

## Growth and dispersal of capybaras (*Hydrochaeris\* hydrochaeris*) in the Llanos of Venezuela

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(With 3 figures in the text)

Growth rates and dispersal patterns of capybaras, *Hydrochaeris\* hydrochaeris*, were studied in a ranch in the Venezuelan seasonally flooded savannas by first marking juvenile animals at specific locations in March–April 1989 and then, on two occasions the following year (February and May 1990), searching a wide area for recaptures. Animals grew a mean 2.8 kg per month in the 10 months between the first and second captures and apparently lost weight over the next three months, possibly due to water scarcity. From 22 recaptures, median dispersal distance was 3366 m, about six times the average home range width. Maximum dispersal distance was 5600 m and minimum was 0. There were no differences between males and females in dispersal distances. A group of three males and three females apparently dispersed together. Competition for resources—water and grass—under a social system involving group-living and territoriality is proposed as the cause of the patterns observed. No correlation was found between distance dispersed and initial and final weight or weight gain. Capybaras appeared to disperse predominantly north or south, possibly in order to reduce the chances of meeting established groups and to increase the probability of finding a stream, since all streams in the region run approximately west–east.

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### Introduction

Dispersal patterns both affect and reflect the social systems of vertebrates. On one hand, they have an important effect on the genetic structure of the population (Shields, 1987), which in turn plays a role in determining many aspects of social behaviour. Thus, the amount of gene flow allowed by dispersal and/or migration will have an influence on the relevance of kin selection (Hamilton, 1964) in the evolution of cooperative or altruistic behaviour (Wade & Breden, 1981).

\*Also known as *Hydrochoerus* but see Husson, A. M. (1978). *Mammals of Surinam*. Leiden: E. J. Brill

On the other hand, dispersal patterns are themselves largely determined by social roles and intraspecific competition (Shields, 1987), thus being a consequence of the social system.

According to Greenwood's (1980) review, in polygynous and promiscuous species (mostly mammals), males are the ones that generally disperse or that disperse longer distances, while females are mainly philopatric. The opposite is true of monogamous species (mostly birds). The alleged causes for these patterns are the relative extent of intra-sexual competition, either for resources or for mates in each social system (Greenwood, 1980; Dobson, 1982; Liberg & von Schantz, 1985) and inbreeding avoidance (e.g. Packer, 1979), although the latter does not conclusively account for the observed sex differences in dispersal (Pusey, 1987). Greenwood (1980) also mentions that in a greater number of mammalian species (15 mammals and six birds), there were no sex differences in dispersal patterns. The costs of dispersal in terms of deterioration of physical condition or other measure of cost are seldom addressed (Dobson, 1982).

In this paper, dispersal patterns of capybaras (*Hydrochaeris hydrochaeris*) as they grow from juvenile (5–7 months) to adult (1.5 years; Ojasti, 1973) are studied and interpreted on the basis of the social system prevailing in the Venezuelan Llanos, as described below. Analysis of changes in weight as they relate to dispersal distances will allow an assessment of one possible cost of dispersal (e.g. a lower growth rate for animals dispersing longer distances).

Capybaras, 50-kg caviomorph rodents, live in groups of 10 adults on average and a varying number of young, although there is substantial variation in group size. These groups are stable, i.e. membership remains largely unchanged for more than one year, each group being composed of a dominant male, several females and young and one or more subordinate males (Herrera & Macdonald, 1987). A rigid dominance hierarchy is evident among the males. Subordinate males are 'proper' group members (as opposed to 'floaters') and remain so for two years or more (Herrera, 1986). Dominant males are larger, have a heavier snout scent gland, and have significantly more matings than subordinates (Herrera, 1986). However, little or no sexual dimorphism in size is present in this species (Ojasti, 1973). A low interaction rate among females precludes an analysis of their social relationships (Herrera, 1986). Apparently, most of them breed at least once a year.

In high density areas of the Venezuelan Llanos, groups of capybaras live in small (10 ha) territories defended by all adult group members, subordinate males included (Herrera & Macdonald, 1989). A territory includes a grazing patch, bush and, significantly, a section of a pond or river (Herrera & Macdonald, 1989), in which capybaras wallow for several hours a day, mate and seek protection from predators. At the beginning of the wet season (see below), most females come into oestrus and have an average of four young five months later, towards the end of the wet season (around October). At this time, Herrera & Macdonald (1987) report that the previous year's young, now one year old, which move in closely knit associations (Macdonald, 1981), tend to wander away from their parental group accompanied by a subordinate male. This has been interpreted as incipient dispersal and as circumstantial evidence for a process whereby aggregations of young from the same social unit found a new group an unknown distance away from the parental group's home range (Herrera & Macdonald, 1987). The subordinate male in these incipient groups would probably turn into the dominant by virtue of his age and size. In Herrera & Macdonald's (1987) report, the sexes of the apparently dispersing young could not be determined but most young of any one group joined the dispersers, suggesting that both sexes were equally represented.

The specific questions addressed in this report are: what distances do capybaras disperse as they grow from juvenile to adult age? Are there differences in dispersal patterns between males and

females? Are associations found among pre-dispersers maintained after dispersal? Are dispersal distances related to growth rates?

### Study area and methods

This study was conducted at Hato El Frio (80,000 ha), a cattle ranch located in the Venezuelan low Llanos (7° 45' N, 68° 55' W). This region is characterized by flat, grassy plains interspersed with isolated patches of woodland. Here, a marked wet-dry seasonal regime causes widespread flooding in the wettest months (July–September) and severe water scarcity in February and March. At El Frio, capybaras are abundant, found around virtually every water body with an overall density of roughly 0.3 capybaras/ha, reaching 1 capybara/ha locally. These densities are likely to have been favoured by a water management system consisting of dykes (several km long by 2 m high) and small dams blocking streams and causing ponds of a few to several hundred ha to be formed, and possibly also by the virtual extinction of some of the major predators (large cats and crocodiles).

At El Frio, and in other ranches in the Llanos, capybaras are harvested every year under a management programme that allows the annual culling of 20–30% of the population (Ojasti, 1973, 1991). The cull has been traditionally carried out for perhaps as much as 200 years (Humboldt, 1816) in February of each year when capybaras are concentrated around the receding pools and breeding is at its yearly minimum (Ojasti, 1973). However, due to a more stringent management policy and an apparent reduction in population size, no animals were taken at El Frio in 1987, 1988 or 1989. Culling resumed in February 1990, with a toll of 4000 animals based on a census of 27,000 animals for the whole ranch.

This study was designed so as to take advantage of the logistic facilities made available by the annual capybara slaughter, which would allow a wide (but not necessarily thorough or systematic; see below) search of the ranch for previously marked animals. The fact that there was no slaughter in the year of first capture (1989) nor in the previous 2 years permitted a study of dispersal under relatively 'normal' conditions.

From 29 March to 8 April 1989, capybaras of juvenile size (10–20 kg) were captured in 3 major ponds centrally located at El Frio (see Fig. 1). The ponds were 2–6 km away from each other, and, since regular movements of capybaras rarely exceed 500 m daily (Azcarate, 1980; Macdonald, 1981; Herrera & Macdonald, 1989), were effectively isolated from each other. The size of the animals chosen corresponded to animals born at the yearly birth peak of September–October (Ojasti, 1973), so they were between 5 and 7 months old. Animals were captured by herding and rounding up a small number of them and either lassoing them in flight, capturing them by hand, or fishing them up with a dog-catcher from bushes. Captured animals were weighed to the nearest 0.25 kg with a Pesola spring balance, marked with coloured and numbered eartags ('rototags': Dalton Supplies, Nettlebed, UK) and released. Location of capture was recorded on a 1:35,000 map. It is estimated that points of capture were recorded with a  $\pm 500$  m error, or roughly the average home range diameter (Herrera & Macdonald, 1989). Thus, animals recaptured within 1000 m of point of original capture were considered to have remained in their natal home range.

The following year (1990), from 2 to 17 February, many, perhaps most, areas within the ranch were searched by following the slaughtermen as they rounded up groups of capybaras killing selected ones. As the cull proceeded, great care was taken to record accurately the place from which the animals were herded since this could be some distance away from the place where they were rounded up. Any marked animals that turned up—not killed because of their small size—were captured with a dog-catcher. The same data were collected as for the original captures. Note that the cull procedure would allow an estimate of both mean and maximum dispersal distance (as long as the latter was within ranch limits, or 10–15 km from the first capture ponds), since it proceeded from the borders inward in a somewhat spiral-like fashion.

A second capture operation using the 1989 technique was carried out between 9 and 12 May 1990 in the original capture areas (Fig. 1). Animals captured in this way were not used for calculating dispersal distances or proportion of animals dispersing since they were deliberately searched for in the areas where they were first captured. They were used to increase the numbers of non-dispersers for comparison with dispersers. It must

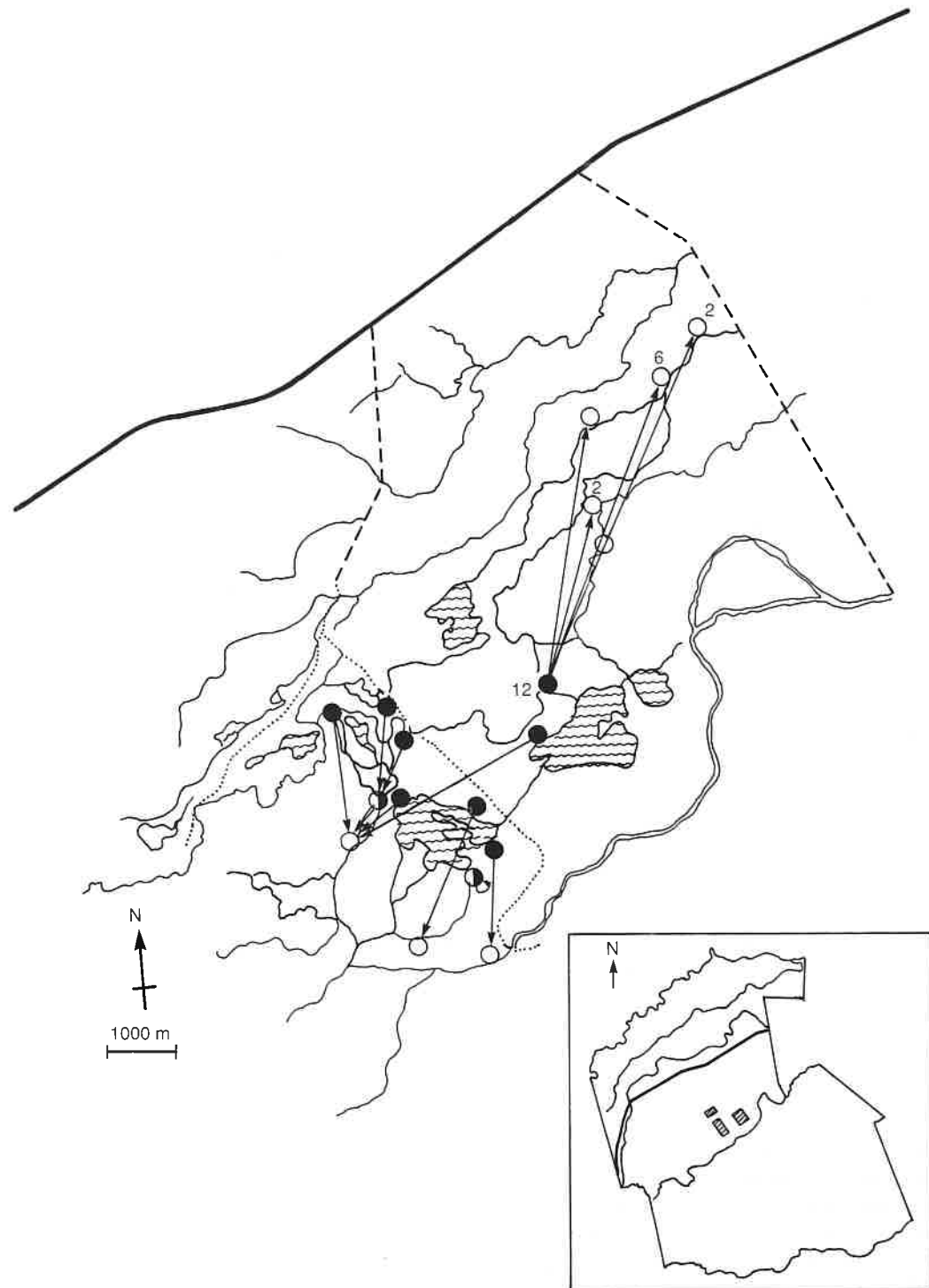


FIG. 1.

TABLE I  
 Statistics of capybaras captured in 1989 (as juveniles) and February 1990 (as adults) at El Frio ranch in Venezuela.  
 Values reported are means and standard deviations

(a) 1989

	N	Weight (kg)	Foot length (mm)
Males	306	13.9 ± 3.3	151.3 ± 14.5
Females	253	14.3 ± 3.3	150.5 ± 13.1
Total	559	14.1 ± 3.3	150.9 ± 13.9

(b) February 1990

	N	Weight (kg)	Foot length (mm)
Males	13	43.1 ± 2.0	193.5 ± 9.7
Females	10	42.2 ± 3.1	181.9 ± 10.4
Total	23	42.7 ± 2.5	188.5 ± 11.4

be noted, however, that, since all 3 ponds were searched, the possibility of capturing animals having moved from one to the other, and therefore having dispersed, existed.

## Results

### Growth rates

A total of 559 animals (306 males and 253 females; sex ratio differing significantly from 1:1;  $\chi^2 = 5.03$ ,  $d.f. = 1$ ,  $P < 0.025$ ) were captured in 1989 (summary statistics in Table Ia). Of these, 24, or 4.3%, of all marked animals (14 males and 10 females), were recaptured during the following year's slaughter (Table Ib; note that sample sizes are not always the same because field conditions did not allow all data to be collected for all animals). In 10 months (May 1989–February 1990) these animals grew on average 28 kg, from a mean 14.1 kg ( $\pm 3.3$  kg) to 42.7 kg ( $\pm 2.5$  kg), or 2.8 kg per month (approximately 91.8 g/day). No difference was found in weight gain (measured as a proportion of initial weight) between females and males (males:  $\bar{x} = 1.91 \pm 0.20$ ,  $n = 10$ ; females:  $\bar{x} = 2.00 \pm 0.41$ ,  $n = 9$ ; Student's  $t$ -test:  $t = 0.59$ ,  $d.f. = 17$ , NS). Interestingly, although there was a positive correlation between weight in 1989 and weight in 1990 ( $r = 0.699$ ,  $d.f. = 17$ ,  $P < 0.01$ ; Fig. 2), the proportional increase in weight was negatively correlated with initial weight, i.e. as a proportion of their weight in 1989, heavier animals grew less than lighter animals, irrespective of sex ( $r = -0.916$ ,  $d.f. = 17$ ,  $P < 0.01$ ).

During the May 1990 search of original capture areas, another eight animals (four males and four females) were recaptured. Although these animals were captured three months later than the

FIG. 1. Map showing points of original capture (●) of young capybaras at El Frio in 1989 linked to their locations of recapture as adults in 1990 (○). Next to dots are numbers of animals captured or recaptured at each site. No number indicates 1. — = streams; ——— = the main road; - - - - - = dykes; ····· = vehicle paths. Inset: location of first capture areas within the ranch.

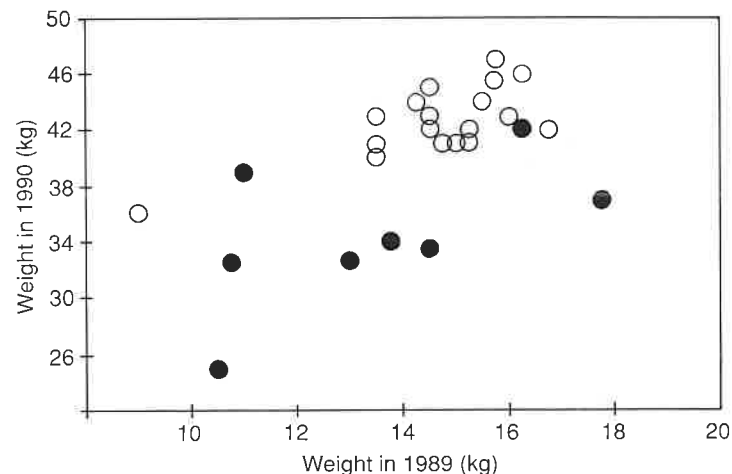


FIG. 2. Body weights of capybaras recaptured at El Frio (Venezuela) as adults in February (○) and May (●) 1990, plotted against their body weights on first capture (as juveniles) in March–April 1989.

first recaptures, their weights were much lower (8 kg on average) than those of February 1990 ( $\bar{x}$  in May 1990 =  $34.5 \text{ kg} \pm 5.1$ ,  $n=8$ ;  $\bar{x}$  in February 1990 =  $42.7 \text{ kg} \pm 2.5$ ,  $n=19$ ;  $t=4.34$ ,  $df.=25$ ,  $P<0.005$ ), while no difference was found in foot length ( $\bar{x}$  in May 1990 =  $186.3 \text{ mm} \pm 6.41$ ,  $n=8$ ;  $\bar{x}$  in February 1990 =  $188.5 \text{ mm} \pm 11.4$ ,  $n=23$ ;  $t=0.68$ ,  $df.=29$ , NS).

#### Dispersal patterns

Maximum dispersal distance was 5600 m and minimum was 0 (Fig. 3), in both cases a male. Besides the male found at the same location, one male and one female moved about 1000 m and

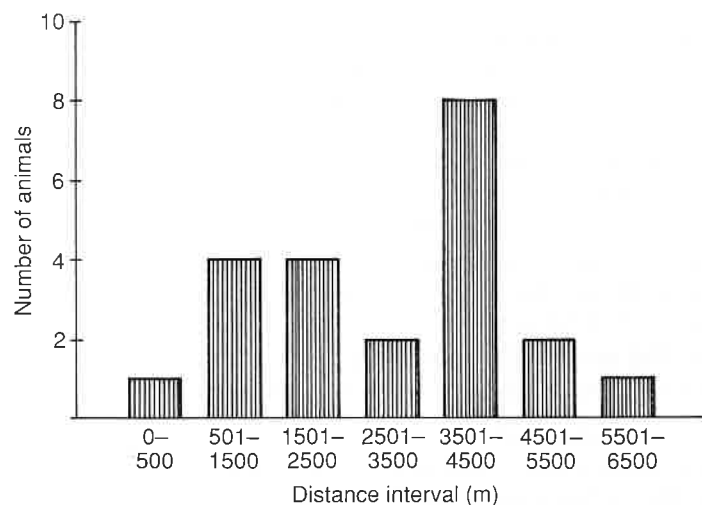


FIG. 3. Frequency histogram of distances dispersed by capybaras recaptured in February 1990 and marked in March–April 1989 at El Frio, Venezuela.

were considered non-dispersers (in the first recapture operation). The median dispersal distance—of those that dispersed—was 3366 m and there was no difference between males and females: median dispersal distance for males = 4025 m,  $n=10$ ; median for females = 3500 m,  $n=9$  (Mann–Whitney test, NS). Of the eight animals recaptured in May 1990, three males moved more than 1000 m, the others are non-dispersers. The median dispersal distance of the three dispersers was 1575 m. Taking animals from both recapture samples (February and May 1990), three out of 16 males and five out of 14 females did not disperse ( $\chi^2=1.099$ ,  $df.=1$ , NS). There was no correlation between initial weight, final weight or weight increase and distance dispersed.

Six animals (three males and three females) that were captured on the same day (6 April) and same location in 1989 were recaptured in a single round-up on the 16 February 1990, 4025 m from the point of first capture. This strongly suggests that these animals dispersed as a group.

Figure 1 shows the directions of movements of the 22 animals from the first recapture for whom this could be determined. Note that most animals moved predominantly north or south. Observations on recapture areas indicate that the habitat in which animals were first caught was in all cases a large lagoon, while that in which they were recaptured was a similarly large pond in 11 cases, in 14 cases a narrow stream, and smaller ponds in the rest.

#### Discussion

Recapture rate (only 4.3%) was low: using the proportion of the population rounded up to predict recapture rate, one would expect perhaps as many as four times the number of recaptures. The probability of finding marked animals was reduced because of: (a) the size of the ranch; and (b) the relatively small area where the animals were captured meaning that the dispersing animals were not uniformly distributed across the ranch. Further, since the way the slaughter works—simply the most convenient way for the workers—is not necessarily a thorough and systematic search of the ranch, it is possible that the areas surrounding first capture locations were not especially searched.

Growth rates found between March–April 1989 and February 1990 were high (weights nearly tripled in 10 months), almost twice the average growth rate for animals within the same ages found by Ojasti (1973:  $53.6 \text{ g/day} \pm 1.9$ ) in similar habitat. However, by the following May, recaptured animals had gained 8 kg less than those caught in February, suggesting that they had lost weight. These values actually reduce the overall growth rate in the 13 months covered to  $51.3 \text{ g/day}$ , much closer to Ojasti's earlier figure. Clearly, this result is related to the fact that the driest months of the year are those between the first and second recaptures (whether the slaughter has any stressing effect on survivors, affecting growth rates, is unknown). This, incidentally, precludes a comparison of changes in weights and condition indices between dispersers and non-dispersers, since most of the latter ones were captured after three months of scarce resources (water and grass). Larger animals were unable to take advantage of the 'good' period, managing only to increase a similar amount (and hence a lower proportion of their own weight) to that of the lighter animals. This is also shown by the lower variability in weight in February 1990 compared with 1989 (Table I a and b), with coefficients of variation going from 24% to 6% between these two dates. However, if the differences in initial weights were due to age, then the reduction in growth rates were to be expected.

Dispersal distances found for capybaras fall within values expected for an animal its size and trophic level (cf. Berger, 1987; Nelson & Mech, 1987). Interestingly, animals moving longer distances had not lost weight, which may indicate that dispersing farther is not necessarily more

costly. If the animals can find water and grass along their route, the cost of moving is possibly negligible; as the dry season progresses, continued movements must certainly become more damaging. As to the directions of movement, since water flows west-east, moving north or south—as the animals mostly did—would increase the probability of finding water. Alternatively, moving north-south would avoid constantly crossing the aggressively-defended territories of established groups, located along the west-east streams.

Two important facts emerged from this study: (1) that dispersers were both male and female with no differences in the distances moved; and (2) that a group of six animals, also of both sexes, apparently dispersed as a group. Both these results corroborate Herrera & Macdonald's (1987) proposition that capybaras disperse in groups of subadults of both sexes accompanied by subordinate males. Species with dispersal by both sexes account for only 23% of Greenwood's (1980) survey of 65 mammalian species, while both Greenwood (1980) and Dobson (1982) argue that dispersal by both sexes should be expected for monogamous mammals. According to these authors and also to Liberg & von Schantz (1985), an important factor underlying these patterns is reproductive competition, i.e. within sex competition, or, in polygynous species, within males.

The capybaras' mating system can be classified as midway between polygyny and promiscuity: more than one male mating with several females in a group, with one male obtaining a greater proportion of the matings (Herrera, 1986). The expected pattern would then be male-biased dispersal (Greenwood, 1980; Dobson, 1982). Under such a system, the dominant male would rather see the subadult males go since their staying would increase the number of competitors.

The pattern found—subadults of both sexes dispersing in groups—must then be related to other aspects of the animals' ecology rather than, although not necessarily exclusive of, reproductive competition. The—perhaps uncommon—social system of capybaras, which combines group-living with territoriality (Herrera & Macdonald, 1987, 1989), is certainly relevant. Competition for limited resources (group membership can be viewed as a vital 'resource'), rather than mates, possibly underlies the patterns observed as argued in the following account. Group territories of capybaras at El Frio are small (10 ha on average), always close to the water, and they apparently occupy all available habitat (Herrera & Macdonald, 1989). Moreover, adult membership of groups (both males and females) varies little from year to year (Herrera & Macdonald, 1987). This suggests that the number of animals in a group is strictly limited by resources available within territories. Since no animal can afford to be outside a group or face extra animals with which to compete, all subadults must disperse.

What is the fate of dispersers? In a high density area such as El Frio, favourable habitat appears to be saturated with territorial groups of capybaras (Herrera & Macdonald, 1989), and possibly more so in 1989–90 after three years without a cull. Under these conditions, an incipient group searching a suitable home range would have to: (1) insinuate itself in between established territories; or (2) move to marginal habitat. The first alternative seems to be a rare occurrence, since Herrera & Macdonald (1989) found few changes in territory shapes and numbers around a pond during three years. The second possibility will no doubt lower survival chances of dispersers. Locations of recapture do not allow a conclusive assessment of habitat quality after dispersal, although, in most cases, it appeared somewhat worse than that from which they came. All this, in any case, points to the existence of an annual surplus of young dispersers, facing a high mortality. While partly explaining the low recapture rate, this scenario supports Ojasti's (1973) management plan which allows the culling of a number of capybaras every year, replacing natural mortality and thus having little effect on overall population density.

The process of group formation described by Herrera & Macdonald (1987) and supported by

the present results will probably lead to inbreeding for the following reasons. Young in a group of capybaras have a greater probability of being the offspring of the dominant male than of any other male (Herrera, 1986), so many members of the incipient groups are at least half sibs. As the ex-subordinate becomes dominant of the new social unit, he will mate with the females (possibly his younger sisters or cousins), while the younger males he recruited along with the females will—at least to some degree—do the same. Inbreeding thus occurs and the recurrent nature of this process will reinforce it. This has important consequences for the social system among capybaras, by making kin selection an important force operating therein (Wade & Breden, 1981). Previous observations such as the dominant male's tolerance of subordinates (Herrera, 1986), the females' apparent cooperation in nursing and caring of young (Macdonald, 1981) and alarm calling behaviour (Herrera, 1986; Yáber, 1990) could then have been favoured by kin selection.

Although inbreeding may 'help' in the evolution of cooperative behaviour through kin selection, it can also be deleterious if it becomes excessive. Thus, many authors suggest that dispersal is a means for avoiding or reducing inbreeding (see Pusey, 1987, for a review). For instance, Wolff, Lundy & Baccus (1988) found that, in *Peromyscus leucopus*, a species with a mating system ranging from polygyny and promiscuity to facultative monogamy, both sexes disperse with 7.6% of the males and 20.0% of the females being philopatric. Their evidence only supports the inbreeding avoidance hypothesis. In capybaras, the mechanism for dispersal seems to have the opposite effect among dispersers, as argued above. If excessive inbreeding has deleterious effects, mechanisms to reduce it within groups may appear, such as emigration of adults followed by immigration into a new group (see e.g. Packer, 1979), or a foreign animal ousting the dominant. Both these phenomena have been observed in capybaras at El Frio (Herrera, 1986), albeit infrequently. Also, the departure of both subadult males and females from the group reduces the probability of parent-offspring mating.

### Summary

Growth rates of capybaras, *Hydrochaeris hydrochaeris*, between six and 16 months of age in the Venezuelan seasonally flooded savannas, were found to be quite high (2.8 kg per month). Both male and female subadults dispersed, at least sometimes in groups, with a median distance of 3366 m (about six home range widths) and no differences between males and females. No relation between growth rates and distance dispersed was found. Resource-related competition in a social system involving group-living and territoriality are believed to be associated with the patterns observed.

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### REFERENCES

- Azcárate, T. (1980). Sociobiología y manejo del capibara. *Doñana Acta Vert.* (Spec. No.) 7–8: 1–228.  
 Berger, J. (1987). Reproductive fates of dispersers in a harem-dwelling ungulate: the wild horse. In *Mammalian dispersal patterns*: 41–54. Chepko-Sade, B. D. & Halpin, Z. T. (Eds). Chicago: Chicago University Press.

- Dobson, F. S. (1982). Competition for mates and predominantly juvenile male dispersal in mammals. *Anim. Behav.* **30**: 1183–1192.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**: 1140–1162.
- Hamilton, D. W. (1964). The genetical evolution of social behaviour I & II. *J. theor. Biol.* **7**: 1–52.
- Herrera, E. A. (1986). *The behavioural ecology of the capybara, Hydrochoerus hydrochaeris*. D.Phil. thesis, University of Oxford.
- Herrera, E. A. & Macdonald, D. W. (1987). Group stability and the structure of a capybara population. *Symp. zool. Soc. Lond.* No. 58: 115–130.
- Herrera, E. A. & Macdonald, D. W. (1989). Resource utilization and territoriality in group-living capybaras. (*Hydrochoerus hydrochaeris*). *J. Anim. Ecol.* **58**: 667–679.
- Humboldt, A. von (1816). *Voyage aux régions équinoxiales du nouveau continent fait en 1799–1804 par A. de Humboldt et A. Bonpland VI*. Paris: N. Mache.
- Liberg, O. & von Schantz, T. (1985). Sex-biased philopatry and dispersal in birds and mammals: the Oedipus hypothesis. *Am. Nat.* **126**: 129–135.
- Macdonald, D. W. (1981). Dwindling resources and the social behaviour of Capybaras, (*Hydrochoerus hydrochaeris*) (Mammalia). *J. Zool., Lond.* **194**: 371–391.
- Nelson, M. E. & Mech, L. D. (1987). Demes within a northeastern Minnesota deer population. In *Mammalian dispersal patterns*: 27–40. Chepko-Sade, B. D. & Halpin, Z. T. (Eds). Chicago: Chicago University Press.
- Ojasti, J. (1973). *Estudio biológico del chigüire o capibara*. Caracas: FONAIAP.
- Ojasti, J. (1991). Capybara exploitation in Venezuela. In *Wildlife use and conservation in the Neotropics*: 236–252. Robinson, J. G. & Redford, K. H. (Eds). Chicago: Chicago University Press.
- Packer, C. (1979). Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* **27**: 1–36.
- Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* **2**: 295–299.
- Shields, W. M. (1987). Dispersal and mating systems: investigating their causal connections. In *Mammalian dispersal patterns*: 3–24. Chepko-Sade, B. D. & Halpin, Z. T. (Eds). Chicago: Chicago University Press.
- Wade, M. J. & Breden, F. (1981). Effect of inbreeding on the evolution of altruistic behaviour by kin selection. *Evolution, Lawrence, Kans.* **35**: 844–858.
- Wolff, J. O., Lundy, K. I. & Baccus, R. (1988). Dispersal, inbreeding avoidance and reproductive success in white-footed mice. *Anim. Behav.* **36**: 456–465.
- Yáber, M. C. (1990). *Comportamiento de alerta y alarma en chigüires, Hydrochoerus hydrochaeris*. Licenciatura thesis, Universidad Simón Bolívar, Caracas, Venezuela.