

tion in Galapagos fur seals and sea lions: cues used and functional significance. *Behaviour*, 78:21-42.  
 TRILLMICH, F., AND P. MAJLUF. 1981. First observations on colony structure, behavior, and vocal

repertoire of the South American fur seal (*Arctocephalus australis* Zimmermann, 1783) in Peru. *Zeitschrift für Säugetierkunde*, 46:310-322.

*Submitted 13 December 1989. Accepted 3 April 1990.*

*J. Mamm.*, 72(1):206-208, 1991

## REPRODUCTIVE BIOLOGY OF CAPTIVE CAPYBARAS

COLIN A. CHAPMAN

*Peabody Museum, Harvard University, Cambridge, MA 02138*

Knowledge about the reproductive biology of the capybara (*Hydrochaeris hydrochaeris*) is limited and where published estimates of reproductive characteristics are available, small samples often limit the reliability and generality of the values. An objective of this study was to describe a series of reproductive characteristics for captive capybaras and compare the findings to published estimates from free-ranging populations. A comparison of this nature not only provides descriptive information, but also provides a basis for speculation on the value of applying zoo observations to the management of free-ranging populations. Further, capybaras are the largest extant species of rodent. This characteristic, in conjunction with their social, group-living behavior, sets them apart from most other rodents, and these anomalous features might be expected to relate to other aspects of their biology. Thus, as a second objective I compared the average litter size of capybaras to other rodents.

A questionnaire was sent to all zoos listed in the *International Zoo Yearbook* from 1971 to 1986 as having breeding colonies of capybaras. Information was requested concerning origin, age, weight, date of birth of litters, reproductive history, sex of infants, and age at death. Thirty-one zoos responded to the request. From the information provided, the following variables were derived for each reproducing individual: sex, age (estimated or known), weight, and age at death (if applicable). The reproductive history of each female was determined, and information was extracted concerning age at first birth, interbirth interval, date of each birth, sex of each infant, and whether each infant survived to 1 year of age. For incomplete questionnaires a series of conservative criteria was established to exclude potentially erroneous or misleading data. As the first criterion, whenever gaps occurred in the zoo records, information related to interbirth interval, mortality rate of infants, and sex of successive infants was extracted only to the beginning of the period when data were not recorded. Secondly, if a litter was born into a colony, but its mother was unknown, subsequent data on all adult females in the colony were excluded. And finally, if an infant survived to 6 months of age, then was shipped to another zoo, they were considered to have survived to 1 year of age. If an infant was transferred between zoos before 6 months, it was excluded from the analysis of survival.

From records provided by zoos, information on 163 litters was obtained. The average litter size was 3.3 young, but litter size ranged from one to seven. There was no significant difference in the size of litters produced over the lifespan of a female (between first through seventh litters; one-way analysis of variance,  $F = 0.500$ ,  $P = 0.811$ ). Ojasti (1983) reported that the average litter size of free-ranging capybaras in the Venezuelan llanos was four. Of the capybaras born in captivity, 66% survived to 1 year of age, and the survival rate of offspring did not increase with age of the mother (survival rate from first through seventh litters,  $F = 1.096$ ,  $P = 0.369$ ). The survival rate of capybaras in zoos was higher than in the wild. Ojasti (1983) reported that infant mortality exceeds 50% in free-ranging populations. The sex ratio of the litters was 1:0.992 in favor of females and did not vary with the number of litters produced by a female ( $F = 1.541$ ,  $P = 0.176$ ). The mean ( $\pm SE$ ) interbirth interval for females was  $251 \pm 12.9$  days (range, 124-523 days,  $n = 58$ ). As with the other reproductive parameters, interbirth interval did not vary with the number of litters a female had produced ( $F = 1.442$ ,  $P = 0.218$ ).

At some localities, free-ranging capybaras breed throughout the year (Alho et al., 1987a, 1987b; Lord and Lord, 1988; Ojasti, 1983), whereas at other sites a seasonal peak in births has been observed near September (Lord and Lord, 1988; Ojasti, 1983). In captivity, capybaras appear to maintain this seasonal breeding pattern

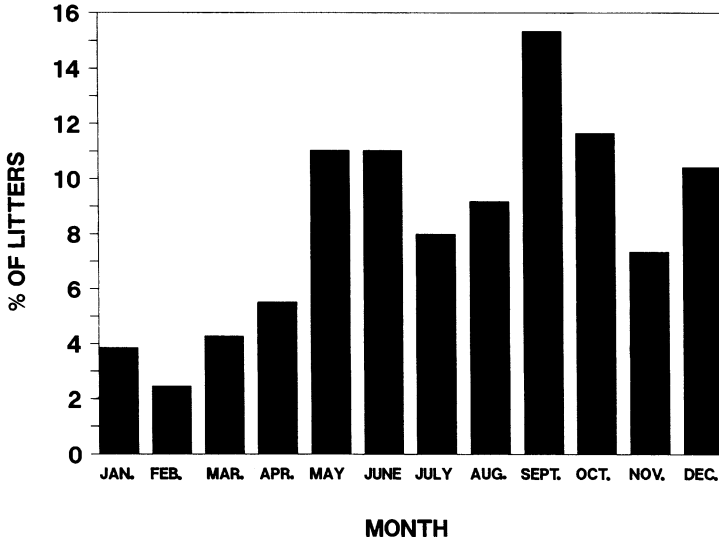


FIG. 1.—A frequency histogram of the percentage of capybara (*Hydrochaeris hydrochaeris*) litters born in zoos that occurred in each month of the year ( $n = 163$  litters).

(Fig. 1). Birth seasonality is maintained in zoos despite removal of cues (such as the seasonal availability of food and water) that potentially could synchronize breeding.

Zoo records indicated an average ( $\pm SE$ ) age at birth of first litters was  $31 \pm 2.5$  months (range, 12–53 months,  $n = 19$ ). Based on a recorded gestation period of approximately 153 days (Weir, 1974; Zara, 1973), females in captivity first reach maturity at ca. 26 months of age. Ojasti (1983) estimated the age at maturity from wild populations as 18 months.

From zoo records, the oldest capybara in captivity lived 11.3 years. In wild populations, the oldest individuals are estimated to be 5 years old; however, these populations are heavily harvested (Lord and Lord, 1988).

To determine if capybaras exhibit atypical reproductive traits when compared to other members of the order, I obtained estimates of average litter size for rodents ( $n = 105$  species) from Eisenberg (1981). Because litter size is a function of body weight (Eisenberg, 1981), I regressed body weight against litter size to determine if capybaras were a significant outlier. For rodents, litter size was a function of body size ( $r^2 = 0.30$ ,  $P = 0.002$ ); however, capybaras did not represent a statistically significant outlier from what would be predicted based on their body size ( $P > 0.05$ ).

Estimating reproductive characteristics for mammals in the wild is difficult. Not only must individually recognizable animals be monitored for long periods, but logistical constraints often limit sample size. One means of obtaining information on the reproductive biology of a species is by analyzing zoo records. However, caution must be used in interpretation and application of these data, as some reproductive parameters may be altered by the living conditions in zoo environments. For example, the estimated age at maturity for capybaras housed in zoos is much greater than for free-ranging animals. One possible reason for this discrepancy is that capybaras often are housed in adult pairs, and a maturing female may be inhibited from mating with her father and may be subordinate to the older female, which may be her mother.

I thank the zoo personnel who collected the information and answered the questionnaire, and L. Chapman, R. Lord, and M. Bryant for helpful comments on this paper. This research was conducted partially while I was a member of the Department of Biology of McGill University and was funded by the National Sciences and Engineering Research Council (Canada).

#### LITERATURE CITED

- ALHO, C. J. R., Z. M. S. CAMPOS, AND H. C. GONCALVES. 1987a. Ecologia de capivara (*Hydrochaeris hydrochaeris*, Rodentia) do Pantanal:—I. Habitats, densidades e tamanho de grupo. *Revista Brasil Biologia*, 47:87–97.
- . 1987b. Ecologia de capivara (*Hydrochaeris hydrochaeris*, Rodentia) do Pantanal:—II. Atividade, sazonalidade, uso do espaço e manejo. *Revista Brasil Biologia*, 47:99–110.
- EISENBERG, J. F. 1981. The mammalian radiations:

- an analysis of trends in evolution, adaptation, and behavior. The University of Chicago Press, Chicago, 610 pp.
- LORD, R. D., AND V. R. LORD. 1988. Cross checking censuses and a model of the annual cycle of mortality and reproduction in capybaras (*Hydrochaeris hydrochaeris*). *Studies on Neotropical Fauna and Environment*, 23:213–224.
- OJASTI, J. 1983. Ungulates and large rodents of South America. Pp. 427–439, *in* Tropical savannas (F. Bourliere, ed.). Elsevier Scientific Publishing Co., Amsterdam, 730 pp.
- WEIR, B. J. 1974. Reproductive characteristics of hystricomorph rodents. Symposium of the Zoological Society of London, 34:265–301.
- ZARA, J. L. 1973. Breeding and husbandry of the capybara *Hydrochoerus hydrochaeris*. *International Zoo Yearbook*, 13:137–139.

Received 21 August 1989. Accepted 8 March 1990.

*J. Mamm.*, 72(1):208–210, 1991

## INFLUENCE OF AGE ON THE REPRODUCTIVE EFFORT OF MALE REINDEER

ILPO KOJOLA

*Finnish Game and Fisheries Research Institute, Game Division,  
Meltaus Game Research Station,  
SF-97340 Meltaus, Finland*

In polygynous mammals, such as reindeer (*Rangifer tarandus*), males usually initiate their reproductive life later than females (Greenwood, 1980; Johnson, 1986). This is an apparent consequence of male–male competition for mates. In ungulates, fighting success of males depends on body size (Bergerud, 1974; Clutton-Brock et al., 1982). Male dominance, the major determinant of mating success in reindeer, largely depends on body size and antler size (Bergerud, 1974; Prowse et al., 1980). Male reindeer reach puberty at the age of 6 months (Leader-Williams, 1988), but in natural populations they rarely breed before the age of 4 years (Bergerud, 1974). Because young males should benefit from rapid growth rates, adult males are not expected to have evolved an ability to invest heavily in reproduction before they reached prime age.

Herein, I report on a study of breeding behavior and reproductive effort of male reindeer in relation to their age and body mass. This study was conducted mainly with semidomesticated reindeer in 1986 in Kaamanen, Finnish Lapland (69°N, 27°E). Before the rut, females were divided by local herders into six groups of 10–12 each. These groups then were introduced into separate enclosures. Adult males were introduced as follows: two yearlings, two yearlings, a 3-year-old male and a yearling, a 3-year-old male, a 4-year-old male, and a 5-year-old male. The area of enclosures were 50, 50, 60, 40, 3, and 2 ha, respectively. Some data were gathered on an enclosed herd of wild reindeer in 1981–1983 in central Finland (69°N, 25°E). This herd was kept in a 15-ha enclosure. It was composed of two prime-aged males, one–three yearling males, one 2-year-old male, and six–nine adult females. The behavior of reindeer was observed by the focal-animal method (Altmann, 1974). A male was a focal animal 1–4 h at a time. Data were gathered during the peak of the rut (for semidomesticated reindeer, 25 September–10 October; for wild reindeer, 1–10 October). I conducted observations during daylight, between 0900 and 1800 h. When measuring the dependence of behavioral traits on the age or body mass, I considered males for which I had >150 observations. For the wild reindeer, the sample was biased toward prime-aged males (Fig. 1). During observation, I recorded activity of male at 30-s intervals, distance from male to farthest female in the group at 5-min intervals, and number of low-stretch postures and hunching postures. Hunching usually involves urination on the hind feet (Bergerud, 1974). Low-stretch posture is one of the most pronounced forms of courtship behavior. Urinating on the hind feet is associated with odor-marking behavior (self-marking—Espmark, 1964). Reindeer were fed daily in all enclosures. In addition to the males in the semidomesticated herd, one 6-year-old male, herding females in a 900-ha, enclosed pasture, was weighed before and after the rut. Nonparametric statistical tests (Siegel, 1956) were used for behavioral data where possible. To measure the dependence of proportional weight loss on age or body mass, I performed simple regressions. All *P* values presented are two-tailed.

Among the semidomesticated males that dominated within their enclosure, the proportion of time spent