



## RESEARCH ARTICLE

# A novel trophic cascade between cougars and feral donkeys shapes desert wetlands

Erick J. Lundgren<sup>1,2,3</sup>  | Daniel Ramp<sup>3</sup>  | Owen S. Middleton<sup>4</sup>  |  
Eamonn I. F. Wooster<sup>3</sup>  | Erik Kusch<sup>1,2</sup>  | Mairin Balisi<sup>5,9</sup>  | William J. Ripple<sup>6</sup>  |  
Chris D. Hasselerharm<sup>1</sup>  | Jessica N. Sanchez<sup>7</sup>  | Mystyn Mills<sup>8</sup>  | Arian D. Wallach<sup>3</sup> 

<sup>1</sup>Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Biology, Aarhus University, Aarhus, Denmark; <sup>2</sup>Section for Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark; <sup>3</sup>Centre for Compassionate Conservation, TD School, University of Technology Sydney, Ultimo, Australia; <sup>4</sup>School of Life Sciences, University of Sussex, Brighton, UK; <sup>5</sup>La Brea Tar Pits and Museum, Los Angeles, California, USA; <sup>6</sup>Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA; <sup>7</sup>One Health Institute, School of Veterinary Medicine, University of California at Davis, Davis, CA, USA; <sup>8</sup>Department of Botany & Plant Sciences, University of California Riverside, Riverside, CA, USA and <sup>9</sup>Raymond M. Alf Museum of Paleontology, Claremont, CA, USA

## Correspondence

Erick J. Lundgren

Email: [erick.lundgren@gmail.com](mailto:erick.lundgren@gmail.com)

## Funding information

Australian Research Council, Grant/Award Number: DP180100272; University of Technology Sydney

Handling Editor: Rafael Raimundo

## Abstract

1. Introduced large herbivores have partly filled ecological gaps formed in the late Pleistocene, when many of the Earth's megafauna were driven extinct. However, extant predators are generally considered incapable of exerting top-down influences on introduced megafauna, leading to unusually strong disturbance and herbivory relative to native herbivores.
2. We report on the first documented predation of juvenile feral donkeys *Equus africanus asinus* by cougars *Puma concolor* in the Mojave and Sonoran Deserts of North America. We then investigated how cougar predation corresponds with differences in feral donkey behaviour and associated effects on desert wetlands.
3. Focusing on a feral donkey population in the Death Valley National Park, we used camera traps and vegetation surveys to compare donkey activity patterns and impacts between wetlands with and without cougar predation.
4. Donkeys were primarily diurnal at wetlands with cougar predation, thereby avoiding cougars. However, donkeys were active throughout the day and night at sites without predation. Donkeys were ~87% less active (measured as hours of activity a day) at wetlands with predation ( $p < 0.0001$ ). Sites with predation had reduced donkey disturbance and herbivory, including ~46% fewer access trails, 43% less trampled bare ground and 192% more canopy cover (PERMANOVA,  $R^2 = 0.22$ ,  $p = 0.0003$ ).
5. Our study is the first to reveal a trophic cascade involving cougars, feral equids and vegetation. Cougar predation appears to rewire an ancient food web, with diverse implications for modern ecosystems. Our results suggest that protecting apex predators could have important implications for the ecological effects of introduced megafauna.

## KEYWORDS

burros, feral equids, invasive species, megafauna, mountain lions, predation, rewilding, trophic cascades

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

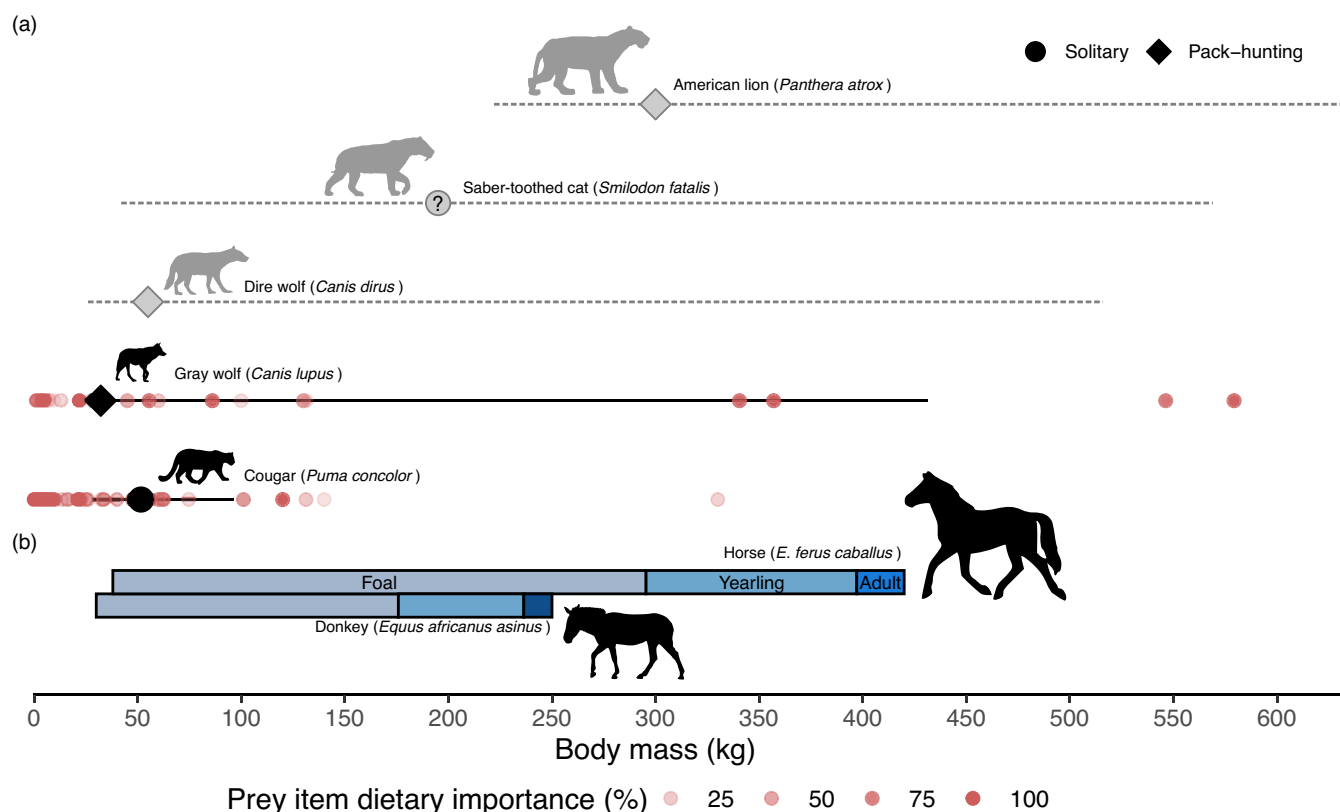
## 1 | INTRODUCTION

Many of the world's large herbivores and predators were lost in the late Pleistocene, most likely due to human impacts (Sandom et al., 2014; Smith et al., 2018). A second wave of decline is ongoing, as the majority of surviving large herbivore species (henceforth megafauna) are now threatened with extinction (Ripple et al., 2015). Conversely, several megafauna species have established thriving populations following introductions, restoring lost species richness and some important ecological traits (Lundgren et al., 2018, 2020). However, many apex predator species, especially the largest, did not survive the late Pleistocene extinctions and those that remain are often persecuted by humans (Middleton et al., 2020; Ripple et al., 2014). This begs the question: can extant apex predators exert top-down influences on introduced megafauna, given that many introduced megafauna are larger than co-occurring native herbivores?

We report on a novel trophic cascade (Wallach et al., 2015) between cougars *Puma concolor*, feral donkeys *Equus africanus asinus* and vegetation in North America. Cougars co-occurred with a diversity of equid species for more than a million years until the North

and South American late Pleistocene extinctions ~9–12,000 years ago (Williams et al., 2018). The little paleoecological evidence that exists, however, suggests that cougar–equid interactions may have been uncommon, with equids mainly preyed upon by larger or pack-hunting now-extinct predators (Figure 1a,b, DeSantis & Haupt, 2014). While research on cougar predation of feral horses is increasing (Andreasen et al., 2021), most policy and ecological literature continues to ignore or explicitly deny the possibility that feral equids experience ecologically significant predation, with oft-repeated claims that they 'have no natural predators' (Bureau of Land Management, 2018; Death Valley National Park, 2018). In contrast, we recorded the first documented predation of feral donkeys by cougars, including a yearling (Figure 2a,b) and foal (Figure 2c,d), and mapped widespread predation of juvenile donkeys in the Mojave Desert (Figure S1).

Predation can control herbivore populations through direct killing. Indeed, cougar predation on juvenile introduced feral horses can reduce or prevent population growth rates in some circumstances (Greger & Romney, 1999; Turner et al., 1992). However, predation also influences prey indirectly, by driving predator-avoidance



**FIGURE 1** Body size and hunting style determine predator–prey interactions and may constrain the ability of extant predators to influence introduced megafauna. X-axis (body mass) is shared across all subplots. (a) North American apex predators before and after the late Pleistocene extinctions. Horizontal lines indicate theoretical optimum prey body mass range of extant (black) and extinct (dashed) predators (from Van Valkenburgh et al., 2016). Points indicate average predator body mass and hunting style, which remains uncertain for *Smilodon fatalis* (denoted with question mark). Red points indicate published prey items by body mass, with transparency denoting the importance of prey in diet (data from CarniDIET, Middleton et al., 2021). Of extant North American predators, only the cougar *Puma concolor* substantially overlaps in geographic distribution with feral equids (IUCN Red List, 2018; Wallach et al., 2020). (b) Estimated body mass ranges for equid age classes.



**FIGURE 2** First photographic evidence of cougar predation on feral donkeys, captured with camera traps. (a, b). Successful predation of a yearling donkey in the Sonoran Desert, Arizona. The cougar is looking up from the ground. Arrow in inset points to the cougar's left eye. (c, d). Predation of a foal in the Death Valley National Park, in the Mojave Desert of California. Donkey ages were determined from tooth eruption sequences of carcasses. Images (a) and (c) were tonally adjusted for visibility (see Figure S2 for original versions).

behaviours that can modify their effects on the environment (Fortin et al., 2005; Landré et al., 2010). These include increased vigilance, reduced consumption rates, shifts in activity rates and temporal patterns, and longer movement distances (Cunningham et al., 2019; Fortin et al., 2005; Landré et al., 2010; van Beeck Calkoen et al., 2021). These changes can emerge even after recent exposure to predators. For example, moose mothers *Alces alces* rapidly changed their behaviour after experiencing the first predation of a calf by range-expanding grey wolves *Canis lupus* (Berger et al., 2001).

Feral donkeys and horses can have strong effects on ecosystems through herbivory and trampling (Baur et al., 2018) and by competitively displacing other species from limiting resources (Hall et al., 2016). For these reasons, many feral equid populations in the United States have been targeted for complete removal and most experience strict population control. However, it remains unknown whether the effects of feral equids could be shaped by predation. If so, this would have implications for policies towards feral equids

and their predators and would contextualize how we understand the effects of feral equids and other introduced megafauna.

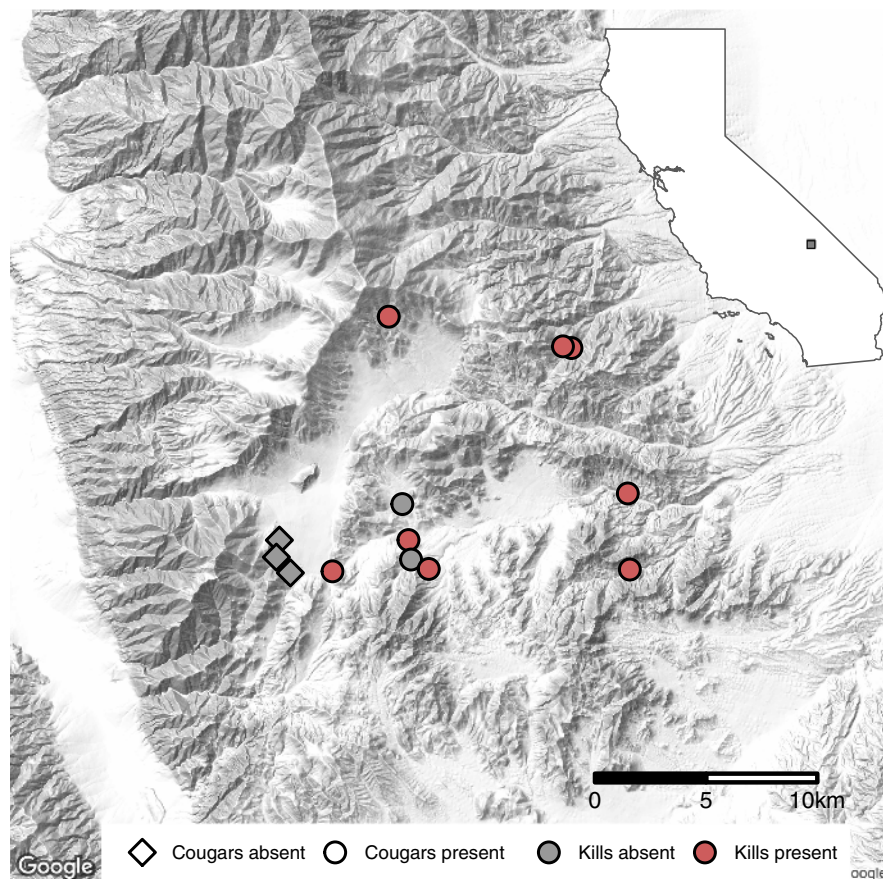
We utilized a 'natural comparisons' approach at desert wetlands with and without cougar predation of feral donkeys to investigate how cougars influenced donkey temporal activity patterns and rates, and how predation was associated with the disturbance and herbivory related effects of donkeys on desert wetlands.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

This research focused on the Southern Panamint mountains of the Death Valley National Park (Figure 3, permit: DEVA-2018-SCI-0036). This ~150km<sup>2</sup> landscape is highly connected by donkey trails, and we regularly witnessed bands of donkeys travelling





**FIGURE 3** Primary study area in the Southern Panamint Mountains of the Death Valley National Park. Points indicate monitored wetlands, which varied by the presence of cougars and kills. The three wetlands where cougars were absent were proximate to campsites. Inset indicates location in the state of California. See Table S1 for camera trap nights per station. See Figure S1 for distribution of kills and the additional study sites used to corroborate donkey temporal activity responses to cougars.

between wetlands within this study region, suggesting that this can be considered a single population of donkeys. Unlike many areas with feral equids, cougars in the Death Valley National Park are strongly protected from hunting. We monitored every known wetland in this region ( $n = 17$ ) but excluded three because of camera malfunctions. All work was non-manipulative and did not require the Institutional Animal Care and Use Committee approval in the USA but received animal ethics approval at the University of Technology Sydney, Australia (ETH16-0237).

The wetlands in this region varied in relation to predation risk. There were eight wetlands (2,530 trap nights) where cougar predation on donkeys was detected, two wetlands where cougars were detected but donkey kills were absent (436 trap nights), and three wetlands without any cougar detections (312 trap nights). These latter wetlands were at campsites. Unfortunately, this led to a discrepancy in trap nights between these treatment levels due to camera thefts at these wetlands. While the mixed effect models we employed (specified below) are robust to differences in sample size (Pinheiro, 2014), all other analyses used resampling methods to ensure that our results were robust to unbalanced sample sizes.

Evidence of predation was determined by surveying for cached carcasses on cougar trails at each wetland (see the Supporting Information) as well as from direct photographic evidence of kills (i.e. Figure 2). Although it is possible that the cached donkey carcasses were the result of non-predation related mortality events and had been scavenged by cougars, the inverse relationship between

the total number of donkey carcasses and feral equid activity rates supports that these carcasses were not caused by some underlying density-dependent process, such as disease ( $z = -3.5$ ,  $p = 0.0005$ , see Supplementary material and Figure S3).

## 2.2 | Temporal activity patterns of donkeys and cougars

Temporal activity patterns were calculated with the 'overlap' (v0.3.3) and 'circular' packages (v0.4-93) in R v4.0.0 (Agostinelli & Lund, 2017; Meredith & Ridout, 2014; R Core Team, 2020). Sampling effort (i.e. number of trap nights) and the number of donkey detections varied between sites with and without cougar predation, which would bias pooled estimates. We therefore resampled our data over 1,000 iterations, sampling equally between sites with and without predation (see Supplementary material for resampling details). From these resampled activity distributions, we calculated 95% confidence intervals (CIs) to test if there was a significant difference in activity between sites with predation and without, based on the overlap or non-overlap of CIs.

Half of the sites (three of six) without kills were at campsites, which could also drive nocturnality if donkeys were avoiding human activity. We therefore compiled data from additional study regions from earlier research efforts to corroborate our results (Lundgren, Ramp, Stromberg, et al., 2021). However, since we did not have

ground survey data of local predation events in this broader region, we conducted this analysis based on whether cougars were locally detected or not (Figure S1; Data S1).

## 2.3 | The influence of cougar predation on the activity duration of feral donkeys

Desert wetlands can become foci of activity for water-dependent animals such as donkeys, particularly at high temperatures, leading to intense herbivory, disturbance and competition (Baur et al., 2018; Hall et al., 2016). Daily donkey activity rates at each wetland were summarized per day as the total duration of 'events'. Events were defined as any donkey detection within 30 min of any other. We chose to evaluate event duration instead of the number of events, given that some wetlands were occupied continuously for nearly 12 hr a day in singular events, while others were occupied for <30 min a day but in several short-duration events.

First, we used a Wilcoxon signed rank test to analyse whether the total duration of activity (henceforth 'activity rate') over 100 trap nights varied between sites with and without cached donkey kills. We then analysed how the presence of cached donkey kills, daily maximum temperature and their interaction, affected daily donkey activity rates in the Southern Panamints of Death Valley. We used negative binomial mixed effect models in the R package GLM-MTMB v1.0.2.1 (Brooks et al., 2017), nesting camera station within site, crossed with date, as random effects. We treated the presence of local donkey kills, daily maximum temperature, and their interactions, as fixed effects. Daily maximum temperatures were extracted from the PRISM Climate Group (2020).

Following Brooks et al. (2017), we used the R package DHARMA (Hartig, 2022) to test for over or under dispersion and zero inflation, of which the latter was significant. To address this, we used the DHARMA function 'testZeroInflation' to evaluate different formulations of zero inflation terms and chose the model with the least evidence of zero-inflation ( $p = 0.088$ ). This model included the presence of kills in its zero-inflation component, thus testing whether there was a higher probability of days with zero donkey activity at sites with kills. To test whether the unexplained variation in this model was related to spatial distribution of sites, we used the function 'Moran.I' in the R package APE v5.4 to test for spatial autocorrelation on the scaled residuals, which we extracted with the function `simulateResiduals` (DHARMA).

## 2.4 | Effects of feral donkeys on wetlands

To understand if cougars influenced the effects of donkeys on wetlands, we collected data from 14 desert wetlands in the Southern Panamints of Death Valley National Park. We excluded wetlands that experienced flood disturbance, as this would confound the effects of donkeys themselves. We focused on pools where donkeys accessed water and measured the percentage of surface water

vegetated by emergent vegetation (e.g. rooted in aquatic substrate), the percent of the water surface covered by canopy foliage, the number of access trails per pool and the percent of the pool's perimeter occupied by vegetation  $\geq 0.5$  m in height.

To quantify the degree of disturbance extending upland from these water access points, we set 3 parallel 30-m long belt transects 10 m apart, with the central transect centered on the spring access point. Every 10 m along each transect, we estimated percent trampled ground, percent undisturbed ground, percent herbaceous cover, and percent woody cover in 1-m<sup>2</sup> quadrats (9 total per access point). Although we collected data on plant cover by type and species, we did not include these in subsequent analyses because it was confounded by elevation and edaphic differences across sites, and thus did not directly capture the effects of donkeys.

To characterize wetland structure, we analysed these data by calculating the Gower distance between sites based on all seven response variables, which we analysed with a PERMANOVA test in the R package VEGAN v 2.5-6, with the presence of kills, the presence of cougars, elevation, and terrain complexity as independent variables. Terrain complexity was calculated from a 1/3 arc-second digital elevation model (USGS National Geospatial Program, 2019), which synthesized terrain roughness, terrain ruggedness and slope with a principal components analysis (PCA). PC1 explained 92.5% of total variation and was subsequently used as a synthetic terrain complexity variable (Figure S4). We visualized this data with a Principal Coordinates Analysis (PCoA) on the Gower distance matrix. The first two axes (PCoA 1 and PCoA 2) explained 47.5% of total variation between sites (28.3% and 19.1% respectively).

To test if these differences could have been driven by other underlying spatial gradients, we calculated a geographic distance matrix with the R package GEOSPHERE v1.5-10. We then conducted a Multiple Regression on Distances Matrices analysis with the function 'MRM' in the R package ECODIST v2.0.7 with 1,000 iterations, which tested whether the dissimilarity between wetlands was explained by their spatial distribution.

## 3 | RESULTS

Donkey temporal activity differed between wetlands depending on the presence of cougars and donkey kills. Donkeys were active throughout the day and night at sites where cougars were absent. However, donkeys were almost exclusively diurnal at sites with cougars, particularly where there was also evidence of cougar predation, thereby avoiding peaks of cougar activity (Figure 4a). Data from additional sites in the Mojave and Sonoran Deserts (Figure S1) corroborated this pattern, showing a transition from nocturnal to diurnal activity in the presence of cougars (Figure S5).

Donkeys were less active overall (hours over 100 trap nights) at wetlands with cougar predation (Wilcoxon signed rank test:  $W = 45$ ,  $p = 0.03$ ). Daily donkey activity rates also differed between sites with and without cougar predation: while daily activity rates increased with maximum daily temperature at all sites ( $z = 11.96$ ,

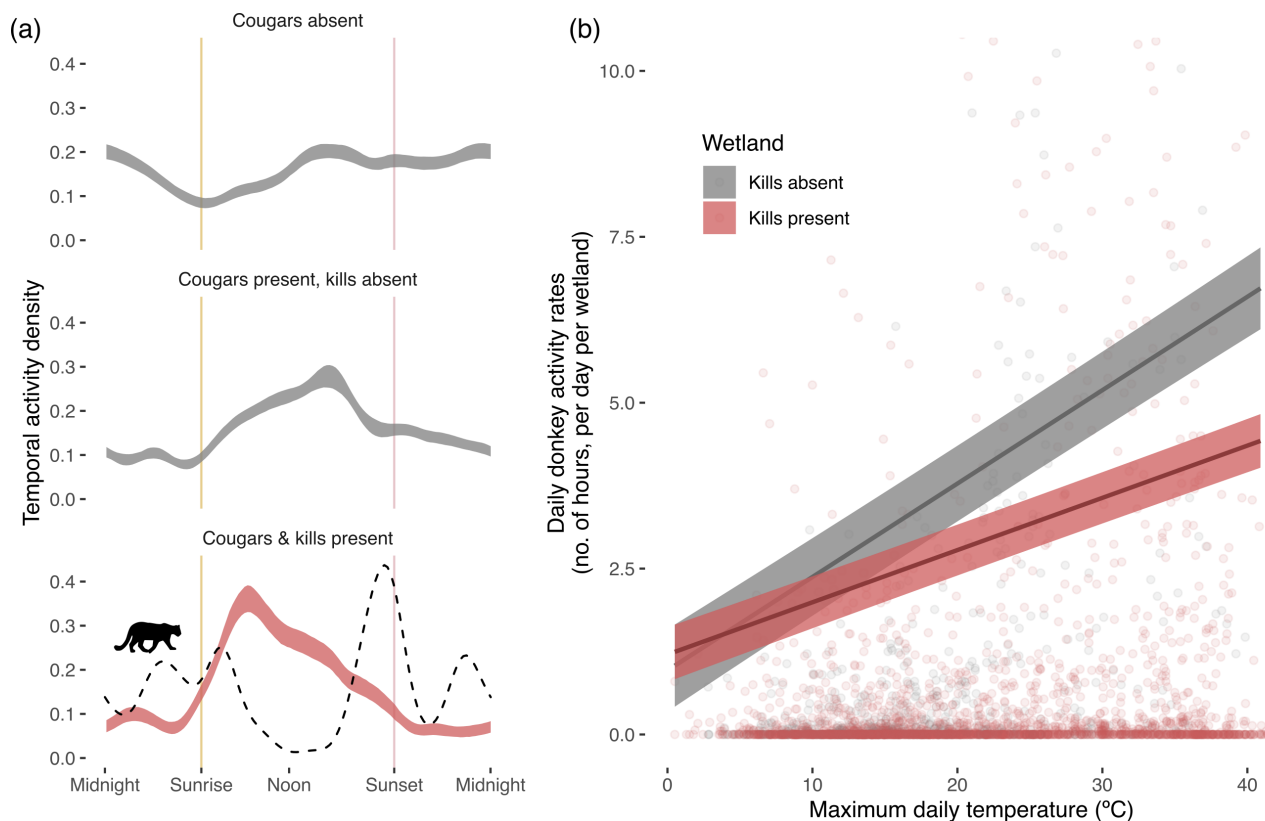


FIGURE 4 Cougars shape donkey activity at desert wetlands. (a) Donkey temporal activity under different levels of predation risk. X-axis indicates time of day. Ribbon indicates 95% confidence intervals from bootstrapped detections. Dashed line indicates cougar activity pattern. Cougar detection frequencies were insufficient at sites without kills to calculate their activity pattern (3 events). Data from additional sites in the Mojave and Sonoran Deserts (Figure S1) corroborated this pattern (Figure S5). (b) Relationship between maximum daily temperature and the daily activity rates of donkeys (hours/day/site) for sites with and without predation. Regression lines are extracted from negative binomial model with error estimates indicating standard error of model prediction.

$p < 0.0001$ , Figure 4b; Table S2; Data S1–S2), this response was reduced at sites with kills (interaction term:  $z = -4.91$ ,  $p < 0.0001$ , Figure 4b; Table S2). At wetlands without kills, activity increased to an average of 5.5 hr/day on days  $\geq 35^\circ\text{C}$  ( $SD = \pm 4.4$ , max = 16.5 hr, see Figure 4b for model predictions, Table S2); while at sites with kills, activity remained low and relatively stable, averaging 0.7 hr/day on days  $\geq 35^\circ\text{C}$  ( $\pm 1.7$ , max = 12.6 hr, Figure 4b; Table S2). Sites with kills also had more donkey-free days (zero-inflated model component:  $z = 3.4$ ,  $p = 0.0007$ , Table S2). There was no evidence of spatial autocorrelation in the responses of donkeys to temperature and predation (Moran's  $I$  on scaled residuals:  $p = 0.22$ ).

Cougar predation on donkeys was associated with reduced herbivory and disturbance-related effects on wetlands (PERMANOVA:  $R^2 = 0.22$ ,  $F = 3.34$ ,  $p = 0.0003$ , Figure 5a–c; Data S3). Wetlands with kills had 192% more canopy cover ( $41.5\% \pm 33.7$  compared to  $14.2\% \pm 16\%$  without kills, mean  $\pm SD$ ), 102% more vegetation around water perimeter ( $60.29\% \pm 18$  to  $29.75\% \pm 24.13$  without kills), 46% fewer trails ( $1.6 \pm 0.74$  to  $3.0 \pm 1.8$  without kills), and 43% less trampled bare ground (from  $50.2 \pm 16.5\%$  to  $88.8 \pm 12.9\%$  without kills, see Figure S6 for responses of individual variables). These differences were not explained by the presence of cougars (independent

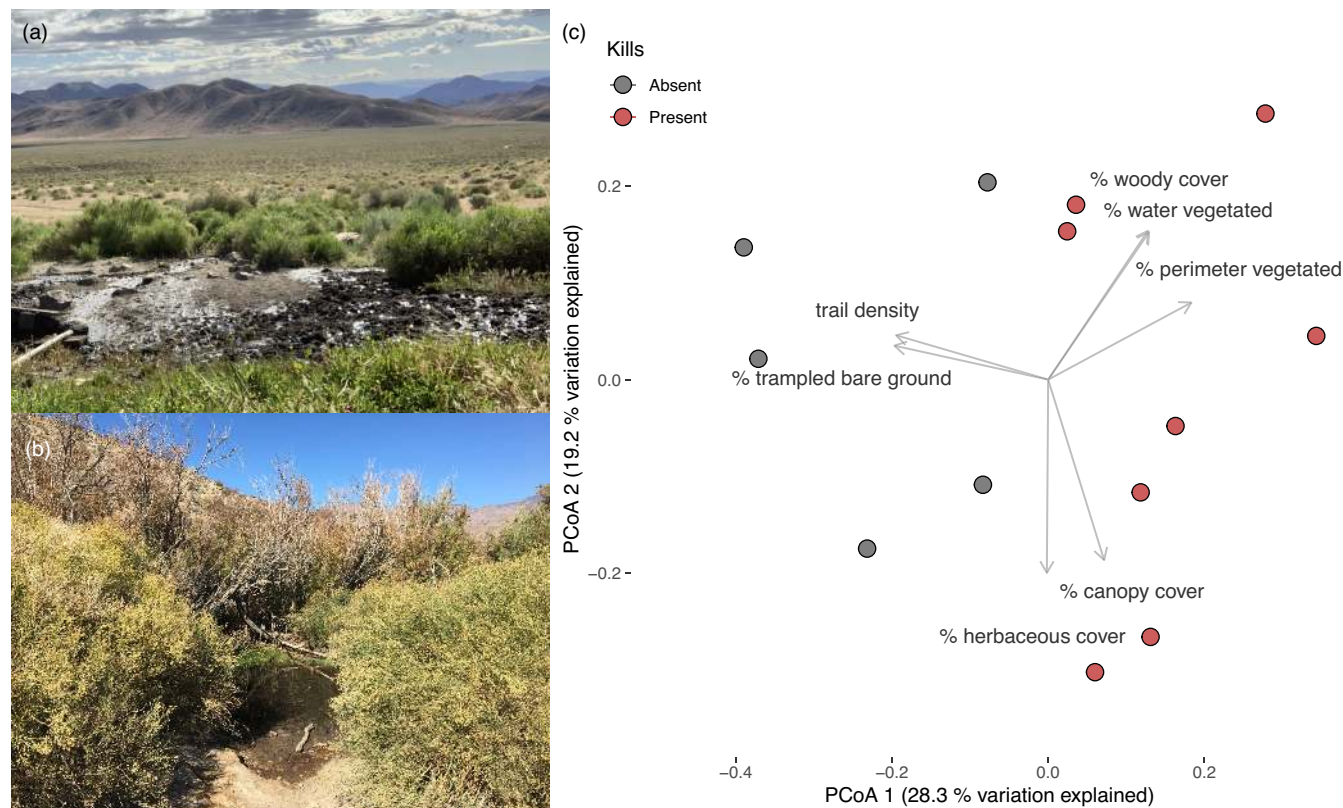
of kills), terrain complexity, elevation ( $p = 0.25$ – $0.36$ , Table S3), nor geographic distances between sites (multiple regression on distance matrices,  $R^2 = 0.02$ ,  $F = 1.35$ ,  $p = 0.35$ ).

## 4 | DISCUSSION

Cougar predation on feral donkeys was associated with altered donkey activity patterns and rates and with reduced herbivory and disturbance-related effects on desert wetlands. This adds to growing evidence that ecologically important predator–prey interactions can emerge rapidly in novel ecosystems, with implications for modern ecosystem functioning (Cattau et al., 2017; Wallach et al., 2015; Zavaleta et al., 2001). These results also suggest that removals or eradications of introduced equids and prevailing policies of predator persecution may have unintended consequences.

Feral donkeys and cougars appear to be linked in an emerging ecological network. Donkeys were the primary recorded prey of cougars at our study sites (24 of 29 cached carcasses). In addition to shaping donkey ecology, cougar predation on donkeys may drive novel evolutionary trajectories in cougars (Cattau et al., 2017) and





**FIGURE 5** Cougar predation is associated with reduced herbivory and disturbance-related influences on desert wetlands. (a) A representative wetland lacking both cougars and kills compared to a similar sized wetland nearby (~6 km apart) (b) where cougars and kills were present (site of the kill in Figure 1c,d). Photos were taken at a similar distance from water's edge, by EJL (a) and OSM (b). (c). Principal coordinates analysis (PCoA) showing differences in wetlands (points) with and without cougar predation on donkeys (PERMANOVA:  $F = 3.5$ ,  $p < 0.001$ ). Relationship between response variables and PCoA axes are indicated by overlaid arrows and text. See Figure S6 for response of individual variables.

reduce predation pressure on their other prey. While we did not conduct exhaustive analysis of cougar diets, the importance of donkeys in cougar caches, and of horses as prey elsewhere (Andreasen et al., 2021), suggests that removals of feral equids could have consequences both for cougars and for their alternative prey (e.g. big-horn sheep) due to prey switching.

Cougars, like most apex predators, are persecuted in service of the meat industry and to increase populations of their prey for sport hunting and conservation (Arizona Department of Game and Fish, 2016; Ripple et al., 2014). As with other apex predators, persecution can reduce the ability of cougar populations to hunt larger and more challenging prey by removing older individuals from the population and by disrupting the transmission of hunting techniques from mother to young (Peebles et al., 2013). Even moderate persecution may thus reduce the potential for ecologically relevant trophic cascades between cougars and feral equids. Policy responses to feral equid populations may benefit from attending to pervasive policies of predator persecution (Phillips, 2018).

Our study took advantage of a natural experiment, comparing sites with cougar predation to sites without. The absence of kills at certain springs appears to have been driven both by the presence of campsites and by terrain complexity (Figure S7). We

did not detect any cougars, or kills, at springs close to campsites (i.e. human shielding, Ripple & Beschta, 2006; Suraci et al., 2019). Likewise, as expected given the ambush cover requirements of cougars (Dickson & Beier, 2006), springs in topographically flat terrain lacked kills and had few cougar detections (Figure S7). Collectively, these sites had the highest donkey activity rates yet few or no cougars, suggesting that cougars were not simply tracking prey availability but were driving the observed differences in donkey behaviour (Smith et al., 2019). Human recreation and terrain differences could have had independent effects on donkey activity rates and wetland vegetation. However, donkeys did not appear disturbed by the presence of campers, nor was there evidence to suggest intrinsic differences in the potential vegetation between sites. Regardless, further research is necessary to strengthen these inferences.

Donkeys, like the majority of extant megafauna, are threatened in their native range (Lundgren et al., 2018; Ripple et al., 2015). This has led to calls for more inclusive conservation approaches to protect species both in their native and introduced ranges (Wallach et al., 2020). Promoting protections for introduced megafauna can find productive common ground with other conservation goals, such as increasing protection and tolerance for apex predators.

Expanding protections for apex predators may further influence the ecologies of feral donkeys and feral horses. For instance, the reestablishment of other documented equid predators (Table S4), such as wolves *Canis lupus* (Webb et al., 2009), could increase predation risk in low ambush terrain, further shaping how these animals influence ecosystems.

For more than a million years, cougars cooccurred with several species of equid across North and South America (Williams et al., 2018). However, much of conservation remains rooted in recent history, with little recognition of the prehistoric and historic legacies of human-caused extinctions and range contractions (Galetti et al., 2017; Monsarrat et al., 2019; Sandom et al., 2014; Smith et al., 2018). As such, the apparently novel effects of feral equids on desert wetlands are cited as the primary reason for their eradication and removal (Death Valley National Park, 2018). However, megafauna influences on wetlands were likely ubiquitous from the early Cenozoic (40–30 million ybp) until the late Pleistocene extinctions (Kodric-Brown & Brown, 2007; Lundgren, Ramp, Stromberg, et al., 2021; Naiman & Rogers, 1997). Indeed, previous donkey removals in the Death Valley region led to the extinction of several endangered and endemic fish populations due to the loss of donkey-maintained open water habitat (Kodric-Brown & Brown, 2007). Despite this, the feral donkeys of Death Valley and surrounding lands are currently being targeted for complete removal (Death Valley National Park, 2018).

If we had studied feral donkeys as 'invaders', without paying attention to predation, our data would contain a great degree of inexplicable noise. Instead, by studying these animals as any other wildlife, we find echoes of the late Pleistocene in a novel trophic cascade. Studying these interactions in light of Earth's history can yield insight into the structure and function of both modern and prehistoric ecological communities (Lundgren, Ramp, Wu, et al., 2021). The introduction of equids after their ~12,000 year hiatus—and predation upon them by cougars—suggests that global patterns of inadvertent rewilding can not only increase biodiversity and restore lost ecological functions (Lundgren et al., 2020; Wallach et al., 2018) but also can rewire ancient food webs (Pires, 2017). Our results suggest that the conservation community should prioritize the protection of apex predators and the world's remaining megafauna, regardless of their nativeness.

## AUTHORS' CONTRIBUTIONS

E.J.L. made the initial observations; E.J.L., E.I.F.W., O.S.M., W.J.R., D.R. and A.D.W. designed and conducted fieldwork; E.J.L., E.K., C.D.H., O.S.M. and E.I.F.W. conducted statistical analyses; all authors contributed to conceptualization and writing.

## FUNDING STATEMENT

Open access publishing facilitated by University of Technology Sydney, as part of the Wiley - University of Technology Sydney agreement via the Council of Australian University Librarians. WOA Institution: University of Technology Sydney Consortium Name: CAUL 2022

## ACKNOWLEDGEMENTS

We thank the Death Valley National Park staff, particularly Alison Ainsworth and Mike Reynolds. We thank Mark Meyers of Peaceful Valley Donkey Rescue—tasked with the non-lethal removals of feral donkeys from Death Valley—for assistance with field work logistics, equipment donations and site information. We thank Melanie Tietje and Sophie Monsarrat for statistical insight and Mark Davis, Martin Schlaepfer, Justin Suraci and two anonymous reviewers for helpful feedback on the manuscript. Work was supported by the Australian Research Council (grant number DP180100272) and crowdfunding. Open access publishing facilitated by University of Technology Sydney, as part of the Wiley - University of Technology Sydney agreement via the Council of Australian University Librarians.

## CONFLICT OF INTEREST

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and custom scripts available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.bvq83bkbk> (Lundgren et al., 2022).

## ORCID

Erick J. Lundgren  <https://orcid.org/0000-0001-9893-3324>  
Daniel Ramp  <https://orcid.org/0000-0003-3202-9898>  
Owen S. Middleton  <https://orcid.org/0000-0002-0813-6995>  
Eamonn I. F. Wooster  <https://orcid.org/0000-0002-2907-4076>  
Erik Kusch  <https://orcid.org/0000-0002-4984-7646>  
Mairin Balisi  <https://orcid.org/0000-0001-6633-1222>  
William J. Ripple  <https://orcid.org/0000-0001-6557-3043>  
Chris D. Hasselerharm  <https://orcid.org/0000-0001-5580-5445>  
Jessica N. Sanchez  <https://orcid.org/0000-0002-7689-0324>  
Mystyn Mills  <https://orcid.org/0000-0001-6775-8738>  
Arian D. Wallach  <https://orcid.org/0000-0002-6640-3887>

## REFERENCES

- Agostinelli, C., & Lund, U. (2017). *R package 'circular': Circular Statistics (version 0.4-93)*. Retrieved from <https://r-forge.r-project.org/projects/circular/>
- Andreasen, A. M., Stewart, K. M., Longland, W. S., & Beckmann, J. P. (2021). Prey specialization by cougars on feral horses in a desert environment. *The Journal of Wildlife Management*, 85, 1104–1120.
- Arizona Department of Game and Fish. (2016). *Arizona mountain lion management plan: Draft August 2016*. Retrieved from [www.azgfd.com](http://www.azgfd.com)
- Baur, L. E., Schoenecker, K. A., & Smith, M. D. (2018). Effects of feral horse herds on rangeland plant communities across a precipitation gradient. *Western North American Naturalist*, 77, 526–539.
- Berger, J., Swenson, J. E., & Persson, I.-L. (2001). Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. *Science*, 291, 1036–1039.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.



- Bureau of Land Management. (2018). *Management options for a sustainable wild horse and burro program*. Report to congress. Retrieved from [https://www.blm.gov/sites/blm.gov/files/wildhorse\\_2018ReporttoCongress.pdf](https://www.blm.gov/sites/blm.gov/files/wildhorse_2018ReporttoCongress.pdf)
- Cattau, C. E., Fletcher, R. J., Jr., Kimball, R. T., Miller, C. W., & Kitchens, W. M. (2017). Rapid morphological change of a top predator with the invasion of a novel prey. *Nature Ecology and Evolution*, 2, 108–115.
- Cunningham, C. X., Scoleri, V., Johnson, C. N., Barmuta, L. A., & Jones, M. E. (2019). Temporal partitioning of activity: Rising and falling top-predator abundance triggers community-wide shifts in diel activity. *Ecography*, 42, 2157–2168.
- Death Valley National Park. (2018). *Invasive Burros*. Retrieved from <https://www.nps.gov/deva/learn/nature/invasive-burros.htm>
- DeSantis, L. R., & Haupt, R. J. (2014). Cougars' key to survival through the Late Pleistocene extinction: Insights from dental microwear texture analysis. *Biology Letters*, 10, 20140203.
- Dickson, B. G., & Beier, P. (2006). Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA. *Journal of Zoology*, 271, 270–277.
- Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86, 1320–1330.
- Galetti, M., Moleon, M., Jordano, P., Pires, M. M., Guimaraes, P. R., Jr., Pape, T., Nichols, E., Hansen, D., Olesen, J. M., Munk, M., de Mattos, J. S., Schweiger, A. H., Owen-Smith, N., Johnson, C. N., Marquis, R. J., & Svenning, J. C. (2017). Ecological and evolutionary legacy of megafauna extinctions. *Biological Reviews*, 93, 845–862.
- Greger, P. D., & Romney, E. M. (1999). High foal mortality limits growth of a desert feral horse population in Nevada. *Great Basin Naturalist*, 59, 374–379.
- Hall, L. K., Larsen, R. T., Westover, M. D., Day, C. C., Knight, R. N., & McMillan, B. R. (2016). Influence of exotic horses on the use of water by communities of native wildlife in a semi-arid environment. *Journal of Arid Environments*, 127, 100–105.
- Hartig, F. (2022). *DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models*. R Project. R package version 0.4.5.
- IUCN Red List. (2018). *The International Union for the Conservation of Nature Red List*. The International Union for the Conservation of Nature.
- Kodric-Brown, A., & Brown, J. H. (2007). Native fishes, exotic mammals, and the conservation of desert springs. *Frontiers in Ecology and the Environment*, 5, 549–553.
- Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *The Open Ecology Journal*, 3, 1–7.
- Lundgren, E. J., Ramp, D., Middleton, O. S., Wooster, E. I. F., Kusch, E., Balisi, M., Ripple, W. J., Hasselerharm, C. D., Sanchez, J. N., Mills, M., & Wallach, A. D. (2022). Data from: A novel trophic cascade between cougars and feral donkeys shapes desert wetlands. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.bvq83bkbbk>
- Lundgren, E. J., Ramp, D., Ripple, W. J., & Wallach, A. D. (2018). Introduced megafauna are rewinding the Anthropocene. *Ecography*, 41, 857–866.
- Lundgren, E. J., Ramp, D., Rowan, J., Middleton, O., Schowanek, S. D., Sanisidro, O., Carroll, S. P., Davis, M., Sandom, C. J., Svenning, J. C., & Wallach, A. D. (2022). Introduced herbivores restore Late Pleistocene ecological functions. *Proceedings of the National Academy of Sciences of the United States of America*, 117, 7871–7878.
- Lundgren, E. J., Ramp, D., Stromberg, J. C., Wu, J., Nieto, N. C., Sluk, M., Moeller, K. T., & Wallach, A. D. (2021). Equids engineer desert water availability. *Science*, 372, 491–495.
- Lundgren, E. J., Ramp, D., Wu, J., Sluk, M., Moeller, K. T., Stromberg, J. C., & Wallach, A. D. (2021). Feral equids' varied effects on ecosystems. *Science*, 373, 973–974.
- Meredith, M., & Ridout, M. (2014). Overview of the overlap package. *Journal of Agricultural, Biological, and Environmental Statistics*, 14, 322–337.
- Middleton, O. S., Scharlemann, J. P., & Sandom, C. J. (2020). Homogenisation of carnivorous mammal ensembles caused by global range reductions of large-bodied hypercarnivores during the late Quaternary. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20200804.
- Middleton, O. S., Svensson, H., Scharlemann, J. P. W., Faurby, S., & Sandom, C. J. (2021). CarniDIET: A database of terrestrial carnivorous mammal diets. *Global Ecology and Biogeography*, 30, 1175–1182.
- Monsarrat, S., Novellie, P., Rushworth, I., & Kerley, G. (2019). Shifted distribution baselines: Neglecting long-term biodiversity records risks overlooking potentially suitable habitat for conservation management. *Philosophical Transactions of the Royal Society B*, 374, 20190215.
- Naiman, R. J., & Rogers, K. H. (1997). Animals and system-level characteristics in river corridors. *Bioscience*, 47, 521–529.
- Peebles, K. A., Wielgus, R. B., Maletzke, B. T., & Swanson, M. E. (2013). Effects of remedial sport hunting on cougar complaints and live-stock depredations. *PLoS ONE*, 8, e79713.
- Phillips, D. (2018). *Let mountain lions eat horses*. The New York Times.
- Pinheiro, J. C. (2014). *Linear mixed effects models for longitudinal data*. Wiley StatsRef: Statistics Reference Online.
- Pires, M. M. (2017). Rewilding ecological communities and rewiring ecological networks. *Perspectives in ecology and conservation*, 15, 257–265.
- PRISM Climate Group. (2020). *PRISM Climate Data* (ed. N.A.f.C.S. Engineering). Oregon State University.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Ripple, W. J., & Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation*, 133, 397–408.
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484.
- Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., Macdonald, D. W., Malhi, Y., Painter, L. E., Sandom, C. J., Terborgh, J., & Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, 1, e1400103.
- Sandom, C., Faurby, S., Sandel, B., & Svenning, J. C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133254.
- Smith, F. A., Elliott Smith, R. E., Lyons, S. K., & Payne, J. L. (2018). Body size downgrading of mammals over the late Quaternary. *Science*, 360, 310–313.
- Smith, J. A., Donadio, E., Pauli, J. N., Sheriff, M. J., Bidder, O. R., & Middleton, A. D. (2019). Habitat complexity mediates the predator-prey space race. *Ecology*, 100, e02724.
- Suraci, J. P., Clinchy, M., Zanette, L. Y., & Wilmers, C. C. (2019). Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters*, 22, 1578–1586.
- Turner, J. W. J., Wolfe, M. L., & Kirkpatrick, J. F. (1992). Seasonal mountain lion predation on a feral horse population. *Canadian Journal of Zoology*, 70, 929–934.
- USGS National Geospatial Program. (2019). *The National Map*. United States Geological Survey.
- van Beeck Calkoen, S. T., Kreikenbohm, R., Kuijper, D. P., & Heurich, M. (2021). Olfactory cues of large carnivores modify red deer behavior and browsing intensity. *Behavioral Ecology*, 32, 982–992.
- Van Valkenburgh, B., Hayward, M. W., Ripple, W. J., Meloro, C., & Roth, V. L. (2016). The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 862–867.

- Wallach, A. D., Lundgren, E., Batavia, C., Nelson, M. P., Yanco, E., Linklater, W., Carroll, S. P., Celermajer, D., Brandis, K. J., Steer, J., & Ramp, D. (2020). When all life counts in conservation. *Conservation Biology*, 34, 997–1007.
- Wallach, A. D., Lundgren, E. J., Ripple, W. J., & Ramp, D. (2018). Invisible megafauna. *Conservation Biology*, 32, 962–965.
- Wallach, A. D., Ripple, W. J., & Carroll, S. P. (2015). Novel trophic cascades: Apex predators enable coexistence. *Trends in Ecology & Evolution*, 30, 146–153.
- Webb, N. F., Merrill, E., & Allen, J. (2009). *Density, demography, and functional response of a harvested wolf population in West Central Alberta, Canada*. University of Alberta.
- Williams, J. W., Grimm, E. G., Blois, J., Charles, D. F., Davis, E., Goring, S. J., Graham, R., Smith, A. J., Anderson, M., Arroyo-Cabral, J., Ashworth, A. C., Betancourt, J. L., Bills, B. W., Booth, R. K., Buckland, P., Curry, B., Giesecki, T., Hausmann, S., Jackson, S. T., ... Takahara, H. S. (2018). The Neotoma paleoecology database: A multi proxy, international community-curated data resource. *Quaternary Research*, 89, 156–177.
- Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology & Evolution*, 16, 454–459.

## SUPPORTING INFORMATION

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

**How to cite this article:** Lundgren, E. J., Ramp, D., Middleton, O. S., Wooster, E. I. F., Kusch, E., Balisi, M., Ripple, W. J., Hasselerharm, C. D., Sanchez, J. N., Mills, M., & Wallach, A. D. (2022). A novel trophic cascade between cougars and feral donkeys shapes desert wetlands. *Journal of Animal Ecology*, 00, 1–10. <https://doi.org/10.1111/1365-2656.13766>