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Feeding behavior of the tuco-tuco (*Ctenomys mendocinus*):its modifications according to food availability and the changes in the harvest pattern and consumption

Comportamiento alimentario del tuco-tuco (*Ctenomys mendocinus*): su modificación en función de la oferta y diferencias entre patrones de cosecha y de consumo

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ABSTRACT

The foraging behavior of *Ctenomys mendocinus* Philippi 1869 has been studied in the laboratory. It has been verified through two experimental series that this behavior is modified according to the quality of the food available that are given to them. Two different criteria were used to test food selection in order to verify coincidence between harvest patterns and consumption patterns. The use of more than one criterion of selectivity precluded the confusion between removal (harvesting) and consumption, allowing us to establish the feeding behavior of *Ctenomys mendocinus* in a more reliable way. Tuco-tucos fed on the aboveground parts of grass avoiding shrubs and roots but they were opportunistic when they harvested the available vegetation. This harvest pattern did not experience changes in response to changes in the offer; it would mean selective advantages because the animal spends less time for aboveground feeding. On the other side, the difference between harvest patterns and consumption patterns suggest that *C. mendocinus*, remove material for distint uses (storage, construction of nest, etc.).

Key words: rodents, fossorial, selectivity, opportunistic, foraging.

RESUMEN

Se estudió el comportamiento alimentario de *Ctenomys mendocinus* Philippi 1869 en laboratorio. Se verificó en dos series experimentales si este comportamiento se modificaba en función de la calidad de alimentos puestos a disposición. Además se verificó si los patrones de cosecha coinciden con los de consumo, utilizando dos criterios diferentes para poner a prueba la selección de alimento. La consideración de más de un criterio de selección evitó confundir remoción con consumo, lo que permitió establecer con mayor confiabilidad el comportamiento alimentario de *C. mendocinus*. Los tuco-tucos consumieron selectivamente la parte aérea de las gramíneas, en detrimento de arbustos y de raíces en general, pero cosecharon el material vegetal en forma oportunista. Este patrón de cosecha no se modificó con el cambio de oferta y podría presentar ventajas selectivas al disminuir el tiempo de exposición fuera de la cueva del animal. Por otro lado las diferencias entre patrones de cosecha y patrones de consumo sugieren que *C. mendocinus* removió material para distintos usos (almacenamiento, construcción de nido, etc.).

Palabras clave: roedores, fosoriales, selectividad,oportunismo, forrajeo.

INTRODUCTION

The theoretical and empirical literature concerning the theory of optimal foraging (Krebs 1978, Krebs *et al.* 1983, Pyke *et al.* 1977, Pyke 1984, Stephen & Krebs 1986, Schoener 1987) has proven to be controversial (Gould & Lewontin 1979, Glasser 1984). Pyke (1984) suggested that the theory needs additional critical tests to evaluate the suitability of its assumptions and predictions in describing and explaining foraging behavior in various animal groups and environments.

Foraging behavior of subterranean rodents is a challenge to the classical foraging theories. Simpler optimal-diet models based on maximizing net rates of energy intake per time unit lead to the prediction that animals should become less

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selective as search costs associated with foraging increase (MacArthur & Pianka 1966). In subterranean rodents, the construction of new tunnels represents the highest energetic cost in the food search. Gophers may spend 360-3400 times as much energy burrowing as they would be traveling an equivalent distance on the surface (Vleck 1979, 1981). This suggests that subterraneal rodents should be relatively nonselective foragers.

The species of *Ctenomys* are the most numerous among the subterraneal ones, being 45% of the living species of fossorial rodents (Reig *et al.* 1990). *Ctenomys mendocinus* lives in a great variety of environments within the province of Mendoza (Argentina). Its foraging behavior is not well known. The few published papers based on field study suggest that tuco-tucos feed in a selective way (Torres-Mura *et al.* 1989), and prefer grasses to shrubs (Madoery, 1993). It is still unknown if tuco-tucos select their food among the different species of grass, or between the aboveground and belowground parts of it. In addition, it is also unknown if *Ctenomys mendocinus* store food for a later use and if the harvest pattern coincides with its immediate consumption pattern. There are few feeding trials for fossorial rodents that measure the availability of different food items or eliminate behavioral constraints (e.g. burrowing costs). There are no trials on this subject about *Ctenomys mendocinus* . Such feeding trials using dry pellets of grasses, plants, and shrubs allow to study the feeding behavior of rodents (Jenkins & Bollinger 1989) and to verify the predictions of the classical models of optimal foraging (Andersen & Mac Mahon 1981, Behrend & Tester 1988, Heth 1989). The aim of this

TABLE 1

Grasses vs Grasses. Figures are rank sums for each item for the six tests of each trial and are selection indices. *Type selected significantly. +Type avoided significantly. *P*: indicates the probable errors made of type I

Gramíneas vs Gramíneas. Las cifras corresponden a la suma de rangos de cada item para los seis tests de cada experimento y son indices de selección. *Tipo seleccionado significativamente. +Tipo evitado significativamente. *P*: indica la probabilidad de cometer error de tipo I

		First Criterion of selectivity (harvest)								Second Criterion of selectivity (consumption)							
		Animals								Animals							
		1		2		3		4		1		2		3		4	
		T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2
Pappophorum sp	tops	5	0	7	7	2	3	3.5	7	7	5	8	8*	5	4	3.5	7
	roots	1.5	7	3.5	4.5	6.5	6.5	0.5+	1.5	2.5	5	2.5	2.5	4.5	5.5	0.5+	1.5
Diplachne sp	tops	3.5	5	4	6	3	1.5	8*	7	5	6	4	7	6	2.5	8*	7
	roots	6.5	2	5	0.5	9	5	3.5	0.5+	6.5	3	5	1+	4	5	3.5	0.5+
Aristida sp	tops	2	5	9	7	3	6	9*	8*	6.5	8	9	8*	7	7	9*	8*
	roots	7.5	5	3	2.5	6.5	6	2.5	1.5	3	3.5	2.5	1.5	4.5	3	2.5	1.5
Trichloris sp	tops	2	6	2.5	7	3	1.5	7	6.5	1	3	2	4.5	3	3.5	7	6.5
	roots	7	6	2	1.5	3	6.5	2	4	4.5	2.5	3	3.5	2	2.5	2	4
Variance of rank sums		5.98	5.42	5.78	7.14	6.21	4.71	9.77	9.00	4.70	3.49	7.02	8.12	2.49	2.28	9.57	9.00
P:		<.19	=.29	=.21	=.07	=.16	=.39	<.006	<.010	<.39	<.63	.09	<.02	<.82	<.83	<.006	<.010

research was to verify the feeding behavior of *Ctenomys mendocinus* and to prove if this behavior is modified according to the quality of the offer, and if the harvest patterns coincide with the consumption patterns.

METHODS

A clear-acrylic-plastic maze (designed by Jenkins & Bollinger 1989) was used. It was designed so as to minimize costs of burrowing and search costs.

The maze consists of a central square body (45 by 45 by 16 cm) containing a smaller body, the nesting box (20 by 20 by 16 cm), inside. The central body has four arms or tunnels (80 by 11 by 16 cm) connected to it by vertical sliding doors. The food was presented cut in pieces, in an attempt to even the handling costs of different items. The first series of trials was done in April-May, 1991 and consisted of the offer of four species of grass: *Aristida sp., Pappophorum sp., Diplachne sp.* and *Trichloris sp.* The second series of trials was done during October-November 1991, and consisted of the offer of two species of shrubs: *Cassia sp.* and *Atriplex sp.* and two species of grass: *Panicum sp.* y *Pappophorum sp.*. There is evidence that the species offered in both experimental series were consumed in a different way (Madoery, 1993).The reason why only grass was offered was to verify if tuco-tucos had the ability to discriminate among different species of that category and between the aboveground and belowground parts of those plants. On the other hand, the second experimental series had the aim of corroborating if these rodents selected grass avoiding shrubs.

The whole plants were collected in Cacheuta (Mendoza, 1,750 m.elevation), and dried in stoves (Jenkins & Bollinger 1989) (60°C, 120 hours); the aboveground and underground parts were separated and weighed. In the same place, that is in Cacheuta, four animals were caught and kept in captivity with a diet that consisted of carrots, potatoes, natural vegetation and alfalfa «ad libitum»during 20 days before the beginning of the first series of trials.

In both experimental series, each tuco-tuco was subjected to two trials of six tests each, representing all possible pair-wise combinations of the four plant species (eight items) presented at random. In each test, three grams of each item were put at the end of each wing (tunnel) of the maze, so that the tuco-tuco had four different items at its disposal (the aboveground and the underground parts of each pair of species). The vegetation was weighed before and after each test.

Two criteria were adopted to determine the food selectivity. The first one considered that the material that was selected was the one that was removed (harvested) from the tunnels, without making any difference between the consumed food and the one that was removed for a later use. The second criterion considered that the material that was selected was the one that was consumed during the two hours of each test (calculated as weight difference).

A test was taken each day under red lights, and lasted for two hours. Between tests, animals were fed with their normal laboratory diet. The experimental design allowed for analizing the feeding behavior of each animal in each of the two trials.

At the end of each test the amount removed from each item were written down. We ranked them on a scale of 0 to 3, with 0 representing the least amount harvested and 3 representing the largest amount harvested. Amounts differing by 0.02 were considered ties and ranked accordingly. Then we wrote down the sum of the ranks for each item during the trials. As each item was paired 3 times in each trial, the sums of ranks could range from 0, for the item that had been less removed to 9 for the item that had been more removed. The variance of the sums of ranks for the 8 items is a measure of the degree of selectivity of an animal during a trial, as it takes into account the degree of dispersion of the data. In this way, the trial with a high degree of variance indicates that the animal selects certain items and avoids others.

A Monte Carlo procedure was used to simulate the variance which agreed with what is stated in the null hypothesis (Ho), according to which the animals harvest food at random. Then certain critical value of the variable (α) was determined, from which the statistical significance of the variance of sums of ranks for each trial was tested. In this way, we could determine if an animal was harvesting food selectively or nonselectively from the array of items offered, and to test which items were selected and which were avoided. We used a FORTRAN program adapted from the BASIC program kindly offered by Dr. Stephen Jenkins, that performed 1000 simulations of feeding trials. If the actual variance of the ranks sums for an experiment was >95% of the variances computed for the simulations, it was judged significant at P<0.05.

Acumulative distribution of the individual sums of ranks was also generated for the 1000 simulated tests, to determine if certain item was selected or avoided. If the actual sums of ranks were in the top or bottom 5% of this distribution, it implied significant selection for or avoidance of a particular plant type with a certainty of 95% (Jenkins & Bollinger 1989).

RESULTS

First experimental series

The variance of the sums of ranks of this experimental series (Table 1) did not indicate any selectivity of *C. mendocinus* for the species offered in 6 out of 8 instances according to the first criterion of selectivity,

TABLE 2

Grasses vs Shrubs. Figures are rank sums for each item for the six tests of each trial and are selection indices. *Type selected significantly. +Type avoided significantly.
P: indicates the probable errors made of type I

Gramíneas vs arbustos. Las cifras corresponden a la suma de rangos de cada item para los seis tests de cada experimento y son indices de selección. *Tipo seleccionado significativamente. +Tipo evitado significativamente.
P: indica la probabilidad de cometer error de tipo I

		First Criterion of selectivity (harvest)								Second Criterion of selectivity (consumption)							
		Animals								Animals							
		1		2		3		4		1		2		3		4	
		T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2	T1	T2
Panicum sp	tops	7	6	9*	8	5	4.5	5.5	7	9*	9*	8	8	9*	7	6	6
	roots	7	5	5	2	2	6.5	3.5	2.5	2	1+	4.5	2	1+	4.5	4	1+
Pappophorum sp	tops	3	7	8*	9	4.5	2	9*	7.5	5.5	8*	8	8.5	5	9	9*	7.5
	roots	4	3	1+	3.5	5	4	5	6	4.5	2	2	4	5	4	4.5	6
Cassia sp	tops	3.5	5	4	3.5	3	5.5	4	6	2.5	3	4	3.5	1+	4.5	4.5	6
	roots	1.5	5	1.5	2.5	6	4	0.5+	0+	2.5	5.5	2	2.5	7	3	0.5+	0+
Atriplex sp	tops	4	7	4.5	4.5	6	4	8*	1+	8*	3	4.5	4.5	5.5	4	7	2
	roots	3	1	3	3	4.5	5.5	0.5+	6	2	4.5	3	3	2.5	0	0.5+	7.5
Variance of rank sums		3.76	4.12	8.07	6.71	1.92	1.85	9.57	8.35	7.71	8.07	5.64	5.99	8.07	7.07	8.71	9.07
P:		<.57	<.50	=.02	<.11	=.91	<.91	<.006	<.02	=.03	=.02	=.23	<.19	=.02	=.09	<.01	=.01

and in 5 out of 8 instances according to the second criterion of selectivity. However, when the value of the variable to determine if an animal removed food selectively or nonselectively was fixed at 10%, opportunism was verified in 5 out of 8 instances for the first criterion of selectivity (Table 1).

Second experimental series

The variances of the sums of ranks of the second series of trials (Table 2) were significantly different depending on the criterion that was used. According to the first criterion, the animals did not select in 5 out of 8 instances. According to the second criterion, in 5 out of the 8 instances, the tuco-tucos were selective. What they preferred were the aboveground parts of *Panicum sp.* and *Pappophorum sp.* and what they mostly avoided were the roots of *Panicum sp.* and *Cassia sp.*

As the value of the variable was fixed at 10% to determine the selective or nonselective behavior, selectivity was verified in 6 out of the 8 instances. If the limit in the distribution of the ranks at random was to determine what items were avoided or selected, and was fixed at a value of 10%, there was an even more consistent selectivity pattern for the abovepart of *Pappophorum sp.* ($P=0.01$, $P=0.01$, $P>0.01$, $P>0.05$), whereas the roots of *Atriplex sp.* were selected once (animal 4).

The animal 4 behaved as selective under any of the two criteria in both experimental series.

DISCUSSION

The results of the first experimental series (grass vs grass) indicate nonselectivity for both criteria of selectivity. The results of the second experimental series (grass vs shrubs) indicate nonselectivity according to the first criterion (harvesting), and selection/avoidance according to the second criterion (consumption).

The difference between both experimental series using the Criterion 2, may be due to the experimental design. The four species that were offered in the Experimental Series 1 were grasses, a category that was highly preferred in other diet tests of *C. mendocinus* (Torres Mura *et al.* 1989). In the Experimental Series 2, the foods that were offered were two species of grasses and two species of shrubs. In this case, selection/avoidance was verified in 5 out of 8 instances. Thus, the use of the terms opportunism and selectivity would depend on the analytic scale that is taken into account. The results also coincide with those obtained by Madoery (1993), who indicated that tuco-tucos selected grasses and avoided shrubs in Cacheuta (Mendoza), although there is a higher availability of shrubs in this area. Other field and laboratory works on several species of fossorial rodents did not agree with our results. Andersen & MacMahon (1981) indicated that *Thomomys talpoides* behaved as an opportunistic rodent. Heth *et al.*(1989) suggested that *Spalax ehrenbergi* search and get their food randomly. Berhend & Tester (1988) suggested that *Geomys bursarius* eats more grasses than shrubs. The feeding trials performed by Jenkins & Bollinger (1989) also suggest selectivity for *Thomomys monticola.*

The results also indicate how important is the criterion that is used to determine food selectivity. When the Criterion 1 (harvest) was used, the Ho was rejected only occasionally in the two experimental series. When Criterion 2 (consumption) was used, the Ho was rejected only in the Experimental Series 2. This may suggest that the harvest pattern is wide, and independent of the available food offered.

During the trials, tuco-tucos moved the plant parts from the arms to the central body or other arms of the maze. This transportation was an active one : tuco-tucos used the mouth or push the plants with their hind feet.

On the other hand if what is taken into account is the removed food at the end of each trial, we would get to the conclusion that they are nonselective foragers. But if what is taken into account is the consumed food, the foraging behavior of these rodents would suggest selectivity/avoidance of certain items.

The aboveground parts of the grasses were preferred for consumption and the roots were rejected in all trials. When the roots were removed from the tunnels, they were not consumed.

Some authors (Reichman 1988, Stuebe & Andersen 1985) pointed out that the animals might select food for immediate consumption and for storage. Thus, feeding behavior may be misunderstood if the harvested amount is used as a substitute of the amount that is actually consumed (Jenkins & Bollinger 1989). In the field studies of Puig *et al* (1992), they mention the existence of important vegetation deposits in the burrows of *C. mendocinus* .

Our experimental design eliminated burrowing costs to increase selectivity in the foraging behavior of *C. mendocinus*. However, the Ho was only rejected in one trial. Considering the lack of selectivity shown in the harvest pattern in both experimental series, we suggest that the elimination of burrowing costs does not induce the selective behavior of *C. mendocinus*.

It is also important to point out individual differences of the animals used in the tests. Animal 4 showed a selective behavior in all the opportunities in which it was tested. In almost every opportunity it consumed the food without moving it from the tunnels. This would indicate that there may be individuals with different foraging tactics within natural populations. Almost all natural behaviors involve elements that meet the decisions made by the animals. There are examples in some species that illustrate how the «prizes» of the trade-off reduced when they involve factors such as predation (Holbrook & Schmidt 1988), risk of inanition (Caraco *et al* 1980) and habitat selectivity (Whitman 1980, Post & Reichman 1991).

Even when the fossorial mammals spend an important part of the day underground, there are occasions in which they are obliged to go up to the surface for different reasons (foraging, territory maintainance, mate search) (Reichman & Smith 1990).

We have observed many times clear evidences of aboveground foraging as beleved shrub stems, grass and cactaceous surrounding the mouth of the burrows of *C. mendocinus*.

The risk of predation becomes then a factor that could affect food choice. Weir (1974) points out that the main predator on *C. talarum* is the owl *Speotyto cunicularia*..

Thus, the opportunistic harvesting pattern observed might be selectively advantageous as it reduces the time the rodent spent in the surface. It may be possible, that once the rodent harvests its food, it may classify it in its cave.

The results presented here confirmes that *C. mendocinus* harvests a variety of plant material although it prefers the aboveground parts of grasses over shrubs and roots in general (Torres Mura *et al.* 1989, Madoery, 1993).

The differences between harvesting patterns and consumption patterns suggest that *C. mendocinus* used the removed material in different ways (storage, nest, etc.).

The use of more than one criterion of selectivity precluded the confusion between removal and consumption and allowed us to establish the feeding behavior of *C. mendocinus* in a more reliable way.

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