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Influence of Summer and Autumn Nutrition on Body Condition and Reproduction in Lactating Mule Deer

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ABSTRACT Recent work suggests that availability and quality of forage in late summer and early autumn, a time when female ungulates face multiple energetic demands, is critical to reproduction in wild ungulates. Therefore, we examined direct links between nutritional quality of diets, body condition, and reproduction of lactating mule deer. Using captive mule deer, we tested the hypothesis that females consuming diets with lower digestible energy (DE; kJ/g) would have lower DE intake rates (DEI; MJ/day), have less body fat and muscle, have later estrus cycles, and have lower pregnancy and twinning rates. Deer fed lower DE diets had lower DEI during summer and autumn. In turn, deer with lower DEI, regardless of diet DE, had lower body mass, body fat, and muscle thickness. When nutritional quality of diets began to decline earlier in the summer, relationships between food quality, DEI, and body condition were stronger. Although DEI did not influence estrus date for deer that became pregnant before 21 December, deer with lower DEI had a lower probability of becoming pregnant and had a lower probability of producing twins. Measures of body condition in October (i.e., body mass, body fat, and muscle depth) predicted pregnancy and twinning rates in mule deer. Serum concentration of hormones leptin and Insulin Growth Factor 1 were not good predictors of body condition or reproduction. These findings suggest that managers concerned with productivity of mule deer populations should consider focusing on assessing and improving quality of forage available in summer and autumn.

KEY WORDS body condition, Insulin Growth Factor 1, intake, lactation, leptin, mule deer, nutrition, *Odocoileus hemionus*, pregnancy, reproduction.

Herbivores survive on foods low and variable in nutritional quality; thus, nutrition has long been recognized as a factor influencing ungulate populations (Pederson and Harper 1978, Van Soest 1996, Beck et al. 2006). The amount of energy and nutrients available and consumed by ungulates can affect both survival and reproduction (Mduma et al. 1999, Cook et al. 2004a). Because winter starvation is the most visible effect of nutrition on wild ungulates, research and management has typically focused on winter nutrition and forage quality (Gray and Servello 1995, Fauchald et al. 2004, Parker et al. 2005, Page and Underwood 2006, and Sauve and Cote 2006). However, research with elk (*Cervus elaphus*; Cook et al. 2001, 2004a), red deer (*C. elaphus*; Loudon et al. 1983), caribou (*Rangifer tarandus*; Cameron and Smith 1993, Adams and Dale 1998, Russell et al. 1998), white-tailed deer (*Odocoileus virginianus*; Verme 1969, White 1992), muskoxen (*Ovibos moschatus*; Adamczewski et al. 1998), cattle (Randel 1990), and sheep (Sosa et al. 2004) suggests that forage quality and nutrient intake during summer and autumn may have even greater effects on ungulate populations than in winter. During summer and autumn, females are subjected to multiple demands, such as lactation, building body reserves for surviving winter, and consuming enough energy for estrus and conception. Poor

nutrition or body condition in ungulates can adversely affect hypothalamic–pituitary function (Cupps 1991, Schillo 1992, Wade et al. 1996), delay puberty (Senger 1999), prevent ovulation (Tanaka et al. 2003), reduce pregnancy rates (Folk and Klimstra 1991, Mani et al. 1996, Tanaka et al. 2003), and reduce production of offspring (Adamczewski et al. 1998, Russell et al. 1998, Cook et al. 2004a, b). Low body fat reserves, especially in lactating animals, may also increase probability of terminating pregnancy shortly after breeding (Sosa et al. 2004).

Although wildlife agencies in the western United States are concerned about declining mule deer (*Odocoileus hemionus*) populations (Gill et al. 2001, Andelt et al. 2004, Wasley 2004), little research has examined links between nutrition during lactation and subsequent reproduction in mule deer (but see Sadleir 1982). However, deer populations and fawn recruitment have been indirectly correlated with forage quality in Oregon (Peek et al. 2002), Arizona, Texas (Marburger and Thomas 1965, Anthony 1976, Lawrence et al. 2004), Utah (Pederson and Harper 1978), and Washington (Gilbert and Raedeke 2004), USA. Because nutrition often acts in a compensatory way with many other mortality factors like predation and disease (Gill et al. 2001), understanding individual effects of nutrition on wild ungulate populations requires separating nutrition from other potential effects under controlled conditions. Therefore, we examined direct links between summer and autumn nutrition and reproduction using controlled pen experiments

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with captive mule deer designed to simulate effects of declining forage quality over summer and autumn in a year in which nutritional quality declines early in the season and in a year in which the decline occurs later in the season.

Specifically, we tested the hypothesis that nutritional quality of forage (i.e., digestible energy [DE] content; KJ/g) would influence daily DE intake (DEI; MJ/day) of lactating females. In turn, we expected that animals with higher DEI would have higher body condition, earlier estrus, greater pregnancy rates, and larger litter sizes. We sought to determine whether measures of body condition (i.e., body mass, body fat, muscle depth) or blood hormones associated with nutritional and reproductive status (i.e., leptin and Insulin Growth Factor 1 [IGF-1]) are useful for predicting pregnancy and litter size in mule deer.

STUDY AREA

We conducted our experiments with captive mule deer at the Washington State University (WSU) Wild Ungulate Facility (WUF) in Pullman, Washington, USA. The Wild Ungulate Facility contained 3 0.2-ha fenced treeless grass pastures, each of which included a covered feeding area and one 3-m^3 covered shelter. To limit the amount of natural vegetation consumed by deer during experiments, we mowed and scraped pastures to ground level as needed throughout the experiment (approx. monthly) from June to October so that their pastures were devoid of substantial vegetation.

METHODS

We obtained male and female mule deer used in our experiments from eastern Washington between May and June 2002 as 0–14-day-old fawns by spotting them from the ground or helicopter and hand-capturing them (Johnstone-Yellin et al. 2006). We hand-raised and habituated all deer to experimental protocols. During their second autumn (2003), we bred yearling females by yearling males. Females gave birth between May and July 2004. We assigned 24 females and their fawns to 1 of 3 nutritional treatments for the late decline experiment beginning in August 2004 (Fig. 1). We stratified groups of 8 so that each treatment group would have equal body mass, litter sizes, and sex ratios of fawns at the beginning of the experiment (Table 1). Following the late decline experiment in June 2005, we randomly stratified 24 lactating females (20 of which we used in the previous yr) and their fawns to 1 of 3 nutritional treatments (we randomly assigned only 6 of 20 deer to the same treatment group as the previous yr: 3 high, 2 medium, 1 low). Because of limitations of facility space, we used some animals in both years of experiments; thus, we acknowledge that there is not complete independence between experimental years. Although we swapped pens used for the high and low nutritional treatments between the late and early decline experiments and pens were virtually identical, we were unable to measure any influences caused by individual pen assignments.

We applied 3 nutritional treatments in both the late and early decline experiments by varying fiber content, and thus the DE content, of completely balanced grain–alfalfa herbivore pellets milled at the WSU Animal Science Feed Preparation Laboratory (Table 2; for ingredients see Tollefson 2007). We selected DE values to mimic natural declines in vegetation available to mule deer and other cervids of temperate North America at the end of summer (Hodgman et al. 1996, Van Soest 1996, Cook et al. 2004a). The high-DE treatment offered a high-DE diet (14.0 kJ/g) that remained constant throughout the summer and autumn (Fig. 1). Digestible energy content of the diet declined from a high of 14.0 kJ/g to a low of 11.9 kJ/g and 9.8 kJ/g in the medium- and low-DE groups, respectively (Fig. 1). For the late decline experiment, high and low DE occurred on 5 August and 13 September 2004, respectively; for the early decline experiment, high and low DE occurred on 29 June and 28 September 2005, respectively. The medium- and low-DE groups remained at those levels for the rest of the experiment, which ended on 4 November in both years. We began recording intake and body mass 2 weeks before declines in DE began, resulting in 12 weeks and 18 weeks of data for the late decline and early decline experiments, respectively; thus, the early decline and late decline experiments began on week 1 and week 5, respectively (Fig. 1). Because we focused on effects of late-summer and early autumn nutrition on pregnancy and litter size, our goal during breeding season was to maintain each female's body mass at her 4 November level during breeding season until 21 December. Therefore, during the late decline experiment in 2004, we switched all animals on 4 November to the high-DE pellet and alfalfa hay fed ad libitum to ensure females did not lose mass during the breeding season. However, we found that females tended to lose or gain weight inconsistently during that period, so during the early decline experiment in 2005, we maintained all females on their nutritional treatment through breeding season until 21 December, which leveled out their body mass (Fig. 1).

We housed treatment groups separately in adjacent, identical 0.2-ha pens with automatic water troughs. We fed females in individual feeders at 0600 hours, 1200 hours, and 1800 hours in the late decline experiment and at 0600 hours and 1800 hours in the early decline year. We allowed females to feed until they were satiated and left the feeders, which lasted up to 1 hour per feeding. We group-fed fawns fed the same DE pellets as their mothers in specially designed feeders that excluded adults, but provided 24-hour access to fawns. We weighed mass of food consumed by each female daily to the nearest 0.1 g to determine dry matter intake (DMI; g/day). We weighed females to the nearest 0.1 kg each week on an electronic platform scale. We measured standing biomass of vegetation in each pen monthly by clipping 10 random plots, drying clippings at 100° C, and weighing them. In addition, we measured biomass production monthly during the growing season in exclosures within each pen.

We determined the gross energy (GE; kJ/g) content of each pelleted diet using bomb calorimetry and neutral detergent fiber (NDF; %), acid detergent fiber (%), and acid detergent lignin (%) from sequential detergent analysis
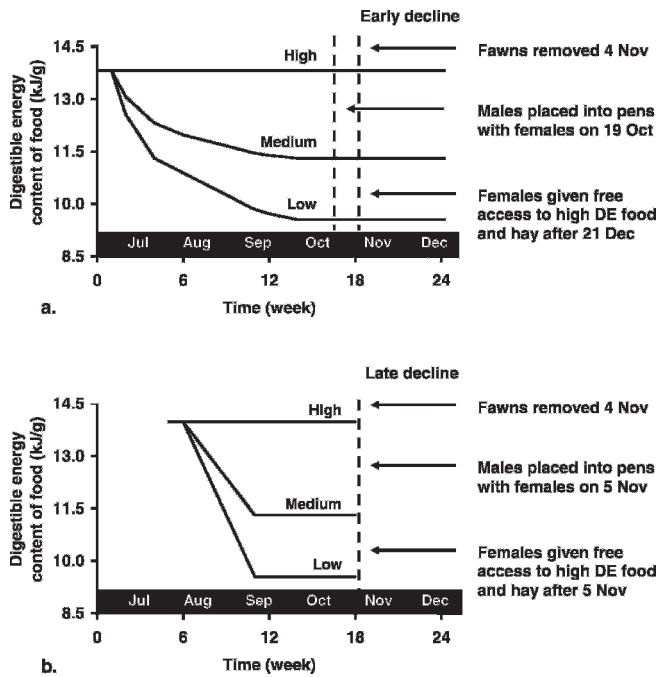
Figure 1. Feeding regime for 24 lactating mule deer, 8 of which we assigned to each of 3 nutritional treatments (high, medium, and low digestible energy [DE]) from 5 August to 2 November 2004, which simulated a late decline in nutritional quality, and 29 June to 21 December 2005, which simulated an early decline in nutritional quality, at Washington State University, Pullman, Washington, USA.

(Goering and Van Soest 1970) with filter bags, sodium sulfite, and alpha amylase (Ankom Fiber Analyzer [200/220®]; Ankom Technology, Fairport NY; Table 2). We determined nitrogen content (%) of food and feces by the Kjeldahl procedure (Bradstreet 1965) and estimated crude protein (CP) content as 6.25 times the nitrogen content (Robbins 1993). We measured in vitro dry matter digestibility (%) using an Ankom Daisy II Incubator (Ankom Technology) and rumen fluid from a fistulated cow fed grain and hay (Table 2). In addition, we conducted in vivo digestion trials with 3 nonlactating females on the high- and low-quality diets. We confined animals to digestion crates and measured the mass of pellets consumed, mass of feces produced, and volume of urine excreted over 5 days with a 14-day pretrial. We corrected mass of food and feces for dry matter. We analyzed feces for GE, CP, and NDF as previously described for food. We calculated dry matter, fiber, CP, and energy digestibility (%) as described in Robbins (1993). We calculated DE of diets from the product of in vivo digestibility and GE (Table 2), and daily DEI was the product of DE and DMI divided by 1,000. We calculated digestible protein (DP; g CP) of the diet from the product of the in vivo digestibility and CP (Table 2), and DP consumed by animals per day (DPI; g CP/day) was the product of DP and DMI.

To measure body condition and serum hormones, we anesthetized each female with 0.4 mg/kg xylazine hydrochloride and reversed them with 0.3 mg/kg yohimbine hydrochloride as needed on 16 September and 2 November in the late decline experiment and biweekly from 30 June to

5 November in the early decline experiment. We measured maximum subcutaneous rump fat thickness (MAXFAT) and thickness of the longissimus dorsi muscle between the 12th and 13th rib, adjacent to the spine (hereafter, loin depth), using a portable ultrasonograph (Sonovet 600; Medison Corp. Universal Medical, Newbedford Hills, NY [Stephenson et al. 1998, Cook et al. 2007]). We scored the rump body condition (rumpBCS) of each animal using palpation, validated for mule deer (Cook et al. 2007). We estimated body fat (y) by the equation $y = -1.3719 + 4.12406 \times (X) - 0.39389 \times (X^2) + 0.03318 \times (X^3)$ where X is rLIVINDEX, an arithmetic combination of subcutaneous rump fat thickness and the rump body condition score (Cook et al. 2001, 2007). If MAXFAT $\geq$ 0.2 cm then rLIVINDEX = (MAXFAT $-$ 0.2) + rump body condition score (rumpBCS). If MAXFAT < 0.2 cm then rLIVINDEX = rumpBCS.

While females were anesthetized, we collected 10 mL blood via a jugular puncture in a serum separator tube and centrifuged samples for 5 minutes. We poured the serum into a glass test tube and froze it at $-20°$ C until we could analyze all samples for leptin and IGF-1. We measured serum concentrations of leptin in triplicate and quantified them using a competitive, liquid–liquid-phase, double-antibody leptin radioimmunoassay procedure described previously (Delavaud et al. 2000) with one modification, whereby we substituted the primary antiserum reported by Delavaud et al. (2000) with rabbit anti-ovine leptin primary antiserum number 7105. We determined serum concentrations of IGF-1 using a competitive, liquid–liquid-phase, double-antibody IGF-1 radioimmunoassay procedure as described previously by Lalman et al. (2000).

To determine effects of the decline experiment, nutritional treatment, nutrient intake (DMI, DEI, and DPI), and body condition (body mass, body fat, and loin depth) on estrus and pregnancy, we placed one adult male mule deer in the pen with each treatment group on 5 November during the late decline experiment in 2004 and 19 October during the early decline experiment in 2005. Although breeding normally begins in mule deer in early November (Wallmo 1981), we placed males in pens with treatment groups 2 weeks earlier during the second year to ensure that we did not inadvertently delay breeding. In both decline experiments, we removed fawns from females on 4 November, by which time fawns were nearly weaned, nursing <0.5 hours/day (Tollefson 2007). From mid-October until 21 December, we observed mating behavior daily for 4 hours at dawn and 4 hours at dusk using focal animal observations from a tower 3 m above the ground. To detect whether a female was in estrus, we used observations of female behavior, such as increase in activity, pacing, urination, calling, attention toward the male, aggressiveness, or erect tails, and observations of male behavior, such as frequent and intense attention to females, guarding, checking urine, performing a Flehmen's response, and mounting. To confirm visual observations of estrus and mating, we collected fresh fecal samples on 28 September–17 December 2004 and 10 September–21 December 2005 from each female every 2 or

Table 1. Mean (±SE) characteristics of 24 lactating mule deer, 8 of which we assigned to each of 3 nutritional treatments (high, medium, and low digestible energy), before we imposed treatments on 5 August 2004, which simulated a late decline in nutritional quality, and 29 June 2005, which simulated an early decline in nutritional quality, at Washington State University, Pullman, Washington, USA.

Yr	Nutritional treatment	Body mass		Body fat		Loin muscle		Offspring born		Total fawns		Parturition date	
		kg	SD	%	SD	cm	SD	$\bar{x}$	SD	Begin	End	Jun	SD
Early decline	High	65.7	6.6	8.7	5.8	3.68	0.27	1.9	0.4	15	15	8 Jun	4.9
	Medium	65.4	3.5	9.2	6.1	3.6	0.24	1.8	0.5	14	11	8 Jun	11.2
	Low	66.7	4.8	9.1	5.6	3.5	0.24	1.9	0.4	15	10	8 Jun	9.8
Late decline	High	63.9	5.5					1.6	0.5	12	11	8 Jun	16.1
	Med	62.3	7.4					1.5	0.5	11	11	2 Jun	7.4
	Low	65.9	8.6					1.6	0.5	14	14	2 Jun	9.8

3 days, freeze-dried samples, then ground and stored them at $-20°$ C until we analyzed progesterone metabolites (progestogens) using radioimmunoassay methods similar to Munro and Stabenfeldt (1984). We used spikes in fecal progesterone to confirm date of estrus as described in Tollefson (2007) as has been used with elk (Cook et al. 2001), fallow deer (*Dama dama*; Asher and Smith 1987), and gazelle (*Nanger dama*; Asher and Smith 1987). We verified pregnancy abdominally in March of both years using a portable ultrasound machine (Sonovet 600, Medison Corp. Universal Medical).

Statistical Analysis

To determine effects of nutritional treatment and decline experiment on DMI, DEI, and DPI across the late and early decline experiments, we used repeated-measures analysis of variance (PROC MIXED, SAS v. 9.1.3; SAS System for Microsoft Windows, Cary, NC) with autoregressive error structure with a lag of one and least-squares means to examine pair-wise comparisons ($\alpha = 0.05$). Our model included decline experiment (early or late), nutritional treatment, week, and interaction terms.

We used autoregression to determine effects of nutritional treatment, decline experiment, and nutrient intake on weekly measures of body mass during both the late and the early decline experiments and biweekly measures of body fat, loin depth, leptin, and IGF-1 during the early decline experiment only. We first examined multicollinarity among variables using the Variance Inflation Factor (VIF) in the full regression model (PROC REG) and with Pearson's correlation (PROC CORR). We did not include in the

same model variables with a VIF > 10 or any pairs of variables with a significant $r > 0.5$. We then further reduced the regression model using a stepwise function with backward elimination with $\alpha = 0.15$ for entry and $\alpha = 0.15$ for retention. Finally, because we measured body mass and condition weekly or biweekly, we determined our final model using autoregression (PROC AUTOREG), with backward elimination of autoregressive terms and variable selection with $\alpha = 0.05$ for entry and $\alpha = 0.05$ for retention in the model. During the late decline experiment, we measured body fat and loin depth twice at the beginning (16 Sep) and end (4 Nov) of the trial, whereas we only measured leptin and IGF-1 once at the end of the experiment on 4 November right before breeding. Therefore, we used analysis of covariance (ANCOVA; PROC GLM) to examine effects of nutritional treatment, decline experiment, and mean DMI, DEI, and DPI averaged for October on body mass, body fat, loin depth, leptin, and IGF-1 on 4 November. We did not include variables with a significant $r > 0.5$ in the same model.

We used ANCOVA (PROC GLM) to examine effects of nutritional treatment, decline experiment, nutrient intake, body condition, and hormones leptin and IGF-1 on date of estrus for animals that became pregnant during the autumn experiment (before 21 Dec). We did not include variables with a significant $r > 0.5$ in the same model.

Finally, we used logistic regression (PROC LOGISTIC) to model relative probability of pregnancy and twinning, in relation to nutritional treatment, decline experiment, 3 measures of nutrient intake (average DMI, DPI, and DEI during Oct), 3 measures of body condition (body mass, body fat, and loin depth), and 2 hormones: leptin and IGF-1. We first assessed all one-variable models, then all combinations of uncorrelated variable sets in forward stepwise logistic regression. We considered variables too correlated to co-occur in models if Pearson's correlation coefficient (PROC CORR) of pair-wise comparisons was >0.5. We included variables in the model based on the chi-square improvement statistic, calculated as the difference between the likelihood ratios of successive models, and selected the model with the largest log-likelihood chi-square (Manly et al. 2002). The relative probability equation for the logistic model was

$$P = \frac{\exp(\beta_o + \beta_1 a + \beta_2 b \ldots)}{1 + \exp(\beta_o + \beta_1 a + \beta_2 b \ldots)},$$

where P is probability of pregnancy or twinning, β_o is a

Table 2. Nutritional composition of high-digestible-energy and low-digestible-energy pelleted diets we used for creating nutritional treatments fed to lactating mule deer at Washington State University, Pullman, Washington, USA, in 2004–2005. We created the medium-digestible-energy diet by mixing the high- and low-quality diets at a ratio of 1:1.

Nutritional parameter	High quality	Medium quality	Low quality
Gross energy (kJ/g)	18.7	18.2	17.6
In vitro digestibility (%)	69.1	61.6	54.0
In vivo digestibility (%)	74.9	65.2	55.5
Digestible energy (kJ/g)	14.0	11.9	9.8
Protein digestibility (%)	71.0	73.8	76.5
Neutral detergent fiber (%)	28.5	41.8	55.0
Acid detergent fiber (%)	25.0	29.7	34.4
Acid detergent lignin (%)	2.6	5.5	8.3
Crude protein (%)	15.6	14.7	13.7
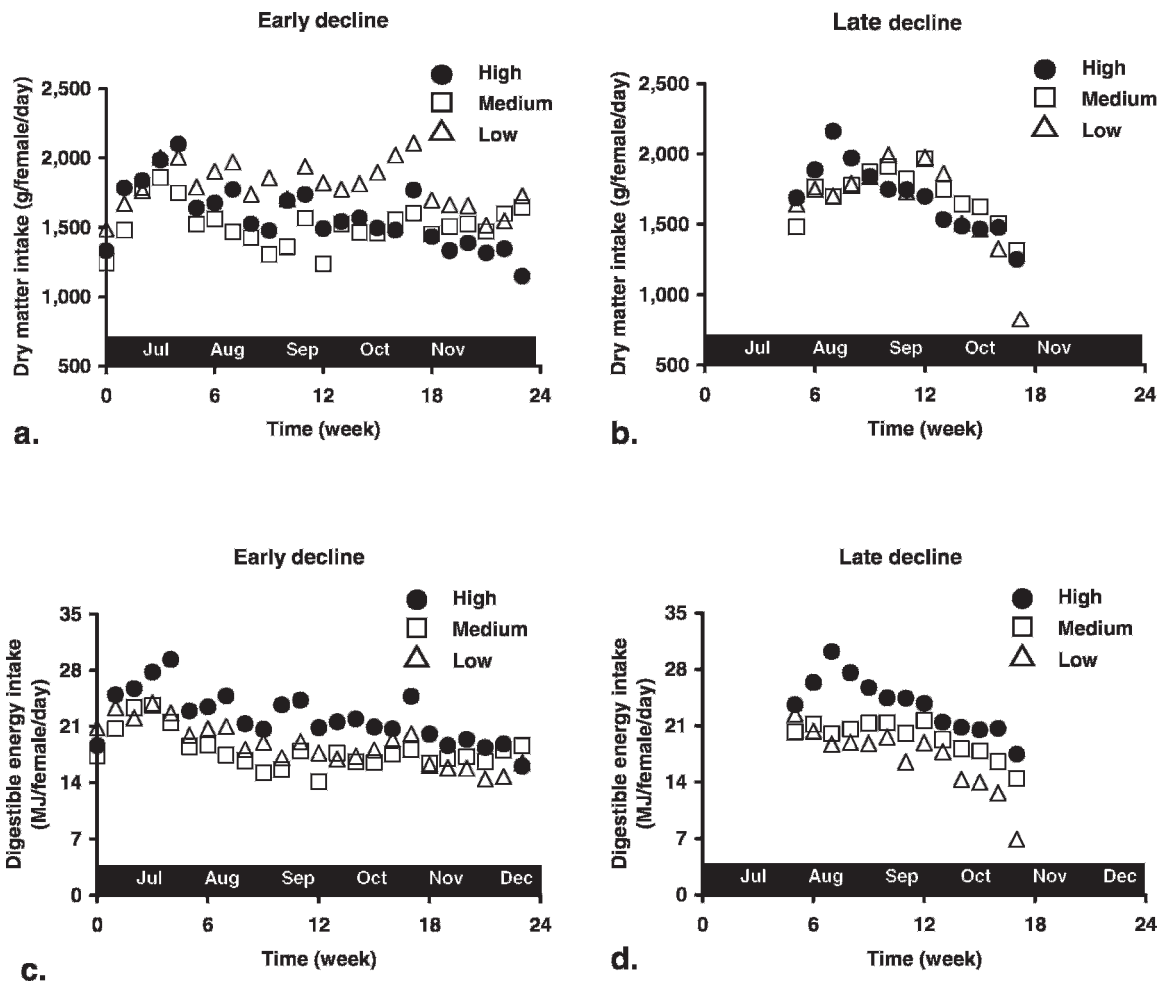
Figure 2. Mean daily dry matter (a, b) and digestible energy intake (c, d), averaged by week, consumed by 24 lactating mule deer, 8 of which we fed either high-, medium-, or low-digestible energy diets, from 5 August to 2 November 2004 (week 5–18), which simulated a late decline in nutritional quality, and 29 June to 21 December 2005 (weeks 0–24), which simulated an early decline in nutritional quality, at Washington State University, Pullman, Washington, USA.

constant, and $\beta_1 a$ to $\beta_1 k$ are parameter coefficients. For analyses we assumed that all adult deer were independent of each other between the 2 decline experiments, although we rerandomized 20 of the 24 deer among the 3 treatments and used them in both late and early decline experiments.

RESULTS

Two female deer in the low-quality treatment group died during our experiments, one by an unidentified bacterial infection on 7 October 2004 before breeding during the late decline experiment and the other by trauma from the breeding male after breeding on 29 November 2005 during the early decline experiment. Although the female in the early decline year had been bred by the male, necropsy reports could not indicate whether she had become pregnant before her death and, therefore, we removed both females from analyses regarding pregnancy.

Biomass of natural vegetation (mostly grass) available to the deer in their pens during the experiment was negligible and equal among the 3 pens, averaging only 6.34 $\pm$ 7.56 g DM/ m^2 ($F = 0.40$, $P = 0.67$). Amount of biomass production available to each female–fawn family during the growing

season ranged from 107.4 $\pm$ 27.6 g per female–fawn family per day in July to 43.4 $\pm$ 37.3 g per female–fawn family per day in September. This production amounted to 1.5–4.9% of the daily intake of each female–fawn family. Therefore, $\geq$ 95% of the diet consumed by lactating mule deer and their fawns came from the pellets we offered them.

In both the late and early decline experiments, DMI (late: $F_{12,248} = 42.29$, $P < 0.001$, early: $F_{23,481} = 18.16$, $P < 0.001$), DEI (late: $F_{12,248} = 50.03$, $P < 0.001$, early: $F_{23,481} = 29.32$, $P < 0.001$), and DPI (late: $F_{12,248} = 41.60$, $P < 0.001$, early: $F_{23,481} = 17.00$, $P < 0.001$) of lactating mule deer differed across weeks of the summer–autumn experiment. Deer DMI, DEI, and DPI generally increased for the 2–4 weeks of the experiments and then declined gradually thereafter (Fig. 2). After the experiment ended on 4 November, body mass in both the early and late decline experiments remained constant during the breeding period. Change in body mass between 4 November and 21 December averaged -0.8 ± 5.4 kg after the late decline experiment and 1.9 $\pm$ 2.5 kg after the early decline experiment. Nutritional treatment, decline experiment, and their interaction influenced nutrient intake across the
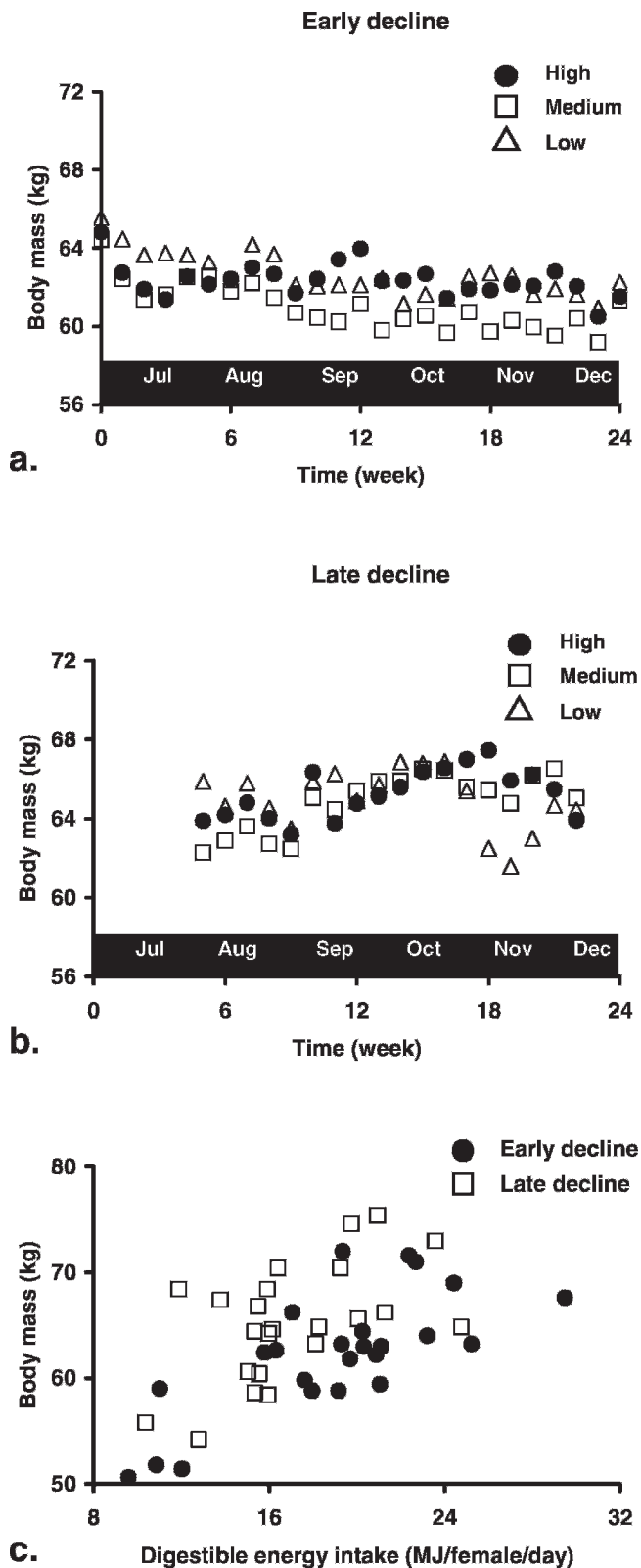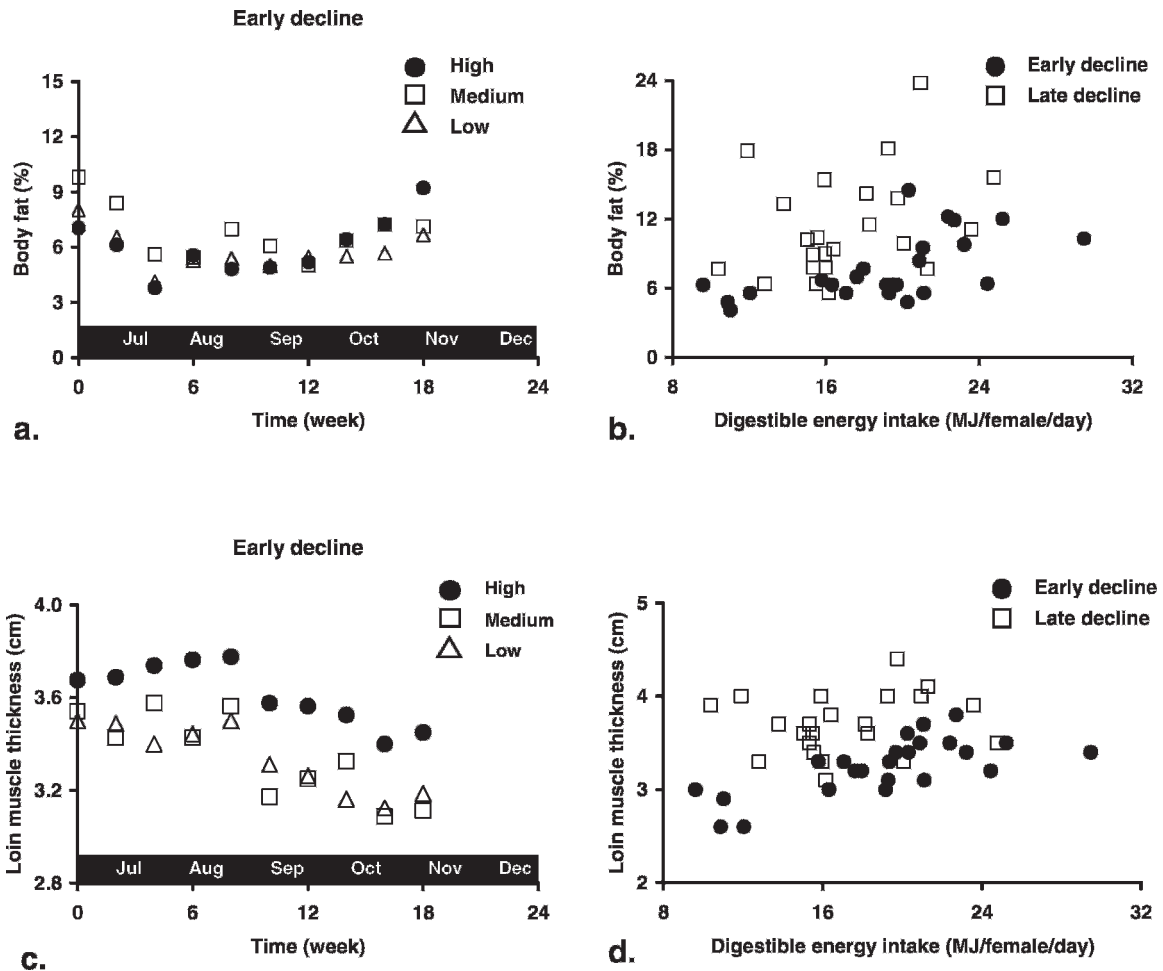
Figure 3. Mean body mass of 24 lactating mule deer fed either high-, medium-, or low-digestible-energy diets from (a) 5 August to 2 November 2004 (weeks 5–18), which simulated a late decline in nutritional quality; (b) 29 June to 21 December 2005 (weeks 0–24), which simulated an early decline in nutritional quality; and (c) the relationship between body mass and digestible energy intake during these periods at Washington State University, Pullman, Washington, USA.

experiment. When consuming medium-and low-DE diets, deer had a higher DMI and DPI in the late decline experiment than in the early decline experiment (all $F_{1,14} > 4.4$, all $P < 0.05$), but were similar between experiments for deer consuming the high-DE diet ($F_{1,14} = 1.25$, $P = 0.29$). However, DEI did not differ between late and early decline experiments on any diet (all $F_{1,14} < 4.2$, all $P > 0.06$). Dry matter intake did not differ among nutritional treatments in the late decline experiment (1,701 ± 494 g/day; $F_{2,21} = 0.02$, $P = 0.98$), whereas in the early decline experiment females on the low-DE diet ate an average of 13.1% more DM (1,785 ± 513 g/day) than those fed the high- (1,551 ± 455 g/day) or medium- (1,515 ± 451 g/day) DE diets ($F_{2,21} = 9.04$, $P = 0.02$). Deer fed the low-DE diet in the late decline experiment had a DEI of only 75% of the high-DE group's DEI (high: 23.7 ± 7.1, medium: 19.3 ± 5.2, low: 17.7 ± 5.5; $F_{2,21} = 17.60$, $P < 0.001$) and in the early decline experiment, deer fed the low-DE diet had a DEI of only 86% of the high-DE group's DEI (high: 21.7 ± 6.4, medium: 18.0 ± 5.6, low: 18.7 ± 5.7; $F_{2,21} = 11.40$, $P < 0.001$). Digestible protein intake did not differ with nutritional treatment in the late decline experiment ($F_{2,21} = 0.99$, $P = 0.30$), but in the early decline experiment, DPI was higher on the low-DE diet than in the medium-DE diet ($t = 3.05$, $P = 0.006$).

During the early decline experiment, weekly measurements of body mass declined steadily across the 12-week and 18-week experiments (Fig. 3a), whereas in the late decline experiment weekly measurements of body mass initially increased for the first 12 weeks and then decreased for the last 6 weeks (Fig. 3b). Models for predicting body mass on a weekly basis across the 12-week to 18-week early and late decline experiments were improved by including autoregressive terms with a lag time of 2 weeks. The most parsimonious model included decline experiment, nutritional treatment (low-DE diet), and DEI, with a lag time of 2 weeks (model: body mass = 6,077.00 − 3.00 × early decline experiment + 1.19 × low-DE diet + 0.143 × DEI; $R^2 = 0.17$). Body mass increased with DEI ($t_1 = 4.30$, $P < 0.001$) but was lower on the low-DE diet ($t_1 = 2.94$, $P < 0.001$) and the early decline experiment ($t_1 = 7.62$, $P < 0.001$; Fig. 3c). Likewise body mass on 4 November right before breeding increased with October DMI ($F_{1,42} = 33.12$, $P < 0.001$), DEI ($F_{1,42} = 23.44$, $P < 0.001$), and DPI ($F_{1,42} = 32.50$, $P < 0.001$) and was lower in the early decline experiment (62.37 ± 1.18 kg) than the late decline experiment (65.24 ± 1.16 kg, all $F_{1,42} > 5.15$, all $P < 0.01$). However, nutritional treatment only predicted body mass when included in the model with DMI and decline experiment ($F_{1,42} = 4.82$, $P = 0.01$). We found no interactions between nutritional treatment and decline experiment (all $F < 0.86$, all $P > 0.43$).

Biweekly measurements of body fat across nutritional treatments during the early decline experiment decreased from the start of the experiment to a low at about 10 weeks (mid-Sep) and then began to increase again until the end of the experiment (Fig. 4a). Biweekly body fat was not associated with nutritional treatment, decline experiment,

Figure 4. Mean body fat composition and thickness of longissimus dorsi (loin) muscle of 24 lactating mule deer fed either high-, medium-, or low-digestible-energy diets from 29 June to 21 December 2005, which simulated an early decline in nutritional quality, and relationship to digestible energy intake at Washington State University, Pullman, Washington, USA.

or measures of nutrient intake when accounting for autocorrelation (all $F < 0.72$, all $P > 0.47$). However, body fat on 4 November increased with October DMI ($F_{1,42} = 7.39$, $P = 0.01$), October DEI ($F_{1,42} = 7.05$, $P = 0.01$; Fig. 4b), and October DPI ($F_{1,42} = 7.67$, $P = 0.008$). Body fat was lower in the early decline experiment ($7.62 \pm 0.56\%$) than the late decline experiment ($11.26 \pm 0.93\%$, all $F_{1,42} > 14.06$, all $P < 0.001$), but nutritional treatment did not influence body fat on 5 November (all $F_{2,42} < 2.64$, all $P > 0.08$).

Biweekly measurements of loin depth declined steadily during the early decline experiment (Fig. 4c). The best model for predicting loin depth on a biweekly basis across the 18-week early decline experiment included nutritional treatment and DEI, with a lag time of 4 weeks ($R^2 = 0.40$, model: loin $= 2.79 + 0.03 \times$ DEI $+ 0.18 \times$ high-DE diet). Loin depth on 5 November increased with October DMI ($F_{1,42} = 8.36$, $P = 0.006$), October DEI ($F_{1,42} = 7.99$, $P = 0.007$; Fig. 4d), and October DPI ($F_{1,42} = 8.39$, $P = 0.006$). Loin depth was lower in the early decline experiment (3.25 ± 0.06 cm) than the late decline experiment (3.68 ± 0.07 cm, all $F_{2,42} > 28.35$, all $P < 0.001$). Loin depth

decreased from the high- to the low-DE treatment (all $F_{1,42} > 3.20$, all $P < 0.05$).

Biweekly measurements of leptin were best predicted by body fat and DMI with a lag of 2 weeks ($R^2 = 0.16$, model: $4.71 + 0.19 \times$ body fat $- 0.0014 \times$ DMI). Although serum leptin on 5 November was higher in the early decline experiment (4.02 ng/mL ± 0.45) than in the late decline experiment (1.64 ng/mL ± 0.18, $F_{1,43} = 27.41$, $P < 0.001$) and higher in the medium-DE treatment (3.76 ng/mL ± 0.73) than the low-DE treatment (2.16 ng/mL ± 0.34, $F_{2,43} = 4.62$, $P = 0.02$), measures of October nutrient intake and body condition did not influence serum leptin values on 5 November (all $F_{1,42} < 1.21$, all $P > 0.28$). There was no significant decline experiment $\times$ treatment interaction ($F = 0.61$, $P = 0.55$). Biweekly IGF-1 generally declined across the 18 weeks of the early decline experiment. The best model for predicting IGF-1 on a biweekly basis across the 18-week early decline experiment included DEI with a lag time of 2 weeks ($R^2 = 0.09$, model: IGF-1 $= 5.50 + 0.30 \times$ DEI). On the other hand, nutrient intake, decline experiment, and treatment did not influence IGF-1 (all $F < 3.19$, all $P > 0.08$).

Table 3. A comparison of mean and standard error characteristics of body condition and digestible energy intake (DEI) among female mule deer that gave birth to 0, 1, and 2 fawns during nutritional treatments at the Wild Ungulate Facility at Washington State University, Pullman, Washington, USA, in the spring of 2004 and 2005. One female died before we could ascertain the number of fetuses. Different letters indicate significant differences among means at $\alpha = 0.05$. A and B denote significant differences between litter sizes.

Characteristic	0 fawns		1 fawn		2 fawns	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
N	6		11		29	
Body mass (kg)	59.10	4.00	64.50	1.20	64.50	1.00
Body fat (%)	7.00	1.30	7.90	0.90	10.60	0.80
Loin depth (cm)	3.07	0.20 B	3.43	0.10 B	3.57	0.06 A
DEI (MJ/day)	13.80	2.00 B	18.50	0.50 A	19.90	0.70 A

Date of estrus did not differ between decline experiments ($F = 3.40$, $P = 0.07$) but averaged 15 November ± 5.8 days. Even though the males were allowed access to females 2 weeks later in the late decline experiment than in the early decline experiment, the earliest date we recorded breeding behavior or estimated estrus from fecal progesterone was 10 November in the late decline experiment and 2 November in the early decline experiment. Nutritional treatment, October DMI, DEI, DPI, body mass, body fat, loin depth, leptin, or IGF-1 measured on 5 November did not predict date of estrus (all $F < 3.97$, all $P > 0.05$).

During the 2 years 6 deer failed to become pregnant, 11 had singles, and 29 had twins. Females with higher DEI and thicker loin depth had more fawns (Table 3). Nutrient intake, body mass, and loin depth predicted probability of pregnancy in mule deer, whereas neither blood hormones, nutritional treatment, nor decline experiment predicted pregnancy (all $\chi^2 < 3.4$, all $P > 0.05$). Body fat was not a significant factor in the model for predicting pregnancy in our captive mule deer ($\chi^2 = 1.99$, $P > 0.15$; Fig. 5a). However, DEI in October alone provided the most parsimonious model for predicting probability that a female would become pregnant (Fig. 5b), and adding measures of body condition (body fat and loin depth), concentrations of blood hormones, nutritional treatment, or decline experiment, with correlation coefficients <0.5, did not improve model fit (all $\chi^2 < 3.4$, all $P > 0.05$; Table 4).

Digestible energy intake in October and body fat and loin depth on 4 November each predicted probability that a lactating female produced twins (Fig. 5c, d; Table 5) and number of offspring born (i.e., 0, 1, 2; Table 6). Likewise, females on the low-DE treatment had a lower probability of having twins (0.36 ± 0.13 vs. 0.75 ± 0.08, $\chi^2_1 = 6.36$, $P = 0.01$) and had fewer fawns (1.21 ± 0.19 fawns/F vs. 1.63 ± 0.13 fawns/F, $\chi^2_1 = 4.48$, $P = 0.03$; Tables 5, 6) than females on the medium and high treatments. However, DMI, DPI, body mass, blood hormone levels, and decline
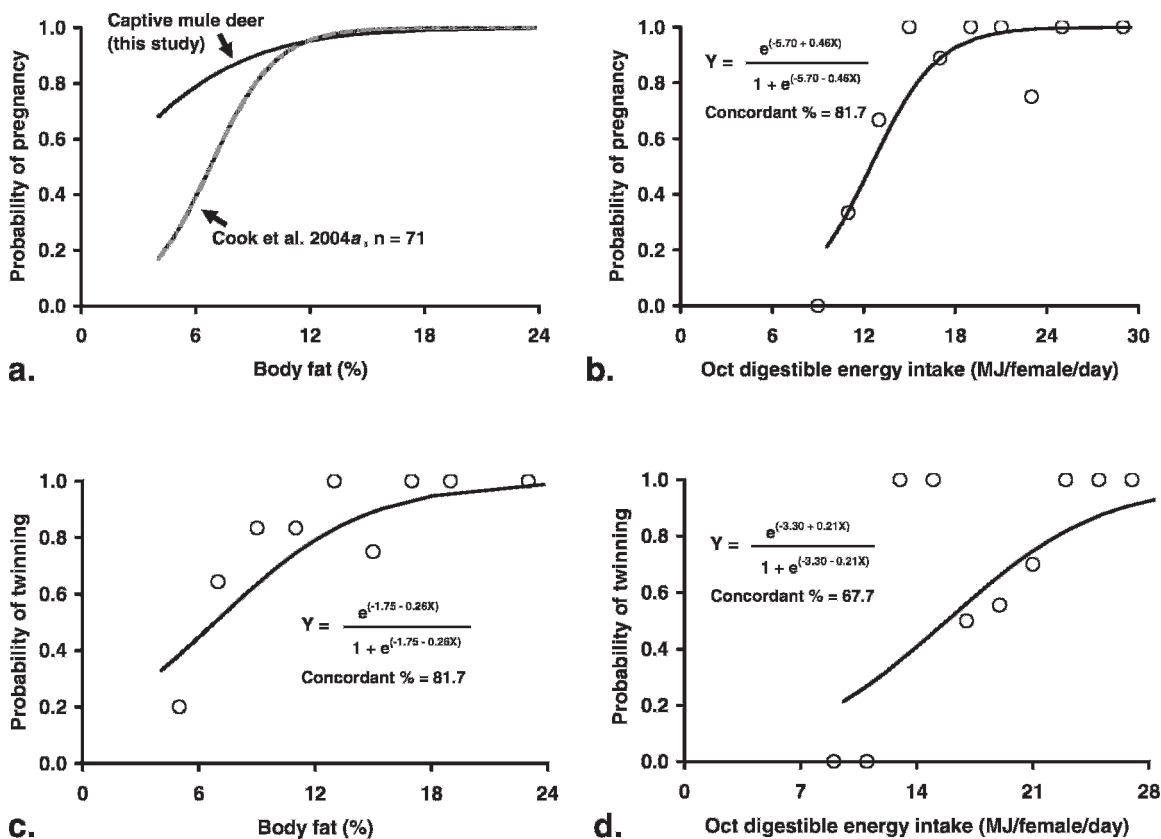
Figure 5. Probability of pregnancy (a, b) and producing twins (c, d) by 24 lactating mule deer fed either high-, medium-, or low-digestible-energy diets 5 August to 2 November 2004, and 29 June to 21 December 2005, at Washington State University, Pullman, Washington, USA, in relation to (a, c) daily digestible energy intake and (b, d) body fat composition measured on 5 November. We provide the relationship between body fat and probability of pregnancy for captive elk (Cook et al. 2004a; $n = 71$) for comparison.

Table 4. Alternative models predicting pregnancy in lactating mule deer from digestible energy intake (DEI; MJ/day), dry matter intake (DMI; g/day), digestible protein intake (DPI; g N/day), thickness of longissimus dorsi muscle (loin; mm), and body mass (kg) at Washington State University, Pullman, Washington, USA, from 5 August to 2 November 2004, and 29 June to 5 November 2005. Asterisk denotes the most parsimonious model that explains the most variation in pregnancy rates.

| Model | Likelihood ratio | | | Variables | Model parameters | | | |
	χ^2	df	P-value		β	SE (β)	Wald χ^2	P-value
DEI*	11.78	1	0.001	Intercept	−5.699	2.592	4.83	0.03
				DEI	0.457	0.165	7.65	0.006
Loin	8.51	1	0.004	Intercept	−11.535	5.406	4.55	0.03
				Loin depth	4.091	1.694	5.83	0.02
DPI	7.77	1	0.005	Intercept	−3.897	2.334	2.79	0.09
				DPI	0.038	0.016	5.52	0.02
DMI	7.08	1	0.008	Intercept	−3.537	2.284	2.40	0.12
				DMI	0.0038	0.002	5.09	0.02
Body mass	4.51	1	0.03	Intercept	−8.450	5.101	2.74	0.10
				Mass	0.168	0.084	3.95	0.05

Table 5. Alternative models predicting twinning in lactating mule deer from digestible energy intake (DEI; MJ/day), thickness of longissimus dorsi muscle (loin; mm), body fat (%), and digestible energy content of food (low-DE diet) at Washington State University, Pullman, Washington, USA, from 5 August to 2 November 2004, and 29 June to 5 November 2005. Asterisk denotes the most parsimonious model that explains the most variation in pregnancy rates.

| Model | Likelihood ratio | | | Variables | Model parameters | | | | |
	χ^2	df	P-value		β	SE (β)	Wald χ^2	P-value	Odds ratio
Loin depth, low-DE diet*	11.18	2	0.004	Intercept	−6.038	3.462	3.04	0.08	
				Low-DE diet	−1.630	0.731	4.99	0.03	5.11
				Loin depth	2.080	1.014	4.19	0.04	0.13
Body fat, low-DE diet	11.60	2	0.003	Intercept	−1.015	1.061	0.92	0.34	
				Body fat	0.232	0.116	4.02	0.04	0.80
				Low-DE diet	−1.533	0.739	4.31	0.04	3.88
DEI, low-DE diet	10.97	2	0.004	Intercept	−2.529	1.826	1.92	0.17	
				Low-DE diet	−1.534	0.722	4.52	0.03	4.64
				DEI	0.196	0.094	3.90	0.05	0.82
Body fat	7.05	1	0.008	Intercept	−1.752	1.009	3.01	0.08	
				Body fat	0.259	0.116	5.02	0.03	
Low-DE diet	6.36	1	0.01	Intercept	1.099	0.408	7.24	0.007	
				Low-DE diet	−1.686	0.691	5.95	0.02	
DEI	6.21	1	0.01	Intercept	−3.304	1.716	3.71	0.05	
				DEI	0.209	0.093	5.03	0.02	
Loin	5.88	1	0.02	Intercept	−6.972	3.410	4.19	0.04	
				Loin depth	2.186	0.996	4.82	0.03	

Table 6. Alternative models predicting the number of fawns (0, 1, 2) produced by lactating mule deer from digestible energy intake (DEI; MJ/day), thickness of longissimus dorsi muscle (loin; mm), body fat (%), and digestible energy content of food (low-DE diet, high-DE diet) at Washington State University, Pullman, Washington, USA, from 5 August to 2 November 2004, and 29 June to 5 November 2005. Asterisk denotes the most parsimonious model that explains the most variation in pregnancy rates.

| Model | Likelihood ratio | | | Variables | Model parameters | | | | |
	χ^2	df	P-value		β	SE (β)	Wald χ^2	P-value	Odds ratio
DEI, high-DE diet*	17.04	2	0.001	Intercept 1	−3.284	1.785	3.39	0.07	
				Intercept 2	−5.102	1.900	7.22	0.007	
				DEI	0.374	0.111	11.38	0.001	0.69
				High-DE diet	−1.868	0.814	5.275	0.02	6.48
DEI	10.88	1	0.001	Intercept 1	−3.346	1.656	4.08	0.04	
				Intercept 2	−5.013	1.761	8.10	0.004	
				DEI	0.300	0.100	9.59	0.002	
Loin	8.98	1	0.003	Intercept 1	−7.515	3.297	5.20	0.02	
				Intercept 2	−9.14	3.393	7.26	0.007	
				Loin depth	2.813	0.998	7.95	0.005	
Body fat	7.66	1	0.006	Intercept 1	−0.335	0.986	0.12	0.73	
				Intercept 2	−1.862	0.998	3.48	0.06	
				Body fat	0.272	0.115	5.56	0.02	
Low-DE diet	4.48	1	0.03	Intercept 1	2.498	0.551	20.52	0.001	
				Intercept 2	1.023	0.399	6.60	0.01	
				DEI	−1.32	0.645	4.19	0.04	

experiment did not influence probability of twinning or number of fawns born, nor did these variables improve models containing body fat, loin, DEI, or low-DE treatment (all $\chi^2_1 < 3.4$, all $P > 0.05$). Including the low-DE treatment in the model improved predictability of body fat ($\chi^2_1 = 4.52$, $P = 0.02$), DEI ($\chi^2_1 = 4.76$, $P = 0.04$), and loin ($\chi^2_1 = 7.97$, $P = 0.005$) on probability of twinning (Table 5). Therefore the most parsimonious models for predicting probability of twinning included either body fat and DE treatment or loin depth and low-DE treatment (Table 5). The most parsimonious model for predicting number of fawns born included DEI and high-DE treatment ($\chi^2_2 = 17.04$, $P < 0.001$; Table 6). For females used in both decline experiments, litter size in the late decline experiment was not correlated with litter size in the early decline experiment ($r = 0.23$, $P = 0.31$).

DISCUSSION

Nutrition during summer and autumn influenced body condition and subsequent reproduction of lactating mule deer. Females that consumed the high-DE diet acquired more total DE/day, despite the higher DMI of deer fed the low-DE diet (i.e., early decline experiment only). Therefore, deer fed the low-DE diet that contained more plant fiber seemed unable to completely compensate for food quality by eating more. Because feeding mule deer large quantities of hay can cause omasal impaction (Schoonveld et al. 1974), we conducted our study with processed grain–alfalfa pellets with small particle sizes that may speed up passage rate through the digestive system. Therefore, any limitations on DMI caused by higher fiber in our low-DE diet would likely be exacerbated in natural forages with the same fiber content but longer fiber particles (Robbins 1993, Van Soest 1994).

The more nutrients females consumed, especially DE during the month before breeding (Oct), the more body fat, mass, and muscle depth they had just before estrus. These effects were stronger in the early decline experiment, where forage quality began to decline 1.5 months earlier than in the late decline experiment (early Jul vs. mid-Aug) and were consistent with other studies in ungulates (Robbins 1993, Chilliard et al. 1998, Senger 1999). Therefore, in dry summers in which vegetation quality declines earlier in the season, lactating mule deer would be expected to enter the breeding season, and ultimately the winter, in lower nutritional condition.

Nutrient intake, particularly DEI, and body condition (i.e., mass, body fat, and muscle stores) predicted probability of pregnancy and litter size in our lactating mule deer across decline experiments and nutritional treatments. Pregnancy rates and litter sizes were similar between decline experiments, even though we maintained deer on their respective nutritional treatments during breeding season in the early decline year, but we maintained all deer on the high-DE diet during breeding in the late decline experiment. Although DEI alone was the best predictor of pregnancy in our mule deer (Table 4; Fig. 5b), daily intake is nearly impossible to measure in wild ungulates. We found that body mass and loin depth were also reasonable predictors of pregnancy (Table 4). Our model indicated that if a female consumed <18 MJ DE/day during October, her chance of becoming pregnant began to decline, and a female was unlikely to become pregnant when consuming <9 MJ DE/day during October (Table 4; Fig. 5a). Likewise, deer weighing <60 kg or having a loin depth <3.2 cm had <80% chance of becoming pregnant (Tables 3, 4). The best models for predicting probability of having twins and number of fawns produced (0, 1, 2) included a combination of nutritional treatment (DE content of food), a measure of body condition (i.e., body fat or loin depth), or DEI (Tables 5, 6). To have >80% chance of having twins, females must have had DEI >23 MJ/day, body fat >6%, or a loin depth >3.9 mm (Fig. 5; Tables 3, 5). Although biweekly concentrations of leptin weakly reflected body fat and IGF-1 reflected DEI of our deer, neither hormone predicted pregnancy or litter sizes and, thus, were likely not useful indicators of nutritional status or reproduction in lactating mule deer.

Similar relationships between body condition and probability of pregnancy and litter size have been reported in other cervids (Ozoga and Verme 1982, Adamczewski et al. 1998, Testa and Adams 1998, Keech et al. 2000, Cook et al. 2004a). However, mule deer seem to be able to conceive at lower fat levels than can elk. For example, captive and wild elk had only a 25% chance of becoming pregnant, whereas at 5% body fat, our captive mule deer had >75% chance of becoming pregnant (Cook et al. 2004a, b). The pregnancy rate differences between these species may reflect the relative importance of DEI and body fat in reproductive physiology or real differences in life history and physiological strategies in different cervid species.

Digestible energy intake and body fat of ruminants are usually correlated and linked in complex ways to influence estrus, ovulation, and conception (Wettemann et al. 2003). However, most studies suggest that DEI, and its effects on blood glucose and insulin, rather than adipose stores themselves, trigger leptin secretion (Ingvartsen and Boisclair 2001). Leptin secretion decreases pulse frequency of luteinizing hormone (LH) and ovarian activity, influencing onset of puberty and estrus (Bronson and Manning 1991, Schillo 1992, Wade et al. 1996, Wettemann et al. 2003, Barb et al. 2005). Inadequate DEI can also disrupt the preovulatory surge of gonadotropin-releasing hormone (GnRH), decreasing the amplitude and pulse frequency of LH, interfering with both ovulation and the animal's receptiveness during breeding (Wade et al. 1996, Chilliard et al. 1998, Tanaka et al. 2003). In addition, food restriction can decrease production of progesterone receptors, thereby decreasing probability of implantation even if ovulation is not impaired (Senger 1999, Sosa et al. 2004). Restricting food for even 2 days can change mating behavior, reduce ovulation rates, and delay estrus (Morin 1986, Verme and Doepker 1988, Temple et al. 2002). However, a resumption of adequate DEI even after a period of nutritional anestrous may cause a female ungulate to resume estrous cycles (Verme 1965, Senger 1999). Livestock producers often refer to this resumption of cycling and conception following an

increase in feed intake as flushing and use this strategy with sheep and pigs before breeding to improve pregnancy rates, even when animals are in poor body condition (Church 1988, Robinson 1990). Thin wild ungulates may experience a similar increase in pregnancy following occasional autumn green-up conditions.

Differences in how nutritional quality of forage affects reproduction in elk, deer, and other wild ruminants may also be related to differences in body size and life history strategies. First, ungulates are generally considered capital breeders that rely on stored energy for reproduction (Stearns 1992). However, Andersen et al. (2000) showed that small roe deer (*Capreolus capreolus*) fall more toward the income breeder side of the continuum because roe deer use energy acquired during the reproductive period to support maternal care. Because mule deer are small and polytocous like roe deer, mule deer may also rely more on energy consumed during late pregnancy and lactation than stored fat for financing future reproduction, falling more toward the income side of the capital-income breeder continuum than do larger monotocous ungulates like elk (Stearns 1992, Andersen et al. 2000). Sadleir (1982) found that some lactating black-tailed deer (*O. h. columbianus*) were capable of consuming enough energy to maintain milk production, whereas others depleted fat stores during the first 4 months postpartum.

Second, larger ungulates like moose and elk may require larger fat stores to conceive because they produce milk and nurse their young to a much greater extent during the breeding season than do mule deer (Wallmo 1981, Clutton-Brock 1982, Landete-Castillejos 2000, Toweill and Thomas 2002, Gallego et al. 2006). The gestation period of elk and red deer is a month longer and their breeding begins at least a month earlier than that of mule deer, whereas by breeding season our mule deer fawns attempted to nurse an average of only 0.5 times/day (Sadleir 1987, Tollefson 2007). Nursing during breeding could prevent elk in low and moderately low body condition from becoming pregnant, an effect that might be exacerbated by the fact that fawns eating poor-quality forage may attempt to nurse more often (Loudon et al. 1983, Tollefson 2007). Nursing places a substantial energy demand on the female at the onset of estrus, interfering with production of GnRH and LH (Landete-Castillejos et al. 2003, Wettemann et al. 2003). Although body reserves can supplement energy requirements from food, 80% of milk fat is derived from acetate that must come from the diet itself (Pond et al. 2005). Lactational anestrus and poor body reserves may be responsible for red deer skipping a breeding cycle every 3 years, yet a similar every-other-year breeding cycle has not been reported for mule deer (Clutton-Brock 1982).

Finally, differences in the amount of fat required to become pregnant among cervids may be related to potential litter sizes. Because relative size at birth and early growth of offspring do not differ between monotocous and polytocous ungulates, polytocous ungulates like mule deer allocate more in maternal care (e.g., milk production) than monotocous ungulates like elk (Robbins and Robbins 1979, Andersen et al. 2000). A litter-bearing life history strategy may allow deer to breed at lower DEI and body fat levels than elk, but at the expense of having only one fawn, as our experiments indicated. For example, our mule deer required an average of 34% more fat stores to produce twins than to become pregnant (Table 3). However, for an animal like an elk that typically has only one calf per season, the life history choice each autumn is all or nothing and, thus, may be tied more directly to energy stores.

MANAGEMENT IMPLICATIONS

Properly managing harvest and preventing declines of mule deer populations in the western United States depends on having adequate tools to both assess and improve reproductive potential of the herd. Although our data suggest that DEI is the most sensitive and important nutritional mechanism governing body condition, pregnancy, and litter size in mule deer, measuring DEI in wild mule deer populations is currently not practical. Our study suggests that concentrations of leptin and IGF-1 in serum, as currently collected and analyzed, have little usefulness to wildlife managers in predicting nutritional and reproductive status of mule deer.

If autumn body condition or pregnancy rates are poor, managers should develop strategies for assessing and providing high-quality forage on summer and autumn ranges. Because mule deer tend to be more dispersed and use larger landscapes in summer than winter (e.g., D'Eon and Serrouya 2005), enhancing forage quality on summer and autumn ranges usually requires integrating forage improvements into large-scale resource management. Therefore, researchers and managers should first investigate nutritional consequences of local activities that manipulate plant succession (e.g., fire, grazing, logging) in their region (e.g., Long et al. 2005). Throughout mule deer range, promoting a variety of native grass, forbs, and shrubs that mature asynchronously will extend the period in which green, nutritious forage is available to mule deer during summer and autumn. Because forage quality in summer and autumn in large part depends on annual precipitation and temperature, managers should include effects of variable summer and autumn weather on forage quality in population and harvest models created for mule deer.

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