

## Quantifying herbivory in heterogenous environments: Methodological considerations for more accurate metrics



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### ABSTRACT

Formative patterns of vegetation responses to cattle grazing can be difficult to detect because of innate heterogeneity of vegetation communities and grazing patterns, especially in semiarid environments. Nonetheless, some of this heterogeneity can be accounted for using appropriate experimental designs and statistical analyses. Bork and Werner (1999) suggested retention of negative vegetation consumption values for paired herbivory studies to concurrently analyze spatial heterogeneity and intensity of herbivory. Yet, inclusion of negative consumption metrics has not been widely utilized. Our objective is to determine if postulates proposed by Bork and Werner (interpretation of effects when negative consumption values are manipulated) are applicable to a real data set utilizing a paired experimental design in a heterogeneous, semiarid environment. We determined manipulation of negative consumptive values affects interpretation; it skews data distribution, over-estimates treatment effect, and results in a statistically weaker treatment effect. Therefore, we recommend employing a biologically paired experimental design and the retention of all negative vegetation consumption values so that: (1) resulting models represent a normally distributed population, (2) standing crop of vegetation resulting from the treatment is not over-estimated and (3) grazer treatment effect in heterogenous environments is recognized if existent. This will ensure conservative metrics guide management decisions.

### 1. Introduction

Heterogeneity is common in semiarid systems and can make it difficult to detect patterns of ecological significance. Ecologically significant patterns can help guide best management practices for the sustainable use of natural resources. Establishing and quantifying formative ecological patterns of vegetation responses to cattle grazing is an ongoing objective in rangeland ecology and management (Powell et al., 2018; Schieltz and Rubenstein, 2016). Despite this, a consensus on vegetation responses to cattle grazing is lacking due to the heterogeneity of environmental factors affecting vegetation growth and its responses to grazing. These contributing factors are confounded across gradients of precipitation, topoedaphic features, and plant community composition and dynamics (Krausman et al., 2009; Fulbright et al., 2008; Vavra, 2005; Georgiadis et al., 1989).

Variation in vegetation responses to cattle grazing also exists within

ecologically similar landscapes. For example, in semiarid landscapes, some researchers concluded cattle grazing had no impact on forbs (Jones, 2000; Ortega et al., 1997), while other researchers concluded cattle grazing increases forbs (Ruthven, 2007; Holechek, 1991; Evans, 1986). Variation in vegetation responses to cattle grazing in semiarid environments may be attributable to: (1) natural spatial variability of vegetation communities (Bork and Werner, 1999), (2) patchiness of cattle grazing across the landscape (Pringle and Landsberg, 2004; Landsberg et al., 1999, 2003; Andrew, 1988), and (3) differences in study design and statistical analyses (Bork and Werner, 1999; Mitchell and Wass, 1996).

Natural spatial variability of vegetation communities and patchiness of cattle grazing across the landscape are exacerbated in semiarid environments. Water is limiting and the overall capacity of the soil to absorb water is typically low. Abiotic heterogeneity in semiarid environments can be ascribed to locally variable water and soil

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redistribution (Bork and Werner, 1999; Koppel et al., 2002). These variable abiotic conditions contribute to high variation in standing crop of herbaceous vegetation (Bork and Werner, 1999). The heterogeneity of standing crop is further confounded by patchiness of vegetation selection by grazing cattle across the landscape. For example, cattle graze more intensely on forages closer to water sources (Andrew, 1988; Landsberg et al., 1999, 2003; Pringle and Landsberg, 2004). Thus, selectivity of grazing cattle typically results in high removal of standing crop by cattle at the patch level relative to the landscape level (Bork and Werner, 1999). The naturally occurring heterogeneity of vegetation communities and grazing cattle in semiarid landscapes are difficult to control in field-based studies. However, the investigator can account for some of this heterogeneity in semiarid environments when developing the experimental design and employing the statistical analyses to examine cattle grazing effects on vegetation.

Bork and Werner (1999) addressed statistical methods for paired herbivory studies to account for high heterogeneity in semiarid and arid environments. They suggested including negative consumption values (i.e., the difference between standing crop and percent utilization) when estimating grazing utilization in a paired sub-plot study design. Negative vegetation consumption values occur in paired study designs when there is a higher standing crop of vegetation inside the control (caged, ungrazed area) compared to the treatment (grazed area). Due to system randomness, statistical theory dictates the difference between paired grazed and ungrazed plots has a one-third probability of resulting in negative, neutral, or positive values in ungrazed systems. When grazing is added to the system, in theory this would shift the normally distributed bell-shaped curve to the right, or further towards a sampling distribution with more positive values. However, some portion of the sampling distribution would remain to the left of center and negative values should be expected. In this study, 24% of our values were negative. When these negative grazing utilization values are set to zero, there is an overestimate of forage use and a higher probability of detecting a significant difference between the intensity of herbivory (Bork and Werner, 1999). However, when a properly employed analysis includes negative vegetation consumption values, non-zeroed data can concurrently analyze spatial heterogeneity and the intensity of herbivory (Bork and Werner, 1999).

Although the benefits of retaining negative vegetation consumption values were identified over twenty years ago (e.g., in 1999), inclusion of negative consumption metrics have not been widely used. Typically, reported vegetation consumption metrics range from zero to positive values (Vermeire et al., 2018). However, by random chance, vegetation response in paired plots could result in one of three potential outcomes: (1) the difference between paired observations could be positive (for example, more vegetation in the control area), (2) the difference between paired observations could be zero (no vegetation difference between control and treatment area), or (3) the difference between paired observations could be negative (for example, more vegetation in the treatment). Additionally, it is often unclear if the negative vegetation consumption metrics are zeroed or deleted from the data set before the data is analyzed.

Our objective is to determine the effects on interpretation when negative consumption values are manipulated utilizing a real data set collected on a landscape scale in a heterogenous, semiarid environment. Specifically, we determine if manipulation of negative consumption values affects interpretation when: (1) employing a true paired experimental design, (2) examining the herbivore-based impact by evaluating the relationship of forb standing crop to the difference in grass standing crop, and (3) examining the impact of herbivory on the vegetation community by evaluating the relationship of forb standing crop as it relates to percent grass utilization (Bork and Werner, 1999).

## 2. Materials and methods

### 2.1. Study area description

We selected six 2500 ha study sites (10–134 km apart) located on 4 East Foundation ranches spanning 134 km of the semiarid region of South Texas, USA from the immediate Gulf Coast to the western edge of the Coastal Sand Plains ecoregion. The East Foundation (San Antonio, TX) is an Agricultural Research Organization devoted to promoting the advancement of land stewardship through ranching, science, and education using its living laboratory (that includes 6 ranches and 88,222 ha in South Texas) as a platform. One study site was on each of the following ranches: (1) Buena Vista (6113 ha; lat 26°57'14.4"N, long -98°27'21.6"W), (2) El Sauz (10,984 ha; lat 26°31'58.8"N, long -97°29'23.9"W), and (3) Santa Rosa (7544 ha; lat 27°10'58.8"N, long -97°51'39.6"W). Three study sites were located on San Antonio Viejo ranch, 60,034 ha, with a study site in the northern (site 1; lat 27°1'44.4"N, long -98°47'13.2"W), central (site 2; lat 26°53'49.2"N, long -98°43'40.8"W), and southern (site 3; lat 26°45'25.2"N, long -98°46'11.9"W) portion of the ranch.

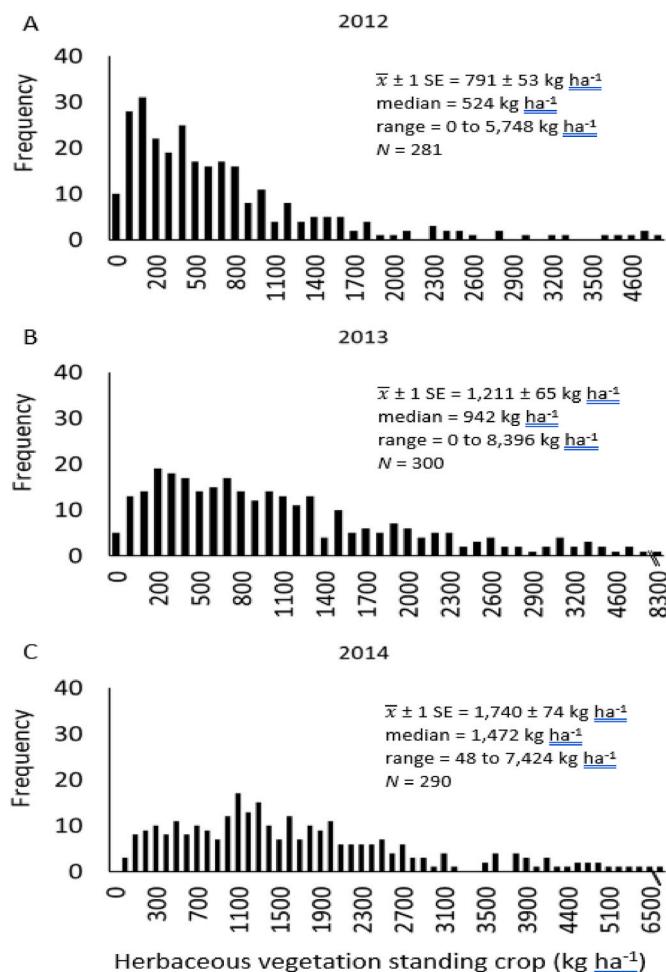
All study sites, except San Antonio Viejo site 3, were in the Coastal Sand Plain ecoregion. San Antonio Viejo site 3 was in the Tamaulipan Thornscrub ecoregion. Vegetation characteristics across the landscape ranged from open grasslands with interspersed woody mottes to thornscrub woodlands. Detailed descriptions of vegetation for the Coastal Sand Plain are in Diamond and Fulbright (1990), Forman et al. (2009), Fulbright (2001), and Fulbright et al. (1990). Detailed descriptions of the Tamaulipan Thornscrub are in Fulbright (2001).

Based on the preceding 20 yrs of data, average yearly rainfall for the region was 46.2 cm (C.J. Fernandez, Texas A&M Research & Extension Center at Corpus Christi, Personal communication). Weather stations that recorded both precipitation and temperature were located within each study site on Buena Vista, El Sauz, and Santa Rosa and within 4.5–9.5 km of study sites on San Antonio Viejo ranch. Regional average annual rainfall received across study area was 32.1 cm, 36.4 cm, and 45.8 cm during 2012, 2013, and 2014, respectively.

The ungrazed, standing crop of herbaceous vegetation (e.g., within grazing exclosures) was heterogenous across the randomly deployed experimental sites during the three years of data collection (Fig. 1). Heterogeneity of the herbaceous vegetation in this semiarid landscape across all years of data collection was corroborated from: (1) the skewed data distribution of herbaceous vegetation standing crop within grazing exclosures, (2) the 1.2–1.5 fold difference between the mean and median annual values of the herbaceous standing crop, and (3) the expansive range of herbaceous vegetation standing crop that fluctuated from zero, or near zero, to upwards of over 5000–8000 kg ha<sup>-1</sup> in a given year (Fig. 1).

### 2.2. True paired experimental design

We installed fifty 1.5 m × 1.5 m grazing exclosures (Chambers and Brown, 1983) within each of the six 2500 ha study sites during 28 January to 11 March 2012. We used ArcMap (ArcGIS software v. 10, ESRI, Redlands, CA) to randomly allocate each grazing exclosure, at least 100 m apart, in each of the study sites. Each grazing exclosure was constructed using four 10 cm × 10 cm spacing, 6-gauge galvanized utility panels (each panel was 1.2 m tall x 1.5 m wide) and 4 t-posts. The center of the grazing exclosure was the non-grazed sampling area. We installed each grazing exclosure in areas dominated by herbaceous vegetation because our research objective was focused on grasses and forbs. Next, at least 10 m away from each grazing exclosure, we searched for a biologically similar vegetation plot to the non-grazed sampling area to serve as a paired, grazed plot. Once located, we marked the paired grazed sampling area with a t-post (Loft et al., 1987). We marked the north corner of the grazed sampling area to guarantee we sampled the initially selected paired sampling plot; it was located 0.5 m south of



**Fig. 1.** Standing crop of herbaceous vegetation inside randomly distributed grazing exclosures across south Texas, USA during (A) 2012, (B) 2013, and (C) 2014. Heterogeneity of vegetation standing crop is corroborated by the skewed data distribution, the 1.2–1.5 fold difference in the mean and median values, and the expansive range of vegetation standing crop values within a given year.

the t-post. The 0.5 m distance from the t-post and sampling plot was the same distance for the grazed (treatment) and ungrazed (control) sampling areas. Our goal was to reduce environmental heterogeneity with a true paired experimental design (paired treatment and control). We ensured paired treatment and control sampling plots were: (1) in close proximity, (2) by visual inspection, initially were judged to be ~90% biologically similar with respect to vegetation species and bare ground (i.e., percent cover and species richness), and (3) located as similar as possible to the composition of surrounding vegetation so that sunlight influences would be similar between paired areas.

### 2.3. Vegetation sampling

In South Texas, autumn is the only season when grasses and forbs are concurrently in their peak growing season (Fulbright and Ortega-S., 2013). Thus, we conducted our sampling immediately after the autumn growing season, when both grasses and forbs had concurrently reached peak biomass (Mitchell and Wass, 1996). Consumption of grasses represents cattle grazing across our study sites because grasses constitute the highest proportion of cattle diets compared to the other large ungulates, white-tailed deer (*Odocoileus virginianus*; hereafter deer) and nilgai (*Boselaphus tragocamelus*), present on our study sites. During autumn, grasses comprised  $87.9\% \pm 1.3\%$  ( $\bar{x} \pm 1 \text{ SE}$ ) of cattle diets compared to  $\leq 38.0\% \pm 1.9\%$  of nilgai (19–38%) and deer (3–11%) diets

based on seasonal stable isotope analyses of feces (Hines, 2016).

Grazing exclosures were in place for 8–12 months on each study site before samples were collected. During November–December 2012 and September–October 2013 and 2014, forage standing crop was clipped at ground level (i.e., destructive sampling) within a 0.5 m × 0.5 m sampling frame placed in the center of each grazing exclosure and 0.5 m from the t-post marking the paired grazed sampling area. Within each grazing exclosure, the distance between the sampled plot and all panels was 0.5 m, which ensured standing crop of sampled forages was not disturbed by large ungulates.

Herbaceous vegetation samples were separated into: (1) grasses, (2) forbs preferred by deer, and (3) forbs not preferred by deer. We separated forb species into those preferred and not preferred by deer due to alignment with a separate research question of interest; effect of grazing on forbs deer select for. Preference of forbs by deer was based on previous research regarding forb palatability to deer in South Texas (DeYoung et al., 2019). Non-preferred forbs consisted of 32 species that deer would consume little compared to the proportion of their availability in the plant community or would consume in greater amounts only as a last resort when all other forage was absent (Appendix A). Because deer are opportunistic feeders (Fulbright and Ortega-S., 2013), all other forbs were considered preferred by deer (Appendix B). We dried vegetation samples at 45 °C until they reached a constant mass and then weighed them to the nearest 0.1 g using a digital, battery operated scale (Ohaus, Parsippany, NJ). After sampling was completed and because destructive sampling was used, we moved grazing exclosures 10 m in a randomly assigned cardinal direction (previously sampled locations were avoided). After the new grazing exclosure was installed, which established the new non-grazed sampling area, we then searched for a new biologically similar area to serve as the paired grazed plot. Once located, the new paired grazed plot was marked with a t-post. Details of paired plots are described above.

### 2.4. Statistical analyses

Each randomly allocated paired sampling location (i.e., grazed and corresponding ungrazed area) was defined as the experimental unit. We initially had 900 paired sampling locations (e.g., experimental units) to analyze during this study (50 at each of the 6 study sites during each of 3 yrs). However, we excluded 26 paired sampling locations from the data set because grazing exclosure panels were compromised allowing ungulates to graze inside the enclosure or because sampling areas were flooded. We evaluated the frequency and simple statistics (i.e., mean, median) for the difference in herbaceous vegetation (calculated as ungrazed minus grazed) to determine if sampling distribution postulates proposed by Bork and Werner (1999) apply to a data set collected in a heterogeneous, semiarid environment with a true paired experimental design.

We then sought to determine if data interpretation postulates regarding manipulation of negative consumption vegetation metrics proposed by Bork and Werner (1999) apply to a data set collected in a heterogeneous, semiarid environment with a true paired experimental design. First, for each of our paired grazing exclosure locations, we estimated the two common grass consumption metrics, difference in standing crop and percent utilization (Bork and Werner, 1999). We calculated the cattle-based consumption metric, the difference in grass standing crop, as grass standing crop in ungrazed minus grass standing crop in grazed. We calculated the herbivory impact consumption metric, percent grass utilization (GU), as:

$$GU (\%) = \left[ \frac{(I - O)}{I} \right] * 100. \quad [1]$$

Where  $I$  was the standing crop of grass in the grazing exclosure (the control) and  $O$  was the standing crop of grass in the grazed sampling area (the treatment). Grass utilization was bound between 0 and 100%

when there was greater standing crop of grass in the grazing enclosure compared to the paired grazed area. However, when standing crop of grass was greater in the grazed area compared to the paired grazing enclosure, negative grass utilization values could be infinite. We scaled negative utilization values, so they were bound between -100 and 0%, by multiplying each negative value by  $(100 \div \text{absolute value of the minimum negative utilization value obtained during our 3 yr study})$ . We maintained all grass consumption values (scaled negative values through unscaled positive values) for our complete data set. We manipulated negative consumption values in the complete data set to create two additional data sets. For our negative values zeroed data set, we set negative consumption values equal to zero (Bork and Werner, 1999). For our negative values deleted data set, we removed negative consumption values from the data set.

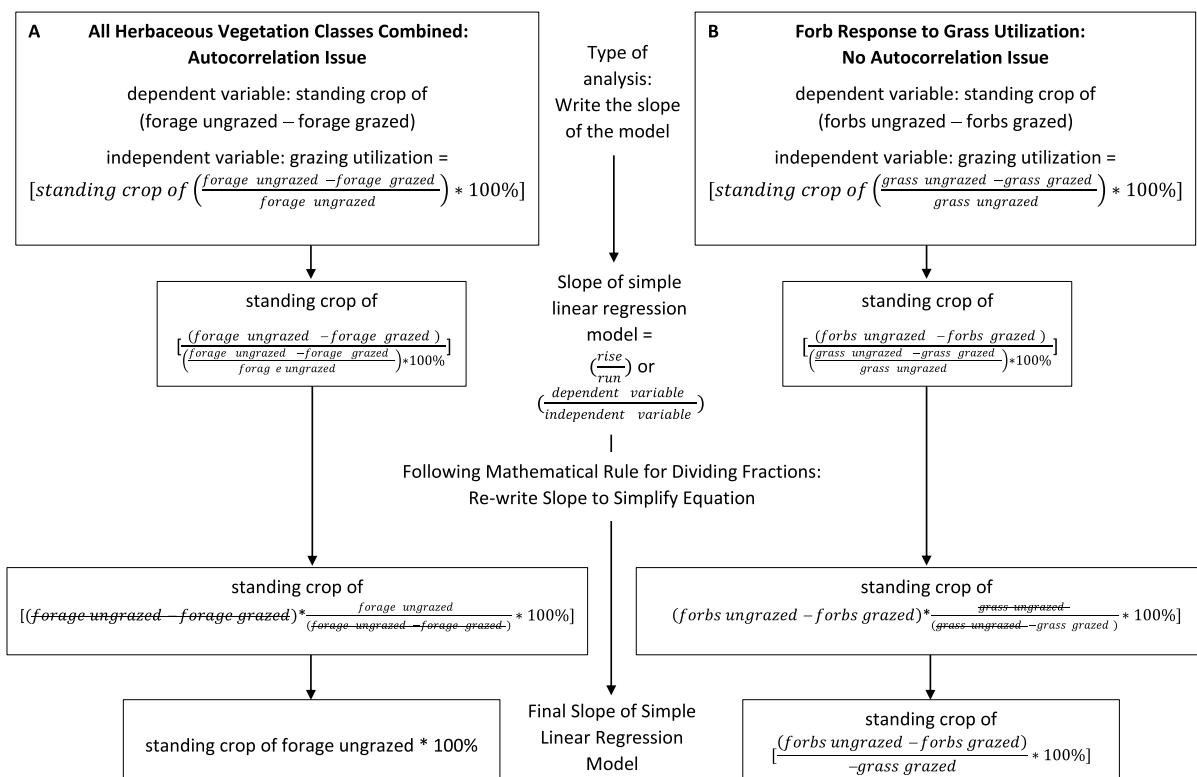
Secondly, we calculated the difference in standing crop of forbs (total, preferred, and non-preferred forbs) in the grazed area (treatment) minus the standing crop of forbs in the ungrazed area (control) for each paired sampling location. We calculated the difference as grazed minus ungrazed because our objective was to investigate the effect of grazing versus a non-grazed area. Our null hypothesis was  $\mu_1 - \mu_2 = 0$ , where  $\mu_1$  = standing crop of forbs in the treatment and  $\mu_2$  = standing crop of forbs in paired control. Hence, any value other than 0 for the difference in the standing crop of forbs indicates a treatment effect on the standing crop of forbs. A positive value indicates forb standing crop increased in the grazed area, while a negative value indicates forb standing crop decreased in the grazed area for each experimental unit pair.

Finally, we devised our standard models to examine if the difference in the standing crop of forbs was related to variation in the difference in grass standing crop and grass utilization. The independent variable in each model was either the difference in grass standing crop or grass utilization. Our dependent variable in each model was the difference in standing crop of forbs between the grazed and ungrazed plots. For each of our data sets (complete, zeroed, and deleted), we ran a separate model

for each of the following dependent variables: (1) total forbs (preferred + non-preferred), (2) preferred deer forbs, and (3) non-preferred deer forbs. To pass normality and homogeneity of variances, the difference in standing crop for each forb category was log transformed. We report back-transformed values in the results. The reported effect size is an approximated percent change in the median difference in forb standing crop ( $e^\beta$  is roughly equal to  $1 + \beta$  for small values) for every unit change of the grass consumption metric.

In our models, we avoided autocorrelation issues that occur when all vegetation classes are combined to calculate percent utilization because we examined the relationship of grass consumption metrics to forb standing crop (Mitchell and Wass, 1996). For example, autocorrelation issues arise when examining the relationship of herbaceous vegetation utilization to forb standing crop and the resulting slope of the model is related to the control (e.g., ungrazed area), not related to the treatment employed (e.g., grazed area; Fig. 2). However, when forage classes are examined separately in a simple linear model of the response of forbs to grass utilization, the final slope of the model is 100% times the difference in the standing crop of forbs in the paired grazed and ungrazed plots relative to the standing crop of grass grazed (Fig. 2). The slope of our models provide insight into the effect size for the treatment – the grazed area.

We determined the influence of grass consumptive metrics on forb standing crop after accounting for the influence of other variables (subsequently listed) that have been documented to affect standing crop of vegetation. In our models we included: (1) year as a random effect, (2) percent sand as our topographic metric for each sampling location as a continuous variable (USDA-NRCS, 2011a; 2011b), (3) distance from each grazing enclosure to nearest water source as a covariate (determined using near analysis tool in ArcMap), (4) autumn (August and September) rainfall received as determined from ranch weather stations as a covariate, and (5) a linear autumn temperature combination variable as a covariate. The 3 individual temperature variables (see



**Fig. 2.** Final slope of simple linear model when examining vegetation standing crop as it relates to percent utilization between paired treatment-control areas: (A) all herbaceous vegetation classes combined - slope is not related to treatment, but rather control (e.g., ungrazed area) and (B) separate forb and grass vegetation classes - slope is related to treatment (e.g., grazed area).

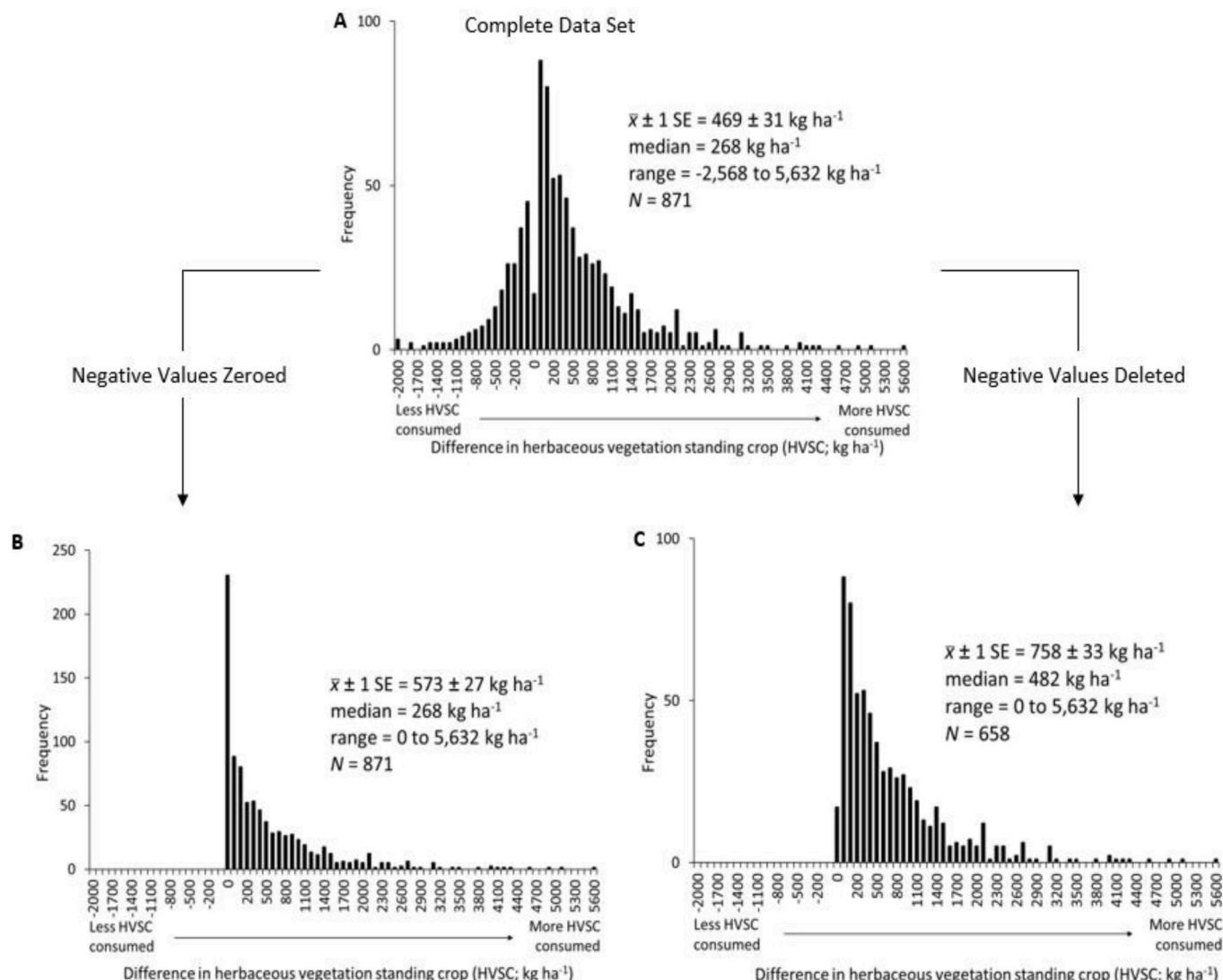
description below) were collinearly related, thus instead, a linear combination variable that retained 78% of variation of the 3 separate temperature variables was included in each model so not to bias model results (Aguilera et al., 2006). The linear temperature combination variable was determined from principle components analysis (Proc Princomp, SAS, version 9.3, SAS Institute, Cary, NC, USA) of 3 individual temperature values: daily (1) minimum and (2) maximum temperature averaged across August–September and (3) average daily temperature during August–September. Additionally, we utilized seasonal weather patterns because they are better predictors of vegetation standing crop than annual weather patterns (Pitt and Heady, 1978). There was no multicollinearity among other predictor variables for each of our models (condition index <19.4; Haque et al., 2002). Finally, we used mixed models because we had both random and fixed effects in our model (Proc Mixed; SAS, 2016).

### 3. Results

#### 3.1. Sampling distribution

##### 3.1.1. Complete data set

Three outliers for the difference in herbaceous vegetation standing crop (e.g., ungrazed minus grazed) were removed from the dataset because they were not representative of most of the data: -5544; 8320; and 17,360 kg ha<sup>-1</sup>. After removal of outliers, the difference in herbaceous standing crop ranged from -2568–5632 kg ha<sup>-1</sup> ( $N = 871$ ). Positive values indicate a higher consumption of herbaceous standing crop in the grazed relative to the ungrazed area. Most values, 74%, were positive and 24% were negative values ( $N = 641$  and 213, respectively). There was no difference in 2% of the paired plots, and most cases (16 of 17 pairs) had no herbaceous vegetation inside or outside of exclosures. The frequency of the difference in herbaceous standing crop (e.g., forb and grass standing crop combined) exhibited a normal sampling distribution, but was slightly positively skewed (Fig. 3A). The most frequent difference in herbaceous standing crop ranged between 1 and 99 kg ha<sup>-1</sup> ( $N = 88$ ), followed by 100–199 kg ha<sup>-1</sup> ( $N = 80$ ). The mean ( $\bar{x} \pm 1 \text{ SE}$ )



**Fig. 3.** Data distribution and sample statistics: mean  $\pm$  standard error ( $\bar{x} \pm 1 \text{ SE}$ ), median, range, for the difference in herbaceous vegetation standing crop for a true paired experimental design in a stochastic semiarid environment. (A) The complete data set, included all negative to positive standing crop values, had a normal distribution. When negative standing crop values were (B) set to equal zero or (C) deleted, the positively skewed data sets over-estimated the central tendency value (s) of forage consumption across south Texas, USA, 2012–2014.

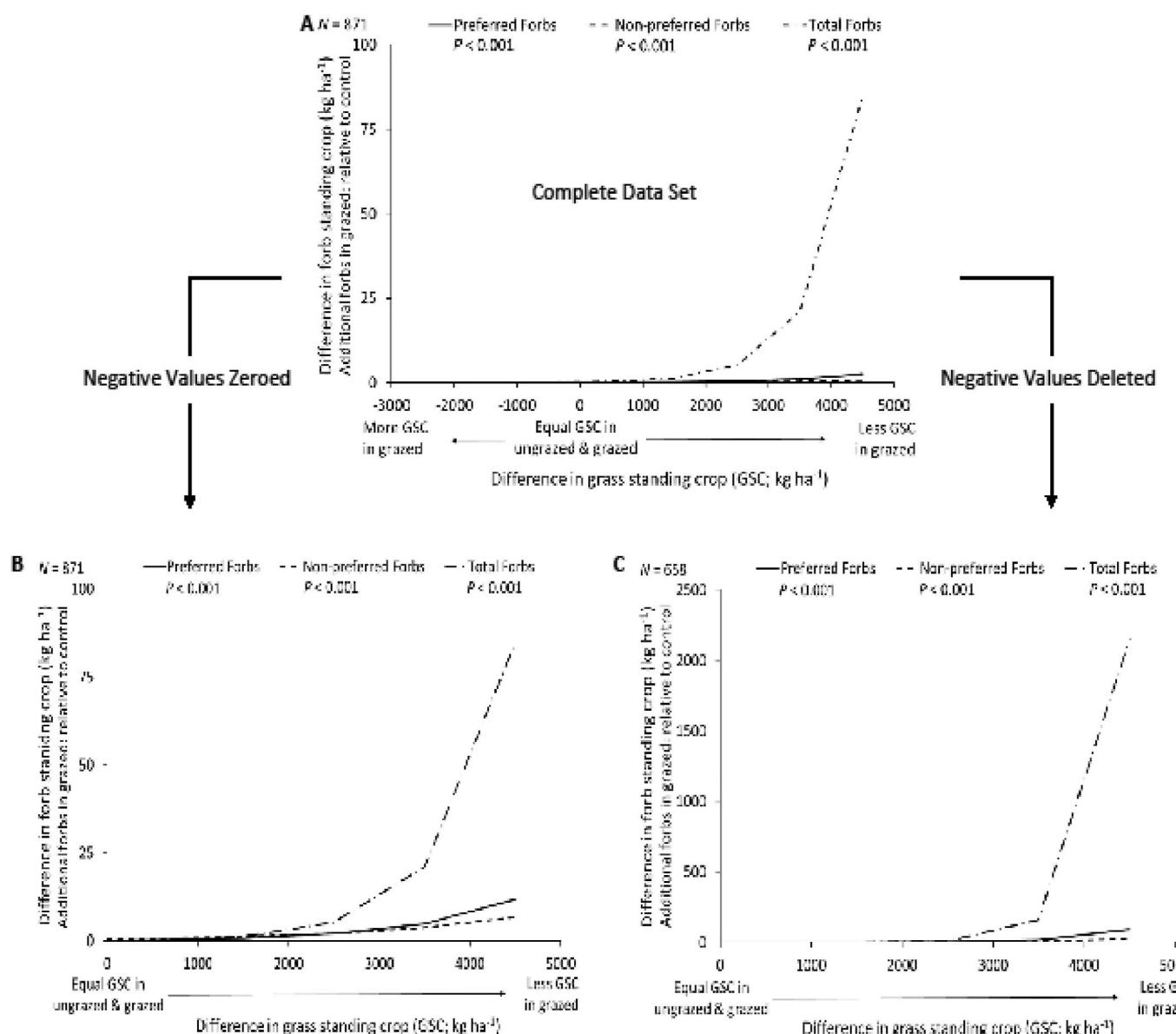
difference in the standing crop of herbaceous vegetation was  $469 \pm 31$  kg ha<sup>-1</sup> with a median value of 268 kg ha<sup>-1</sup>.

### 3.1.2. Negative values zeroed data set

Negative values indicate a lower consumption of standing crop, thus a higher standing crop of herbaceous forage in the grazed relative to the ungrazed area. These negative values were set equal to zero for this data set. The difference in herbaceous standing crop ranged from 0 to 5632 kg ha<sup>-1</sup> ( $N = 871$ ). The frequency of the difference in herbaceous standing crop exhibited a positively skewed sampling distribution (Fig. 3B). The most frequent difference in herbaceous standing crop was 0 kg ha<sup>-1</sup> ( $N = 230$ ). The mean ( $\bar{x} \pm 1\text{SE}$ ) difference in the standing crop of herbaceous vegetation was  $573 \pm 27$  kg ha<sup>-1</sup> with a median value of 268 kg ha<sup>-1</sup>. The median value for the zeroed data set was the same as the complete dataset. However, the mean consumption of herbaceous vegetation was 104 kg ha<sup>-1</sup> higher than the complete data set (Fig. 3A and B).

### 3.1.3. Negative values deleted data set

Negative values for the difference in standing crop of herbaceous vegetation were deleted for this data set. The difference in herbaceous standing crop ranged from 0 to 5632 kg ha<sup>-1</sup> ( $N = 658$ ). This data set had 213 fewer observations compared to the complete and zeroed data sets. The frequency of the difference in herbaceous standing crop exhibited a positively skewed sampling distribution (Fig. 3C). The most frequent difference in herbaceous standing crop was the same as the complete data set; ranged between 1 and 99 kg ha<sup>-1</sup> ( $N = 88$ ), followed by 100–199 kg ha<sup>-1</sup> ( $N = 80$ ). The mean ( $\bar{x} \pm 1\text{SE}$ ) difference in the standing crop of herbaceous vegetation was  $758 \pm 33$  kg ha<sup>-1</sup> with a median value of 482 kg ha<sup>-1</sup>. The median value was 214 kg ha<sup>-1</sup> higher than the complete and zeroed data sets. In addition, the mean consumption of herbaceous vegetation was 185–289 kg ha<sup>-1</sup> higher than the zeroed and complete data sets (Fig. 3).



**Fig. 4.** The standing crop of total forbs (preferred + non-preferred), preferred, and non-preferred deer forbs as it related to the difference in grass standing crop for the (A) complete data set, included all negative to positive difference in grass standing crop values, (B) negative difference in grass standing crop values were set equal to zero data set, and (C) negative difference in grass standing crop values were deleted data set. When negative grass consumption values were manipulated (zeroed or deleted), the models over-estimated the additional standing crop of forbs in the grazed area (relative to forb standing crop in control) that resulted from the treatment across south Texas, USA, 2012–2014.

### 3.2. Herbivore-based models – standing crop

#### 3.2.1. Complete data set

There were 871 observations in the complete data set. The difference in grass standing crop displayed a similar pattern as the difference in herbaceous vegetation (forbs + grass) standing crop. The difference in grass standing crop was negative for 204 paired plots ( $N = 204$ ). Thus, 24% of paired plots had a higher standing crop of grasses the grazed plot compared to the non-grazed paired plot. There was no difference in grass standing crop in 7% of paired plots, and most cases (55 of 65 pairs) had no grass inside or outside the exclosure. Most paired plots, 69%, had positive values for the difference in grass standing crop ( $N = 603$ ). The difference in standing crop of total forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,863} = 41.12$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of total forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00139)} = 1.00139\%$ ; Fig. 4). This model predicted an increase in total forbs of 84.9 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed (Fig. 4A).

The difference in standing crop of preferred forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,863} = 20.46$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of preferred forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00089)} = 1.00009\%$ ; Fig. 4). This model predicted an increase in preferred forbs of 2.6 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed (Fig. 4A).

The difference in standing crop of non-preferred forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,863} = 11.06$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of non-preferred forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00058)} = 1.00058\%$ ; Fig. 4). This model predicted an increase in non-preferred forbs of 0.7 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed (Fig. 4A).

#### 3.2.2. Negative values zeroed data set

Negative values for the difference in grass standing crop were set equal to zero for this data set. The sample size was the same as the complete data set ( $N = 871$ ).

The difference in standing crop of total forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,863} = 41.12$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of total forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00139)} = 1.00139\%$ ; Fig. 4). This model predicted an increase in total forbs of 84.9 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed (Fig. 4B). These results are the same for effect size and prediction as the complete data set model for the difference in total forbs.

The difference in standing crop of preferred forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,863} = 20.46$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of preferred forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00089)} = 1.00009\%$ ; Fig. 4). This was the same effect size as the complete data set model for the difference in preferred forbs. However, this model predicted an increase in preferred forbs of 11.8 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed; a 9.2 kg ha<sup>-1</sup> greater increase in preferred forbs compared to the complete data set model (Fig. 4B).

The difference in standing crop of non-preferred forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,863} = 11.06$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of non-preferred forbs in the grazed area relative to the ungrazed

area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00058)} = 1.00058\%$ ; Fig. 4B). This was the same effect size as the complete data set model for the difference in non-preferred forbs. However, this model predicted an increase in non-preferred forbs of 6.7 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed; a 6.0 kg ha<sup>-1</sup> greater increase in non-preferred forbs compared to the complete data set model (Fig. 4B).

#### 3.2.3. Negative values deleted data set

Negative values for the difference in grass standing crop were deleted for this data set. There were 658 observations in this data set, 213 fewer observations compared to the complete and zeroed data sets.

The difference in standing crop of total forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,650} = 169.20$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of total forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00261)} = 1.00261\%$ ; Fig. 4C). This was the same relationship prediction, but slightly larger (0.00122%) effect size when compared to the complete data set and zeroed data set models. However, this model predicted an increase in total forbs of 2149.8 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed; a 2064.9 kg ha<sup>-1</sup> greater increase in total forbs compared to the complete data set and zeroed data set models (Fig. 4C).

The difference in standing crop of preferred forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,650} = 61.27$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of preferred forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00159)} = 1.00159\%$ ; Fig. 4C). This was the same relationship prediction, but slightly larger (0.00070%) effect size when compared to the complete data set and zeroed data set models. However, this model predicted an increase in preferred forbs of 91.0 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed; 88.4 kg ha<sup>-1</sup> greater increase in preferred forbs compared to the complete data set model prediction and 79.2 kg ha<sup>-1</sup> greater increase compared to the zeroed data set model (Fig. 4C).

The difference in standing crop of non-preferred forbs was positively related to grass standing crop consumed (ungrazed grass standing crop – grazed grass standing crop;  $F_{1,650} = 33.01$ ;  $P < 0.001$ ); for every 1 kg ha<sup>-1</sup> increase in grass consumed, there was a 1% increase in standing crop of non-preferred forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}$ :  $\exp^{(0.00159)} = 1.00159\%$ ; Fig. 4C). This was the same relationship prediction, but slightly larger (0.00101%) effect size when compared to the complete data set and zeroed data set models. However, this model predicted an increase in non-preferred forbs of 24.2 kg ha<sup>-1</sup> when 4500 kg ha<sup>-1</sup> of grass was consumed; a 23.5 kg ha<sup>-1</sup> greater increase in non-preferred forbs compared to the complete data set model and 17.5 kg ha<sup>-1</sup> greater increase compared to the zeroed data set model (Fig. 4C).

### 3.3. Herbivore impact on vegetation models – utilization

#### 3.3.1. Complete data set

There were 792 observations in the complete data set. This was 79 fewer observations compared to the complete data set when the independent variable was the difference in grass standing crop. These 79 observations were removed from the grass utilization complete data set because there was 0 kg ha<sup>-1</sup> of grass standing crop in the ungrazed area – you cannot divide by zero to calculate grass utilization. Mostly, this reduced the frequency of negative values and values of no difference between paired plots in the dataset. The difference in grass standing crop was negative for 177 paired plots. Thus, 22% of the paired plots had more grass standing crop in the grazed compared to the non-grazed plot. Few paired plots had no difference in grass standing crop inside and outside exclosures ( $N = 10$ ). Most, 76%, of paired plots had more grass standing crop in the non-grazed compared to the grazed plot ( $N = 603$ ).

The difference in standing crop of total forbs was positively related to

grass utilization ( $F_{1,784} = 15.30; P < 0.001$ ); for every 1% increase in grass utilization, there was a 1% increase in standing crop of total forbs in the grazed area relative to the ungrazed area (Fig. 5A). This model predicted an increase in total forbs of  $0.6 \text{ kg ha}^{-1}$  when 100% grass was consumed (Fig. 5A).

The difference in standing crop of preferred forbs was positively related to grass utilization ( $F_{1,784} = 10.14; P = 0.001$ ); for every 1% increase in grass utilization, there was a 1% increase in standing crop of preferred forbs in the grazed area relative to the ungrazed area (Fig. 5A). This model predicted an increase in preferred forbs of  $0.6 \text{ kg ha}^{-1}$  when 100% grass was consumed (Fig. 5A).

The difference in standing crop of non-preferred forbs was not related to grass utilization ( $F_{1,784} = 1.23; P = 0.269$ ; Fig. 5A).

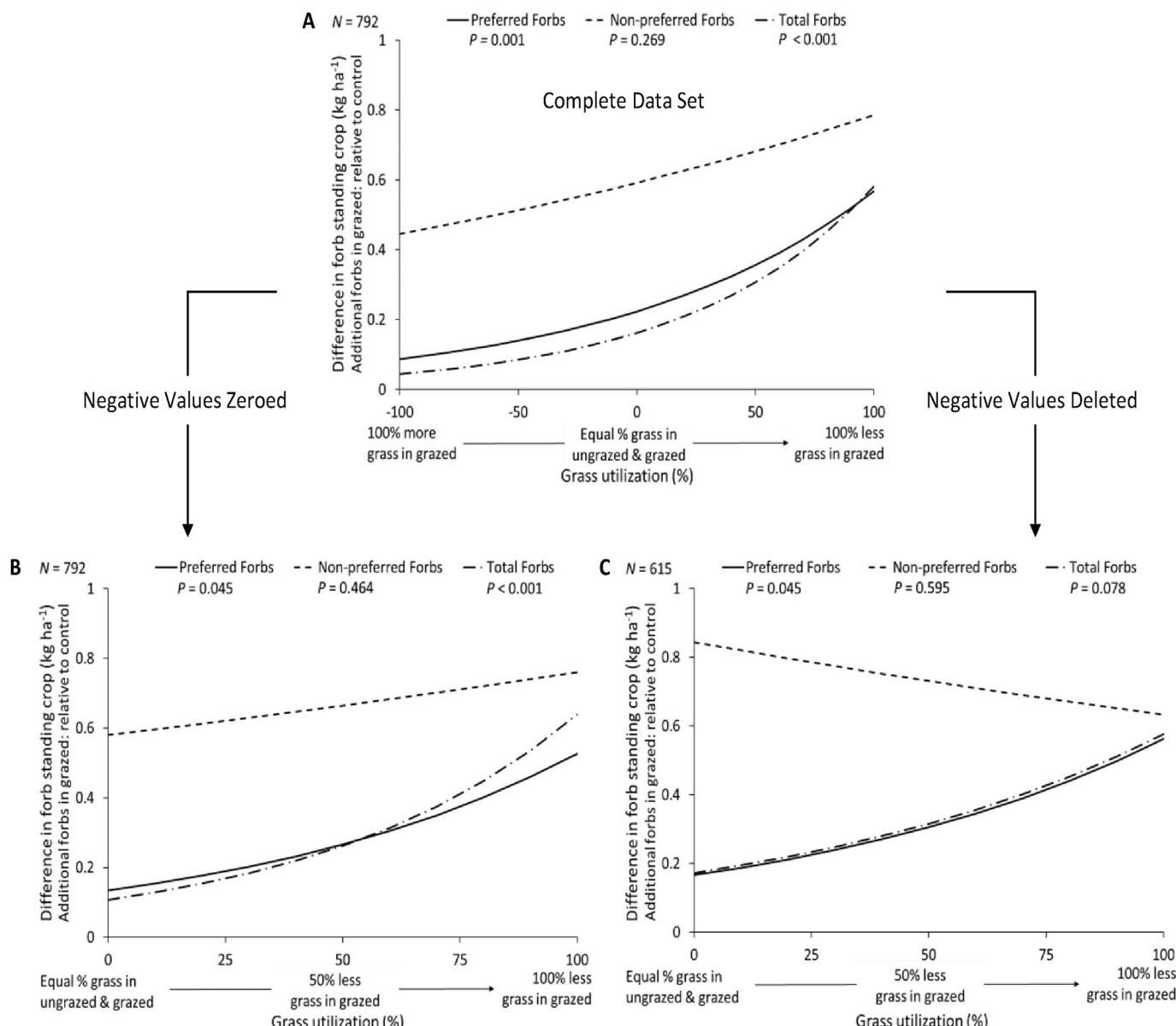
### 3.3.2. Negative values zeroed data set

Negative values for grass utilization were set equal to zero for this data set. The sample size was the same as the complete data set ( $N = 792$ )

792).

The difference in standing crop of total forbs was positively related to grass utilization ( $F_{1,784} = 14.34; P < 0.001$ ); for every 1% increase in grass utilization, there was a 1% increase in standing crop of total forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}: \exp^{(0.01781)} = 1.01797\%$ ; Fig. 5B). This model also predicted an increase in total forbs of  $0.6 \text{ kg ha}^{-1}$  when 100% grass is consumed (Fig. 5B). This was the same relationship and prediction as the complete data set model.

The difference in standing crop of preferred forbs was positively related to grass utilization ( $F_{1,784} = 10.51; P = 0.001$ ); for every 1% increase in grass utilization, there was a 1% increase in standing crop of preferred forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}: \exp^{(0.01368)} = 1.01377\%$ ; Fig. 5B). This was the same relationship prediction as the complete data set model. However, this model predicted an increase in preferred forbs of  $0.5 \text{ kg ha}^{-1}$  when 100% grass was consumed (Fig. 5B);  $0.1 \text{ kg ha}^{-1}$  lower standing crop of forbs



**Fig. 5.** The standing crop of total forbs (preferred + non-preferred), preferred, and non-preferred deer forbs as it related to percent grass utilization for the (A) complete data set, included all negative to positive grass utilization values, (B) grass utilization negative values were set equal to zero data set, and (C) grass utilization negative values were deleted data set. Mostly, the final interpretation of all model predictions for the additional standing crop of forbs (relative to forb standing crop in control) that resulted from the treatment was similar across all data sets across south Texas, USA, 2012–2014.

compared to the complete data set model.

The difference in standing crop of non-preferred forbs was not related to grass utilization ( $F_{1,784} = 0.54; P = 0.464$ ; Fig. 5B). This was the same relationship prediction as the complete data set model.

### 3.3.3. Negative values deleted data set

Negative values for grass utilization were deleted for this data set. There were 615 observations in this data set, 177 fewer observations compared to the complete and negative values zeroed data sets.

The difference in standing crop of total forbs had a weak, but positive relationship to grass utilization ( $F_{1,607} = 3.13; P = 0.078$ ); for every 1% increase in grass utilization, there was a 1% increase in standing crop of total forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}: \exp(0.01207) = 1.01214\%$ ; Fig. 5C). This model also predicted an increase in total forbs of  $0.6 \text{ kg ha}^{-1}$  when 100% grass is consumed (Fig. 5C). While the relationship was statistically weaker, the overall prediction was the same as the complete and zeroed grass utilization data set models.

The difference in standing crop of preferred forbs was positively related to grass utilization ( $F_{1,607} = 4.03; P = 0.045$ ); for every 1% increase in grass utilization, there was a 1% increase in standing crop of preferred forbs in the grazed area relative to the ungrazed area ( $B_{\text{grass utilization}}: \exp(0.01222) = 1.01229\%$ ; Fig. 5C). This was the same, but statistically weaker relationship than predicted with the complete and zeroed grass utilization data set models. This model also predicted an increase in preferred forbs of  $0.6 \text{ kg ha}^{-1}$  when 100% grass was consumed (Fig. 5C); the same prediction as the complete grass utilization data set model, but  $0.1 \text{ kg ha}^{-1}$  more forbs compared to the zeroed data set model.

The difference in standing crop of non-preferred forbs was not related to grass utilization ( $F_{1,607} = 0.28; P = 0.595$ ; Fig. 5C). This was the same relationship prediction as the complete and zeroed grass utilization data set models.

## 4. Discussion

Contrary to most data analyses conducted in our field, we retained negative consumptive values and compared retention to analyses in which the negative consumptive values were manipulated by zeroing or deleting values (Vermeire et al., 2018). We engaged in this data analyses because of inherent system randomness, even when treatments such as grazing are added to the system (Bork and Werner 1999). To elucidate, in an ungrazed system, differences between protected and unprotected plots would approximate a bell-shaped curve. Thus, when calculating the difference in standing crop vegetation between paired grazed and ungrazed plots, statistical theory dictates there is one-third probability the difference could result in negative, neutral, or positive values. In theory, grazing simply shifts the curve to the right, or more positive. However, some portion of the curve remains to the left of center, or negative. This was established in this study. Across datasets, most of our calculated grass consumptive values were positive, 69–76%. Meaning grazing shifted the curve to the more positive end due to the consumption of grasses in the grazed plots. However, some of our sampling distribution, 24%, remained to the left of center and resulted in negative grass consumptive values. When these negative values are set to zero, there is an overestimation of forage use (Bork and Werner, 1999). Indeed, we determined manipulation of negative consumptive values does affect the interpretation of the data (Table 1). First, when negative consumptive values are zeroed or deleted, the sampling distribution is skewed. Second, when negative consumptive values are zeroed or deleted from the data set, the treatment effect is almost always overestimated. Third, when negative consumptive values are deleted from the data set, the treatment effect is statistically weaker (e.g., smaller F-values and larger P-values).

**Table 1**

Summary comparison of the effect on sampling distribution and interpretation of model results when negative consumptive herbaceous vegetation values are manipulated in a real data set collected across south Texas, USA, 2012–2014. The non-manipulated (complete) and manipulated (zeroed or deleted) negative consumptive values were the explanatory variable in the model calculated as the difference in grass standing crop in the ungrazed minus grazed paired plot. Preferred forbs are selected for by deer; nonpreferred forbs are rarely selected for by deer; total forbs are preferred + nonpreferred forbs. When negative consumptive values were zeroed or deleted, the data distribution was positively skewed and there was almost always an overestimate of the grazing effect of grass removal on forb standing crop. When negative consumptive values were deleted, the relationship was statistically weaker (e.g., smaller F-values and larger P-values).

	Complete data set	Negative values zeroed data set	Negative values deleted data set
Frequency of sampling distribution	normal, slightly positively skewed	positively skewed	positively skewed
Herbivore impact on forb standing crop model predictions:			
+ or – change in forb standing crop when 4500 kg ha <sup>-1</sup> grass is consumed; F-stat; and P-value			
Total Forbs	+84.9 kg ha <sup>-1</sup> ; $F_{1,863} = 41.12; P < 0.001$	+84.9 kg ha <sup>-1</sup> ; $F_{1,863} = 41.12; P < 0.001$	+2149.8 kg ha <sup>-1</sup> ; $F_{1,650} = 169.20; P < 0.001$
Preferred Forbs	+2.6 kg ha <sup>-1</sup> ; $F_{1,863} = 20.46; P < 0.001$	+11.8 kg ha <sup>-1</sup> ; $F_{1,863} = 20.46; P < 0.001$	+91.0 kg ha <sup>-1</sup> ; $F_{1,650} = 61.27; P < 0.001$
Nonpreferred Forbs	+0.7 kg ha <sup>-1</sup> ; $F_{1,863} = 11.06; P < 0.001$	+6.7 kg ha <sup>-1</sup> ; $F_{1,863} = 11.06; P < 0.001$	+24.2 kg ha <sup>-1</sup> ; $F_{1,650} = 33.01; P < 0.001$
Herbivore impact on vegetation models – utilization model predictions:			
+ or – change in forb standing crop when 100% of grass is consumed; F-stat; and P-value			
Total Forbs	+0.6 kg ha <sup>-1</sup> ; $F_{1,784} = 15.30; P < 0.001$	+0.6 kg ha <sup>-1</sup> ; $F_{1,784} = 14.34; P < 0.001$	+0.6 kg ha <sup>-1</sup> ; $F_{1,607} = 3.13; P = 0.078$
Preferred Forbs	+0.6 kg ha <sup>-1</sup> ; $F_{1,784} = 10.14; P = 0.001$	+0.5 kg ha <sup>-1</sup> ; $F_{1,784} = 10.51; P = 0.001$	+0.6 kg ha <sup>-1</sup> ; $F_{1,607} = 4.03; P = 0.045$
Nonpreferred Forbs	<sup>a</sup> NR; $F_{1,784} = 1.23; P = 0.269$	<sup>a</sup> NR; $F_{1,784} = 0.54; P = 0.464$	<sup>a</sup> NR; $F_{1,607} = 0.28; P = 0.595$

<sup>a</sup> NR is no statistical relationship; thus, no prediction of forb standing crop at 100% grass removal.

### 4.1. Sampling distribution

When negative consumptive values were set to zero or deleted from the data set, the sampling distribution was skewed (Table 1). However, the complete data set that included the scaled negative consumptive values exhibited a normal sampling distribution. This is contrary to the findings of Bork and Werner (1999). They established that the data set for a paired-subplot sampling method in stochastic environments would not follow a normal sampling distribution. Bork and Werner (1999) attributed a skewed sampling distribution to the paired-subplot sampling method and the stochastic nature of plant communities in a heterogeneous environment. In the paired-subplot method referenced by Bork and Werner (1999), first, the grazed and ungrazed subplots are randomly chosen. Next, the data are averaged across grazed sampling subplots and averaged across ungrazed sampling subplots. Finally, the averaged grazed and averaged ungrazed subplots are paired. The pairing of the sampling plots occurs last – after the initial statistical manipulation of the data. Additionally, averaging data across subplots in stochastic environments does not reduce heterogeneity associated with the data set (Bork and Werner 1999). In heterogeneous plant communities, randomly chosen ‘paired’ plots are not analogous to a true paired study design because plant communities are highly variable. Yet, data set heterogeneity can be reduced in stochastic environments by pairing plots first, in the field. First, locate and cage the randomly allocated

ungrazed sampling area. Then, seek out and mark a biologically paired, grazed sampling location. Select paired grazed and ungrazed plots based on visually judging the similarity of the biotic (i.e., species and percent cover of plants present) and abiotic factors (i.e., percent soil, sunlight intensity). This biological pairing reduced heterogeneity, as evident by a more normally distributed sampling distribution in our complete dataset.

Our results did align with some of [Bork and Werner's \(1999\)](#) conclusions. We also established that forage consumption is over-estimated when negative consumption values are manipulated (e.g., difference in herbaceous vegetation standing crop and percent utilization). Manipulation of negative consumption values in a data set positively skews the sampling distribution. Positive skewing of the distribution results in over-estimation of mean vegetation consumption metrics. [Bork and Werner \(1999\)](#) advised against zeroing negative values. However, our analysis revealed that deleting all negative consumption values from the data set has a greater over-estimation impact compared to when negative values are zeroed. For example, there was a 1.6x greater mean estimate of herbaceous vegetation consumed when negative values were deleted, but only a 1.2x greater mean consumption when negative values were zeroed. Furthermore, only the mean value was positively skewed when negative values were zeroed; the median value did not change. However, when negative values were deleted, both the mean and median values were positively skewed resulting in a higher over-estimate of herbaceous vegetation consumed.

#### 4.2. Manipulation of negative values and model predictions

When negative consumptive values are manipulated, it affects the interpretation of the model parameters ([Table 1](#)). Model estimates of the treatment effect were over-estimated when negative consumptive values are manipulated. We determined that deleting negative consumptive values further exacerbated the over-estimation of the treatment effect compared to when negative consumptive values were zeroed. For example, when negative values were deleted, the models predicted a 35x greater increase in forb standing crop (preferred and non-preferred forbs) compared to the complete data set models when  $4500 \text{ kg ha}^{-1}$  of grass is consumed. When negative values were zeroed, the models did have a greater estimate of the standing crop of forbs (3.6–7.7x greater increase in the standing crop of non-preferred and preferred forbs, respectively) compared to the complete data set when  $4500 \text{ kg ha}^{-1}$  of grass is consumed. However, the over-estimate of the treatment ensuing forb standing crop was much lower when negative consumption values were zeroed compared to when they were deleted. Our results agreed with findings of [Bork and Werner \(1999\)](#), the treatment effect was overestimated when we examined the consumptive metric as herbaceous standing crop.

While our models agreed with their findings for the difference in standing crop, we did not come to the same conclusion when we examined percent utilization as the consumption metric. [Bork and Werner \(1999\)](#) employed a paired-subplot experimental design while we employed a true paired experimental design. Across our models, regardless of the data set (complete, zeroed, deleted), our model estimates of the treatment effect were mostly similar when we examined percent grass utilization ([Table 1](#)). The estimated effect of 100% grass utilization was a small increase ( $0.5\text{--}0.8 \text{ kg ha}^{-1}$ ) in forb standing crop. However, the statistical power of the relationship was affected by manipulating negative consumptive values. When negative grass utilization values were deleted, there was a weaker statistical relationship between grass utilization and forb standing crop. Additionally, the relationship was opposite between non-preferred forb standing crop and grass utilization when negative consumptive values were deleted. However, we did find non-significant relationships between non-preferred forbs and grass utilization across all models, all datasets.

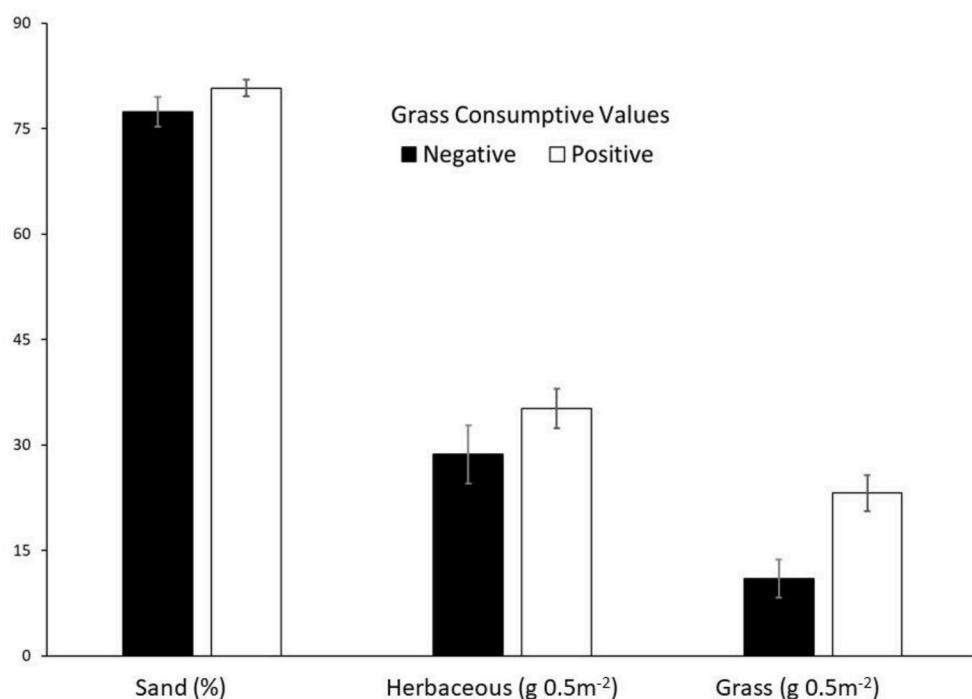
#### 4.3. Conclusion and implications

There are principles that support the probability of observing negative consumptive values, or a higher standing crop of grass in the grazed compared to its paired ungrazed plot. The first has been discussed at length in the literature. The grazing optimization hypothesis elucidates plants compensate through growth when grazed and at higher growth rates than ungrazed plants ([Li et al., 2021](#); [Mipam et al., 2019](#); [Hilbert et al., 1981](#)). However, it was [Briske \(1993\)](#) that provided the best summarized potential for compensatory growth as it related to our study sites. The grazing optimization hypothesis was most supported when: (1) the density of herbivores in the system was not directly controlled by humans, (2) grazing occurred over expansive areas, and (3) there was an increase in the interval between consecutive grazing events ([Briske, 1993](#)). While we did not directly observe this (e.g., we did not have GPS collared cattle or cameras at each paired plot), this description matches the grazing management system in our study. Thus, the observation of negative grass consumptive values could be due to compensatory growth. However, it may not be fully attributed to biological explanations. We further investigated the biology of this phenomenon.

We conducted simple t-tests to determine if any of the biological parameters we recorded during our study provided insight into the occurrence of negative compared to positive grass consumptive values. We did not include neutral values in this exploratory analysis because most neutral values were due to the absence of vegetation in both paired plots. We discovered mean annual rainfall and distance of paired plots to the nearest accessible water source were not factors ( $P \geq 0.488$ ). Soil texture, the percentage of sand, was an influencing factor ( $P = 0.007$ ). However, it was not biologically significant. The mean difference in percent sand was less than 3.4% between the occurrence of positive and negative grass consumptive values ([Fig. 6](#)). However, annual productivity, as determined by herbaceous vegetation in the protected, ungrazed plot, did influence the occurrence of negative and positive consumptive values ( $P \leq 0.011$ ). This was mostly driven by the productivity of grasses ( $P < 0.001$ ; [Fig. 6](#)). Cattle selectively graze across the landscape and avoid areas of low productivity ([Fulbright et al., 2021](#)). Thus, biologically, these areas may be a measure of the ungrazed portion of the system. As such, statistical theory predicts that a small portion of the sampling distribution will remain left of center, and thus negative, due to inherent system randomness. This is supported by our data.

In our study, most paired plots, 69–76%, had positive consumptive values and were in areas with higher grass productivity. This supports cattle grazing in areas of higher grass productivity which resulted in positive consumptive values. Most paired plots that had a neutral grazing effect were due to the absence of vegetation. However, some paired plots, 24%, had negative consumptive values and were in areas of lower grass productivity. This supports the probability that cattle did not graze in these areas and the resulting negative consumptive values were most likely attributed to system randomness and supported by statistical theory. Thus, the occurrence of negative consumptive values could also be attributed to biological and statistical theory. Regardless of the underlying cause for observing negative consumptive values in paired plot designed grazing studies, deleting or zeroing these negative values can result in management decisions that are not representative of the entire grazing system, especially in semiarid areas with expansive grazing management practices.

Deleting negative vegetation consumption values from the data set over-estimates vegetation metrics (i.e., vegetation standing crop resulting from treatment employed). Deleting negative consumption values has a more profound over-estimation effect compared to zeroing negative values. Over-estimation of vegetation metrics resulting from the treatment is more prevalent when the independent variable is the difference in standing crop. Therefore, managers and researchers relying on models with manipulated negative consumption values would predict that cattle grazing grasses resulted in a higher standing crop of forbs across the landscape. This overestimation of the treatment effect could



**Fig. 6.** Biological factors that influenced ( $P \leq 0.011$ ) if grass consumptive values, the difference between paired grazed and ungrazed plots, were negative (e.g., more grass in the grazed area) or positive (e.g., more grass in the ungrazed area). Mean values  $\pm 95\%$  CI are displayed for the occurrence of negative or positive grass consumptive values as it related to: (1) soil texture determined as percentage of sand, (2) annual production of herbaceous forbs and grasses (e.g., herbaceous), and (3) annual production of grasses. Annual production was measured as standing crop of vegetation in the protected, ungrazed plot. Positive grass consumptive values were observed in most paired plots, 76%. Negative grass consumptive values were observed in 24% of paired plots and appear to be most influenced, and thus, most likely occurred in areas where annual grass production was low.

result in higher yield management decisions, such as increased cattle stocking rate or increased deer harvest, that may stress the system.

Our analyses revealed similar results between non-manipulated and manipulated negative consumptive values datasets when investigating percent utilization. However, the effect of percent vegetation utilization was statistically weaker when negative values were manipulated. Manipulation of negative consumptive values could result in analyses that return an interpretation of a weak or even no treatment effect, especially for smaller datasets (e.g., less than 900 paired plots). This could lead researchers or managers to conclude cattle utilization of vegetation in a stochastic environment does not affect vegetation standing crop. In other words, that coupling between herbivores and vegetation dynamics is weak in stochastic environments (Von Wehrden et al., 2012; Ellis and Swift, 1988).

Employing a true paired experimental design reduces the occurrence of over-estimating treatment effects. Therefore, we recommend employing a biologically paired experimental design and the inclusion of all negative vegetation consumption values so that: (1) resulting models represent a normally distributed population, (2) standing crop of vegetation resulting from the treatment is not over-estimated and (3) any grazer treatment effect in heterogeneous environments is recognized if existent.

However, these mathematical calculations are not always biologically intuitive and must be explained. For example, if the vegetation metric is calculated as treatment (i.e., grazed, prescribed burn, etc.) minus the control (i.e., ungrazed, unburned, etc.), then relative to the control: (1) a negative value indicates vegetation standing crop decreased as a result of the treatment, (2) zero indicates no change in vegetation standing crop as a result of the treatment, and (3) a positive value indicates vegetation standing crop increased as a result of the treatment. To increase biological understanding, explain the calculations with biological definitions in all figures and in pertinent locations within the text. Ensuing, this will ensure researchers effectively convey biologically understandable, yet conservative results to better guide management decisions.

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## CRediT authorship contribution statement

**Stacy L. Hines:** Conceptualization; Formal analysis; Investigation; Methodology; Project administration; Validation; Visualization; Writing – original draft, Writing – review & editing. **Timothy E. Fulbright:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Alfonso Ortega Santos:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **David B. Wester:** Formal analysis, Methodology, Validation. **David G. Hewitt:** Writing – review & editing. **Thomas W. Boutton:** Writing – review & editing. **Tyler Campbell:** Writing – review & editing

## 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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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2021.104698>.

## References

- Aguilera, A.M., Escabias, M., Valderrama, M.J., 2006. Using principal components for estimating logistic regression with high-dimensional multicollinear data. *Comput. Stat. Data Anal.* 50, 1905–1924.
- Andrew, M.H., 1988. Grazing impact in relation to livestock watering points. *Trees (Berl.)* 3, 336–339.
- Bork, E.W., Werner, S.J., 1999. Viewpoint: implications of spatial variability for estimating forage use. *J. Range Manag.* 52, 151–156. <https://doi.org/10.2307/4003509>.
- Briske, D.D., 1993. Grazing optimization: a plea for balanced perspective. *Ecol. Appl.* 3, 24–26.
- Chambers, J.C., Brown, R.W., 1983. Methods for Vegetation Sampling and Analysis on Revegetated Mined Lands. Forest Service, Ogden, Utah. GTR-INT-151. US Department of Agriculture.
- DeYoung, C.A., Fulbright, T.E., Hewitt, D.G., Wester, D.B., Draeger, D.A., 2019. Linking white-tailed deer density, nutrition, and vegetation in a stochastic environment. *Wildl. Monogr.* 202, 1–63.
- Diamond, D.D., Fulbright, T.E., 1990. Contemporary plant communities of upland grasslands of the coastal sand plain, Texas. *Southwest Nat.* 35, 385–392.
- Ellis, J.E., Swift, D.M., 1988. Stability of African pastoral ecosystems: alternate paradigms and applications for development. *J. Range Manag.* 41, 450–459.
- Evans, C.C., 1986. The Relationship of Cattle Grazing to Sage-Grouse Use of Meadow Habitat on the Sheldon National Wildlife Refuge [MS Thesis]. University of Nevada, Reno, Nevada, USA.
- Forman, S.L., Nordt, L., Gomez, J., Pierson, J., 2009. Late Holocene dune migration on the south Texas sand sheet. *Geomorphology* 108, 159–170.
- Fulbright, T.E., Drabek, D.J., Ortega-S, J.A., Hines, S.L., Saenz III, R., Campbell, T.A., Hewitt, D.G., Wester, D.B., 2021. Forb standing crop response to grazing and precipitation. *Rangel. Ecol. Manag.* 79, 175–185.
- Fulbright, T.E., Ortega-S, J.A., 2013. White-tailed Deer Habitat: Ecology and Management on Rangelands, second ed. Texas A&M University Press, College Station, Texas.
- Fulbright, T.E., Ortega-S, J.A., Rasmussen, A., Redeker, E.J., 2008. Applying ecological theory to habitat management: the altering effect of climate. In: Fulbright, T.E., Hewitt, D.G. (Eds.), *Wildlife Science: Linking Ecological Theory to Management Applications*. CRC Press, Boca Raton, Florida.
- Fulbright, T.E., 2001. Human-induced vegetation changes in the Tamaulipan semiarid scrub. In: Webster, G.L., Bahre, C.J. (Eds.), *Changing Plant Life of La Frontera*. University of New Mexico Press, New Mexico.
- Fulbright, T.E., Diamond, D.D., Rappole, J., Norwine, J., 1990. The coastal sand plain of southern Texas. *Rangelands* 12, 337–340.
- Georgiadis, N.J., Ruess, R.W., McNaughton, S.J., Western, D., 1989. Ecological conditions that determine when grazing stimulates grass production. *Oecologia* 81, 316–322.
- Haque, A., Jawad, A.F., Cnaan, A., Shabbout, M., 2002. Detecting multicollinearity in logistic regression models: an extension of BKW diagnostic. In: Proceeding of the 2002 Joint Statistical Meeting, pp. 11–15. August 2002; New York.
- Hilbert, D.W., Swift, D.M., Detling, J.K., Dyer, M.I., 1981. Relative growth rates and the grazing optimization hypothesis. *Oecologia* 51, 14–18.
- Hines, S.L., 2016. Cattle, Deer, and Nilgai Interactions [PhD Dissertation]. Texas A&M University-Kingsville, Kingsville, Texas, USA.
- Holechek, J.L., 1991. Chihuahuan desert rangeland, livestock grazing, and sustainability. *Rangelands* 13, 115–120.
- Jones, A., 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. *West. N. Am. Naturalist* 60, 155–164.
- Koppel, J., Van De, Rietkerk, M., Langevelde, F., Van, Kumar, L., Klausmeier, C.A., Fryxell, J.M., Hearne, J.W., Andel, J., Van, Ridder, N., De, Skidmore, A., Stroosnijder, L., Prins, H.H.T., 2002. Spatial Heterogeneity and Irreversible Vegetation Change in Semiarid Grazing Systems, vol. 159.
- Krausman, P.R., Naugle, D.E., Frisina, M.R., Northrup, R., Bleich, V.C., Block, W.M., Wallace, M.C., Wright, J.D., 2009. Livestock grazing, wildlife habitat, and rangeland values. *Rangelands* 31, 15–19.
- Landsberg, J., James, C.D., Morton, S.R., Müller, W.J., Stol, J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. *J. Appl. Ecol.* 40, 1008–1024.
- Landsberg, J., Lavorel, S., Stol, J., 1999. Grazing response groups among understorey plants in arid rangelands. *J. Veg. Sci.* 10, 683–696.
- Li, W., Hooper, D.U., Wu, L., Bakker, J.D., Gianuca, A.T., Wu, X.B., Taube, F., Wang, C., Bai, Y., 2021. Grazing regime alters plant community structure via patch-scale diversity in semiarid grasslands. *Ecosphere* 12, e03547. <https://doi.org/10.1002/ecs2.3547>.
- Loft, E.R., Menke, J.W., Kie, J.G., Bertram, R.C., 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. *J. Wildl. Manag.* 51, 655–664.
- Mipam, T., Zhong, L., Liu, J., Miehe, G., Tian, L., 2019. Productive overcompensation of alpine meadows in response to yak grazing in the eastern Qinghai-Tibet plateau. *Front. Plant Sci.* 10 <https://doi.org/10.3389/fpls.2019.00925> article 925.
- Mitchell, S.F., Wass, R.T., 1996. Quantifying herbivory: grazing consumption and interaction strength. *Oikos* 76, 573–576.
- Ortega, I.M., Soltero-Gardea, S., Bryant, F.C., Drawe, L., 1997. Evaluating grazing strategies for cattle: deer forage dynamics. *J. Range Manag.* 50, 615–621.
- Pitt, M.D., Heady, H.F., 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. *Ecology* 59, 336–350.
- Powell, J., Martin, B., Dreitz, V.J., Allred, B.W., 2018. Grazing preferences and vegetation feedbacks of the fire-grazing interaction in the northern great Plains. *Rangel. Ecol. Manag.* 71, 45–52. <https://doi.org/10.1016/j.rama.2017.09.003>.
- Pringle, H.J.R., Landsberg, J., 2004. Predicting the distribution of livestock grazing pressures in rangelands. *Austral Ecol.* 29, 31–39.
- Ruthven III, D.C., 2007. Grazing effects on forb diversity and abundance in a honey mesquite parkland. *J. Arid Environ.* 68, 668–677.
- SAS, 2016. Random-effects Analysis, SAS/STAT(R) 9.2 User's Guide, second ed. [https://support.sas.com/documentation/cdl/en/statug/63033/HTML/default/viewer.htm#statug\\_glm\\_sect037.htm](https://support.sas.com/documentation/cdl/en/statug/63033/HTML/default/viewer.htm#statug_glm_sect037.htm). (Accessed 29 April 2016).
- Schieltz, J.M., Rubenstein, D.I., 2016. Evidence-based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? *Environ. Res. Lett.* 11 <https://doi.org/10.1088/1748-9326/11/11/113003>.
- USDA-NRCS, 2011a. Soil Survey Geographic (SSURGO) Database. <http://www.nrcs.usda.gov>. (Accessed 21 March 2011).
- USDA-NRCS, 2011b. Soil Data Viewer v.6.0. <http://www.nrcs.usda.gov>. (Accessed 25 July 2011).
- Vavra, M., 2005. Livestock grazing and wildlife: developing compatibilities. *Rangel. Ecol. Manag.* 58, 128–134.
- Vermeire, L.T., Strong, D.J., Waterman, R.C., 2018. Grazing history effects on rangeland biomass, cover and diversity responses to fire and grazing utilization. *Rangel. Ecol. Manag.* 71, 770–775.
- Von Wehrden, H., Hanspach, J., Kaczensky, P., Fischer, J., Wesche, K., 2012. Global assessment of the non-equilibrium concept in rangelands. *Ecol. Appl.* 22, 393–399.