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Oikos, Vol. 72, No. 3. (Apr., 1995), pp. 333-342.

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OIKOS 72: 333–342. Copenhagen 1995

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Grantham, Ö. K., Moorhead, D. L. and Willig, M. R. 1995. Foraging strategy of the giant rams-horn snail, *Marisa cornuarietis:* an interpretive model. – Oikos 72: 333–342.

A linear programming model was used to examine the foraging strategy of the giant rams-horn snail, *Marisa cornuarietis*, based on its consumption of two aquatic macrophytes, *Ludwigia repens* and *Vallisneria americana*, in laboratory feeding experiments. A model was constructed for each of 27 snails, incorporating estimates of daily energy requirement, digestive capacity, and feeding time of each individual. An index of foraging strategy was developed to assist the evaluation of individual deviation from predicted optimal diets; energy-maximized and time-minimized diets have index values of 1.0 and 0.0, respectively. As a population, *M. cornuarietis* does not maximize energy intake or minimize time spent foraging, rather it forages in an intermediate fashion (mean index value = 0.565). Individual snails exhibited all possible strategies: 11% minimized time spent foraging, 30% maximized energy intake, 41% were intermediate, and 18% had unresolved strategies resulting from high variation in daily consumption patterns. Uncertainty analyses of the linear programming model revealed that it is robust with regard to changes in key parameter values.

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Herbivores forage under constraints related to digestive capacity, nutrient requirements, and time (Pulliam 1975). In general, optimal foraging behavior is hypothesized to maximize the intake of energy or nutrients (Pyke et al. 1977, Vadas 1977, Belovsky 1978, 1984a, b, Huebner and Edwards 1981, Owen-Smith and Novellie 1982), to maximize the rate of digestion (Westoby 1974), to minimize the intake of toxins (Freeland and Janzen 1974), or to minimize the time spent foraging (Pyke et al. 1977). Many foraging models predict a single optimal diet for an entire population, although individuals in the population may deviate from predicted optima (Krebs et al. 1977, Rechten et al. 1983). In fact, high intraspecific variation among consumers generally characterizes diet selection (Heinrich 1976, Werner et al. 1981, Sandlin and Willig 1993).

Intraspecific variation in diet can be explored with mathematical models in which morphological and physiological differences among individuals are incorporated as factors that influence food choice. For example, Ritchie (1988) used a linear programming (LP) model to examine variation in the diets of Columbian ground squirrels, and found that the diet of 37% of 109 individuals deviated significantly from an energy-maximizing diet. In many cases, LP models have been used successfully to predict optimal foraging strategies of terrestrial herbivores (Belovsky 1978, 1984a, 1986, Belovsky and Schmitz 1991, Doucet and Fryxell 1993). However, this approach has not been applied to aquatic organisms such as freshwater gastropods.

Accepted 14 September 1994

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Table 1. Description of parameters included in the linear programming (LP) model. Lr = *Ludwigia repens*, Va = *Vallisneria americana*.

Parameter	Description (units)	Value	Equation(s)
E	daily energy requirement (cal · d^{-1})	variable	1, 2 and 9
a	activity coefficient (unitless)	1	1
α	constant (ml O_2 · h^{-1} · mg^{-1})	0.98	1
β	constant (unitless)	0.789	1
W	snail weight (mg)	variable	1 and 8
e_{Lr}	digestible energy content of Lr (cal · mg^{-1})	2.05	2, 6 and 7
e_{Va}	digestible energy content of Va (cal · mg^{-1})	1.025	2, 6 and 7
LR	amount of Lr consumed (mg · d^{-1})	variable	2, 4 and 5
VA	amount of Va consumed (mg · d^{-1})	variable	2, 4 and 5
D	daily gut capacity (mm^3 · d^{-1})	variable	3 and 4
V	gut volume (mm^3)	variable	3
gtt	gut turnover time (d^{-1})	1.6	3
b_{Lr}	bulk volume of Lr (mm^3 · mg^{-1})	13.43	3 and 4
b_{Va}	bulk volume of Va (mm^3 · mg^{-1})	16.90	3 and 4
T	maximum feeding time (min)	variable	5
c_{Lr}	cropping rate of Lr (min · mg^{-1})	variable	5
c_{Va}	cropping rate of Va (min · mg^{-1})	variable	5
M	shell diameter (mm)	variable	8
z	exponent (unitless)	2.4	8
E_{max}	maximum energy intake (cal · d^{-1})	variable	6 and 9
E_{min}	minimum energy intake (cal · d^{-1})	variable	7 and 9
FSI	foraging strategy index (unitless)	variable	9

Background

The giant rams-horn snail, *Marisa cornuarietis* (Ampullariidae), is a discodial prosobranch gastropod that recently was introduced from South America into the San Marcos and Comal Rivers of Central Texas, USA (Jobin 1970, Neck 1984). *M. cornuarietis* grazes on *Ludwigia repens* (Lr) and *Vallisneria americana* (Va), two dominant macrophytes in the Comal River (Horne et al. 1992). In laboratory experiments, *M. cornuarietis* consumes Lr at higher rates than it does Va, but this snail exhibits partial preferences when both macrophytes are present (Grantham et al. 1993). Although the consumption of Va remains low, it is remarkably constant in the presence of Lr. Grantham et al. (1993) concluded that Va supplies some essential nutrient(s) that the preferred Lr does not, thus explaining the partial preference for Va even though Lr has higher digestibility. Although diet choice can be influenced by avoidance of toxins, there is no evidence suggesting that secondary plant substances constrain the foraging of *Marisa*. Moreover, Grantham et al. (1993) found no significant differences in tannin content of Lr and Va.

Herein, we utilize an LP model to elucidate the foraging strategy of *M. cornuarietis* based on consumption of Lr and Va. LP models are well-suited to this type of study because they allow simultaneous consideration of several foraging constraints. For example, minimum daily energy must be obtained within a finite amount of time, given a particular digestive capacity. Also, individual differences in body size, and digestive and foraging abilities, can be incorporated into model structure. Finally, LP models can be used to predict conditions under which partial preferences should occur. Specifically, our goals are to examine individual deviation from predicted optimal diets (i.e., time-minimized or energy-maximized), and evaluate the effects of snail size on diet selection. In this study we examine three null hypotheses: 1) *M. cornuarietis* forages in a manner that maximizes energy intake, 2) diet composition is independent of snail size, and 3) foraging strategy is consistent among individuals.

Modelling rationale

An LP model was developed to describe foraging behavior of *M. cornuarietis* based on two variables: consumption of Lr and Va (LR and VA, respectively; mg dry wt · d^{-1}). Three primary factors affect foraging in this approach: 1) minimum daily energy requirement, 2) gut capacity, and 3) maximum time feeding or available to feed.

Daily energy requirement

The minimum daily energy requirement (E) of a rams-horn snail is a function of body mass (Akerlund 1969, 1974):

$$E = a \cdot \alpha W^{\beta} \quad (1)$$

where, a is an activity coefficient (Aldridge 1983), W is the dry mass (mg) of the individual, and α and β are coefficients (Akerlund 1974; see Table 1 for parameter values). For the purposes of convenience in this study, E

is converted to units of calories per day, instead of ml O_2 uptake per hour estimated by Akerlund. This energy requirement must be met by consuming plants such that:

$$E < e_{Lr} \cdot LR + e_{Va} \cdot VA \quad (2)$$

where e_{Lr} and e_{Va} are digestable energy contents of Lr and Va ($cal \cdot mg^{-1}$), respectively.

Digestive capacity

Digestive capacity limits the amount of food an individual can ingest and small herbivores have proportionately smaller gut capacities than do large ones (Milton 1979). Daily digestive capacity (D; $mm^3 \cdot d^{-1}$, can be estimated as a function of gut volume (V; mm^3) and turnover (gtt; d^{-1}):

$$D = gtt \cdot V \quad (3)$$

In this case, digestive capacity limits plant consumption:

$$D > b_{Lr} \cdot LR + b_{Va} \cdot VA \quad (4)$$

where b_{Lr} is the bulk volume ($mm^3 \cdot mg^{-1}$) of Lr and b_{Va} is the bulk volume of Va.

Time constraint

A daily time frame is used in the LP model to estimate feeding time (T; $min \cdot d^{-1}$), excluding all other activities. Energy intake during this feeding time can be expressed in terms of potential plant consumption:

$$T > c_{Lr} \cdot LR + c_{Va} \cdot VA \quad (5)$$

where c_{Lr} and c_{Va} are the cropping rates ($min \cdot mg^{-1}$) associated with the consumption of Lr and Va, respectively.

Interactions

In defining the constraints on food intake (above equations), E, D, and T are expressed in terms of plant material consumed (VA and LR), and the diet may comprise various ratios of Va and Lr. Accordingly, each snail may have a range of possible diets that satisfy its minimum daily energy requirement without exceeding daily feeding time or gut capacity. The LP model identifies the point at which gut capacity is obtained in the available time with a diet composition that maximizes energy intake. This point (E_{max}; $cals \cdot d^{-1}$) corresponds to an energy-maximizing strategy that can be expressed in terms of plant consumption:

$$E_{max} = e_{Lr} \cdot LR_{max} + e_{Va} \cdot VA_{max} \quad (6)$$

where LR_{max} and VA_{max} are the quantities of Lr and Va ($mg \cdot d^{-1}$) that compose this diet. Similarly, the point at which minimum daily energy requirements are met in the least possible time (E_{min}; $cal \cdot d^{-1}$) represents a time-minimizing foraging strategy that also can be expressed in terms of energy intake:

$$E_{min} = e_{Lr} \cdot LR_{min} + e_{Va} \cdot VA_{min} \quad (7)$$

where LR_{min} and VA_{min} are the quantities of Lr and Va ($mg \cdot d^{-1}$) that compose this diet. This model provides a basis to determine if *M. cornuarietis* is an energy-maximizer or a time-minimizer with respect to foraging.

Methods and materials

The methods of collection and laboratory maintenance of *M. cornuarietis* and the macrophytes used in this study are described in detail by Grantham et al. (1993). However, a brief overview of relevant procedures follow.

Dietary patterns

Adult snails (>30 mm shell diameter) and macrophytes were collected from the Comal River near San Marcos, Texas. Animals were maintained at 20°C in aerated 76-l aquaria, and offered a mixture of Lr and Va for consumption before the feeding trials. Water in all aquaria was changed weekly and the laboratory was illuminated for 12 h per day. During feeding trials, each of 27 snails was placed in an aerated 4-l aquarium (acclimated for 3–6 h), and simultaneously offered equal amounts of Lr and Va for four consecutive days. Measurements of plant consumption (wet mass, blotted to remove excess water) were taken daily. Samples of five plants of each species were dried at 60°C for 48 h to obtain dry weight to wet weight ratios that were used to convert measurements to dry weight. Mean daily food consumption (LR and VA, respectively) was measured as mg dry mass of Lr and Va eaten per day.

Model parameters

Each snail was transferred to an aerated container (4×4×6 cm) 4–6 h before the measurement of cropping rates. The cropping rates of snails when feeding on Lr or Va (c_{Lr} and c_{Va}; eq. 5) were determined by observing each of 27 individuals continually for 1–2 h when plant species were offered separately. The reduction in plant weight during each observation period defined total consumption (mg) of plant material by the snail. This quantity was divided by the amount of time each snail fed, to estimate the cropping rate of each individual for each plant species.

The total time that snails spent foraging per day was determined by placing individuals with known cropping rates (N = 27) in a 76-l aquarium that contained both Lr and Va. The activity of each snail was recorded (e.g., found on plants, crawling separate from plants or inactive) every 20 min for 24 h. From these observations, we estimated the fraction of time each individual spent feeding during each hour of the day, as well as the total amount of time spent feeding (min).

Average gut turnover (i.e., number of times gut is emptied per day) for *M. cornuarietis* was estimated in two ways. First, three individuals (not used in LP modelling) were placed in separate aquaria, starved for 24 h, and fed a diet of 5% agar containing colored cotton fibers mixed with dry plant material. During the next day, feces produced by these snails were examined for the presence of the colored fibers. The inverse of the time (d^{-1}) at which the fibers first appeared in the feces defined gut turnover (gtt; d^{-1}). This method provided a maximum estimate (gtt = 2.0). Alternatively, six snails (not used in LP modelling) were starved for 24 h and then fed lettuce until satiated. Three of these individuals were dissected after 12 h (0.5 d), and three were dissected after 15 h (0.625 d) to estimate the rate at which snails empty 95% of their stomach contents. The ratio of number of food particles in the stomach fluid to the total number of particles in the entire gut was used to determine the turnover of stomach contents. When ≤ 5% of the total particles were present, stomachs were classified as empty, and the inverse of the time required to reach this state (d^{-1}) provided an estimate of average gut turnover for *M. cornuarietis*. This method provided the lowest estimate (gtt = 1.34).

Shell diameter of each individual was measured to the nearest mm. These measurements were used to estimate shell-free snail weight according to Skalberg and Arsuffi (pers. comm.):

$$W = M^z \tag{8}$$

where W is shell-free dry mass (mg), M is shell diameter (mm) and z is a constant (see Table 1). These estimates of individual snail mass were used to calculate minimum daily energy requirement (E; eq. 1).

After determining consumption patterns and gut turnover, snails were fed lettuce for 24 h and then anesthetized in a solution of 7.5% MgCl. Entire animals were fixed in 10% neutral formalin. The length and perimeter of the esophagus-stomach complex was measured in each individual, and gut volumes were calculated assuming that the esophagus and stomach were cylinders. Bulk volumes of Lr and Va (b_{Lr} and b_{Va}; see eq. 4) were measured by weighing measured volumes of each plant species (length by width by thickness of leaf samples).

Energy contents of Lr and Va used for model parameters (e_{Lr} and e_{Va}; see eq. 2 and Table 1) represent the digestable fraction of the total caloric content of each plant type. The total caloric content of both Lr and Va was assumed to be 4.1 cal · mg^{-1} because Boyd (1970) reported that aquatic macrophytes generally have similar caloric contents (i.e., 4.1 ± 0.45 cal · mg^{-1}, N = 11 [number of species in Boyd]). However, Grantham et al. (1993) found that the *M. cornuarietis* could digest only a fraction of Lr and Va, i.e., 52% and 26%, respectively. In estimating the energy content of the digestible fractions of these macrophytes, we assumed that the caloric concentrations within digestible and undigestible components of each plant species were constant.

We evaluated the assumption of equal caloric contents of plant tissues from Va and Lr by analyzing plant materials remaining at the end of the feeding experiments, by bomb calorimeter. The quantities remaining were insufficient for multiple samples, but the gross caloric content of a bulked sample for Lr was the same as that for Va (ca 3.0 cals · mg^{-1}). This value falls into the range reported for Va, at 1.6–4.3 cals·mg^1 (Muztar et al. 1978, Donnermeyer and Smart 1985, respectively).

Quantitative analyses

The relationships between size (32–44 mm, shell length) and 1) mean consumption rate, 2) feeding time, 3) cropping rate, and 4) gut capacity of snails were examined via separate linear regression analyses. A paired t-test was used to evaluate differences in cropping rates on Lr and Va.

For each of the 27 individual LP models, the coordinates at which diets were energy-maximized (E_{max}) and time-minimized (E_{min}) were calculated in terms of caloric values rather than consumption rates (see eqs 6 and 7). To examine inter-individual deviation from these optimal strategies, an index of individual foraging strategy (FSI) was calculated for each snail:

$$FSI = (E - E_{min}) / (E_{max} - E_{min}) \tag{9}$$

where E is calories obtained from the observed diet, E_{min} (see eq. 7) is calories obtained from a time-minimized diet, and E_{max} (see eq. 6) is calories obtained from an energy-maximized diet. According to eq. 9, the values of FSI for time-minimized and energy-maximized diets correspond to 0 and 1, respectively. For each individual, a 95% confidence interval (CI) of FSI was calculated based on daily individual consumption during the 4 d of the feeding trials. If the 95% CI included unity (1.0), the snail was considered to be an energy-maximizer; if the 95% CI included 0, the snail was considered to be a time-minimizer; if the CI included both 0 and 1, the strategy was considered to be unresolved; if CI included neither 0 nor 1, the strategy was considered to be intermediate. Regression analysis of FSI as a function of snail size assessed if deviations from optimal strategies were related to size.

Uncertainty analyses of three key model parameters were conducted to examine the effects of potential experimental error on individual deviations (as determined by

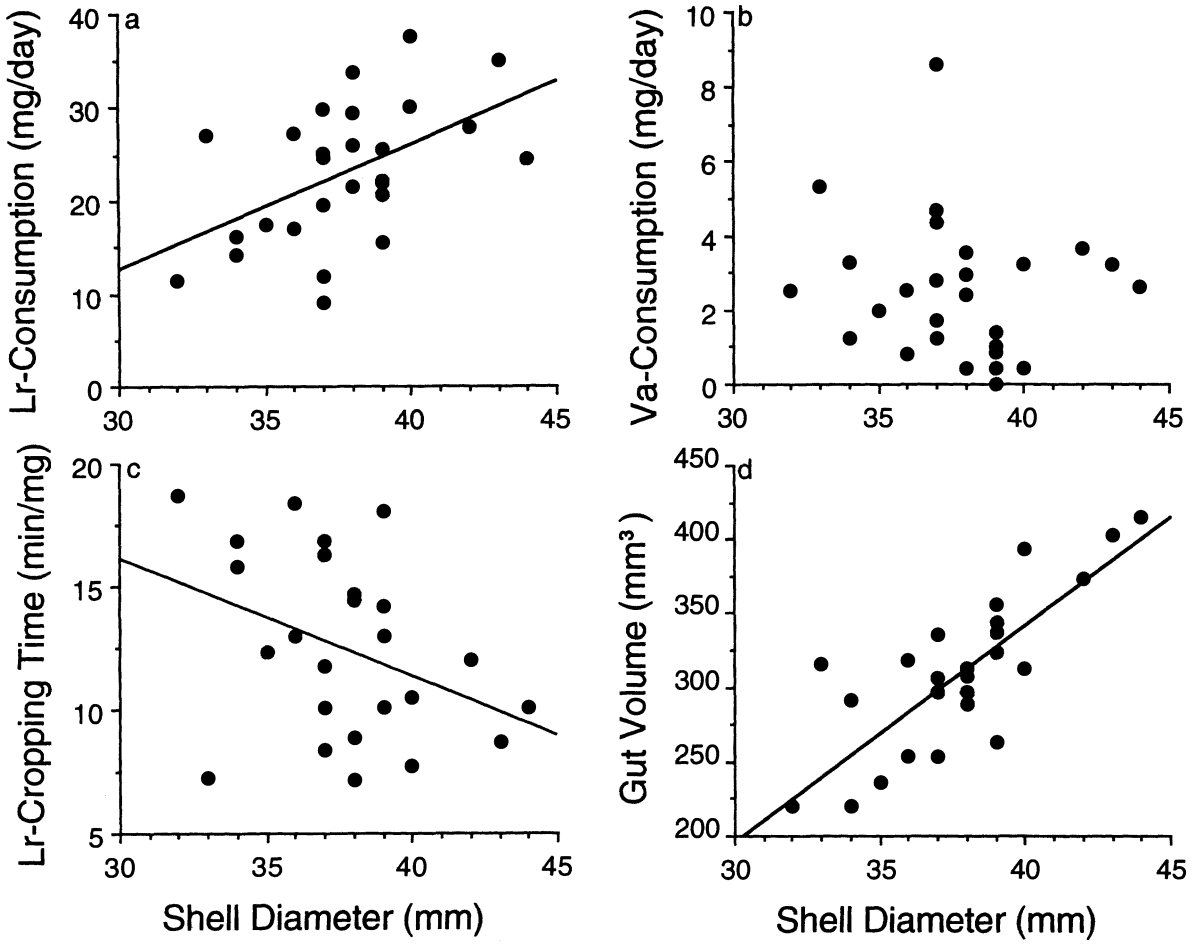

Fig. 1a. The relation between daily consumption of *Ludwigia repens* (Lr) and snail size ($y = 1.35x - 27.7$; $r^2 = 0.259$; $P = 0.007$). b. The non-significant relation between daily consumption of *Vallisneria americana* (Va) and snail size ($r^2 = 0.004$, $P = 0.75$). c. The relation between the cropping rate of Lr and snail size ($y = 30.66 - 0.48x$; $r^2 = 0.143$, $P = 0.018$). d. The relation between the gut volume and snail size ($y = 14.6x - 240.6$; $r^2 = 0.613$, $P < 0.001$).

FSI values) from the optimal diets. Key model parameters were the activity coefficient (a; see eq. 1), gut turnover (gtt; see eq. 2), and maximum daily feeding time (T; see eq. 3). Values of these parameters were modified to reflect the actual range of observations for mollusks, in general, or specifically for *M. cornuarietis*. For example, the activity coefficient was doubled (from 1 to 2) to include the energetic costs associated with feeding and digestion, as reported for other gastropods (Aldridge 1983). Changes in daily gut turnover, estimated by two methods, reflected the lowest and highest turnover values estimated for *M. cornuarietis* (gtt = 1.34 d^{-1} and 2.0 d^{-1}, respectively). Finally, the observed daily feeding times of individuals were probably overestimated because these values were measured as the total time spent on plants, and likely included time that was not spent foraging. Consequently, a fraction (65%) of this parameter, representing the average time required to fill the gut, given volume and cropping rate, also was used in uncertainty analyses. Normality of the FSI values resulting from this model was tested via Kolmogorov-Simirnov goodness-of-fitness tests (SPSS 1988).

Results

Observed diet

The mean (± SE) daily consumption rates of Lr and Va (N = 27) were 23.06 ± 7.40 and 2.49 ± 0.36 mg · d^{-1}, respectively. A significant linear relationship occurred between Lr consumption (mg) and size of the snails (Fig. 1a); however, no relationship existed between daily consumption of Va and snail size (Fig. 1b).

Table 2. Parameters values from linear programming (LP) models of four different individuals represented in Fig. 2a-d.

Parameter	Snail 4	Snail 8	Snail 14	Snail 16
Snail mass (mg)	501	614	655	655
Cropping rates ($min \cdot mg^{-1}$)				
Ludwigia repens	15.78	10.1	14.43	16.63
Vallisneria americana	20.89	8.21	11.49	9.82
Digestible energy content ($cal \cdot mg^{-1}$)				
Ludwigia repens	2.050	2.050	2.050	2.050
Vallisneria americana	1.025	1.025	1.025	1.025
Food bulk ($mm^3 \cdot mg^{-1}$)				
Ludwigia repens	13.43	13.43	13.43	13.43
Vallisneria americana	16.90	16.90	16.90	16.90
Feeding time ($min \cdot d^{-1}$)	660	660	760	620
Gut capacity ($mm^3 \cdot d^{-1}$)	467	474	474	493
Energy requirement ($cal \cdot d^{-1}$)	15.23	17.88	18.82	18.82

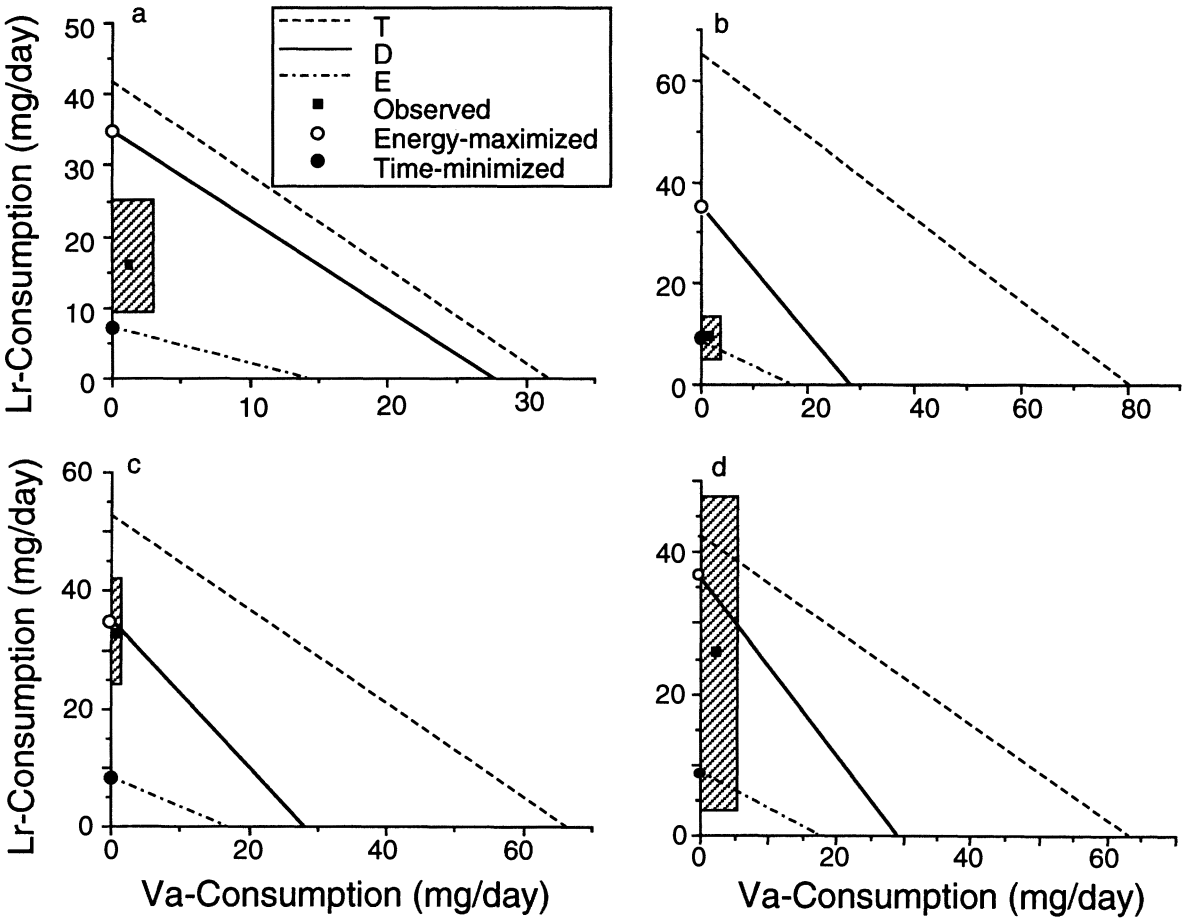

Fig. 2a. Linear programming (LP) model for an individual that is neither an energy-maximizer nor a time-minimizer (snail 4; see Table 2). b. LP model for a time-minimizer (snail 8). c. LP model for an energy-maximizer (snail 14). d. LP model for an individual whose foraging strategy could not be categorized with confidence because of high variation in daily consumption (snail 16). In all cases, the cross-hatched area represents 95% confidence intervals of the mean observed consumption, shown by a solid square. Constraint lines are time (dashed; T), digestive capacity (solid; D), and energy (dot-dash; E) isoclines; Lr = *Ludwigia repens*, Va = *Vallisneria americana*.

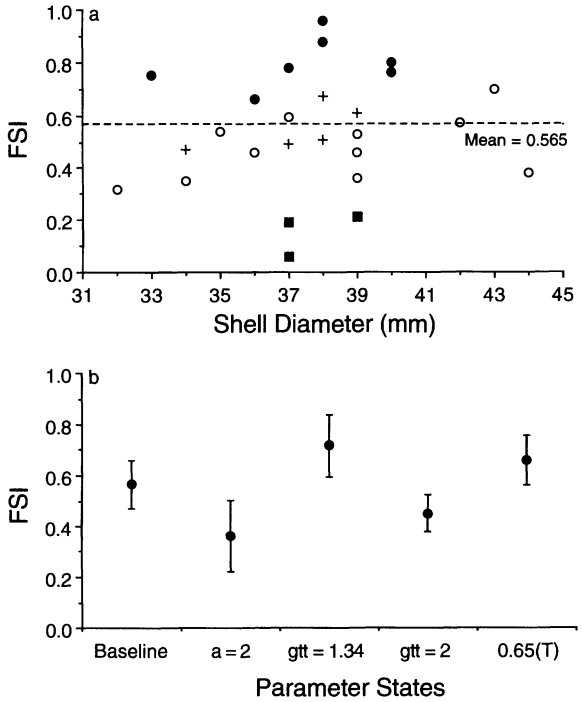

Fig. 3a. The relation between individual deviation from optimal strategy and snail size. Open circles represent intermediate foragers, closed circles represent energy-maximizers, closed squares represent time-minimizers, and crosses represent unresolved foraging strategies. b. The 95% confidence intervals of mean FSI (individual deviation from time-minimized strategy) for LP models with different parameter values (a = snail activity coefficient, gtt = daily gut turnover, T = maximum daily feeding time; energy-maximized strategy occurs when FSI = 1, and time-minimized strategy occurs when FSI = 0).

Model parameters

Mean (± SE) cropping times of Lr and Va (N = 27) were 12.42 ± 0.69 and 14.39 ± 1.02 $min \cdot mg^{-1}$, respectively, with the difference approaching significance (t = –2.041, P = 0.052). Cropping time decreased with increasing snail size for Lr (Fig. 1c), but remained constant for Va.

Snails spent an average of 46% of the day feeding with no significant relationship existing between maximum daily feeding time and snail size ($r^2 = 0.061$, P = 0.213). More than 80% of the snails spent less than 57% of the day feeding. When not feeding, snails were either crawling or inactive. A positive linear relationship existed between gut volume (mm^3) and body size (Fig. 1d).

The greatest gut turnover was estimated as 2 times a day (i.e., the dissection method indicated that 12 h [0.5 d] were necessary to empty 95% of the stomach contents) and the slowest turnover was calculated to be 1.34 times a day (i.e., 18 h [0.75 d] required for labelled food to appear in feces). The average gut turnover was estimated as 1.6 times a day (i.e., 15 h [0.625 d] were necessary to empty 95% of the stomach contents), used in model simulations.

LP model

An LP model was developed for each individual (N = 27), but only one representative of each foraging strategy is illustrated herein (Table 2). For all 27 individuals, LP models predicted that both time-minimized (E_{min}) and energy-maximized (E_{max}) diets should comprise exclusively Lr, due to the higher digestibility of Lr compared to Va (52% vs 26% dry wt., respectively; Grantham et al. 1993). In summary, 41% of the snails had neither energy-maximizing nor time-minimizing diets, and were classified as intermediate foragers (Fig. 2a). Only 11% of the snails were time-minimizers (Fig. 2b) and 30% were energy-maximizers (Fig. 2c). The rest of the snails (18% of the total) varied so much in daily Lr consumption that it was impossible to classify their strategy as other than indeterminate (Fig. 2d).

The FSIs for all snails indicated that the population as a whole did not exhibit a consistent pattern of diet selection (Fig. 3a). As a population, *M. cornuarietis* adopted an intermediate foraging strategy, because the largest number of classifiable, individual diets were intermediate and the mean of individual FSIs (0.565) was approximately halfway between energy-maximizing and time-minimizing strategies. Furthermore, individual deviations from optimal diets were independent of snail size, reducing the likelihood that foraging patterns were influenced by age.

Uncertainty analysis

Uncertainty analysis of the LP model, incorporating reasonable variations in parameter estimates, continued to produce FSI values indicative of an intermediate foraging strategy (Fig. 3b). For example, increasing daily energy requirements by doubling the activity coefficient of the energy constraint (a = 2) decreased the mean value of FSI by 36%, but did not result in a time-minimizing diet. The mean value of FSI decreased by a relatively small amount when gut turnover (gtt) was varied from 1.34 to 2.0 Similarly, decreasing the time available for foraging (T) by 35% increased the mean FSI value for the population, but did not result in an energy-maximizing diet. In short, none of the parameter modifications resulted in the predominance of energy-maximimizing or time-minimizing foraging strategies. As a consequence, even if substantial errors exist in parameter estimates, they do not affect the overall interpretation of foraging strategies for *M. cornuarietis* by this LP model.

Discussion

Energy and time are currencies that affect foraging decisions of herbivores (Shoener 1971, Belovsky 1978); time minimizers forage the least amount of time needed to meet minimum energy requirements, whereas energy

maximizers obtain the greatest amount of energy in the available feeding time. Our studies suggest that the overall foraging strategy of *M. cornuarietis* is neither energy-maximizing (30% of the sample population) nor time-minimizing (11% of the sample population). If foraging strategy is an inherent characteristic of a species or an individual (cf. Ritchie 1988), *M. cornuarietis* is more likely to be classified as an intermediate forager based on the composite picture provided by individual diets (41% of individuals overlapped neither energy-maximized nor time-minimized strategies). Further supporting this conclusion, the mean value of the foraging strategy index for the entire population also represented an intermediate strategy (FSI = 0.565; Fig. 3a).

According to classical models of optimal diet, natural selection favors energy-maximizing strategies because they facilitate potentially higher growth and reproduction. However, physiological changes in organisms and varying environmental conditions may result in diet variation. For example, a generalist grassland herbivore may adopt an overall energy-maximizing strategy to survive periods of energy deficiency during times of poor forage quality (Belovsky 1986). Alternatively, an individual may increase fitness by minimizing time spent foraging if it is involved in activities such as parental care, avoiding predators, or searching for mates (Belovsky 1978). However, we believe that the intermediate foraging strategy exhibited in these trials by *M. cornuarietis*, as a population, is not a product of changing environment, forage quality, or physiological variability. Fluctuations in foraging strategy resulting from fluctuating environmental conditions were unlikely because laboratory conditions of temperature and light regime remained constant. The quality of food offered to individual snails might have varied, but the plants used for feeding trials were collected from the same beds of plants at the same time and the short duration of the feeding trials reduces the possibility of much change having occurred in plant quality during utilization. Furthermore, no predators were present and no indication of changes in reproductive status or behavior of the population occurred during the study period.

Although foraging models generally predict a single optimal diet for an entire population, individual diets often deviate from predicted optima (Heinrich 1976, Krebs et al. 1977, Werner et al. 1981, Rechten et al. 1983, Sandlin and Willig 1993). Consistent with such observations, LP model evaluations of *M. cornuarietis* diets illustrated high inter-individual variation (Fig. 3a). We are aware of only one other study using LP models to elucidate individual variation in diet selection, in which diets of ground squirrels were examined (Ritchie 1988). Diets consisted of two food types (dicots and monocots), and LP models were used to define the relative proportion of each plant type in an energy-maximized diet. Energy-maximized diets were reported for 63% of the squirrels (N = 109), demonstrating that about one-third of the population had diets deviating from the predicted optimum. In spite of these inter-individual variations, Ritchie (1988) reported that the predicted diet composition of ground squirrels was highly correlated (r = 0.97) to observations.

In our study, the amount of food consumed by snails fluctuated considerably on a daily basis, due to variations in the absolute consumption of Lr, but not of Va. For this reason, the proportion of Lr (or Va) in the diet was inconsistent and could not be used to predict the foraging strategies of *M. cornuarietis* in the manner used by Ritchie (1988). Instead, confidence intervals (95%) of mean daily consumption were used to classify individuals as being energy maximizers or time minimizers (Fig. 2). The relative differences between predicted and observed diets (FSI), based on caloric intake, also were used to quantify individual deviations from optimal strategies. All of our LP models of *M. cornuarietis* predicted that both time-minimized (E_{min}) and energy-maximized (E_{max}) diets should comprise exclusively Lr, because Lr supplies more energy than does Va (Grantham et al. 1993). Nonetheless, Va was included in the diet of all but one snail. Partial consumption of Va apparently was not a consequence of energy requirements; nonetheless other currencies, such as nutrients, might account for this pattern (Belovsky 1978, 1984b, Lacher et al. 1982, Willig and Lacher 1991). In particular, nitrogen and phosphorus contents of Va exceed those of Lr (Riemer and Toth 1968, Muztar et al. 1978, Terry and Tanner 1986), so that observed diets of *M. cornuarietis* may balance energy and nutrient requirements (Grantham et al. 1993).

Partial preferences resulting in deviation from energy-maximizing diets have been reported in other studies using LP models (e.g., Belovsky 1978, 1984b, Doucet and Fryxell 1993). For example, Doucet and Fryxell (1993) found that an energy-maximizing diet for beaver (*Castor canadensis*) should comprise solely aspen (*Populus tremuloides*) but animals consistently exhibited partial preference for water lily (*Nymphaea odorata*). Clearly, LP models based on the acquisition of a single resource, such as energy, cannot represent fully the dynamics of multiple-resource capture.

Both the utility and limitations of LP models for evaluating individual foraging strategy are demonstrated by this study. Twenty-five of the individual diets contained quantities of Lr and Va that were consistent with simultaneous operation of energy and digestive constraints. Only two individuals consumed Lr and Va in amounts that exceeded estimates of digestive capacity or were less than minimum requirements. This suggests that the LP model accurately incorporated essential constraints in the foraging behavior of *M. cornuarietis*. Moreover, this modeling approach is robust with regard to uncertainty in parameter estimates; none of the parameter modifications in uncertainty analyses significantly affected the classification of foraging strategy by *M. cornuarietis* as a population. Thus, it is unlikely that we have obtained serendipitous correspondence between observed diets and model predictions because of inaccurate parameter estimates. How-

ever, this study also illustrates the limitations of a single-resource based model of foraging behavior. Since all organisms must balance a multitude of resource requirements for survival and reproduction, a precise characterization of foraging strategy must consider these additional needs. For example, Tilman's work with models of multiple-resource limitations on growth or survival in plants (Tilman 1982, 1988) provides a conceptual framework that might be applied to patterns of animal foraging. As plant species may have different strategies regarding acquisition of different resources, animals also may have different foraging strategies with regard to various nutritional requirements. Although we are unaware of any attempts to apply Tilman's theories to animal behavior, we believe that it would be fruitful to expand the LP modeling methodology to include multiple dimensions represented by various resources.

In summary, as a population, *M. cornuarietis* does not maximize energy or minimize time, rather it forages in an intermediate fashion. However, energy-maximizing, time-minimizing, and intermediate strategies were adopted by different individuals and some snails were so highly variable in daily consumption patterns that their foraging strategy could not be classified. Although individuals may utilize a single foraging strategy over long times or change strategies frequently, the time domain of our study could not examine this possibility. Partial preferences of *M. cornuarietis* suggest that foraging patterns are influenced by nutritional requirements in addition to energy procurement, which should be considered in future work to more accurately predict consumption patterns.

Acknowledgements – This work contributed to the partial completion of Master of Science degree requirements for Ms. Özlen Grantham at Texas Tech Univ. We wish to thank M. K. Rylander and T. L. Arsuffi for providing critical input and reviewing earlier versions of the manuscript. Also, we would like to thank M. Skalberg and T. L. Arsuffi for assistance with field collections and for sharing unpublished data.

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