

Feral horses influence both spatial and temporal patterns of water use by native ungulates in a semi-arid environment

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Abstract. The horse (*Equus caballus*) is a feral ungulate that currently exceeds target population sizes in many areas of western North America. Horses are behaviorally dominant over native ungulates and outcompete the latter for access to water sources. However, a better understanding of the broader spatial and temporal implications of horse-induced competition on access to water by native ungulates will enable better conservation and management of native species. Our objective was to determine whether pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) spatially or temporally altered their use of water to minimize interactions with horses. From 2010 to 2014, we used remote cameras to monitor ungulates at 32 water sources in the Great Basin Desert. We evaluated spatial and temporal partitioning by these species at water sources using generalized linear models, mixed-effects models, and Mann–Whitney *U* tests. We found that both native ungulates used water sources less often where horse activity at water sources was high, indicating that spatial avoidance occurred. Further, we observed significant differences in peak arrival time for pronghorn, but not mule deer at horse-occupied sites versus sites where horses were absent or uncommon, indicating that temporal avoidance may be more important for pronghorn than mule deer. Because mule deer are primarily crepuscular and nocturnal whereas horses are largely diurnal, we did not expect to observe a temporal shift for mule deer. We also found strong support for the interactive negative effect of elevated temperature and subsequent increased activity of horses at water sources on drinking patterns of pronghorn and mule deer. Our findings indicate that feral horses further constrain access to an already limited resource for native species in a semi-arid environment.

Key words: competition; horse; mule deer; pronghorn; temperature; ungulates; water.

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INTRODUCTION

The horse (*Equus caballus*) is an exotic and feral ungulate that was introduced to North America during the 16th century (Mills and McDonnell 2005). Since its introduction, the horse has become widespread in western North America. Numbers of horses currently exceed appropriate management levels by almost 46,000 animals and can increase by 15–20% per year (Palmer et al. 2013, Bureau of Land Management 2017). However,

because horses are federally protected and share close relationships with humans, management options are limited, costly, and controversial (Linklater et al. 2002, Taggart 2008, Bies et al. 2011, Garrott and Oli 2013). In fact, the management of feral horses is often met with public debate and criticism (Symanski 1996, Linklater et al. 2002). Because public opinion and sentiment can take priority over conservation needs for ecosystems, the ability to mitigate the negative effects of large populations of horses on western rangelands can

be compromised (Linklater et al. 2002, Bies et al. 2011). Despite efforts to manage populations of horses, current practices and methodologies appear inadequate to achieve target population sizes in much of western North America (Palmer et al. 2013, Bureau of Land Management 2017).

Increased numbers of horses are associated with negative impacts to arid and semi-arid landscapes and some of the species inhabiting these environments (Beever 2003, Beever and Aldridge 2011, Davies et al. 2014, Hall et al. 2016b). Horses can degrade habitat features (e.g., soil and vegetation) via trampling, excessive nutrient deposition, and overgrazing (Loydi and Zalba 2009, de Villalobos et al. 2011, Parvage et al. 2011). Horse-related shifts in soil and vegetation are linked to altered community composition of fossorial invertebrates and small vertebrates (Beever and Brusard 2004, Beever and Herrick 2006). Increased grazing by horses can result in higher rates of predation for some species by removing vegetative cover used for concealment (Levin et al. 2002, Zalba and Cozzani 2004). While evidence suggests that horses can influence habitat components and relatively small animals, there is substantially less information supporting the idea that horses affect larger species (e.g., native ungulates). Because desert environments are generally resource-poor areas, increased numbers of horses may influence resource acquisition by native ungulates (Ostermann-Kelm et al. 2008, Perry et al. 2015, Gooch et al. 2017).

Water is a limiting resource for horses and native ungulates such as pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*). Horses have a relatively high water demand (up to 33 L/d; Groenendyk et al. 1988). During periods of water stress (e.g., increased temperatures), horses visit water sources more often and for longer periods (up to 73% of the day; Miller 1983, Stevens 1988, Hall et al. 2016b). Pronghorn and mule deer drink less water than horses (pronghorn up to 3.4 L/d, mule deer up to 6 L/d; Hazam and Krausman 1988, Fox et al. 2000), but depend on water during periods of water stress (e.g., lactation during summer months; Bowyer 1984, Clemente et al. 1995, Boroski and Mossman 1996, Fox et al. 2000, McKee et al. 2015). Unfortunately, when the physiological dependence on water is greatest for ungulates during the hot and dry summer months, water is often least available. Reduced availability

of an already limited resource, such as water, could heighten competitive interactions between horses and native ungulates during stressful summer conditions (Perry et al. 2015, Gooch et al. 2017).

Horses are dominant over native ungulates (Berger 1985) and can negatively influence their use of water. For example, horses have excluded desert bighorn sheep (*Ovis canadensis*) from water (Ostermann-Kelm et al. 2008), chased elk (*Cervus elaphus*) away from water (Perry et al. 2015), and increased vigilance behavior in pronghorn at water sources (Gooch et al. 2017). Understanding the broader spatial and temporal implications of horse-induced competition for water with native ungulates will facilitate conservation and management of native species. As water is projected to become even more limiting in western North America over the course of this century (Cook et al. 2004, 2015, Seager et al. 2013), a better understanding of how non-native feral species negatively influence the conservation of native species is imperative. Furthermore, a more developed comprehension of the interacting effects of increased temperatures and subsequent high activity of horses near water (Hall et al. 2016b) on drinking patterns of native ungulates will enhance our ability to better manage native species and natural resources in light of oncoming environmental change.

Our objective was to determine whether horses influenced spatial and temporal drinking patterns of native ungulates. If horses excluded native ungulates from water as suggested by previous work, we would predict the latter to avoid water sources used by horses or alter arrival times to minimize interactions with horses. Because mule deer are primarily crepuscular and nocturnal whereas horses are largely diurnal, we did not predict as large of a difference in visitation times to water in response to presence of horses, compared to pronghorn. We also predicted that the interactive effects of high temperatures and subsequent increased activity of horses (Hall et al. 2016b) would negatively affect the use of water by native ungulates.

METHODS

Study areas

We conducted this study in the Great Basin Desert of western Utah, USA (Fig. 1). Our study area consisted of 1200 km² of land managed by the U.S. Department of Defense, U.S. Army

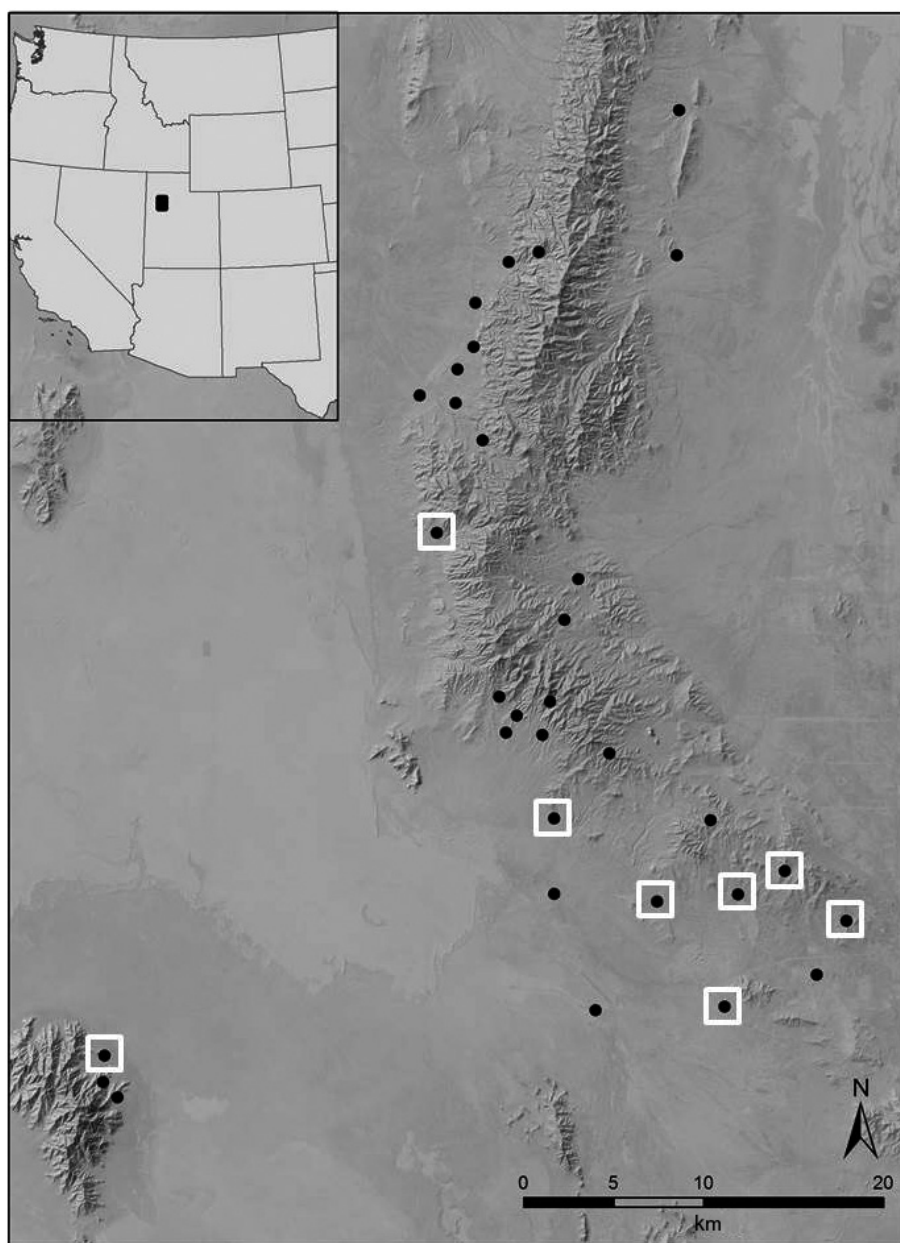


Fig. 1. Distribution of water sources that were monitored with remote cameras for pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and horses (*Equus caballus*) in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014. White squares around water sources indicate horse-exclusionary fencing.

Dugway Proving Ground and the U.S. Department of the Interior, Bureau of Land Management. Elevations across the study area ranged from 1300 to 1850 m. The terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats dominated by black greasewood (*Sarcobatus vermiculatus*). Along the foothills,

invasive annual grasslands (*Bromus tectorum*) were commonly mixed with desert shrubs (*Chrysothamnus* spp.), sagebrush (*Artemisia* spp.), and juniper (*Juniperus osteosperma*), transitioning to pinyon (*Pinus edulis*)-juniper woodlands at higher elevations. Annual weather consisted of mean air temperatures of 13.6°C and mean precipitation of

160 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center).

Data collection

We used infrared-triggered cameras (Reconyx PC900 Hyperfire, Holmen, Wisconsin, USA) to monitor ungulate activity at 32 water sources in our study area (Fig. 1). These water sources consisted of nine water developments for wildlife (i.e., guzzlers), eight livestock troughs, 11 natural springs/seeps, and four ponds. Seven water developments and one spring had exclusionary fencing for livestock that prevented horses from accessing water sources. To encourage use by native ungulates, perimeter fencing was ≥ 5 m from the water source, with the top cable 92 cm from the ground, the bottom cable 44 cm from the ground, and a 48 cm space in between both cables. Based on documented occurrence from prior research, these fence dimensions provided ample space to crawl underneath or jump over the fencing and both pronghorn and mule deer regularly occurred at fenced water sources (Hall et al. 2016b).

We secured cameras to metal posts and placed them approximately 3 m from the edge of water where animals accessed water for drinking. At water sources with multiple locations of drinking access (e.g., paired tanks of water, ponds), we placed cameras at a minimum of two locations where animals could drink. We considered proximity to trails and recent ungulate sign (i.e., tracks, pellet droppings) to determine the location of cameras at larger ponds or springs. Despite our efforts to optimally place cameras at large sources, our estimates of water usage are likely conservative as we may have missed the existence of other trails used by native ungulates. We checked the battery status, changed memory cards, and performed any necessary maintenance to cameras approximately every two weeks. Cameras were set to trigger on both motion and heat following which they recorded an image every 30 s. We monitored 16 water sources from June to October, 2010–2014, and monitored an additional 16 water sources (for a total of 32 water sources) from June to October, 2013–2014. This seasonal window captured periods of increased temperatures and decreased precipitation where visitation rates to water by ungulates were greatest (Shields et al. 2012).

To determine relative patterns of visitation by ungulates, we first summarized the images of

ungulate species captured by remote cameras. We extracted the time and date associated with each camera image. With date and time information, we then sorted camera images into species visits. Due to the difficulty of identifying individuals (particularly females and juveniles), we followed the methodology of previous research using remote cameras to monitor wildlife and defined independent visits as consecutive images of a species separated by at least 30 min (Michalski and Peres 2007, Hall et al. 2016b).

To account for the potential influence of site characteristics on the use of water by wildlife (Larsen et al. 2012, Hall et al. 2013), we measured vegetative and topographical characteristics within a 1785 m radius around each water source (Larsen et al. 2011). We selected a 1785 m radius based on summer home range sizes and daily distances traveled for pronghorn and mule deer (Gregg 1955, Kitchen 1974, Yoakum 1978, Hoskinson and Tester 1980, Garrott et al. 1987, Hayes and Krausman 1993, O’Gara and Yoakum 2004). We used tree cover and topographical ruggedness (terrain roughness) as our primary habitat variables to follow what has been done with pronghorn and mule deer at water sources in the Great Basin Desert (Larsen et al. 2011). We derived tree cover using vegetative cover types available in LANDFIRE (Landscape Fire and Resource Management Planning Tools) data provided by the U.S. Department of Agriculture Forest Service and the U.S. Department of the Interior. We defined tree cover as the proportion of pixels within a 1785 m radius around water sources containing vegetation dominated by trees (Larsen et al. 2011). Using ArcGIS (ArcMap, version 10.3; Environmental Systems Research Institute, Redlands, California, USA), we calculated ruggedness within the 1785 m radius buffer around water sources using a 30-m resolution digital elevation model. We used the vector ruggedness metric and set the ruggedness neighborhood to a 3×3 cell size (Sappington et al. 2007).

Statistical analyses

We employed a two-stage modeling approach to determine whether spatial partitioning occurred between horses and native ungulates. In the first stage, we identified the most appropriate statistical distribution (Gaussian, Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial [ZINB]) for visitation rates

(counts) of mule deer and pronghorn (Larsen et al. 2011). Count data for wildlife at water sources can often result in data that do not meet the assumptions of normality for standard linear models. These data are often not easily normalized via transformations due to the presence of large numbers of zero counts (where no target species were detected). Within the last two decades, however, statistical distributions designed to handle non-normal data with large numbers of zeros have been identified and used in ecological modeling. To determine the best distribution for ungulate data, we used model selection and Akaike's information criterion, corrected for sample sizes (AIC_c) model weights to evaluate the relative performance of a simple model (ungulate visits as a function of elapsed sampling time [number of camera days; EST]) with each of the distributions.

In the second stage of our analysis, we created two sets of models to measure any influence that horses may have on the selection of water sources by native ungulates (Larsen et al. 2011). One model of each set contained a habitat covariate such as tree cover or ruggedness (or both). The other model of each set was identical to the first but included horse activity (number of pictures of horses at a water source) as an additional parameter. We included EST in each model to account for differences in total sampling time across water sources over the 5 yr as some water sources were sampled the entire time and others for only two years. Because EST was included in every model, we did not need to standardize horse photographs by the number of days cameras were operable. We limited our models to no more than three variables considering our overall sample size of water sources was rather modest ($n = 32$) and the general rules of thumb regarding model selection and linear models (Burnham and Anderson 2002). We intentionally excluded any variables referencing time (e.g., temperature, year) to explicitly test for spatial avoidance and therefore used only a single photograph count of ungulates at each sampled water source in this stage of analysis. Prior to model selection, we conducted correlation analyses with all variables. In the case where variables were highly correlated ($|r| > 0.6$), we retained the variable that was associated with a model having the lower AIC_c score. Using AIC_c model weights (w_i), we ranked competing models (Burnham and Anderson 2002). We considered

models to be competing if they received $\geq 5\%$ of the cumulative AIC_c model weight. We then evaluated both the AIC_c model weight and log-likelihood associated with top models to identify any models with uninformative parameters. We judged parameters as uninformative when competing models differed from the top model by a single parameter and little to no improvement in log-likelihood was evident (Burnham and Anderson 2002, Anderson 2008, Arnold 2010). Where we encountered multiple competing models, we did not model average to acquire β coefficients, but instead calculated predicted values with 85% confidence intervals and then averaged these values based on relative AIC_c weight of the top models (Cade 2015). This model comparison coupled with the β estimates from supported models allowed us to evaluate the relative influence of horses on the spatial use of water by native ungulates after accounting for known habitat factors.

We then determined whether native ungulates experienced temporal shifts or altered time usage (Valeix et al. 2007) at water sources where activity of horses was high. For this analysis, we identified the hour of peak arrival for pronghorn and mule deer at each water source. We then compared hour of peak arrival for native ungulates at water sources where horses were common and absent (or rare) using Mann–Whitney U tests. We considered water sources as horse common if horses visited more than once per day. This categorization resulted in a natural break in water sources based on horse activity and resulted in 17 that were horse common and 15 that were horse absent or rare. On average, activity of horses was 16.5 times greater at horse common water sources compared to horse absent or rare water sources.

We constructed several generalized linear mixed models to determine whether the interactive increase of temperature and activity levels of horses negatively influenced daily visitation to water by native ungulates. In these models, we limited ourselves to a ZINB distribution for pronghorn and mule deer photograph counts, due to the excess numbers of zero counts occurring across days and sites. These models were similar to the spatial partitioning models in that we included tree cover and ruggedness at the summer home range scale to account for known habitat characteristics, but we also included maximum daily temperature ($^{\circ}\text{C}$) and daily photograph counts of horses. We

then included a temperature $\times$ horse variable to capture the interaction between daily maximum temperature and daily activity of horses (number of pictures/d). A potential concern for our interaction term could arise from a correlation between horse activity and daily temperature, but the correlation coefficient was low ($r = 0.17$) and well below generally accepted thresholds for correlation coefficients of $|r| > 0.6$. To account for variation between water sources and years, we included these variables as random effects in these models. We then followed the same evaluation as before and compared AIC_c model weights, log-likelihoods, and β estimates of candidate models with and without the horse $\times$ temperature interaction to determine whether the multiplicative effects of increased temperatures and high horse activity better explained drinking patterns of native ungulates. We performed all analyses using Program R (R Development Core Team 2014). We used the glmmADMB package (<http://glmmadmb.r-forge.r-project.org/>) to run generalized linear mixed models in Program R. We set the level of significance for all statistical tests at $\alpha = 0.05$.

RESULTS

From 2010 to 2014, we accrued a total of 29,666 pictures of pronghorn and 39,605 pictures of mule deer in 27,700 camera days. Of these pictures, there were 7465 visits of pronghorn and 7363 visits of mule deer. Horses accounted for an additional 780,452 pictures comprising 20,202 visits. All three ungulates occurred at the majority of water sources that we sampled. Pronghorn visited 26 of the 32 water sources (81%), mule deer visited 29 water sources (91%), and horses visited 23 water sources (72%).

From stage one of our modeling, we determined that a ZINB distribution best fits the pronghorn data and a negative binomial distribution best fits the mule deer data (Table 1). In stage two of our modeling (to determine spatial selection of water sources), we found that in nearly all analyses, the models that contained horse activity were best supported by the data. In fact, models with the horse activity covariate comprised 93% of model weight for pronghorn and 76% of model weight for mule deer (Table 2). Our models revealed that horse activity was negatively associated with visitation to water by pronghorn and mule deer (Figs. 2, 3).

Table 1. AIC_c scores for the statistical distribution of camera trap images for pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) at water sources.

Species	Distribution	AIC _c
Pronghorn	ZINB	381
	Negative binomial	386
	Gaussian	462
	ZIP	8355
	Poisson	11,423
Mule deer	Negative binomial	393
	ZINB	396
	Gaussian	472
	ZIP	11,648
	Poisson	13,076

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes; ZINB, zero-inflated negative binomial; ZIP, zero-inflated Poisson. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

Table 2. Model selection results evaluating overall spatial partitioning of water sources by pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) with horses (*Equus caballus*).

Model†	K‡	LL§	ΔAIC _c ¶	w _i #
Pronghorn				
EST + Trees + Horse	8	−207.20	0.00	0.76
EST + Rugged + Horse	8	−208.90	3.38	0.14
EST + Trees	7	−212.60	5.09	0.06
EST + Horse	7	−213.30	6.47	0.03
EST + Rugged	7	−214.50	8.91	0.01
EST	5	−219.80	10.23	0.00
Mule deer				
EST + Rugged + Horse	4	−181.72	0.00	0.63
EST + Rugged	3	−184.65	3.24	0.13
EST + Trees + Horse	4	−183.68	3.72	0.10
EST + Trees	3	−184.98	3.90	0.09
EST + Horse	3	−186.00	5.93	0.03
EST	2	−187.64	6.77	0.02

Notes: AIC_c, Akaike's information criterion, corrected for sample sizes. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

† EST, elapsed sampling time; trees, proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse, log base 10 of activity (no. of pictures) of horses; rugged, ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model.

‡ Number of parameters; pronghorn models contained nearly 2 $\times$ as many parameters compared to mule deer models because of the zero-inflated distribution model counts and excess zeros with separate estimates.

§ Model log-likelihood.

¶ Change in AIC_c value compared to top model.

AIC_c weight.

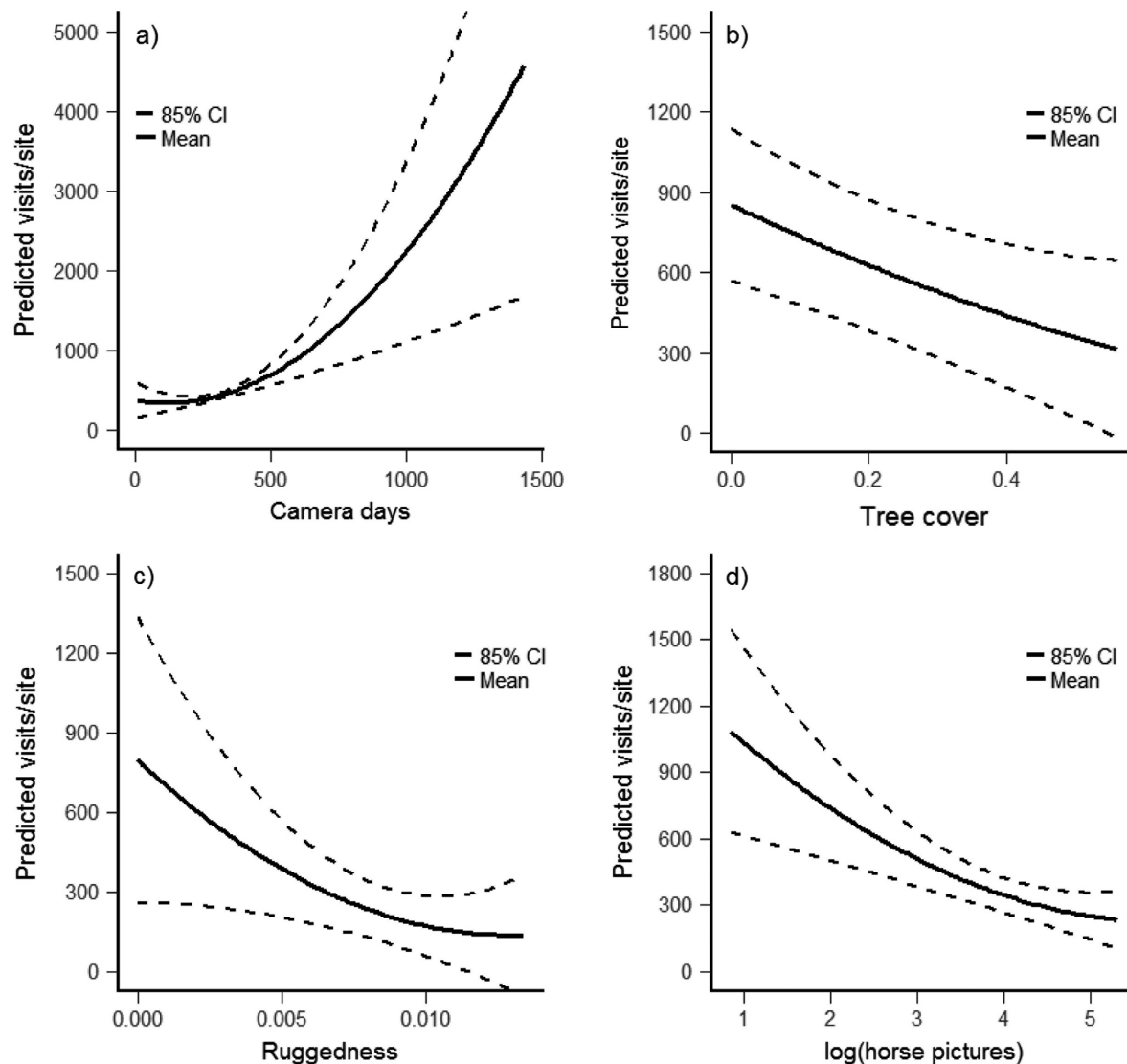


Fig. 2. Predicted visits (with 85% confidence intervals) to water by pronghorn (*Antilocapra americana*) based on variables from the top generalized linear models evaluating spatial partitioning with horses (*Equus caballus*). Camera days = number of camera-sampling days; tree cover = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); log(horse pictures) = log base 10 of activity (no. of pictures) of horses; and ruggedness = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

Native ungulates exhibited relatively distinct patterns of temporal activity at water sources, whereas horses were active throughout day, but most active during diurnal hours (Fig. 4). Horse activity did not appear to influence arrival times to water by pronghorn and mule deer in the same fashion. At water sources where horses

were common, pronghorn exhibited differences in arrival times compared to water sources where horses were absent or rare ($U = 81.00$, $P = 0.04$; Fig. 5). Pronghorn also experienced a greater amount of variation in arrival times where horses were common (Fig. 5). Alternatively, there were no differences in arrival time to water for mule

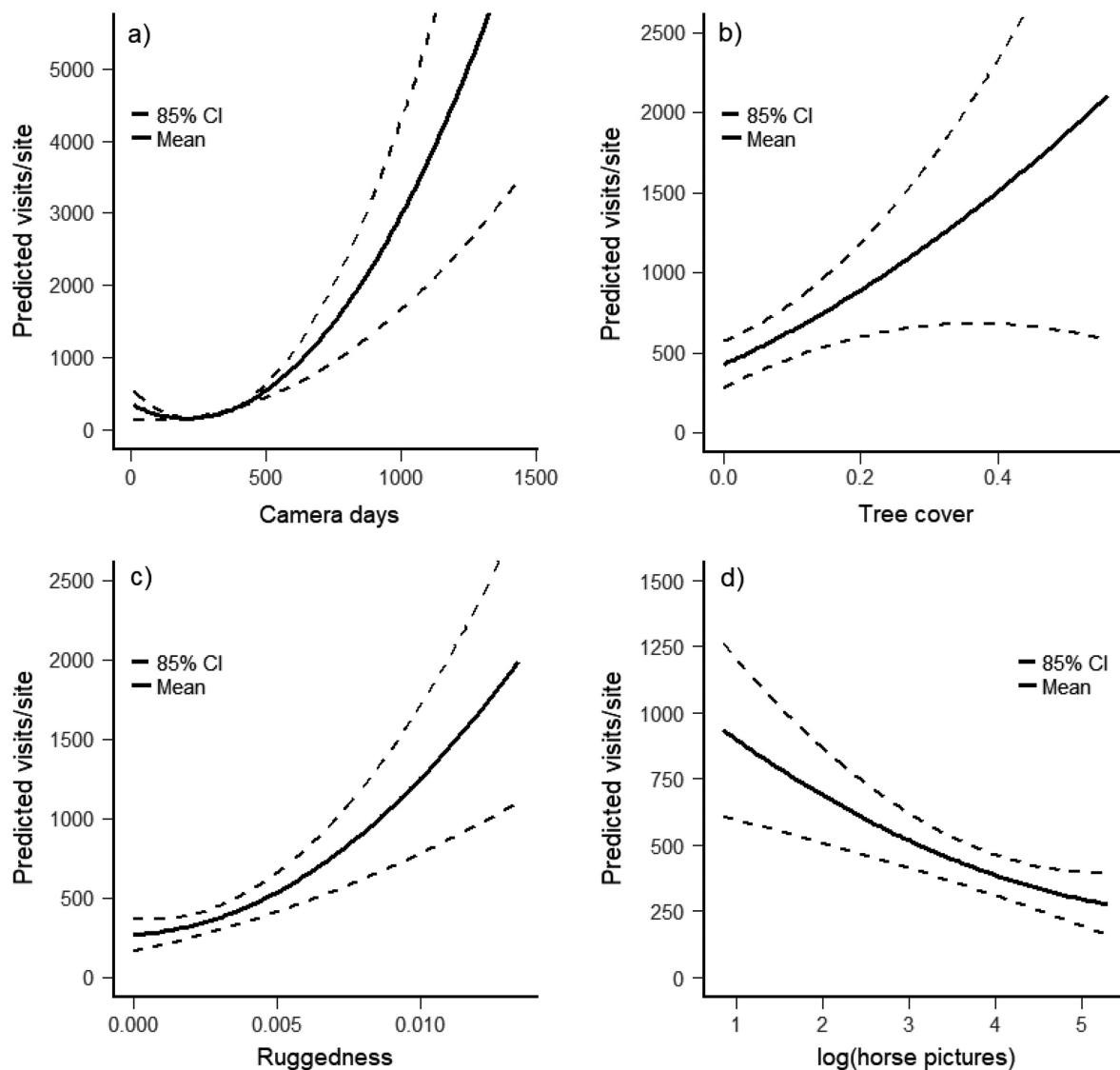


Fig. 3. Predicted visits (with 85% confidence intervals) to water by mule deer (*Odocoileus hemionus*) based on variables from the top generalized linear models evaluating spatial partitioning with horses (*Equus caballus*). Camera days = number of camera-sampling days; tree cover = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); log(horse pictures) = log base 10 of activity (no. of pictures) of horses; and ruggedness = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

deer, regardless of horse activity ($U = 159.00$, $P = 0.95$; Fig. 6).

With our mixed-effects models, we found strong support for the temperature $\times$ horse interaction. Pronghorn models containing the temperature $\times$ horse interaction accounted for 95% of the cumulative model weight (Table 3).

While the individual model estimates for horse and temperature variables were both positively correlated with water use by pronghorn, the estimate for the interaction of these variables had a negative correlation with the use of water by pronghorn (Fig. 7). Similar to pronghorn, mule deer models with the temperature $\times$ horse

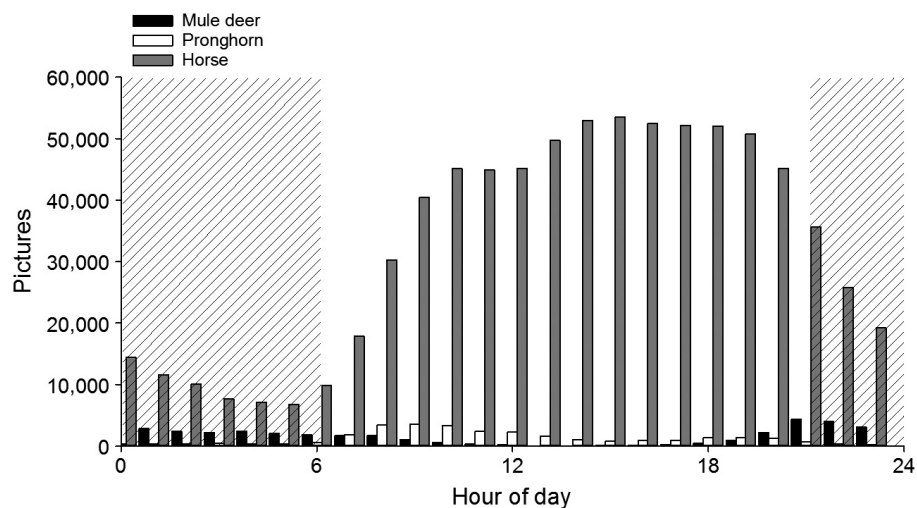


Fig. 4. Temporal activity (number of pictures from remote cameras by hour of day) of pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and horses (*Equus caballus*) at water sources in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014. Hatched (shaded) regions depict nocturnal hours.

interaction accounted for nearly all (99%) of the cumulative model weight and that interaction was negatively correlated with use of water by mule deer (Table 3, Fig. 8).

DISCUSSION

Our study demonstrated that horses negatively influenced how pronghorn and mule deer

accessed a limiting resource. Our findings also provided corroborating evidence that horses out-competed native ungulates for water (Miller 1983, Ostermann-Kelm et al. 2008, Perry et al. 2015, Gooch et al. 2017). We observed resource partitioning (indirect evidence of competition) between horses and native ungulates; specifically, we found evidence for spatial partitioning as pronghorn and mule deer avoided water

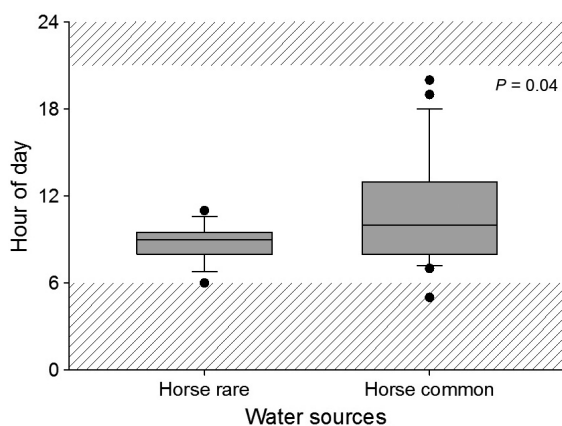


Fig. 5. Peak arrival hour for pronghorn (*Antilocapra americana*) at water sources where horses (*Equus caballus*) were rare (or absent) and where horses were common. Hatched (shaded) regions depict nocturnal hours. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

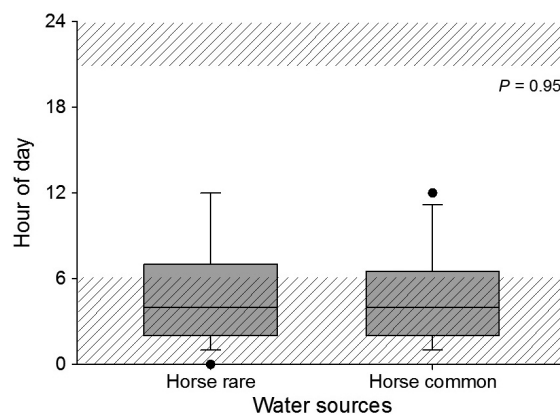


Fig. 6. Peak arrival hour for mule deer (*Odocoileus hemionus*) at water sources where horses (*Equus caballus*) were rare (or absent) and where horses were common. Hatched (shaded) regions depict nocturnal hours. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

Table 3. Model selection results evaluating the interactive effect of daily temperature and horse activity on daily visitation to water by pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*).

Model†	K‡	LL§	ΔAIC_c ¶	w_i #
Pronghorn				
Trees + Temp + Horse + Temp $\times$ Horse	9	-14,257.20	0.00	0.65
Trees + Rugged + Temp + Horse + Temp $\times$ Horse	10	-14,257.20	2.00	0.24
Rugged + Temp + Horse + Temp $\times$ Horse	9	-14,259.80	5.20	0.05
Trees + Temp + Horse	8	-14,261.20	6.00	0.03
Temp + Horse + Temp $\times$ Horse	8	-14,261.70	7.00	0.02
Trees + Rugged + Temp + Horse	9	-14,261.20	8.00	0.01
Rugged + Temp + Horse	8	-14,263.70	11.00	0.00
Trees + Temp	7	-14,287.20	55.99	0.00
Trees + Rugged + Temp	8	-14,287.20	58.00	0.00
Rugged + Temp	7	-14,289.80	61.19	0.00
Trees + Horse	7	-14,376.40	234.39	0.00
Trees + Rugged + Horse	8	-14,376.40	236.40	0.00
Rugged + Horse	7	-14,379.00	239.59	0.00
Mule deer				
Rugged + Temp + Horse + Temp $\times$ Horse	9	-16,654.60	0.00	0.45
Trees + Rugged + Temp + Horse + Temp $\times$ Horse	10	-16,654.00	0.80	0.30
Trees + Temp + Horse + Temp $\times$ Horse	9	-16,655.30	1.40	0.22
Temp + Horse + Temp $\times$ Horse	8	-16,658.70	6.20	0.02
Rugged + Temp + Horse	8	-16,660.30	9.40	0.01
Trees + Rugged + Temp + Horse	9	-16,659.70	10.20	0.00
Rugged + Temp	7	-16,662.00	10.79	0.00
Trees + Temp + Horse	8	-16,661.00	10.80	0.00
Trees + Rugged + Temp	8	-16,661.40	11.60	0.00
Trees + Temp	7	-16,662.80	12.39	0.00
Rugged + Horse	7	-16,805.70	298.19	0.00
Trees + Horse	7	-16,806.00	298.79	0.00
Trees + Rugged + Horse	8	-16,805.10	299.00	0.00

Notes: AIC_c , Akaike's information criterion, corrected for sample sizes. Data were collected in the Great Basin Desert of western Utah, USA, from June to October, 2010–2014.

† Trees, proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse, activity (no. of pictures) of horses; rugged, ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Temp, maximum daily temperature.

‡ Number of parameters.

§ Model log-likelihood.

¶ Change in AIC_c value compared to top model.

AIC_c weight.

sources more heavily used by horses. We also observed temporal shifts in water use by pronghorn in response to increased activity of horses. However, we did not detect temporal shifts for mule deer in response to horse activity; likely due to horses being primarily diurnal, while mule deer accessed water during crepuscular or nocturnal periods, suggesting horses may impact pronghorn more than mule deer.

Large herbivores can influence patterns of water use by smaller, less competitive species (Valeix et al. 2007, 2008, Hall et al. 2016b). For example, relatively small African herbivores generally avoided times of peak visitation to waterholes by

elephants (Valeix et al. 2007). Desert bighorn sheep exhibited a similar pattern using alternative water sources when a horse was present at a regularly used water source (Ostermann-Kelm et al. 2008). Similarly, Nubian ibex (*Capra nubiana*) avoided water sources that had been recently used by feral donkeys (*Equus africanus asinus*) in northern Africa (Attum et al. 2009). In a more direct fashion, horses were observed on multiple occasions actively preventing elk (*Cervus elaphus*) from accessing water (Perry et al. 2015). In each of these examples, larger dominant herbivores outcompeted smaller herbivores for water. Moreover, the latter three studies highlighted how a feral equid

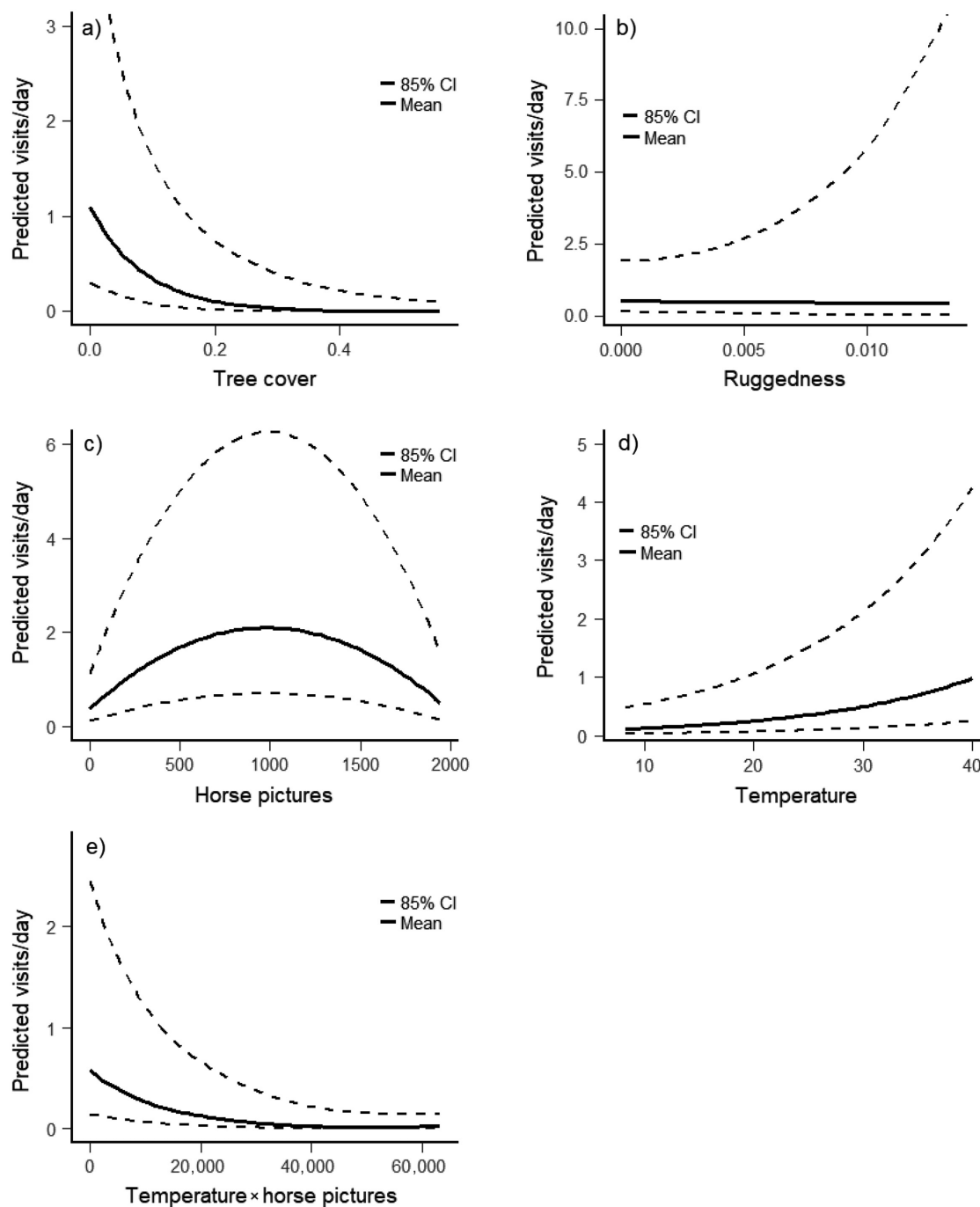


Fig. 7. Predicted visits (with 85% confidence intervals) to water by pronghorn (*Antilocapra americana*) based on variables from the top generalized linear mixed models evaluating the interactive effect of daily temperature and horse (*Equus caballus*) activity. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014. Tree cover = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse pictures = activity (no. of pictures) of horses; and ruggedness = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

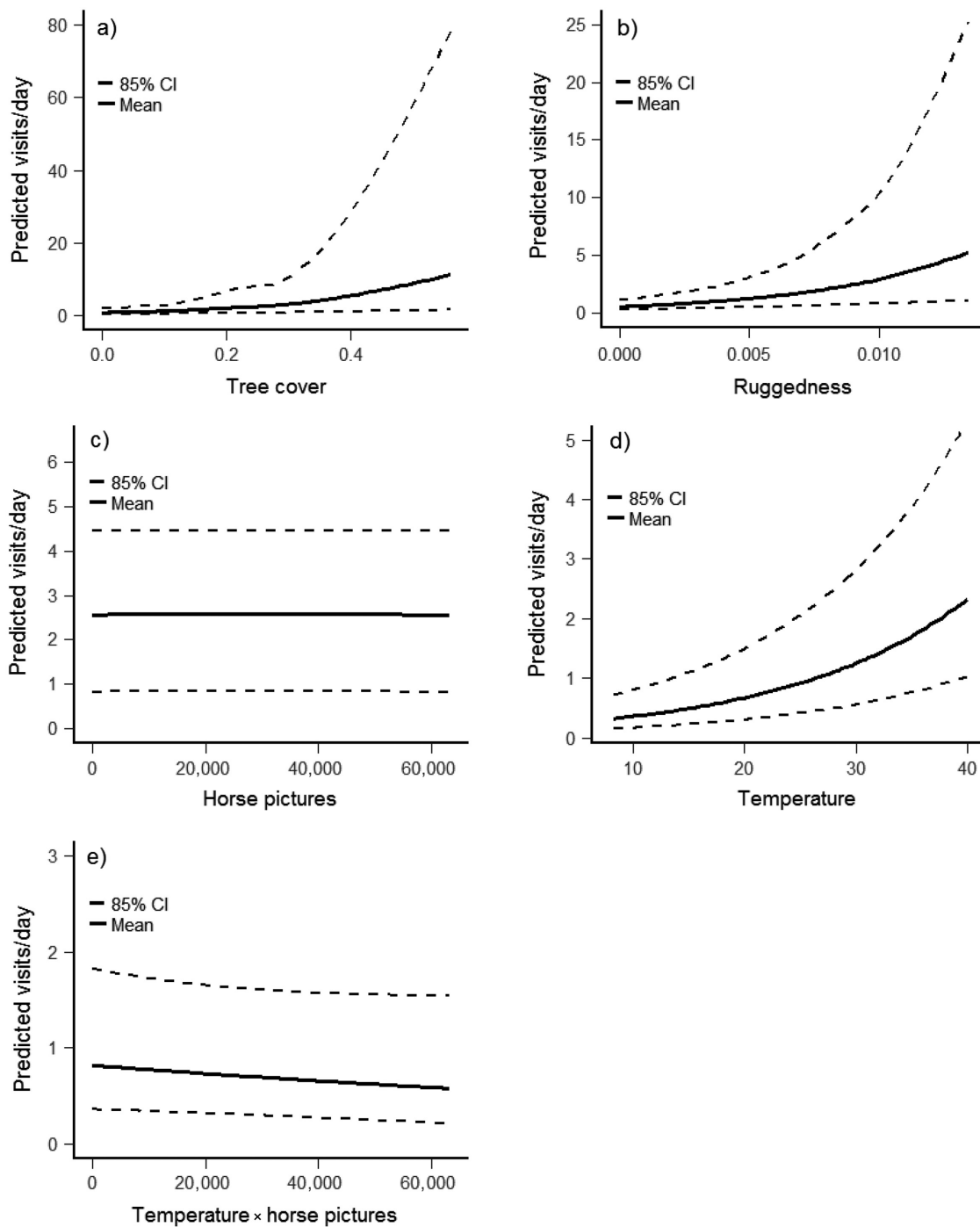


Fig. 8. Predicted visits (with 85% confidence intervals) to water by mule deer (*Odocoileus hemionus*) based on variables from the top generalized linear mixed models evaluating the interactive effect of daily temperature and horse (*Equus caballus*) activity. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014. Trees = proportion of pixels identified as trees within 1785 m of each water source (representing home range tree cover); horse = activity (no. of pictures) of horses; and rugged = ruggedness metric calculated within 1785 m of each water source using a 30-m resolution digital elevation model. Data were collected in the Great Basin Desert in western Utah, USA, from June to October, 2010–2014.

can influence patterns of resource acquisition by smaller native species (Ostermann-Kelm et al. 2008, Attum et al. 2009, Perry et al. 2015).

Competing for limiting resources can result in trade-offs for the species involved. In arid and semi-arid regions, many species face a trade-off associated with accessing limited water resources and minimizing conflict with more competitive species (Atwood et al. 2011, Edwards et al. 2015). In our study system, there may be fitness costs associated with the trade-off of directly competing with horses versus using different water sources or allocating use at different times, when horses are absent. Prior work conducted in the Great Basin Desert on use of water by horses and pronghorn found the latter devoted more time to vigilance behavior and foraged and drank less in the presence of horses (Gooch et al. 2017). While the long-term implications of this behavioral modification are largely unknown and may be negligible, our work supports previous research, indicating that horses can alter the drinking patterns of pronghorn.

The intense use of water by horses during periods of increased temperatures and physiological stress (Perry et al. 2015, Hall et al. 2016b) raises conservation concerns for native species that compete with horses for water. Based on our mixed-effects models, visits to water sources for pronghorn and mule deer were reduced on particularly hot days when activity of horses was high. With models of global climate change predicting increased temperatures and aridity in many deserts, water will likely become less available for species inhabiting these areas (Ault et al. 2014, Cook et al. 2014, Wanders et al. 2015). While reduction of water availability is not a novel challenge for desert species, the rapid loss of water in these systems (due to contemporary climate change) will likely pose additional challenges for desert biota (Hall et al. 2016a). Water already serves as a major selective force in warm and dry environments (Noy-Meir 1973). Further loss of water from the environment combined with competition with increasing populations of feral species will likely create additional conservation and management issues for native species.

Our study provides a multi-year perspective on how a behaviorally dominant, feral species such as the horse can alter the spatial and temporal use of a limiting resource by native species.

While we did not experimentally manipulate the density of horses to identify a causal relationship for the patterns that we observed, we capitalized on differences already occurring in horse activity across water sources. We also monitored multiple water sources for five years providing extensive spatial and temporal context to our findings. We provide evidence that horses competed with and spatially displaced pronghorn and mule deer from water sources. Horses also temporally displaced pronghorn from water sources, but not mule deer. In addition, we found strong support for the interactive negative effect of increased temperature and activity of horses on drinking patterns of pronghorn and mule deer. Our findings indicated that feral horses further constrained access to an already limited resource for native species in a semi-arid environment.

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