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Author(s): Gary E. Belovsky and Oswald J. Schmitz

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# PLANT DEFENSES AND OPTIMAL FORAGING BY MAMMALIAN HERBIVORES

GARY E. BELOVSKY AND OSWALD J. SCHMITZ

*Department of Fisheries and Wildlife and Ecology Center, Utah State University,  
Logan, UT 84322-5210*

*School of Forestry and Environmental Studies, Yale University,  
New Haven, CT 06511*

We examined, using an optimal-foraging model, the conditions under which particular plant defenses (e.g., structural, digestive-inhibiting chemicals, toxic chemicals, and nutritional content) should be effective in reducing intake of plants by mammalian herbivores. We demonstrated that no type of plant defense can guarantee reduced consumption, because defense efficacy depends not only upon other characteristics of the defended plant (e.g., its nutrient content, its passage rate through the herbivore's digestive tract, and its ability to be harvested by the herbivore), but also the characteristics of other plants available to the herbivore in the environment. Consequently, some defenses will be effective in some environments, but not others, making generalizations about the efficacy of defenses conditional.

**Key words:** mammalian herbivores, plant defenses, optimal foraging

Documenting plant defenses and their potential for reducing consumption by mammalian herbivores has become a major area of study over the past decade (Palo and Robbins, 1991). For herbivores in general, several cycles of synthesis, empirical evaluation, and re-synthesis of the role played by antiherbivore defenses have transpired (Stamp, 1992). Yet, despite these efforts, there remains a general failure to construct a theoretical framework that explains the empirical findings, because existing theory often is incongruent with empirical work (Stamp, 1992).

The majority of empirical studies have relied upon one or more of four approaches. The first approach relates plant traits, including defenses, with the herbivore's consumption or preferences in the laboratory or field using statistical correlation, while the other three approaches are experimental. The second approach investigates plant defenses using controlled feeding trials to assess a herbivore's preferences for plants that differ in presumed levels of defense. The third approach investigates defenses using

controlled feeding trials to determine whether variation in the presumed defensive trait of plants (e.g., concentration of digestion inhibitor and density or length of thorns) reduces consumption, when other plant traits that might influence consumption are allowed to naturally vary and are statistically controlled for, or the defenses are held constant using an artificial diet. The fourth approach relates the presence of a defense in the plant to a physiological response in the herbivore that might reduce the herbivore's fitness (e.g., the concentration of a toxin in the plant and liver damage).

The four approaches can identify that a plant trait potentially operates as a defense against herbivores. However, while it is necessary to demonstrate that a defense can be effective, this is not sufficient for understanding the role that the defense plays in reducing consumption by herbivores in nature. For example, a plant may possess a defense, but, when consumption by herbivores in the field is studied, the defense does not always appear to be effective

(Stamp, 1992). Extrapolating the findings of these approaches to consumption by herbivores in the field assumes that defense efficacy is immutable, meaning that it is not dependent on the defended plant's absolute or relative abundance nor the characteristics and abundances of other sympatric plants. This perspective treats the herbivore as if it is a "hard-wired machine" incapable of varying its feeding behavior in response to environmental conditions. This is one of the reasons why Stamp (1992) found that empirical observations of plant-antiherbivore defenses can be incongruent.

Consequently, there is an additional element that must be considered in assessing the efficacy of a plant's defenses; the foraging of the herbivore, whose behavioral response is "plastic" to environmental conditions (e.g., availability of other plants, the characteristics of other plants, and abiotic conditions that affect feeding). Employing established models of diet selection in herbivores, we investigate the environmental conditions under which plant traits that have been demonstrated to be potential defenses by the described approaches can be effective against mammalian herbivores.

#### MODEL OF DIET SELECTION IN HERBIVORES

Studies of foraging by mammalian herbivores have followed two major avenues: 1) diet selection is based upon the acquisition of nutrients; 2) diet selection is based upon the avoidance of antiherbivore defenses of plants. Although ecologists often view these as alternative hypotheses, this is a false dichotomy, because even when plant defenses are important to diet selection, the herbivore cannot ignore nutritional considerations or it may perish and fail to reproduce. Furthermore, given that natural selection favors individuals that survive and reproduce better than other individuals, and this may frequently increase with the amount of food ingested (Robbins, 1993), a herbivore cannot simply select a diet based upon considerations of plant defenses

once a minimal level of nutritional intake is attained. Therefore, nutritional considerations can never be overlooked, and defenses operate to modify feeding decisions based solely on nutrition. This becomes a "trade-off" in which nutritional considerations have primacy.

In light of the primacy of nutritional considerations, our models of diet selection in herbivores initially focused upon decision-making given the herbivore's goal to attain nutrients (Belovsky, 1978, 1981, 1984*a*, 1984*b*, 1984*c*, 1986*a*, 1986*b*, 1987*a*, 1990*a*, 1991; Belovsky and Slade, 1987; Schmitz, 1990). Two simple goals generally have been employed: the herbivore attempts to maximize its nutrient intake, given that greater nutrient intake converts directly into greater survival and reproduction (nutrient maximization); the herbivore attempts to attain some minimal level of nutrient intake in the least amount of time spent feeding, given that feeding increases the risk of encountering a predator or reduces time for other activities such as mating (time minimization). Finding solutions to the goals is trivial if the individual is not constrained in its actions, i.e., either it feeds on the most nutritious food to maximize nutrient intake or it feeds on the food that can be found and harvested in the least time to minimize feeding time. However, the imposition of limits on individual action (constraints) makes the problem more difficult and interesting, because the forager must balance the ingestion of one food against the consumption of other foods to attain the "best" solution for either nutrient maximization or time minimization, given that each food differentially impacts the constraints.

The constraints imposed upon the forager are set by the forager's physiology (e.g., digestion and thermal, nutritional, and sensory traits) and characteristics of the foods (e.g., nutrient content, digestibility, and rate of digestion). However, the forager and food characteristics can only be integrated within the context of environmental influences (e.g., thermal conditions that affect

feeding time and absolute and relative abundances of the foods and their distribution over the landscape that affect how frequently the forager will encounter each food) before the "best" diet choices can be made. Therefore, understanding and defining foraging constraints are exercises in physiological ecology, because physiology and specifics about the environment are examined to assess what an animal can and cannot undertake behaviorally. Finally, within these constraints, the "best" feasible (not violating any constraints) diet can be identified.

For herbivorous mammals, we have identified several potential constraints on diet selection. Digestive capacity within a time period (e.g., wet mass/day) may be set by the volume of the portion of the alimentary tract that most retards the breakdown of plant tissue ( $D$ ; e.g., rumen capacity in wet mass) divided by the rate at which a unit of each plant food passes through the organ ( $R$ ; days/rumen capacity). This constraint is imposed through the amount of organ capacity displaced by a unit intake of each food plant ( $d$ ; e.g., wet mass/dry mass) and the total amount of each food ingested ( $x$ ; dry mass). The constraint algebraically becomes:

$$D \geq \sum R_i d_i x_i,$$

where  $i$  refers to each potential plant food.

Feeding time within a larger time period ( $T$ ; e.g., min/day) may be set by the forager's thermal physiology and the abiotic environment. This constraint is imposed through the amount of time required to find and harvest a unit of each food plant ( $t$ ; e.g., min/dry mass) and the total amount of each food ingested ( $x$ ; dry mass). The algebraic expression for the feeding-time constraint depends upon how the foods are distributed over the landscape, which affects how the herbivore will encounter each food plant in its search for food. One simple, but apparently common, pattern from our empirical studies of mammalian herbivores is that food plants of one type are found together

and not in association with other food plants (e.g., leaves of shrubs do not grow with aquatic vegetation and grasses and forbs tend to grow in different places). Therefore, the herbivore must decide on which foods to feed at any point in time, because the individual cannot be in two places at once. This time constraint can be algebraically expressed as:

$$T \geq \sum t_i x_i.$$

Other distributions of plants in the landscape produce different expressions (Belovsky et al., 1989).

Minimal energy requirements within a time period ( $E$ ; e.g., kJ/day) are set by the forager's maintenance requirements, as well as its thermal physiology and the abiotic environment. The constraint is imposed through the net energy content of each food plant ( $e$ ; e.g., kJ/dry mass) and the total amount of each food ingested ( $x$ ; e.g., dry mass). Net energy is the product of the food plant's digestibility and gross-energy content, less the energy expended in acquiring the food given the distribution and abundance of food plants in the environment. Algebraically, the constraint is:

$$E \leq \sum e_i x_i.$$

Other nutritional requirements within a time period can be written in the same manner as the energy constraint by substituting the desired nutritional component (e.g., protein, sodium, and water) for energy.

The given constraints are linear functions, this assumes that there are no synergistic interactions between the intakes of different foods. For example, if the consumption of food A modifies the passage rate of food B through the alimentary organ in such a way that passage rate of food B does not equal that of food A or when each is consumed alone and the passage rate of food B is not a weighted average of the passage rates of the two foods based on their relative intake, a synergism emerges, making the digestive constraint nonlinear. For example, if the protein value of food A

and B are enhanced by the intake of both foods due to each possessing complementary amino acids, a synergism emerges, making the nutrient constraint for protein nonlinear. However, feeding-time constraints, even for complex distributions of foods over the landscape and over different time periods, produce linear constraints, because the constraint is composed of several linear segments (Belovsky et al., 1989). Linear constraints are most parsimonious, given no evidence to the contrary, and provide first-order approximations, even when they might be nonlinear (Belovsky, 1990b; Belovsky and Schmitz, 1993).

Given linear constraints, the diet combination that does not violate any of the constraints and achieves either the nutrient-maximizing or the feeding-time-minimizing goals can be predicted by employing the optimization technique of linear programming. Several examples of linear-programming solutions are presented in Fig. 1 (also see Table 1) for ungulates feeding in early spring at the National Bison Range, Montana, before the prairie vegetation has started to grow. In each case, the solution that maximizes energy intake is not significantly different from the observed diet, while the solution that minimizes feeding time is significantly different from the observed diet.

Each of these ungulates may exhibit synergisms in their passage rates of foods through the rumen at this time (Baker and Hobbs, 1987). When the observed synergisms are used to construct nonlinear constraints and nonlinear programming is employed to predict the diets that achieve the foraging goals, we find that the diet predictions are either unchanged from linear-programming predictions (*Odocoileus hemionus*, mule deer; *Cervus elaphus*, elk) or, even if the diet predictions differ, they lead to the same conclusion that the herbivore selects a diet that maximizes energy intake (*Ovis canadensis*, bighorn sheep). Therefore, the application of linear constraints does not appear to distort our conclusions

TABLE 1.—The linear-programming parameters ( $\pm 1$  SE) presented in Fig. 1 for those mammalian herbivores at the National Bison Range. The maintenance-energy requirement was calculated using allometric relationships (Belovsky, 1986b), and energy content for the foods was calculated using their gross contents (Belovsky, 1986b) and the herbivores' dry-matter digestibilities (Baker and Hobbs, 1987).

Species	Constraint equation	Type of food	
		Grass	Browse
Elk ( <i>Cervus elaphus</i> )	Feeding time (min/day) <sup>a</sup>	317 $\pm$ 31 <i>n</i> = 131 animal-h	0.029 $\pm$ 0.003 <i>n</i> = 16 (min/g dry mass)
	Maintenance energy (kJ/day) <sup>b</sup>	20,851 kJ/day	7.73 kJ/g dry mass
Bighorn sheep ( <i>Ovis canadensis</i> )	Feeding time (min/day) <sup>a</sup>	370 $\pm$ 18 <i>n</i> = 179 animal-h	0.31 $\pm$ 0.02 <i>n</i> = 50 (min/g dry mass)
	Maintenance energy (kJ/day) <sup>b</sup>	9,691 kJ/day	9.89 kJ/g dry mass
Mule deer ( <i>Odocoileus hemionus</i> )	Feeding time (min/day) <sup>a</sup>	358 $\pm$ 40 <i>n</i> = 358 animal-h	0.18 $\pm$ 0.02 <i>n</i> = 16 (min/g dry mass)
	Maintenance energy (kJ/day) <sup>b</sup>	7,150 kJ/day	8.30 kJ/g dry mass

<sup>a</sup> Constraint  $\geq$  type of food.

<sup>b</sup> Constraint  $\leq$  type of food.

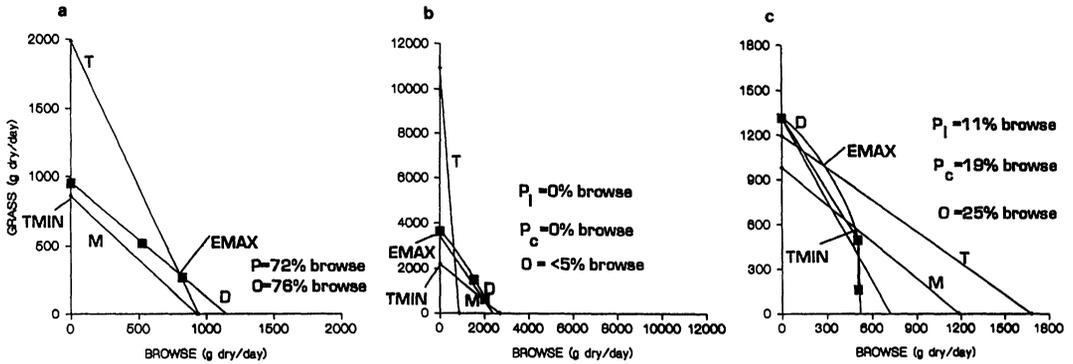


FIG. 1.—Graphical foraging models for three mammalian herbivores (a, mule deer; b, elk; c, bighorn sheep) at the National Bison Range in early spring (first 2 weeks of April, 1980) are presented; the methods are described by Belovsky (1986b), and parameter values are presented in Table 1. The model is examined for two food categories: grasses, browse (twigs). In each case, the digestive constraint (D) is presented as a linear function (regression) using data (squares) collected by Baker and Hobbs (1987) on the passage rates of the two food categories through the alimentary tract of these animals and as a nonlinear function (DWLS smoothing—Wilkinson, 1993). The maintenance metabolism constraint (M) and feeding time constraint (T) are presented as linear functions. EMAX refers to the energy-maximizing solution for the nonlinear digestive constraint, and TMIN refers to the time-minimizing solution. O is the observed diet,  $P_1$  is the energy-maximizing diet predicted using the linear digestive constraint, and  $P_c$  is the energy-maximizing diet predicted using the nonlinear digestive constraint. Only for bighorn sheep is there a difference in the predictions based on linear and nonlinear digestive constraints, and while the nonlinear constraint provides a better prediction of the observed diet in this case, it is not significantly different from the prediction based on a linear constraint.

on foraging by mammalian herbivores based on linear constraints.

We have employed linear programming to examine >94 cases of foraging by mammalian herbivores, involving 33 species. These studies have examined foraging in boreal forest, temperate deciduous forest, temperate prairie, alpine tundra, Arctic tundra, tropical savanna, and semiarid shrubland and foraging during different times of the year and for individuals of each sex and at different ages (see Table 2). Other linear-programming studies with mammalian herbivores (188 cases) have reported on additional species, habitats or seasons (Table 2). The linear-programming predictions for nutrient maximization, with the nutrient usually being energy, explain 85% of the observed variation in diet composition. In two cases, feeding-time minimization was detected, and, in five cases, neither nutrient maximization or time minimization was de-

tected. All of these cases were for adult males during mating. Other studies that utilized linear programming have examined herbivores from other taxa (e.g., five insects and two birds for 29 cases) and other types of foragers (e.g., omnivores for 65 cases) with similar results.

Nonetheless, the validity of linear-programming models has been questioned (Hanley, 1980; Hobbs, 1990; Owen-Smith, 1993a, 1993b; Ward, 1993) on a number of points varying from the functional form of the constraints, the definition of foraging goals, model sensitivity, and model circularity. These criticisms specifically have been addressed (Belovsky, 1990b, 1991; Belovsky and Schmitz, 1993), and these concerns usually arise from misunderstandings about what linear-programming models represent and how they should be appropriately employed. The most serious concern is that the linear-programming model is inherently

TABLE 2.—A summary of available results of linear-programming model for diets of mammalian herbivores. The number of cases refers to the number of independent attempts to validate linear-programming predictions. Comments on the studies' general findings also are presented.

Species	Habitat	Season	Cases	Conclusion	Study
<i>Alces alces</i>	Boreal/northern hardwood forest	Summer	4	Energy maximizing	Belovsky, 1978
<i>Alces alces</i>	Boreal/northern hardwood forest	Winter	2	Energy maximizing	Belovsky, 1981
<i>Microtus pennsylvanicus</i>	Temperate grassland (xeric and mesic sites)	Summer	3	Energy maximizing	Belovsky, 1984a
<i>Tragelaphus strepsiceros</i>	Tropical shrubland	Wet season			
<i>Castor canadensis</i>	Boreal/northern hardwood forest	Summer	1	Energy maximizing	Belovsky, 1984c
<i>Lepus americanus</i>	Boreal/northern hardwood forest	Summer and winter	2	Energy maximizing	Belovsky, 1984b
<i>Microtus pennsylvanicus</i>	Temperate grassland	Summer	15	Energy maximizing, except for male pronghorn during the rut are time minimizing	Belovsky, 1986b
<i>Spermophilus columbianus</i>	Temperate grassland	Summer			
<i>Sylvilagus nutalli</i>	Temperate grassland	Summer (two years)			
<i>Marmota flaviventris</i>	Temperate grassland	Summer (two years)			
<i>Antilocapra americana</i>	Temperate grassland	Summer (different age and sex categories)			
<i>Ovis canadensis</i>	Temperate grassland	Summer			
<i>Odocoileus virginianus</i>	Temperate grassland	Summer			
<i>Odocoileus hemionus</i>	Temperate grassland	Summer			
<i>Cervus elaphus</i>	Temperate grassland	Summer			
<i>Bison bison</i>	Temperate grassland	Summer			
Data on mammalian herbivores from the literature	Temperate forest and grassland, tropical grassland, temperate desert, and alpine tundra	Variety of seasons	26	Energy maximizing	Belovsky, 1986a
<i>Microtus pennsylvanicus</i>	Temperate grassland	Summer (different age and sex categories)	6	Energy maximizing	Belovsky, 1987a
<i>Odocoileus virginianus</i>	Temperate deciduous forest	Summer	1	Energy maximizing	Belovsky, 1987b
<i>Equus caballus</i>	Temperate grassland	Summer (with and without grain)	4	Energy maximizing	Belovsky and Slade, 1987
<i>Ovis aries</i>	Temperate grassland	Summer			

TABLE 2.—Continued.

Species	Habitat	Season	Cases	Conclusion	Study
<i>Bos taurus</i>	Temperate grassland	Summer	8	Energy maximizing	Belovsky, 1991
<i>Rangifer tarandus</i>	Arctic tundra	Summer		Energy maximizing	Present paper
<i>Odocoileus hemionus</i>	Temperate grassland	Late winter/early spring	3	Energy maximizing	
<i>Ovis canadensis</i>	Temperate grassland	Late winter/early spring			
<i>Cervus elaphus</i>	Temperate grassland	Late winter/early spring	7	Energy maximizing except for adult males of one kangaroo species which become time minimizing when mating	G. E. Belovsky, pers. obser.
<i>Oryctolagus cuniculus</i>	Arid shrubland	Summer			
<i>Macropus robustus</i>	Arid shrubland	Summer			
<i>Macropus rufus</i>	Arid shrubland	Summer			
<i>Ovis aries</i>	Arid shrubland	Summer			
<i>Bos taurus</i>	Arid shrubland	Summer			
<i>Marmota flaviventris</i>	Temperate grassland	Summer (different months and age/sex categories)	12	Energy maximizing	G. Edwards, in litt.
<i>Castor canadensis</i>	Boreal/northern hardwood forest	Summer	10	Energy maximizing	Doucet and Fryxell, 1993
<i>Ovibos moschatus</i>	Arctic tundra	All seasons (different age and sex categories)	21	Energy or sodium maximizing—adult males (5 additional cases) did not appear to be energy or sodium maximizing, or time minimizing	Forchhammer and Boomsma, in press
<i>Ammospermophilus leucurus</i>	Temperate desert	Summer	1	No result because of missing constraint	Karasov, 1985
<i>Tragelaphus strepisceros</i>	Tropical shrubland	Wet season	3	Energy maximizing	Owen-Smith, 1993a
<i>Spermophilus columbianus</i>	Temperate grassland	Summer (individual by individual in the population)	131	Energy maximizing	Ritchie, 1988
<i>Spermophilus columbianus</i>	Temperate grassland and alpine tundra	Summer	20	Energy maximizing	Ritchie and Belovsky, 1990
<i>Odocoileus virginianus</i>	Temperate deciduous forest	Winter (different months and with and without supplemental feed)	6	Energy maximizing	Schmitz, 1990
<i>Lepus americanus</i>	Boreal forest	Winter	4	Energy maximizing	Schmitz et al., 1992
<i>Odocoileus hemionus</i>	Conifer forest	Summer	1	No result because of missing constraint	Spalinger, 1980
<i>Bos taurus</i>	Temperate pasture	All seasons	14	Energy maximizing	Vulink and Drost, 1991

flawed due to circularities (Owen-Smith, 1993a). First, the inherent logical structure of linear programming can be mathematically demonstrated to be void of circularities and robust to circularities that can arise with parameterization (Belovsky and Schmitz, 1993). Second, while circularities can emerge with parameterization, this is not a fault with linear programming, but with the investigator, the empirical tests listed in Table 2 largely appear to avoid this problem (Belovsky and Schmitz, 1993). In fact, Owen-Smith (1994) appears to have rescinded this criticism.

Another criticism of the linear-programming model warrants particular attention. Linear-programming models generally have defined diets of herbivores in terms of plant categories, such as grasses, forbs, leaves from trees, and aquatic plants, not by plant species, and linear-programming models have not specifically incorporated the actions that different plant defenses play on diet selection by herbivores. To examine the actions of different plant defenses, the linear-programming model must examine diet choices between different plant species. The addition of plant defenses to optimal foraging models like linear programming is not a new concept (Pulliam, 1975). However, given the predictive successes of linear-programming models for mammalian herbivores, it would seem logical that this modeling format should be extended to this problem. This extension provides a perspective where plant defenses do not have primacy as argued by some (e.g., Bryant and Kuropat, 1980; Bryant et al., 1990), but integrates nutrition and plant defenses into a unified theory, as suggested by Stamp (1992), to examine one element of plant-animal interactions: how do defenses modify diet selection from predictions based solely on nutrition?

#### APPLICATION OF LINEAR PROGRAMMING TO ASSESS PLANT DEFENSES

The actions of three types of plant defenses (structural defenses such as thorns,

digestion-reducing chemicals such as tannins and lignin, and toxic chemicals such as nontannin phenolics) on diet choices of herbivores will be examined using a graphical, linear-programming model. The predictions made with these models can be tested with examples of feeding data from mammalian herbivores. The linear-programming predictions will be restricted to a foraging goal that maximizes nutrient intake (e.g., energy and protein), because previous work indicated that this goal was observed most commonly (>98% of the cases). Specific algebraic, rather than graphic depictions, of the linear-programming models are presented elsewhere (Belovsky and Schmitz, 1991).

*Structural defenses.*—Structural defenses, at least for mammalian herbivores, generally act by inhibiting the rate at which plant tissue can be ingested. Thorns and spines require the herbivore to maneuver before harvesting so that the thorns or spines do not “prick” the forager. Twigs that are difficult to bite off and plant parts that are tough and require more chewing require more time spent harvesting. Therefore, structural defenses modify the feeding-time constraint; e.g., thorny plants should take longer, on average, to harvest than unthorned plants (Cooper and Owen-Smith, 1986).

A graphical example can be developed to illustrate the effects of structural defenses by considering that a herbivore can choose to feed on two plants, one thorned and the other unthorned. In Fig. 2a, the thorns successfully defend the plant by reducing the herbivore’s consumption of the thorned plant; however, in Fig. 2b, the thorns have no effect on the herbivore’s consumption of the thorned plant. The condition required for the thorns to be an effective defense is that the nutrient content (e.g., digestible energy/g dry mass) per unit of digestive constraint utilized (g daily digestive capacity used/g dry mass) must be greater for the defended plant.

Studying five species of mammalian her-

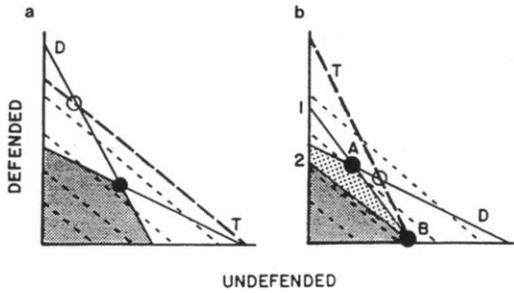


FIG. 2.—The graphical, linear-programming model is used to examine when structural defenses are effective. The digestive constraint is labeled as D. The feeding time constraint is labeled as T; the large-dashed line represents this constraint without the defense, and the solid lines that intersect the undefended plant's axis at the same point as the large-dashed line represent this constraint when the structural defense reduces harvesting rates. Successive solid lines for the feeding-time constraint (b; numbered lines) represent increasing structural defense effectiveness at reducing harvesting rate. The small-dashed lines that are parallel represent the energy-maximizing goal. The point farthest from the origin where one of the small-dashed lines is tangent to the region of feasible diets (shaded area) represents the energy-maximizing diet. a) The structural defense reduces consumption of the defended plant (diet shifts from the open to filled circle). b) The structural defense (T represented by line 1) increases consumption of the defended plant (diet shifts from the open circle to filled circle A) and then as the defense continues to reduce harvesting rate (T represented by line 2), the defended plant's consumption decreases (diet shifts from filled circle A to B).

bivores in semi-arid Australian shrubland (rabbits, *Oryctolagus cuniculus*; hill kangaroos, *Macropus robustus*; red kangaroos, *Macropus rufus*; sheep, *Ovis aries*; cattle, *Bos taurus*), we demonstrated that the condition for thorns to be effective was met for thorned plants that these herbivores did not prefer, but was not met by thorned plants that were preferred (Belovsky et al., 1991). Furthermore, we found that the effectiveness of thorns as a defense varied between the herbivores. This was expected, because the condition defining thorn effectiveness

depends upon the herbivore's feeding constraints, especially the degree to which thorns increase harvesting time, and these constraints vary between the different herbivores, especially with body mass (Belovsky et al., 1991). Therefore, empirical evidence supports the linear-programming model modified for structural defenses. This may be the only dataset that is applicable for testing model predictions, because other studies do not assess concurrently thorn effects on harvesting times and other parameters needed to measure the condition for defense efficacy.

The modeling results and empirical evidence indicate that structural defenses cannot be attributed with universal efficacy. Rather, efficacy depends upon the context of body mass of herbivores and the attributes of other plants available to the herbivore in the immediate environment.

*Digestion-reducing chemicals.*—Digestion-reducing chemicals as defenses are being down-played today by some ecologists (e.g., Bryant et al., 1991, 1992), because many of these chemicals now have been demonstrated to act principally as toxins. Nonetheless, others still argue for the digestive-reducing effects of some chemicals such as tannins, because they do reduce the assimilation of nutrients and do not appear to be toxic (e.g., Hagerman et al., 1992; McArthur et al., 1993). If there are such digestion-reducing chemicals in plants, and lignin is an example that does not seem to be debated, how can their actions be incorporated into the linear-programming model?

A graphical example can be developed to illustrate the effects of digestion-reducing defenses by considering that a herbivore can choose to feed on two plants, one with the chemical (or more of the chemical) and the other without the chemical (or less of it). The digestion-reducing chemical operates in two ways, unlike the structural defense. First, it changes the nutrient constraint(s) by increasing the amount of nutrient that must be ingested to satisfy re-

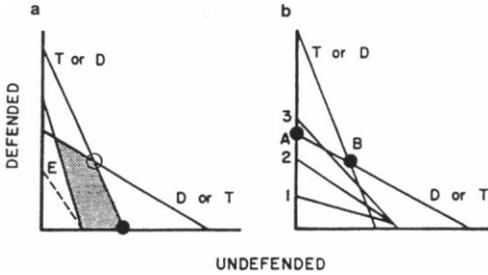


FIG. 3.—A graphical, linear-programming model is used to examine when digestion-reducing chemical defenses are effective. The feeding time (T) and digestive (D) constraints are interchangeable. a) The forager's energy constraint (E) is a dashed line if the chemical has no effect in reducing digestion and a solid line if it has an effect. The chemical changes the energy-maximizing diet from the open circle to the filled circle, decreasing consumption of the defended plant. b) The energy constraint is a solid line labeled with a 1–3, where an increasing number reflects the chemical's increasing ability to reduce digestion. The chemical reduces consumption of the defended plant from filled circle A to B as the energy constraint shifts from 1 to 2, but has no further effect (diet remains at filled circle B) as the energy constraint shifts to 3.

quirements. Second, it reduces the function defining the nutrient-maximizing goal, because the chemical decreases the nutritional value of the foods.

In Fig. 3a, the chemical successfully defends the plant (with the chemical or more of it) by reducing the herbivore's consumption of the plant (i.e., totally preventing consumption). The chemical to be a successful defense must attain a threshold of digestion-inhibition before it reduces consumption and any further ability to reduce digestion does not reduce consumption any further. However, the effects of the chemical are not always so apparent. For example (Fig. 3b), as the chemical successfully defends the plant by reducing consumption (consumption reduced from point A to B), further defense effectiveness (never consuming the defended plant) cannot be attained. Therefore, more of the chemical

does not always lead to reduced consumption.

The algebraic condition required for the digestion-reducing chemical to be an effective defense depends upon whether the herbivore's maximum consumption of the defended plant is limited by feeding time or digestive capacity (Belovsky and Schmitz, 1991). If feeding time limits intake, the ratio of nutrient content for the undefended plant : nutrient content for the defended plant (e.g., digestible energy/g dry mass of undefended plant : digestible energy/g dry mass of defended plant) must be greater than the ratio of the harvesting time for the undefended plant : harvesting time for the defended plant (e.g., min/g dry mass of the undefended plant : min/g dry mass of the defended plant). If digestive capacity limits intake, the ratio of nutrient content of the undefended plant : nutrient content of the defended plant must be greater than the ratio of the digestive capacity utilized by the undefended plant : digestive capacity utilized by the defended plant (e.g., g wet mass of digestive capacity filled/g dry mass of the undefended plant : g wet mass of digestive capacity filled/g dry mass of the defended plant). The fill of digestive capacity depends upon the passage of each of the foods through the digestive organ(s) and the volume displaced by each food.

Data provided on the digestion-reducing effects of tannins in twigs consumed by white-tailed deer (*Odocoileus virginianus*) and mule deer (Robbins et al., 1987) indicate that the model's criteria for efficacy, when intake is limited by digestive capacity, are met. Schmitz et al. (1992) provide stronger support for the model's predictions, because they explicitly tested the model's predictions using feeding trials in which snowshoe hares (*Lepus americanus*) were provided twigs whose characteristics pertinent to the model were manipulated. Consumption of the twigs decreased when the model's conditions for defense efficacy were met, and consumption increased when the criteria were not met. The model's con-

ditions were modified by varying the twigs' protein content, digestive-capacity utilization, and the concentration of the active chemical. Whether or not the active chemical in these twigs was correctly identified by the researchers (J. Bryant, pers. comm.), the chemical was experimentally demonstrated to reduce digestibility without any apparent toxic effects, which is the only necessary observation, because chemical identification has no particular meaning to the model.

The modeling results and empirical evidence indicate that defenses based upon digestion-reducing chemicals cannot be attributed with universal efficacy. Rather efficacy depends upon the context of other plants available to the herbivore in the immediate environment. For example, defense efficacy depends not only upon the digestion-inhibiting effects of the chemical and nutrient content in the plant thought to be defended, but also the nutrients and digestibility of the undefended plant. Defense efficacy is further controlled by the other characteristics (e.g., digestive capacity utilized and harvesting times) of the available plants. Therefore, demonstrating the ability of a chemical to reduce digestion and its presence in a plant does not indicate that it is an effective defense in nature.

*Toxic chemicals.*—Toxic plant chemicals often are considered the most important defenses, especially because these were the defenses first focused upon by ecologists studying plant-animal interactions (Ehrlich and Raven, 1964). A graphical example can be developed to illustrate the effects of toxic-chemical defenses by considering that a herbivore can choose to feed on two plants, one with the chemical (or more of the chemical) and the other without the chemical (or less of it). Toxic chemicals are easy to incorporate into linear-programming models, as claimed by Pulliam (1975), by adding a constraint that depicts a level of toxin intake that cannot be exceeded, because further intake either kills the forager or more subtly reduces fitness. Consequent-

ly, the toxic chemical operates in a single way unlike the digestion-reducing-chemical defense that modifies two functions in the linear-programming model. In Fig. 4c, the chemical successfully defends the plant (with the chemical or more of it) by reducing the herbivore's consumption of it; in Fig. 4b, the chemical can effectively reduce the herbivore's consumption under some conditions, and, in Fig. 4a, the chemical never has an effect.

The algebraic condition required for the toxic chemical to be an effective defense depends on whether the herbivore's maximum consumption of the defended plant is limited by feeding time or digestive capacity. If feeding time limits intake, the ratio of toxin content from the undefended plant : toxin content for the defended plant (e.g., toxin content/g dry mass of undefended plant : toxin content/g dry mass of defended plant) must be greater than the nutrient content for the undefended plant : nutrient content for the defended plant (e.g., digestible energy content/g dry mass of undefended plant : digestible energy content/g dry mass of defended plant), and both must be greater than the ratio of the harvesting time for the undefended plant : harvesting time for the defended plant (e.g., min/g dry mass of undefended plant : min/g dry mass of defended plant). If digestive capacity limits intake, then the first two ratios presented must be greater than the ratio of the digestive capacity utilized by the defended plant : digestive capacity utilized by the undefended plant (e.g., g digestive capacity filled/g dry mass of undefended plant : g digestive capacity filled/g dry mass of defended plant).

Data for desert woodrats (*Neotoma lepida*) foraging in the laboratory on foods containing toxic phenolic resins (Meyer and Karasov, 1989) meet the model's conditions for toxin efficacy. Data on voles (*Microtus pennsylvanicus*) foraging in the laboratory on foods containing toxic nontannin phenolics (Richter, 1988) meet the model's conditions for toxin efficacy. A study of

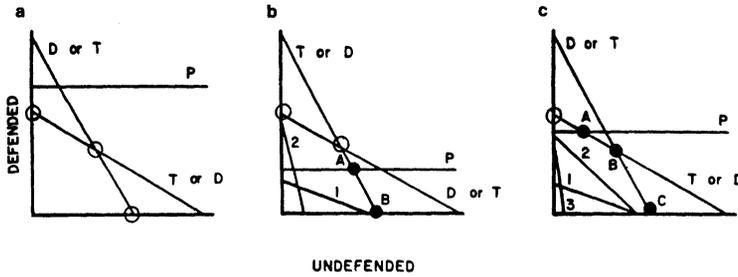


FIG. 4.—The graphical, linear-programming model is used to examine when toxins are effective. The digestive (D) and feeding-time (T) constraints are interchangeable. Numbered constraint lines denote different energy constraints; and the toxin constraint is labeled with a P. a) Because the toxin constraint is positioned above all other constraints, it cannot reduce consumption (i.e., the herbivore cannot consume enough of the defended plant for the toxin to have an effect). In this case, the diet will be represented by one of the open circles, depending upon the slope of the energy constraint. b) If the energy constraint is line 1, the toxin reduces consumption of the defended plant from the diet represented by one of the open circles to the diet represented by filled circle A; if the energy constraint is line 2, the toxin cannot reduce consumption of the defended plant, because it would not be consumed, even without the toxin (filled circle B). c) If the energy constraint is line 1, the toxin reduces consumption of the defended plant from the diet represented by the open circle to the diet represented by filled circle A; if the energy constraint is line 2, the toxin has no effect on consumption (the diet would be filled circle B with or without the toxin); and if the energy constraint is line 3, the toxin has no effect on consumption, because the defended plant would not be included in the diet, with or without the toxin (filled circle C).

mule deer foraging in pens indicates that nontannin phenolics in leaves meet the model's conditions when the leaves are not preferred (defended; McArthur et al., 1993). Furthermore, this study illustrates the absence of a universal relationship between a toxin and a particular herbivore as indicated by the linear-programming model. For example, the leaves of a species of toxic plants can be preferred relative to another species' leaves, but unpreferred relative to a third species' leaves. Preferences depend upon more than the presence or absence of a toxin, but also must consider the nutritional characteristics of each species. Therefore, the linear-programming model appears to predict the conditions needed for a toxin to be an effective defense.

The results for toxin efficacy are surprising, because it is commonly assumed that toxins always are effective in reducing consumption. The linear-programming model, however, indicated that toxin efficacy (e.g., concentration and toxicity) cannot be attrib-

uted without considering the traits (e.g., digestive capacity utilized, harvesting time, and nutrient content) of the toxin-containing and other plants in the environment. Therefore, demonstrating a chemical's toxic effects and the chemical's presence in a plant does not indicate that the chemical is an effective defense in nature.

#### INSIGHTS GAINED ON PLANT DEFENSES AGAINST MAMMALS

A number of realizations emerge from the inclusion of plant defenses in the linear-programming model for foraging by herbivores. These insights help to explain why plant-animal ecology has been plagued with inconsistent observations (Stamp, 1992) and the limitation of existing data on understanding plant-animal interactions.

*Plants and their defenses cannot be viewed in isolation.*—Plants and their defenses must be viewed in the context of the characteristics of other available plants and the herbivore's foraging characteristics.

This was explicitly indicated by the experiments conducted by Belovsky et al. (1991), McArthur et al. (1993), and Schmitz et al. (1992).

A simple example is provided by considering a herbivore foraging in two environments composed of the same two species of plants, where the plants differ in their absolute abundances or distributions in the two environments. Abundance and distribution of plants will change the harvesting rates for each plant by the herbivore. Because harvesting rate can appear as a factor in determining the efficacy of either digestion-reducing or toxic chemicals, the linear-programming model indicates that the plant with the chemical (or greater concentration of it) could be effectively defended so that consumption of it decreases and consumption of the other plant species increases at one set of abundances, but not at a lower set of abundances.

Differences in sunlight or soil moisture could likewise modify defense efficacy, if the two plants differentially responded to the conditions and if this differentially modified their nutrient concentrations or water content (digestion-fill), which in turn modified the conditions of the linear-programming model for defense efficacy. Therefore, we should not be surprised to observe that a plant defense is only sometimes effective, when we compare the same species of plants in different environments or between different sets of plants.

In a short time period (e.g., few days or weeks), a herbivore can learn to forage more efficiently on different plants and acclimate physiologically and biochemically to different plants as the plants change in relative abundances (Provenza and Balph, 1990). This can further complicate defense efficacy.

The failure to observe consistent responses of herbivores to plant defenses and defense effectiveness was one of the reasons why Stamp (1992) questioned the predictive success of studies in plant-animal ecology. However, the linear-programming

model tells us that uniform responses and efficacies are not to be expected. We do not argue that plant-animal interactions are either too complex to understand or that general theory will not emerge. The linear-programming model appears to provide a general framework for addressing defense efficacy and is instructive for which parameters need to be collected to make predictions about plant-animal interactions.

*What to measure in studies of plant-animal interactions.*—Because a plant's defenses must be evaluated in the context of the characteristics of other plants available in the environment, many past studies provide necessary, but insufficient, knowledge to evaluate defense efficacy. For example, when a laboratory study demonstrates that a plant chemical is toxic or digestion-reducing, this does not mean that the chemical is an effective deterrent to herbivory in all or any environments. These studies only illustrate that the chemical can potentially act as a defense. As indicated previously, even studies comparing consumption of pairs or assemblages of plant species in the laboratory, where all are equally abundant, cannot determine whether plant defenses are effective at field sites, because of different absolute abundances and distributions that affect harvesting rates. We need to have the matrix of pertinent characteristics of plants defined by the linear-programming model for all the common species available at a site. This means that diet selection by herbivores must be studied for particular environmental scenarios rather than piecemeal (i.e., the herbivore's response to one plant).

An interesting perspective on the necessary measurements emerges from the study of toxic nontannin phenols on intake by mule deer conducted by McArthur et al. (1993). In one study (Pullman, Washington), the plants were dried before assessing preference by deer, and, in this case (four tests of pairs of plant species), the linear-programming model predicted the effectiveness of the toxin as a defense. In the

other study (Juneau, Alaska), the plants were fresh when preference by deer was assessed, and, in this case (seven tests of pairs of plant species), the linear-programming model predicted toxin efficacy in five cases. It was pointed out that toxin efficacy depends upon a third consideration, either harvesting rates or digestion capacity-fill, depending upon which constraint (feeding time or digestive capacity) limits maximum intake of the defended plant. Because the plants were presented to the deer ad lib, harvesting rates are no longer a consideration. When the plants were dried (Pullman trials), digestive capacity may no longer be a consideration. However, when fresh plants were used (Juneau trials), digestive capacity may affect the model's predictions, making a toxin ineffective. Interestingly, the Juneau trials contain two cases where the toxin appeared to be ineffective, while the linear-programming model predicted that all should be effective if digestive-fill is not considered, which was not measured in the study.

Therefore, the study of plant-animal interactions needs to adopt a more holistic approach. A particular chemical or plant trait cannot be focused upon to the exclusion of other plant traits if we are to adequately evaluate plant defenses and diet selection by herbivores.

*What defenses potentially are most effective.*—All three categories of plant defenses (structural, digestive-reducing, and toxins) evaluated with the linear-programming model were shown to be effective under certain conditions. However, which is more likely to be effective in a variety of environmental circumstances? The linear-programming model indicates that toxin defenses are more likely to be effective than digestive-reducing-chemical defenses or structural defenses, because the conditions for efficacy are more likely to be met for toxins. This supports the argument that chemical toxicity may be more important than digestion-reduction (Bryant et al., 1991, 1992), but this does not imply that all

chemical defenses are toxic, rather than digestion-reducing, because digestion-reduction is a viable defensive strategy.

When referring to defense effectiveness, we also must be cognizant of the potential for two defenses, both in a single plant or one in each of two plants, either to enhance their effectiveness or be antagonistic. The linear-programming model indicates that structural and digestion-reducing or toxic chemical defenses in the same plant can be antagonistic. Antagonism arises when each defense requires opposite plant conditions to be effective. The linear-programming model also indicates that digestive-reducing defenses in two plants are antagonistic, because the same plant conditions cannot be met by both plant species to make each defense effective. Two plants containing the same toxic chemical enhance the defense's effectiveness, because ingestion of either plant results in greater toxin intake. However, if the two plants have different toxic chemicals that operate independently on the physiology of herbivores, the two defenses become antagonistic.

*Simplifications suggested for the study of plant-animal interactions.*—The holistic perspective toward plant-animal interactions provided by the linear-programming model indicates that a wide variety of parameters must be measured and evaluated. This is an extremely detailed approach that may appear insurmountable for many environments, especially those with numerous species of plants, but the degree of detail required may vary with the question being addressed.

The question of defense efficacy addresses whether a particular plant characteristic reduces consumption by herbivores, an important topic from the perspective of plant fitness, because the focus is upon how a plant avoids consumption. Therefore, the linear-programming analysis of plant-defense efficacy requires a perspective that is based upon individual species of plants, because the pertinent characteristics of all

common plants in an environment must be compared.

A different question is what particular foraging goal (e.g., nutrient maximization versus feeding-time minimization) is adopted by the herbivore, an important topic from the perspective of herbivore fitness. This question is addressed by comparing the diet observed to be selected by the herbivore against the diet predicted to produce each foraging goal. This can be accomplished employing the same level of detail used to address defense efficacy (i.e., diet selection based upon individual plant species, e.g., Doucet and Fryxell, 1993), but an approach requiring less detail might suffice to address this question (i.e., diet selection based on plant categories composed of species with similar traits, e.g., the analyses earlier in this paper).

The empirical applications of linear programming to address the herbivore's foraging goal have been criticized (Hobbs, 1990; Owen-Smith, 1993a, 1993b, 1994), because the consumption of plant categories (e.g., grasses and forbs) were examined, not the selection between plant species. However, this simplification employed to address foraging goals of herbivores may be supported by the more detailed approach required to address defense efficacy.

Structural and digestion-reducing chemical defenses do not add any new constraints to the linear-programming model. This permits calculation of average constraint parameters by plant categories, because the characteristics of the species that are averaged do not require specific consideration of the presence or absence of structural or digestion-reducing chemical defenses.

Toxins add a new constraint(s) to the model, the intake of each class of toxin that leads to mortality or reduced herbivore fitness. We know that some plants possess effective toxin defenses, and this might negate the simplification provided by plant categories. However, the linear-programming model using plant categories appears

to predict observed diets of mammalian herbivores in >272 cases (Table 2). How can this be explained? The plant-species approach to the linear-programming model provides two possible explanations. First, as previously pointed out, a toxin's efficacy can easily be negated by the defenses and characteristics of other available plants. Second, if a toxin is so effective that small amounts ingested lead to reduced herbivore fitness, the plants containing the toxin may not be "viewed" as food by the herbivore and would not be included in the linear-programming model. Therefore, the successful use of plant categories as a simplification to examine herbivore foraging goals may be expected.

#### CONCLUSION

Linear-programming models of foraging, for all of their simplifications and assumptions, appear to be able to predict the foraging behavior of mammalian herbivores and the actions of plant defenses on mammalian herbivores. These models explicitly integrate herbivore physiology, plant characteristics, and environmental parameters into a unified framework that quantitatively addresses why certain plants are consumed. Qualitative models (e.g., McArthur et al., 1993) may provide the same general predictions, but cannot make specific predictions for diet selection by herbivores or plant defenses. Furthermore, the linear-programming model indicates that a herbivore's adoption of a specific foraging goal (e.g., energy-intake maximization) does not lead to that currency in different plants (e.g., digestible energy/g dry mass) being the sole determinant of the herbivore's intake. This is contrary to claims that a herbivore does not maximize its energy intake if it does not preferentially consume the plant species with the greatest digestible energy per grams of dry mass (e.g., Dearing and Schall, 1992), because the holistic approach provided by the linear-programming model indicates that other characteristics of plants must be considered as well.

No doubt more realistic models of herbivore foraging will emerge; however, linear-programming models have identified what parameters must be considered. Linear-programming models may provide a unifying perspective for the study of plant-animal interactions, whether an investigator wishes to address defense efficacy of plants or diet selection by herbivores; this may help to alleviate some of the inconsistencies in this fertile area of ecological investigation that were identified by Stamp (1992).

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