Journal of Wildlife Management 74(4):808–815; 2010; DOI: 10.2193/2009-207

Management and Conservation Article

Habitat Characteristics of Lowland Leopard Frogs in Mountain Canyons of Southeastern Arizona

J. ERIC WALLACE,[1] *School of Natural Resources, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85721, USA*
ROBERT J. STEIDL, *School of Natural Resources, University of Arizona, 325 Biological Sciences East, Tucson, AZ 85721, USA*
DON E. SWANN, *Saguaro National Park, 3693 South Old Spanish Trail, Tucson, AZ 85730, USA*

ABSTRACT Many aquatic species in the arid southwestern United States are imperiled, persisting primarily in isolated, low-order streams that are increasingly vulnerable to stochastic disturbances. During 2003 and 2004, we surveyed 39 mountain canyons in southeastern Arizona, USA, for lowland leopard frogs (*Rana yavapaiensis*), a species that has declined in abundance and distribution across its range in the United States. We quantified habitat features at 2 spatial scales, canyon and pool, to identify features that distinguished sites inhabited by frogs from those uninhabited by frogs. Canyons inhabited by frogs had watersheds that averaged 8.1 km^2 larger (SE = 2.52), pools that averaged 37.8 m^3 greater (9.30) in volume, gradients that averaged 4.1% (1.40%) less steep, and locations that averaged 3.2 km closer (1.06) to the nearest valley stream than did uninhabited canyons. Plunge pools inhabited by frogs averaged 13.5% (5.66%) more perimeter vegetation, 11.2% (5.34%) more canopy cover, and 1.9 (0.60) more refuges than uninhabited pools. In general, canyons that provided more perennial water during dry summer months and plunge pools that provided more bank heterogeneity were more likely to be inhabited by frogs. Conservation of lowland leopard frogs and other aquatic species that inhabit xeric systems in the southwestern United States depends principally on maintaining riparian ecosystems that provide habitat for these species and the adjacent uplands that influence the structure and function of these systems. Therefore, both riparian areas and their adjacent uplands must be managed to maintain habitat for organisms that inhabit these rare and diverse ecosystems.

KEY WORDS Arizona, canyons, freshwater ecosystems, habitat, intermittent stream, leopard frogs, lowland, plunge pool, *Rana yavapaiensis*, tinaja.

Freshwater ecosystems are imperiled worldwide; however, they are of special concern in the arid southwestern United States because they are rare, constituting <1% of land area in Arizona and New Mexico; support a unique and diverse fauna; and are especially vulnerable to adverse effects of human activities (Briggs 1996, Olson and Dinerstein 1998, Abell et al. 2000). Most of these ecosystems have been altered, degraded, or destroyed through pumping of ground water, impounding of surface water, dredging and draining of channels, and livestock grazing (Briggs 1996, Abell et al. 2000, Rieman et al. 2003). Consequently, many of the aquatic organisms that inhabit these ecosystems are declining and at increasing risk of extinction (Ricciardi and Rasmussen 1999, Abell et al. 2000).

In the United States, for example, 8 of 10 faunal groups considered most endangered are freshwater inhabitants, including mussels, crayfish, fish, and amphibians (Wilcove and Master 2005). In the western United States, many aquatic species have decreased in distribution and abundance, particularly native fish and ranid frogs (Rieman et al. 2003, Bradford 2005). Declines of native ranids are especially apparent in the southwestern United States, where all 7 species depend on stream environments for habitat and are classified as species of conservation concern (Degenhardt et al. 1996, Brennan and Holycross 2006). In Arizona, for example, Tarahumara frogs (*Rana tarahumarae*) have been extirpated, and the distribution and abundance of all 5 species of native leopard frogs have decreased in the past 30 years (Clarkson and Rorabaugh 1989, Witte et al. 2008). Chiricahua leopard frogs (*Rana chiricahuensis*) are listed as threatened and relict leopard frogs (*Rana onca*) are listed as a candidate species under the Endangered Species Act (U.S. Fish and Wildlife Service 2002*a*, *b*). Remaining populations of ranid frogs persist primarily in undisturbed, isolated, low-order streams (Degenhardt et al. 1996, Sredl 2005) that are increasingly vulnerable to stochastic disturbances including flooding, drought, wildfire, and sedimentation and to introductions of nonnative organisms (Degenhardt et al. 1996, Pilliod et al. 2003, Sredl 2005, Witte et al. 2008).

Lowland leopard frogs (*Rana yavapaiensis*) are medium-sized aquatic frogs distributed from southern Arizona and southwestern New Mexico to northwestern Mexico that inhabit low- to mid-elevation rivers, streams, springs, and livestock impoundments (Degenhardt et al. 1996, Sredl 2005). Because of habitat destruction and introductions of nonnative animals, the geographic range of lowland leopard frogs in the United States has contracted, their populations have declined, and they no longer inhabit many of the valley-bottom environments where they were likely once most abundant (Arnold 1940, Pace 1974, Clarkson and Rorabaugh 1989, Degenhardt et al. 1996, Sredl 2005). Further, a pathogenic chytrid fungus, *Batrachochytrium dendrobatidis*, implicated in amphibian declines worldwide, has been identified in lowland leopard frogs, although its role in population declines is uncertain (Bradley et al. 2002, Schlaepfer et al. 2007, Skerratt et al. 2007). Throughout their range in the southwestern United States, lowland leopard frogs are classified as species of concern by natural resource agencies (New Mexico Department of Game and

[1] *E-mail: batrachia@yahoo.com*

Fish 2008); therefore, wildlife biologists have sought increasingly to conserve this species and the small, isolated aquatic environments where it persists.

To foster strategies for conserving lowland leopard frogs, their habitat must be characterized clearly so that remaining habitat can be identified and protected, degraded habitat restored, and potential translocation sites identified and prioritized. Therefore, in 2003 and 2004, we surveyed mountain canyons in southeastern Arizona for lowland leopard frogs and quantified habitat features at 2 spatial scales, canyon and pool, and identified those features that distinguished canyons and pools inhabited by frogs from those uninhabited by frogs.

STUDY AREA

We studied intermittent streams in the Rincon and Santa Catalina mountains of southeastern Arizona, USA, that drained via deeply incised canyons into the Santa Cruz and San Pedro rivers. The mountain ranges are part of the Basin and Range physiographic province and are geologically one metamorphic core complex, encompassing an area of approximately 1,420 km^2 and ranging in elevation from approximately 850 m to 2,765 m. Rainfall in the region is bimodal, averaging 300 mm per year at the lowest elevations and 800 mm per year at the highest elevations, with peaks during summer (Jul–Sep) and winter (Nov–Mar; Desilets et al. 2007). Summer rains can be especially intense, resulting in short-duration, high-velocity floods (Bogan and Lytle 2007). Within the 850-m to 1,460-m elevational range we studied, average daily air temperatures ranged from 21° C to 38° C during summer and from 3° C to 20° C during winter, and water temperatures ranged from lows of 5° C during winter to highs of 24° C during summer (Wallace 2008).

Low-order streams in the region typically did not flow from late spring to early summer, when the only available surface water was restricted to small, isolated, perennial pools that typically ranged from 3 m^2 to 12 m^2 in size; surface flows typically resumed during late summer and winter (Bogan and Lytle 2007). Pools varied from simple bedrock depressions with no perimeter vegetation to pools with soil banks that supported stands of grasses (*Muhlenbergia rigens*, *Cynodon dactylon*), sedges (*Eleocharis* spp., *Carex* spp.), shrubs (*Acacia gregii*, *Cephalanthus occidentalis*, *Baccharis* spp.), and trees (*Quercus* spp., *Juglans major*, *Fraxinus velutina*, *Salix gooddingii*, *Populus fremontii*, *Platanus wrightii*). Vegetation within pools included floating and submerged algal mats (e.g., *Cladophora* spp., *Chara* spp.) and emergent species such as cattails (*Typha* spp.). Upland vegetation communities in the elevational range we studied ranged from Sonoran Desert Scrub at lower elevations to Madrean Evergreen Woodlands at upper elevations (Brown 1982). Land uses in the mountains included scattered livestock grazing at low elevations and recreation throughout the area, with a large portion of the area designated as wilderness by Saguaro National Park and Coronado National Forest.

METHODS

We identified 39 canyons likely to contain perennial water or that supported leopard frogs historically, were free of nonnative animals, and were not predominately in private ownership (E. Wallace, University of Arizona, and D. Swann, Saguaro National Park, unpublished data). We began surveys at canyon mouths, which we defined as the junction of the upper bajada (conjoined alluvial fans) and base of the mountains. Canyon mouths usually occurred at approximately 850 m although in some cases were located at higher elevations. We ended surveys between 1,350 m and 1,460 m, the approximate upper elevational limit of lowland leopard frogs in the region. When canyon mouths were inaccessible due to private land ownership, we began surveys at the lowest elevation possible.

During 2003 and 2004, we surveyed 39 canyons for frogs 3 times each unless we 1) detected a lowland leopard frog on the first or second survey ($n = 12$); 2) found that a canyon contained no water, in which case we excluded it from analysis because of the low likelihood of supporting frogs ($n = 6$); or 3) determined that a canyon had been adversely affected by wildfires in 2002 and 2003 ($n = 8$) such that our ability to survey for frogs and to reliably quantify some habitat characteristics was compromised. Consequently, number of canyons in our sample varied by habitat characteristic and ranged from 24 to 33 (Table 1). We classified canyons or pools as inhabited if we detected frogs of any life stage during any survey and as uninhabited if we never observed frogs during any survey.

Detectability of lowland leopard frogs is high and likely linked to abundance, because we always detected frogs at sites where frogs were most abundant. Based on a subset of canyons known to be inhabited that we surveyed ≥ 3 times between 2002 and 2004, we estimated detectability of frogs by computing the proportion of surveys at individual sites in which we detected a frog of any life stage; we estimated detectability to be 0.82 (95% CI = 0.63–1.0, $n = 11$). Although we cannot be certain that frogs were absent from canyons where we did not detect them, their abundances were likely extremely low.

We surveyed leopard frogs throughout their activity period of February to November but focused surveys between May and July when water levels in canyons were lowest and individuals congregated at isolated pools and detectability of frogs was likely highest (Frost and Platz 1983, Clarkson and Rorabaugh 1989). Consequently, our inferences apply to the driest season of the year when pool availability was lowest. We surveyed the entire bank perimeter of all pools >1 m wide and >0.3 m deep using visual encounter surveys during daylight hours. We approached pools silently and searched the pool edge and water column for frogs and tadpoles while probing and searching vegetation and undercut banks by hand and with flashlights. Lowland leopard frogs are rarely found far from water and are active both day and night (Degenhardt et al. 1996; Stebbins 2003; Sredl and Jennings 2005; E. Wallace, personal observation). Although detectability was likely higher at night, the steep rocky terrain of

Table 1. Habitat characteristics of canyons inhabited and uninhabited by lowland leopard frogs, southeastern Arizona, USA, 2003–2004.

Canyon characteristics	Inhabited			Uninhabited				
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	t	P
Tinajas (%)	13	61.7	6.59	18	73.0	5.60	1.31	0.20
Plunge pools (%)	13	38.3	6.59	18	27.0	5.60	1.31	0.20
Available water								
Vol/pool (m^3)[a]	13	61.6	7.08	18	23.9	6.02	4.56	<0.001
Vol/distance (m^3/km)[a]	13	287.1	67.70	18	110.8	57.54	3.95	0.005
Pool substrate (%)[b]								
Bedrock	11	57.8	6.61	14	64.7	5.86	0.79	0.44
Boulder and cobble[a]	11	5.2	1.78	14	2.2	1.57	1.59	0.13
Gravel and sand[a]	11	37.0	6.68	14	33.1	5.92	0.44	0.67
Pool vegetation (%)[a,b]								
Perimeter	11	11.0	2.84	14	9.7	2.52	0.43	0.67
Submergent	11	2.2	0.80	14	0.7	0.71	1.29	0.21
Floating	11	3.6	1.30	14	1.1	1.15	1.12	0.27
Emergent	11	1.5	3.18	14	5.4	2.82	0.32	0.75
Midstory	11	4.5	0.94	14	2.9	0.83	0.94	0.35
Canopy	11	10.9	4.05	14	3.5	3.59	1.67	0.11
Undercut banks (%)[a]	11	5.2	0.94	14	1.9	0.83	2.55	0.018
Watershed area (km^2)[a]	15	14.3	1.85	18	6.2	1.70	3.37	0.002
Stream gradient (%)	15	9.5	1.03	18	13.6	0.94	−2.89	0.007
Stream sinuosity	15	1.23	0.030	18	1.16	0.028	1.67	0.10
Distance to valley stream (km)[a]	15	2.0	0.79	18	5.3	0.72	−3.34	0.002
Canyon width (m)	11	23.0	2.91	13	17.7	2.68	1.32	0.20
SD of canyon width	11	11.1	1.63	13	7.3	1.50	1.98	0.048
Stream channel width (m)[a]	11	3.4	0.36	13	2.0	0.33	2.42	0.024
Slickrock (m/km)	11	244.6	37.08	13	190.1	34.11	1.08	0.29

[a] Untransformed estimates reported, although we transformed data for analysis.
[b] Averaged across all pools in a canyon.

these mountain canyons precluded safe, effective nighttime surveys. Immediately after visual surveys, we used D-frame dip-nets of 3.2-mm mesh to sweep systematically for tadpoles through areas of shallow water, along undercut banks, and in patches of debris and vegetation. Number of dip-net sweeps per pool ranged from 2 to 12 and varied with pool size and structural heterogeneity. To reduce risks of transferring potential pathogens among study sites, we followed standardized sterilization protocols (Fellers et al. 2001). Sampling was approved under the University of Arizona Institutional Animal Care and Use Committee (protocol no. 02-110).

We characterized habitat of lowland leopard frogs at 2 spatial scales, canyon and pool, by measuring a set of characteristics potentially important to leopard frogs during either the second or third frog survey in each canyon. We characterized canyons based on watershed-scale variables extracted from digital maps (DeLorme 3-D Topoquads, Yarmouth, ME; National Geographic TOPO!, San Francisco, CA) and in the field. From digital maps, we calculated gradient as the change in elevation divided by the stream distance surveyed, and we calculated sinuosity as the actual stream distance surveyed divided by straight-line distance across the survey reach. We also used digital maps (National Geographic TOPO!) to measure distance to valley stream as the distance from the lowest-elevation pool in each canyon to the confluence with the nearest valley-bottom stream, which we defined as a stream channel, whether or not wetted or inhabited by frogs, that drained areas below the mountain bajada. In the field, we characterized geomorphological and hydrological attributes of canyons by sampling between 9 and 11 locations established systematically throughout each canyon and averaged attributes across locations within the canyon for analysis. At each point, we estimated canyon width perpendicular to the channel using range finders. We estimated channel width to the nearest 0.1 m at high flow as demarcated by stream banks at bank-full (Platts et al. 1983) or by water-stained bedrock, which represented width of flow for unconstrained flow over bedrock. We used a simplified Wentworth scale to estimate percentage of coverage of dominant channel substrates including bedrock, boulder and cobble, and gravel and sand in a 4-m long strip centered on each point. We computed standard deviation of canyon-width measurements within a canyon as an estimate of variability in canyon width throughout the survey reach. We combined estimated pool volumes (described below) across each canyon as an index to available water in the survey reach based on the average volume per pool and average volume per distance surveyed. We characterized dominant pool substrate types and vegetation for each canyon by averaging measures taken for all pools in a canyon (described below).

We classified pools as either tinajas or plunge pools based on their structural characteristics. We defined tinajas as bedrock-bound pools with little to no soil deposition along banks and plunge pools as pools with some soil-bank development that generally formed below exposed bedrock slides or boulder piles. We recorded locations of pools with

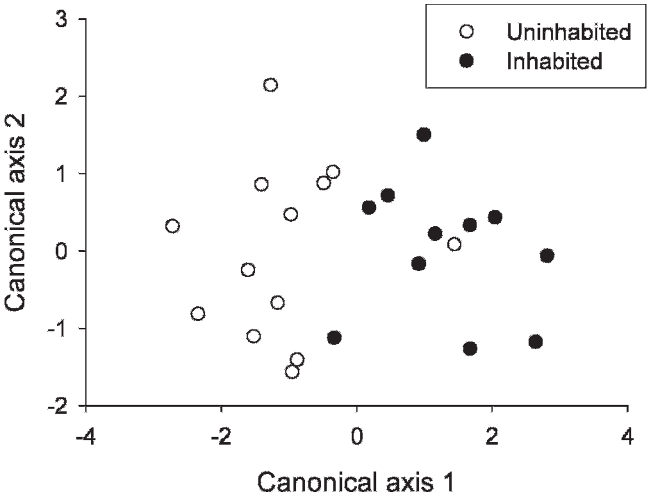

Figure 1. Plot of scores along the first and second canonical discriminant axes of canyons inhabited (n = 11) and uninhabited (n = 13) by lowland leopard frogs in southeastern Arizona, USA, 2003–2004. Canonical axis 1 represents a continuum, from larger well-watered canyons with potentially less-erosive flow regimes that were more likely to be inhabited by frogs, to smaller drier canyons that were less likely to be inhabited by frogs. Canonical axis 2 contained no discriminatory information.

handheld Global Positioning System units and photo-documented pools to aid in relocating pools between surveys.

We estimated length (L), width (W), and depth (D) of pools to the nearest 0.1 m and estimated maximum potential volume based on the formula for an elliptic depression ($4/3 \times \pi \times L \times W \times D$; Van Haveren 1983), the shape that best approximated pool shape in our system. We visually estimated percentage of coverage of perimeter vegetation within 1 m of the entire pool bank, which we defined as the lip surrounding pools at maximum potential volume as demarcated by high-water marks. We visually estimated percentage of coverage of emergent, floating, and submergent vegetation within the pool as well as percentage of coverage of groundcover (0–0.5 m), midstory (0.6–2.5 m), and canopy vegetation (>2.5 m) within 2 m of the pool bank perimeter. We estimated percentage of coverage of dominant pool substrates including bedrock, boulder and cobble, and gravel and sand visually and by probing pool bottoms with dip-nets. We also estimated number of discrete refuges, which we defined as any recess approximately 0.1 m in diameter that extended $\geq$0.1 m back from the bank lip. Finally we estimated percentage of the pool perimeter with undercut banks, which we defined as areas extending $\geq$0.1 m back from the bank lip.

We used t-tests to compare habitat characteristics between canyons and pools classified as inhabited or uninhabited by frogs. At the pool scale, we analyzed data from tinajas and plunge pools separately because of inherent differences in their physical characteristics. At the canyon scale, we used canonical discriminant function analysis (CDFA; SAS Proc STEPDISC, SAS Institute Inc., Cary, NC) to determine a set of habitat characteristics that best distinguished canyons classified as inhabited or uninhabited (McGarigal et al. 2000); because we measured many variables at this scale, we included only those variables that differed ($P < 0.1$) between inhabited and uninhabited canyons as indicated by t-tests. At the pool scale, we used CDFA separately for each type of pool and included pools only from inhabited canyons and used all variables measured. To reduce redundancy of habitat variables, we used Pearson's correlations to identify pairs of variables that were highly correlated ($r > 0.8$) and retained the variable we felt most biologically meaningful. We transformed variables for analysis with natural log, natural log + 1, or square root when necessary to better meet assumptions of parametric statistical tests.

Table 2. Standardized canonical coefficients for habitat characteristics of lowland leopard frogs that distinguished inhabited (n = 11) from uninhabited (n = 13) canyons along the first canonical discriminant axis, southeastern Arizona, USA, 2003–2004.

Canyon characteristic	Coeff.
Vol/distance (log m^3/km)	1.70
Undercut banks (log %)	0.13
Watershed area (log km^2)	−0.99
Stream gradient (%)	−1.16
Stream sinuosity	−0.77
Distance to valley stream (km)	0.19
SD of canyon width	0.03
Stream channel width (m)	0.65

RESULTS

We observed postmetamorphic frogs or tadpoles in 15 of 33 canyons (45%) and counted up to 104 frogs per survey in inhabited canyons ($\bar{x}$ = 15.4, SE = 4.99, n = 30). We observed evidence of breeding based on presence of tadpoles or recently metamorphosed frogs in 11 of 15 inhabited canyons (73%).

Structurally, canyons inhabited by frogs had larger watershed areas, larger pools, and lower stream gradients than uninhabited canyons, characteristics that increased water availability relative to uninhabited canyons (Table 1). Specifically, watershed area averaged 8.1 km^2 larger (SE = 2.52), volume per pool averaged 37.8 m^3 greater (9.30), and total amount of water available within the surveyed reach averaged 176.3 m^3 greater (88.85) in inhabited than uninhabited canyons (Table 1). Stream channels averaged 1.4 m wider (0.49), stream gradients were 4.1% (1.40%) less steep, and pools had 3.3% (1.26%) more undercut banks in inhabited than uninhabited canyons (Table 1). Distance to the nearest valley stream was 3.2 km closer (1.06) and canyon width more variable in canyons inhabited by frogs (Table 1). Canyon characteristics associated with geomorphic and hydrological processes, including watershed area, stream width, and gradient and available surface water best distinguished inhabited and uninhabited canyons along the first canonical axis (Fig. 1). This axis represented a continuum of larger well-watered canyons with potentially less-erosive flow regimes that were more likely to be inhabited by frogs, to smaller, drier canyons that were less likely to be inhabited by frogs (Table 2).

Plunge pools inhabited by frogs averaged 13.5% (5.66%) more perimeter vegetation, 11.2% (5.34%) more canopy cover, and 1.9 (0.60) more refuges than uninhabited pools

Table 3. Habitat characteristics of lowland leopard frogs in plunge pools (n = 18 inhabited, n = 15 uninhabited) and tinajas (n = 23 inhabited, n = 31 uninhabited) in southeastern Arizona, USA, 2003–2004.

	Plunge pools						Tinaja					
	Inhabited		Uninhabited				Inhabited		Uninhabited			
Characteristics	$\bar{x}$	SE	$\bar{x}$	SE	t	P	$\bar{x}$	SE	$\bar{x}$	SE	t	P
Pool size (m^3/pool)[a]	94.4	18.75	84.2	20.54	0.51	0.61	38.4	10.06	28.2	8.66	0.40	0.69
Depth[a]	1.4	0.12	1.3	0.13	0.42	0.67	1.3	0.13	1.1	0.11	1.36	0.18
Substrate (%)												
Bedrock	40.2	6.82	49.1	7.62	−0.88	0.39	71.1	5.33	70.1	4.60	0.05	0.96
Boulder and cobble[a]	11.1	3.44	5.3	3.78	1.50	0.14	5.2	2.01	1.3	1.72	1.40	0.17
Gravel and sand[a]	51.1	7.04	46.0	7.72	0.36	0.72	23.1	5.03	27.2	4.31	−0.67	0.51
Vegetation (%)[a]												
Perimeter	27.5	3.82	14.0	4.18	3.29	0.002	2.8	1.47	0.3	1.27	0.88	0.38
Submergent	0.6	2.19	8.0	2.40	−2.48	0.019	1.3	0.85	0.0	0.73	1.16	0.25
Floating	1.1	4.28	21.0	4.69	−2.97	0.006	2.2	2.47	4.7	2.13	−0.99	0.32
Emergent	8.8	2.48	2.3	2.71	2.26	0.031	0.0	0.00	0.0	0.00		
Canopy	15.8	3.60	4.7	3.94	2.44	0.021	0.2	0.14	0.0	0.12	1.16	0.25
Undercut banks (%)[a]	10	2.4	8	2.7	1.62	0.11	3	1.4	2	1.20	1.36	0.18
No. of refuges[a]	2.7	0.40	0.8	0.44	3.35	0.002	0.4	0.14	0.3	0.12	0.94	0.35

[a] Untransformed estimates reported, although we transformed data for analysis.

(Table 3). Characteristics of plunge pools associated with vegetation structure best distinguished inhabited and uninhabited plunge pools along the first canonical axis (Fig. 2A). This axis represented a gradient of pools with well-vegetated banks and greater canopy cover that were more likely to be inhabited by frogs, to pools with banks nearly devoid of vegetation that were less likely to be inhabited by frogs (Table 4). In contrast, no measured characteristics distinguished inhabited from uninhabited tinajas in the univariate analysis (Table 3). Similarly, no characteristics distinguished inhabited from uninhabited tinajas along the first canonical axis because of their structural simplicity (Table 4; Fig. 2B).

DISCUSSION

Canyons inhabited by lowland leopard frogs differed from uninhabited canyons primarily in structural characteristics associated with geomorphic and fluvial processes, because frogs were more likely to inhabit canyons with larger watersheds, wider stream channels, lesser stream gradients, and larger pools. In general, these characteristics distinguish canyons that are likely to maintain more surface water, with geological features that promote formation of large, deep pools that are more likely to persist through drought periods. Although amount of water available in the surveyed reach was mostly explained by watershed area ($r = 0.74$, $P < 0.001$), hydrological features that supply pools through subsurface seeps, hyporheic flow, or small, perched aquifers also may have affected amount of available surface water (Schneider 1996, Cunningham et al. 1998, Wigington et al. 2006). Wider channels, higher variation in canyon width, and lesser stream gradients of inhabited canyons also might reduce adverse effects of flash floods that could displace larvae from natal pools or scour soil and vegetation from in and around pools (Degenhardt et al. 1996). The combination of large watershed area that intercepts limited precipitation and subsurface physical features that provide reliable perennial surface water for frogs in all life stages during the driest season likely enhances population persistence of lowland leopard frogs. For example, canyons unaffected by fire where we observed breeding contained 3 times as much surface water as inhabited canyons where we did not observe breeding. The influence of these geomorphological and hydrological processes on availability of perennial surface water is critical to maintenance of frogs and other biota in these xeric environments (Montgomery 1999, Wigington et al. 2006).

Although abiotic features were important determinants of habitat for frogs, biological features were also influential. Canyons inhabited by frogs were nearer to valley streams than uninhabited canyons and therefore less isolated geographically. Although it is difficult to determine absence of many species with certainty, lowland leopard frogs appear to have been extirpated from several canyons in our study area because they were not observed during multiple surveys spanning periods of $\geq$4 years (D. Swann, unpublished data). Recolonization after local extirpation likely depends on proximity and suitable connections to other frog populations (Witte et al. 2008). Because canyons are surrounded by a desert matrix unsuitable for leopard frogs, long-distance movements likely occur along watercourses during rainy periods when streams flow (Sredl 2005, Sredl and Jennings 2005, Wells 2007). Therefore, if the amount and persistence of surface water linking canyons through valley streams is reduced further by lowering of water tables, or if canyons or valley streams are degraded by presence of aquatic nonnative animals, connectivity among frog populations will be reduced, disrupting large-scale demographic processes. Maintaining or restoring function of stream corridors that connect mountain canyons will help maintain

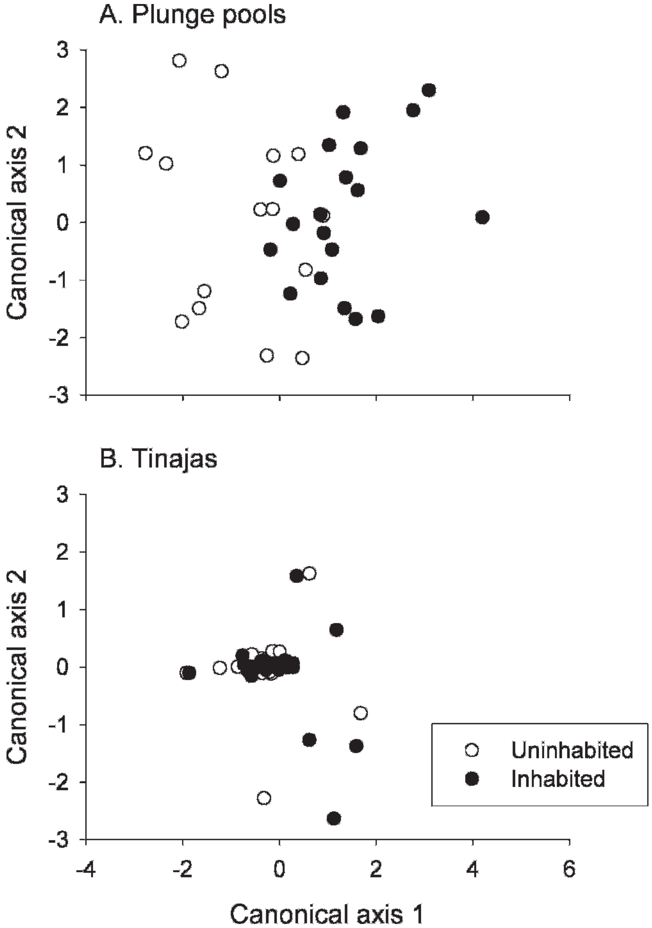

Figure 2. Plot of scores along the first and second canonical discriminant axes of (A) plunge pools inhabited ($n = 19$) and uninhabited ($n = 15$) and (B) tinajas inhabited ($n = 24$) and uninhabited ($n = 33$) by lowland leopard frogs in mountain canyons of southeastern Arizona, USA, 2003–2004. Canonical axis 1 for plunge pools represented a gradient of pools with well-vegetated banks and greater canopy cover that were more likely to be inhabited by frogs, to pools with banks nearly devoid of vegetation that were less likely to be inhabited by frogs. Canonical axis 2 contained no discriminatory information. Canonical axis 1 for tinajas contained no discriminatory information, nor did canonical axis 2.

populations of frogs and other aquatic organisms across this arid region (Fagan et al. 2002, Hall and Steidl 2007, Witte et al. 2008).

Like most leopard frogs, lowland leopard frogs are habitat generalists. Pools inhabited by frogs in our study area ranged in character, from well-vegetated plunge pools similar to those used by leopard frogs in other areas (Degenhardt et al. 1996, Sredl 2005, Sredl and Jennings 2005), to tinajas devoid of vegetation. Structure of plunge pools varied considerably, with frogs more likely to inhabit pools with greater bank heterogeneity and canopy cover. Bank heterogeneity provided by vegetation, refuges, and undercut banks likely provided cover from predators, moist stable microclimates, and more diverse foraging substrates (Sredl and Jennings 2005, Wells 2007). In contrast, habitation of tinajas was unaffected by any of the characteristics we measured, possibly because of the structural simplicity of these pools. In some inhabited canyons, including several with high numbers of frogs, tinajas were used readily by

Table 4. Standardized canonical coefficients for habitat characteristics of lowland leopard frogs that distinguished inhabited ($n = 19$) from uninhabited ($n = 15$) plunge pools and inhabited ($n = 24$) from uninhabited ($n = 33$) tinajas along the first canonical discriminant axis in mountain canyons of southeastern Arizona, USA, 2003–2004.

Pool characteristics	Plunge pools	Tinajas
Vol/pool (log m^3)	−0.01	−0.42
Max. depth/pool (log m)	0.46	1.02
Substrate (log %)		
Bedrock	0.42	−0.05
Boulder and cobble	0.20	0.32
Terrestrial vegetation (log %)		
Perimeter	1.34	−0.39
Overhanging	−0.12	0.91
Ground cover	0.92	0.01
Midstory	−1.56	0.00
Canopy	0.83	0.17
Aquatic vegetation (log %)		
Floating	−0.78	−0.30
Submergent	0.21	0.02
Emergent	−0.04	0.08
Undercut banks (log + 1%)	−0.75	0.53
No. of refuges (log)	0.41	0.49

frogs when these pools were the dominant type ($\geq 75\%$) and provided most of the available surface water. Therefore, any pools that contain water during the physiologically challenging summer drought season might be used by frogs, because availability of perennial water during this season is likely the most limiting resource for persistence of all life stages of leopard frogs, particularly tadpoles. Lowland leopard frogs breed most frequently in late winter and early spring, the period immediately preceding the driest time of the year (Collins and Lewis 1979, Frost and Platz 1983). Because tadpoles need approximately 3–9 months to metamorphose, drying of breeding pools likely affects breeding success and recruitment (Collins and Lewis 1979, Sredl 2005).

Canyons that provide perennial water during dry summer months in the desert environment of southeastern Arizona are vital resources for leopard frogs and a variety of other aquatic and terrestrial organisms, many of which persist at the periphery of what was once a larger, more perennial system of interconnected aquatic environments (Hall and Steidl 2007). Intermittent, low-order streams are also critical to persistence of other aquatic organisms in areas that are much less arid than the area we studied (Wigington et al. 2006), underscoring the importance of these streams to aquatic biota in desert environments (Reiman et al. 2003, Bogan and Lytle 2007, Hall and Steidl 2007). Increased human uses of water and widespread introductions of nonnative species during the past century have diminished quantity and quality of these surface waters, at least partially explaining declines of leopard frog populations across the region (Briggs 1996, Rieman et al. 2003, Witte et al. 2008). Despite their limited size, the rarity of these aquatic environments and their high conservation value merits management attention disproportionate to the area they occupy on the landscape.

MANAGEMENT IMPLICATIONS

Although particular features of canyons and pools affect habitation by lowland leopard frogs, many of the features important to frogs are influenced by larger-scale processes, specifically those that function to maintain perennial water in pools during summer droughts. Land-use practices such as mining, timber management and harvest, fire suppression, livestock grazing, and road building can affect these upland processes and increase erosive flows and sediment loads in streams following rain events, altering the structure of pools required by leopard frogs. Therefore, conservation of lowland leopard frogs and other aquatic organisms that inhabit these rare environments depends principally on managing riparian ecosystems and their adjacent uplands to maintain the integrity of large-scale processes that function to provide and maintain habitat for these vulnerable organisms.

ACKNOWLEDGMENTS

We appreciate the efforts of C. Butler, M. Ward, R. Miller, E. Zylstra, and E. Stitt, who assisted with field surveys, and T. Skinner, who provided logistical support. C. Schwalbe, W. J. Matter, and 2 anonymous referees provided constructive reviews of earlier drafts. Our work was funded by Saguaro National Park, T & E Inc., Western National Parks Association, Coronado National Forest, and the School of Natural Resources, University of Arizona.

LITERATURE CITED

Abell, R. A., D. M. Olson, E. Dinerstein, P. T. Hurley, J. T. Diggs, W. Eichbaum, S. Walters, W. Wettengel, T. Allnut, C. J. Loucks, and P. Hedao. 2000. Freshwater ecoregions of North America: a conservation assessment. Island Press, Washington, D.C., USA.

Arnold, L. W. 1940. An ecological study of the vertebrate animals of the mesquite forest. Thesis, University of Arizona, Tucson, USA.

Bogan, M. T., and D. A. Lytle. 2007. Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. Freshwater Biology 52:290–304.

Bradford, D. F. 2005. Factors implicated in amphibian population declines in the United States. Pages 915–925 *in* M. Lanoo, editor. Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, USA.

Bradley, G. A., P. C. Rosen, M. J. Sredl, T. R. Jones, and J. E. Longcore. 2002. Chytridiomycosis in native Arizona frogs. Journal of Wildlife Diseases 38:206–212.

Brennan, T. C., and A. T. Holycross. 2006. A field guide to amphibians and reptiles in Arizona. Arizona Game and Fish Department, Phoenix, USA.

Briggs, M. K. 1996. Riparian ecosystem recovery in arid lands; strategies and references. University of Arizona Press, Tucson, USA.

Brown, D. E., editor. 1982. Biotic communities of the American Southwest—United States and Mexico. Desert Plants 4:1–342.

Clarkson, R. W., and J. C. Rorabaugh. 1989. Status of leopard frogs (*Rana pipiens* complex: Ranidae) in Arizona and Southeastern California. Southwestern Naturalist 34:531–538.

Collins, J. P., and M. A. Lewis. 1979. Overwintering tadpoles and breeding season variation in the *Rana pipiens* complex in Arizona. Southwestern Naturalist 24:371–373.

Cunningham, E. B., A. Long, C. Eastoe, and R. L. Bassett. 1998. Migration of recharge waters downgradient from the Santa Catalina Mountains into the Tucson basin aquifer, Arizona, USA. Hydrogeology Journal 6:94–103.

Degenhardt, W. G., C. W. Painter, and A. H. Price. 1996. Amphibians and reptiles of New Mexico. University of New Mexico Press, Albuquerque, USA.

Desilets, L. E., B. Nijssen, B. Ekwurzel, and T. P. A. Ferre. 2007. Post-wildfire changes in suspended sediment rating curves: Sabino Canyon, Arizona. Hydrological Processes 21:1413–1423.

Fagan, W. F., P. Unmack, C. Burgess, and W. L. Minckley. 2002. Rarity, fragmentation, and extinction risk in desert fishes. Ecology 83:3250–3256.

Fellers, G. M., D. E. Green, and J. E. Longcore. 2001. Oral chytridiomycosis in the mountain yellow-legged frog (*Rana muscosa*). Copeia 2001:945–953.

Frost, J. S., and J. E. Platz. 1983. Comparative modes of reproductive isolation among four species of leopard frogs (*Rana pipiens* complex) in Arizona. Evolution 37:66–78.

Hall, D. H., and R. J. Steidl. 2007. Movements, activity, and spacing of Sonoran mud turtles (*Kinosternon sonoroiense*) in interrupted mountain streams. Copeia 2007:403–412.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer, New York, New York, USA.

Montgomery, D. R. 1999. Process domains and the river continuum. Journal of the American Water Resources Association 35:397–410.

New Mexico Department of Game and Fish. 2008. Threatened and endangered species of New Mexico 2008 biennial review. New Mexico Department of Game and Fish, Santa Fe, USA.

Olson, D. M., and E. Dinerstein. 1998. The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. Conservation Biology 12:502–515.

Pace, A. E. 1974. Systematic and biological studies of the leopard frogs (*Rana pipiens* complex) of the United States. Miscellaneous Publications of the Museum of Zoology University of Michigan 148:1–140.

Pilliod, D. S., R. B. Bruce, E. J. Hyde, C. A. Pearl, and P. S. Corn. 2003. Fire and amphibians in North America. Forest Ecology and Management 178:163–181.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service Intermountain Forest and Range Experiment Station General Technical Report INT-138, Ogden, Utah, USA.

Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater fauna. Conservation Biology 13:1220–1222.

Rieman, B., D. Lee, and D. Burns. 2003. Status of native fishes in the western United States and issues for fire and fuels management. Forest Ecology and Management 178:197–211.

Schlaepfer, M. A., M. J. Sredl, P. C. Rosen, and M. J. Ryan. 2007. High prevalence of *Batrachochytrium dendrobatidis* in wild populations of lowland leopard frogs *Rana yavapaiensis* in Arizona. Ecohealth 4:421–427.

Schneider, S. H., editor. 1996. Encyclopedia of climate and weather. Oxford University Press, New York, New York, USA.

Skerratt, L. F., L. Berger, R. Speare, S. Cashins, K. R. McDonald, A. D. Phillott, H. B. Hines, and N. Kenyon. 2007. Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. Ecohealth 4:125–134.

Sredl, M. J. 2005. Species account: *Rana yavapaiensis*. Pages 596–599 *in* M. Lanoo, editor. Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, USA.

Sredl, M. J., and R. D. Jennings. 2005. Species account: *Rana chiricahuensis*. Pages 546–549 *in* M. Lanoo, editor. Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, USA.

Stebbins, R. C. 2003. A field guide to western reptiles and amphibians. Third edition. Houghton Mifflin, Boston, Massachusetts, USA.

U.S. Fish and Wildlife Service. 2002*a*. Endangered and threatened wildlife and plants; listing of the Chiricahua leopard frog (*Rana chiricahuensis*); final rule. Federal Register 67(114):40790–40811.

U.S. Fish and Wildlife Service. 2002*b*. Endangered and threatened wildlife and plants; review of species that are candidates or proposed for listing as endangered or threatened; annual notice of findings on recycled petitions; annual description of progress on listing actions. Federal Register 67(114):40657–40679.

Van Haveren, B. 1986. Hydrologic properties. Pages 613–632. *in* A. Y. Cooperrider, R. J. Boyd, and H. R. Stuart, editors. Inventory and monitoring of wildlife habitat. U.S. Department of the Interior, Bureau of Land Management Service Center, Denver, Colorado, USA.

Wallace, J. E. 2008. Habitat of lowland leopard frogs in mountain canyons of southeastern Arizona. Thesis, University of Arizona, Tucson, USA.

Wells, K. D. 2007. The ecology and behavior of amphibians. University of Chicago Press, Chicago, Illinois, USA.
Wigington, P. J., Jr., J. L. Ebersole, M. E. Colvin, S. G. Leibowitz, B. Miller, B. Hansen, H. R. Lavigne, D. White, J. P. Baker, M. R. Church, J. R. Brooks, M. A. Cairns, and J. E. Compton. 2006. Coho salmon dependence on intermittent streams. Frontiers in Ecology and the Environment 4:513–518.
Wilcove, D. S., and L. L. Master. 2005. How many endangered species are there in the United States? Frontiers in Ecology and the Environment 3:414–420.
Witte, C. L., M. J. Sredl, A. L. Kane, and L. L. Hungerford. 2008. Epidemiological analysis of factors associated with local disappearances of native ranid frogs in Arizona. Conservation Biology 22:375–383.

Associate Editor: Gray.