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Poor soils and density-mediated body weight in deer: forage quality or quantity?

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Cervid studies have demonstrated body weight and lactation may be limited in areas with poor-quality soils, with the underlying mechanism often attributed to poor forage quality resulting from poor soil quality. However, if highly nutritious foods are produced but in limited quantities, selective foraging may alleviate nutritional stressors associated with poor soil productivity when adequate quantities of high-quality forage are obtained. We tested whether poor soil productivity limits forage from being high quality or conversely limits the abundance of high-quality forages. To do so, we determined whether nutrient concentrations in selected and non-selected forages on our poor soil study site met the nutritional requirements of lactating white-tailed deer *Odocoileus virginianus* assuming adequate amounts of forage are obtained. Also, we compared body weight of yearling males at a high density (13–17 deer km^{-2}) and low density (3–5 deer km^{-2}), because previous studies concluded soils on the study site were too poor for morphometrics (e.g. body weight) to be density-mediated. Deer selected plant species from each of five forage classes that would meet their nutritional requirements (i.e. assuming adequate forage intake) but also selected for different nutrients across forage classes. Phosphorus was limited in most forages, but deer selected forages that met P-requirements 10 times more than expected. We demonstrated body weight was 7.3% greater when deer density was low than high. Contrary to previous reports from poor productivity soil regions, deer on our study site should be able to meet lactation requirements when the quantity of high-quality forage is not limiting, and similarly body weight should be density-mediated. Hence, management strategies that alter the amount of forage per animal (i.e. decreasing animal density and/or increasing forage abundance) are viable options to promote desirable ungulate morphometrics in poor soil regions.

There are two competing hypotheses regarding the role of poor soil productivity in deer (Cervidae) nutrition: either poor quality soils limit forages from being high quality (hypothesis 1) or soil nutrients limit the amount of high-quality forages produced (hypothesis 2). Understanding the relationship between soil productivity and forage nutrition is important because animal productivity is directly linked to forage quality (Verme 1969, Hobbs and Swift 1985). In support of the first hypothesis, studies have suggested the existence of a threshold in low soil productivity that limits forage quality to an extent that deer morphometrics (e.g. body weight) are no longer affected by mechanisms associated with intraspecific competition and forage distribution (Shea et al. 1992, Shea and Osborne 1995, Keyser et al. 2005). In this case, there is no competition over high-quality forages because of soil limitations; therefore, body weight cannot be density-mediated (Shea et al. 1992). Under the second hypothesis, if soils limit the quantity but allow the existence of some high-quality forages, then morphometrics should respond to changes in intraspecific competition (i.e. density-mediation).

Wildlife population demographics are influenced by forage quality and quantity (Hobbs and Swift 1985). For example, forage quality is known to correlate positively to body weight variations in a variety of deer, including moose *Alces alces* (Herfindal et al. 2006), red deer *Cervus elaphus* (Mysterud et al. 2001, Pettorelli et al. 2001), roe deer *Capreolus capreolus* (Gaillard et al. 1996, Lehoczki et al. 2011), and white-tailed deer *Odocoileus virginianus* (Simard et al. 2008, Hefley et al. 2013). Also, body weight, particularly of yearling males, has been demonstrated to negatively correlate with intraspecific competition for limited quantities of forage (i.e. density dependence; Keyser et al. 2005, Hefley et al. 2013). However, previous studies have reported that body weight is not density-mediated in areas with poor soils, presumably because of low forage quality (Shea et al. 1992, Keyser et al. 2005). Forage quality has been reported as affected by soil productivity (Jones et al. 2008), though young tissues selected by concentrate selectors (Hofmann 1989) should not be affected by soil nutrients (Jones and Case 1990). These discrepancies fall between the agricultural and wildlife literature and may be explained by the inappropriate inclusion of physiologically mature plant tissues in analyses of wildlife forage quality (Lashley et al. 2014a), particularly when the study species is a concentrate selector. Unlike physiologically young plant tissues, nutrients in mature plant tissues correlate to nutrients available in the soil (Jones and Case 1990).

Management options for deer populations may be quite different depending on which hypothesis is supported in poor soil regions. For example, increasing forage available per animal either by decreasing animal density or implementing habitat management strategies that promote increased forage production can be effective at increasing body weight or antler quality if soils only limit the abundance of high-quality forages (Simard et al. 2008, Hefley et al. 2013). Alternatively, if soils limited forages from being high quality, then animals could not obtain a diet high enough in quality to meet peak growth requirements regardless of competition, so management strategies that manipulate forage per animal would not be as effective. Because management of ungulate populations increasingly is focused on desirable individual physical qualities (Hamilton et al. 1995), the distinction between the role of soils in deer nutrition is important. Common management strategies that rely on concepts of density dependence to manage populations (i.e. quality deer management in North America; Hamilton et al. 1995) may be ineffective if high quality forages cannot be produced (Shea et al. 1992).

To determine which hypothesis was supported in a soil region previously reported below the lower threshold of soil productivity (i.e. soil quality limits forages from being high enough quality to support density-mediation; Keyser et al. 2005), we tested whether soil quality limits forage quality by collecting forage samples from 72 genera. We compared the nutrient levels in selected and non-selected forages to the nutritional requirements of lactating white-tailed deer to evaluate whether deer would be able to meet their dietary nutritional requirements of peak lactation (i.e. support maximum growth of two fawns) if forage availability was not limiting intake. Further, we compared body weights of hunter-harvested yearling males over a high and low population density. Our results would support hypothesis 1 if forage quality did not meet the nutritional requirements of peak lactation and body weight did not respond to changes in density. Our data would support hypothesis 2 if forage quality did meet the nutritional requirements of peak lactation and body weight did respond to changes in density.

Material and methods

Study area

Fort Bragg Military Installation (Fort Bragg; 73 469 ha) was located in the Sandhills physiographic region in the northern-most remnants of the longleaf pine *Pinus palustris* ecosystem in North Carolina (35.1°N, 79.2°W). Fort Bragg managed most forested stands on a 3-year growing-season fire-return interval (Lashley et al. 2014b). The Sandhills region has been described as extremely poor productivity for white-tailed deer (Shea and Osborne 1995). Further, Perry and Amacher (2007) reported soils in the Sandhills region rank in the lower 20% in terms of productivity in the US. They based this rank on an index developed by Amacher et al. (2007), incorporating 19 variables of soil quality from soil nutrient analyses. However, to ensure soils at Fort Bragg ranked similar to these other reports for the Sandhills region, we pooled 10 soil samples at each of seven sites randomly located across Fort Bragg and performed a soil nutrient assay. We used results from the assay to rank soil productivity at Fort Bragg in comparison to soils across the US according to the soil quality index as reported in Perry and Amacher (2007). We confirmed that Fort Bragg scored an 8 out of 26 on the soil quality index, which is lower in productivity than $>$ 80% of the soil classes ranked on this scale in the US. Additionally, high-quality forage quantity at Fort Bragg was relatively low in comparison to reports in higher productivity soils (Edwards et al. 2004, Jones et al. 2009, Shaw et al. 2010, Lashley et al. 2011, Lashley 2014).

Deer densities were estimated using spotlight surveys during 1984–1990 (13–17 deer km^{-2}) and 2000–2010 (3–5 deer km^{-2}) in accordance with methods suggested by McCullough (1982) to standardize sources of variance for relative comparison among years (Fort Bragg Military Installation Wildlife Branch, unpubl. data). Deer harvest adjusted to hunter effort indicated deer density declined by 30–60% from 1989 to 2010 (J. Jones and C. Brown pers. comm.). There were no apparent changes in habitat quality between the time periods or changes in hunter selectivity of yearling males (J. Jones and C. Brown pers. comm.). White-tailed deer density declines were concurrent with the establishment of coyotes *Canis latrans* and likely resulted from the high predation rates on adult females and neonates (Chitwood et al. 2014a, 2015a, b). Our intention was to use these density measures to compare relative density at the study site, not to report an accurate density estimate. Methods to estimate deer density each have unique limitations, so we used a combination of methods to demonstrate density declines on Fort Bragg over the two time periods (Imperio et al. 2010, Collier et al. 2013). Therefore, we assumed white-tailed deer density was lower in 2000–2010 than 1984–1990 because methods to estimate deer density showed consistent results across the two time periods.

The average winter temperature was 6.9°C and the average summer temperature was 26.0°C. Average yearly rainfall was 120 cm, average yearly snowfall was 7.5 cm, and there were ~175 frost-free days per year (Sorrie et al. 2006). Primary forest types included longleaf pine, upland hardwoods and bottomland hardwoods, with managed openings intermixed (see Sorrie et al. 2006 for detailed floristic accounts).

Plant collection and analyses

During June, July and August of 2011 and 2012, we collected samples from 72 genera (28 forbs, 18 trees, 12 shrubs, 8 grasses, 6 vines). We collected only physiologically young plant parts to mimic herbivory of deer (Lashley et al. 2014a). Plants were bagged in paper sacks and immediately transported to a dryer. We dried forages at 47°C, weighing forages every 12 h until they reached constant mass (Lashley et al. 2014a). Dried samples were shipped to the Clemson Univ. Agricultural Service Laboratory, which is certified by the National Forage Testing Association. A full nutrient array was performed yielding crude protein (CP), phosphorus (P), calcium (Ca), acid detergent fiber (ADF), and neutral detergent fiber (NDF) content. We calculated gross energy (GE) of each plant based on equations developed by Park et al. (2012). Though their study was on feedstuffs for domestic swine, the equations they used to calculate GE yielded lower values (3.7 kcal g^{-1}) than recommended in the literature (i.e. 4.4 kcal g^{-1}, Hewitt 2011); therefore, we assumed our GE calculations were conservative. We calculated digestible energy (DE) by multiplying GE by dry matter digestibility (DMD) which we calculated in accordance with equations developed by Robbins et al. (1987) and Hanley et al. (1992) for white-tailed deer. Lignin values are relatively low in physiologically young plant tissues, especially in forbs (Ball et al. 2007), so we used lignin values reported in Robbins et al. (1987) for older plant tissues (i.e. 11% late-cut alfalfa *Medicago sativa*) to ensure DMD estimates were conservative. We did not adjust CP levels for condensed tannins because prevalence of condensed tannins in forages of the southeastern United States was reported minimal (Jones et al. 2010a). Moreover, because white-tailed deer generally avoid foods high in condensed tannins, our treatment of tannins in forages provides a conservative estimate of the magnitude of difference between selected and non-selected diets (Hofmann 1989).

We randomly placed 60 50-m line transects to determine plant selection by deer at Fort Bragg during mid-June and 60 during mid-August of 2011. Three plot centers were located at 10, 25 and 40 m along the transect ($n = 360$), and we recorded all stems of each species (i.e. availability) and number of stems browsed (i.e. use) in a $1.5 \times 1.2 \times 1.2$ m plot (Lashley et al. 2011). We used the structure of damage in remaining forage tissues and the foraging ecology of deer and other wildlife to distinguish herbivory between wildlife species (Lashley et al. 2014b). We calculated a selection index (Chesson index; Chesson 1978, 1983, Edwards et al. 2004, Lashley et al. 2011, Lashley and Harper 2012) by dividing the ratio of use and availability for a given species by the sum of ratios for all species (index cutoff value = 0.007). This allowed us to group plants based on the selectivity of white-tailed deer on the site. Further, we grouped selected and non-selected plants into the appropriate forage classes (i.e. Forb, Shrub, Tree and Vine). We did not include grasses in subsequent analyses because none were selected at Fort Bragg as indicated by the selection transects (i.e. bite count surveys). Also, we did not include fruits in the bite count surveys because fruits that are readily eaten by deer were low in abundance at Fort Bragg (Lashley 2014). Further, our subsequent estimations of digestible energy intake are increasingly more conservative as intake of fruits increased because of the high concentration digestible energy in most fruits (Short and Epps 1976).

We compared nutrient levels within selected and non-selected forages with and without considering forage class. Also, we compared nutrient levels in selected forages to the requirements of an adult female white-tailed deer with single and twin fawns during peak lactation, which represents the most nutritionally demanding physiological condition in white-tailed deer (Hewitt 2011). Therefore, using lactation requirements is the most stringent metric to test for limiting nutrients.

We used an intake of 4.8% body weight or 2.16 kg day^{-1} (dry matter) for a 45 kg animal (National Research Council 2007), which is the physiologically limited dry matter intake for white-tailed deer during peak lactation. Our intention with this calculation was to measure whether forage quality is high enough for white-tailed deer to meet their peak lactation requirements when forage quantity is not limiting, and not to conclude whether deer were actually meeting their nutritional requirements during the study. By assuming forage availability was not limiting forage intake, we were able to explicitly compare forage nutritional quality to white-tailed deer physiological requirements (hypothesis 1). We calculated each nutrient requirement as a function of the maximum physiologically possible intake for a 45 kg female deer during lactation. The basal metabolic rate (BMR) of mammals is estimated at 70 kcal $kg^{-0.75}$ day^{-1} (Kleiber 1961). Minimum energy requirements for peak lactation with a single deer fawn are $3.49 \times$ BMR and $4.73 \times$ BMR with twins (National Research Council 2007). Therefore, a 45 kg female with 1 fawn would require 1.96 kcal g^{-1} of forage (i.e. $3.49 \times (70 \times 45^{75})/2160$) or 2.66 kcal g^{-1} with twin fawns. Crude protein requirements have been reported as 14 g CP/100 g of dried forage for one fawn and 19 g CP/100 g of dried forage (i.e. 216 g day^{-1} for body maintenance and an additional 203 g day^{-1} for sufficient milk production) for two fawns at the maximum daily intake of 2.16 kg (National Research Council 2007, Hewitt 2011). The calcium requirement for a female with twin fawns during peak lactation is 0.038 g g^{-1} and the phosphorus requirement is 0.035 g g^{-1} at the given intake rate (National Research Council 2007, Hewitt 2011). The phosphorus requirement for lactation with one fawn is suggested to be near 0.025 g g^{-1} (McEwen et al. 1957, Barnes et al. 1990).

We used a general linear model in SPSS (2008) to test for differences between each nutrient level within selected and non-selected forages and between each nutrient level within selected and non-selected forages by forage classes. We used a conservative Tukey's mean separation test when interactions were detected. We used a log transformation to correct for non-normality when necessary.

Body weight collection and analysis

We obtained body weight measurements from all harvested yearling males at Fort Bragg during 1984–1990 ($n = 996$) and 2000–2010 ($n = 1867$). We used yearling males because the tooth wear and replacement technique may not accurately assign older age classes (Gee et al. 2002), and yearling males were the best indicators of density as reported in Keyser et al. (2005). We used a general linear model in SPSS (2002) to test for differences in body weight between periods. We used a conservative Tamhane's T2 mean separation test, which does not assume equal variances, when interactions were detected.

Results

Deer selected plants on average should meet their DE and Ca requirements of lactation for two fawns and CP requirements of lactation for one fawn assuming that forage intake was not limited (Table 1). Deer selected forages high in P 10 times more than expected. The magnitude of selection of forages high in P, without regard to forage class, may indicate deer had the ability to adjust selectivity of plants to

Table 1. Mean (SE) digestible energy (DE), crude protein (CP), phosphorus (P), and calcium (Ca) in selected and non-selected forages at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

	Requirements			
Nutrient	One fawn[a]	Two fawns[a]	Selected[b]	Non-selected[b]
DE[c]	1.96	2.66	3.36 (0.05)	3.34 (0.04)
CP[c]	14	19.40	14.22 (0.51)	11.25 (0.34)
P[c]	0.25	0.35	0.18 (0.01)	0.15 (0.01)
Ca[c]		0.38	0.71 (0.04)	0.56 (0.03)

[a] requirement for a female white-tailed deer during peak lactation with a given number of fawns.

[b] selected forages were selected as or more than available and non-selected forages were selected less than available.

[c] digestible energy is reported as kcal g^{-1}; crude protein, phosphorus, and calcium are reported as percent of dry matter.

capitalize on high concentrations of nutrients that are limited in the majority of available forages. We failed to detect a difference in DE between selected and non-selected plants ($F = 3.2$, $p = 0.15$). However, selected forages had greater levels of CP ($F = 22.5$, $p < 0.01$), P ($F = 4.7$, $p = 0.03$) and Ca ($F = 17.9$, $p < 0.01$) than non-selected forages.

Digestible energy was similar in selected and non-selected forbs ($p = 0.37$), shrubs ($p = 0.92$), vines ($p = 0.68$) and trees ($p = 0.48$) (Table 2). There was no difference in CP between selected and non-selected shrubs ($p = 0.32$), trees ($p = 0.98$) or vines ($p = 0.97$); however, deer selected forbs with greater CP ($p = 0.02$) relative to other forbs available (Table 2). There was no difference in Ca between selected and non-selected forbs ($p = 0.99$), shrubs ($p = 0.99$) or vines ($p = 0.81$); however, deer selected trees with greater Ca ($p < 0.01$) relative to other trees available (Table 2). There was no difference in P between selected and non-selected forbs ($p = 0.87$) or vines ($p = 0.91$); however, deer selected shrubs with greater P ($p < 0.01$) and trees with lower P ($p = 0.03$) relative to non-selected shrubs and trees available (Table 2). The general linear model revealed body weight of yearling males was 7.3% greater at the lower deer density (40.4 kg versus 43.7 kg) ($F = 278.3$, $p < 0.01$) indicating deer morphometrics at Fort Bragg were density-mediated.

Table 2. Measure of digestible energy (DE), crude protein (CP), phosphorus (P), and calcium (Ca) in forages selected and non-selected by white-tailed deer in each forage class at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Nutrient[a]	Forage class	Selected	Non-selected
Digestible energy	Forb	3.42 (0.08)	3.28 (0.05)
	Shrub	3.34 (0.09)	3.27 (0.08)
	Tree	3.24 (0.04)	3.33 (0.11)
	Vine	3.27 (0.08)	3.30 (0.10)
Crude protein	Forb[b]	16.81 (0.77)	12.11 (0.55)
	Shrub	11.34 (0.81)	8.95 (1.00)
	Tree	10.21 (0.59)	12.57 (0.60)
	Vine	13.80 (0.99)	11.38 (0.72)
Phosphorus	Forb	0.185 (0.012)	0.152 (0.008)
	Shrub[b]	0.164 (0.018)	0.099 (0.015)
	Tree[b]	0.122 (0.013)	0.187 (0.011)
	Vine	0.221 (0.025)	0.164 (0.017)
Calcium	Forb	0.737 (0.054)	0.796 (0.060)
	Shrub	0.534 (0.068)	0.536 (0.057)
	Tree[b]	0.951 (0.174)	0.468 (0.042)
	Vine	0.643 (0.067)	0.950 (0.159)

[a] digestible energy is reported as kcal g^{-1}; crude protein, phosphorus and calcium are reported as percent of dry matter.

[b] indicates deer selected and non-selected forages were different at alph = 0.05.

Table 3. Genera meeting the crude protein (CP) or phosphorus (P) requirements of lactation for twins at Fort Bragg Military Installation, North Carolina, 2011 and 2012.

Genus	Forage class	CP	P	Deer selection[a]
Ambrosia sp.	Forb	27.5	0.45	+
Chamaechrista sp.[b]	Forb	19.7		+
Clitoria sp.[b]	Forb	25.1		+
Cnidosculus sp.	Forb	20.4		=
Desmodium sp.[b]	Forb	21.9		+
Galactia sp.[b]	Forb	22.0		+
Lupine sp.[b]	Forb	20.3		–
Phytolacca sp.	Forb	28.6	0.38	+
Tephrosia sp.[b]	Forb	21.0		–
Callicarpa sp.	Shrub	24.3	0.45	+
Gleditsia sp.[b]	Shrub	23.0		+
Acer spp.	Tree		0.38	=
Magnolia sp.	Tree	20.4		=
Prunus sp.	Tree	29.5	0.44	+
Smilax spp.	Vine	24.7	0.47	+
Vitis spp.	Vine		0.36	+

[a] a + indicates deer selection greater than expected, an = indicates deer selection as expected, and a – indicates deer selection less than expected.

[b] leguminous genus.

Of the 72 forages collected and analyzed, 14 genera met the CP requirements and eight genera met the P requirements to support lactation for twins (Table 3). Of the 16 genera that met one or both of the nutrient requirements, seven were leguminous. However, none of the legumes met the P requirements. Five genera met CP and P requirements of lactation for two fawns. Deer relied heavily on these species because on average they selected them ~10 times more than expected.

Discussion

Our results support hypothesis 2, that soil productivity limits the abundance of high quality forages but does not limit forages from being high quality, because some plant taxa exceeded the nutritional requirements of lactation. Although deer-selected plants on average did not meet the CP and P requirements for females with two fawns, several individual plant taxa did meet these requirements. Deer tended to select these high-quality forages (i.e. high in P) at much greater rates than less nutritious forages, but the quantity of these high-quality forages often was quite limited on the study site (Lashley 2014). Selection for forages high in P may be common in poor soil regions where P commonly is limited in forages (Grasman and Hellgren 1993). However, CP is less likely limiting in marginal conditions because ruminants are capable of making their own proteins when they have sufficient DE and a source of nitrogen in their diet (Hewitt 2011). All plant taxa we collected on Fort Bragg met DE and Ca lactation requirements for two fawns, indicating they would not be limiting regardless of deer selectivity.

As evidence that quantity of high-quality forage is a limiting factor on poor soils, radiocollared fawns at Fort Bragg had high starvation rates (29% of fawns monitored) and 0 of 23 sets of twins had both individuals survive (Chitwood et al. 2014b, 2015b). Although some high-quality forage plant species were available across the study site, females apparently were not able to intake enough high-quality forage to meet their lactation requirements. Therefore, because poor soils limit the availability of high-quality forages, management practices that increase the quantity of selected forages with high P, particularly plants also high in CP, may be most important for the conservation of herbivores in nutrient-poor soils (Chapin 1980, Biere 1995, Fraser and Grime 1998). Because some land uses can increase forage available by an order of magnitude, they may be particularly effective in managing ungulate populations where high-quality forage is limited (Lashley et al. 2011, Hefley et al. 2013).

Deer likely selected for forage qualities other than DE because DE was not limiting in any forage we sampled at Fort Bragg (Jones et al. 2010b). Therefore, in support of hypothesis 2, the only limitation of DE in the diet would stem from low quantity of high-quality forage and not low DE in the forages. Although DE may be limited in arid (Meyer et al. 1984) and boreal (Parker et al. 1999) environments, forage selection by ungulates may be predominantly driven by mineral requirements, even at the cost of reducing energy or protein intake when forage quality is poor during the growing season (Belovsky and Jordan 1981, Ben-Shahar and Coe 1992). Our results support the notion that DE is unlikely a limiting factor during the lactation period on our study area because other nutrients such as P will be limiting first.

Body weight of yearling males was greater at the low density than the high density, indicating body weight was density-mediated at Fort Bragg. The increase in body weight demonstrated that forage quantity and not forage quality was the limiting factor. If forage quality was limited by soil productivity, deer weights would not have shifted with changes in density because there would have been no high-quality resources to compete over (Shea et al. 1992). Keyser et al. (2005) concluded body weight at Fort Bragg was not density-mediated based on their analysis across 15 years with a reported range in density from 6–10 deer km^{-2}. We suspect that deer density was too high at each end of the range in their study to demonstrate a change in body weight or the density did not change enough to affect deer body weights. This may highlight an important difference between high- and low-quality soils – that density dependence may only be evident in a range of relatively low densities for poor soil regions in comparison to more fertile areas. Similarly, Shea et al. (1992) reported body weight of yearling males did not increase in response to an estimated 75% reduction in population density in the Florida flatwoods region, which is characterized by poor soil productivity. They suggested the insensitivity of body weight to density reductions was a result of the poor quality of forages on site. Based on our results, forage quality on poor sites like Fort Bragg should allow density-mediated body weight responses as long as high-quality forage availability is not limiting at lower densities. Thus, any insensitivity of body weight to changes in density is because soil productivity determines the overall forage availability (Polis 1999), rather than forage quality as suggested previously.

Our study provides an interesting insight into mechanisms behind density-mediation. Poor quality soils may produce and maintain a high biomass of vegetation, but the overall quality of the vegetation is poor as a result of species composition (Polis 1999). Thus, a wide range of deer densities can be sustained at maintenance nutritional levels. This phenomenon has been demonstrated in a long-term study on the Haida Gwaii archipelago (Canada), where deer populations were sustained at high densities for decades despite the depletion of high-quality forages on the landscape (Saout et al. 2014). However, because soils do not limit forages from being high-quality, low quantities of high-quality forage may persist on the landscape and allow density-mediation at a range of low densities.

Conclusions

Poor soil productivity is widely accepted as limiting to the demography of ungulates, specifically because high quality forage cannot occur on low quality soils. However, our data indicate poor soil productivity has a greater effect on high-quality forage quantity, which limits ungulates via the interaction of forage availability and ungulate density (i.e. density mediated). This is in contrast to the previously accepted idea that poor soils translate to poor forage quality, which in turn limits peak genetic expression at any density. Because morphometrics are density-mediated on poor sites, management strategies that adjust the amount of forage per animal to promote desirable herd characteristics can be effective, though at lower densities than on more fertile soils. Conservation efforts should focus on managing ungulates within the nutritional constraints of existing habitat. Attention should be on high-quality forage quantity and its relationship with ungulate density.

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