THE EFFECT OF HARVESTING ON THE AGE STRUCTURE AND BODY SIZE OF A CAPYBARA POPULATION

EFECTO DE LA EXPLOTACION SOBRE LA ESTRUCTURA DE EDADES Y EL TAMAÑO CORPORAL DE UNA POBLACION DE CHIGÜIRES

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ABSTRACT

During a three-year period (1982-1984), a 400 ha section of a ranch in the Venezuelan seasonally flooded savannas was spared from the annual cull of 20-30% of the capybara (Hydrochaeris hydrochaeris) population. In that period, the average body weight of adult capybaras of both sexes increased from 38.2 to 41.1 kg. Adult weight of males increased by 4 kg (38.4 to 42.4 kg) while females went from a mean of 37.9 to 39.9 kg. These results also show the development of a slight but significant sexual dimorphism. The age distribution of adult capybaras at the end of the moratorium had more animals in older age-classes than the harvested population. This was reflected in a statistically significant increase in the average age of adult animals of approximately one year. A sample of humeri from killed animals taken in 1990 after another three years without a cull (1987-1989) did not differ in average age from the 1984 study area (no slaughter) sample. Neither was this sample different in average age or length from a sample taken from animals dead of natural causes in the same year. The results suggest that the harvested population is below its maximum potential productivity due to the low average age and body weight of the individuals, since older and bigger females have greater reproductive success than younger ones.

Key words: capybara, Llanos, harvesting, wildlife, Venezuela, age structure, body weight.

RESUMEN

Durante un período de tres años (1982-1984), una sección de unas 400 ha del hato El Frío en los Llanos inundables de Venezuela fue excluida de la matanza anual de chigüires, Hydrochaeris hydrochaeris, la cual extrae 20-30% de la población cada año. En ese período, el peso promedio de los chigüires aumentó de 38,2 a 41,1 kg. El peso de los machos aumentó en promedio 4 kg (de 38,4 a 42,4 kg) mientras las hembras crecieron de un promedio de 37,9 a 39,9 kg. Estos resultados muestran asimismo el surgimento de un dimorfismo sexual en peso pequeño pero significativo. El largo de un pie trasero (como medida de tamaño esqueletal) de los chigüires en la zona excluida de matanza no cambió en forma significativa durante estos tres años. La distribución por edades de los chigüires adultos al final del período sin matanza en el área de estudio tenía una proporción de animales en clases de edad alta mayor que la de la población cosechada. Esto se vió reflejado en un aumento de aproximadamente un año (estadísticamente significativo) en la edad promedio de los animales. No se encontraron diferencias al comparar la estructura por edades de una muestra tomada en 1990, luego de otros tres años sin matanza (1987-1989), con la muestra del área de estudio en 1984 (sin matanza). Tampoco se encontraron diferencias en edad o largo humeral

HERRERA

entre esta muestra y una muestra de húmeros recogidos en el campo de animales muertos de muerte natural ese mismo año. Estos resultados sugieren que la población cosechada se encuentra bajo su máximo de productividad potencial debido a la baja edad y peso de los animales, ya que las hembras de mayor edad y tamaño tienden a tener mayor éxito reproductivo que las menores.

Palabras clave: chigüire, Llanos, explotación, fauna silvestre, Venezuela, estructura por edades, peso corporal

INTRODUCTION

Capybaras, Hydrochaeris hydrochaeris, 50 Kg caviomorph rodents, are semi-aquatic dwellers of the seasonally flooded savannas (Llanos) of Venezuela and other lowland regions of tropical South America. This species has been commercially hunted for meat in Venezuela for more than 150 years (Humboldt 1816, Ojasti and Medina 1972). Since 1968, a management plan, presently run by the Ministry of the Environment (MARNR) of Venezuela, has been in operation, based on the guidelines of Ojasti (1973). Ranches applying for permits are censused by direct count of the animals present and a proportion is allowed to be culled. Up to 1985, this number was 30% in ranches with adequate capybara populations, but since 1986 the proportion has been reduced to 20%. This plan has been generally successful in that both population levels and extraction rates have remained relatively stable (Ojasti 1980; 1991).

The harvesting program consists of a slaughter carried out once a year during the dry season (usually in February), when the animals are concentrated around the dwindling pools. Only adult animals, as estimated by their size (officially 35 kg minimum) are killed. Visibly pregnant females are usually spared, but this is not always practicable. In some ranches, up to 200 animals are processed each day for about three weeks. The meat is salted, dried and the whole production is sold within a month in markets in central Venezuela.

Harvesting can have important consequences on several population parameters (besides the obvious density), such as age structure (e.g., Logan et al. 1986). This, in turn, can have an effect on the efficiency of the harvesting program itself since age structure affects the reproductive potential of any population (e.g., Krebs 1985; Begon et al. 1990). Thus, in the case of capybaras, Ojasti (1973) found that older and bigger females had greater reproductive success.

Cordero and Ojasti (1981) found that the average weight of capybaras in the savannas of a ranch in southern Venezuela during the dry season was 39.6 kg (N=232), significantly lower than the average fullygrown, dry-season body weight of 47.5 kg (N=67) reported by Ojasti (1973). They attributed this result to

the effect of the slaughter. Ojasti's earlier figure resulted from weighing animals which had not been affected by a slaughter for at least five years.

During a study on the social behavior of capybaras in the wild (Herrera and Macdonald 1987), a 400 ha section of a capybara-producing ranch in the Venezuelan Llanos was spared from the slaughter for three years (1982-1984). Stability of social groups and land tenure patterns evidenced in that study (Herrera and Macdonald 1987; 1989) indicate that adult capybaras rarely migrate or move a significant distance away from a small (10 ha on average) home range defended as a common territory by all adult group members for three years or more. Therefore, the two 'populations' formed were effectively isolated from each other as there was little or no interchange of animals between the two. In the present report, the average body weight and age structure of the capybara populations from these two areas, one harvested and one spared, are compared. Also, as the ranch failed to obtain a license to slaughter capybaras in 1987, 1988 or 1989, the age structure of animals killed in the 1990 slaughter was compared to that in the 1982-84 sanctuarium. The relevance of the differences in relation to the management program are discussed.

During the slaughter, managerial guidelines require workmen to kill the largest and apparently older

Tabla 1. Correspondence between humeral age classes and actual age for capybaras (after Ojasti, 1973).

Humerus age class	Real age		
I	0-3 months		
II	5-12 months		
III	12-18 months		
IV	18-36 months		
V	4 years*		
VI	5 or more years		

^{*}This age class is not well defined, according to Ojasti's results. Its time bracket was assumed to lie between that of age classes IV and VI, on the basis on the intermediate state of its sutures.

animals, especially males. To test the efficacy of their method while assessing in more detail how the slaughter affects the structure of the population, the age distribution of a sample of animals from the 1990 slaughter was compared with that of animals having died of natural causes within the previous few months. Skeletal size, assessed from humerus length, was also compared.

STUDY AREA AND METHODS

This study was carried out at Hato El Frio (7° 46' N; 68° 57' W) a cattle ranch in the Llanos of southern Venezuela, a vast region of open, seasonally flooded grassy plains (see habitat details in Herrera and Macdonald 1989). This ranch holds a population of more than 20,000 capybaras in an area of approximately 80,000 ha. Capybaras have been harvested for commercial purposes in this ranch at least since the beginning of this century.

A marked wet-dry seasonality is the most important climatic feature of the Llanos, causing widespread flooding in the wet season (generally May to October) and severe drought during the driest months (November to April). Land in this region is used almost exclusively for extensive cattle ranching (cattle densi-

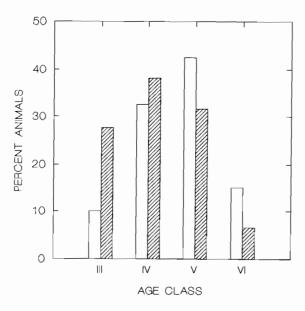


FIGURE 1. Percentage of dead capybaras in each of the four adult age-classes at Hato El Frío (Venezuela) in 1984 (see text and Table 1). Open bars: Within the 1982-1984; 400-ha sanctuarium (without a slaughter), N = 40; Striped bars: In the rest of the ranch (20-30% animals culled every year), N = 76.

ty: one head per 2 to 4 ha) but in some ranches a substantial profit is made from the management of capybaras.

Under an agreement with the ranch management, an area of some 400 ha was spared from the slaughter during the three years that the first stage of field work lasted. In February of 1982, 1983 and 1984, capybaras were captured in the spared area with the help of cowboys and marked with plastic collars and eartags for individual identification. The length of one hind foot of all captured animals was measured to the nearest millimeter. The weight of the animals was estimated using a device called 'weighband' (Dalton Supplies, Nettlebed, Oxon, UK) designed to estimate the weights of pigs and cows. This band is placed around the girth of the animal and gives a measure in Kg. Girth circumference has been shown to be the best indicator of weight in several wild mammalian species (Talbot and MacCullock 1965, Nagy et al. 1984). The band was calibrated by weighing on a spring balance (±⁸1 kg) 12 captive individuals (six males and six females) and obtaining the weighband estimate. The correlation coefficient found between weighband estimate and real weight was highly significant (0.918, d.f.=10, p<0.01). Weight estimates in the field were converted to actual weights using the regression line equation ($r^2 = 0.820$):

$$RW = -18.20 + 1.13 WW$$

where RW is the real weight of the animals and WW is the weighband weight estimate.

Note that the equation is linear because the scale on the weighband is not. Young (less than 1 year old) animals captured were excluded from this analysis since the weighband could not be used on them.

The age of dead animals was estimated from the order of ossification of humerus sutures (Ojasti 1973). Humeri from marked individuals dead in 1984 in the spared area and from animals dead the same year of natural causes (not killed in the slaughter) from the rest of the ranch (where the slaughter had been carried out normally) were collected and assigned to one of Ojasti's (1973) six age classes, whose approximate correspondence to real age appears in Table 1.

Young animals are under-represented in both samples, since their carcasses either disappear completely or are more difficult to find. Furthermore, because of difficulties at capturing young animals, the biases against young are probably not equal in both samples. For this reason, only age classes III-VI will be used in the analysis.

In 1990, a sample of humeri was collected from animals killed in the slaughter. These bones were assigned to age classes and measured (nearest mm) to assess skeletal size. A further sample was collected from animals having died of natural causes within the dry season prior to the slaughter. Animals dead in the wet season or before could be recognized easily since rain would have left the carcasses much cleaner; such animals were not collected. Age and size were also recorded for these bones.

RESULTS

Mean weight of capybaras of both sexes captured in the 1982-1984 study area (sex ratio in all years did not depart significantly from 1:1) increased about 1.5 kg per year (Table 2). The 1982 sample can be considered a random sample of the harvested population since the animals had been affected by a slaughter less than a year earlier. Weights probably correspond to yearly minima since they were all taken in the dry season, a time of year when the animals have lost weight (Ojasti 1973). The differences found between years (pooling both sexes) are significant (ANOVA: F=14.36; d.f.=2, 784; p<0.001; Table 2). Note also a slight reduction in variability (see SD values) over the years.

Foot length, on the other hand, did not significantly increase over the three years (both sexes pooled, ANOVA: F=0.05; df=2, 781; N.S. Table 2). This apparently contradictory result is not inconsistent with the observed change in body weight since Ojasti (1973) found that a capybara's weight continues to increase after foot length has ceased to grow.

In 1982, no sexual dimorphism in weight was found, but by 1983 a slight dimorphism had developed, which was increasingly apparent in 1984 (Table 2). In foot length, however, sexual dimorphism was present in all years with only a slight increase towards 1984 (Table 2).

Forty-two humeri from marked animals dead within the study area in 1984, i.e. from animals spared from the slaughter for three years, and 98 from animals dead in other parts of the ranch were collected and assigned to Ojasti's (1973) six age groups. Figure 1 shows the distributions of age classes III to VI in these samples. This Figure shows that, within the study area, 57.5% of the adult animals were four years old or more (age classes V and VI), while only 38.2% were that old in the harvested population. The median age of animals dead within the study area in 1984 was age-class V while that of the general population in the rest of the

ranch was IV. This difference is significant (Mann-Whitney test, p=0.0194). Since age class IV covers ages 1.5 to 3 years old while animals of age class V are on average 4 years old (see Table 1), this difference represents between one and two years of actual age.

The age structure of animals dead of natural causes in 1990 (again after three years without a slaughter) did not differ significantly from that of animals in the 1982-84 sanctuarium (median age in 1990= 5, n=74; Mann-Whitney test, p=0.4344; Figs. 1 and 2). Nor did the age structure of the sample of natural deaths differ from the 1990 slaughter sample in age structure (Median age of culled animals = 5; n=483; Mann-Whitney test, p=0.1291; Fig. 2) or humerus length (Mean length of 1990 natural death sample = 175.4; n=483; 1990 slaughter sample = 176.1; n=74; Student's t-test, t=0.59, p=0.55).

DISCUSSION

The increase in body weight observed in capybaras after three years of no harvesting is probably due to the fact that, because the slaughter takes preferentially larger individuals, the harvested population is maintained at a low average body weight, while the animals in the 'sanctuarium' had a chance to grow. Also, the

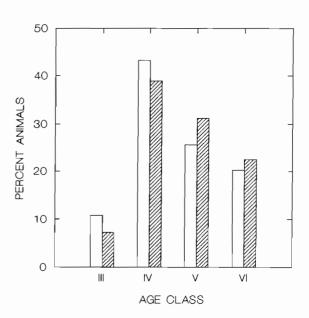


FIGURE 2. Percentage of dead capybaras in each of the four adult age-classes at Hato El Frío (Venezuela) in 1990 (see text and Table 1). Open bars: From natural causes, N = 74. Striped bars: Killed in the slaughter, N = 483.

THE EFFECT OF HARVESTING ON THE AGE STRUCTURE

Tabla 2. Sexual dimorphis in body weight (kg) and hind foot lenght (mm) adult capybaras for each year of capture in the study area (without slaughter). Entries are means \pm standard deviations. Results of a one-way ANOVA are presented for each year for a between-sex comparison. N = sample size.

Year	Variable	Box sexes	Males	Females	\mathbf{F}	
					Between	Sexes
	Weight	38.2 ± 6.3	38.4 ± 6.6	37.9 ± 6.1	0.23	***
1982	Foot lenght	227.0 ± 10.1	230.5 ± 9.5	223.7 ± 9.6	21.83	
	N	174	84	90		
	Weight	39.6 ± 6.1	40.3 ± 6.2	38.9 ± 5.8	4.02	
	•					*
1983	Foot lenght	227.3 ± 9.6	230.7 ± 9.4	223.6 ± 8.3	44.28	
	N	289	138	151		***
	Weight	41.1 ± 5.7	42.4 ± 5.8	39.9 ± 5.5	16.39	

1984	Foot lenght	227.3 ± 9.8	231.5 ± 9.0	223.0 ± 8.7	73.03	
	N	324	160	164		***

^{*} p < 0.05

way the slaughter is carried out in the field is likely to locally enhance its effect, in the following sense. Although the census covers the whole ranch systematically, and the number to be culled is calculated on the population estimate thus obtained, the slaughtermen proceed in the most convenient way for them, which is to progress along the more easily accessible areas killing all adults found until the quota is reached. Since the study area was easily accessible, the slaughter had probably been affecting most adult animals equally and not just 30% of them. Also, since the number to be culled is calculated on the basis of total population size -including young-, the proportion of animals in adult age classes killed is greater than 30%.

Ojasti (1973), using animals out of the harvesting program for five years, did not find sexual dimorphism in body weight. Although a significant sexual dimorphism in body weight in animals spared from the slaughter for three years was observed in this study, it should be pointed out that differences found were only slight: in 1984, males averaged only 6.3% heavier than females. The dominance relations existing among male capybaras, in which the largest male in the group held the highest rank and also had greater reproductive success (Herrera 1986), suggest that through male competition and possibly sexual selection males should tend to become bigger than females. However, the differences in reproductive success of heavier males are relatively small (Herrera 1986), especially when

compared to other highly polygynous and highly dimorphic mammals such as Red deer (Clutton-Brock et al. 1982) or Elephant seals (LeBoeuf and Reiter, 1988), suggesting that selection for larger size in capybara males is not strong. Harsh conditions during the dry season and perhaps thermoregulation (Pereira et al. 1980) are also likely to place a ceiling to the largest size a male can reach, thereby limiting the degree of dominance he can exert.

The increase in mean age in the 1982-1984 study area and in the whole ranch in 1990 (in both cases after three years without a slaughter) is probably also a consequence of the moratorium, as explained above for body weight, and it probably is the underlying cause of the change in body weight observed, since Ojasti (1973) found a correlation between humeral age and body weight. It is probable that dispersal also played a role in the reduction of mean age in heavily harvested areas, as young animals from higher density areas (forested or spared) are able to colonize the lower density areas produced by the slaughter (see Cordero and Ojasti, 1981). Thus, heavily harvested areas would have a greater proportion of young individuals.

The fact that the age structures and skeletal sizes of animals killed and those of animals dead from natural causes in 1990 are not different suggests that the slaughter does indeed take the same portions of the adult populations that would have died anyway. Thus, it seems that the principle behind the management

^{***} p < 0.001

program of Ojasti (1973) -to replace natural mortality by a cull- is being maintained in practice.

The lower average age and body weight of animals in the harvested population suggests that the productivity of a capybara population under the current management program may be below its potential maximum, since older females have bigger litters and heavier females are more often pregnant at any one time than smaller ones (Ojasti 1973). Thus, a population of greater average age and weight is likely to be more productive (in terms of number of young produced every year) than the presently managed population. It would be possible, then, to include a "fallow" season every few years that would increase the average age of females and thereby increase productivity. To kill a lower proportion of females or to spare the larger ones might have a similar effect. However, side effects of an increase in productivity -and therefore densitysuch as overgrazing or dispersal to marginal habitats or to neighboring ranches with lower capybara densities are unknown and need to be taken into account. Only longer-term studies will make clearer which is the best management strategy.

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LITERATURE CITED

- Begon, M., S. Townsend and T. Harper. 1990. Ecology 2nd ed. Blackwell Scientific Publications, Oxford.
- Clutton-Brock, T.H., F.E. Guinness and S.D. Albon. 1982. Red deer: Behaviour and ecology of two sexes. Chicago University Press, Chicago.
- Cordero, G.A. and J. Ojasti. 1981. Comparison of capybara populations of open and forested habitats. Journal of Wildlife Management 45: 267-271.
- Herrera, E.A. 1986. The behavioural ecology of the capybara, *Hydrochoerus hydrochaeris*. D. Phil. Thesis, University of Oxford.
- Herrera, E.A. and D.W Macdonald. 1987. Group stability and the structure of a capybara population. Symposium of the Zoological Society of London 58: 115-130.
- Herrera, E.A. and D.W. Macdonald. 1989. Resource utilization and territoriality in group-living capybaras (Hydrochoerus hydrochaeris). Journal of Animal Ecology 58: 667-669.
- Humboldt, A. von, 1816. Voyage aux régions equinoxiales du nouveau continent. Imprimerie J. Smith. Paris 13 vols.
- Krebs, C.J. 1985. Ecology: The experimental analysis of distribution and abundance. 3rd ed. Harper & Row, New York.
- LeBoeuf, B.J., and J. Reiter. 1988. Lifetime reproductive success in Northern elephant seals, p 344-363. *In Clutton-Brock*, T.H. (ed.), Reproductive success. The University of Chicago Press, Chicago.
- Logan, K.A., L.L. Irwin and R. Skinner. 1986. Characteristics of a hunted lion population in Wyoming. Journal of Wildlife Management 50: 648-654.
- Nagy, J.A., M.C. Kingsley, R.A. Russell, A.M. Pearson and B.C. Gorki. 1984. Relationship of weight to chest girth in the grizzly bear. Journal of Wildlife Management 48: 1439-1440.
- Ojasti, J. 1973. Estudio biológico del chigüire o capibara. FONAIAP, Caracas.
- Ojasti, J. 1980. Ecology of capybara raising on inundated savannas of Venezuela. Tropical Ecology and Development 1980: 287-293.
- Ojasti, J. 1991. Human exploitation of capybara. *In*: Robinson, J.G. and K.H. Redford (eds.), p 236-252. Neotropical Wildlife Use and Conservation. University of Chicago Press. Chicago.
- Ojasti, J. and G. Medina. 1972. The management of capybaras in Venezuela. Transactions of the North American Wildlife and Natural Resources Conference 37: 268-277.
- Pereira, J.N., D. McEvan and E. Finley. 1980. The structure of the skin of the capybara. Acta Cientifica Venezolana 31: 361-364.
- Talbot, M. and J.S.G. McCullock. 1965. Weight estimates for East African mammals from body measurements. Journal of Wildlife Management 29: 84-89.