Research Article

Artificial Water Catchments Influence Wildlife Distribution in the Mojave Desert

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ABSTRACT Water often limits the distribution and productivity of wildlife in arid environments. Consequently, resource managers have constructed artificial water catchments (AWCs) in deserts of the southwestern United States, assuming that additional free water benefits wildlife. We tested this assumption by using data from acoustic and camera trap surveys to determine whether AWCs influenced the distributions of terrestrial mammals (>0.5 kg), birds, and bats in the Mojave Desert, California, USA. We sampled 200 sites in 2016–2017 using camera traps and acoustic recording units, 52 of which had AWCs. We identified detections to the species-level, and modeled occupancy for each of the 44 species of wildlife photographed or recorded. Artificial water catchments explained spatial variation in occupancy for 8 terrestrial mammals, 4 bats, and 18 bird species. Occupancy of 18 species was strongly and positively associated with AWCs, whereas 1 species (i.e., horned lark [*Eremophila alpestris*]) was negatively associated. Access to an AWC had a larger influence on species' distributions than precipitation and slope and was nearly as influential as temperature. In our study area, AWCs functioned as an important influence on wildlife occupancy, which supports the long-held assumption that AWCs may benefit wildlife in arid habitats. We encourage managers to maintain existing AWCs, particularly those in areas forecasted to have the largest decrease in water availability. We also recommend long-term, systematic monitoring of AWCs, which will facilitate more informed management decisions. © 2019 The Wildlife Society.

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Water is a fundamental need of wildlife (Leopold 1933). This need is met through a combination of pre-formed water available in food, metabolic water created as a byproduct of internal processes (e.g., the breakdown of carbohydrates), and free water available for drinking (Robbins 2001). In arid environments where free water is scarce or absent, many species have developed behavioral and physiological adaptations to maximize their intake and retention of pre-formed and metabolic water. For example, Gambel's quail (*Callipepla gambellii*) are generally able to meet their water needs by consuming succulent foods (Schemnitz 1994). Alternatively, kit fox (*Vulpes macrotix*) can survive without free water by acquiring water from prey, relying on thermal conductance to cool, and limiting activity to nighttime when temperatures are cooler (Golightly and Ohmart 1984). In times of severe

heat and drought when food quantity and quality are limited, however, even these xeric-adapted species may require free-standing water to meet their physiological needs or to alleviate physiological stresses (Larsen et al. 2012, Hall et al. 2013). Further, for species like large mammals, it is unclear if they can meet their water requirements through pre-formed and metabolic water alone during all seasons of the year (Morgart et al. 2005).

The scarcity and unreliability of free water in desert regions of the southwestern United States has led managers to believe it is one of the primary factors limiting the distribution and productivity of many wildlife species (Roberts 1977, Rosenstock et al. 1999, Krausman et al. 2006). This concern has been amplified in recent years as the desert southwest becomes increasingly arid. Mean annual temperatures have increased by >2°C over the last 50 years, and in many areas, precipitation has decreased by approximately 20% in the last century (Shriner et al. 1998, Seager et al. 2007, Rapacciuolo et al. 2014).

In the Mojave Desert, these long-term reductions in precipitation have resulted in a 40% decline in avian species

richness (Iknayan and Beissinger 2018). The negative effects of increased aridity are further amplified by land use changes. Urbanization and energy development have resulted in the loss or degradation of naturally occurring water sources (deVos et al. 1983, DeStefano et al. 2000, Krausman et al. 2006), and anthropogenic alterations like water diversions and groundwater pumping have lowered water tables (Lynn et al. 2008, Patten et al. 2008).

To mitigate the negative influences that limited or absent free water may have on wildlife distributions, survival, and reproduction, resource managers have expended substantial time and money enhancing existing water sources and developing new sources (Benolkin 1990, Rosenstock et al. 1999, Krausman et al. 2006). New water sources, which we term artificial water catchments (AWCs), generally consist of aboveground or belowground tanks that catch and store rainwater from steep-sided gullies, rock surfaces, or desert pavement (Bleich et al. 2006). When AWCs were first constructed across the desert southwest, they were created with the specific purpose of benefiting game species like chukar (*Alectoris chukar*), mourning doves (*Zenaida macroura*), desert bighorn sheep (*Ovis canadensis*), and mule deer (*Odocoileus hemionus*; Wright 1959). Because many game species require free water (e.g., mourning doves) or are positively associated with free water (e.g., desert bighorn sheep; Bleich et al. 1997, Rosenstock et al. 1999, O'Brien et al. 2006), managers assumed that AWCs would improve species' fitness and allow species to expand their distributions (Rosenstock et al. 1999, Turner et al. 2004, Longshore et al. 2009). In the 1980s, these perceived benefits were broadened to both game and nongame species, and AWCs began functioning as a means for mitigating the loss of naturally occurring water sources resulting from human development (deVos et al. 1983, Burkett and Thompson 1994).

The assumption that AWCs benefitted wildlife populations in arid habitats continued unquestioned for many years (Rosenstock et al. 1999). Recently, however, these benefits have been debated (Burkett and Thompson 1994, O'Brien et al. 2006). Results from prior studies evaluating the influence of water catchments are equivocal and appear to be both species- and region-specific. For example, AWCs may benefit some bird species but not all; they receive little use by migratory passerine species but are heavily used by resident passerine species, raptors, and owls (Rosenstock et al. 1999; DeStefano et al. 2000; Lynn et al. 2006, 2008; O'Brien et al. 2006).

The influence of AWCs on small mammals, however, may vary by region. In Utah, USA, there was no evidence that water developments influenced small-mammal abundance (Kluever et al. 2016), whereas in New Mexico and Arizona, USA, sites with water developments had greater small-mammal abundance and richness, respectively (Burkett and Thompson 1994, Switalski and Bateman 2017). Additionally, several negative effects of AWCs have been proposed, including increased predation and interspecific competition, health issues related to water quality, and disease transmission (Rosenstock et al. 1999). These negative effects,

however, have received less support in the literature (DeStefano et al. 2000, Bleich et al. 2006, O'Brien et al. 2006).

California, USA, has one of the largest historical and current water catchment programs. As of 2000, there were over 2,500 AWCs in the state (Rosenstock et al. 1999). This number may increase as water catchments become increasingly used to mitigate the negative effects of land use and climate change (Krausman et al. 2006, Longshore et al. 2009, Iknayan and Beissinger 2018). Given the capital investment required to develop and maintain this program, it is vital to invest in monitoring and managing existing water catchments to determine if they are achieving their stated purpose (Rosenstock et al. 1999, Cain et al. 2008). Further, few studies have assessed how AWCs influence the distributions of multiple taxonomic groups. Previous efforts have generally focused on a single species (Marshal et al. 2006, Cain et al. 2008, Longshore et al. 2009), a specific group of species (Lynn et al. 2008, Hall et al. 2013, Kluever et al. 2016), or were descriptive in nature (e.g., reporting which wildlife species use AWCs; Burkett and Thompson 1994, O'Brien et al. 2006).

We used data from acoustic and camera trap surveys to determine whether AWCs influenced the distributions of terrestrial mammals (>0.5 kg), bats, and birds in the Mojave Desert, California. Our specific objectives were to model occupancy probabilities for terrestrial mammal, bat, and bird species, to assess if the presence of AWCs helped explain variation in species-specific occupancy probabilities, and to determine if species' body mass, diet, or land cover preference were predictors of their association with AWCs.

STUDY AREA

Our study area was in the southern portion of the Mojave Desert ecoregion of California. Elevations ranged from 147–2,414 m (Fig. 1) and rainfall patterns varied seasonally, with most rain falling in the winter as storms originating over the Pacific Ocean moved inland (Bachelet et al. 2016). Precipitation during our study period was limited, however, with just 0–20 mm of precipitation per month. The dominant plant species was creosote scrub (*Larrea tridentata*), but the area encompassed a mosaic of vegetation types including saltbrush (*Atriplex polycarpa*), Joshua trees (*Yucca brevifolia*), single-leaf pinyon (*Pinus monophylla*), and mesquite (*Prosopis glandulosa*; California Department of Fish and Wildlife [CDFW] 2017). The area is also home to a diverse array of fauna, including species of special concern like the burrowing owl (*Athene cunicularia*), Mojave ground squirrel (*Xerospermophilus mohavensis*), desert bighorn sheep, and flat-tailed horned lizard (*Phrynosoma mcallii*; CDFW 2015). Most of the land was designated as federally protected (e.g., Mojave National Preserve and Bureau of Land Management public lands), as recreation management areas (e.g., Stoddard-Johnson, Ward Valley, and Lava Hills), or as military land (i.e., Twentynine Palms). Federally protected land was used primarily for recreational purposes, with limited livestock grazing.
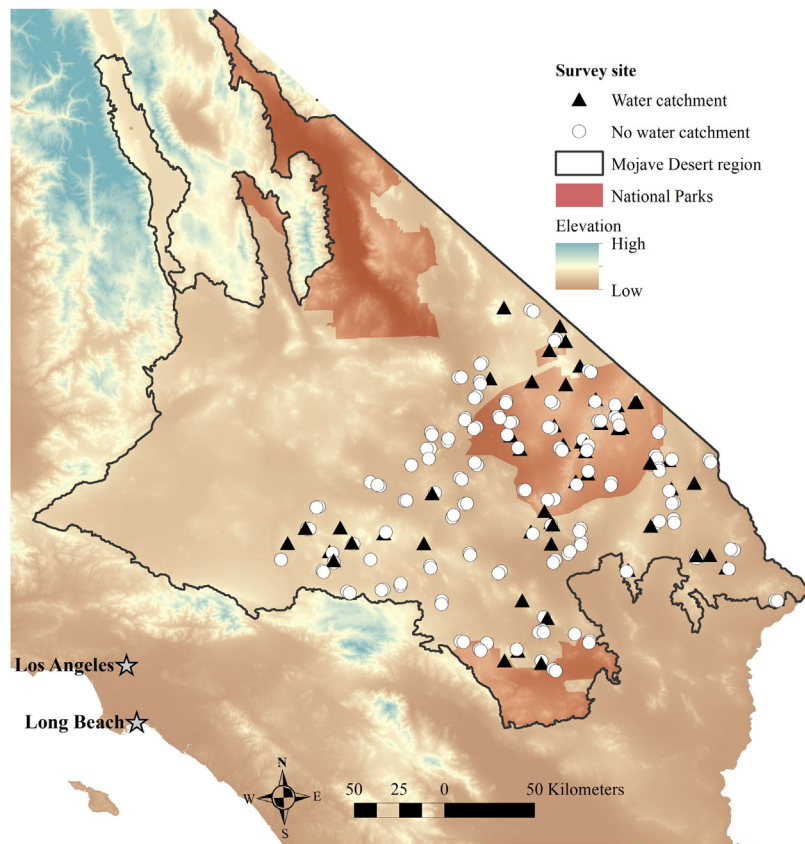
Figure 1. Survey site locations in the southern portion of the Mojave Desert ecoregion, California, USA, 2016–2017, and whether the site was located by an artificial water catchment.

METHODS

Camera Trap and Acoustic Recorder Surveys

We surveyed 200 sites between March and July of 2016–2017 (Fig. 1). We sampled during this time because it aligned with the breeding season for songbirds and thus, increased the probability that birds were vocalizing and would be detected by the acoustic recorders. In the March to July period, we spread out our spatial sampling of sites with respect to month (vs. sampling from north to south) to help minimize the influences of seasonal changes in water availability.

We identified survey locations by first selecting a spatially balanced random sample of hexagons, stratified by vegetation community, from the United States Department of Agriculture (USDA) Forest Inventory and Analysis program's hexagon grid (hexagon radius is ~2.6 km). We then randomly selected 1–3 survey locations within each hexagon, which were spaced by 1–2 km and stratified by vegetation community. To ensure that a representative number of sites were near AWCs, we randomly selected 50 hexagons that contained a catchment and included them as a separate vegetation community during our initial stratification process. For these hexagons, survey sites were strategically located in proximity to the AWC. Our study area included both aboveground AWCs (i.e., aboveground tanks that store rainwater flowing in from deep-sided gullies or rock surfaces;

$n = 12$) and underground AWCs (i.e., systems that catch rain from desert pavement and store it in underground tanks; $n = 40$; Bleich et al. 2006; Fig. 2).

At each survey location, we concurrently deployed a PC900 camera trap (Reconyx, Holmen, WI, USA) and a SM3-BAT bioacoustic recorder with microphone (Wildlife Acoustics, Inc., Maynard, MA, USA). We cable-locked cameras and acoustic recorders to securely placed T-posts 1 m and 2 m above the ground, respectively; T-posts were separated by ≥30 m. If T-post mounting was not possible, we secured devices to a tree or other rigid vegetation.

We deployed cameras for an average of 34 ± 7.6 (SD) days and baited them during their initial deployment with a 250-g salt lick, 100 mL of rolled oat-peanut butter mixture, and 150 g of fish cat food, a combination of baits that is attractive to a broad range of mammalian species. It is possible that baits attracted mammals from outside of their home range, but we believe it was unlikely given we did not re-bait and bait effects decline with time (Furnas et al. 2017). We programmed cameras to take 3 photos at each trigger event, with a delay of 1 second between trigger events to help ensure we would get ≥1 clear image of photographed animals. After the field season, we identified photos to the species-level, omitting photographs when this was not possible (e.g., blurry image).

We programmed acoustic recorders to record 3 5-minute sessions on 3 consecutive days during the survey period,

Figure 2. Artificial water catchments (AWC) in the Mojave Desert ecoregion, California, USA, including A) an aboveground AWC that stores rainwater flowing in from deep-sided gullies or rock surfaces, and B) an underground AWC that catches rain from desert pavement and stores it in an underground tank.

following the protocol of Furnas and Callas (2015). The first session was at 30 minutes before sunrise, the second at sunrise, and the third at 30 minutes after sunrise (Furnas and Callas 2015). We had an expert in aural identification of California desert birds review each 5-minute recording and identify bird species by song, call, wing noise, or drumming. To aid in bird identification, the expert examined spectrograms in Raven Pro software (version 1.5; Cornell Lab of Ornithology Bioacoustics Research Program, Ithaca, NY,

USA). We omitted recordings that could not be identified to the species level.

We also programmed the acoustic recorders to record full spectrum (i.e., 6–192 kHz) ultrasonic triggers from 30 minutes before sunset until 0400 the following morning for 8 consecutive days on average (range = 3–10 days). We used Kaleidoscope Pro version 4.3.2 with the KPro classifier (Wildlife Acoustics, Maynard, MA, USA) to auto-classify file recordings to the bat species level. Using the probabilistic output from the classifier, we filtered files to retain only those determined to have a misidentification probability <0.05. We then manually reviewed (e.g., examined diagnostics and spectrograms) all the remaining files to confirm, reject, or correct the auto-classified species identification.

Spatial Covariates of Occupancy

We expected that topography and climate would influence wildlife distributions across our study area (McCain 2009, Serra-Diaz et al. 2014, Bachelet et al. 2016, Iknayan and Beissinger 2018). We represented topography by determining site-specific elevation and slope using the 30-m resolution National Elevation Dataset (U.S. Geological Survey 2016). To represent climate, we downloaded 4-km resolution monthly precipitation and monthly, mean daily temperature data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM Climate Group 2018) for March–July 2016 and 2017. We calculated the mean precipitation and temperature values from March through July at each survey site during the respective survey year. Temperature and elevation were correlated ($r = -0.82$), so we retained only temperature for our analyses. Lastly, given our interest in assessing how AWCs influence species distributions, we also included categorical variables indicating whether the survey site was located by an aboveground AWC ($n = 12$) or an underground AWC ($n = 40$).

On average, AWC sites were in areas with comparable slope and precipitation values to non-AWC sites, but these areas tended to have cooler temperatures (Table 1). The range of temperature values sampled at AWC sites, however, was comparable to that of non-AWC sites (Table 1). We note that we did not account for naturally occurring water in our modeling framework. We found only a coarse measure of water availability (Pekel et al. 2016), which did not representatively capture ephemeral, perennial, and annual water sources. Further, this coarse measure suggested that distances to natural water were similar at AWC and non-AWC sites (Welch's $t_{103} = 0.87$; $P = 0.387$), and preliminary analyses showed that the addition of this variable only nominally influenced species' occupancy.

Table 1. Mean ($\bar{x}$), standard error (SE), and range of slope, mean monthly precipitation (mm), and mean daily temperature (°C) values sampled at sites with and without artificial water catchments (AWCs) in the Mojave Desert, California, USA, 2016–2017, and results from a Welch's t-test assessing if there were differences in mean covariate values at AWC and non-AWC sites including the t-statistic (t), degrees of freedom (df) and P-value (P).

Covariate	AWC sites				Non-AWC sites				t	df	P
	$\bar{x}$	SE	Min.	Max.	$\bar{x}$	SE	Min.	Max.			
Slope	5.77	0.95	0.34	35.15	5.04	0.42	0.04	31.76	0.66	85	0.51
Precipitation	7.81	0.92	0.02	16.38	6.66	0.55	0.00	20.49	1.12	80	0.27
Temperature	21.96	0.41	16.38	28.60	23.80	1.98	16.38	29.61	−3.81	92	0.001

Occupancy Models

We estimated species' occupancy probabilities and conducted model selection using the UNMARKED package (Fiske and Chandler 2011) in Program R. Given our goal was to assess species-specific associations with AWCs, we used single-season, single-species occupancy models. We included year (2016 = 1, 2017 = 0) as a categorical variable influencing occupancy and detection in all models to account for potential inter-annual variation. We also restricted our analyses to species that had a minimum of 15 detections.

Occupancy models distinguish the true absence of a species from the non-detection of a species (i.e., species present but not photographed or recorded) using spatially or temporally replicated survey data (MacKenzie et al. 2018). Thus, for each survey location, we treated each 24-hour camera trapping period, each 5-minute acoustic recording, and each night of triggered ultrasonic recordings as a repeat survey at that particular site. We then created species-specific detection histories where a 1 indicated species i was detected at site j during sampling occasion k, a 0 indicated it was not detected, and an NA indicated the recorder or camera was inactive at site j during sampling occasion k. We assumed demographic and geographic closure during our repeat surveys at each site.

In addition to year, we modeled detection probability to be a function of mean ordinal day given that the phenology of birds' vocal behavior can change over the course of a breeding season (Furnas and McGrann 2018) and that mammal movement and activity patterns may fluctuate based on environmental factors and human activity (Ordiz et al. 2017). Keeping the model structure for detection constant, we then modeled occupancy probability using 2 model structures (i.e., we ran 2 models for each species). First, we modeled occupancy as a function of slope, temperature, and precipitation. We standardized these covariates to have a mean of zero and standard deviation of one. In the second model structure, we added a categorical variable indicating whether the site was located by an AWC. For each species, we included the AWC variable (i.e., aboveground AWC, underground AWCs, or any type of AWC) found to have the largest univariate effect size. We used Akaike's Information Criterion (AIC; Burnham and Anderson 2002) to compare model fit. If after controlling for climate and topography the addition of the AWC covariate improved model fit (i.e., resulted in a lower AIC value), then we had support that AWCs were influencing the respective species' probability of occupying an area. We used the model with the lower AIC value to estimate occupancy, detection, and covariate relationships (Burnham and Anderson 2002).

Species Traits and AWC Use

We used AIC values to compare the fit of models that included species' body mass, diet, or land cover preference as predictors of whether the species' occupancy was associated with AWCs. We restricted our trait analysis to bird species because of the small number of terrestrial mammal and bat species detected. We compiled species traits from individual species' accounts in Birds of North America Online (Rodewald 2018) and Animal Diversity Web (University of Michigan 2018; Table S1, available online in Supporting Information). We log-transformed body mass values, classified species as carnivores, herbivores, or omnivores, and identified if species preferred arid lands (i.e., open areas like deserts, scrublands, or grasslands) or were habitat generalists (Table S1). We then carried out 3 generalized linear models where we used a single species trait as a continuous (i.e., mass) or categorical (i.e., diet and land cover preference) predictor of whether the bird species had a strong, positive association with AWCs or not.

RESULTS

We obtained 5,760 detections of 44 wildlife species during our 6,365 camera trap nights, 1,794 5-minute recordings, and 1,574 acoustic recorder nights for bats (Table 2). Wildlife species with a minimum of 15 detections included 9 terrestrial mammal, 7 bat, and 28 bird species (Table 2). Black-tailed jackrabbits (*Lepus californicus*), canyon bats (*Parastrellus hesperus*), and black-throated sparrows (*Amphispiza bilineata*) were among the most detected species, whereas American badgers (*Taxidea taxus*), fringed myotis (*Myotis thysanodes*), and common poorwills (*Phalaenoptilus nuttallii*) were among the least detected species. The mean probability of occupancy was 0.21 for terrestrial mammals, 0.17 for birds, and 0.33 for bats (Table 2). This varied considerably among species, however, ranging from <0.01 for mule deer, Crissal thrasher (*Toxostoma crissale*), LeConte's thrasher (*T. lecontei*), and fringed myotis to >0.7 for black-throated sparrow, white-crowned sparrow (*Zonotrichia leucophrys*), and canyon bat (Table 2). Site-level detection probabilities also varied among species, ranging from 0.09 to 1.00 (Table 2).

Model fit improved for 68% of the species ($n = 30$) when AWC was included as a covariate for occupancy (Table 3). This included 89% of terrestrial mammal, 57% of bat, and 64% of bird species (Table 3). The influence of AWCs on species-specific occupancy probabilities was strong (i.e., 95% CI did not overlap 0) and positive for 7 terrestrial mammal species (78%), 1 bat species (14%), and 10 bird species (36%; Table 3). Desert bighorn sheep, Gambel's quail, and mourning doves were among the game species positively associated with AWCs, whereas Audubon's cottontail (*Sylvilagus audubonii*), loggerhead shrike (*Lanius ludovicianus*), and California myotis (*M. californicus*) were among the nongame species positively associated (Table 3). Bighorn sheep, gray fox (*Urocyon cinereoargenteus*), canyon bat, Mexican free-tailed bat (*Tadarida brasiliensis*), and Say's phoebe (*Sayornis saya*) were the only species that had their strongest association with aboveground AWCs (Table 3). The remaining species, conversely, had their strongest association with underground AWCs ($n = 13$) or all AWCs combined ($n = 12$). Horned larks (*Eremophila alpestris*) were the only species strongly and negatively related to the presence of water catchments (Table 3).

For species that were strongly associated with AWCs, we estimated occupancy probabilities at sites with and without these features (while holding other covariates at their mean value). Occupancy probabilities were significantly higher

Table 2. Terrestrial mammal, bird, and bat species detected during camera trap and automated recorder surveys in the Mojave Desert, California, USA, 2016–2017, including numbers of detections (det.), estimated occupancy probabilities (ψ), standard error estimates (SE), and site-level detection probabilities (p).

Common name	Scientific name	det.	ψ	SE	p
Terrestrial mammals					
Coyote	*Canis latrans*	57	0.3	0.04	1
Black-tailed jackrabbit	*Lepus californicus*	307	0.7	0.05	1
Bobcat	*Lynx rufus*	41	0.2	0.03	1
Mule deer	*Odocoileus hemionus*	36	0	0.01	0.9
Bighorn sheep	*Ovis canadensis*	22	0	0.01	1
Audubon's cottontail	*Sylvilagus audubonii*	184	0.2	0.04	1
American badger	*Taxidea taxus*	18	0.2	0.04	0.8
Gray fox	*Urocyon cinereoargenteus*	40	0.1	0.02	1
Kit fox	*Vulpes macrotis*	170	0.3	0.05	1
Birds					
Black-throated sparrow	*Amphispiza bilineata*	756	0.8	0.04	1
Bell's sparrow	*Artemisiospiza belli*	28	0.1	0.03	0.7
Verdin	*Auriparus flaviceps*	94	0.2	0.03	1
Gambel's quail	*Callipepla gambelii*	141	0.2	0.03	1
Costa's hummingbird	*Calypte costae*	19	0	0.02	0.8
Cactus wren	*Campylorhynchus brunneicapillus*	239	0.2	0.04	1
Canyon wren	*Catherpes mexicanus*	32	0	0.01	1
Lesser nighthawk	*Chordeiles acutipennis*	67	0.1	0.03	0.9
Common raven	*Corvus corax*	124	0.3	0.05	0.9
Horned lark	*Eremophila alpestris*	183	0.2	0.05	1
House finch	*Haemorhous mexicanus*	207	0.3	0.04	1
Scott's oriole	*Icterus parisorum*	51	0	0.02	0.8
Loggerhead shrike	*Lanius ludovicianus*	70	0.3	0.05	0.7
Northern mockingbird	*Mimus polyglottos*	161	0.1	0.03	1
Ash-throated flycatcher	*Myiarchus cinerascens*	278	0.3	0.04	1
Phainopepla	*Phainopepla nitens*	32	0.1	0.04	0.6
Common poorwill	*Phalaenoptilus nuttallii*	18	0	0.01	0.7
Ladder-backed woodpecker	*Picoides scalaris*	26	0.1	0.03	0.7
Black-tailed gnatcatcher	*Polioptila melanura*	90	0.2	0.04	0.9
Rock wren	*Salpinctes obsoletus*	192	0.2	0.04	1
Say's phoebe	*Sayornis saya*	59	0.1	0.02	0.9
Brewer's sparrow	*Spizella breweri*	25	0.1	0.06	0.1
Eurasian collared dove	*Streptopelia decaocto*	25	0	0.02	1
Bewick's wren	*Thryomanes bewickii*	82	0.1	0.02	1
Crissal thrasher	*Toxostoma crissale*	41	0	0.01	0.8
LeConte's thrasher	*Toxostoma lecontei*	51	0	0.15	0.9
Mourning dove	*Zenaida macroura*	302	0.3	0.04	1
White-crowned sparrow	*Zonotrichia leucophrys*	135	0.7	0.08	0.2
Bats					
Pallid bat	*Antrozous pallidus*	47	0.1	0.03	0.8
Townsend's big-eared bat	*Corynorhinus townsendii*	29	0.1	0.08	0.7
Greater bonneted bat	*Eumops perotis*	24	0.1	0.03	0.6
California myotis	*Myotis californicus*	300	0.6	0.04	0.9
Fringed myotis	*Myotis thysanodes*	16	0	0.01	0.5
Canyon bat	*Parastrellus hesperus*	786	0.9	0.17	1
Mexican free-tailed bat	*Tadarida brasiliensis*	155	0.5	0.06	0.8

(i.e., 95% CIs did not overlap) at catchment sites for 11 of the 19 species (Fig. 3), and mean occupancy across all species increased from 0.19 ± 0.032 (SE) to 0.41 ± 0.094.

Temperature had a strong association with the distributions of 48% of species ($n = 21$), including 56% of the terrestrial mammals and 57% of the birds (Table 3). The spatial occurrence of 17 species was strongly and negatively associated with temperature, whereas the occurrence of kit fox, black-tailed gnatcatcher (*Polioptila melanura*), lesser nighthawk (*Chordeiles acutipennis*), and LeConte's thrasher was strongly and positively associated with temperature (Table 3). Our second climatic variable, precipitation, strongly influenced the distributions of 27% of species ($n = 12$), the majority positively ($n = 8$; Table 3). Lastly, the spatial occurrence of 30% of the species ($n = 13$) was strongly

influenced by slope, 9 positively (e.g., canyon wren) and 4 negatively (e.g., kit fox; Table 3).

Avian traits were weakly associated with AWC use. Diet was the only species' trait that improved model fit when compared to the null model (Table 4). Omnivores and carnivores were less likely to use AWCs than herbivores, but all associations were weak (i.e., 95% CI for beta estimate overlapped zero). Body mass and land cover preference did not improve model fit, as compared to the null model, and beta estimates indicated that these trait associations were weak (i.e., large SE estimates; Table 4).

DISCUSSION

Artificial water catchments are influencing wildlife distributions in California's Mojave Desert. The distributions of

Table 3. Covariate relationships for explaining spatial variation in the occupancy of terrestrial mammal, bird, and bat species in the Mojave Desert, California, USA, 2016–2017. We compared 2 model structures and present covariate relationships from the top-ranked model based on Akaike's Information Criterion (AIC). In the first model, we included slope, temperature (temp), and precipitation (precip) as covariates for occupancy and in the second model, we added a categorical variable indicating whether the site was located by an artificial water catchment (AWC). Covariate relationships marked with an asterisk were significant (i.e., 95% CI did not overlap zero). We also present the change in AIC values (ΔAIC) between the 2 model structures, where a negative value indicates that the model including the AWC variable had a lower AIC value.

| Common name	AWC type[a]	AWC	Slope	Temp	Precip	ΔAIC
Terrestrial mammals						
Coyote	Either	1.51*	−0.81*	−0.95*	−1.14*	−11.21
Black-tailed jackrabbit	UG	1.51*	−1.55*	−0.18	0.52*	−5.30
Bobcat	Either	1.29*	0.37*	−1.10*	0.14	−7.47
Mule deer	Either	1.49	0.76	−3.70*	0.99	−0.26
Bighorn sheep	AG	2.03*	0.74*	−0.07	−0.77	−2.56
Audubon's cottontail	UG	1.61*	−0.48	−1.43*	0.85*	−9.97
American badger	UG	1.61*	−0.01	−0.38	0.42	−7.29
Gray fox	AG	1.75*	0.62*	−0.57	−0.33	−2.96
Kit fox			−1.79*	0.99*	−0.25	0.99
Birds						
Black-tailed gnatcatcher	Either	1.49*	0.01	0.76*	0.15	−8.91
Bell's sparrow			−0.37	0.16	0.36	0.75
Verdin	UG	1.62*	−0.22	0.38	0.27	−8.26
Gambel's quail	Either	1.27*	−0.31	−0.39	0.14	−7.45
Costa's hummingbird			0.35	−1.42*	−0.93	1.79
Cactus wren	UG	0.67	−0.09	−1.24*	0.88*	−0.28
Canyon wren			1.35*	0.2	0.84	1.29
LeConte's thrasher			−0.24	0.84*	0.58	1.51
Common raven			−0.24	−1.32*	−0.78*	4.39
House finch	Either	1.58*	0.52*	−1.24*	−0.75*	−12.36
Horned lark	Either	−1.33*	−1.11*	−0.02	−0.33	−5.45
Scott's oriole			−0.45	−2.68*	−0.30	1.01
Loggerhead shrike	UG	1.69*	−0.49	−0.36	0.21	−7.96
Northern mockingbird	UG	1.29*	−0.31	−0.83*	1.11*	−3.26
Ash-throated flycatcher	UG	1.29*	−0.01	−0.90*	0.63*	−6.69
Phainopepla	Either	1.39	0.18	−0.74	1.40*	−2.02
Common poorwill	UG	2.14*	0.18	−0.64	0.85	−1.35
Ladder-backed woodpecker	UG	1.32	−0.38	−1.58*	−0.46	−1.38
Brewer's sparrow	Either	1.36	−0.13	−0.15	0.32	−0.38
Rock wren			1.11*	−0.83*	−0.65*	1.12
Say's phoebe	AG	1.45*	0.2	−0.41	−0.22	−1.45
Black-throated sparrow	UG	1.07	0.48*	−1.78*	1.44*	−0.81
Eurasian collared dove			−0.05	0.72	−1.45	1.94
Bewick's wren			0.32	−1.62*	0.36	1.92
Crissal thrasher	UG	1.68	−1.43	−2.94*	0.89	−1.26
Lesser nighthawk			−0.30	2.01*	1.66*	1.07
Mourning dove	UG	0.97*	−0.21	−1.09*	0.1	−3.06
White-crowned sparrow	Either	1.22	−0.37	−0.52	0.45	−0.17
Bats						
Pallid bat	Either	0.85	0.58*	−0.03	−0.14	−0.26
Townsend's big-eared bat			0.64	−0.61	−0.29	0.87
Greater bonneted bat			0.46	0.44	−0.39	2
California myotis	Either	1.23*	0.40*	0.19	0.37	−7.64
Fringed myotis			0.3	−2.00	0.69	6.7
Canyon bat	AG	1.24	0.48	−0.15	0.01	−0.55
Mexican free-tailed bat	AG	2.15	−0.03	0.09	0.14	−1.95

[a] UG = underground tank where water is funneled from desert pavement; AG = aboveground tank that stores rainwater flowing in from deep-sided gullies or rock surfaces; Either = either type of artificial water catchment.

18 species of terrestrial mammals, birds, and bats were strongly and positively associated with the presence of AWCs, meaning these features influenced the occupancy of a greater number of species than precipitation and slope, and nearly as many species as temperature. Although our study did not permit assessments of survival, recruitment, or shifts in distributions, our results do provide a critically needed first step in testing the long-held assumption that AWCs benefit a diversity of wildlife species in arid habitats and help mitigate the negative influences that limited or absent free water may have (Benolkin 1990, Rosenstock et al. 1999, Krausman et al. 2006). Our results also showcase how simultaneous deployment of camera traps and acoustic recorders can facilitate inferences on multiple taxonomic groups, as compared to just a single species.

The occupancy of 3 game species, desert bighorn sheep, Gambel's quail, and mourning doves, were strongly and positively associated with AWCs. Water is consistently found to be an important correlate of desert bighorn sheep use (Bleich et al. 1997, Epps et al. 2004, Turner et al. 2004,
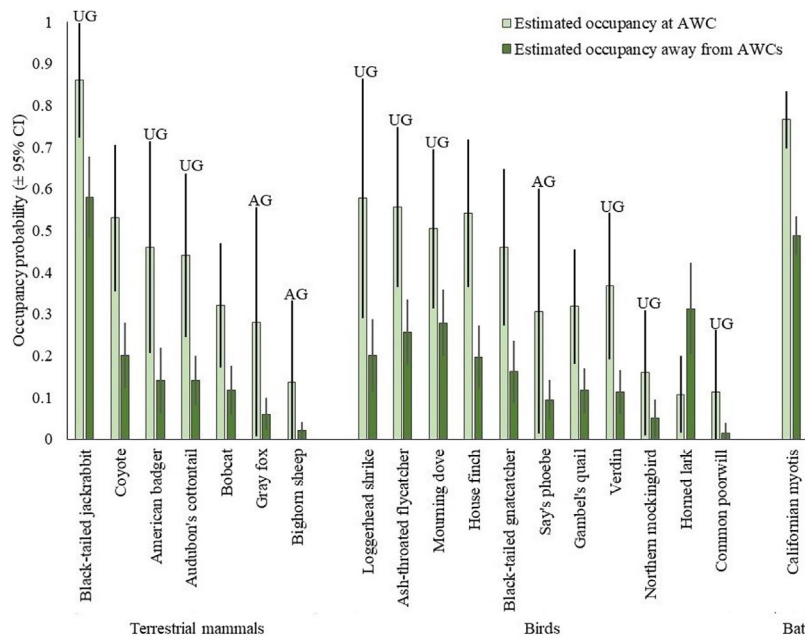
Figure 3. Estimated occupancy probabilities for 19 terrestrial mammal, bat, and bird species at sites with and without artificial water catchments (AWCs) in the Mojave Desert, California, USA, 2016–2017. We label which type of AWC was included, where UG = underground tank, AG = aboveground tank, and no label = either type of AWC.

Longshore et al. 2009). Our research was no exception; we found that desert bighorn sheep were 7 times more likely to occupy areas near aboveground AWCs. These results support that aboveground AWCs are achieving their primary management goal of providing water for desert bighorn sheep (Bleich et al. 2006). Gambel's quail, alternatively, were 2.7 times more likely to occupy areas near above- or belowground AWCs. Gambel's quail are a desert-adapted species and as such, may be able to meet their water needs by consuming succulent foods (Schemnitz 1994). Easy access to free water, however, likely helps to alleviate physiological stresses and improve fitness (Hall et al. 2013). Further, aboveground AWCs may serve the dual function of acting as an elevated perch from which males can vocalize (i.e., to attract females or to protect their young brood when

disturbed; Schemnitz 1994). Mule deer, another game species of interest, were positively associated with AWCs, but this association was weak (i.e., 95% CI overlapped zero). Our mule deer results were likely due to a limited number of mule deer detections ($n = 36$) and limited sampling at aboveground AWCs ($n = 12$). Given the bevy of contrasting literature regarding the species' association with artificial sources of water (Krausman and Etchberger 1995, DeStefano et al. 2000, Marshal et al. 2006, O'Brien et al. 2006), we encourage additional, targeted sampling at aboveground AWCs.

More nongame species were positively associated with areas near AWCs than game species, ranging from lagomorphs to mammalian predators to songbirds to bats. Lagomorphs (i.e., black-tailed jackrabbits and Audubon's cottontails) were positively associated with belowground AWCs, the only type of AWC accessible to small mammals. In addition to water, these AWCs may have provided cleared vegetation or sheet metal that could be used as cover and increased foraging opportunities (Burkett and Thompson 1994, Switalski and Bateman 2017). Artificial water catchments helped explain variation in the spatial occurrences of numerous bird species. Similar results have been reported for breeding birds, particularly resident species, which use AWCs and associated vegetation as sources of food, water, and nesting habitat (Cutler and Morrison 1998, Rosenstock et al. 1999, Lynn et al. 2006). Although free water may not be necessary for these birds to survive, it likely affects reproduction and may facilitate larger clutch sizes (Coe and Rotenberry 1983, Lynn et al. 2008). Lastly, AWCs explained variation in the occupancy patterns of 4 of the 7 bat species. These insectivorous species may be using AWCs as a foraging site for insects and a source of surface water. California

Table 4. Regression models where we used bird species traits, including body mass, diet, and land cover preference, as predictor variables for whether the spatial occurrences of bird species in the Mojave Desert, California, USA, 2016–2017, were strongly and positively associated with artificial water catchments (1) or not (0). K = number of estimable parameters, ΔAIC = difference in Akaike's Information Criterion, ω_i = Akaike weight, β = beta estimate for the species' trait, and SE = standard error.

Variable	K	ΔAIC	ω_i	β	SE
Diet	3	0.00	0.54		
Carnivore				−0.29	0.540
Herbivore				0.69	1.061
Omnivore				−1.79	1.190
Null	1	2.11	0.19		
Body mass	2	2.36	0.17		
Body mass (ln)				0.03	0.339
Land cover preference	2	3.39	0.10		
Arid land				−0.44	0.427
Generalist				0.85	1.008

myotis, the species that had the strongest association with AWCs, were also among the most commonly detected bat species at water developments in Arizona (Rosenstock et al. 2004).

In recent years, researchers and managers have suggested that manipulating a limiting resource like free water may have unintended, negative effects on native populations. Artificial water catchments may, for example, have poor water quality that poses a health risk to animals, promote disease transmission, or act as foci of interspecific competition (Rosenstock et al. 1999). We found minimal evidence supporting that AWCs negatively influenced the distributions of wildlife populations. Among the 44 terrestrial mammal, bat, and bird species that we modeled, occupancy of only a single species (i.e., horned larks) was negatively associated with AWCs, whereas 29 species were positively associated with these features. Further, horned lark prefer open, barren country (Wiens et al. 1987), so their negative association with AWCs may be due to the accompanying vegetation and debris rather than the structures themselves.

Our research did support, however, the possibility that AWCs influence interspecific competition. The potential costs of interspecific competition are likely amplified at AWCs compared to other shared resources because they are spatially fixed (Thrash et al. 1995, Atwood et al. 2011). We found that coyotes (*Canis latrans*) and bobcats (*Lynx rufus*), which are dominant competitors in the Mojave, had stronger positive associations with AWCs than gray fox and kit fox, which are subordinate competitors (Atwood et al. 2011). We also found that the limited number of AWCs where gray fox and kit fox were photographed had few or no detections of coyotes and bobcats, and in the case of gray fox were close to rugged escape terrain. These findings suggest that foxes may be partitioning their use of AWCs to minimize the risk of encountering dominant competitors (Hayward and Slotow 2009, Atwood et al. 2011).

Our research demonstrates the utility of simultaneous camera trap and acoustic recorder surveys, and occupancy models, for assessing a diverse array of species' responses to AWCs. Our study did, however, have several limitations. First, it was a short-term study carried out at already constructed AWCs. Thus, we were unable to determine whether the construction of AWCs improved species' fitness or resulted in range expansions, and whether the influence of AWCs varied seasonally or annually. If, for example, low levels of precipitation in 2016 made wildlife more likely to occupy areas near AWCs, then occupancy at AWCs may have been biased high. It would be advantageous if future monitoring efforts were conducted before and after the construction of AWCs to more clearly identify species that are benefitting from the installation of these manmade features and over a long enough duration to capture the range of variability inherent in the desert southwest (Burkett and Thompson 1994, Cain et al. 2008). Our study was also limited in that we did not account for naturally occurring water. Future studies should consider mapping and including a detailed measure of natural water availability. Finally, our study cannot separate the direct effects of AWCs as sources of free water for wildlife from the indirect effects AWCs may foster such as altering the structure and composition of adjacent vegetation and invertebrate communities.

MANAGEMENT IMPLICATIONS

We recommend that managers expend the time and resources needed to maintain existing AWCs. If time and resources are limited, managers should prioritize maintenance based on current and forecasted distributions of water, where areas forecasted to have the largest decrease in water availability are prioritized. We also recommend modifying AWC structures, if needed, to make them accessible to as many species as possible. This will help maximize the net gains of maintaining these features. Lastly, we recommend systematically monitoring species' presence at AWCs during times of high, low, and average water availability, and monitoring survival and reproduction for a limited set of focal species. This information would facilitate a more efficient use of labor and capital resources, help ensure the decision to maintain AWCs is influenced by empirical data, and enable assessments of fitness and range shifts.

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LITERATURE CITED

Atwood, T. C., T. L. Fry, and B. R. Leland. 2011. Partitioning of anthropogenic watering sites by desert carnivores. Journal of Wildlife Management 75:1609–1615.

Bachelet, D., K. Ferschweiler, T. Sheehan, and J. Strittholt. 2016. Climate change effects on southern California deserts. Journal of Arid Environments 127:17–29.

Benolkin, P. 1990. Strategic placement of artificial watering devices for use by chukar partridge. Pages 59–62 *in* G. K. Tsukamoto and S. J. Stiver, editors. Wildlife Water Development Symposium. The Wildlife Society —Nevada Chapter, U.S. Bureau of Land Management, Nevada Department of Wildlife, 29 November–1 December 1988, Las Vegas, Nevada, USA.

Bleich, V. C., N. G. Andrew, M. J. Martin, G. P. Mulcahy, A. M. Pauli, and S. S. Rosenstock. 2006. Quality of water available to wildlife in desert environments: comparisons among anthropogenic and natural sources. Wildlife Society Bulletin 34:627–632.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:3–50.

Burkett, D. W., and B. C. Thompson. 1994. Wildlife association with human-altered water sources in semiarid vegetation communities. Conservation Biology 8:682–690.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cain III, J. W., P. R. Krausman, J. R. Morgart, B. D. Jansen, and M. P. Pepper. 2008. Responses of desert bighorn sheep to removal of water sources. Wildlife Monographs 171:1–32.

California Department of Fish and Wildlife [CDFW]. 2015. California State Wildlife Action Plan, 2015 update: a conservation legacy for Californians. A. G. Gonzales and J. Hoshi, editors. Prepared with assistance from Ascent Environmental, Inc., Sacramento, California, USA.

California Department of Fish and Wildlife [CDFW]. 2017. Vegetation Classification and Mapping Program. https://www.wildlife.ca.gov/Data/VegCAMP. Accessed 10 Oct 2017.

Coe, S. J., and J. T. Rotenberry. 1983. Water availability affects clutch size in a desert sparrow. Ecology 84:3240–3249.

Cutler, T. L., and M. L. Morrison. 1998. Habitat use by small vertebrates at two water developments in southwestern Arizona. Southwestern Naturalist 43:155–162.

DeStefano, S., S. L. Schmidt, and J. C. deVos Jr. 2000. Observations of predator activity at wildlife water developments in southern Arizona. Journal of Range Management 53:255–258.

deVos Jr., J. C., C. R. Miller, S. L. Walchuk, W. D. Ough, P. E. Taylor. 1983. Biological resource inventory, Tucson Division- Phase B, Central Arizona Project. U.S. Bureau of Reclamation, Final Report, Phoenix, Arizona, USA.

Epps, C. W., D. R. McCullough, J. D. Wehausen, V. C. Bleich, and J. L. Rechel. 2004. Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18:102–113.

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Furnas, B. J., and R. L. Callas. 2015. Using automated recorders and occupancy models to monitor common forest birds across a large geographic region. Journal of Wildlife Management 79:325–337.

Furnas, B. J., R. H. Landers, R. L. Callas, and S. M. Matthews. 2017. Estimating population size of fishers (*Pekania pennanti*) using camera stations and auxiliary data on home range size. Ecosphere 8:e01747.

Furnas, B. J., and M. C. McGrann. 2018. Using occupancy modeling to monitor dates of peak vocal activity for passerines in California. Condor 120:188–200.

Golightly Jr. R. T., and R. D. Ohmart. 1984. Water economy of two desert canids: coyote and kit fox. Journal of Mammalogy 65:51–58.

Hall, L. K., R. T. Larsen, R. N. Knight, K. D. Bunnell, and B. R. McMillan. 2013. Water developments and canids in two North American deserts: a test of the indirect effect of water hypothesis. PLoS ONE 8:e67800.

Hayward, M. W., and R. Slotow. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. South African Journal of Wildlife Research 39:109–125.

Iknayan, K. J., and S. R. Beissinger. 2018. Collapse of a desert bird community over the past century driven by climate change. Proceedings of the National Academy of Sciences 115:8597–8602.

Kluever, B. M., E. M. Gese, and D. J. Dempsey. 2016. The influence of wildlife water developments and vegetation on rodent abundance in the Great Basin Desert. Journal of Mammalogy 97:1209–1218.

Krausman, P. R., and R. C. Etchberger. 1995. Response of desert ungulates to a water project in Arizona. Journal of Wildlife Management 59:292–300.

Krausman, P. R., S. S. Rosenstock, and J. W. Cain. 2006. Developed waters for wildlife: science, perception, values, and controversy. Wildlife Society Bulletin 34:563–569.

Larsen, R. T., J. A. Bissonette, J. T. Flinders, and J. C. Whiting. 2012. Framework for understanding the influences of wildlife water developments in the western United States. California Fish and Game 98:148–163.

Leopold, A. S. 1933. Game management. Charles Scribner's Sons, New York, New York, USA.

Longshore, K. M., C. Lowrey, and D. B. Thompson. 2009. Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73:280–286.

Lynn, J. C., C. L. Chambers, and S. S. Rosenstock. 2006. Use of wildlife water developments by birds in southwest Arizona during migration. Wildlife Society Bulletin 34:592–601.

Lynn, J. C., S. S. Rosenstock, and C. L. Chambers. 2008. Avian use of desert wildlife water developments as determined by remote videography. Western North American Naturalist 68:107–112.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2018. Occupancy estimation and modeling, second edition. Elsevier, San Diego, California, USA.

Marshal, J. P., V. C. Bleich, P. R. Krausman, M. L. Reed, and N. G. Andrew. 2006. Factors affecting habitat use and distribution of desert mule deer in an arid environment. Wildlife Society Bulletin 34:609–619.

McCain, C. M. 2009. Global analysis of bird elevational diversity. Global Ecology and Biogeography 18:346–360.

Morgart, J. R., J. J. Hervert, P. R. Krausman, J. L. Bright, and R. S. Henry. 2005. Sonoran pronghorn use of anthropogenic and natural water sources. Wildlife Society Bulletin 33:51–60.

O'Brien, C. S., R. B. Waddell, S. S. Rosenstock, and M. J. Rabe. 2006. Wildlife use of water catchments in southwestern Arizona. Wildlife Society Bulletin 34:582–591.

Ordiz, A., S. Sæbø, J. Kindberg, J. E. Swenson, and O. G. Støen. 2017. Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? Animal Conservation 20:51–60.

Patten, D. T., L. Rouse, and J. C. Stromberg. 2008. Isolated spring wetlands in the Great Basin and Mojave Deserts, USA: potential response of vegetation to groundwater withdrawal. Environmental Management 41:398–413.

Pekel, J. F., A. Cottam, N. Gorelick, and A. S. Belward. 2016. High-resolution mapping of global surface water and its long-term changes. Nature 540:418.

PRISM Climate Group. 2018. Daily precipitation and mean temperature data. http://www.prism.oregonstate.edu/recent/. Accessed 10 Jan 2018.

Rapacciuolo, G., S. P. Maher, A. C. Schneider, T. T. Hammond, M. D. Jabis, R. E. Walsh, K. J. Iknayan, G. K. Walden, M. F. Oldfather, D. D. Ackerly, and S. R. Beissinger. 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology 20:2841–2855.

Robbins, C. T. 2001. Wildlife feeding and nutrition. Academic Press, San Diego, California, USA.

Roberts, R. F. 1977. Big game guzzlers. Rangeman's Journal 4:80–82.

Rodewald, P., editor. 2018. Birds of North America. Cornell Laboratory of Ornithology, Ithaca, New York, USA. https://birdsna.org/Species-Account/bna/home. Accessed 16 Aug 2018.

Rosenstock, S. S., W. B. Ballard, and J. C. Devos Jr. 1999. Benefits and impacts of wildlife water developments. Journal of Range Management 52:302–311.

Rosenstock, S. S., M. J. Rabe, C. S. O'Brien, and R. B. Waddell. 2004. Studies of wildlife water developments in southwestern Arizona: wildlife use, water quality, wildlife diseases, wildlife mortalities, and influences on native pollinators. Arizona Game and Fish Department, Research Branch Technical Guidance Bulletin 8:1–15.

Schemnitz, S. E. 1994. Scaled quail. Birds of North America 106:1–14.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H. P. Huang, N. Harnik, A. Leetmaa, N. C. Lau, and C. Li. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Serra-Diaz, J. M., J. Franklin, M. Ninyerola, F. W. Davis, A. D. Syphard, H. M. Regan, and M. Ikegami. 2014. Bioclimatic velocity: the pace of species exposure to climate change. Diversity and Distributions 20:169–180.

Shriner, D. S., R. B. Street, R. Ball, D. D'Amours, K. Duncan D. Kaiser, A. Maarouf, L. Mortsch, P. Mulholland, R. Neilson, J. A. Patz, J. D. Scheraga, J. G. Titus, H. Vaughan, and M. Weltz. 1998. North America. Pages 255–332 *in* R. T. Watson, M. C. Zinyowera, R. H. Moss, and D. J. Dokken, editors. The regional impacts of climate change: an assessment of vulnerability. Cambridge University Press, Cambridge, United Kingdom.

Switalski, A. B., and H. L. Bateman. 2017. Anthropogenic water sources and the effects on Sonoran Desert small mammal communities. PeerJ 5: e4003.

Thrash, I., G. K. Theron, and J. D. P. Bothma. 1995. Dry season herbivore densities around drinking troughs in the Kruger National Park. Journal of Arid Environments 29:213–219.

Turner, J. C., C. L. Douglas, C. R. Hallum, P. R. Krausman, and R. R. Ramey. 2004. Determination of critical habitat for the endangered Nelson's bighorn sheep in southern Calfornia. Wildlife Society Bulletin 32:427–448.

United States Geological Survey. 2016. National Elevation Dataset. https://lta.cr.usgs.gov/NED. Accessed 10 Jan 2017.

University of Michigan. 2018. Animal Diversity Web. https://animaldiversity.org/. Accessed 16 Aug 2018.

Wiens, J. A., J. T. Rotenberry and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132–147.

Wright, J. T. 1959. Desert wildlife: a research study. Arizona Game and Fish Department, Phoenix, USA.

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