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Compatibility of Dual Enterprises for Cattle and Deer in North America: A Quantitative Review



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ABSTRACT

Grazing by livestock, particularly cattle (Bos spp.), is the dominant land use across North American rangelands and often co-occurs in habitats used by wildlife. Deer (Odocoileus spp.) are an ecologically and economically important native wildlife species in North America. Sustainable management and profitable economic returns require an understanding of the factors driving cattle-deer compatibility. Cattle are compatible with deer when cattle grazing does not negatively impact deer or their habitat requirements (food, cover, and space). We reviewed 2,685 publications on cattle-deer interactions across North American ecosystems to assess the compatibility of these two important genera. We extracted data from 85 of the publications, years ranged from 1930-2015, that met criteria for quantifying cattle-deer diet overlap, and cattle effects on deer food, cover, and space. We determined that cattle-deer compatibility across North American ecosystems is dictated: mostly by geographic region; followed by cattle stocking rate and season; and marginally by soil texture. Cattle and deer were compatible across North American ecosystems when cattle stocking rate was less than 0.12-0.17 AUY ha⁻¹. Cattle-deer diet overlap was lowest during summer and autumn. Although, cattle had the greatest potential to decrease forbs in the northeastern forested ecoregion on clay soils during autumn. Cattle had little measurable effect on habitat variables important to deer in open North American ecoregions dominated by herbaceous vegetation. In contrast to rangelands, cattle had the greatest potential to adversely impact deer food, cover, and use of space in forest-dominated ecoregions in North America. However, observations in eastern forested ecoregions only represented 6-16% our data sets. Our review reveals a range of conservative cattle stocking rates (0.12-0.17 AUY ha⁻¹) that will have minimal impact on deer using rangelands, and that stocking rates in forested ecoregions may need to be reduced further to minimize impacts to deer and their habitat requirements.

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Introduction

Livestock grazing is the dominant land use on rangelands, which comprise 30–40% of terrestrial area globally and 61% of terrestrial area in the United States (Fuhlendorf & Engle 2001; Briske et al. 2015). Because rangelands are mostly natural landscapes, they are also important habitat for wildlife (Holechek et al. 1998). For example, most (84%) mammal species in the United

States spend part of their time on rangelands (Hart 1994). Consequently, potential livestock impacts on wildlife have received much attention in natural resource management (Graham et al. 2010). Livestock-wildlife interactions are context and species dependent (Schieltz and Rubenstein 2016; Gordon 2018) that typically lacks a clear definition and solution (du Toit et al. 2017). For example, among small mammals, species adapted to dense cover were impacted negatively by livestock grazing and species adapted to open plant communities were impacted positively (Schieltz and Rubenstein 2016). Developing a sustainable solution for multiple land uses or enterprises will require land managers to make informed decisions of livestock production in conjunction with natural resource management, particularly management of wildlife and their habitats (Herrero et al. 2009).

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The effects of cattle grazing on habitat components important to deer

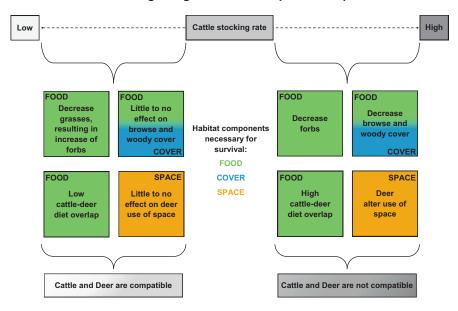


Fig. 1. Hypothetical relationship of cattle-deer compatibility as defined by the effect of grazing by cattle on habitat components important to deer. We predict that cattle stocking rate will be a key component governing the effect of cattle grazing on deer and habitat components important to deer.

Most reviews of livestock effects on wildlife have been qualitative and were concentrated in western United States, with little inclusion of studies conducted in other regions of North America (Fleischner 1994; Belsky & Blumenthal 1997; Belsky et al. 1999; Jones 2000; Krausman et al. 2009). Qualitative reviews conducted to evaluate natural resource management issues may be biased because they are a subjective summarization of data (Jones 2000). In addition, these reviews focused on small and often geographically constrained species, ranging from aquatic organisms to small mammals (Fleischner 1994; Jones 2000). In contrast, quantitative reviews extract data for statistical analysis and thus objectively evaluate impacts and reduce biases reflected in qualitative reviews. However, recent quantitative reviews may have been focused too broadly, searching for positive or negative impacts of multiple livestock species on a wide array of wildlife species (Schieltz and Rubenstein 2016; Gordon 2018).

A well-defined, focused quantitative review of literature to investigate livestock-wildlife compatibility begins with the selection of specific species. After livestock and wildlife species are selected, then compatibility between these species can be conducted by evaluating the effects of livestock on habitat components important to wildlife - food, cover, and space (Fulbright & Ortega-S. 2013). We selected cattle (Bos species) and deer (Odocoileus species) because: (1) cattle are economically important and the most numerous form of livestock in North America (Belsky et al. 1999), (2) deer are the most economically important native wildlife species on North American rangelands for wildlife recreation (Curtis 2002; Watkins et al. 2007), (3) more research has been completed on deer and cattle than most other species, thus providing a large database for review (Schieltz and Rubenstein 2016), and (4) a comprehensive, quantitative review focused on cattle-deer interactions is unavailable in peer-reviewed literature.

Our objective was to quantitatively evaluate the effects of cattle grazing on deer habitat across North American ecosystems. Habitat is species specific and requires characterization (Hall et al. 1997). Habitat components important to deer include food, cover, and space (Fig. 1). First, quantifiable habitat components related to deer food includes cattle grazing impacts on forbs,

the primary food when available, and woody vegetation, a year-round food resource (Krausman et al. 1997; Fulbright & Ortega-S. 2013). Additionally, cattle-deer diet overlap can provide insight into cattle grazing effects on deer food. Second, a quantifiable habitat component related to deer cover includes cattle grazing impacts on woody vegetation because woody plants provide deer with hiding cover from predators and alleviation from extreme weather conditions (Krausman et al. 1997; Fulbright & Ortega-S. 2013). Finally, comparison of deer home range size or selection of vegetation communities in the presence and absence of cattle can quantify cattle grazing impacts on deer use of space (Hygnstrom & VerCauteren 2000; Stewart et al. 2011). We predict that cattle stocking rate will be a key component governing the effect of cattle grazing on deer and their habitat components (Fig. 1).

Methods

Overview of literature review

We reviewed 2,685 publications, consisting of peer-reviewed literature, conference proceedings, and theses/dissertations, on cattle-deer interactions in North America that reported: (1) the influence of cattle grazing on forb availability because forbs are an important constituent in deer diets (Krausman et al. 1997; Fulbright & Ortega-S. 2013), (2) woody plant responses to grazing by cattle because woody plants are an important source of food and cover (e.g., browse and mast) for deer (Krausman et al. 1997; Fulbright & Ortega-S. 2013), (3) diet overlap among cattle and deer because increasing diet-overlap may result from or indicate potential competition for the same food items between the species when forage is limiting (Garrott et al. 1987; Stewart et al. 2011), and (4) cattle effects on deer use of space because deer may be displaced to suboptimal habitats or exhibit changes in fitness producing activities.

We extracted data from 85 of the 2,685 publications (Fig. 2; Appendix A) that met the following criteria: (1) cattle were the only domestic livestock species influencing deer or their habitat, (2) disturbance such as fire or human-induced alteration to vegetation community within 2 yr of data collection was absent, and (3)

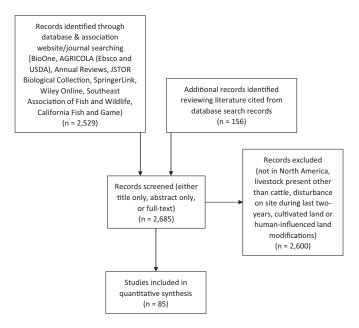


Fig. 2. Overview of systematic literature review methods to extract data for quantitative analysis regarding cattle impact on deer and habitat components important to deer.

research was not conducted on cultivated lands such as croplands or non-native, seeded and improved pasture. We ensued this strict criterion for data extraction because it provided a focused study design to extrapolate cattle-only effects on deer and their habitat. Cattle-deer research that met our criteria and that was included in our quantitative analysis was conducted in North America from 1930 to 2015 (Fig. 3).

Overview of statistical analysis

Vegetation communities influence cattle-deer interactions and vary spatially and temporally (Bork & Werner 1999). Repeated measures are when data is collected from the exact same subject multiple times (Cleophas et al. 2009). However, spatially (between areas) and temporally (between seasons or years), randomly selected vegetation plots are not the exact same (Bork & Werner 1999). Even in the exact same location, successional theory of plant communities dictates that plants in a given area change over time (Clements 1916; Gleason 1926). Therefore, spatially and temporally distinct observations (hereafter, observations) extracted from publications were not considered repeated measures.

Multiple methods (e.g., cover, density, frequency, species richness, or standing crop) were employed across publications to quantify vegetation (forbs, grasses, woody plants; Table B.1–B.2), so for this reason, vegetation metrics were recorded as an ordinal response variable (i.e., decreased, not affected, or increased) in cattle grazed versus non-grazed areas. We also extracted data on cattle and deer stocking rates, annual rainfall the year of the study, dominant soil texture, season, and geographic location because these independent variables influence vegetation communities. When aforementioned independent variables were not included in the publication, we contacted multiple sources (including but not limited to, authors, federal and state government agencies, and other publications) to obtain information to include in our statistical analyses.

We conducted all our statistical analyses using SAS® version 9.3 (SAS Institute, Inc., Cary, North Carolina, USA). For each data set described below (forbs, woody plants, diet overlap, use of space), we developed a full model with all covariates as main effects and re-

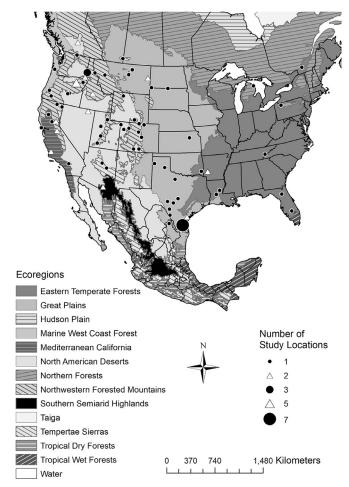


Fig. 3. Locations of 85 studies conducted across North American ecoregions on interactions between cattle and deer. Research that met our criteria spanned an 85-year time period (1930–2015) and may have been conducted at same location for >1 publication or >1 location for one publication.

moved variables from each model data set when P > 0.10 for more than one variable (Peterman 1990). Full models included: season and soil texture as categorical independent variables, animal stocking rate (cattle and/or deer) and annual rainfall as continuous explanatory variables, and latitude and longitude of study location as covariates. We included latitude and longitude to capture the geographic location of each study area and to account for the vast spatial distribution of research conducted across North America. To avoid over-fitting each model and biasing variances of parameter estimates, collinear predictors (condition index of model > 30) were not included in models (Haque et al. 2002); thus annual rainfall was omitted from all models with latitude and longitude because rainfall was collinear with latitude and longitude.

Forbs dataset analysis

We obtained 351 observations from 24 publications (1930–2015) where researchers reported response of forbs to grazing by cattle relative to non-grazed areas. Observations were deleted from models due to missing values for the explanatory variables; in our models, we included 325 observations from 20 publications (1930–2015). These observations included the response of forbs in areas where cattle grazed versus non-grazed areas estimated as; canopy cover (area or percent cover), density, frequency, species richness, and standing crop of forbs (Table B.1). Forb response (nominal distribution) was modeled with a

multinomial logistic regression using Proc Logistic (generalized logit link function). Forb response was not modeled as ordinal distribution, due to failing assumptions for both full and partial proportional odds model.

Woody plants dataset analysis

We obtained 161 observations from 32 publications (1930–2014) when researchers reported response of woody plants to grazing by cattle relative to non-grazed areas. Observations were deleted from models due to missing values for the explanatory variables; in our models, we included 148 observations from 28 publications (1930–2014). We quantified reported responses of woody plants, that were within the useable space of deer, as changes that could affect potential food and/or woody cover for deer. These changes included the response of woody plants in areas where cattle grazed versus non-grazed areas estimated as; canopy or stem cover (area or percent cover), woody plant density, woody plant frequency, and standing crop of browse (Table B.2). Woody plant response (ordinal distribution) was modeled with a proportional odds model using Proc Logistic (cumulative logit link function).

Diet overlap dataset analysis

We obtained 142 observations from 26 publications (1949-2006) when researchers reported percent diet overlap among cattle and deer. Observations were deleted from models due to missing values for the explanatory variables; in our reduced model, we included 118 observations from 17 publications (1949-2006). We also calculated percent diet overlap from studies that did not report diet overlap, but provided the necessary values for calculating percent diet overlap. Multiple methods were employed in the publications to observe diets of species (i.e., bite counts, microhistological, rumen content analysis) and to calculate percent diet overlap (i.e., Kulcyznski's Similarity Index, Morista-Horn Index, Pianka Index; Table B.3). Percent diet overlap was modeled using general linear models in Proc GLM. Because percent diet overlap is bound between 0-100%, residuals were tested to corroborate general linear model assumptions; in addition, results were verified with a generalized linear mixed model with a beta distribution (logit link function) using Proc Glimmix (Dickey 2010). Results were corroborated using Proc Glimmix. Thus, we report Proc GLM results because it provides additional statistics, such as an R2 value.

Use of space dataset analysis

We obtained 70 observations from 32 publications (1965–2014) when researchers compared and reported deer use of space when cattle were present and when cattle were absent. Observations were deleted from models due to missing values for the explanatory variables; in our reduced model, we included 70 observations from 32 publications (1965–2014). Data were entered as binary response, either cattle had no effect on deer use of space or affected deer use of space. Cattle had no effect on deer use of space when deer only maintained their distance from cattle (50–100 m), but did not otherwise alter their use of space. Cattle affected deer use of space when deer used alternative plant communities or increased their home range size. Deer shift in use of space was modeled with a binary logistic regression using Proc Logistic (logit link function).

Results

Forbs: primary deer food when available

Most research investigating the response of grasses and forbs to cattle grazing was conducted in drier ecoregions of western North America; 51% of the observations were from study sites in western North America, followed by central (33%) and eastern (16%) North America. Most researchers (81%; 285 of 351 observations) reported standing crop or area of coverage of vegetation (Table B.1). Forbs: increased in 29% (n=102 of 351); were not affected in 38% (n=133 of 351); and decreased in 33% (n=116 of 351) of the reported observations in response to cattle grazing.

In our full model (no effect from cattle grazing on forbs as reference; n = 325); season ($\chi^2 = 11.296$; df = 4, P = 0.023), soil ($\chi^2 = 19.567$; df = 4; P < 0.001), and geographic location (latitude and longitude; $\chi^2 \ge 37.450$; df=2; P < 0.001) influenced forb response to cattle grazing, but cattle stocking rate ($\chi^2 = 0.120$; df=2; P=0.942) did not influence forb response. Autumn exacerbated both positive and negative effects; forbs were as likely to increase ($\chi^2 = 4.486$; df = 1; P = 0.034) as decrease ($\chi^2 = 4.577$; df = 1; P = 0.032) as compared to not being affected by cattle grazing during autumn (Table C.1). During spring, forbs were not affected by cattle grazing ($\beta = -1.166$; = 3.716; df = 1; P = 0.054). Clay soils also exacerbated both positive and negative effects; forbs were more likely to increase ($\chi^2 = 12.560$; df = 1; P < 0.001) than decrease ($\chi^2 = 8.419$; df=1; P = 0.004) as compared to not being affected by cattle grazing on clay soils. Geographic location also intensified both positive and negative effects. Forbs were just as likely to increase ($\chi^2 = 52.125$; df=1; P < 0.001) as decrease $(\chi^2 = 23.080; df = 1; P < 0.001)$ with eastward progression (e.g., increase in longitude) across North America as compared to not being affected by cattle grazing. However, forbs were more likely to decrease ($\chi^2 = 37.088$; df = 1; P < 0.001) than increase ($\chi^2 = 5.737$; df = 1; P = 0.017) with northern progression (e.g., increase in latitude) across North America as compared to not being affected by cattle grazing (Table C.1).

We also ran a full model with cattle grazing decreasing forbs as the reference category to illuminate when forbs were more likely to increase versus decrease ($n\!=\!325$). It illuminated that forbs most likely increase with southern progression (e.g., decrease in latitude; $\beta\!=\!-0.121$; $\chi^2\!=\!9.244$; df=1; $P\!=\!0.002$; Table C.1) compared to forbs decreasing in response to cattle grazing. Thus, forbs are most likely to decrease with eastward and northern progression across North America as compared to not being affected by cattle grazing. Additionally, forbs are most likely to increase with eastward and southern progression across North America as compared to decreasing in response to cattle grazing (Fig. 4).

Woody plants: year-round deer food and cover

Most published research (78%; n=126 of 161 observations) was conducted in western North America. Most researchers (77%; n=124 of 161; Table B.2) reported standing crop or area of coverage of vegetation. Cattle stocking rate ranged from 0.0017–1.8333 AUY ha⁻¹. The reported cattle grazing effect on woody plants was: increased in 14% (n=23); had no effect or change in 37% (n=60); and decreased in 49% (n=78) of the 161 observations.

In the full model, model fit was poor when latitude and longitude were included as explanatory variables (Hosmer and Lemeshow Goodness-of-Fit Test; $\chi^2 = 28.239$; df=13; P=0.008), but model fit improved in the full model when latitude and longitude were replaced by North American Ecoregion and annual rainfall (Hosmer and Lemeshow Goodness-of-Fit Test; $\chi^2 = 16.266$;

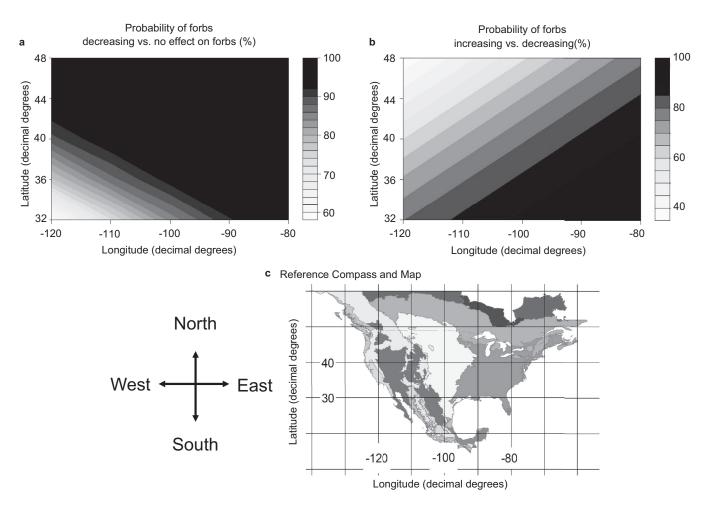


Fig. 4. Cattle grazing effect on forbs (deer food habitat component; a–b) as it related to geographic location across North America (c) in cattle grazed versus non-cattle grazed areas determined from 325 observations reported in 25 publications (1930–2015; Table C.1). Forbs most likely decreased in the northeast (a) and increased in the southeast (b) in response to cattle grazing.

df=15; P=0.3646). In the adjusted full model (n=147), the probability that woody plants decreased in response to cattle grazing was not related to season (χ^2 =1.3, df=4, P=0.857), soil (χ^2 =0.6, df=2, P=0.731), but was related to cattle stocking rate (χ^2 =5.2, df=1, P=0.023), North American Level I Ecoregion (χ^2 =16.2, df=4, P=0.003) and potentially influenced by annual rainfall during the study (χ^2 =1.9, df=1, P=0.163; Table C.2); EPA 2020.

In the reduced model, woody plant response to cattle grazing was strongly influenced by ecoregion ($\chi^2 = 16.1$, df = 4, P = 0.003), followed by cattle stocking rate ($\chi^2 = 6.0$, df = 1, P = 0.014), and then annual rainfall during the study ($\chi^2 = 4.1$, df = 1, P = 0.043; Table C.2). The odds of no effect or a positive effect on woody plants decreased as annual rainfall ($\beta = -0.017$) and cattle stocking rate $(\beta = -5.265)$ increased. The odds that woody plants decreased in response to cattle grazing was most prevalent in the Northwestern Forested Mountains ecoregion (n = 50; $\chi^2 = 12.5$, df = 1, P <0.001), followed by the North American Deserts ecoregion (n = 58; $\chi^2 = 3.2$, df = 1, P = 0.072; Fig. 5). In the Great Plains ecoregion, cattle grazing most likely had no effect on woody plants (n = 8; $\beta = 1.423$; $\chi^2 = 4.7$, df = 1, P = 0.030; Table C.2) until cattle stocking rate was greater than 0.5 AUY ha⁻¹ at which point cattle grazing most likely decreased woody plants (Fig. 5). There was no substantial relationship between the response of woody plants to cattle grazing in Eastern Temperate Forests (n = 27; $\chi^2 = 2.1$, df = 1, P = 0.144; Table C.2) or Mediterranean California (n = 4; $\chi^2 = 0.0$, df = 1, P = 0.973) ecoregions.

Diet overlap

Diet overlap observations were dispersed nearly equally across North America; 28% from western, 37% from central, and 35% from eastern North American study sites. Most researchers (73%; $n\!=\!105$ of 143 observations) reported using Kulcyznski's Similarity and Morista-Horn indices for calculating cattle-deer diet overlap (Table B.3). Cattle and deer dietary overlap ranged from $0.6\!-\!65.0\%$. Cattle stocking rate ranged from $0.00002\!-\!0.41700$ AUY and deer abundance ranged from $0.00002\!-\!0.01669$ AUY.

The full model ($n\!=\!90$) indicated deer abundance (deer AUY; $F_{1,80}\!=\!0.12$; $P\!=\!0.727$), soil ($F_{2,80}\!=\!0.12$; $P\!=\!0.888$), latitude and longitude ($F_{1,80}\!\leq\!0.95$; $P\!\geq\!0.333$) were not related to cattle and deer dietary overlap. However, cattle stocking rate ($F_{1,80}\!=\!15.73$; P<0.001) and season ($F_{3,80}\!=\!14.59$; P<0.001) were related to cattle and deer dietary overlap (Table C.3).

In the reduced model ($n\!=\!118$), when we accounted for geographic location, cattle stocking rate ($F_{1,111}\!=\!31.92;\ P<0.001$) and season ($F_{3,111}\!=\!15.50;\ P<0.001$) explained 47% of the variation in predicted cattle-deer diet overlap (Table C.3). Cattle-deer diet overlap increased 5% with every 0.1 AUY (Animal Unit Year) ha $^{-1}$ increase in cattle stocking rate. In addition, our model revealed that diet overlap was 12–14% greater (Tukey-Kramer; P<0.001) during winter (μ , 95% CI; 32.7%, 28.5–36.8%) and spring (31.6%, 27.4–35.8%) compared to autumn (19.5%, 15.8–23.1%) or summer (18.1%, 14.6–21.6%; Fig. 6).

- Decrease -- No Effect -- Increase

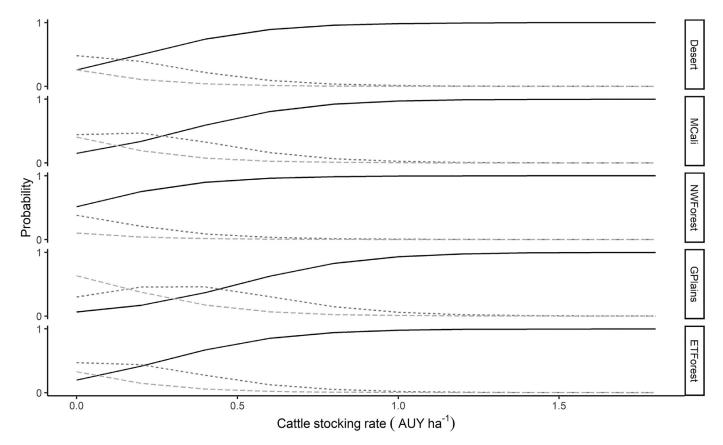


Fig. 5. Cattle grazing effect on woody plants (deer food and cover habitat components) at the mean annual rainfall reported in studies for each Level I North American ecoregion as it related to cattle stocking rate determined from 147 observations reported in 24 publications (1930–2014; Table C.2). From top to bottom, ecoregion panels are displayed from least to greatest mean annual rainfall: North American Deserts (Deserts) 35 cm; Mediterranean California (MCali) 48 cm; Northwestern Forested Mountains (NWForest) 71 cm; Great Plains (GPlains) 77 cm; and Eastern Temperate Forests (ETForest) 115 cm. Woody plants most likely decreased in response to cattle grazing; the relationship was meaningful (P < 0.073) in NWForest, Deserts, and GPlains, but not (P > 0.143) in MCali and ETForests. However, our model indicated as cattle stocking rate and rainfall increased, cattle grazing would most likely decrease woody plants (P < 0.043).

Use of space

Most research (55%) on deer use of space was conducted in western North America, followed by central (39%), and then eastern (6%) North America. In two-thirds of observations (n = 45 of 70), deer were reported to shift their use of space; meaning in the presence of cattle, deer either increased home-range size or utilized an alternative vegetation community compared to when cattle were absent.

The full model (n=34) indicated that deer abundance (deer AUY; $\chi^2 = 0.967$, df = 1, P = 0.326), season ($\chi^2 = 1.261$, df = 4, P = 0.868), and soil ($\chi^2 = 0.021$, df = 3, P = 0.999) did not influence deer use of space in the presence of cattle (Table C.4). However, cattle stocking rate ($\chi^2 = 2.340$, df = 1, P = 0.126), latitude $(\chi^2 = 1.923, df = 1, P = 0.166)$, and longitude $(\chi^2 = 2.691, df = 1,$ P = 0.100) may influence deer use of space in the presence of cattle. The first reduced model (n=46; parameters included: cattle stocking rate, latitude, and longitude) indicated cattle stocking rate (AUY; $\chi^2 = 4.06$, df = 1, P = 0.044) was a significant predictor of deer use of space, but the point estimate for cattle stocking rate (>999.999; 95% CI 1.28- >999.999) was not reliable. The final reduced model (n = 70; parameters included latitude and longitude) indicated longitude ($\chi^2 = 5.90$, df = 1, P = 0.015) was a significant predictor for when deer shift space use in the presence of cattle. However, the Hosmer and Lemeshow Goodness-of-Fit test indicated the final reduced model exhibited a lack of fit (χ^2 =18.37, df=8, P=0.019; Table C.4).

Discussion

Our quantitative review of 85 years of cattle-deer research in North America revealed prognostic associations into the sympatric use of landscapes between cattle and deer. We initially hypothesized that cattle stocking rate would be a key component governing the effect of cattle grazing on deer and their habitat components (Fig. 1). Our hypothesis was not completely incorrect because cattle stocking rate was influential. However, cattle stocking rate was not the most prevalent and was not the only component governing cattle-deer compatibility (Table 1). Geographic location was the most prevalent indicator because it influenced three of the four deer habitat variables (e.g., forbs, woody plants, and space use). Season and cattle stocking rate both influenced two of the four deer habitat variables. Albeit each influenced a different combination of variables; season influenced cattle grazing effect on forbs and cattle-deer diet overlap while cattle stocking rate influenced cattle grazing effect on woody plants and cattledeer diet overlap. Soil texture (e.g., clay, sand, or loam) influenced one of the four deer habitat variables - cattle grazing effect on forbs.

Table 1Qualitative and quantitative summary of literature review on cattle-deer compatibility, as determined by cattle effects on habitat parameters important to deer extracted from 85 publications for research conducted across North America during 1930 to 2015. Cattle effects were determined as the comparison between cattle grazed vs. non-cattle grazed areas in all studies. The qualitative summary is based on summary statistics. The quantitative summary is based on results from regression models.

Deer Habitat Parameter	Qualitative Summary		Quantitative Summary	
	Location of research in North America (NA)	Effect of cattle grazing on parameter	Explanatory influential variables	Effect of cattle grazing on deer habitat parameter
Forbs (Food)	51% Western NA, 33% Central NA, 16% Eastern NA	38% No Effect, 33% Decreased, 29% Increased	season, soil, geographic location	During autumn on clay soils, forbs most likely increase in SE North America and decrease in NE North America.
Woody Plants (Food, Cover)	78% Western NA, 5% Central NA, 17% Eastern NA	49% Decreased, 37% No Effect, 14% Increased	cattle stocking rate, geographic location, rain	As cattle stocking rates and rainfall increase, woody plants most likely decrease; especially in Northwestern Forested Mountains.
Diet Overlap (Food)	28% Western NA, 37% Central NA, 35% Eastern NA	Ranged 0.6–65.0% Overlap	cattle stocking rate, season	Greater probability of increasing diet overlap with increasing cattle stocking rate during winter and spring compared to summer and autumn.
Use of Space (Space)	55% Western NA, 39% Central NA, 6% Eastern NA	64% Changed use of space, 36% Did not change use of space	geographic location	More likely for deer to use an alternative vegetation community or increase home range size in forested compared to open or mixed open-forested ecoregions.

Food habitat component

The primary rationale for employing cattle grazing as a wildlife habitat management tool originates from the theory that in climax grasslands, cattle grazing decreases grasses, thereby making grasses less competitive with forbs resulting in an increase in forbs (Leopold 1933; Vavra 2005). Reducing grasses, thereby increasing forbs, would benefit deer because when available, forbs comprise a larger proportion of deer diets than other vegetation classes (Krausman et al. 1997; Fulbright & Ortega-S. 2013). Our review revealed that forbs were most likely not affected by cattle grazing in western North America, but did respond to cattle grazing in eastern North American ecoregions. The western ecosystems in our review received < 52 cm mean annual rainfall compared to at least 2 x greater mean annual rainfall (112 cm) in northern and eastern North American ecosystems. In drier ecosystems of western North America, forb response is most likely influenced more by stochastic abiotic factors (i.e., annual rainfall) than biotic factors, such as cattle grazing (Ellis and Swift 1988; Von Wehrden et al. 2012). Conversely, forbs did respond to cattle grazing in mesic ecoregions of eastern North America. However, our model indicated forb response was not unidirectional; forbs were more likely to decrease in northeastern ecoregions and increase in southeastern ecoregions. Cattle may be more likely to decrease forbs in areas with cooler temperatures and shorter growing seasons, such as in the northeastern North American ecoregions (Wolfe et al. 2018). However, these trends need to be continually monitored as they may alter with impending climate change. For example, northeastern North American ecoregions are predicted to have a longer growing season with more frost-free days and warmer temperatures (Wolfe et al. 2018; Karmalkar and Bradley 2017). This climate change prediction could potentially change forb response to cattle grazing in northeastern ecoregions.

Diet overlap can indicate potential competition between sympatric species when forage becomes limiting. Daily consumption of forage on a dry matter basis averages 11.8 kg day⁻¹ for a mature cow and 2.4 kg day⁻¹ for a mature deer (Fulbright & Ortega-S. 2013). If diet overlap among cattle and deer is 20%, and 20% of 11.8 kg of forage is 2.4 kg of forage, then at 20% diet overlap one mature cow consumes the daily equivalent of the same forage as one deer. If forage is limiting, then 20% diet overlap would indicate one mature cow is consuming the essential daily forage to support

one deer. During seasons when grasses were less available, winter and spring, diet overlap exceeded 20%. During peak growing seasons for grasses, summer and autumn, diet overlap only exceeded 20% when cattle stocking rate was \geq 0.15 AUY ha $^{-1}$ (Fulbright & Ortega-S. 2013). Therefore, when forage is limiting, cattle potentially only adversely impact deer food habitat components during seasons when grasses are less available and when cattle stocking rates are greater than 0.15–0.17 AUY ha $^{-1}$.

Food and Cover habitat component

Woody plants provide deer with hiding cover from predators and cover to alleviate extreme weather conditions (Krausman et al. 1997; Fulbright & Ortega-S. 2013). Deer in North America do not respond positively to a decrease in woody vegetation (Fulbright et al. 2018). Our review uncovered that cattle grazing activities most often resulted in woody plants decreasing, with the effect being more predominate as rainfall and cattle stocking rate increased. However, the magnitude of the effect was not congruent across all North American ecoregions.

Using our model results, we can predict the cattle stocking rate threshold (e.g., has a 99% chance; probability = 0.99) where essentially all cattle grazing activity results in a decrease in woody plants across ecoregions. The Northwestern Forested Mountains ecoregion has the lowest cattle stocking rate threshold at 0.8 AUY ha⁻¹ (Fig. 5). In Eastern Temperate Forests, North American Deserts, and Mediterranean California ecoregions, the predicted cattle stocking rate threshold is 1.2 AUY ha⁻¹. Finally, cattle grazed areas in the Great Plains have the highest predicted cattle stocking rate threshold at 1.4 AUY ha⁻¹ before woody plants will decrease (Fig. 5). In forested ecoregions, researchers concurrently reported a reduction in native grasses (herbaceous vegetation) and woody vegetation due to cattle consumption (Bratton 1979; Kay & Bartos 2000). Thus, it is understandable that ecoregions characteristically dominated by woody plants (e.g., forested and shrub dominated ecoregions) would tolerate a lower cattle stocking rate before cattle consumed woody plants compared to the Great Plains which is characteristically dominated by herbaceous vegetation (CEC 1997; Omernik and Griffith 2014). This is furthermore exacerbated in forested ecoregions at high elevation. The Northwestern Forested Mountain ecoregion contains the highest mountains in North

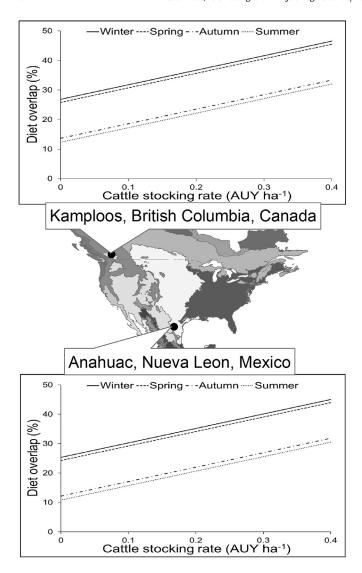


Fig. 6. Diet overlap (%) among cattle and deer displayed at an extreme northern (Canada) and southern (Mexico) North American study site as it related to cattle stocking rate expressed as AUY (animal unit year) ha $^{-1}$ determined from 118 observations reported in 17 publications (1949–2006; Table C.3). When accounting for geographic location, cattle stocking rate and season explained 47% of variation in cattle-deer diet overlap (P<0.001). Cattle-deer diet overlap increased 5% (P<0.001) for every 0.1 AUY ha $^{-1}$ increase in cattle stocking rate.

America with colder temperatures and dry grasslands; conditions that potentially further limit herbaceous vegetation (CEC 1997).

Space habitat component

Deer select habitat to meet their basic needs for survival while minimizing expenditure of energy (Brown 1992; Hygnstrom & Ver-Cauteren 2000). Additionally, deer home range sizes are typically smaller in locations with abundant forage and less competition with other herbivores (Garrott et al. 1987; Stewart et al. 2011). Thus, deer that utilize alternative vegetation communities may be displaced to suboptimal habitats or deer that increase home range size may exhibit changes in fitness producing activities. Our review uncovered that in the presence of cattle, most researchers reported that deer either utilized an alternative vegetation community or increased home-range size compared to when cattle were absent.

The probability that deer would or would not change their use of space in the presence of cattle was influenced by geographic location across North America. However, our model was unable

to detect a predictable and reliable trend. Therefore, we investigated the frequency at which deer would or would not change their use of space in the presence of cattle across North American ecoregions because deer use of space was related to longitude (Table C.4). Deer were equally likely to change their space use as to not change space use in to not change space use in non-forested, open ecoregions (i.e., Great Plains, North American Deserts: 21% changed; n = 15 compared to 19% did not change; n = 13) and in mixed forested/open ecoregions (i.e., Mediterranean California, Southern Semiarid Highlands; 4% changed; n=3 compared to 3% did not change; n=2) in the presence of cattle. In contrast, deer were mostly likely (39% changed; n = 27 compared to 14% did not change; n = 10) to change their use of space in response to the presence of cattle forested ecoregions (i.e., Eastern Temperate Forest, Northern Forests, Northwestern Forested Mountains, Temperate Sierras: Fig. 7).

In forested ecoregions, most researchers reported that deer were more likely to use alternative vegetation communities, with less herbaceous forage or on steeper slopes, and deer had larger home range sizes when cattle were present. For example, Compton et al. (1988) reported radio-collared deer immediately exited from a Montana riparian forest when cattle were introduced but returned to the area once cattle were removed. In a *Quercus* woodland in Oregon, Smith and Coblentz (2010) reported deer shifted their center of activity by 23–75 m and made exploratory trips when cattle were present. Finally, Kie et al. (1991) reported deer increased home range size by 15–29% and used areas that had steeper slopes when cattle were present. Thus, it was most often observed that deer displayed behaviors to avoid cattle and cattle-grazed areas in forested ecoregions.

Summary of cattle-deer compatibility from this quantitative review

The difference in forb response to cattle grazing between mesic and drier rangelands sheds light on why wildlife managers in mesic areas might view cattle grazing as a tool to increase forbs (Lutz 1930; Leopold 1933; Hayes and Holl, 2003; Towne et al., 2005). In contrast, wildlife managers on drier rangelands may not find a strong effect of grazing on abundance of forbs selected for by deer (Jones 2000; Ortega et al., 1997). Conversely, cattle grazing might be viewed as destructive by deer managers in forested ecoregions because cattle decrease woody plants that serve as security cover and year-round food resource (Bratton et al. 1980; Belanger and Picard 1999; Moore and Terry 1979). Finally, perspectives on cattle grazing and deer may differ depending on cattle stocking rate. For example, a negative viewpoint on cattle grazing might result if someone only observed areas with high cattle stocking rates. Our analysis revealed high stocking rates (≥ 0.12 AUY ha⁻¹) negatively impact habitat variables important to deer.

Additionally, our quantitative review revealed that most of the research regarding cattle effects on habitat variables important to deer (food, cover, and space) were from western (51-78%) and central (33-39%) North America, with little research conducted in eastern forested ecoregions. This is a justifiable trend given most beef cattle producing states are in the open, grassland-dominated ecoregions in central and western North America (CEC 2015). Subsequently, our review revealed that cattle, when properly stocked, have little measurable effect on habitat variables important to deer in areas where cattle producing operations are in greatest abundance in North America. On the contrary, cattle had the greatest potential to adversely impact deer food, cover, and use of space in forested-dominated ecoregions in North America. However, we cannot formally conclude these trends exist throughout forested areas because observations in eastern forested ecoregions only represented 6-16% our data sets. Rather, our review simultaneously exposes the need for more conservative cattle grazing management

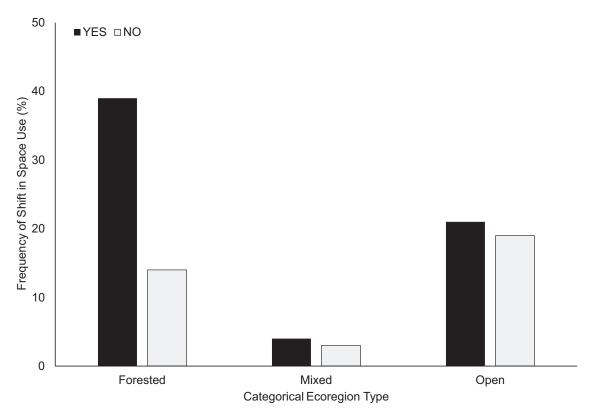


Fig. 7. The frequency that deer shifted use of space in the presence of cattle as determined from 70 observations reported in 32 publications (1965–2014). Level I North American ecoregions were categorized by dominate vegetation growth forms: Forested included Eastern Temperate Forest, Northern Forests, Northwestern Forested Mountains, Temperate Sierras; Mixed forested/open included Mediterranean California and Southern Semiarid Highlands; and Open included Great Plains and North American Deserts. Deer were most often reported to use alternative vegetation communities or increase home range size when cattle were present in forested ecoregions.

strategies in all forested ecoregions and the need for more research in eastern forested ecoregions.

Finally, our quantitative review revealed that two variables, cattle stocking rate and season, explained almost half of the variation in cattle-deer diet overlap across North America. This is exceptional considering the multitude of natural variability across North America that influence available forages, such as varying climatic influences and different vegetation communities. The peak growing seasons for grasses are usually during summer and autumn, with characteristically less grass available during winter and spring (NRCS 2005). Cattle select primarily for grasses (Mackie 1970; Armstrong 1981; Gallina 1993). Our models indicated that when potentially less grass was available, during non-peak grass growing seasons and due to higher cattle stocking rate, cattle switched to forages consumed by deer. This resulted in an increase in cattledeer diet overlap. Thus, the availability of grasses appears to be the determining factor when cattle-deer diets overlap. Managers across North America can reduce cattle-deer diet overlap by seasonally adjusting cattle-stocking rate to be within the available and sustainable grass biomass regenerative capabilities for the grazable cattle management area (Findholt et al. 2004; Beck and Peek 2005). If forage is limiting, our models indicate that during peak growing seasons for grasses, cattle stocking rate should be maintained at or below 0.15 AUY ha^{-1} .

Implications

While our initial hypothesis, that cattle stocking rate would best explain cattle-deer compatibility across North America (Fig. 1) was not supported, cattle stocking rate did influence food and cover habitat variables important to deer (Table 1). Our analyses revealed cattle and deer were compatible across all North American

ecosystems when cattle stocking rate was less than 0.12-0.17 AUY ha⁻¹. Additionally, we were able to reveal other prognostic associations suitable to guide management actions to maximize cattledeer compatibility in North American ecosystems. In addition to cattle stocking rate, cattle-deer compatibility is influenced by season and geographic location (Table 1). For example, in forested North American ecoregions, it is more likely that cattle grazing will decrease forbs (especially during autumn in northeast), decrease woody plants, and alter deer use of space. Thus, managers in forested ecoregions will have to monitor impacts of cattle grazing on these important deer habitat variables to ensure cattledeer compatibility. Conversely, in open North American ecoregions, it is less likely that cattle grazing will decrease forbs or woody plants or alter deer use of space (Table 1). However, the abundance and availability of herbaceous vegetation is unpredictable in these open ecoregions because of their semi-arid to arid climate (Bork and Werner, 1999). Thus, managers must mitigate potential cattle-deer diet competition by closely monitoring the abundance of herbaceous vegetation during winter and spring (regardless of cattle stocking rate) and during autumn and summer when cattle stocking rate is > 0.15 AUY ha⁻¹ (Fig. 6). Managing for cattle-deer compatibility in North America will mitigate livestock-wildlife interactions and ensure the sustainability of financial returns from ecosystem services and goods provided by two of the most ecologically and economically important species for millions of humans in North America (Curtis 2002; Watkins et al. 2007; Graham et al. 2010; Sayre et al. 2013).

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Declaration of Competing Interest

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

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Supplementary materials

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