



Resource Utilization and Territoriality in Group-Living Capybaras (*Hydrochoerus hydrochaeris*)

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RESOURCE UTILIZATION AND TERRITORIALITY
IN GROUP-LIVING CAPYBARAS
(*HYDROCHOERUS HYDROCHAERIS*)

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SUMMARY

(1) Groups of capybaras living in the seasonally flooded savannas of Venezuela showed seasonal shifts in habitat use in relation to changes in availability of favourable habitat (mainly grassland) caused by the alternation of drought and flooding.

(2) Group home-ranges were stable; certain activities (e.g. resting, grazing, wallowing) were largely restricted to specific localities within each range. Although groups fed on the most favourable ('grazing') habitat in relation to its availability, individuals fed for similar amounts of time in this habitat irrespective of its availability per head.

(3) Groups of capybaras were territorial. The small amount of overlap between neighbouring home-ranges corroborated observations of intruder rejection. Territory size varied between 5 and 16 ha (mean = 10.4 S.D. \pm 3.7 ha) and was positively correlated with group size.

(4) All home-ranges (with one exception) had a section of each of four major habitat types. Comparing home-ranges, the areas of two of these habitat types (bush scrub and low-lying grassy patches) correlated significantly with group size. Furthermore, the area of bushy scrub in each home-range correlated with the reproductive success of females occupying it. These two habitats are essential for survival in the dry season (grassy patches) and wet season (bushy scrub).

(5) Capybaras depend upon access to permanent surface water. Where there is such water, it appears that their territories are configured to encompass sufficient resources to ensure survival under widely different seasonal conditions. These results are discussed in relation to the pattern of availability and dispersion of the critical resources.

INTRODUCTION

Patterns in the availability and utilization of resources are important constraints on the social organization of mammals, e.g. primates (Crook & Gartlan 1966), antelopes (Jarman 1974), carnivores (Macdonald 1983). In particular, the temporal and spatial dispersion of their food and shelter, along with other factors such as predation pressure, affect whether it is advantageous to form groups. In this paper, we attempt to identify the ecological constraints imposed on the social organization of a population of capybaras (*Hydrochoerus hydrochaeris* L.), described in Azcarate (1981), Macdonald (1981), Herrera (1986) and Herrera & Macdonald (1987), using data on their spatial organization and habitat utilization.

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Capybaras, 50-kg caviomorph rodents, are semi-aquatic grazers. They are abundant in the seasonally flooded savannas (llanos) of Venezuela (Ojasti 1973), reaching overall population densities of 0.5 animals per ha, and up to 2 animals per ha locally (Mones & Ojasti 1986). They have anatomical and physiological adaptations to a herbivorous diet (Ojasti 1973; Gonzalez-Jimenez 1977; Herrera 1985). Water is an important resource for capybaras. It is used for drinking, for thermoregulation (wallowing) and for escape from predators. They invariably mate in water, and many of the plants on which they feed are aquatic (Azcarate 1981; Macdonald 1981; Schaller & Crawshaw 1981; Herrera 1985; Jorgenson 1986).

Capybaras breed throughout the year in the Llanos, but there is a marked peak in sexual activity at the beginning of the wet season, and in births at the height of the wet season (Ojasti 1973). Dry seasons in the Llanos are harsh (see below), and Ojasti (1978) found a high (up to 33%) and density-independent mortality of adults during this period; 'the demographic strategy of capybaras in the Llanos is to breed and grow in the wet season and survive the drought' (Ojasti 1983, p. 435).

In the population under study, capybaras live in stable groups of 4–40 individuals, including adults and young (Herrera & Macdonald 1987). At the height of the dry season, most of the groups form temporary aggregations of up to 100 animals around the receding waterholes, but subsequently these aggregations fragment into the original groups. During our study, groups retained their identity over at least 2 years, and intruders were rejected aggressively by all adult group members. A stable dominance hierarchy characterized relationships between males within groups (E. A. Herrera & D. W. Macdonald, unpublished). At least 50%, and up to 100%, of identified group members remained in the same group for at least 2 years, whereas most of the young dispersed when 1 year old, possibly in groups accompanied by a subordinate male (Herrera & Macdonald 1987).

STUDY AREA

This study was carried out on a ranch (Hato El Frio, 7°46'N, 68°57'W) in the low Llanos of Venezuela, a region characterized by tropical floodplain savannas (described in Herrera & Macdonald 1987). The alternation of dry (November–April) and wet (May–October) seasons, causes severe water shortage at the height of the dry season and extensive flooding in the wettest months. The region comprises three physiographic units: (i) esteros (ponds), most of which dry up completely in the dry season, but in the early wet season dense stands of *Hymenachne* spp. and other aquatic grasses grow in the shallows, replaced by reed (Cyperaceae) and other aquatic vegetation late in the wet season. (ii) bajios (up to 0.5 m higher than the esteros), areas that comprise c. 70% of the low llanos (Ramia 1974) and are covered with short highly palatable grasses (e.g. *Leersia hexandra* and *Panicum laxum*). Bajios flood in the wet season to depths of 10–120 cm: (iii) bancos (2 m higher than the esteros), areas with a vegetation cover of tall grasses (e.g. *Imperata contracta*, *Elyonurus tripsacoides*) or bushes (e.g. *Sida* spp., *Cassia* spp.), which are rarely flooded. The lower bancos, which are more prone to flooding, are characterized by the grasses, the highest ones by the bushes. Isolated patches of semi-deciduous woodland grow on some high bancos.

METHODS

Observations were made from March to August in 1982 and from March to October in 1983 and 1984. In February of each year, capybaras were captured from horse-back using a lasso or noose on a pole and marked for individual identification (ear tags and PVC collars, described in Herrera & Macdonald 1987). Detailed observations were made on four groups in 1982, and on seven groups in 1983, four of which were also observed in 1984. One group (P5) was studied in all 3 years. Groups were observed in rotation, in sessions of 2–12 hours, with pre-determined start and stop times, samples of similar sizes being drawn from each group for each hour between 07.00 and 19.00 hours. Behaviour patterns considered in this report are of 'state' type (i.e. of measurable duration) and were recorded using the scan sampling regime (Altmann 1974) at 10-minute intervals. Nine habitats were categorized, and each capybara in the focal group was scored as being in one of these when its behaviour was recorded during each scan.

A habitat map of the study area was prepared, using colour aerial photographs, to distinguish the distribution of major habitats (esteros, bajios, grassy and bushy bancos). The geometric centre of the focal group was plotted on this map (at an estimated accuracy of ± 25 m) during each 10-min scan. These data were used to estimate home-range size as defined by irregular polygons (allowing up to 45° concavity) configured to exclude areas never visited (or visited only when fleeing a predator) (Macdonald, Ball & Hough 1980). To facilitate comparisons with other studies, home-range sizes were also calculated by two other methods: (i) cumulative use of 50×50 m grid-cells (e.g. Voigt & Tinline 1980; Newdick 1983); (ii) convex polygon (e.g. Southwood 1966).

RESULTS

Habitat use

There were clear differences in habitat use as the seasons progressed (Fig. 1). Grouping monthly data into three seasons—dry (March), early wet (April–June), late wet (July–August)—a *G*-test showed that the differences in habitat use with seasons were significant ($G = 381.8$, $P < 0.001$, d.f. = 5 for 1982; $G = 857.0$, $P < 0.001$, d.f. = 5 for 1983). Capybaras fed on bajios throughout the year, although they spent less time in this habitat as it became more deeply flooded late in the wet season (July–August). Bancos were virtually unused until the peak of the rains, when they became the only dry land available. Aquatic grasses were eaten mostly during the mid-wet season, before they were replaced in the habitat by less palatable reeds (Cyperaceae, *Eleocharis* spp.), water hyacinth (Pontederiaceae, *Eichhornia* spp.) and other aquatic vegetation. Differences in the relative use of 'bajio' and 'dry reed' in the dry seasons of 1982 and 1983 are shown in Fig. 1. These arose because flooded bajios were more extensively covered by reed in the wet season of 1982 (which formed a blanket of dry reed in the following dry season).

These seasonal shifts in habitat did not involve migratory movements. On the contrary, in their search for dry land in the wet season, capybaras rarely moved their centre of activity more than 300 m from their dry season wallow. Furthermore, at the height of the wet season, capybaras were seen to select individual blades of grass from amongst a sward of less nutritious reed (Cyperaceae, *Eleocharis* spp.).

Habitat use followed a daily pattern, as indicated by the percentage of animals engaged in given activities in each habitat for each hour of the day (data pooled for all groups). Bajio was used for resting in the early morning (07.00–09.00 h, 41–51%), avoided at midday (11.00–15.00 h, maximum 26%) and grazed in the evening (18.00–19.00 h,

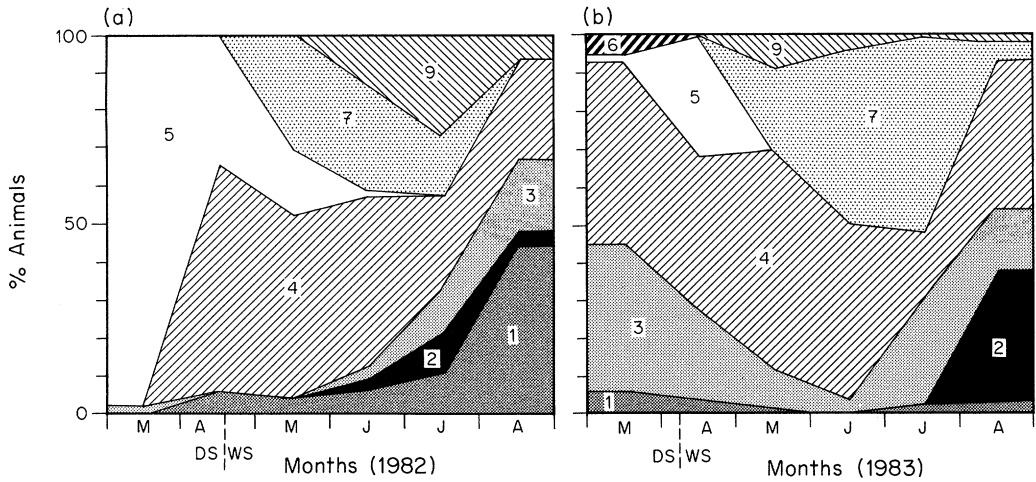


FIG. 1. Proportion of feeding time spent in each of nine major habitats by capybaras. Data from all groups combined. Habitats numbered as follows: 1, bushy banco; 2, grassy banco; 3, ecotone banco/bajio; 4, bajio; 5, dry reed; 6, dry lagoon bed; 7, aquatic grass; 8, pond with no vegetation; 9, water hyacinth and other aquatic vegetation.

53–59%). Ponds were used principally for wallowing, especially around midday (12.00–16.00 h, 34–46%) and were avoided in the mornings and evenings (07.00–09.00 h and 18.00–19.00 h, maximum (6%). Bush banco was used largely for resting in the morning (before 10.00 h, maximum 22%; other times of day, for any activity, maximum 7%). These findings corroborate those of Azcarate (1981) and Macdonald (1981).

Home range: utilization and configuration

A schematic map of the study area (see Fig. 2) shows the utilization distributions (as contour plots) for the home-ranges of groups observed in 1983. Some groups show a bi- or multi-modal distribution of utilization scores (e.g. C1 and VQ in 1983), whereas for others the distribution is more uniform (e.g. NC in 1983). All home-ranges encompassed at least part of a pond or ponds, and in all cases their configurations either expanded radially around the pond or extended longitudinally along the shore to include one or more patches of grazing habitat. The multi-modal pattern of utilization arose where ponds, bajios and bancos were separated, the uni-modal pattern where they were adjacent. In the former cases, most peaks were associated with a specific activity (e.g. the western peak of P5's range corresponded, in all 3 years, to their resting and wallowing area, while the eastern peak was their grazing patch). Groups with a uni-modal utilization distribution grazed more or less evenly around their wallows.

Most of the groups that were observed systematically for more than 1 year showed great constancy in the location and configuration of their home-ranges (e.g. Fig. 2, group P5, the only change in 3 years being a north-westward expansion of about 100 m in 1984, concomitant with a similar contraction to the east; groups NC, VQ and C2 used much the same areas in 1983 and 1984). The only known exception to this general result was a group of twenty-three animals observed in 1982 (not illustrated here) which used the eastern end of the study area until the beginning of the rains, and then moved *en masse* about 800 m to the east (approximately twice the average home-range width), before settling temporarily (4 weeks) prior to emigrating altogether from the study area and environs.

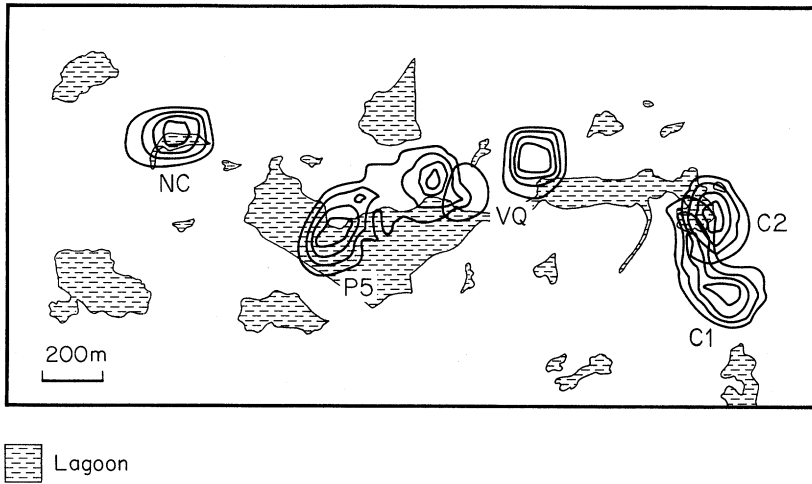


FIG. 2. Contour plots of intensity of use for capybara groups observed in 1983. Intensity of use is a relative measure obtained by dividing the number of visits to each 50 × 50 cm cell by the number of visits to the most frequently visited cell. Contours are spaced in 0.2 stages (innermost is 0.8). Environmental features shown are all boundaries of ponds and small streams as they look in the early wet season before extensive flooding.

Home range: area, group size, reproduction and habitat

Home-ranges, measured as irregular polygons (IP), varied in size between 5 and 16.3 ha. The average home-range measured $10.4 \text{ SD} \pm 3.7$ ha, comprising 1.8 ± 1.3 ha of pond, 6.6 ± 2.3 ha of bajio, 0.6 ± 0.4 ha of grassy banco and 1.3 ± 0.9 ha of bushy banco. The data were sufficiently abundant (14000 locations) and the pattern of the capybaras' movements sufficiently clear to give confidence that these irregular polygons were accurate representations of their home ranges. The grid-cell (GC) and convex polygon

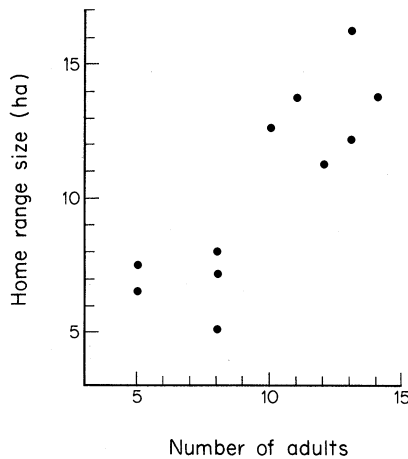


FIG. 3. Correlation between home-range size (ha) and number of adults in the group. Data from all years.

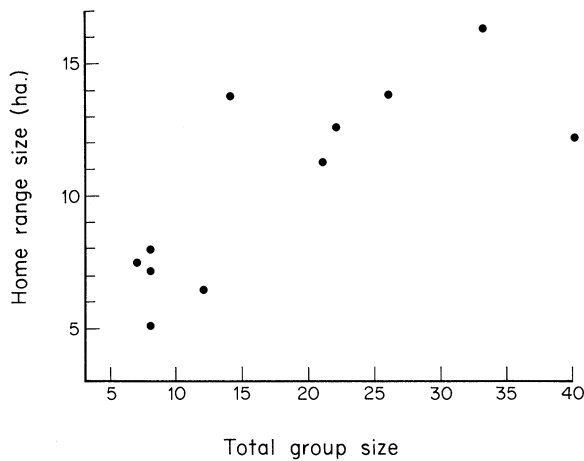


FIG. 4. Correlation between home-range size (ha) and total group size (i.e. adults plus young). Data from all years.

(CP) methods gave significantly larger estimates of home-range size than that of irregular polygons (IP) (mean GC = 18.8 ± 5.4 ha, $t = 4.44$, $P < 0.001$; mean CP = 16.1 ± 5.6 ha, $t = 2.93$, $P < 0.01$) but did not differ significantly themselves ($t = 1.19$, $P = 0.25$). Grid-cell and CP area estimates were strongly influenced by peripheral locations (Don & Rennolls 1983). Furthermore, both tended manifestly to over-estimate range sizes, the GC method being flawed by the effect of grid-cell size, the CP method by its inclusion of areas not used by the subjects (Macdonald, Ball & Hough 1980).

Home-range size was correlated significantly with both the number of adults in the group and the total group size (Figs 3, 4). (for adults only: $r_s = 0.820$, $P < 0.01$, $n = 11$; for

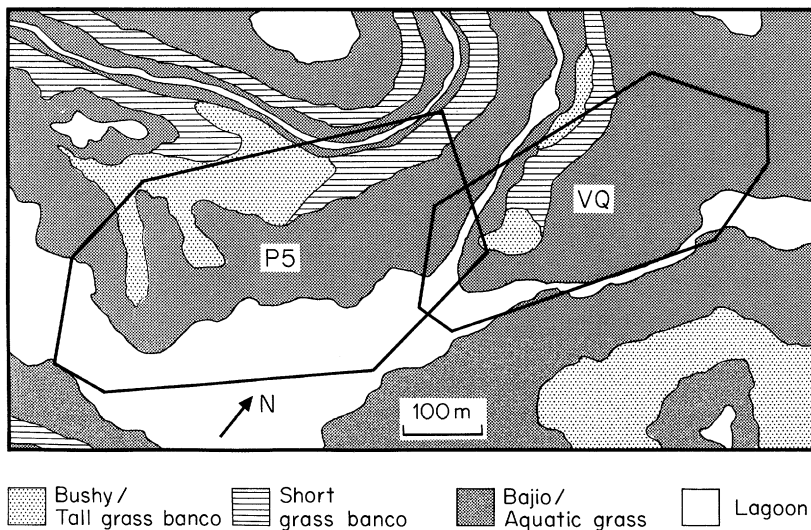


FIG. 5. Boundaries of home-ranges of two primary groups (P5 and VQ in 1983) drawn on the habitat map of the study area. Four habitat types are represented.

total group size: $r_s = 0.743$, $P < 0.01$, $n = 11$), i.e. larger groups occupied larger home-ranges. Was this trend related to the habitat composition of the home ranges? All habitat types were present in all home-ranges, apart from the absence of bushy banco from the home-range of group C1 in 1983 (Fig. 5). The areas of bushy banco and, to a lesser extent, bajio correlated significantly with the number of adults in the group, and with total group size (Table 1), i.e. larger home-ranges had greater areas of bushy banco and bajio. The total area of bushy banco in each home-range was also highly correlated with the number of young surviving per female ($r_s = 0.886$, $n = 6$, $P = 0.05$). The only group which had no bushy banco in its home-range was the only group that produced no surviving young throughout the study. In this context, female reproductive success was also correlated with adult group size ($r_s = 0.9$, $n = 6$, $P < 0.05$, see Herrera & Macdonald 1987), whereas the association between female reproductive success and home-range size falls just short of significance ($r_s = 0.886$, $n = 6$, N.S.).

Areas of bajio and grassy ponds supported the most palatable and productive grasses (Escobar & Gonzalez-Jimenez 1979) and can be combined as 'grazing' habitat. The percentage of each group's feeding time spent in these grazing habitats increased with the relative availability of these habitats in their home-range ($r_s = 0.636$, $n = 11$, $P < 0.05$). However, the area of grazing habitats tends to be greater in larger ranges, as does group size (see above), and there is no correlation between the proportion of each group's feeding time spent on grazing habitats and the area of these habitats available per head within the group ($r_s = -0.109$, N.S., $n = 11$), i.e. capybaras grazed on the most nutritious grasses for a similar proportion of their time (c. 70%) irrespective of their availability.

Territoriality

Attacks by group members on non-members have been described elsewhere for capybaras (Herrera & Macdonald 1987). Such observations suggest a territorial organization and this is further corroborated in our present study by the spatial arrangement of home-ranges. During 1983 and 1984, regular records were kept of the locations of all identifiable groups. The dispersion of group ranges is given in Fig. 6, together with the more accurately delineated ranges of focal groups. These maps show: (i) minimal overlap (equivalent to less than 10% of average home-range size) between neighbouring home ranges (mean area of overlap = 0.81 ± 0.70 ha; percentage overlap = 0–29.3%); (ii) an effectively contiguous blanket of home-ranges throughout the study area; and (iii) no evidence of new groups establishing themselves.

Two pairs of groups departed from the general pattern of non-overlapping ranges: (i) groups P5 and VQ in 1984 (17.2% overlap of VQ range). Both groups extended their ranges to the west during the prolonged dry period of 1984, when surface water in the

TABLE 1. Spearman rank correlation coefficients between the area covered by each major habitat type in the home-ranges and two measures of group size: Adults only and total. $n = 11$ in all cases

Variable	Bajio	Short grassy banco	Bushy banco	Pond
Number of adults	0.668*	0.539	0.866***	0.498
Group size	0.615*	0.569	0.826**	0.569

* $P < 0.05$.

** $P < 0.01$.

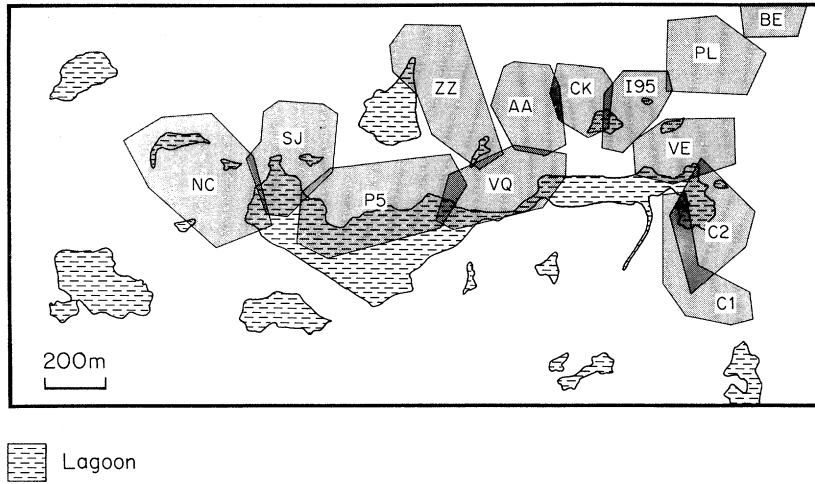


FIG. 6. Approximate boundaries of home-ranges of all groups using the study area in 1983. All features delineated are ponds and streams. The southern part of the central pond was also inhabited by capybara groups but they were inaccessible to study.

Central Pond was limited to its westernmost tip. Interpretation of cause and effect is complicated by the partial take-over of group P5's home-range by VQ, following the defeat of members of P5 during territorial encounters with members of group VQ in 1984 (detailed in Herrera 1986); (ii) groups C1 and C2 in 1983–84 (e.g. 29.3% of C1 range in 1983 and 27.9% of C2 in 1983). Almost every evening members of C1 crossed part of C2's range *en route* between their wallow and their main grazing patch to the south. Travelling swiftly, members of C1 crossed the overlap zone without eliciting the aggression which otherwise characterized their encounters with members of C2.

DISCUSSION

The shape, size and location of the home-ranges emphasize the importance of a permanent waterhole for the capybaras' survival and reproduction. Activity centres were always located close to water and distances from the main grazing patches to the nearest pond were never greater than 300 m. In consequence, the home-ranges of these groups of capybaras were small compared with those of other tropical herbivores of similar size (cf. Eisenberg 1981, Fig. 47). For instance, both the density and biomass of capybaras within an average home-range were roughly ten times greater than those of the Bohor reedbeek (*Redunca redunca*, Hendrichs 1975), perhaps the closest equivalent of capybaras in terms of size (36–50 kg) and habits (a grazing herbivore of tropical marshes in Africa). Escobar & Gonzalez-Jimenez (1979) found that grassy ponds and flooded bajios have the highest primary productivity of the habitats in these savannas, and several authors have pointed out that *Leersia hexandra* and the *Hymenachne* species typical of these habitats are nutritious for grazers and predominate in the capybaras' diet (Ramia 1974; Escobar & Gonzalez-Jimenez 1976a). The llanos receive over twice the rainfall (1600 mm) of the African plains (750 mm in the wettest section of the Serengeti plains). Furthermore, in the llanos, the only potential native competitor is the white-tailed deer, *Odocoileus virginianus* Zimmerman 1771, which is more of a browser than a grazer (Ojasti 1981). Introduced

grazing stock do not seem to compete with capybara (Escobar & Gonzalez-Jimenez 1976b). In contrast, in the African savannas, there are as many as ten sympatric species of grazing antelope (Jarman & Sinclair 1979). The semi-aquatic habits of capybaras confine them to the vicinity of water and thus to the most productive habitat of the llanos, thereby restricting their distribution while facilitating their relatively high population densities. The density in those parts of the llanos further than 300 m from waterholes falls to almost zero.

The home-range sizes, varying between 6 and 16 ha, observed in this study, are similar to those found by Azcarate (1981) and Macdonald (1981), for the same population. Schaller & Crawshaw (1981), however, found home-range sizes (CP) for capybaras in the Brazilian Pantanal of up to 200 ha and a minimum of 12 ha. In the same habitat, Alho, Campos & Gonclaves (1987a) record home-ranges of *c.* 33–196 ha (mean 78.9 ha). Alho, Campos & Gonclaves (1987b) also mention 'core areas' of *c.* 3–50 ha (mean 9.4 ha) of home-ranges in this habitat. These descriptions of the habitat in the Pantanal suggest that it is less productive than that of the llanos (and the average population density is markedly lower at 0.14 capybaras per ha).

Despite major seasonal shifts in the dispersion of water bodies and grazing areas, capybaras did not substantially alter the size or juxtaposition of their home-ranges between years, in contrast to the large-scale movements of some of the other tropical, mammalian grazers living in seasonal regions (e.g. Leuthold 1977; Maddock 1979). We conclude that capybara home-ranges encompass sufficient resources to ensure survival under widely different seasonal conditions. However, the pattern of habitat utilization by capybaras follows the availability of water, grasses and dry land as the seasons progress. Bajios are used in the dry and early-wet seasons, while the aquatic grasses are used as they begin to grow in the mid-wet season. Deep flooding and displacement of the best grasses by reed and water hyacinth force the animals up to the higher, bushier bancos at the end of the wet season.

It can be seen from Fig. 6 that the home-ranges of capybaras are territorially organized, a conclusion further supported by observations of the expulsion of intruders (Herrera & Macdonald 1987). Analyses of territory economics (e.g. Brown 1964; Davies 1978) have shown that, for territoriality to evolve, there must be some critical resource that makes a territory economically defensible, i.e. the costs of defence are lower than the benefits thereby obtained. Typically, large gregarious grazers are non-territorial or seasonal territorial behaviour is displayed by males only (e.g. Leuthold 1977). This is because an evenly distributed, low quality and widely available resource, such as grass in a tropical savanna, is not economically defensible (Jarman 1974). As capybaras are grazers of open areas, the question arises: which features of the capybaras' circumstances in the llanos promote formation of groups and maintenance of territories?

In capybaras, defence from predators is likely to be an important factor favouring grouping (Macdonald 1981; Herrera & Macdonald 1987). A different, but not incompatible, suggestion is that aggregation by herbivores might help maintain a high quality and quantity of forage (McNaughton 1984). This suggestion is based on the controversial premise that grazing stimulates grass growth and quality (for the arguments against, see Belsky 1986). However, in favour of McNaughton's proposal, Ojasti (1978) found a slight increase in primary production at a density of 1.6 capybaras per ha compared with ungrazed control areas.

In our study area, we have shown that each home-range included patches of each major habitat type, including a water body. However, in the low llanos of Venezuela, there are

vast expanses of bajio without permanent surface water, and these are invariably devoid of capybaras. Around waterholes big enough to retain water well into the dry season (as in our study area) capybara territories cover contiguously the land available (Fig. 6). Thus, it appears that grazing patches next to waterhole(s) are economically defensible for capybaras in the llanos. As all other habitat types (those within bancos and bajios) can exist in the absence of waterholes, it appears that the waterhole is the key resource that makes a territory defensible.

The components of a territory necessary to sustain even one capybara throughout the changing seasons are (i) bushy banco (for food and harbourage during the height of the wet season), (ii) pond (for drinking water, thermoregulation, mating and sanctuary from predators during the dry season) and (iii) bajio (for grazing during the peak of the dry season). The size and shape of an economically defensible territory (*sensu* Brown 1964) with these minimal requirements will be determined by the dispersion of these three resources. In such a minimum territory (*sensu* Carr & Macdonald 1986), i.e. one that supports the requirements of a minimal social unit (in this case we have never seen stable groups smaller than three adults), the resource patches may be sufficiently rich to support a larger group. In so far as group size is determined by resource availability (as opposed to, for example, predation or disease), it will be limited by whichever was the most limited of the three critical resources (the 'narrowest' of the 'bottlenecks'), banco, bajio or pond. In our groups, over 3 years, the close correlation between adult group size and area of bushy banco indicates that this is a limiting resource. The failure to rear young by the one group whose territory had no bushy banco probably indicates that the dry ground provided by this habitat is a prerequisite for the survival of new born young. It is also plausible that, having survived the wet season, the subsequent survival of young is affected by the availability of dry season grazing; but our sample is insufficient to test this.

In these circumstances, territory size and group size might be determined independently, and respectively, by the dispersion and abundance ('richness') of available resources, a possibility described by the Resource Dispersion Hypothesis (see Macdonald 1983; Carr & Macdonald 1986), which has been applied to various group-living mammals (e.g. Bradbury & Vehrencamp 1976; Kruuk & Parish 1982; Mills 1982). In minimum territories, the relationship between group size and territory size could be explained solely by a correlation between patch dispersion and patch richness, e.g. if territories sufficiently large to encompass widely spaced ponds and/or bajios in the dry season automatically encompassed additional banco for the wet season (Hypothesis 1). In this case, the *dispersion* of one (or two) critical resources in one season would be correlated with the *richness* of the third critical resource (in this case, the bottleneck) in the other season. The observation that larger territories are apparently configured to embrace two ponds, and thereby acquire additional intervening banco (and bajio), is compatible with this suggestion.

If the territories are larger than the minimum needed to sustain the basic social unit, the capybaras would meet the definition of expansionists (*sensu* Kruuk & Macdonald 1985). Expansionism (Hypothesis 2) is a successful strategy when the advantages of larger group size outweigh the costs of maintaining the increased area of territory necessary to support the additional group members (interaction of such costs and benefits are discussed in Macdonald & Carr 1989). We have no direct evidence that larger groups are able to oust smaller ones; there are several putative advantages to membership of larger groups (e.g. increased vigilance, defence against predators, opportunity for allomaternal behaviour) and a proven association between group size and female reproductive success

(Macdonald 1981; Herrera 1986; Herrera & Macdonald 1987). This association may arise from either one or both of the sociological corollaries of larger group size (e.g. defence against predators) and from the ecological corollaries (e.g. larger groups are sustained by, or can commandeer, larger and thus higher quality territories which favour survival of young).

There are, however, intermediate explanations which take into account the annual variation in the severity of the alternating floods and droughts and the costs of adjusting territory size to such fluctuating resource availability, which are likely to be high (as emphasized by von Schantz 1984, see also Carr & Macdonald 1986). For example, territorial configuration of capybaras could be adapted to the worst conditions likely to occur over a number of years. In the mild, intervening years, the capybaras resist the pressure to contract their borders because of the costs of such a short-term strategy (e.g. territorial clashes in the subsequent expansion in the next severe year). Furthermore, precipitous re-adjustment of territorial borders would forestall any opportunity of benefiting from the larger group sizes that might develop on the additional resources (e.g. slightly lower banco that is not submerged, slightly shallower ponds that are not evaporated to dryness). Only in exceptionally wet or dry years, when the resource bottleneck patches are at their 'narrowest', would the group size drop to its minimum level, thereby possibly destroying the correlation (notwithstanding Hypothesis I) that would otherwise generally hold between group size and home-range size.

These hypotheses yield testable predictions. For example, the existence of minimum (contractionist, *sensu* Kruuk & Macdonald 1985) territories could be explored by a manipulation of patches and group sizes. Removal of patches that were bottle necks would make a minimum territory inviable, whereas the addition of new patches would cause it to shrink (the enrichment or impoverishment of existing bottleneck patches would lead, respectively, to increase or decrease in group size). A complementary approach could arise from the annual harvest of capybaras in the llanos (our population was protected by a moratorium between 1982 and 1984). The cull, or experiment, would alter the relative sizes of neighbouring groups; expansionist tactics would lead to groups with more survivors increasing their territory at the expense of their neighbours. In contrast, pure contractionists would not expand their minimum territories even if their neighbours were removed (as in Cheeseman's observations of badgers, *Meles meles*, cited in Kruuk & Macdonald 1985).

In practice, the erratic and seasonally shifting fragmentation of habitat patches, their variable juxtaposition and the likely involvement of confounding variables complicate such experiments. Nonetheless, the feasibility of manipulating resources by fencing, damming and draining in the llanos, and of manipulating the cull, combined with the fact that the results could have agronomic implications for capybara ranching (see Ojasti 1978), should encourage such experiments.

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