

## CONTRIBUTED PAPER

# Indirect effects of African megaherbivore conservation on bat diversity in the world's oldest desert

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**Article impact statement:** Conservation of large desert mammals may indirectly benefit insectivorous bat activity and species richness through herbivory.

## Abstract

In extreme environments, temperature and precipitation are often the main forces responsible for structuring ecological communities and species distributions. The role of biotic interactions is typically thought to be minimal. By clustering around rare and isolated features, like surface water, however, effects of herbivory by desert-dwelling wildlife can be amplified. Understanding how species interact in these environments is critical to safeguarding vulnerable or data-deficient species. We examined whether African elephants (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), and southern giraffe (*Giraffa giraffa*) modulate insectivorous bat communities around permanent waterholes in the Namib Desert. We estimated megaherbivore use of sites based on dung transects, summarized vegetation productivity from satellite measurements of the normalized difference vegetation index, and surveyed local bat communities acoustically. We used structural equation models to identify relationships among megaherbivores and bat species richness and dry- (November 2016–January 2017) and wet- (February–May 2017) season bat activity. Site-level megaherbivore use in the dry season was positively associated with bat activity—particularly that of open-air foragers—and species richness through indirect pathways. When resources were more abundant (wet season), however, these relationships were weakened. Our results indicate that biotic interactions contribute to species distributions in desert areas and suggest the conservation of megaherbivores in this ecosystem may indirectly benefit insectivorous bat abundance and diversity. Given that how misunderstood and understudied most bats are relative to other mammals, such findings suggest that managers pursue short-term solutions (e.g., community game guard programs, water-point protection near human settlements, and ecotourism) to indirectly promote bat conservation and that research includes megaherbivores' effects on biodiversity at other trophic levels.

## KEYWORDS

Chiroptera, food webs, foraging guild, Namib Desert, Namibia, structural equation modeling, vegetation productivity

Efectos Indirectos de la Conservación de Mega Herbívoros Africanos sobre la Diversidad de Murciélagos en el Desierto Más Antiguo del Mundo

**Resumen:** Es común que en los ambientes extremos la temperatura y la precipitación sean las principales responsables de la estructura en las comunidades ecológicas y en la distribución de las especies. Con frecuencia se cree que el papel de las interacciones bióticas en estas características es mínimo. Sin embargo, si nos enfocamos en características raras y aisladas, como el agua superficial, los efectos de la herbivoría ocasionada por la fauna del desierto puede ser amplificada. El entendimiento de cómo las especies interactúan en estos

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ambientes es importante para salvaguardar a las especies vulnerables o con datos insuficientes. Examinamos si los elefantes africanos (*Loxodonta africana*), los rinocerontes negros (*Diceros bicornis*) y la jirafa sureña (*Giraffa giraffa*) modulan las comunidades de murciélagos insectívoros alrededor de los abrevaderos permanentes en el Desierto del Namib. Estimamos el uso que le dan los mega herbívoros a ciertos sitios con base en transectos, en la productividad de la vegetación resumida a partir de las medidas satelitales del índice normalizado de diferencias en la vegetación (INDV) y en censos acústicos de las comunidades locales de murciélagos. Usamos modelos de ecuaciones estructurales para identificar las relaciones entre los mega herbívoros y la riqueza de especies de murciélagos con la actividad de los quirópteros durante la temporada seca (noviembre 2016 - enero 2017) y la lluviosa (febrero - mayo 2017). El uso a nivel de sitio dado por los mega herbívoros durante la temporada seca estuvo asociado positivamente con la actividad de los murciélagos—particularmente para aquellos que forrajearon a cielo abierto—y la riqueza de especies por vías indirectas. Sin embargo, cuando los recursos fueron más abundantes (temporada de lluvias), estas relaciones fueron débiles. Nuestros resultados indican que las interacciones bióticas contribuyen a la distribución de las especies en áreas desérticas y sugieren que la conservación de los mega herbívoros en este ecosistema puede beneficiar indirectamente a la abundancia y la diversidad de los murciélagos insectívoros. Ya que los murciélagos suelen ser poco valorados y poco estudiados en comparación con otros mamíferos, nuestros descubrimientos sugieren que los gestores buscan soluciones a corto plazo (p. ej.: programas de guardias comunitarias de las presas de caza, protección de puntos de abastecimiento de agua cercanos a establecimientos humanos, ecoturismo) para promover indirectamente la conservación de murciélagos y que la investigación incluye los efectos de los mega herbívoros sobre la biodiversidad en otros niveles tróficos.

**PALABRAS CLAVE:**

Chiroptera, Desierto del Namib, gremio de forrajeo, modelado con ecuación estructural, Namibia, productividad de la vegetación, redes alimentarias

## INTRODUCTION

In extreme desert environments, the role of biotic interactions in structuring ecological communities is expected to be small relative to abiotic forces (Brown & Ernest, 2002; Darwin, 1859). Animal populations may regularly collapse due to frequent droughts and high variation in interannual precipitation. Consequently, effects on vegetation or at different trophic levels may be subtle or go unnoticed (Illius & O'Connor, 1999; von Wehrden et al., 2012). In ancient deserts, however, a longer history of aridity may have allowed more species to coexist despite intense competition for resources (Simmons et al., 1998), such as surface water in highly ephemeral river systems (Kingsford et al., 2006). Sometimes, top-down forces structure desert communities (Polis, 1991). Yet, where predator densities are low or too variable to structure prey populations in these low-productivity habitats (Hatton et al., 2015), 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). The relationships between large ungulates and small mammals at different trophic levels are not frequently addressed.

Among the world's oldest deserts, the Namib extends along southern Africa's Atlantic coast and is a biodiversity hotspot among arid zones globally (Simmons et al., 1998). Despite the extreme environment, its northern reaches host African

elephants (*Loxodonta africana*), black rhinoceroses (*Diceros bicornis*), southern giraffes (*Giraffa giraffa*), mountain zebras (*Equus zebra*), greater kudu (*Tragelaphus strepsiceros*), gemsboks (*Oryx gazella*), springboks (*Antidorcas marsupialis*), and steenboks (*Raphicerus campestris*) and localized herds of domestic livestock and large and small carnivores. Herbivores alter vegetation density, biomass, and species composition in a roughly 2-km high-impact zone around surface water (Leggett et al., 2003a). Piospheric effects (i.e., radial pattern of attenuating impact [Landman et al., 2012]) are likely magnified in the Namib due to the presence of megaherbivores, such as elephants that topple and debark large trees (Ogada et al., 2008; Owen-Smith, 1992; Shannon et al., 2008).

The concentrated and visible impacts of herbivores on vegetation near surface water in deserts may affect organisms in other trophic levels. Butterflies and moths, for instance, can benefit from mammalian herbivory of intermediate intensities and duration (Moranz et al., 2012; Pöyry et al., 2004), which in turn can benefit communities of diverse insectivorous taxa, including birds (Cardinal et al., 2012), lizards (McCauley et al., 2006), and rodents (Keasing, 1998; Keasing & Young, 2014; Young et al., 2015). Bats that consume insects may indirectly benefit from herbivory in a similar manner. Bats in Zimbabwe's miombo woodlands, however, remain relatively unchanged with increasing elephant densities in comparison with sympatric bird communities (Fenton et al., 1998). The intensity of such biotic

interactions between distantly related taxa in deserts remains unclear.

The presumption of a relationship between megaherbivores and insectivorous species has conservation implications. Although elephants and rhinoceroses are important conservation targets, their protection may induce a trade-off between ecological function and biodiversity by counteracting the conservation of small insectivores, such as bats. Alternatively, large herbivores may create disturbances that benefit other organisms, including bats.

We examined the extent to which the abundance of localized desert-dwelling herbivores modulates insectivorous bat communities. Because desert bats concentrate in riparian areas where herbivores affect plant communities (Adams & Thibault, 2006; Razgour et al., 2010), we hypothesized that the spatial heterogeneity of large herbivores affects bat species richness and activity (Appendix S1). If elephants, giraffes, and black rhinoceroses reduce the food or habitat available for bats' plant-dependent insect prey, then chiropteran species richness and activity may be inversely related to megaherbivore use. Alternatively, insect prey may increase with megaherbivore activity or dung density and positively affect bat species richness and activity. A further possibility is that megaherbivores 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 foraging bats, but increasing herbivory eventually becomes detrimental for clutter and clutter-edge foraging bats (details on hypothesized relationships in Appendix S2).

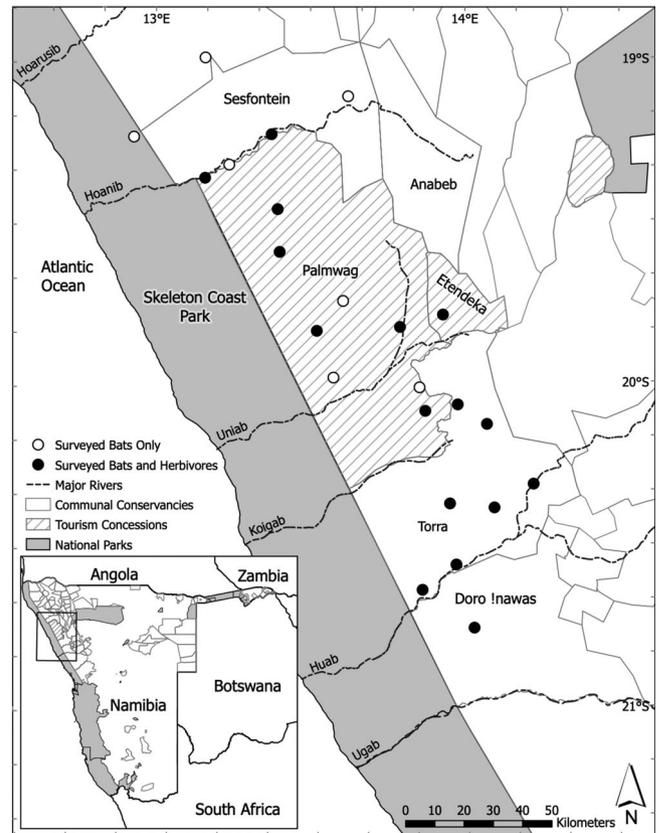
We sought to highlight the complexity of conservation when targets are very different. By studying biotic interactions between bats, for which much ecology is unknown, and charismatic megafauna, short-term solutions to enhance megaherbivore and bat conservation could be devised.

## METHODS

### Study area

In the northern Namib Desert, we studied 4 of Namibia's 12 major ephemeral river catchment systems (Figure 1). This region receives an average 30–100 mm annual precipitation at the western and eastern edges of our study area, respectively (Jacobson & Jacobson, 2013). Permanent water exists as natural springs, artificial pools constructed for wildlife or livestock, and short ( $\leq 3$  km) stretches of flowing river. Rivers sustain above-ground flows only during the wet season (i.e., January–April), on average fewer than 20 days/year.

We collected data during the hot, dry season (November 2016–January 2017) and the wet season (February–May 2017) and focused on 23 permanent bodies of open water, including artificial pools ( $n = 5$ ) and natural springs ( $n = 18$ ) (Figure 1; Appendix S3), but did not include elephant wells or megaher-



**FIGURE 1** Study area in the northern Namib Desert (closed circles, sites where bats and herbivores were sampled [ $n = 16$ ]; open circles, sites where only bats were sampled [ $n = 7$ ])

bivore willow sites. Maximum water surface area varied across these sites, but not by season (mean [SD]: 515 m<sup>2</sup> [855],  $n = 46$ ) (Lavery & Berger, 2020). All sites retained water from February 2016 to May 2017, and even the smallest waterholes were used by wildlife, including bats.

### Bat sampling

Using ultrasonic bat detectors (Wildlife Acoustics Song Meter SM4BAT FS, Maynard), we monitored bat activity and species richness at each site once per season: total 46 nights (dry season: 21 November 2016–21 January 2017; wet season: 16 March 2017–16 May 2017 [Lavery & Berger, 2020]). Bat detectors were deployed from 30 min before sunset to 30 min after sunrise within 3 m of surface water. We avoided sampling bats within 3 days of full moon nights because moonlight reduces activity in some bats (Lang et al., 2006). Survey protocols were approved by Colorado State University's Institutional Animal Care and Use Committee (protocol 15-6140A) and the Namibian Ministry of Environment and Tourism (permits 2122/2016 and 2225/2016).

We identified species on recorded calls with the cluster analysis option in the program Kaleidoscope Pro Version 5.1.3 (Wildlife Acoustics, Maynard). Under this method, full-spectrum calls recorded by bat detectors were analyzed by the

software with enhanced zero crossing (Ross et al., 2018). Clusters were created and sorted based on their similarity after a signal detector searched for candidate vocalizations in the recordings. We manually reviewed all calls in every cluster to classify the species present based on reference calls recorded from bats physically captured in mist nets and identified over different sampling periods at the same sites (Appendix S4; Laverty & Berger, 2020). Calls were also compared with those in Monadjem et al.'s (2010) field guide.

Spectrograms of most Namib bat calls are distinct from one another and readily identifiable, with the exception of 3 pairs of species: Angolan wing-gland bat (*Cistugo seabrae*) and Zulu serotine (*Neoromicia zuluensis*); Cape serotine (*Laephotis capensis*) and Schlieffen's twilight bat (*Nycticeinops schlieffeni*); and long-tailed serotine (*Eptesicus hottentotus*) and yellow-bellied house bat (*Scotophilus dinganii*) (Laverty & Berger, 2020). Thanks to our mist-netting efforts and paired acoustic recordings of bats across our study area during different sampling periods (i.e., 1477 bats captured and released—many with hand-release calls recorded—from December 2014 to May 2017), we were confident in our assignment of species to the call files in question. However, the activity of many gleaning bats (e.g., Hipposideridae and Nycteridae) may be underestimated in studies relying on acoustic recordings due to the attenuation of their high-frequency calls or the whispering nature of their calls.

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 in 1 night at each site.

## Megaherbivore activity sampling

To estimate megaherbivore activity, we conducted monthly site-specific dung surveys from 21 November 2016 to 5 April 2017 with 3, 120 × 4 m belt transects radiating away from 16 of the bodies of water where bats were sampled (Appendix S3). We did not sample 7 sites due to their proximity to tourism lodges or an office, their location in a national park and tourism concession, and their distance from the subsequent site (i.e., we could not sample a site for herbivore activity and reach our next site in a day).

Dung counts offer more reliable estimates of relative habitat use by a given species within habitats and seasons relative to live animal aerial and ground counts (Barnes, 2001; Riginos, 2015), although such data can be affected by variations in decomposition rates (Plumptre & Harris, 1995). Identification of dung piles for all megaherbivores—African elephant, southern giraffe, and black rhinoceros—was confirmed using Gutteridge and Liebenberg's (2013) field guide, enumerated, and removed from the transect to prevent recounting. We pooled the number of dung piles for these species as a measure of megaherbivore use at a site. To align these data with our bat sampling, 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).

## Measuring vegetation productivity

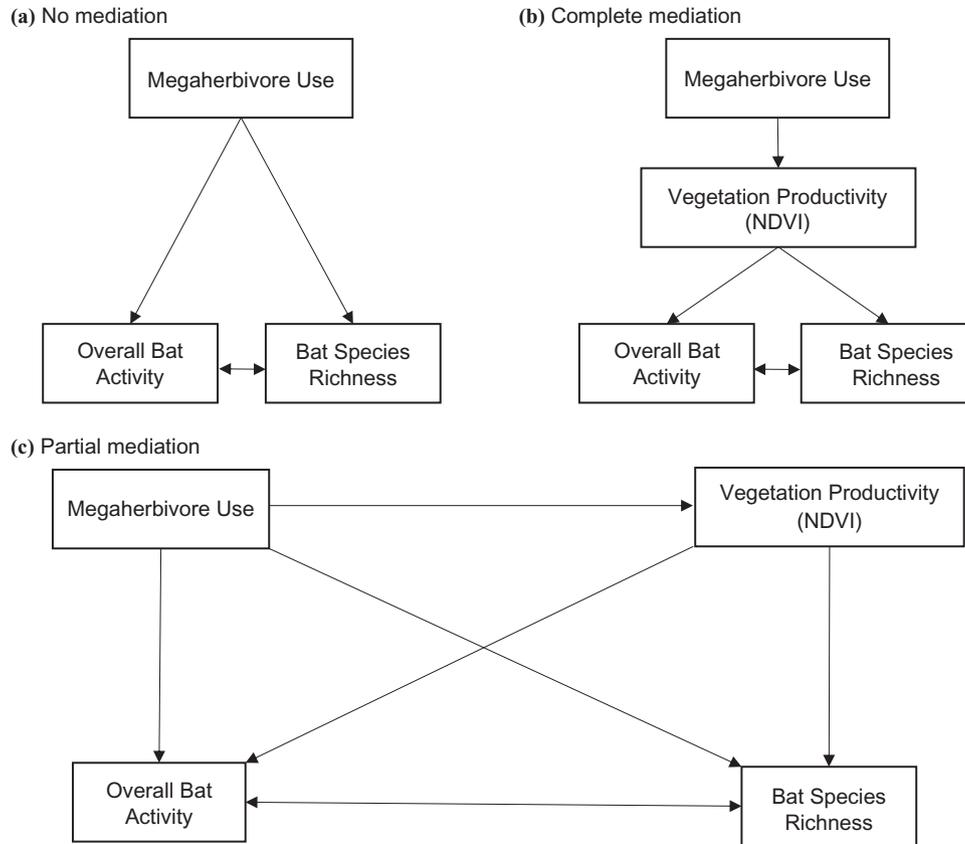
We approximated vegetation productivity for each season with the normalized difference vegetation index (NDVI) (Rouse Jr. et al., 1974) derived from 10-m resolution satellite imagery (Sentinel-2A Level-1C imagery) (Drusch et al., 2012) for the periods we sampled bats. Using Google Earth Engine (Gorelick et al., 2017), we computed the mean NDVI value in 50 m, 100 m, 250 m, 500 m, 1 km, 1.5 km, and 2 km radii of each sampling point, based on the median value for each pixel on days with <15% cloud coverage (i.e., 3–18 and 3–21 days of imagery for the dry and wet seasons, respectively).

## Statistical analyses and predictions

To choose a scale at which bats may be responding to vegetation properties, we related the NDVI values from each radius to bat species richness and overall activity with linear regression models carried out in the `lm` function in R version 3.5.3 (R Core Team, 2019). We used small-sample corrected Akaike information criterion (AICc), a relative metric of model quality that accounts for parsimony and overfitting, to select models (Burnham & Anderson, 2004). Only the 500-m radius resulted in  $\Delta\text{AICc} < 2$  for models of both bat species richness and overall activity, and it was used for all subsequent analyses.

We evaluated data normality with the `shapiro.test` function in R. We transformed values to the square root to normalize megaherbivore activity and overall bat activity and to the fourth root to normalize the activity of each bat foraging guild. These transformed data were used for all subsequent analyses. We tested for seasonal differences among our 4 variables with paired  $t$  tests in the `t.test` function and calculated Bonferroni-adjusted  $p$  values to account for multiple comparisons with the `p.adjust` function. We assessed bat species richness and overall activity for spatial autocorrelation with the `Moran.I` function in R's `ape` package (Paradis & Schliep, 2019). We also built structural equation models (SEMs) with 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 (Figure 2, Appendix S2).

We investigated individual relationships with linear regression models with the `lm` function. To identify which hypothesized relationships were most consistent with our observations, we examined each relationship as a separate SEM model structure and then performed model selection with AIC. Because our missing megaherbivore activity data were not random, we used only the 16 sites with complete data in our SEM models. 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. For each season, we tested whether the relationships between megaherbivores and bat communities were direct or mediated through NDVI by comparing the AIC scores of 3 alternate SEM structures (Grace, 2006): megaherbivores directly affect bat species richness and



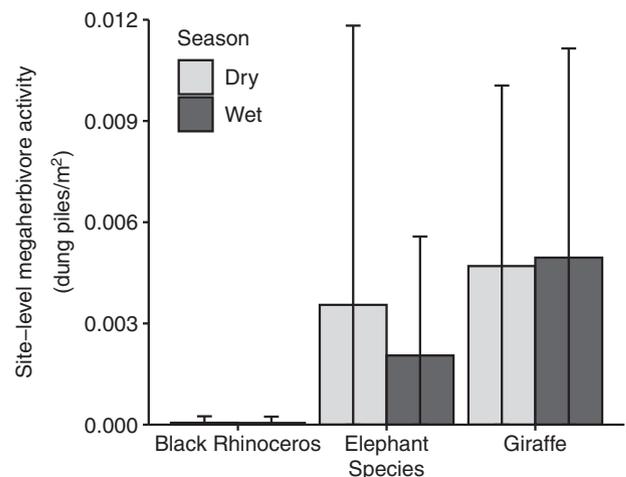
**FIGURE 2** Three hypothesized relationships among megaherbivores, vegetation productivity, and bat communities in northwestern Namibia evaluated through structural equation modeling: (a) direct relationship of megaherbivore use at a site with bat species richness and overall activity, (b) the same model as in (a) but the effects of megaherbivores on bat communities are completely mediated through vegetation productivity, and (c) both the direct and indirect effects of megaherbivores are represented (double-headed arrows, anticipated correlation between bat species richness and overall activity)

activity (no mediation [Figure 2a]); megaherbivores only affect bat species richness and activity indirectly through their effects on NDVI (complete mediation [Figure 2b]); or megaherbivores directly and indirectly affect bat species richness and activity (partial mediation [Figure 2c]). We selected the best-fitting model (i.e., model with the lowest AIC value) for the dry and wet seasons separately. We then substituted the activity of the 3 bat foraging guilds (i.e., clutter, clutter-edge, and open-air foragers) in place of overall bat activity in the best-fitting SEMs to examine whether relationships may be due to different feeding behaviors and flight patterns. Data and code are in Appendix S5.

## Results

### Seasonal megaherbivore use and NDVI

Monthly dung surveys showed our Namib Desert sites were used primarily by giraffes and elephants (Figure 3). Although mean NDVI near these bodies of water was approximately 60% greater in the wet season than the dry season (Appendix S6), site-level megaherbivore use did not vary between seasons (Table 1). A significant positive relationship between megaherbivore use and NDVI was evident during the



**FIGURE 3** Mean site-level megaherbivore use estimated from monthly dung surveys in northwestern Namibia over the dry season (light gray;  $n = 37$ ; 21 November 2016–24 January 2017) and wet season (dark gray;  $n = 27$ ; 6 February 2017–5 April 2017) (error bars, 1 SD)

dry season (NDVI = 0.01 + 0.11\* megaherbivore use [square-root transformed];  $R^2 = 0.47$ ;  $p = 0.002$ ), but relaxed during the wet season (NDVI = 0.02 + 0.17\* megaherbivore use [square-root transformed];  $R^2 = 0.15$ ;  $p = 0.074$ ) (Appendix S7a).

**TABLE 1** Mean (SD) megaherbivore use (transformed to the square root), normalized difference vegetation index (NDVI, proxy for vegetation productivity), nightly bat species richness, and overall bat activity (transformed to the square root) in the dry (November 2016–January 2017) and wet (February–May 2017) seasons in the northern Namib Desert, Namibia

Variable	<i>n</i> <sup>a</sup>	Dry season	Wet season	<i>t</i>	Bonferroni-adjusted <i>p</i>
Megaherbivore use (dung piles/m <sup>2</sup> ) <sup>1/2</sup>	16	0.15 (0.12)	0.14 (0.11)	0.512	1.000
NDVI	23	0.024 (0.021)	0.039 (0.037)	−3.215	0.0160 <sup>b</sup>
Bat species richness	23	5.6 (2.6)	6.1 (2.2)	−1.594	0.5012
Overall bat activity (passes/night) <sup>1/2</sup>	23	32.5 (20.4)	53.5 (31.2)	−4.057	0.0007 <sup>b</sup>

<sup>a</sup>Number of sites sampled during each season.

<sup>b</sup>Significant *p* value.

**TABLE 2** Foraging guild and mean (SD) species-specific bat activity (mean passes per night) recorded during the conclusion of dry (November 2016–January 2017) and wet (March–May 2017) seasons in the northern Namib Desert, Namibia

Species	Foraging guild*	Dry season activity ( <i>n</i> = 23)	Wet season activity ( <i>n</i> = 23)
Angolan wing-gland bat ( <i>Cistugo seabrae</i> )	clutter-edge	378 (414)	840 (1260)
Long-tailed serotine ( <i>Eptesicus hottentotus</i> )	clutter-edge	87.2 (153)	52.3 (76.7)
Sundevall's leaf-nosed bat ( <i>Hipposideros caffer</i> )	clutter	16.8 (33.7)	29.5 (48.1)
Cape serotine ( <i>Laephotis capensis</i> )	clutter-edge	52.0 (249)	90.0 (432)
Striped leaf-nosed bat ( <i>Macronycteris vittata</i> )	clutter-edge	0	0.304 (1.46)
Greater long-fingered bat ( <i>Miniopterus inflatus</i> )	clutter-edge	0.217 (1.04)	0.130 (0.626)
Natal long-fingered bat ( <i>Miniopterus natalensis</i> )	clutter-edge	0.652 (2.17)	0.783 (3.33)
Zulu serotine ( <i>Neoromicia zuluensis</i> )	clutter-edge	200 (597)	140 (330)
Schlieffen's twilight bat ( <i>Nycticeinops schlieffeni</i> )	clutter-edge	143 (687)	279 (340)
Egyptian slit-faced bat ( <i>Nycteris thebaica</i> )	clutter	0	0.565 (2.11)
Damara horseshoe bat ( <i>Rhinolophus damarensis</i> )	clutter	19.4 (41.5)	10.4 (46.2)
Dent's horseshoe bat ( <i>Rhinolophus denti</i> )	clutter	0.957 (2.06)	2.35 (7.03)
Rüppell's horseshoe bat ( <i>Rhinolophus fumigatus</i> )	clutter	5.65 (21.6)	1.70 (7.50)
Roberts's flat-headed bat ( <i>Sauromys petrophilus</i> )	open-air	373 (451)	1720 (2140)
Yellow-bellied house bat ( <i>Scotophilus dinganii</i> )	clutter-edge	9.83 (44.2)	1.78 (6.59)
Egyptian free-tailed bat ( <i>Tadarida aegyptiaca</i> )	open-air	166 (503)	625 (874)

\*Foraging guilds determined by Monadjem et al. (2010).

## NDVI and bat species richness and overall bat activity

We recorded 120,749 bat passes in 45 of the 46 nights of sampling (i.e., no bat calls were identified in recordings at one site during the dry season [Lavery & Berger, 2020]). Across all sites, bat species richness did not differ significantly across seasons (Table 1): 14 insectivorous species were detected in the dry season and 16 in the wet season (Table 2). However, overall bat activity was significantly greater during the wet season (Table 1): mean site-level activity was 160% higher during this period. This

was mostly due to an increase in activity of resident species rather than due to the 2 additional species recorded in the wet season (Table 2).

The relationship between NDVI and bat species richness was strong and positive during the dry season (bat species richness = 3.5 + 87.0\*NDVI,  $R^2 = 0.45$ ,  $p < 0.001$ ) and weaker during the wet season (bat species richness = 5.2 + 25.0\*NDVI,  $R^2 = 0.13$ ,  $p = 0.050$ ) (Appendix S7b). A strong, positive, significant relationship also existed between NDVI and overall bat activity during the dry season (overall bat activity [square-root transformed] = 16.1 + 679.1\*NDVI,  $R^2 = 0.45$ ;  $p < 0.001$ ),

but not during the wet season (overall bat activity [square-root transformed] =  $49.2 + 112.9 \cdot \text{NDVI}$ ,  $R^2 = 0.03$ ;  $p = 0.545$ ) (Appendix S7c). Bat species richness was not spatially autocorrelated across sites (dry season: Moran's  $I = 0.029$ ,  $p = 0.14$ ; wet season:  $I = -0.033$ ,  $p = 0.80$ ), and spatial autocorrelation in bat activity was weak and positive during the wet season only (dry season:  $I = 0.015$ ,  $p = 0.22$ ; wet season:  $I = 0.086$ ,  $p = 0.0095$ ).

### Megaherbivore use and bat species richness and overall bat activity

Site-level megaherbivore use and bat species richness during the dry and wet seasons were not significantly related (dry season: bat species richness =  $4.9 + 8.5 \cdot \text{megaherbivore use}$  [square-root transformed],  $R^2 = 0.15$ ,  $p = 0.078$ ; wet season: bat species richness =  $5.7 + 3.9 \cdot \text{megaherbivore use}$  [square-root transformed],  $R^2 = 0.002$ ,  $p = 0.34$ ) (Appendix S7d). Similarly, megaherbivore use and overall bat activity were not significantly related (dry season: overall bat activity [square-root transformed] =  $27.6 + 41.2 \cdot \text{megaherbivore use}$  [square-root transformed],  $R^2 = 0.02$ ,  $p = 0.263$ ; wet season: overall bat activity [square-root transformed] =  $69.2 - 89.5 \cdot \text{megaherbivore use}$  [square-root transformed],  $R^2 = 0.01$ ,  $p = 0.292$ ) (Appendix S7e).

### Structural equation models

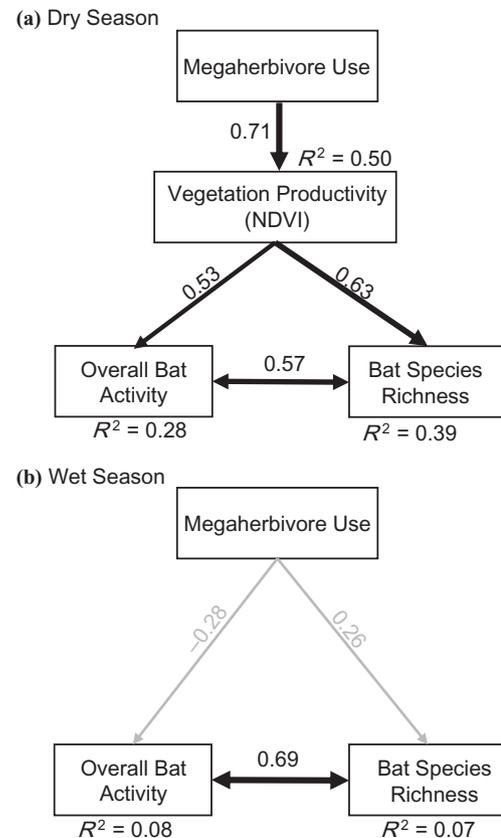
During the dry season, the best-fitting SEM was the complete mediation model in which the relationships between megaherbivore use and bats—both species richness and overall bat activity—were mediated through NDVI (Figure 4a; Appendix S8). Specifically, megaherbivore use was positively associated with local NDVI, which in turn had a positive relationship with bat species richness and overall activity. The latter relationship was primarily driven by the positive association between megaherbivore use and activity of open-air foraging bats (Appendix S10a).

In contrast to dry-season results, a significant herbivore–bat relationship was not supported by models during the wet season (Figure 4b; Appendices S9 and S10b). Consistent with the prior regression analyses, the partial regressions among megaherbivore use and bat activity and species richness were not significant. The  $R^2$  values were also low in all 3 of the SEM models. Together, this suggests minimal direct or indirect relationships between megaherbivores and bats during the wet season when water is less limiting.

## DISCUSSION

### Big animals as modulators of insectivorous bat diversity

Beyond weather and aridity per se, water can concentrate species and shape adaptive capacity (Brown & Ernest, 2002; Davis et al.,



**FIGURE 4** The most supported structural equation models (i.e., models with the lowest Akaike information criterion values) of the relationships between megaherbivore and bat communities in the northern Namib Desert for the (a) dry and (b) wet seasons (black,  $p \leq 0.05$ ; gray,  $p > 0.05$ ;  $R^2$ , total variation explained by a model up to those points in the diagram; arrow width, the wider the stronger the path strength; double-headed arrows, correlation between bat species richness and overall activity). Megaherbivore use and overall bat activity are transformed to the square root to meet model assumptions. Pathways are accompanied by standardized partial regression coefficients. See Appendices S8 and S9 for all candidate models

2017). In 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 available. Although previous studies in the Namib show seasonal differences in elephant and giraffe distributions (Fennessy, 2009; Leggett, 2006), we detected no seasonal effects in either bat species richness or megaherbivore use of the areas immediately adjacent to permanent waterholes. This may be due to the true absence of a temporal relationship because water points may attract megaherbivores and bats year-round, to seasonal differences in dung decomposition rates among megaherbivores, or to a sample-size artifact. However, the significant seasonal differences among some of our other variables (i.e., NDVI and overall bat activity) supported our choice of conducting separate SEM analyses of species and plant interactions for each season.

During the dry season, bat species richness and overall activity were indirectly, positively associated with megaherbivore use as mediated by vegetation productivity. We hypothesized that elephants in particular change the vertical complexity of shrubs

and trees (i.e., reduce the number of branches and canopy cover [Asner et al., 2009]), providing new habitat for less maneuverable, open-air foraging bat species, such as Roberts's flat-headed bat (*Sauromys petrophilus*) and the Egyptian free-tailed bat (*Tadarida aegyptiaca*). Although our models appear to support this relationship, direct measurements of horizontal and vertical vegetative cover and bat activity in vegetation patches are needed to better understand this perceived pattern. Land-cover and land-use data sets that accurately represent this region's vegetation are not currently available, and the isolated nature of dry-land tree cover limits nonforest inferences from remote sensing data (Brandt et al., 2020). Although this prevented further analysis of the role of vegetation structure and communities on Namib Desert bats, vegetation complexity is a prominent factor that affects bat communities in many habitats (e.g., Froidevaux et al., 2016; Suarez-Rubio et al., 2018). To discern megaherbivore habitat use in relationship to NDVI patterns, researchers should focus on fine-scale megaherbivore movement ecology. It is possible that the positive relationship between bats and megaherbivores stems from overlapping preferences of similar vegetation types. This alternative hypothesis could be tested by classifying vegetation types, collecting megaherbivore movement data, conducting large-scale acoustic monitoring of bats, and mapping bat roosts in different habitats.

Alternatively, bat species richness and activity may depend more on water availability than vegetation productivity. Natural springs in deserts are important to insectivorous bats for drinking and foraging. Bat species richness and overall activity increase around small waterholes in the semiarid Limpopo Province of South Africa (Taylor et al., 2020) and are positively related to water surface area around natural springs and artificial pools in the Namib Desert (although water surface area of surveyed sites does not differ between seasons [Lavery & Berger, 2020]). Insect communities may respond to water availability and herbivore activity in terrestrial environments around our surveyed waterholes. Insect community responses to herbivore use, however, were only inferred in our modeling, and we recommend abundance and diversity of insects be measured directly. Although we tested insect community sampling with light traps (BioQuip UV LED CDC Trap, Rancho Dominguez) for 1–3 h each night at a subset of sites ( $n = 12$ ) during different sampling periods, we avoided simultaneous use of light traps and acoustic monitoring because this can affect bat activity (Froidevaux et al., 2018). Therefore, we recommend monitoring the insect community on the night following bat sampling and perhaps deploying a variety of traps to address taxonomic biases in insect sampling methods.

Our study could have benefited from additional information on Namib bats. Roost locations are unknown, but most of the species we recorded roost in caves and rock crevices in other parts of their range (Monadjem et al., 2010). Some species may also roost in tree hollows, under the bark of trees, or in houses. We could not be certain of the independence of bat ensembles at waterholes without knowledge of bat roost locations, species' home ranges, and foraging distances. With the exception of bat activity in the wet season, however, bat species richness and overall activity were not spatially autocorrelated.

## Food webs and muting of top-down effects in the wet season

The relationships among megaherbivore use of an area, bat activity, and species richness we detected in the dry season dwindled in the wet season. In other parts of sub-Saharan Africa, ungulates disperse throughout the wet season when water is more widely distributed (Holdo et al., 2009; Wittemyer et al., 2007). Spatial and temporal variability of resources strongly influence the movements and composition of wildlife communities in many ecosystems as species track food and avoid predators (Holdo et al., 2009; Sabo & Power, 2002). Access to water often limits species distributions in desert environments, but this constraint varies seasonally. In the Namib, alternative water sources during the wet season (e.g., flooding rivers and ephemeral pools) provide species with greater access to food resources in areas distant from permanent bodies of water.

Localized precipitation events also strongly affect vegetation productivity and the distributions of many large mammals in this desert (Fennessy, 2009; Leggett, 2006) and across arid regions worldwide (Acebes et al., 2013; Singh et al., 2010; Wittemyer et al., 2007). Small mammals, including bats, 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). Nightly bat activity was approximately double in the wet season, which may correspond to bats temporarily immigrating into the region with the seasonal pulse in resources, as occurs for migratory birds in Namibia (Lavery & Berger, 2020; Loutit, 1991).

## Conservation and dwindling effects of desert-dwelling megaherbivores

Many of the world's largest herbivores occur in Africa, but have undergone severe range declines (Ripple et al., 2015). African elephants, for instance, are widely distributed across the continent and use a range of habitats, from semidesert to tropical forests (Owen-Smith, 1992). Their current presence in deserts, however, is unique and restricted to the northern Namib Desert in Namibia and the edges of the Sahara and the Sahel in Mauritania and Mali (Leggett, 2006; Wall et al., 2013). Despite the low human densities in deserts, megaherbivores in these regions have not escaped the effects of poaching, civil war, and drought. Populations of black rhinoceroses 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 (Brodie et al., 2011; Leggett et al., 2003b).

Conservation efforts, especially by nongovernmental organizations, have understandably focused on these large charismatic species, but have yet to employ a multispecies recovery approach that recognizes the strength of interactions among broader levels of biodiversity, including insectivores. Understanding how 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 (Caro, 2010). Body size is not, however, always the best indicator of an umbrella species. 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 interannual rainfall (von Wehrden et al., 2012), and our efforts highlight the need for future research across multiple years to meet intensive data requirements of SEMs and improve understanding of the biotic and abiotic drivers of species distributions over time. Despite these challenges, we provide novel insights on associations between large herbivores and bat biodiversity and confirmed that these interactions have abiotic influences as demonstrated through seasonal differences in SEM performance. Whether these interspecific relationships hold true in other deserts around the world remains to be tested. The threats to bats in other regions, such as wind energy development, mining, and white-nose syndrome in North American deserts (Frick et al., 2020), may overpower biotic interactions with large herbivores. If so, perhaps the strength of these biotic relationships between such distantly related species in deserts may be inversely related to the scope and severity of threats due to anthropogenic activities (e.g., land-use change, overexploitation of species, introduction of invasive species, and climate change).

Adaptations to the physical environment are important drivers of speciation and survival in harsh climates (Darwin, 1859), although the interplay between biotic and abiotic factors in shaping species distributions remains unclear or understudied for many taxonomic groups in such realms. We found bat species richness and the activity of open-air foraging bats was positively related to megaherbivore habitat use, but only during the dry season. This supports the idea that biotic interactions structure desert communities 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 may indirectly benefit Namib Desert bat activity and species diversity. By supporting elephant, giraffe, and black rhinoceros populations through community game guard programs, water-point protection, and ecotourism opportunities, local people may have been conserving insectivorous wildlife for years. The conservation of large herbivores does not come without consequences to people living among these species (Laverly et al., 2019), but our findings highlight the opportunity for integrating ecological findings with social research in this system to promote the sustainable coexistence of people, livestock, and wildlife—large and small—in this unique desert ecosystem.

## ACKNOWLEDGMENTS

We are grateful to the Namibian Ministry of Environment and Tourism and Anabeb, Sesfontein, and Torra conservancies for permitting this research and to Etendeka Mountain Camp, Skeleton Coast Safari's Kuidas Camp, Wilderness Safari's Desert Rhino Camp, and Wilderness Safari's Hoanib Skeleton Coast Camp for permitting access to nearby waterholes. We thank L.

Mushabati for assistance with study design, M. Davies for help with data collection, S. Eiseb for use of the acoustic detectors, V. Landau for coding assistance in Google Earth Engine, and S. Carroll for assistance in ArcGIS Pro and with land-cover and land-use data sets. We are grateful to K. Crooks, G. Wittemyer, T. Teel, and J. Field for their comments on an earlier version of this manuscript. T.M.L. received funding from the National Science Foundation (GRFP, DGE-1321845), the National Geographic Society (YE 9514-14), and The Explorers Club. J.B. received funding from the Wildlife Conservation Society.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Laverty TM, Berger J.

Indirect effects of African megaherbivore conservation on bat diversity in the world's oldest desert. *Conservation Biology*. 2022;*36*:e13780.

<https://doi.org/10.1111/cobi.13780>

