Temporal partitioning and the effects of climate change on two ecologically similar desert bats

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Climate change is predicted to create increasingly arid deserts with fewer and smaller water sources. Because free water is already limiting for arid-adapted animals, reductions in water likely will impact desert species and how they compete for this limited resource. Our objective was to examine how the size of water sources influenced competition between 2 ecologically similar bats, *Parastrellus hesperus* and *Myotis californicus*, in the American Southwest. Bats are a highly successful taxon in deserts, although many rely upon access to free water. We examined bat activity observationally over 35 different-sized water sources throughout the Mojave Desert in southwestern Utah, United States, and experimentally reduced the surface area of 2 water sources. *Parastrellus hesperus* and *M. californicus* typically occurred at the same water sources, but both species temporally partitioned their use of shared water sources regardless of the surface area of the water. Experimentally reducing surface area of water sources negatively affected drinking behaviors of both species and resulted in higher overall activity, but temporal partitioning still occurred. While loss of water may influence some competitive interactions, mechanisms such as temporal partitioning can potentially allow continued co-use of limited resources by competing species.

Key words: arid environments, bats, competition, temporal partitioning, water

Climate change is predicted to affect ecosystems worldwide (Pecl et al. 2017). Arid environments are predicted to experience increased temperatures, aridity, frequency, and intensity of droughts, and a corresponding decrease in surface water (Cayan et al. 2010; Cook et al. 2010, 2015; Seager et al. 2013). Increasing anthropogenic use of surface water and groundwater in areas such as the American Southwest likely will further impact water resources (MacDonald 2010; Taylor et al. 2013; Wada et al. 2013). The combination of rising temperatures, prolonged drought, and increased water usage will lead to decreases in the number and size of water sources in arid environments (Seager et al. 2013; Ting et al. 2018). As competition for limiting resources influences the structure of communities (Ronconi and Burger 2011; Robles et al. 2012), species in arid environments likely will be faced with increased competition as communal use of water intensifies due to projected loss of water (Thrash et al. 1995; Valeix 2011). However, predicting how species interactions will be influenced by rapid loss of water and prolonged droughts due to climate change is difficult (Urban et al. 2012; Dell et al. 2014).

Desert bats provide an ideal system for evaluating the synergistic effects of water loss and subsequent altered competition (Jones et al. 2009; Rebelo et al. 2010; Jones and Rebelo 2013). Desert bats largely are reliant on free water due to their predisposition to water loss (e.g., individuals of some species can lose more than 30% of overall body mass in evaporative water loss in a single day of roosting—Webb 1995, but see Muñoz-Garcia et al. 2016), especially during lactation (O'Farrell and Bradley 1970; Adams and Hayes 2008), and locating water via echolocation is an innate behavior in some bats (Greif and Siemers 2010). Multiple species of bats often use the same water sources (Adams and Simmons 2002; Adams and Thibault 2006; Razgour et al. 2011; Hall et al. 2016) and coordinate drinking passes to avoid collisions (Adams and Simmons 2002;

Adams and Thibault 2006). Because of this overlapping use of water, the surface area of a water source is an important influencer of the bat community that uses the water source (Rabe and Rosenstock 2005; Razgour et al. 2010). Smaller water sources typically have less-diverse communities characterized by species of bats with high maneuverability (i.e., relatively lower aspect ratio and wing loading—Rabe and Rosenstock 2005; Taylor and Tuttle 2007; Razgour et al. 2010; Hall et al. 2016), whereas larger water sources are used by more diverse communities of bat species. As competition for water likely is most intense between species that have incomplete niche differentiation (Razgour et al. 2011), ecologically similar species should display the greatest competitive responses to each other as they compete for water and prey above the water source.

Previous studies have documented evidence for high levels of competition through both spatial and temporal partitioning between species of desert bats (Adams and Thibault 2006; Razgour et al. 2011; Hall et al. 2016). Most commonly, competing species of bats will temporally partition periods of time when competitors are most active (O'Farrell and Bradley 1970; Adams and Thibault 2006; Razgour et al. 2011), or spatially partition those water sources most frequented by their closest competitor (Razgour et al. 2011). The size and availability of water sources in an area may mediate competitive interactions in arid environments. However, the only previous study on this topic, in the Negev Desert, Israel, found that spatial partitioning between bat species occurred during wetter parts of the year, but was replaced by temporal partitioning during drier parts of the year when there were fewer and smaller water sources (Razgour et al. 2011).

Parastrellus hesperus and *Myotis californicus* are 2 of the most common, maneuverable species of insectivorous bats in the American Southwest and likely compete with each other (as well as other bats) for access to water sources (O'Farrell et al. 1967; O'Farrell and Bradley 1970; Rabe and Rosenstock 2005; Hall et al. 2016). Both species are year-round residents of the American Southwest and are the most active species at water sources directly after sunset (O'Farrell and Bradley 1970; Hall et al. 2016), with their total activity an order of magnitude higher than all other species at our study site (Hall et al. 2016). *Parastrellus hesperus* is one of the most abundant bats in the American Southwest (Mumford et al. 1964, Ruffner et al. 1979), and as they are often the most abundant species at water sources around sunset (Cockrum and Cross 1964; Mumford et al. 1964; Jones 1965; O'Farrell et al. 1967; Bradley and O'Farrell 1969) they likely influence access to water during this time for other bat species. *Myotis californicus* are not only active around the same time as *P. hesperus* (Jones 1965; O'Farrell et al. 1967) but are often detected at the same water sources (O'Farrell and Bradley 1970; Bell 1980). There is evidence of temporal partitioning (competition) between *P. hesperus* and *M. californicus* as the activity peaks of these species occur at different times, regardless of the time of year (O'Farrell et al. 1967; O'Farrell and Bradley 1970). Both are low-level aerial foragers with moderate- to high-intensity echolocation (Mumford et al. 1964; Black 1974; Bell 1980) and prey heavily on lepidopterans (Black 1974). However, the extent of competition between these similar species and how loss of surface water will influence their interactions is uncertain.

Our objective was to determine how loss of surface water affects competitive interactions between 2 ecologically similar species of maneuverable bats. We hypothesized that there would be minimal evidence of competition between *P. hesperus* and *M. californicus* at large water sources, but that spatial or temporal partitioning would occur at small water sources. We first sampled 35 water sources of varying sizes in the Mojave Desert of southwestern Utah, to examine the influence of surface area on spatial and temporal partitioning between *P. hesperus* and *M. californicus* under natural conditions, predicting either spatial or temporal avoidance at smaller water sources. We then experimentally reduced the size of 2 large water sources to determine if the loss of surface water directly affected species' activity and competitive interactions (Razgour et al. 2010; Hall et al. 2016). We predicted that a reduction in the surface area of water sources would negatively affect drinking ability of both species and intensify competitive interactions.

MATERIALS AND METHODS

Study area.—We conducted this study in the Mojave Desert in extreme southwestern Utah (37°08′N, 114°01′W). Our study area was characterized by rolling hills and ridges and dry desert washes radiating from the Beaver Dam Mountains and emptying into the Beaver Dam Wash to the southwest. Common vegetation at lower elevations included creosote (*Larrea tridentata*), Joshua tree (*Yucca brevifolia*), blackbrush (*Coleogyne ramosissima*), and red brome (*Bromus rubens*). Along the foothills, the vegetation primarily consisted of big sagebrush (*Artemisia tridentata*) and juniper (*Juniperus osteosperma*), transitioning to pinyon pine (*Pinus edulis*) at higher elevations. Elevations across our study area ranged from approximately 835 to 1,385 m. Annual weather consisted of mean air temperatures of 19.91°C (range: −10.20 to 40.10° C) and mean precipitation of 126 mm (MesoWest, Bureau of Land Management and Boise Interagency Fire Center). All methods conformed to the guidelines of the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2016).

Observational data collection.—To examine how water surface area relates to competitive interactions between *P. hesperus* and *M. californicus*, we sampled bat activity over water sources of various sizes in the Mojave Desert. From May to August 2010 and May to July 2011, we sampled 35 water sources with AR125 full-spectrum, time-expansion bat detectors and FR125-III data recorders (Binary Acoustic Technology, Tucson, Arizona). Water sources consisted of natural springs and ponds (8), water tanks for livestock (10), and water developments for wildlife (17). We classified water sources as "small" (< 2 m length) or large (> 2 m length), because water sources < 2 m are used by few bat species and make drinking in flight difficult for most species (Taylor and Tuttle 2007; Jackrel and Matlack 2010; Hall et al. 2016). Only 2 of the water sources we sampled were routinely filled with water by resource managers; the other water sources were considered self-maintaining and contained relatively consistent levels of water throughout the duration of our study. The 7 natural springs we sampled can be ephemeral during some years and dry up towards the end of the

summer, but these springs were relatively constant during our sampling. We did not sample (or resample) a water source that was either dry or very low in water.

All known perennial (or near-perennial) water sources within our study areas had the potential of being selected for acoustic sampling, but not all were sampled. We selected water sources using a clustered sampling design: we randomly selected a point in space within a geographic information system and located the nearest known water source. We then located the 2 nearest water sources to that water source and deployed bat detectors at all 3 sites for 1 night (due to equipment limitations, we could only sample 3 locations each night). Water sources selected for sampling averaged 2.35 km apart (range: 0.60–6.20 km). The following evening, a new random point was chosen, and 3 new water sources were sampled. We sampled with replacement, meaning that our protocol allowed for water sources to be sampled multiple times during the study (and many were). We positioned microphones at 45° angles on tripods (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 h (approximately sunset) to 0100 h (4 h total; this time period encompassed nearly all activity over water sources for *P. hesperus* and *M. californicus* in this region—Cockrum and Cross 1964; O'Farrell et al. 1967; Ruffner et al. 1979). Additionally, because temperature can be important in determining drinking by and nightly activity of bats (Korine and Pinshow 2004), we acquired temperature data from a weather station in our study area (MesoWest, Bureau of Land Management and Boise Interagency Fire Center). We calculated the average daily temperature for each date by averaging all hourly temperature readings for the given date, and these values were used as potential covariates in the applicable analyses.

Experimental design.—To determine the influence of a reduction of water surface area on competition, we experimentally manipulated the surface area of 2 water sources with high bat activity. Our surface area experiment occurred in August 2011 at 2 livestock water tanks located 3.51 km apart in the Mojave Desert. These tanks were selected because they were the largest water sources available in our study area, identical in design, void of flight obstructions, were filled with water during the summers of 2010 and 2011, and were located within the same habitat type (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 m^2 of surface area. We used AR125 full-spectrum, time-expansion bat detectors and FR125-III data recorders (Binary Acoustic Technology, Tucson, Arizona), along with an infrared video camera (Sony Handycam DCR-DVD610) supplemented with an infrared lamp, to monitor bat activity at these water sources. We positioned microphones at 45° angles on tripods (1 m in height) approximately 1 m from the edge of the water (Razgour et al. 2011). We oriented microphones over the center of the water source to capture the majority of airspace above water (Razgour et al. 2011). We recorded bat activity from 2100 h (approximately sunset) to 0100 h, just as in our observational study.

We conducted our surface area experiment using a "crossover" design (Tuttle et al. 2006; Jackrel and Matlack 2010). At Tank A, we restricted the surface area to 2.25 m^2 (average surface area of small water sources from both study areas) using a plywood cover, while Tank B was unmodified. After 1 night (to allow bats to adjust to the experimental modification—Jackrel and Matlack 2010), we recorded bat activity and behavior for 5 subsequent nights. Following the 5-night manipulation period, we switched the surface area restrictions from Tank A to Tank B. One night later, we recorded for another 5 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 (Tuttle et al. 2006).

Acoustic analysis.—We used SonoBat version 3 (SonoBat, Arcata, California) 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. 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 discriminant function model trained on calls from a reference library from the western United States (Clement et al. 2014; Slough et al. 2014). We used call sequences for species identification with an estimated probability of correct identification ≥ 95% (Barnhart and Gillam 2014; Clement et al. 2014). SonoBat has no known difficulties distinguishing call sequences between *P. hesperus* and *M. californicus*.

We used The Observer XT10 behavioral analysis software (Noldus, Leesburg, Virginia) to view video recordings and record observations related to drinking and non-drinking passes. We considered a drinking pass as when a bat made contact with the surface of the water (Adams and Simmons 2002; Russo et al. 2016). We then matched timestamps between audio and video files to determine drinking behavior of identified species (Razgour et al. 2010; Hall et al. 2016).

Analysis of observational data.—We used our observational sampling of water sources to compare both spatial and temporal activity between *P. hesperus* and *M. californicus*. We tested for spatial partitioning with a Fisher's exact test on the number of sites that had 1, both, or neither of the species present. We further tested for spatial partitioning by using a linear mixed-effects model to examine the relationship between the total activity of each species—if spatial partitioning was prevalent, we expected a negative relationship between the activity of each species across water sources, especially at small (< 2 m length) water sources. For these analyses, we used the total number of calls for each species at the site (calls per night) during the entire 4-h recording period. We first created a "base" model for each species based on the combination of the following variables that yielded the best fit (lowest Akaike information criterion [AIC] value): the type of water source (natural spring,

livestock, wildlife) as a potential random effect, the average daily temperature as a potential fixed effect, and then location and date were always included as random effects to account for repeated measures of sites and dates. We used AIC model selection to compare the base model to models that included our fixed effects of interest: heterospecific activity, size of the water source, a model with both of these, and a model with the interaction of heterospecific activity and size of water source.

We tested for temporal partitioning with our observational data using 2 approaches. First, we examined the proportional activity of each species over 30-min intervals (species' activity within a 30-min interval divided by the total species activity that site-night) using G-tests for sites with sufficient activity (Sokal and Rohlf 1981; Hall et al. 2016). We then examined the difference between peak activity intervals of *P. hesperus* and *M. californicus* on those sites that had sufficient activity to adequately conduct G-tests. If a tank was sampled multiple nights, we used the night with the highest overall activity of the 2 species combined (so there were no repeated measures in the Wilcoxon test, see below). We determined peak arrival by identifying the 30-min interval with the highest activity for each species during each tank-night sampled (Hall et al. 2016), and if there were multiple peaks in activity we averaged all of the differences between the peak intervals of each species. We then identified the absolute difference in peak activity between the species for each night at each tank and used a 1-way Wilcoxon sign-ranked test to determine if these peaks differed from zero. If the difference in peak activity between species was significantly different from zero, this indicated temporal partitioning, whereas no difference from zero suggested both species were simultaneously using the water source. We then compared the difference in peak activity intervals using 3 different tests of 3 variables: a Wilcoxon sign-ranked test comparing small and large water sources; a Wilcoxon sign-ranked test comparing low activity (< 100 calls per night) to high activity (> 100 calls per night) water sources; and a Kruskal–Wallis rank-sum test on the interaction of size and activity to see if peak activity was influenced by both. We used a Bonferroni correction to account for multiple comparisons.

Analysis of experimental data.—To determine if competition occurred during our experiment, we used similar analyses of temporal partitioning as used for the observational data. For every night at each tank, we determined the activity for *P. hesperus* and *M. californicus* in 30-min intervals and performed G-tests on the proportional activity of each species. We tested for differences in the peak activity between each species using a 1-way Wilcoxon sign-ranked test. We also used Wilcoxon sign-ranked tests to determine if differences in peak activity were affected by the surface area treatment, level of activity, and the interaction of treatment and activity.

With our video recordings, we analyzed the individual passes of each species over each tank to determine how water surface area and competition influenced the drinking behaviors of each species. Bat passes from videos were aligned with timestamps from our audio data to identify the species of each pass (and every call was associated with a pass—Razgour et al. 2010;

Hall et al. 2016). We classified passes where the bat contacted the water as drinking passes (Adams and Simmons 2002; Hall et al. 2016; Russo et al. 2016), and determined the drinking rate of each species as the number of drinking passes divided by the total number of passes during the 4-h recording period. We then created 2 linear mixed-effects models for each species to examine how their drinking passes were affected by reduced surface area (as predicted by climate change) and activity of the other species (competition to access water): one model analyzing the drinking rate, and another analyzing the total number of drinking passes during the night. Each of these models accounted for date as a random effect and tank as a fixed effect, with the interactions of treatment (surface area reduction) and activity (total calls per night) of the other focal species as fixed effects, to determine if these factors affected the 2 drinking measures of either species. These models allowed us to determine if bat drinking rates and total drinking passes were similarly affected by our manipulation. All data analyses were done in R (R Development Core Team 2017).

RESULTS

Observational study.—We sampled 35 water sources, 13 of which were resampled 2–4 times, for 56 sample nights. Of these water sources, we classified 20 as "small" (< 2 m maximum length) and 15 as "large" (> 2 m maximum length). Four of these samples experienced equipment malfunction and were excluded from analyses, and 2 sites failed to record activity from *P. hesperus* or *M. californicus* and were used only for the presence analysis. During our sampling, we recorded 965 identifiable bat calls comprising 16 species. *Parastrellus hesperus* accounted for 47.7% of the total activity, while *M. californicus* accounted for 34.7%, for a total of 82.4% of the total activity recorded during our sampling. At sites with activity from at least 1 of our focal species, *M. californicus* had a mean (± *SE*) of 30.6 (± 5.3) calls at a given site per night, whereas *P. hesperus* had a mean (± *SE*) of 79.5 (± 19.5) calls at a given site per night.

In our analysis of spatial partitioning, we did not find any evidence of broad-scale spatial partitioning as both species were present at 29 of the 35 sites (Fisher's exact test $P = 0.047$). Our model selection results of bat activity at 33 water sources and 50 sample nights further suggested a lack of spatial partitioning regardless of the size of the water source. Total activity (calls per night) of *P. hesperus* and *M. californicus* was positively correlated (Fig. 1) and not affected by the size of the water source. The best model of *M. californicus* activity did not provide evidence for spatial partitioning with *P. hesperus*, regardless of the size of the water source. Rather, activity of *P. hesperus* was positively correlated with that of *M. californicus* ($t_{46.9} = 4.33$, $P < 0.01$) and the size of the water source did not influence activity of *M. californicus* ($t_{31.2} = -1.29$, $P = 0.21$; Table 1), and neither temperature nor water source type were included in the final model. Similarly, the best model for activity of *P. hesperus* did not provide evidence for spatial partitioning; instead, both activity of *M. californicus* and size of the water source were positively correlated with activity of

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Fig. 3.—The absolute differences between peak activity intervals of *Parastrellus hesperus* and *Myotis californicus* during our observational (A) and experimental (B) studies in the Mojave Desert, southwestern Utah, United States. There was a significant difference in peak activity intervals between the 2 species across all water sources during both the observational and experimental studies ($P < 0.001$ for both); this was not affected by water source size (small < 2 m, large > 2 m) in our observational study or the surface area reduction treatment in our experiment. Observational sampling occurred at 27 water sources during the summers of 2010 and 2011. The experiment was performed on 2 livestock water tanks over 12 nights in August 2011, and one outlier is not visualized here (a difference of 210 min on a treatment night).

by reducing the surface area of water sources (as predicted by climate change) and competition from conspecific activity, albeit in different ways (specific parameters from these models are presented in Table 2). Contrary to our predictions, the drinking rate of *P. hesperus* was not affected by treatment, conspecific activity, or the interaction of both of these (Table 2). However, consistent with our predictions, the total number of drinking passes by *P. hesperus* was significantly affected by the treatment and the interaction of treatment and activity, although *M. californicus* activity alone had a positive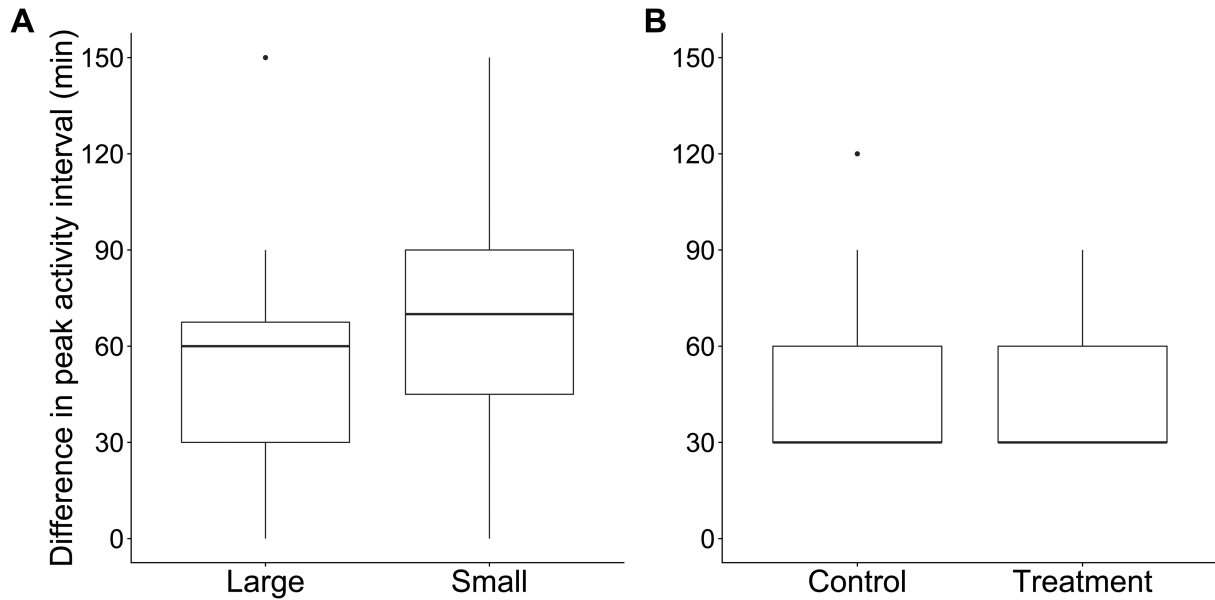 but not statistically significant effect. Specifically, *P. hesperus* took significantly more drinking passes on treatment nights that were negatively affected by *M. californicus* activity, but this affect of conspecific activity was not found during control nights (Table 2). Our models for *M. californicus* revealed that, consistent with our predictions, the drinking rate for *M. californicus* was negatively affected by both treatment and total activity of *P. hesperus*, although contrary to our predictions their interaction was not significant (Table 2). However, the total number of drinking passes by *M. californicus* was not significantly affected by treatment, the activity of the other species, or their interaction (Table 2).

DISCUSSION

Our study provides evidence of temporal partitioning between *P. hesperus* and *M. californicus* at water sources, even when facing reduced surface water (a predicted outcome of climate change). During nearly every night of both our observational and experimental monitoring, we detected distinct patterns of temporal partitioning between *P. hesperus* and *M. californicus*. This was evidenced by differences in peak arrival times and

overall activity patterns at both small and large water sources, and we did not detect significant alterations of temporal partitioning when we reduced surface area during our experiment. While both species decreased their proportion of drinking passes during our experimental treatments, these responses were similar between the species. The competitive interaction between the 2 species was evidenced by the consistent presence of temporal partitioning and the negative effects of each species' activity on the other in our experiment.

We found evidence for temporal partitioning between *P. hesperus* and *M. californicus* that occurred irrespective of water source size or the overall activity levels of heterospecifics, in both our observational and experimental approaches. While it is difficult to determine if either of these species had a competitive advantage over the other (i.e., some sort of dominance in close interactions), *P. hesperus* generally was the more abundant or active of the 2 species and typically was most active only shortly after sunset. *Myotis californicus* showed more variability in time of peak activity, although it typically reached its peak activity after that of *P. hesperus*. Whether *M. californicus* were locally avoiding *P. hesperus*, the more abundant species, or a mutual avoidance was occurring is unclear. However, neither surface area nor activity affected the partitioning of water sources. While we predicted that temporal partitioning might not be evident, or at least be less common, at larger water sources (where multiple bats can drink simultaneously with less risk of collision), this was not the case in our observational or experimental results. Peak activity of our focal species never occurred during the same time interval in our experiment. Regardless of size of the water source, we detected a difference in peak activity between these 2 species, similar to that found in

Table 2.—Mixed-effects models of the proportion (drinking rate) and number of drinking passes of *Myotis californicus* and *Parastrellus hesperus* and their effect estimates. Treatment indicates nights when the surface area of water sources was decreased. The experiment was performed on 2 livestock tanks in the Mojave Desert, southwestern Utah, United States, over 12 nights in August 2011.

Model	Effect	Estimate	SE	t	P
Parastrellus hesperus					
p(drinking passes)	Intercept	0.63	0.049	12.84	< 0.01
	Treatment	−0.14	0.13	−1.05	0.31
	M. californicus activity	0.0005	0.001	0.48	0.64
	Treatment*Act[a]	−0.0006	0.002	−0.28	0.78
	Tank B	0.08	0.04	1.99	0.07
Total drinking passes	Intercept	44.85	25.06	1.79	0.09
	Treatment	196.56	68.99	2.85	0.01
	M. californicus activity	1.02	0.58	1.77	0.09
	Treatment*Act	−4.22	1.13	−3.73	< 0.01
	Tank B	258.98	21.99	11.78	< 0.01
Myotis californicus					
p(drinking passes)	Intercept	0.79	0.06	12.53	< 0.01
	Treatment	−0.32	0.11	−2.91	0.01
	P. hesperus activity	−0.0008	0.0003	−2.85	0.01
	Treatment*Act	0.0005	0.0003	1.55	0.14
	Tank B	0.30	0.11	2.59	0.02
Total drinking passes	Intercept	22.99	7.85	2.93	0.01
	Treatment	12.60	13.62	0.93	0.25
	P. hesperus activity	−0.04	0.04	−1.18	0.37
	Treatment*Act	−0.03	0.04	−0.65	0.52
	Tank B	34.96	14.38	2.43	0.03

[a] "Act" is the activity of other focal species.

other studies (Cockrum and Cross 1964; Mumford et al. 1964; Jones 1965; O'Farrell et al. 1967; O'Farrell and Bradley 1970).

Based on our observational results, there was no evidence of spatial partitioning between *P. hesperus* and *M. californicus*; instead, we found that these species often occurred at the same water sources, and their activity levels were even positively correlated. This correlation was expected given that previous work observed similar sympatry at water sources, which, along with our data, suggested that these species often use the same habitat and water sources (O'Farrell and Bradley 1970; Bell 1980). While other species of ecologically similar bats have been shown to spatially partition water (Razgour et al. 2011) or foraging space or resources (Arlettaz 1999), temporal partitioning between our focal species seems to lessen the need for spatial partitioning at water sources.

Drinking rates were negatively affected by the loss of surface area of water in both species. *Parastrellus hesperus* did not have a significant reduction in proportion of drinking passes on treatment nights, but they did have more total drinking passes. This increase in drinking passes while maintaining their drinking rate indicates *P. hesperus* took more high (non-drinking) and drinking passes when facing reduced surface area of water, which is likely indicative of the increased difficulty of accessing water. In contrast, *M. californicus* experienced a decrease in the proportion of drinking passes on treatment nights, but no decline in the total number of drinking passes, indicating this species had more passes in total over the water source when surface area was restricted. This increase in total passes while maintaining the total number of drinking passes may suggest that, while the drinking requirements were similar across nights

for these bats, the reduced ability to access water requires more total passes until a successful drinking pass can occur.

Our analysis of drinking detected further evidence of competition between these species that could not be examined in our observational study. Although *M. californicus* activity was positively associated with *P. hesperus* drinking passes, the interaction of activity and treatment actually resulted in a negative effect on the number of *P. hesperus* drinking passes. While *P. hesperus* attempted more drinking passes when surface area was reduced, the increase in total activity from *M. californicus* on treatment nights may curtail this increase. Alternatively, the proportion of drinking passes by *M. californicus* was negatively affected by *P. hesperus* activity, irrespective of the treatment. While each species responded slightly differently to the reduction in surface area and the activity of the other, in both cases there was evidence of increased activity during treatment nights and increased competition between the species. While these patterns were not detected in our observational sampling, our repeated examination of the same water sources and experimental manipulation allowed such competitive interactions to become apparent, similar to previous studies (Tuttle et al. 2006; Razgour et al. 2010).

It should be noted that both species had comparable drinking rates (~70% of all passes were drinking passes for both species); although the drinking needs of individuals of either species are not known, it is a consideration. While little is known of the adaptations that *P. hesperus* or *M. californicus* have for dealing with aridity and water loss, the high drinking rates for each species suggests that either certain individuals (e.g., lactating females) have high drinking requirements (Adams and Hayes 2008), large numbers of individuals require at least 1 or a few drinks near the beginning of the evening, or a combination of these 2. Although species with

higher drinking rates (rates comparable to our species) have been shown to use larger more permanent ponds (Razgour et al. 2010), this contrasts with our findings that both species were found at small water sources. This contrast in findings likely is related to the maneuverability of our focal species that allows them to easily drink from small water sources (Hall et al. 2016).

Temporal partitioning may mediate the effects that reduced surface area and competitors have on the drinking behaviors of each species. The fact that *M. californicus* maintained the same number of drinking passes and *P. hesperus* increased its total drinking passes on treatments nights, despite some evidence of negative interactions between the 2 species, highlights the need for temporal partitioning. While our observational work did not detect negative relationships between the species (likely due to the coarse focus of our sampling), our experiment assessing drinking behaviors indicated that competition occurred between both species. Especially for *M. californicus* (the species with lower activity), concentrating activity before or after the most intense period of *P. hesperus* activity may allow the former to maintain similar numbers of drinking passes despite the increased difficulty of accessing the reduced water source.

Our study suggests that mechanisms such as temporal partitioning may mediate some negative effects of climate change in water-limited ecosystems. We found that *P. hesperus* and *M. californicus* co-occurred at water sources of all sizes and types and that temporal partitioning facilitated this co-occurrence even when the surface area of a water source was reduced. Although there is growing evidence that desert bats and other desert species are already facing declines and will be impacted by climate change (Adams 2010; Korine et al. 2016; Wu 2016; Hayes and Adams 2017), some species may fare better than others, at least in the short term. Our study does not address the other ways in which climate change might impact desert bats that are ecologically similar, but our results do indicate that mechanisms such as temporal partitioning contribute to the resiliency of biotic communities during sudden environmental disturbance.

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