



Meta-Analysis of Diet Composition and Potential Conflict of Wild Horses with Livestock and Wild Ungulates on Western Rangelands of North America[☆]



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ABSTRACT

Wild horse (*Equus ferus caballus*) management in western North America is an escalating concern for ecological integrity on these landscapes. Identifying potential diet overlap among horses, livestock, and wildlife will inform management decisions to optimize multiple interests. To understand dietary relationships, we conducted a quantitative synthesis of microhistological fecal studies for wild horse, beef cattle (*Bos* spp.), domestic sheep (*Ovis aries*), elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) diet composition on western rangelands of North America. Our search yielded 60 studies from 14 states, 1 Canadian province, and 2 Mexican states with 392 unique species-season samples. We summarized plant species into graminoid, forb, and browse functional groups. For wild horses, seasonal diet composition means for graminoids (77–89%), forbs (4–15%), and browse (3–10%) did not vary seasonally for any plant group ($P \leq 0.05$). Univariate analyses and the calculation of effect sizes corroborated our finding that graminoid composition explained the potential overlap of wild horses with cattle regardless of season, with sheep and elk in the spring, with sheep in the summer, and with elk in the fall and winter. Although data indicate wild horse diets are primarily composed of graminoids, several studies reported unusual, regionally specific shifts in response to winter snow that limited graminoid accessibility, leading to higher browse composition. Season, plant composition, and ungulate assemblage may all influence dietary competition between wild horses and other large ungulate sharing western North American rangelands; however, the low and nonsignificant heterogeneity values at alpha 0.01 for cattle:horse effect size comparisons suggest that cattle and horses respond to regional and seasonal variation similarly—a result not observed for other ungulate:horse comparisons. Our meta-analysis provides a robust data set for evaluations of diet composition for wild horses, livestock, and wildlife, whereas no empirical studies have assessed all species together.

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Introduction

Management of wild horses (*Equus ferus caballus*) is an ecological and sociological issue of escalating concern on western North American rangelands and other areas of the world such as eastern North American salt marshes, Africa, Asia, Argentina, Australia, and New Zealand (Turner, 1988; Linklater et al., 2004; Zalba and Cozzani, 2004; Mallon and Zhigang, 2009; Hampson et al., 2010; Odadi et al., 2011). In North America, wild equids became extinct about 10 000 years ago, and extant wild horse populations are the result of

introductions of domesticated horses by Spaniards in the 1500s, repeated escapes from domestic herds, and successive commingling with present free-roaming herds (Haines, 1938; Wagner, 1983; Beaver, 2003). The Wild Free-Roaming Horses and Burros Act of 1971 directs the federal management of these wild equids as part of the natural system (Public Law 92-195). More recently, the Federal Land Policy and Management Act of 1976 (Public Law 94-579) and the Public Rangelands Improvement Act of 1978 (Public Law 95-514) have further established the enforcement authority of the Bureau of Land Management (BLM) to remove excess wild horses, from both public and private lands, when populations exceed appropriate management levels to maintain the ecological integrity of western rangelands.

Since 1971, the BLM has removed 195 000 wild horses from western rangelands and offered many of these horses to the public for adoption (Garrott and Oli, 2013). However, a struggling adoption program coupled with annual population growth rates that can exceed 20% has

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relegated many horses to temporary holding facilities (Eberhardt et al., 1982; Garrott and Taylor, 1990; Garrott et al., 1991). Removal of horses alone is not anticipated to effectively meet population objectives, and more recent strategies have included fertility control (Gross, 2000; Bartholow, 2010). As of March of 2015, there were approximately 47 329 wild horses and 10 821 wild burros roaming western rangelands, more than twice the national appropriate management levels of 26 715 wild horses and burros. Furthermore, there are currently 46 298 in temporary holding corrals or long-term pastures—as many that are currently free roaming (BLM, 2015). Federal expenditures for the adoption and relocation program in FY 2013 were \$76 million, with \$51 million accounting for holding, gathering, and removal costs. The annual cost of managing horses in temporary holding facilities is expected to exceed \$1 billion by 2030 (Garrott and Oli, 2013).

Management of the escalating wild horse population in the United States is critical because federal lands are mandated to be managed for multiple uses, including livestock grazing and providing habitat for native wildlife species (Bastian et al., 1991). Many studies have quantified diet composition of wild horses, but not all studies have compared wild horse diet composition with livestock and/or wildlife; they have only measured overlaps for a certain season of the year or for only a subset of co-occurring ungulates (Hansen, 1976; Hansen et al., 1977; Salter and Hudson, 1980; Krysl et al., 1984; Stephenson et al., 1985a). Further complicating wild horse management in some areas is the movement of horses across the largely unfenced matrix of public-private land ownership known as “checkerboard,” a relic of the Union Pacific Railroad (Calef, 1952). Evidence also suggests that wild horses may disproportionately use features of the landscape, such as riparian areas and wet meadows, more than other areas, thus having negative effects on riparian function (Crane et al., 1997; Hampson et al., 2010).

Given the burgeoning wild horse population, a federal mandate to manage for multiple uses, variation in diet compositional comparisons of wild horses with other ungulate across regions and seasons, and the inevitable seasonal diet overlap between wild horses and livestock and native wildlife, we sought to quantify diet overlap of the most common large rangeland ungulate in western North America. The primary objective of our study was to identify potential dietary overlap between wild horses and livestock and wild ungulates across seasons, geographical boundaries, and limitations of prior studies. We systematically reviewed and synthesized microhistological fecal studies for wild horse, beef cattle (*Bos* spp.), domestic sheep (*Ovis aries*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) diet composition on western rangelands of North America. To understand broad ecological interactions on western rangelands, we used univariate and meta-analytic effect size calculations to compare functional group diet composition of these six ungulate in spring, summer, fall, and winter and on an annual basis.

Materials and Methods

Literature Search Criteria

We searched the peer-refereed and gray literature (theses, dissertations, reports, and proceedings) using Google Scholar and Web of Science scholastic search engines for wild horse diet studies based on the following combinations of search terms: Animal species searched individually for “wild horse” (or “feral horse,” “horse,” or “equid” singularly), “cattle” (or “cow”), “sheep” (or “livestock”), “elk” (or “wapiti” or “Cervus”), “pronghorn” (or “antelope” or “Antilocapra”), “mule deer” (or “deer” or “Odocoileus”), and “ungulate” or “herbivore.” Each individual animal species term was also used in combination with “diet composition” and “microhistological,” and searches were conducted with and without the term “rangeland.” We also searched the bibliographies of relevant papers for other potential sources of data that might have been missed with the initial search protocol. To be included, studies must have presented percentage diet composition or availability data

for graminoid, forb, and browse plant functional groups and presented data for at least one season (spring, summer, fall, winter). We only considered studies from the western United States; Alberta and British Columbia, Canada; and northern Mexico. The literature search and data extraction process were conducted between August 2014 and August 2015.

We intentionally restricted our search to studies that used the microhistological fecal analysis technique, thus removing studies that solely evaluated diets through bite counts, forage use (e.g., visual observations of feeding sites and plant selection), ingesta samples, and rumen content analysis. Restricting our study to this single technique was important because studies have shown disagreements with other techniques, particularly esophageal fistula sampling and forb estimates (McInnis, 1977; Vavra et al., 1978). Microhistological studies use a microscopic comparison of fecal plant fragments to reference specimens to determine botanical diet composition, especially for dominant plant species across western North America since the 1930s (Johnson, 1982). Microhistological procedures are advantageous because they are practical for free-roaming animals, are less intrusive than esophageal-fistulation for in vitro estimation, are less subject to observer error than forage use estimates, do not disrupt behavior of grazing animals, and are ideal for comparing multiple ungulate using the same rangeland (Crocker, 1959; Anthony and Smith, 1974; Smith and Shandruk, 1979; Mayes and Dove, 2000).

From a practical standpoint, fecal microhistological analysis has been suggested to be one of the best techniques for quantifying dietary composition of large ungulate on rangelands (Holechek et al., 1982b; Mohammad et al., 1995). However, this technique is not without its limitations including that a portion of plant fragments may remain unidentifiable, differential digestion of different fragments by species may be influenced by maturity, observer skill and bias can influence accuracy, and some studies have demonstrated disagreement between fecal analyses with the analyses of stomach contents (Holechek et al., 1982b, 1982c; Mayes and Dove, 2000). However, Mayes and Dove (2000) concluded in a detailed review that microhistological fecal analysis can be used for both ruminants and nonruminants as the limitations to the technique apply regardless of digestive strategy. Furthermore, a recent study concluded that microhistological fecal analyses can be a useful tool to determine the botanical diet composition of horses (Morrison, 2008). We did not censor cattle dietary information by animal age or class because the fecal samples from wild horses and native ungulates were not censored in such a way. Thus, we included mature cows, yearling stocker cattle, heifers, and/or calves from beef cattle studies.

Data Analyses

Our statistical analyses were designed to answer three specific questions: 1) Do wild horse, livestock, and native wildlife diets fluctuate seasonally? 2) Are seasonal mean plant functional group components for wild horse, livestock, and native wildlife diets similar? 3) What is the magnitude of the diet comparison effect on an annual basis for livestock and native wildlife that potentially share rangelands with wild horses?

We pooled plant species data from scientific studies that met our search criteria by plant functional groups to make generalizations about animal species diet composition across different plant communities. Specifically, we grouped grasses and grasslike plants inclusive of grasses (Poaceae), sedges (Cyperaceae), and rushes (Juncaceae) as graminoids; herbaceous, broad-leaved flowering plants as forbs; and woody plants and cacti (Cactaceae) as browse (including all woody deciduous and coniferous shrub and tree species). Because some studies reported total diets with plant functional group components that did not equal 100% due to the lack of reporting rare or uncommon food species, we corrected percentages as the percent of the total diet accounted for following Christianson and Creel (2007). This correction results in all diets summing to 100% but assumes that unreported portions of the diet were composed of equal proportions of graminoids, forbs, or browse.

We first compared seasonal plant functional group means by ungulate species diet for each season using analysis of variance (ANOVA) to determine if diets were influenced by season (SAS Institute, 2011). Seasonal designations were based on either sample study definitions or the following categorization of months into seasons (winter—December, January, February; spring—March, April, May; summer—June, July, August; fall—September, October, November). If multiple months were presented, we took the average of the months to indicate the season. In separate analyses, we used graminoid, forb, and browse means as the dependent response variable and ungulate species as the fixed main effect. We then conducted an ANOVA to compare means for all pairwise comparisons between horses and each of the other five ungulate species and grouped each analysis by season. For each pairwise comparison we noted the level of significance at $P \leq 0.001$, $P \leq 0.05$, or $P > 0.05$. For each ANOVA, we used a generalized linear model assuming negative binomial distribution in PROC GENMOD (SAS Institute, 2011) to account for the non-normal distribution and nonindependence due to the unit sum constraint of diet components inherent in the plant functional group diet data (White and Bennets, 1996; Ver Hoef and Rohlf, 2007; O'Hara and Kotze, 2010). Adjusted standard errors to correct for overdispersion were used to separate means, but we also present unadjusted standard errors and raw means.

Before calculating effect sizes, we transformed plant functional group diet data using the arcsine transformation because percentage data are non-normally distributed and asymptotic (i.e., cannot be lower than 0 or exceed 100; Cohen, 1988; Prendergast et al., 2002; Nakagawa and Cuthill, 2007). We calculated effect sizes using Hedges' d (\bar{d} ; Gurevitch and Hedges, 1993; Osenberg et al., 1997) for potentially co-occurring ungulate annual diets and potential direct overlap with wild horses by making comparisons for each potential wild horse and livestock or wild ungulate species combination (*other*) for the three plant functional groups by:

$$\text{Hedges' } d = \frac{(\bar{x}^{\text{horse}} - \bar{x}^{\text{other}})}{S} \quad J \quad (1)$$

where \bar{x}^{horse} was the mean diet for a given plant functional group for wild horses and \bar{x}^{other} was the mean diet for the given plant functional group for each other livestock or wildlife species. Effect sizes used an estimate of the pooled sampling variance by calculating the pooled standard deviation (S) as

$$S = \sqrt{\frac{(N^{\text{horse}} - 1)(S^{\text{horse}})^2 + (N^{\text{other}} - 1)(S^{\text{other}})^2}{(N^{\text{horse}} + N^{\text{other}} - 2)}} \quad (2)$$

where S^{horse} was the standard deviation of each plant functional group diet mean for wild horses, S^{other} was the standard deviation of each plant functional group diet mean for each other livestock or wildlife species, N^{other} was the total number of studies for each other livestock or wildlife species, and N^{horse} was the total number of studies for wild horses. We chose Hedges' d over Hedges' g , in part, because it includes a correction term for small sample sizes (J) calculated as:

$$J = 1 - \frac{3}{4(N^{\text{other}} - N^{\text{horse}} - 2) - 1} \quad (3)$$

where N^{other} was the total number of studies for each other livestock or wildlife species and N^{horse} was the total number of studies for wild horses. To compare effect sizes and for evaluating the magnitude of

the effect size, we calculated the variance (v) in the effect as:

$$v = \frac{N^{\text{other}} + N^{\text{horse}}}{(N^{\text{other}})(N^{\text{horse}})} + \frac{d^2}{2(N^{\text{other}} + N^{\text{horse}})} \quad (4)$$

We calculated 95% confidence intervals for each comparison to assess significance of dietary overlap (at $P \leq 0.05$). If confidence interval bars overlapped zero, the effect size was considered insignificant and reflected potential dietary overlap with wild horses for that plant functional group during a specific season. If the confidence interval bars did not overlap zero, the effect size was significant and reflected no potential dietary overlap with wild horses for that plant functional group. All effect size analyses and calculations were computed in MetaWin v 2.0 (Rosenberg et al., 1999).

To assess variability of effect sizes we used Q statistics as a measure of heterogeneity (Hedges and Olkin, 1985). Total heterogeneity (Q_T), a weighted sum of squares similar to the calculation of the total sum of squares used in ANOVA, was calculated as an indication of effect size homogeneity (tested against a χ^2 distribution) and as an indicator of additional structure in the data (Rosenberg et al., 1999). Within-group heterogeneity (Q_W) was calculated for each categorical group (in this case for each ungulate species compared with wild horses) to determine if diet comparisons were homogenous or confounded by other external factors.

Results

Our literature search yielded 60 peer-refereed studies with 392 unique diet composition samples (combinations of animals species and season considered as cases) from 14 states (Arizona, California, Colorado, Idaho, Montana, North Dakota, New Mexico, Nevada, Oregon, South Dakota, Texas, Utah, Washington, Wyoming), Alberta, Canada, and 2 states in Mexico (Fig. 1; Table 1). On average, only two animal species were assessed per study, and none of the studies assessed all six ungulate together—further justification for our study.

We found no difference in seasonal diet composition for horses ($P \leq 0.05$). Seasonal diet means (\pm SE) ranged from $77 \pm 7\%$ to $89 \pm 5\%$ for graminoids, $4 \pm 1\%$ to $15 \pm 6\%$ for forbs, and $3 \pm 1\%$ to $10 \pm 4\%$ for browse (Table 2). In all seasons, wild horse diets always included a similar proportion of graminoids as cattle and significantly more than mule deer or pronghorn (see Table 2). In the spring, wild horse diets were composed of a similar proportion of forbs as elk but less than livestock or other wildlife species (see Table 2). In summer, wild horse diets were composed of lower proportions of forbs than livestock or wildlife species. In the fall and winter, wild horse diets were composed of a similar proportion of forbs as all herbivore species except for pronghorn in winter, which included a significantly higher proportion of forbs in their diets as compared with wild horses. Wild horse diets were composed of a lower proportion of browse than livestock or wildlife species in the spring, a similar proportion of browse as cattle and sheep in the summer and winter, a similar proportion to cattle in the fall, and always a smaller proportion than elk, mule deer, or pronghorn regardless of season (see Table 2).

When we analyzed the variance of diets for each herbivore species individually, there were no differences in the seasonality of plant functional group diet composition for wild horses, mule deer, pronghorn, or sheep. However, cattle diets were composed of a higher proportion of graminoids in the summer ($79 \pm 3\%$) than in the winter ($64 \pm 6\%$) ($P = 0.046$) but there were no seasonal differences for forbs or browse. Furthermore, elk diets included three times more forbs in the summer ($31 \pm 6\%$) than in the winter ($9 \pm 2\%$) ($P = 0.009$) (see Table 2).

Effect sizes across all comparisons ranged from -5.1 to $+2.6$ depending on the animal species and plant functional group comparison to wild horses (Fig. 2). Total heterogeneity was high and significant ($Q_T = 604.1$, $df = 59$, $P < 0.001$), rejecting the null hypothesis that all

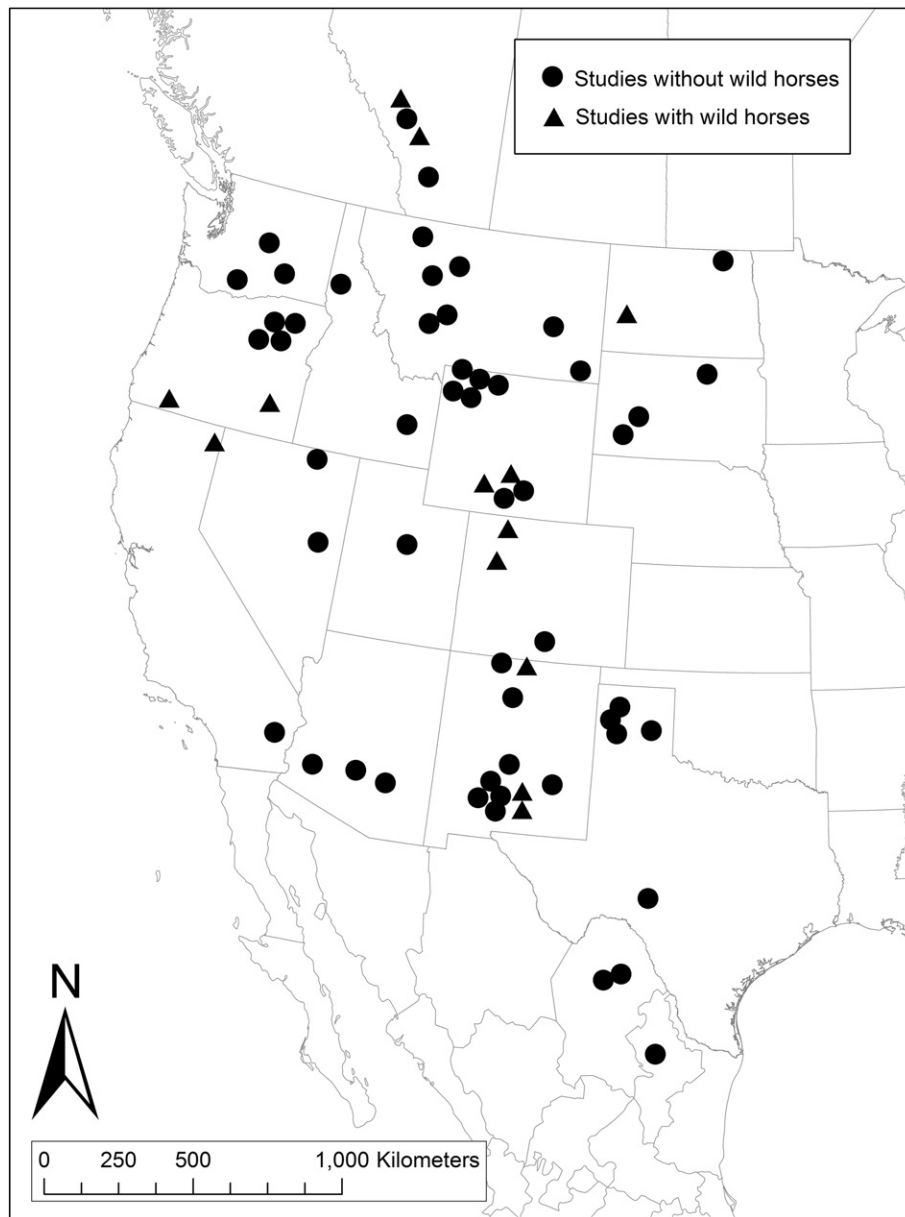


Figure 1. Study locations assessing wild horse ($n = 12$) or domestic livestock or native wildlife ($n = 100$) diet composition with microhistological analyses on rangelands of western North America. Each symbol represents a single study with the exception of the two triangles in Wyoming, which denote two different locations within a single study from Krysl et al. (1984).

diet overlaps between horses and other ungulates were equal and further justifying the calculation of individual effect sizes for each species relative to wild horses (i.e., a categorical meta-analysis). When wild horses were compared with cattle, effect sizes overlapped zero for all plant functional groups (graminoid $\bar{E} = -0.63$; 95% CI: -1.26 to 0.002 ; forb $\bar{E} = 0.42$; 95% CI: -0.21 to 1.05 ; browse $\bar{E} = 0.28$; 95% CI: -0.34 to 0.91) (see Fig. 2). The weighted mean effect size for cows ($\bar{E} = 0.03$; 95% CI: -0.22 to 0.28) indicated diet overlap between cattle and horses for all plant functional group types and similar diet composition on an annual basis. Heterogeneity for cattle:horse comparisons was the lowest for all ungulate:horse comparisons and the only one that was nonsignificant at $\alpha = 0.01$ ($Q_w = 21.4$, $df = 11$, $P = 0.03$), suggesting that all diet comparisons between cattle and horses were similar and likely did not vary by season or location.

When wild horses were compared with domestic sheep, effect sizes overlapped zero for browse ($\bar{E} = 0.68$; 95% CI: -0.09 to 1.45) but not for graminoids ($\bar{E} = -1.33$; 95% CI: -2.16 to -0.49) or forbs ($\bar{E} = 0.87$; 95% CI: 0.09 – 1.65 ; see Fig. 2). Horse diet composition was equal for browse

but included more graminoids and fewer forbs than sheep (see Fig. 2). The weighted mean effect size for sheep ($\bar{E} = 0.14$; 95% CI: -0.18 to 0.45) overlapped zero, indicating overlap between domestic sheep and horses for diet composition on an annual basis. Heterogeneity for sheep:horse comparisons was low but significant ($Q_w = 49.5$, $df = 11$, $P < 0.001$), suggesting that not all diet comparisons between wild horses and sheep were similar and varied by season or region.

When wild horses were compared with elk, effect sizes overlapped zero for forbs ($\bar{E} = 0.044$; 95% CI: -0.22 to 1.10) but not for graminoids ($\bar{E} = -1.46$; 95% CI: -2.16 to -0.75) or browse ($\bar{E} = 1.03$; 95% CI: 0.36 – 1.70 ; see Fig. 2). The effect size was negative for graminoids, indicating that wild horses ate more grass than elk but the effect size was positive for browse, indicating that wild horses ate less browse than elk. The weighted mean effect size for elk ($\bar{E} = 0.06$; 95% CI: -0.21 to 0.33) indicated diet overlap between elk and horses for diet composition in general on an annual basis, and the primary function of that overlap appeared to be for forbs. Heterogeneity for elk:horse comparisons was moderate and significant ($Q_w = 86.0$, $df = 11$, $P < 0.001$),

Table 1
Summary of studies with suitable diet composition data using microhistological fecal analyses of wild horses, livestock, and wildlife on western rangelands of North America. Please see Literature Cited for full citations

Author and yr	Location	Data type	Horse	Cattle	Sheep	Elk	Prong-horn	Mule deer
Morgantini and Hudson, 1985	Alberta	winter	—	—	—	x	—	—
Salter and Hudson, 1979	Alberta	all seasons	x	—	—	—	—	—
Salter and Hudson, 1980	Alberta	winter (horse/elk), summer (horse/cattle)	x	x	—	x	—	—
Telfer, 1994	Alberta	winter	—	x	—	x	—	x
Krausman et al., 1997	AZ	all seasons	—	—	—	—	—	x
Hanley, 1982	CA/NV	all seasons	x	x	x	—	x	x
Marshal et al., 2004	CA	all seasons	—	—	—	—	—	x
Hansen and Reid, 1975	CO	all seasons (mule deer/elk), summer/fall (cattle)	—	x	—	x	—	x
Hansen et al., 1977	CO	summer	x	x	—	—	—	x
Hubbard and Hansen, 1976	CO	summer	x	x	—	—	—	x
Johnson, 1979	ID	summer (cattle/sheep/pronghorn), winter (pronghorn)	—	x	x	—	x	—
Mitchell and Rodgers, 1985	ID	spring, summer, fall	—	x	—	—	—	—
Mellado et al., 2005a	Coahuila	all seasons	—	—	x	—	—	—
Mellado et al., 2005b	Coahuila	all seasons	—	x	—	—	—	—
Ramirez et al., 1996	Nuevo Leon	all seasons	—	—	—	—	—	x
Alexander et al., 1983	MT	summer	—	—	x	—	—	—
Canfield, 1984	MT	winter	—	—	—	x	—	—
Daneke, 1980	MT	all seasons	—	—	—	x	—	—
Frisina et al., 2008	MT	winter	—	—	—	—	—	x
Grings et al., 2001	MT	spring, summer, fall	—	x	—	—	—	—
Jenkins and Wright, 1987	MT	winter	—	—	—	x	—	—
Kasworm et al., 1984	MT	winter and spring (mule deer/elk), summer (cattle)	—	x	—	x	—	x
Beasom et al., 1982	NM	fall, winter	—	—	x	—	x	—
Hamadeh et al., 1990	NM	spring, fall, winter	—	—	x	—	—	—
Hansen, 1976	NM	all seasons	x	—	—	—	—	—
Hulet et al., 1992	NM	summer	—	x	x	—	—	—
Mofareh et al., 1997	NM	all seasons	—	x	—	—	—	—
Mohammad et al., 1996	NM	all seasons	—	x	—	—	—	—
Rosiere et al., 1975	NM	all seasons	—	x	—	—	—	—
Sandoval et al., 2005	NM	all seasons	—	—	—	x	—	x
Smith et al., 1998	NM	all seasons	x	—	—	—	x	—
Stephenson et al., 1985a	NM	winter	x	—	—	x	x	x
Stephenson et al., 1985b	NM	spring, winter	—	x	x	—	x	—
Osborn et al., 1997	ND	fall, winter	—	—	—	x	—	—
Sullivan, 1988	ND	all seasons	x	—	—	x	—	x
Beck and Peek, 2005	NV	spring and summer (elk), summer (mule deer/ cattle/sheep)	—	x	x	x	—	x
Kolada, 2011	NV	summer	—	x	—	x	—	x
Clark et al., 2013	OR	summer	—	x	—	—	—	—
Darambayar et al., 2013	OR	summer	—	x	—	—	—	—
Holechek et al., 1982a	OR	spring, summer, fall	—	x	—	—	—	—
Hosten et al., 2007	OR	all seasons	x	x	—	x	—	x
McInnis and Vavra, 1987	OR	all seasons	x	x	—	—	x	—
Stewart et al., 2003	OR	summer	—	x	—	x	—	x
Plumb and Dodd, 1993	SD	summer and fall	—	x	—	—	—	—
Jacques et al., 2006	SD	all seasons	—	—	—	—	x	—
Uresk ,1984	SD	spring, summer, fall	—	x	—	—	—	—
Koerth et al., 1984	TX	all seasons	—	—	—	—	x	—
Sowell et al., 1985	TX	all seasons	—	—	—	—	—	x
Warren et al., 1984	TX	all seasons	—	—	x	—	—	—
Mower and Smith, 1989	UT	winter	—	—	—	x	—	x
Jenkins and Starkey, 1993	WA	spring, fall, winter	—	—	—	x	—	—
McArthur, 1977	WA	all seasons	—	—	—	x	—	—
McCorquodale, 1993	WA	spring, fall, winter	—	—	—	x	—	—
Compton, 1974	WY	all seasons	—	—	—	x	—	x
Delgiudice et al., 2001	WY	winter	—	—	—	x	—	—
Krysl et al., 1984	WY	summer	x	x	—	—	—	—
Ngugi et al., 1992	WY	all seasons	—	x	x	x	x	x
Singer and Norland, 1994	WY	winter	—	—	—	x	x	x
Torstenson et al., 2006	WY	all seasons	—	x	—	x	—	x
Vales and Peek, 1993	WY	all seasons	—	—	—	x	—	—
TOTAL STUDIES			12	29	11	26	11	23

suggesting that not all diet comparisons between wild horses and elk were similar and varied by season or region. Furthermore, heterogeneity for elk:horse comparisons, specifically for forbs, was the highest and significant ($Q_w = 86.0$, $df = 11$, $P < 0.05$), the only time this occurred for any of the specific plant functional group comparisons to wild horses for any of the other ungulate. This indicates that elk respond to environmental factors that dictate forb abundance differently than other ungulate species.

When wild horses were compared with mule deer, effect sizes did not overlap zero for any plant functional group; graminoids ($\bar{E} = -5.08$; 95% CI: -6.31 to -3.85), forbs ($\bar{E} = 0.71$; 95% CI: 0.07 – 1.36), browse ($\bar{E} = 2.62$; 95% CI: 1.78 – 3.45) (see Fig. 2). The relative magnitude between elk and mule deer effects compared with wild horses was an order of magnitude greater for mule deer for graminoids and browse (see Fig. 2). The weighted mean effect size for mule deer ($\bar{E} = 0.47$; 95% CI: 0.14 – 0.80) indicated no overlap between mule deer and

Table 2

Pair-wise mean comparisons (± 1 standard error; n = number of cases) for plant functional group diets by livestock and wild ungulates compared with wild horses in western rangelands of North America. Values in parentheses after standard errors are adjusted standard errors calculated in a generalized linear model assuming a negative binomial distribution to correct for overdispersion and to separate means. Mean comparisons based on least-squares output from analysis of variance with statistical differences between herbivore species noted within season and plant functional groups

Season	Herbivore species	n	% Graminoid	% Forb	% Browse
Spring					
	Horse	7	89 \pm 5 (20)	8 \pm 4 (3)	3 \pm 1 (1)
	Cattle	26	70 \pm 4 (8) ¹	17 \pm 4 (3) ²	13 \pm 3 (2) ³
	Domestic sheep	8	56 \pm 8 (12) ¹	29 \pm 9 (10) ²	15 \pm 4 (4) ²
	Elk	22	54 \pm 6 (7) ¹	15 \pm 3 (3) ¹	31 \pm 5 (5) ³
	Mule deer	18	8 \pm 2 (1) ³	22 \pm 4 (5) ²	70 \pm 4 (13) ³
	Pronghorn	7	9 \pm 3 (2) ³	32 \pm 9 (12) ²	59 \pm 11 (17) ²
Summer					
	Horse	12	88 \pm 4 (18)	4 \pm 1 (1)	8 \pm 3 (2)
	Cattle	48	79 \pm 3 (8) ¹	13 \pm 3 (2) ²	7 \pm 1 (1) ¹
	Domestic sheep	13	66 \pm 6 (13) ¹	21 \pm 5 (7) ²	13 \pm 4 (4) ¹
	Elk	11	41 \pm 7 (8) ²	31 \pm 6 (10) ²	28 \pm 6 (8) ²
	Mule deer	25	9 \pm 3 (1) ³	24 \pm 5 (6) ²	67 \pm 6 (14) ³
	Pronghorn	8	10 \pm 4 (3) ³	46 \pm 9 (19) ²	44 \pm 9 (16) ²
Fall					
	Horse	7	84 \pm 8 (13)	8 \pm 4 (4)	8 \pm 4 (3)
	Cattle	25	78 \pm 4 (7) ¹	9 \pm 3 (2) ¹	13 \pm 3 (2) ¹
	Domestic sheep	7	47 \pm 8 (8) ²	27 \pm 12 (12) ¹	25 \pm 8 (8) ²
	Elk	14	54 \pm 6 (6) ¹	18 \pm 4 (5) ¹	28 \pm 6 (6) ²
	Mule deer	16	4 \pm 1 (1) ³	15 \pm 4 (5) ¹	81 \pm 5 (16) ³
	Pronghorn	6	8 \pm 3 (2) ³	35 \pm 11 (17) ¹	57 \pm 12 (19) ²
Winter					
	Horse	11	77 \pm 7 (17)	15 \pm 6 (6)	10 \pm 4 (2)
	Cattle	12	64 \pm 6 (13) ¹	21 \pm 4 (6) ¹	15 \pm 4 (3) ¹
	Domestic sheep	8	57 \pm 9 (15) ¹	25 \pm 9 (9) ¹	18 \pm 5 (4) ¹
	Elk	31	52 \pm 5 (7) ¹	9 \pm 2 (2) ¹	39 \pm 5 (5) ³
	Mule deer	24	6 \pm 2 (1) ³	20 \pm 3 (4) ¹	74 \pm 4 (10) ³
	Pronghorn	12	13 \pm 4 (3) ²	34 \pm 9 (1) 0 ²	53 \pm 9 (10) ³

¹ NS (nonsignificant) = $P > 0.05$.

² $P \leq 0.05$.

³ $P \leq 0.001$.

horses for diet composition on an annual basis. Heterogeneity for mule deer:horse comparisons was the highest for all animal:horse comparisons and significant ($Q_W = 284.9$, $df = 11$, $P < 0.001$), suggesting that not all diet comparisons between wild horses and mule deer were similar and varied by season or region.

None of the plant functional group effect sizes overlapped zero for the pronghorn comparisons (graminoids $\bar{E} = -3.8$; 95% CI: -5.12 to -2.52; forbs $\bar{E} = 1.33$; 95% CI: 0.48–2.19; browse $\bar{E} = 1.82$; 95% CI: 0.91–2.73) (see Fig. 2). The weighted mean effect size for pronghorn ($\bar{E} = 0.55$; 95% CI: 0.16–0.94) indicated no overlap between pronghorn and horses for diet composition in general on an annual basis, similar to the pattern for elk and mule deer. Heterogeneity for pronghorn:horse comparisons was high and significant ($Q_W = 155.4$, $df = 11$, $P < 0.001$), suggesting that not all diet comparisons between wild horses and pronghorn were similar and varied by season or region.

Discussion

We compiled diet composition data to develop broad comparisons of wild horses with domestic and wild ungulates that share western North American rangelands. Results from our statistical analyses considered season and study location and provide strong support that wild horse and cattle diets overlapped in plant functional group composition, primarily for graminoids (Smith, 1986). The low and nonsignificant Q_W heterogeneity values at $\alpha = 0.01$ for cattle:horse effect size comparisons suggest cattle and horses were similar in diets and likely responded to regional and seasonal variation similarly, a result that was not the case for other comparisons of livestock and native wild ungulates to wild horses. Rather, diet overlap between wild horses

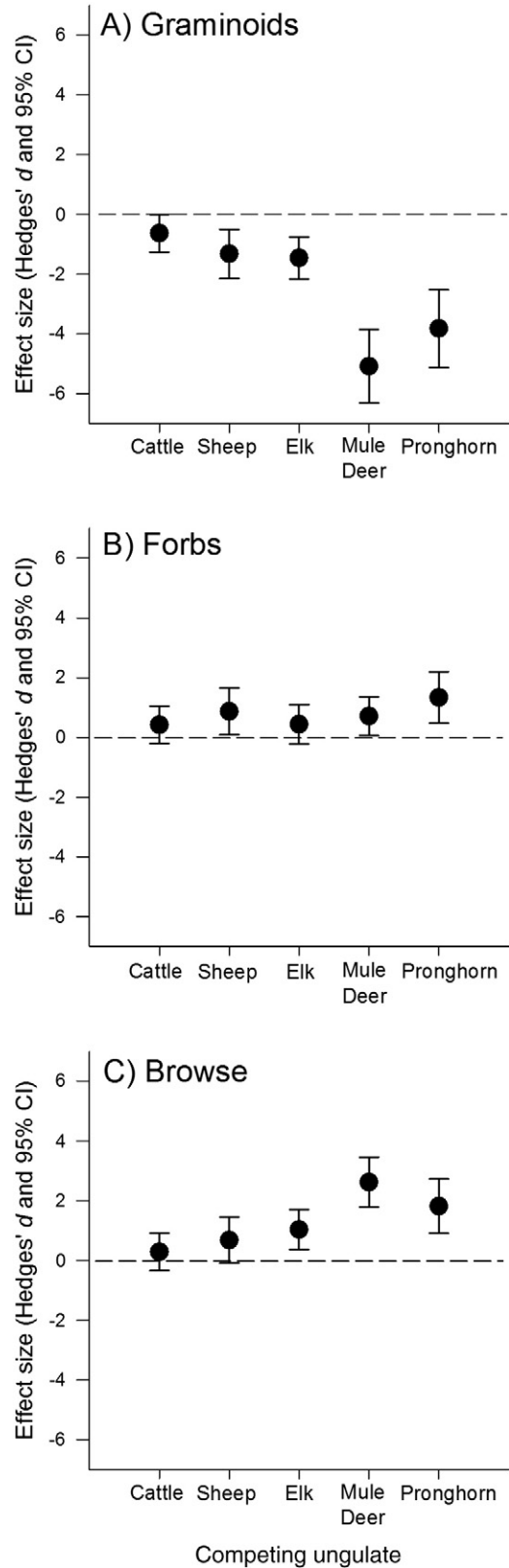


Figure 2. Effect sizes using Hedges' d and 95% confidence intervals for potentially co-occurring ungulate annual diets and potential direct overlap with wild horses for **A**, graminoids, **B**, forbs, and **C**, browse. If confidence interval bars overlap zero, the effect size is insignificant, reflecting potential diet overlap with wild horses for that plant functional group. If the confidence interval bars do not overlap zero, the effect size is significant, reflecting no potential diet overlap with wild horses for that plant functional group.

and domestic sheep and elk was more related to similarities in seasonal diet composition for specific plant functional groups. The effect size pattern when comparing wild horses with all native wild ungulates was similar for all species with negative effect sizes for graminoids and positive effect sizes for browse and forbs, indicating that wild horses ate more grass but less browse and forbs than elk, pronghorn, or mule deer. Furthermore, our results are corroborated by studies that we did not consider because they lacked specific data that met our search criteria, but that also report substantial diet overlap between wild horses and cattle (e.g., Olsen and Hansen, 1977; Crane et al., 1997).

Although we employed systematic search criteria to include microhistological studies from western North America, our results have limitations inherent in the assumptions that all species within a plant functional group were similar in quantity and quality, that all regions had similar plant functional groups available to ungulate, and that all seasonal designations represented similar phenological expression of various plant functional groups and plant species comprising those groups. Despite these assumptions, we compiled data in a robust and interpretable manner, and we also demonstrated that the variation in descriptions of wild horse diet composition were influenced more by regionally specific weather or plant species availability than general seasonal shifts. The application of meta-analytic techniques and effect sizes to data from existing studies is a well-accepted tool used to provide information to answer important questions for organisms with different traits that occur across ecological gradients by identifying fundamental processes while minimizing extraneous factors (Osenberg et al., 1997, 1999).

Wild horses are not necessarily ecologically comparable with cattle or other ungulates due to different mouth structures (incisor presence/absence and prehensile ability of the lips) and digestive system (rumen fermentation or foregut in true ruminants versus cecal fermentation or hindgut in horses; Beever, 2003). This different digestive strategy places a greater time-energy constraint and limits the use of low-quality forage by horses (Hanley and Hanley, 1982). These anatomical and physical adaptations in horses results in a high-intake foraging strategy of 20–65% greater consumption by volume of plant herbage than a domestic cow of equivalent size (Hanley, 1982; Menard et al., 2002). Consequently, horses consume small, frequent meals with daily estimates of time spent grazing ranging from 10–17 hours (Fleurance et al., 2001). A review of comparative anatomy suggests that digestive tracts in true ruminants comprise a greater proportion of total body weight at 40% compared with 15% in horses, and that horses only achieve 70% efficiency in comparison (i.e., a tradeoff; Janis, 1976). These physiological differences result in a more rapid passage time in horses compared with cattle—14 to 50 h for horses versus 57 to 90 h for cattle or, more approximately, 1.6× greater mean retention time for ruminants than hindgut fermenters (Janis, 1976; Illius and Gordon, 1992; Huhtanen and Kukkonen, 1995; Van Weyenberg et al., 2006). However, our results indicate that these differences may not result in differences between wild horses and cattle in the high graminoid composition of their diets relative to forbs or browse.

Although our findings indicate mean browse composition of wild horse diets did not exceed 10%, several studies have reported unusually high composition of browse by wild horses with seasonal variation. In northern New Mexico, Stephenson et al. (1985a) reported 43% browse composition in wild horse winter diets, whereas Smith et al. (1998) reported 2% browse composition from January to March (cool/dry period) and 28% browse composition from July to November (warm/wet period) in southern New Mexico. The increase of browse composition of horse diets in northern New Mexico in winter was attributed to the low volatile oil content of common winter fat (*Krascheninnikovia lanata*) and fourwing saltbush (*Atriplex canescens*), as well as the inaccessibility of graminoids due to snow cover for half of the winter (Stephenson et al., 1985a). Krysl et al. (1984) reported a similar increase of browse composition due to winter conditions for both wild horses and cattle in Wyoming, ranging from 33–39% browse composition. However, in

the winter wild horses consumed equal amounts of the two preferred winter browse, common winter fat and gray horsebrush (*Tetradymia canescens*), whereas cattle consumed ~ 1.5× more common winter fat than gray horsebrush, and in the summer neither ungulate diet was composed of more than 2% gray horsebrush (Krysl et al., 1984). However, in southern New Mexico the increase of browse composition in the late summer/early fall was attributed to the use of mesquite beans (*Prosopis* spp.) by wild horses, a legume that contains 9–14% protein and serves as an important part of ruminant diets in arid and semiarid regions of the southwest (Fagg and Steward, 1994; Smith et al., 1998). Thus, horses are strong grazers of graminoids but may employ regionally specific shifts in response to winter stress and limited graminoid accessibility or use of leguminous browse resulting in greater browse composition in diets. Furthermore, severe winters may increase selection by all rangeland ungulates for sites with reduced wind and snow, thus increasing potential for diet overlap (Miller, 1983). These types of unusual scenarios lead to overdispersion of horse diet estimates and large adjustments of standard errors under the generalized linear model and negative binomial distribution assumptions (see Table 2).

Dietary overlap by plant functional groups is just one aspect of overlap among wild horses, livestock, and wild ungulates. A less understood aspect of overlap that influences foraging and diet composition is the spatial competition for optimum habitat and site selection. For example, Salter and Hudson (1980) reported 66% overlap in summer diets between wild horses and cattle but low contemporaneous spatial overlap in western Alberta. However, others have reported that wild horse occupancy of sites may physically displace other ungulates (Miller, 1983). Several studies have also demonstrated that the availability of water affects horse distribution, and when water becomes scarce, interspecific aggression occurs and wild horses may force both cattle and pronghorn off watering sites (Miller, 1983).

The temporal effects of wild horse grazing year-round on federal allotments before turning livestock out on allotments in the spring, as well as the potential grazing effects that may have occurred before livestock grazing is initiated, are areas that need additional research. This issue is an ongoing concern for public-lands ranchers (personal communication). Producers and managers should note that wild horses are not ecologically synonymous with livestock or native wild ungulates due to physiological and morphological differences (Beever, 2003), but our results demonstrate that they may target graminoid components of the plant community before cattle have been turned out (Beever et al., 2008). The effects of horse social behavior, interspecific and intraspecific aggression in site selection and dominance, and how site occupancy influences site selection by wildlife species are also not well understood. Given the burgeoning wild horse population and recent negative population trends of mule deer and pronghorn (Pojar and Bowden, 2004; Ellenberger and Byrne, 2011), this is an area that needs additional research. Finally, the importance of water to the distribution of all rangeland ungulate in the context of escalating warming and drought cycles, trends that may be especially acute in western North America, may increase wild horse overlaps with livestock and native wildlife (Beever and Brussard, 2000; Meehl and Tebaldi, 2004; Westerling et al., 2006; Burke and Brown, 2008).

Management Implications

Our results suggest that potential diet overlap between wild horses and co-occurring rangeland ungulates is greatest for cattle, domestic sheep, and elk—a concerning result relative to managing allotments for multiple use. Finally, adjustments in stocking rates should be considered in areas dually grazed by wild horses and livestock or wild ungulates because wild horses appear to prefer graminoids and the hindgut fermentation physiology and relative digestive inefficiency of horses compared with other ungulates increases intake of herbage relative to body mass in wild horses (Hanley, 1982; Menard et al., 2002). Furthermore, the potential negative effects of concentrated horse use in areas

composed of perennial grasses and sagebrush should be considered in the management of sage-grouse (*Centrocercus spp.*) (Beever and Aldridge, 2011; Davies et al., 2014). This meta-analysis provides a robust data set for modeling diet composition of wild horses, cattle, domestic sheep, elk, mule deer, and pronghorn, whereas no empirical studies have assessed all species together.

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