys.

2. Methods

2.1. Study area

Our study area was Big Bend National Park (BBNP), which consists of approximately 315,000 ha, located in southwestern Texas along the Rio Grande River in the Chihuahuan Desert ecoregion. Annual precipitation averages approximately 38 cm with nearly 75% of the rainfall recorded at the main visitor center (1150 m elevation) occurring from May to September. Elevation ranges from 600 m along the Rio Grande River to nearly 2400 m in the Chisos Mountains, with most of the land between 762 and 1370 m. Mean summer and winter daytime temperatures are approximately 33 °C and 18 °C respectively, with extremes of 46 °C and −4 °C. Creosote bush (*Larrea tridentata*) and lechuguilla (*Agave lechuguilla*) dominate the vegetation community over approximately 72% of the park (Plumb, 1987). Major soil units are Lajitas-rock outcrop, Lozier-rock, Chamberino, and Chilicotol, together comprising approximately 69% of soils found in BBNP (Cochran and Rives, 1985).

2.2. Spatial data layers

Variables included in our habitat suitability models were elevation, soil texture, soil water holding capacity, slope, and proximity to drainage channels. These landscape variables have been shown to be important in influencing amphibian species distributions. Spatial data layers used were digital elevation models (DEM), digitized soil survey maps, and drainage channel maps. Digital elevation models (30 m resolution) were acquired from the Texas Natural Resources Information System (TNRIS), soil characteristics maps were obtained from digitized USDA soil maps of Big Bend National Park (Cochran and Rives, 1985), and drainage/hydrology maps were created from digitized USGS 1:100,000 topographic maps. Spatial attributes (slope and distance to drainage channels) were created using Arc View Spatial Analyst (ESRI, 1998). Data were converted to raster format and projected in NAD 83 with 30 m resolution. Georeferenced data of breeding sites detected during field surveys were used to create GIS "species" distribution layers.

2.3. Rationale for selection of environmental features included in habitat suitability models

2.3.1. Soil characteristics

Soil properties influence the distribution of many amphibians species (Diller and Wallace, 1999; Bradford et al., 2003; Dayton et al., 2004). Coarse-rocky soils have relatively low water holding capacity and drain quickly (Cochran and Rives, 1985). These characteristics limit the duration water is available for breeding and reduce a species' ability to dig into the soil (Hardy, 1945). The capacity of soil to hold available water (available water capacity) is expressed as inches of water per inch of soil depth (in./in.). In BBNP available water holding capacities of soils range from 0.02 in./in. (0.51 mm) in rocky areas to 5 mm/mm (0.2 in./in.) in clay loams (Cochran and Rives, 1985). Soils with relatively high available water capacity are likely to be important for burrowing amphibians, as they provide moist refuge sites that prevent amphibians from desiccating (McClanahan, 1967; Shoemaker, 1988) and are easier to burrow in compared to rocky hard soils that typically have low water holding capacities. In rocky terrain water will pool in areas with slight depressions and may hold water for several months at a time. Although rock bound pools provide suitable habitat for amphibian larvae, habitat for adults is limited, especially for burrowing species. Thus, soils with high water holding capacities are likely to be important for burrowing amphibians such as *S. couchii* (Dayton et al., 2004); however, for non-burrowing species rocky soils may provide important habitat for adult amphibians. For burrowing species, and species associated with fine soils, we ranked soils based on their water holding capacity.

2.3.2. Slope

Steepness of a region significantly influences runoff. Some amphibian species are associated with habitats that have steep slopes (Diller and Wallace, 1996; Diller and Wallace, 1999); these species tend to inhabit permanent or long-lasting streams in mountainous regions. In desert environments where accumulation of water is primarily a result of short-lived thunderstorms, steep sloped regions provide relatively little area where water can accumulate to create potential breeding pools. Flat regions provide more opportunities for water to pool opposed to areas with steeper slopes.

2.3.3. Elevation

Elevation is an important factor limiting the persistence of many amphibian species (Fauth et al., 1989; Bradford et al., 2003; Pineda and Halffter, 2004). In BBNP there are no records of *S. couchii*, *B. debilis*, *B. punctatus*, or *G. olivacea* above ~1400 m (Dayton, unpublished data). The majority of amphibians in BBNP inhabit areas with elevations ranging between 550 and 1000 m with the exception of *B. punctatus* which has been found at higher elevations in the Chisos Mountains (Dayton, 2001).

2.3.4. Proximity to drainage channels

Drainage channels, and areas in close proximity to them, receive runoff from seasonal floods. Runoff often pools in drainage channels providing potential breeding habitat for some amphibian species. Another source of water in desert environments are man-made cattle tanks. We excluded cattle tanks from our analyses because although amphibians certainly use these habitats, they represent unnatural habitat and are not being maintained by the National Park Service and will soon be reverted back to natural conditions.

2.4. Model framework

We assigned different suitability values to selected habitat variables (i.e. specific soil type, slope category, etc.) based on published accounts and field observations of habitat associations for *S. couchii*, *B. debilis*, *B. punctatus*, and *G. olivacea* (see Sections 2.5–2.7 for habitat suitability values for each species). Pixel values for each habitat suitability variable were reclassified from 0 to 3 in ArcView. Higher numbers corresponded to more suitable habitat. GIS layers for each reclassified habitat variable were multiplied using the Map Calculator in ArcView to create a single landscape map. This is a multiplicative approach in which all layers are combined to create a single layer of all the habitat variables. The final step in creating the habitat suitability model was to reclassify the combined map into categories based on the value of each cell. Thus, potential habitat suitability was determined by a combination of the landscape variables based on species specific habitat affinities. Some habitat features were ranked as 0 because the species is not known to occur with that particular feature. For example, in BBNP *S. couchii* do not occur in the higher elevations of the Chisos Mountains, thus all elevation above 1200 m was ranked as 0. Because we used a multiplicative approach, all areas within BBNP that fell above 1200 were scored as 0 for potential habitat suitability for *S. couchii* regardless of the other landscape level factors associated with that specific spot. For each species we provide a detailed description on natural history affinities as well as a detailed compilation of how each predicted habitat category was created.

2.5. Scaphiopus couchii and Bufo debilis habitat affinities

Scaphiopus couchii and *B. debilis* are associated with similar habitats in BBNP (Dayton et al., 2004). For this reason we developed a single habitat suitability model that predicted suitable habitat for both species (Fig. 1). Both species are associated with clay loam soils with relatively high water holding capacities and breed primarily in temporary pools in alluvial floodplains (Strecker, 1926; Newman, 1987; Dayton et al., 2004) and metamorphose in relatively few days. *S. couchii* metamorphosis in as little as 8 days (Mayhew, 1965; Newman, 1989) and *B. debilis* in as few as 20 days (Strecker, 1926). In BBNP, *S. couchii* is distributed throughout the park with the greatest number of individuals occurring in the northern regions and near the Rio Grande River at the lower elevations

Landscape-Scale Model for *Scaphiopus couchii* and *Bufo debilis*

SOIL RATING

3 High Likelihood
- Available water capacity > 2.5 mm/mm

2 Medium Likelihood
- Available water holding capacity 2.0 to 2.5 mm/mm

1 Low Likelihood
- Available water holding capacity < 2.0 mm/mm

SLOPE RATING

2 High Likelihood
- Flat areas (slope < 3°)

1 Medium Likelihood
- Moderate slopes (slope 3-6°)

0 Very Low Likelihood
- Steep slopes (> 6°)

ELEVATION

2 High Likelihood
- Low elevation (500-1000 m)

1 Medium Likelihood
- Medium elevation (1000-1200 m)

0 Very Low Likelihood
- High elevation (> 1200 m)

POSSIBLE ENVIRONMENTAL FACTOR COMBINATIONS

Elevation Rating	*Slope Rating*	*Soil Rating*	*Predicted Habitat Suitability*
0	—	—	Very Low
—	0	—	Very Low
1	1	1 or 2	Low
1	2	1	Low
2	1	1	Low
1	1	3	Medium
1	2	2	Medium
2	1	2	Medium
2	2	1	Medium
1	2	3	High
2	1	3	High
2	2	2	High
2	2	3	Very High

— = any category rating

Fig. 1 – Variables selected and criteria used in habitat suitability models for *Scaphiopus couchii* and *Bufo debilis*.

up to approximately 1200 m (Dayton, 2001; Dayton et al., 2004). *Bufo debilis* occur primarily in the northern region of the park at elevations ranging from 700 to 900 m; however, a few individuals have been observed along the Rio Grande River and near the western park boundary at lower elevations (Dayton, unpublished data). Relatively little natural history information exists for *B. debilis;* though, it is also thought to burrow into the soil and seek refuge beneath vegetation and rocks and in animal burrows (Creusere and Whitford, 1976; Dayton, unpublished data).

2.6. *Bufo punctatus* habitat affinities

Bufo punctatus is associated with temporary and permanent water bodies throughout their range and breed in a wide variety of habitats including temporary bedrock pools, rocky canyons, low gradient flood plains, steeply sloped tributaries, and permanent springs (Fig. 2) (Mayhew, 1965; Tevis, 1966; Sullivan and Fernandez, 1999; Bradford et al., 2003). Adults are often associated with rocky stream beds and drainage channels in well drained rocky soils (Sullivan, 2005). In the desert southwest breeding primarily occurs following a rain event and continues for several weeks (Sullivan, 1989). During the summer months breeding occurs primarily in small temporary pools in rocky upland habitat (Tevis, 1966; Creusere and Whitford, 1976; Sullivan, 2005). Although adults are believed to burrow and dig into the ground during dry periods (Tevis, 1966), they often take refuge beneath stones, vegetation, and other cover (Strecker, 1926; Turner, 1959; McClanahan et al., 1994). In BBNP, *B. punctatus* is distributed widely throughout the park but has not been found in the high elevations Chisos Mountains (Dayton, unpublished data).

2.7. *Gastrophryne olivacea* habitat affinities

Gastrophryne olivacea is associated with a wide variety of habitats including stock tanks, tinajas, temporary pools, and frequently inundated alluvial floodplains (Smith, 1934; Sullivan et al., 1996; Anderson et al., 1999) (Fig. 3). Adults seek refuge beneath fallen vegetation and rocks as well as within tarantula burrows (Fitch, 1956; Dundee, 1999; Dayton, 2000). Breeding takes place after seasonal rain storms and adults continue to call for several days following a rain event (Dayton, unpublished data). *Gastrophryne olivacea* has been reported to be rare throughout BBNP; however, recent surveys indicate they are relatively common (Dayton, unpublished data). In BBNP, *G. olivacea* is distributed widely throughout the park and occurs primarily in low and mid elevation ranges across a broad range of habitat types ranging from sloped well-drained rocky areas to clay-loam flats with relatively high water holding capacity (Dayton, 2001; Dayton, 2005). Although we used published data to develop criteria for *G. olivacea* a significant portion of the information was based on our observations over 7 years of survey work.

2.8. Survey of amphibian breeding sites

During the summer months of May–August from 1998 to 2004 we conducted area-constrained surveys (where each pool represented the sample area) at more than 500 permanent and temporary water bodies throughout all of BBNP for the presence of amphibians. Sites ranged from ephemeral pools to permanent springs. Because the goal of our study was to cover as much area as possible the majority (approximately 75%) of the sites were surveyed only once; however, some sites were surveyed multiple times during the 7 years. This survey method allowed us to survey more sites; however, we may have missed the presence of a given species at a particular site (e.g. the species was absent when we surveyed but bred their later). Location of each site was recorded using a handheld Global Positioning System (GPS) unit. Sites were sampled opportunistically and assumed to be a random representative sample due to the stochastic nature of rain distribution patterns in BBNP. Site selection was determined based upon recent rain events. Surveys were conducted over

Landscape-Scale Model for ***Bufo punctatus***

SOIL RATING

3 High Likelihood
- Cobble

2 Medium Likelihood
- Gravel

1 Low Likelihood
- Sandy or fine

SLOPE RATING

2 High Likelihood
- Flat to moderate slopes (slope 0-6°)

1 Medium Likelihood
- Moderate to steep (slope 6-9°)

0 Very Low Likelihood
- Steep (> 9°)

DRAINAGE CHANNEL RATING

2 High Likelihood
- < 50 m from drainage channel

1 Medium Likelihood
- > 50 m from drainage channel

ELEVATION RATING

2 High Likelihood
- < 1450

1 Very Low Likelihood
- > 1450

POSSIBLE ENVIRONMENTAL FACTOR COMBINATIONS

Elevation Rating	*Drainage Rating*	*Slope Rating*	*Soil Rating*	*Predicted Habitat Suitability*
—	—	0	—	Very Low
1	1	1	1	Very Low
1	1	1	2 or 3	Low
1	1	2	1	Low
1	2	1	1	Low
2	1	1	1	Low
1	1	2	2 or 3	Medium
1	2	1	2 or 3	Medium
2	1	1	2 or 3	Medium
1	2	2	1	Medium
2	1	2	1	Medium
2	2	1	1	Medium
1	2	2	2 or 3	High
2	1	2	2 or 3	High
2	2	1	2 or 3	High
2	2	2	1	High
2	2	2	2 or 3	Very High

— = any category rating

Fig. 2 – Variables selected and criteria used in habitat suitability models for *Bufo punctatus*.

Landscape-Scale Model for *Gastrophryne olivacea*

SOIL RATING

3 High Likelihood
- Cobble or available water capacity > 2.5 mm/mm

2 Medium Likelihood
- No cobble and available water holding capacity 2.0 to 2.5 mm/mm

1 Low Likelihood
- No cobble and available water holding capacity < 2.0 mm/mm

SLOPE RATING

2 High Likelihood
- Flat to moderate slopes (slope 0-6 °)

1 Medium Likelihood
- Moderate to steep (slope 6-9°)

0 Very Low Likelihood
- Steep (> 9°)

ELEVATION

2 High Likelihood
- Low elevation (500-1000 m)

1 Medium Likelihood
- Medium elevation (1000-1200 m)

0 Very Low Likelihood
- High elevation (> 1200 m)

POSSIBLE ENVIRONMENTAL FACTOR COMBINATIONS

Elevation Rating	*Slope Rating*	*Soil Rating*	*Predicted Habitat Suitability*
0	—	—	Very Low
—	0	—	Very Low
1	1	1 or 2	Low
1	2	1	Low
2	1	1	Low
1	1	3	Medium
1	2	2	Medium
2	1	2	Medium
2	2	1	Medium
1	2	3	High
2	1	3	High
2	2	2	High
2	2	3	Very High

— = any category rating

Fig. 3 – Variables selected and criteria used in habitat suitability models for *Gastrophryne olivacea*.

a 7-year period, and covered the range of available habitats throughout the entire study region. We used extensive dip-net sampling throughout each pool to capture tadpoles and document species presence. Because we were interested in detecting species presence/absence rather than calculating abundance or density we sampled the banks and interior regions of each pool in a manner that ensured we covered as much area as possible rather than sampling along fixed transects or plots. Dip-net surveys provide a good estimate of species presence (Shaffer et al., 1994) and are effective in detecting tadpoles even when densities are relatively low (Jung et al., 2002). Tadpoles collected in the field were identified to species (Altig and McDiarmid, 1998). Locality data for each species were recorded in DBF file format and converted to point shape files and then grid themes. Wetlands within 30 m of one another were grouped together as a single site. Our rationale for the 30 m distance is based upon water connectivity rather than dispersal abilities of adults. We were concerned that pools that were very close to each other may have initially been a single pool that because of evaporation appeared as two pools. Furthermore, because surveys were conducted over multiple years we wanted to be sure that we did not include a particular breeding site multiple times. Thus, we decided to group sites that were within 30 meters of one another. This reduced our overall sample size but was necessary to be certain we were not counting a single pool multiple times.

2.9. Model evaluation and data analysis

Evaluating the effectiveness of a habitat suitability model typically entails using independent data to test the ability of the model to accurately predict occurrence and or abundance of target species. Although we did not explicitly use data from our breeding site surveys to generate habitat suitability models, our observations on habitat affinities were used as one of the sources of information in selecting model variables and classification criteria. Accuracy of the model was examined by overlaying GIS species occurrence layers onto predicted habitat suitability maps. We then used chi-square goodness-of-fit tests to examine whether the observed frequencies of occurrence in each habitat category were different than would be expected if the number of breeding sites simply reflected the availability of each predicted habitat category. To determine which habitat categories were drivers of significant differences, we compared 95% confidence intervals for the proportions of used, versus available, predicted habitat categories (Bonferroni adjusted)

$$o_i - Z_{(1-\alpha/2k)}\sqrt{o_i(1-o_i)/n} \leqslant \pi_i \leqslant O_i + Z_{(i-\alpha/2k)}\sqrt{o_i(1-o_i)/n}$$

where i is habitat category, o_i is the proportion of the sample of used resources in category i, k is number of simultaneous estimates being made, and π_i is the proportion of available resources units that are in category i. This method evaluates whether the observed proportions of sites in a specific habitat category fall outside the predicted 95% confidence interval for that habitat category (Neu et al., 1974; Manly et al., 2002).

3. Results

3.1. *Scaphiopus couchii*

Predicted suitable habitat for *S. couchii* is scattered throughout BBNP, with the majority of Very High quality habitat occurring in the northern region of the park (Fig. 4). Approximately 75% of all *S. couchii* breeding sites detected during our surveys occurred in High and Very High habitat suitability categories (Table 1). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occurred in the categories relative to their availability ($\chi^2 = 353$, df = 4, $P < 0.0001$). *Scaphiopus couchii* occurred in the Very High category significantly more frequently than expected, and less frequently than expected in Low and Very Low categories. (This can be determined for *S. couchii*, and other species, by comparing the observed vs. expected values by category, and by comparing the *pi* statistic with the confidence limits (Table 1).

3.2. *Bufo debilis*

Predicted suitable habitat for *B. debilis* is scattered throughout BBNP, with the majority of Very High quality habitat occurring in the northwestern region of the park (Fig. 4). Approximately 89% of all *B. debilis* breeding sites detected during our surveys occurred in the Very High habitat suitability category (Table 1). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occupied the

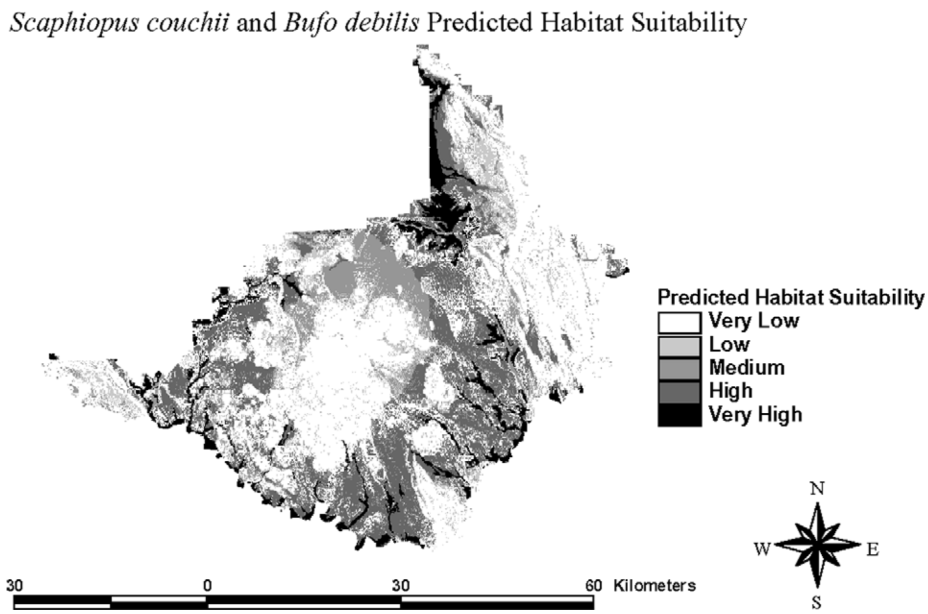

Fig. 4 – Predicted habitat suitability for *S. couchii* and *B. debilis* in Big Bend National Park, Texas.

Table 1 – Occurrence of, and habitat selection indices for, *Scaphiopus couchii*, *Bufo debilis*, *Gastrophryne olivacea*, and *Bufo punctatus* in each of the five predicted habitat categories

Species	Predicted habitat category (i)	Proportion of total area of predicted habitat category (π)	Observed # of sites in habitat category (u)	Expected # of sites in category (πu^+)	Proportion sites in habitat category (o)	Confidence intervals (Bonferroni adjusted)
Scaphiopus couchii	Very low	0.46[a]	9	40	0.10	$0.02 \leqslant p_i \leqslant 0.19$
	Low	0.09[a]	2	9	0.03	$-0.02 \leqslant p_i \leqslant 0.06$
	Medium	0.16	10	14	0.11	$0.03 \leqslant p_i \leqslant 0.20$
	High	0.21	16	18	0.18	$0.08 \leqslant p_i \leqslant 0.29$
	Very high	0.07[a]	50	6	0.57	$0.44 \leqslant p_i \leqslant 0.70$
Bufo debilis	Very low	0.46[a]	1	12	0.04	$-0.03 \leqslant p_i \leqslant 0.10$
	Low	0.10	0	3	0	N/A
	Medium	0.16	2	4	0.08	$-0.01 \leqslant p_i \leqslant 0.16$
	High	0.21	0	5	0	N/A
	Very high	0.07[a]	23	2	0.88	$0.78 \leqslant p_i \leqslant 0.99$
Bufo punctatus	Very Low	0.36[a]	15	35	0.15	$0.02 \leqslant p_i \leqslant 0.28$
	Low	0.01	0	0.5	0	N/A
	Medium	0.15	25	14	0.26	$0.10 \leqslant p_i \leqslant 0.42$
	High	0.45	45	44	0.46	$0.28 \leqslant p_i \leqslant 0.64$
	Very high	0.04	13	4	0.13	$0.01 \leqslant p_i \leqslant 0.26$
Gastrophryne olivacea	Very Low	0.36[a]	3	17	0.06	$-0.03 \leqslant p_i \leqslant 0.15$
	Low	0.06	1	3	0.02	$-0.03 \leqslant p_i \leqslant 0.07$
	Medium	0.13	4	6	0.09	$0.02 \leqslant p_i \leqslant 0.19$
	High	0.20	11	10	0.23	$0.08 \leqslant p_i \leqslant 0.39$
	Very high	0.25[a]	28	12	0.60	$0.42 \leqslant p_i \leqslant 0.78$

Confidence intervals were not constructed for categories in which no sites were detected.
u^+ = Total number of sites for each species.
a Significant at $P < 0.05$ after Bonferroni corrections.

categories relative to their availability ($\chi^2 = 240$, df = 4, $P < 0.0001$). *Bufo debilis* occurred in the Very High category significantly more frequently than expected and less frequently than expected in the Very Low category (Table 1).

3.3. *Bufo punctatus*

Predicted suitable habitat for *B. punctatus* is widely distributed throughout BBNP, with the majority of High quality habitat occurring throughout the southern regions of BBNP but with large patches scattered throughout the entire park (Fig. 5). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occurred in the categories relative to their availability ($\chi^2$28, df = 4, $P < 0.0001$). Approximately 59% of all *B. punctatus* breeding sites occurred in High and Very High habitat suitability categories (Table 1). More *B. punctatus* individuals occurred in Very High and High habitat categories than expected; however the results were not significant (Table 1). The only significant difference detected was for the Very Low category, where fewer individuals occurred than expected (Table 1).

3.4. *Gastrophyrne olivacea*

Predicted suitable habitat for *G. olivacea* is scattered throughout BBNP, with the majority of Very High quality habitat occurring in the northern and eastern regions of the park with isolated patches throughout the southern and western boundaries (Fig. 6). Approximately 83% of all *G. olivacea* breeding sites detected during our surveys occurred in High and Very High habitat suitability categories (Table 1). Breeding sites occurred in predicted habitat categories disproportionately than would be expected if they occurred in the categories relative to their availability ($\chi^2 = 35$, df = 4, $P < 0.0001$).

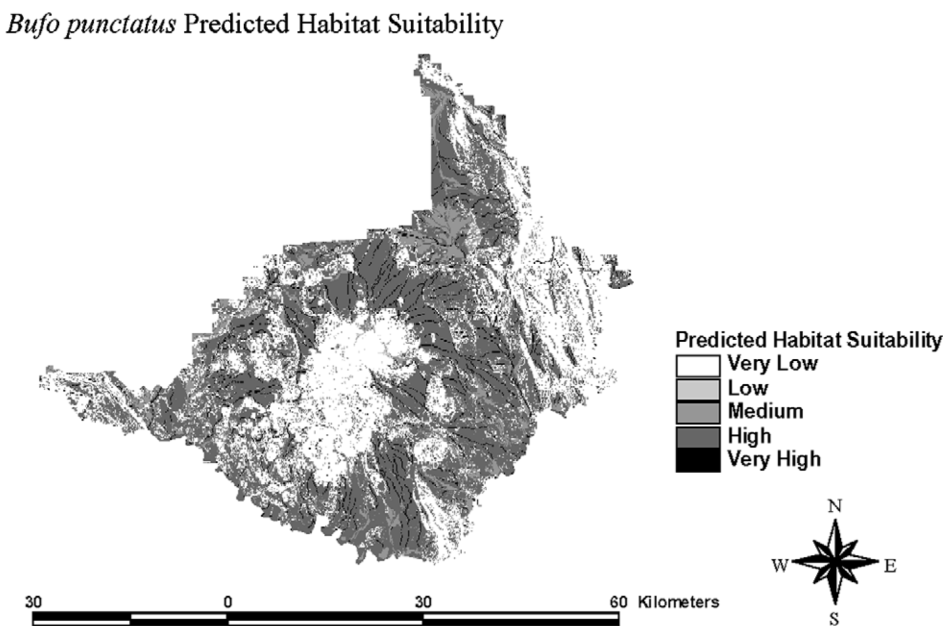

Fig. 5 – Predicted habitat suitability for *B. punctatus* in Big Bend National Park, Texas.

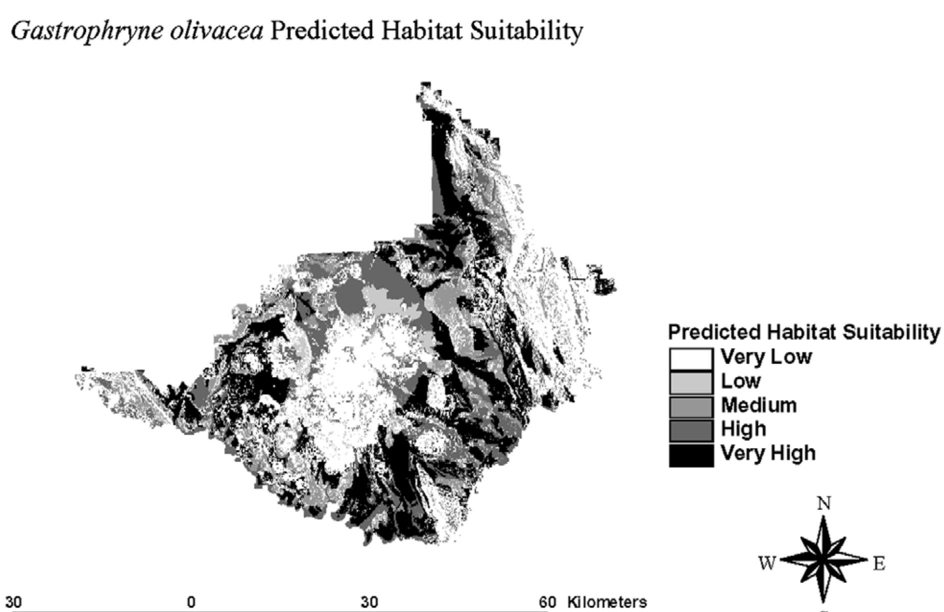

Fig. 6 – Predicted habitat suitability for *Gastrophryne olivacea* in Big Bend National Park, Texas.

Gastrophryne olivacea occurred in the Very High category significantly more frequently than expected, and less frequently than expected in the Very Low category (Table 1).

4. Discussion

Our study is the first to provide habitat suitability models for desert amphibians. By utilizing species-specific habitat associations, we were able to accurately predict habitat suitability for three of the four amphibian species. Model evaluation demonstrated that habitat suitability models performed well for predicting species occurrence in Very High suitable habitat categories and species absence in Very Low habitat suitability categories for *S. couchii*, *B. debilis*, and *G. olivacea*. The inability of our model to predict the presence or absence of individuals of all species in many of the intermediate predicted habitat categories indicates that our models perform best in discriminating between Very Low and Very High predicted habitat categories. This discrepancy is likely due to the coarseness of our model input (e.g. small pockets of potential habitat may exist within areas we classified as low quality habitat), inaccuracies in GIS data (e.g. modeled slope values may not correspond perfectly to slope on the ground), or be an artifact of small sample sizes in some regions.

Very High and High suitable habitat categories for *G. olivacea* and *B. punctatus* extended over greater areas of BBNP compared to *S. couchii* and *B. debilis*. Suitable habitat for *S. couchii* and *B. debilis* was limited primarily to the northern regions of the BBNP and along the Rio Grande River, with fingers of Very High quality habitat extending into the interior of the park. *Gastrophryne olivacea* and *B. punctatus* also occurred in these areas, as well as in other regions of the park. Although the model was significant for *B. punctatus*, the fit was not as informative for as it was for the other species. This is likely due to the fact that *B. punctatus* utilize a wide variety of habitats and may not be as restricted in their habitat use. The data used in our models may be too coarse to pick up small scale environmental features that may actually be suitable habitat for *B. punctatus*.

For many amphibian species that inhabit desert environments suitable habitat is relatively sparse and patchily distributed. Thus, populations may be isolated by unsuitable xeric regions. Furthermore, amphibian populations in desert environments are likely to exhibit significant fluctuations in size over time due to the stochasticity and unpredictability of the presence and duration of aquatic habitats. Desert amphibians often do not breed on an annual basis due to unpredictable environmental conditions (Bragg, 1945), commonly lose entire clutches due to desiccation (Mayhew, 1965; Tevis, 1966; Newman, 1987), have extremely low juvenile survivorship (Creusere and Whitford, 1976), are susceptible to predation in all stages of their development (Newman, 1987; Dayton and Jung, 1999; Bonine et al., 2001; Dayton and Wapo, 2002), and often persist in isolated populations (Turner, 1959; Mayhew, 1965). Combined, these factors presumably lead to frequent extinction events at local breeding sites. Species persistence over the long-term relies upon recolonization from neighboring sites (Hanski, 1987; Rustigian et al., 2003). The ability of amphibians to move between isolated populations is largely dependent on the suitability of habitat among populations (Marsh and Trenham, 2001; Gray et al., 2004a; Gray et al., 2004b). Thus, regions with high quality terrestrial and aquatic habitat are likely to provide a source of emigrants that maintain satellite populations.

4.1. *Implications for conservation*

An important implication of the habitat suitability models is that high quality habitat may play an important role in facilitating movements among isolated breeding sites. Therefore, protecting areas where high quality habitat is abundant should positively influence the persistence of local populations that depend on the dynamics of local extinction and colonization (Vos and Stumpel, 1996; Marsh et al., 1999; Bulger et al., 2003; Green, 2003). This is particularly important for species such as *S. couchii* and *B. debilis* that had patchily distributed areas of high quality habitat that were often isolated from one another by relatively large distances. In comparison, *B. punctatus* and *G. olivacea* seem to be habitat generalists and persist in a relatively broad range of habitats. The variation in the predicted suitable habitat among these four functionally similar species (i.e. xeric adapted amphibians) elucidates the fact that developing single species habitat suitability models is a more appropriate approach then trying to develop multi-species models which assume species will respond to changes in habitat in a similar manner (Lindenmayer et al., 2002). The fact that we used field surveys to examine the measure of agreement between our model output and breeding site localities significantly increases their usefulness and relevance for conservation and management purposes as we have provided evidence that these models work (Fleishman et al., 2001; Pullin and Knight, 2001; Pullin et al., 2004). We are optimistic these results will be very useful to BBNP resource managers in identifying sites for future surveys as well as areas of high species richness. Although it is important to realize the scope of this study was constrained within the boundaries of BBNP, the framework of our model provides a valuable tool for land managers and conservation biologists interested in determining suitable habitat for other xeric adapted amphibians.

Acknowledgements

This work would not have been possible without the tremendous support of the staff at Big Bend National Park, especially R. Skiles and V. Davila. S. Walls, R. Jung, and S. Droege all had a big hand in helping to make the Big Bend amphibian research continue for 7 years. Field assistance was provided by K. Bonine, S. Claeson, E. Dayton, P. Dayton, A. De la Reza, S. Raimondo, M. Rosenshield, W. A. Ryberg, J.E. Wallace, and S. Williamson. J. Dixon, T. Lacher, and X. B. Wu provided important comments on many facets of this study. Our work was supported in part by funding from the NPS and the EPA through the PRIMENet program, the U.S.G.S. Amphibian Research and Monitoring Initiative, Tom Slick Graduate Fellowship, Francis Bacon Memorial Fund, Society of Wetlands Scientists student research grant, and the Texas Water Resource Initiative Mills Scholarship. We appreciate the significant comments of two anonymous reviewers as well as E. Dayton for her important contributions.

REFERENCES

Akcakaya, H.R., Atwood, J.L., 1997. A habitat based metapopulation model of the California gnatcatcher. Conservation Biology 11, 422–434.

Altig, R.A., McDiarmid, R.W., 1998. A key to the anuran tadpoles of the United States and Canada. Contemporary herpetology Information Series.

Anderson, A.M., Haukos, D.A., Anderson, J.T., 1999. Habitat use by anurans emerging and breeding in playa wetlands. Wildlife Society Bulletin 27, 759–769.

Banks, S.C., Lindenmayer, D.B., Ward, S.J., Taylor, A.C., 2005. The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, *Antechinus agilis*. Molecular Ecology 14, 1667–1680.

Blaustein, A.R., Kiesecker, J.M., 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecology Letters 5, 597–608.

Bonine, K.E., Dayton, G.H., Jung, R.E., 2001. Attempted predation of Couch's spadefoot (*Scaphiopus couchii*) juveniles by ants (*Aphaenogaster cockerelli*). Southwestern Naturalist 46, 104–106.

Bradford, D.F., Neale, A.C., Nash, M.S., Sada, D.W., Jaeger, J.R., 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology 84, 1012–1023.

Bragg, A.N., 1945. The spadefoot toads in Oklahoma with a summary of our knowledge of the group II. American Naturalist 79, 52–72.

Brook, B.W., Sodhi, N.S., Ng, P.K.L., 2003. Catastrophic extinctions follow deforestation in Singapore. Nature 424, 420–423.

Bulger, J.B., Scott, N.J., Seymour, R.B., 2003. Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. Biological Conservation 110, 85–95.

Burnside, N.G., Smith, R.F., Waite, S., 2002. Habitat suitability modeling for calcareous grassland restoration on the South Downs, United Kingdom. Journal Of Environmental Management 65, 209–221.

Cochran, R.A., Rives, J.L., 1985. Soil survey of Big Bend National Park, part of Brewster County, Texas. U.S. Department of Agriculture, Soil Conservation Service, pp. 117.

Cowles, H.C., 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27, 95–117.

Creusere, F.M., Whitford, W.G., 1976. Ecological relationships in a desert anuran community. Herpetologica 32, 7–18.

Dayton, G.H., 2000. *Gastrophryne olivacea* (narrow-mouthed toad). Vocalization. Herpetological Review 31, 40.

Dayton, G.H., 2001. Abiotic and biotic factors affecting distributions of desert anurans. Masters Thesis, Texas A&M University, College Station, Texas, 56 pp.

Dayton, G.H., 2005. Community assembly of xeric-adapted anurans at multiple spatial scales. Texas A&M University, College Station, 162 pp.

Dayton, G.H., Jung, R.E., 1999. *Scaphiopus couchii*. Predation. Herpetological Review 30, 164.

Dayton, G.H., Jung, R.E., Droege, S., 2004. Large-scale habitat associations of four desert anurans in Big Bend National Park, Texas. Journal of Herpetology 38, 619–627.

Dayton, G.H., Wapo, S.D., 2002. Cannibalistic behavior in *Scaphiopus couchii*: more evidence for larval anuran oophagy. Journal of Herpetology 36, 531–532.

Diller, L.V., Wallace, R.L., 1999. Distribution and habitat of *Ascaphus truei* in streams on managed, young growth forests in north coastal California. Journal of Herpetology 33, 71–79.

Diller, L.V., Wallace, R.L., 1996. Distribution and habitat of *Rhyacotriton variegatus* in managed, young growth forests in north coastal California. Journal of Herpetology 30, 184–191.

Dundee, H.A., 1999. *Gastrophyrne olivacea* (Great Plains Narrow-mouthed Toad). Aggregation with tarantula. Herpetological Review 30, 91–92.

Fauth, J.E., Crother, B.I., Slowinski, J.B., 1989. Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. Biotropica 21, 178–185.

Ficetola, G.F., De Bernardi, F., 2004. Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. 119, 219–230.

Fitch, H.S., 1956. Field study of the Kansas ant eating frog, *Gastrophryne olivacea*. University of Kansas Museum of Natural History 8, 275–306.

Fleishman, E., Mac Nally, R., Fay, J.P., Murphy, D.D., 2001. Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. Conservation Biology 15, 1674–1685.

Gibson, L.A., Wilson, B.A., Cahill, D.M., Hill, J., 2004. Modelling habitat suitability of the swamp antechinus (*Antechinus minimus maritimus*) in the coastal heathlands of southern Victoria, Australia. Biological Conservation 117, 143–150.

Gray, M.J., Smith, L.M., Brenes, R., 2004a. Effects of agricultural cultivation on demographics of Southern High Plains amphibians. Conservation Biology 18, 1368–1377.

Gray, M.J., Smith, L.M., Leyva, R.I., 2004b. Influence of agricultural landscape structure on a Southern High Plains, USA, amphibian assemblage. Landscape Ecology 19, 719–729.

Green, D.M., 2003. The ecology of extinction: population fluctuation and decline in amphibians. Biological Conservation 111, 331–343.

Greenberg, C.H., Tanner, G.W., 2005. Spatial and temporal ecology of eastern spadefoot toads on a Florida landscape. Herpetologica 61, 20–28.

Grinnell, J., 1917. The niche relationship of the California Thrasher. Auk 34, 427–433.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147–186.

Hanski, I., 1987. Colonization of ephemeral habitats. In: Gray, A.J., Crawley, M.J., Edwards, P.J. (Eds.), Colonization, Succession and Stability. Blackwell Scientific Publications, Oxford, pp. 155–185.

Hardy, R., 1945. The influence of types of soil upon the local distribution of some mammals in southwestern Utah. Ecological Monographs 15, 71–108.

Hazell, D., 2003. Frog ecology in modified Australian landscapes: a review. Wildlife Research 30, 193–205.

Hermann, H.L., Babbitt, K.J., Baber, M.J., Congalton, R.G., 2005. Effects of landscape characteristics on amphibian distribution in a forest-dominated landscape. Biological Conservation 123, 139–149.

Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayek, A.C., Foster, M.S., 1994. Measuring and monitoring biological diversity: standard methods for amphibiansBiological Diversity Handbook Series. Smithsonian Institution, Washington, DC.

Jung, R.E., Dayton, G.H., Williamson, S.J., Sauer, J.R., Droege, S., 2002. An evaluation of population index and estimation techniques for tadpoles in desert pools. Journal of Herpetology 36, 465–472.

Lindenmayer, D.B., Manning, A.D., Smith, P.L., Possingham, H.P., Fischer, J., Oliver, I., McCarthy, M.A., 2002. The focal-species approach and landscape restoration: a critique. Conservation Biology 16, 338–345.

Lips, K.R., Mendelson, J.R., Munoz-Alonso, A., Canseco-Marquez, L., Mulcahy, D.G., 2004. Amphibian population declines in montane southern Mexico: resurveys of historical localities. Biological Conservation 119, 555–564.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Kluwer Academic, Dordrecht, The Netherlands.

Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15, 40–49.
Marsh, D.M., Fegraus, E.H., Harrison, S., 1999. Effects of breeding pond isolation on the spatial and temporal dynamics of pond use by the tungara frog, *Physalaemus pustulosus*. Journal of Animal Ecology 68, 804–814.
Mayhew, W.W., 1965. Adaptations of the amphibian, *Scaphiopus couchi*, to desert conditions. American Midland Naturalist 74, 95–109.
McClanahan, L., 1967. Adaptations of spadefoot toad *Scaphiopus couchi* to desert environments. Comparative Biochemistry and Physiology 20, 73–99.
McClanahan, L.L., Ruibal, R., Shoemaker, V.H., 1994. Frogs and toads in deserts – amphibians seem unlikley desert denizens – but those living in dry climates reveal a diverse and unusual array of adaptations to life at the extremes. Scientific American 270, 82–88.
Neu, C.W., Byers, C.R., Peek, J.M., 1974. Technique for analysis of utilization – availability data. Journal of Wildlife Management 38, 541–545.
Newman, R.A., 1987. Effects of density andpredation on *Scaphiopus couchi* tadpoles in desert ponds. Oecologia 71, 301–307.
Newman, R.A., 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology 70, 1775–1787.
Pereira, J.M.C., Itami, R.M., 1991. GIS-based habitat modeling using logistic multiple regression – a study of the Mt Graham red squirrel. Photogrammetric Engineering and Remote Sensing 57, 1475–1486.
Pineda, E., Halffter, G., 2004. Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico. Biological Conservation 117, 499–508.
Plumb, G.A., 1987. An algorithmic approach to automated vegetation mapping of Big Bend National Park, Texas. Dissertation Thesis, University of Kansas, 499 pp.
Pope, S.E., Fahrig, L., Merriam, N.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81, 2498–2508.
Porej, D., Micacchion, M., Hetherington, T.E., 2004. Core terrestrial habitat for conservation of local populations of salamanders and wood frogs in agricultural landscapes. Biological Conservation 120, 399–409.
Pullin, A.S., Knight, T.M., 2001. Effectiveness in conservation practice: pointers from medicine and public health. Conservation Biology 15, 50–54.
Pullin, A.S., Knight, T.M., Stone, D.A., Charman, K., 2004. Do conservation managers use scientific evidence to support their decision-making? Biological Conservation 119, 245–252.
Ray, N., Lehmann, A., Joly, P., 2002. Modeling spatial distribution of amphibian populations: a GIS approach based on habitat matrix permeability. Biodiversity and Conservation 11, 2143–2165.
Root, K.V., Akcakaya, H.R., Ginzburg, L., 2003. A multispecies approach to ecological valuation and conservation. Conservation Biology 17, 196–206.
Rustigian, H.L., Santelmann, M.V., Schumaker, N.H., 2003. Assessing the potential impacts of alternative landscape designs on amphibian population dynamics. Landscape Ecology 18, 65–81.
Shaffer, B.H., Alford, R.A., Woodward, B., Richards, S.J., Altig, R.G., Gascon, C., 1994. Quantitative sampling of amphibian larvae. In: Heyer, W.R., Donnelly, M.A., McDiarmid, R.W., Hayekand, A.C., Foster, M.S. (Eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians, Biological Diversity Handbook Series. Smithsonian Institution Press, Washington, pp. 130–141.
Shoemaker, V.H., 1988. Physiological ecology of amphibians in desert environments. Journal of Arid Environments 14, 145–153.
Smith, H.M., 1934. The amphibians of Kansas. American Midland Naturalist 15, 377–527.
Strecker, J.K., 1926. Chapters from the life-histories of Texas reptiles and amphibians: Part one. Contributions from Baylor University Museum 8, 1–12.
Sullivan, B.K., 2005. *Bufo punctatus*. In: Lannoo, M.J. (Ed.), Amphibina Declines: The Conservation Status of United States Species. University of California Press, Berkeley, CA, pp. 430–432.
Sullivan, B.K., 1989. Desert environments and the structure of anuran mating systems. Journal of Arid Environments 17, 175–183.
Sullivan, B.K., Fernandez, P.J., 1999. Breeding activity, estimated age-structure, and growth in Sonoran Desert anurans. Herpetologica 55, 334–343.
Sullivan, B.K., Bowker, R.W., Malmos, K.B., Gergus, E.W.A., 1996. Arizona distribution of three Sonoran Desert anurans: *Bufo retiformis*, *Gastrophryne olivacea*, and *Pternohyla fodiens*. Great Basin Naturalist 56, 38–47.
Tevis, L., 1966. Unsuccessful breeding by desert toads (*Bufo Punctatus*) at limit of their ecological tolerance. Ecology 47, 766–775.
Turner, F.B., 1959. Some features of the ecology of *Bufo punctatus* in Death Valley, California. Ecology 40, 175–181.
Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), 1986. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, Wisconsin.
Vos, C.C., Stumpel, A.H.P., 1996. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the tree frog (*Hyla arborea*). Landscape Ecology 11, 203–214.
Woodward, B.D., Mitchell, S.L., 1991. The community ecology of desert anurans. In: Polis, G.A. (Ed.), The Ecology of Desert Communities. Arizona University Press, Tucson, AZ, pp. 223–248.
Wu, X.B., Smeins, F.E., 2000. Multiple-scale habitat modeling approach for rare plant conservation. Landscape and Urban Planning 51, 11–28.