

DISSERTATION

BATS, ELEPHANTS, AND THEIR FOOD: A CONSERVATION PERSPECTIVE ON
TROPHIC INTERACTIONS IN THE NAMIB DESERT

Submitted by

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ABSTRACT

BATS, ELEPHANTS, AND THEIR FOOD: A CONSERVATION PERSPECTIVE ON TROPHIC INTERACTIONS IN THE NAMIB DESERT

Deserts are often seen as relatively simple ecosystems characterized by low productivity and species richness. Rarely are they considered bastions of biodiversity. Nevertheless, desert ecosystems harbor six percent of the global human population, and a surprising number of unique species adapted to these harsh and highly variable environments that cover 17% of Earth's terrestrial surface. Bats are one of the most diverse and successful groups of mammals in deserts. Relative to their body size, they travel large distances (e.g., several kilometers) and consume vast quantities of insects (e.g., up to 100% of their body weight) each night. Despite their recognized importance in community ecology, many aspects of basic bat biology, including interspecific interactions with closely and distantly related taxa, remain unknown due to the difficulties of studying nocturnal, volant organisms. My dissertation contributes to addressing these gaps by quantifying abiotic and biotic drivers of bat distributions and activity patterns in the Namib Desert of northwestern Namibia, and documenting the perceived challenges and proposed solutions to living with wildlife in this ecosystem held by local pastoralists.

The Namib is considered to be one of the world's oldest deserts, with evidence suggesting a semi-arid or drier state persisting for at least the last 80 million years. Perhaps owing to this antiquity and historical stability, the desert – and its northern

Kaoko escarpment in particular – is considered to be the most important hotspot for endemic and near-endemic flora and fauna in Namibia and Angola, with the majority of regional vertebrate taxa represented. While temperature and rainfall fundamentally limit the population sizes and distributions of species in this hot, dry desert, the interplay between biotic and abiotic factors in shaping species distributions remains unclear for many taxonomic groups.

Water abundance, flow, and quality are known as key elements affecting species distributions in arid environments, yet how exactly they interact to structure specific animal communities is often unclear. In Chapter 1, we examined relationships between bodies of water and bat communities in the Namib Desert, and explored whether these flying mammals may serve as new bioindicators of water quality. 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 field work at the terminus hot, dry season from November 2016 to January 2017 and at the conclusion of the 2017 wet season from March to May 2017, collecting water samples and acoustic recordings of bat activity at both natural springs and artificial pools. Bat species richness and overall activity increased during the wet season, but variations in water quality were not predicted by neither seasonality nor water body type. Bat distributions showed only modest association with water quality. Although individual artificial pools harbored a greater number of species and activity, more than 35% of the species we recorded were present only at natural springs. While particular bat species (rather than the entire bat community as a whole) may still be

useful water quality indicators, other factors (e.g., roost and prey availability) requiring further investigation likely also affect the distributions of Namib Desert bats.

In extreme desert environments, temperature and precipitation (i.e., abiotic factors) are expected to be the main forces responsible for structuring ecological communities, and the role of biotic interactions are often thought to be minimal. The uneven distribution of resources in arid landscapes, however, causes many species to cluster around limiting features like surface water, particularly during the dry season. In Chapter 2, we investigated how large mammalian herbivores (i.e., elephants, black rhinoceros, and giraffe), may modulate insectivorous Namib Desert bat communities. In addition to the acoustic data analyzed in Chapter 1 describing bat communities, we estimated megaherbivore use of sites using dung transects, and vegetation productivity around bodies of water using satellite measurements of Normalized Difference Vegetation Index (NDVI). We designed structural equation models to test for direct and indirect (i.e., mediated through NDVI) effects of megaherbivores on bat species richness and activity in both the dry (November 2016 – January 2017) and wet (February – May 2017) seasons. We found site-level megaherbivore use to be positively associated with bat activity and species richness through direct and indirect pathways, respectively, in the dry season. During the wet season when resources were more abundant, however, these effects were insignificant. Our results not only indicate that biotic interactions can contribute to species distributions in desert habitats, but also suggest that the conservation of megaherbivores in the Namib Desert may directly and indirectly benefit insectivorous bat abundance and diversity.

Understanding how organisms relate to one another and to their physical surroundings is important for facilitating ecological knowledge, but only sometimes aids in the conservation of these species. The protection of large mammals, for example, does not come without conflict for the people living among these species. People's values, attitudes, and behaviors toward wildlife not only contribute to the severity of human-wildlife conflicts, but also shape how people respond these problems. Therefore, we sought to not only understand species richness and distribution patterns of small and large mammals in the northern Namib Desert, but also the frequency and types of interactions of local pastoralists with these species.

Integrating social and ecological knowledge is key to finding solutions to human-wildlife conflicts and other global conservation problems, but gathering the requisite data has often proved difficult. Social-ecological systems models have also traditionally overlooked how individual human thought and behavior that can affect the success of management interventions. In response to these challenges, Chapter 3 drew upon psychological theory and long-term ecological data on wildlife populations and conflict occurrence to conduct qualitative research on pastoralists' values toward wildlife in the northern Namib Desert. We explored how values and ecological conditions shaped individuals' interactions with and tolerance of species, and their perceptions of challenges and potential solutions to living with wildlife. Semi-structured interview data revealed a prevailing domination value orientation toward wildlife, reflected in concerns for human and livestock wellbeing. Despite these concerns and high rates of reported conflicts, pastoralists were generally tolerant of predators and other wildlife, and offered a variety proposed management solutions. In addition to its practical implications for

informing human-wildlife coexistence strategies in the Namibian context, our approach advances knowledge about wildlife values globally, offers insights on the utility of qualitative assessments for cross-cultural social-ecological systems research, and furthers our understanding of conservation challenges and opportunities in extreme arid environments.

In sum, our research resulted in key ecological, theoretical, and applied insights for desert mammal conservation. First, bat species richness and overall activity differed by season, but were largely unrelated to variations in water quality across our study area. Bat distributions are likely determined by other factors, such as roost and prey availability, in addition to water quality. Second, bat species richness and overall activity positively related to megaherbivore use at our sites, but only during the dry season. This supports the theory that the strength of biotic interactions in structuring desert communities is strongest when resources are most limited. Lastly, we determined that pastoralists value interactions with large mammals despite their threats to human and livestock safety. By having local pastoralists describe and identify the greatest challenges and potential solutions to living with wildlife, our findings should indicate which management practices have the strongest public support, benefiting the conservation of the Namib's unique wildlife.

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CHAPTER 1

ARE BATS SEEKING OUT CLEAN WATER? A PERSPECTIVE FROM THE NAMIB DESERT

Introduction

Deserts are rarely considered bastions of biodiversity due to limited rainfall, low primary production, and resultant low standing biomass. Arid environments, however, often harbor a surprising number of unique species (Safriel et al. 2005; Durant et al. 2012). Deserts cover only 17% of the world's land mass yet are utilized by 25% of all terrestrial vertebrate species (Millenium Ecosystem Assessment 2005) as well as 6% of the global human population. Water plays an important role in structuring desert communities (Noy-Meir 1974), and precipitation totals – while low on average – show extreme inter-annual variation (von Wehrden et al. 2010). Desert mammal distributions and behaviors (e.g., well digging by elephants; Ramey et al. 2013) are strongly affected by 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 recognized as global biodiversity hotspots (Brown & Ernest 2002; Bogan et al. 2014; Davis et al. 2017). Herein is this challenge – both abiotic factors and humans and their livestock intercede strongly in affecting extant biological diversity and nowhere is this clearer than in deserts.

Bodies of water vary in chemistry and 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 research rarely do we understand the effects of water quality and chemistry on species richness. Desert waters can sometimes be unsuitable for wildlife consumption (Broyles 1995), and in extreme circumstances can lead to heavy metal or toxin bioaccumulation in (e.g., Ratcliffe 1967; Olsson et al. 1998) or even poisoning of (e.g., cyanide poisoning and cyanobacteria blooms; Koenig 2000; Stewart et al. 2008) wildlife and livestock. Species differ, however, in their sensitivity to water quality. Aquatic invertebrates, fish, and amphibians have been traditionally used as indicators of freshwater quality, particularly in mesic habitats (Innis et al. 2000). Since surface water is rare and widely-dispersed in deserts such as the Kalahari and the Namib in southern Africa (Durant et al. 2012), more mobile species (e.g., flying mammals) may be additional and perhaps more useful bioindicators in arid landscapes provided they are sufficiently sensitive to water quality. The enhanced ability of these species to move across the landscape can provide information not only about water quality of individual water sources, but also about the use of and connectivity among dispersed sources. We ask if the distributions of bats across the landscape relate to differences in water quality in arid environments.

Bats account for approximately 20% of the world's mammals (Voigt & Kingston 2016), and comprise one of the most diverse and successful groups of mammals living in deserts (Carpenter 1969). Although flying bats have high mobility and dispersal ability, their small body sizes and high metabolic rates suggest that local distributions are driven by microhabitat features, such as the availability of water and insect prey. Insectivorous bats in arid environments can lose relatively large amounts of water (e.g.,

15-31% of body mass) daily through evaporation (Studier 1970; Webb 1995).

Unsurprisingly, desert bat activity is typically highest around water, where bats replenish those losses through direct water consumption (Kurta et al. 1990; McLean & Speakman 1999) and indirectly through feeding (Adams & Thibault 2006; Rebelo & Brito 2007; Korine et al. 2015). Bats may also supplement nutrient deficiencies by drinking from bodies of water rich in dissolved ions and minerals (e.g., calcium; Adams et al. 2003), which can be particularly important for reproductive individuals. In the Negev Desert in Israel, studies 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 (McCain 2007). This effect of water quality on bat species distributions remains debated in published literature, particularly in desert ecosystems (Korine et al. 2015, 2016).

Our study aims to better understand spatial relationships among the distribution of bat species, water availability, and water quality in one of the world's oldest deserts, the Namib in southern Africa (Ward et al. 1983; Frossard et al. 2015). More specifically, we test the hypothesis that bat distributions are driven by differences in water quality between artificial pools and natural springs during both dry and wet seasons. We predicted poorer water quality (i.e., higher electrical conductivity and ion concentration indices) would occur during the dry season and at artificial pools, and that bat species richness and activity would be lower at these sites as a result. Such a relationship, if present, would suggest that bats may serve as additional mammalian indicators of

water quality in desert landscapes where systematic sampling of individual bodies of water is difficult.

Methods

Study Area

Our study area was in the northern Namib Desert, specifically the Kunene Region of Namibia (Fig. 1.1). 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). While mean annual rainfall exceeds 300 mm in the eastern headwater regions within these catchments, it declines to near zero in the west where the rivers meet the Atlantic Ocean (Berger 1997; Jacobson & 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; Leggett et al. 2001; Jacobson & Jacobson 2013).

Water Sampling

We sampled water quality and volume at 23 permanent bodies of open water including both artificial pools ($n = 5$) and natural springs ($n = 18$; Fig. 1.1; Appendix 1.1) at the end of the 2016 dry season (21 November 2016 – 21 January 2017) and 2017 wet season (16 March 2017 – 16 May 2017). Each site was sampled twice, once during each season. Following Razgour et al. (2010), we estimated water availability by measuring the maximum length, width, and depth of each body of water and then

multiplying these three metrics to calculate an index of maximum pond volume. Just prior sunset each night, we collected a one-liter water sample per site for subsequent standard water quality laboratory analysis. 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 until their delivery to the Analytical Laboratory Services in Windhoek, Namibia for analysis within three weeks of collection.

The standard water quality analysis kit measured several commonly-used water quality indicators including pH, electrical conductivity, turbidity, total dissolved solids (TDS), and total alkalinity as 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, which was only evaluated during our wet season sampling, consisted of 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 1.2; Olsen et al. 2012). We used these indices to estimate general differences in water quality between the two water body types and tested for seasonal differences as described in the Statistical Analysis section below.

Surveying Bat Communities

We deployed an ultrasonic bat detector (Song Meter SM4BAT FS, Wildlife Acoustics) to monitor activity during the nights on which water sampling was conducted (i.e., the bat community at each site was sampled once in the dry season and once in the wet season). 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. 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).

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 calls in each of the clusters to classify the species present based on a set of calls that we tagged and recorded from bats physically captured and identified over different sampling periods at the same sites. Calls were also compared to those provided in the field guide by Monadjem et al. (2010). 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. Species richness was defined as the total number of species recorded within a night at each site.

Statistical Analysis

To test for seasonal effects, we analyzed patterns in water chemistry using only the standard water quality analysis kit's results (i.e., not the heavy metal analysis) because these data were collected over both sampling periods. We further excluded Mn^{2+} , NO_3^- , and NO_2^- from our analyses because these ions were not detected in approximately half of our samples. We also ignored TDS because its measurements were highly correlated with electrical conductivity (Pearson correlation, $r = 0.9992$). 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 and overall bat activity with a cube root transformation (Olsen et al. 2012). Both F^- and Mg^{2+} still did not fit a normal distribution after the natural log transformation, so we also excluded these measurements from our subsequent analyses.

We tested all of our remaining normally-distributed data for differences between artificial and natural bodies of water as well as between wet and dry seasons using principal components analysis (PCA) with the *PCA* function in the FactoMineR package (Le et al. 2008), and discriminant function analysis (DFA) with the *lda* function in the MASS package (Venables & Ripley 2002). We used multivariate analysis of variance (MANOVA) with the *manova* function in the stats package to compare all water chemistry and, separately, overall bat activity and species richness across the different water body types and seasons. We also tested for interactions between water body type and season. We conducted *post hoc* analysis of variance (ANOVA) to verify all significant differences identified by the MANOVA test.

Further, we used the Kruskal-Wallis test (*kruskal.test* in R) to compare activity within species at different water body types across seasons. For all significant Kruskal-Wallis results, we used the Conover-Iman test (*conover.test* in package *conover.test*; Dinno 2017) as *post hoc* tests with the Benjamini-Hochberg adjustment for multiple comparisons (Benjamini & Hochberg 1995).

Lastly, we applied non-metric multidimensional scaling (NMDS) ordination of the bat community data (presence/absence) from both seasons in two dimensions (*metaMDS* in package *vegan*; Oksanen et al. 2013) with Bray-Curtis dissimilarity distances. Using *envfit* in package *vegan* based on 5000 permutations, we fit vectors for maximum water volume and water chemistry variables without any transformations to the NMDS of the bat community data and plotted the vectors of correlated variables in which $p \leq 0.1$. Since we conducted additional water quality sampling in the wet season, we also investigated how observed wet season bat activity and species richness patterns were related to this larger suite of water chemistry variables (i.e., including all heavy metal analysis variables excluding those that were undetected – Cd^{2+} , Co^{2+} , Cr^{3+} , Cu^{2+} , Pb^{2+} , Ni^{2+} , and Zn^{2+}) in a separate NMDS ordination with maximum water volume and water quality variables again fit with *envfit* based on 5000 permutations (vectors plotted when $p \leq 0.1$). All statistical analyses were done in R (R Core Team 2017) with $\alpha = 0.05$ unless otherwise noted.

Results

Variation in Water Quality

We attempted to distinguish differences in water chemistry between natural and artificial bodies of water based on two PC scores, which together explained 59.5% of

the variance. PC1 accounted for 39.6% of the variance, PC2 22.6%, and PC3 11.3% of the variance (eigenvalues = 4.35, 2.49, and 1.24, respectively). PC1 was highly weighted with higher measurements of electrical conductivity as well as with greater concentrations of Na^+ , Cl^- , K^+ , and SO_4^{2-} (Table 1.1). PC2 was weighted with higher measurements of Fe^{3+} , turbidity, total alkalinity as CaCO_3 , and pH, as well as lower measurements of Ca^{2+} . PC3 was primarily weighted with higher maximum pond volume measurements. Artificial pools were generally distributed at the lower range of PC2 (i.e., lower iron and calcium concentrations) and upper range of PC1 (i.e., higher salt concentrations), while natural springs were more often found at the lower range of PC1 (i.e., lower salt concentrations; Fig. 1.2). DFA leave-one-out cross-validation, however, correctly classified 0% of artificial and 88.9% of natural springs, indicating that water body type was not easily distinguished among our samples despite the differences indicated by the PCA. This could be due to the low sample sizes of artificial pools ($n = 5$) relative to natural springs ($n = 18$), and hence low power to detect differences between water body types. Or, this result might stem from underlying differences between river catchments (e.g., differences in geology or groundwater quality) not tested by our study.

We were unable to detect differences in water chemistry between wet and dry seasons, as their distributions largely overlapped on PCA plot (Fig. 1.2). Similarly, we could not distinguish between seasons using DFA leave-one-out cross-validation, correctly categorizing only 56.5% and 65.2% of dry and wet season samples, respectively.

Results from the MANOVA indicated that certain water chemistry variables used in the PCA described above differed significantly for season ($p = 0.0023$) and water body type ($p = 0.0013$), but the interaction between water type and season was insignificant ($p = 0.59$). Using *post hoc* ANOVA, we determined concentrations of K^+ and SO_4^{2-} were significantly higher at artificial pools (K^+ : $p = 0.0046$; SO_4^{2-} : $p = 0.022$), and concentrations of Fe^{3+} were higher in the dry season ($p = 0.0002$).

Bat Species Richness and Activity

We recorded a total of 120,749 bat passes among 16 different species during our 46 nights of sampling. Bats were detected at all sampling sessions at all sites except one (i.e., we did not record any bats at Ganias, a natural spring, during the dry season). Across all sites, 14 species of bats were detected during the dry season, while 16 species were found during the wet season. Using a MANOVA test, we found that both species richness and overall activity of bats differed between water body type ($p = 0.0158$) and season ($p = 0.0165$), with no significant interaction between water body type and season ($p = 0.785$). On average, we recorded 6.00 ± 1.87 (mean $\pm$ SD) bat species and 2440 ± 1520 bat passes at each artificial pool during the dry season, and 5.76 ± 2.56 species and 1250 ± 1420 passes at each natural spring (Fig. 1.3). During the wet season, we recorded 7.20 ± 1.10 bat species and 6660 ± 3630 bat passes at each artificial pool, and 5.83 ± 2.38 species and 3000 ± 3060 passes at each natural spring (Fig. 1.3).

With respect to activity, species differed between seasons and/or water body types for three of the 16 species (Table 1.2) – Sundevall's leaf-nosed bat *Hipposideros caffer* ($p = 0.0159$), the Egyptian slit-faced bat *Nycteris thebaica* ($p = 0.0163$), and the

Egyptian free-tailed bat *Tadarida aegyptiaca* ($p = 0.0102$). Specifically, Sundevall's leaf-nosed bat was more active at artificial pools, the Egyptian slit-faced bat was only detected in the wet season (although the activity of this species may have been underestimated due to the whispering nature of their echolocation calls), and the Egyptian free-tailed bat was more active in the wet season than dry season. There was suggestive, but inconclusive evidence of a difference between seasons and/or water body types for three additional species ($p \leq 0.1$). The long-tailed serotine *Eptesicus hottentotus* ($p = 0.0872$) was more active at artificial pools in the wet season than at natural springs during both seasons. Dent's horseshoe bat *Rhinolophus denti* ($p = 0.0889$) was most active artificial pools in the wet season as was Roberts's flat-headed bat *Sauromys petrophilus* ($p = 0.0607$). Six species were only detected at natural springs: the striped leaf-nosed bat *Hipposideros vittatus* (only recorded on one night of sampling), the greater long-fingered bat *Miniopterus inflatus*, the Cape serotine *Neoromicia capensis*, Schlieffen's twilight bat *Nycticeinops schlieffeni*, Rüppell's horseshoe bat *Rhinolophus fumigatus*, and the yellow-bellied house bat *Scotophilus dinganii*.

With data pooled across both seasons, we found some degree of partitioning among bat species through the NMDS analysis (stress = 0.126; Fig. 1.4). Roberts's flat-headed bat, the Egyptian free-tailed bat, and the Angolan wing-gland bat *Cistugo seabrae* were located at the center of the NMDS plots as they were the most ubiquitous species across the study area, regardless of season or water body type (Table 1.2). In contrast, Schlieffen's twilight bat and the Cape serotine were only present at a single spring (Sesfontein) during both seasons, and the striped leaf-nosed bat only at a single

spring (Fonteine) during the wet season; hence, these species fall at the periphery of the NMDS plot, and roughly orthogonal to each other (i.e., they fall ~90 degrees away from each other relative to the central cluster of results). Of the 16 water quality variables and maximum water volume estimates that we measured in both seasons (i.e., all standard analysis kit variables excluding TDS due to its strong correlation with electrical conductivity), only Mn^{2+} and season were correlated ($p \leq 0.1$) with the two-dimensional species spaces (Fig. 1.4; Appendix 1.3). The distributions of the Angolan wing-gland bat, Sundevall's leaf-nosed bat, and the Damara horseshoe bat *Rhinolophus damarensis* were associated with higher concentrations of Mn^{2+} .

To study how heavy metal concentrations may affect bat distributions, we also examined the bat community and broader water quality variables collected during the wet season only. When fitting these water quality data onto an ordination plot, electrical conductivity, Na^+ , Cl^- , K^+ , Ca^{2+} , and Sr^{2+} all correlated ($p \leq 0.1$) with the two-dimensional species spaces (NMDS stress = 0.074; Fig. 1.5; Appendix 1.4), and individually explained variation in the bat community data fairly well ($r^2 \geq 23\%$). These ions tended to correlate with one another across the wet season sites, hence their vectors almost perfectly overlap on the NMDS plot (Fig. 1.5). The distributions of yellow-bellied house bat and Rüppell's horseshoe bat, in particular, were associated with higher concentrations of salts, K^+ , Ca^{2+} , and Sr^{2+} . Most other species were associated with lower concentrations of these ions (Fig. 1.5)

Discussion

Water Quality of Artificial Pools Relative to Natural Springs

The provisioning of artificial water points in arid regions as a conservation tactic has historically been controversial due to concerns over environmental degradation and the exclusion of wildlife from surrounding areas due to increased human and livestock use (Du Toit & Cumming 1999; O'Brien et al. 2006). The remoteness and erratic grazing availability in this region of Namibia may limit, however, the expansion of human settlements and livestock distributions and minimize such risks (Leggett et al. 2004; Leggett 2006a; Lavery et al. 2019). Large differences in water quality were measured across the water bodies in our study area (Fig. 1.2), but surprisingly these differences were only minimally affected by the factors we investigated (i.e., water body type and season). Our inferences, however, may be limited by the small sample size of artificial pools examined ($n = 5$) and thus the relationship between water body type and water quality deserves further investigation. Artificial pools were constructed in the northern Namib Desert by the government of Namibia and tourism operations to supplement wildlife populations with water sources away from human settlements (Leggett 2006), which limits the risk of degradation of water quality from anthropogenic pollution. The water chemistry of artificial pools most closely resembled that of nearby natural springs, which suggests that broader spatial differences in water quality may be due to differences in the underlying geology or groundwater quality at the scale of river catchments.

Are Bats Seeking Out Clean Water?

Bat activity and species richness differed by water body type and season. We observed higher species richness and much greater activity levels during the wet season, which may be indicative of seasonality in species' occupancy and/or their

overall activity levels. In addition, individual artificial pools, on average, supported higher species richness and overall bat activity than natural springs. However, six of the 16 recorded bat species were only detected at natural springs. Due to our small sample sizes (artificial pools, $n = 5$; natural springs, $n = 18$), we are unable to determine if these species avoided artificial pools or if their absence at these pools was due to other factors, such as the distance of these waterholes from bat roosts.

Other studies investigating the role of water quality on bat communities over natural and artificial bodies have focused on wastewater treatment pools or around large urban centers (Naidoo et al. 2013; Korine et al. 2015; Straka et al. 2016; Li & Kalcounis-Rueppell 2018), where water quality differences exist and negatively affect the activity of sensitive bat species. While our sample sizes limited our ability to detect differences, water chemistry only showed minimal differences between artificial pools and natural springs in our study region, and water quality effects on bat activity and species richness were similarly subtle. Several factors (Mn^{2+} , Na^+ , Cl^- , K^+ , Ca^{2+} , Sr^{2+} , and electrical conductivity) were consistently correlated with bat communities across sites as indicated by the NMDS analyses. Contrary to previous expectation (Griffiths et al. 2014), we did not find that bats avoided saline bodies of water. In particular, Roberts's flat-headed bat and the Egyptian free-tailed bat – two of our most ubiquitous species – were most active over sites with Cl^- concentrations above 9000 mg/L and used these sites for drinking. These concentrations were above the recommended maximum chloride concentration for human consumption of 1200 mg/L recommended by the Namibian Department of Water Affairs (1991). The concentration of Ca^{2+} , which is limiting in other arid regions and affects the spatial distributions of insectivorous bats

(Barclay 1994; Adams et al. 2003), was relatively high – and thus accessible – in the Namib Desert (Table 1.1). Namib Desert bats likely do not need to alter their distributions to obtain this resource.

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? Obviously, 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; Razgour et al. 2011; Hagen & Sabo 2014). Ironically, the yellow-bellied house bat was almost exclusively recorded at sites disassociated with human settlements. In contrast, two species – the Cape serotine and Schlieffen's twilight bat – appeared to limit use of water by restricting activities near human settlements on the more mesic eastern extremities of our study area. This suggests these species do not tolerate extreme arid conditions, but may instead rely on human settlements for reliable access to water, roosts, and/or prey. We did not find the size of water bodies (estimated herein as maximum pond volume) to associate with species richness as was found in other studies (e.g., Razgour et al. 2010). The size of water bodies may yet be an important predictor of the probability of bats drinking at a site, particularly for fast-flying species (e.g., free-tailed bats, including Roberts's flat-headed bat and the Egyptian free-tailed bat) that require larger sloop zones (i.e., larger surface areas) to drink on the wing (Tuttle et al. 2006). However, bats may visit bodies of water and not drink there, so their presence at a site could be misinterpreted to mean that they drink water from a larger range of pond volumes than in fact are used. Future studies should address the

importance of water bodies 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).

The primary purpose of artificial pools in the Namib Desert has not been for bats, per se, but these pools individually harbored bat diversity similar to that found at natural springs despite their distance from human settlements. This was contrary to our expectations. We originally predicted that fewer bats would use natural springs due to their homogeneity in shape, size, water chemistry, and vegetation cover relative to that of natural springs. Clutter foragers and gleaning bats, in particular, may benefit from the habitat complexity surrounding natural springs. As such, the construction of artificial pools – at least in the Namib Desert where these pools were designed to attract wildlife populations – were not expected to benefit certain guilds of bat biodiversity. Human-constructed pools were thought to favor generalist bat species or open-air foragers rather than specialists or clutter or edge foragers (Lisón & Calvo 2011). However, we note that higher activity levels of the Namib Desert endemic Angolan wing-gland bat, a clutter-edge forager (Monadjem et al. 2010), occurred at artificial pools. This suggests these synthetic pools do play some role in bat conservation and function to provide habitat for needs beyond those related to foraging.

Conservation Implications and Future Work

Life in deserts clusters around rare and often isolated bodies of water. In the face of increasing rainfall variability predicted with climate change, understanding the roles that water availability, water quality, and the vegetation structure around water sources

play in structuring mammal communities in arid ecosystems is essential to biodiversity conservation. If we can untangle the underlying mechanisms and then identify reliable bioindicators, it may be possible to prioritize the protection of specific bodies of water for bat and broader biodiversity conservation.

Our study builds upon the work of others who also investigated the relationships between bat communities and water availability and quality in other deserts (e.g., the Negev in Israel, Razgour et al. 2010; Korine et al. 2015). Similar to the findings of Korine et al. (2015) in the Negev Desert, we found community measurements of species richness and overall activity to be poorly correlated with water quality in the Namib Desert, but that activity levels of specific species were restricted to particular natural springs. Due to the complexity of water quality measurements (i.e., using the concentrations of many ions as indices of water quality) and studying a relatively unknown bat community, future research should focus on increasing the spatial and temporal sampling of both water quality and bat communities to gain a better understanding of the seasonal abiotic drivers of bat distributions. While bats may be useful predictors of environmental conditions (Jones et al. 2009), species most dependent on water quality will likely vary by geographic location. Therefore, any use of bats as bioindicators will require more species-specific research. By better characterizing bat species compositions across this previously-unstudied region, we hope that this work contributes a solid foundation for such future studies.

Table 1.1. Mean ($\pm$ 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 Namib Desert, Namibia.

Variable ^a	Dry Season		Wet Season		PC loadings ^b		
	Artificial Pools (<i>n</i> = 5)	Natural Springs (<i>n</i> = 18)	Artificial Pools (<i>n</i> = 5)	Natural Springs (<i>n</i> = 18)	PC 1	PC 2	PC 3
Maximum water volume	7.1 $\pm$ 5.0	247.4 $\pm$ 546.7	10.9 $\pm$ 9.2	154.2 $\pm$ 302.9	- 0.220	0.202	0.841
<i>Standard Analysis Kit</i>							
pH	7.7 $\pm$ 0.3	8.1 $\pm$ 0.5	8.0 $\pm$ 0.9	8.1 $\pm$ 0.5	0.327	0.584	0.460
Electrical conductivity (mS/m)	456.8 $\pm$ 140.3	558.3 $\pm$ 721.1	891.3 $\pm$ 825.6	860.5 $\pm$ 1273.6	0.966	-0.112	0.107
Turbidity (NTU)	3.4 $\pm$ 3.0	27.6 $\pm$ 38.1	8.8 $\pm$ 5.7	44.8 $\pm$ 122.5	0.176	0.687	-0.087
Total dissolved solids (determined)	2777.1 $\pm$ 837.9	3458.9 $\pm$ 4530.1	5971.4 $\pm$ 5531.3	5765.5 $\pm$ 8533.0	-	-	-
Total alkalinity as CaCO ₃	403.0 $\pm$ 118.0	469.6 $\pm$ 426.4	471.2 $\pm$ 381.2	477.2 $\pm$ 607.7	0.307	0.673	0.107
Calcium (Ca ²⁺)	107.0 $\pm$ 36.6	84.5 $\pm$ 81.5	76.0 $\pm$ 59.5	144.6 $\pm$ 223.1	0.394	-0.787	0.077
Chloride (Cl ⁻)	901.0 $\pm$ 282.9	1370.9 $\pm$ 2270.4	2297.0 $\pm$ 2343.0	2519.5 $\pm$ 4628.1	0.954	-0.172	0.045
Fluoride (F ⁻)	1.4 $\pm$ 0.2	2.0 $\pm$ 1.5	1.4 $\pm$ 0.8	2.2 $\pm$ 2.4	-	-	-
Iron (Fe ³⁺)	0.24 $\pm$ 0.22	1.17 $\pm$ 1.73	0.08 $\pm$ 0.15	0.18 $\pm$ 0.42	- 0.052	0.705	-0.499
Sulfate (SO ₄ ²⁻)	568.2 $\pm$ 289.6	432.3 $\pm$ 531.0	1423.8 $\pm$ 1842.7	288.7 $\pm$ 347.0	0.673	0.137	-0.147
Magnesium (Mg ²⁺)	105.6 $\pm$ 39.2	92.5 $\pm$ 107.9	189.8 $\pm$ 194.5	86.6 $\pm$ 90.6	-	-	-
Manganese (Mn ²⁺)	0.02 $\pm$ 0.02	0.04 $\pm$ 0.05	0.05 $\pm$ 0.08	0.01 $\pm$ 0.01	-	-	-
Nitrate (NO ₃ ⁻)	6.5 $\pm$ 12.2	5.9 $\pm$ 8.7	1.6 $\pm$ 2.4	7.4 $\pm$ 9.6	-	-	-
Nitrite (NO ₂ ⁻)	0.40 $\pm$ 0.69	0.07 $\pm$ 0.11	0.37 $\pm$ 0.80	0.24 $\pm$ 0.31	-	-	-
Potassium (K ⁺)	38.9 $\pm$ 22.1	14.1 $\pm$ 19.0	86.5 $\pm$ 79.6	27.7 $\pm$ 61.9	0.831	-0.015	-0.099

Sodium (Na ⁺)	708.6 ± 290.2	1079.2 ± 1612.6	1791.8 ± 2083.8	1577.7 ± 2447.0	0.964	0.067	-0.004
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Heavy Metal Analysis

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	-	-	-

^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.

Table 1.2. Bat activity (mean passes per night $\pm$ 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 Namib Desert, Namibia. Kruskal-Wallis tests were used to compare activity within species at different water body types across seasons.

Species	Dry Season		Wet Season		Kruskal-Wallis test		
	Artificial Pools (<i>n</i> = 5)	Natural Springs (<i>n</i> = 18)	Artificial Pools (<i>n</i> = 5)	Natural Springs (<i>n</i> = 18)	χ^2	df	<i>p</i> *
<i>Cistugo seabrae</i>	515 $\pm$ 420	360 $\pm$ 421	2160 $\pm$ 1900	474 $\pm$ 736	4.07	3	0.254
<i>Eptesicus hottentotus</i>	167 $\pm$ 203	69.0 $\pm$ 139	110 $\pm$ 83.0	36.4 $\pm$ 68.9	6.56	3	0.0872
<i>Hipposideros caffer</i>	23.6 $\pm$ 18.3	15.9 $\pm$ 38.0	71.2 $\pm$ 72.5	17.9 $\pm$ 33.3	10.3	3	0.0159
<i>Hipposideros vittatus</i>	-	-	-	0.4 $\pm$ 1.7	1.50	3	0.683
<i>Miniopterus inflatus</i>	-	0.3 $\pm$ 1.2	-	0.2 $\pm$ 0.7	0.591	3	0.898
<i>Miniopterus natalensis</i>	2.6 $\pm$ 4.3	0.1 $\pm$ 0.5	-	1.0 $\pm$ 3.8	5.10	3	0.164
<i>Neoromicia capensis</i>	-	70.3 $\pm$ 290	-	115 $\pm$ 488	0.585	3	0.900
<i>Neoromicia zuluensis</i>	547 $\pm$ 1210	109 $\pm$ 275	108 $\pm$ 160	149 $\pm$ 366	1.31	3	0.727
<i>Nycticeinops schlieffeni</i>	-	194 $\pm$ 800	-	357 $\pm$ 1510	0.584	3	0.900
<i>Nycteris thebaica</i>	-	-	2.2 $\pm$ 4.4	0.1 $\pm$ 0.5	10.3	3	0.0163
<i>Rhinolophus damarensis</i>	48.8 $\pm$ 74.3	11.9 $\pm$ 25.2	45.8 $\pm$ 98.5	0.6 $\pm$ 1.8	3.92	3	0.271
<i>Rhinolophus denti</i>	0.6 $\pm$ 1.3	1.1 $\pm$ 2.3	9.4 $\pm$ 13.6	0.4 $\pm$ 1.4	6.52	3	0.0889
<i>Rhinolophus fumigatus</i>	-	7.6 $\pm$ 25.0	-	2.2 $\pm$ 8.5	1.99	3	0.574
<i>Sauromys petrophilus</i>	612 $\pm$ 651	325 $\pm$ 380	3070 $\pm$ 2160	1350 $\pm$ 2040	7.38	3	0.0607
<i>Scotophilus dinganii</i>	-	13.3 $\pm$ 51.3	-	2.3 $\pm$ 7.4	1.93	3	0.587
<i>Tadarida aegyptiaca</i>	523 $\pm$ 1070	71.4 $\pm$ 105	1090 $\pm$ 1060	495 $\pm$ 800	11.3	3	0.0102

* Significant p-values are indicated in bold.

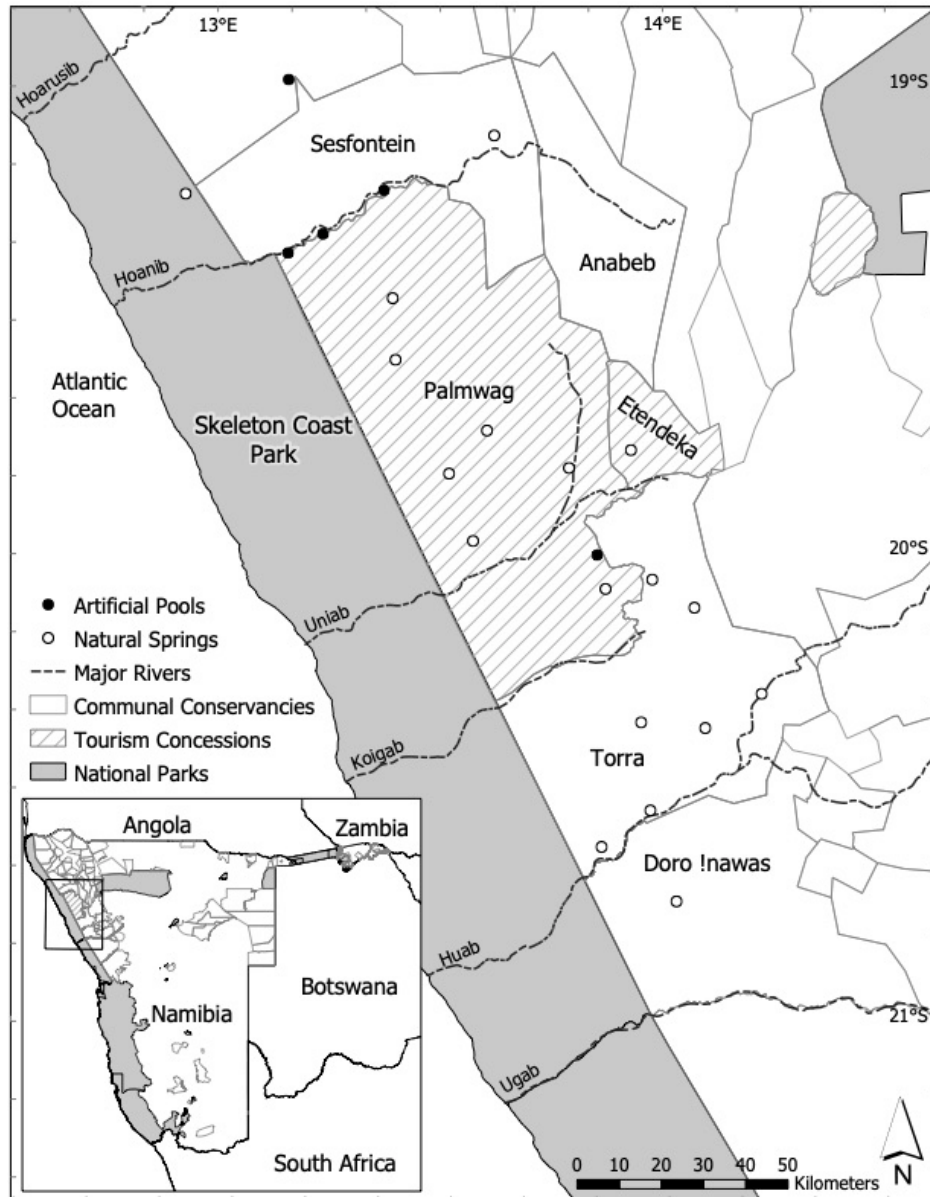


Figure 1.1. Map of our study area in the northern Namib Desert. Closed and open circles represent sampled artificial pools ($n = 5$) and natural springs ($n = 18$), respectively.

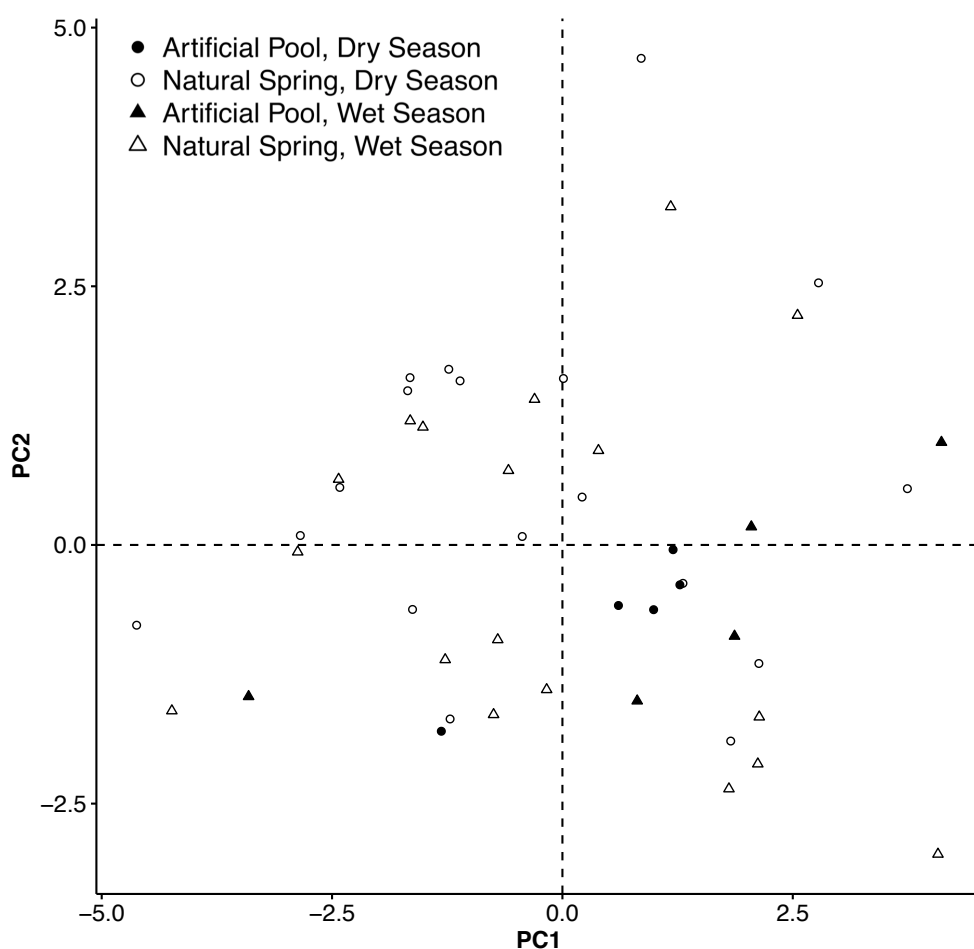


Figure 1.2. Ordination diagram of the first two axes of the principal component analysis (PCA) for water chemistry across water types. Closed and open circles represent artificial pools ($n = 5$) and natural springs ($n = 18$), respectively, sampled at end of the dry season (November 2016 – January 2017), while closed and open triangles represent artificial pools ($n = 5$) and natural springs ($n = 18$), respectively, sampled at end of the wet season (March – May 2017). The two axes of the PCA explained 62.2% of the total variation in water quality, with PC1 accounting for 39.6% and PC2 22.6% of the variance. PC1 was highly weighted with higher measurements of electrical conductivity as well as with greater concentrations of Na^+ , Cl^- , K^+ , and SO_4^{2-} . PC2 was weighted with higher measurements of Fe^{3+} , turbidity, total alkalinity as CaCO_3 , and pH, as well as lower measurements of Ca^{2+} .

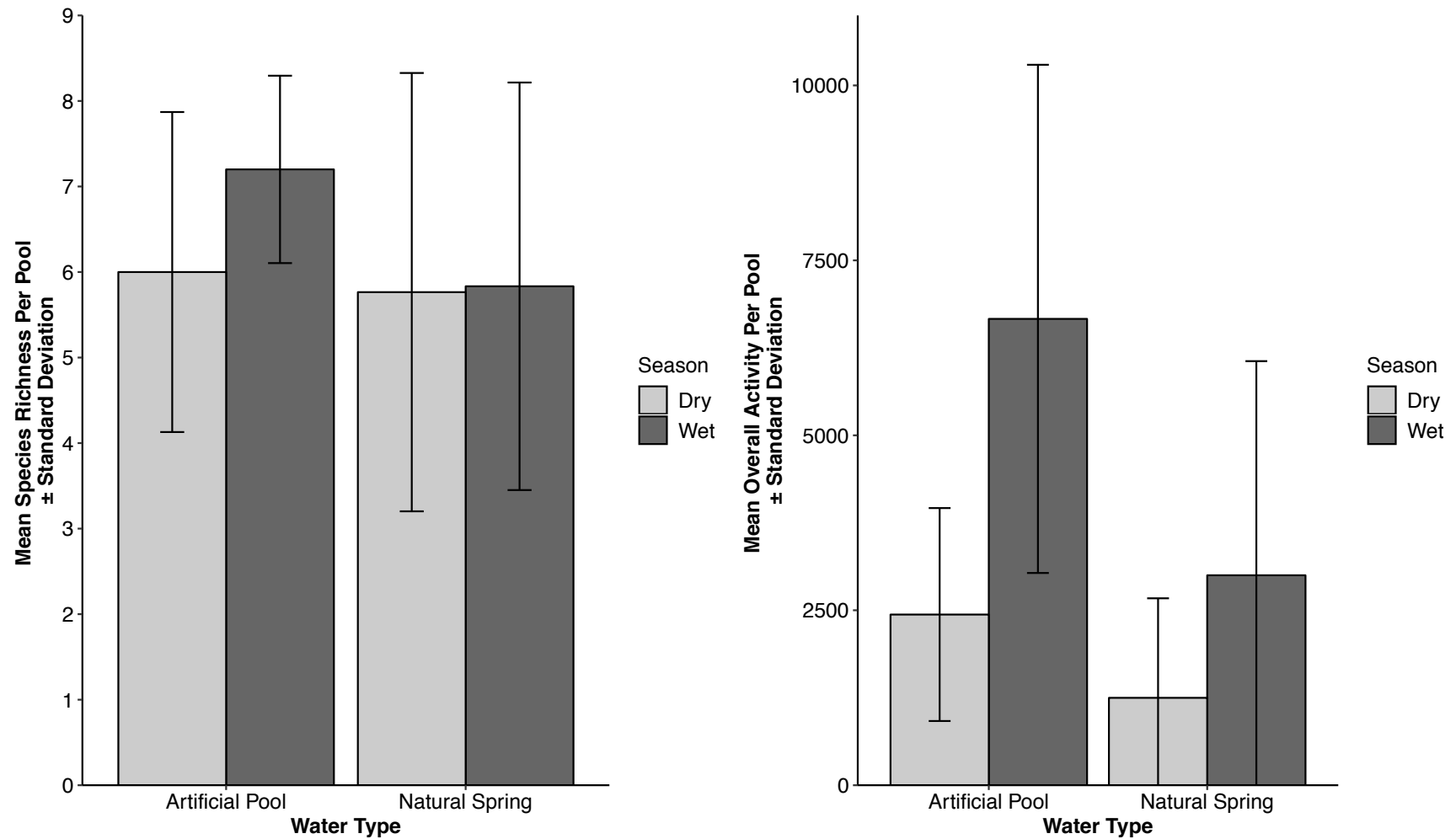


Figure 1.3. Relationship between a) species richness and b) overall activity per pool (mean $\pm$ SD) for bats sampled at artificial pools ($n = 5$) and natural springs ($n = 18$) once at the end of the dry season (light gray bars; November 2016 – January 2017) and once at the end of the wet season (dark gray bars; March – May 2017).

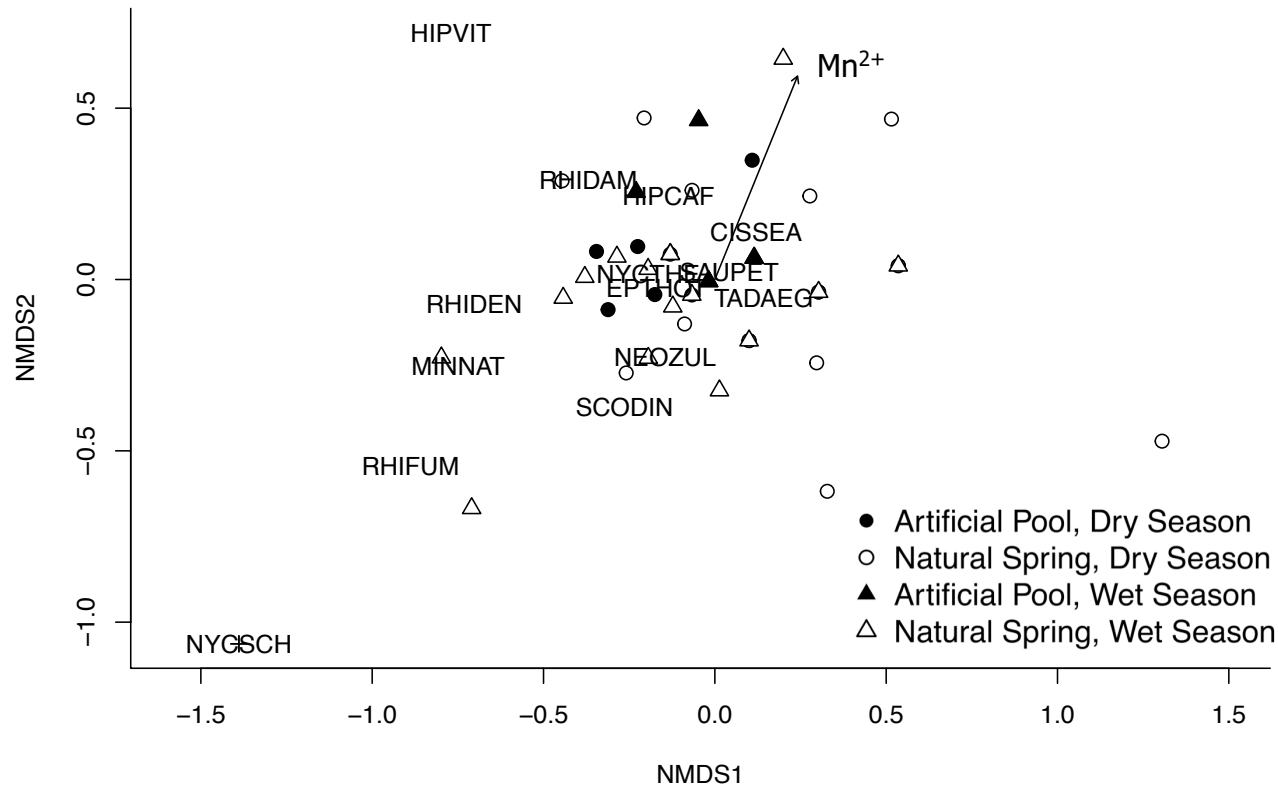


Figure 1.4. Relationship between two-dimensional non-metric multidimensional scaling (NMDS) of bat community structure (species presence/absence) at two types of bodies of water and two seasons in the Namib Desert, Namibia. Closed and open circles represent artificial pools and natural springs, respectively, sampled at the end of the dry season (November 2016 – January 2017), while closed and open triangles represent artificial pools and natural springs, respectively, sampled at the end of the wet season (March – May 2017). The arrow indicates that manganese significantly correlated with the bat community ordination calculated with *envfit* and arrow direction signifies increasing manganese concentration. Bat species include *Cistugo seabrae* (CISSEA), *Eptesicus hottentotus* (EPTHOT), *Hipposideros caffer* (HIPCAF), *Hipposideros vittatus* (HIPVIT), *Miniopterus inflatus* (MININF), *Miniopterus natalensis* (MINNAT), *Neoromicia capensis* (NEOCAP), *Neoromicia zuluensis* (NEOZUL), *Nycticeinops schlieffeni* (NYCSCH), *Nycteris thebaica* (NYCTHE), *Rhinolophus damarensis* (RHIDAM), *Rhinolophus denti* (RHIDEN), *Rhinolophus fumigatus* (RHIFUM), *Sauromys petrophilus* (SAUPET), *Scotophilus dinganii* (SCODIN), and *Tadarida aegyptiaca* (TADAEG).

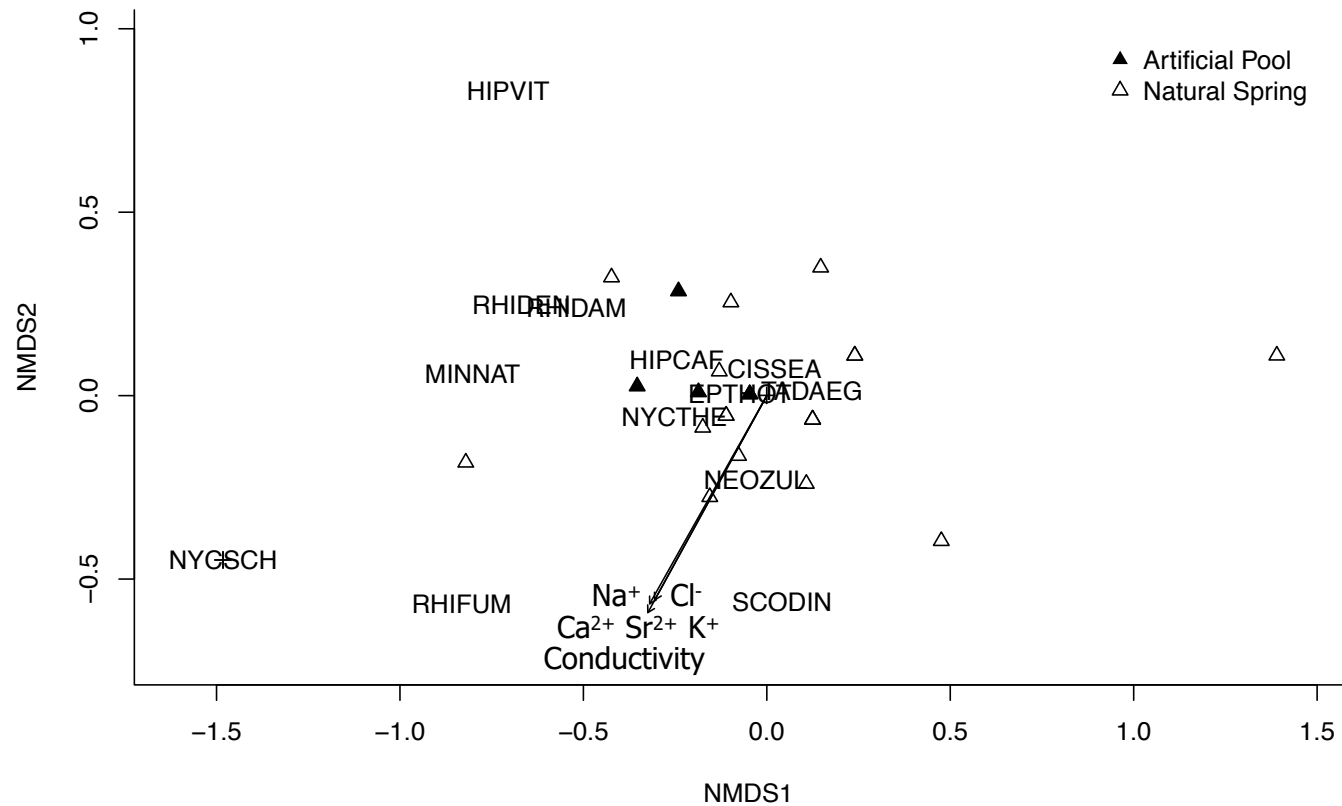


Figure 1.5. Relationship between two-dimensional non-metric multidimensional scaling (NMDS) of bat community structure (species presence/absence) at two types of bodies of water (insets) in the Namib Desert, Namibia at the end of the wet season (March – May 2017). Arrows indicate that sodium, chloride, calcium, strontium, potassium, and electrical conductivity were all significantly correlated with the bat community ordination calculated with *envfit* and arrow direction signifies increasing concentrations of these variables. Bat species include *Cistugo seabrae* (CISSEA), *Eptesicus hottentotus* (EPTHOT), *Hipposideros caffer* (HIPCAF), *Hipposideros vittatus* (HIPVIT), *Miniopterus inflatus* (MININF), *Miniopterus natalensis* (MINNAT), *Neoromicia capensis* (NEOCAP), *Neoromicia zuluensis* (NEOZUL), *Nycticeinops schlieffeni* (NYCSCH), *Nycteris thebaica* (NYCTHE), *Rhinolophus damarensis* (RHIDAM), *Rhinolophus denti* (RHIDEN), *Rhinolophus fumigatus* (RHIFUM), *Sauromys petrophilus* (SAUPET), *Scotophilus dinganii* (SCODIN), and *Tadarida aegyptiaca* (TADAEG).

CHAPTER 2

BATS, ELEPHANTS, AND THEIR FOOD: HOW MEGAHERBIVORES MODULATE MAMMALIAN INSECTIVORY IN DESERTS

“When we reach absolute deserts, the struggle for life is almost exclusively with the elements... Not until we reach the extreme confines of life, in the Arctic regions or on the borders of an utter desert, will competition cease.” – Charles Darwin, *On the Origin of Species* (1859)

Introduction

In extreme desert environments, the role of biotic interactions in structuring ecological communities is expected to be small relative to abiotic forces (Darwin 1859; Brown & Ernest 2002). Animal populations regularly collapse in arid environments due to frequent droughts and high variation in interannual precipitation, and thus may have relatively subtle effects on vegetation or on different trophic levels (Illius & O'Connor 1999; von Wehrden et al. 2012). In old deserts, however, a longer history of aridity may have allowed more species to adapt and coexist in spite of intense competition for resources (Simmons et al. 1998). Nearly all desert life concentrates and interacts around surface water in the form of natural springs, manmade pools, or short running water sections within highly ephemeral river systems (Kingsford et al. 2006), and this sort of local abundance provides an opportunity for top-down forces to structure desert communities (Polis 1991). In more mesic environs, carnivores play substantive roles in managing food webs and preventing ecological meltdowns (Crooks & Soulé 1999;

Terborgh et al. 2001; Estes et al. 2011). Where predator densities are too low or variable to limit prey in arid environments (Hatton et al. 2015), mammalian herbivores may alternately structure communities. Herbivores with large body sizes and steep energy requirements may exert “rampant indirect effects” on species of other trophic levels via their consumption of vegetation (Paine 2000), particularly in low-productivity habitats such as deserts (Pringle et al. 2007).

The Namib Desert along southern Africa’s Atlantic coast is one of the world’s oldest deserts, and a biodiversity hotspot among arid zones globally (Ward et al. 1983; Simmons et al. 1998). Despite its extreme nature, the northern reaches of this desert are utilized by African elephants (*Loxodonta africana*), black rhinoceroses (*Diceros bicornis*), giraffe (*Giraffa giraffa*), mountain zebra (*Equus zebra*), greater kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*), and steenbok (*Raphicerus campestris*) in addition to localized herds of domestic livestock. Herbivores alter vegetation density, biomass, and species composition in a roughly two-kilometer high-impact zone around surface water in the Namib (Leggett et al. 2003a). This influence is often referred to as the piosphere effect (i.e. a radial pattern of attenuating impact; Lange 1969; Unmack & Minckley 2008; Landman et al. 2012), and is likely magnified in the Namib due to the presence of megaherbivores like elephants that topple and debark large trees (Owen-Smith 1992; Fenton et al. 1998; Ogada et al. 2008; Shannon et al. 2008).

The concentrated and often visible impacts of herbivores on the vegetation communities near surface water in deserts may have cascading effects on other species. Insects including butterflies and moths can benefit from mammalian herbivory

of intermediate intensities and duration (Pöyry et al. 2004; Vogel et al. 2007; Moranz et al. 2012), which in turn can benefit communities of diverse insectivorous taxa including birds and lizards (McCauley et al. 2006; Pringle et al. 2007; Cardinal et al. 2012).

Insectivorous bats may also be indirectly affected by herbivory in a similar manner. In Zimbabwe's miombo woodlands, however, bat communities remained relatively unchanged with increasing elephant densities in comparison to bird communities (Fenton et al. 1998). The intensity of such biotic interactions between distantly-related taxa in deserts remains unclear.

If a relationship between megaherbivores and insectivorous species exists, there may be important conservation implications. While elephants understandably continue to be a main target for conservation efforts, their protection may induce a trade-off with ecological function or biodiversity by counteracting the conservation of smaller insectivores (Ogada et al. 2008), such as bats. On the other hand, elephants or other large herbivores may create habitat disturbances that benefit other organisms, including bats. Such potential trophic links require investigation.

Our research asks, to what extent does the relative abundance of localized desert-dwelling herbivores modulate insectivorous bat communities? Since desert bats concentrate in the same riparian areas where herbivores impact plant communities (Adams & Thibault 2006; Razgour et al. 2010; Korine et al. 2015), we hypothesized that the spatial heterogeneity of large herbivores would affect Namib bat species richness and activity (Fig. 2.1). Bat species richness and activity might also be inversely related to megaherbivore use at water sites if elephants, giraffes, and black rhinoceroses reduce the food or habitat available for bats' plant-dependent insect prey. Alternatively,

insect prey may increase with megaherbivore activity and dung density at a site and positively relate to bat species richness and activity. A last possibility is that megaherbivores may create or restructure habitats by changing the vegetation layer near water, with a consequent effect on the distribution of aerial insectivores. If so, relationships between large herbivores and bats may be nonlinear and consistent with the intermediate disturbance hypothesis (Connell 1978) such that moderate herbivory restructures vegetation to benefit less maneuverable open-air foragers, but increasing herbivory eventually becomes detrimental for clutter-edge foraging bats.

By examining the above question and associated predictions, our aims are twofold. First, we contribute to the body of literature and ideas initially posed by Darwin with respect to the strength of biotic interactions in abiotically extreme locales. Second, given the challenges experienced by impoverished pastoralists persisting at the edge of deserts among species as different as elephants and little-known bats, we aim to increase attention on the complexity of conservation when targets may be very different.

Methods

Study Area

We conducted our research in the northern Namib Desert in the Kunene Region of Namibia (Fig. 2.2). We worked within the catchments of the Hoanib, Uniab, Koigab, and Huab Rivers – four of Namibia's twelve major ephemeral rivers (Jacobson et al. 1995). This region features a strong rainfall gradient with average annual precipitation increasing from ~ 30 mm to 100 mm from the western to the eastern edge of our study area (Berger 1997; Jacobson & Jacobson 2013). Permanent water exists as natural springs, artificial pools constructed for wildlife and/or livestock use, and short (≤ 3 km)

stretches of flowing river. Other river sections sustain aboveground flows only during the wet season (i.e., January to April), on average less than 20 days per year (Jacobson et al. 1995; Leggett et al. 2001; Jacobson & Jacobson 2013).

We collected all ecological data during the hot, dry season of November 2016 – January 2017 and the wet season of February – May 2017. Our measurements focused on 23 permanent bodies of open water (Fig. 2.2) including both artificial pools ($n = 5$) and natural springs ($n = 18$).

Bat Community Sampling

Using ultrasonic bat detectors (Song Meter SM4BAT FS, Wildlife Acoustics), we monitored bat activity and species richness at each site once per season, for a total of 46 nights of sampling (dry season: 21 November 2016 – 21 January 2017; wet season: 16 March 2017 – 16 May 2017). Bat detectors were deployed from 30 min before sunset to 30 min after sunrise. For each night of sampling, we positioned one bat detector within 3 m of surface water with the microphone 2.5 m above the ground at a 45-degree downward angle. We avoided sampling bat communities within three days of full moon nights, as moonlight is known to reduce the activity patterns of some bat species (Lang et al. 2006; Kingston 2009).

A call library for Namibian bats does not currently exist, so we identified species within recorded calls using the cluster analysis option in the software program Kaleidoscope Pro Version 5.1.3 (Wildlife Acoustics, Maynard, MA). Full spectrum calls recorded by bat detectors were analyzed by the software using enhanced zero crossing (Ross et al. 2018). Clusters were created and sorted based on their similarity after a signal detector searches for candidate vocalizations in the recordings. We then

manually reviewed all calls in every cluster to classify the species present using a set of reference calls recorded from bats physically captured in mist nets and identified over different sampling periods at the same sites. Calls were also compared to those provided in the field guide by Monadjem et al. (2010). We calculated overall bat activity as the number of passes (i.e., sequence of calls; Fenton 1970) per night of recording at each site, regardless of species. Species richness was defined as the total number of species recorded within a night at each site.

Sampling Megaherbivore Activity

To estimate megaherbivore use at a site, we conducted monthly dung surveys between 21 November 2016 and 5 April 2017 using three 120 x 4 m belt transects radiating away from 16 of the water bodies where bats were sampled. Dung counts offer more reliable estimates of relative habitat use within a given species, habitat, and season as compared to live animal aerial and ground counts (Barnes 2001; Marques et al. 2001; Riginos 2015), though such data can be affected by variations in decomposition rates (Fuller 1991; Plumptre & Harris 1995). Dung piles of all megaherbivores – African elephant, giraffe, and black rhinoceros – were identified from published accounts (Gutteridge & Liebenberg 2013), enumerated, and then removed from the transect to prevent re-counting. For each site, we averaged the number of dung piles across the total transect area for the dry ($n = 37$; 21 November 2016 – 24 January 2017) and wet seasons ($n = 27$; 6 February – 5 April 2017) to align with our bat community sampling. We pooled the number of dung piles for these three species as a measure of megaherbivore use at a site.

Measuring Vegetation Productivity

We approximated vegetation productivity using the Normalized Difference Vegetation Index (NDVI; Rouse Jr. et al. 1974) derived from 10 m resolution satellite imagery (Sentinel-2A Level-1C imagery; Drusch et al. 2012) over the same periods of time that we sampled bat communities (dry season: 21 November 2016 – 21 January 2017; wet season: 16 March 2017 – 16 May 2017). We used Google Earth Engine (Gorelick et al. 2017) to compute the mean NDVI value within a 1 km circular buffer of each sampling point, based on the median value for each pixel on days with <15% cloud coverage (i.e., 9 and 12 days of imagery for the dry and wet seasons, respectively).

Statistical Analysis and Predictions

We tested for seasonal differences among our variables using paired t-tests with the *t.test* function in the stats package of R version 3.5.3 (R Core Team 2019). We also built structural equation models (SEMs) using the *sem* function in the lavaan package (Rosseel 2012). Construction of our SEMs was guided by ecological theory and prior observations of how desert communities function (Fig. 2.3). Specifically, we hypothesized relationships between:

1. Megaherbivore use and NDVI. We note that although grazing and browsing can stimulate subsequent vegetation growth (e.g., McNaughton et al. 1997), herbivory also removes biomass. Therefore, we predicted that increased activity by elephants, giraffe, and black rhinoceroses near water sources would negatively relate to mean NDVI over time, particularly in the less productive dry season (Pettorelli et al. 2011; Charles et al. 2017);

2. NDVI and bat species richness / overall activity. Higher NDVI values may indicate greater amounts of biomass that support a higher abundance and species richness of insects (i.e., bat prey) as suggested previously (e.g., Pringle et al. 2007; Pettorelli et al. 2011), but such a relationship can also imply differences in vegetation structure and thus bat habitat complexity. We predicted that bat species richness and overall activity would positively relate to NDVI; and
3. Megaherbivore use and bat species richness / overall activity. Greater megaherbivore use at a site can support higher insect abundance (i.e., bat prey) both around the herbivores themselves (Braverman et al. 1991; Mooring et al. 2003) and around their piles of dung (Schoenly 1983; Piñero & Avila 2004), which could in turn support higher bat species richness and overall activity. Alternatively, megaherbivores may reduce insect abundance through excessive herbivory (e.g., Ogada et al. 2008), and thus may reduce bat activity (Fenton et al. 1998). We predicted that bat species richness and overall activity would positively relate to megaherbivore use until a threshold is reached after which bat species richness and overall activity would decrease as high rates of herbivory may exclude clutter-foraging bats.

We first investigated these individual relationships with linear regression models using the *lm* function in the stats package of program R. To identify which of the hypothesized relationships are most consistent with our observational data, we implemented each relationship as a separate SEM model structure and then performed model selection using the Akaike Information Criterion (AIC), a relative metric of model quality that accounts for parsimony and over-fitting (Burnham & Anderson 2004).

Expecting these relationships to be stronger in the dry season when resources are more limiting and spatially discrete than in the wet season, we analyzed the potential for seasonal effects separately. More specifically, for each season we tested whether the relationships between megaherbivores and bat populations were direct or mediated through NDVI by comparing the AIC scores of three alternate SEM structures (Grace 2006) in which: 1) megaherbivores directly affect to bat species richness and activity (i.e., no mediation; Fig. 2.3a), 2) megaherbivores solely affect bat species richness and activity indirectly through their effects on NDVI (i.e., complete mediation, Fig. 2.3b), or 3) megaherbivores both directly and indirectly affect to bat species richness and activity (i.e., partial mediation; Fig. 2.3c). We selected the best-fitting model (i.e., the model with the lowest AIC value) for the dry and wet seasons separately.

Results

Seasonal Megaherbivore Use and NDVI

Monthly dung surveys showed our Namib Desert sites to be primarily utilized by giraffe and elephants, with minimal black rhinoceros presence (Fig. 2.4). While the mean NDVI in the vicinity of these bodies of water was approximately 60% greater in the wet season than the dry (Fig. 2.5; Table 2.1), megaherbivore use did not vary between seasons (Table 2.1). A positive relationship between megaherbivore use and NDVI was evident during the dry season ($\text{NDVI} = 0.02 + 0.75 \cdot \text{Megaherbivore Use}$; $R^2 = 0.23$; $p = 0.036$), but not during the wet season ($\text{NDVI} = 0.02 + 1.36 \cdot \text{Megaherbivore Use}$; $R^2 = 0.03$; $p = 0.245$; Appendix 2.1a).

NDVI and Bat Species Richness / Overall Activity

We recorded a total of 120,749 bat passes over 45 of the 46 nights of sampling (no bat calls were identified in recordings at one site during the dry season; Lavery 2019). Across all sites, 14 insectivorous species were detected in the dry season, while 16 were recorded during the wet season. Mean overall bat activity at the site level was 160% greater in the wet season, but bat species richness did not significantly differ across seasons (Table 2.1).

We found a strong, positive relationship between NDVI and bat species richness during the dry season (Bat Species Richness = $3.2 + 98.8 \cdot \text{NDVI}$, $R^2 = 0.51$, $p < 0.001$) and a weaker relationship between those factors during the wet season (Bat Species Richness = $5.1 + 26.6 \cdot \text{NDVI}$, $R^2 = 0.14$, $p = 0.047$; Appendix 2.1b). While the relationship between NDVI and overall bat activity was not significant in the wet season (Overall Bat Activity = $3495 + 7983 \cdot \text{NDVI}$, $R^2 = 0.01$; $p = 0.716$), this relationship was strong in the dry season (Overall Bat Activity = $174.3 + 53663.3 \cdot \text{NDVI}$, $R^2 = 0.46$; $p < 0.001$; Appendix 2.1c).

Megaherbivores and Bat Species Richness / Overall Activity

No significant relationship between megaherbivore use of an area and bat species richness was detected in either the dry or the wet season (dry season: Bat Species Richness = $5.4 + 84.1 \cdot \text{Megaherbivore Use}$, $R^2 = 0.13$, $p = 0.096$; wet season: Bat Species Richness = $5.9 + 52.2 \cdot \text{Megaherbivore Use}$, $R^2 = 0.001$, $p = 0.331$; Appendix 2.1d). A moderate, positive relationship was observed between megaherbivore use and overall bat activity in the dry season (Overall Bat Activity = $815.0 + 65834.3 \cdot \text{Megaherbivore Use}$, $R^2 = 0.35$, $p = 0.009$; Appendix 2.1e), whereas overall bat activity appears to decline with megaherbivore use during the wet season

(though not statistically significant; Overall Bat Activity = 5146 - 115522*Megaherbivore Use, $R^2 = 0.001$, $p = 0.330$).

Structural Equation Models

During the dry season, the best-fitting SEM was the partial mediation model in which the relationship between megaherbivore use and bat species richness was mediated primarily through NDVI, but megaherbivore use directly related to overall bat activity (Fig. 2.6a; Appendix 2.2). Specifically, megaherbivore use positively associated with local NDVI, which in turn had a positive effect on bat species richness. The same model also highlighted the positive direct effect of megaherbivore use on bat activity.

By contrast, a significant herbivore – bat relationship was not supported by our models during the wet season (Fig. 2.6b; Appendix 2.3). Consistent with the prior simple regression analysis, the partial regressions among megaherbivore use, NDVI, and bat activity / species richness were not significant, and R^2 values were low within all three of the SEM models tested. Together, this suggests minimal direct and/or indirect relationships between megaherbivores and bats during seasons when water is less limiting.

Discussion

Elephants and Other Big Animals as Modulators of Insectivorous Bats

Numerous biotic and abiotic factors affect species richness and abundance (MacArthur 1984; Martin 2001; Lortie et al. 2004; Benton 2009). Beyond weather and aridity per se, water has the ability to concentrate species and shape adaptive capacity (Broyles 1995; Brown & Ernest 2002; Davis et al. 2017). With respect to the Namib Desert, bat activity and NDVI increased during the wet season due to phenological

drivers of biological activity including a putative pulse of vegetative-mediated profusion of insects when water was also readily available. Although previous studies in the Namib found seasonal differences in elephant and giraffe distributions (Leggett 2006b; Fennessy 2009), we detected no seasonal effects in either megaherbivore use of an area or bat species richness. This may be due to the true absence of a temporal relationship or an artefact of our sample size. However, the significant seasonal differences observed among some of our other variables (i.e., NDVI and overall bat activity) supported our choice of conducting separate SEM analysis of species and plant interactions for each season.

In the dry season, bat activity was positively related to megaherbivore use through direct pathways, while bat species richness was positively associated with megaherbivore use through indirect pathways. Elsewhere in sub-Saharan Africa disturbance from browsing and grazing of plants by megaherbivores promotes higher vegetation growth rates and productivity in the dry season (e.g., Pringle et al. 2007; Charles et al. 2017). The observed positive relationship between dry season ungulate use and NDVI may have similar origin. This could also be due to megaherbivores selecting sites with more productive vegetation (i.e., higher NDVI), but our study did not directly test the directionality of this relationship. To address this limitation, we suggest monitoring megaherbivore movement patterns via GPS collars or tags for a fine-scale understanding of habitat use in relationship to NDVI patterns. We did find a higher diversity of insectivorous bats at the sites of greater NDVI values and higher megaherbivore use. Elephants in particular may have changed the vertical complexity of shrubs and trees (i.e., reduced the number of branches and canopy cover; Asner et al.

2009), opening up new habitat for less maneuverable bat species (e.g., free-tailed bats, including Roberts's flat-headed bat *Sauromys petrophilus* and the Egyptian free-tailed bat *Tadarida aegyptiaca*). We suggest collecting measurements of horizontal and vertical vegetative cover with densiometers and cover boards to confirm the possibility of such a relationship. As more research is conducted on the foraging ecology of Namib bats, we also suggest analyzing bat activity and foraging behavior (i.e., open aerial, clutter-edge, intermediate) as it relates to a site's herbivore complex.

In contrast, our SEM analysis suggests that the relationship between megaherbivores and overall bat activity was direct rather than mediated through NDVI. In this case, the presence of megaherbivores and their dung may have increased insect abundance, which supported greater activity within individual bat species. Insect community responses to herbivore use are only inferred in our modeling, however, and we recommend that the abundance and diversity of insects be directly measured in future SEM-based studies. Alternatively, both elephants and bats may select sites that happen to have high insect diversity, which could be tested in the future by modifying insect abundance in specified areas of our study area.

Muting of Top-Down Effects in the Wet Season

The relationships among megaherbivore use of an area, bat activity, and species richness that we detected in the dry season disappeared in the wet season. In other parts of sub-Saharan Africa, ungulates disperse throughout the wet season when water is more widely distributed (Wittemyer et al. 2007; Holdo et al. 2009). Spatial and temporal variability of resources strongly influence the movements and composition of wildlife communities in many ecosystems, as many species follow these patterns for

food acquisition (e.g., Sabo & Power 2002; Holdo et al. 2009; Coogan et al. 2012; Schindler et al. 2013). Ephemeral rivers not only sustain brief flows that bring nutrients to the desert during the wet season (Jacobson & Jacobson 2013), but ephemeral pools also fill during localized rainfall events, supporting species with greater access to food resources in areas distant from permanent bodies of water.

Localized precipitation events strongly affect vegetation productivity and alter the distributions of many large mammals in not only the Namib Desert (Leggett 2006b; Fennessy 2009), but also across arid regions worldwide (Wittemyer et al. 2007; Singh et al. 2010; Acebes et al. 2013). Small mammals including bats presumably also capitalize on changes in food availability by tracking seasonally ephemeral resources with pulses in vegetation blooms where insects become more abundant following floods or rainfall events (Kingsford et al. 2006). We found nightly bat activity more than doubled in the wet season, suggesting that the relative abundance of bats increased with the seasonal pulse in resources.

Dwindling Effects of Desert-Dwelling Giants

Many of the world's largest herbivores are found in Africa, but have undergone severe range declines due to hunting, habitat loss or fragmentation, and human encroachment or conflict (Ripple et al. 2015). African elephants, for instance, are widely distributed across the continent, utilizing a wide variety of habitats ranging from semi-desert to tropical forests (Laws 1970; Owen-Smith 1992). Their presence in deserts, however, is unique and restricted to the northern Namib Desert in Namibia and on the edges of the Sahara and the Sahel in Mauritania and Mali (Viljoen 1989; Leggett 2006b; Wall et al. 2013). Despite the low human densities in deserts, megaherbivores in these

regions have not escaped the effects of poaching (due in large part to the economic value of elephant ivory and rhinoceros horn), civil war, and drought (Viljoen 1987; Cunningham & Berger 1997; Barnes 2001; Brodie et al. 2011). Populations of black rhinoceros and elephants underwent severe ($\geq 90\%$) declines in the northern Namib Desert from the 1880s to the 1980s (Viljoen 1987), but have been stable or increasing since around the time of Namibia's independence in 1990 (Leggett et al. 2003b; Brodie et al. 2011).

Conservation efforts, especially by non-governmental organizations have understandably focused on these large charismatic species but have yet to employ a multi-species recovery approach that recognizes the strength of interactions among broader levels of biodiversity, including insectivores. Understanding how the conservation of large herbivores affects other trophic levels may guide wildlife management to maximize local biodiversity. It is often assumed that the large habitat requirements of megaherbivores makes them suitable “umbrella species” – species whose protection indirectly benefits many other species (Caro 2010). Body size is not always the best indicator of appropriate umbrella species, however. Conserving the spatial extent of the black rhinoceros in the northern Namib Desert, for instance, does not support populations of other large herbivores (Berger 1997). Short-term studies have clear limitations in desert ecosystems characterized by highly variable inter-annual rainfall (von Wehrden et al. 2012), and our efforts highlight the need for future research across multiple years to both meet the intensive data requirements of SEMs and capture a better understanding of the biotic and abiotic drivers of species distributions over time. These challenges notwithstanding, we gained novel insights on the

associations of large herbivores and bat biodiversity, and confirmed that these interactions had abiotic influences as demonstrated through seasonal differences in SEM performance.

Darwin (1859) noted that adaptations to the physical environment are important drivers of speciation and survival in harsh climates, though the interplay between biotic and abiotic factors in shaping species distributions remains unclear or understudied for many taxonomic groups in such realms. Our research found bat species richness and overall activity to positively relate to megaherbivore use, but only during the dry season. This supports the theory that the strength of biotic interactions in structuring desert communities is strongest when resources are most limited. Despite the many differences that exist between the world's largest terrestrial mammals and some of the smallest, our findings imply that the continued protection and recovery of megaherbivores (i.e., elephants, giraffe, and black rhinoceroses) may directly and indirectly benefit Namib Desert bat populations and species diversity.

Table 2.1. Megaherbivore use, the Normalized Difference Vegetation Index (NDVI, a proxy for vegetation productivity), bat species richness, and overall bat activity summarized (mean $\pm$ SD) for each for the dry (November 2016 – January 2017) and wet (February – May 2017) seasons in the Namib Desert, Namibia.

Variable	n^a	Dry Season	Wet Season	t	p^b
Megaherbivore Use (dung/m ²)	16	0.0090 $\pm$ 0.0118	0.0076 $\pm$ 0.0082	0.512	0.6164
NDVI	23	0.024 $\pm$ 0.019	0.038 $\pm$ 0.035	-3.183	0.0043
Bat Species Richness	23	5.6 $\pm$ 2.6	6.1 $\pm$ 2.2	-1.594	0.1253
Overall Bat Activity (passes/night)	23	1453.3 $\pm$ 1469.8	3796.6 $\pm$ 3467.0	-4.057	0.0005

^a Sample size n represents the number of samples for each season.

^b Significant p-values are indicated in bold.

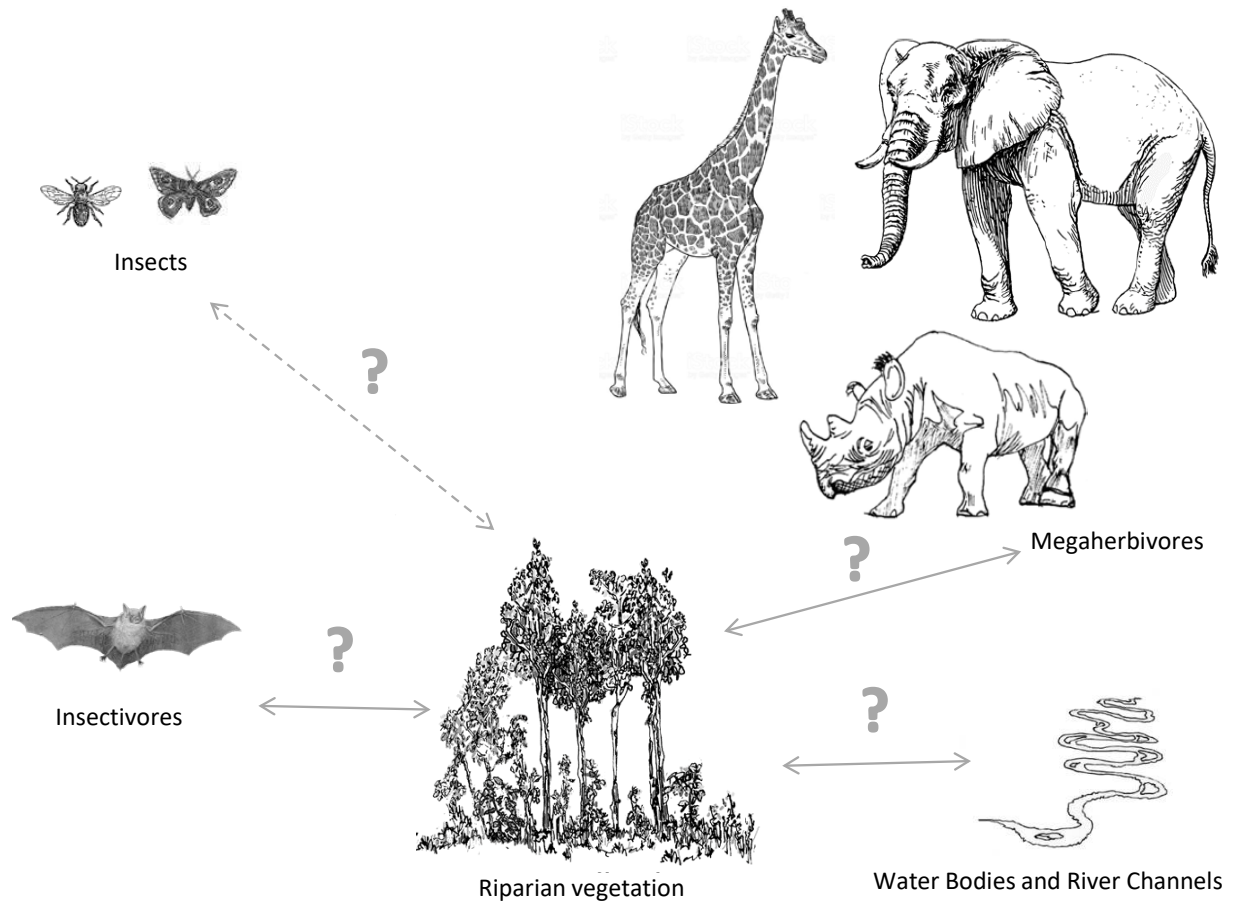


Figure 2.1. Conceptual diagram displaying the trophic levels we studied in the northern Namib Desert. Not all arrows are drawn for simplicity. The dotted arrows between riparian vegetation and insects represents assumed relationship that we did not measure in this study.

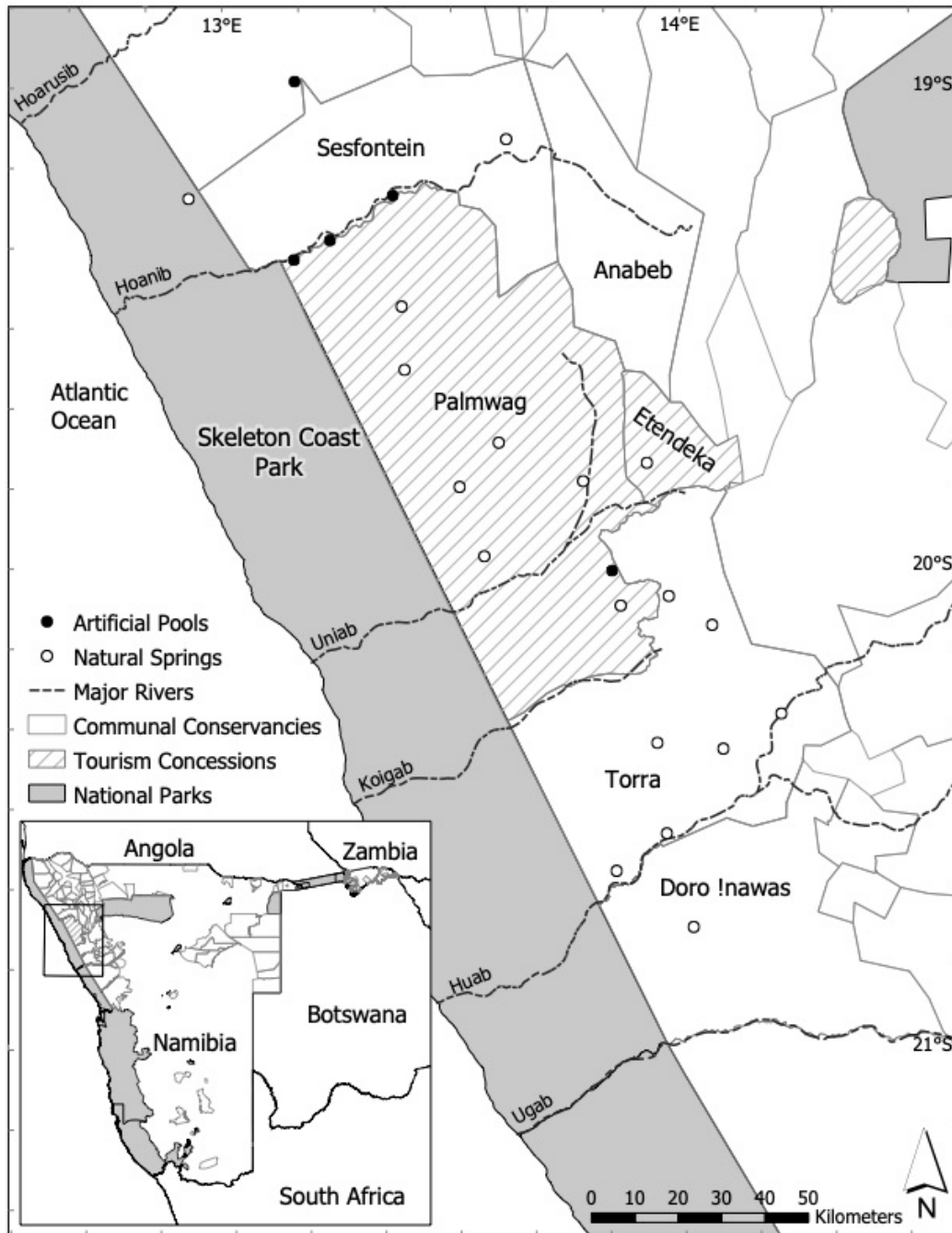
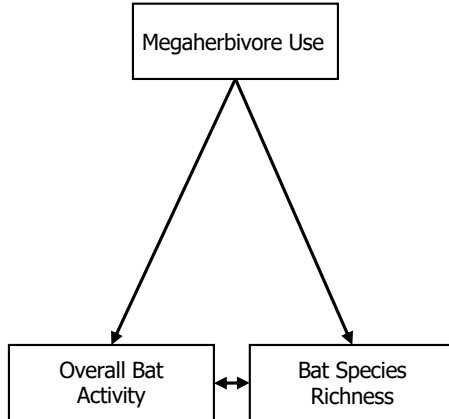
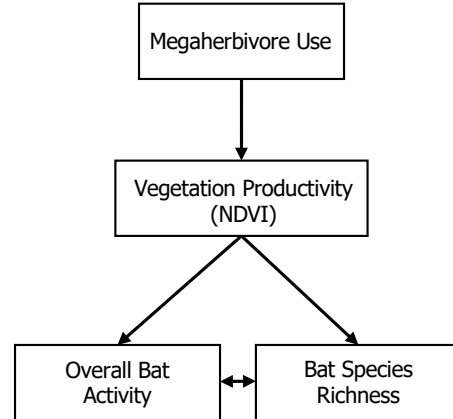


Figure 2.2. Map of the study area in the northern Namib Desert. Closed and open circles represent sampled artificial pools ($n = 5$) and natural springs ($n = 18$), respectively.

a) No mediation



b) Complete mediation



c) Partial mediation

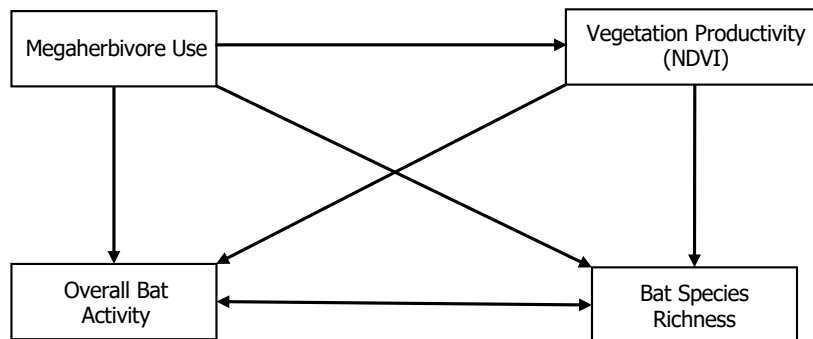


Figure 2.3. Three hypothesized relationships among megaherbivores, vegetation productivity, and bat communities that we evaluated through structural equation modeling. The theory-driven models include: a) the direct relationship of megaherbivore use at a site with bat species richness and overall activity, b) the same model but the effects of megaherbivores on bat communities are completely mediated through vegetation productivity, and c) a final model in which both the direct and indirect effects of megaherbivores are represented. The double headed arrows indicate an anticipated correlation between bat species richness and overall activity.

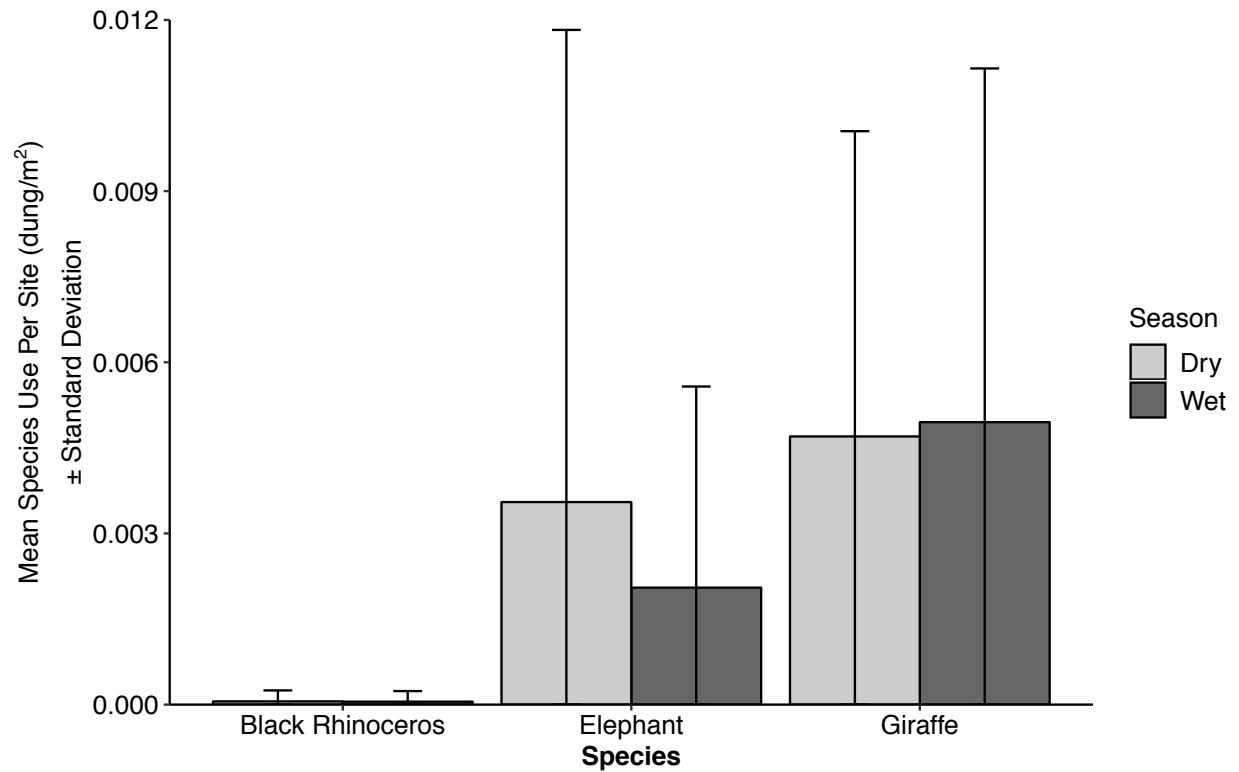


Figure 2.4. Megaherbivore use per site (mean $\pm$ SD) estimated from monthly dung surveys in northwestern Namibia over the dry season (light gray bars; $n = 37$; 21 November 2016 – 24 January 2017) and wet season (dark gray bars; $n = 27$; 6 February 2017 – 5 April 2017).

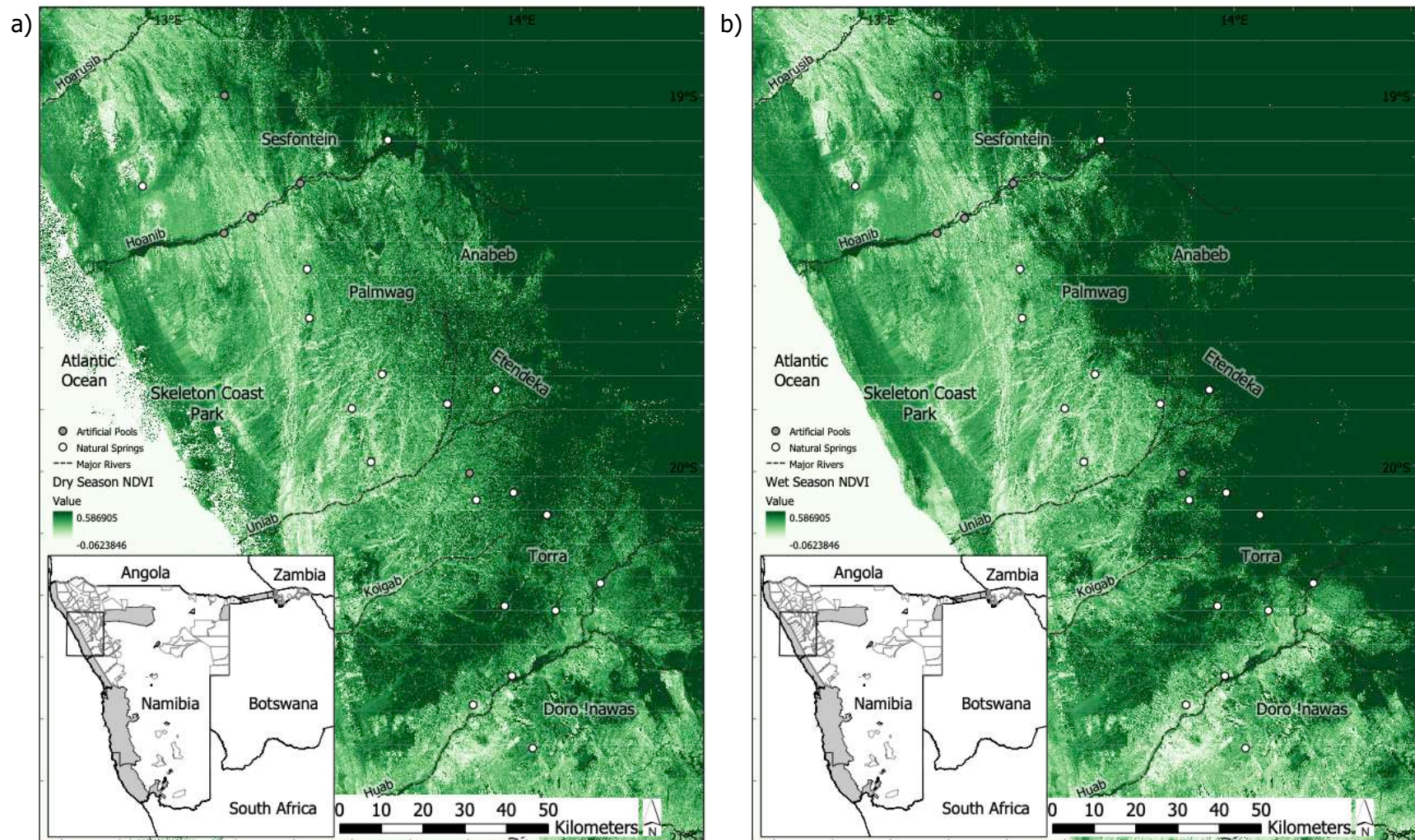


Figure 2.5 Maps displaying the median Normalized Difference Vegetation Index (NDVI) values for the a) dry (21 November 2016 – 21 January 2017) and b) wet (16 March 2017 – 16 May 2017) season at a 30 m resolution.

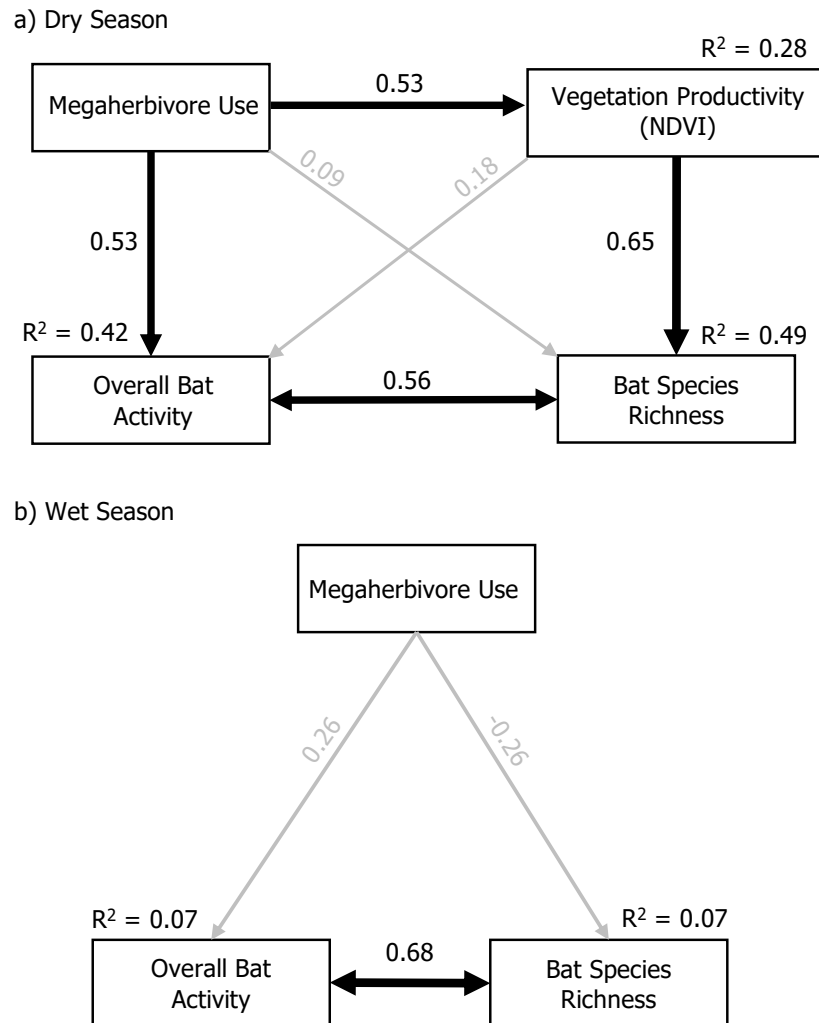


Figure 2.6. The most supported structural equation models (i.e., models with the lowest AIC values) for the a) dry and b) wet seasons. Pathways are accompanied by standardized partial regression coefficients. The significance of the coefficients is shown with different colors (black: $p \leq 0.05$; grey: $p > 0.05$). Arrow width corresponds to path strength (wider = stronger). The double headed arrows indicate a correlation between bat species richness and overall activity. R^2 values indicate the total variation explained by a model up to those points in the diagram.

CHAPTER 3

USING PASTORAL IDEOLOGY TO UNDERSTAND HUMAN-WILDLIFE COEXISTENCE IN ARID AGRICULTURAL LANDSCAPES¹

Introduction

Conflicts between humans and wildlife are escalating worldwide due to human population growth, urbanization, growth of agricultural and industrial activities, and, in certain areas, increasing wildlife populations (Woodroffe et al. 2005). Humans incur costs in the form of attacks on people, game or livestock depredation, crop-raiding, disease transmission to stock or humans, opportunity costs to human livelihoods, and diminished psychosocial wellbeing due to stress and fear of attack (Woodroffe et al. 2005, 2007; Barua et al. 2013). The costs of conflict to human livelihoods may be more severe in extreme environments, such as desert ecosystems. Severe droughts have become more frequent, for example, in deserts worldwide, exacerbating competition between wildlife and people for resources (Fig. 3.1; Durant et al. 2014). As another illustration, carnivores are threefold more prevalent per kilogram of prey in dry deserts than in lush savannas (Hatton et al. 2015), contributing to greater potential for carnivore-related conflicts with people and livestock. Despite being among the poorest and most marginalized people in the world in the face of these challenges (Middleton et

¹ Originally published as: Lavery TM, Teel TL, Thomas REW, Gawusab AA, Berger J. 2019. Using pastoral ideology to understand human-wildlife coexistence in arid agricultural landscapes. *Conservation Science and Practice* 1:e35. doi: 10.1111/csp2.35.

al. 2011), desert pastoralists and their livestock have historically coexisted with and tolerated wildlife more so than other groups (Gadd 2005; Browne-Nuñez et al. 2013). However, these relationships could shift as pastoralists become less nomadic and resources become more variable in space and time due to phenomena such as modernization and climate change. These anticipated changes in social-ecological conditions could affect human value systems as well as the frequency and severity of human-wildlife conflicts over time (Galvin 2009; Manfredo et al. 2017).

Acknowledging the diversity of factors operating across social and ecological systems can lead to a broader understanding of the underlying causes of human-wildlife conflict (Redpath et al. 2013; Carter et al. 2014; Morzillo et al. 2014). While conflicts occur largely at the interface of human and wildlife behaviors, the context that shapes these interactions includes multiple, nested levels of internal and external social and ecological processes (Manfredo et al. 2014, 2017; Lischka et al. 2018). These range from society- and ecosystem-level influences, down to individual attributes of humans (e.g., values) and wildlife (e.g., physiological conditions). Furthermore, social and ecological systems are not independent, but rather they interact through feedback mechanisms. For example, desert rivers and springs (i.e., ecosystem characteristics) drive both wildlife distributions and human settlement patterns (i.e., societal-level drivers; Lischka et al. 2018). At the individual and population levels, predators in arid landscapes may focus their hunting efforts around these scarce water resources that act to concentrate prey populations. Pastoralists and their livestock, which often occur in higher densities than wild prey, also rely on these areas where they may, as a consequence, be more likely to experience conflict with predators.

Research that integrates social and ecological knowledge through this systems lens can lead to more proactive and innovative solutions to conservation problems like human-wildlife conflict, though collection and analysis of the requisite data has often proved difficult. Limitations can stem from misperceptions about the quality and utility of social science information, particularly of qualitative research, and from epistemological differences across disciplines (Fox et al. 2006; Pooley et al. 2014; Bennett et al. 2017). Challenges also arise from inadequate attention in social-ecological systems models to individual human thought and behavior that can form the basis for conservation problems and ultimately determine the course and success of management interventions (Manfredo et al. 2014, 2017; Lischka et al. 2018). Given the global nature of human-wildlife conflicts, it is also important to document and understand these social dimensions across cultures to enhance transferability of findings and inform more broad-based solutions (Manfredo & Dayer 2004; Dickman 2010; Teel et al. 2010).

To help address these gaps, we paired theory from social psychology that emphasizes individual thought and behavior with a unique suite of long-term ecological data to inform a qualitative investigation of pastoralists' values toward wildlife in the northern Namib Desert of Namibia.

Conceptual Background

Values are basic patterns of thought formed early in life that guide behavior over a wide array of situations and events (Schwartz 1992; Rohan 2000). They allow people to determine what is good and bad or right and wrong, and inform rules of behavior for members of a social group. Once formed, values persist within individuals and across generations (Manfredo et al. 2016). Recognizing the importance of values in

conservation, Manfredo et al. (2017) recently called for a broader social-ecological systems approach to expand and improve the concept's application. According to this approach, values are embedded in a complex, multilevel social structure and manifest in daily routines, communication patterns, societal culture, and ways that people perceive and relate to their surroundings.

Wildlife value orientations, which serve to strengthen and give personal meaning to more basic values in relation to wildlife, form the foundation for individual behavior in wildlife-related contexts (Teel & Manfredo 2009; Manfredo et al. 2016). Recent studies have primarily focused on two core orientations: mutualism (emphasizing equality, caring, and compassion for wildlife) and domination (prioritizing human wellbeing over wildlife). These orientations can explain variation in attitudes and behaviors across a diversity of wildlife-related issues, particularly those involving harm to wildlife and trade-offs between human interests and wildlife protection (e.g., Teel & Manfredo 2009; Teel et al. 2010; Hermann et al. 2013; Manfredo et al. 2016; Cerri et al. 2017). Individuals with a domination orientation tend to be less tolerant of wildlife when it competes with human interests and more supportive of management actions like lethal control for dealing with human-wildlife conflicts (Manfredo et al. 2016). Tolerance is an indicator of attitudes toward wildlife, defined more specifically as an individual's acceptance of negative effects and desire for positive effects that arise from interactions with wildlife (Bruskotter et al. 2015). People who have high tolerance of a wildlife species prefer larger populations of that species. In contrast to domination, individuals with a mutualism orientation are more likely to prioritize concerns for animal welfare and wildlife-focused interests (e.g., habitat protection, support for endangered species) in

their attitudes and behaviors. Differences in these orientations can form the basis for social conflict among stakeholder groups over wildlife conservation and management efforts.

Recent research has suggested that a shift from domination to mutualism wildlife value orientations may be occurring globally, in line with broader value shifts due to modernization (Inglehart & Welzel 2005; Manfredo et al. 2016), with important implications for biodiversity conservation. However, knowledge of the cognitive basis for human-wildlife relationships is geographically limited, and prior research has largely been conducted using quantitative survey assessments in modernized societies such as the United States and western Europe. Recent exceptions in the Netherlands, China, Estonia, Mongolia, Republic of the Congo, and Thailand (see *Human Dimensions of Wildlife* volume 12, issue 5; Rickenbach et al. 2017) that were more exploratory in nature utilized a qualitative technique consisting of semi-structured interviews to measure wildlife value orientations among people of variable literacy and comprehension skills (Dayer et al. 2007). A need to better integrate ecological data in a way that both informs and reinforces interpretation of wildlife value orientation data (including both qualitative and quantitative) is also needed to better understand the challenges of coexisting with wildlife across cultures.

Recognizing these gaps in cross-cultural understanding and the important role of values in influencing human attitudes and behaviors, we explored pastoralists' value orientations toward wildlife in the northern Namib Desert and how those value orientations may affect: (1) local levels of species tolerance on the landscape; and (2) perceptions of challenges and potential solutions to living with wildlife. We also

interpreted our findings in relation to concurrent ecological data on wildlife populations and conflict occurrence in Namibia. We sought to further our understanding of human-wildlife relationships in arid landscapes to inform more effective solutions for conflict management. More broadly, this approach advances understanding of wildlife values globally and offers insights on the utility of qualitative assessment tools for cross-cultural social-ecological systems research.

Methods

Study Area

We conducted research in pastoralist communal conservancies in the Kunene Region of the Namib Desert, a region receiving ~100 mm of rainfall, on average, between January and April each year (Fig. 3.2; Jacobson & Jacobson 2013). Surface water is limited temporally and spatially, with ephemeral rivers typically sustaining aboveground flows less than 20 days per year during the wet season (Jacobson et al. 1995). Plants, animals, and people tend to be concentrated around these sparse water resources throughout the majority of the year, contributing to potentially higher rates of human-wildlife interactions. Communities in this region ranged in size from 2 to ~150 households.

Northwestern Namibia has been the focus of conservation efforts since the early 1980s, following large declines in wildlife populations due to expanding human settlements, war, intensive hunting and poaching, and drought (Leggett et al. 2003b). With effective law enforcement, the creation of communal conservancies, and the shift in natural resource ownership from government entities to property owners, wildlife populations have stabilized or increased since the country's independence in 1990

(Scanlon & Kull 2009; NACSO 2016). Communal conservancies in Namibia are demarcated land areas collectively managed by a group of land residents who agree to conserve and share their natural resources in a sustainable and economically beneficial manner (Shaw & Marker 2010). Torra, Anabeb, and Sesfontein conservancies were among the first conservancies established in Namibia after the 1996 Nature Conservation Amendment Act (in 1998, 2003, and 2003, respectively), and comprise a mix of ethnic groups (e.g., Damara, Herero, Himba, and Riemvasmaker) due in part to forced relocations of people imposed by successive colonial governments (Jones & Mosimane 2000). Local pastoralists in the region rely on livestock for income, although ecotourism and trophy hunting are also increasingly important (Bandyopadhyay et al. 2004; Lindsey et al. 2007). These conservancies are mostly unfenced, which permits free movement of wildlife and livestock (Rust & Marker 2014). As in other areas in southern Africa using community-based natural resource management (CBNRM), these conservancies allow both consumptive and non-consumptive uses of wildlife, and have devolved management responsibility to local people (Van Schalkwyk et al. 2010).

Data Collection

Our qualitative data collection approach consisted of face-to-face semi-structured interviews, which also addressed other research questions as part of a larger investigation. The first and fourth authors, the latter being a former Sesfontein Conservancy committee member and ecological field assistant across the Kunene Region, collaboratively developed the interview questions, and piloted the full interview instrument with four residents of different ethnic groups in Sesfontein Conservancy to ensure the questions were culturally appropriate and contextually clear (see Appendix

3.1). In May 2017 (i.e., immediately after the wet season), the first and fourth authors conducted 86 interviews in 31 villages in Sesfontein, Anabeb, and Torra conservancies (Appendix 3.2). In total, we conducted 64 individual interviews and 22 focus group interviews comprised of two to six individuals each (Appendix 3.3). Focus groups helped to enhance the comfort level and gender diversity of respondents, as some women denied consent to be interviewed individually without their husbands who were absent at the time of the interviews. This resulted in a total of 112 conservancy residents who were interviewed, ranging in age from 19 to 88 years. One man and four women declined to participate, and we excluded responses from one man who chose not to complete the full interview. In addition to attempting to achieve a gender balance in our sample, we prioritized obtaining representation of all ethnic groups within each conservancy.

Given the low density of occupied households in our study area, we used snowball sampling to identify potential participants after beginning at a randomly selected, occupied household in each village (Newing et al. 2011). At the conclusion of each interview, we asked respondents to provide a list of nearby occupied households. Interviews typically occurred at the location where we encountered recommended participants. Most interviews were at private residences, but a few were in public locations (e.g., restaurants, hotels).

The fourth author translated interview questions into Khoekhoegowab, Otjiherero, or Afrikaans as appropriate in real time, allowing the first author to ask follow-up questions as necessary. We recorded all interviews after receiving verbal consent from participants. Interview duration ranged from 19 to 129 minutes for the full suite of

questions and English translation. All interviews were transcribed verbatim by the first author from the fourth author's English translation. Final interview procedures were approved for use with human subjects prior to implementation by Colorado State University's Institutional Review Board (Protocol #043-18H) and the Namibian Ministry of Environment and Tourism (Permit #2225/2016).

To measure wildlife value orientations, we followed the cross-cultural interview guide developed by Dayer et al. (2007). This technique, which relies on basic human emotions as being universally understood across cultures, is designed to elicit stories about wildlife through emotional prompts. More specifically, this method asks respondents for depictions of personal experiences with wildlife that made them happy, sad, angry, and afraid in addition to a description of how they feel about wildlife in general. As an indicator of tolerance, we asked which species, if any, respondents thought should not be conserved or protected by their conservancy. For this measure, we relied on the assumption from the relevant literature (e.g., Bruskotter et al. 2015) that people with lower tolerance of a species prefer smaller populations or complete exclusion of that species. We also recorded which species were mentioned in responses to the emotional prompt questions and whether each interaction was perceived by respondents to be a positive or negative experience. We asked two additional questions to elicit perceived challenges and solutions to human-wildlife coexistence (see Appendix 3.1).

External ecological data sources were used to inform interview questions and interpret responses. Wildlife road surveys have occurred in the study area every June since 2001 as part of the North-West Game Count, with data publicly available from the

Namibian Association of CBNRM Support Organizations (NACSO 2018a). These survey results are used to estimate populations of large-bodied species, including oryx (*Oryx gazella*), ostrich (*Struthio camelus*), springbok (*Antidorcas marsupialis*), and Hartmann's mountain zebra (*Equus zebra hartmannae*), using distance sampling in the program DISTANCE (Laake et al. 1993), which accounts for reductions in species' detections with distance from the transect line. These population estimates, which are likely conservative due to a lack of system-wide accessibility, are in turn used to set annual harvest quotas for each conservancy. In addition to these population data, long-term records of monthly reports of human-wildlife conflicts at the species level are also available for each conservancy (NACSO 2018b). We analyzed these records from June 2004 to May 2017, as data were inconsistently recorded prior to 2004. By assessing the frequency and types of human-wildlife conflicts documented in the region as well as general trends in wildlife populations, we were able to obtain a broader understanding of the conditions that may be affecting pastoralists' wildlife-related perceptions and interactions reported in the interviews. It also allowed us to explore whether interviews disproportionately reported conflicts with particular species.

Analysis

To analyze wildlife value orientation data, the first author coded the relevant responses for each interview without pre-determined categories (i.e., inductive *in vivo* coding), with attention given to repeated codes (Levy et al. 1998), and then used existing studies on wildlife value orientations as guides for creating and grouping codes into axial categories (i.e., deductive coding; Strauss & Corbin 1998). Research objectives were then used to integrate, refine, and organize axial codes into broader

theoretical categories, or selective codes (Appendix 3.4). Interviews were our unit of analysis rather than individuals because some interviews involved more than one respondent.

Triangulation was accomplished through peer review by the third author, who was not part of the original study team but has expertise in cross-cultural qualitative research and wildlife value orientations. After the first author generated a list of themes, the third author reviewed the interview responses independently and coded 68 (15.8%) passages selected by the first author to contain the entire suite of value orientations and corresponding belief dimensions (i.e., sets of basic beliefs; Teel & Manfredi 2009) identified across interviews. Inter-coder agreement (95.8%) was calculated for each code based on the number of passages in which both coders determined the presence or absence of a code divided by the total number of passages (Appendix 3.4; Coffey & Atkinson 1996). After the two authors reached agreement on code definitions and interpretation, the first author independently reviewed the codes that were previously assigned to the remaining 362 coded passages and made minor adjustments.

For responses to questions about tolerance, challenges, and solutions, the first author again took an *in vivo* coding approach to generate a list of themes, which were grouped into categories (Appendix 3.5; Appendix 3.6). We determined these responses were more straightforward and less open to variable interpretation, reducing the need for a second reviewer. After coding all responses for a question, previously coded responses were reexamined and adjustments were made where necessary (Creswell 1998; Glesne 2006). Following our final coding procedures, results and interpretations drawn from data on wildlife populations and human-wildlife conflicts were used to

provide more context for interpretation of interview responses and to assess, in particular, potential differences in reported conflicts across data sources.

Results

Wildlife Value Orientations

Responses predominately reflected a domination wildlife value orientation (Table 3.1). Concern for property, including livestock, crops, and water structures, and human safety were the most commonly identified belief dimensions for this orientation, detected in 96.5% and 75.6% of all interviews, respectively (Appendix 3.4). Personal stories reflecting these themes often included predator attacks on livestock and humans, or elephants (*Loxodonta africana*) destroying crops or water structures. Responses also contained beliefs about economic gains from wildlife (29.1%), including monetary benefits or opportunities from conservation efforts, and hunting (18.6%), mostly for meat consumption. Fewer interviews (24.4%) expressed a mutualism value orientation toward wildlife. Of those that did, they described wildlife as “like [my] own children” that were deserving of trust, respect, and care. Other orientations identified in previous cross-cultural research on wildlife value orientations were also detected (see *Human Dimensions of Wildlife* volume 12, issue 5). Attraction or interest was a commonly reported value orientation, with 83.7% of interviews indicating a desire to see wildlife and 12.8% expressing the importance of future generations being able see and know all local wildlife species. A rational or scientific value orientation, tied to stories about how the natural world works and animals behave, was detected in 11.6% of interviews. Lastly, 5.8% of interviews indicated a spiritual or religious value orientation in which wildlife and the environment are thought to be created and controlled by a higher power.

Interactions with and Tolerance of Wildlife Species

Respondents were relatively tolerant of wildlife, although tolerance varied by species (Table 3.2). When asked which species, if any, should not be conserved, most interviews (67.4%) indicated that all species should be protected, although many (30.2%) also suggested the need for managing predator populations. Many interviews mentioned the importance of conserving all species for future generations to experience, with one man reporting that, “our children should not just hear from our stories, but the next generation should also see the wildlife [themselves].” When interviews did provide a species that they thought should not be conserved, lions (*Panthera leo*) were by far the most frequently listed animal (20.9%) because they kill livestock. One woman remarked that, “the conservancy program’s compensation is very weak. If the lion kills my cattle, I am supposed to pay [my children’s] school fees from those cattle. Because we are getting almost [no compensation], we don’t want lions to be conserved. However, if the system changes, then it would be fine.” The predominant value orientation – domination – influenced pastoralists’ tolerance of particular species as tolerance was lower for species, such as lions, leopards (*Panthera pardus*), and elephants, that threaten human and livestock wellbeing.

From the emotional prompt questions, we gathered stories describing both positive and negative interactions with 18 wildlife species (Table 3.2). Most positive interactions were with prey species, such as Hartmann’s mountain zebra, springbok, ostrich, elephants, and giraffes (*Giraffa camelopardalis angolensis*), and primarily emerged in interviews where the attraction and mutualism value orientations were also detected. One man described his encounter with zebra and springbok as, “we stood for

almost two hours [watching] the way they were grazing and running and [how they] came close to us. It was amazing.” Some respondents were also thankful for the meat received from prey species as indicated in interviews in which the hunting belief dimension (linked to domination) was detected. Interviews expressing a mutualism value orientation were more likely to describe positive interactions with several species otherwise prone to reports of human-wildlife conflict (i.e., hyenas *Crocuta crocuta* and *Hyaena brunnea*, lions, black rhinoceroses *Diceros bicornis*, black-backed jackals *Canis mesomelas*, and baboons *Papio ursinus*). We often detected a domination value orientation in interviews describing negative interactions with wildlife. These stories related to concerns over human safety and livestock wellbeing. One man described it as, “The elephants are destroying the fields and the lions and leopards are killing our cattle.”

The ecological data revealed how prey population sizes (and presumably those of predators) have widely fluctuated across conservancies over the last 16 years, varying more than ten-fold (Fig. 3.3a). Population sizes recorded in 2017 appear near the median of 6787 individuals per conservancy (Fig. 3.3b). Despite this variation, annual reports of human-wildlife conflicts remained consistently high, with only 7 of 42 measured conservancy-years recording less than 80 attacks on livestock (Appendix 3.7). The species responsible for conflicts (primarily predators and elephants) differed by conservancy (Appendix 3.8), and corresponded to negative interactions described in the interviews. For instance, median reported attacks on livestock by cheetah (*Acinonyx jubatus*) were over two times greater in Sesfontein Conservancy, where interviews described three times as many negative experiences with cheetah, as compared to

other conservancies. Interviews across all conservancies, however, consistently offered more negative stories about lions than any other wildlife species (Table 3.2), even though lions were not reported as causing the highest number of conflicts each year according to the conflict record data (Appendix 3.8).

Challenges and Proposed Solutions to Human-Wildlife Coexistence

The most commonly reported challenges were predators that kill livestock and drought, as noted in 91.9% and 53.5% of interviews, respectively (Table 3.3; Appendix 3.5). Indeed, our ecological data confirmed that livestock predation occurred consistently across years, regardless of environmental conditions (Appendix 3.8). Other challenges included elephants destroying crops or water structures (14.0%), wildlife threatening human safety (8.1%), and unreliable access to water (8.1%). These problems were often associated with a domination orientation and accounts of negative interactions with elephants and predators. Challenges also included ethnic conflicts (14.0%), such as the recent arrival of Himba immigrants with many livestock, and conservancy management issues (10.5%), including confusion about conservancy goals, poaching, overgrazing, and the inability to control wildlife populations. As one man stated, “I cannot implement the policies that I do not know. I do not understand even what the conservancy is, what are its goals, [and] why the conservancy has been set up.”

Proposed solutions to these challenges were more variable. Most frequently reported were methods designed to reduce human-wildlife conflict (Table 3.3; Appendix 3.6), including harvesting predators through trophy or community hunts (31.4%), translocating wildlife to other protected areas (29.1%), fencing predators within portions

of the conservancies themselves (23.3%), and increased monitoring of wildlife movements (17.4%). Many of these solutions reflected a perception that human-wildlife conflicts are a constant threat (Appendix 3.8) no matter the natural prey population size (Fig. 3.3a). Interviews that suggested fencing predators frequently noted the value of those species for attracting tourists. Interviews mentioning challenges around ethnic conflicts often suggested that conservancies enact stricter immigration laws and greater penalties for stealing livestock (10.5%).

Few interviews addressed water-related concerns, but those that did requested continued access to drought-relief feed for livestock (7.0%) and better access to water (7.0%) by fixing existing boreholes and constructing others away from human settlements. One man suggested that, “Where no one is living, they should drill more water points for wildlife so that [the wildlife] can stay there. If there's enough water points in the field, the wildlife might stay [away from settlements].” Concerns about subsistence needs, such as access to water, human safety, and livestock wellbeing, all tied to a domination orientation, prevailed in both reported challenges and solutions to living with wildlife.

Discussion

Our study investigated pastoralists’ value orientations toward wildlife and impacts of these orientations on species tolerance and perceptions of challenges and potential solutions to living with wildlife in the northern Namib Desert. The conditions of extreme environments like deserts may uniquely shape human-wildlife relationships and thought patterns in complex ways. Where desert pastoralists settle and how often they move with their livestock are driven by basic human needs, such as access to food and water.

The strong prevalence of a domination value orientation toward wildlife expressed in all of our interviews is reflective of these subsistence needs. This orientation promotes a view prioritizing human well-being over wildlife and relegating wildlife to roles and uses that benefit humans. At the same time, however, a mutualism orientation was also detected in nearly one-quarter of the interviews, emphasizing notions of caring, compassion, and equality in wildlife treatment. Other research in western societies suggests that this orientation surfaces as modernization contributes to greater emphasis on belongingness and social affiliation needs; wildlife, as a reflection of those needs, are then seen as more human-like and part of one's extended social network (Manfredo et al. 2016). In the Namibian context, however, mutualism may also be an extension of how livestock are treated, given that they are not only sold to cover living expenses and used as sources of transportation, milk, and meat, but are also considered part of a pastoralist's family. Indeed, we found evidence of this complexity in similar conceptions of both wildlife and livestock in our interviews, consistent with findings of wildlife value orientation assessments in certain other non-western cultural contexts including Mongolia and Kenya (Kaczensky 2007; Browne-Núñez et al. 2013).

Wildlife value orientations were also reflected in pastoralists' tolerance of wildlife and their perceptions of human-wildlife interactions. Our respondents indicated a strong affinity for herbivores among pastoralists as found in other studies (e.g., Gadd 2005; Browne-Núñez et al. 2013), notwithstanding inferred competition with livestock for access to water and pasture. These prey species (e.g., Hartmann's mountain zebra, springbok) often resemble livestock (e.g., donkeys, goats) in appearance and behavior (Kaczensky 2007), and interviews, particularly those in which mutualism and attraction

value orientations surfaced, revealed how pastoralists enjoyed seeing and living among them. However, pastoralists' tolerance of these species also reflected beliefs tied to a domination value orientation, in that participants highlighted the importance of herbivores for providing sustenance (i.e., meat for human consumption).

While pastoralists in our study were generally favorable toward wildlife as a whole, their relationship with predators is strained due to significant livestock depredation (e.g., Thomas et al. 2015). As in other parts of the world, Namibians kill predators due to the real and perceived threats they pose to livestock (Marker et al. 2003; Stein et al. 2010; Rust & Taylor 2016), a growing challenge in Namibia despite concerted efforts to limit such conflicts (NACSO 2016). Negative interactions with lions, in particular, were reported across a majority (66.3%) of interviews, although the conflict report data we accessed for the same region showed that lions were not the most damaging species to livestock (NACSO 2018b). Despite these interactions, a much lower percentage (20.9%) of interviews reported that lions should not be conserved, indicating that pastoralists may still be relatively tolerant of the species.

Our respondents identified a greater diversity of potential solutions, compared to perceived challenges, to living with wildlife in the northern Namib Desert. Challenges were related to subsistence needs, such as access to water and grazing as well as human and livestock safety, reflective of a domination value orientation. Living in extreme deserts likely magnifies these issues, many of which are also associated with poverty (Middleton et al. 2011; Durant et al. 2014). Pastoralists in our study suggested multiple ways to reduce the primary challenge of predators killing livestock. Some supported harvesting predators to manage to population sizes. Others favored

translocating them to parks, private farms, or concession areas (i.e., removing some proportion of individual animals from the conservancies). Nearly one-quarter of interviews favored fencing predators on the conservancies, but away from human settlements. This would allow them to retain the benefits that predators bring as tourist attractions (reflective of beliefs about economic gains tied to domination), but also would provide local residents and their children the chance to still encounter these species (reflective of the attraction value orientation). Although drought was also frequently described as a challenge to living in the region, many felt that little can be done to address this problem and instead focused their responses on ways to reduce conflicts with predators.

Our findings can be used to inform future conservation efforts in northwestern Namibia and other similar arid landscapes. The data we collected not only offer a baseline for future studies, but also identified several potential solutions to reduce human-wildlife conflicts in the region. While most interviewees showed relatively high levels of tolerance of the local wildlife community, including predators, many also recognized the threats that predators pose for livestock and human safety. Participants suggested means to address these risks through reductions in predator populations or limiting the spatial overlap between predator species and people with their livestock. Our research initially focused on identifying wildlife value orientations among Namibian pastoralists (a new geographic contribution to previous cross-cultural research on wildlife value orientations) because, by understanding existing value structures, one can anticipate human attitudes and behaviors and work within those value structures to design more effective solutions to conservation challenges (Manfredo et al. 2016,

2017). Our findings suggest that pastoralists would not favor the complete removal of predators, as they value their existence, but recognize that management efforts are needed to mitigate the conflicts affecting livestock and human safety. Combined with our results on value orientations in the region, the solutions identified in this study highlight potential opportunities for management interventions that may have a greater likelihood of success based on local pastoralists' support. Managing these issues over time, however, will require further monitoring to understand the dynamic social and ecological factors at play that could alter the system.

Some of our findings point to areas where future research would be beneficial to contribute to this need for monitoring. Modernization, globalization, and climate change are likely to affect the social-ecological conditions of this pastoralist society over time (e.g., increased drought, transitions to less nomadic lifestyles), which could in turn result in changes to value structures, rates of human-wildlife conflicts, and species tolerance. We detected traces of these outside influences that may warrant further exploration. For example, responses indicating a spiritual/religious value orientation referenced a Judeo-Christian God, suggestive of the far-reaching influence of missionaries in rural Namibia. Additionally, as Namibian pastoralists increasingly settle and adopt small-scale subsistence farming, their tolerance for conflict-prone species may be reduced, as was the case in central Kenya (Gadd 2005). We recommend exploring these dynamics of tolerance in greater depth, perhaps with additional questions and methods that could expand upon our qualitative approach.

Our methodology consisted largely of semi-structured interviews, which included questions containing emotional prompts to elicit stories about wildlife. The latter allowed

us to build upon and extend previous cross-cultural research on wildlife value orientations employing a similar approach (e.g., see *Human Dimensions of Wildlife* volume 12, issue 5). Replication of these qualitative methods and thorough descriptions of local contexts can allow for comparison across societies, including those where barriers to quantitative survey research such as limited literacy may exist (Dayer et al. 2007). In addition, had we used quantitative survey methods typical of wildlife value orientation assessments in more modernized countries (e.g., Teel & Manfredo 2009; Manfredo et al. 2016), we would not have obtained an in-depth understanding of pastoralists' relationships and interactions with specific species. Nor would we have been able to adequately understand some of the ecological and cultural conditions shaping these relationships, an understanding that was also enhanced by the inclusion of an ecological component in our study. In the future, we suggest using a plurality of quantitative and qualitative methods to allow researchers the flexibility to generalize across a larger sample of respondents, while still maintaining credibility by remaining grounded in the participants' lived realities and the local context of the conservation issues of interest.

Our work advances knowledge about wildlife values globally as part of a social-ecological systems approach, illustrating the preponderance of a domination ideology in an African pastoralist society not previously explored in cross-cultural wildlife value orientation assessments. In addition to domination, we identified a diverse suite of other value orientations and belief dimensions, some of which have been detected in these earlier assessments for other cultures and geographic locations. Our qualitative approach was also useful for eliciting pastoralists' perceptions of challenges and

potential solutions to human-wildlife coexistence, furthering our understanding of conservation issues and opportunities in extreme arid environments. Our findings, as a whole, can contribute to development of more effective conservation initiatives, management interventions, and monitoring efforts that better account for the local cultural context, particularly in similar regions practicing community-based natural resource management.

Table 3.1. Wildlife value orientations and belief dimensions from a 2017 interview of Namibian pastoralists.

Wildlife value orientations and belief dimensions	Example quotation(s)*
Domination	
Hunting	"Sometimes you are so hungry at home, you think it is better to go around in the bush and shoot the animal"
Economic gains	
Compensation	"Now-a-days there's less farmers because of predators and so on, so that's the sad side of the story, but we gain something like a certain compensation, but... it's not really market-related"
Employment	"In general, he's quite happy with wildlife because it brings, it creates employment and the conservancy all them enter in joint ventures and they make also money out of it, so he just wants to be more educated, to be more involved in wildlife management"
Tourism	"They do make not only me, but all of us in Namibia happy because we get tourism from the outside. They come look at animals they do not have [where they are from] and it brings income to Namibia"
Concern for human safety	"And then he saw the leopard coming down with the klipspringer in her mouth and then he ran down. And then he moved on the other mountain and ran away... He was never coming so close in his life to the leopard"
Concern for property	
Livestock wellbeing	"So he was also a farmer, but when the lions and the cheetah went in his corral and killed all his animals that is the day when he quit or gave up farming." "Zebra [will make you sad]. It's grazing too close to the people and using a lot of grazing"
Crops	"The elephants come and they come and destroy our gardens..."
Water structures/buildings	"[The elephants] break our pump and the pipes that bring the water to our homes..."
Mutualism	

Caring	"One day I was on my patrol... and when I went somewhere I saw an oryx in a foot trap. He was still alive maybe for two to three days. It made me really sad"
Extended family/friends	"For me there's some wildlife that makes me sad, like for me I like mostly the elephant, so I have been adapted from elephant currently. I'm just feeling like if I saw an elephant die, [it would] just feel like I have saw my own cattle [die]"
Trust/respect	"All you have to do is just train [wild animals]. They will understand it." "It's wrong if I caught a snake there at the mountain and I want to kill it- it's totally wrong and I will not even support such an activity- just killing because you come together. I don't think that that snake will enter up here, so that's the snake's habitat. Respect and I also want [my habitat] to be respected"
Attraction/Interest	
For self	"For me, it makes me happy to see wild animals roaming freely all over"
For future generations	"I like wild animals because I don't want them to die out because if those wild animals are dying out, my future generation will never see what it's looking like and those kind of business"
Rational/Scientific	"[Elephant manure] was also used to help us with medicine- maybe the blood, your nose is running, or you're having a headache or you're scratching your body then you put in the water and then you shower [in] it."
Spiritual/Religious	"You know God created everything and after that he went to sit and said to himself now I must create the human being to guard over these things"

* Additional example quotations and code descriptions can be found in Appendix 3.4.

Table 3.2. Measurements of species tolerance from a 2017 interview of Namibian pastoralists (n = 86).

Species	Positive Interactions % of interviews ^b	Negative Interactions % of interviews ^b	Would not conserve ^a % of interviews ^b
Herbivores			
Elephant	27.9%	54.7%	4.7%
Giraffe	15.1%	—	—
Kudu	5.8%	—	—
Oryx	7.0%	—	—
Rhino	4.65%	5.8%	1.2%
Springbok	34.9%	1.2%	—
Zebra	24.4%	2.3%	—
Predators			
Cheetah	—	23.3%	4.7%
Hyena	1.2%	23.3%	2.3%
Jackal	2.3%	12.8%	3.5%
Leopard	—	36.0%	5.8%
Lion	5.8%	66.3%	20.9%
Predators ^c	—	3.5%	—
Other			
Baboon	2.3%	3.5%	1.2%
Honey badger	1.2%	—	—
Ostrich	3.5%	—	—
Snakes	—	3.5%	—
Vultures	—	1.2%	—
Warthog	1.2%	—	—

^a Interview responses to the question, “which wild animals, if any, do you think should not be conserved or protected?”

^b We report the percentage of total interviews, including focus groups, that mention these themes as opposed to individual respondents.

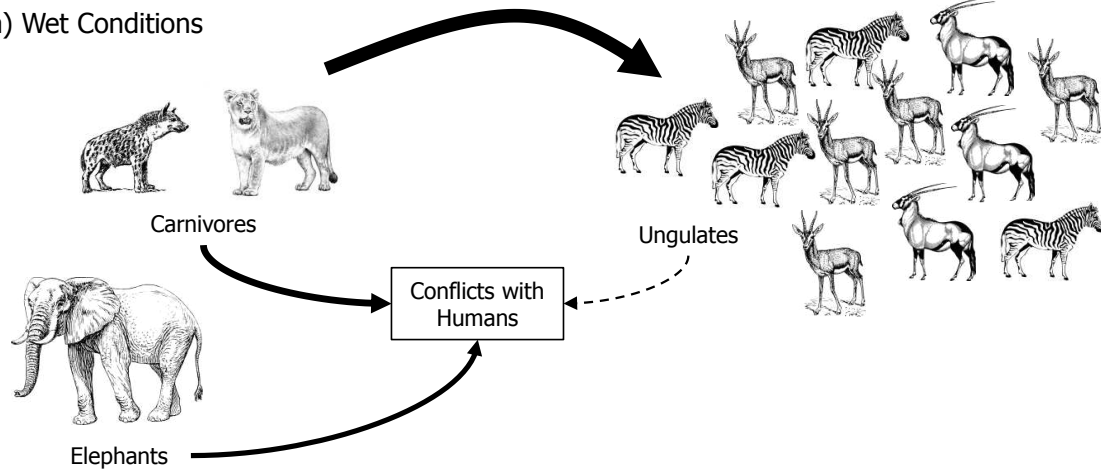
^c Interview responses that failed to specify a particular predator species.

Table 3.3. The top five themes mentioned as perceived challenges and solutions to living with wildlife from a 2017 interview of Namibian pastoralists (n = 86).

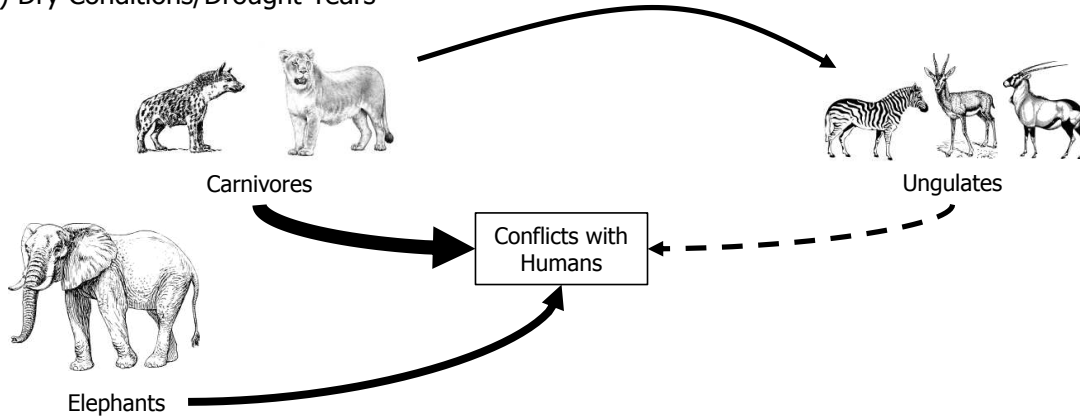
Themes	% of interviews*
Challenges	
Predators killing livestock	91.9%
Drought	53.5%
Elephants destroying crops and water structures	14.0%
Ethnic conflicts over land and cattle	14.0%
Problems related to conservancy management (e.g., poaching, overgrazing, and a lack of understanding of the conservancy system's goals)	10.5%
Solutions	
Harvest or trophy hunt predators	31.4%
Translocate wildlife to parks, private farms, or concession areas	29.1%
Fence predators within conservancy boundaries	23.3%
Hire more people to monitor wildlife movements and notify residents of their whereabouts	17.4%
Stricter immigration laws and greater penalties for stealing livestock	10.5%

* We report the percentage of total interviews, including focus groups, that mention these themes as opposed to individual respondents.

(a) Wet Conditions



(b) Dry Conditions/Drought Years



(c) Food Pyramid

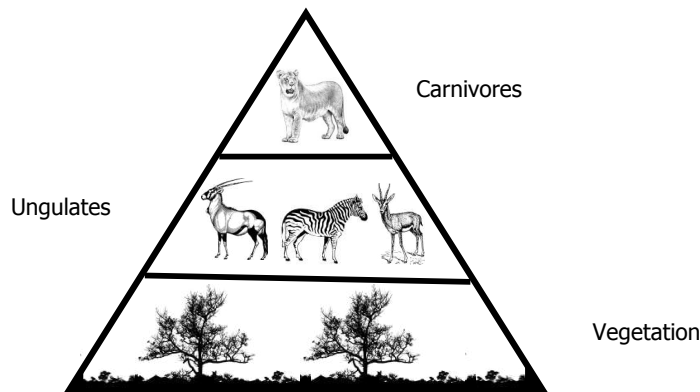


Figure 3.1. Wildlife behaviors, relative abundance, and threats to human livelihood differ between (a) wet conditions and (b) dry conditions or drought years. Arrow width signify the relative strength of interactions. Solid arrows indicate direct effects of one trophic level on another or their contribution to human-wildlife conflicts, while dashed arrows indicate the indirect effect of ungulates on pastoralists' livestock through competition for grazing. Conflicts with humans also refers to the destruction of water structures and crops, as well as threats to livestock and personal safety. The food pyramid (c) illustrates that biomass reduces at higher trophic levels and is dependent on the amount of vegetation in desert landscapes.

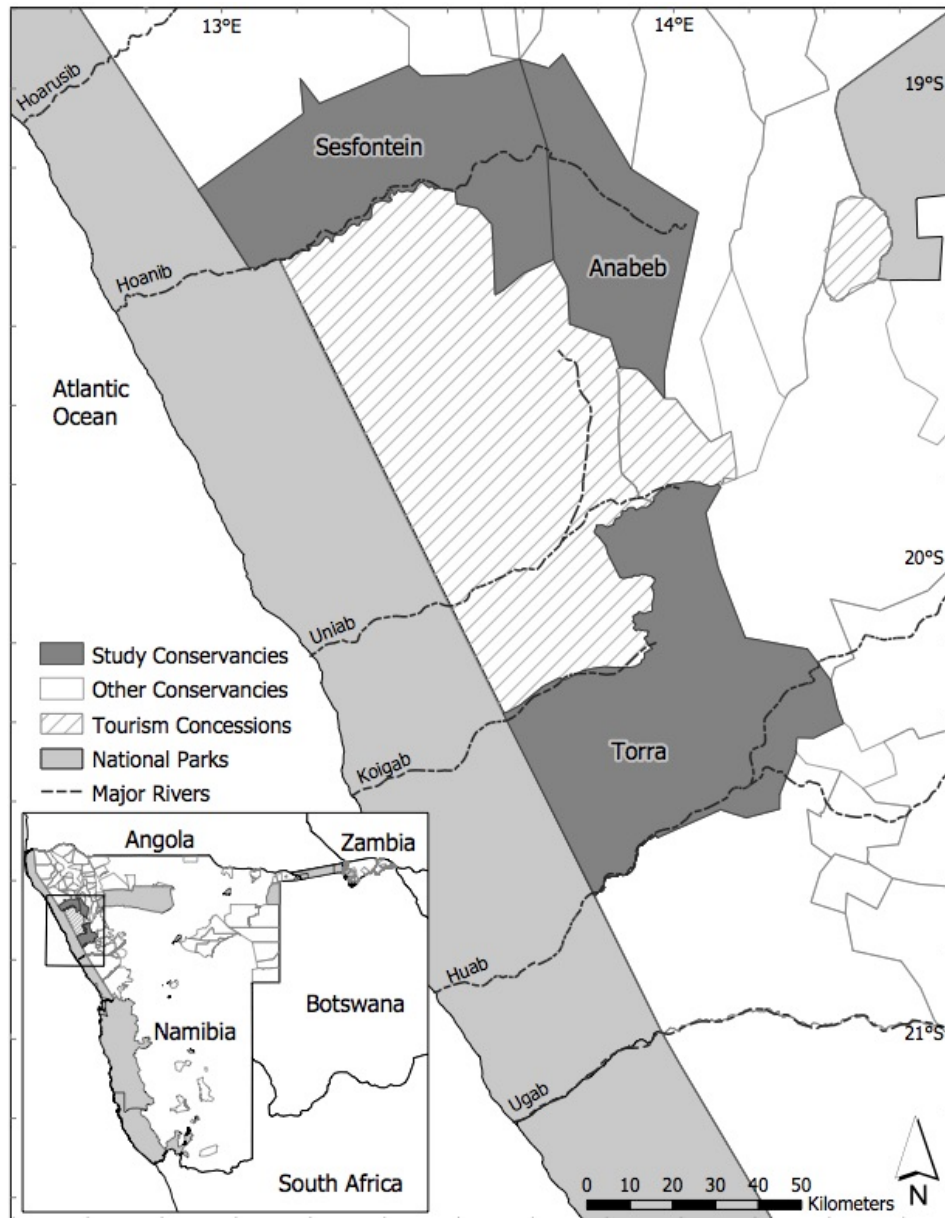


Figure 3.2. Study area map featuring conservancies in northwestern Namibia.

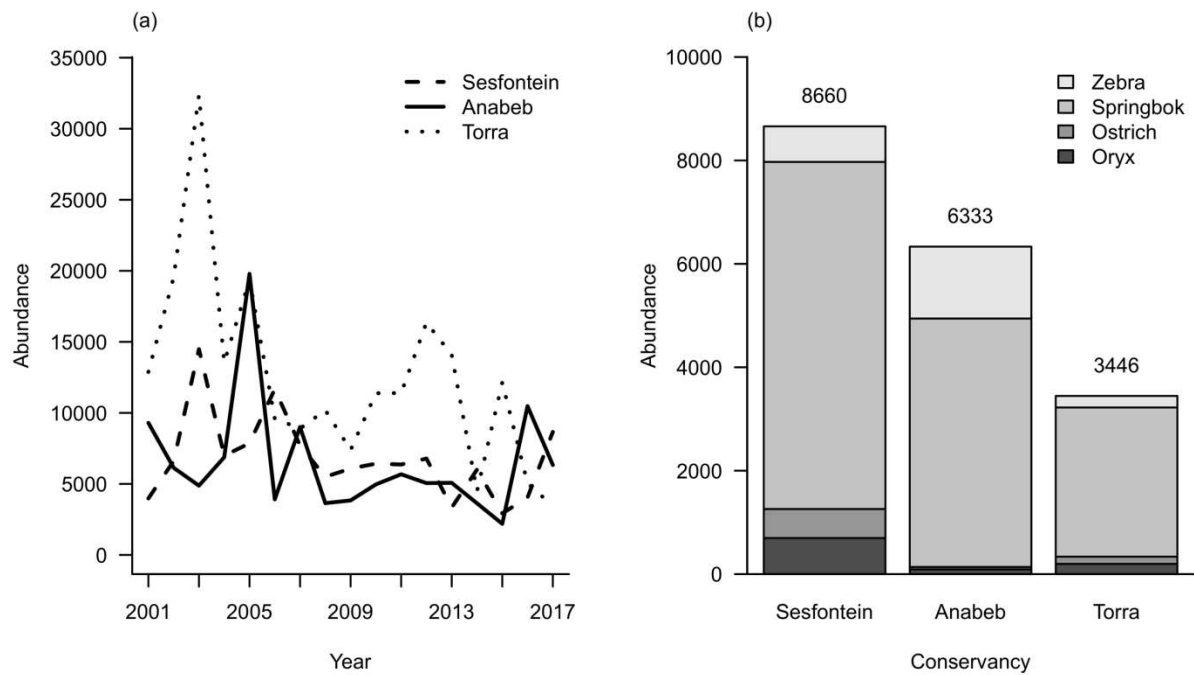


Figure 3.3. Wildlife abundance trends estimated from road surveys (a) for summed populations of oryx, ostrich, springbok, and Hartmann's mountain zebra across time, and (b) for the year of 2017 alone. Numbers above the bars in (b) represent the summed abundance of oryx, ostrich, springbok, and Hartmann's mountain zebra for each conservancy. Annual estimates are presented from June 2001 to 2017 (NACSO 2018a).

LITERATURE CITED

- Acebes P, Malo JE, Traba J. 2013. Trade-offs between food availability and predation risk in desert environments: the case of polygynous monomorphic guanaco (*Lama guanicoe*). *Journal of Arid Environments* **97**:136–142.
- Adams RA, Pedersen SC, Thibault KM, Jadin J, Petru B. 2003. Calcium as a limiting resource to insectivorous bats: can water holes provide a supplemental mineral source? *Journal of Zoology* **260**:189–194.
- Adams RA, Thibault KM. 2006. Temporal resource partitioning by bats at water holes. *Journal of Zoology* **270**:466–472.
- Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences* **106**:4947–4952.
- Bandyopadhyay S, Shyamsundar P, Wang L, Humavindu MN. 2004. Do households gain from community-based natural resource management? An evaluation of community conservancies in Namibia. DEA Research Discussion Paper 68. Directorate of Environmental Affairs, Ministry of Environment and Tourism, Windhoek, Namibia.
- Barclay RM. 1994. Constraints on reproduction by flying vertebrates: energy and calcium. *The American Naturalist* **144**:1021–1031.
- Barnes RF. 2001. How reliable are dung counts for estimating elephant numbers? *African Journal of Ecology* **39**:1–9.

- Barua M, Bhagwat SA, Jadhav S. 2013. The hidden dimensions of human–wildlife conflict: Health impacts, opportunity and transaction costs. *Biological Conservation* **157**:309–316.
- Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **57**:289–300.
- Bennett NJ, Roth R, Klain SC, Chan KM, Clark DA, Cullman G, Epstein G, Nelson MP, Stedman R, Teel TL. 2017. Mainstreaming the social sciences in conservation. *Conservation Biology* **31**:56–66.
- Benton MJ. 2009. The Red Queen and the Court Jester: Species diversity and the role of biotic and abiotic factors through time. *Science* **323**:728–732.
- Berger J. 1997. Population constraints associated with the use of black rhinos as an umbrella species for desert herbivores. *Conservation Biology* **11**:69–78.
- Bleich VC, Andrew NG, Martin MJ, Mulcahy GP, Pauli AM, Rosenstock SS. 2006. Quality of water available to wildlife in desert environments: comparisons among anthropogenic and natural sources. *Wildlife Society Bulletin* **34**:627–632.
- Bogan MT, Noriega-Felix N, Vidal-Aguilar SL, Findley LT, Lytle DA, Gutiérrez-Ruacho OG, Alvarado-Castro JA, Varela-Romero A. 2014. Biogeography and conservation of aquatic fauna in spring-fed tropical canyons of the southern Sonoran Desert, Mexico. *Biodiversity and Conservation* **23**:2705–2748.
- Braverman Y, Kitron U, Killick-Kendrick R. 1991. Attractiveness of vertebrate hosts to *Culex pipiens* (Diptera: Culicidae) and other mosquitoes in Israel. *Journal of Medical Entomology* **28**:133–138.

- Brodie JF, Muntifering J, Hearn M, Loutit B, Loutit R, Brell B, Uri-Khob S, Leader-Williams N, Du Preez P. 2011. Population recovery of black rhinoceros in north-west Namibia following poaching. *Animal Conservation* **14**:354–362.
- Brown JH, Ernest SM. 2002. Rain and rodents: Complex dynamics of desert consumers. *BioScience* **52**:979–987.
- Browne-Núñez C, Jacobson SK, Vaske JJ. 2013. Beliefs, attitudes, and intentions for allowing elephants in group ranches around Amboseli National Park, Kenya. *Wildlife Society Bulletin* **37**:639–648.
- Broyles B. 1995. Desert wildlife water developments: Questioning use in the southwest. *Wildlife Society Bulletin* **23**:663–675.
- Bruskotter JT, Singh A, Fulton DC, Slagle K. 2015. Assessing tolerance for wildlife: Clarifying relations between concepts and measures. *Human Dimensions of Wildlife* **20**:255–270.
- Burnham KP, Anderson DR. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* **33**:261–304.
- Cardinal E, Martin J-L, Côté SD. 2012. Large herbivore effects on songbirds in boreal forests: lessons from deer introduction on Anticosti Island. *Ecoscience* **19**:38–47.
- Caro T. 2010. Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species. Island Press, Washington, D.C.
- Carpenter RE. 1969. Structure and function of the kidney and the water balance of desert bats. *Physiological Zoology* **42**:288–302.

- Carter NH, Viña A, Hull V, McConnell WJ, Axinn W, Ghimire D, Liu J. 2014. Coupled human and natural systems approach to wildlife research and conservation. *Ecology and Society* **19**:43.
- Cerri J, Mori E, Vivarelli M, Zaccaroni M. 2017. Are wildlife value orientations useful tools to explain tolerance and illegal killing of wildlife by farmers in response to crop damage? *European Journal of Wildlife Research* **63**:70.
- Charles GK, Porensky LM, Riginos C, Veblen KE, Young TP. 2017. Herbivore effects on productivity vary by guild: cattle increase mean productivity while wildlife reduce variability. *Ecological Applications* **27**:143–155.
- Coffey A, Atkinson P. 1996. Making sense of qualitative data: Complementary research strategies. Sage Publications, Inc, Thousand Oaks, CA.
- Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302–1310.
- Coogan SC, Nielsen SE, Stenhouse GB. 2012. Spatial and temporal heterogeneity creates a “brown tide” in root phenology and nutrition. *ISRN Ecology* **2012**:618257.
- Creswell JW. 1998. Qualitative inquiry and research design: Choosing among five traditions. Sage Publications, Inc, Thousand Oaks, CA.
- Crooks KR, Soulé ME. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**:563.
- Cunningham C, Berger J. 1997. Horn of darkness: Rhinos on the edge. Oxford University Press, New York, NY.

- Darwin C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London.
- Davis JA, Kerezszy A, Nicol S. 2017. Springs: conserving perennial water is critical in arid landscapes. *Biological Conservation* **211**:30–35.
- Dayer AA, Stinchfield HM, Manfredo MJ. 2007. Stories about wildlife: Developing an instrument for identifying wildlife value orientations cross-culturally. *Human Dimensions of Wildlife* **12**:307–315.
- Department of Water Affairs. 1991. Guidelines for the evaluation of drinking water for human consumption with reference to the chemical, physical and bacteriological quality. Pages 1–5. Windhoek, Namibia.
- Dickman AJ. 2010. Complexities of conflict: The importance of considering social factors for effectively resolving human–wildlife conflict. *Animal Conservation* **13**:458–466.
- Dinno A. 2017. conover.test: Conover-Iman test of multiple comparisons using rank sums. R package version 1.1.5. Available from <https://CRAN.R-project.org/package=conover.test>.
- Drusch M, Del Bello U, Carlier S, Colin O, Fernandez V, Gascon F, Hoersch B, Isola C, Laberinti P, Martimort P. 2012. Sentinel-2: ESA's optical high-resolution mission for GMES operational services. *Remote Sensing of Environment* **120**:25–36.
- Du Toit JT, Cumming DH. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity & Conservation* **8**:1643–1661.

- Durant SM, Pettorelli N, Bashir S, Woodroffe R, Wacher T, De Ornellas P, Ransom C, Abáigar T, Abdelgadir M, El Alqamy H. 2012. Forgotten biodiversity in desert ecosystems. *Science* **336**:1379–1380.
- Durant SM, Wacher T, Bashir S, Woodroffe R, Ornellas P, Ransom C, Newby J, Abáigar T, Abdelgadir M, El Alqamy H. 2014. Fiddling in biodiversity hotspots while deserts burn? Collapse of the Sahara's megafauna. *Diversity and Distributions* **20**:114–122.
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JB. 2011. Trophic downgrading of planet Earth. *Science* **333**:301–306.
- Fennessy J. 2009. Home range and seasonal movements of *Giraffa camelopardalis angolensis* in the northern Namib Desert. *African Journal of Ecology* **47**:318–327.
- Fenton MB. 1970. A technique for monitoring bat activity with results obtained from different environments in southern Ontario. *Canadian Journal of Zoology* **48**:847–851.
- Fenton MB, Cumming DH, Rautenbach IL, Cumming GS, Cumming MS, Ford G, Taylor RD, Dunlop J, Hovorka MD, Johnston DS. 1998. Bats and the loss of tree canopy in African woodlands. *Conservation Biology* **12**:399–407.
- Fox HE, Christian C, Nordby JC, Pergams OR, Peterson GD, Pyke CR. 2006. Perceived barriers to integrating social science and conservation. *Conservation Biology* **20**:1817–1820.

- Frossard A, Ramond J-B, Seely M, Cowan DA. 2015. Water regime history drives responses of soil Namib Desert microbial communities to wetting events. *Scientific Reports* **5**:12263.
- Fuller TK. 1991. Do pellet counts index white-tailed deer numbers and population change? *Journal of Wildlife Management* **55**:393–396.
- Gadd ME. 2005. Conservation outside of parks: Attitudes of local people in Laikipia, Kenya. *Environmental Conservation* **32**:50–63.
- Galvin KA. 2009. Transitions: Pastoralists living with change. *Annual Review of Anthropology* **38**:185–198.
- Glesne C. 2006. Making words fly: Developing understanding through interviewing. Pages 79–108 *Becoming qualitative researchers: An introduction*, 3rd edition. Pearson, Boston.
- Gorelick N, Hancher M, Dixon M, Ilyushchenko S, Thau D, Moore R. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment* **202**:18–27.
- Grace JB. 2006. *Structural equation modeling and natural systems*. Cambridge University Press, Cambridge.
- Griffiths SR, Donato DB, Lumsden LF, Coulson G. 2014. Hypersalinity reduces the risk of cyanide toxicosis to insectivorous bats interacting with wastewater impoundments at gold mines. *Ecotoxicology and Environmental Safety* **99**:28–34.
- Gutteridge L, Liebenberg L. 2013. *Mammals of southern Africa and their tracks and signs*. Jacana Media, Auckland Park, South Africa.

- Hagen EM, Sabo JL. 2014. Temporal variability in insectivorous bat activity along two desert streams with contrasting patterns of prey availability. *Journal of Arid Environments* **102**:104–112.
- Hatton IA, McCann KS, Fryxell JM, Davies TJ, Smerlak M, Sinclair AR, Loreau M. 2015. The predator-prey power law: Biomass scaling across terrestrial and aquatic biomes. *Science* **349**:aac6284.
- Hermann N, Voß C, Menzel S. 2013. Wildlife value orientations as predicting factors in support of reintroducing bison and of wolves migrating to Germany. *Journal for Nature Conservation* **21**:125–132.
- Holdo RM, Holt RD, Fryxell JM. 2009. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist* **173**:431–445.
- Illius AW, O'Connor TG. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. *Ecological Applications* **9**:798–813.
- Inglehart R, Welzel C. 2005. Modernization, cultural change and democracy: The human development sequence. Cambridge University Press, New York.
- Innis SA, Naiman RJ, Elliott SR. 2000. Indicators and assessment methods for measuring the ecological integrity of semi-aquatic terrestrial environments. *Hydrobiologia* **422**:111–131.
- Jacobson PJ, Jacobson KM. 2013. Hydrologic controls of physical and ecological processes in Namib Desert ephemeral rivers: Implications for conservation and management. *Journal of Arid Environments* **93**:80–93.

- Jacobson PJ, Jacobson KM, Seely MK. 1995. Ephemeral rivers and their catchments: Sustaining people and development in western Namibia. Desert Research Foundation of Namibia, Windhoek, Namibia.
- Jones BTB, Mosimane A. 2000. Empowering communities to manage natural resources: Where does the new power lie? Case studies from Namibia. Directorate of Environmental Affairs (DEA) Research Discussion Paper **40**:1–32.
- Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA. 2009. Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* **8**:93–115.
- Kaczensky P. 2007. Wildlife value orientations of rural Mongolians. *Human Dimensions of Wildlife* **12**:317–329.
- Kingsford RT, Georges A, Unmack PJ. 2006. Vertebrates of desert rivers: Meeting the challenges of temporal and spatial unpredictability. Pages 154–200 in R. T. Kingsford, editor. *Ecology of desert rivers*. Cambridge University Press, Cambridge.
- Kingston T. 2009. Analysis of species diversity of bat assemblages. *Ecological and behavioral methods for the study of bats* **2**:195–215.
- Koenig R. 2000. Wildlife deaths are a grim wake-up call in Eastern Europe. *Science* **287**:1737–1738.
- Korine C, Adams AM, Shamir U, Gross A. 2015. Effect of water quality on species richness and activity of desert-dwelling bats. *Mammalian Biology* **80**:185–190.
- Korine C, Adams R, Russo D, Fisher-Phelps M, Jacobs D. 2016. Bats and water: Anthropogenic alterations threaten global bat populations. Pages 215–241 in C.

- C. Voigt and T. Kingston, editors. Bats in the Anthropocene: Conservation of bats in a changing world. Springer International Publishing, Cham, Switzerland.
- Kurta A, Kunz TH, Nagy KA. 1990. Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. *Journal of Mammalogy* **71**:59–65.
- Laake JL, Buckland ST, Anderson DR, Burnham KP. 1993. DISTANCE user's guide V2.0. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.
- Landman M, Schoeman DS, Hall-Martin AJ, Kerley GI. 2012. Understanding long-term variations in an elephant piosphere effect to manage impacts. *PLoS One* **7**:e45334.
- Lang AB, Kalko EK, Römer H, Bockholdt C, Dechmann DK. 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* **146**:659–666.
- Lange RT. 1969. The piosphere: sheep track and dung patterns. *Journal of Range Management*:396–400.
- Laverty TM. 2019. Bats, elephants, and their food: A conservation perspective on trophic interactions in the Namib Desert. Ph.D. dissertation. Colorado State University, Fort Collins, CO.
- Laverty TM, Teel TL, Thomas REW, Gawusab AA, Berger J. 2019. Using pastoral ideology to understand human-wildlife coexistence in arid agricultural landscapes. *Conservation Science and Practice* **1**:e35.
- Laws RM. 1970. Elephants as agents of habitat and landscape change in East Africa. *Oikos*:1–15.

- Le S, Josse J, Husson F. 2008. FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software* **25**:1–18.
- Leggett K. 2006a. Effect of artificial water points on the movement and behaviour of desert-dwelling elephants of north-western Namibia. *Pachyderm* **40**:24–34.
- Leggett K, Fennessy J, Schneider S. 2003a. Seasonal vegetation changes in the Hoanib River catchment, north-western Namibia: A study of a non-equilibrium system. *Journal of Arid Environments* **53**:99–113.
- Leggett K, Fennessy J, Schneider S. 2003b. Seasonal distributions and social dynamics of elephants in the Hoanib River catchment, northwestern Namibia. *African Zoology* **38**:305–316.
- Leggett K, Schneider S, Fennessy J. 2004. A study of animal movement in the Hoanib River catchment, northwestern Namibia. *African Zoology* **39**:1–11.
- Leggett KE. 2006b. Home range and seasonal movement of elephants in the Kunene Region, northwestern Namibia. *African Zoology* **41**:17–36.
- Leggett KEA, Fennessy J, Schneider S. 2001. Rainfall, water sources and water use in the Hoanib River catchment, northwestern Namibia. *Desert Research Foundation of Namibia Occasional Paper* **15**:37–75.
- Levy RI, Hollan DW, Bernard HR. 1998. Person-centered interviewing and observation. Pages 333–364 *Handbook of methods in cultural anthropology*. Altamira Press, Walnut Creek, CA.
- Li H, Kalcounis-Rueppell M. 2018. Separating the effects of water quality and urbanization on temperate insectivorous bats at the landscape scale. *Ecology and Evolution* **8**:667–678.

- Lindsey PA, Roulet PA, Romanach SS. 2007. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological Conservation* **134**:455–469.
- Lischka SA, Teel TL, Johnson HE, Reed SE, Breck S, Carlos AD, Crooks KR. 2018. A conceptual model for the integration of social and ecological information to understand human-wildlife interactions. *Biological Conservation* **225**:80–87.
- Lisón F, Calvo JF. 2011. The significance of water infrastructures for the conservation of bats in a semiarid Mediterranean landscape. *Animal Conservation* **14**:533–541.
- Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI, Callaway RM. 2004. Rethinking plant community theory. *Oikos* **107**:433–438.
- MacArthur RH. 1984. *Geographical ecology: Patterns in the distribution of species*. Princeton University Press, Princeton, NJ.
- Manfredo MJ, Bruskotter JT, Teel TL, Fulton D, Schwartz SH, Arlinghaus R, Oishi S, Uskul AK, Redford K, Kitayama S. 2017. Why social values cannot be changed for the sake of conservation. *Conservation Biology* **31**:772–780.
- Manfredo MJ, Dayer AA. 2004. Concepts for exploring the social aspects of human–wildlife conflict in a global context. *Human Dimensions of Wildlife* **9**:1–20.
- Manfredo MJ, Teel TL, Dietsch AM. 2016. Implications of human value shift and persistence for biodiversity conservation. *Conservation Biology* **30**:287–296.
- Manfredo MJ, Teel TL, Gavin MC, Fulton D. 2014. Considerations in representing human individuals in social-ecological models. Pages 137–158 in M. J. Manfredo, A. Rechkemmer, and J. J. Vaske, editors. *Understanding society and*

- natural resources: Forging new strands of integration across the social sciences. Springer Press, New York.
- Marker LL, Mills MGL, Macdonald DW. 2003. Factors influencing perceptions of conflict and tolerance toward cheetahs on Namibian farmlands. *Conservation Biology* **17**:1290–1298.
- Marques FF, Buckland ST, Goffin D, Dixon CE, Borchers DL, Mayle BA, Peace AJ. 2001. Estimating deer abundance from line transect surveys of dung: Sika deer in southern Scotland. *Journal of Applied Ecology* **38**:349–363.
- Martin TE. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: Climate change impacts? *Ecology* **82**:175–188.
- McCain CM. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* **16**:1–13.
- McCauley DJ, Keesing F, Young TP, Allan BF, Pringle RM. 2006. Indirect effects of large herbivores on snakes in an African savanna. *Ecology* **87**:2657–2663.
- McLean JA, Speakman JR. 1999. Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation in lactation. *Functional Ecology* **13**:360–372.
- McNaughton SJ, Banyikwa FF, McNaughton MM. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* **278**:1798–1800.
- Middleton N, Stringer L, Goudie A, Thomas D. 2011. The forgotten billion: MDG achievement in the drylands. Pages 1–64 United Nations Office at Nairobi,

- Publishing Services Section, ISO 14001:2004. Available from http://catalogue.unccd.int/39_Forgotten_Billion.pdf (accessed October 3, 2018).
- Millenium Ecosystem Assessment. 2005. Ecosystems and human well-being: Biodiversity synthesis. World Resources Institute, Washington, D.C.
- Monadjem A, Taylor PJ, Cotterill W, Schoeman MC. 2010. Bats of southern and central Africa: A biogeographic and taxonomic synthesis. Wits University Press, Johannesburg.
- Mooring MS, Fitzpatrick TA, Fraser IC, Benjamin JE, Reisig DD, Nishihira TT. 2003. Insect-defense behavior by desert bighorn sheep. *The Southwestern Naturalist*:635–643.
- Moranz RA, Debinski DM, McGranahan DA, Engle DM, Miller JR. 2012. Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. *Biodiversity and Conservation* **21**:2719–2746.
- Morzillo AT, de Beurs KM, Martin-Mikle CJ. 2014. A conceptual framework to evaluate human-wildlife interactions within coupled human and natural systems. *Ecology and Society* **19**:14.
- NACSO. 2016. The state of community conservation in Namibia: A review of communal conservancies, community forests and other CBNRM initiatives. 2016 Annual Report. NACSO, Windhoek, Namibia.
- NACSO. 2018a. Resources and publications: Game count data. Available from <http://www.nacso.org.na/resources/game-count-data> (accessed December 13, 2018).

- NACSO. 2018b. Resources and publications: Conservancy profile data. Available from <http://www.nacso.org.na/resources/conservancy-profile-data> (accessed December 13, 2018).
- Naidoo S, Vosloo D, Schoeman MC. 2013. Foraging at wastewater treatment works increases the potential for metal accumulation in an urban adapter, the banana bat (*Neoromicia nana*). *African Zoology* **48**:39–55.
- Newing H, Eagle CM, Puri R, Watson CW. 2011. Conducting research in conservation: Social science methods and practice. Routledge, London.
- Noy-Meir I. 1974. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**:25–51.
- O'Brien CS, Waddell RB, Rosenstock SS, Rabe MJ. 2006. Wildlife use of water catchments in southwestern Arizona. *Wildlife Society Bulletin* **34**:582–591.
- Ogada DL, Gadd ME, Ostfeld RS, Young TP, Keesing F. 2008. Impacts of large herbivorous mammals on bird diversity and abundance in an African savanna. *Oecologia* **156**:387.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Wagner H. 2013. *Vegan: Community Ecology Package*. Available from <http://CRAN.R-project.org/package=vegan/>.
- Olsen RL, Chappell RW, Loftis JC. 2012. Water quality sample collection, data treatment and results presentation for principal components analysis—literature review and Illinois River watershed case study. *Water Research* **46**:3110–3122.

- Olsson P-E, Kling P, Hogstrand C. 1998. Mechanisms of heavy metal accumulation and toxicity in fish. Pages 321–350 *Metal metabolism in aquatic environments*. Springer, New York.
- Owen-Smith RN. 1992. Megaherbivores: The influence of very large body size on ecology. Cambridge University Press, Cambridge.
- Paine RT. 2000. Phycology for the mammalogist: marine rocky shores and mammal-dominated communities—how different are the structuring processes? *Journal of Mammalogy* **81**:637–648.
- Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jędrzejewska B, Lima M, Kausrud K. 2011. The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Climate Research* **46**:15–27.
- Piñero FS, Avila JM. 2004. Dung-insect community composition in arid zones of south-eastern Spain. *Journal of Arid Environments* **56**:303–327.
- Plumptre AJ, Harris S. 1995. Estimating the biomass of large mammalian herbivores in a tropical montane forest: A method of faecal counting that avoids assuming a “steady state” system. *Journal of Applied Ecology*:111–120.
- Polis GA. 1991. Complex trophic interactions in deserts: An empirical critique of food-web theory. *The American Naturalist* **138**:123–155.
- Pooley SP, Mendelsohn JA, Milner-Gulland EJ. 2014. Hunting down the chimera of multiple disciplinarity in conservation science. *Conservation Biology* **28**:22–32.
- Pöyry J, Lindgren S, Salminen J, Kuussaari M. 2004. Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications* **14**:1656–1670.

- Pringle RM, Young TP, Rubenstein DI, McCauley DJ. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *Proceedings of the National Academy of Sciences* **104**:193–197.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from Available from <https://www.R-project.org/>.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from Available from <https://www.R-project.org/>.
- Ramey EM, Ramey RR, Brown LM, Kelley ST. 2013. Desert-dwelling African elephants (*Loxodonta africana*) in Namibia dig wells to purify drinking water. *Pachyderm* **53**:66–72.
- Ratcliffe DA. 1967. Decrease in eggshell weight in certain birds of prey. *Nature* **215**:208.
- Razgour O, Korine C, Saltz D. 2010. Pond characteristics as determinants of species diversity and community composition in desert bats. *Animal Conservation* **13**:505–513.
- Razgour O, Korine C, Saltz D. 2011. Does interspecific competition drive patterns of habitat use in desert bat communities? *Oecologia* **167**:493–502.
- Rebelo H, Brito JC. 2007. Bat guild structure and habitat use in the Sahara desert. *African Journal of Ecology* **45**:228–230.
- Redpath SM et al. 2013. Understanding and managing conservation conflicts. *Trends in Ecology & Evolution* **28**:100–109.

- Rickenbach O, Reyes-García V, Moser G, García C. 2017. What explains wildlife value orientations? A study among Central African forest dwellers. *Human Ecology* **45**:293–306.
- Riginos C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology* **84**:124–133.
- Ripple WJ, Newsome TM, Wolf C, Dirzo R, Everatt KT, Galetti M, Hayward MW, Kerley GI, Levi T, Lindsey PA. 2015. Collapse of the world's largest herbivores. *Science Advances* **1**:e1400103.
- Rohan MJ. 2000. A rose by any name? The values construct. *Personality and Social Psychology Review* **4**:255–277.
- Ross SRP-J, Friedman NR, Dudley KL, Yoshimura M, Yoshida T, Economo EP. 2018. Listening to ecosystems: Data-rich acoustic monitoring through landscape-scale sensor networks. *Ecological Research* **33**:135–147.
- Rosseel Y. 2012. lavaan: An R Package for structural equation modeling. *Journal of Statistical Software* **48**:1–36.
- Rouse Jr. JW, Haas RH, Schell JA, Deering DW. 1974. Monitoring vegetation systems in the Great Plains with ERTS. Pages 309–317 *Proceedings of the Third Earth Resources Technology Satellite Symposium*, NASA SP-351. U.S. Government Printing Office, Washington, D.C.
- Russo D, Ancillotto L, Cistrone L, Korine C. 2016. The buzz of drinking on the wing in echolocating bats. *Ethology* **122**:226–235.
- Rust NA, Marker LL. 2014. Cost of carnivore coexistence on communal and resettled land in Namibia. *Environmental Conservation* **41**:45–53.

- Rust NA, Taylor N. 2016. Carnivores, colonization, and conflict: A qualitative case study on the intersectional persecution of predators and people in Namibia. *Anthrozoös* **29**:653–667.
- Sabo JL, Power ME. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. *Ecology* **83**:3023–3036.
- Safriel U et al. 2005. Dryland systems. Pages 623–662 in R. M. Hassan, R. Scholes, and N. Ash, editors. *Millennium Ecosystem Assessment: Ecosystems and human well-being*. Island Press, Washington, D.C.
- Scanlon LJ, Kull CA. 2009. Untangling the links between wildlife benefits and community-based conservation at Torra Conservancy, Namibia. *Development Southern Africa* **26**:75–93.
- Schindler DE, Armstrong JB, Bentley KT, Jankowski K, Lisi PJ, Payne LX. 2013. Riding the crimson tide: Mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters* **9**:20130048.
- Schoenly K. 1983. Arthropods associated with bovine and equine dung in an ungrazed Chihuahuan desert ecosystem. *Annals of the Entomological Society of America* **76**:790–796.
- Schwartz SH. 1992. Universals in the content and structure of values: Theoretical advances and empirical tests in 20 countries. *Advances in Experimental Social Psychology* **25**:1–65.
- Shannon G, Druce DJ, Page BR, Eckhardt HC, Grant R, Slotow R. 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology* **24**:281–289.

- Shaw D, Marker LL. 2010. The Conservancy Association of Namibia (CANAM): An Overview of Freehold Conservancies. CANAM, Windhoek, Namibia.
- Simmons RE, Griffin M, Griffin RE, Marais E, Kolberg H. 1998. Endemism in Namibia: Patterns, processes and predictions. *Biodiversity & Conservation* **7**:513–530.
- Singh NJ, Grachev IA, Bekenov AB, Milner-Gulland EJ. 2010. Tracking greenery across a latitudinal gradient in central Asia—the migration of the saiga antelope. *Diversity and Distributions* **16**:663–675.
- Stein AB, Fuller TK, Damery DT, Sievert L, Marker LL. 2010. Farm management and economic analyses of leopard conservation in north-central Namibia. *Animal Conservation* **13**:419–427.
- Stewart I, Seawright AA, Shaw GR. 2008. Cyanobacterial poisoning in livestock, wild mammals and birds—an overview. Pages 613–637 *Cyanobacterial harmful algal blooms: state of the science and research needs*. Springer.
- Straka TM, Lentini PE, Lumsden LF, Wintle BA, van der Ree R. 2016. Urban bat communities are affected by wetland size, quality, and pollution levels. *Ecology and Evolution* **6**:4761–4774.
- Strauss A, Corbin J. 1998. Axial coding. Pages 123–142 *Basics of qualitative research: Techniques and procedures for developing grounded theory*. Sage Publications, Inc, Thousand Oaks, CA.
- Studier EH. 1970. Evaporative water loss in bats. *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology* **35**:935–943.
- Teel TL, Manfredo MJ. 2009. Understanding the diversity of public interests in wildlife conservation. *Conservation Biology* **24**:128–139.

- Teel TL, Manfredo MJ, Jensen FS, Buijs AE, Fischer A, Riepe C, Arlinghaus R, Jacobs MH. 2010. Understanding the cognitive basis for human-wildlife relationships as a key to successful protected-area management. *International Journal of Sociology* **40**:104–123.
- Terborgh J et al. 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**:1923–1926.
- Thomas RE, Bruyere B, Sundaresan S, Bouzo S, Welden R, Trimarco J. 2015. Youth experiences with wildlife during a period of significant cultural change in Laikipia, Kenya. *Human Dimensions of Wildlife* **20**:133–146.
- Tuttle SR, Chambers CL, Theimer TC. 2006. Potential effects of livestock water-trough modifications on bats in northern Arizona. *Wildlife Society Bulletin* **34**:602–608.
- Unmack PJ, Minckley WL. 2008. The demise of desert springs. Pages 11–34 in L. E. Stevens and V. J. Meretsky, editors. *Aridland springs in North America: Ecology and conservation*. University of Arizona Press, Tucson, AZ.
- Van Schalkwyk DL, McMillin KW, Witthuhn RC, Hoffman LC. 2010. The contribution of wildlife to sustainable natural resource utilization in Namibia: A review. *Sustainability* **2**:3479–3499.
- Venables WN, Ripley BD. 2002. *Modern Applied Statistics with S*, 4th edition. Springer, New York.
- Viljoen PJ. 1987. Status and past and present distribution of elephants in the Kaokoveld, South West Africa/Namibia. *African Zoology* **22**.

- Viljoen PJ. 1989. Spatial distribution and movements of elephants (*Loxodonta africana*) in the northern Namib Desert region of the Kaokoveld, South West Africa/Namibia. *Journal of Zoology* **219**:1–19.
- Vogel JA, Debinski DM, Koford RR, Miller JR. 2007. Butterfly responses to prairie restoration through fire and grazing. *Biological Conservation* **140**:78–90.
- Voigt CC, Kingston T. 2016. Bats in the Anthropocene. Pages 1–9 in C. C. Voigt and T. Kingston, editors. *Bats in the Anthropocene: Conservation of bats in a changing world*. Springer International Publishing, Cham, Switzerland.
- von Wehrden H, Hanspach J, Kaczensky P, Fischer J, Wesche K. 2012. Global assessment of the non-equilibrium concept in rangelands. *Ecological Applications* **22**:393–399.
- von Wehrden H, Hanspach J, Ronnenberg K, Wesche K. 2010. Inter-annual rainfall variability in Central Asia—a contribution to the discussion on the importance of environmental stochasticity in drylands. *Journal of Arid Environments* **74**:1212–1215.
- Wall J, Wittemyer G, Klinkenberg B, LeMay V, Douglas-Hamilton I. 2013. Characterizing properties and drivers of long distance movements by elephants (*Loxodonta africana*) in the Gourma, Mali. *Biological Conservation* **157**:60–68.
- Ward JD, Seely MK, Lancaster N. 1983. On the antiquity of the Namib. *South African Journal of Science* **79**:175–183.
- Webb PI. 1995. The comparative ecophysiology of water balance in microchiropteran bats. Pages 203–218 in P. A. Racey and S. M. Swift, editors. *Ecology, evolution and behaviour of bats*. Oxford University Press, Oxford.

- Witemyer G, Getz WM, Vollrath F, Douglas-Hamilton I. 2007. Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology* **61**:1919–1931.
- Woodroffe R, Frank LG, Lindsey PA, ole Ranah SM, Romanach S. 2007. Livestock husbandry as a tool for carnivore conservation in Africa's community rangelands: A case–control study. *Biodiversity and Conservation* **16**:1245–1260.
- Woodroffe R, Thirgood S, Rabinowitz A, editors. 2005. *People and wildlife: Conflict or coexistence?* Cambridge University Press, Cambridge.

APPENDIX 1.1

The names, types, and coordinates of bodies of water sampled in the northern Namib Desert, Namibia. We collected water to be analyzed and recorded bat activity at these sites during the the conclusion of dry (November 2016 – January 2017) and wet (March – May 2017) seasons.

Site	Type of Water Body	Latitude	Longitude
Okongwe	Artificial Pool	-18.993088	13.1574094
Hoanib Camp	Artificial Pool	-19.364167	13.1518401
Mudorib	Artificial Pool	-19.324346	13.2308721
Ganamub	Artificial Pool	-19.231961	13.3696712
Rhino Camp	Artificial Pool	-20.016573	13.8448633
Ganias	Natural Spring	-19.234752	12.9223756
Sesfontein	Natural Spring	-19.116877	13.6191753
Karkappie	Natural Spring	-19.792494	13.9228461
Aub-Barab Junction	Natural Spring	-19.829824	13.782439
Kai Ais	Natural Spring	-19.748333	13.5974807
Crowthersquelle	Natural Spring	-19.839847	13.5107871
Salvadora	Natural Spring	-19.984498	13.5638275
Hunkap	Natural Spring	-19.595162	13.3920793
Upper Mudorib Spring	Natural Spring	-19.463277	13.3870023
Poacher's Camp	Natural Spring	-20.070087	13.9693218
Spaarwaterpos	Natural Spring	-20.13068	14.064505
Zincfontein	Natural Spring	-20.375458	13.9420704
Upper Achab	Natural Spring	-20.089324	13.8631905
Upper Huab	Natural Spring	-20.315757	14.2161023
Fonteine	Natural Spring	-20.3885	14.0876052
Peter's Pool	Natural Spring	-20.564081	13.9617669
Kuidas Camp	Natural Spring	-20.641477	13.850214
Gai Ais	Natural Spring	-20.759119	14.0198895

APPENDIX 1.2

Concentration detection limits for water quality tests (95% confidence) used by Analytical Laboratory Services in Windhoek, Namibia.

Test	Method description*	Detection limit
pH	Electrometric	–
Electrical conductivity	Electrometric	0.1 mS/m
Turbidity	Nephelometric	0.05 NTU
Total dissolved solids (determined)	Gravimetric	1 mg/L
Total alkalinity as CaCO ₃	Titrimetric	20 mg/L
Chloride (Cl ⁻)	Argentometric	1 mg/L
Fluoride (F ⁻)	Electrometric	0.1 mg/L
Sulfate (SO ₄ ²⁻)	Automated methylene blue	1 mg/L
Nitrate (NO ₃ ⁻)	Automated Cd reduction	0.1 mg/L
Nitrite (NO ₂ ⁻)	Colorimetric	0.01 mg/L
Aluminium (Al ³⁺)	ICP-OES	0.01 mg/L
Arsenic (As ³⁺)	ICP-OES	0.01 mg/L
Barium (Ba ²⁺)	ICP-OES	0.01 mg/L
Boron (B ³⁺)	ICP-OES	0.05 mg/L
Cadmium (Cd ²⁺)	ICP-OES	0.01 mg/L
Calcium (Ca ²⁺)	ICP-OES	0.1 mg/L
Cobalt (Co ²⁺)	ICP-OES	0.01 mg/L
Chromium (Cr ³⁺)	ICP-OES	0.01 mg/L
Copper (Cu ²⁺)	ICP-OES	0.01 mg/L
Iron (Fe ³⁺)	ICP-OES	0.01 mg/L
Lead (Pb ²⁺)	ICP-OES	0.01 mg/L
Lithium (Li ⁺)	ICP-OES	0.01 mg/L
Magnesium (Mg ²⁺)	ICP-OES	0.1 mg/L
Manganese (Mn ²⁺)	ICP-OES	0.01 mg/L
Nickel (Ni ²⁺)	ICP-OES	0.01 mg/L
Potassium (K ⁺)	ICP-OES	0.1 mg/L
Selenium (Se ²⁻)	ICP-OES	0.01 mg/L
Silica (SiO ₂)	ICP-OES	0.01 mg/L
Sodium (Na ⁺)	ICP-OES	0.1 mg/L
Strontium (Sr ²⁺)	ICP-OES	0.01 mg/L
Zinc (Zn ²⁺)	ICP-OES	0.01 mg/L

* ICP-OES signifies inductively coupled plasma mass spectroscopy.

APPENDIX 1.3

Water chemistry variables fit with *envfit* that are significantly correlated ($p \leq 0.1$) with the two-dimensional non-metric multidimensional scaling (NMDS) axes for community structure of bats recorded in the Namib Desert, Namibia at the conclusion of the dry (November 2016 – January 2017) and wet (March – May 2017) seasons.

Variable	NMDS Axis 1	NMDS Axis 2	r^2	p
Manganese (Mn^{2+})	0.377	0.926	0.139	0.056
Factor: Season			0.060	0.071
Dry	0.112	0.0053		
Wet	-0.107	-0.0051		

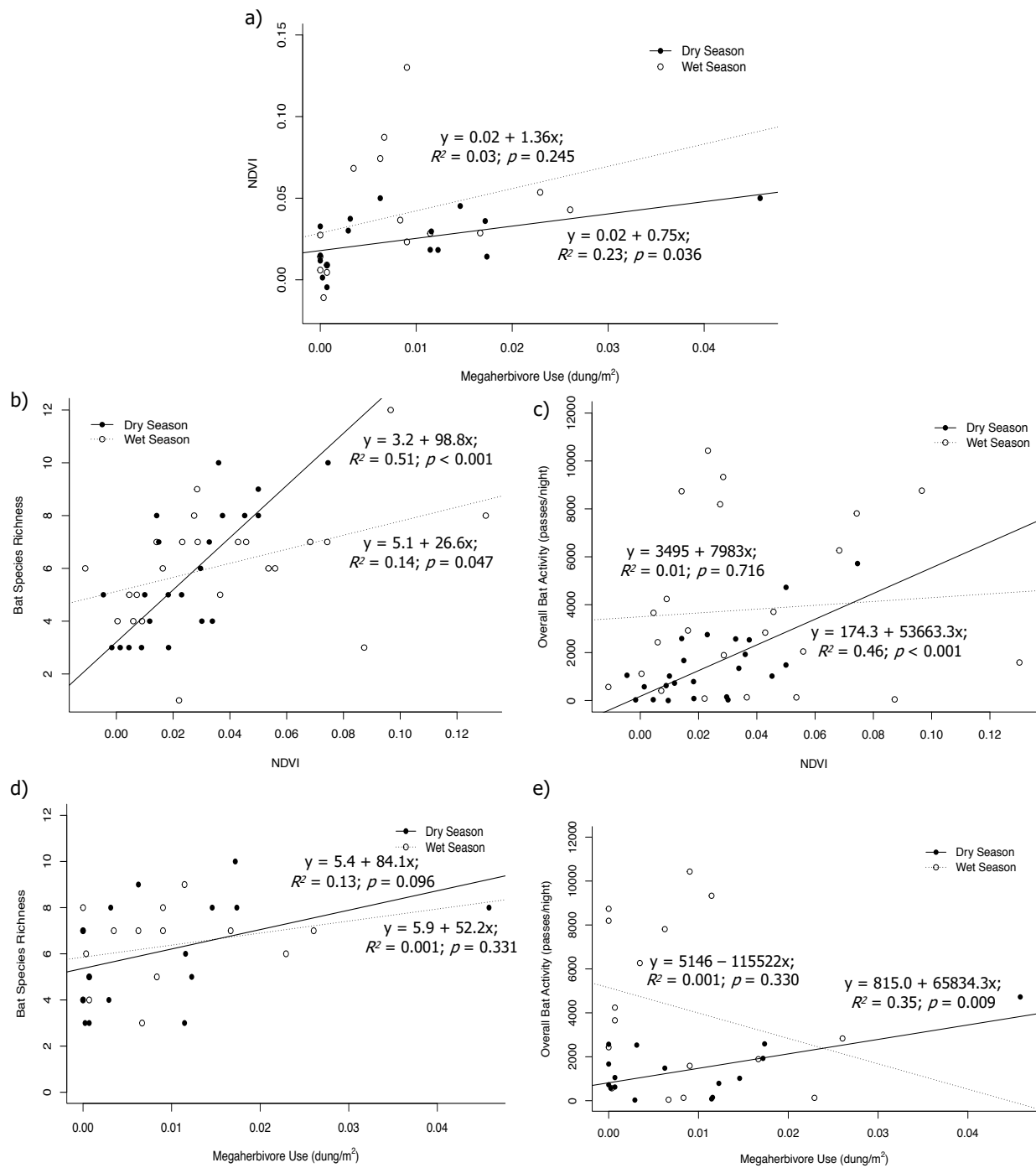
APPENDIX 1.4

Water chemistry variables fit with *envfit* that are significantly correlated ($p \leq 0.1$) with the two-dimensional non-metric multidimensional scaling (NMDS) axes for community structure of bats recorded in the Namib Desert, Namibia at the conclusion of the wet (March – May 2017) season only.

Variable	NMDS Axis 1	NMDS Axis 2	r^2	p
Electrical conductivity	-0.488	-0.877	0.246	0.0862
Chloride (Cl ⁻)	-0.499	-0.867	0.255	0.0848
Potassium (K ⁺)	-0.488	-0.873	0.244	0.0894
Sodium (Na ⁺)	-0.510	-0.860	0.231	0.0964
Strontium (Sr ²⁺)	-0.494	-0.870	0.262	0.0892

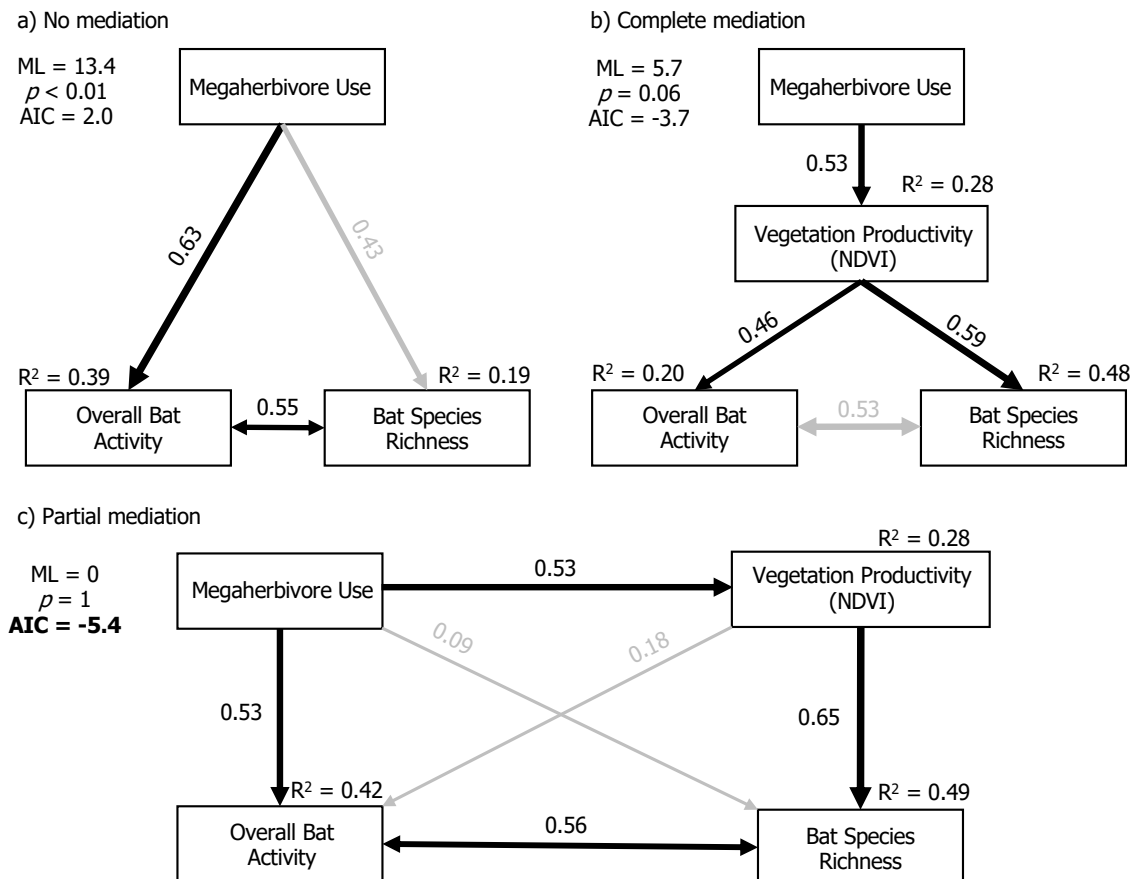
APPENDIX 2.1

Results from linear regression models exploring the relationships between a) megaherbivore use and NDVI, b) NDVI and bat species richness, c) NDVI and overall bat activity, d) megaherbivore use and bat species richness, and e) megaherbivore use and overall bat activity. Lines represent linear relationships and adjusted R^2 values are reported. Closed and open circles represent data from the dry and wet seasons, respectively.



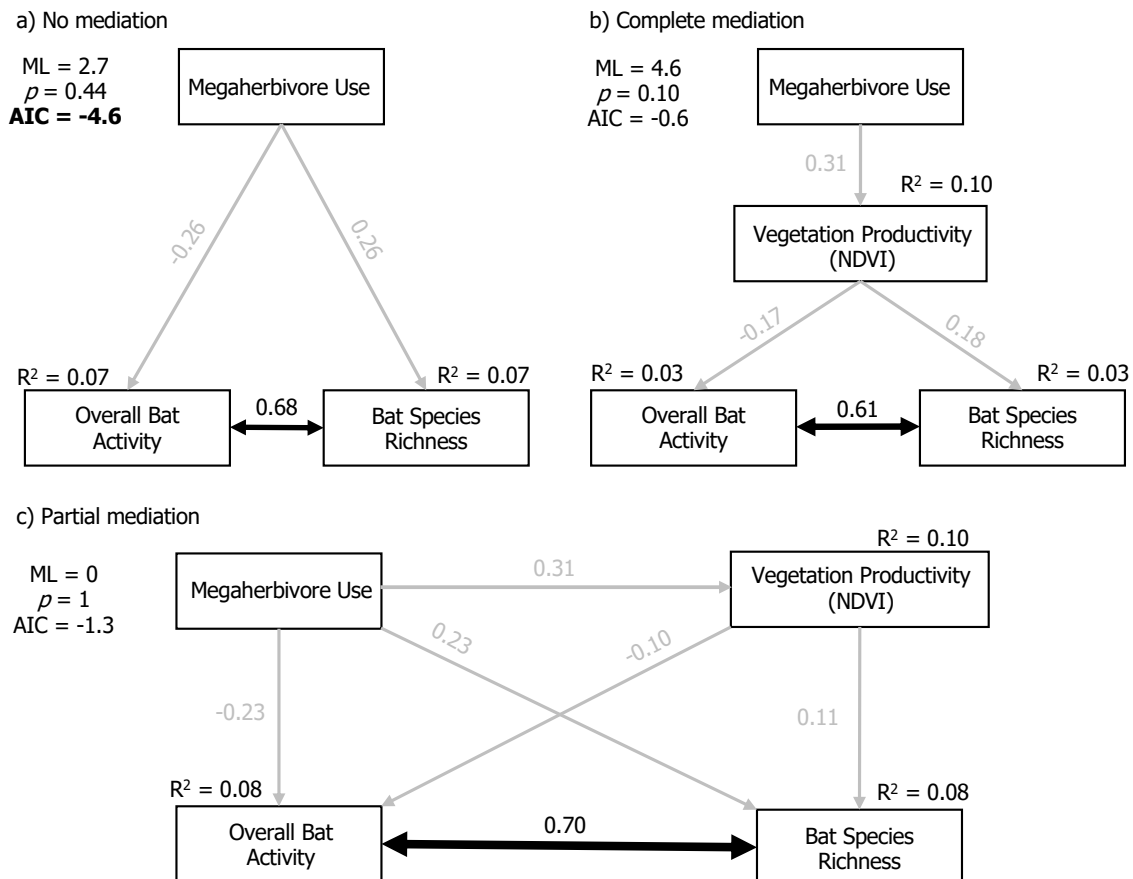
APPENDIX 2.2

Structural equation models (SEMs) of bat community responses to megaherbivore use during the dry season (November 2016 – January 2017) in northern Namib Desert, Namibia. Results of the a) no mediation, b) complete mediation, and c) partial mediation SEMs test the direct and indirect effects of megaherbivore use at a site on bat species richness and overall activity. Black and gray arrows are significant and non-significant paths, respectively, and numbers on arrows indicate standardized path coefficients. Arrow width corresponds to path strength (wider = stronger). The double headed arrows indicate a correlation between bat species richness and overall activity. R^2 values indicate the total variation explained by a model up to those points in the diagram. Maximum likelihood (ML), p -value (p ; $p < 0.05$ indicating significant lack of fit between the model and the data), and AIC for each SEM are shown. The partial mediation SEM was the best model (indicated in bold) for the dry season data based on AIC values (also shown in Fig. 2.6a).



APPENDIX 2.3

Structural equation models (SEMs) of bat community responses to megaherbivore use during the wet season (February 2017 – May 2017) in northern Namib Desert, Namibia. Results of the a) no mediation, b) complete mediation, and c) partial mediation SEMs test the direct and indirect effects of megaherbivore use at a site on bat species richness and overall activity. Black and gray arrows are significant and non-significant paths, respectively, and numbers on arrows indicate standardized path coefficients. Arrow width corresponds to path strength (wider = stronger). The double headed arrows indicate a correlation between bat species richness and overall activity. R^2 values indicate the total variation explained by a model up to those points in the diagram. Maximum likelihood (ML), p -value (p ; $p < 0.05$ indicating significant lack of fit between the model and the data), and AIC for each SEM are shown. The no mediation SEM was the best model (indicated in bold) for the wet season data based on AIC values (also shown in Fig. 2.6b).



APPENDIX 3.1

2017 semi-structured interview guide for northwestern Namibia residents adapted from Dayer et al. (2007)*.

Demographics

What is your...

- First/Primary Language?
- Gender?
- Age?
- Ethnicity?
- Length at Current Residence?

Wildlife Value Orientations (Basic Beliefs about and Experiences with Wildlife)

Please share with me any experiences you have had with wild animals that make you happy (repeat with sad, angry, and afraid). [Can you give a more detailed description of what happened? Do you have another example of this?]

In general, could you describe how you feel about wild animals?

* These questions represent a subset of the overall interview questions. The full interview recruitment script and guide is available on request from the corresponding author.

Human-Nature Interactions

Which wild animals, if any, do you think should not be conserved or protected? Why?

In general, what challenges do you face while living in this area? More specifically, what types of wildlife-related challenges/conflicts do you face and how frequently do you face them?

Do you think these challenges are worse and/or more frequent here than in other areas nearby in Kunene Region?

What, if anything, do you think could or should be done to address these challenges?

What specifically could be done to address the challenges associated with wild animals?

Lastly, are there any nearby farms or people that I should also consider interviewing?

APPENDIX 3.2

Interview locations for a 2017 study of Namibian pastoralists.

Conservancy	Villages
Sesfontein	Okohere, Okamazema, Otjindakui, Sesfontein, and Skelm River Pos
Anabeb	!Nao-dais, Anabeb, Eiland, Khowarib, Okaturua, Ongongo, Otjiperongo, Otjihavarero, Otjondumbu, and Warmquelle
Torra	Bergsig, Bergsig Pos, De-Reit, Driefontein, Fontainepos, Jackalsvlei, Middelpoos, Opdraendpos, Otjihavera, Palm, Palmpos, Palmwag, Rooivlak, Spaarwater, Spaarwaterpos, and Vrede

APPENDIX 3.3

Summary of respondents by sex and ethnic group within each conservancy from a 2017 interview of northwestern Namibia residents.

Conservancy and ethnic groups	No. of women	No. of men	Total interviews
Sesfontein (n = 20)			
Damara			4
Individual	0	4	
Herero			13
Individual	3	6	
Focus group 1	0	2	
Focus group 2	2	0	
Focus group 3	0	2	
Focus group 4	1	1	
Himba			3
Individual	0	2	
Focus group 1	2	0	
Anabeb (n = 24)			
Damara			3
Individual	0	1	
Focus group 1	1	1	
Focus group 2	1	1	
Herero			19
Individual	4	10	
Focus group 1	1	1	
Focus group 2	1	1	
Focus group 3	1	2	
Focus group 4	0	2	
Focus group 5	2	0	
Himba			2
Focus group 1	0	2	
Focus group 2	2	0	
Torra (n = 42)			
Damara			20
Individual	7	9	
Focus group 1	1	1	
Focus group 2	0	2	
Focus group 3	1	1	
Focus group 4	1	1	
Herero			8
Individual	3	2	

Conservancy and ethnic groups	No. of women	No. of men	Total interviews
Focus group 1	1	1	
Focus group 2	0	2	
Focus group 3	0	2	
Himba			1
Focus group 1	5	1	
Riemvasmaker			13
Individual	4	9	

APPENDIX 3.4

Coding strategy and descriptions of codes for wildlife value orientations and belief dimensions.

Wildlife value orientations and belief dimensions	Percent of interviews containing code (n = 86)	Percent intercoder agreement*	Code description and sample quotations
Domination	100%		Wildlife exists for human use; human welfare is prioritized over that of wildlife
Hunting	18.6%	94.1%	Focus on wildlife as the object of hunting and an important source of protein; includes subsistence and trophy hunting (1) "Sometimes you are so hungry at home, you think it is better to go around in the bush and shoot the animal." (2) "Also through the conservancy, they bring the hunting season and so on so they are also getting meat from the wildlife and so on."
Economic gains	29.1%		Monetary benefits or opportunities from wildlife conservation efforts
Compensation	7.0%	95.6%	Focus on wildlife as sources of income for offsetting loss (1) "Now-a-days there's less farmers cause of predators and so on, so that's the sad side of the story, but we gain something like a certain compensation, but... it's not really market-related." (2) "But if they sometimes lost the animals, the conservancy is giving them compensation fee."
Employment	8.1%	97.1%	Focus on wildlife as the object of providing employment opportunities (1) "In general, he's quite happy with wildlife because it brings, it creates employment and the conservancy all them enter in joint ventures and they make also money out of it, so he just wants to be more educated, to be more involved in wildlife management."

Wildlife value orientations and belief dimensions	Percent of interviews containing code (n = 86)	Percent intercoder agreement*	Code description and sample quotations
Tourism	22.1%	98.5%	(2) "It's a good thing for us because I also get a job from this." Focus on wildlife as the object of attracting tourists (1) "They do make not only me, but all of us in Namibia, happy because we get tourism from the outside. They come look at animals they do not have [where they are from] and it brings income to Namibia." (2) "Like other people coming from other sides like overseas come seeing a rhino that they don't even have in their country. Yes, it's good."
Concern for human safety	75.6%	92.7%	Concern related to interacting with wildlife because of the possibility of harm (1) "Elephant, I don't know was the elephant so angry... we were in the field and it was just chasing the donkey cart because we make firewood and we really saw the elephant so late and the elephant was so angry- started throwing sand all around and when we just jump on the donkey cart to get out, it followed us and it was really scary." (2) "If he sees his child in the bush, they will come back. Springbok will never do any harm to his child."
Concern for property	96.5%		Concern related to the possibility of wildlife causing harm to objects
Livestock wellbeing	94.2%	92.7%	Concern over predation risks and competition for grazing for livestock (1) "So he was also a farmer, but when the lions and the cheetah went in his corral and killed all his animals that is the day when he quit or gave up farming." (2) "So there was one day when the lions- more than nine- were killing her six donkeys during the night."

Wildlife value orientations and belief dimensions	Percent of interviews containing code (n = 86)	Percent intercoder agreement*	Code description and sample quotations
			(3) "Now the springboks were so many and the mountain zebras as well. They almost ate up the grazing, the grass, so she was feeling angry."
Crops	17.4%	98.5%	Concern over the damage of small subsistence crops (1) "The elephants come and they come and destroy our gardens..." (2) "The elephants, they make him afraid because he became tired to build his corrals around for gardening and so on because every time if he makes a fence around the garden, the elephants come and then they destroy them."
Water structure/buildings	19.8%	95.6%	Concern over the destruction of water structures, buildings, and fences (1) "[The elephants] break our pump and the pipes that bring the water to our homes..." (2) "[The elephants] come... breaking our pump, the pump, and the pipes that bring the water to our places and things like that."
Mutualism	24.4%		Wildlife are viewed as capable of relationships of trust with humans and have rights like humans
Caring	8.1%	89.7%	Personal emotional attachment to animals; humans want to help and prevent the suffering of wildlife (1) "One day I was on my patrol... and when I went somewhere I saw an oryx in a foot trap. He was still alive maybe for two to three days. It made me really sad." (2) "I am there to protect my animals and I always come across the things so there's a lot of day that I was angry seeing people poaching."
Extended family/friends	10.5%	97.1%	Wildlife are friends or part of an extended family

Wildlife value orientations and belief dimensions	Percent of interviews containing code (n = 86)	Percent intercoder agreement*	Code description and sample quotations
			(1) "So as I said I got the animals like your own children, so they are children. You can't get rid of them. Yes, because they are part of the family, so I found wildlife here when I was born, so I believe okay we are born like that so we have to stay." (2) "The animals like giraffe, oryx, springbok, and other small [animals] even if you check behind the house there you can see them. They are used to staying with our livestock without a problem... the livestock and wild animals I can say are a bit the same..."
Trust/respect	7.0%	97.1%	Wildlife are capable of relationships of trust with humans; wildlife and their habitat should be respected and valued (1) "Last year one elephant, he came all the way- he was a bull- up to this tree and he shouted at him and he turned around and he walked down to the water and drank water and took his way. So he was so much happy with that elephant- he was quite happy because the elephant listened to him when he shouted." (2) "It's wrong if I caught a snake there at the mountain and I want to kill it- it's totally wrong and I will not even support such an activity- just killing because you come together. I don't think that that snake will enter up here, so that's the snake's habitat. Respect and I also want [my habitat] to be respected"
Attraction/interest	84.9%		Interest in and a desire to see and know more about wildlife; feeling that wildlife enhances life experiences
For self	83.7%	92.7%	An individual's desire to see and know more about wildlife (1) "For me, it makes me happy to see wild animals roaming freely all over."

Wildlife value orientations and belief dimensions	Percent of interviews containing code (n = 86)	Percent intercoder agreement*	Code description and sample quotations
			(2) "There was one day- the elephants were here at the water hole and they drank water- it was about 10 elephants- and he was outside standing next to the house and watching how they drink and how they throw away the water and so on."
For future generations	12.8%	100%	Belief that humans must retain wildlife populations for future generations to see and know these species (1) "I like wild animals because I don't want them to die out because if those wild animals are dying out, my future generation will never see what it's looking like and those kind of business." (2) "The fact that our children, my sister's children, children in the conservancy, the schools can also see wildlife is also a good thing."
Rational/scientific	11.6%	98.5%	Rational or scientific explanations about the way the natural world works and the way animals behave (1) "The elephant always, we know the group of elephants, if a group comes together that day then they fight because the bull wants to take that group others. That's a time when he makes noise and things... [Elephant manure] was also used to help us with medicine- maybe the blood, your nose is running, or you're having a headache or you're scratching your body then you put in the water and then you shower [in] it." (2) "When I was out with the guests and the rhino was eating, feeding on <i>Euphorbia damarensis</i>- how she eats and how she also eats those base plants, she was happy because it was green."

Wildlife value orientations and belief dimensions	Percent of interviews containing code (n = 86)	Percent intercoder agreement*	Code description and sample quotations
Spiritual/religious	5.8%	97.1%	Viewing wildlife and the environment as created and controlled by a higher power(s) (1) "You know God created everything and after that he went to sit and said to himself now I must create the human being to guard over these things." (2) "He said those are the creatures of the God and they feel very happy." (3) "We know also if there's no rain we check the wild animals- mostly the birds, jackal, and also the elephant we know."

* Intercoder agreement was calculated for each code based on the number of passages in which both coders determined the presence or absence of a code divided by the total number of passages (n = 68). For example, if the first author recorded four passages with the tourism belief dimension, while the third author had coded five (with four passages shared between authors), intercoder agreement equaled 67 agreements divided by 68 passages, or 98.5% agreement for the tourism dimension.

APPENDIX 3.5

Coding strategy and descriptions of codes for perceived challenges to human-wildlife coexistence faced by respondents in northwestern Namibia.

Categories and descriptions of challenges	Percent of interviews containing code (n = 86)	Sample quotations
Wildlife		
Predators killing livestock	91.9%	(1) "It's only the baboons, baboons who kill their small animals." (2) "So the lions, if they find nothing in the wild, they used to come to these animals because these animals are not that much wild. That's why they come here and kill their livestock. Lion and the leopard and the hyena..."
Elephants destroying crops/property	14.0%	(1) "The elephants... the gardens they eat their vegetables, destroy pipes, and so on." (2) "Only the elephants come and destroy our gardens..."
Wildlife threatening personal safety	8.1%	(1) "Now-a-days, it doesn't help if [you] hire, whether you hire a shepherd, you put that, it's a life risk, so you try to save your livestock, but on the other side the people that you have hired are also at risk, but they don't understand." (2) "If you are going to look after the goats, then you must first check in your phone where is the lion then it's okay, but the new lion- those newcomers- are a problem because they have the place where you think there's none and then you can find them."
Water		

Categories and descriptions of challenges	Percent of interviews containing code (n = 86)	Sample quotations
Drought, includes increased distance to grazing	53.5%	(1) "The past four years there was also drought, but now they are a little bit happy because the grass is also good now." (2) "Because it's a drought and if the drought is here the animals used to graze... they are going to graze far..."
Access to water, includes boreholes breaking and sanitation problems	8.1%	(1) "The one problem is the borehole. Yes, it's always breaking." (2) "Only the water. The water is a little bit far from their homes- they use a donkey cart."
Social		
Problems related to conservancy management, includes confusion about conservancy goals, poaching, overgrazing, and the inability to control wildlife populations	10.5%	(1) "I cannot implement the policies, I don't know. I don't understand even what the conservancy is, what are their goals, why the conservancy has been set up, so that's actually the very problem that one is having." (2) "So in the old days if a lion killed your cattle, they used to kill him, but now-a-days it's prohibited to kill them, so their numbers are now many." (3) "Another challenge we have is the killing of wildlife by unknown people- the poaching, yes. Rhino, oryx, and kudu- those are the most challenges we are having in this area." (4) "There are no fences dividing the grazing areas like in the commercial areas... to use the grazing areas sparingly- this month this camp and the other one another."
Interpersonal/ethnic conflict and competition, includes people stealing livestock and competition for grazing with immigrants	14.0%	(1) "Sometimes it's people who come and steal livestock from other people." (2) "So the people who moved in, they came in with many cattle, many animals..."

Categories and descriptions of challenges	Percent of interviews containing code (n = 86)	Sample quotations
Resources		
Lack of resources and capacity to deal with human-wildlife conflict, includes poor road conditions, lack of access to electricity or communications networks, and insufficient compensation payments	7.0%	(1) "As I said, me and my family hate lions, we do not have any mean of tracking those lions- no cars, you cannot track it by foot, not even on your feet, so we are just sitting here while they are roaming." (2) "The challenges that we are facing in this area are the network problem, the radio- the radio is very poor, the network they recover it nearly- and transport, public transport."

APPENDIX 3.6

Coding strategy and descriptions of codes for perceived solutions to human-wildlife coexistence faced by respondents in northwestern Namibia.

Categories and descriptions of solutions	Percent of interviews containing code (n = 86)	Sample quotations
Wildlife		
Harvest/trophy hunt predators	31.4%	(1) "One way of managing, you kill them. One way of another managing is bring in [a foreigner] as a trophy hunter." (2) "Maybe they should reduce it, bring the number down so that they can control that are there and maybe hunt these that are outside and maybe leave those that are in that camp."
Translocate wildlife to parks/private farms/concession areas	29.1%	(1) "They don't want to shoot it, but just to relocate lions to some other or even to the park also, so that the lions' population can just decrease at least to have control over the lions or what's the movement because now there are a lot and they stay in groups." (2) "They should be moved to the national parks."
Fence predators within conservancy boundaries	23.3%	(1) "I think they should build more fences so the wildlife can stay on the other side instead of coming to us." (2) "It must be somewhere a place where the lions should be locked up even in the conservancy somewhere one place for them to be locked up."
Hiring more people responsible for monitoring wildlife movements, includes notifying residents of local	17.4%	(1) "According to my opinion, we have rhino rangers- those people help those lions. To me, I can say it, it can also put

Categories and descriptions of solutions	Percent of interviews containing code (n = 86)	Sample quotations
threats and increased general awareness of wildlife movements		the collar on each lion, so that we can see where is the lion.” (2) “So all we should do, us as human beings, is take care also of ourselves and then know our movements and then take care of our cattle as possible as we can do.” (3) “... and people can be controlled or the movements can also be more controllable and people can be informed also what side lions move- today that side... game guards or so we can inform people.”
Better livestock herding/tending practices, includes building stronger corrals and the use of conservation dogs	5.8%	(1) “Better corrals, proper corrals for the livestock.” (2) “It's only to go together with the animals-to go together with cows and goats [make sure the herders are with the animals] to make sure the lions and the predators cannot kill them, so he doesn't have other ideas.” (3) “She was buying the dogs from the other farm there. We put them in the work that side, but those dogs were old... Dogs must [kill] the lion or the dog must chase it away.”
Water		
Provide more drought relief hay for livestock	7.0%	(1) “The drought like the government used to give us also grass- [drought relief] food and yes.” (2) “Sometimes the government is also helping them with the drought relief food.”
Provide better access to water, includes building new boreholes, fixing existing ones, and building more toilet blocks	7.0%	(1) “He said there are some open places not far away from here where there's nice grazing areas, but there's no water, so what could be done is just setting up water points there and that the wildlife could be taken there, or maybe could be taken there, and that would decrease their numbers a

Categories and descriptions of solutions	Percent of interviews containing code (n = 86)	Sample quotations
		bit, reduce their numbers in this area, so rather than setting up a fence or whatever.” (2) “During the drought period there should be places to look around where the grass is to drill boreholes.” (3) “People should fix the borehole.”
Social		
Changes related to conservancy management, includes holding more conservancy meetings, fencing areas for rotational grazing, and poaching deterrents	5.8%	(1) “Maybe you can try like I said we hold regular meetings for the members and be honest with them [about] what’s the challenge that we are facing and we have to work to manage those challenges.” (2) “You should think of a zone and zoning with fences, not only just zoning with imaginary borders or something like that and to keep animals in a certain area for grazing...” (3) “I think two years ago I heard that our government will provide us with cameras in the field- we are talking about the poaching now- so that maybe people can be afraid to hunt illegally and I can know where it has been stopped. Such an idea must come again for putting up cameras in the field.”
Changes related to conservancy management, includes holding more conservancy meetings, fencing areas for rotational grazing, and poaching deterrents		
Change land use from wildlife utilization to wildlife protection, includes moving to areas further east	4.7%	(1) “So I don't want to say to people to move out from these areas, but these people they need some good farms in commercial areas, so that they can move in because there's also stories going around of People's Park and National Park, so these things cannot come together so that they must get other farms.” (2) “I always told the guys it has become time for us to make a choice whether we want to go ahead with farming or wildlife

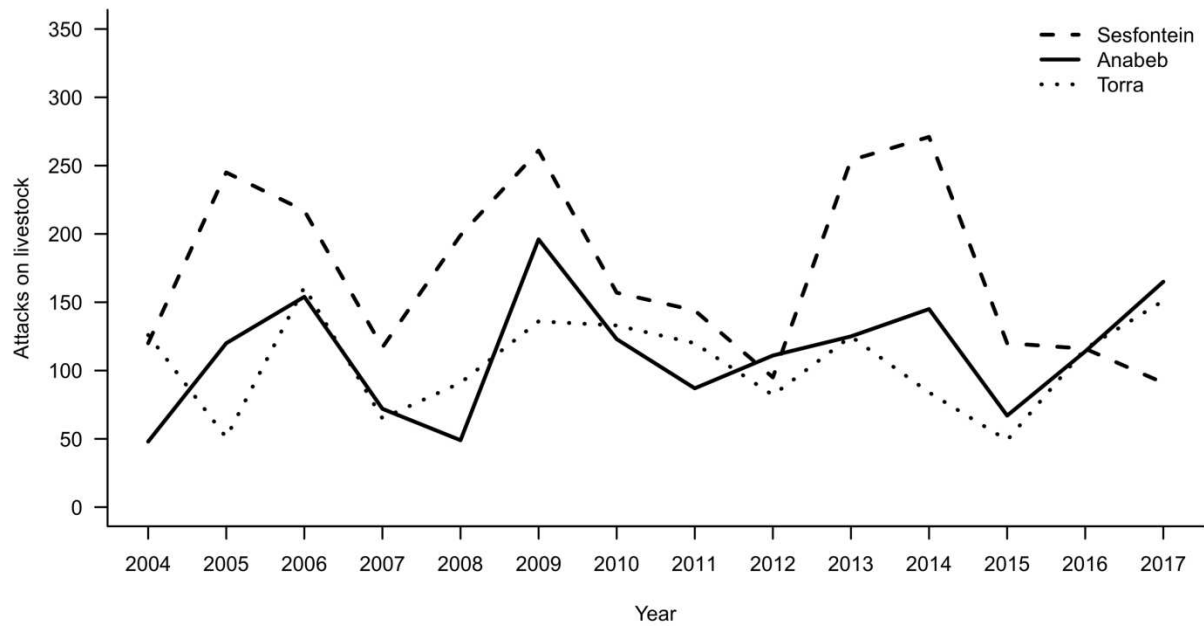
Categories and descriptions of solutions	Percent of interviews containing code (n = 86)	Sample quotations
		because together there will be no solution, so we have to make a choice."
Means to reduce interpersonal/ethnic conflict and competition, includes enacting stricter immigration laws and greater penalties for stealing livestock	10.5%	(1) "I don't know what to do about the people, maybe they have to change the law there. It depends and maybe to pay back what you have stolen or to stay in prison maybe for even a year if you steal one. Maybe it will change." (2) "Now they came in within this area without permission, so now the rain is all over so they must go back to their original farmlands."
Resources		
Provide physical resources and capacity to deal with human-wildlife conflict, includes better road conditions, access to electricity or communications networks, and greater compensation payments	7.0%	(1) "Transport and radios- our government must just negotiate with relevant authorities like telecommunications just to expand their transmissions to the rural areas, so that we must just communicate." (2) "Some of the guys don't have tents, so the guys must give them the tents." (3) "Compensation should be increased- compensation fee."
Provide physical resources and capacity to deal with human-wildlife conflict, includes better road conditions, access to electricity or communications networks, and greater compensation payments		
Other*		
Live sale of predators and/or elephants to other countries	2.3%	(1) "There's no way in the case of the elephants, no solutions. Maybe live sale to any other countries who might need them because their numbers are too much."

Categories and descriptions of solutions	Percent of interviews containing code (n = 86)	Sample quotations
Invest more in education	1.2%	(1) "... playground for kids and nice kindergartens, and facilities for schools."
Can and sell elephant meat	1.2%	(1) "We are starving as Africans of hunger. Will it be wrong if you can elephant meat? That's the other story you've never ate an elephant, but you do believe on earth there are people who are eating elephant. And what is wrong with maybe canning the meat and export it or use it for local purposes...?"
Allow more lodges to be built to deter lion movements	1.2%	(1) "Like in the edge of the Hoanib River there was one guy who was interested to put a lodge there. Then I was saying you know we should give permission to that guy because I thought that if we put a lodge there, the car might be moving in and out from Sesfontein to that specific point. Then I think during the day the movement of the lion will be eliminated, so that lodge will try to keep them very much far into the concession area there."

* These proposed solutions were reported in only one or two interviews and were not combined to fit within other themes.

APPENDIX 3.7

Trends in predator attacks on livestock in northwestern Namibia from June 2004 to May 2017. Annual reported numbers of attacks on livestock in three conservancies in northwestern Namibia. Data presented are from June 2004 to May 2017 and are likely underestimated as not all attacks are reported (NACSO 2018b).



APPENDIX 3.8

Species-specific trends in human-wildlife conflict data in northwestern Namibia from June 2004 to May 2017. Boxplots depict median, upper and lower quartile, and 95% percentiles for the annual number of conflicts caused by five wildlife species in three conservancies in northwestern Namibia. Data presented are from June 2004 to May 2017 (NACSO 2018b).

