Do bats seek clean water? A perspective on biodiversity from the Namib Desert

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Acknowledgements

We are grateful to the Namibian Ministry of Environment and Tourism in addition to Anabeb, Sesfontein, and Torra conservancies for permitting this research. We thank Mallory L. Davies for assistance with data collection, Seth J. Eiseb for use of the acoustic detectors, Kapoi Kasaona of Palmwag Lodge for storing water samples during fieldwork, and Sarah L. Carroll for her ArcGIS expertise. We are grateful to Kevin R. Crooks, George Wittemyer, Tara L. Teel, and John L. Field for their comments on an earlier version of this manuscript as well as to Rick A. Adams and Lina M. Mushabati for assistance with the study design. This work was supported by the National Science Foundation (GRFP, DGE-1321845 to T.M.L.), Bat Conservation International (to T.M.L), and Sigma Xi, The Scientific Research Society (GIAR, G2016100180021278 to T.M.L.).

Declaration of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Abstract

Water abundance, distribution, and quality are key elements affecting species distributions in arid environments, yet how their interactions structure specific animal communities is often unclear. To address this knowledge gap, we examined relationships between bodies of water and bat communities in the northern Namib Desert. We predicted that water quality would be poorer (i.e., higher indices of electrical conductivity and ion concentrations) during the dry season and at artificial pools, and that bat species richness and activity would consequently be lower at these sites. We conducted extensive fieldwork at the terminus of the hot, dry season from November 2016 to January 2017 and at the conclusion of the following wet season from March to May 2017, collecting water samples and acoustic recordings of bat activity at both natural springs (n = 18) and artificial pools (n = 5). Overall activity (but not species richness) was greater during the wet season and at artificial pools, but we did not find systematic differences in water quality driven by seasonality or water body type. Although individual artificial pools harbored significantly greater bat activity, more than 35% of the species that we recorded were present only at natural springs. While bat species richness was reduced at saline sites, only the activity of the Zulu serotine also related to water quality. In general, water surface area was more often associated with bat activity in the Namib Desert than was water quality.

Keywords

Chiroptera; community ecology; deserts; Namibia; water availability; water quality

1. Introduction

Deserts cover 17% of the world’s land mass yet are utilized by 25% of all terrestrial vertebrate species and 6% of the global human population (Durant et al., 2012; Millennium Ecosystem Assessment, 2005; Safriel et al., 2005). Water plays an important role in structuring wildlife communities in these arid environments (Noy-Meir, 1974), where precipitation totals – while low on average – show extreme inter-annual variation (von Wehrden et al., 2010). Mammal distributions and behaviors in deserts (e.g., well digging by elephants; Ramey et al. 2013) are strongly affected by their daily water losses, though some species (e.g., giraffe; Fennessy 2009) are less sensitive than others. In general, surface water availability concentrates desert life, such that springs in arid landscapes are global biodiversity hotspots (Bogan et al., 2014; Brown and Ernest, 2002; Davis et al., 2017). Nowhere is water so limiting as in deserts.

Beyond water availability, the chemistry of bodies of water can vary spatially, temporally, and with anthropogenic disturbance, which consequently can have profound and cascading influences on human, livestock, and wildlife health (Bleich et al., 2006; Korine et al., 2015). Water availability affects the distributions of flora and fauna in arid environments, but rarely are the effects of water quality and chemistry on species richness known. Surface water in deserts can sometimes be unsuitable for consumption (Broyles, 1995), and in extreme circumstances can lead to heavy metal or toxin bioaccumulation in or poisoning of (e.g., cyanide poisoning and cyanobacteria blooms) wildlife and livestock (Koenig, 2000; Naidoo et al., 2013; Olsson et al., 1998; Ratcliffe, 1967; Stewart et al., 2008). High nitrogen and phosphorus concentrations contribute to eutrophication, toxic algal blooms, and overall reduced water quality (Carpenter, 2008; Strauch, 2013). High alkalinity levels (> 500 mg/L) can have a laxative effect on animals (Rosenstock et al., 2004). Sodium and chloride ions not only contribute to dehydration and can be lethal for animals in high concentrations (Gereta and Wolanski, 1998), but can also dissolve suspended heavy metals and introduce them into food chains (Bradford et al., 1990). In general, poor water quality is associated with high concentrations of ions (Korine et al., 2015), as well as large measurements of electrical conductivity (i.e., a measurement of the charged ions in water that often correlates with concentrations of sodium, chloride, and sulfate; Christensen, 2001).

Species differ, however, in their sensitivity to water quality. Traditionally, aquatic invertebrates, fish, and amphibians have been used as indicators of freshwater quality, particularly in mesic environments, as they spend all or parts of their lives in water. Since surface water is rare and widely-dispersed in deserts like the Kalahari and the Namib in southern Africa (Durant et al., 2012), highly mobile species (e.g., flying mammals) may provide information not only about water quality of individual water sources, but also about the use of and connectivity among dispersed sources. Bats (Order Chiroptera) account for approximately 20% of the world's mammals (Voigt and Kingston, 2016), and comprise one of the most diverse and successful groups of mammals living in deserts (Carpenter, 1969). Although bats have high mobility and dispersal ability by flying, their small body sizes and high metabolic rates suggest that local distributions are driven by microhabitat features, such as water, roost, and prey availability. Insectivorous bats can lose relatively large amounts of water (e.g., 15-31%

of body mass) daily through evaporation (Studier, 1970; Webb, 1995). Unsurprisingly, bat activity (particularly in deserts) is typically highest around water, where bats replenish those losses directly through water consumption (Kurta et al., 1990; McLean and Speakman, 1999) and indirectly through feeding (Adams and Thibault, 2006; Korine et al., 2015; Rebelo and Brito, 2007). Bats may also seek out bodies of water rich in dissolved ions and minerals (e.g., calcium; Adams et al. 2003) to supplement nutrient deficiencies, which can be particularly important for reproductive individuals.

In addition to water quality, the surface area of water sources may limit the accessibility of drinking water for larger, less-maneuverable species (i.e., often fast-flying open-air foragers with large aspect and wing-loading ratios), introducing a confounding factor. In the United States, less-maneuverable desert bats were more active over larger water sources while maneuverable bats exhibited no preference for water size (Hall et al., 2016). In the Negev Desert in Israel, studies also found bat activity and species richness to increase with water body size (Razgour et al., 2010), with no difference between artificial pools and natural springs despite significant differences in water chemistry (Korine et al., 2015). However, certain species were only found at natural springs, suggesting that water quality may affect the distribution of individual species (Korine et al., 2015; McCain, 2007). The effect of water quality on bat species distributions and activity levels varies by species in published literature (Salvarina, 2016), particularly in desert ecosystems (Blakey et al., 2018; Korine et al., 2016). Worldwide, many of these studies linking water quality and bat communities have yielded conflicting results, including differences in activity between and sometime within species ascribed to water chemistry (Salvarina, 2016). Research involving seasonal comparisons of bat activity over bodies of water is needed, especially in lentic systems (i.e., lakes and ponds) where declines in water quality and eutrophication risks can be more severe.

Our study aims to better understand spatial relationships among the distributions of bat species, water availability, and water quality in one of the world's oldest deserts, the Namib in southern Africa (Frossard et al., 2015; Ward et al., 1983). More specifically, we test the hypothesis that insectivorous bat distributions are driven by differences in water quality between artificial pools and natural springs during both dry and wet seasons. We predicted that: 1) poorer water quality (i.e., higher electrical conductivity and ion concentrations) would occur during the dry season and at artificial pools; 2) bat activity and species richness would generally be lower at sites with poorer water quality and smaller pond surface area—with both expected to have stronger negative effects during the dry season when bats may be lactating and water is generally more limiting—and at artificial springs due to presumably lower food availability in human-constructed environments; and 3) slower-flying, more maneuverable bat species (e.g. clutter-edge foragers, or those species that feed in cluttered environments) would seek out sites with better water quality, whereas fast-flying species (e.g., open-air foragers) would be limited to ponds of larger surface areas due to accessibility issues. Such relationships, if present, would suggest that the management of water quality in desert landscapes may be just as important, if not more, than overall water availability for the presence and activity of bats.

2. Materials and Methods

2.1 Study Area

Our study took place in the northern Namib Desert within the Kunene Region of Namibia (Fig. 1). We worked primarily within the catchments of the Hoanib, Uniab, Koigab, and Huab Rivers – four of the twelve major ephemeral rivers of Namibia (Jacobson et al., 1995; Laverty, 2019). While mean annual rainfall exceeds 300 mm in the eastern headwater regions within these catchments, it declines to near zero in the west where these rivers meet the Atlantic Ocean (Berger, 1997; Jacobson and Jacobson, 2013). The eastern and western edges of our particular study area receive on average ~ 100 mm and 30 mm of annual precipitation, respectively. Permanent surface water sources in this region consist of natural springs, artificial pools constructed for wildlife and/or livestock use, and short (≤ 3 km) running water stretches. During the wet season (January to April), rivers sustain aboveground flows for on average less than 20 days per year (Jacobson et al., 1995; Jacobson and Jacobson, 2013; Leggett et al., 2001).

We sampled water quality and bat communities at 23 permanent bodies of open water including both artificial pools (n = 5) and natural springs (n = 18), with a minimum straight-line distance between sites of 8.28 km (Fig. 1; Appendix S1). None of these sites were illuminated by floodlights with the exception of the artificial pool at Wilderness Safaris' Rhino Camp, which is lit every night for the entire evening by one floodlight. While illumination generally has negative effects on bat activity, limiting the number of passes to drink water in particular (Russo et al., 2017, 2019), habituation or phenotypic plasticity may occur for some species in areas where artificial illumination at night is widespread and has been present for a long time as it has been at our study site (Altermatt and Ebert, 2016). Only one site was located in a village, the natural spring found ~100 m behind the Sesfontein Conservancy headquarters in Sesfontein, Kunene Region. Three bodies of water were situated near ecotourism lodges: artificial pools at Wilderness Safaris' Hoanib Skeleton Coast Camp (358 m from lodge) and Wilderness Safaris' Rhino Camp (~100 m from lodge), and the natural spring at Skeleton Coast Safaris' Kuidas Camp (2.15 km from lodge). The natural springs at Fonteine and Spaarwaterpos were ~100 m and ~1.5 km away, respectively, from adjacent small, semi-nomadic ranches comprised of 1-3 households. All other sites were > 10 km from villages, active ranches, or lodges. Artificial pools and natural springs varied in having aquatic vegetation and/or terrestrial vegetation within 5 m of each body of water (Appendix S1). Vegetation was sparse enough at our study areas that it did not limit access to surface water for drinking bats and was therefore not included on our analyses.

2.2 Water Sampling

We sampled water quality and surface area at each of the 23 sites twice—once at the end of the 2016 dry season (21 November 2016 – 21 January 2017) and once at the end of the 2017 wet season (16 March 2017 – 16 May 2017). We estimated water availability by measuring the maximum length and width of each body of water and then multiplying these together to calculate an index of maximum pond surface area. Just prior sunset each night, we collected a one-liter water sample per site for subsequent laboratory analysis of water quality. Samples were drawn from the center of each body of water's surface. During the wet season only, we also collected a 250 mL acidified sample for heavy metal analysis. We stored all samples in a cool, dry place before delivering them to the Analytical Laboratory Services in Windhoek, Namibia within three weeks of collection.

During both seasons, we measured several commonly-used indicators of water quality including pH, electrical conductivity, turbidity, total dissolved solids (TDS), and total alkalinity as calcium carbonate ($CaCO_3$), in addition to concentrations of major and trace ions: calcium (Ca^{2+}), chloride (Cl^-), fluoride (F^-), iron (Fe^{3+}), magnesium (Mg^{2+}), manganese (Mn^{2+}), nitrate (NO_3^-), nitrite (NO_2^-), potassium (K^+), sodium (Na^+), and sulfate (SO_4^{2-}). The heavy metal analysis was only conducted during our wet season sampling, and not included in our regression analyses. We report, however, on these results for comparison with other sites for the following ions: aluminum (Al^{3+}), arsenic (As^{3+}), barium (Ba^{2+}), boron (B^{3+}), cadmium (Cd^{2+}), chromium (Cr^{3+}), cobalt (Co^{2+}), copper (Cu^{2+}), lead (Pb^{2+}), lithium (Li^+), nickel (Ni^{2+}), selenium (Se^{2-}), silica (SiO_2), strontium (Sr^{2+}), and zinc (Zn^{2+}). Poor water quality is generally associated with higher concentrations of these indices (Korine et al., 2015). Measurements falling below a detection limit were recorded as half of that detection limit (see Appendix S2; Olsen et al. 2012). We used these indices to estimate general differences in water quality between natural springs and artificial pools and tested for seasonal differences as described in the Statistical Analysis section below. For each sample, we also interpreted the overall water quality based on guidelines for the evaluation of drinking water for human consumption (Department of Water Affairs, 1991). This classification system divides water into four groups: excellent water quality, good water quality, water with low health risks, and water unsuitable for human consumption. Overall water quality is determined by the ion concentration that complies the least with these drinking water quality guidelines. Consequently, our 46 water samples were all classified in the latter three categories (i.e., no sample was considered excellent quality water).

2.3 Surveying Bat Communities

At each of the 23 sites (artificial pools, *n* = 5, and natural springs, *n* = 18), we also monitored nightly bat activity and species richness twice (once in each season) for a total of 46 nights of sampling. More specifically, we deployed an ultrasonic bat detector (Song Meter SM4BAT FS, Wildlife Acoustics) to monitor activity during the nights on which water sampling was conducted (Laverty, 2019). Recordings began 30 min before sunset and ended 30 min after sunrise. We positioned the microphone 2.5 m above the ground at a 45-degree downward angle within 3 m of surface water. While the downward angle of the microphone adjacent to surface water may result in steeper than usual frequency-modulated echolocation calls, this orientation is preferred in the event of inclement weather such as rain or fog (Loeb et al., 2015). We did not record bat calls or sample water quality within three days of the full moon, since moonlight is known to reduce the activity patterns of some bat species (i.e., lunar phobia; Lang et al. 2006; Kingston 2009). Survey protocols were approved prior to implementation by an Institutional Animal Care and Use Committee [institution and protocol # removed for blind review] and the Namibian Ministry of Environment and Tourism [protocol # removed for blind review].

Since a call library does not exist for Namibian bats, we used the bat call identification software program Kaleidoscope Pro Version 5.1.3 (Wildlife Acoustics, Maynard, MA) to perform cluster analysis. Under this method, full spectrum calls are analyzed using enhanced zero crossing (Ross et al., 2018). A signal detector searches for candidate vocalizations in the recordings, which are then sorted into a number of clusters based on their similarity. We then manually reviewed all call files in each of the clusters to classify the species present (Appendix S3). Calls were compared to those provided in a field guide by Monadjem et al. (2010). We also based our identifications on a set of reference calls that we tagged and recorded from bats physically captured and identified over different sampling periods at the same sites.

In total, we captured 1,477 bats in mist nets during 16 months of bat research in this region. Since each night of mist netting was paired with a concurrent acoustic survey, calls from known hand-released individuals could be compared with those recorded by free-flying bats, reducing the error in our species identification. Most species' calls are distinct from one another and readily identifiable. However, three pairs of species in this area have similar calls that made differentiation difficult: the Angolan wing-gland bat (*Cistugo seabrae*) and the Zulu serotine (*Neoromicia zuluensis*); the Cape serotine (*Neoromicia capensis*) and Schlieffen's twilight bat (*Nycticeinops schlieffeni*); and the long-tailed serotine (*Eptesicus hottentotus*) and the yellow-bellied house bat (*Scotophilus dinganii*). After careful evaluation of the spectrograms for these six species and reviewing the capture histories of bats netted at these 23 sites during different sampling periods, we were confident in assigning a species to each of the call files in question. Additionally, the activity of many gleaning bats (e.g., those in the family Hipposideridae and Nycteridae) may have been underestimated due to the whispering nature of these bats' echolocation calls.

We defined bat activity as the number of passes (i.e., sequence of calls; Fenton 1970) per night of recording at each site. We calculated overall activity as the total number of bat passes per night recorded at each site, regardless of species. Lastly, species richness was defined as the total number of species recorded within a night at each site.

2.4 Statistical Analysis

All statistical analyses were done in R (R Core Team, 2017) with $\alpha = 0.05$. We used principal components analysis (PCA) and multivariate analysis of variance (MANOVA) to test for differences in water quality across seasons and water body types. We first used PCA with the *PCA* function in the FactoMineR package (Le et al., 2008), which included 10 water chemistry variables (pH as well as natural log transformations of electrical conductivity, turbidity, total alkalinity as calcium carbonate, chloride, sulfate, sodium, potassium, calcium, and iron), measured twice (once in each season) at 23 sites (artificial pools, $n = 5$, and natural springs, $n = 18$) for a total sample size of 46. We used only those measurements collected over both sampling periods (i.e., we did not include the heavy metal analysis). We further excluded manganese, nitrate, and nitrite from our analyses because these ions were not detected in approximately half of our samples. We also omitted total dissolved solids (TDS) because its measurements were highly correlated with electrical conductivity (Appendix S4). For all other variables, we tested for normality using the Shapiro-Wilk normality test (*shapiro.test* in R) and transformed all non-normal water chemistry variables (i.e., all variables except for pH) using a natural log transformation (Olsen et al., 2012). Both fluoride and magnesium were extremely right skewed and failed to fit a normal distribution after the natural log transformation. Twelve of our 46 water samples produced fluoride or magnesium concentrations that were classified as unsuitable for human consumption (Department of Water Affairs, 1991). Given the recommendations to normalize our data before further analysis (Olsen et al., 2012), however, we also excluded measurements of these ions from our subsequent analyses.

We then used MANOVA with the *manova* function in the stats package to test for differences in water quality across seasons and water body types. In this analysis, our response variables were the first two principal components from the PCA described above (PC1, $n = 46$, and PC2, $n = 46$) and the dependent categorical variables were the effects of season, water body type, and the interaction between season and water body type.

To test for the effects of water quality and availability (measured here as maximum pond surface area) between seasons and water body types on overall bat activity and species richness, we used generalized linear models. Initial data exploration indicated that the distribution of overall bat activity was positively skewed and the variance was much greater than the mean. For species richness, however, the variance and mean of this distribution were approximately equal. Therefore, we used generalized linear model procedures (*glm* and *glm.nb*) in R to compare the fit of log-linked Poisson, quasi-Poisson, and negative binomial models to our data (Crawley, 2013; Venables and Ripley, 2002). The different regression models were compared using visual evaluation of quantile-quantile (QQ) plots, comparison of residual deviance versus residual degrees of freedom, and assessment of Akaike's information criterion (AIC; Crawley, 2013). After determining the best-fitting distributional model for the complete set of predictor variables, we performed backward selection starting with full models that all included the following predictors: interactions between season and water quality represented as the first two principal components from the PCA described above to avoid multicollinearity between variables, an interaction between season and maximum pond surface area normalized with a natural log transformation, and water body type. Water quality and maximum pond surface area were all measured twice (once in each season) at 23 sites (artificial pools, *n* = 5, and natural springs, *n* = 18) with a total sample size of 46. Bat activity and species richness were surveyed for the entirety of those 46 nights. With the *drop1* function in R, we dropped variables using F tests for quasi-Poisson models and chi-square tests for Poisson and negative binomial models until only variables significant at the 0.05 level remained.

Further, we investigated species-specific responses to water quality and availability by using the generalized linear model comparison and selection procedures described above with the same predictor variables and full model structure. The response variable in these models was the activity of an individual species rather than the overall activity of the entire bat community. We limited this analysis to species that were recorded on 50% of the sampled nights or more and that also had greater than 1,000 total recorded passes summed across all surveyed nights. This included six species in total: two fast-flying bats in the family Molossidae (Roberts's flat-headed bat, *Sauromys petrophilus*, and the Egyptian free-tailed bat, *Tadarida aegyptiaca*), and four slower-flying, more maneuverable species in the families Cistugidae (the Angolan wing-gland bat), Vespertilionidae (the long-tailed serotine and the Zulu serotine), and Hipposideridae (Sundevall's leaf-nosed bat, *Hipposideros caffer*).

3. Results

3.1 Variation in Water Quality

We examined for differences in water quality across our 46 samples using PCA. PC1 accounted for 43.2% of the variance and PC2 24.6% (eigenvalues = 4.32 and 2.46, respectively). The first principal component (PC1) was highly weighted with higher measurements of electrical conductivity as well as with greater concentrations of sodium, chloride, potassium, and sulfate (Table 1). The second principal component (PC2) was weighted with higher measurements of iron, turbidity, total alkalinity as calcium carbonate, and pH, as well as lower measurements of calcium. Lower measurements of PC1 and PC2 were generally associated with better overall water quality as determined by the classifications made by the Department of Water Affairs in Namiba (1991; Fig. 2). Our MANOVA results did not, however, provide support for our prediction 1 in which we expected that water quality would be poorer during the dry season and at artificial pools. Neither season ($p = 0.327$), water body type ($p = 0.204$), nor the interaction between season and water body type ($p = 0.684$) significantly related to PC1 and PC2 (Appendix S5; Appendix S6).

3.2 Bat Species Richness and Activity

In total, we recorded 120,749 individual passes from 16 bat species in our 46 nights of sampling. Bats were detected at all sites during all sampling sessions except one (i.e., no bats were recorded at the natural spring Ganias during the dry season). Nine species were detected at artificial pools in both the dry and wet seasons, while 14 species were recorded at natural springs in the dry season versus 16 in the wet season (Table 2). Notably, six species were only detected at natural springs: the striped leaf-nosed bat (*Macronycteris vittatus*; only recorded on one night of sampling), the greater long-fingered bat (*Miniopterus inflatus*), the Cape serotine, Schlieffen’s twilight bat, Rüppell’s horseshoe bat (*Rhinolophus fumigatus*), and the yellow-bellied house bat. Additionally, the striped leaf-nosed bat and the Egyptian slit-faced bat (*Nycteris thebaica*) were only detected during the wet season.

Due to differences in sample sizes across water body types, we report the mean number of species found at individual artificial pools (*n* = 5) and natural springs (*n* = 18) rather than the raw totals. Mean bat species richness was similar across water body types (mean ± SD: artificial pools = 6.60 ± 1.58, natural springs = 5.64 ± 2.59) and seasons (dry = 5.57 ± 2.63, wet = 6.13 ± 2.22; Fig. 3). Bat activity varied more across these factors, with activity as high as 6,660 ± 3,630 bat passes at artificial pools in the wet season to as low as 1,250 ± 1,420 passes at natural springs in the dry season (Fig. 3).

3.2.1 Effects of Water Quality and Availability on Bat Communities

Results from generalized linear model selection suggested a positive significant relationship between overall bat activity and pond surface area (Table 3). The wet season harbored significantly more bat activity than the dry season, and artificial springs hosted more activity than did natural springs. Contrary to our expectations (prediction 2), statistical support for a relationship between bat activity and water quality was lacking (Table 3).

Bat species richness, on the other hand, did significantly relate to water quality and pond surface area (prediction 2). Our analysis found a significant negative relationship between PC1 (weighted with higher measurements of electrical conductivity and larger concentrations of sodium, chloride, potassium, and sulfate; Table 1) and species richness, but a significant positive relationship between pond surface area and species richness (Table 3). Species richness was also higher at artificial pools than at natural springs.

3.2.2 Species-Specific Effects of Water Quality and Availability on Bat Activity

We found support for our prediction that bat activity of the fast-flying species would relate to pond surface area rather than water quality (prediction 3). The activity of both of the fast-flying molossid species (Roberts's flat-headed bat and the Egyptian free-tailed bat) had a significant positive relationship with pond surface area (Table 4). Both species were also more active at artificial pools than at natural springs, as well as during the wet season relative to the dry season.

Of the four clutter-edge foraging species with more maneuverable flight patterns (the Angolan wing-gland bat, the long-tailed serotine, the Zulu serotine, and Sundevall's leaf-nosed bat), only the activity of the Zulu serotine was related to water quality in agreement with prediction 3 (Table 4). More specifically, the activity of the Zulu serotine had a significant negative relationship with PC2 (weighted with higher measurements of turbidity, iron, total alkalinity as calcium carbonate, and pH, as well as lower measurements of calcium; Table 1). The activity of Sundevall's leaf-nosed bat had a significant positive relationship with pond surface area and was greater at artificial pools than at natural springs (Table 4). Neither water quality nor surface area related to the activity of the long-tailed serotine, but, like Sundevall's lead-nosed bat, its activity was greater at artificial pools than at natural springs (Table 4). The activity of the Angolan wing-gland bat had a significant positive relationship with pond surface area and was more active during the wet season. This was the only species whose activity also had a significant interaction term in its top model, such that the effect of pond surface area on the activity of the Angolan wing-gland bat was greater during the dry season than during the wet season (Table 4).

4. Discussion

4.1 Seasonal Variation in Bat Activity

Bat activity, but not species richness, differed by season. We observed significantly greater activity levels during the wet season consistent with our prediction that seasonality affects overall bat activity. The wet season roughly corresponds to the period in which bat pups are weaned and fledge in the northern Namib Desert (e.g., juveniles were captured in mist nets between January and March, pers. obs.), which may explain some of the additional activity recorded during these months. While it is reasonable to think that bats may increasingly concentrate around limited surface water in the dry season – particularly if this season coincides with lactation (Adams and Hayes, 2008) – we believe the observed increase in bat activity during the wet season may also be due to individuals temporarily immigrating into the region when prey and water resources are more abundant, as has been noted for Namib Desert migratory birds (Loutit, 1991; Ryan et al., 1984). In agreement with this prediction of bat migration (Fleming and Eby, 2003), our observations included two bat species—the striped leaf-nosed bat and the Egyptian slit-faced bat—only recorded during the wet season. Future research should include long-term acoustic monitoring and tracking of individuals to understand seasonal patterns of movement for Namib Desert bats.

4.2 Bat Use of Artificial Pools Relative to Natural Springs

Artificial pools were constructed in the northern Namib Desert by the government of Namibia and tourism operations to supplement wildlife populations away from human settlements (Leggett 2006), a tactic to reduce risks of degradation of water quality from anthropogenic pollution. Due to their homogeneity in shape, size, water chemistry, and lack of aquatic vegetation relative to that of natural springs, we predicted that human-constructed pools would favor generalist bat species or open-air foragers rather than specialists or clutter-edge foragers (Lisón and Calvo, 2011). Surprisingly, artificial pools individually harbored bat diversity similar to that found at natural springs. As expected, the open-air foraging Egyptian free-tailed bat and Roberts's flat-head bat were significantly more active at artificial pools. In contrast, clutter foragers and gleaning bats, in particular, may benefit from the habitat complexity surrounding natural springs. Indeed, six of the 16 bat species observed—all clutter-edge foragers—were only recorded at natural springs and never detected at artificial pools. However, due to our small sample sizes, we are unable to determine if these species avoided artificial pools, or if their absence at these sites was a consequence of other factors, such as the distance of artificial pools to bat roosts. Contrary to our predictions, we found significantly higher activity levels of the long-tailed serotine and Sundevall's leaf-nosed bat at these manmade pools. Across the entire bat community, artificial pools supported, on average, approximately twice the overall activity of natural springs regardless of season.

Our findings support the notion that these synthetic pools may play a role in broader bat conservation and function to provide habitat for needs beyond those related to foraging (e.g., drinking; Tuttle et al., 2006). However, constructing additional artificial pools across the landscape may attract generalist bats and other animals that are not native to these regions, which may function to competitively exclude desert-adapted bats from these bodies of water (Korine and Pinshow, 2004; Polak et al., 2011; Razgour et al., 2011). Future studies should aim to document bat communities before and after the construction of artificial pools. Additional research should address whether distance to human settlements and/or livestock areas may be useful covariates for predicting wildlife activity and water quality at these sites.

4.3 Do Bats Seek Large Bodies of Water or Clean Water?

The size of bodies of water may be an important predictor of whether bats consume water at sites, particularly for fast-flying species (e.g., molossids) that require larger swoop zones to drink on the wing (Tuttle et al., 2006). Water availability, measured as maximum pond surface area in this study, had an expected positive relationship with the activity of the two fast-flying, open-air foraging species—the Egyptian free-tailed bat and Roberts's flat-headed bat. Additionally, the activity of two other species showed significant relationships with pond surface area. The highly-maneuverable Sundevall's leaf-nosed bat was more active over larger bodies of water, as was the highly-maneuverable Angolan wing-gland bat, but the effect of pond surface area on the activity of the Angolan wing-gland bat was stronger during the dry season than during the wet season. Our results support the findings of Hall et al. (2016) that less-maneuverable desert bats are more active over larger bodies of water, but maneuverable bats exhibit no preference on average. In agreement with other studies (e.g., Razgour et al., 2010), both bat species richness and overall activity of the entire bat community had significant positive relationships with pond surface area.

Water quality only had a significant relationship with bat species richness in the northern Namib Desert. As predicted, species richness was negatively related to water salinity (measured as PC1). The activity of only one species—the Zulu serotine—had a significant relationship with water quality consistent with our original predictions, with reduced activity at more turbid, alkaline, iron-rich, and calcium-poor bodies of water (measured as PC2). The top models for the five other species did not contain water quality variables.

Other investigations of water quality and bat communities involving natural and artificial bodies of water have focused on wastewater treatment pools or other bodies of water around large urban centers (Korine et al., 2015; Li and Kalcounis-Rueppell, 2018; Naidoo et al., 2013; Straka et al., 2016), where water quality differences exist and at times negatively affect the activity of sensitive bat species. Results from our study in the Namib Desert revealed no significant differences in water chemistry between artificial pools and natural springs. Water quality effects on bat activity and species richness were more complex. While there is no single accepted definition or standards for "clean" water for wildlife, some of our results suggest bats may incur physiological consequences from drinking at or foraging over certain bodies of water. Specifically, bats did not avoid saline bodies of water contrary to our expectations (Griffiths et al., 2014), which may result in dehydration. Roberts's flat-headed bat and the Egyptian free-tailed bat—two of our most ubiquitous species— were most active over sites with chloride concentrations above 9000 mg/L (although the effect of salinity on the activity of these two species was not significant). These values are well above the maximum chloride concentration for human consumption (1200 mg/L) recommended by the Namibian Department of Water Affairs (1991). Not only did we record these species at these saline bodies of water, but we also observed them drinking water at these sites during our study. Calcium is another limiting ion in arid regions that possibly affects the spatial distributions of insectivorous bats (Adams et al., 2003; Barclay, 1994). In the Namib Desert, the concentration of calcium (averaging 110 mg/L; Table 1) was relatively high— and thus more accessible to bats— compared to calcium-rich sites in the arid regions of Colorado in the United States, where concentrations of 29 mg/L were reported by Adams et al. (2003). Bats, at least in this African ecosystem, likely do not need to alter their distributions or behaviors to obtain this resource.

4.4 Other Drivers of Bat Distributions

If water chemistry does not appear to be the main driving force in bat species richness and activity in the Namib Desert, what might be? Species distributions—bats included— are products of many factors; beyond water chemistry, roost and prey availability, reproductive condition, and interspecific competition play roles (Barclay, 1994; Hagen and Sabo, 2014; Razgour et al., 2011). Two species—the Cape serotine and Schlieffen’s twilight bat—appeared to limit use of water by restricting activities near the human settlement of Sesfontein on the more mesic eastern extremities of our study area. This suggests these two species do not tolerate extreme arid conditions, but may instead rely on human settlements for reliable access to water, roosts, and/or prey.

Bats also frequent bodies of water without drinking, so their presence over these sites might wrongly be interpreted to signify water consumption. Natural springs may host higher densities of potential prey for foraging bats since riparian vegetation provides habitat for terrestrial and aquatic insects (Hackett et al., 2013; Hagen and Sabo, 2014). Therefore, while bats may be expected to visit artificial pools primarily for drinking, natural springs may serve multiple purposes (i.e., both drinking and foraging habitats). A previous study found Roberts's flat-headed bat and the Zulu serotine to survive for months in captivity without access to water, suggesting that these species may obtain sufficient water from their insect prey alone (Roer, 1970). Roberts's flat-headed bat, however, was one of the most frequently observed species to drink water at our study sites (pers. obs.). Therefore, these species will likely drink water when and where it is available to them. Future studies should address the importance of bodies of water as foraging habitats versus solely space for drinking by calculating the ratio of feeding buzzes, which occur during the final stage of insect capture (Griffin et al., 1960), to drinking buzzes, which occur as bats approach water to drink (Russo et al., 2016). Additionally, studies should directly measure horizontal and vertical vegetation cover and plant species diversity, as bats may choose to associate with specific plant species for foraging and roosting.

4.5 Conclusions

Life in deserts is often focused around rare and isolated bodies of water. In the face of increasing rainfall variability predicted with climate change (Jacobson and Jacobson, 2013), understanding the roles that water availability and quality play in structuring mammal communities in arid ecosystems is essential to biodiversity conservation. As we untangle the underlying mechanisms, it will become increasingly possible to prioritize protection of specific bodies of water for bats and broader biodiversity conservation.

Similar to findings from the Negev Desert in Israel (Korine et al., 2015; Razgour et al., 2010), our study found activity of the entire bat community in the northern Namib Desert, and that of several individual species, to be related to water surface area, and only poorly associated with “clean” water. Only activity of the Zulu serotine decreased with turbid, alkaline, iron-rich, and calcium-poor bodies of water in agreement with our predictions and species richness declined with water salinity. Six of the 16 species recorded in this study appeared to be restricted to natural springs. We also documented large seasonal differences in bat activity, with wet season activity approximately twice that of the dry season. Species most dependent on water quality will likely vary their habitat use and behavior due to seasonal changes in resources and differ by geographic location. Therefore, future research should focus on increasing the spatial and temporal sampling of water quality, water availability, and bat communities in arid landscapes to gain a better understanding of the seasonal abiotic drivers of bat distributions.

Appendix A. Supplementary information

Additional tables and a figure are provided.

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Table 1. Mean (± SD) and principal component (PC) loadings of water chemistry from artificial pools and natural springs sampled during the conclusion of dry (November 2016 – January 2017) and wet (March – May 2017) seasons in the northern Namib Desert, Namibia.

Variable[a]	Dry Season		Wet Season		Principal component (PC) loadings[b]	
	Artificial Pools (*n* = 5)	Natural Springs (*n* = 18)	Artificial Pools (*n* = 5)	Natural Springs (*n* = 18)	PC 1	PC 2
Maximum water surface area (m^2)	25.0 ± 12.9	652.0 ± 985.4	30.9 ± 25.1	647.3 ± 886.1	-	-
Standard Analysis Kit						
pH	7.7 ± 0.3	8.1 ± 0.5	8.0 ± 0.9	8.1 ± 0.5	**0.350**	**0.552**
Electrical conductivity (mS/m)	456.8 ± 140.3	558.3 ± 721.1	891.3 ± 825.6	860.5 ± 1273.6	**0.968**	-0.135
Turbidity (NTU)	3.4 ± 3.0	27.6 ± 38.1	8.8 ± 5.7	44.8 ± 122.5	0.189	**0.681**
Total dissolved solids (determined)	2777.1 ± 837.9	3458.9 ± 4530.1	5971.4 ± 5531.3	5765.5 ± 8533.0	-	-
Total alkalinity as $CaCO_3$	403.0 ± 118.0	469.6 ± 426.4	471.2 ± 381.2	477.2 ± 607.7	**0.324**	**0.657**
Calcium (Ca^{2+})	107.0 ± 36.6	84.5 ± 81.5	76.0 ± 59.5	144.6 ± 223.1	**0.388**	**-0.804**
Chloride (Cl^-)	901.0 ± 282.9	1370.9 ± 2270.4	2297.0 ± 2343.0	2519.5 ± 4628.1	**0.952**	-0.191
Fluoride (F^-)	1.4 ± 0.2	2.0 ± 1.5	1.4 ± 0.8	2.2 ± 2.4	-	-
Iron (Fe^{3+})	0.24 ± 0.22	1.17 ± 1.73	0.08 ± 0.15	0.18 ± 0.42	-0.054	**0.734**
Sulfate (SO_4^{2-})	568.2 ± 289.6	432.3 ± 531.0	1423.8 ± 1842.7	288.7 ± 347.0	**0.667**	0.142
Magnesium (Mg^{2+})	105.6 ± 39.2	92.5 ± 107.9	189.8 ± 194.5	86.6 ± 90.6	-	-
Manganese (Mn^{2+})	0.02 ± 0.02	0.04 ± 0.05	0.05 ± 0.08	0.01 ± 0.01	-	-
Nitrate (NO_3^-)	6.5 ± 12.2	5.9 ± 8.7	1.6 ± 2.4	7.4 ± 9.6	-	-
Nitrite (NO_2^-)	0.40 ± 0.69	0.07 ± 0.11	0.37 ± 0.80	0.24 ± 0.31	-	-
Potassium (K^+)	38.9 ± 22.1	14.1 ± 19.0	86.5 ± 79.6	27.7 ± 61.9	**0.828**	-0.022
Sodium (Na^+)	708.6 ± 290.2	1079.2 ± 1612.6	1791.8 ± 2083.8	1577.7 ± 2447.0	**0.963**	0.054

Heavy Metal Analysis[c]						
Aluminium (Al^{3+})	-	-	0.09 ± 0.17	0.07 ± 0.14	-	-
Arsenic (As^{3+})	-	-	0.02 ± 0.01	0.02 ± 0.02	-	-
Barium (Ba^{2+})	-	-	0.04 ± 0.02	0.05 ± 0.06	-	-
Boron (B^{3+})	-	-	1.22 ± 0.86	1.67 ± 1.84	-	-
Cadmium (Cd^{2+})	-	-	0.01 ± 0	0.01 ± 0	-	-
Cobalt (Co^{2+})	-	-	0.01 ± 0	0.01 ± 0	-	-
Chromium (Cr^{3+})	-	-	0.01 ± 0	0.01 ± 0	-	-
Copper (Cu^{2+})	-	-	0.01 ± 0.01	0.01 ± 0	-	-
Lead (Pb^{2+})	-	-	0.01 ± 0	0.01 ± 0	-	-
Lithium (Li^{+})	-	-	0.14 ± 0.14	0.06 ± 0.16	-	-
Nickel (Ni^{2+})	-	-	0.01 ± 0	0.01 ± 0	-	-
Selenium (Se^{2-})	-	-	0.04 ± 0.03	0.03 ± 0.04	-	-
Silica (SiO$_2$)	-	-	12.34 ± 7.41	26.40 ± 16.58	-	-
Strontium (Sr^{2+})	-	-	3.71 ± 2.06	4.76 ± 8.40	-	-
Zinc (Zn^{2+})	-	-	0.01 ± 0	0.01 ± 0	-	-

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[a] Results are in mg/L unless otherwise stated.

[b] Variables accounting for significantly more variation in each principal component PC are shown in bold. See methods for further details.

[c] The heavy metal analysis was not included in our analyses, but is provided here to allow comparison across other study areas.

Table 2. Bat activity (mean passes per night ± SD) for each species recorded at artificial pools and natural springs during the conclusion of dry (November 2016 – January 2017) and wet (March – May 2017) seasons in the northern Namib Desert, Namibia.

Species	Dry Season		Wet Season	
	Artificial Pools (*n* = 5)	Natural Springs (*n* = 18)	Artificial Pools (*n* = 5)	Natural Springs (*n* = 18)
Angolan wing-gland bat (*Cistugo seabrae*)	515 ± 420	360 ± 421	2160 ± 1900	474 ± 736
Long-tailed serotine (*Eptesicus hottentotus*)	167 ± 203	69.0 ± 139	110 ± 83.0	36.4 ± 68.9
Sundevall's leaf-nosed bat (*Hipposideros caffer*)	23.6 ± 18.3	15.9 ± 38.0	71.2 ± 72.5	17.9 ± 33.3
Striped leaf-nosed bat (*Macronycteris vittatus*)	0	0	0	0.4 ± 1.7
Greater long-fingered bat (*Miniopterus inflatus*)	0	0.3 ± 1.2	0	0.2 ± 0.7
Natal long-fingered bat (*Miniopterus natalensis*)	2.6 ± 4.3	0.1 ± 0.5	0	1.0 ± 3.8
Cape serotine (*Neoromicia capensis*)	0	70.3 ± 290	0	115 ± 488
Zulu serotine (*Neoromicia zuluensis*)	547 ± 1210	109 ± 275	108 ± 160	149 ± 366
Schlieffen's twilight bat (*Nycticeinops schlieffeni*)	0	194 ± 800	0	357 ± 1510
Egyptian slit-faced bat (*Nycteris thebaica*)	0	0	2.2 ± 4.4	0.1 ± 0.5
Damara horseshoe bat (*Rhinolophus damarensis*)	48.8 ±74.3	11.9 ± 25.2	45.8 ± 98.5	0.6 ± 1.8
Dent's horseshoe bat (*Rhinolophus denti*)	0.6 ± 1.3	1.1 ± 2.3	9.4 ± 13.6	0.4 ± 1.4
Rüppell's horseshoe bat (*Rhinolophus fumigatus*)	0	7.6 ± 25.0	0	2.2 ± 8.5
Roberts's flat-headed bat (*Sauromys petrophilus*)	612 ± 651	325 ± 380	3070 ± 2160	1350 ± 2040
Yellow-bellied house bat (*Scotophilus dinganii*)	0	13.3 ± 51.3	0	2.3 ± 7.4
Egyptian free-tailed bat (*Tadarida aegyptiaca*)	523 ± 1070	71.4 ± 105	1090 ± 1060	495 ± 800

* Significant p-values are indicated in bold.

Table 3. Top model results from generalized linear models describing the relationships between bat community responses (overall activity and species richness), water body type (artificial pools and natural springs), and seasonal interactions with water quality (represented as principal components[a]) and availability (represented as maximum pond area) measured at the conclusion of dry (November 2016 – January 2017) and wet (March – May 2017) seasons in the northern Namib Desert, Namibia.

Response	Family	Predictor[b]	df	Test statistic[c]	p	Estimate (± SE)
Overall bat activity	Quasi-Poisson	Intercept				6.96 (0.40)
		ln(Pond area)	1	9.66	0.0034	0.28 (0.09)
		Water body type: Natural spring	1	18.10	0.0001	-1.52 (0.36)
		Season: Wet	1	12.74	0.0009	0.92 (0.26)
Species richness	Poisson	Intercept				1.62 (0.18)
		PC1	1	4.32	0.038	-0.06 (0.03)
		ln(Pond area)	1	6.48	0.011	0.10 (0.04)
		Water body type: Natural spring	1	6.83	0.009	-0.47(0.18)

[a] Full models included the effects of two principal components: PC1 (weighted with higher measurements of electrical conductivity and larger concentrations of chloride, potassium, sodium, and sulfate) and PC2 (weighted with higher measurements of turbidity, iron, total alkalinity as calcium carbonate, and pH, as well as lower measurements of calcium).

[b] Predictors are all on the log scale.

[c] The test statistic represents either a F test for Quasi-Poisson models or a χ^2 test for Poisson models.

Table 4. Top model results from generalized linear models describing the relationships between species-specific activity, water body type (artificial pools and natural springs), and seasonal interactions with water quality (represented as principal components[a]) and availability (represented as maximum pond area) measured at the conclusion of dry (November 2016 – January 2017) and wet (March – May 2017) seasons in the northern Namib Desert, Namibia.

Response: Species' activity	Family	Predictor[b]	df	Test statistic[c]	p	Estimate (± SE)
Robert's flat-headed bat	Quasi-Poisson	Intercept				4.56 (0.57)
		ln(Pond area)	1	25.28	< 0.001	0.60 (0.13)
		Water body type: Natural spring	1	27.70	< 0.001	-2.51 (0.50)
		Season: Wet	1	20.80	< 0.001	1.47 (0.35)
Egyptian free-tailed bat	Negative binomial	Intercept				4.58 (0.72)
		ln(Pond area)	1	5.33	0.021	0.37 (0.15)
		Water body type: Natural spring	1	13.16	< 0.001	-2.34 (0.68)
		Season: Wet	1	10.93	0.001	1.73 (0.48)
Angolan wing-gland bat	Negative binomial	Intercept				5.06 (0.87)
		ln(Pond area)				0.18 (0.17)
		Season: Wet				3.90 (1.31)
		ln(Pond area) * Season: Wet	1	5.90	0.015	-0.69 (0.25)
Long-tailed serotine	Quasi-Poisson	Intercept				4.93 (0.39)
		Water body type: Natural spring	1	5.14	0.028	-1.00 (0.52)
Zulu serotine	Quasi-Poisson	Intercept				4.91 (0.45)
		PC2	1	5.64	0.022	-0.45 (0.29)
Sundevall's leaf-nosed bat	Negative binomial	Intercept				2.24 (0.73)
		ln(Pond area)	1	6.67	0.010	0.49 (0.16)

	Water body type: Natural spring	1	10.08	0.001	-2.32 (0.72)

[a] Full models included the effects of two principal components: PC1 (weighted with higher measurements of electrical conductivity and larger concentrations of chloride, potassium, sodium, and sulfate) and PC2 (weighted with higher measurements of turbidity, iron, total alkalinity as calcium carbonate, and pH, as well as lower measurements of calcium).

[b] Predictors are all on the log scale.

[c] The test statistic represents either a F test for Quasi-Poisson models or a χ^2 test for negative binomial models.

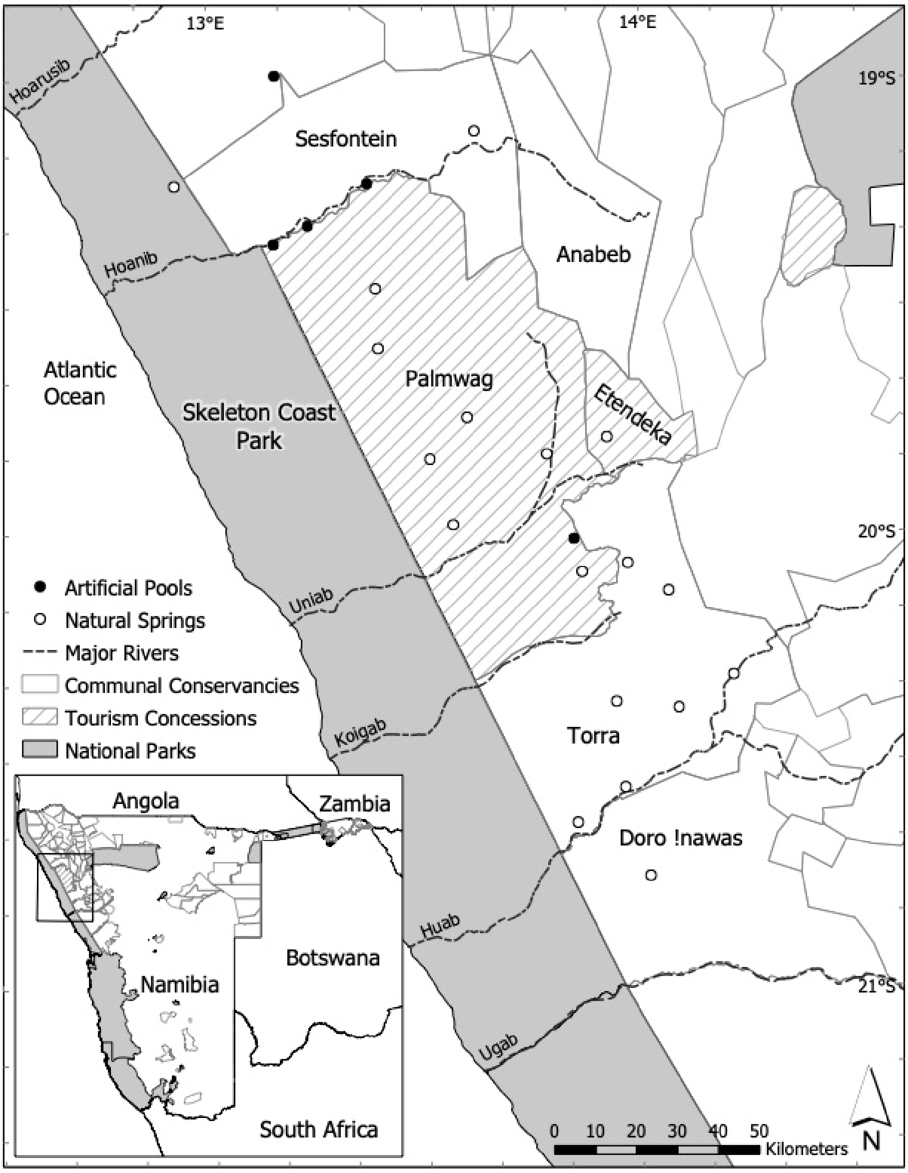

Figure 1. Map of our study area in the northern Namib Desert, Namibia. Closed and open circles represent sampled artificial pools (*n* = 5) and natural springs (*n* = 18), respectively. The minimum straight-line distance between sites was 8.28 km.

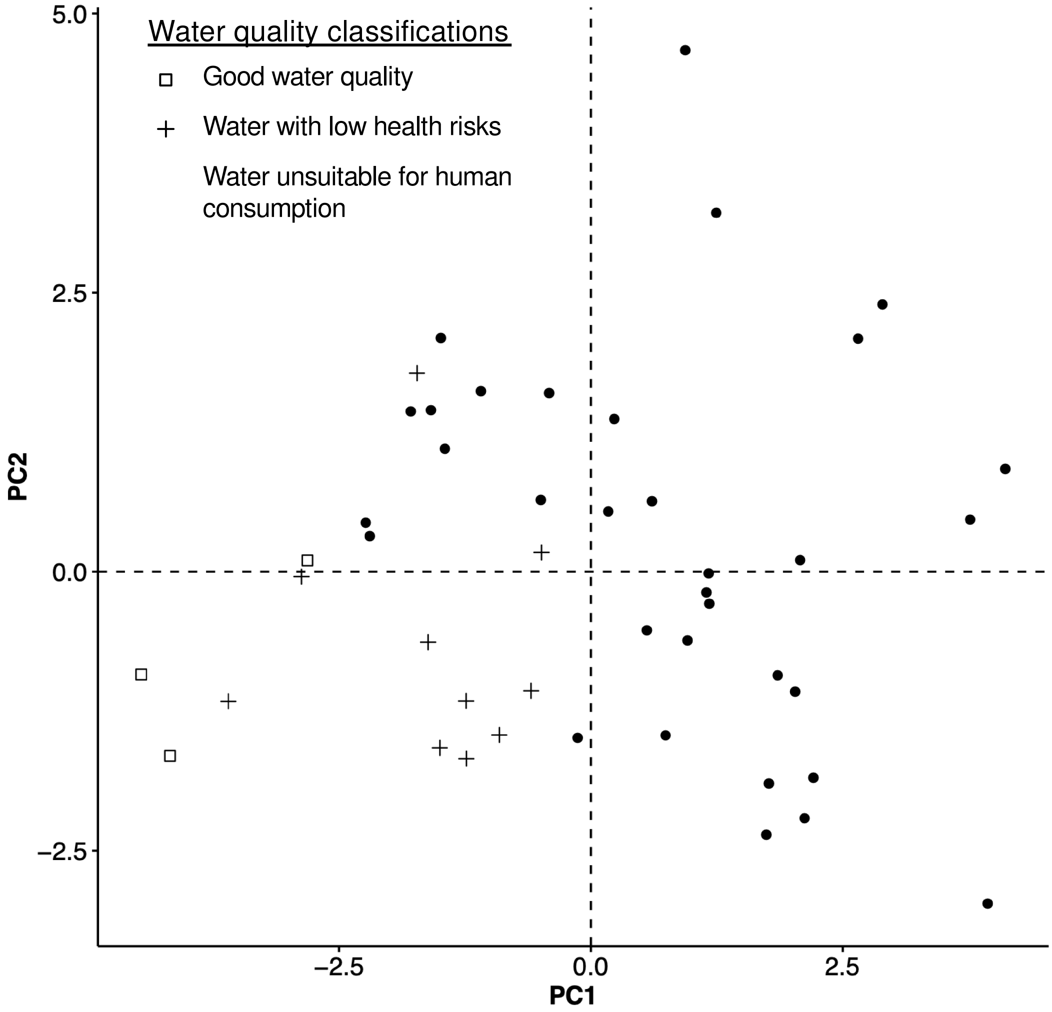

Figure 2. Ordination diagram of the first two axes of the principal component analysis (PCA) for water chemistry across water body types in the northern Namib Desert. Symbols represent overall water quality classifications determined by the Department of Water Affairs (1991). Water samples were collected from artificial pools (*n* = 5) and natural springs (*n* = 18) sampled once at end of the dry season (November 2016 – January 2017) and once at end of the wet season (March – May 2017) for a total of 46 samples. The two axes of the PCA explained 67.8% of the total variation in water quality, with PC1 accounting for 43.2% and PC2 24.6% of the variance. PC1 was highly

weighted with higher measurements of electrical conductivity as well as with greater concentrations of chloride, potassium, sodium, and sulfate. PC2 was weighted with higher measurements of iron, turbidity, total alkalinity as calcium carbonate, and pH, as well as lower measurements of calcium.

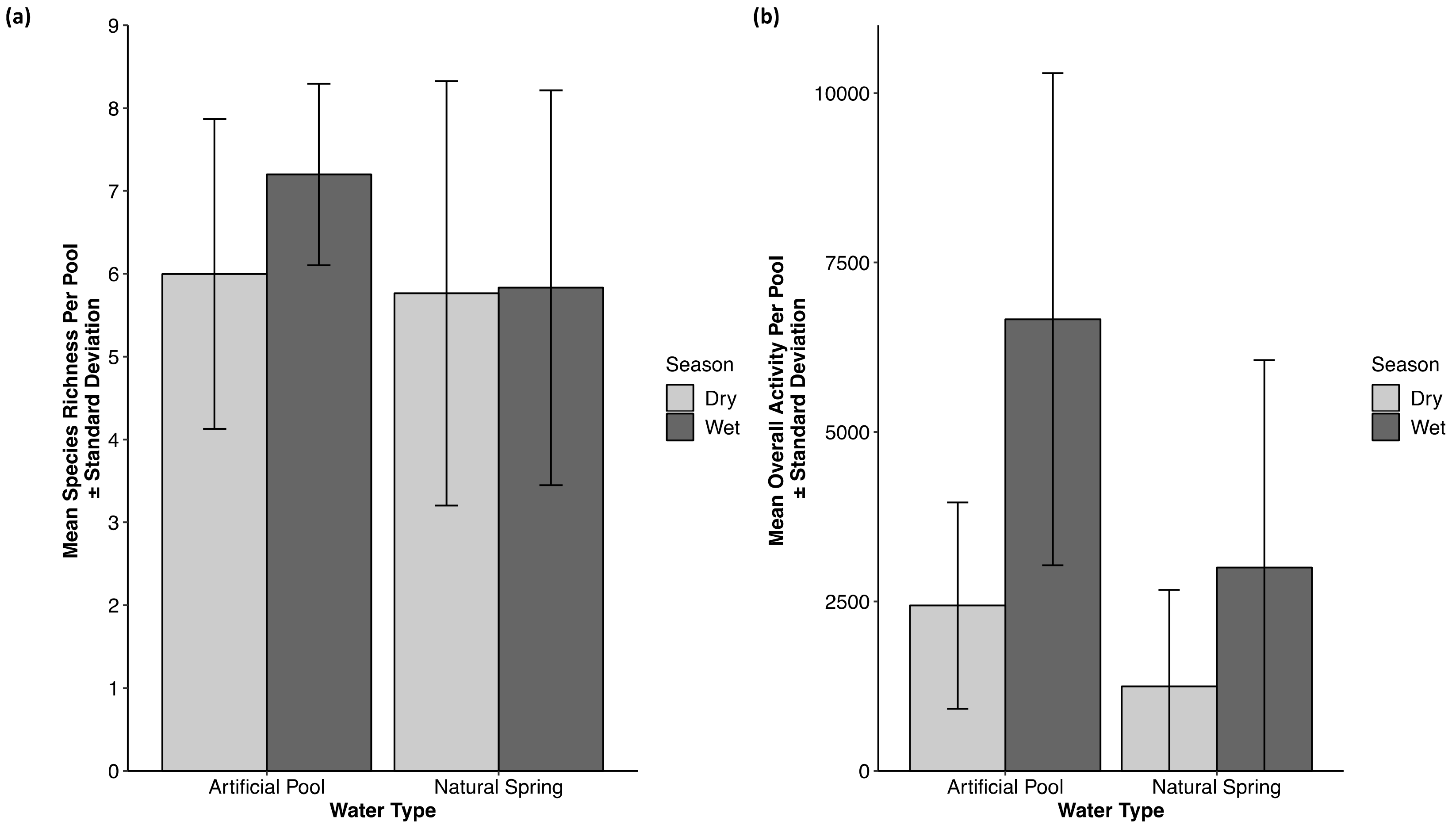

Figure 3. Relationship between a) species richness and b) overall activity per pool (mean ± SD) for bats sampled at artificial pools (*n* = 5) and natural springs (*n* = 18) in the northern Namib Desert. Recordings took place at each site once

at the end of the dry season (light gray bars; November 2016 – January 2017) and once at the end of the wet season (dark gray bars; March – May 2017).