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Original article

Foraging behaviour of coypus *Myocastor coypus*: why do coypus consume aquatic plants?

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Abstract

Foraging behaviour of wild coypu was studied to examine two hypotheses that had been previously proposed to explain the species' preference for aquatic plants. First, the nutritional benefit hypothesis which states that aquatic plants are more nutritional than terrestrial plants. Second, the behavioural trade-off hypothesis which states that coypus avoid foraging far from the water because of the costs associated with other types of behaviour. In order to test the nutritional benefit hypothesis, we studied the diet composition of coypus in relation to the protein content of the diet and of the plants available in the environment. Fieldwork was conducted seasonally from November 1999 to August 2000 at one study site located in the Province of Buenos Aires, east central Argentina. Behavioural observations showed that coypus remained foraging in the water and microhistological analysis of faeces indicated that their diet was principally composed of hygrophilic monocotyledons (*Lemna* spp. and *Eleocharis* spp.) throughout the year. We did not find support for the nutritional benefit hypothesis: nutritional quality (based on nitrogen content) of hygrophilic plants was not higher than that of terrestrial plants, and seasonal changes in diet quality did not match either fluctuations in vegetation quality or proportion of hygrophilic plants in the diet. Although not directly tested, the behavioural trade-off hypothesis may explain why coypus prefer to forage in or near the water as a mechanism for reducing predation risk.

Keywords: Diet selection; Diet quality; Foraging ecology; Nutria

1. Introduction

The coypu (*Myocastor coypus*) is a semi-aquatic herbivorous rodent indigenous to southern South America (Gosling and Baker, 1991). This species was introduced into several regions around the world early this century, including North America, Europe, the Middle East, Africa, and Japan (Carter and Leonard, 2002). In some of these regions the coypu is considered a pest because of the damage caused to crops, native flora and fauna, and drainage systems (Kinler et al., 1987; Gosling and Baker, 1989; Reggiani et al., 1993; Verheyden and Abbas, 1996).

In order to predict the potential impact of an invasive herbivore species like the coypu on crops or native vegetation, it is important to understand the behavioural mechanisms underlying diet selection (Gosling, 1981). Previous studies have indicated that foraging is the major activity of coypus when outside their burrows (D'Adamo et al., 2000; Guichón et al., 2003), and that their diet has a strong dependence on aquatic and semi-aquatic plants (Shirley et al., 1981; Kinler et al., 1987; Wilsey et al., 1991; Borgnia et al., 2000). This high consumption of hygrophilic vegetation was also evident in areas where terrestrial plants constituted a non-limiting, high quality resource (i.e. crops) located a few meters from the water body (Gosling, 1981; Borgnia et al., 2000; D'Adamo et al., 2000). Gosling (1981) suggested three hypotheses that could explain the feeding pattern of coypus: (1) nutritional benefit: aquatic plants are better sources of nutrients than terrestrial plants; (2) innate preference: coypus have digestive mechanisms to deal with this type of vegetation as one of several adaptations to live in aquatic environ-

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ments; and (3) behavioural trade-off: coypus avoid foraging far from the water as a means of diminishing costs associated with other types of behaviour, e.g. to reduce predation risk or to thermo-regulate more efficiently. The latter hypothesis assumes that the high representation of aquatic plants in a coypu's diet is the result of a process of microhabitat selection rather than a product of choosing plant types.

Borgnia et al. (2000) tested the hypotheses 2 and 3 above and found evidence to support the behavioural trade-off hypothesis against the innate preference hypothesis. In a field experiment, they showed that consumption of a plant species was dependent on its location, either near or far from the water. The authors were unable to test the nutritional benefit hypothesis because they did not estimate the nutritional quality of the vegetation. Aquatic plants typical of wetland habitats tend to have high nutritional quality and easy digestibility and floating aquatics constitute a good potential source of crude protein (Garner, 1962; Lebreton, 1982; Hubac et al., 1984). Protein is critical for the growth, reproduction, and survival of herbivores that must consume large quantities of food to fulfil their nutritional requirements (Sinclair, 1975; Crawley, 1983). Therefore, a diet based on aquatic plants rather than terrestrial plants could be preferable because of the nutritional benefits.

In this study, we analysed the foraging behaviour of indigenous coypus in relation to the composition and nitrogen content of their diet and of the plants available in the environment. Under the nutritional benefit hypothesis, the high consumption of aquatic plants is explained by their greater nutritional quality in comparison to terrestrial plants. Under the behavioural trade-off hypothesis, coypus will consume aquatic plants regardless of plant quality and their diet will be composed of aquatic plants, unless these plants show a significant decrease in abundance. This is the first study that combines information on diet composition, nutritional quality, and foraging behaviour of coypus.

2. Material and methods

2.1. Study area

The work was conducted at a study site of agricultural pampas located near Jáuregui town (34°35'S, 59°11'W), in the Province of Buenos Aires, east-central Argentina. The original habitat of grassland steppe has been widely modified by arable and livestock farming and urbanisation (Cabrera, 1971). The area has a temperate climate, with mean temperatures of 9.1 °C in winter and 23.8 °C in summer, and a mean annual rainfall of 944 mm (Goldberg et al., 1995).

Fieldwork was conducted around a pond (4.3 ha) located in a large field of cattle pasture and forestation. The pond had been constructed for recreational purposes in 1960 by modifying a natural watercourse, but was rarely used for this purpose during the study. The water was covered by *Lemna* spp., and the dominant surrounding vegetation was grasses and planted trees. During the study period, 25–44 coypus were present in the pond (Guichón et al., 2003).

2.2. Data collection

Faeces and vegetation were sampled seasonally from November 1999 to August 2000: spring (November–December), summer (February), autumn (May), and winter (August). In each season, we collected all faeces deposited within the first 2 m of the bank around the whole perimeter of the pond. We listed all of the plant species that were present in the water and within 15 m of the pond edge. Previous studies reported that use of space by coypus is mainly restricted to an area of 10 m on either side of the water's edge (Doncaster and Micol, 1989; Borgnia et al., 2000; D'Adamo et al., 2000; Guichón et al., 2003). Therefore, only the vegetation present within this area was taken into account when estimating plant availability. Plant availability was sampled in two vegetation zones: (1) 0–5 m from pond edge into water, and (2) 0–5 m from pond edge out of water. The available vegetative cover was estimated every 60 m around the pond by using a sampling quadrat (50 × 50 cm) that was subdivided into five sections. At each sampling point, we randomly placed the quadrat within each vegetation zone and recorded the presence of hygrophilic monocotyledons, terrestrial monocotyledons, hygrophilic dicotyledons, and terrestrial dicotyledons in each subdivision. In each quadrat, we randomly placed a 20 × 20 cm subquadrat where we collected the aboveground biomass to analyse the nutritional quality of the vegetation. The plants were clipped at soil surface. For this latter analysis, we also sampled vegetation that was 10–15 m from the pond edge following the same procedure described for the other two vegetation zones.

Behavioural observations were conducted following Guichón et al. (2003). Fifty-seven hours of observation were performed between December 1999 and March 2000. We observed animals during the evening, using a telescope (60×) and binoculars (12 × 50) from two vantage points simultaneously. Scan sampling separated by 15-min intervals (Martin and Bateson, 1993) allowed us to record the location of the foraging animals and the type of vegetation consumed. Changes in foraging behaviour throughout the year might have been undetected due to the limited observation period. However, data resulting from sampling of signs of activity (faeces, paths, tracks, grazed areas, excavations) and quarterly trapping sessions conducted from July 1999 to August 2000 indicated that the use of foraging sites was similar throughout the study period (Guichón, 2003).

2.3. Diet analysis

Diet composition was determined by microhistological analysis of the faeces collected each season, following Borgnia et al. (2000). Twenty-five faeces were chosen at random from the pool of faeces collected each season, blanched with 50% hypo-chlorite, and filtered with water to retain fragments 0.05–1 mm. Five random samples were

Table 1
Percentage of plant availability and consumption, and estimated Manly's selection index (±95% confidence interval) for each plant category in each season

Season/parameter	Hygrophilic monocotyledons	Terrestrial monocotyledons	Hygrophilic dicotyledons	Terrestrial dicotyledons	χ^2 (d.f. = 3)
Spring					
Availability	46.8	25.5	13.8	13.8	
Consumption	90.9	9.1	0.0	0.0	
Selection index	1.9 ± 0.4 (P)	0.4 ± 0.3 (A)	0.0	0.0	31.4*
Summer					
Availability	47.6	22.4	5.4	24.5	
Consumption	92.6	7.4	0.0	0.0	
Selection index	1.9 ± 0.4 (P)	0.3 ± 0.3 (A)	0.0	0.0	28.2*
Autumn					
Availability	37.6	42.3	3.4	16.8	
Consumption	76.3	13.0	0.0	10.7	
Selection index	2.0 ± 0.6 (P)	0.3 ± 0.2 (A)	0.0	0.6 ± 0.5	43.3*
Winter					
Availability	38.3	32.9	3.0	25.7	
Consumption	74.6	23.9	0.0	1.5	
Selection index	1.9 ± 0.5 (P)	0.7 ± 0.3	0.0	<0.1 ± 0.1 (A)	57.6*

(P) indicates preference and (A) indicates avoidance.
* $P < 0.001$.

extracted from the sieve and examined to identify all the epidermic fragments contained in 100 predetermined fields (20/slide) at 100× magnification. Fragments were compared to a reference collection of epidermis tissue collected from leaves, stems, and fruits from the area.

Data on consumption, obtained from microhistological analysis, and availability of plants were analysed by using the selection index proposed by Manly et al. (1993). A log-likelihood chi-square test was used to test the hypothesis of no selection, and Bonferroni confidence intervals were estimated to evaluate if each resource category was significantly selected or avoided (Manly et al., 1993).

The quality of the diet and of the vegetation available was determined by using percent nitrogen content (Robbins, 1983). Twenty-five faeces were selected at random from the pool of faeces collected in each season, dried at 60 °C, ground, and analysed. Four samples were analysed each season. The aboveground biomass collected in each vegetation zone was dried at 60 °C, crumbled, and analysed. Two samples were analysed from the pool of aboveground vegetation of each zone and their average gave the percent nitrogen value for each season. The Kjeldahl technique (AOAC, 1980) was used to determine nitrogen content in faecal and aboveground biomass samples.

3. Results

When plant consumption was compared to availability, we found that coypus foraged selectively in all seasons (Table 1). The diet was based almost exclusively on hygrophilic monocotyledons, which were preferred in all seasons (Table 1). Coypus rejected terrestrial monocotyledons (except in winter), and the hygrophilic and terrestrial (except in autumn) dicotyledons throughout the year (Table 1).

The microhistological analysis of faeces indicated that coypus consumed only eight of the 45 plants that were available in the water and near the bank (Table 2). More than 80% of the year-round diet was composed of two hygrophilic monocotyledons: *Lemna* spp. and *Eleocharis* spp. (Fig. 1). Coypus also consumed terrestrial grasses, mainly *Cynodon* sp., and *Dichondra* sp.

Foraging observations indicated that coypus primarily fed in the pond (99.8% of 1572 recordings). The few times that animals were observed foraging outside the pond, they were within 5 m from the pond edge. Coypus consumed *Lemna* spp. in 92% of the foraging records. This result is consistent

Table 2
List of herbaceous plant genera available in the water and near the pond edge. Plants in bold were present in the diet of coypus, as determined by microhistological analysis of faeces

Vegetation category	Plant species
Hygrophilic monocotyledons	*Azolla* [a], *Cortaderia, Cyperus,* ***Eleocharis****, Iris, Juncus,* ***Lemna****, Triglochin, Typha*
Terrestrial monocotyledons	***Bromus, Cynodon****, Hordeum,* ***Lolium****, Paspalum, Phyllostachys, Piptochaetium, Polypogon,* ***Stenotaphrum, Stipa****, Tradescantia*
Hygrophilic dicotyledons	*Alternanthera, Hydrocotyle, Ludwigia*
Terrestrial dicotyledons	*Asclepias, Baccharis, Carda, Centaurium, Ciclospermum,* ***Dichondra****, Dicliptera, Eclipta, Gamochaeta, Hypericum, Leonurus, Lotus, Medicago, Oxalis, Oxypetalum, Parietaria, Picrosia, Plantago, Pluchea, Polygonum, Rumex, Verbena*

[a] We included the pteridophyte *Azolla* within the group of hygrophilic monocotyledons.

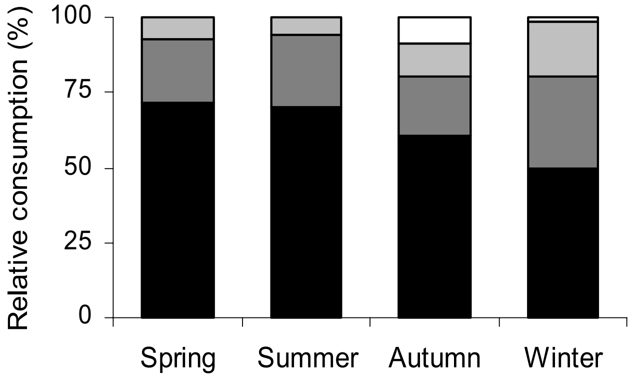

Fig. 1. Diet composition of coypus as determined by microhistological analysis of faeces. Hygrophilic monocotyledons: *Lemna* sp. (black) and *Eleocharis* sp. (dark grey); terrestrial monocotyledons: grasses (light grey) including *Bromus* sp., *Cynodon* sp., *Lolium* sp., *Stenotaphrum* sp., and *Stipa* sp.; and terrestrial dicotyledons: *Dichondra* sp. (white).

with the microhistological analysis of the faeces in showing that *Lemna* spp. was the main component of the diet. However, the percentage consumption of *Lemna* spp. estimated by behavioural observations was larger than that estimated by faecal analysis in the same season (Fig. 1: 70%), probably due to limitations of the observation period.

Hygrophilic plants comprised the majority of the diet, but the hypothesis of nutritional benefit could only explain these results if hygrophilic plants had higher nitrogen content than terrestrial plants. No significant differences were found in the nitrogen content of the plants present in the three vegetation zones (Kruskal–Wallis test: $n = 12$, $H = 2$, $P = 0.27$). Furthermore, the percentage of hygrophilic vegetation in the diet was larger in spring and summer than in autumn and winter (Table 3). If hygrophilic plants are selected for their nutritional value, a larger relative consumption of hygrophilic vegetation should have resulted in better diet quality. Diet quality diminished from summer to autumn, but the increased nitrogen content of the diet in winter cannot be explained by an increased consumption of hygrophilic plants nor by their larger nitrogen content (Table 3).

4. Discussion

The diet of coypus was mainly composed of hygrophilic vegetation throughout the year. Coypus foraged primarily on hygrophilic monocotyledons and, secondarily, on terrestrial monocotyledons (grasses). Similar results were obtained in previous studies conducted in the coypu's native range (Murúa et al., 1981; Borgnia et al., 2000) and in regions of introduction (Warkentin, 1968; Gosling, 1974; Willner et al., 1979; Shirley et al., 1981; Abbas, 1991; Wilsey et al., 1991). Despite their preference for hygrophilic plants, we found no evidence to support the nutritional benefit hypothesis: nitrogen content of hygrophilic plants was not higher than that of terrestrial plants and seasonal changes in diet quality did not match fluctuations in vegetation quality. Other constraints than nitrogen content could be important in coypus' diet selection and should be analysed in further studies. However, our results tackle a key question given the high protein content reported for the most preferred food items of this species (Garner, 1962; Hubac et al., 1984). Even if food quality was not determined for each species, the nitrogen content of hygrophilic plants offered a reliable estimation of the nutritional value of the plants consumed by coypus given the high representation of *Lemna* sp. and *Eleocharis* sp. throughout the year and the comparative purpose of our analysis.

In a previous study, Borgnia et al. (2000) suggested that diet selection by coypus depended on the distribution of food relative to distance to water. In a field experiment that equalised the availability of a terrestrial (*Lolium multiflorum*) and an hygrophilic (*Eleocharis bonariensis*) species at two distances from water, the authors found evidence in support of the behavioural trade-off hypothesis. In this study we did not directly test the behavioural trade-off hypothesis. However, coypus remained foraging in the water the majority of the time and they fed mainly on hygrophilic plants that were not significantly higher in nitrogen content, suggesting that the behavioural trade-off hypothesis may explain their foraging behaviour. Other studies in similar environments (i.e. excluding marshlands) also reported that coypus foraged in or close to the water (Doncaster and Micol, 1989; Gosling and Baker, 1991; D'Adamo et al., 2000), and that they consumed hygrophilic plants when they were available, only turning to terrestrial vegetation (mainly grasses) when hygrophilic vegetation was scarce (Abbas, 1991).

The behavioural trade-off hypothesis assumes that the costs and benefits of other behaviours related to food acquisition modulate the foraging behaviour of coypus. In this case, foraging in or near the water results from a feeding site selection process rather than from a plant choice decision. Two types of behaviours could be involved in this decision making process: thermo-regulation requirements and predation risk avoidance. Observations of coypu behaviour in the wild and in enclosures indicated a weak or null relationship

Table 3
Nitrogen content (%N) of the three vegetation zones (0–5 m on the water, and 0–5 and 10–15 m on land) and of the faeces. The percentage of hygrophilic vegetation in the diet is also shown

Season	%N of vegetation			%N of faeces	Percentage of hygrophilic plants in diet
	0–5 m water	0–5 m land	10–15 m land		
Spring	3.85	3.28	3.08	1.98	91
Summer	2.53	2.67	2.17	2.30	93
Autumn	2.57	1.98	1.92	1.60	76
Winter	2.24	2.40	2.15	2.02	75

between air temperature and use of water (Doncaster et al., 1990; Moinard et al., 1991). Coypus remained in the water even under the freezing conditions of temperate winters in France, and also under a wide range of temperatures when air temperature was experimentally manipulated in enclosures (Doncaster et al., 1990). This evidence suggests that use of water does not depend on temperature regulation. Selection of feeding sites in coypus could be modulated by predation risk avoidance, even if this behaviour may incur nutritional (Gosling, 1981) or thermo-regulatory (Doncaster et al., 1990; Moinard et al., 1991) costs. Water serves as shelter for coypus, a species that commonly dives into water to escape, and either remains under water for several minutes or enters submerged burrow openings (personal observations; Gosling and Baker, 1991). This escape behaviour was also observed in capybaras *Hydrochaeris hydrochaeris* (Quintana, 1996). The selection of foraging sites near the shelter appears as a common pattern among caviomorph rodents, for example, in cavies *Cavia aperea* (Cassini, 1991; Guichón and Cassini, 1998), degus *Octodon degus* (Vásquez, 1997), and vizcachas *Lagostomus maximus* (Branch and Sosa, 1994), and in several bird and mammal prey species (Lima and Dill, 1990).

The foraging behaviour of coypus described in this study can have management applications when trying to diminish or prevent damage to crops. Coypus are not a threat to agricultural systems in their native range (Guichón and Cassini, 1999; Borgnia et al., 2000; D'Adamo et al., 2000), probably because cultivated lands in the Pampas region typically have a fringe of natural vegetation growing between the water body and the crop. This non-cultivated fringe of vegetation near the watercourse is often not available in European farmlands, where intensive land cultivation extends to the water's edge and crops growing next to the water are damaged by coypus (e.g. canals of irrigation systems in France: Abbas, 1988). A more effective reduction of crop losses can be attained, therefore, if trapping control is complemented with relatively simple actions of habitat management, such as leaving a 5-m wide fringe of natural vegetation near the water's edge and promote the growth of hygrophilic plants.

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