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Group stability and the structure of a capybara population

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Synopsis

A capybara population in the seasonally flooded savannas of Venezuela was found to be structured in groups of five to 14 adult individuals of both sexes, with a socionomic sex ratio biased towards females (♀:♂ = 1.7:1.0, $N = 16$), and a variable number of young (range 0–68% of group membership). Although such groups amalgamated during the dry season, they appeared to be of closed membership, and remained stable in size and composition for two or more years. Social integrity of groups was maintained by territorial aggressive behaviour exhibited by all adult group members against intruders.

Although some groups produced many young, these were rarely recruited as adults into their parental group. There was no support for the hypothesis that groups develop from a breeding pair. However, we present circumstantial evidence that yearling subadults disperse together from their natal group in the company of a subordinate adult male. Favourable habitat was saturated with capybara groups, therefore such dispersing, incipient groups probably had little chance of successful establishment, with the probable result that subadult mortality was high.

The importance of group living in capybaras is discussed with reference to the distribution of essential resources and the reproductive success of females.

Introduction

The social behaviour and grouping patterns of individuals of any species have a strong influence on the structure and dynamics of their population (e.g. Dunbar 1985: Łomnicki 1978). Thus, the mating system, mechanisms of dispersal and other elements of a species' social system will affect each individual's survival and reproduction. The aggregate outcomes of these

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individual life histories will determine population parameters such as density and growth rate. In this paper, we present data on the grouping patterns of capybaras (*Hydrochoerus hydrochaeris*) in the seasonally flooded savannas of Venezuela, and discuss the relevance of those patterns for the structure of the population at large. Details of the social relationships within groups, which may also be relevant to population structure, are discussed elsewhere (Herrera 1986).

Capybaras are caviomorph rodents of up to 50 kg in weight which feed mainly by grazing (Escobar & Gonzalez-Jimenez 1976). They are abundant in the northern neotropical savannas, where they live in groups, invariably associated with water (Macdonald 1981; Schaller & Crawshaw 1981). In the study area, most of the matings occur at the beginning of the wet season and the young—on average four per female—are born five months later. A general account of capybara biology is given in Herrera & Macdonald (1984), and the population dynamics are described by Ojasti (1973).

The data reported here come from our three-year study of capybara social behaviour and ecology (Herrera 1986). Our study has shown that the groups of capybaras in the Llanos are constructed of a dominant male, several females and young, and one or more subordinate males. Among the males there is a social hierarchy, one consequence of which is that each dominant male mates more often than any of the subordinates in his group. The relationships between females are less well understood since females interact very little with each other.

In our study area the mean size of groups of capybaras in the dry season was 10.9, but this figure embraces some significantly smaller groups in areas that were artificially irrigated (mean group size = 7.8) and larger groups in areas which dried up naturally (mean group size = 18.6) (Macdonald 1981). The same factors may underlie a similar seasonal difference: small groups are typical of the wet season, but some large groups of up to 60 members can be found in the dry season (Ojasti 1973). In addition to seasonal and local variations in mean group sizes, up to 7% of individuals appear to be solitary (Macdonald 1981).

Hitherto, nothing has been known of the stability or social dynamics of groups of capybara in either the short or the long term. In seeking to determine how stable and cohesive are groups of capybaras in the Llanos, we ask how groups relate to one another, how groups are formed and whether group size affects the reproductive success of females. We also discuss the ecological factors that may underlie the social organization observed and, more specifically, we ask whether the larger dry-season groups are actually aggregations of smaller wet-season groups and, if so, whether they fall into their original component units when they subsequently fragment again.

Study area

We carried out our study on a cattle ranch, Hato El Frio (7° 46′ N, 68°57′ W), located in the low Llanos region of Venezuela. This area consists of tropical savannas, i.e. vast flat plains dominated by grasses (Sarmiento 1984), and its climate is dominated by a marked wet/dry seasonality. The wet season lasts approximately from May to October, the dry season from November to April. In the late dry season (February and March), evaporation from surface water reaches a rate of 1 cm per day, with the result that most lakes and ponds dry up, leaving a parched landscape. The wet season receives 90% of the annual average rainfall of 1600 mm, leading to extensive flooding over most of the savanna. In this habitat, Ojasti (1978) found a high (up to 30%) density-independent adult mortality of capybaras due to starvation. Capybaras may also starve during the wet season if the flooding is unusually severe. In a later review, Ojasti (1983:435) concluded that 'the demographic strategy of a capybara in the Llanos region is to breed and grow in the rainy season and survive the drought'.

Methods

The behaviour of individual capybaras was studied from March to October in 1982, 1983 and 1984. To achieve this, it was necessary to capture and mark animals. This was done with the help of cowboys (llaneros) in February of each year. The most successful method of marking involved a combination of expanding Darvic PVC (ICI) collars (designed by Fiona Guinness, see Clutton-Brock, Guinness & Albon 1982), painted with unique combinations of two letters, and coloured plastic eartags (Dalton Supplies, Nettlebed).

Capybaras were observed by means of 10×22 binoculars or a 60mm telescope, and their behaviour was recorded according to both the scan (10 min intervals) and instantaneous sampling regimes (Altmann 1974). Animals were classified into four age groups (infants, juveniles, sub-adults and adults) on the basis of size, and each class was aged on the assumption that most individuals were born during September and October at the end of the wet season.

Results

Five groups were observed in detail during 1983 and 1984, and one of these (P5) was also observed in 1982. The numbers of animals present in each group were scored at each scan throughout every observation session. The analyses of group size and group stability were decoupled in so far as data on both marked and unmarked animals were used in the former, whereas only data on marked individuals could be used for the latter.

Group stability

Table 1 presents examples of the pattern of presence and absence of marked individuals across observation sessions for two groups in 1983. It can be seen that some animals were present repeatedly throughout the study period while others were seen only rarely (once or twice). The pattern observed is caused by factors of both biological and methodological origin. Capybara groups generally moved and rested as a cohesive unit; in these circumstances it was straightforward to note which animals were 'in' the group. It was not uncommon, however, for a group to be more scattered; for example, one or a few animals might lag behind, sometimes for several hours. There were also occasions when animals from neighbouring groups strayed so close together that members of one might mistakenly be recorded as members of the other. Despite these sources of confusion, the recurrent presence of a cadre of animals in each group (and the fact that these individuals were never seen in other groups) demonstrates the existence of a social cohesion among group members. The behaviour of animals towards each other provided a further clue to membership of groups. As will be shown below, group members aggressively reject intruders. So, individuals were recorded as group members (as indicated on Table 1) on the grounds that they were frequently present and generally tolerated.

It should be noted, nonetheless, that the presence of group members was less consistent in the dry season: until the rains started in mid-April, there appeared to be more members absent and more non-members present. This was due in part to the difficulty of defining groups when they had coalesced into the larger, and sometimes rather diffuse, aggregations typical of that season (see below). We conclude that capybara groups are stable social units during one year, but that at a given moment a minority of animals may be more or less loosely affiliated with the group.

Group size

Group size and composition appeared to vary, but prolonged observation revealed that this was largely caused by animals moving into and out of view (cf. Aldrich Blake 1970). Over several hours all of the marked animals present would be seen, even if they were never all in sight simultaneously. The number of unmarked animals was estimated from the proportion of those marked individuals known to be present that were in sight on average; assuming that marked and unmarked animals were equally likely to be in view, the total group size could be estimated from the number in sight. Since both the confounding variables (absentee members and interloping non-

Table 1. Presence of identified individuals in all systematic observation sessions in 1983 (dates across the top) of (a) group C2 and (b) group NC. An X means presence, blank absence. The last column indicates whether each individual is considered a member (Y) of the group or not (N).

(a) Date of observation session

Age/sex and status[a]	Identity code	Mar	Apr				May				June						July		Aug		Member of group
		29	6	14	20	25	7	10	17	31	3	16	20	21	24	28	9	10	11	19	
DM	OJA				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	Y
F	OXH	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	Y
F	OXB				X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	Y
F	OVN	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	Y
M	OHX				X	X		X	X	X	X		X							X	Y
M	OHD				X	X	X	X	X	X			X							X	Y
M	M14							?	X	X		X	X	X	X	X					Y
F	YCZ							X													N
M	OJX	X	X	X						X											N
M	OEL					X															N
M	WNT		X																		N

(b) Date of observation session

Age/sex and status[a]	Identity code	Mar	Apr			May				June					July	Aug		Sept		Oct	Member of group
		23	4	8	21	6	10	18	24	1	2	17	23	27	1	9	25	9	23	7	
DM	R15	X	X	X	X	X	X	X	X		X	X	X	X		X	X	X		X	Y
F	YCC	X	X	X		X	X	X	X	X	X	X	X		X	X	X	X			Y
F	YBV				X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	Y
F	YED	X	X			X	X	X	X		X	X	X	X		X		X			Y
F	YCH			X		X	X	X	X			X	X			X		X	X		Y
F	YVI					X	X	X	X		X	X	X	X		X	X	X	X		Y
M	WTE		X	X	X	X	X	X	X	X	X	X	X	X	X		X	X		X	Y
M	WNA	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	Y
M	1DG						X		X			X	X	X	X		X	X			Y
M	WPT	X	X	X																	N
M	WLH		X																		N
M	WNH		X																		N
F	YVA	X																			N
F	YDN				X																N
M	WNT			X																	N

[a] DM, dominant male; F, adult female; M, adult male.

members) proved to be rare events, we may expect the estimated group sizes to be accurate.

Figure 1 shows a histogram of the numbers of adults in 16 groups. In this histogram, for those groups that were seen for more than one field season, only the first year is used, since the values of one year and the next are not independent. This sample gives a mean group size of 9.6 (± 3.8), with an average composition of 3.6 males (± 1.8) and 6.1 females (± 2.4), giving a socionomic sex ratio of 1.7:1.0 (female:male). Including juveniles, the mean group size is 14.0 (± 9.9) with juveniles contributing 0–68% of group membership (0–27 individuals). These figures do not include solitary individuals or pairs and may therefore be biased towards the more stable social situations (see below).

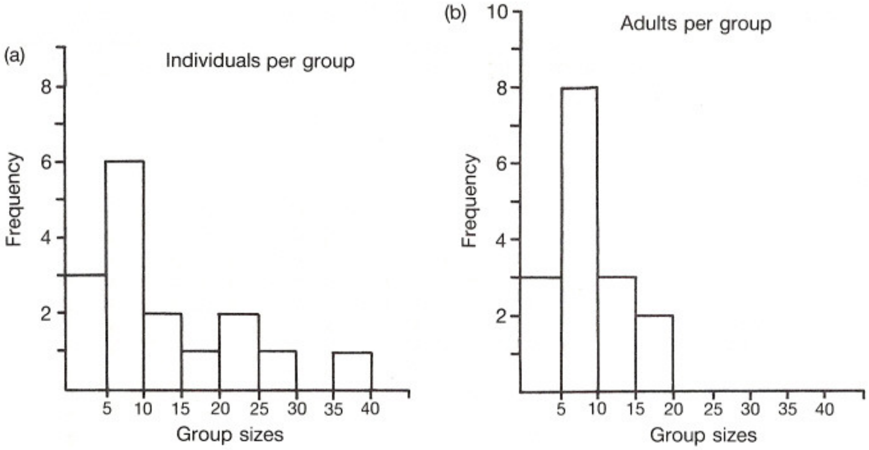

Fig. 1. Histograms showing the distributions of the sizes of (a) 16 capybara groups and (b) the numbers of adults in these groups.

Jarman (1982) has pointed out that the commonly used mean for group size may not represent the group size that the average animal experiences. He proposes the formula:

$$\bar{g} = \frac{\sum_{i=1}^{n} g_i^2}{\sum_{i=1}^{n} g_i}$$

where g represents group sizes and n, number of groups. This formula indicated that the average female capybara is found in a group of 7.0 females, the average male in a group of 4.4 males, and young among 17.8 of their contemporaries.

The histogram in Fig. 1 indicates that sizes of capybara groups vary from four to 16 individuals with a peak at eight and a long tail towards the larger groups. These features are consistent with the interpretation that there is a threshold size below which a group is not advantageous, while to be in a large group has fewer disadvantages than being in one that is smaller than this threshold or in no group at all (see Sibly 1983).

Interannual group stability

Because of the difficulties in determining group membership described above, and because collars were so often shed between field seasons, the structures of only five groups could be accurately determined in two successive years. Diagrams of these structures for all five groups in 1983 and 1984 are given in Tables 2a–e. These show that many, and probably most, adult capybaras remained in the same group from year to year. In the five groups shown in Table 2a–e, five out of 11 males marked in 1983 (excluding the dominants of each group) and nine out of 19 females were still present in 1984. There was no indication from these data of any difference between the sexes in terms of tendency to stay or disappear ($\chi^2 = 0.001$, *d.f.* = 1, N.S.).

It is unlikely that all the adults which disappeared also died. Thorough searches of the study area, combined with field signs such as circling vultures, led to the discovery of many corpses but few of the missing marked animals were among them. The likely provenances of some of the adults first marked in 1984 (Table 2) were determined on the basis of their size and appearance. If an animal was a young adult, it was listed as a possible recruit from that group's young of the previous year. If its size and appearance indicated that it was older than 1.5 years, it could have been either an immigrant or an unmarked animal from the previous year. From Table 2a–e it is clear that there must be some immigration of adults, since some animals could not have been either recruits from the previous year's young or previously (i.e. 1983) unmarked members of that group. However, of 858 animals marked over the three years, we never saw one case of an adult member of one group transferring permanently to another group within the study area. These newcomers were, therefore, probably immigrants from outside the study area. One female (YCA: Table 2d) was seen some 5 km south of the study area two weeks before she was first seen in Group P5. Two other females were observed to leave their groups. Thereafter they were both found alone, or occasionally accompanied by a male and occupying small home ranges next to those of their former groups.

The few changes observed in the adult composition of groups (Tables 2a–e) imply that there was little recruitment of young into their parental groups and little change in group size from one year to the next. For instance, Group NC had 27 young in 1983 but only four of the newly marked adult members of 1984 could have been young recruited from the previous year. Similarly, the number of adults in Group P5 from 1983 to 1984 rose by only four, although this group had 12 young in 1983. In fact, the general trend was for a decrease in the number of adult members of groups. From the changes in group composition (Table 2), it can be seen that the net change in the number of male members is 0 while that of females is −2.

Relations between groups

All groups of capybaras observed in the study area occupied stable home ranges of 6–16 ha (Herrera & Macdonald in prep.). The overlap between

Table 2. Changes in group composition from 1983 to 1984 in five groups (a) C1, (b) C2, (c) NC, (d) P5 and (e) VQ. Identification codes (three characters) of animals unambiguously identified in both years appear joined by a solid line: unmarked animals in either year that could have been marked the previous or subsequent year are joined by a broken line. Total number of animals in each age/sex class is shown.

(a)

	1983		1984
Females	OXD	————	OXD
	YBH	- - - - -	YQK
	YCZ		
	Fem	- - - - -	YLL
			YL4 Newcomers
			Fem
N =	4		5
Males	WSC	————	WSC
	OJX	————	OJX
	WTC		
	Male	- - - - -	WHI
			Male Newcomer
N =	4		3
Young	0		0

(b)

	1983		1984
Females	OVN (Died)		
	OXH	————	OXH
	OXB		
	Fem1	- - - - -	YLU
N =	4		2
Males	OJA	————	OJA
	M14	————	M14
	OHD	————	OHD
	OHX		
N =	4		3
Young	0		2

(c)

	1983		1984
Females	YCC	————	YCC
	YVI	————	YVI
	YBV	————	YBV
	YED		
	YCH		
	Fem1	- - - - -	YQB
	Fem2	- - - - -	YT4
			YLQ
			YSB Young recruits
			WWD Newcomer?
N =	7		8

Males	R15	
	WTE	WTE
	WNA	WNA
	1DG	
	Male1	WHC
	Male2	Male
		W14 Young recruit
N =	6	5
Young	27	20

(d)

	1983	1984
Females	2GB	2GB
	YDS	YDS
	YVA	YVA
	YCA	YCA
	Fem1	2LW
	Fem2	YPU
		YST Newcomer
N =	6	8
Males	165	165
	D14	Male1
	WLJ	
		W14 Young recruit
		WW7 Newcomer
		Male2
		Male3 Newcomers?
N =	4	6
Young	12	7

(e)

	1983	1984
Females	OVP Died	
	YBI	Y76
	YBD	YTS
	YCD	
	Fem1	
	Fem2	
N =	6	2
Males	1BY	1BY
	WTN	Male1
		Male2
N =	2	3
Young	0	7

neighbouring ranges was minimal, so we regarded them as territories. During 729 hours of observation, a total of 31 group territorial border encounters involving 13 groups was observed. In general, these encounters were aggressive. The typical course of events was that the members of two groups would stray closer together as they grazed. Peripheral members of each group would gradually intermingle, and those that were closest would launch attacks on the individual nearest them. Other individuals of both groups, who happened not to meet a stranger, would show no interest in these individual squabbles. During territorial encounters, several ritualized behaviour patterns were noted. These included walking in parallel along the territorial border, with both capybaras co-ordinating their movements so that they started and stopped in synchrony. Very aggressive, all-out fights were also observed during inter-group encounters, involving animals of either sex.

In total, during 31 inter-group encounters, 67 such aggressive interactions between two males from different groups were recorded, 41 between a male and a female, 42 between two females, and 13 in which the sex of either or both of the participants could not be determined. It is noteworthy that intersexual aggressive interactions between groups involved a high proportion of female–female clashes. This is in marked contrast to the situation within groups, where female–female aggression constituted only 8.3% of all aggressive interactions (Herrera 1986). In three of the 31 cases, several members of both interacting groups were simultaneously involved in the rejection of intruders. In one of these cases 16 chases between individuals of both sexes were recorded in the 15 min for which the episode lasted. It is noteworthy that males which were low-ranking during interactions within their own group were actively involved in aggression towards other groups and, in at least one case, a subordinate from one group was able to drive away the dominant from another.

Despite the great variation in group size, there was no evidence of any group being consistently dominant over another. Rather, the outcome of an interaction between members of neighbouring groups was determined by its location: each individual acted as dominant over its neighbour when inside its own territory.

How does this general finding of antagonism between neighbours bear on the possibility of groups coalescing during the dry season? During observations at the end of the 1983–1984 dry season, three large aggregations were found of which members in each case included marked individuals known to have belonged to up to four separate groups from the preceding wet season. When the rains returned, these same individuals reverted to their original groupings. There was no evidence of any exchange of members between the groups composing each aggregation. These observations made clear that the recurrent reports of dry season groups being larger than wet season ones (Ojasti 1973; Azcarate 1980; Macdonald 1981) reflect the combination of several independent social units rather than the breakdown and amalgamation of such units.

The splitting and coalescing of groups occurred on a daily basis with groups forming aggregations while resting and wallowing in the mornings and separating to a greater or lesser extent to graze in the evenings. When separating from the large aggregations, members of each group would move as a unit. The spatial tolerance of the dry season does not destroy the group's integrity since neighbouring groups appear simply to rest side by side around receding pools. The observation of territorial behaviour in the dry season indicates that the groups can maintain their identities despite the apparent mingling.

Group formation

Ojasti (1973) postulated that new groups arise when newly formed pairs breed, the parents and offspring subsequently remaining together. In the present study, at least three possible pairs were recorded within the 300 ha study area. None of these animals that was relocated was still in the same company. No pair was seen to rear young (the smallest group to do so numbered five). Of course, in an area where suitable habitat is saturated with group territories the establishment of new groups (and therefore sightings of pairs) might be a rare event. Nonetheless, group sizes were fairly constant (Table 2) and numbers of young surviving to April averaged 7.2 (± 7.8, $N = 6$) per group annually. What was the fate of this surplus annual production, and was there any possibility of some of them forming new groups?

On 20 occasions during the latter part of the wet seasons of 1983 and 1984 (September and October), marked subordinate males from nine different groups were seen grazing between 30 and 50 m from the core of their group accompanied by a number (ranging from one to 11) of that group's young. In the context of mean nearest-neighbour distances between grazing group members of 12.5 m (Macdonald 1981), the distances between these cliques and the remainder of the group were notable, and the fact that they invariably involved subordinate males was striking. In September and October, the young of the year are approaching sub-adult status and the next generation is about to be born. At this time of year systematic observation of behaviour is hampered by extensive flooding and thick vegetation, so it was not possible to monitor any change in adult–young aggression that might presage dispersal. These observations of subordinate males accompanied by sub-adult individuals of unknown sex suggested that they were in the process of splitting from the parent group. In this case the subordinate male would be expected to become dominant in the incipient group by virtue of being bigger and older.

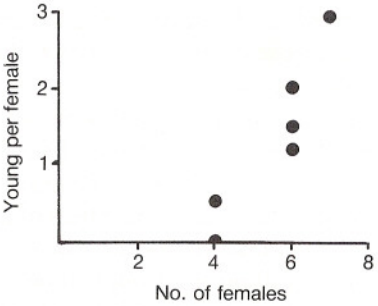

Fig. 2. Reproductive success of females and group size: number of young surviving to April per female plotted against number of females in the group the previous year.

Group size and the reproductive success of females

The observation that pairs failed to breed in our study area raises the question of which factors affect capybara reproductive success and, in particular, whether survival of offspring is related to group size. The reproductive success of an individual is best measured as the number of its offspring that survive to sexual maturity or to a certain critical age. In the case of capybaras, most young are born at the end of the wet season, a time of relatively abundant forage and cover. But soon after this, they face their first dry season, a time of high adult mortality (Ojasti 1978). Survival during this first dry period is crucial. Thus, it seems appropriate to use the number of young surviving to April as an indicator of the reproductive success of females.

The number of young born to any particular female is difficult to determine. This is because of the social system of the capybaras: female capybaras give birth away from the group and hidden under cover, and the mothers are wary and retiring when their offspring are very young; within the first week of life the young join creches; and females nurse each others' young communally (Macdonald 1981; Schaller & Crawshaw 1981). Hence only the total number of young born to a group could be observed reliably, and from this the average number of young per female was calculated. For five groups accurate estimates of adult membership in 1983 and the number of young in April 1984 are available, along with comparable data for one group from 1982 to 1983. Figure 2 shows that there is a significant positive correlation between the mean number of surviving young per female and the number of females in a group (Spearman rank correlation coefficient, $Rs = 0.926, p < 0.05, N = 6$).

Discussion

The niche occupied by the capybara has much in common with those of many species of tropical ungulates (see Jarman 1974; Leuthold 1977; see also Dubost 1968). Like them, the capybara is a relatively large grazer and subject to predation on open plains. Capybaras are both group-living and territorial, but the selective forces favouring these two facets of their social system may be separate. Capybaras are, or have been in the recent past, prey to puma, *Felis concolor*, jaguar, *Panthera onca*, feral dogs, *Canis familiaris*, caiman, *Cayman crocodilus*, and man. Macdonald (1981) described how a group of capybaras, under attack by feral dogs, bunched together with youngsters within a protective cordon. There are three reasons why capybaras might form groups in response to predation: 1. increased vigilance to forestall attack, 2. increased possibility of intimidating the predator through greater strength of numbers; 3. the 'selfish herd' effect (Hamilton 1971), in which individuals share the risk of capture, whether or not this also reduces the capture rate of the predator. Bertram (1978) reviews evidence for these commonly presumed advantages of grouping among some other species. Turner & Pitcher (1986) present a model in which the dilution effect (predator is less likely to find a group than an individual) and the avoidance effect (point 3 above) are combined to produce what they call 'attack abatement', so that animals living in groups may have greater fitness than scattered ones. A separate possible function of group living relates to McNaughton's (1984) suggestion that the stimulating effect of a group of grazers on a patch of grass is advantageous in maintaining a nutritious grazing lawn. However, the premise that grazing stimulates grass growth has recently been challenged (Belsky 1986).

The demands of predation and perhaps grazing may explain why capybaras are gregarious, but alone they do not explain either why they are territorial or why their groups sizes are not larger. The answers to these questions are probably to do with the dwindling of resources as the dry season progresses. In particular, capybaras are dependent upon water to sustain their food plants, and they also thermoregulate in water, mate in water, and seek refuge from predators in water (Ojasti 1973; Azcarate 1980; Macdonald 1981; Herrera & Macdonald 1984; Herrera 1986). As the dry season progresses, lakes that were previously almost contiguous over the landscape contract until they are little more than puddles surrounded by kilometres of dry, dusty and, to the capybaras, useless land. The remaining pools and the associated food become limiting, and highly patchy, resources. We suggest that it is the need to guarantee access to a permanent dry-season lagoon that favours territoriality. The presence of the water hole next to a grazing patch makes a piece of land defensible (Brown 1964). We observed that every territory did indeed contain both a waterhole and a grazing lawn (Herrera & Macdonald in prep.).

The foregoing discussion of predation, together with the fact that females nurse each other's infants (and occasionally carry them on their backs while swimming from danger) might suggest that individual capybaras should benefit from being members of groups that are as large as possible. This suggestion is compatible with the observed distribution of group sizes with its long tail towards large groups (Fig. 1). Within the range of group sizes that we found, any possible disadvantages of larger membership (e.g. greater discord with more males) were apparently overridden by the advantages, since females in larger groups reared more young. However, data on reproductive success are lacking for the largest groups observed (16 adults). It would be premature to conclude that there was a causal link between the postulated advantages of gregariousness and this increased reproductive success. Another possibility is that group size and reproductive success are both affected, partially or completely independently, by a third variable, such as the nutritional quality of the grassy patches in each territory.

The stability of groups observed in these rodents is comparable to that of several territorial species of primates and carnivores (e.g. Hrdy 1977; Rasa 1985). In the case of capybaras, the interannual group stability, particularly the fact that subordinate males remained in their groups for two years or more while being deprived of some resources (particularly access to sexually receptive females), demonstrates the importance of group living for these individuals.

The stability of group sizes between years was particularly notable in those groups in which a large number of young was not reflected in an increase in the number of adults the following year. Clearly, many young were not recruited into their parental groups, and their fate is crucially important to understanding the structure of the capybara population in the Llanos. If the young of a group do indeed disperse as a unit, as suggested above, they would find the area surrounding the water holes in our study area populated by contiguous capybara territories, and these were maintained over at least three years (Herrera 1986). In fact, between 1983 and 1984 virtually all groups using the study area were known, and there was no evidence of any new group becoming established. This suggests that incipient groups would have little chance to find a vacant territory adjoining that of their parents. The alternatives would be to colonize suboptimal habitat close at hand or to disperse over greater distances. The second option is likely to be hazardous since suitable blocks of habitat are widely dispersed and, anyway, likely to be fully colonized. Therefore, the circumstantial evidence is that dispersing sub-adults have poor prospects and probably suffer high mortality.

How do these patterns fit with Ojasti's (1973) apparently correct finding (Ojasti 1980) that there is a sustained yield of 30% of the population which can be harvested every year? This 30% is calculated on the basis of the total population, including all age and sex classes. However, the slaughtermen only kill adult individuals and they attempt to spare pregnant females. In practice, the cull moves from a selected point across favourable areas killing all adults found until the quota is reached. Field observations revealed large areas which were populated almost exclusively by young capybaras after the cull, thereby indicating that in some areas most of the adult population is wiped out. Having no adults with which to compete, these young are probably able to remain in their natal territories. Conditions in our study area were a marked contrast to this, since it was spared from the annual slaughter; in this case the majority of young faced dispersal at 1.5 years of age. Thus, the cull probably has the effect of reducing dispersal and mortality among sub-adults. These animals and the surviving adults will form the population to be harvested one year later.

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