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Effect of dietary composition on food selection and assimilation in the leaf-eared mouse (*Phyllotis darwini*) inhabiting central Chile

Efecto de la composición dietaria sobre la selección y asimilación de alimento en el lauchón orejudo (*Phyllotis darwini*) en Chile central

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ABSTRACT

In this work we investigated the criterion by which a granivorous rodent selects food and the relationship between the diet selected and the nutrients that become assimilated. We conducted tests of food preference and nutrient assimilation in the sigmodontine leaf-eared mouse *Phyllotis darwini*, which inhabits the mediterranean and semiarid regions of Chile and lives in open scrub habitats subjected to summer drought. We found that this rodent does not select food based on a single criterion. When given a choice, individuals select food with the highest content of nutrients to satisfy a minimal assimilation of 4.34 g dry-matter/day. Thus, animals seem to use criteria in addition to energy content in choosing food.

Key words: Dietary chemistry, feeding behavior, assimilation, *Phyllotis darwini*.

RESUMEN

En este trabajo investigamos el criterio que utiliza un roedor granívoro en la selección de alimento y la relación entre la dieta seleccionada y los nutrientes que son asimilados. Se realizaron pruebas de preferencias alimentarias y asimilación de nutrientes en el lauchón orejudo sigmodontino *Phyllotis darwini* que vive en las regiones mediterréneas y semiáridas de Chile y en hábitats arbustivos sujetos a veranos secos. Encontramos que este roedor selecciona el alimento basado en múltiples criterios. Cuando se les da la oportunidad, los individuos seleccionan el alimento con un alto contenido de nutrientes tal que satisfaga una asimilación mínima de 4,34 g materia-seca/día. Luego, en la selección de alimento, estos animales parecen usar criterios adicionales al contenido de energía de los ítemes tróficos.

Palabras clave: Química dietaria, conducta de alimentación, asimilación, *Phyllotis darwini*.

INTRODUCTION

The criterion by which animals select food remains a puzzle to those who study nutritional ecological physiology and foraging behavior. Feeding choices depend on the ecological context in which foraging behavior takes place, as well as the physiological characteristics of the animals and the chemical and structural features of their food (Bozinovic & Martínez del Río 1996).

Diet selection by granivorous rodents is commonly used as a model to test hypotheses about foraging behavior and nutritional ecology (e.g. see Brown 1989). Indeed, Vickery (1984) and Kerley & Erasmus (1991), suggested that berry-eating and seed-eating rodents select foods on the basis of a single criterion, usable energy. Frank (1988) demonstrated that water requirements influence diet choice when experimental diets have identical energy contents. He demonstrated that desert granivorous rodents preferred those diets with combinations of proteins, lipids and carbohydrates, that produced the greatest net amount of metabolic

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water gain. Thus, animals are able to use criteria in addition to energy content in choosing food.

Foraging theory has emphasized pre-ingestional determinants or cues of profitability. Nevertheless, minor differences in the chemical content or physical structure of diets can have profound consequences for the feeding behavior and assimilation of nutrients by animals (Martínez del Río et al. 1992), as well as on their rate of energy expenditure (Veloso & Bozinovic 1993). Thus, observed variation in feeding choices may not only reflect changes in food availability or foraging profitability, but it may also depend on dietary chemistry and the animal's physiological state.

Because animals do not simply feed on any food item they encounter, but rather apparently select food higher in certain chemical compounds and lower in other components, we investigate the criterion by which a granivorous rodent selects food and the relationship between the diet selected and the nutrients that become assimilated. We conducted tests of food preference and nutrient assimilation in the sigmodontine leaf-eared mouse *Phyllotis darwini* (Waterhouse 1837). The leaf-eared mouse inhabits the mediterranean and semiarid regions of Chile and lives in open scrub habitats subjected to summer drought. It is mainly granivorous but also feeds occasionally on insects (Meserve 1981).

MATERIAL AND METHODS

Ten adult non-reproductive individuals (six males and four females) with a body mass of 50.13 ± 6.43 g were captured in the central Chile matorral at Quebrada de la Plata (70°50'W, 33°31'S). The locality has the typical climate of the Chilean mediterranean semiarid environments, with hot dry summers and and cold rainy winters. In the laboratory, they were first maintained on rabbit food pellet and water ad libitum in our animal room with natural photoperiod of 10L:14D and ambient temperature of 10 - 20 °C.

For experiments of food selection, all individuals were transferred and maintained during two days in individual plastic cages (35 X 30 X 15 cm) divided into three areas, a nest compartment with water and two feeding chambers with equal chance of free access to both chambers. In these cages, we offered a weighed amount (ca. 20 g) of each of two experimental diets, with one food type in each feeding chamber. The position of the food type was changed randomly. Food consumption was measured gravimetrically (± 0.1 g). To correct for evaporation, blank-diets were left for the same length of time in cages without animals and then weighed. All mice were tested on paired diets (low lipids versus high lipids, low albumin versus high albumin, low starch versus high starch and low energy versus high energy).

For experiments on assimilation, individuals were kept with one diet in metabolic cages with metal underneath to collect faeces. All eight experimental food items were tested during three days after dietary acclimation. Water and each of the experimental diets were provided ad *libitum.* We conducted feeding trials offering an equal amount of food (ca. 20 g) and collecting faeces and orts. Animals remained three days with rabbit food pellets between tests. Each day, the collected feces and food refuse were weighed and stored, after drying at 60 °C (Bozinovic 1995, Bozinovic & Muñoz-Pedreros 1995). The experimental room was maintained at 20 °C (range = 16 °C to 24 °C) and photoperiod of 12L:12D. Apparent assimilation (A) of dry-matter, energy, protein, lipids and carbohydrates was calculated for each experimental diet according to Qi - Qe, where Qi = daily rate of food/nutrients intake and Qe = daily rate of egestion. Assimilation is apparent because this method underestimates digestion by the contribution of metabolic wastes and nonreabsorbed secretions of the digestive system. Animal's body mass was recorded before and after each measurement of food selection and assimilation.

The diets used in the experiments (see Table 1) were prepared based on the method proposed by Lindroth et al. (1984). Faeces were analyzed following the Proximal Chemical Analyses Methods (AOAC 1980), energy content of food and feces was measured in a

TABLE 1

Composition (g/100g) of the experimental diets used for preference and assimilation trials.
Composición (g/100g) de las dietas experimentales usadas en las pruebas de preferencia y de asimilación

	Diets							
Ingredient	Low lipids (1)	High lipids (2)	Low albumin (3)	High albumin (4)	Low starch (5)	High starch (6)	Low energy (7)	High energy (8)
Albumin	24.5	22.9	10.0	20.0	15.0	10.0	20.0	20.0
Cornstarch	49.0	45.9	46.5	38.0	45.0	57.0	57.0	38.0
Vitamin/salt	1.2	1.1	1.0	1.0	1.0	1.0	1.0	1.0
Corn oil	0.7	7.0	22.5	21.0	11.0	14.7	1.9	21.0
Cellulose	24.5	22.9	20.0	20.0	27.9	12.0	20.0	20.0
Energy (kJ/g)	18.3	18.8	20.6	20.8	14.6	17.5	17.5	21.2

Parr 1261 computerized calorimeter (Parr Instrument, Moline, IL). Two replicates were determined to be ash free and were considered reliable when the difference between two measurements was less that 1%.

Comparisons between two groups were conducted by the Wilcoxon test, and correlation by Spearman rank correlations. Differences between treatments were assessed by a one-way ANOVA (Steel & Torrie 1985).

RESULTS

When animals were allowed to choose between the pairs of experimental foods, they selected dietary nutrients in the following order: high lipid > low lipid (Fig 1a), high protein > low protein (Fig. 1b), high energy > low energy (Fig 1d), but they did not discriminate between low and high dietary starch (Fig. 1c).

Although body mass did not differ significantly between diets at the beginning of the assimilation trials (ANOVA, $F = 0.384$, $P > 0.566$), percentage of body mass change did (Fig. 2). It was positive in the group of individuals offered the high energy, high albumin, low lipid, and low starch diets. The amount of assimilated dry matter required to maintain a constant body mass was 4.34 g/day (see Fig. 2). Apparent assimilation coefficients were all highly related with the concentration of the specific dietary compound tested (Fig. 3); except for assimilation of energy (Fig. 3d). Across diets, energy assimilation increased significantly with increased dry matter consumption (Fig. 4), following a trend similar to the one observed in Fig. 2 for each dietary treatment. Albumin and starch assimilation were also highly correlated with dry matter intake ($r_s = 0.917$, $P = 0.0001$; $r_s = 0.819$, $P = 0.0001$ respectively).

DISCUSSION

We postulated that food selection may not only reflect changes in food availability or foraging profitability, but it may also depend on dietary chemistry and the animal's physiological state. This is because animals do not simply feed on any food item they encounter, but rather they select food higher in certain chemical compounds and lower in other components. Here we conducted experiments to investigate the criterion by which a granivorous rodent *(P. darwini)* selects food and the relationship between the diet selected, food consumption and the nutrients that become assimilated.

Our data suggest that this granivorous rodent does not select food based on a single criterion. When given a choice, individuals select food with the highest content of nutrients other than starch (Fig. 1); to satisfy a minimal assimilation of 4.34 g dry-matter/day (Fig. 2). Thus, animals seem to use nutrients (lipid, albumin) for contain energy in choosing food. Depending on the abundance and availability of food resources in the environment, it will select food by using multiple criteria, such as lipid, carbo-

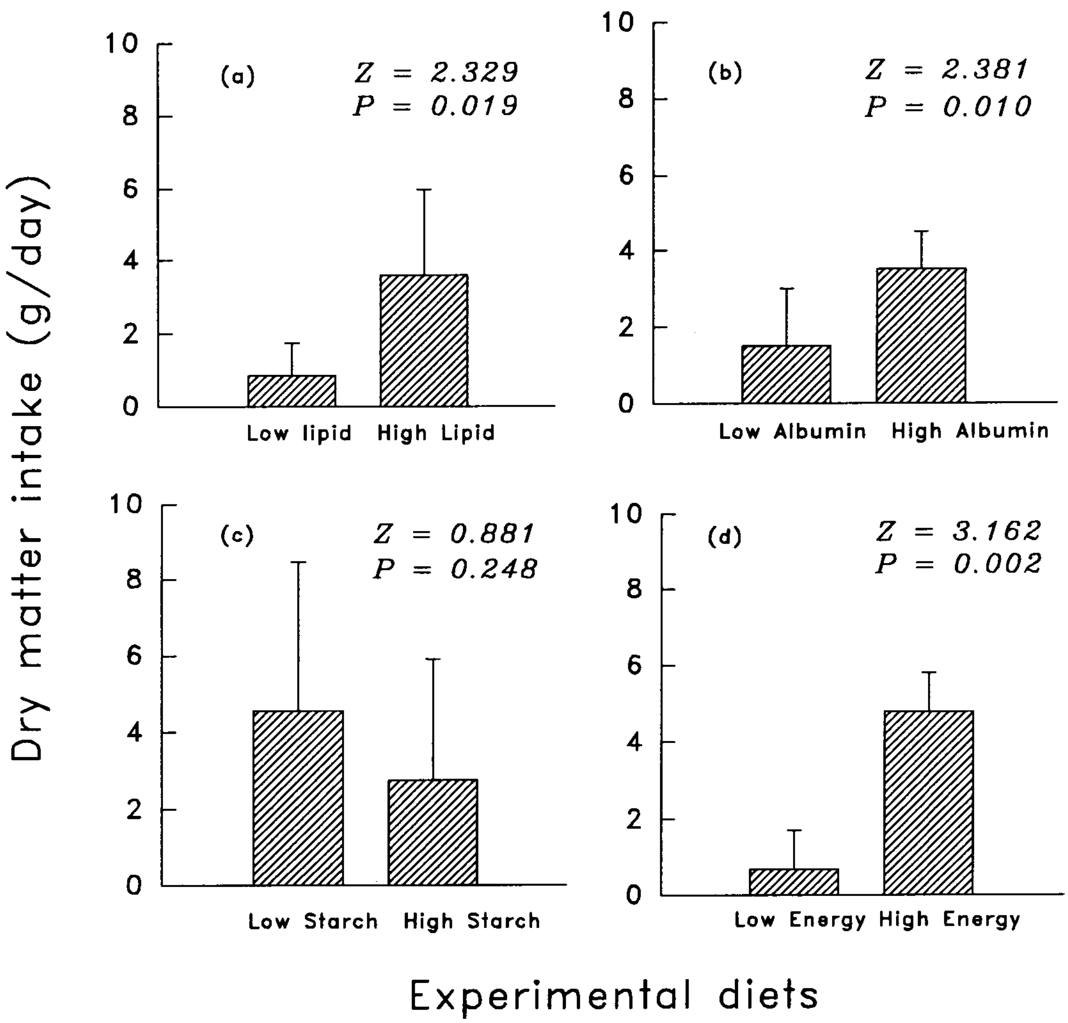

Fig. 1: Food selection between experimental food items (mean ± SD). a) lipid selection, b) protein selection, c) carbohydrate selection and d) energy selection.

Selección de alimento entre ítemes tróficos experimentales (media ± DE). a) Selección de lípidos, b) selección de proteína, c) selección de carbohidratos y d) selección de energía.

hydrate, protein, and energy contents, and its own metabolic and nutritional requirements. Nevertheless, it is also possible that different nutrients are abundant enough in just one dietary item, to guarantee the animal's nutrition.

Variations in food preferences among animals depend of multiple factors. Bozinovic & Martínez del Río (1996) postulated that knowledge about the mechanisms of nutrient assimilation may provide a straigtforward explanation of diet choice in nature (see Martínez del Río et al. 1992). Here, we found in the leaf-eared mouse, that dry matter intake was positively and significantly correlated with energy, protein and carbohydrate assimilation. It appears interesting that the total amount of food eaten varied among trials. *Phyllotis darwini* ate less food, expressed as dry-matter, when energy/nutrients assimilation was lower. However, the assimilation of different nutrients was positively related with the proportion of dietary nutrients.

There are two possible multiple criteria selection procedures. One is that animals select based on a primary criterion but when two diets are equal for that criterion, a secondary criterion may be used. The alternative is that both criteria are always im-

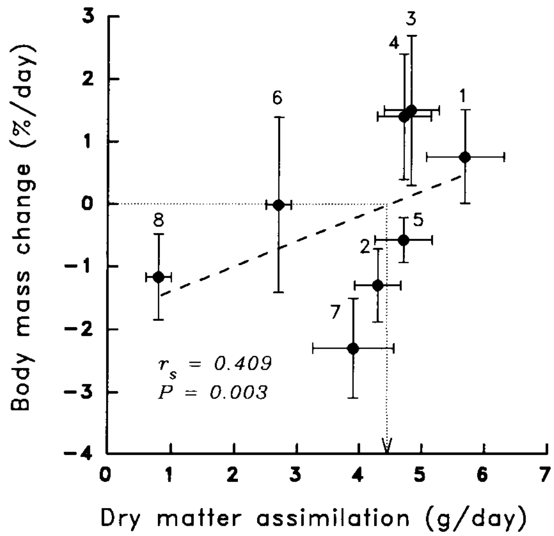

Fig. 2: Relationship between dry matter assimilation and change in body mass for *Phyllotis darwini* maintained with different diets (mean ± SD). 1) Low lipids, 2) high lipids, 3) high albumin, 4) high energy, 5) low energy, 6) low starch, 7) high starch, and 8) low albumin.

Relación entre asimilación de materia seca y cambio en masa corporal en *Phyllotis darwini* mantenido con diferentes dietas (media ± DE). 1) Baja en lípidos, 2) alta en lípidos, 3) alta en albúmina, 4) alta en energía, 5) baja en energía, 6) baja en almidón, 7) alta en almidón y 8) baja en albúmina.

portant, such as trying to attain sufficient energy and protein from food that is rich in only one of them. The latter case differs from simple diet choice models and may be better treated by linear modelling (see Pulliam 1975) whereas the former does not present an important problems for simple diet choice models. Our results appear compatible with sequential criteria (the former case), however, our methods do not permit us to test the latter. The leaf-eared mouse may attempt to obtain a certain amount of resources, once attained, individuals stop consuming the diet. Total dry-matter ingestion during preference trials (Fig. 1a,b,c and d) seems to support this hypothesis since minor differences were observed between experiments when consumption per trial was summed (range = 7.30 g/d in Fig. 1c to 4.42 g/d in Fig. 1a).

Based on these observations, we suggest that digestive characteristics, such as the assimilation rate, may be important contributors to the profitability of food items (but see Kaiser et al. 1992). That is, food preferences may be determined in part by the efficiency and rate with which the nutrients contained in food are assimilated. As demonstrated by Martínez del Río & Karasov (1990), these preferences and gut processing are in turn determined by the interaction between intestinal hydrolysis of nutrients, their uptake by the small intestine and their time of gut retention. Obviously, foraging decisions depend on multiple factors. Predation risk, for example, is one of the several factors affecting diet selection (e.g. Lima & Dill 1990). Nevertheless, we argue here that, although selection of different items will depend of the ecological context in which foraging behavior takes place (e.g. Vásquez 1994 for an example in *P. darwini*), as well as prey value and handling time, the criterion of food choice may be also related to the physiological mechanisms of nutrient assimilation and to an animal's metabolic requirements.

Kerley & Erasmus (1991) pointed out that seed selection by granivorous rodents is highly correlated with the energy intake, supporting classical predictions that consumers should maximize their net energy intake. Nevertheless, these authors also pointed out that rodent preferences for seeds may also be a response to some nutritional factor, arguing that the efficiency of food assimilation should be considered as another criterion of food selection. For example, as postulated by Frank (1988), the amount of metabolic water gain appears to be an important factor in food selection.

Since chemical components of food influence dietary preferences, and since there are physiological capabilities and constraints to deal with in food chemistry, both dietary chemistry and an animal's physiology should be considered in explaining behavioral patterns of food use by small mammals. In other words, species-specific physiological strategies may determine potential diet, but also chemical characteristics of available food item will influence feeding, digestion and metabolism.

A complicating factor in the extrapolation of our results to the field is the unknown relationship between the physiological responses of this rodent and

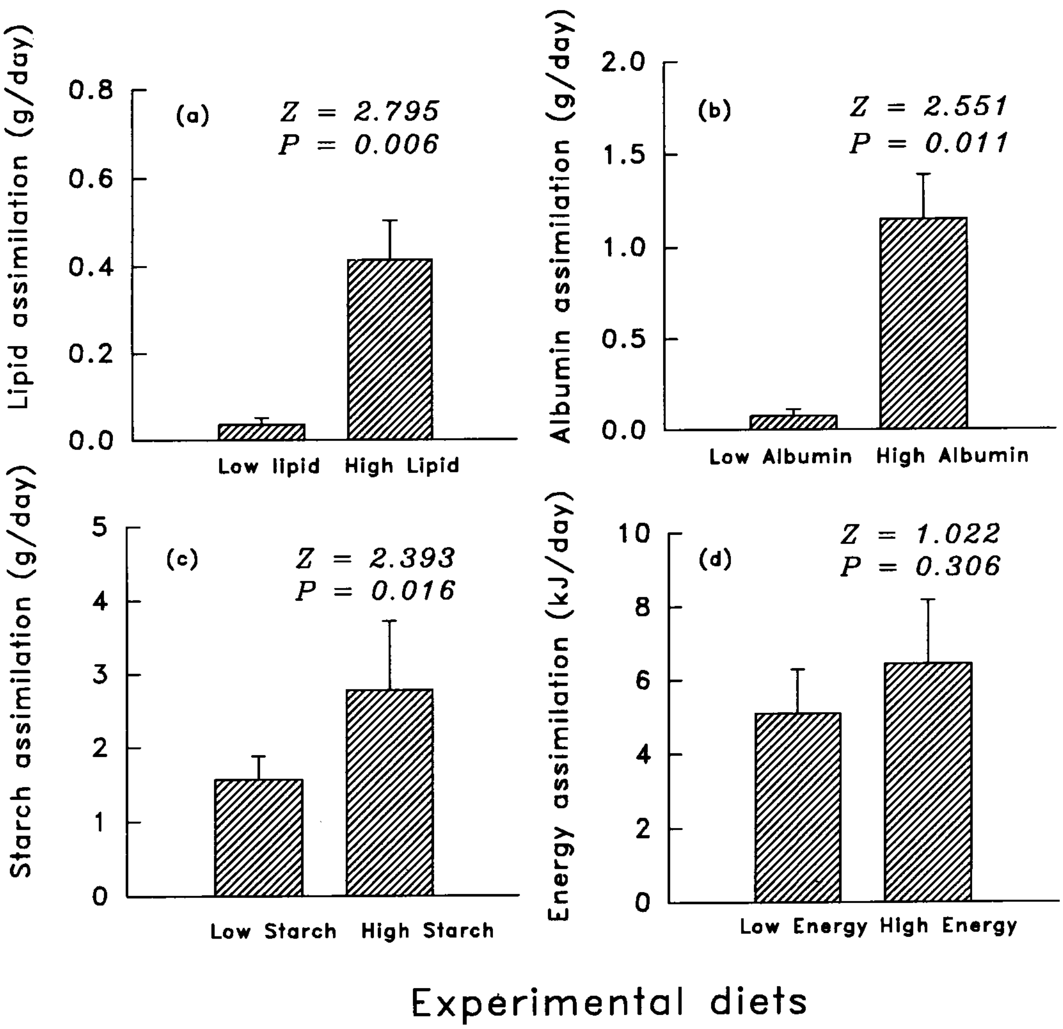

Fig. 3: Assimilation of nutrients by *Phyllotis darwini* (mean ± SD).

Asimilación de nutrientes por *Phyllotis darwini* (media ± DE).

fluctuating dietary chemistry in their habitats, as well as the role of its nutritional requirements and assimilation rates of different dietary items on food selection. Another methodological problem in this kind of study is that diets are constructed in a way that may produce confusion among the factors (nutrients). For instance, the low and high starch diets also differ in cellulose content. Lipid content also varies slightly. When rodents do not show a clear choice between them, we may not conclude that they have no preference for starch. Perhaps a preference for starch and lipids has been counterbalanced by lipid preference. Similar problems may arise because the low and high albumin diets differ in starch and slightly in lipid content. Also, the low and high lipid diets differ slightly in albumin and starch content. Perhaps, only in the low and high energy diets is the situation clear enough. This problem is unavoidable because one cannot change the proportion of one nutrient in the experimental diet without affecting the proportion of at least one other. The challenge is thus to produce diets which will, nonetheless, allow the behavioral ecologist to test hypotheses. Until such methods become available, our working

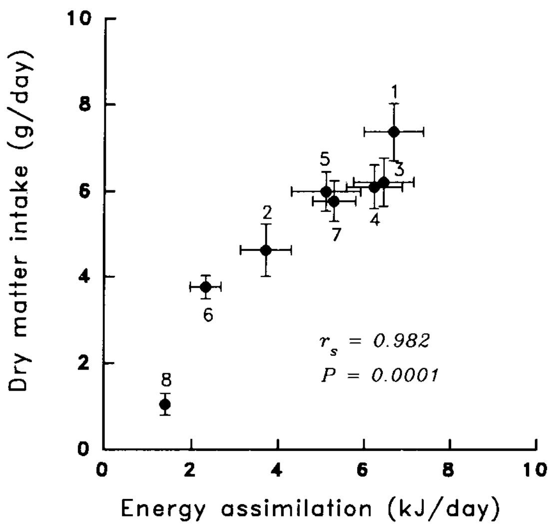

Fig. 4: Relationship between energy assimilation and dry matter intake for *Phyllotis darwini* maintained with different experimental diets (mean ± SD). See Fig 2 for identification of dietary items.

Relación entre asimilación de energía e ingesta de mataria seca en *Phyllotis darwini* mantenido con diferentes dietas experimentales (media ± DE). Véase Fig. 2 para la identificación de los ítemes dietarios.

hypothesis is that a dietary item will be selected and consumed in the field when that item is more highly assimilated than an alternative dietary item in the foraging area.

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