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Effects of Forage Nutritional Quality (Energy and Protein) on Deer Acceptance of Foods Containing Secondary Metabolites

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ABSTRACT: Deer foraging on tree seedlings is recognized as the most widespread detriment to reforestation efforts. Non-lethal approaches to reduce deer damage to seedlings are highly desirable. Avoidance of natural secondary metabolites contained in conifers may provide feasible means to develop non-lethal measures. Other studies have demonstrated that sheep and goats fed diets with high protein-to-energy ratios, or allowed to select between concentrates high in either energy or protein, ate much more of a high-terpene diet and of a high-tannin diet than when they were fed diets high in energy-to-protein ratios. Thus, manipulating foraging options for deer may impact their ability to ingest terpenes contained in conifers. We conducted a series of studies to determine whether deer acceptance of terpene-containing foods can be affected by altering the ratio of energy and protein in their maintenance diet. We determined relative consumption of a high-energy and low-protein diet, and a low-energy and high-protein diet, when deer are given the opportunity to self-regulate their intake. We also determined if deer modified their relative intake of these diets when offered an alternative terpene-treated diet. Penned deer were offered variable diets (e.g., high energy-low protein, low-energy-high protein, or both foods), then their acceptance of terpene- and tannin-containing foods was determined. Deer consumed more and demonstrated a strong preference for the high-energy diet relative to the high-protein diet. However, the varied diets did not appear to affect their intake of terpene or tannin-containing foods. This paper discusses the potential of manipulating maintenance rations as a non-lethal tool, presents initial results and possible explanations for differences between our study with deer and prior work with domestic ruminants.

KEY WORDS: black-tailed deer, energy, foraging behavior, metabolites, nutritional status, *Odocoileus hemionus columbianus*, protein, toxins

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INTRODUCTION

Deer (*Odocoileus* spp.) and other wild ungulates occur across the United States, providing desirable recreational and aesthetic opportunities. Unfortunately, foraging deer can cause conflicts with humans, particularly where population densities are high. Deer damage a variety of grain crops, forage crops, vegetables, fruit trees, nursery trees, and ornamentals (Craven and Hyngstrom 1994). Ungulates also are the most widespread constraint inflicted by wildlife to establishing tree seedlings after a fire or a harvest (Rochelle 1992). Ungulate browsing suppresses growth and delays regeneration, and it can increase mortality among seedlings that are uprooted or repeatedly browsed (Crouch 1976, Evans 1987, Tilghman 1989).

Multiple approaches to minimize ungulate damage have been attempted (Nolte 1999). Fencing that excludes ungulates from problem areas is probably the most effective tool (Craven and Hygnstrom 1994), but it is expensive to install and to maintain (Reed et al. 1982). Individual barriers work well when properly installed, but they too can be expensive to treat large areas (Nolte 1999). Some contact repellents can reduce deer browsing for a few months before efficacy declines (Nolte 1998, Nolte and Wagner 2000, Wagner and Nolte 2001). Other approaches used to impede deer activity have had marginal success (Schafer and Penland 1985, Conover et al. 1995). Additional efforts to identify additional feasible approaches to alleviate ungulate damage are ongoing.

Most, if not all, ungulate damage to forest resources is inflicted while animals are foraging for food. Their exhibited choices reflect preferences for nutritious forage and not merely relative abundance (Weckerly 1994). Understanding why deer select some foods and avoid others may enable us to manipulate their choices. Knowing how to reduce their interest in eating seedlings would greatly enhance our ability to manage their negative impacts. In general, herbivore diet selection is attributed to obtaining a balanced intake of nutrients (Westoby 1978) and minimizing toxins or plant secondary metabolites (Freeland and Janzen 1974). Proteins and energy are essential for survival (Parker et al. 1999). Secondary metabolites can be deleterious to an animal's health, limiting digestibility of other nutrients, or at least requiring additional resources to detoxify toxins (Cheeke and Shull 1985). An animal's ability to cope with toxins reflects not only the kind and amount of toxins, but available nutrients in all forages on offer (Villalba et al. 2002a).

An ungulate's choice to consume a tree seedling therefore depends on the type and concentration of secondary metabolites and the animal's nutritional state. Deer tend to prefer foods with low concentrations of terpenes (Scholl et al. 1977, Connolly et al. 1980, Duncan et al. 1994) and tannins (Radwin et al. 1978, Alm et al. 2002). Deer given protein supplements, however, increase their intake of tannin-containing sagebrush (*Artemisia* spp.; Chris Peterson, Utah St. University, pers. comm.). Similarly, domestic ungulates fed supplemental macro-nutrients increased their intake of foods that contain toxins as diverse as lithium chloride (Wang and Provenza 1996), terpenes (Banner et al. 2000, Villalba et al. 2002b), menthol (Illius and Jessop 1996), and tannins (Villalba et al. 2002c). Conversely, animals ingesting low-sodium diets restrict their intake of toxins, and the sodium-depleting effects of many toxins may deter herbivores from eating plants that are low in sodium (Provenza et al. 2003). Thus, manipulating nutrients available to an animal may offer the potential to increase their intake of plants habitually avoided or to decrease their intake of plants habitually eaten.

We conducted a series of experiments to assess whether diets with varied levels of energy and protein affect deer acceptance of foods containing secondary metabolites. Specific objectives addressed in these studies were: 1) to determine relative consumption of a high-energy and low-protein diet, and a low-energy and high-protein diet, when deer are given the opportunity to self-regulate their intake; 2) to determine if deer modified their relative intake of these diets when offered an alternative terpene- or tannin-treated diet; and 3) to determine whether deer acceptance of terpene- and tannin-containing foods can be affected by altering the ratio of energy and protein in their maintenance diet.

METHODS

Subjects

Captive adult black-tailed deer (*Odocoileus hemionus columbianus*) served as experimental subjects. These animals were reared at the National Wildlife Research Center's Olympia Field Station, Olympia, Washington, and maintained with free access to a special formulated deer pellet (Table 1) and limited natural forage. Deer were weighed prior to the study and ranked by weight. Outliers (heavy or light animals) were excluded from the study. The 36 intermediate animals were then assigned among 12 herds. Herds were created by randomly assigning one deer from the 12 heaviest to each herd, one deer from the middle 12 weights, then another deeer from the 12 weighing the least. Mean weight of all deer within each herd was then calculated to ensure it was within at least 10% of the mean weight of all deer in the study. Subsequently, the 12 deer herds were randomly assigned to pastures where they were offered one of three maintenance diets. Test pastures, approximately 0.125 ha, contained minimal native vegetation, a shelter, and fresh water. All feed was offered to deer in open troughs placed beneath their shelters. Problems with some pregnant does during early phases of the adaptation period caused us to reduce deer herds from 3 deer to 2 deer. Average weight of animals among herds remained within the targeted 10% mean weight of all animals in the study.

Treatments

Experimental treatments were applied by incorporating them into the maintenance diets offered deer during the study. Four herds were given a high-energy and low-protein diet (HELP; Table 2), 4 herds were given a low-energy and high-protein diet (LEHP; Table 3), and 4 herds were given a choice between HELP and LEHP diets allowing them to self-regulate their protein and energy intake. Deer were given free access to these foods except during periods as described for testing their acceptance of treated foods. Approximate weight of diets consumed by each herd was monitored by tracking the amount offered minus amount remaining at weekly or daily intervals.

The test diet contained relatively low levels of protein and energy, similar to concentrations identified within Douglas-fir (Table 4). All diets were created by mixing appropriate ground products in 22.25-kg batches, then adding and thoroughly mixing in 1.15 L of corn oil. Separate bins were used for mixing HELP, LEHP, terpene, and tannin diets to minimize cross-contamination. Terpene composition was similar to that identified in Douglas-fir (Table 5, Kimball et al. 1998). Terpene diet was made by incorporating 1 L of the terpene mixture (ingredients purchased from Sigma-Aldrich, Saint Louis, MO, or TCI America, Portland, OR) into the corn oil prior to mixing it with the test diet. For the tannin diet, 1.0 kg quebracho (Tannin Corp., Peabody, MA) was mixed with the ground food before adding the liter of corn oil.

Table 1. Composition of special deer diet fed deer prior to experimental manipulation; CP/DE ratio: 41.0.

Ingredient	Composition	DE* (Mcal/kg)	CP* (g/kg)
Millrun	15.0%	0.54	2.8
Corn	25.7%	0.99	26.0
Barley	25.0%	0.97	33.8
Soybean Meal	13.7%	0.51	65.3
Alfalfa	10.0%	0.25	14.5
Molasses	6.5%	0.22	0.6
Dicalcium P	1.0%		
Perma Pell	1.6%		
Salt	1.0%		
Lime Flour	0.5%		
Total	*100%*	*3.48*	*142.9*

* DE = digestible energy; CP = crude protein

Table 2. Composition of high-energy and low-protein diet (HELP) used to maintain deer; CP/DE ratio: 30.5.

Ingredient	Composition	DE* (Mcal/kg)	CP* (g/kg)
Beet Pulp	62.0%	2.11	59.5
Barley	21.0%	0.81	28.4
Alfalfa	2.5%	0.06	3.6
Soybean Meal	1.0%	0.04	4.8
Oat Hulls	11.0%	0.15	0.5
Limestone fl	0.5%		
Dicalcium P	1.0%		
Salt	1.0%		
Total	*100%*	*3.17*	*96.8*

* DE = digestible energy; CP = crude protein

Table 3. Composition of low-energy and high-protein diet (LEHP) used to maintain deer; CP/DE ratio: 78.6.

Ingredient	Composition	DE* (Mcal/kg)	CP* (g/kg)
Beet Pulp	3.0%	0.10	2.9
Barley	3.0%	0.12	4.1
Alfalfa	41.0%	1.03	59.4
Soybean Meal	29.0%	1.09	138.3
Oat Hulls	21.5%	0.28	1.0
Limestone fl	0.5%		
Dicalcium P	1.0%		
Salt	1.0%		
Total	*100%*	*2.62*	*205.7*

* DE = digestible energy; CP = crude protein

Table 4. Composition of test diet mixed with terpene and tannins to assess deer response to secondary metabolites; CP/DE ratio: 30.1.

Ingredient	Composition	DE* (Mcal/kg)	CP* (g/kg)
Beet Pulp	38.0%	1.29	36.5
Barley	14.0%	0.54	18.9
Alfalfa	2.0%	0.05	2.9
Soybean Meal	3.5%	0.13	16.7
Oat Hulls	40.0%	0.53	1.8
Limestone fl	0.5%		
Dicalcium P	1.0%		
Salt	1.0%		
Total	*100%*	*2.55*	*76.8*

* DE = digestible energy; CP = crude protein

Table 5. Composition of terpene mixture added to test diet to assess deer response to terpene-treated food.

(-) alpha-Pinene	1500 mL
(-) Camphene	17 g
(-) beta-Pinene	250 mL
Myrcene	50 mL
(+) 3-Carene	100 mL
alpha-Terpinene	5 mL
p-Cymene	13 mL
(-) Limonene	125 mL
γ-Terpinene	5 mL
Terpinolene	100 mL
(±) Linalool	50 mL
(-) Terpinen-4-ol	50 mL
(-) Bornyl acetate	7 mL
Citronellyl acetate	50 mL
(+) Longifolene	5 mL
Caryophyllene	10 mL

Procedures

The preliminary adaptation period to maintenance diets was 6 weeks. Relative preference between HELP and LEHP was determined by monitoring weekly intake by deer. A series of 1- and 2-choice tests was then conducted to determine whether deer acceptance of terpene- and tannin-containing foods could be affected by altering the ratio of energy and protein in their maintenance diet. First, a 1-choice test assessed intake of a terpene-treated diet when offered to animals maintained on a HELP diet, a LEHP diet, or both HELP and LEHP diets. After deer had 6 weeks with their respective maintenance diets, they were conditioned to the 1-choice test regime. On 5 consecutive days during a pretreatment period, deer were given 4 hours with their respective maintenance diet followed by a 20-hour exposure to an untreated test diet. Maintenance diet and test diet intake was measured daily. The procedure was then repeated the following week, except deer were offered the terpene-treated diet during the 20-hour test period for 5 consecutive days. Subsequently, we assessed deer response when offered their choice between their respective maintenance diets and the terpene-treated food. Therefore, one treatment was a choice between HELP and the terpene test diet, another treatment was a choice between LEHP and the terpene test diet, and the third treatment was a choice between HELP, LEHP, and the terpene test diet. Foods were weighed every 24 hours for 5 consecutive days to monitor deer consumption of all foods.

Deer response to the tannin test diet was assessed as described for the terpene test diet. A single-choice test regime (4/20 hr) was conducted first, followed by a multiple-choice test. The only differences were the test food was treated with quebracho rather than the terpene mixture, and the test was conducted for 4 consecutive days instead of 5 days.

Whether deer modified their preference for HELP and LEHP when offered food containing teprenes or tannins was determined by comparing the proportion of HELP consumed relative to both diets (HELP/HELP + LEHP) when deer were offered their maintenance diets and food without secondary metabolites added, when offered food containing terpenes, or when offered food containing tannins.

Statistical Analysis

A 2-factor repeated measures ANOVA was used to assess intake of deer offered HELP and LEHP during the conditioning period. Foods (2) were nested within subjects and the repeated measure was weeks (6 levels).

Deer response to terpene-treated diet among treatment groups during the single-choice test was assessed in a 3-factor repeated measures ANOVA. The dependent variable was the amount of terpene diet consumed by respective treatment groups (3 levels). Periods (pre-treatment and treatment) and days (5 levels) were the repeated measures. Assessing deer response to the tannin-treated diet during the single-choice test was similar, except periods were not included because the pre-treatment period was not repeated and there were fewer days (4-levels).

Deer responses to treated foods in multiple-choice tests were assessed similarly for the terpene test and the tannin test. A 2-factor repeated ANOVA was to use to compare responses of the treatment groups (3 levels) and days (4 levels) was the repeated measure. The dependent variable was intake of the respective test diet.

Additional statistical analysis was conducted to provide further insight into the results. A 2-factor repeated measures ANOVA was used to assess total food consumed by all treatment groups (3 levels) during the multiple-choice test using terpene-treated food. A similar but separate analysis compared the same groups when animals were offered tannin-treated food. Days (4 levels) was the repeated measure. A single-factor ANOVA was used to compare consumption of terpene- and tannin-treated diets by deer offered HELP and LEHP during the multiple-choice test.

A single-factor ANOVA was used to assess whether deer altered their preference for HELP and LEHP when also offered food containing secondary metabolites. Proportion of HELP consumed was the dependent variable.

RESULTS

Deer exhibited a preference ($P < 0.00001$) for the HELP diet when offered with the LEHP diet (Figure 1). Amount of food ingested by deer increased with each subsequent week ($P = 0.00002$). There was a food by week interaction ($P = 0.0422$). Although deer intake of both foods increased over time, the increased intake of HELP was greater than the increase exhibited for LEHP. Deer offered only HELP or LEHP food during the adaptation period ate similar ($P > 0.35$) amounts of both (mean HELP = 18.313 kg, mean LEHP = 16.113 kg; Figure 2). Deer increased their consumption of both foods over time ($P < 0.0001$), but they increased their intake of HELP quicker ($P = 0.0316$) than they did LEHP.

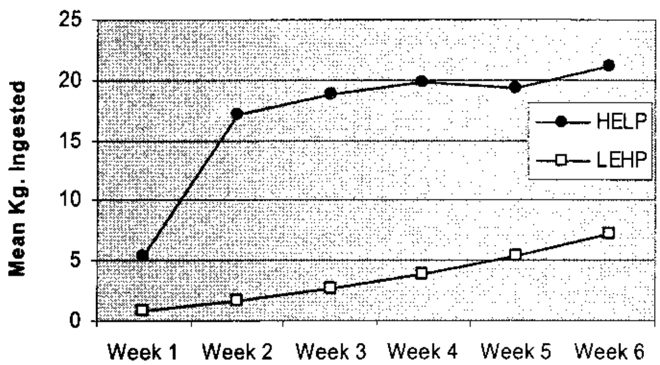

Figure 1. Mean weekly intake of a high-energy and low-protein diet (HELP) and a low-energy and high-protein diet (LEHP) by deer offered both diets during a 6-week adaptation period.

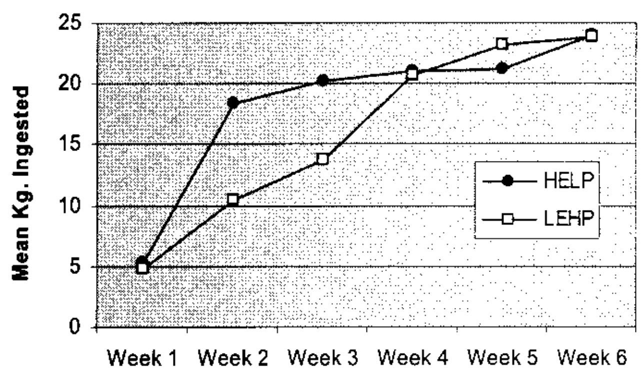

Figure 2. Mean weekly intake by deer offered only a high-energy and low-protein diet (HELP) and mean weekly intake by other deer offered only a low-energy and high-protein diet (LEHP).

Deer consumption of terpene-treated food was similar ($P > 0.35$) for all treatment groups during the single-choice test (Figure 3). All groups ate more ($P = 0.0001$) test food during the pre-treatment period (mean intake =

2.8 kg/day) than they did during the treatment period when the test food contained terpenes (mean intake = 1.9 kg/day). Although daily intake varied ($P = 0.0243$) for all groups, there was not a consistent pattern. Mean daily intake for all groups from day 1 through day 5 was 2.3, 2.4, 2.0, 2.5, and 2.5 kg, respectively. There were no significant interactions ($P > 0.15$). Deer consumption of tannin-treated food also was similar ($P > 0.35$) for all treatment groups during the single-choice test (Figure 4). There was a day effect ($P = 0.0002$). Mean daily consumption was 1.8, 2.5, 2.2, and 2.4 kg for days 1 through 4, respectively. The treatment by day interaction was not significant ($P > 0.35$).

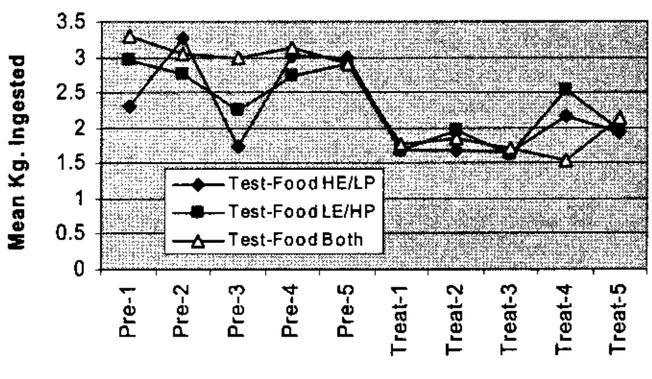

Figure 3. Mean daily intake of a terpene-treated food by deer fed a high-energy and low-protein diet (HELP), or a low-energy and high-protein diet (LEHP), or permitted to self-regulate their intake between both diets (BOTH) during a single-choice test.

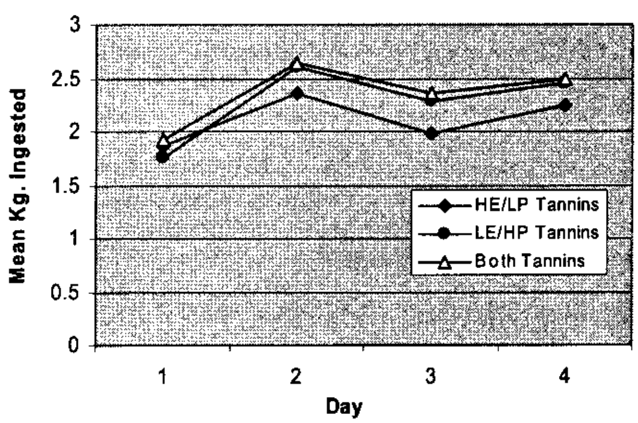

Figure 4. Mean daily intake of a tannin-treated food by deer fed a high-energy and low-protein diet (HELP), or a low-energy and high-protein diet (LEHP), or permitted to self-regulate their intake between both diets (BOTH) during a single-choice test.

Deer maintained on the LEHP diet ingested more ($P = 0.0261$) terpene-treated food during the multiple-choice test than deer maintained on the HELP diet or permitted to self-regulate (Figure 5). There was not a day effect ($P = 0.1052$) or a day by treatment interaction ($P = 0.1006$). Deer fed LEHP during the multiple-choice test also ingested more ($P = 0.0359$) tannin-treated food than did the other two groups. Overall, deer consumption of tannin-treated food declined ($P = 0.0064$) with progressive days (1.8, 1.6, 1.4, 1.2 kg, respectively). There was not a day by treatment interaction ($P > 0.35$).

The total amount of food consumed by deer was similar among all treatment groups during the multiple-choice test when deer were offered terpene-treated food ($P > 0.35$) and when deer were offered tannin-treated food ($P > 0.35$). The total food intake did not vary across days during the terpene test ($P > 0.35$), but declined as the test progressed when deer were offered tannin-treated food ($P = 0.0011$, Figure 6). There was not a day by treatment interaction detected for either analysis ($P > 0.35$).

Deer did not alter their relative intake of HELP and LEHP when offered in conjunction with food containing secondary metabolites ($P > 0.35$). The proportion of HELP diet consumed when offered with LEHP and no other food was 0.804; the ratio when offered in 3conjunction with terpene-treated food was 0.811; and the ratio when offered with tannin-treated food was 0.774. Deer allowed to self-regulate between the HELP and LEHP diets ingested less ($P = 0.013$) terpene-treated food (0.219 kg/day) during the 2-choice test than they did tannin-treated diet (2.356 kg/day) during a similar test.

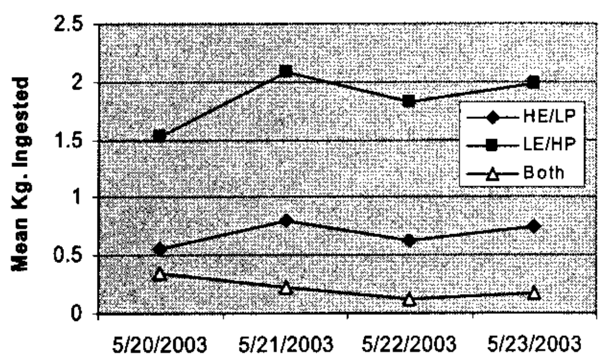

Figure 5. Mean daily intake of a terpene-treated food by deer offered the treated food with a high-energy and low-protein diet (HELP), or the treated food with a low-energy and high-protein diet (LEHP), or the treated food and both HELP and LEHP (BOTH) in a multiple-choice test.

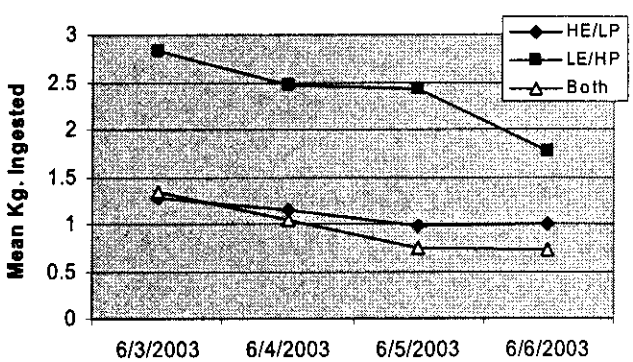

Figure 6. Mean daily intake of a tannin-treated food by deer offered the treated food with a high-energy and low-protein diet (HELP), or the treated food with a low-energy and high-protein diet (LEHP), or the treated food and both HELP and LEHP (BOTH) in a multiple-choice test.

DISCUSSION

Deer exhibited a persistent preference for the HELP diet relative to the LEHP diet. Thus, although ground to a similar texture, deer distinguished between the foods. Their initial preference for HELP may have been in part caused by their prior experience. Animals tend to select familiar rather than novel foods (Provenza 1995). Therefore, HELP similarity to the regular diet (Table 1) fed at the station may have initially affected their choice. However, this preference persisted throughout the experiment. Deer offered HELP and LEHP in the last multiple-choice test continued to ingest more HELP. However, when not offered an alternative, deer ingested the LEHP diet in amounts similar to the amount ingested by deer offered only the HELP diet. These results suggest that deer exhibited a relative preference for HELP, but not necessarily an avoidance of LEHP, when choices were limited.

Our results are similar to other findings where ruminants typically show stronger preferences for energy than protein (Villalba and Provenza 1996). White-tailed deer (*Odocoileus virginianus*), when offered dietary choices, selected foods higher in energy and lower in protein (Berteaux et al. 1998). They considered these choices consistent with physiological needs of deer wintering at the study site, where digestible energy in natural forages was low. Free-ranging black-tailed deer in Alaska were routinely energy-deficient and selected for high-energy foods to compensate (Parker et al. 1999). Other studies have demonstrated that domestic (Kyriazakis et al. 1990, Nicholson et al. 1992, Kyriazakis and Oldham 1993) and wildlife (Prins and Beekman 1989, Vickery et al. 1994, Berteaux 1998) species select foods that meet their protein requirements, but when given the choice do not ingest excess proteins. Wintering cervids were thought to avoid ingesting excessive proteins because of an apparent cost in excreting them (Soppela et al.1992). Within our experiment, deer may have been able to meet their protein needs by ingesting small quantities of LEHP. Natural forage was sparse and considered to contribute minimally to their nutritional status.

Within this experiment, deer did not alter their intake of terpene- or tannin-treated food regardless of their base diet during single-choice tests. Other studies reported animals ingesting more food containing toxins when permitted to regulate their macro-nutrients or given a high-protein diet (Illius and Jesop 1996; Wang and Provenza 1996; Banner et al. 2000; Villalba et al. 2002b, 2002c). Differences demonstrated in our experiment may have been because deer respond differently than domestic ruminants. However, mule deer ate more tannin-containing sagebrush when they were supplemented with a high-protein diet (Chris Peterson, Utah St. University, pers. comm.). Therefore, our failure to detect differences may merely reflect our experimental paradigm. Further efforts may provide better insights of conditions (e.g, experience, satiety or nutritional status, toxin or macro-nutrient concentrations) necessary to elicit varied responses.

Energy and protein availability did affect deer consumption of treated foods in multiple-choice tests. Deer maintained on the LEHP diet consumed more terpene- and tannin-treated food than deer maintained on HELP or permitted to self-regulate between the two maintenance diets. This increase may reflect a greater tolerance for these toxins because of the high-protein diet, such as demonstrated with sheep (Villalba et al. 2002a). Deer did not increase their LEHP consumption when eating terpene- or tannin-treated food; they ate less. Therefore, an alternate explanation is that deer were compensating for their low preference for LEHP by ingesting more of the treated diets. All three treatment groups ate similar total amounts of food during both multiple-choice trials. Therefore, if they ate less LEHP, they had to make up the caloric difference. Regardless, it is difficult to ascertain whether deer response to tannin-treated diet reflected an increased capacity because of the protein-enriched diet or merely reflected relative preferences, or possibly a combination of the two explanations. Deer repeatedly demonstrated a greater willingness to ingest tannin-treated food than terpene-treated food, perhaps because deer produce salivary proteins capable of binding to tannins and minimizing their deleterious effects on digestibility (Robbins et al. 1991).

SUMMARY

Deer will selectively browse plants with lower terpene concentrations (Radwan 1972, Scholl et al. 1977, Connolly et al. 1980, Behan and Welch 1985), probably to avoid the associated negative consequences (Smith 1992). Therefore, applications increasing terpene concentrations within a plant or decreasing deer tolerance of existing concentrations will cause relative preference for that plant to decline. Our study was inconclusive as to whether altering nutrient composition may provide a means to manage deer foraging on tree seedlings. Conversely, altering diets may increase deer acceptance of plants normally not readily ingested. Protein supplements increased deer browsing of sagebrush (Chris Peterson, Utah St. University, pers. comm.). Manipulating browsing pressure on select plants may permit managers to alter forest plant assemblages by increasing foraging on undesirable invasive plant species, or at least reduce pressure on highly palatable plants. Regardless whether the mechanism is reduced preference for seedlings or increased preference for alternative forages, the resultant reduced browsing pressure will increase seedling survival. Therefore, further efforts are warranted to improve our understanding of the role macro-nutrient intake has on deer consumption of secondary metabolites.

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