



## Short communication

## Exotic oryx interact with shrub encroachment in the Chihuahuan Desert

Kieran J. Andreoni<sup>a</sup>, Casey J. Wagnon<sup>a</sup>, Brandon T. Bestelmeyer<sup>b</sup>, Robert L. Schooley<sup>a,\*</sup><sup>a</sup> Department of Natural Resources and Environmental Sciences, University of Illinois, 1102 S. Goodwin Ave, Urbana, IL, 61801, USA<sup>b</sup> USDA-ARS Jornada Experimental Range, New Mexico State University, MSC 3JER, Box 30003, Las Cruces, NM, 88003, USA

## ARTICLE INFO

## Keywords:

Diel activity  
Habitat use  
Invasive species  
*Oryx gazella*  
Shrub encroachment

## ABSTRACT

Biotic invasions can interact with ongoing landscape transitions in introduced ranges, acting synergistically to accelerate landscape change. The African oryx (*Oryx gazella*), a large ungulate native to the Kalahari Desert in southern Africa, was intentionally released into the Chihuahuan Desert of southern New Mexico to provide increased hunting opportunities. Oryx have subsequently dispersed widely, including into the adjacent Jornada Basin Long Term Ecological Research site, which contains native grassland communities imperiled due to shrub encroachment. We examined how landscape use and diel activity of oryx interacts with shrub encroachment at Jornada Basin. We hypothesized that oryx would be more common on unencroached grasslands that provide preferred forage, and that oryx would be most active at dawn and dusk (crepuscular) when ambient temperatures were favorable and predator surveillance was possible. We sampled 24 sites across a broad gradient of shrub encroachment from 2014 to 2018 using camera traps to evaluate our hypotheses. Oryx relative abundances were higher on unencroached grasslands, especially in years of low to moderate precipitation. We found oryx were most active during crepuscular periods, and this behavior was consistent across the shrub encroachment gradient. Our research suggests exotic oryx could contribute to shrub encroachment by focusing their foraging on remaining grasslands, especially during drier years, which may adversely affect livestock production and other ecosystem services.

## 1. Introduction

Biotic invasions and landscape change are two drivers of biodiversity loss and altered ecosystems globally (Crowl et al., 2008; Norbury et al., 2013). Moreover, these threats may act synergistically to accelerate changes in ecosystem structure and function (Brook et al., 2008). Understanding how exotic species interact with landscape change is critical for informing management intended to restore native ecosystems and species (Hobbs et al., 2009). A first step toward assessing such interactions is to quantify the space use and behavior of exotic species in relation to alternative ecosystem states on a landscape (Bradley and Mustard, 2006).

The African oryx (*Oryx gazella*; Fig. S1), or gemsbok, is a large ungulate (often >200 kg) native to the Kalahari Desert of southern Africa that some local government institutions consider invasive in southern New Mexico. Intentionally released into the White Sands Missile Range (WSMR) from 1969 to 1977, populations have increased from 95 individuals to >3400 (Bender et al., 2019). Due to physiological tolerances to aridity, predator release, and continuous reproduction (Bender,

2006), oryx have expanded their exotic range well beyond WSMR into the greater Chihuahuan Desert. Because oryx feed on perennial grasses, their range expansion could have far-reaching consequences for landscapes in which shrub encroachment is already endangering native grasslands and reducing forage production for livestock.

Shrub encroachment is a global phenomenon producing persistent alternative stable states with increased bare soil coverage, wind erosion, edaphic droughts, and possible biodiversity loss compared to historically extensive grassland states (D'Odorico et al., 2012; Ratajczak et al., 2012). Shrub encroachment is a pervasive issue across the northern Chihuahuan Desert (Peters et al., 2012). Adjacent to WSMR, the Jornada Basin Long Term Ecological Research (LTER) site (Jornada Basin) is a landscape containing sensitive grassland communities whose imperilment due to shrub encroachment has been well-documented. From 1858 to 1998, estimated cover by grasslands at Jornada Basin decreased from 82% to 8%, while cover by native honey mesquite (*Prosopis glandulosa*) increased from 15% to 59% (Peters et al., 2012). Overgrazing by cattle and extended droughts were likely triggers of the shrub expansion (Peters et al., 2012). However, ungulates can also alter plant community

\* Corresponding author.

E-mail address: [schooley@illinois.edu](mailto:schooley@illinois.edu) (R.L. Schooley).<https://doi.org/10.1016/j.jaridenv.2020.104302>

Received 13 June 2020; Received in revised form 24 August 2020; Accepted 27 August 2020

Available online 6 September 2020

0140-1963/© 2020 Elsevier Ltd. All rights reserved.

composition, through foraging and trampling, and such landscape-scale disturbance can promote invasive plant species (Vavra et al., 2007). Thus, we investigated oryx in the Chihuahuan Desert because this exotic ungulate could exacerbate shrub encroachment through herbivory focused on remaining grasslands.

We sought to clarify how shrub encroachment influences landscape use and diel activity of oryx within Jornada Basin and consider feedbacks to rangeland condition. African oryx feed mainly on grasses during wet periods but have broader diets that include more forbs and succulents during dry periods (Lehmann et al., 2013; Cain et al., 2017). Hence, we hypothesized they would be more common on unencroached grassland habitats that provide preferred forage. We also hypothesized oryx would be most active at dawn and dusk (i.e., crepuscular) when ambient temperatures were favorable and predator surveillance was possible (Boyers et al., 2019), assuming oryx remain wary even though large, nocturnal predators are rare. Moreover, we expected oryx might extend activity on shrub-dominated sites into daytime if shrubs provide favorable microclimates (Boyers et al., 2019) or into nighttime if shrubs provide concealment from predators.

## 2. Study area

We conducted our research at Jornada Basin LTER site (Fig. S2) in southern New Mexico, USA (32°35' N, 106°51' W; 1334 m a.s.l.). Jornada Basin encompasses 100,000 ha of arid grassland and shrubland communities within the northern Chihuahuan Desert (Peters et al., 2012). The site is located ~30 km to the west of WSMR where oryx were first introduced. Grasslands within our study area were dominated by black grama (*Bouteloua eriopoda*), dropseed (*Sporobolus* spp.), threeawn (*Aristida* spp.), and tobossa (*Pleuraphis mutica*), whereas shrublands were dominated by honey mesquite. Seasonal monsoons (July–September) typically drive annual precipitation, which is patchily distributed.

## 3. Materials and methods

We conducted our study across grassland-to-shrubland transitions associated with the long-term monitoring of mammals and their feedbacks to vegetation dynamics (i.e., the Ecotone Study; Bestelmeyer et al., 2007; Schooley et al., 2018; Wagnon et al., 2020). Specifically, we used a network of camera traps across 24 sites to measure oryx spatial abundance patterns and diel activity. In 2014, we established camera traps at 15 sites within five core pastures. Each pasture included three sites (grassland, ecotone, and shrubland). Each site was three ha. In 2015, we expanded our sampling effort to include nine additional sites. Collectively, these 24 sites provided a strong gradient of perennial grass cover ( $\bar{x} = 14.5\%$ ; range: 1.7–50.2%) and shrub cover ( $\bar{x} = 12.3\%$ ; range: 1.5–27.1%). The minimum distance between sites ranged from 188 to 4400 m. The spatial extent of the camera-trap monitoring network was ~200 km<sup>2</sup>.

At each site, we established two unbaited camera traps separated by 196 m (Bushnell Trophy Cam, model no. 119436). We combined data from the two cameras on a site for our analyses. We positioned camera traps 0.5 m aboveground, attached to fenceposts, and programmed cameras to take three photographs in a short burst with a 30-s delay before rearming. We sampled sites from mid-July through October each year from 2014 to 2018.

The sites included no vehicle tracks. There is only one main road in Jornada Basin, which has occasional traffic. Camera traps were located >75 m from the main road, and normally much farther. As such, we assumed space use by oryx was not strongly affected by disturbance from vehicles.

We characterized vegetation cover for each site using line-point-intercept methods (Herrick et al., 2005) to evaluate how shrub encroachment affects oryx. Within each site, we established five or six 50-m transects that were offset from each other in a staggered formation by 20 m. We measured vegetation cover at 25-cm intervals along each

transect (200 points) and then averaged values across all transects to estimate cover of grasses, shrubs, total foliar, and bare ground. We conducted vegetation sampling in 2017.

We anticipated that precipitation may influence the space use of oryx through forage production because of strong associations between precipitation and aboveground net primary productivity (Peters et al., 2012; Schooley et al., 2018). Hence, we measured total precipitation from November to October using the nearest rain gauge to each site ( $\bar{x} = 0.93$  km; range: 0.16–2.31 km) and included it as a predictor variable. We also evaluated whether water sources affect oryx space use because oryx frequently visit water tanks for cattle in New Mexico (Harris et al., 2015). We created a proximity metric that integrated the number and distances of water tanks within two km to sites using ArcGIS (ArcMap Ver. 10.7.1). We used a threshold of two km from sites because oryx in New Mexico have mean daily movement distances between 1.6 and 2.6 km (Bender, 2006). Specifically, we used the following equation:  $Tanks = \sum_{n=1}^w 1/\bar{d}_{sw}^2$ , where  $\bar{d}_{sw}$  is the mean distance ( $\bar{d}$ ) from the two cameras on site  $s$  to water tank  $w$ . Generally, the proximity metric for a site increased with a greater number of water tanks and with shorter distances to tanks.

All oryx photographs were relabeled, sorted, and stored using the procedures and computer programs described by Sanderson and Harris (2013). We considered photographs to be independent if sequential photographs of oryx at a site were separated by  $\geq 60$  min. We used the photographic rate (no. of independent photographs at a site per year) as a measure of relative abundance for oryx (Carbone et al., 2001; Rovero and Marshall, 2009). We included the total number of trap-nights (no. of 24-h cycles completed by an active camera) as a measure of sampling effort in our statistical models. We then used the time stamps from independent photographs to examine diel activity patterns of oryx.

To assess how oryx photographic rate was related to environmental covariates, we fit generalized linear mixed models (GLIMMIX procedure, SAS). We used a negative binomial distribution appropriate for over-dispersed count data and applied log (trap-nights) as an offset variable. We also included a first-order autoregressive covariance structure to account for our yearly repeated measures design. We used only the percentage of grass and shrub cover as vegetation predictors, excluding foliar cover and bare ground. Grass cover was highly correlated with foliar cover ( $r = 0.886$ ,  $P < 0.0001$ ) and bare ground ( $r = -0.846$ ,  $P < 0.0001$ ), so we used grass cover to index these vegetation components. Grass and shrub cover were negatively correlated but not strongly ( $r = -0.346$ ,  $P = 0.098$ ). Hence, the predictors in our model of oryx photographic rate included our water tank metric, grass cover, shrub cover, yearly precipitation, and a shrub\*precipitation interaction, in case landscape use depended on rangeland condition.

We assessed diel activity using the time of day for each independent photograph across all cameras and years using the Chi-square goodness-of-fit test. Specifically, we tested whether diel activity patterns of oryx varied among diurnal, nocturnal, and crepuscular periods. We defined crepuscular activity as 1 h before and after sunrise and sunset, diurnal activity as 1 h after sunrise to 1 h before sunset, and nocturnal activity as 1 h after sunset to 1 h before sunrise. We used the 'sunrise' function in package 'maptools' (Bivand and Lewin-Koh, 2019) in R (RStudio Ver. February 1, 5001) to obtain spatially referenced time of day values of sunrise and sunset for each independent photograph via the National Oceanic and Atmospheric Administration solar calculator. We also assessed whether oryx diel activity varied with vegetation cover by categorizing sites as having "High" or "Low" levels of grass and shrub cover, based on whether they were above or below the mean for all sites. We tested for differences in activity between "High" and "Low" cover sites using the Chi-square test of independence. We visualized oryx diel activity using the 'sunTime' function in the 'overlap' package in R (Ridout and Linkie, 2009). Finally, we used the Chi-square test of independence to assess whether diel activity differed between individuals and groups (two or more individuals in a photograph).

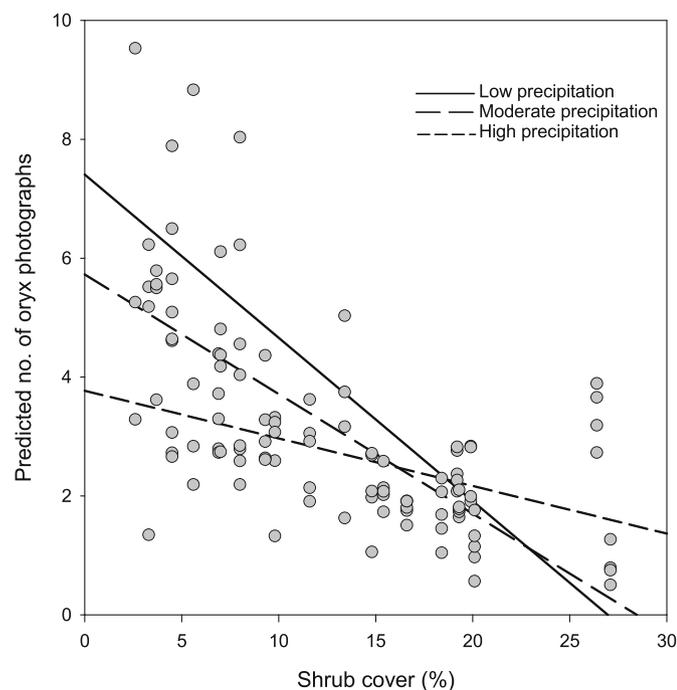
### 4. Results

We obtained 2339 oryx photographs across 19,097 trap-nights, producing 359 independent photographs. Photographic rate was variable across years but generally increased over time (Table S1). Oryx photographic rate was negatively related to shrub cover (Fig. 1) and to yearly precipitation ( $\bar{x} = 237$  mm, range: 99–406 mm; Table 1). Moreover, there was a positive interaction between shrub cover and yearly precipitation (Table 1), suggesting increased abundances of oryx in habitats with low shrub cover were most pronounced in drier years (Fig. 1). Oryx photographic rate was unrelated to grass cover or cattle water tanks (Table 1).

Oryx diel activity differed among activity periods, showing distinct peaks centered around sunrise and sunset ( $\chi^2 = 39.687$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 2a). Diel activity was also consistent across years ( $\chi^2 = 8.828$ ,  $df = 8$ ,  $P = 0.357$ ). Diel activity patterns for oryx did not differ between sites with high or low grass cover ( $\chi^2 = 2.729$ ,  $df = 2$ ,  $P = 0.256$ ) or shrub cover ( $\chi^2 = 0.648$ ,  $df = 2$ ,  $P = 0.723$ ). However, we found differences in diel activity between individuals and groups ( $\chi^2 = 14.447$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 2b), and this outcome was consistent between levels of grass and shrub cover (Table S2). Individuals were more active during the nocturnal period than were groups of oryx.

### 5. Discussion

Using a multiyear data set collected across a broad grassland-to-shrubland gradient, we provide evidence linking an exotic ungulate to the potential exacerbation of shrub encroachment in the Chihuahuan Desert. Specifically, we demonstrate that relative abundances of oryx were greater on habitats with low shrub cover, where grasses and herbaceous forage are typically more abundant (Peters et al., 2012; Schooley et al., 2018). We also demonstrate that this association of oryx

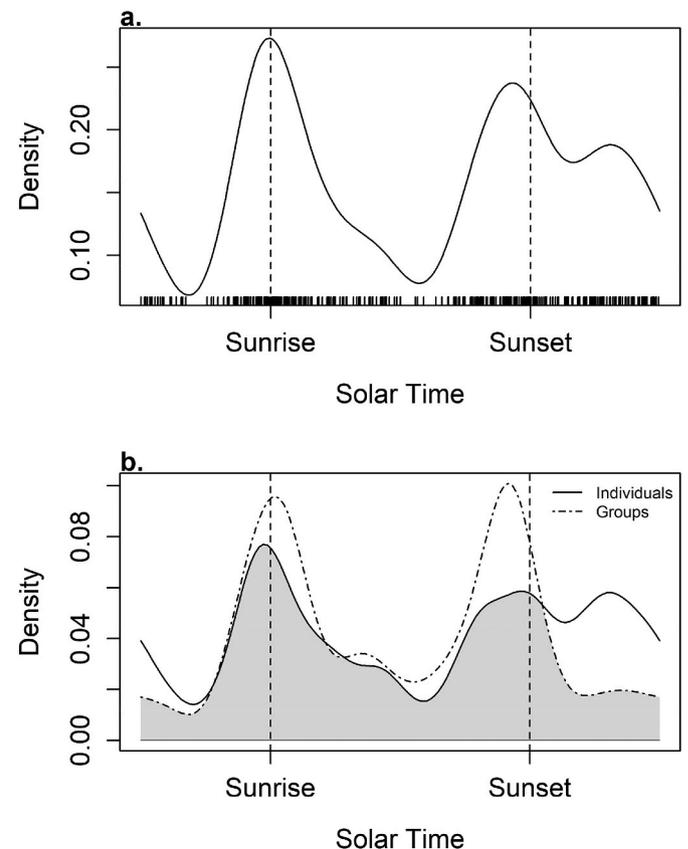


**Fig. 1.** Interactive effects of shrub cover and precipitation on relative abundance of exotic oryx at the Jornada Basin Long Term Ecological Research site, New Mexico, 2014–2018. Each circle represents the predicted number of independent photographs of oryx on a site from our negative binomial model (see Table 1). Lines indicate relationships for three levels of annual precipitation (Low  $\leq$  33rd percentile, Moderate = 34th – 66th percentile, High  $>$  66th percentile). The positive association of oryx with sites with low shrub cover is strongest in years of low-to-moderate precipitation.

**Table 1**

Estimates of beta coefficients from our negative binomial model of photographic rate of exotic oryx across shrub encroachment gradients at the Jornada Basin Long Term Ecological Research site, New Mexico, USA, 2014–2018.

Covariate	$\hat{\beta}$	SE	95% CI	df	P
Water Tanks	0.0899	0.0711	[-0.058, 0.240]	20	0.220
Grass Cover	0.0133	0.0213	[-0.031, 0.058]	20	0.537
Shrub Cover	-0.1880	0.0664	[-0.330, -0.050]	20	0.010
Precipitation	-0.0088	0.0032	[-0.015, -0.0025]	85	0.007
Shrub*Precipitation	0.000492	0.000226	[0.000042, 0.00094]	85	0.032



**Fig. 2.** Oryx diel activity from 2014 to 2018 plotted as a kernel density estimate, adjusted from clock times to solar times. (a) Oryx displayed an overall crepuscular pattern. Tick marks on the x-axis indicate times of independent photographs. (b) Overlapping kernel density estimates of oryx individuals and groups (gray shading) illustrate a shift in diel activity of individuals toward greater nocturnality.

with low shrub cover increases during years of low to moderate precipitation, which has implications for rangeland health. More broadly, our research highlights that ongoing landscape change may interact with biotic invasions, potentially accelerating landscape transitions.

Oryx were more common on unencroached grasslands during dry years when grasslands are most vulnerable to degradation and subsequent shrub encroachment (D’Odorico et al., 2012). Compared to shrublands, grasslands at Jornada Basin typically have over twice the cover of perennial grasses plus greater net productivity of annual grasses and forbs (Schooley et al., 2018). Moreover, perennial forbs were negatively correlated with shrub cover ( $r = -0.754$ ,  $P < 0.001$ ; Fig. S3) and should provide additional forage in grasslands during dry years when grasses are less abundant (Cain et al., 2017). Thus, oryx may be attracted to sites with low shrub cover that have more food resources in

general instead of tracking perennial grasses directly. Nevertheless, the outcome would be greater herbivory pressure in grasslands and the opportunity to promote further shrub encroachment.

To our knowledge, our study is the first to quantify diel activity of African oryx in their exotic range. Our findings support the hypothesis that oryx are most active during crepuscular periods, which is similar to their diel activity during the hot-wet season in their native range (Boyers et al., 2019). Limiting activity to crepuscular periods likely ensures oryx can forage while maintaining thermoregulatory processes, limiting water loss, and remaining vigilant for predators. Oryx diel activity was unrelated to variations in shrub or grass cover, indicating shrub encroachment does not alter their behavior over short temporal scales (i.e., the 24-hr diel cycle). Interestingly, however, we documented differences in diel activity between groups and individual oryx. The apparent shift of individual oryx toward more nocturnal activity may be due to predator release in New Mexico. If perceived risk of predation is reduced, individual oryx may be expanding their diel niche as a means to reduce intraspecific pressures. Individual oryx may also represent particular sex or age classes that require extended activity for foraging.

Here, we demonstrate how landscape use of an exotic ungulate species could potentially exacerbate shrub encroachment in the Chihuahuan Desert. This issue, along with potential increases in human-wildlife conflicts (i.e., vehicle collisions, property destruction; Bender et al., 2019), disease transmission to native ungulates (Bender et al., 2019), and spread of exotic plant species (Vavra et al., 2007) may become increasingly magnified if oryx populations expand their range across the desert southwest. If oryx are indeed exacerbating grass loss, different stakeholders may have conflicting perspectives on oryx management strategies. Ranchers who depend on these grasslands for cattle grazing could see diminishing returns if oryx are not controlled, whereas recreational hunters would derive continued benefits from presence of oryx and could be in favor of expanding the population.

Thus, there is a need to weigh the costs and benefits of exotic oryx in the Chihuahuan Desert and whether the ecological and economic outcomes warrant the widespread consideration of oryx as an invasive species. Further research is necessary to identify (1) specific pathways by which oryx interact with shrub encroachment, native herbivores, and livestock; (2) current and potential extents of oryx distribution in North America; and (3) effective methods of population control that produce positive outcomes for rangeland ecosystems and relevant stakeholders.

#### CRedit authorship contribution statement

**Kieran J. Andreoni:** Methodology, Formal analysis, Data curation, Writing - original draft. **Casey J. Wagnon:** Methodology, Formal analysis, Data curation, Writing - review & editing. **Brandon T. Bestelmeyer:** Resources, Funding acquisition, Writing - review & editing. **Robert L. Schooley:** Conceptualization, Formal analysis, Writing - review & editing, Funding acquisition.

#### Declaration of competing interest

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

#### Acknowledgments

We thank NSF for funding to the Jornada Basin LTER program (Nos. DEB-1235828 and DEB-1832194); Seth Hall, Laura Burkett, and Neeshia Macanowicz for conducting fieldwork; John Anderson, Amalia Slaughter, and David Thatcher for providing supporting data; and Niko Mendes and Ryan Hagan for compiling photographic data.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2020.104302>.

#### References

- Bender, L.C., 2006. Population Demographics, Dynamics, and Movements of South African oryx (*Oryx gazella gazella*) in South-Central New Mexico. Final Report. U.S. Department of Defense – White Sands Missile Range, New Mexico. Department of Game and Fish.
- Bender, L.C., Morrow, P.C., Weisenberger, M.E., Krueger, B., 2019. Population dynamics and control of South African oryx in the Chihuahuan Desert, south-central New Mexico. *Human-Wildlife Interactions* 13, 158–166. <https://doi.org/10.26076/dbdm-9c32>.
- Bestelmeyer, B.T., Khalil, N.I., Peters, D.P.C., 2007. Does shrub invasion indirectly limit grass establishment via seedling herbivory? A test at grassland-shrubland ecotones. *J. Veg. Sci.* 18, 270–363. <https://doi.org/10.1111/j.1654-1103.2007.tb02548.x>.
- Bivand, R., Lewin-Koh, M., 2019. Maptools: tools for handling spatial objects. R package version 0.9-9. <https://CRAN.R-project.org/package=maptools>.
- Boyers, M., Parrini, F., Owen-Smith, N., Erasmus, B.F.N., Hetem, R.S., 2019. How free-ranging ungulates with differing water dependencies cope with seasonal variation in temperature and aridity. *Conservation Physiology* 7 (1), coz064. <https://doi.org/10.1093/conphys/coz064>.
- Bradley, B.A., Mustard, J.F., 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecol. Appl.* 16, 1132–1147. [https://doi.org/10.1890/1051-0761\(2006\)016\[1132:CTLDOA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1132:CTLDOA]2.0.CO;2).
- Brook, B.W., Sodhi, N.S., Bradshaw, C.J.A., 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* 23, 453–460. <https://doi.org/10.1016/j.tree.2008.03.011>.
- Cain III, J.W., Avery, M.M., Caldwell, C.A., Abbott, L.B., Holecheck, J.L., 2017. Diet composition and overlap of sympatric American pronghorn and gemsbok. *Wildl. Biol.* 4, 00296 <https://doi.org/10.2981/wlb.00296>.
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J.R., Griffiths, M., Holden, J., Kawanishi, K., Kinnaird, M., et al., 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Anim. Conserv.* 4, 75–79. <https://doi.org/10.1017/S1367943001001081>.
- Crowl, T.A., Crist, T.O., Parmenter, R.R., Belovsky, G., Lugo, A.E., 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. *Front. Ecol. Environ.* 6, 238–246. <https://doi.org/10.1890/070151>.
- D’Orazio, P., Okin, G.S., Bestelmeyer, B.T., 2012. A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecohydrology* 5, 520–530. <https://doi.org/10.1002/eco.259>.
- Harris, G., Sanderson, J.G., Erz, J., Lehnen, S.E., Butler, M.J., 2015. Weather and prey predict mammals’ visitation to water. *PLoS One* 10 (11), e0141355. <https://doi.org/10.1371/journal.pone.0141355>.
- Herrick, J., Van Zee, J.W., Havstad, K.M., Whitford, W.G., 2005. *Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems*. USDA-ARS Jornada Experimental Range, Las Cruces, New Mexico, Tucson, Arizona, USA. University of Arizona Press.
- Hobbs, R.J., Higgs, S., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24, 599–605. <https://doi.org/10.1016/j.tree.2009.05.012>.
- Lehmann, D., Mfune, J.K.E., Gewers, E., Cloete, J., Brain, C., Voigt, C.C., 2013. Dietary plasticity of generalist and specialist ungulates in the Namibian Desert: a stable isotopes approach. *PLoS One* 8 (8), e0072190. <https://doi.org/10.1371/journal.pone.0072190>.
- Norbury, G., Byrom, A., Pech, R., Smith, J., Clarke, D., Anderson, D., Forrester, G., 2013. Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. *Ecol. Appl.* 23, 1707–1721. <https://doi.org/10.1890/12-1958.1>.
- Peters, D.P.C., Yao, Y., Sala, O.E., Anderson, J.P., 2012. Directional climate change and potential reversal of desertification in arid and semiarid environments. *Global Change Biol.* 18, 151–163. <https://doi.org/10.1111/j.1365-2486.2011.02498.x>.
- Ridout, M., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. *J. Agric. Biol. Environ. Stat.* 14, 322–337. <https://doi.org/10.1198/jabes.2009.08038>.
- Ratajczak, Z., Nippert, J.B., Collins, S.L., 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology* 93, 697–703. <https://doi.org/10.1890/11-1199.1>.
- Rovero, F., Marshall, A.R., 2009. Camera trapping photographic rate as an index of density in forest ungulates. *J. Appl. Ecol.* 46, 1011–1017. <https://doi.org/10.1111/j.1365-2664.2009.01705.x>.
- Sanderson, J.G., Harris, G., 2013. Automatic data organization, storage, and analysis of camera trap pictures. *Journal of Indonesian Natural History* 1, 11–19.
- Schooley, R.L., Bestelmeyer, B.T., Campanella, A., 2018. Shrub encroachment, productivity pulses, and core-transient dynamics of Chihuahuan Desert rodents. *Ecosphere* 9 (7). <https://doi.org/10.1002/ecs2.2330> e02330.
- Vavra, M., Parks, C.G., Wisdom, M.J., 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. *For. Ecol. Manag.* 246, 66–72. <https://doi.org/10.1016/j.foreco.2007.03.051>.
- Wagnon, C.J., Schooley, R.L., Cosentino, B.J., 2020. Shrub encroachment creates a dynamic landscape of fear for desert lagomorphs via multiple pathways. *Ecosphere* (in press).