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Research Article

A Connectivity and Wildlife Management Conflict in Isolated Desert Waters

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ABSTRACT In deserts, amphibian reproduction is restricted to a dynamic network of small, isolated, ephemeral water sites, which support gene flow between isolated populations. Establishment of artificial catchments to augment natural water sources for target species other than amphibians (e.g., larger-bodied and more-vagile game species) can increase connectivity between potential breeding sites and populations of amphibians. These anthropogenic waters, however, may differ in quality from natural waters, with ammonia concentrations high enough to potentially affect amphibian health, reproduction, and population persistence. Thus, water supplementation has set up a potential conflict for managing landscape connectivity for sympatric species differing in dispersal abilities. To explore this possibility, we used graph theory to examine potential connectivity under current and potential future scenarios among natural, modified natural, and human-made waters on the United States Air Force's Barry M. Goldwater Range East (BMGR-E) and adjacent Bureau of Land Management (BLM) lands in Arizona. The network of 117 waterbodies on the study site (82 natural and unmodified, 35 anthropogenic or modified) coalesced at 15.7 km, meaning that wildlife must be capable of traveling $\geq$15.7 km from any water to the next to traverse the network, assuming all the waterbodies are in fact wet. At this threshold dispersal distance, we identified those waters that played important linkage roles in supporting connectivity through the network, 23% (5 of 22) of which were found to be either anthropogenic or modified waters, indicating that human activities play an outsized role in countering natural isolation of the waters. Two of these important waters were hubs (i.e., waters linked to a high number of nearby wetlands), meaning that the potential negative factors in a catchment could affect relatively more wildlife than in waters not associated with a hub. Because the coalescence distance exceeded the dispersal range of many smaller-bodied species, we also examined 2 smaller dispersal distances more appropriate for smaller-bodied and less-vagile species like amphibians (0.6 km and 6 km). We identified 2 wetland clusters that contained anthropogenic or modified waters. When we performed simulated removal of catchments (representing potential management action), the network showed surprisingly few effects: coalescence distance did not increase, and although the number of wetland clusters changed slightly, wetland density in the majority of clusters was not reduced. These results suggest that catchments could be removed without much negative impact on larger, high-vagility (i.e., those capable of dispersing $\geq$15.7 km; large mammals) or smaller, low-vagility (e.g., amphibians) species. Simulated removal of waters allowed us to generate a prioritized list of waters found to be consistently important for connectivity conservation for wildlife (large and small) on BMGR-E and adjacent BLM lands. Such an approach could be adopted in any situation where a quantitative assessment of connectivity among habitat patches and management options is needed. © 2016 The Wildlife Society.

KEY WORDS amphibian, catchment, connectivity, graph theory, network, wildlife water.

Temporary freshwater wetlands are simultaneously among the most important and most vulnerable habitats on Earth (Brinson and Malverez 2002) crucial for supporting biodiversity globally (Griffiths 1997). In arid regions, these wetlands provide the foundation for much of the faunal biodiversity and are a critically limiting resource (Rosenstock et al. 1999, O'Brien et al. 2006). Although there is controversy regarding their effectiveness and potential negative impacts (Broyles 1995, Larsen et al. 2012), federal state and private land management agencies have established water developments throughout the United States to improve water availability for a variety of wildlife species (Rosenstock et al. 1999).

Arid-land waters serve a variety of wildlife species ranging from large mammals to amphibians. Many arid-land waters

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are isolated in independent watersheds (hereafter, isolated desert waters) and are intermittent, filling only from precipitation runoff. These waters are especially vulnerable because of a changing climate that is projected to significantly alter habitat availability for many species (Bates et al. 2008, Kunkel et al. 2013). For example, even the most conservative climate models predict that the arid southwestern United States will become hotter and rainfall more unpredictable, causing increased scarcity of reliable water sources and significantly affecting resource availability for a variety of wildlife species (Seager et al. 2007, Romero-Lankao et al. 2014). Awareness of the need to manage landscapes and resources in ways that promote adaptation to climate change is growing (Vos et al. 2008, Mawdsley et al. 2009, Groves et al. 2012). Hence, management and maintenance of these waters will increase in importance with increased climatic variability.

Two of the primary management activities to mitigate water scarcity are to 1) modify existing natural water sources to increase their volume and, consequently, hydroperiod, and 2) supplement available natural waters with constructed catchments supplied with water. Both such activities have occurred on numerous federal, state, and private lands in the United States. In 11 western states, almost 6,000 catchments have been constructed (Rosenstock et al. 1999) at such places as Desert National Wildlife Refuge (NV; Loeheffner 2009), Big Desert Game Management Unit (ID; Ogden 1990), Kaibab National Forest (AZ; U.S. Forest Service 2008), Cabeza Prieta National Wildlife Refuge (AZ; Slone 2011), Kofa National Wildlife Refuge (AZ), Sonoran Desert National Monument (AZ), and various Bureau of Land Management (BLM) lands and military installations (BLM 1995*a*,*b*; U.S. Department of the Air Force et al. 2013; Arizona Game and Fish Department 2014). These activities have primarily focused on supplementing water for game species, namely desert bighorn (*Ovis canadensis nelsoni*) and mule deer (*Odocoileus hemionus*; Bleich 1992, Rosenstock et al. 1999, Rosenstock et al. 2004), but game cameras have documented use of these catchments by additional wildlife species, including various amphibians (O'Brien et al. 2006).

Installed catchments increase resource density but differ in structure from natural sites, with implications on water quality. Specifically, ammonia accumulates from the decomposition of organic matter in Sonoran Desert catchments (Griffis-Kyle et al. 2014). Natural and modified natural waterbodies are flushed of accumulated debris during rain events (Fig. 1), but there is no such natural mechanism to remove organic material from anthropogenic catchments. Recent work has reported that over half of catchments surveyed in the Sonoran Desert in 2 separate studies in 2 different years exceeded the Environmental Protection Agency's (EPA's) Guidelines for Freshwater Aquatic Life for ammonia concentration, some by a factor of 10 (Griffis-Kyle and Jenness 2013, Hermosillo 2013) and at levels that were toxic to amphibians (Camargo and Alonso 2006). Amphibians also attempt reproduction in these ammoniated sites (Griffis-Kyle et al. 2014, Kiesow 2015), suggesting that in a very stochastic and water-limited environment, amphibians may respond simply to the presence of water rather than assessing other aspects of habitat quality (Griffis-Kyle et al. 2014). Adding water sites to boost connectivity for large species may thus inadvertently affect smaller, non-target species such as amphibians. The potential negative effects of anthropogenic waters create a potential conflict for managing landscape connectivity for sympatric species differing in dispersal abilities. Given our knowledge of how ammonia affects the suitability of individual water sites for organisms, this poses a challenge to valuation of waters for habitat connectivity.

Habitat connectivity (i.e., how, when, and where landscape structure facilitates or impedes movement) is a key determinant of extinction risk for many species and a factor in the success of invasive species, and is thus a primary focus of conservation (Taylor et al. 1993). We used techniques from graph (network) theory to examine a large network of isolated desert waters, weighting the importance of each water body on its contribution to connectivity. A network is described as a collection of nodes (habitat patches; i.e., isolated desert waters) connected by actual or potential dispersal routes, termed links, which we approximated as Euclidean distances between water centroids, although other measures, including actual estimates of movement to define linkages, can also be used (Andersson and Bodin 2008). Graph theory can effectively quantify structural connectivity among nodes and is an efficient tool for conservation planning because it is used with occurrence data rather than detailed demographic data that most other conservation prioritization methods require but that are lacking for most species and take time and resources to acquire

Figure 1. Time series photos of the Black Bottom Tank tinaja on the Barry M. Goldwater Range in southern Arizona, showing flooding during a large rain event in August 2014. Photo credits: 56th Range Management Office, United States Air Force.

(Bunn et al. 2000, Fall et al. 2007, Minor and Urban 2007). A graph-theoretic approach assumes a fully permeable landscape mosaic; related techniques that include some influence of terrestrial habitat and thus assess functional connectivity (e.g., landscape resistance models; Adriaensen et al. 2003, McRae 2006, Zeller et al. 2012) require additional information that is lacking for most species and most regions. Moreover, graph-theoretic methods allow for a quantitative assessment of the role of each node in facilitating connectivity. A graph-theoretic approach thus provides a relatively rapid assessment of structural habitat connectivity, and a useful null model for landscape resistance models when terrestrial data are available (Bunn et al. 2000, Urban and Keitt 2001, Minor and Urban 2007). Such speed and efficiency in quantifying connectivity are critical given the pace and magnitude of wetland losses due to projected climate change in the southwestern United States.

Our objectives were to compare connectivity under different potential scenarios (representing possible management actions and drought or climate change) at the landscape and more localized scales over a range of potential dispersal distances to determine whether anthropogenic waters are facilitating connectivity, and the implications of their possible removal. We also examined the role of the most abundant (but most ephemeral) water type, and generated a list of the most important waters for maintaining connectivity. Our approach allowed for evaluating changes in landscape connectivity for various species simultaneously under different management options. The range of dispersal distances we examined are relevant for many taxa, but our concentration was on connectivity at distances relevant to the large game species that were the target of the management action and to amphibians, which could suffer negative effects from the creation of anthropogenic water sources.

STUDY AREA

We conducted our study primarily on the Barry M. Goldwater Range East (BMGR-East), managed by the United States Air Force (USAF) in southern Arizona, an area >688,000 ha where wildlife management is mandated by the Department of Defense. We focused on the eastern portion of BMGR-East and 3 waters on adjacent BLM lands that were formerly managed by the USAF and are currently co-managed by the BLM (Fig. 2). Our study area was a heterogeneous mosaic consisting of Sonoran Desert bajadas interspersed with igneous rocky outcrops that led to rocky arroyos, and with paved and unpaved roads. There were also small areas with buildings or other human structures. Outside of the study area to the north was the Gila River and associated agricultural fields, and urban areas (including Yuma and Gila Bend, AZ). This area experienced average high daily air temperatures up to 42.7°C and averaged 15.6 cm annual precipitation (data for Gila Bend, AZ, from 1892 to 2005 from the Western Regional Climate Center, www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?azgila, accessed 20 Jun 2014). In our study area, as elsewhere in southwestern Arizona south of the Gila River, the only natural water sources were isolated desert waters. On our study area as of

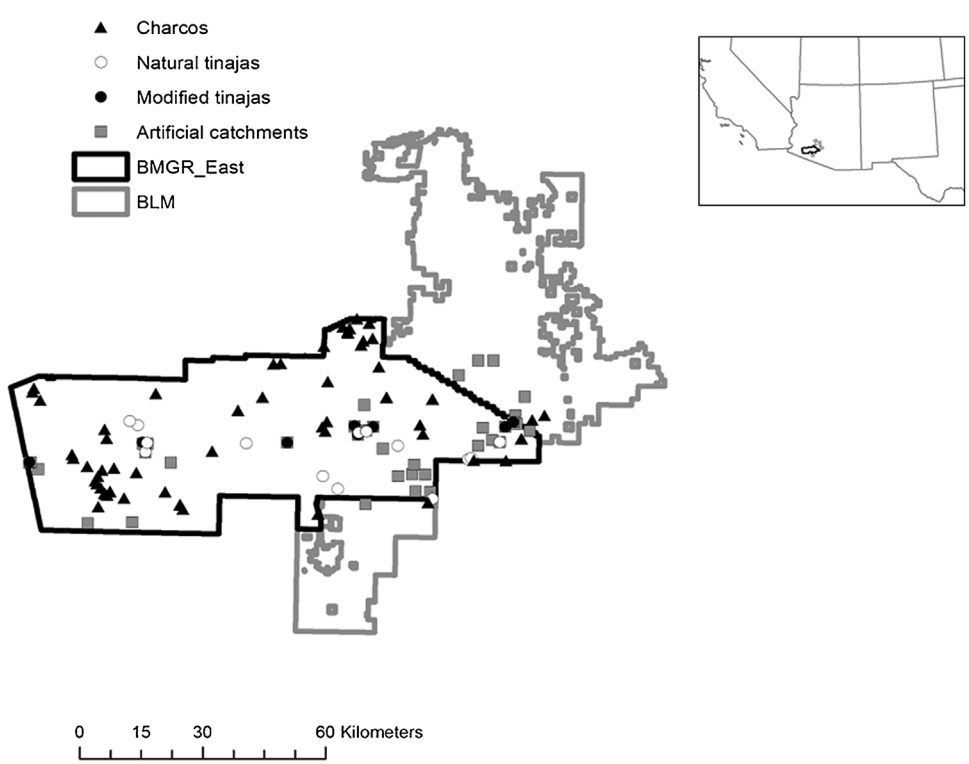

Figure 2. Natural (15 natural tinajas and 67 charcos), modified (13 modified tinajas), and artificial (22 artificial catchments) waters of the eastern portion of the Barry M. Goldwater Range (BMGR-E; outlined in black) and adjacent Bureau of Land Management lands (BLM; outlined in gray), Arizona, 2014. Inset at upper right shows the location of these sites within Arizona and the southwestern United States.

2014, there were 117 waterbodies (82 natural and unmodified, 35 anthropogenic or modified) within a roughly 9,000-km^2 area (Figs. 2 and 3). Coordinate data of these waters came from BMGR-E personnel and were verified with ground-truthed data or visual inspection of low-altitude imagery from Google Earth (Google, Mountain View, CA). The natural waters included 67 charcos (i.e., very shallow areas that collect runoff, formed in otherwise flat areas via wind scour; Bryan 1920) and 15 tinajas (i.e., eroded areas on rock slopes that collect runoff; Fig. 3a and b). Thirteen additional tinajas were modified via construction of earthen or concrete dams to deepen their basins and increase their hydroperiods, or had dams constructed to block large debris from entering the basin (Fig. 3c). Finally, there were 22 artificial catchments (Fig. 3d) that consisted of concrete, steel, or fiberglass tanks and concrete troughs; these were installed from 1951 to 1995 to increase the density and connectivity of waters, decreasing the distance between them. The tinajas (both natural and modified) of our study area (and 1 artificial catchment) were located in rocky areas, but the charcos and most artificial catchments occurred in flat areas. The natural waters were seasonal, filling when there was sufficient precipitation, whereas the catchments contained water year-round. The modified tinajas were intermediate between these 2 endpoints of hydroperiod length. Because the charcos were the shallowest, they had the shortest hydroperiods of any of the water types.

METHODS

We sampled water quality at 6 tinajas and 17 catchments between July and October 2012, with sites selected based on access and logistics. We measured pH, conductivity, and total dissolved solids with hand-held probes (MP-6p Portable Meter; Hach, Loveland, CO) and ammonia and nitrate+nitrite concentrations using a handheld colorimeter (DR/890 Portable Colorimeter; Hach). We measured water quality parameters at mid-water column from the edge of the water body. We took all measurements between 0600 and 1400 Standard Mountain time zone. We used analysis of variance (ANOVA) to compare water-quality parameters by water type.

A connected landscape is one defined by the property of coalescence, a critical threshold that defines whether a landscape is traversable or not, given a species' vagility and the distribution of resources. A single coalescence distance value is present for a given network; this distance indicates the presence of a system change (a critical threshold in landscape status from fragmented to connected), such that dispersal capacity below the coalescence distance means that an organism would be unable to move through the network (at some point, the next node would be sited too far away, beyond the organism's dispersal capacity). Conceptually, at a smaller given distance (such as the size of an animal's daily foraging movements), a given number of waters will be available for an animal to use. These waters thus form a cluster (defined as $\geq$2 waters within a given distance) that is separated from other waters that are farther away. As the potential dispersal distance is increased, clusters grow and merge until, eventually, there is a single cluster comprising every wetland in the network. At that point, a highly vagile animal could cross the entire network, moving from water to water. Network coalescence thus represents a transition from

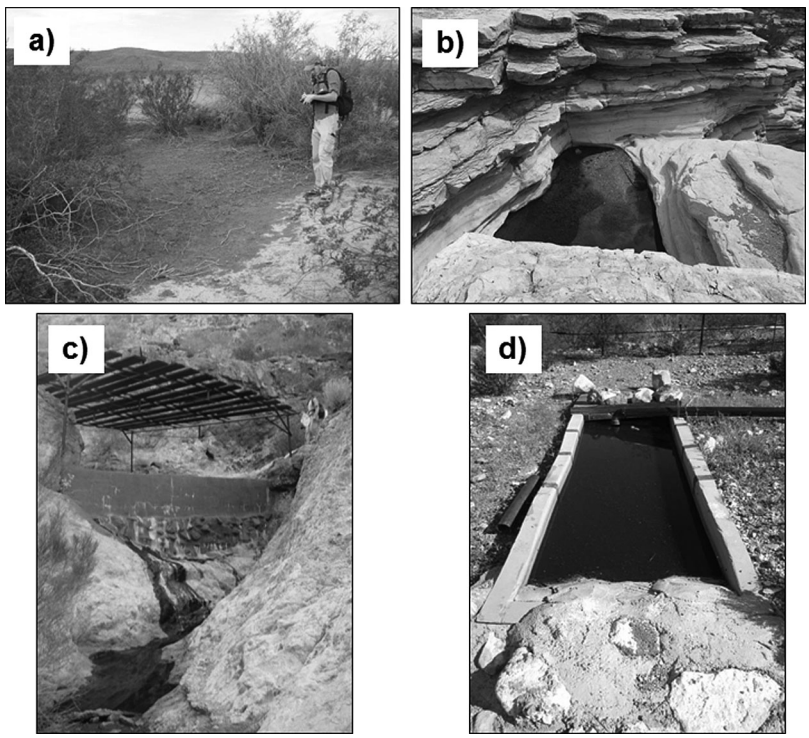

Figure 3. Examples of a) charco, b) natural tinaja, c) modified tinaja (with a concrete dam and a wooden shade structure), and d) catchment on the eastern portion of the Barry M. Goldwater Range, Arizona, 2010–2014. Photo credits: a) J. Goetting, b) N. E. McIntyre, c) J. Goetting, d) J. C. Drake.

a fragmented landscape to a connected one (Keitt et al. 1997). An assumption behind this approach is that all waters in the network are wet simultaneously. This can potentially happen during the 2 rainy seasons of the Sonoran Desert (Pacific fronts in the winter and convective thunderstorms in the summer monsoon season; Whitford 2002).

Using the package igraph (Csardi and Nepusz 2006) in R 3.0.2 (R Core Team 2014), we determined when the network of waters coalesced (within the nearest 0.1 km). At coalescence, we ranked individual waters according to their importance in supporting connectivity. Ranking habitat patches according to their importance in supporting connectivity through a habitat network is common (Bodin and Saura 2010), although the rankings can be influenced by the connectivity metric used (Laita et al. 2011). Thus, we used 3 conceptually and computationally different measures of connectivity, identifying patches as stepping-stones, cutpoints, or hubs (Ruiz et al. 2014). Stepping-stones are determined via betweenness centrality, a standard network metric that identifies the number of shortest paths through each node within the network; thus a stepping-stone is a node through which most of the shortest paths pass (Csardi and Nepusz 2006). A cutpoint (or articulation point) is a node that, if removed, causes the network to become fragmented (i.e., increases the number of clusters present; Csardi and Nepusz 2006). Finally, Kleinberg's hub scores are proportional to the number of links from a node, with a node that is connected to a large number of other nodes (within a specified dispersal distance) receiving a high hub score (Csardi and Nepusz 2006). These 3 metrics (out of a large number of possible connectivity metrics; Tischendorf and Fahrig 2000) quantify structural connectivity. At the coalescence distance, we ranked waters according to their betweenness centrality and hub scores; cutpoint designation is categorical rather than continuous and so could not be ranked. Stepping-stones, cutpoints, and hubs do not exist except at the coalescence distance (or above) because they are identified as nodes that permit connectivity through the network, which can only occur at coalescence or above.

In addition to identifying the overall network connectivity threshold distance, we also examined topology at distances more relevant to species with lower vagility, such as amphibians. Although different desert amphibians have species-specific habitat requirements, they are, as a group, rather more similar in their breeding habitat requirements than are other small taxa such as birds or small mammals, which makes amphibians a good focal taxon for examining wetland connectivity. We gathered information on observed maximum dispersal distances for native amphibians (all anurans) in our area (Table 1). Although dispersal distances were not known for several of our species, they could be inferred from data from congeners (see footnotes of Table 1). In addition, because the distances we used (Table 1) may underestimate true maximum dispersal capacity, we examined distances on the relatively low and high ends (0.6 km and 6 km) to provide a broad representation of dispersal or daily movement distances well below the coalescence threshold for many non-target taxa. Focusing on only an average, median, or modal estimated distance moved by species of concern would effectively ignore the majority of species that also use these waterbodies, and would also ignore the infrequent, but potentially crucial, longer-distance movements that could be made by any species. By including relatively small and much larger distances, our approach includes a wide potential spectrum of species of management concern.

Table 1. Reported maximum dispersal distances for native amphibian species in the southwestern United States.

Species	Distance (km)
Great Plains toad (*Anaxyrus cognatus*)	0.914[a]; 1.6[b]
Red-spotted toad (*Anaxyrus punctatus*)	0.95[c]
Sonoran green toad (*Anaxyrus retiformis*)	0.95[d]
Southwestern Woodhouse's toad (*Anaxyrus woodhousii australis*)	0.95[d]
Lowland leopard frog (*Lithobates yavapaiensis*)	0.272[e]; 2.2–7.7[f]
Couch's spadefoot toad (*Scaphiopus couchii*)	0.762[g]
Mexican spadefoot toad (*Spea multiplicata*)	0.762[g]
Lowland burrowing treefrog (*Smilisca fodiens*)	0.008–2[h]

[a] Ewert (1969).
[b] Creusere and Whitford (1976).
[c] Weintraub (1974).
[d] Inferred based on data for red-spotted toad (*Anaxyrus punctatus*) from Weintraub (1974).
[e] Zylstra et al. (2015).
[f] Rosen et al. (2013).
[g] Inferred based on data for eastern spadefoot toad (*Scaphiopus holbrookii*) from Pearson (1955).
[h] Inferred based on data for western narrow-mouthed toad (*Gastrophryne olivacea*) from Fitch (1956).

At the 0.6 km and 6 km distances, we calculated the number of wetland clusters present, with each cluster consisting of wetlands within these distances. Stepping-stones, cutpoints, or hubs can be calculated for individual clusters, if such clusters are treated as entire, separate networks. Clusters exist, by definition, at scales lower than the coalescence distance (at coalescence, there is a single cluster), and different distances (scales) render different numbers, sizes, and configurations of clusters. This is where it becomes important to use species-relevant scales to identify clusters. If the primary management objective is to ensure that all waterbodies are linked, then the focus should be on identifying the coalescence threshold under current network topology, comparing that to the dispersal distances of the species of management interest, and determining whether waters need to be added to the network to reduce the coalescence distance. If the species of management interest have drastically different dispersal capacity (e.g., large mammals compared to amphibians), then identification of clusters at dispersal distances smaller than coalescence would be necessary. In contrast, if the objective is to minimize for loss of waterbodies, which could decrease overall connectivity, then identification of those waters that play important roles as stepping-stones, cutpoints, or hubs would be needed. Because all 3 of these situations are at play in our study region, we identified the coalescence threshold, examined cluster structure under dispersal distances relevant to amphibians, and identified waters as stepping-stones, cutpoints, and hubs.

Table 2. Number of isolated desert waters by type that we identified as playing key roles in supporting connectivity at the 15.7-km threshold in the 117-water network of the eastern portion of the Barry M. Goldwater Range and adjacent Bureau of Land Management lands, Arizona, 2014.

Role	Catchment	Modified tinaja	Natural tinaja	Charco
Stepping-stone (top 10)	2	1	1	6
Hub (top 10)	1	1	1	7
Cutpoint (all 2)	0	0	0	2

We then expanded on these analyses to explore the potential impacts of removing water sites under 3 scenarios (representing possible management actions or due to drought or climate change), compared to the full network of all the waters. Under the first scenario, all of the catchments were removed (hereafter scenario 1, catchments removed), representing management of actual and potential ammoniated waters, or potential loss of financial or other support for maintenance of these waters. During rare and brief periods of very high rainfall, however, these catchments would likely not be as important to amphibian dispersal as would be charcos, the most numerous water type on the study area. Therefore, we also examined another scenario where charcos were removed (scenario 2, charcos removed), which would allow us to isolate the influence of catchments from these shallow and highly ephemeral (but numerous) waters. Because charcos are dry more often than they are wet, scenario 2 represents typical conditions (and ones that would be increasingly likely under drought or climate change). Finally, we combined these scenarios to represent management under drought or climate change, leaving only the more persistent modified and natural tinajas (scenario 3, catchments and charcos removed). We compared results from each of these scenarios to results from the full network of all waters assumed to be wet, representing maximum water availability; we repeated the comparisons for the coalescence distances 0.6 km and 6 km. In every scenario, we identified the most important waters that assumed >1 role (i.e., as a top 10 stepping-stone, top 10 hub, or cutpoint) in supporting connectivity at network coalescence; those waters that were identified as important (playing >1 role) in >1 scenario were deemed to be the highest priorities for conservation. Although waterbodies that rank highly in >1 metric are not inevitably more important than others, there is no precedent as to how to prioritize on the basis of connectivity. Our approach provides one such guide.

RESULTS

For the network of all 117 waters, coalescence was achieved at 15.7 km, indicating that an animal must be capable of moving at least 15.7 km (going from water to water) if it is to traverse the entire network (i.e., the farthest separation of waters was 15.7 km). At this coalescence threshold of network connectivity, we identified the top 10 stepping-stones, top 10 hubs, and all ($n = 2$) cutpoints; 3 of these 22 key sites were catchments, and 2 more were modified tinajas. Of the catchments identified as key sites, one was sampled for ammonia and was found to have an extremely high ammonia concentration (Sand Tank #8, at 55 mg/L N-NH_3). One of the catchments and one of the modified tinajas were hubs, which have the potential to influence a larger amount of wildlife than would be expected at just 2 waters, because of their connections to other waters (Table 2). Both of the cutpoints were charcos, and most of the stepping-stones and hubs were charcos as well (not surprising because 57% of all the waters were charcos). At the 2 smaller scales examined (0.6 km and 6 km), we identified numerous wetland clusters (Table 3), several of which contained catchments (Fig. 4). This was expected, given that many of the catchments were located close to other waters, increasing the potential for dispersal of amphibians among the waters within a cluster (and less or no dispersal between clusters).

When the 22 catchments were removed via simulation in scenario 1, representing management action to mitigate negative effects from high ammonia levels, 95 water bodies remained and the network coalescence distance (15.7 km) did not change. This was somewhat surprising, because decreasing the density of waters should increase the distance needed to move among the remaining waters, thereby increasing the coalescence distance. However, the catchments were mostly concentrated in the center of the network and were sited near other waters (Fig. 2), so their removal did not alter network topology enough to change the minimum dispersal distance necessary to traverse the network. When we examined scenario 1 at the 0.6 km and 6 km scales relative to the overall network, the numbers of wetland clusters changed and the density of waters within a majority of clusters decreased (Table 3, Fig. 5).

Table 3. Number of wetland clusters and cluster size range at 2 dispersal scales in the 117-water network of the Barry M. Goldwater Range and adjacent Bureau of Land Management lands, Arizona, 2014, and the various culling scenarios.

Scenario and metric	0.6 km	6 km
All 117 waters on study area		
No. of clusters containing >2 waters	21	17
Cluster size range (i.e., no. of waters within a cluster)	2–3	2–27
Scenario 1, catchments removed		
No. of clusters containing >2 waters	18	19
Cluster size range (i.e., no. of waters within a cluster)	2–3	2–24
Scenario 2, charcos removed		
No. of clusters containing >2 waters	8	6
Cluster size range (i.e., no. of waters within a cluster)	2–3	2–12
Scenario 3, catchments and charcos removed		
No. of clusters containing >2 waters	5	6
Cluster size range (i.e., no. of waters within a cluster)	2–3	2–8

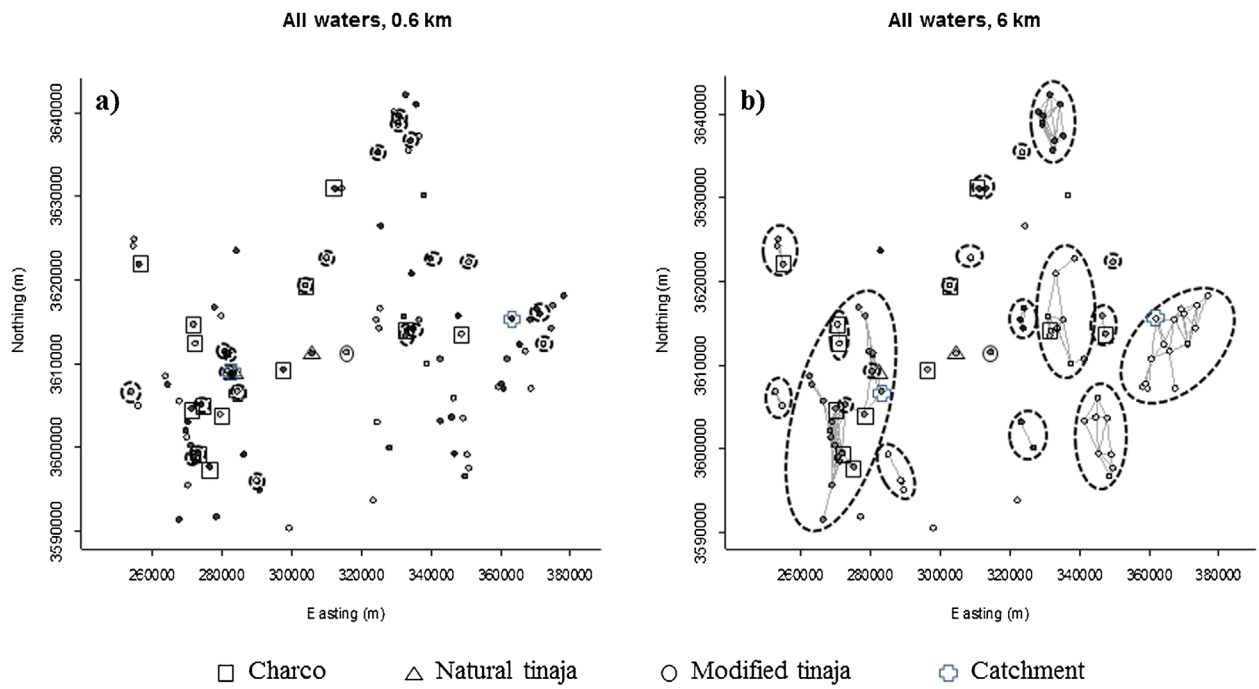

Figure 4. Clusters of all 117 isolated desert waters on our study area in southern Arizona, 2014, at a) 0.6 km and b) 6 km. Waters that are within the specified distance are linked by gray lines; these linked wetlands are circled in dashed lines and the waters within each cluster are grouped by color (grayscale). At the 0.6-km scale, only 1 out of 21 clusters contained a catchment, and none of the clusters contained a modified tinaja. At the 6-km scale, 2 of the 17 clusters contained catchments and all also contained other (natural) waters, but none contained a modified tinaja.

The results from scenario 1 were highly influenced by the sheer abundance and distribution of charcos, which were more numerous than all the other types of waters combined and thus masked the relative connectivity importance of anthropogenic catchments. When we simulated removal of charcos ($n = 67$) in scenario 2, the resulting coalescence distance (22.4 km) was farther compared to all waters and scenario 1 (15.7 km), meaning that catchments did facilitate connectivity through the network when the most abundant water type (charcos) were removed. Furthermore, 5 out of the top 10 stepping-stones, 7 out of the top 10 hubs, and 2 of the 3 cutpoints (when charcos were ignored) were catchments. Additionally, half (4 of 8) of the clusters at the 0.6 km scale and 5 out of the 6 clusters at the 6 km scale contained catchments (Fig. 6). There were 12 catchments in these clusters; we measured 9 for ammonia and found that 100% had concentrations that exceeded the EPA's Guidelines for Freshwater Aquatic Life. Although they may serve a valuable role during times when other waterbodies may be dry, their topology within the network increases the danger of these catchments being potential wildlife hazards. Finally, when both catchments and charcos were removed in scenario 3, coalescence occurred at the greatest distance for any scenario, at 26.6 km. Given that there were only 28 waters present in this scenario, it is not surprising that an animal would need to travel farther through a relatively sparse network even with tinajas present and all assumed wet. Anthropogenic effects on connectivity were still apparent in even this scenario, with modified tinajas occurring in 8 out of 11 clusters at the 0.6-km and 6-km scales (Fig. 7).

For each of our scenarios, we identified waters that played >1 role in supporting connectivity (i.e., >1 of the following: top 10 stepping-stone, top 10 hub, or a cutpoint; Table 4). All 4 water types (charco, natural tinaja, modified tinaja, and catchment) were important in more than 1 role, but there were no waters that played all 3 roles. We identified 2 natural tinajas that played >1 role in >1 scenario; E Pass was a stepping-stone and cutpoint and Javelina Tank was a stepping stone and hub (Table 4). These 2 waters (out of the 117 on the study area) thus deserve the highest connectivity conservation priority.

The only water-quality parameter that differed with water type was ammonia, with higher concentrations in anthropogenic catchments than in tinajas (Table 5; $F_1 = 5.9$, $P = 0.02$). This is consistent with previous work that reported ammonia levels that exceeded EPA standards at 12 out of 16 catchments surveyed (Griffis-Kyle et al. 2014).

DISCUSSION

The heterogeneous nature of our study area may facilitate or impede animal movement among the isolated desert waters. Approaches that incorporate how landscape structure may affect movement among habitat patches (i.e., resistance-based approaches, including use of circuit theory or least-cost paths to quantify functional connectivity) are often touted as being more detailed and realistic than the relatively simple straight-line approach taken in graph theory that ignores intervening landscape heterogeneity (McRae et al. 2008). However, these approaches use the same principles as does graph theory (indeed, they are based in graph theory; Bunn et al. 2000) with

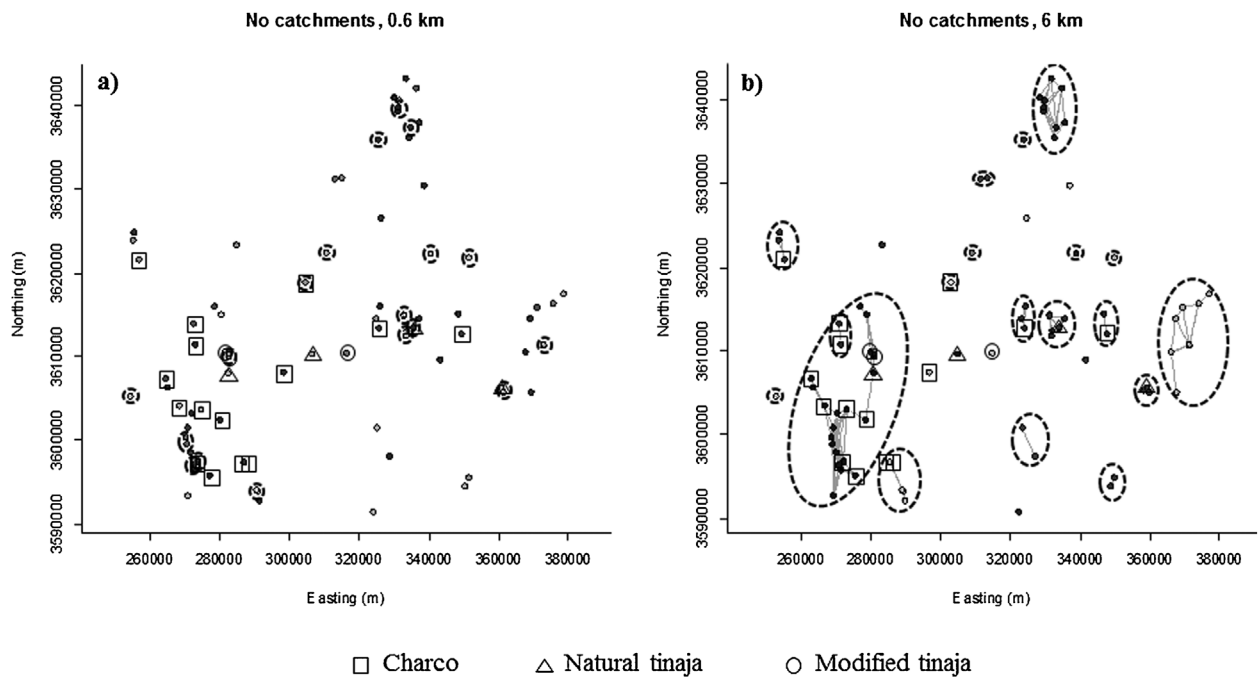

Figure 5. Clusters of isolated desert waters on our study area in southern Arizona, 2014, under scenario 1, catchments removed at a) 0.6 km and b) 6 km. Waters that are within the specified distance are linked by gray lines; these linked wetlands are circled in dashed lines and the waters within each cluster are grouped by color (grayscale). At the 0.6-km scale, only 1 of the 18 wetland clusters contained a modified tinaja. At the 6-km scale, 1 out of 19 clusters did.

both being capable of identifying areas in which to concentrate management attention. Network analyses that rely on thresholds of Euclidean distance (e.g., max. dispersal distance) to examine connectivity (such as our study), can lead to unreliable conclusions on connectivity compared to methods that incorporate more realistic characterizations of the movement process (e.g., via theoretically or conceptually based dispersal kernels; Fletcher et al. 2011). However, such movement data are lacking for most species and systems; our approach was a straightforward, first-step analysis that could be

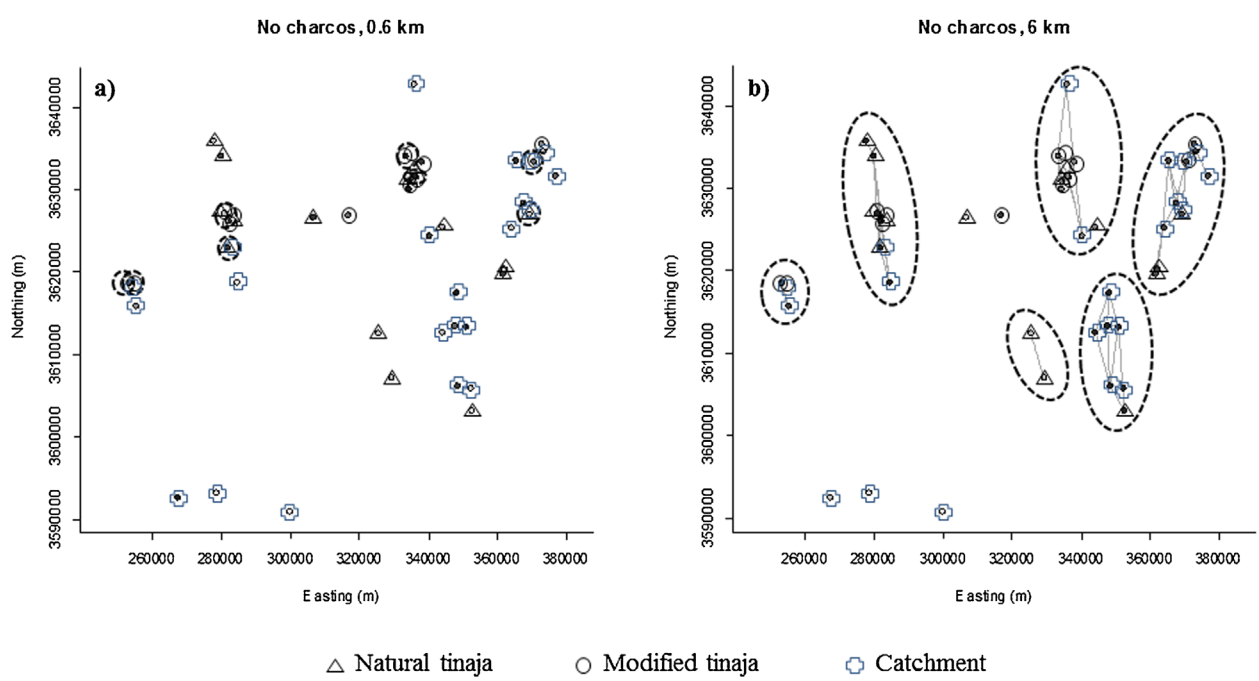

Figure 6. Clusters of isolated desert waters on our study area in southern Arizona, 2014, under scenario 2, charcos removed at a) 0.6 km and b) 6 km. Waters that are within the specified distance are linked by gray lines; these linked wetlands are circled in dashed lines and the waters within each cluster are grouped by color (grayscale).

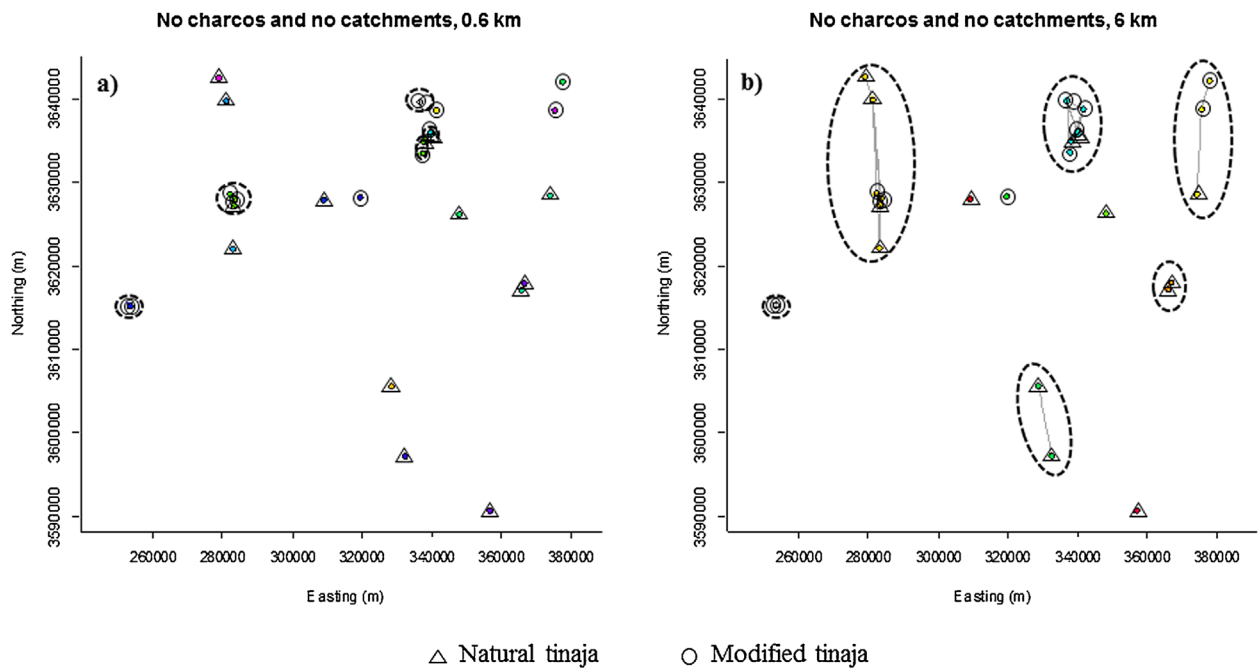

Figure 7. Clusters of isolated desert waters on our study area in southern Arizona, 2014, under scenario 3, charcos and catchments removed at a) 0.6 km and b) 6 km. Waters that are within the specified distance are linked by gray lines; these linked wetlands are circled in dashed lines and the waters within each cluster are grouped by color (grayscale).

applied to obtain an initial assessment to advise more in-depth studies, or in the absence of resources to obtain more detailed movement data. The logical follow-up to our work would be an assessment of functional connectivity for this system, and a comparison to our structural results.

Specific wetlands in our study system can play multiple roles in facilitating connectivity (compare Figs. 4–6). The biological relevance of each role, however, may necessitate different management activities. For example, although it may be desired to conserve both stepping-stones and cutpoints to promote connectivity, they differ in how they do so and thus may differ in conservation priority; cutpoints are single nodes that, if removed, induce system fragmentation, whereas stepping-stones are nodes that lie along expeditious paths through the network. The presence of multiple paths through a network would reduce priority of stepping-stones over cutpoints. Similarly, hubs play a biologically different role from either stepping-stones or cutpoints in supporting connectivity, with possibly the lowest priority of all. Moreover, these roles can change over time as overall network topology changes with rainfall or human activity (Ruiz et al. 2014), meaning that an isolated desert wetland that is important in a given role under the current configuration of wetlands may not be important in that same role under different circumstances. Finally, promoting connectivity may not be desirable if an invasive species or infectious disease is present in the system; in

Table 4. List of waters of the Barry M. Goldwater Range and adjacent Bureau of Land Management lands, Arizona, 2014, that assumed >1 connectivity role (top 10 stepping-stones, top 10 hubs, all cutpoints) by scenario. Waters with an asterisk were important in >1 scenario. UTM coordinates (easting, northing) for Zone 12N are provided.

Scenario	Water type	Water name	Easting	Northing
All 117 waters on study area	Charco	Unnamed	297552.375	3609619.937
	Catchment	New Halliwill	283963.9192	3606964.177
Scenario 1, catchments removed	Charco	Unnamed	273543.017	3605422.458
	Charco	Unnamed	297552.375	3609619.937
Scenario 2, charcos removed	Natural tinaja	E Pass*	305835.6493	3611650.805
	Natural tinaja	Javelina Tank*	342961.875	3610996.5001
	Natural tinaja	Chris Glyph	324555.8455	3603275.8071
	Catchment	Mohawk Mts. #3	267083.3036	3591385.488
	Catchment	Granite Mt. SPH	278038.4774	3591732.9365
Scenario 3, catchments and charcos removed	Natural tinaja	E Pass*	305835.6493	3611650.805
	Natural tinaja	Javelina Tank*	342961.875	3610996.5001
	Natural tinaja	Unnamed	335204.5481	3614698.8465
	Natural tinaja	Aguila N1	277338.1151	3617165.9674
	Natural tinaja	White Tank	328237.125	3600097.0001
	Modified tinaja	Black Tank	315857.5331	3611802.6152

Table 5. Water quality of sampled wildlife waters on the Barry M. Goldwater Range-East in southern Arizona, summer 2012. Ammonia was significantly higher in anthropogenic catchments than in tinajas. No other water quality parameter varied between water type.

	Catchment ($n = 17$)			Tinaja ($n = 6$)		
Parameter	Average	SE	Range	Average	SE	Range
pH	8.2	0.3	(6.3–10.2)	7.7	0.3	(6.6–9.9)
Conductivity (μS/cm)	570.1	113.7	(147.4–1,863.0)	315.0	76.8	(158.5–916.6)
Total dissolved solids	460.1	106.1	(99.3–1,648.0)	214.2	53.8	(100.6–630.0)
Nitrate ($N\text{-}NO_3^-$) mg/L	0.5	0.05	(0–0.8)	1.8	0.5	(0.3–3.7)
Ammonia ($N\text{-}NH_3$) mg/L	22.2	5.4	(0–55)	0.3	0.2	(0–1.0)

such cases, restricted connectivity for quarantine purposes may be desired. All of these factors highlight the difficulty of connectivity conservation.

Our analyses revealed the importance of considering charcos when assessing wetland network connectivity. Charcos may play an important role in the episodic dispersal of some species (Bryan 1920). One tacit assumption in our assessments was that all waters were wet simultaneously, which is not a common event; thus, our results represent potentially best-case situations. Only after an extreme regional rainfall would such a situation potentially occur, and even then it would only be brief because charcos dry quickly after infiltration and evaporation of their small, shallow basins.

We did not assess the influence of the terrestrial surroundings (land cover permeability) that influence dispersal probability and success (Buskirk 2012, Zeller et al. 2012), but our results indicate that the removal of catchments would have a larger effect on organisms that generally travel less than 6 km in a single bout than on more vagile organisms. When catchments were removed (scenario 1), the number of wetland clusters declined from 21 to 18, although cluster size was relatively unchanged. For native amphibians, the isolation of clusters can be important. Invasive species like the American bullfrog (*Lithobates catesbeianus*) require perennial waters, and many of the anthropogenic catchments are managed for year-round access to water. The bullfrogs are a threat to native amphibians in this area in that bullfrogs are a voracious predator, efficient competitor, and are carriers of pathogens such as *Batrachochytrium dendrobatidis*, the fungal disease causing declines in amphibian populations globally (Kraus 2009, Kilpatrick et al. 2010). The bullfrog is much more vagile than are native amphibians in this region (Table 1; Rosenstock et al. 2004, Griffis-Kyle and Jenness 2013), so increased connectivity between clusters and increased hydroperiod at anthropogenic waters could cause population declines and extirpations of native species due to bullfrogs (Hayes and Jennings 1986, Rosen and Schwalbe 2002). Hence, connectivity at the small scale (within clusters) may be important for native amphibians, whereas large-scale connectivity (between clusters) could lead to population declines from invasive species and/or diseases.

Simulated removal of catchments (scenario 1) had little effect on connectivity or network topology at the landscape scale, suggesting that the removal of catchments will likely have little effect for larger and more vagile species when considering the landscape during most years (i.e., dry charcos). Even when charcos are ignored, removal of catchments (scenario 3) caused the coalescence distance to increase by only 4.2 km, suggesting that species that are the primary targets for water supplementation via catchments (e.g., desert bighorn, mule deer) should still be able to traverse the network. Additionally, there was no change in the number of wetland clusters for species that could travel >6 km (Table 3). Cluster size was reduced, but this should not affect these species' access to water because the sites within a cluster would be within an accessible distance. These results indicate that management activity (i.e., catchment removal) could be taken that would benefit amphibians and not harm larger game species (if all catchments are equal).

Catchments are not structurally or functionally the same as natural water sources, which may influence how beneficial they are to amphibians and other wildlife. Unfortunately, amphibians will breed in catchments with high ammonia concentrations (Kiesow 2015). Amphibians are inherently tied to water, and in desert systems, there is a strong selective pressure to locate this ephemeral resource. This is especially insidious for catchments with high ammonia levels nested within wetland clusters. Managers of desert wildlife waters did not consider water quality a concern because previous work did not assess ammonia concentrations and found no marked impairment of water quality (e.g., in terms of total dissolved solids, alkalinity, and a variety of ions; Rosenstock et al. 2005, Bleich et al. 2006), although recent work also reports cases of biological toxins (e.g., *Clostridium botulinum*) impairing water quality in deserts (Swift et al. 2000). Humans have changed breeding resources in ways that desert amphibians may not be assessing, and we have not quantitatively evaluated the impacts of these alterations. Differences in water quality, combined with their inherent isolation, mean that management of these waters and their associated wildlife will not be effective without quantifying connectivity routes and integrating differences in water quality.

MANAGEMENT IMPLICATIONS

Constructing catchments to enhance connectivity has led to elevated ammonia concentrations and there is evidence that these waters may negatively affect non-target species. Management of desert waters is inherently a landscape-level problem, but management needs to include more than an analysis of spatial connectivity. Managers have target species they are trying to assist with the provision of

supplemental waters, species that are generally game animals or species of conservation concern. However, a more comprehensive assessment of connectivity among sites could be applied that considers other species (including invasive species). Furthermore, site attributes, such as habitat quality and permanence, should be considered. Sites that function as attractive traps may appear as if they are enhancing connectivity and population persistence while actually doing harm to populations because they provide poor habitat. Enhanced connectivity may not be desirable in all situations (e.g., for control of invasive species), meaning that simply constructing more habitat patches to facilitate movement across a landscape can be counter-productive to wildlife management goals (Rahel 2013).

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