Revista Chilena de Historia Natural
70: 67-71, 1997

Diet selection in rodents: an experimental test of the effect of dietary fiber and tannins on feeding behavior

Selección de dieta en roedores: una prueba experimental del efecto de fibra y taninos dietarios sobre la conducta de alimentación

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ABSTRACT

The individual effects of chemical plant defenses on food preferences in small mammals have been explored in many studies. However, the combined effects of dietary fiber and tannins on feeding preference have received considerably less attention. Here I search for differences in feeding behavior of alternative experimental diets differing in fiber (cellulose = F) and a secondary metabolite (the hydrolyzable tannin, tannic acid = TA) in two sympatric rodent species that live in the Mediterranean environments of central Chile. I used the herbivorous burrowing caviomorph rodent *Octodon degus* (specialist), and the granivorous Sigmodontine *Phyllotis darwini* (generalist). These species differ in their trophic niche, and likely in behavioral and physiological features to cope with plant defenses. In preference trials with isocaloric diets, both species prefered dietary items with low F and TA. I conclude that non-energetic dietary features influence feeding strategies, and that generalist and specialist species behave in the same way. Future studies dealing with the ecology of foraging on chemical plant defenses should focus more explicitly on the interactive effect of different plant defensive compounds instead of on the isolated effect of single factors.

Key words: Feeding behavior, fiber, tannin, rodents.

RESUMEN

Muchos estudios han explorado el efecto individual de las defensas químicas de las plantas sobre las preferencias dietarias de micromamíferos. Sin embargo, poca atención se ha puesto en el estudio del efecto combinado de fibra y taninos sobre la conducta de alimentación. En este artículo se estudió el efecto de dietas con diferentes concentraciones de fibra (celulosa = F) y un metabolito secundario (el tanino hidrolizable, ácido tánico = TA) sobre la preferencia de alimentación en dos especies de roedores simpátridos que habitan en el matorral mediterráneo de Chile central. Se usó al roedor caviomorfo herbívoro *Octodon degus* (especialista), y al Sigmodontino *Phyllotis darwini* (generalista). Estas especies difieren en su nicho trófico, y probablemente en características conductuales y fisiológicas en el uso de defensas vegetales. Se encontró que en pruebas de preferencias con dietas isocalóricas, ambas especies prefieren ítemes dietarios con bajas F y TA. Se concluye que las características dietarias no energéticas influyen sobre las estrategias de alimentación, y que las especies especialistas y generalistas se comportan de la misma forma. Se propone que los estudios futuros orientados a la ecología del forrajeo de defensas químicas de plantas debiesen centrarse en forma más explícita en el rol de los efectos interactivos de los compuestos defensivos de las plantas más que en el estudio de factores aislados.

Palabras clave: Conducta de alimentación, fibra, taninos, roedores.

INTRODUCTION

As postulated by foraging theory (e.g. Stephens & Krebs 1986), a selective feeding behavior coupled to an efficient digestion are two of the most important factors determining the value of food consumed by animals. For small mammalian herbivores, plant fiber and secondary metabolites should influence foraging behavior, affecting consumers' fitness. Mammalian herbivores may therefore select plants rich in nutritional components and poor in fiber and secondary metabolites (Belovsky & Schmitz 1991). Finally, what may determines whether or not a plant is consumed depends on many factors, such as its biomass, the concentration of chemical defenses in those parts of the plant exposed to herbivores, and the herbivores' own behavioral and

(Received 4 March 1996; accepted 10 September 1996; managed by Javier Simonetti)

physiological capabilities (Harborne 1991) among others.

In seasonal environments, like the Mediterranean ecosystems, herbivores must also cope with temporal changes in forage quality and abundance (Palo et al. 1992, Montenegro et al. 1980). Two of the most conspicuous chemical compounds of plants such as tannins and fiber, are independently able to reduce food digestion, and their combined effects may play an important role in shaping dietary preferences (McArthur et al. 1993). These compounds decrease the nutritive quality and digestibility of the plant tissues, and hence plants benefit from reduced preference, and palatability to herbivores. Consequently, a selective feeding behavior may be a first line of defense against these compounds, followed by physiological adaptations to the chemical composition of food.

The effects of variation in level of a single chemical defensive compound on diet preferences have been previously explored (see Palo & Robbins 1991 and references therein). The combined effects of subchronic levels of dietary fiber and tannins on feeding behavior have received less attention (but see Hay et al. 1994).

In this paper I investigate diet preferences in two sympatric species of rodents inhabiting central Chile subjected to experimental diets differing in fiber (cellulose = F) and secondary metabolites (the hydrolyzable tannin, tannic acid = TA). These two species differ in diet, and probably have different feeding behavior to cope with plant defenses. I analyzed the combined effect of subchronic dietary cellulose and tannic acid in the herbivorous caviomorph rodent *Octodon degus* (degu), and the largely granivorous Sigmodontine *Phyllotis darwini* (leaf-eared mouse). Both species live in open scrub habitat subjected to summer droughts, but they have dietary differences in the relative proportions of shrub, grass foliage and seeds. Degus is a herbivore feeding primarily on grasses, forb, shrub foliage, and conductive tissue and was classified here as specialist. The leaf-eared mouse is mainly granivorous, but it also feed on insects being defined here as generalist (Meserve 1981, Meserve et al. 1984).

Animals do not simply feed on any dietary item they encounter, they are able to use criteria in choosing food in addition to simply energy. Thus, to test the hypothesis that a selective feeding behavior is the first line of defense of small mammals against "poor" food, I gave these rodents four combinations of experimental isocaloric diets with different concentrations of TA and F.

MATERIALS AND METHODS

Animals and maintenance

The experimental animals were non-reproductive, all captured in Quebrada de la Plata, central Chile (70°50'W, 33°31'S). In the animal room, they were first maintained on rabbit food pellets and later randomly assigned to dietary groups. Powdered diets were prepared by adding and homogenizing cellulose and tannic acid (Sigma Chemical Company) to commercial rabbit food pellets. Diets were analyzed for neutral (NDF) and acid (ADF) detergent fiber, or simply fiber (see Bjorndal & Bolten 1993); nitrogen content of the diets was also measured using the microKjeldahl method (AOAC 1980).

Groups of six *O. degus* and six *P. darwini* were each tested on diets with high TA-high F, low TA-low F, high TA-low F, and low TA-high F, respectively. Following Karasov et al. (1992) we choose high TA to be 4% addition of TA into the diet. Low dietary TA was 1%. The level of F incorporated into the diet was 52%-NDF and 32%-ADF for high fiber, and 43%-NDF and 20%-ADF for the low fiber diet, following Bozinovic (1995). This author documented that at Quebrada de la Plata, the grass consumed by O. degus contained 61.1% NDF during the dry season (summer), and 37.3% NDF during the wet season (fall-winter). After chemical and caloric analysis, the caloric content, and the nitrogen and fiber (ADF and NDF) composition of the experimental diets were: a) high TA-high F: 18.00 kJ/g, 2.36% N, 32.04% ADF and 51.92% NDF; b) low TA-low F: 17.92 kJ/g, 2.31% N, 20.25% ADF and 42.68% NDF; c) high TA-low F: 17.95

kJ/g, 2.59% N, 20.49% ADF and 43.60% NDF; and d) low TA-high F: 18.05 kJ/g, 2.63% N, 30.63% ADF and 51.50 NDF. Dietary energy content was determined in a Parr 1261 computerized calorimeter following Bozinovic (1995).

Preference trials

Preference trials were conducted to determine whether rodents feed selectively to dietary items with low dietary fiber and low tannic acid. Before the preference trials were conducted, rodents were maintained for 10 days in two large outdoors enclosures (120 by 70 by 90 cm) with natural photoperiod of LD = 10:14 and ambient temperature of 10-20°C, with water and rabbit food pellets provided ad lib. Dietary preference trials were conducted in another outdoor enclosure (110 by 60 by 80 cm high) with water ad lib., and natural photoperiod and ambient temperatures previously described. Trials of one day were conducted in animals deprived of food for the previous 8 h. Ingestion was measured gravimetrically, and a standard amount of 30 g of each diet was offered each time.

Statistics

The significance of the effect of dietary TA and F on food intake was assessed by a multifactor analysis of variance (ANOVA), using the a posteriori Tukey test for multiple comparisons between groups with (= 0.05. In the ANOVA we evaluated F and TA effects and the interaction between factors, and arcsin transformations were applied when data were not normally distributed (Steel & Torrie 1985). Results are given as means ± 1 SD.

RESULTS

Rodents' preference for food with low fiber and low tannic acid was significantly greater than for alternative dietary items. When animals were allowed to choose between the experimental diets, they always minimized F and TA ingestion (Fig. 1). Regardless

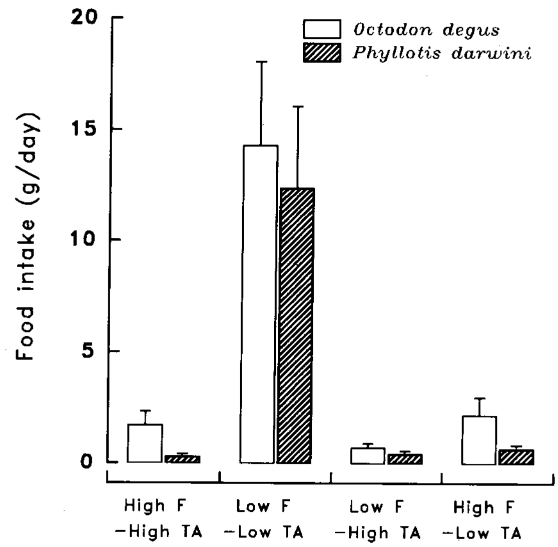

Fig. 1: Food preferences of the herbivorous *Octodon degus* and the omnivorous *Phyllotis darwini*, measured by food intake for experimental diets with combinations of high and low fiber (F) and tannic acid (TA).

Preferencias de alimento por el roedor herbívoro *Octodon degus* y el omnívoro *Phyllotis darwini* medida por la ingesta de dietas experimentales con combinaciones de alta y baja fibra (F) y ácido tánico (TA).

of species, animals strongly preferred the low TA-low F. Statistics for *O. degus* were: ANOVA, F-ratio = 12.354, d.f. = 2, P = 0.0003 for main effects; F-ratio = 13.170, d.f. = 1, P = 0.0017 for F effect; F-ratio = 11.537, d.f. = 1, P = 0.0029 for TA effect; and F-ratio = 8.245, d.f. = 1, P = 0.0094 for the interaction F*TA; whilst for *P. darwini* statistics were: ANOVA, F-ratio = 10.113, d.f. = 2, P = 0.0009 for main effects; F-ratio = 10.707, d.*f.* = 1, P = 0.0038 for F effect; F-ratio = 9.518, d.f. = 1, P = 0.0058 for TA effect; and F-ratio = 9.907, d.f. = 1, P = 0.0051 for the interaction F*TA.

The a posteriori Tukey test revealed for both species significant differences in food selection between low TA-low F, and high TA-high F, high TA-low F, and low TA-high F, but not between the last three dietary treatments (Fig. 1). Thus, in all cases the two species showed pronounced preferences for low F and low TA dietary items, avoiding others with high F and TA, high F-low TA, and low TA-high F; as revealed by the Tukey test.

DISCUSSION

The results of this study may be used to examine the following questions: 1.- What are the combined effects of tannic acid and fiber (the most common type of exposure of animals to plant food) on the feeding behavior in herbivorous and omnivorous rodents?, and 2.- Can behavior act as a first line of defense of small mammals to chemical compounds of plant foods?. The answers are important for understanding the behavioral significance in animals feeding on chemically-defended plants.

Milton (1979) pointed out that the protein to fiber ratio may determine the food preference of mammalian herbivores, as well as plant defensive compounds. For example, herbivorous rodents in the genus Neotoma behaviourally reduce the fiber content in their diet (Justice & Smith 1992). Meyer & Karasov (1989) demonstrated that woodrats feed selectively to minimize resin intake, preferring foliage with low resin contents.

According to Bryant et al. (1992), the high fiber and low water content, and thick cutticule of many evergreens are adaptive traits to unfavorable environmental conditions such as the Mediterranean summer drought. In addittion, mature leaves of evergreens frequently contain secondary metabolites that deter feeding by mammals (see Rosenthal & Berenbaum 1992 and references therein).

Based on my results (Fig. 1), it seems that consumers may select or reject a given type of food item simply based on pre-ingestive behavioral perception, including sight, smell and taste (Illius & Gordon 1993). It is also probably that consumers decrease ingestion of foods that contain higher concentrations of F and/or TA, presumably on the basis of post-ingestive feed-back. In fact, and according to Provenza & Cincotta (1993), when foraging, it is important that consumers sample food because, as results of sampling, animals are able to ingest a diverse array of dietary items, can change the intake of poor food, and finally can discover new dietary items in different patches of the environment. Indeed when *O. degus* is experimentally exposed to young or mature leaves of different species of Chilean shrubs and different levels of artificial dietary fiber, it prefers young leaves over mature leaves (Simonetti & Montenegro 1991), probably as a consequence of different concentrations of chemical defensive plant compounds, and also select low dietary fiber (Bozinovic 1995). Palo et al (1992) pointed out that both chemical defenses and fiber probably impose a handling cost to the consumer in terms of a large proportion of indigestible material in the digestive tract, depressed gut microbial activity and/or toxic properties.

I did not observed marked differences between rodent species in behavioral response to experimental diets, but both species preferred the "highest quality" diet (i.e low F-Low TA). It thus appears that the first line of defense of these small mammals to plant chemistry and nutritional content is a common selective feeding behavior, without species-specific differences. Individuals of both species may ingest and sample different amounts of dietary items in the environment, which may reduce the chance of consumption of plant defensive compounds and enhance the probablity of meeting their nutritional and energetic requirements. Thus, individuals may change or decrease intake of plants with different defensive compounds as plant chemical composition changes over time if changes in flavour caused by a change in plant chemistry is associated with a temporal or spatial variation in secondary metabolites or toxins.

In spite of the similar behavioral responses of the two rodent species have to food quality, after ingestion, there are important differences between the two species in their physiological and anatomical response to plant chemistry and food quality (Bozinovic et al. 1995)[1]. Future studies dealing with the behavioral ecology of animal foraging on chemical plant defenses should focus more explicitly on the

1 BOZINOVIC F, FF NOVOA & P SABAT (1995) Ecología digestiva y costos metabólicos de la alimentación de defensas químicas de plantas: efecto de la interacción entre fibra y taninos. Noticiero de Biología, IV Reunión Anual Sociedad de Ecología de Chile, R-74.

interactive effect of different plant defensive compounds than on the isolated effect of single factors. The combined effect of chemical, structural and nutritional food characteristics can be much more than the sum of their separate effects.

ACKNOWLEDGMENTS

This work was funded by a Fondo Nacional de Desarrollo Científico y Tecnológico grant, FONDECYT 1950394; P. A. Camus, M. Rosenmann and a referee made useful comments on a draft of this manuscript.

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