

# Unique utilisation pattern responses of five sympatric ungulates to local phenological gradients

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## ABSTRACT

**Context.** Ungulate life-history strategies and behaviour are driven by two dominant factors, namely, acquisition of nutrients and avoidance of predation. Although many studies have investigated single species resource/habitat selection, there are still gaps in our understanding of multi-species systems and resource partitioning. **Aim.** We explored the habitat selection of five sympatric resident ungulates in relation to seasonal phenological gradients in a temperate grassland (Northern Great Plains) system. We identified and compared habitat-utilisation strategies across the vegetation-growing season and related to established forage acquisition hypotheses. **Methods.** We collected ungulate detection data during two field seasons (July–October 2018, May–September 2019) across 202 sites and deployed 1202 cameras (29 284 camera-nights). We modelled ungulate detections in relation to normalised difference vegetation index (NDVI) and NDVI slope (rate and direction of change) to learn about ungulate resource selection in four habitat types (grass, prairie dog colonies, forest and riparian). **Results.** We found unique foraging strategies for each of the focal species throughout the growing season (spring, summer, early autumn), which resulted in seasonal partitioning of resources among sympatric ungulate species. **Conclusions.** The temporal and spatial patterns observed emphasise that multiple species can experience the same vegetation phenology and respond differently in their movements and foraging behaviour. At local scales, some ungulates selected for higher forage quantity (selection of higher NDVI) and some for higher forage quality (selection of positive NDVI slope or greening up). **Implications.** The unique foraging strategies presented here indicated that generalisations are problematic when managing wildlife resources and emphasise the need to conduct multi-species studies to understand resource utilisation at local scales. Furthermore, understanding variation in foraging strategies of resident sympatric species can direct management planning where decreased connectivity or loss of migration pathways alters traditional behaviours.

**Keywords:** habitat selection, elk, mule deer, NDVI, Northern Great Plains, plains bison, pronghorn, white-tailed deer.

## Introduction

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Ungulate life-history strategies and behaviour are driven by two dominant factors: acquisition of nutrients (Parker *et al.* 2009) and avoidance of predation (Hebblewhite and Merrill 2009; Shamoon *et al.* 2018; Maor Cohen *et al.* 2020). Although ungulates must consider inter- and intra-specific interactions, their core requirement is nutritional demand (Parker *et al.* 2009). Ungulates allocate their space use to specific phenological conditions (Hebblewhite *et al.* 2008) during each life stage, that is, juvenile growth (Pettorelli *et al.* 2007), body mass gain prior to winter, or reproduction (Proffitt *et al.* 2016a).

Current theory holds that spatio-temporal resource/habitat partitioning among ungulate species is a function of a species' body size (Hopcraft *et al.* 2010), anatomy (Arsenault and Owen-Smith 2008), physiology (Codron and Clauss 2010), the number

of coexisting individuals in a given space (van Beest *et al.* 2014), forage quantity and quality (Villamuelas *et al.* 2016), and resource availability (Macandza *et al.* 2012). Thus, we would expect the spatial and temporal overlap of species to vary across phenological gradients (i.e. resource availability) and in relation to population composition and densities. Here we explore habitat selection of five sympatric, resident ungulate species in relation to the seasonal phenological gradients found in a temperate grassland ecosystem (Northern Great Plains). We identify and compare resource utilisation strategies across the vegetation growing season and discuss implications of changes in resource availability for the focal species.

Ungulate feeding anatomy (i.e. mouth size and anatomy, and dental pattern) are the result of evolutionary adaptations that facilitate their co-existence by feeding on different plants, grass heights (Murray and Illius 2000; Arsenault and Owen-Smith 2008), and stages of grass maturation, all of which allow species to maximise intake of energy and protein (Illius 1997). These studies provided a body of evidence to support coexistence theories in relation to anatomy and physiology, and can be expanded by exploring coexistence based on plant productivity at the landscape level. Remote sensing methodologies provide the tools needed to survey vegetation trends across landscapes and seasons at different resolutions that can be used as predictors of ungulate space use (Wu *et al.* 2014; Villamuelas *et al.* 2016; Xue and Su 2017). Here, we used satellite imagery to evaluate multi-ungulate resource-utilisation strategies in relation to phenological gradients.

The forage-maturation hypothesis (FMH) states that ungulates migrate to maximise energy intake by utilising high-quality forage (Hebblewhite *et al.* 2008). This phenomenon is described for many migrating ungulates such as wildebeest (*Connochaetes taurinus*) in Africa, and elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) in North America (Hebblewhite *et al.* 2008; Boone *et al.* 2010; Scurlock *et al.* 2016). FMH can be extended to the green-wave hypothesis (GWH) that ties resource utilisation to phenological condition, and to the spatial and temporal distribution of vegetation or the rate of change in NDVI, termed instantaneous rate of green-up (IRG; Merkle *et al.* 2016).

Studies of GWH have shown that many ungulates ‘surf’ along phenological gradients, timing their movements and distribution to shifts in plant productivity (Scurlock *et al.* 2016). Ungulates can also ‘jump’ over the green wave and arrive to summer ranges before they peak, possibly to obtain first access to high-quality forage (Bischof *et al.* 2012; Lendum *et al.* 2014; Geremia *et al.* 2019). These green-wave movements are not only across landscapes, but can traverse elevational gradients, such as the seasonal migrations of takin (*Budorcas taxicolor*) in the mountains of China (Guan *et al.* 2013).

Although many ungulate populations are migratory, most are composed of both residents and migrants

(Fryxell *et al.* 1988), with alternative foraging strategies pointing to behavioural flexibility within a population. For example, migrating elk ‘surfing’ the green wave gain more body fat than do resident elk (Middleton *et al.* 2018). However, anthropogenic activities, such as supplemental feeding, can alter elk migration (Jones *et al.* 2014) and resident elk were shown to be more flexible with nutritional requirements, thereby occupying less productive, although less predation-prone, locations (Hebblewhite and Merrill 2009). There is contradicting evidence that resident elk can become habituated to humans and thus increase their predation risk because of increased hunter access (Robinson *et al.* 2010). Similarly, examination of the niche space of resident and migrant mule deer found the former’s preference for sites closer to developed areas (Robb *et al.* 2019).

Behaviour flexibility can be advantageous in changing environments. Courtemanch *et al.* (2017) suggested that migrants have flexible behavioural strategies to help individuals cope with shifting migration pathways. The authors showed that a bighorn sheep (*Ovis canadensis*) population persisted after migration pathways were lost by adapting foraging strategies similar to those of resident bighorn sheep. Other work on bighorn sheep (Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*) showed that migration strategies are highly plastic and individuals can shift strategies between years (Spitz *et al.* 2018). Similar findings have been observed with elk (Eggeman *et al.* 2016). This body of work supports the argument that ungulate life strategies are flexible and interchangeable, and are affected by environmental, climatic and anthropogenic variables. Such information can inform wildlife managers on a species’ capacity to persist with and without migration pathways, and the importance of resource options for resident animals.

While many studies have investigated ungulate migration in relation to foraging strategies (Hebblewhite *et al.* 2008; Raynor *et al.* 2015; Scurlock *et al.* 2016; Debeffe *et al.* 2017), there are still gaps in our understanding of foraging strategies at local scales. The hypotheses mentioned above can be down-scaled to learn about ungulate resource utilisation along local phenological gradients that vary annually. Technological advances, for example, GPS-tagging, enable examination of multi-species foraging strategies and resource selection (Schweiger *et al.* 2015), but simultaneous movement data from multiple species is difficult to obtain. Camera-trap data present an opportunity to explore foraging behaviour and nutritional requirements for multiple species within a landscape. We explore the habitat selection of elk (*C. canadensis*), white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and plains bison (*Bison bison bison*) by using an array of camera traps.

Early studies on resource selection of ungulates indicated that species feeding strategies are affected by body size and anti-predator behaviour (Jarman 1974), and smaller body-size species generally select for higher-quality forage

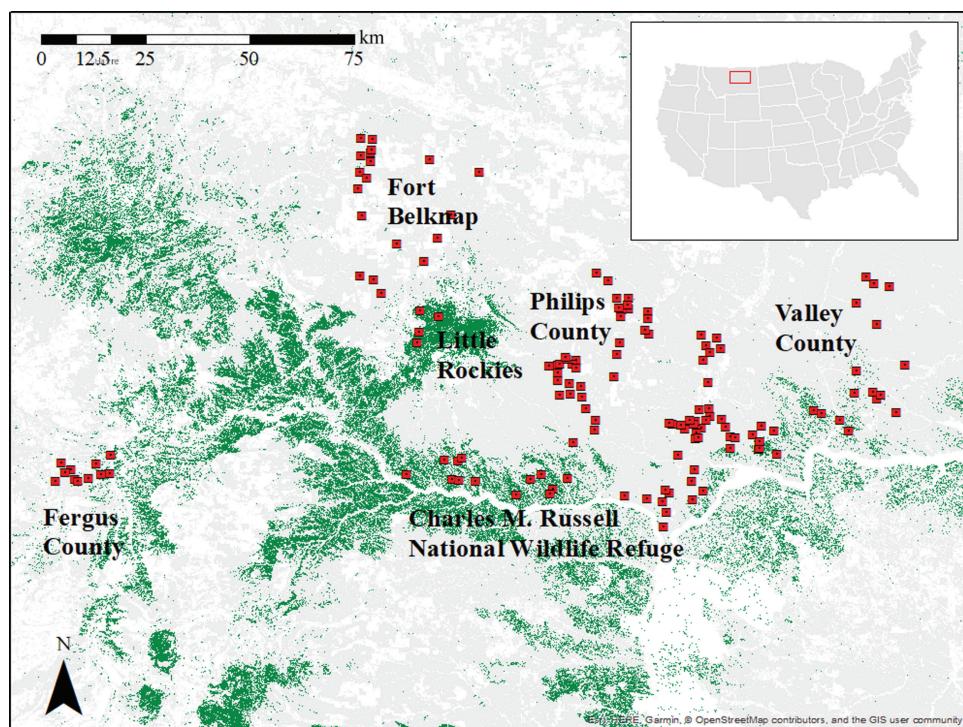
(Schwartz and Ellis 1981). In Hofmann (1989) review on ecophysiological adaptation and diversification of ruminants, species diet habits were characterised into the following three types on the basis of their digestive systems: (1) concentrate selectors (e.g. white-tailed deer); (2) intermediate opportunistic mixed feeders (e.g. pronghorn, elk, mule deer); and (3) grass and roughage eaters (e.g. bison). Codron *et al.* (2008) showed that in complex African systems, taxonomic diversification is correlated with differentiation in ecological niche, and grass quality dictates selection for short to tall grasses. In short-grass prairies, we hypothesise that pronghorn (Jakes 2015), mule deer (Merkle *et al.* 2016) and elk (Middleton *et al.* 2018) will track vegetation productivity (as per the GWH), and will switch between habitat types to take advantage of higher-quality diet. We predict that white-tailed deer will be selective and mainly utilise riparian areas, characterised by dense woody vegetation. While foraging strategies have been documented that bison both support (Merkle *et al.* 2016) and not support (Geremia *et al.* 2019) GWH, we predict bison in this study will not follow GWH because their movements are constrained by fences. We predict that bison will adapt foraging patterns to maximise protein intake in higher-biomass/high-fibre grass patches and high-quality/low-biomass prairie dog patches (Raynor *et al.* 2016). Furthermore, landscape level productivity trends will differ among upland grasslands, riparian areas and forests, resulting in species shifting their activity among habitats on the basis of their digestive systems. We link their habitat selection to remote measurements of NDVI and to the slope of changes in NDVI to

examine whether these ungulates differ in their utilisation of shared patches during stages of vegetation growth and productivity.

## Materials and methods

### Study area

Work was conducted in a mixed-grass prairie ecosystem within the Northern Great Plains of central Montana (Fig. 1). The study area is a mixture of private and public lands used mostly for cattle (*Bos taurus*) ranching operations. Four herds of plains bison occur in large pastures (35–110 km<sup>2</sup>) within the study area and all were sampled during this study. The Fort Belknap Indian Reservation occupies the northwestern region of the study area and is mainly composed of mixed-grass prairie ecosystem. The Little Rockies, a forested island mountain range that extend to 2000 m elevation, also occurs across the region. The southern part of the study region is the 1.1 million-acre Charles M. Russell Wildlife Refuge managed by the US-Fish and Wildlife Service (Fig. 1). Exposed soils throughout the area contain high percentages of bentonite clay (Knechtel and Patterson 1962). The climate is characterised as arid (average annual precipitation 325–384 mm), with dramatic weather changes between seasons, from cold winters (average temperature –7.6°C) to warm to hot summers (average temperature 33.8°C; Whitlock *et al.* 2017). Elevation ranges from approximately 1100 to 1700 m,



**Fig. 1.** Survey sites. Ungulate detection data were collected in north central Montana, USA, in July–October 2018 and May–September 2019. Forest (green); grasslands (grey); survey sites (red cells).

with an upland plateau that varies little in terms of elevation and slope.

The study area can be divided into two main habitat types, namely, uplands (prairie) and forest (Little Rockies and Missouri Breaks). Outside of the Missouri River, waterways in the study area are primarily seasonal streams. Upland vegetation is a mixture of native perennial grasses, annual grasses (many non-native), a diverse community of native and non-native forbs, and woody shrubs (*Artemisia cana*, *Artemisia tridentata*, *Juniperus horizontalis* and *Krascheninnikovia lanata*; [Charboneau 2013](#)). Seasonal streams are bordered by woody riparian vegetation comprising mainly *Acer negundo* and species of Salicaceae ([Charboneau 2013](#)). Black-tailed prairie dog (*Cynomys ludovicianus*) colonies occur within the grasslands. Prairie dogs are considered ecosystem engineers and their foraging creates short grass and forb patches that are continuously grazed ([Archer et al. 1987](#)). Around the Missouri River, gentle to steep slopes occur along buttes, canyons, rock outcrops and ravines. The breaks are woodlands dominated by ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*) and Rocky Mountain juniper (*Juniperus scopulorum*). Undergrowth is predominantly composed of bluebunch wheatgrass (*Pseudoroegneria spicata*) with no or few shrubs present.

The only remaining resident ungulate predators are puma (*Puma concolor*), coyotes (*Canis latrans*), and a small number of recolonising black bears (*Ursus America*). Wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) were eliminated from this region about 1900.

## Focal species

Seven native ungulates occur in the study area, including elk, white-tailed deer, mule deer, pronghorn, plains bison, moose (*Alces alces*), and bighorn sheep. Bighorn sheep are restricted to the Missouri breaks, and moose are primarily transients. Both were excluded from our analyses. Plains bison were reintroduced in the late 1970s (Fort Belknap Indian reservation) and 2005 (American Prairie Reserve) to four pastures that range between 32 and 106 km<sup>2</sup> and do not occur in forested areas. Elk, white-tailed deer, mule deer and pronghorn are free-roaming.

The ungulates in this study can be classified as grazers, browsers and intermediate feeders. Pronghorns are intermediate feeders and their diet consists of grasses, forbs and shrubs ([Jenks et al. 2006](#)). In early spring, pronghorns select grasses with high concentrations of nitrogen, timed with pre-parturition. Later in the summer, pronghorns select forbs and shrubs ([Jakes 2015](#)). Bison diet is flexible across the growing season. During spring and fall, bison consume more forbs and shrubs than they do during the summer, at which time bison diet mainly consists of grasses ([Bergmann et al. 2015](#)). Elk diet is dominated by grasses in early spring, although they also consume forbs and browse during

summer and fall ([Mackie 1970; Torstenson et al. 2006](#)). Mule deer and white-tailed deer are primarily browsers, with the majority of their diet comprising forbs and browse, but mule deer diet does include grasses ([Watkins et al. 2007; Innes 2013](#)).

## Survey design

We detected ungulates with camera traps (model Reconyx HyperFire 2) during two growing seasons (July–October 2018, May–September 2019). We deployed camera traps to 202 sites within four habitat types (grass; prairie dog colony; riparian; forest). We placed 3–6 cameras in each survey site spaced 250–400 m apart. We deployed cameras at 65 sites in 2018 ( $n = 406$  camera setups) and 137 sites in 2019 ( $n = 796$  camera setups). Cameras were rotated among sites and data were collected following 3–6 consecutive weeks at each site. Sites were resampled two or three times during each year. Sites were randomly chosen within each habitat type and the number of sites was relative to the available area ( $n_{\text{Forest}} = 88$ ;  $n_{\text{Grass}} = 593$ ;  $n_{\text{Prairie dog}} = 280$ ;  $n_{\text{Riparian}} = 241$ ). In total, we collected data during 29 284 camera-trap nights (10 752 in 2018 and 18 532 in 2019). Cameras were set 50 cm above ground facing north to avoid false triggers. Images were sorted, identified to species, and stored in the eMammal repository (emammal.si.edu user project ‘Smithsonian Grassland Ecology Program’). eMammal partitions the images into sequences, meaning the software groups together images that are spaced < 1 min apart. The surveyor will view the entire sequence and count the number of individuals that pass the camera. This ensures that the same individual is not counted multiple times if it is standing in front of a camera. We collected habitat data at each camera location to assess detection bias. These data included the percentage of ground cover vegetation (bare ground, grass, forb and shrub), percentage of canopy cover, mean shrub height within 5 m in front of each camera, distance at which the camera sensor was triggered in response to an approaching human, and whether or not the camera was set on an obvious animal trail. Note that bison are confined to four large pastures (35–110 km<sup>2</sup>) which included three habitat types excluding forest. We only considered camera sites within those pastures when constructing the bison models.

## Statistical analysis

### Normalised difference vegetation index (NDVI) trends

NDVI is a proxy for vegetation productivity and an indicator of green/photosynthetic vegetation ([Wang et al. 2004](#)), and can be linked to phenological stage ([Studer et al. 2007](#)). NDVI trends are correlated with the crude protein amounts in ungulate faecal matter, which is a measure of forage quality ([Hamel et al. 2009](#)). Vegetation

nitrogen content peaks with peak NDVI slope and total biomass peaks occur during maximum increases in NDVI measures. Early in the growing season, biomass is of highest quality but of low quantity. As green-up advances, quality decreases and quantity increases until late maturation when NDVI peaks, then gradually forage quality and quantity decrease. As a result, NDVI has been used as an effective proxy for annual changes in high-quality forage (Hamel *et al.* 2009; Borowik *et al.* 2013; Creech *et al.* 2016; Hogrefe *et al.* 2017).

We extracted the mean NDVI within 250 m resolution for time series of the Terra Vegetation Indices 16-Day NDVI (MOD13Q1) at each camera-trap location. Datasets are freely accessible via Google Earth Engine (<https://doi.org/10.5067/MODIS/MOD13Q1.006>).

We calculated a harmonic regression (Shumway and Stoffer 2017) for each time-series dataset by using the equation:

$$\text{NDVI}_t = \beta_0 + \beta_1 t + \beta_2 \cos(2\pi\omega t) + \beta_3 \sin(2\pi\omega t) + e_t \quad (1)$$

where  $\omega$  is frequency of harmonic (in this case, one cycle per unit time), and  $\varphi$  is phase (equals to  $\text{atan}(\beta_3/\beta_2)$ ).  $\beta_0$  is intercept,  $\beta_1$  is linear rate of change over time,  $\beta_2$  is amplitude  $\times$   $\cos(\varphi)$ ,  $\beta_3$  is amplitude  $\times$   $\sin(\varphi)$ , and  $e_t$  is a random error. Amplitude equals to square root of  $(\beta_2^2 + \beta_3^2)$ .

To estimate trends of vegetation (greening and drying), we calculated the slope of the linear regression line through every three consecutive ( $i, j, k$ ) points in the time series:

$$\sum_i^k (x_i - \bar{x}) \times (y_i - \bar{y}) / (x_i - \bar{x})^2 \quad (2)$$

where  $x$  is time the sample was collected, and  $y$  is the value of NDVI at a given point.

## Ungulate responses to NDVI and vegetation trends

We modelled ungulate detections against values for the estimated NDVI and slope trend to characterise ungulate habitat utilisation for each of the four habitat types (grass, prairie dog colonies, forest and riparian). We examined linear and non-linear (quadratic) relationships of these factors with animal detections. Each species was modelled separately in each habitat, resulting in 17 model combinations for the five species and four habitats (bisons do not occur in forest habitat). Bisons were not present in forest areas and pronghorn detections were too low in riparian and forest habitats to construct models. We use N-mixture models to estimate the number of detections for each species within a given time frame, while accounting for imperfect detection (Royle 2004; Joseph *et al.* 2009; Zhou and Carin 2015). N-mixture models are sometimes used to estimate densities; however, we do not, given that our camera-trap

array is based on a plotless design; modelling detection counts is best considered an index of activity level (Shamoon *et al.* 2017). Model calculation was undertaken in a two-step process where we first identified the variables that effect detection probability (binomial distribution; see detection covariates in sampling design). Detection models were ranked by Akaike information criterion (AIC) and the best-fitting model (Table 1) was used in each N-mixture model for the mammal-habitat combinations (count model using negative binomial distribution). To test species responses to vegetation greenness (NDVI) and green-up (NDVI slope), we constructed state-level models that include linear and quadratic relationship for both covariates. We also considered year to account for variation between the two consecutive years; however, this variable was not significant. Different combinations were tested and competing models were ranked by AIC score for each species. Final model prediction was undertaken by model averaging according to AIC weights of all considered models.

## Results

During the 2-year survey we recorded 12 903 animal detections of elk ( $n = 827$ ), white-tailed deer ( $n = 1372$ ), mule deer ( $n = 3609$ ), pronghorn ( $n = 1062$ ) and bison ( $n = 6033$ ) (Fig. 2). Annual NDVI estimates at each camera site indicated that the average NDVI peak occurred on Day 203 ( $\pm 9.18$  days) in forest, Day 195 ( $\pm 7.03$  days) in grasslands, Day 197 ( $\pm 8.28$  days) on prairie dog colonies, and Day 196 ( $\pm 6.37$  days) in riparian areas (Fig. 3a). The average maximum NDVI values for forest, grass patches, prairie dog colonies and riparian were  $(0.71 \pm 0.1)$ ,  $(0.50 \pm 0.02)$ ,  $(0.05 \pm 0.02)$  and  $(0.61 \pm 0.02)$  respectively (Fig. 3b). The ungulates in this study region showed different utilisation in relation to vegetation productivity (NDVI) and greenness trend (NDVI slope) within the four habitat types (Table 2, Fig. 4). Elk and mule deer had a negative quadratic relationship with NDVI in forest sites, meaning that they selected for intermediate NDVI values. White-tailed deer had a positive relationship with NDVI values at forest sites (i.e. higher forage quantity aligned with FMH; Fig. 4).

In riparian sites, elk had a negative quadratic relationship with NDVI, white-tailed deer had a positive relationship with NDVI but negative relationship with NDVI slope, and mule deer had negative relationship with NDVI and NDVI slope (Table 2, Fig. 4). This resulted in seasonal partitioning of riparian sites among the deer species, where elk utilises riparian sites in the middle of the growing season (high NDVI values), followed by white-tailed deer (NDVI peak skewed towards the second half of the season; i.e. drying of vegetation) and mule deer near the end of the growing season (selection of lower NDVI and drying portion of the season; Table 2, Fig. 4). Bison did not show any preference

**Table 1.** Leading detection function models for each species and habitat combination.

<b>Species</b>	<b>Habitat</b>	<b>Intercept</b>	<b>Factor trail</b>	<b>Shrub</b>	<b>Forbs</b>	<b>Grass</b>
Elk	Forest	$-5.656 \pm 0.262$	–	$-0.012 \pm 0.006$	$0.016 \pm 0.005$	$0.043 \pm 0.005$
	Grass	$-4.099 \pm 0.1$	$1.095 \pm 0.362$	$0.011 \pm 0.004$	–	–
	Prairie dog	$-6.457 \pm 0.526$	.	$0.036 \pm 0.008$	$0.041 \pm 0.022$	$0.022 \pm 0.006$
	Riparian	$-4.77 \pm 0.307$	–	.	$-0.02 \pm 0.005$	$0.011 \pm 0.003$
White-tailed deer	Forest	$-4.617 \pm 0.316$	–	–	–	–
	Grass	$-5.38 \pm 0.56$	–	$0.002 \pm 0.011$	$0.002 \pm 0.011$	$-0.002 \pm 0.006$
	Prairie dog	$-4.549 \pm 0.367$	–	$-0.021 \pm 0.008$	–	–
	Riparian	$-3.545 \pm 0.163$	–	$-0.012 \pm 0.003$	$-0.008 \pm 0.002$	$-0.004 \pm 0.002$
Mule deer	Forest	$-4.72 \pm 0.171$	$0.202 \pm 0.097$	$0.006 \pm 0.003$	–	–
	Grass	$-4.285 \pm 0.078$	–	–	–	$-0.002 \pm 0.001$
	Prairie dog	$-5.155 \pm 0.257$	$1.04 \pm 0.506$	–	–	–
	Riparian	$-3.937 \pm 0.105$	–	–	–	$-0.004 \pm 0.001$
Pronghorn	Grass	$-4.544 \pm 0.088$	$-0.347 \pm 0.167$	–	–	–
	Prairie dog	$-5.133 \pm 0.198$	–	–	–	$0.007 \pm 0.002$
Plains bison	Grass	$-4.559 \pm 0.049$	$0.713 \pm 0.074$	$0.022 \pm 0.001$	–	–
	Prairie dog	$-3.842 \pm 0.038$	–	$0.004 \pm 0.001$	$-0.011 \pm 0.003$	–
	Riparian	$-4.469 \pm 0.136$	–	–	–	$0.005 \pm 0.002$

Detection covariates: Trail (factor: open (intercept) or animal trail); vegetation cover within 5 m radius plot in front of camera (grass, forbs, bare ground, shrub, and canopy).

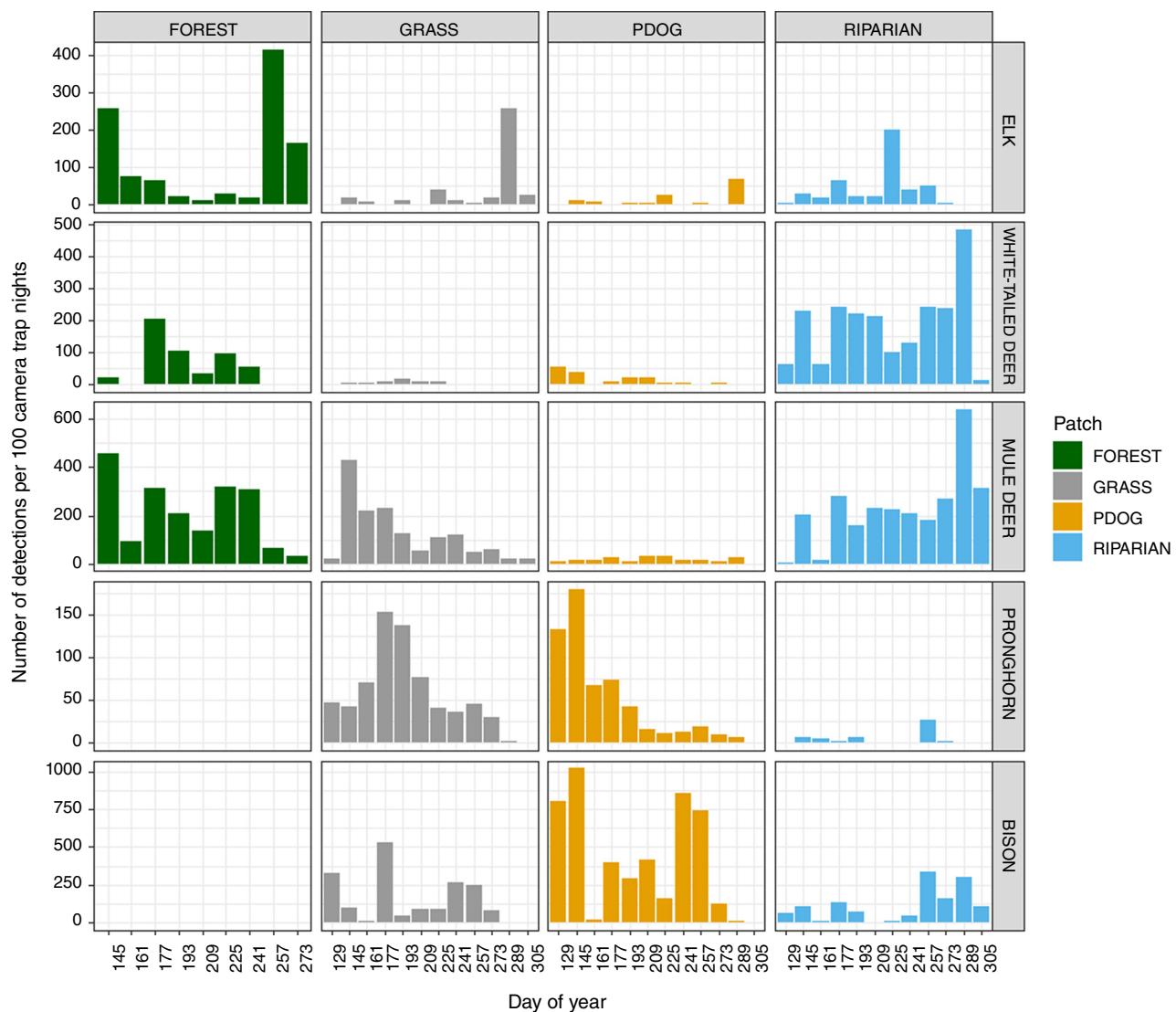
to riparian sites (*intercept only* leading model; Table 2, Fig. 4).

At grass sites and prairie dog colonies, elk overall use was low, and utilisation was higher during the drying of vegetation (low NDVI values; Table 2, Fig. 4). Mule deer trends at grass sites were consistent with GWH, where leading model showed a strong positive relationship with NDVI slope (Table 2, Fig. 4). At prairie dog colonies, mule deer had a negative relationship with NDVI slope and a positive relationship with the quadratic NDVI. This resulted in higher mule deer activity mid-season that was skewed towards the second half of the growing season (Table 2, Fig. 4). White-tailed deer preferred peak NDVI (positive relationship with NDVI) at both grass and prairie dog colonies. Pronghorn leading model for grass sites had a positive relationship with NDVI slope and a negative relationship with the quadratic NDVI term (Table 2, Fig. 4). Pronghorn activity at grass sites was consistent with GWH, but the trends were skewed towards the middle of the growing season (Table 2, Fig. 4). At prairie dog colonies, pronghorn activity was consistent with GWH (positive relationship with slope NDVI). Bison did not follow either NDVI or NDVI slope trends at grass and prairie dog colonies; however, the estimated number of detections was higher at prairie dog colonies which acted as small islands of continuously grassed patches (by prairie dog) and with a high cover of forbs in a sea of mixed grass (Table 2, Fig. 4).

## Discussion

We found seasonal spatial partitioning among ungulates that points to resource partitioning across the growing season (May–October). The focal species shifted their activity between habitats, each taking advantage of shared habitats at different times of the growing cycle. We found a unique foraging pattern for each of the focal species, and these patterns partially supported both the forage maturation hypothesis (FMH) and the green-wave hypothesis (GWH).

Plant nutrient composition changes throughout the plant annual cycle and forage quality decreases as the growing season progresses. Forage quality in grasslands is highest during early vegetation growth, typically before stem elongation and flowering (George and Rice 2016). By relating phenological state to NDVI trends, we would expect higher forage quality during the vegetation growth phase (i.e. green-up), which is reflected in a positive NDVI slope. Following forage maturation hypothesis (FMH) and green-wave hypothesis (GWH), we predicted that pronghorn, mule deer and elk activity would be higher when forage is most nutritious (Jakes 2015; Merkle *et al.* 2016; Middleton *et al.* 2018). We also expected these sympatric ungulates to partition high-quality resources in space (i.e. select between grass/shrub, prairie dog towns, forest, or deciduous riparian). We found partial evidence for this; for example, pronghorn individuals timed their peak activity to the green-up of



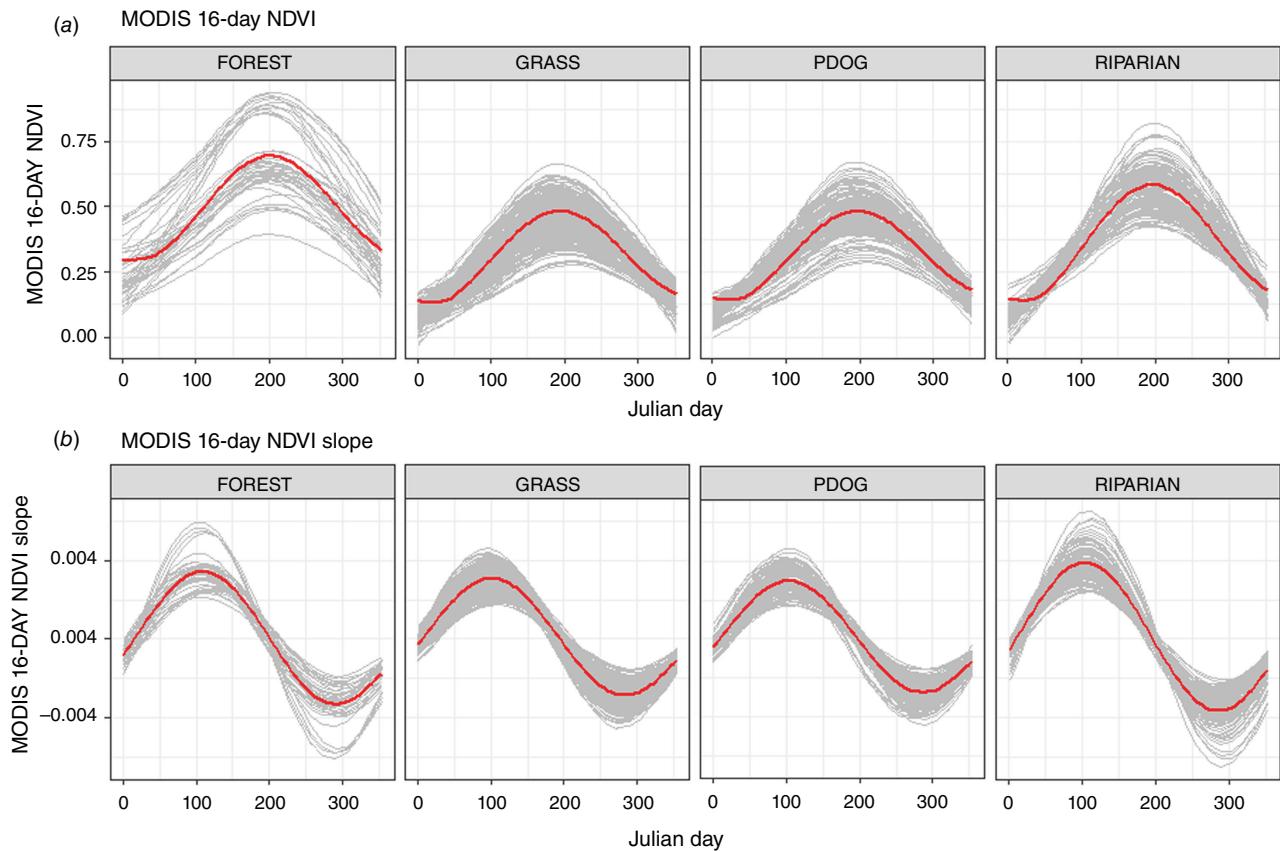
**Fig. 2.** Number of detections per 100 camera-trap nights in relation to day of year (i.e. 16-day Landsat NDVI interval).

grasslands and prairie dog colonies. Similar findings were found for migrating pronghorn, where individuals timed their migration north with seasonal green-up; high activity in May and early June coincides with pronghorn post-parturition diet, primarily forbs, that are abundant in prairie dog colonies (Jakes 2015).

As with pronghorn, mule deer activity also peaked at grass sites during green-up. This is consistent with previous studies that showed that mule deer follow the edge of green-up (Merkle *et al.* 2016). However, unlike pronghorn, mule deer selected prairie dog towns when NDVI peaked (July, August). Given the fact that forbs are a major component of mule deer diet, this finding was counterintuitive to our prediction, because we expected mule deer would take advantage of forbs earlier in the season, when they are most nutritious (May and June; Johnson-nistler *et al.* 2020). Similarly, this was also the case for white-tailed

deer that selected forage in prairie dog towns when NDVI peaked (July, August). Biomass is correlated with NDVI (Todd *et al.* 1998; Olson and Cochran 2003); thus, this may indicate that mule deer and white-tailed deer select peak NDVI as a trade-off between forb quality and quantity. We suggest that prairie dog colonies may attract ungulates because the continuous grazing by prairie dogs is likely to keep the vegetation in the growing stage longer, similar to the foraging of bison (Geremia *et al.* 2019), and they accelerate nutrient cycles, thus promoting a more diverse plant community and a higher net nitrogen than in off-colony sites (Fahnestock and Detling 2002).

In uplands, bison did not time activity to green-up or peak NDVI, indicating that there are other factors that affect bison foraging patterns. Recent evidence shows that bison has unique grazing strategies in comparison to other ungulates (Geremia *et al.* 2019). In environments with significant



**Fig. 3.** (a) MODIS 16-day NDVI and (b) slope (resolution 250 m). Individual site curves are shown in grey and the mean curve in red. Each grey curve represents a camera site in a given year (2018, 2019).

altitudinal gradients where bisons seasonally migrate (Yellowstone National Park), bison did not follow the ‘green-wave’, but engineered the green-wave through their grazing activity (Geremia *et al.* 2019). Whether other species follow the bison’s ‘green-wave’ is yet to be determined. Geremia’s (2019) finding contradicts our observation, and possibly an artefact of bison being confined to fenced pastures. Bison is characterised as a grass and roughage eater (fibre-rich diets) by Hofmann (1989), and has been shown to adaptively move between higher-biomass/lower-quality patches and low-biomass/high-quality patches (Raynor *et al.* 2016). These observations are aligned with studies on African buffalo (*Synacerus caffer*), which balance fibre and protein intake by moving between higher and shorter grass patches (Prins 1996). This could explain the patterns observed in this study, where bison moves between prairie dog colonies (low biomass, high quality) and grass patches (higher biomass, lower quality).

We found seasonal habitat partitioning among the deer species at riparian sites. In riparian sites, peak activity was sequential among the deer species; elk activity peaked earlier in the season (June), followed by white-tailed deer activity (July, August) and ending with mule deer activity (September, October). At forest sites, we found that elk and

mule deer timed their peak activity early and late in the growing season (May–June and September–October), whereas white-tailed deer timed peak activity with peak NDVI (July–August). This is supported by a previous study (Stewart *et al.* 2002) that investigated elk, mule deer and cattle resource partitioning and found that elk and mule deer show temporal partitioning in a hourly scale, but not spatial partitioning within a weekly interval. They also investigated mule deer and elk resource partitioning and found that grass/shrublands were essential for both species but the two differed in that forests were used more by elk than mule deer during summer (Stewart *et al.* 2010). We found a similar pattern, where elk was more active in forests and mule deer in uplands. The authors also found evidence for dietary niche partitioning between the two species, meaning that they use the same habitats but consume different plants (Stewart *et al.* 2003). We did not explore dietary niches but did document that the three deer species’ activity peaks differed through the growing season, pointing to spatio-partitioning of habitat (or resources).

White-tailed deer were sympatric with both mule-deer and elk in forest and riparian habitats but timed their peak activities to when mule deer and elk were less active. These results agree with a study on resource partitioning between

**Table 2.** Single species N-mixture model estimates (negative binomial distribution).

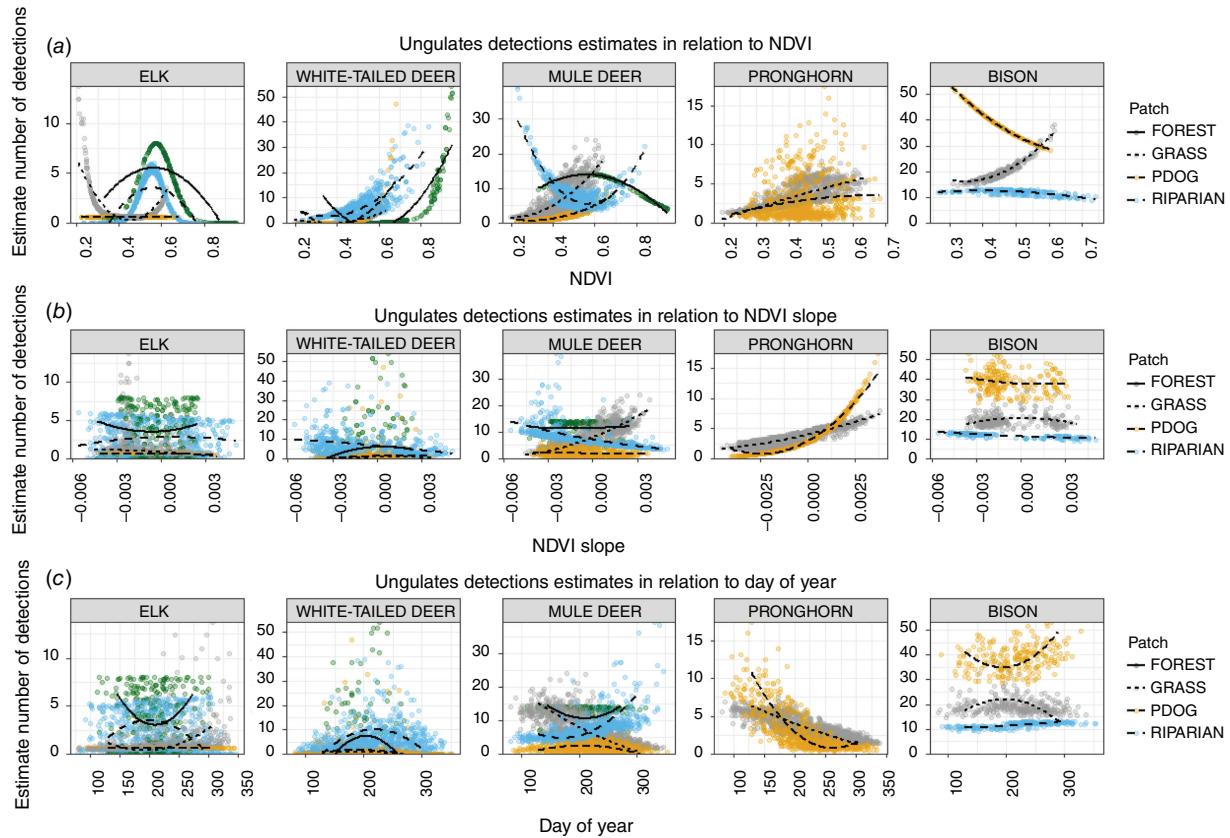
Species	Habitat	Intercept	NDVI	Slope	NDVI	Slope	negLog-Like	nPars	AIC	delta	AICwt	cumlt-vWt
Elk	Forest	-26.14 ± 10.398	98.515 ± 35.809		-85.979 ± 30.631		566.81	8	1149.62	0	0.729	0.729
		-26.571 ± 10.534	100.086 ± 36.285	-1.282 ± 5.522	-87.375 ± 31.052		566.811	9	1151.62	2	0.268	0.997
		1.286 ± 0.289					579.84	6	1171.68	22.06	0	1
	Grass	16.754 ± 7.212	-80.644 ± 34.642		91.255 ± 40.462		1132.87	7	2279.74	0	0.487	0.487
		-0.227 ± 0.274					1136.2	5	2282.4	2.658	0.129	0.761
	Prairie dog	-0.553 ± 0.443					265.588	6	543.177	0	0.444	0.444
		-0.527 ± 0.543		-7.081 ± 52.356			265.575	7	545.15	1.973	0.166	0.61
		-0.338 ± 2.143	-0.492 ± 4.796				265.583	7	545.166	1.989	0.164	0.775
	Riparian	-50.821 ± 11.483	189.718 ± 42.936		-171.283 ± 39.695		936.831	7	1887.66	0	0.653	0.653
		-51.466 ± 11.489	192.01 ± 43.016	-53.6 ± 88.132	-173.44 ± 39.818		936.461	8	1888.92	1.261	0.347	1
		0.879 ± 0.233					954.681	5	1919.36	31.7	0	1
Mule Deer	Forest	-1.075 ± 2.064	12.627 ± 6.035		-10.679 ± 4.334		1718.48	6	3448.96	0	0.6	0.6
		-1.084 ± 2.072	12.658 ± 6.074	1.592 ± 64.691	-10.7 ± 4.368		1718.46	7	3450.91	1.95	0.226	0.826
		2.462 ± 0.159					1725.01	4	3458.03	9.066	0.006	0.996
	Grass	0.18 ± 0.51	4.088 ± 1.13	226.581 ± 43.695			5682.28	6	11376.6	0	0.727	0.727
		0.176 ± 0.509	4.083 ± 1.126	223.276 ± 43.39		-0.054 ± 8.267	5682.27	7	11378.5	1.989	0.269	0.997
		1.882 ± 0.095					5713.19	4	11434.4	57.829	0	1
	Prairie dog	-3.03 ± 1.24	7.802 ± 2.537	-146.521 ± 117.346			579.328	6	1170.66	0	0.407	0.407
		-2.302 ± 1.081	6.534 ± 2.294				581.031	5	1172.06	1.406	0.201	0.608
		-4.491 ± 4.502	14.268 ± 19.654	-158.515 ± 117.781	-6.998 ± 21.304	-	579.266	7	1172.53	1.876	0.159	0.767
	Riparian	0.703 ± 0.294					585.263	4	1178.53	7.87	0.008	0.996
		7.268 ± 2.044	-20.359 ± 7.759	-101.011 ± 43.508	18.658 ± 7.254		3242.22	7	6498.43	0	0.773	0.773
		2.119 ± 0.118					3253.07	4	6514.15	15.715	0	1
White-tailed Deer	Forest	-12.69 ± 1.593	17.552 ± 1.83	71.632 ± 96.87			529.758	5	1069.52	0	0.255	0.255
		-14.021 ± 12.405	21.304 ± 32.289	203.786 ± 92.543	-2.56 ± 20.676		528.802	6	1069.6	0.087	0.244	0.498
		-12.511 ± 1.541	17.329 ± 1.768	195.847 ± 90.988		0.142 ± 0	528.816	6	1069.63	0.117	0.24	0.739
	Grass	1.491 ± 0.376					595.732	3	1197.46	127.948	0	1
		-8.59 ± 1.85	16.751 ± 3.615				280.492	7	574.984	0	0.499	0.499
		-8.589 ± 1.931	16.749 ± 3.732	0.114 ± 6.378			280.492	8	576.984	2	0.183	0.682

(Continued on next page)

**Table 2.** (Continued)

Species	Habitat	Intercept	NDVI	Slope	NDVI	Slope	negLog-Like	nPars	AIC	delta	AICwt	cumlt-vWt
Prairie dog	Grass	-7.77 ± 8.999	13.126 ± 38.567		3.917 ± 4.922		280.493	8	576.987	2.003	0.183	0.865
		-0.557 ± 0.502					293.568	6	599.136	24.152	0	1
		-11.705 ± 2.341	22.778 ± 4.521				254.403	5	518.806	0	0.477	0.477
	Riparian	-11.868 ± 2.478	23.076 ± 4.789	8.573 ± 7.712			254.351	6	520.702	1.896	0.185	0.662
		-9.059 ± 12.982	11.966 ± 53.789		10.851 ± 15.137		254.439	6	520.877	2.072	0.169	0.832
		-0.212 ± 0.436					271.104	4	550.207	31.402	0	1
Pronghorn	Grass	-1.893 ± 0.683	6.693 ± 1.249	-185.672 ± 42.223			2752.48	8	5520.96	0	0.658	0.658
		-1.907 ± 0.684	6.719 ± 1.251	-186.98 ± 42.263		0.76 ± 0	2752.48	9	5522.96	1.999	0.242	0.901
		1.927 ± 0.139					2769.12	6	5550.24	29.277	0	1
	Prairie dog	-3.838 ± 2.239	21.077 ± 10.509	107.381 ± 56.309	-20.707 ± 12.136		2944.48	7	5902.95	0	0.36	0.36
		0.128 ± 0.573	2.811 ± 1.258	175.17 ± 56.225		-0.441 ± 6.33	2944.55	7	5903.11	0.156	0.333	0.692
		1.376 ± 0.125		202.359 ± 53.351			2947.13	5	5904.26	1.308	0.187	0.879
Plains bison	Grass	1.222 ± 0.116					2955.02	4	5918.05	15.097	0	1
		1.012 ± 0.206		451.666 ± 69.234			1078.88	5	2167.77	0	0.331	0.331
		1.501 ± 0.706	-1.024 ± 1.534	534.019 ± 72.436			1077.95	6	2167.89	0.123	0.311	0.641
	Prairie dog	1.053 ± 0.205		506.198 ± 69.419		0.028 ± 0	1078.19	6	2168.37	0.605	0.244	0.886
		1.162 ± 0.206	-	-	-	-	1105.25	4	2218.5	50.73	0	1
		0.778 ± 1.416	4.856 ± 3.164	-	-	-	6225.89	6	12463.8	0	0.272	0.272
Riparian	Grass	2.976 ± 0.187	-	-	-	-	6227.21	5	12464.4	0.637	0.198	0.471
		4.973 ± 8.711	-14.043 ± 36.506	-102.325 ± 98.886	20.4 ± 37.91	-	6224.73	8	12465.5	1.679	0.118	0.588
		3.65 ± 0.205	-	-	-	-	8907.77	5	17825.5	0	0.309	0.309
	Prairie dog	5.537 ± 1.423	-4.301 ± 3.153	-	-	-	8906.91	6	17825.8	0.263	0.271	0.579
		3.65 ± 0.217	-	0.447 ± 11.336	-	-	8907.77	6	17827.5	1.996	0.114	0.693
		2.472 ± 0.172	-	-	-	-	2111.97	4	4231.94	0	0.304	0.304
Riparian	Riparian	2.329 ± 0.192	-	-78.617 ± 55.797	-	-	2111.02	5	4232.04	0.105	0.288	0.592
		3 ± 0.899	-1.057 ± 1.754	-	-	-	2111.79	5	4233.58	1.638	0.134	0.726

Presented are top three models and  $\Delta AIC < 2.5$ . The null model is presented as well (intercept only) for each species and habitat type combination. Model estimates the number of detections per 16-day interval in relation to phenological conditions. Model covariates: NDVI, slope of NDVI and quadratic relationship of each.



**Fig. 4.** (a) Ungulate predicted detections in relation to MODIS 16-day NDVI in four habitats. (b) Ungulate predicted detections in relation to MODIS 16-day NDVI slope in four habitats. (c) Ungulate predicted detections in relation to number day of year in four habitats. Forest (green); grass (grey); prairie dog colonies (PDOG; yellow); riparian (blue).

white-tailed deer and black-tailed deer that found diet overlap but spatial separation (Whitney *et al.* 2011). In our case, each of the deer species utilised the same space, but at different times throughout the growing season. In addition, white-tailed deer activity peaked in all habitats with the peak of NDVI, suggesting selection of forage quantity over quality.

We note that elk did not utilise grassland, shrublands or prairie dog towns and confined their activities more strongly to forest habitats than has been observed in other studies (Mackie 1970; Frisina 1992; Chaikina and Ruckstuhl 2006). This could be because of spatial segregation and resource partitioning between elk and other mega-grazers (i.e. bison or cattle; Coe *et al.* 2004; Chaikina and Ruckstuhl 2006), or it could be due to local human-mediated effects such as hunting (Proffitt *et al.* 2013; Proffitt *et al.* 2016b).

## Management implications

Co-occurring ungulates are found worldwide in ecosystems such as North American forests and grasslands (Naples 2000), Eurasia steppe or the African savannas (Leuthold 2012). Persistence of many of these communities is

challenged because of environmental changes, habitat degradation and habitat loss (Sawyer *et al.* 2009; Morrison and Bolger 2014). One of the main mechanistic strategies of co-occurring sympatric ungulates is habitat and/or resource partitioning (van Beest *et al.* 2014); however, in a changing world, persistence of healthy ungulate populations will greatly depend on the species ability to cope with habitat change (Courtemanch *et al.* 2017; Shamoan *et al.* 2018; Veldhuis *et al.* 2020). Ungulates' ability to adjust behaviour, habitats or resources is key of understanding co-occurrence under future landcover and landuse changes. Further research is needed to determine the degree of flexibility of multiple co-occurring ungulates in landscapes undergoing changes and the implications of these changes to intra- and inter-specific interaction. In addition, wildlife managers need to develop adaptive management plans that account for dynamic multi-species resource needs.

We have shown that the distribution of sympatric ungulates is flexible, as is evident by their shifts in habitat selection throughout the growing season, which allow multiple species to co-exist and utilise one ecosystem. Whereas the species in this study present spatio-temporal segregation, in other parts of the world, resource partitioning is a stronger driver of co-occurrence (as in African savanna; Leuthold

2012). The temporal and spatial patterns observed emphasised that multiple species can experience the same vegetation phenology and respond differently. At local scales, some ungulates showed support for FMH (forage quantity, selection of higher NDVI) and some for GWH (forage quality, selection of positive NDVI slope or greening-up), and the unique patterns observed defy generalisations. This further suggests that seasonal studies of habitat selection for individual species do not reflect the niche flexibility of species to shift habitats in response to changes in phenology. Finally, resident ungulate communities may partition habitats differently from communities composed of migratory species. Therefore, understanding variation in foraging patterns of resident sympatric species can direct management planning where decreased connectivity alters traditional movements.

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**Data availability.** The data used to generate the results in the paper are available in eMammal repository under Smithsonian Grassland Ecology Program: <https://emammal.si.edu/>.

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