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DISTRIBUTIONAL CHANGES AND POPULATION STATUS OF AMPHIBIANS IN THE EASTERN MOJAVE DESERT

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ABSTRACT.—Several amphibian species historically inhabited sparsely distributed wetlands in the Mojave Desert of western North America, habitats that have been dramatically altered or eliminated as a result of human activities. The population status and distributional changes of amphibians were investigated over a 20,000-km^2 area in the eastern Mojave Desert in 2 ways. For upland sites (i.e., sites outside of major valleys and river floodplains), where wetland habitat is almost exclusively springs, encounter surveys were conducted at 128 sites in 1997–1999, and results were compared to historical (pre-1970) locality records. For lowland sites (i.e., sites within major valleys and river floodplains), locality records and field surveys in 1995–2004 were reviewed to detect changes in distribution over time. Amphibians were found at 79% of upland sites. By far the most common species was the red-spotted toad (*Bufo punctatus,* 73% of sites), followed by the Pacific chorus frog (*Pseudacris regilla*), Woodhouse's toad (*B. woodhousii*), relict leopard frog (*Rana onca*), and the introduced American bullfrog (*R. catesbeiana*). Taxa observed or collected in the lowlands since 1990 were Woodhouse's toad, Pacific chorus frog, American bullfrog, and the introduced tiger salamander (*Ambystoma tigrinum*). Four taxa (Vegas Valley leopard frog [*Rana* sp.], Arizona toad [*B. microscaphus*], Great Plains toad [*B. cognatus*], and Great Basin spadefoot [*Spea intermontana*]) had historical records but no evidence of occurrence in the study area within the past 5 decades. The amphibian fauna of the study area has changed dramatically in the past century, primarily at lowland sites where habitat loss and modification have been extreme. Striking changes are the nearly complete replacement of native leopard frogs (i.e., Vegas Valley and relict leopard frogs) with the introduced bullfrog, and the complete replacement of the Arizona toad in Las Vegas Valley with Woodhouse's toad or hybrids with predominantly Woodhouse's traits. In contrast, the distributions of 2 species characteristic of upland springs, red-spotted toad and Pacific chorus frog, appear to have changed little from their historical distributions, despite habitat modification at many sites.

Key words: amphibian, desert, distribution, distributional change, Mojave Desert, population status, springs, wetland.

Populations of amphibians around the globe have been declining for the past several decades, although patterns of population change have varied among geographic regions and time intervals (Alford and Richards 1999, Houlahan et al. 2000, Stuart et al. 2004). Amphibians may be especially susceptible to decline in desert environments because wetland habitats are generally scarce and are often the focus of human activities. Several amphibian species inhabit the eastern Mojave Desert of western North America (see MacMahon [1985] for a general regional description). Within the Mojave Desert, the eastern region historically had the greatest extent of wetland habitat and the richest amphibian fauna. More recently, part of the region, Las Vegas Valley, has become one of the fastest growing urban areas in the United States.

The amphibians of this region all require surface water for breeding and are restricted year-round to the vicinity of ephemeral or permanent wetlands, springs, or water catchments. Prior to modern development in the 1900s, large wetland habitats consisted of rivers with scattered wetlands in the floodplains and spring-fed wetlands in some of the major valleys. Small and often ephemeral springs and catchments occurred mostly in the uplands. Unfortunately, nearly all of the original wetlands in the region have been modified by human activities, often to the extent of eliminating the native riparian and aquatic habitats entirely. Such activities include impoundments, water diversions, groundwater pumping, and grazing/trampling. Artificial wetlands, however, have been created by perched water tables, urban

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runoff, and wastewater (Malmberg 1965, Jones and Cahlan 1975). Changes to the original wetland ecosystems have further resulted from introductions of numerous species comprising predators, competitors, or agents of habitat change that may affect amphibians, including many fishes, American bullfrog (*Rana catesbeiana*), tiger salamander (*Ambystoma tigrinum*), crayfish (*Procambarus clarkii*), and saltcedar (*Tamarix* spp.; Jennings and Hayes 1994, Stebbins 2003).

Concomitant with these changes, declines in native aquatic fauna of the eastern Mojave Desert have been dramatic. The Vegas Valley leopard frog (sometimes treated as a subspecies of *Rana onca* [Stebbins 2003], but referred to herein as *R. fisheri* because of its taxonomic uncertainty [Jaeger et al. 2001]) became extinct in the 1940s (Stebbins 1951, Jennings and Hayes 1994). The relict leopard frog (*Rana onca*) has been reduced in distribution to as few as 5 populations (Jaeger et al. 2001, Bradford et al. 2004). Three fish from Las Vegas or Pahrump Valleys have become extinct (*Rhinichthys deaconi, Empethrichys latos pahrump, E. l. concavus;* Miller et al. 1989), and several other fish taxa have been federally listed as endangered or threatened (Deacon 1979). At least 1 springsnail, *Pyrgulopsis coloradensis*, has become extinct (Hershler 1998, D.W. Sada unpublished data).

Other than the aforementioned 2 leopard frog taxa and the red-spotted toad (*Bufo punctatus;* Bradford et al. 2003), the status of amphibians in the region is essentially unknown. Within recent decades, 10 amphibians had nominal geographic ranges that included portions of the eastern Mojave Desert (Stebbins 2003). These species are *Ambystoma tigrinum* (introduced—see Discussion), *Bufo cognatus* (Great Plains toad), *B. microscaphus* (Arizona toad), *B. punctatus*, *B. woodhousii* (Woodhouse's toad), *Pseudacris regilla* (Pacific chorus frog), *Rana catesbeiana* (introduced), *R. fisheri, R. onca,* and *Spea intermontana* (Great Basin spadefoot). Although the occurrence of *R. yavapaiensis* (lowland leopard frog) has been indicated within the study area (Stebbins 2003), it is not included in the study because populations formerly ascribed to *R. yavapaiensis* in the study area and further up the Virgin River have been shown to be *R. onca* (Jaeger et al. 2001). In this paper we use historical records and survey data from 1997 to 2004 to evaluate changes in the population status and distribution of the 10 amphibians in the eastern Mojave Desert.

METHODS

The study area consists of ca. 20,000 km^2 primarily in southern Nevada, extending into California and Arizona (Fig. 1). This region includes a number of distinct mountain ranges and intervening valleys, ranging in elevation from 210 m along the Colorado River to 3630 m in the Spring Mountains. The area drains primarily to the Colorado River system, but it also includes or drains to several closed basins. In recent decades land use has been mostly low-density livestock grazing, although other uses have included urban development, military activities, water development, agriculture, mining, and recreation.

Most springs in the upland portion of the study area continue to produce surface water, although some have been destroyed and many have been greatly modified. Such changes have often resulted from the development of water for livestock, domestic use, mining, wild horses and burros, and native terrestrial wildlife. Large spring systems in the Las Vegas and Pahrump Valleys, in contrast, have been destroyed by diversion and groundwater pumping, with the exception of Corn Creek Springs, an isolated locality in northern Las Vegas Valley that has been greatly modified (Jones and Cahlan 1975, Soltz and Naiman 1978). Wetlands remain in these valleys as a result of urban or agricultural runoff, perched water tables, wastewater flow, and creation of urban ponds. Several washes that formerly rarely contained water now flow year-round. Formation of Lake Mead in 1935 and Lake Mojave in 1951 resulted in the inundation of the entire length of the Colorado and Virgin Rivers within the study area. The springs that produce the Muddy River persist, but the river and its floodplain have been modified primarily by agricultural development and water diversion (Eakin 1964).

The status and distributional changes of amphibians were evaluated separately for the upland and lowland portions of the study area because upland habitats were mostly discrete and comprehensively surveyed, whereas lowland habitats were largely interconnected and surveyed at a subset of locations. Thus, results for upland sites are presented by site, whereas

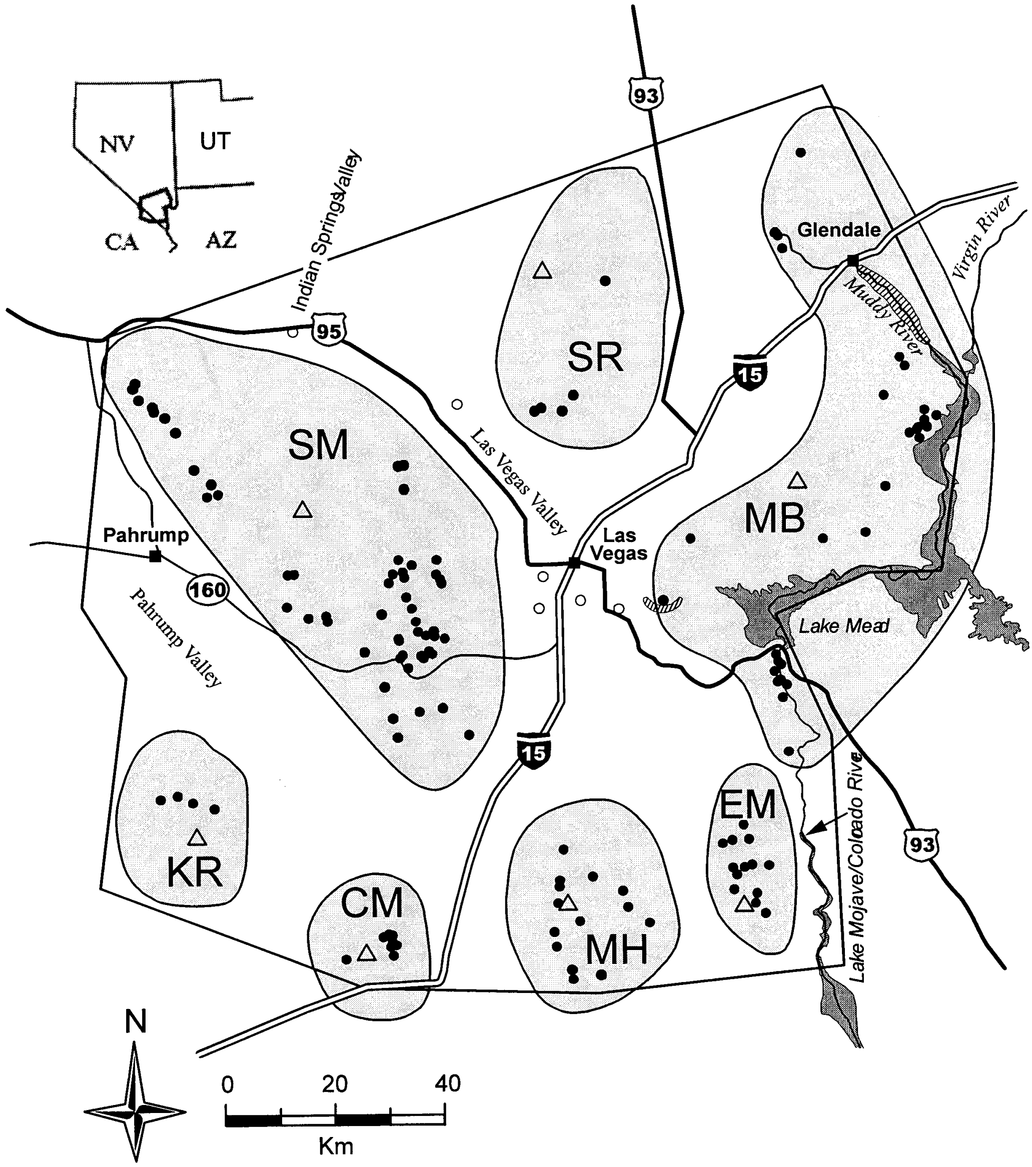

Fig. 1. Study area (outline) and sites surveyed for amphibians in the eastern Mojave Desert. Closed circles indicate sites in the Upland Springs Survey (n = 128). Shaded areas represent mountain range groups: CM = Clark Mountain Range, EM = Eldorado Mountains, KR = Kingston Range, MB = Muddy and Black Mountains, MH = McCullough and Highland Ranges, SM = Spring Mountains, SR = Sheep Range. High point in each mountain range group is indicated by a triangle. The Lowland Records Review and Survey included sites within the Las Vegas, Pahrump, and Indian Springs valleys; floodplains of the Muddy River and the former Colorado and Virgin Rivers (now submerged by Lakes Mead and Mojave); and shorelines of Lakes Mead and Mojave. Sites surveyed for amphibians in these areas are depicted by cross-hatching (Las Vegas Wash and Muddy River) and open circles.

results for lowland sites are presented by geographic area.

For upland sites (sites outside the major valleys and river floodplains), wetland habitat was almost exclusively springs, most of which were ephemeral. Encounter surveys were conducted at these sites, and the results were compared to historical records from specimens and literature (hereinafter the Upland Springs Survey). For lowland sites (sites within the major valleys and river floodplains), status and distributional changes were evaluated by reviewing amphibian specimen and literature records and by conducting encounter surveys at selected areas (hereinafter the Lowland Records Review and Survey). Lowland sites comprised the Las Vegas, Pahrump, and Indian Springs Valleys, and the floodplains of the Colorado, Virgin, and Muddy Rivers (Fig. 1). Some upland sites were within a few hundred meters of lowland sites along the Colorado and Muddy Rivers. For both the Upland Springs Survey and Lowland Records Review and Survey, historical records are defined as pre-1970 because records became sparse after this time.

For the Upland Springs Survey, potential sites for survey were identified as a spring or natural catchment (a single site) shown on USGS 7.5′ topographic maps (n = 141) or identified from agency records (n = 12). Potential sites located within 350-m linear distance of each other, or within 1.6 km via a drainage channel, were considered a single site. Sites above 1735 m elevation were omitted because this was the upper elevation limit for the most commonly encountered amphibian, *B. punctatus* (Bradford et al. 2003), and it approximated the upper limit for the sparse shrub vegetation characteristic of the Mojave Desert. Only *P. regilla* in the Spring Mountains is known to range higher (unpublished data). Of the 153 total sites that met the criteria for inclusion in the survey, 11 were dry over 2 years of repeated visits (including 1 year with above-normal precipitation); fourteen others were not reached during the proper season, were destroyed by urban development, or were inaccessible because of either private property or physical limitations. The remaining 128 springs comprised the Upland Springs Survey (Fig. 1). Two of these sites form part of the headwaters of the Muddy River and are only a few hundred meters from the domain of the Lowland Records Review and Survey (i.e., the floodplain of the river).

In the Upland Springs Survey, 2 individuals surveyed amphibians by visual and aural search for adults, tadpoles, and eggs in all aquatic habitat along 400 m of drainage channel. Surveys were conducted in April–July 1997, 1998, and 1999. In 1997 and 1999 annual precipitation (9.2 and 9.5 cm, respectively, in Las Vegas) was slightly below average (10.7 cm), whereas in 1998 (18.7 cm) it was well above average. All sites were searched during daylight and again at night, except for 5 sites where at least 1 amphibian species had already been detected during the day. Night surveys, conducted using headlamps and a 50,000-lux light, included the aquatic habitat plus adjacent terrestrial habitat within several meters of water. A 2nd night survey was conducted at 35 of the 41 sites where no amphibian was found during previous surveys. Species identifications were based on observations of adults for all species except *P. regilla,* which have easily identifiable tadpoles, and 2 occurrences of *B. punctatus* (identified by presence of tadpoles, following Altig et al. [1998], and/or presence of newly metamorphosed toads).

For the Lowland Records Review and Survey, nighttime visual and aural encounter surveys were conducted along multiple segments of a 9.5-km reach of Las Vegas Wash in Las Vegas Valley and a 23.1-km reach of the Muddy River. Reach segments were surveyed between 1 and 4 times in March–July 2004. Other localities were also visited 1 to several times in 1995–2004 in Las Vegas Valley (Corn Creek Springs, Duck Creek near Highway 95, Flamingo Wash at Decatur Boulevard, vicinity of Flamingo Wash at Swenson Avenue, Las Vegas Springs Preserve) and in Indian Springs valley (Cactus Spring). All localities contain permanent water.

For both the Upland Springs Survey and Lowland Records Review and Survey, specimen records were solicited from 35 museums deemed likely to have holdings from the region. Selected specimens were examined to verify species identification, particularly for 3 taxa that have sometimes been confused: *B. cognatus, B. microscaphus,* and *B. woodhousii* (Appendix). Identifications were made by R. Jennings (unpublished) for *R. fisheri* and DFB for other taxa, except where noted. *Bufo cognatus* was identified according to Stebbins (2003), and *B. microscaphus* and *B. woodhousii* were identified using the morphological hybrid-index scheme of Sullivan (1995) for individuals with >50 mm snout-vent length (SVL). Evaluations of specimens for *Rana fisheri* and *R. onca* refer to other studies (Jennings and Hayes 1994, Jaeger et al. 2001, Bradford et al. 2004). Collection symbolic codes follow Leviton et al. (1985) except the University of Nevada Las Vegas, Marjorie Barrick Museum, represented as MBM. Of the 35 museums contacted, 12

TABLE 1. Number of sites where amphibians were found in the Upland Springs Survey during 1997–1999 (n = 128 sites). For the 5 sites not surveyed at night, daytime surveys revealed *B. punctatus* at all 5 and *P. regilla* at 2. Locations of sites by mountain range group are given in parentheses (defined in Fig. 1) in order of frequency. "Historical" refers to pre-1970 specimen records. At least 1 specimen was verified for all historical sites except 3 sites for *B. punctatus*, 2 for *B. woodhousii*, and 2 for *P. regilla*.

Species	Historical sites	Historical sites occupied	Total sites occupied
Ambystoma tigrinum	1 (MB)	0	0
Bufo punctatus	16 (all ranges except SR)	16 (all ranges except SR)	93 (all ranges except SR)
B. woodhousii	4 (MB)	4 (MB)	12 (MB, SM)
Pseudacris regilla	6 (SM, MB)	3 (SM)	20 (SM, MB)
Rana catesbeiana	2 (MB)	2 (MB)	5 (MB, SM)
R. onca	5 (MB)	2 (MB)	5 (MB)
Spea intermontana	1 (MB)	0	0
Any amphibian	—	—	101 (all ranges except SR)

held amphibian specimens from the study area (AMNH, BYU, CAS, CM, KU, LACM, MBM, MVZ, UMMZ, UNR, USNM, and UU).

RESULTS

Upland Springs Survey

Five species of amphibians were found during the surveys (Table 1). Amphibians occurred at 79% (101/128) of the surveyed sites and were found in 6 of 7 mountain range groups, the exception being the Sheep Range. Sites with 1, 2, 3, and 4 species comprised 56%, 20%, 2%, and 1% of the surveyed sites, respectively. By far the most common amphibian among study sites was *B. punctatus*, which occurred at 73% (93) of the locations. This species occurred typically at rocky sites with relatively open bank cover, which were mostly sites with ephemeral water (Bradford et al. 2003). *Bufo punctatus* occurred in all mountain range groups except the Sheep Range, and it was found at all 16 historical (pre-1970) upland spring localities surveyed. Two additional historical localities for this taxon in the uplands were not visited.

Pseudacris regilla was found at 20 sites: 19 in the Spring Mountains (17 on east side, 2 on west) and 1 in the Muddy/Black Mountains group. Sites where this species occurred were generally rocky with relatively open bank cover, but with more extensive riparian vegetation than at many of the sites occupied by *B. punctatus* (e.g., the trees *Populus*, *Salix*, or *Fraxinus* were often present at *P. regilla* sites). At 3 of the 6 historical upland localities (White Rock, Mountain, and Rogers Springs), *P. regilla* was not encountered. All 3 springs in which *P. regilla* disappeared had been substantially modified, although this species was found at other sites relatively close to the first 2 localities (11 and 10 km away, respectively). An additional historical spring locality was not included in the survey because it was largely destroyed by urban development (Cottonwood Spring, now Blue Diamond), although *P. regilla* was found at a site 1.6 km away.

Bufo woodhousii was found at 12 sites: 11 in the Muddy/Black Mountains group and 1 in the Spring Mountains. This species was found at all 4 of its historical upland sites. Site characteristics were variable, including both permanent and ephemeral water sources and banks that were either densely vegetated or open.

Rana onca was found at 5 sites, all of which occurred in the Muddy/Black Mountains group. All sites had permanent water sources that were geothermally influenced (Bradford et al. 2004). This species was found at 2 of the 5 historical upland localities within the study area.

Spea intermontana was not encountered, and historically it has been reported from only 1 of the spring sites surveyed, the northeasternmost spring in the study area (Fig. 1; UMMZ 84764, collected 1938, specimen verified by G. Schneider personal communication). It was also reported in 1937 within the Valley of Fire (La Rivers 1942). The nearest specimens outside the study area are from the vicinity of Riverside to Mesquite, Nevada, ca. 27 km east of the study area (MVZ records, years 1923 and 1986; specimens verified by DFB or J.R. Macey).

Rana catesbeiana was encountered at 5 sites: 3 in the Muddy/Black Mountains group and 2 in the Spring Mountains. All sites had permanent water sources. This introduced species

TABLE 2. Lowland Records Review and Survey for specimen records and post-1990 observations of metamorphosed amphibians (and larvae as indicated) in the major valleys and river floodplains within the study area (Fig. 1). Geographic areas represented are Las Vegas Valley (LV), Pahrump Valley (PV), Indian Springs valley (IS), and floodplains of the Muddy and Virgin Rivers (MV) and Colorado River (CR). Records for the Colorado River include Lake Mead and Lake Mojave. Localities refer to sites ≥1.6 km apart. For numbers in parentheses, "v" refers to number of localities or specimens verified by examination of specimens; "ob" refers to number of localities or individuals identified by observation at one time by the authors.

	Pre-1970		Post 1990	
Species/Area	Localities	Specimens	Localities	Specimens/Individuals
Ambystoma tigrinum				
Colorado River	2[a] (2 v)	2[a] (2 v)	—	—
Las Vegas Valley	4 (4 v)	8 (8 v)	1 (1 v)	2 (2 v)
Bufo cognatus				
Colorado River	2 (1 v)	13 (4 v)	—	—
Muddy/Virgin Rivers	1 (1 v)	1 (1 v)	—	—
B. microscaphus				
Las Vegas Valley	1 (1 v)	23 (9 v)	—	—
B. punctatus				
Colorado River	3[b] (1 v)	15 (6 v)	1 (1 ob)	6 (6 ob)
B. woodhousii				
Colorado River	3 (2 v)	118 (22 v)	—	—
Las Vegas Valley	—	—	9 (3 v, 6 ob)	26 (3 v, 23 ob)
Muddy/Virgin Rivers	10 (8 v)	105 (34 v)	4 (4 ob)	54 (54 ob)
Pseudacris regilla				
Las Vegas Valley	12 (10 v)	250 (61 v)	3 (1 v, 2 ob)	5 (1 v, 4 ob)
Muddy/Virgin Rivers	1 (0 v)	1 (0 v)	3 (3 ob)	142 (142 ob)
Pahrump Valley	2 (1 v)	18 (3 v)	—	—
Rana catesbeiana				
Las Vegas Valley	1[c] (0 v)	4[c] (0 v)	6 (6 ob)	204 (204 ob)
Indian Springs valley	—	—	1 (1 ob)	15 (15 ob)
Muddy/Virgin Rivers	3 (3 v)	30 (8 v)	8 (8 ob)	208 (208 ob)
Pahrump Valley	2 (2 v)	10 (4 v)	—	—
R. fisheri				
Las Vegas Valley	4 (4 v)	160 (32 v)	—	—
R. onca				
Colorado River	1[b] (0 v)	—	—	—
Muddy/Virgin Rivers	4 (3 v)	15 (14 v)	—	—

[a]Includes 1 larval specimen
[b]Includes 1 record (no specimens) from Cowles and Bogert (1936)
[c]Larval specimens

was found at both of its pre-1970 upland localities. *Ambystoma tigrinum*, another apparently invasive species (see Discussion), was not encountered, but 2 larvae were collected in 1963 at Blue Point Spring, a geothermal spring near Lake Mead that contains a number of exotic aquarium fishes (Courtenay and Deacon 1982).

Lowland Records Review and Survey

Specimens, literature records, and survey results for amphibians in the major valleys and rivers within the study area are summarized in Table 2. *Rana fisheri* specimens date from 1891 to 1942, and the frog has not been seen since the 1940s (Stebbins 1951, Jennings and Hayes 1994). *Rana onca* specimens and 1 literature record date from 1935 to 1964 at 4 sites along the Muddy and Colorado Rivers within the study area, but surveys along the Muddy River did not reveal the species, and the locality on the Colorado River was destroyed by the formation of Lake Mead. Several adult *R. onca* have been recorded at Willow Beach, Arizona, but these individuals are believed to have dispersed from upriver locations included in our Upland Spring Survey results (see Bradford et al. 2004).

Bufo microscaphus specimens were collected from Las Vegas Valley in 1891, 1913, and 1923 (Appendix), and Wright and Wright (1949) observed the species here in 1925. This species, however, was not found in our surveys. Linsdale (1940) examined the specimens from

USNM (originally reported as *B. lentiginosus woodhousii;* Stejneger 1893) and MVZ (catalogued as both *B. microscaphus* and *B. woodhousii*) and assigned them to *B. compactilis compactilis,* now considered *B. microscaphus* (Gergus 1998). Linsdale also assigned the CAS specimens to *B. compactilis,* although it is not clear whether he examined these specimens. Stebbins (1951) agreed that the Las Vegas Valley specimens are *B. microscaphus* but indicated that they show "traces of *woodhousii.*" Hybrid-index scores (Sullivan 1995) for the 5 specimens >50 mm SVL from CAS and MVZ were calculated for the present study and found to be consistent with *B. microscaphus* (median 3, range 1–3). Two of the MVZ specimens were also examined by B. Sullivan (personal communication), who assigned them to *B. microscaphus.* Two specimens (UMMZ) cataloged as *B. microscaphus* from elsewhere in the study area were not of sufficient size to identify to species (G. Schneider personal communication).

Bufo woodhousii specimens dating as far back as 1936 were collected at a number of localities within the study area along the Colorado, Virgin, and Muddy Rivers, and from multiple localities in the Las Vegas Valley since 1976 (Appendix). Linsdale (1940) and Stebbins (1951) reported that regional specimens from the Colorado, Virgin, and Muddy Rivers are closest to *B. woodhousii,* although some show traces of *B. microscaphus.* The median hybrid-index score for 38 specimens from the Muddy, Virgin, and Colorado Rivers examined in the present study was 9 (range 6–11), indicative of *B. woodhousii* or hybrids with predominantly *woodhousii* traits. Blair (1955) and Sullivan (1993, 1995) described a hybrid zone for the 2 species along the Virgin River between approximately the former confluence of the Virgin and Colorado Rivers, Nevada, and the vicinity of St. George, Utah. The toads in the Las Vegas Valley and nearby sites in the Spring Mountains appear the same as those along the Muddy and Virgin Rivers. That is, the hybrid index scores for 39 specimens from the former area (median 9, range 4–12) did not differ significantly from those from the latter area (Mann-Whitney U-test, $P > 0.05$). *Bufo woodhousii* was commonly encountered during our surveys along the Muddy River valley, Las Vegas Wash, and other localities in Las Vegas Valley. Historical specimen localities along the Virgin and Colorado Rivers within the study area were inundated by the formation of Lake Mead beginning in 1935 and Lake Mojave in 1951.

Bufo cognatus were collected many decades ago at 3 localities within the study area (Appendix). These sites were 2 miles southeast of Overton (1936), 1.5 miles north of Cottonwood Landing (1950; now Lake Mojave), and approximately at the confluence of Aztec Wash and the Colorado River (1950; now Lake Mojave). Linsdale (1940) and Stebbins (1951) include the Overton locality in their treatment of *B. cognatus.* We examined the specimens from the Overton site and from Aztec Wash and determined them to be consistent with *B. cognatus.* All 3 historical locations have been greatly modified or destroyed by the formation of Lake Mead and Lake Mojave. The nearest locality records outside the study area are from the Colorado River near Mesquite, Nevada, approximately 37 km to the east (1952), and near Laughlin, Nevada, approximately 36 km to the south (1954).

Specimens of *Bufo punctatus* in the lowlands of the study area have been collected only at Willow Beach, Arizona, between 1938 and 1955. Cowles and Bogert (1936), however, reported that individuals were found clinging to driftwood at the mouth of Boulder Wash, Colorado River, as Lake Mead was filling. Whether the species persists at Willow Beach today is unknown, but it does occur at nearby upland sites that extend down to the Colorado River.

Pseudacris regilla specimens date from 1891 to 1976 in Las Vegas Valley, 1891 in Pahrump Valley, and 1952 in the Muddy River valley. The species was encountered at several sites during our surveys in the Las Vegas and Muddy River valleys, although multiple visits failed to reveal the species at Corn Creek springs where specimens exist from several dates between 1891 and 1950.

Specimen records for the introduced *Rana catesbeiana* date from 1936 in Las Vegas Valley, 1938 in Pahrump Valley, and 1939 in the Muddy and Virgin River valleys. This species was frequently encountered in surveys along the Muddy River, Las Vegas Wash, other localities in Las Vegas Valley including Corn Creek springs, and Cactus Spring in Indian Springs valley. Specimens of *Ambystoma tigrinum* have been collected at scattered localities in Las Vegas (1962–1992), Willow Beach (1965), and Lake Mead (1966).

DISCUSSION

The amphibian fauna of the study area has changed dramatically in the past century. Striking changes are the nearly complete replacement of native leopard frogs, *Rana fisheri* and *R. onca,* with the introduced *R. catesbeiana,* and the complete replacement of *Bufo microscaphus* in Las Vegas Valley with *B. woodhousii* or hybrids with predominantly *woodhousii* traits. *Rana fisheri,* known only from Las Vegas Valley, was last seen in the 1940s (Stebbins 1951, Jennings and Hayes 1994). The known historical distribution of *R. onca* once extended from Black Canyon below Lake Mead to southwestern Utah (Bradford et al. 2004), but it is now restricted to the 5 springs identified within the study area. Possible causes for the population extinction of *R. fisheri* and substantial decline of *R. onca* include the loss and extensive modification of aquatic habitat due to urban, agricultural, and water storage development, and the introduction of predators or competitors including game fishes, crayfish, and, possibly more importantly, *R. catesbeiana* (Jennings and Hayes 1994, Bradford et al. 2004). *Rana catesbeiana,* a major predator and competitor of native ranid frogs (Carey et al. 2003) and potentially a pathogen vector among amphibians (Mazzoni et al. 2003), was introduced to the area around 1920 (Jennings and Hayes 1994). It is now widespread among wetlands in the Las Vegas, Muddy River, and Virgin River valleys and occurs at a few scattered springs elsewhere. The status of *R. catesbeiana* in the artificial wetlands in Pahrump Valley is unknown.

Bufo microscaphus was apparently the only toad originally inhabiting the Las Vegas Valley prior to development in the early 1900s. The only *Bufo* species collected or observed between 1891 and 1925, it was reported as "common" by Slevin (1928). Had *B. woodhousii* cooccurred with *B. microscaphus* in the valley at this time, hybrids would have been expected because such has been the case at virtually all areas where the 2 taxa occur in sympatry (Sullivan 1995). Linsdale (1940) reported that specimens of *B. microscaphus* from Las Vegas Valley, Virgin Mountains, and Meadow Valley wash (specimens from the latter 2 areas are outside the study area) were "rather uniform structurally," and historical specimens from Las Vegas Valley examined in the present study showed hybrid-index scores consistent with *B. microscaphus.*

Sometime between 1925 and 1976, *B. microscaphus* populations disappeared from the Las Vegas Valley, and *B. woodhousii* (inclusive of hybrids with predominantly *woodhousii* traits) appeared and became widespread. Such replacement has occurred at several localities in central Arizona, typically in association with extensive alterations to riparian habitat (Sullivan 1986, 1993, 1995). *Bufo microscaphus* is typically associated with stream habitats, whereas *B. woodhousii* is associated with more lentic habitats (Sullivan 1986, 1995). During development of the Las Vegas area, groundwater pumping and diversion destroyed the original few small permanent streams (Malmberg 1965, Jones and Cahlan 1975), whereas artificial ponds, new small permanent streams, and a large wastewater stream were created. Whether *B. woodhousii* invaded the valley after the demise of *B. microscaphus,* or whether the former replaced the latter through competition and/or interbreeding, is unknown. Access to the Las Vegas Valley by *B. woodhousii* from locations along the Colorado River may have occurred via the Las Vegas Wash, which now contains a permanent wastewater stream flowing to Lake Mead. Prior to extensive development in the valley, a reach of at least 18 km of the Las Vegas Wash between the Colorado River and the valley was apparently dry except during periodic flood events. Early groundwater studies indicated that virtually no subsurface water left the valley through Las Vegas Wash, and wetland and phreatophytic vegetation were historically absent in the mapped portion of this reach (Malmberg 1965). Alternatively, *B. woodhousii* may have been introduced to the valley directly by humans, along with bullfrogs and crayfish. The expansion of *B. woodhousii* to nearby sites on the east side of the Spring Mountains may have occurred following its colonization of Las Vegas Valley. Elsewhere in the study area, *B. woodhousii* continues to occur (1936 to present) along the Muddy River and is present at a number of the springs in the Upland Springs Survey, primarily near the Muddy River and the former Virgin River.

Two other species, *B. cognatus* and *Spea intermontana,* appear to no longer occur in the region. *Bufo cognatus* formerly occurred along the Colorado and Virgin Rivers prior to the formation of Lakes Mead and Mojave. The destruction of habitat by the formation of these reservoirs and the lack of specimens or observations within or near the study area since their formation suggest that *B. cognatus* no longer occurs in this region. For *S. intermontana,* with only 2 historical records, the study area has been at the southern fringe of its range during historical times (Stebbins 2003).

The occurrence of *Ambystoma tigrinum* in the study area is likely the result of introductions through the use of larvae as fishing bait. The study area lies outside the main body of distribution of *A. trigrinum,* and the species was formerly used as bait at many localities in the western United States, including the Colorado River (Riley et al. 2003, Stebbins 2003; museum specimen). Specimens from Las Vegas may have resulted from an agency-funded project in the 1960s to commercially rear *A. trigrinum* for bait in backyard ponds (J. Deacon personal communication). It is unknown, however, whether any specimens collected from the study area represent escapees or members of established populations.

Changes in the amphibian fauna noted above have occurred primarily in the major valleys, and less so in the springs and spring-fed wetlands outside the major valleys. The only species whose distribution in the lowlands is about the same today as in the past is *P. regilla,* although it has disappeared from Corn Creek springs in Las Vegas Valley, and its status in the artificial wetlands of Pahrump Valley is unknown. In contrast, the distributions of species characteristic of upland springs, *B. punctatus* and, in the Spring Mountains, *P. regilla* appear to have changed relatively little. *Bufo punctatus* populations inhabit most of the extant springs and persist at all 16 historical localities surveyed. Interestingly, this species inhabits a number of springs that have been substantially degraded by water development; trampling by livestock, wild horses, or burros; or other forms of disturbance. Nevertheless, a significant environmental factor determining site occupancy by the species in the study area is wetland size (Bradford et al. 2003), implying that water development may reduce the viability of a population. *Pseudacris regilla,* although it remains common in the Spring Mountains, may be less tolerant of disturbance than *B. punctatus.* It was not found at 2 of 5 historical sites in this area, both of which have been substantially degraded. Moreover, like *B. punctatus,* site occupancy was strongly dependent on wetland size, based on an analysis similar to that done in Bradford et al. (2003) for *B. punctatus* (unpublished)

Although the causes for declines of many amphibian populations around the world are poorly understood (Alford and Richards 1999), the most parsimonious explanations for the causes of the distributional changes in the eastern Mojave Desert are the anthropogenic activities of water development (i.e., impoundment, diversion, groundwater pumping) and the introduction of exotic species that act as predators, competitors, or agents of habitat change. Protection of the remaining native amphibian fauna in this region from further decline in distribution and population size requires protection of remaining wetland habitat from further loss and degradation and restoration of altered habitat where feasible. Control of exotic species would greatly facilitate the restoration of native conditions, but such control also poses a great challenge (Carey et al. 2003).

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LITERATURE CITED

ALFORD, R., AND S.J. RICHARDS. 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30:133–165.

ALTIG, R., R.W. MCDIARMID, K.A. NICHOLS, AND P.C. USTACH. 1998. A key to the anuran tadpoles of the United States and Canada. Contemporary Herpetology Information Series 1998 (2), 24 September 1998. http://alpha.selu.edu/ch/chis/1998/2.

BLAIR, A.P. 1955. Distribution, variation, and hybridization in a relict toad (*Bufo microscaphus*) in southwestern Utah. American Museum Novitates 1722: 1–38.

BRADFORD, D.F., A.C. NEALE, M.S. NASH, D.W. SADA, AND J.R. JAEGER. 2003. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. Ecology 84:1012–1023.

BRADFORD, D.F., J.R. JAEGER, AND R.D. JENNINGS. 2004. Population status and distribution of a decimated amphibian, the relict leopard frog (*Rana onca*). Southwestern Naturalist 49:218–228.

CAREY, C., D.F. BRADFORD, J.L. BRUNNER, J.P. COLLINS, E.W. DAVIDSON, J.E. LONGCORE, M. OUELLET, ET AL. 2003. Biotic factors in amphibian population declines. Pages 153–208 *in* G. Linder, D.W. Sparling, and S.K. Krest, editors, Amphibian decline: an integrated analysis of multiple stressor effects. Society of Environmental Toxicology and Chemistry.

COURTENAY, W.R., JR., AND J.E. DEACON. 1982. Status of introduced fishes in certain spring systems in southern Nevada. Great Basin Naturalist 42:361–366.

COWLES, R.B., AND C.M. BOGERT. 1936. The herpetology of the Boulder Dam region (Nev., Ariz., Utah). Herpetologica 1:33–42.

DEACON, J.E. 1979. Endangered and threatened fishes of the West. Great Basin Naturalist Memoirs 3:41–64.

EAKIN, T.E. 1964. Groundwater appraisal of Coyote Spring and Kane Spring valleys and Muddy River springs area, Lincoln and Clark Counties, Nevada. U.S. Geological Survey, Groundwater Resources-Reconnaissance Series Report 25.

HERSHLER, R. 1998. A systematic review of the hydrobiid snails (Gastropoda: Rissooidea) of the Great Basin, western United States. Part I. Genus *Pyrgulopsis*. Veliger 41:1–132.

HOULAHAN, J.E., C.S. FINDLAY, B.R. SCHMIDT, A.H. MEYER, AND S.L. KUZMIN. 2000. Quantitative evidence for global amphibian population declines. Nature 404: 752–755.

GERGUS, E.W.A. 1998. Systematics of the *Bufo microscaphus* complex: allozyme evidence. Herpetologica 54: 317–325.

JAEGER, J.R., B.R. RIDDLE, R.D. JENNINGS, AND D.F. BRADFORD. 2001. Rediscovering *Rana onca:* evidence for phylogenetically distinct leopard frogs from the border region of Nevada, Utah, and Arizona. Copeia 2001:339–354.

JENNINGS, M.R., AND M.P. HAYES. 1994. Decline of native ranid frogs in the desert Southwest. Pages 183–211 *in* P.R. Brown and J.W. Wright, editors, Herpetology of the North American deserts. Southwestern Herpetologists Society, Special Publication 5.

JONES, F.L., AND J.F. CAHLAN. 1975. Water: a history of Las Vegas. Volume 1. Las Vegas Valley Water District, Las Vegas, NV.

LA RIVERS, I. 1942. Some new amphibian and reptile records for Nevada. Journal of Entomology and Zoology 34:53–68.

LEVITON, A.E., R.H. GIBBS, JR., E. HEAL, AND C.E. DAWSON. 1985. Standards in herpetology and ichthyology. Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

LINSDALE, J.M. 1940. Amphibians and reptiles in Nevada. Proceedings of the American Academy of Arts and Sciences 73:197–257.

MACMAHON, J.A. 1985. Deserts. Alfred A. Knopf, Inc., New York.

MALMBERG, G.T. 1965. Available water supply of the Las Vegas ground-water basin Nevada. Geological Survey Water-Supply Paper 1780, U.S. Department of Interior, Geological Survey, Washington, DC.

MAZZONI, R., A.A. CUNNINGHAM, P. DASZAK, A. APOLO, E. PERDOMO, AND G. SPERANZA. 2003. Emerging pathogen of wild amphibians in frogs (*Rana catesbeiana*) farmed for international trade. Emerging Infectious Diseases 9:995–998.

MILLER, R.R., J.D. WILLIAMS, AND J.E. WILLIAMS. 1989. Extinctions of North American fishes during the past century. Fisheries 14:22–38.

RILEY, S.P.D., H.B. SHAFFER, S.R. VOSS, AND B.M. FITZPATRICK. 2003. Hybridization between a rare, native tiger salamander (*Ambystoma californiense*) and its introduced congener. Ecological Applications 13: 1263–1275.

SLEVIN, J.R. 1928. The amphibians of western North America. Occasional Papers of the California Academy of Science 16:1–152.

SOLTZ, D.L., AND R.J. NAIMAN. 1978. The natural history of native fishes in the Death Valley system. Natural History Museum of Los Angeles County Science Series 30:1–76.

STEBBINS, R.C. 1951. Amphibians of western North America. University of California Press, Berkeley.

______. 2003. A field guide to western reptiles and amphibians. 3rd edition. Houghton Mifflin, New York.

STEJNEGER, L. 1893. Annotated list of the reptiles and batrachians collected by the Death Valley Expedition in 1891, with descriptions of new species. North American Fauna 7(2):159–228.

STUART, S.N., J.S. CHANSON, N.A. COX, B.E. YOUNG, A.S.L. RODRIGUES, D.L FISCHMAN, AND R.W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

SULLIVAN, B.K. 1986. Hybridization between the toads *Bufo microscaphus* and *Bufo woodhousii* in Arizona: morphological variation. Journal of Herpetology 20: 11–21.

______. 1993. Distribution of the southwestern toad (*Bufo microscaphus*) in Arizona. Great Basin Naturalist 53: 402–406.

______. 1995. Temporal stability in hybridization between *Bufo microscaphus* and *Bufo woodhousii* (Anura: Bufonidae): behavior and morphology. Journal of Evolutionary Biology 8:233–247.

WRIGHT, A.H., AND A.A. WRIGHT. 1949. Handbook of frogs and toads of the United States and Canada. 3rd edition. Comstock Publishing Co., Ithaca, NY.

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APPENDIX. Specimens examined for *Bufo cognatus, B. microscaphus,* and *B. woodhousii* from localities within the study area. Museum codes are defined in text except DFB, which refers to uncatalogued specimens of the 1st author.

B. cognatus

NEVADA.—Clark Co.: MVZ 19393, 2 mi SE Overton, 1300 feet elev. (1936); MVZ 52054–52057, 18 mi NE Searchlight, Colorado River (1950).

B. microscaphus

NEVADA.—Clark Co.: CAS 36959–36975, Las Vegas (1913); MVZ 8903–8906, Las Vegas (1923).

B. woodhousii
(including hybrids
with *B. microscaphus*)

ARIZONA.—Mohave Co.: MVZ 33402, 33410, 33421–33423, 33425, 33427–33431, 33433, Willow Beach Colorado River (1940).

NEVADA.—Clark Co.: CAS 8413–8416, 13070, DFB 643, MVZ 19461–19465, 20428, 20430–20431, 20646, 20648–20650, 54579, MBM 12010, 12013–12014, 12055, 12141–12142, 12145, 12158, 12233, 12469, 12676–12677, 12682, multiple localities, vicinity Muddy River (1936–1998); DFB 635–636, 644–645, MVZ 19211–19212, MBM 12726, multiple localities, vicinity Virgin River (now Overton Arm, Lake Mead; 1935–1998); CAS 6436–6438, MBM 12144, 2 localities, Meadow Valley Wash, vicinity Lincoln-Clark County line (1938–1964); DFB 550, 579, MBM 12674A–B, 12678A,C–L, 12679A–D, 12680A–C,E–F, 12681B,D–E, 12683A–B,D, 12684A, 12808, multiple localities, Las Vegas Valley (1976–1998); DFB 603, MBM 12708–12712, 2 localities, Spring Mountains, vicinity Blue Diamond (1992–1997); MVZ 52058, 52060, 52071, 52073–52078, 52080, 18 mi NE Searchlight, Colorado River (1950); Lincoln Co.: DFB 571–572, MBM 12728–12729, 2 localities, Meadow Valley Wash, vicinity Lincoln-Clark County line (1993–1997).