Will climate change leave some desert bat species thirstier than others?

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Abstract

The combined effects of global climate change and increased anthropogenic use of free water are likely to cause decreases in availability and surface area of water in arid environments. Climate change and water loss are predicted to alter community dynamics, but identifying mechanisms underlying differential responses of species remains a critical conservation challenge. Bats drink in flight and rely on accessible water sources, yet the ability to access water is a function of flight maneuverability. By reducing the size of water sources (to simulate predicted water loss due to climate change/increased human use), we demonstrated species-specific responses by desert bats based on differences in morphology and flight maneuverability. Under natural conditions, less-maneuverable bats selected larger water sources while maneuverable bats exhibited no preference. When we experimentally reduced surface area, larger, less-maneuverable bats experienced a 69% decrease in proportion of drinking passes ($p < 0.05$) and increased competition with smaller, maneuverable bats. Our study illustrates how morphology can mediate access to a resource and highlights conservation implications as water becomes more limited in arid environments. Selection for differences in wing morphology and flight ability in insectivorous bats has allowed for coexistence and high species richness at a local scale. However, anticipated reductions in the sizes of water sources due to climate disruption may lead to species with less maneuverability being unable to access water efficiently and facing increased competition from more agile bats.

Keywords: bats, climate change, flight, maneuverability, morphology, water

1. Introduction

Models of global climate change predict decreasing availability of free water in arid environments due to increased aridity and frequency of drought (Ault et al. 2014; Cook et al. 2015; Dai 2011; Seager et al. 2013). Western North America, for example, recently lost 63 trillion gallons of surface water due to long-term drought (Borsa et al. 2014). Decrease of water coupled with increasing human demand is expected to further reduce water availability in arid regions (MacDonald 2010; Taylor et al. 2013; Wada et al. 2013). The combined effects of climate change and loss of water will likely have profound impacts on biotic communities (Brusca et al. 2013; Lecomte et al. 2009; Maestre et al. 2015; Ogston et al. 2016; Parmesan and Yohe 2003; Walther et al. 2002; Westphal et al. 2016), but there is little information regarding mechanisms that predict how species will respond to these changes. Understanding how variability among species can lead to differential responses to a rapidly changing climate will increase our ability to forecast shifts in biotic communities (Chen et al. 2011; Jump and Peñuelas 2005; Sherwin et al. 2013; van Gils et al. 2016).

The sensitivity of bats to rising temperatures and concomitant loss of water makes them important indicators of climate change (Adams 2010; Jones et al. 2009; Razgour et al. 2013). Although many species of bats have adaptations that help them locate water sources (Greif and Siemers 2010) and limit evaporative water loss (Bell et al. 1986; Geluso 1978; Muñoz-Garcia et al. 2016), most species face challenges associated with water retention (Carpenter 1969; Hattin 1972; Studier 1970; Webb et al. 1995). Consequently, bats rely on access to free water for thermoregulation in addition to foraging and reproduction (Adams and Hayes 2008; Carpenter 1969; Hagen and Sabo 2012; Kurta et al. 1989; Kurta et al. 1990). Significant decreases in surface area of water sources in a water-limited environment may increase inter- and

intraspecific competition among bats attempting to drink and result in reductions in local and regional species richness and/or reductions in reproductive yields for some species (Adams 2010; McCain 2007; Razgour et al. 2011).

Because bats drink in flight, their ability to access water is mainly dependent on their maneuverability and to some extent on their echolocation. Larger, less-maneuverable bats forage high off the ground or in open areas where obstacles are few and speed is favored over maneuverability, while smaller maneuverable bats forage near the ground or on and around vegetation where avoiding obstacles and collisions is critical (Norberg and Rayner 1987). Thus, less-maneuverable bats are more likely affected by reduced surface area of water sources than smaller, more maneuverable species (Cross 1986; Rabe and Rosenstock 2005; Razgour et al. 2010). The potential for morphological differences between ecologically-similar species to drive responses to contemporary climate change has received little attention. Understanding how biotic communities respond to increasingly limited water is integral for their conservation, particularly as free water becomes less available in arid and semi-arid regions (Adams 2010; Jones and Rebelo 2013; Maestre et al. 2015; Ogston et al. 2016).

We studied bat communities to determine if reduced water availability (an expected outcome of climate change) leads to species-specific responses based on morphological traits. Bats provide a model system because they have evolved differing morphologies for flight maneuverability to partition foraging niches, but are still reliant upon and compete for access to water sources (Adams and Hayes 2008; Findley and Wilson 1982). We used corroborating lines of evidence by first employing an observational approach to acoustically sample 60 water sources across two North American deserts to determine if surface area of water sources predicted the presence of bats based on morphology. Second, we experimentally reduced the

surface area of water sources to assess changes in drinking behavior and competition between maneuverable and less-maneuverable bats. Since competition can be difficult to observe directly, we relied on indirect evidence for the occurrence of competition (e.g., temporal shifts in resource use to minimize direct competitive interactions). We hypothesized that less-maneuverable species of bats would occur less frequently at smaller water sources and respond more strongly to reductions in surface area of water sources than more maneuverable species. Specifically, we predicted that 1) surface area would positively correlate with the presence of less-maneuverable bats under natural conditions, 2) the ratio of drinking passes to non-drinking passes would decrease for less-maneuverable bats when water sources were experimentally reduced, and 3) less-maneuverable bats would experience altered temporal partitioning with maneuverable bats when surface area of water was reduced.

2. Methods

2.1. Study areas

We conducted this study at water sources in the Mojave and Great Basin Deserts. The Mojave Desert study area was located in extreme southwestern Utah (Figure 1) and was characterized by alternating rolling ridges and dry washes. Common vegetation included red brome (*Bromus rubens*), creosote (*Larrea tridentata*), Joshua tree (*Yucca brevifolia*), and blackbrush (*Coleogyne ramosissima*). The Great Basin Desert study area was located in west-central Utah, approximately 360 km north of Mojave (Figure 1), and was characterized by dune systems and alkaline flats. Vegetation characteristic of this area included greasewood (*Sarcobatus vermiculatus*), cheatgrass (*B. tectorum*), big sagebrush (*Artemisia tridentata*), and juniper (*Juniperus osteosperma*).

2.2. *Observational data collection*

From May to August of 2010 and May to July 2011 we sampled 35 water sources at Mojave and 25 water sources at Great Basin with AR125 full-spectrum, time-expansion bat microphones (operating range: 1 to 125 KHz; sensitivity: 0 to 90 dB) and FR125-III data recorders (Binary Acoustic Technology, Tucson, AZ, USA). Water sources consisted of natural springs and ponds (16), water tanks for livestock (13), water developments for wildlife (27), and water treatment ponds and ditches (4). Only two of the water sources that we sampled were routinely filled with water; the other water sources were considered self-maintaining and contained water throughout the duration of our study. Surface area of water sources ranged from 0.25 to 10,000 m² (mean: 186.60 m², SE: 99.10 m²). We categorized water sources into three size groups based on surface length: small (surface length < 2 m), medium (surface length between 2 and 5 m), and large (surface length > 5 m). We considered all known perennial (or near perennial) water sources within our study areas for acoustic sampling, but not all were sampled. We selected water sources using a clustered sampling scheme by randomly selecting a point in space within a geographic information system and then locating the nearest known water source. From that water source we located the two nearest water sources and deployed bat detectors at all three sites for one night (due to equipment limitations, we could only sample three locations each night). On average, water sources selected for sampling were 2.35 km apart (range: 0.60 to 6.20 km). The following evening, a new random point was chosen and three new water sources were selected for sampling. We sampled with replacement so each water source was eligible for re-sampling. We positioned microphones at 45° angles on tri-pods (1 m in height) approximately 3 m from the edge of the water (Adams and Simmons 2002; Jackrel and

Matlack 2010; Razgour et al. 2010). We oriented microphones over the center of the water source and placed them at the longest edge to capture the majority of airspace above water (Razgour et al. 2011). We recorded bat activity from 2100 hr (approximately sunset) to 0100 hr (4 hrs total; this time period encompassed nearly all bat activity for species in this region (Cockrum and Cross 1964; O'Farrell et al. 1967; Ruffner et al. 1979)).

2.3. *Experimental design*

Our surface area experiment occurred in August of 2011 at two livestock water tanks located 3.51 km apart in Mojave. These tanks were selected because they were the largest water sources available in our study area, identical in design, void of flight obstructions, had been filled with water during the summers of 2010 and 2011, and were still close enough to be found within the same habitat (i.e., creosote flats with Joshua trees). Each tank was 0.60 m tall and circular in design, measuring 6.25 m in diameter and provided 30.66 m² of surface area. At each tank, we used an infrared video camera (Sony Handycam DCR-DVD610) and a supplemental infrared lamp along with an AR125 bat detector and FR125-III recorder for species identification. We initiated video and audio recording at 2100 and concluded at 0100. We used The Observer XT10 behavioral analysis software (Noldus, Leesburg, VA, USA) to view video recordings and record observations related to drinking and non-drinking passes. We considered a drinking pass when a bat made contact with the surface of the water (Adams and Simmons 2002). We then matched timestamps between audio and video files to determine drinking behavior of identified species (Razgour et al. 2010).

We conducted our surface area experiment using a “crossover” design (Jackrel and Matlack 2010; Tuttle et al. 2006). At Tank A, we restricted the surface area to 2.25 m² (average

surface area of small water sources from both study areas) using a plywood cover while Tank B was unmodified. After one night (to allow bats to adjust to the experimental modification (Jackrel and Matlack 2010)), we recorded bat activity and behavior for five subsequent nights. Following the five night manipulation period, we switched the surface area restrictions from Tank A onto Tank B. One night later, we recorded for another five nights with Tank B as our treatment and Tank A as our control. This “crossover” design allowed each tank to serve as the control and the experimental unit (Dean and Voss 1999).

2.4. Acoustic analysis

We used SonoBat version 3 (SonoBat, Arcata, CA, USA) to identify call sequences to species. SonoBat uses a decision-based engine to quantitatively analyze recorded call sequences from the field against known recordings from species and has an identification accuracy rate of 98% (J. Szewszak, Humboldt State University, unpubl. data). Prior to analysis of call sequences, we removed any noise or low-quality call sequences. SonoBat then classified call sequences based on several parameter values (e.g., maximum and minimum frequency, duration of call, frequency of the knee, steepness of the slope, etc.) and estimated probabilities for identified call sequences using a discriminate function model trained on calls from a reference library from the western U.S. (J. Szewszak, Humboldt State University, unpubl. data; Clement et al. 2014; Slough et al. 2014). We used call sequences for species identification with an estimated probability of correct identification $\geq 95\%$ (Barnhart and Gillam 2014; Clement et al. 2014). Despite a high accuracy rate, SonoBat can have difficulty distinguishing fragmented calls between pairs of certain species, such as *Tadarida brasiliensis*/*Lasiurus cinereus*, *Myotis lucifugus*/*M. volans*, *M. thysanodes*/*Corynorhinus townsendii*, and *Eptesicus fuscus*/*Lasionycteris noctivagans* (J.

Szewsak, Humboldt State University, unpubl. data). However, none of these pairings included species with differing maneuverability and any misclassification between these species was unlikely to influence our results.

2.5. Data analysis

We used a non-metric multidimensional scaling (NMDS) analysis to assign bats into less-maneuverable or maneuverable groups based on aspect and wing-loading ratios (Brigham 1988; Holloway and Barclay 2001; Norberg and Rayner 1987). Species of bats that are more morphologically similar with regards to characters conducive to different types of flight will tend to “cluster” in ordinal space, whereas species that are more morphologically distinct will be farther apart. We plotted each species in ordinal space and then looked for a natural break to assign individuals into a group.

With our observational data we used mixed-effects logistic models and model selection to determine if the size of water sources influenced the presence of maneuverable and less-maneuverable bats (Burnham and Anderson 2002). We established base models for both groups of bats that included temperature ($^{\circ}\text{C}$; Korine and Pinshow 2004), mean wind speed (m/sec) over the 4-hr sample period (O'Farrell et al. 1967), nearest neighbor distances (average distance of the 3 nearest water sources to the sampled water source (Razgour et al. 2010; Ruffner et al. 1979)), and flight obstructions (e.g., vegetation, rocks, catchment canopies, fences) adjacent to the water and taller than 0.5 m (Jackrel and Matlack 2010). Since our microphones were set 3 m away from water sources, potential obstructions adjacent to water sources did not influence our general set up procedure for bat detectors. To account for the variation between study areas (Great Basin and Mojave), cluster samples, and water sources, we included these variables as random effects

in our models. Because we sampled with replacement some water sources were re-sampled more than once on different nights and by including “water source” as a random effect we accounted for the potential dependency between samples. The “cluster sample”, “water source”, and “nearest neighbor” variables helped account for any potential lack of independence between neighboring samples due to individual bats potentially visiting > 1 water source in a single night. In addition, we conducted Mantel tests with Monte-Carlo permutations for each study area to identify if spatial patterns of bat activity occurred (Besag and Diggle 1977; Mantel 1967). This way, we ensured that the proximity of water sources (regardless of their size and associated habitat features) was not a driving influence on our analysis.

After creating base models incorporating temperature, wind, nearest neighbor distance, obstructions, study area, cluster sample, and water source variables, we then included a “water size” variable to each of the base models to determine the relative influence of the size of water sources on the presence of different maneuverability groups. We used Akaike’s Information Criterion adjusted for small sample size (AIC_c) to compare base models to water models (Akaike 1974). We considered models to be competing if they were within two ΔAIC_c values of the model with the lowest AIC_c value and accounted for the majority of model weight (w_i) (Burnham and Anderson 2002). We also included both marginal (variance explained by fixed effects) and conditional (variance explained by fixed and random effects) R^2 values to provide a measure of model strength (Nakagawa and Schielzeth 2013).

For our experimental data we first compared drinking behaviors of maneuverability groups between control and treatment nights. Since our crossover design resulted in a treatment and control measure for each night, we did not incorporate temperature or wind into this analysis since the same climatic patterns occurred at both tanks each night (an assumption based on the

relative proximity of the two tanks). We also excluded the nearest neighbor distance covariate (used in the logistic regression) because it was an unlikely contributor to drinking ratios (drinking passes/total passes). We compared measures of drinking ratios for each group between treatment and control nights using a mixed-effects ANOVA. In this model, we included “group” (maneuverability group), “treatment”, and a “group x treatment” interaction as fixed effects. The group x treatment interaction allowed us to simultaneously test for relative differences in drinking ability between both groups of bats and between control and treatment nights. To account for variation associated with differences between sample nights and experimental tanks, we included “night” and “tank” as random effects in our model. We then calculated least-squares means for each treatment and group combination.

Second, we compared two measures of bat activity for both maneuverability groups between control and treatment nights: peak arrival times (time when the majority of bat activity occurred at the water source) and proportional activity (number of calls during each 30-min interval/total number of calls for that group in a night) (Adams and Thibault 2006; Razgour et al. 2011). We used 30-min intervals to make our results comparable with previous studies conducted in the American Southwest (Cockrum and Cross 1964; Kuenzi and Morrison 2003; O'Farrell and Bradley 1970; O'Farrell et al. 1967). We used *G*-tests of independence (Sokal and Rohlf 1981) to determine if the proportion of activity differed between 30-min intervals on control and treatment nights at each tank. This analysis allowed us to evaluate shifts in temporal partitioning (indirect evidence of competition) at each tank when water was significantly reduced. If competition occurred, we would expect the less competitive species to exhibit shifts (differences) in proportional activity when the resource was reduced to minimize competition with the more competitive species. Since activity measures used for comparison occurred across

multiple nights at a single tank, there existed the possibility of climatic variability to influence our comparisons. However, there were no differences in mean temperature ($t = 0.11$, $df = 4$, $p = 0.92$) or wind speed ($t = 0.31$, $df = 4$, $p = 0.77$) between the first five and latter five nights based on two-sample t -tests. Furthermore, precipitation was not a factor as it did not rain during the experiment. Therefore, we did not include these climatic variables in the analyses for our experiment. We used Program R for all statistical analyses (R Development Core Team 2014). We set the level of significance for all statistical tests at $\alpha = 0.05$ and used Bonferroni adjusted α -levels of $\alpha = 0.025$ for Mantel tests and $\alpha = 0.013$ for G -tests.

3. Results

The groups of bats that we studied exhibited relatively distinct aspect and wing-loading ratios based on the clustering apparent in the NMDS analysis (Global $R = 0.98$, $p < 0.01$; Figure 2). Species of less-maneuverable bats included *E. fuscus*, *Euderma maculatum*, *L. noctivagans*, *L. blossevillii*, *L. cinereus*, and *T. brasiliensis*, which have greater aspect and wing-loading ratios and are relatively larger bats with faster, less maneuverable flight. Maneuverable species consisted of *Antrozous pallidus*, *C. townsendii*, *M. californicus*, *M. ciliolabrum*, *M. evotis*, *M. lucifugus*, *M. thysanodes*, *M. volans*, *M. yumanensis*, and *Parastrellus hesperus*, all of which have lower aspect and wing-loading ratios and slower, more maneuverable flight.

During our observational data collection from May to August of 2010 and May to July 2011, we sampled 60 water sources from Mojave and Great Basin Deserts (Figure 1). We were able to re-sample 23 of these water sources on > 1 night resulting in 92 total nights of sampling. We detected 16 species at Mojave and 13 species at Great Basin (Table 1). During our surface area experiment at Mojave in August of 2011, we detected 15 species over the 10 night period

(Table 1). Mantel tests did not reveal spatial aggregations of bat activity at Mojave ($p = 0.46$) or Great Basin ($p = 0.35$). Our modelling efforts demonstrated that the size of water sources was significantly correlated with the presence of less-maneuverable, but not maneuverable bats (Table 2, Figure 3). Including “water size” as a variable better explained variation in species presence for less-maneuverable bats, but not maneuverable bats (Tables 2, 3).

Data from our experiment indicated that maneuverability groups responded differently to restricted surface areas in terms of drinking. The “group x treatment” interaction for drinking ratios was significant ($p < 0.01$) in the mixed-effects ANOVA model (Table 4). After inspecting the least-squares means for this model, we found that less-maneuverable bats exhibited a 69% decrease ($p < 0.05$) in drinking ratios during treatment nights relative to control nights (Figure 4). Conversely, maneuverable bats only experienced a 13% decrease in drinking ratios which was not different ($p > 0.05$) between control and treatment nights (Figure 4).

We also detected differences in peak arrival times and proportional activity for less-maneuverable bats during our experiment. During control nights, peak arrival times for both groups overlapped; however, during treatment nights, peak arrival time for less-maneuverable bats was delayed 30 min (Figure 5). Maneuverable bats did not appear to alter peak arrival time at either tank, which occurred 1 hour after sunset on control and treatment nights. The proportional activity of less-maneuverable bats during treatment nights differed significantly compared to control nights ($G = 20.08$, $df = 7$, $p < 0.01$; Figure 5). However, the proportional activity of maneuverable bats did not differ between control and treatment nights ($G = 1.59$, $df = 7$, $p = 0.98$; Figure 5).

4. Discussion

Using observational and experimental approaches, we demonstrated that less-maneuverable species of bats occurred less frequently at smaller water sources and responded more strongly to reductions in surface area than maneuverable species. During our observational surveys, we detected less-maneuverable bats at larger water sources more often than at smaller water sources, corroborating previous work (Rabe and Rosenstock 2005; Razgour et al. 2010) and supporting our first prediction (i.e., that surface area would positively correlate with the presence of less-maneuverable bats under natural conditions). However, this correlation was not apparent for maneuverable bats. In fact, there was no difference in the presence of maneuverable bats at water sources of different sizes. Experimentally manipulating the size of water sources allowed us to examine the mechanisms likely underlying the differential visitation to small water sources by bats and test our other two predictions.

Our experimental findings revealed that reduced surface area of water affected drinking success and timing of use by less-maneuverable bats. Our prediction that less-maneuverable bats would experience lower drinking ratios upon reduction of water sources was supported. Maneuverable bats, on the other hand, did not exhibit significantly reduced drinking ratios when surface areas were restricted. Data also supported our prediction that less-maneuverable bats would experience altered temporal partitioning (i.e., competition) with maneuverable bats. We detected shifts in peak arrival times and proportional activity by less-maneuverable, but not maneuverable bats when water size was reduced. On nights when the surface area of the water source was not restricted, the peak arrival of both groups of bats occurred at the same time, suggesting a lack of competition. However, during nights when surface area of water was restricted, less-maneuverable bats arrived at water sources 30 min later than on control nights.

This temporal shift in activity is likely a response to restricted surface area of water and the resulting increase in competition with maneuverable bats. A half-hour delay in drinking may be of no fitness consequence to bats. However, since bats have high metabolic rates (Voigt et al. 2010) and can lose significant amounts of water while roosting (Webb et al. 1995), visiting water sources shortly after sunset is likely necessary to recover water lost during roosting (Adams and Hayes 2008). Therefore, a delay or increased difficulty in drinking during hot and dry conditions may have physiological consequences for bats, especially for lactating females that have an increased demand for water (Adams 2010; Adams and Hayes 2008).

The competitive advantage of maneuverable bats in accessing experimentally-restricted water likely contributed to the decrease in drinking ratios by less-maneuverable bats. There is a high risk of collisions during flight around small water sources, thus, bats coordinate their drinking passes using a “runway” system where one bat drinks at a time (an observation we confirmed in our videos) (Adams and Simmons 2002). The difficulty of accessing small water sources coupled with competition from maneuverable bats will likely create additional challenges for less-maneuverable bats as water becomes increasingly limited. Decreases in surface area of water sources across arid landscapes will likely lead to heightened competition for this increasingly limited resource as species concentrate on fewer, smaller bodies of water. Our study provides additional evidence that climate change may alter competition dynamics within biotic communities.

We recognize the limitations inherent in sampling only two water sources for an experiment. To minimize the limitations, we implemented a crossover design using each water tank as both treatment and control over multiple nights of sampling. While sample size may limit the inference of our experiment, the experimental design and significant results allowed us

to identify potential mechanisms leading to the differential ability of some bats to better access water than others. Despite reducing the surface area on only two experimental tanks, we were able to detect differences in drinking success and peak arrival time for less-maneuverable bats, both of which supported our predictions and helped explain large-scale patterns of water source use observed across our study areas. The logistically and cost-intensive nature of video-monitoring over multiple nights naturally limits sample sizes and our approach was consistent with previous studies that have investigated drinking patterns of bats (Adams and Thibault 2006; Jackrel and Matlack 2010; Razgour et al. 2010; Tuttle et al. 2006).

Bats may be considered bioindicators of climate change due to their sensitivity to environmental conditions (Jones and Rebelo 2013; Sherwin et al. 2013). Due to the high demand of water by lactating females, loss of water due to climate change will likely impact reproduction (Jones and Rebelo 2013). Bats have experienced decreased reproduction and undersized young during times of prolonged drought (Tuttle 1976). Decreased reproduction is likely unsustainable for *k*-selected species, which lends credence to the predicted distributional shifts of some bat species as climates continue to warm (Jones and Rebelo 2013; McCain 2007; Razgour et al. 2013; Sherwin et al. 2013). Our study further supports the forecasted impacts of climate change on bat communities and proposes a morphological mechanism which may lead to community divergence as water loss continues in arid environments.

While our results propose that less-maneuverable bats will encounter added difficulty in accessing and competing for water when it is reduced, we recognize that these species are still well adapted to the challenges of inhabiting arid environments. Less-maneuverable bats are typically large in body size, which likely allows them to maintain better water balance than smaller species (Carpenter 1969). Larger bats with fast flight can also more efficiently cover

longer distances to locate suitable water sources while expending less energy than smaller bats (Chambers et al. 2011; Robinson and Stebbings 1997). Also, some larger bats can consume larger prey items that provide greater water content than can smaller-bodied, more agile species (Barclay and Brigham 1991). Less-maneuverable bats may be able to persist in a rapidly changing climate with limited water availability as long as they can commute to large water sources (with minimal energy loss) to meet basic water demands. However, if trends of water loss continue as projected it may become energetically unfeasible for large, less-maneuverable bats to inhabit areas of increasingly limited water availability.

It is presumed that water sources introduced by humans can help stabilize the unpredictable nature of water availability in desert landscapes (Longshore et al. 2009), but the use of anthropogenic water sources may inadvertently affect other wildlife and should be used with caution (Broyles 1995). Despite the presumption that anthropogenic water sources can offset the natural loss of water, it is unknown whether these water sources can completely mitigate the predicted effects of climate change. The majority of water sources that we sampled during our study were anthropogenic, however all but two were self-maintaining and relied on natural occurring precipitation (i.e., rain, snow, and springs). Therefore, it could be expected that even these anthropogenic water sources would be subjected to the effects of future drying projected over the course of this century (Ault et al. 2014; Cook et al. 2015; Seager et al. 2013; Wada et al. 2013). If water availability significantly decreases, it is likely that efforts would be made to maintain these water sources via supplementation. But these efforts would be costly, time-intensive, and likely short-lived due to the difficulty of maintaining water availability in so many water sources across such a large area.

Our study provides evidence that the reduction of water can differentially impact competing species of bats based on their morphologies. In addition, these findings illustrate how ecomorphology mediates access to a resource and highlights conservation implications as water becomes more limited in arid environments. Based on our findings, less-maneuverable species of bats will likely experience difficulty or delayed access from increasingly smaller bodies of water as water loss continues throughout desert regions. Selection for differences in wing morphology and flight ability in insectivorous bats has allowed for coexistence and high species richness at a local scale. However, anticipated reductions in the sizes of water sources due to climate disruption may lead to less-maneuverable species being unable to access water efficiently or being outcompeted by more agile fliers.

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List of Figures

Figure 1. Distribution of water sources acoustically sampled from May to August 2010 and May to July 2011 in the Mojave (top panel) and Great Basin (bottom panel) Deserts. Small water sources had a surface length < 2 m, medium water sources had a surface length between 2 and 5 m, and large water sources had a surface length > 5 m.

Figure 2. Non-metric multidimensional scaling (NMDS) plot illustrating differences between less-maneuverable and maneuverable species of bats based on aspect and wing-loading characteristics that influence flight maneuverability ($p < 0.01$).

Figure 3. Proportion of water sources ($\pm 95\%$ CI) where less-maneuverable and maneuverable bats visited. Data were collected across 60 water sources of different sizes in Mojave and Great Basin Deserts from May to August 2010 and May to July 2011. Small water sources had a surface length < 2 m, medium water sources had a surface length between 2 and 5 m, and large water sources had a surface length > 5 m.

Figure 4. Mean drinking ratios (i.e., number of drinking passes/total number of passes; $\pm 95\%$ CI) for less-maneuverable and maneuverable bats at two water tanks on control and treatment nights when we experimentally reduced surface area in a crossover design. On treatment nights, less-maneuverable bats experienced a reduction of drinking ratios, whereas maneuverable bats did not. Data were collected in August 2011 in the Mojave Desert.

Figure 5. Proportion of activity (number of calls during each 30-min interval/total number of calls for that group in a night) of less-maneuverable and maneuverable bats at each experimental water tank on control and treatment nights where surface area was experimentally reduced. There was a difference in proportional activity (plotted lines) between control and treatment nights for less-maneuverable bats ($p < 0.01$), but not maneuverable bats ($p = 0.98$). Data were collected in August 2011 in the Mojave Desert.

Table 1. Distribution of bat calls across species at Mojave and Great Basin Deserts during our observational and experimental sampling from May to August 2010-11. Observational sampling occurred at 60 water sources of different sizes over a total of 92 nights. Experimental sampling occurred at two large water tanks (30.66 m²) over a total of 10 nights.

Species	Number of calls		
	Mojave ^{obs}	Mojave ^{exp}	Great Basin ^{obs}
<u>Less-maneuverable</u>			
<i>Eptesicus fuscus</i>	182	129	11
<i>Euderma maculatum</i>	74	*	6
<i>Lasionycteris noctivagans</i>	10	3	7
<i>Lasiurus blossevillei</i>	3	7	*
<i>Lasiurus cinereus</i>	58	3	8
<i>Tadarida brasiliensis</i>	82	20	7
<u>Maneuverable</u>			
<i>Antrozous pallidus</i>	46	74	3
<i>Corynorhinus townsendii</i>	65	30	1
<i>Myotis californicus</i>	1563	2095	9
<i>Myotis ciliolabrum</i>	127	238	1163
<i>Myotis evotis</i>	6	5	*
<i>Myotis lucifugus</i>	3	23	39
<i>Myotis thysanodes</i>	31	6	8
<i>Myotis volans</i>	4	20	6
<i>Myotis yumanensis</i>	100	77	*
<i>Parastrellus hesperus</i>	3923	9404	68

^{obs} Observational sampling (surveys).

^{exp} Surface area experiment.

* denotes lack of detection of species.

Table 2. Coefficients from mixed-effects logistic models for the presence of less-maneuverable and maneuverable bats. Data were collected at 60 water sources in the Mojave and Great Basin Deserts from May to August 2010 and May to July 2011.

Model	Coefficient	Estimate	SE	<i>p</i>
Less-maneuverable base ^a	Intercept	-2.72	1.52	0.07
	NearNeighbor ^c	0.00	0.00	0.15
	Obstructed ^d	0.00	0.00	0.82
	AvgTemp	0.11	0.05	0.04
	AvgWind	0.16	0.10	0.13
Less-maneuverable water ^b	Intercept	-6.30	3.40	0.06
	WaterSize	2.61	1.17	0.03
	NearNeighbor ^c	0.00	0.00	0.24
	Obstructed ^d	0.00	0.00	0.79
	AvgTemp	0.18	0.11	0.09
	AvgWind	0.15	0.16	0.36
Maneuverable base ^a	Intercept	-6.29	17.36	0.44
	NearNeighbor ^c	0.01	0.03	0.66
	Obstructed ^d	0.04	0.53	0.95
	AvgTemp	5.66	6.50	0.38
	AvgWind	-1.46	12.56	0.91
Maneuverable water ^b	Intercept	-4.80	12.09	0.06
	WaterSize	-3.78	4.85	0.16
	NearNeighbor ^c	0.02	0.01	0.07
	Obstructed ^d	0.05	0.08	0.51
	AvgTemp	7.18	2.91	0.01
	AvgWind	-5.44	2.39	0.02

^a Base models accounted for variation in site (random effect), cluster sample (random effect), water source (random effect), temperature (°C), average wind speed (m/sec), presence of flight obstructions, and nearest neighbor distances (m) for water sources.

^b Water models were identical to base models with the exception of the “WaterSize” variable.

^c Mean distance (m) from the three nearest water sources to water source sampled.

^d Obstruction of ≥ 0.5 m in height adjacent to the water source.

Table 3. Mixed effects logistic models for the presence of less-maneuverable and maneuverable bats. Data were collected from May to August 2010 and May to July 2011 in the Mojave and Great Basin Deserts.

Model	K^a	AIC_c^b	ΔAIC_c^c	LL^d	w_i^e	$R^2_{\text{marg}}^f$	$R^2_{\text{cond}}^g$
Less-maneuverable bats							
Base ^h + Water size	8	104.50	0.00	-43.20	1.00	0.49	0.81
Base ^h	7	122.40	18.25	-53.20	0.00	0.25	0.53
Maneuverable bats							
Base ^h	7	72.20	0.00	-36.20	0.70	0.05	0.71
Base ^h + Water size	8	73.50	1.71	-36.30	0.30	0.02	0.57

^a Numbers of parameters.

^b Akaike's Information Criterion corrected for small samples.

^c Change in AIC_c value compared to top model.

^d Model log-likelihood.

^e AIC_c weight.

^f Marginal R-squared values (variance explained by fixed effects).

^g Conditional R-squared values (variance explained by fixed and random effects).

^h Base models accounted for variation in site (random effect), cluster sample (random effect), water source (random effect), temperature (°C), average wind speed (m/sec), presence of flight obstructions, and nearest neighbor distances (m) for water sources.

Table 4. Coefficients from a mixed effects ANOVA model comparing drinking ratios (number of drinking passes/total passes) between control and treatment nights for less-maneuverable and maneuverable bats. Data were collected at two livestock water tanks in the Mojave Desert that were experimentally manipulated in a crossover fashion over 10 nights in August of 2011.

Coefficient	Estimate	SE	<i>df</i>	<i>t</i>	<i>p</i>
Intercept	0.70	0.05	12.68	14.82	< 0.01
Group ^a	0.11	0.07	35	1.65	0.11
Treatment ^b	-0.13	0.07	35	-1.91	0.06
Group ^a x Treatment ^b	-0.56	0.09	35	-5.93	< 0.01

^a Maneuverability group (i.e., maneuverable and less-maneuverable).

^b Experimental reduction of surface area.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5