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Foraging patterns of capybaras in a seasonally flooded savanna of Venezuela

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ABSTRACT. The foraging behaviour of capybaras (*Hydrochaeris hydrochaeris*) was assessed in relation to habitat and season in a flooded savanna of Venezuela from February (dry season) 1993 to June (rainy season) 1994. Direct observations were carried out to record group movements and foraging activities of individual capybaras when feeding on specific plant species. The time devoted to feeding upon some species was recorded in relation to total foraging time (feeding + searching). Capybaras spent similar times feeding on reeds (*Eleocharis interstincta*; Cyperaceae) and *Paratheria prostrata* (Poaceae) patches during the dry season though plant quality was different. During the rainy season, reeds were almost ignored by the animals which fed mainly on *Hymenachne amplexicaulis*, a grass with a significantly higher content of energy and protein. Capybaras fed for longer time during the dry season but more selectively during the rainy season. Capybaras were the dominant grazers in this flooded savanna as inferred from the comparative effects they produced in the height, biomass and quality of the pasture in relation to those effects produced by other vertebrate herbivores, namely, cattle, feral horses and asses.

KEY WORDS: capybara, foraging behaviour, grazing, herbivory, *Hydrochaeris*, savannas, Venezuela

INTRODUCTION

Mammalian grazers are faced with a sometimes abundant and widespread food resource whose quality can vary widely. Grazers have to adjust their feeding strategy according to time of year and the types of grasses present in the various patches of the environment (Sibly 1981). Thus, in a good patch during the growing season, a herbivore can selectively feed on the best grasses and obtain more than adequate nourishment; conversely, in a poor patch or during

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the non-growing period, a herbivore may procure for itself a large quantity of low quality food by reducing its selectivity and increasing its intake rate (Hume 1989; Sibly 1981,1986).

In order to understand how a particular herbivore adjusts its foraging strategy to cope with differences in food abundance and quality, both in time and in space, four levels of analysis can be used (Pyke 1984, Pyke *et al*. 1977, Stephens & Krebs 1986). At a broad level, patterns of habitat use provide a first approximation to the problem. A study of the use of specific patches within a habitat constitutes the next slightly finer level of analysis. One level further down involves the searching strategy within a patch, while the final and finest level has to do with the plant species and plant parts that the animal actually feeds on (Stephens & Krebs 1986).

A further aspect of a herbivore's feeding strategy involves the plants themselves. Plant responses to herbivory are widely documented but the actual effects herbivores induce on plants have been the object of a long debate (*e.g*. Belsky 1986, Belsky *et al*. 1993, Hilbert *et al*. 1981; McNaughton 1985, 1993). Such responses could be evidenced both in the short and in the long term (Karban & Myers 1989). In particular, an increase in the quality (protein content) of leaves under herbivory has been both theoretically predicted (Hobbs & Swift 1988) and empirically found (*e.g*. Ydenberg & Prins 1981) followed by a hypothesis on 'resource management' by herbivores (Gordon & Lindsay 1990). According to these authors, herbivores manage their patterns of resource utilisation, so as to maximise the flow of nutrients from these resources. Long-term territoriality or the exclusive use of a home range are the social systems most likely to favour selection for prudent resource exploitation (Gordon & Lindsay 1990).

In capybaras (*Hydrochaeris hydrochaeris*; Caviomorpha), 50–60 kg grazing rodents of the South American savannas, a first level of analysis of feeding strategies (habitat use) was carried out by Herrera & Macdonald (1989). They found that the home range of a group of capybaras included the three major habitat types in the area. Their results showed that the 10-ha (on average) home range was in fact a territory defended by all adult group members (Herrera & Macdonald 1989). These authors also mentioned that capybaras can selectively bite a specific plant species within a patch, but they did not study the foraging behaviour of capybaras in relation to habitat quality or seasonality.

The diet of capybaras in Venezuela has been found to consist mostly of grasses, especially *Hymenachne amplexicaulis*, *Leersia hexandra*, *Paratheria prostrata* and *Reimarochloa acuta* and, to a lesser extent, *Panicum laxum* and reeds (*Eleocharis* spp.; Cyperaceae) (Escobar & Gonzalez-Jimenez 1976). In Argentina, the diet of capybaras consisted mainly of Cyperaceae and grasses (Quintana *et al*. 1994). Coprophagy, which is practised during the morning resting period (Herrera 1985) and several adaptations to grazing make the digestive efficiency of capybaras comparable to that of ruminants (Borges *et al*. 1996, Gonzalez-Jimenez 1977, Ojasti 1973). The daily routine of capybaras involves resting in the morning, wallowing

in the hot midday hours and grazing in the afternoon and evening (Herrera 1986, Macdonald 1981, Schaller & Crawshaw 1981). These rodents live in stable, mixed-sex social groups where a rigid dominance hierarchy develops among the males (Herrera & Macdonald 1987, 1993).

In this paper, we studied patterns in the foraging behaviour of capybaras in relation to differences in resource quality both according to habitat and to season. We also assess the effect of capybaras on the plants on which they feed by measuring plant quality with and without herbivory.

STUDY SITE

This study was carried out on Hato El Frio, an 80,000-ha cattle ranch in the low Llanos of Venezuela (7°46′N; 68°57′W). The region is characterized by tropical seasonally flooded savannas. The relief is virtually flat with an eastward slope of 0.02%. Climate is strongly seasonal with a dry period from November to April, which causes severe water shortage, and a wet season from May to October, during which extensive flooding occurs. Average temperatures are around 26 °C and annual rainfall is 1565 mm (data from El Saman Weather Station, 30 km east of the study area). The region comprises three physiographic units (Sarmiento 1984): (i) *esteros* (ponds), most of which dry up completely in the dry season, but in the early wet season dense stands of *Hymenachne amplexicaulis* and other aquatic grasses grow throughout the shallow parts of the pond, to be replaced by reeds (*Eleocharis* spp.; Cyperaceae) and other aquatic vegetation later on in the wet season. (ii) *bajios* (up to 0.5 m higher than esteros) comprise *c*. 70% of the low Llanos (Ramia 1974) and are covered with short, highly palatable grasses (*e.g. Leersia hexandra*, *Panicum laxum*). Bajios flood in the wet season to depths of 10–20 cm. (iii) *bancos* (2 m higher than esteros) are areas generally covered by tall grasses (*e.g. Imperata contracta*, *Elyonurus tripsacoides*), short grasses (*e.g. Reimarochloa acuta*, *Paratheria prostrata*) or bushes (*e.g. Sida* spp., *Cassia aculeata*). Lower bancos are prone to flooding whereas isolated patches of semi-deciduous woodland grow on some high bancos. Census of capybaras conducted by the Venezuelan Wildlife Service revealed that *c*. 13000 animals inhabited the ranch during the time this study was carried out (1993–1994).

METHODS

Foraging behaviour

Direct observations of individuals in social groups were carried out under natural conditions. Capybaras were watched during the afternoon and evening activity peaks (Herrera & Macdonald 1989, Macdonald 1981) for up to 4 h continuously. Observations were made during the onset of the wet season of 1993 and 1994 and during the mid dry season in 1994. We focused our observations on two aspects: (i) Group movements throughout the territory during foraging hours, and (ii) Feeding time on a particular plant species in relation to total foraging

time (feeding and searching) defined from now on as effective feeding time, a measure of the probability of eating an individual plant once encountered.

The area occupied by two contiguous groups was mapped and marked with numbered poles as landmarks. Two additional non-contiguous groups were also observed. Groups were observed with a telescope 15–60x from a distance not more than 50–60 m and their movements were recorded on the map. The time spent in each of the various vegetation stands by both groups was recorded.

In order to measure the effective feeding time, we chose a member of the group (focal animal sampling; Martin & Bateson 1993) and observed it while foraging, noting the plant species being taken. This was possible in the cases of the grasses *Reimarochloa acuta*, *Paratheria prostrata* and *Hymenachne amplexicaulis* and the reed *Eleocharis interstincta* as these plants formed distinguishable stands in the study area. Once an animal was chosen, we measured with a stopwatch the time it spent feeding on a given plant species during 5-min recording sessions. During each session when the animal was foraging, we distinguished between the animal searching for, or actually feeding (biting, swallowing) on, plants or plant parts. We did this only in the cases where we were certain of the species on which the animal was feeding and we stopped recording if the animal was interrupted by alarm calls or displaying alert-type behavioural activities (see Yaber & Herrera 1994). Only continuous 5-min sessions were taken into account. Most animals in four different groups were chosen. Individuals were distinguished on the basis of sex, size, behaviour (level of dominance), marks and group to which the individual belonged. Results were expressed as percent time. Effective feeding time was used as a measure of selectivity by the animal: low values mean more time searching and less time feeding, i.e. high selectivity. Mann-Whitney or Kruskal-Wallis tests were used for comparison of effective feeding times between two or three different plant species respectively.

Food quality

Samples of the plant species considered were taken from the same place where capybaras were foraging in order to determine the caloric content of each one. We took three samples of 30 individual plants of *H. amplexicaulis* and 50 shoots of *E. interstincta* both during the wet and dry season study periods, three samples of 0.25 m^2 aboveground biomass of *R. acuta* during the wet season and three samples of 0.25 m^2 aboveground biomass of *P. prostrata* during the dry season. Samples were oven-dried at 50 °C, ground and the caloric content determined in triplicate in a Parr-1241 adiabatic calorimeter (caloric equivalent = 10.07 Kjoule/°C). Crude protein and fibre content of the green fraction (the fraction eaten by capybaras) were also determined by the Kjeldahl method (multiplying % nitrogen $\times$ 6.25) and neutral-detergent fibre analyses (Goering & Van Soest 1970). Results were expressed as percentages of dry weight (% DW).

Six exclosure plot systems were built as part of a simultaneous experiment that intended to assess the short term impact of herbivory by capybaras on natural pastures (Barreto 1994). Each system consisted of (i) a 16-m^2 total

exclosure plot with no access to vertebrate herbivores, (ii) another 16-m^2 partial exclosure plot allowing capybaras but no other herbivore (cattle, horses or asses) to graze in, and (iii) a 16-m^2 control plot where all animals were allowed. Three of these systems (three replicates) were set on *H. amplexicaulis* stands, two on *R. acuta* stands and one on a *P. prostrata* stand. All exclosures were established toward the end of the dry season (5–6 April 1993). Two samples of 0.25 m^2 of the aboveground biomass were taken from each plot just after they were established and 9 wk afterwards in the cases of *R. acuta* and *P. prostrata* or 12 wk in the case of *H.amplexicaulis*. Each sample was divided into dead and green biomass, oven-dried at 40 °C and ground. Crude protein and fibre content of the green fraction were determined as stated above. Both height and biomass were measured in each plot. Mean values for each plot were used and analysed by using two-way analysis of variance.

RESULTS

Effective feeding time

(i) *Wet season*. The amount of time spent on the various patches differed remarkably. Capybaras spent 27% of the time on *H. amplexicaulis* stands, but only 3 or 1% feeding on reeds or unidentified plants respectively (total observation time = 31.9 h). The remaining time was devoted to moving from one patch to another or resting. The animals did not follow the same route for foraging during consecutive days (Figure 1a). The effective feeding time did not differ between reeds (65%) and *H. amplexicaulis* (69%, n = 56) although few 5-min sessions were conducted on reeds (n = 7). Figures stand for the proportion of time devoted to actually feeding on a specific plant species in relation to the total time devoted to foraging (feeding on and searching for that species). Conversely, *R. acuta* effective feeding time values (81%, n = 47) were significantly higher (less selective) than those from *H. amplexicaulis* (Mann-Whitney U test; P < 0.0001). Caloric content was significantly higher in *H. amplexicaulis* than in *E. interstincta* ($F_{2,6}$ = 16.7; P < 0.01) and protein content in *H. amplexicaulis* was significantly higher than the other two species ($F_{2,6}$ = 11.09; P < 0.01) (Table 1).

(ii) *Dry season*. Capybaras were observed during the dry season for 24.9 h. They fed on reed patches for 21% of the time, 17% was devoted to *P. prostrata* patches and 11% to *Paspalum chaffanjonii* stands. The latter, however, were quite diverse and rich in tall grasses making it difficult to ascertain the plant species being eaten. The remaining time was spent moving from one patch to another or resting. In general, animals did not follow the same route for more than two consecutive days even if the midday resting place was the same. Individuals from group A, for example, foraged the second recorded day on a different area they had foraged the previous day. They follow almost the same route during days 6 and 7 and changed to another area on days 8 and 9 (Figure 1b).

Effective feeding time of capybaras feeding on reeds was lower (68%, n = 45) than that on *P. prostrata* (86%, n = 45) and *H. amplexicaulis* (84%, n = 33)
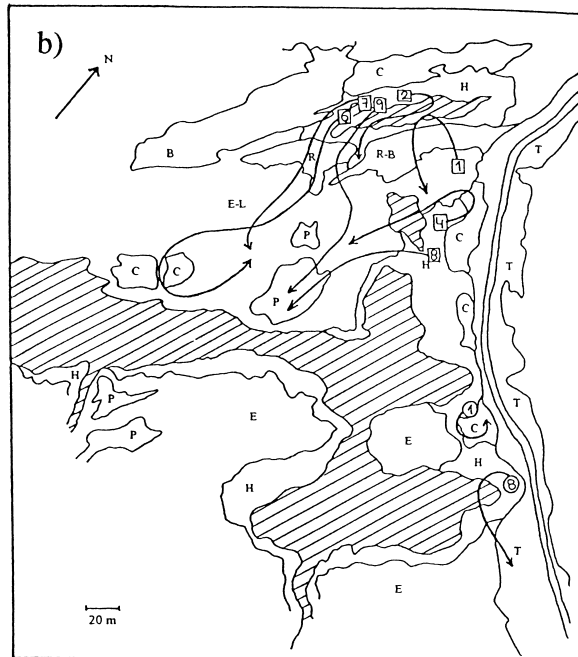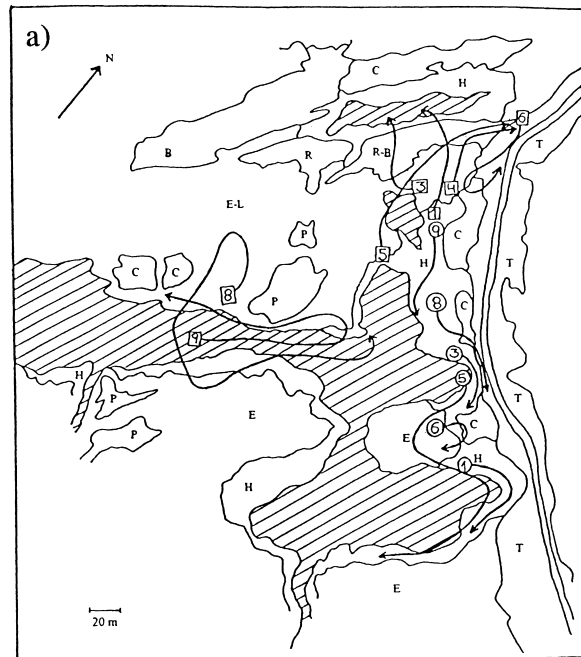
Figure 1.   Movements of two groups of capybaras during the (a) wet season, and (b) dry season. Squares and circles identify the two groups. The figures inside them represent the recorded day. The map shows the different plant associations in the area: B, bank with tall grasses; C, *Cassia* sp.; E, *Eleocharis* sp.; H, *Hymenachne* sp.; L, *Leersia* sp.; P, *Paratheria* sp.; R, *Paspalum* sp.; T, dam with road 2 m higher than the pond (striped area).

Table 1. Ash-free caloric content, crude protein and fibre content of three plant species (green biomass) of the flooded savannas of Venezuela during wet season (mean ± SE). For all cases n = 3. Different superscripts indicate significant differences between species.

Species	C.C. (Kjoule g^{-1})	Protein (% DW)	Fibre (% DW)
H. amplexicaulis	19.26 ± 0.03[a]	10.31 ± 0.86[a]	65.0 ± 1.3[ab]
E. interstincta	18.72 ± 0.11[b]	8.07 ± 0.30[b]	67.6 ± 1.1[a]
R. acuta	19.54 ± 0.13[a]	7.29 ± 25.8[b]	62.8 ± 1.4[b]
P	<0.05	<0.01	<0.01

(Kruskal-Wallis H = 67.5; df = 2; P < 0.001 after multiple contrasts). Although caloric content of *P. prostrata* was significantly higher than that of *E. interstincta*, their protein contents were not significantly different (Table 2). Protein content of *H. amplexicaulis* was higher than that of reeds ($F_{2,6}$ = 19.9; P < 0.01) (Table 2) whereas ash free caloric content was similar to *P. prostrata* but higher than reeds ($F_{2,6}$ = 5.48; P < 0.05).

Exclosure experiment.

(i) *H. amplexicaulis*. Vegetation in the total exclosure plots was significantly taller than in the other treatments after 12 wk ($F_{2,4}$ = 19.1; P < 0.01) reaching up to 1.2 m height. Grazing reduced the height of the vegetation by 10–15%. Green biomass was reduced by grazing by 55% in relation to the biomass in the total exclosure plots. There were no differences between the biomass in the partial exclosure plot (91.7 ± 16.1 g m^{-2}) and the control plot (97.3 ± 33.0 g m^{-2}) though both were significantly lower than the biomass in the total exclosure plot (172.1 ± 29.4 g m^{-2}) ($F_{2,4}$ = 6.98; 0.05 > P > 0.01) (Figure 2).

Fibre content at the beginning of the growing season was 61.8%, and crude protein 19.39% DW. Protein : fibre ratio was 0.33. Protein : fiber ratio is used here as a measure of quality. After 12 wk, fibre and protein in control plots were 55.2% and 18.97%. Table 3 shows fibre and protein contents in total exclosure, partial exclosure and control plots 12 wk after the beginning of the experiment. Although differences were not significant, a trend towards better quality was observed from ungrazed to grazed plots as revealed by an increment in the protein content and a decrease in the fiber content from total exclosure to control plots.

(ii) *R. acuta*. Vegetation in the grazed plots was 40–80% shorter than that in the total exclosure plot. Total biomass in the total exclosure plot

Table 2. Ash-free caloric content, crude protein and fibre content of three plant species (green biomass) of the flooded savannas of Venezuela during the dry season (mean ± SE) (n = 3). Different superscripts indicate significant differences between species.

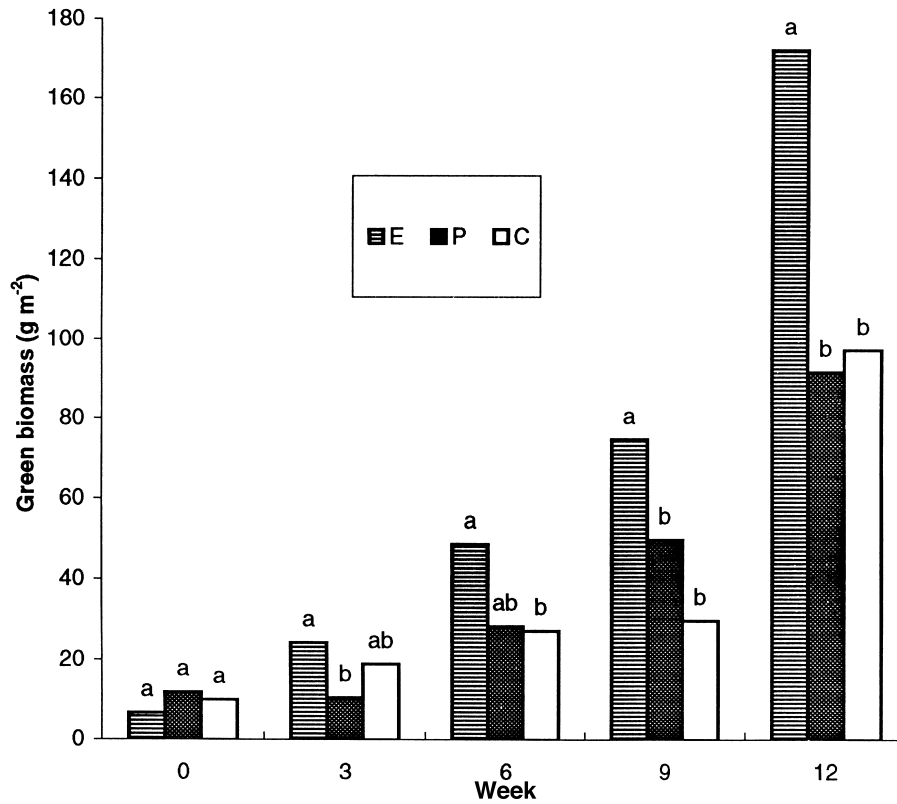| Species	C.C. (Kjoule g^{-1})	Protein (% DW)	Fibre (% DW)
H. amplexicaulis	19.54 ± 0.35[a]	16.62 ± 0.30[a]	54.5 ± 1.3[b]
E. interstincta	18.64 ± 0.08[b]	11.32 ± 1.00[b]	64.4 ± 0.2[a]
P. prostrata	19.44 ± 0.10[a]	12.25 ± 1.58[b]	63.8 ± 3.3[a]
P	<0.05	<0.005	<0.005

Figure 2. Green biomass in stands of *Hymenachne amplexicaulis* under three treatments: E, total exclosure (no vertebrate herbivore allowed); P, partial exclosure (capybaras only) and C, control (no exclosure at all) from the beginning of the experiment until the 12th wk. Different letters above the bars indicate significant differences after two-way analysis of variance (P < 0.05).

Table 3. Protein content (% DW) and fibre content (% DW) in green biomass of *Reimarochloa acuta* and *Hymenachne amplexicaulis* in total exclosures (no major herbivores allowed), partial exclosures (only capybaras allowed) and control plots 9 and 12 wk respectively after the beginning of the experiment. Means and SEs are shown. Different superscripts represent significant differences between treatments (P < 0.01).

	Treatment	Protein (% DW)	Fibre (% DW)
R. acuta	Total exclosure	6.75 ± 0.30^a	64.88 ± 0.68^a
	Partial exclosure	7.25 ± 0.70^a	64.55 ± 1.44^a
	Control	8.50 ± 0.65^b	63.42 ± 1.19^a
H. amplexicaulis	Total exclosure	8.81 ± 0.50^a	58.06 ± 0.94^a
	Partial exclosure	9.81 ± 0.37^a	56.68 ± 1.57^a
	Control	10.12 ± 0.40^a	55.22 ± 1.96^a

$(243.5 \pm 18.3 \text{ g m}^{-2})$ was significatively higher than in the grazed plots ($F_{1, 2} = 40.1$; $P < 0.0001$): $70.8 \pm 26.5 \text{ g m}^{-2}$ in the partial exclosure plots and $68.2 \pm 27.9 \text{ g m}^{-2}$ in the control plots. Fibre and protein contents were 59.6% and 7.1% DW respectively at the beginning of the experiment with a protein: fibre ratio of 0.11. Nine weeks later, crude protein content in control plots was

significantly higher than those in the other two plots ($F_{1, 2} = 18.6$; $P < 0.01$; LSD $P < 0.05$) (Table 3).

(iii) *P. prostrata*. We did not have true replicates for *P. prostrata* so no statistical test can be provided. The pasture was 50% shorter in the grazed plots and the mean total biomass was 233.0 ± 58.5 g m^{-2} in the protected (total exclosure) plot, and 207.5 ± 12.5 g m^{-2} and 182.0 ± 14.0 g m^{-2} in the partially grazed (capybaras only) and control plots respectively. Fibre and crude protein contents were 65.8 and 8.41% DW at the beginning of the experiment. Pasture quality was similar to *R. acuta*, as inferred from a protein:fibre ratio of 0.12. After 9 wk no differences could be observed between treatments in fibre or crude protein contents. Fibre contents were almost identical among treatments (68.7% in total exclosure, 68.7% in partial exclosure and 68.5% in control plot) whereas crude protein contents were 0.10% (total exclosure), 0.10% (partial exclosure) and 0.09% (control).

DISCUSSION

Our observations confirmed previous findings (Herrera & Macdonald 1989) that capybaras are selective feeders, exhibiting distinct foraging patterns in relation to environmental variables. During the wet season an increase in available resources allows the animals to be more selective choosing the more profitable food items (in terms of protein and fibre content) as predicted by optimal foraging theory (see Pyke 1984). Indeed, capybaras almost ignored the reeds during this season as previously pointed out by Herrera & Macdonald (1989). Capybaras spent most of the time foraging in adjacent patches of the more profitable *H. amplexicaulis* with higher values of caloric and protein content and lower fibre content. Comparing *R. acuta* and *H. amplexicaulis* with an energetic content higher than that of reeds, we would expect animals to behave more selectively (lower effective feeding time) when foraging on more profitable items during a high availability period (wet season). Energetic content of both species did not differ but the effective feeding time was significantly lower in *H. amplexicaulis* (see Table 1). This result suggests that factors other than energy are being selected by the animals. In fact, both protein content and protein:fibre ratio were significantly higher in *H. amplexicaulis* as compared with *R. acuta* (protein: 10.31% vs 7.29 %; protein:fibre ratio: 0.16 vs 0.12). Capybaras were less selective when foraging the less (but not least) palatable *R. acuta*.

Conversely, during the dry season, when resource availability for herbivore decreases, greater but less-selective food intake is to be expected (see for example Hume 1989; Sibly 1981, 1986; Stephens & Krebs 1986, among others). Capybaras spent almost the same time foraging in patches of the lower quality reeds as in those of the grass *P. prostrata* with higher caloric content but with similar percentages of protein and fibre. In this case, protein and fibre content also may be more important than caloric content. Intriguingly, capybaras were more selective when foraging on reeds than on *P. prostrata* and the only explanation we

found for such a result is the fact that during dry season, reeds were found spread among water hyacinth stands so the animals had to walk more and take the reed shoots while rejecting the water hyacinth leaves. Our measure of selectivity might not take into account this effect. The harsh conditions during the dry season lead the animals to feed on even less profitable items, so during the severe drought of 1992, when most of the ponds dried up, we observed animals feeding on hyacinth stems, although rejecting their leaves.

Such results are predicted by the marginal value theorem of Charnov (1976). In accordance with this theorem, consumers will choose the more profitable items but they will include less profitable ones if the energy obtained from them is less than the average energy content of all available resources. Reeds (*E. interstincta*) are widely available but low quality resources, and capybaras fed on them during the dry season when overall availability was low. Similar results were reported by Owen-Smith (1994) in South Africa on kudus (*Tragelaphus strepsicerus*) which, during the driest months, consumed plant species of low protein content, including the less palatable deciduous ones. With the onset of the rainy season, as plant protein content increased, the animals favoured the more palatable evergreen species, though they had to travel longer distances (Owen-Smith 1994).

Grasses and reeds pose several limitations to herbivores that feed on them, such as high fibre contents, low nutritional levels and silica accumulations (Sibly 1986). A number of adaptations, other than behavioural ones, allow animals to live by feeding on a graminoid diet. These adaptations are both anatomical and morphological in kind (Hume 1989, Sibly 1981). Capybara teeth, for example, can reduce particle size to 0.001–0.3 mm, comparable to sizes reached in the rumen of ruminants (Ojasti 1973). The digestive efficiency of capybaras has also been found to be similar to that of ruminants (Gonzalez Jimenez 1977) and the presence of celulolitic microorganisms in the caecum has been reported (Borges *et al*. 1996). This makes capybaras the largest caecum fermenters in the world. Evidence for seasonal modifications of the length of the digestive tract has been found elsewhere (Borges 1993), which would allow capybaras to increase their food intake during the poorest months. In addition, coprophagy is practised by capybaras mainly during the dry season (Herrera 1985), possibly increasing nutrient intake. All of these adaptations and the behavioural features described here allow us to assert that capybaras behave as optimal consumers. This certainly plays a role in the capybaras' success in the flooded savannas of Venezuela, where they reach the highest population levels throughout their distribution range (Mones & Ojasti 1986, Ojasti 1991).

Do capybaras 'manage' their resources? Gordon & Lindsay (1990) proposed that as herbivores induce changes in the vegetation they feed on, positive changes to the herbivores could be expected depending on their foraging behaviour. Results from our exclosure experiment showed that capybaras produced the most important effects on the vegetation as both height and biomass in 'capybara plots' were similar to those in the control plots where other herbivores were

allowed to graze. They may also induce changes in the quality of the grasses as it was shown for the case of *R. acuta*. Moreover, it can be shown that capybaras can maintain available pastures in places where they forage. An adult capybara consumes *c*. 690 g dry weight of food daily (Ojasti 1973) and the daily primary production of *H. amplexicaulis* and *R. acuta* measured in the study area was 0.96 g m^{-2} d^{-1} and 0.60 g m^{-2} d^{-1} respectively (Barreto 1994). This means that an average of 10 animals in a group have to graze daily on a 0.7 ha stand of *H. amplexicaulis* or 1.2 ha of *R. acuta* to meet their needs and keep a sustainable level of primary production. Since the average group territory is 10 ha composed mostly of bajio vegetation (Herrera 1986), it can be expected that at least the area occupied by *H. amplexicaulis* stands within a territory exceeds the area required daily by a capybara group. Moreover, several observations suggest that a group tends to graze on different sites within its territory each day (Figure 1), and we have already noted that food quality tended to improve when grazed. Gordon & Lindsay (1990) suggested that resource management is likely to occur in social animals which exclude other herbivores. Capybaras are social animals that defend a territory (Herrera & Macdonald 1987) and no other natural grazer occurs in these savannas as white-tailed deer (*Odocoileus virginianus*) are mostly browsers (Ojasti 1983), and cattle, horses and donkeys are of recent introduction. Capybaras seem to match Gordon & Lindsay's (1990) hypothesis in the flooded savannas of Venezuela.

LITERATURE CITED

BARRETO, G. R. 1994. *Herbivoría en chigüires: un estudio de campo de las relaciones planta-animal*. MSc. Thesis, Universidad Simón Bolívar, Caracas.

BELSKY, A. J. 1986. Does herbivory benefit plants? A review of recent evidence. *American Naturalist* 127:870–892.

BELSKY, A. J., CARSON, W. P, JENSEN, C. L. & FOX, G. A. 1993. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* 7:109–121.

BORGES, P. A. 1993. *Ecofisiología digestiva del chigüire (Hydrochaeris hydrochaeris)*. Unpublished BSc. Thesis, Universidad Simón Bolívar, Caracas.

BORGES, P. A., DOMINGUEZ, M. G. & HERRERA, E. A. 1996. Digestive physiology of capybaras. *Journal of Comparative Physiology, B* 166:55–60.

CHARNOV, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9:129–136.

ESCOBAR, A. & GONZALEZ-JIMENEZ, E. 1976. Estudio de la competencia alimentaria de los herbívoros

mayores del llano inundable con especial referencia al chiguire (*Hydrochoerus hydrochaeris*). *Agronomía Tropical* 26:215–227.

GOERING, H. K. & VAN SOEST, P.J. 1970. *Forage fiber analysis* (*apparatus, reagents, procedures and some applications*). USDA Research Station. Agriculture Handbook No 379.

GONZALEZ-JIMENEZ, E. 1977. Digestive physiology and feeding of capybaras. Pp. 163–177 in Rechligl, M. (ed.) *Handbook series in nutrition and food*. CRC Press, Boca Raton.

GORDON, I. J. & LINDSAY, W. K. (1990). Could mammalian herbivores 'manage' their resources? *Oikos* 59:270–280.

HERRERA, E. A. 1985. Coprophagy in the capybara, *Hydrochaerus hydrochaeris*. *Journal of Zoology (London)* 207:616–619.

HERRERA, E. A. 1986. *The behavioural ecology of the capybara*, *Hydrochoerus hydrochaeris*. D.Phil. Thesis. University of Oxford, Oxford.

HERRERA, E. A. & MACDONALD, D. W. 1987. Group stability and the structure of a capybara population. *Symposia of the Zoological Society of London* 58:115–130.

HERRERA, E. A & MACDONALD, D. W. 1989. Resource utilization and territoriality in group-living capybaras (*Hydrochaerus Hydrochaeris*). *Journal of Animal Ecology* 58:667–679.

HERRERA, E. A. & MACDONALD, D. W. 1993. Aggression, dominance, and mating success among capybara males (*Hydrochaeris hydrochaeris*). *Behavioural Ecology* 4:114–119.

HILBERT, D. W., SWIFT, D. M., DETLING, J. K. & DYER, M. J. 1981. Relative growth rates and the grazing optimization hypothesis. *Oecologia* 51:14–18.

HOBBS, N. T. & SWIFT, D. M. 1988. Grazing in herds: when are nutritional benefits realized? *American Naturalist* 131:760–764.

HUME, I. D. 1989. Optimal digestive strategies in mammalian herbivores. *Physiological Zoology* 62:1145–1163.

KARBAN, R. & MYERS, J. H. 1989. Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* 20:331–348.

MACDONALD, D. W. 1981. Dwindling resources and the social behaviour of capybaras (*Hydrochaeris hydrochaeris*) (Mammalia). *Journal of Zoology* (London) 194:371–391.

MARTIN, P. R. & BATESON, P. P. 1993. *Measuring behaviour: an introductory guide*. (2nd edition). Cambridge University Press, Cambridge. UK. 222 pp.

MCNAUGHTON, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259–294.

MCNAUGHTON, S. J. 1993. Grasses and grazers, science and management. *Ecological Applications* 3:17–20.

MONES, A. & OJASTI, J. 1986. *Hydrochoerus hydrochaeris*. *Mammalian Species* 264:1–7.

OJASTI, J. 1973. *Estudio biológico del chigüire o capibara*. Fondo Nacional de Investigaciones Agropecuarias, Caracas.

OJASTI, J. 1983. Ungulates and large rodents of South America. Pp. 427–439 in Bourlière, F. (ed.). *Tropical savannas*. Elsevier, Amsterdam.

OJASTI, J. 1991. Human exploitation of capybara. Pp. 236–252 in Robinson, JG. & Redford, K.H. (eds). *Neotropical wildlife use and conservation*. University of Chicago Press, Chicago.

OWEN-SMITH, N. 1994. Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology* 75:1050–1062.

PYKE, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15:523–575.

PYKE, G. H., PULLIAM, H. R. & CHARNOV, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 2:137–154.

QUINTANA, R. D., MONGE, S. & MALVAREZ, A. I. 1994. Feeding habits of capybara (*Hydrochaeris hydrochaeris*) in afforestation areas of the Lower Delta of the Paraná River, Argentina. *Mammalia* 58:569–580.

RAMIA, M. 1974. Estudio ecológico del Módulo Experimental de Mantecal (Alto Apure). *Boletín de la Sociedad Venezolana de Ciencias Naturales* 31:117–142.

SARMIENTO, G. 1984. *The ecology of neotropical savannas*. Harvard University Press, Cambridge, Mass.

SCHALLER, G. B. & CRAWSHAW, P.G. 1981. Social dynamics of a capybara population. *Saugetierkundliche Mitteilungen* 29: 3–16.

SIBLY, R.M. 1981. Strategies of digestion and defecation. Pp. 109–139 in Townsend, C. R. & Calow, P. (eds). *Physiological ecology*. Blackwell Scientific Publications, Oxford, UK.

SIBLY, R. M. 1986. Feeding and digestion. Pp. 28–43 in Sibly, R. M. & Calow, P. (eds) *Physiological ecology of animals*. Blackwell Scientific Publications, Oxford, UK.

STEPHENS, D. W. & KREBS, J. R. 1986. *Foraging theory*. Princeton University Press, New Jersey.

YABER, M. C. & HERRERA, E. A. 1994. Vigilance, group size and social status in capybaras. *Animal Behaviour* 48:1301–1307.

YDENBERG, R. C. & PRINS, H. H. T. 1981. Spring grazing and the manipulation of food quality by barnacle geese. *Journal of Applied Ecology* 18:443–453.