This is to certify that the

thesis entitled

POPULATION CHARACTERISTICS OF *AGOUTI PACA* (RODENTIA) IN COLOMBIA

presented by

Stephen Frederick Collett

has been accepted towards fulfillment
of the requirements for

Ph.D degree in ZOOLOGY

Rollin H. Baker

Major professor

Date 23 February 1981

POPULATION CHARACTERISTICS
OF *AGOUTI PACA* (RODENTIA)
IN COLOMBIA

By

Stephen Frederick Collett

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1981

ABSTRACT

POPULATION CHARACTERISTICS
OF *AGOUTI PACA* (RODENTIA)
IN COLOMBIA

by

Stephen Frederick Collett

The paca (*Agouti paca*) is a large (> 7 kg) nocturnal rodent that is intensively hunted by peoples of tropical America. Characteristics of reproduction and age structure were evaluated for a sample of 205 pacas collected from narrow gallery forests in the Llanos Orientales of Colombia. Fecundity was estimated from gross examination of female reproductive tracts and from thin sections of ovaries. Individual age was determined from counts of seasonal annulations seen in thin sections of the cementum tissue of the first upper molar. Observations on foods, behavior, use of habitat, and burrows, were made in the course of hunting. Crude estimates of abundance were also obtained.

Females first gave birth at approximately one year of age, with only one of 43 females less than one year old having given birth. Forty-two of 69 females of reproductive age were pregnant. There was no indication of seasonal clustering of births, or of significant age-specific variation in fecundity. A post-partum estrus was indicated by twelve females that were simultaneously parous and pregnant. The mean interval between births was calculated at 191 days. All pregnancies were of single fetuses. The estimate of fecundity for all adult females was 0.95 ♀♀/♀/yr.

Among subsamples defined by collecting methods or collecting sites, both sex ratios and age-structure regressions proved to be heterogeneous. Significantly more males than females were obtained when hunting from canoes. For the combined sample, adult age structure was best described by log-linear regression of numbers on age, both for males and for females, implying a pattern of constant annual survivorship if the population is assumed to be stationary. Annual survivorship was estimated to be 0.800 for females and 0.867 for males. The age of the oldest individuals was estimated to be between 12 and 13 years.

Examination of stomach contents and direct observations of feeding indicated that pacas ate fruits almost exclusively. Twenty-three specific food items were identified. Availablity of suitable fruits did not appear to be limited at any time of the year. All observations of paca activity occurred in gallery forests at night. Of 108 observations of pacas in the wild, 86 were of solitary individuals. Most instances of intraspecific contacts involved females with small offspring. Pacas in the Llanos spend daylight hours in extensive, individual burrows, eleven of which were excavated. Abundance estimates ranged from 38 to 56 adult pacas per km^2 of forest.

Relationships among fundamental demographic parameters for the paca are described by an algebraic model in five terms, using simplifying assumptions of constant adult survivorship, constant fecundity, and stationary population. The modcl estimates survivorship of juveniles at 0.23 from birth to the age of 1 1/2 years. Effects of increasing or decreasing population size on estimated juvenile survivorship are also considered. Exploitation by man appears to be a major source of mortality for the population, accounting for as much as 40% of adult deaths. The impact of local hunters is probably ameliorated as a result of hunting efforts being concentrated in relatively few, accessible forest galleries. Intraspecific interactions such as territorial behavior may function in determining population size and recruitment of young adults into heavily-harvested populations. The demographic pattern of high adult survivorship and low fecundity is more comparable to game ungulates than to most rodents.

ACKNOWLEDGMENTS

I wish to thank the members of my guidance committee, Rollin H. Baker (Chairman), Richard Hill, Peter Murphy, and Howard Hagerman.

In the initial stages of the paca project, I was greatly aided by John Beaman, Walt Conley, Thomas Yuill, and Eustorgio Méndez. The assistance of Dr. John Hunter of the Latin American Studies Center, MSU, was instrumental in accomplishing a preliminary trip to prospective field sites in Panama and Colombia during March of 1975. Initial funding for the field work was provided by Grant 71-3432 to R. H. Baker from Midwest Universities Consortium for International Activities (MUCIA). The collaboration of Instituto del Desarollo de los Recursos Naturales Renovables (INDERENA), and of Instituto Colombiano Agropecuario (ICA), is gratefully acknowledged. I thank Carlos Uribe, Ceferino Hernández, Joaquín Castiblanco, Raimundo Evaristo, Teófilo Villamizar, and Alejandro Jerez of INDERENA for their contributions to the field work at Territorio Faunistico El Tuparro, and Jorge Hernández Camacho and Victor Vásquez for administrative support in Bogotá. Invaluable assistance was provided by Cesar Lobo, Guillermo Restrepo, and Fernando Lozano of ICA.

Completion of the study would not have been possible without the generous logistical, financial, and interpersonal help of the people of the Tulane University International Center for Medical Research (CIDEIM) of Cali, Colombia. In particular, I thank Paul Beaver,

Thomas Orihel, Margarita de Izquierdo, Stephen Ayala, Wieslaw Kozek, Pablo Barreto, and Kirby Kloter. I am especially indebted to Antonio D'Alessandro, director of CIDEIM-Cali, for constant and unselfish support and encouragement.

Many members of the Centro Internacional de Agricultura Tropical (CIAT) organization provided invaluable assistance, both in Cali and at the Carimagua field station. James and Joyce Spain cheerfully provided logistical and moral support, often under trying circumstances. Administrative support was provided by Fernando Bernal, Guillermo Matéus, and Orlando Martínez. Ablelardo Cardenas, Ramón Gualdrón, Jorge Quintero, and Juan Reyes also helped in various ways.

During the last two years of my stay in Colombia, I was supported by Peace Corps/Colombia. Ernesto Barriga was a great help in all phases of the study. I also thank José Sorzano and Grace de Murillo for essential non-technical help. Volunteers Charles McClung, Raleigh Blouch, Bill Lamar, Paul Gertler, Wally McKay, and Marc Weitzel all contributed substantially to my research. Tom Defler and Paul Vincelli provided information essential to identifying many of the plants involved in the study.

I am particularly indebted to Jon Yates, Mauricio Barreto, and Sharon Halstead de Porre of the CIDEIM field station at El Porvenir for unfailing cooperation. The entire people of El Porvenir earned my eternal appreciation for their interest in furthering the research efforts of the CIDEIM program. Simon Peña of Hato Caviona collaborated most willingly with all of us.

The mathematical treatment presented here would not have been possible without fruitful discussions with Donald Hall, John Hart, and

Robert Boling. Patient tutoring by Ira Longhini and Ronald Hamelink was equally essential. Donald Straney and Charles Cress provided advice regarding portions of the statistical treatments.

Many people in Colombia provided support in various non-professional ways. I especially appreciate the help of Paul and Sue Barry, Tony and Eve Salmon, Bill and Nancy Lamar, Sharon Fish, Richard Cross, Brian Hempstead, Flavio Barney, and Cutto Maniglia.

The greatest contributions to my knowledge of the elusive paca came from experienced local hunters, who still know much more than I about the species. To these men, Darío Angel, Fernando Camico, Genaro Useche, Raimundo Evaristo, Jorge Ramírez, Cipriano Rodríquez, Fernando Batista, and Jose Gutiérrez, I express my most humble gratitude.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF SYMBOLS

x	Age. The midpoint of each year class.
α	Age at which females first give birth.
∞	Infinity.
ω	Longevity. The midpoint of the oldest age class.
λ	Finite rate of increase.
l_x	Survivorship. The probability at birth of an individual surviving to age x.
l_α	Juvenile survivorship. The probability of surviving from birth to age $x = \alpha$.
p	Annual adult survivorship. The probability of surviving from age x to age $(x+1)$ for all $x \geqslant \alpha$.
m_x	Fecundity. Expected number of female offspring per year per female of age x.
$\bar{m}$	Mean annual fecundity for females age $x \geqslant \alpha$.
s_x	Age class. The proportion of the population that consists of individuals of age x.
Π	Product function.
Σ	Summation function.
e	The base of the natural logarithms (= 2.3026).
ln	Natural logarithm.
μm	Micrometers (= 1.0×10^{-6} meters).

INTRODUCTION

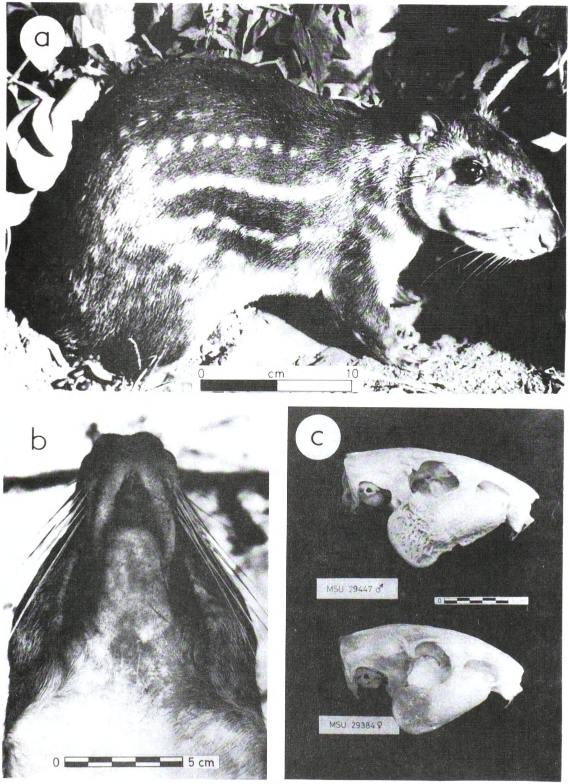
The paca, Agouti paca, is a large, nocturnal, frugivorous rodent found in a variety of forest habitats from southern Mexico to northern Argentina. It belongs to the infraorder Caviomorpha (sensu Wood 1955), a group which first appears in the fossil record in the early Oligocene of South America. Isolated from other rodent groups until later invasions from North America when the land bridge was formed in late Pliocene or early Pleistocene (Hershkovitz 1969), the Caviomorpha have had approximately 60 million years during which to diversify. Recent species occupy a wide variety of ecological niches and have become a major component of the Neotropical mammal fauna. The larger species are especially remarkable for the convergences they demonstrate with various small ungulates of tropical Africa and Asia (Dubost 1968, Eisenberg and McKay 1974). Striking similarities can be seen in the morphology, behavior, dietary specializations, and habitat preferences of New World and Old World "ecological equivalents," with the paca most resembling the water chevrotain (Hyemoschus aquaticus) of central Africa.

Of the several larger caviomorph species which are hunted for their flesh -- and indeed are major sources of "bushmeat" in the Neotropical Region -- the paca is regarded as having the most flavorful meat. Beginning with the earliest accounts of New World mammals (i.e., Marcgrave 1648), naturalists have repeatedly made mention of the paca's edibility and of the methods used by local hunters to obtain it.

The genus *Agouti* Lacépède 1799 is included in the family Dasyproctidae, along with the genera *Dasyprocta* and *Myoprocta*. The synonym *Cuniculus* Brisson 1762 has been frequently but incorrectly used for the pacas (see Hopwood 1947). Two species of *Agouti* are currently recognized: *A*. (*Stictomys*) *taczanowskii* Stolzmann 1889, occurring above approximately 2000 m elevation in the Andes of Venezuela, Colombia, Ecuador, and Peru; and *A*. *paca* (Linnaeus 1766), living in virtually all forest habitats of the New World tropics below 2000 m. Eight subspecies of *A*. *paca* have been described (Ellerman 1940, Cabrera 1961).

The paca has a moderately robust and stout body. Adults typically attain a total length of 550 to 700 mm and a weight of 6.5 to 12 kg. The color of the upper parts varies from reddish brown to dark chocolate or smokey gray, with a variable number (two to seven) of irregular rows of white spots on the flanks (Figure 1(a)). The underparts are white. Pacas are characterized by the presence of unique pockets formed by a ventrolateral expansion of the maxillary bones in association with large lateral plates of the jugal portion of the zygomatic arch (Figure 1(b)). An external, fur-lined cheek pouch is associated with the maxillary pocket. The zygomatic plate is larger and more rugous in males than in females (Figure 1(c)). The montane *A*. *taczanowskii*, which will not be considered in the present study, is distinguishable from *A*. *paca* by its thick, wool-like fur, by splayed digits with long phalanges and weaker, characteristically curved claws, and by a somewhat reduced zygomatic plate that is less

Figure 1. Characteristics of Agouti paca. (a) Profile view of yearling male. (b) Ventral view of head of male. The external zygomatic pouches are visible as dark apertures on either side of the lower jaw. (c) Skulls of adult male (upper) and female (lower) pacas.


a
0
cm
10
b
0
5 cm
c
MSU 29447 ♂
0
MSU 29384 ♀

rugous and distinctively compressed dorsoventrally as compared to *A. paca*. The approximate distributions of the two species of *Agouti* are shown in Figure 2. Although *A. paca* appears to be restricted to forest, it does occupy a wide variety of forest habitats, including mangrove swamps, thin riparian growth, and dense upland scrub (Dalquest 1953, Leopold 1959, Mondolfi 1972). It occasionally becomes a pest of cultivated crops (Alvarez del Toro 1977). Pacas are terrestrial and nocturnal. They spend the day in burrows, the entrances to which they conceal with wads of leaf litter (Smythe 1970a). Their diet consists of fruits of a wide variety of sizes and textures (Smythe *et al*. in press).

It is somewhat difficult for the North American biologist to appreciate the commercial importance of medium- and large-sized Neotropical rodents. Game biologists generally think of sporting and edible mammals chiefly in terms of ungulates, some lagomorphs, and perhaps only tree squirrels among the rodents. Several surveys, however, have demonstrated the importance of the meat of agoutis (*Dasyprocta* spp.), the capybara (*Hydrochoerus hydrochaeris*), and especially the paca, in rural markets. In Manaus, Brazil, for example, the meat of the paca was found to be the most popular mammal dish on local restaurant menus, and ranked behind only tapirs and peccaries in total amount consumed (Wetterberg *et al*. 1976). Similar preferences were found among peoples of eastern Peru (Pierret and Dourejeanni 1966, 1967; Moro 1976). Rural peoples of tropical America depend upon caviomorphs such as pacas, agoutis, capybaras, and spiny rats (family Echimyidae) as much as they do ungulates, fish, and birds for bushmeat protein. The special preference for paca meat is almost universal

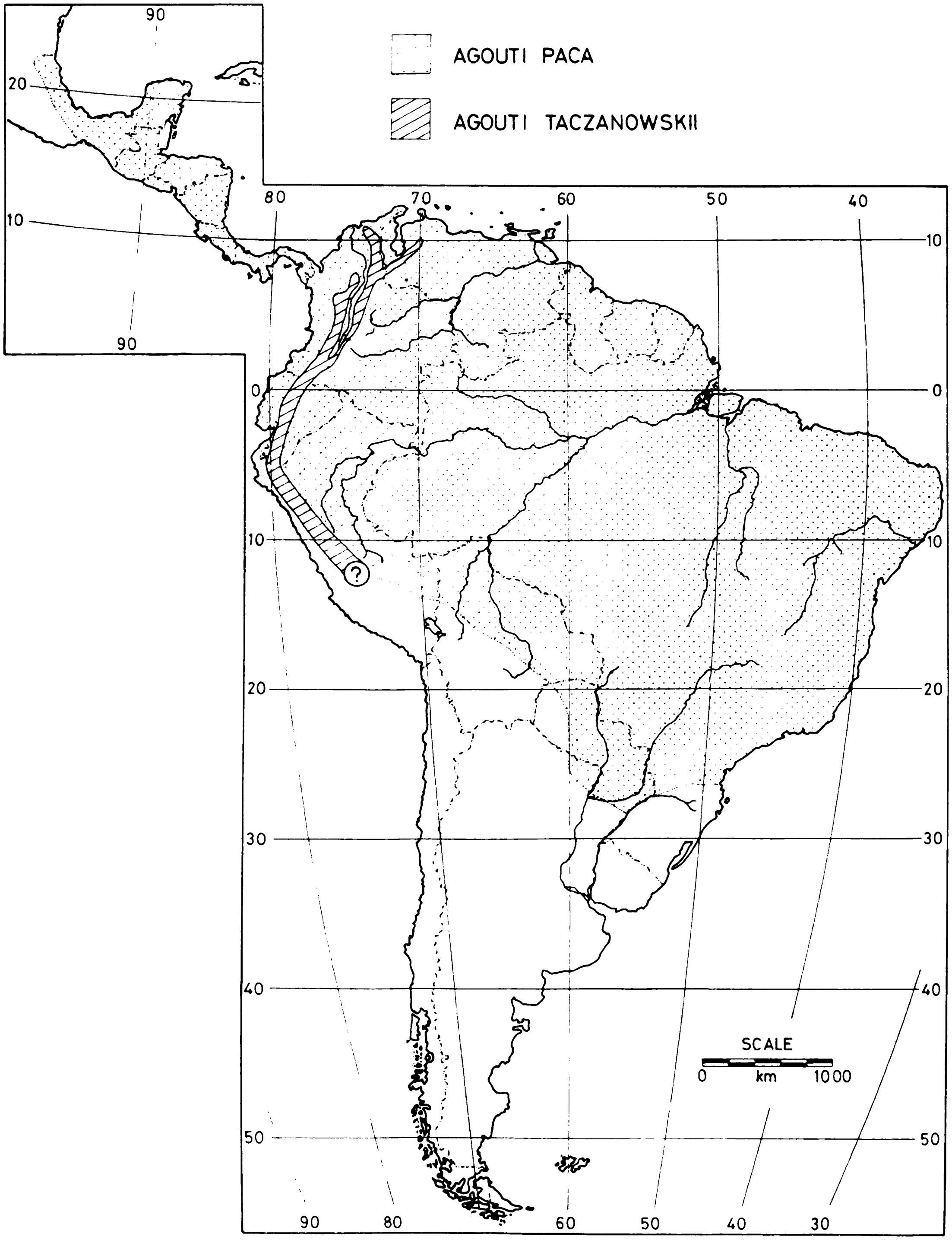


Figure 2. Geographical distribution of the genus Agouti.

throughout the species' range and is amply documented in the literature (e.g., Hingston 1932, Leopold 1959, Mendez 1970, Mondolfi 1972, Pine 1973).

The importance of pacas and agoutis in Neotropical forest communities is profound but difficult to quantify. From a survey of mammals in forest habitats at Parque Nacional Guatopo in Venezuela, Eisenberg et al. (1980) found that pacas and agoutis represented 16% and 13%, respectively, of the biomass of the thirty-five species comprising the community of non-volant mammals. Similar representations have been demonstrated for these two species in other Venezuelan habitats (ibid.) and in Panama (Eisenberg and Thorington 1973). If these figures are representative of mammalian communities elsewhere in the Neotropics, these two caviomorphs should command attention as heavily-exploited sources of food for man.

Only recently has attention been focused on the need to evaluate and to manage rationally the exploitation of edible caviomorphs. To date only the massive capybara has been studied in the context of a harvested resource (Ojasti and Padilla 1972, Ojasti 1973). Smythe (1970a, 1978) has investigated the behavior and ecology of the hare-sized Central American agouti (*Dasyprocta punctata*), a diurnal species in many ways similar to the larger paca. That author has repeatedly emphasized the developing problem of overexploitation of pacas and agoutis in Central America. Even so, long-term studies using live-trapping techniques in the relatively undisturbed situation of Barro Colorado Island, Panama (Smythe et al. in press) have thus far produced only very preliminary findings on the population density and reproduction of agoutis and pacas.

Much of the present knowledge of several aspects of the biology of caviomorph rodents is summarized in the reviews assembled by Rowlands and Weir (1974). These rodents show great diversity in reproductive patterns (Weir 1974a), behavior and social organization (Kleiman 1974, Eisenberg 1974), and ecology (Weir 1974b, Rowlands 1974). Nonetheless, with the notable exception of the domestic guinea pig, only a few of the more than 40 genera of caviomorphs have been studied in any detail. Other than an excellent review by Mondolfi (1972) and detailed observations by Smythe (1970a) and Lander (1974), the literature on pacas is scattered and consists primarily of numerous small notes or comments found in larger treatments of systematics or natural history. Despite its economic importance, the population biology of the paca, and the effects on paca populations of exploitation by man, have not been studied.

The principal objective of this study was to determine and describe the demographic characteristics of the paca, based on samples collected from a population in eastern Colombia. Demographic characteristics are patterns of the processes of birth, death, immigration, and emigration which in combination determine the numbers of individuals in a population and thus are the ultimate means by which population size changes over time. The traditional approach used in demographic studies is to determine the rate of increase of the population by actuarial methods such as life tables or projection matrices. However, these methods require large volumes of data obtained under rigorously defined conditions (Caughley 1966) and are acutely sensitive to sampling errors (Tait and Bunnell 1980), to inaccuracies of methods used to determine individual age (Rice 1980), and to residual effects of past fluctuations in reproduction and/or mortality (*e.g.*, Laws 1969). An alternative approach is to census population numbers repeatedly over time, which does little to explain the demographic changes underlying changes in numbers. It is perhaps more useful to attempt to understand how fundamental demographic parameters combine to form an overall life-history strategy (see review by Stearns [1976]). By life-history strategy, I mean the combination of age-specific fecundity and mortality functions by which a population maintains a favorable balance between births and deaths.

Mathematical models of hypothetical life-history strategies have long been used as heuristic tools for understanding the variety of strategies seen in nature (Cole 1954, Lewontin 1965, Emlen 1966, Charnov and Shaffer 1973). A body of theory has been developed which in large measure predicts the behavior of demographic parameters under different sets of biologically-meaningful simplifying assumptions. More recently, however, mathematically elegant descriptions of demographic relationships have been applied to natural populations of birds (Goodman 1974) and mammals (Shaffer and Tamarin 1973, Siler 1979).

The following analysis uses simple mathematical models to assess the degree to which the population of pacas is likely to exhibit temporal variations in the values of specific parameters such as litter size, frequency of breeding activity, age of first reproduction, length of reproductive life, and age-specific patterns of mortality. The goal of the model is to rank relevant parameters in terms of the sensitivity of the overall life-history strategy to changes in each of them. This elementary analysis serves two purposes: First, as a basis for more detailed studies of the relationships of natural factors, and of exploitation by man, on the overall population process of the species; and second, as a way of comparing the demographic patterns of the paca with those of other exploited species about which more is known concerning population regulation and management techniques.

With a view toward understanding the proximate biological mechanisms by which ultimate deomgraphic processes operate, observations on aspects of the behavior, feeding habits, use of habitat, and burrows, of the pacas I studied were recorded as a secondary objective in the course of collecting the sample of demographic analysis.

DESCRIPTION OF THE STUDY AREAS

The Llanos Region

Field studies were based at El Tuparro, Comisaría del Vichada, from November 1975 until October 1977, and at El Porvenir, Departamento del Meta, from April 1978 until October 1979. Both study areas are located in the Llanos Orientales ("Eastern Plains") of Colombia, a large lowland zone of seasonally dry savannas dissected by narrow gallery forest dendrites bordering the various streams (known locally as caños) of the watershed of the Orinoco River. The Llanos covers the entire northeastern lowlands of Colombia, comprising more than 260,000 km^2, or 22% of the surface area of the country. The locations of the two study areas within the region are shown in Figure 3. Brunnschweiler (1972) provides a review of the climate, soils, geomorphology, and economic demography of the region. The savanna vegetation is discussed in Beard (1953) and Blydenstein (1967), and detailed soil studies are presented in FAO (1965).

A profile view of a typical forest gallery along the lower Tomo River approximately 10 km upstream from the Orinoco is presented in Figure 4(a). The canopy, approximately 15 to 20 m above the forest floor, is in many respects similar to most of the collecting localities in the two study areas. Palms are conspicuous in many areas and are more abundant in swampy galleries than in the better-drained forest shown in Figure 4(a). This gallery is approximately 75 to 100 m

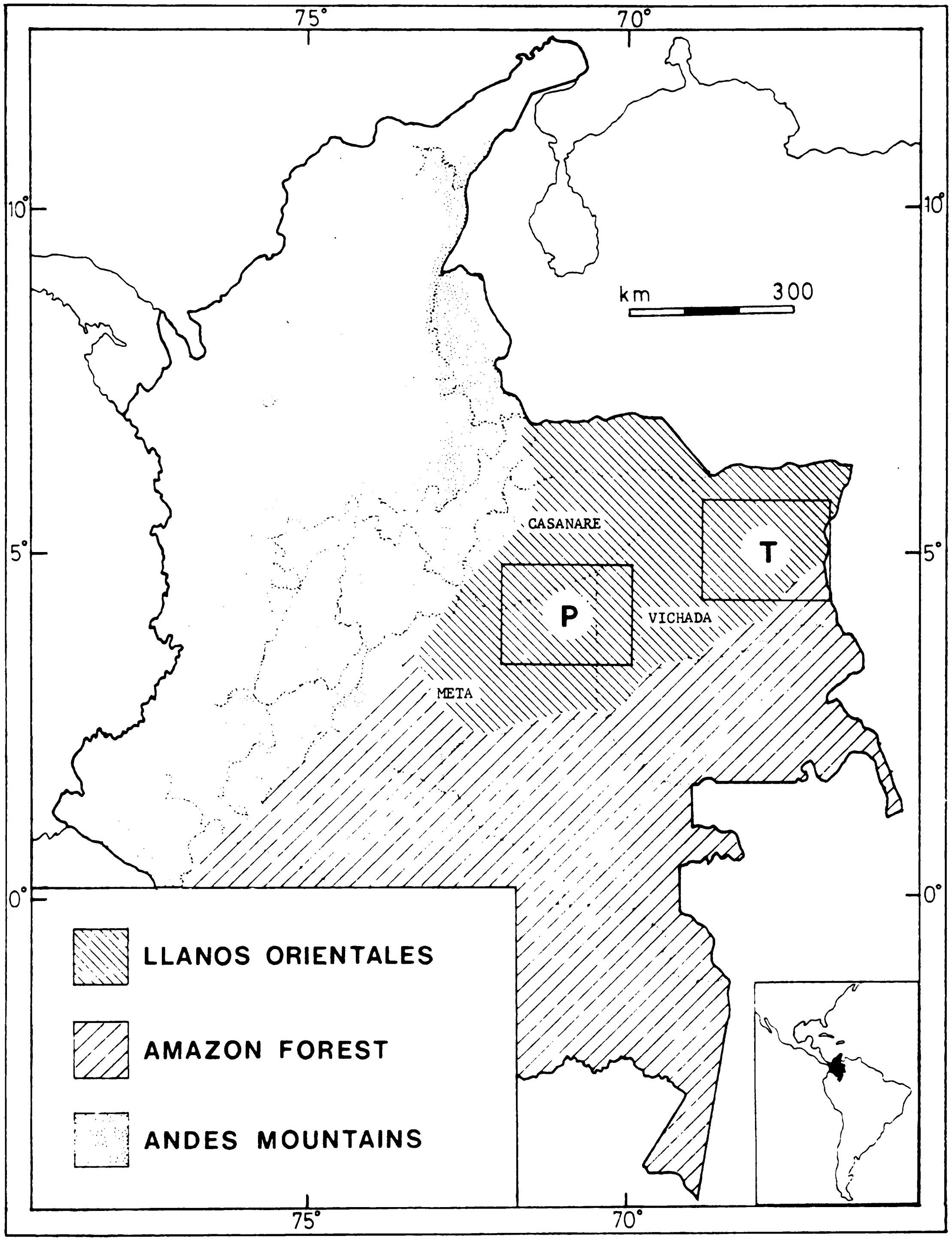
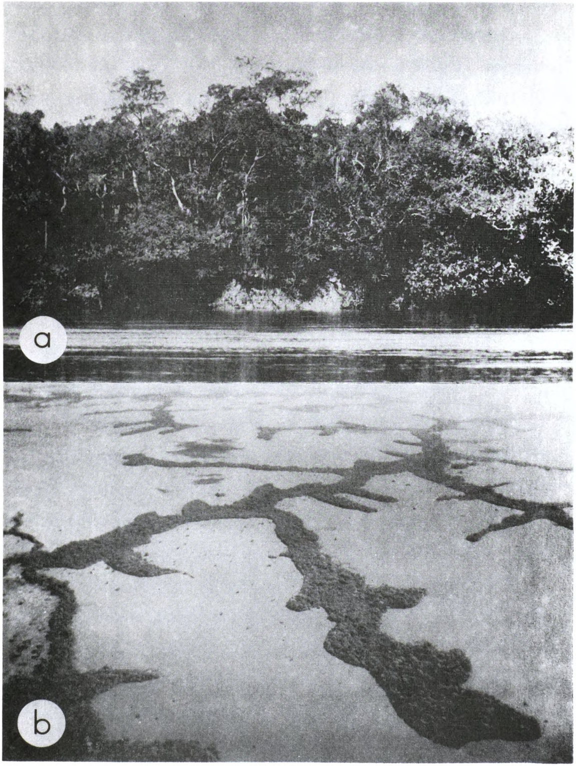


Figure 3. Locations of the study areas: T = El Tuparro; rectangle shows the location of Figure 8: P = El Porvenir; rectangle shows the location of Figure 9.

Figure 4. Gallery forests: (a) Profile view of forest along the lower Tomo River near Centro Administrativo, El Tuparro; (b) Aerial view of the gallery forests of the upper Tomo west of El Tapón, El Tuparro.


a
b

wide on either side of the river, as is typical of the galleries of smaller streams. Most forests along the main rivers are considerably wider, extending for 100 to 150 m on each side. A great variety of broadleaf tree species is present, with abundant lianas and epiphytes. Relatively fewer palm species are found, but these comprise a disproportionate part of the flora. In large-stream galleries, the palms Attalea regia, Acrocomia spp., and Socratea exorriza virtually dominate the well-drained galleries, accounting for approximately 20% of the trunks present. In swampy forests, Oenocarpus mino and other Oenocarpus spp., Mauritia flexosa, and Euterpe precatoria are the dominate palms. In most areas, understory palms such as Bactris spp. and Syagurus inajai are major elements of the flora. Species of Phytolaccaceae, Marantaceae, Melastomaceae, and Heliconia abound in disturbed areas such as treefalls and at the forest edge.

The topography of the Llanos is almost flat, with elevation declining from only 600 m above sea level at Villavicencio, near the base of the Andes, to approximately 250 m at the Orinoco some 800 km east of the Andes. A noteworthy feature of virtually all Llanos galleries is the morichal, a nearly pure stand of Mauritia flexosa palm found at the headwaters of each gallery stream. Morichales are restricted to the uppermost several hundred meters of El Tuparro galleries, but may extend for several kilometers in flatter areas of the Llanos, as is the case just north of the Meta River near the El Porvenir study area. Mauritia flexosa also occurs in occasional patches in other parts of gallery forests, especially in areas which are flooded seasonally.

Within the Llanos, rainfall patterns are reflected in an overall gradient in relative forest cover from north to south, and to a lesser degree from east to west. In the driest areas, where rainfall totals less than 150 cm per year, streams are widely separated by broad savannas and their gallery forests are narrow. An aerial view of the gallery forests near El Tapón, El Tuparro, shown in Figure 4(b), gives an impression of the relationship between gallery forest and savanna in moderately dry mid-Llanos areas. Farther south, the relative amount of gallery forest gradually increases with increasing total rainfall, finally merging into closed jungle where annual rainfall totals more than 200 cm and the dry season is less than four months long. The boundary between continuous forest versus Llanos vegetation types largely coincides with the course of the Guaviare River. Approximate total rainfall isohyets and curves showing the number of months per year with less than 10 cm of rain are presented in Figure 5, adapted from Brunnschweiler (1972:11). The resultant pattern in relative amount of forest cover is strikingly shown in the LANDSAT images presented in Figure 6. Several hypotheses concerning the origin and development of the Llanos vegetation are discussed in Sarmiento and Monasterio (1975).

The two study areas described below differ somewhat in total annual precipitation and in the seasonal distribution of rainfall. Histograms of the seasonal patterns of rainfall for the two reporting stations closest to the study areas (Puerto Ayacucho, Venezuela, and Carimagua, Meta) are shown in Figure 7. Although total rainfall is greater at El Tuparro, it appears to be concentrated into a slightly shorter rainy season than is the case at El Porvenir. Indeed the

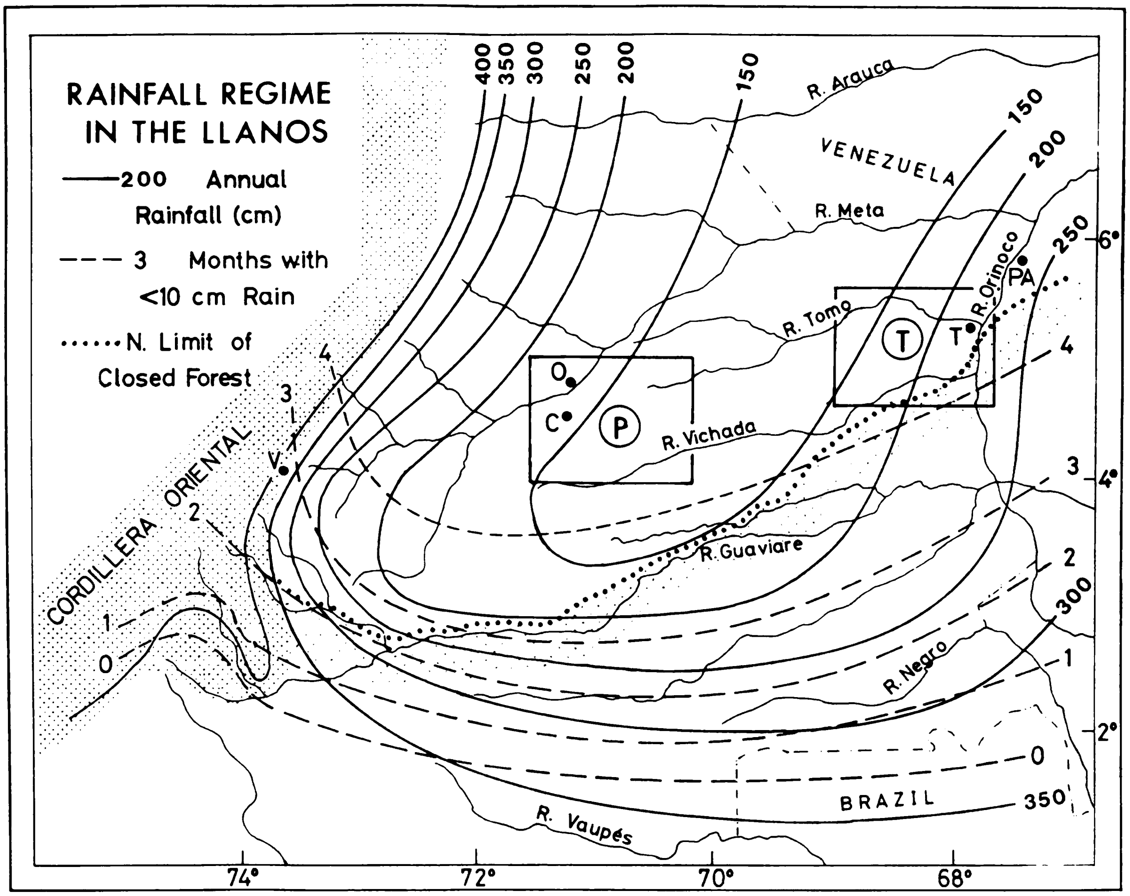
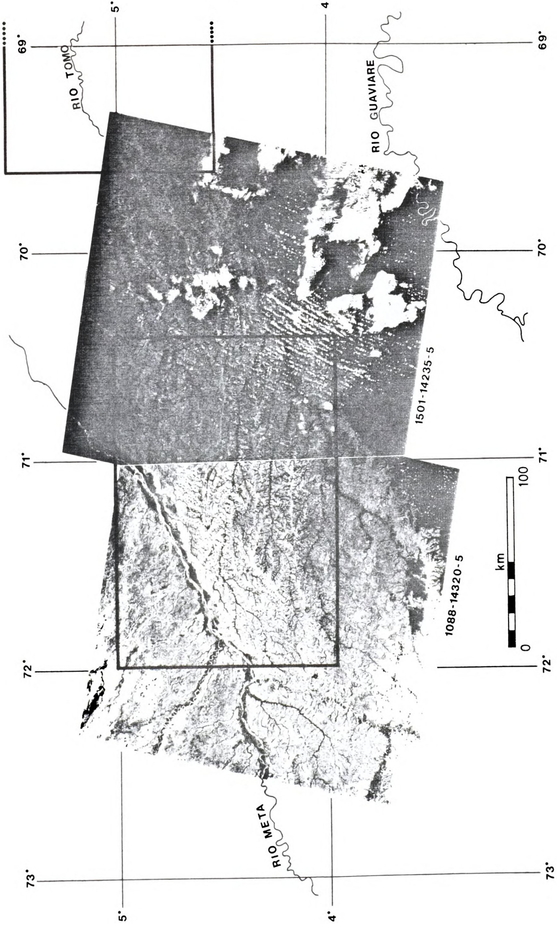


Figure 5. Map of isohyets of total annual rainfall (solid lines) and number of months per year with less than ten cm rainfall (broken lines). Rectangles are the study areas: T = El Tuparro, P = El Porvenir. Solid circles are population centers (C = Carimagua, O = Orocué, PA = Puerto Ayacucho, T = Centro Administrativo, V = Villavicencio).

Figure 6. LANDSAT images of part of the Llanos Orientales. Forest cover appears as irregular black lines or solid black. Savanna is light gray. The left portion is Image 1088-14320-5, taken 19 October 1972. The right portion is Image 1501-14235-5, taken 6 December 1973. A portion of the margin of Figure 8 is indicated by the open rectangle at right. The central rectangle corresponds to the margins of Figure 9.


69°
70°
71°
72°
73°
5°
4°
RIO TOMO
RIO GUAVIARE
RIO META
1501-14235-5
1088-14320-5
km
0
100

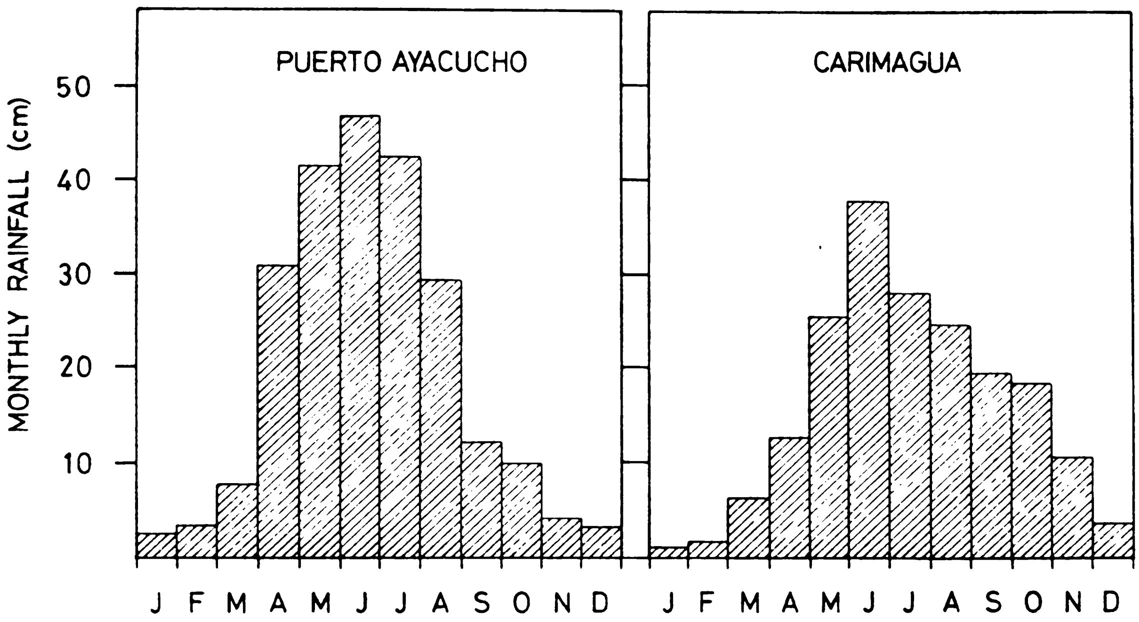


Figure 7. Seasonal distribution of rainfall near the study areas. Histograms of average monthly rainfall for: Puerto Ayacucho (left), 56 km N of Centro Administrativo, for the years 1961-1970 (data from Instituto Geografico Agustín Codazzi 1973); Carimagua (right), 30 km S of El Porvenir, for the years 1973-1978 (data courtesy of Dr. J. M. Spain of CIAT).

severity and length of the dry season is effectively equal for both study areas. The El Tuparro wet season begins in late April and irregular strong rains continue through June. After a brief drier period in late June and early July, rains are more frequent but less intense, with light rains occurring almost daily in August and September. In contrast, at El Porvenir the rainy season is distinguished by two periods of heavy rains separated by a pronounced dry spell or *veranillo* of two to three weeks' duration in late July and early August. The *veranillo*, not apparent in the histogram of Figure 7, is a totally dry hiatus in the middle of the wet season.

The El Tuparro Study Area

As an administrative unit ("faunistic territory"), Territorio Faunístico El Tuparro is part of the system of national parks and natural areas administered by Instituto del Desarollo de los Recursos Naturales Renovables (INDERENA), a division of the Ministry of Agriculture of the Government of Colombia. Comprising some 250,000 ha, El Tuparro is located in eastern Vichada between the Tomo River to the north and the Tuparro River to the south, and extends from the Orinoco on the east to a site called El Tapón, on the Tomo some 180 km to the west of the Orinoco. The majority of the pacas collected in this study area were taken from just outside the Park itself, principally from small tributaries south of the Tuparro River.

INDERENA facilities for the administration of the Park are located at three sites (Figure 8): (1) Centro Administrativo (5°18'N, 67°52'W), the park headquarters; (2) El Tapón, at the western end of the Park; and (3) on the south bank of the Tuparro River at its mouth

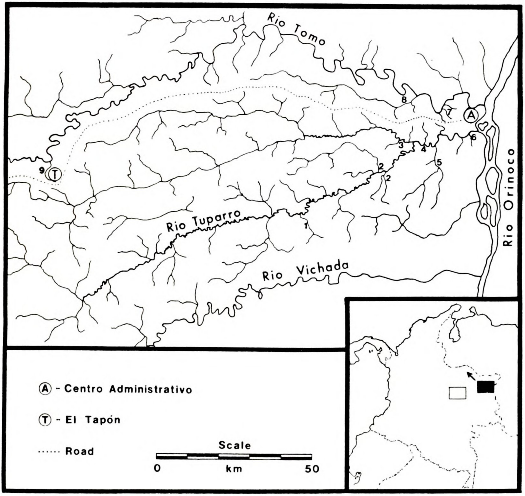


Figure 8. Map of collecting sites for the El Tuparro study area. Numerals correspond to collecting sites discussed in the text.

on the Orinoco. The remainder of the Park is uninhabited except for several small bands of nomadic Indians.

Ecologically, El Tuparro occupies the extreme southeast corner of the Llanos Orientales near the point where savanna merges into continuous forest. Thus the gradient of increasing amounts of forest is pronounced along the eastern end of the Park. Less than 10% of the watershed of the lower Tomo River is forest whereas more than 30% of the Tuparro River watershed is forest. Vincelli (in press) has described the plant communities of Territorio Faunístico El Tuparro, and other aspects of the vegetation are discussed by Defler (1980).

Flat topography and friable soil conditions often combine to result in serpentine rivers that change course frequently, leaving "oxbow" lakes and associated swamps along old riverbeds. This is especially true of the collecting localities along the Tuparro River.

Two additional factors contribute to habitat diversity near the eastern end of the El Tuparro study area. First, the Orinoco itself rises and falls approximately 15 to 18 m over the annual rainfall cycle, and since this cycle is due to rainfall patterns some 300 to 500 km to the south, the river rises well before the start of the local rainy season and falls to its lowest level just shortly after the local rains end in October. Forests on the lower 30 km of the Tuparro River appear to reflect this factor more than the local rainfall cycle. The lower Tomo River, occupying higher, slightly better drained terrain, is much less markedly influenced by the level of the Orinoco. The second locally important factor is the presence of a row of small granitic outcrops (<u>tepuis</u> in the sense of Haffer 1974) located near the Orinoco. As minor extensions of the adjacent Guiana

Shield of Venezuela, these hills rise approximately 200 m above the surrounding plain and support a distinct xeric forest as a result of the low water holding capacity of their thin soils.

Specific collecting sites for the El Tuparro study area are shown in Figure 8. Although widely separated, the nine sites fall into five groups on the basis of habitat characteristics and general location.

Collecting sites 1, 2, and 3 (Caño Alto, Caño Macazaba, and Caño Tuparrito), along the upper Tuparro River, are the wettest sites visited. This portion of the river is characterized by an extremely serpentine course with numerous oxbow lakes and other swamps. Swamps of these oxbows and of the numerous small tributaries of the river tend to coalesce into broad floodplains near the river itself. Although far enough upstream to be isolated from the effects of the yearly rise and fall in the level of the Orinoco, this area is very flat and so large parts of it remain flooded for three to four months during each rainy season. Specimens were collected from five small navigable streams, including two unnamed streams outside the El Tuparro Park opposite Caño Macazaba. The forests of these streams tend to have relatively fewer palms present than is the case for most gallery forests in the Llanos. There appears to be a corresponding increase in the diversity of broadleaf tree species. This distinction reflects the same climatic factors which result in continuous wet forest beginning only 30 km to the south at the Vichada River.

Sites 4 and 5 are on the middle portion of the Tuparro River below Caño Tuparrito. Caño Lapa (site 4) is one of the most accessible and suitable sites in the region for the hunting of pacas. The lower 4 km of this stream consist of low-lying swamps which are flooded for more than six months of the year. A high, well-drained, small stream is separated from the swamps by a small rapids. The stream maintains relatively constant water level in a rich but narrow (less than 200 m) gallery forest, from which all Caño Lapa specimens were obtained. *Oenocarpus* spp., *Socratea*, and *Bactris* palms are particularly abundant there, along with a variety of broadleaf trees. The forest understory is quite open. Signs of other hunting parties were seen during all five of my visits to the area.

The five specimens taken from well-drained, uplifted banks along portions of the lower Tuparro River (site 5) below Caño Tuparrito represent a sample from habitats very similar to upper Caño Lapa. These forests are not subjected to seasonal flooding as are nearby oxbows, and are in fact somewhat narrow (generally less than 200 m) for main-river galleries.

Site 6 is Caño Rana, a tiny seasonal stream less than 3 km long. It drains seasonally-flooded swamp forests and *morichal* just west of the *tepuis* uplands on the south bank of the Tuparro near its mouth. The stream disappears completely for several weeks in February and March, and the forest which it drains is completely innundated by the Tuparro, influenced by the Orinoco just 4 km to the east, from late June to late August.

Puerto Alegre (site 7) is a large patch of forest drained by three separate small tributaries of the Tomo. These streams are not quite flooded in mid-rainy season, but in the dry season are so dry as to be inaccessible by canoe. Palms are not common, presumably as a result of the total lack of saturated soil conditions, although a belt of *Mauritia flexosa* palm is found where seasonal flooding occurs at the margins of the surrounding savanna. The lower portions of Caño Peinillas (site 8) are in most respects similar to Puerto Alegre except that the stream is larger and does not dry out in the dry season.

Site 9, Caño Hormiga, is a fairly large stream located near the INDERENA guard station at El Tapón. The topography there is diverse, with bluffs of old alluvium rising slightly above narrow (less than 200 m) gallery forests. During the dry season, the stream is well below the gallery floor. The stream rises dramatically in the wet season. Palms are not particularly abundant except for Oenocarpus, Socratea, and Bactris.

The El Porvenir Study Area

In March and April of 1977, I participated in an effort by investigators from Tulane University's Centro Internacional de Investigaciones Médicas (CIDEIM) to collect a series of pacas from the vicinity of the Centro Internacional de Agricultura Tropical (CIAT) agricultural experiment station at Carimagua, Meta. Twenty-four pacas were obtained as part of a continuing study of cestode parasites of the genus Echinococcus. Most specimens collected at that time were examined by me. After continued logistical problems at El Tuparro, and in view of the success achieved at Carimagua, it was decided to move the paca study to the village of El Porvenir (4°45'N, 71°25'S), located on the south bank of the Meta River 30 km north of Carimagua. In April of 1978, a field station, with basic laboratory facilities, was set up by CIDEIM, and field work was based there until termination of the paca study in October of 1979.

Although still very sparsely populated, the area around El Porvenir has been settled for centuries. The only significant industry is cattle ranching. Virtually all of the savanna land in the area is dedicated to ranching. Collecting sites involved eight large ranches and also small portions of the Carimagua property. The typical ranching operation consists of 6,000 to 30,000 ha. A limited amount of agriculture is practiced on the rich, broad floodplains of the Meta River, with corn, rice, beans, and cassava being the principal crops. The town of Orocué (pop. ca. 3,000), Intendencia del Casanare, lies 17 km downstream from El Porvenir.

Specific collecting localities in the vicinity of El Porvenir are somewhat more scattered than was the case for El Tuparro. This results primarily from the cooperation of several local hunters who brought in specimens from sites of their own choosing. In all cases except for one ranch in Casanare upstream from El Porvenir, such sites were subsequently visited by me. All of the localities fall quite naturally into four categories, treated below in the order in which they are numbered in Figure 9.

Sites 1 through 4 are parts of Caño Caviona, a small tributary of the Meta River which originates in part in Carimagua and also in the ranches known as El Tranquero, El Piñal, and Hato Caviona. The localities used are all readily accessible by road from El Porvenir. Site 1 (Puente Gloria) is most significant since it is the locality which was most intensively hunted by me and is thus where many of my observations of pacas occurred. This is a single branch of forest approximately 2½ km long extending to the north of Caño Caviona from a point 4 km NE of the bridge where the road from Carimagua crosses the

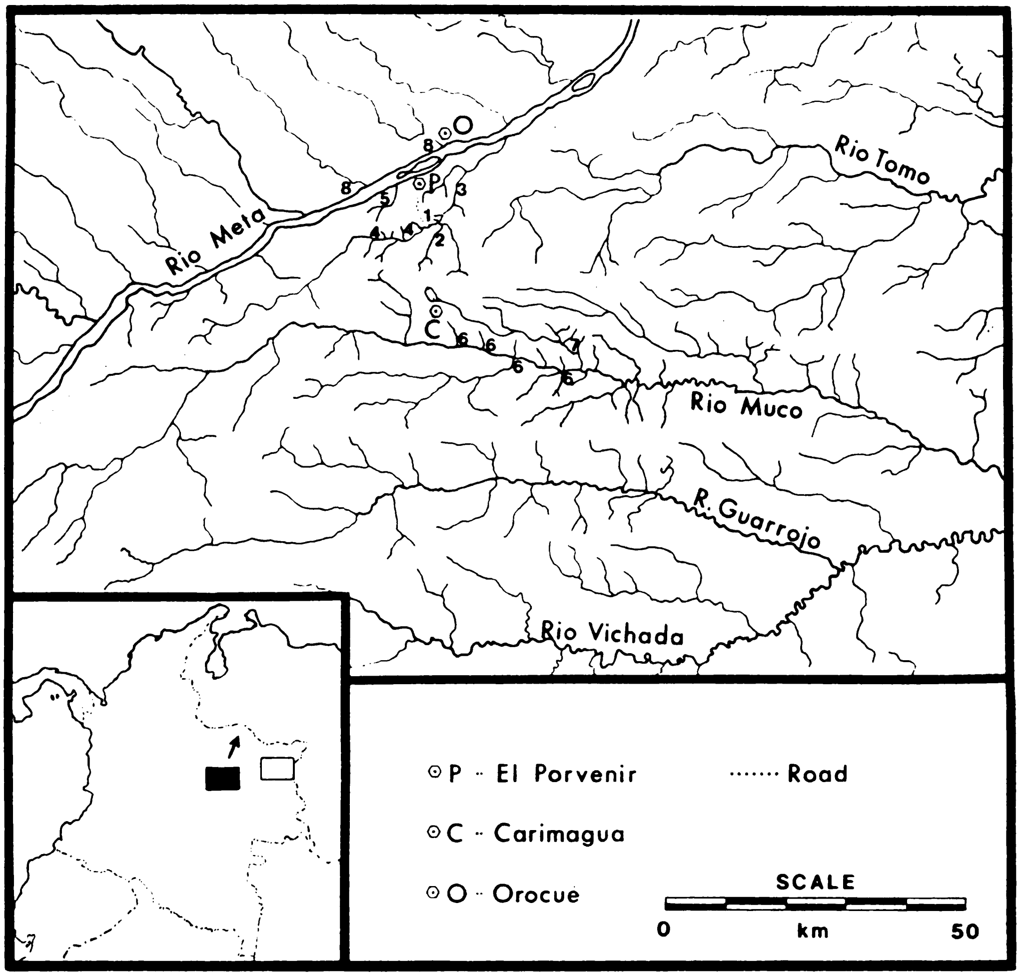


Figure 9. Map of collecting sites for the El Porvenir study area. Numerals correspond to collecting sites discussed in the text.

main stream. Site 2 (La Arepa) is a much larger branch off of the south side of Caño Caviona slightly downstream from site 1 and extending 6 to 7 km toward Carimagua. Site 3 (Rincón Masato) is a segment of Caño Caviona west of Puente Gloria and downstream from site 1, and site 4 (Upper Caño Caviona) includes several points west of Puente Gloria and their associated minor galleries.

West of Puente Gloria, the forests of this stream are low-lying and drain poorly. There are numerous small _morichales_ and streamside stands of _Mauritia_ palm. The gallery forest along Caño Caviona itself is narrow (generally less than 100 m) yet the forest is swampy and has a dense understory with abundant _Bactris_ and _Socratea_ palms and various shrubs. The surrounding savanna is high and well-drained, but the course of the stream is so flat as to result in temporary flooding of much of the gallery forest after most heavy rains. Sites 1 and 2 are associated with slightly higher savanna and thus are drained rapidly after rains. Their forests are more open and have abundant _Attalea_ and _Socratea_ palm.

Site 5 (Paso Ancho) is a part of the floodplain of the Meta River located approximately 7 km west of El Porvenir. The eleven pacas collected there were all taken from the vicinity of a grove of mango trees located in a small farm where corn and rice were grown.

Sites 6 and 7 refer to all tributaries of the Muco River sampled in the course of the study. Many of the specimens from site 6 were taken from four small galleries within the Carimagua station property during March and April of 1977. During 1978-79 hunting on Carimagua land was discouraged, but some pacas were collected from minor tributaries of the Muco near the mouth of Caño Carimagua. Site 7 is Caño

Limici, the small tributary of Caño Carimagua just upstream from its mouth on the Muco. During the last five months of the study, Sr. Genaro Useche Osorio, a native of the region and a former assistant at the CIDEIM field station, established a homestead on Caño Limici. The 42 pacas from that site were all collected by Sr. Useche, whom I had previously trained to take appropriate data and to preserve skulls, genital tracts, and parasite materials.

The forests of the Muco in this area are in many respects similar to Caño Caviona, except that the larger main stream fluctuates less dramatically in water level and supports much wider forest galleries, typically 300 m wide. Numerous oxbows and other swamps are inundated by the Muco during the wet season, but for much of the dry season, no forested areas are flooded. Palms associated with seasonal flooding are somewhat more abundant than in Caño Caviona, especially species of _Oenocarpus_ and _Mauritiella_.

Site 8 (Casanare) refers to several localities in the Intendencia del Casanare, the political division north of the Meta River. Twelve specimens were collected by a local fisherman from four ranches near the Meta River (Hato El Boral, Carocaro, and two smaller ranches on Caño Gurripe) and examined by me. The gallery forests are low and seasonally flooded. _Scheelea_ and _Attalea_ palms predominate. Savannas are very flat and borad, and separated by narrow (less than 150 m) gallery forests. Rainy-season flooding is extensive.

METHODS

Collecting Methods

It was planned originally that two parallel population assessments would be carried out; a live-trapping regime for estimating density, disappearance rates, and fecundity parameters; and a series of four quarterly collecting trips employing local hunters to obtain samples of 100 individuals each three months, for a sample of the standing age distribution and the occurrence of reproductive activity by season and by age. The live-trapping program, using twenty-five 22.5×22.5×80 cm double-door wire mesh traps over a period of five months, was abandoned after approximately 800 trap-nights yielded no pacas. Plans for quarterly samples were changed as it became apparent that sufficient numbers of pacas would be more difficult (and much more expensive) to obtain than had been anticipated. For these reasons, the principal approach used in the study was to hunt pacas whenever logistical and financial conditions permitted. Local residents were hired as hunters, and during the course of the study, I learned much from them about hunting techniques, eventually collecting 49 specimens myself.

The traditional hunting methods used by residents of the study areas were used to obtain all specimens examined. Most were taken by local hunters who worked in collaboration with me and were paid on a per-specimen basis as funds allowed, and were also given the meat from the pacas that they shot. Sites for hunting trips were chosen in consultation with these hunters. This practice had several advantages. I was able to learn which factors of habitat, season, and transportation were of importance to local hunting methods, and usually discussions with the hunters provided details about the recent history of the use by hunters of the site. Often my travel resources enabled us to hunt at sites that had not been visited by local hunters for several years.

Hunting practices were dictated by the habits of the animal being hunted. In the Llanos, there are no government regulations or sporting traditions constraining hunters, since hunting is generally undertaken to meet a major dietary need and not conducted for sport. Weapons used are shotguns and small-caliber rifles of all descriptions, including homemade muzzle-loaders. Finding a paca to shoot involves the use of either a six-volt battery-powered headlamp at night, or a tracking dog in the daytime.

One can readily learn to recognize pacas at night by the strikingly bright orange-red reflection of the hunter's lamp in the animal's eyes. A uniform, large (ca. 10 mm) disk is seen, and it can easily be distinguished from other often-encountered forest animals by color and luminosity: The eyes of the paca do not "sparkle" as do reptile eyes, but instead reflect a soft, uniformly bright light. Often only the eye can be detected in dense cover, yet this is usually sufficient for the hunter to identify his quarry.

Usually pacas were actively pursued in the course of a night's hunting. In advance, either a portion of stream (several km) was cleared of obstructions, then traversed repeatedly by canoe (the principal method used at El Tuparro), or a narrow trail (usually about one km long, often longer) was cut along or near the stream bank, then partially cleared of leaf litter and traversed on foot (at El Porvenir). Some hunters preferred either to clear a short trail (less than 50 m) or to construct a simple platform low in a tree, near a fruitfall or clear sign of paca activity, and wait quietly for a paca to approach. At best, only one paca per night was obtained by these passive methods. The primary considerations in selecting galleries for cutting hunting trails were the ease of transportation to the site and the acquiring of maximum visibility into the surrounding forest. This effectively restricted hunting on foot to the drier, more open, mature galleries -- much less than half of the forest in the Llanos. On the other hand, relatively few streams are sufficiently navigable for hunting by canoe, so that except in flat, wet regions such as El Tuparro, even less gallery forest is traversible by this method.

Sign of paca activity and the presence of concentrated fruitfalls were always considered in selecting galleries for hunting, but were thought by the hunters to be of relatively minor importance. For hunting by canoe, the first consideration was usually the water level relative to the bank of the stream. In a flooded forest, the pacas would be remote from the navigable channel of the stream, while at low water, the hunter would not be able to see the forest floor above the stream bank. Experienced hunters in the El Tuparro area were very astute at visiting particular streams during those few weeks of the year when the water level was especially suitable.

Dogs trained to recognize paca scent can be effective, but truly skilled dogs are rare (and considered quite valuable), and so my experience with them was, unfortunately, limited. Five different dogs were used with some degree of success in this study. The procedure involved two to four men walking in the forest in the morning with one or more dogs which tracked paca scent until they located an occupied burrow. Small dogs could enter the burrow and thereby (hopefully) induce the paca to leave in search of other shelter. Three of the dogs I used were too large for this, but harrassment in the form of dogs barking or sticks poked down burrow entrances usually was sufficient to convince the paca to move into the open. It would then sometimes seek other cover, but more generally headed for the nearest stream and tried to lose its pursuers by swimming underwater. Usually the animal could subsequently be located by carefully probing under overhanging streamside vegetation. Only four of the 42 pacas obtained using dogs had to be literally dug out of their burrows. The remainder were collected while the animals were swimming or when driven from above-ground cover.

The use of dogs has several advantages over other methods. There is no need for the hunter to be especially quiet (noise being a significant factor when hunting at night) since this activity is carried out in the daytime when the animals are in their burrows. Once located, burrows can be excavated to obtain information on their structure and locations in the habitat. Eleven burrows, from eight of which the occupant was collected, were partially or fully excavated in the course of the study. The greatest advantage to the use of dogs, however, is that the hunter has a much better opportunity to capture the paca alive, either in the process of burrow excavation or by grabbing the paca as it attempts to escape by swimming. Six young pacas were captured while swimming. Seven adults were also captured but none became well adjusted to captivity. All but one, a young adult male kept for four months at El Porvenir, had to be sacrificed because of injuries suffered during capture or in captivity.

The use of dogs is also inefficient, especially if the dog is not particularly skilled at recognizing paca scent. The most successful day of hunting using dogs yielded two adult females, each with small offspring. On only three other occasions were two pacas taken with dogs in a single day. In contrast, one skilled hunter at El Tuparro shot as many as seven pacas in an exceptionally good night of hunting by canoe. It was not unusual for one hunter to collect two or three pacas in one night while hunting on foot along trails. I invested 18 days in trying out dogs that were unable to locate pacas at all.

At El Porvenir, a standing offer of 300 pesos (U.S. $10 approximately) was made to local people for each paca brought in fresh for examination. Except for nearby skilled hunters with readily-available transportation, this was not sufficient incentive, and only 24 specimens (many incomplete) were obtained in this manner. Much greater success (46 specimens) resulted from the cooperation of Sr. Genaro Useche, a local hunter trained by me to examine specimens, record data, and preserve materials from pacas collected in my absence, from his homestead on Caño Limici from May to October of 1979. Most of the pacas collected with the aid of tracking dogs were obtained by Sr. Useche.

Cursory notes were kept of observations made while hunting: How many pacas seen, what they were doing when encountered, what foods they were eating, the habitat in which they were seen, times of encounters, other pacas or other mammals seen together with them, the animal's reactions to the hunter and flight behaviors, vocalizations, or any unusual circumstances or behaviors. I personally saw approximately twice as many pacas as I was able to collect, and hunters working with me usually contributed observations on and descriptions of their own encounters with pacas. Some comments were also noted on the types and compositions of forests entered, hydrology of the area, stream levels, densities of ground cover, trees producing fruit, and tracks, runways and related signs of pacas and other mammals.

Examination of Specimens

A detailed necropsy form was prepared for recording external and reproductive characteristics, tooth-wear patterns, fat deposits, tissues preserved, and any abnormalities. These data were later transferred to key-sort cards, indexed by weeks one through fifty-two of the calendar year, which were then used in collating and summarizing all results.

Specimens were examined in detail within sixteen hours of the time of death. Each paca was weighed with a spring scale (Zebco^{R} De-Liar) to 0.1 kg. Standard mammalogical measurements were taken in mm using a steel tape. Whenever possible, photographs of the pelage were taken in profile view. Any lesions or abnormalities were noted. The relative extent of fat deposits was recorded and internal organs were briefly examined for pathologies or parasites. Stomach contents were classified as either fruit pulp, foliage, animal remains, or other matter. In some cases, the species of fruit present in the stomach was determined on the basis of color, texture, and/or characteristic fruit parts.

Length and width of the testes and seminal vesicles were recorded in mm, and selected specimens were preserved in ten percent formalin for sectioning. Vaginae were inspected for copulatory plugs. The position and size of each conceptus was noted. Each fetus was weighed to the nearest gram and the total length measured in mm. Small fetuses (less than 20 g) were subsequently weighed to 0.1 g. For very small conceptuses, the diameter of the entire sphere of fetal membranes was measured from the outside of the uterus and recorded in mm. The method of Huggett and Widdas (1951, and see Appendix B) was used to estimate fetal age. The degree of distortion and rugosity of the uterus (placental scarring) was noted and the greatest width of the uterus was recorded in mm. The uteri, together with ovaries and fetuses, were preserved in formalin. Females were considered to be lactating if milk could be expressed by squeezing the nipples with forceps. The breast tissue was also incised to check for milk.

The time at which birth had occurred was estimated for all young pacas (less than 5 kg), using growth data based on four pacas raised in captivity (see Appendix B).

All ovaries and selected testes, seminal vesicles, and uteri were sectioned for detailed study of reproductive condition. Representative sections of gonads, uteri, and pathological tissures from El Tuparro pacas were prepared by Dr. F. Lozano of the Veterinary Medical Research Laboratory (LIMV) of Instituto Colombiano Agropecuario in

Bogotá. Ovaries of El Porvenir specimens were serially sectioned at 0.1 mm intervals, and representative sections of placental scars and new conceptuses were prepared at CIDEIM-Cali.

Right upper first molars were removed for use in determining individual age on the basis of annulations in the cementum tissue. The teeth were decalcified, sectioned at 12 µm, and stained with haematoxylin and esosin, by Matson's Commercial Microtechnique (Box 308, Milltown, MT 59851). Development of the techniques used to determine age is detailed in Appendix A.

Skulls from 118 specimens (MSU 29363 - 29485), three skins, and all fetuses and tissue sections, are housed in the research collections at The Museum, Michigan State University. Eighty-seven skulls, three fluid-preserved specimens, and seven skins were donated to the INDERENA collections in Bogotá. Four skulls were lost.

Abundance

Discrete forest galleries at three sites (Caño Rana, Puente Gloria, and Caño Limici) were sampled for pacas with such intensity that I used the number of specimens collected at each as a crude estimate of the number of pacas originally present in those areas. The surface area of the forest sampled at Caño Rana was estimated from measurements taken on the ground. Areas from Puente Gloria and Caño Limici forest were measured from LANDSAT images 1088-14320-5 and 1501-14235-5 (EROS Data Center, Sioux Falls, SD 57198), presented above in Figure 6, page 19. Density was estimated as the number of pacas collected divided by the area sampled.

Estimates of the amount of forest present (as percent of surface area) were obtained by different methods for the two study areas. An 11" by 14" photograph of an aerial photo array of the El Tuparro study area was obtained from INDERENA. A transparent grid of 625, 1-mm^2 squares was laid over representative portions of the photograph. Percent forest was calculated as the number of squares which contained at least 0.5 mm^2 of forest, divided by 625, times 100%. For the El Porvenir study area, the LANDSAT images were evaluated using the Spatial Data Systems Datacolor 704 Color Enhancer-Densitometer video system housed at the Department of Geography, Michigan State University. The densitometer distinguishes between forest and savanna portions of the image and computes the proportion of each in any selected portion of the image. To estimate the total number of pacas in the vicinity of each study area, the total surface area of forest was estimated by the above methods and multiplied by the density estimates obtained for the three intensively hunted collecting sites. Suitable LANDSAT images are not available for most of the El Tuparro study area, and aerial photos of the El Porvenir area were not available to me through INDERENA.

Statistical tests and mathematical models are described where they are used in the following sections. The primary statistical reference used was Steele and Torrie (1960). Calculations were performed on the Wang 600-14 programmable calculator housed at The Museum, Michigan State University, using pre-recorded statistical programs developed by Wang and also my own programs.

RESULTS

In total, 213 pacas were examined in the course of the study. Numbers of specimens from each of the collecting sites, together with the primary collecting method(s) used at each site, are listed in Table 1. Seventy-five pacas were obtained by hunting from canoes, 96 by hunting on foot, and 42 by tracking with dogs. Eight specimens (five males and three females) are excluded from much of the following analysis because I was unable to determine their ages due to loss of appropriate materials.

Female Reproduction

In order to obtain a reasonably complete representation of the annual cycle, all 105 females (from both study areas and for all four years of field studies) were combined for the analysis of reproduction and the estimation of fecundity. The two study areas are approximately 350 km apart (see Figure, page 12). Nevertheless, since rainfall patterns and habitats are fundamentally similar for the two areas, I must assume that there was no significant difference in reproductive pattern for pacas between them.

Fifty-five of the 57 females that were one year old or older were reproductively active (either pregnant or recently parous) when collected, irrespective of the time of the year. There were 69 females as heavy or heavier than the lightest (6.5 kg) pregnant female. Of

TABLE 1. Numbers of Pacas Obtained from Each Collecting Site.

STUDY AREA Collecting Site	Collecting Methods[c]	Number of Specimens		
		Males	Females	Both
EL TUPARRO[a]		49	32	81
1) Caño Alto	C	11	6	17
2) Caño Macazaba	C	2	2	4
3) Caño Tuparrito	C	5	1	6
4) Lower Río Tuparro	C,D	3	2	5
5) Caño Lapa	C	7	9	16
6) Caño Rana	C	6	4	10
7) Puerto Alegre	C	9	3	12
8) Caño Peinillas	C	1	0	1
9) Caño Hormiga	D,F	5	5	10
EL PORVENIR[b]		59	73	132
1) Puente Gloria	F,D	5	5	10
2) La Arepa	F	0	5	5
3) Rincón Masato	F	5	4	9
4) Upper Caño Caviona	F,D	12	10	22
5) Paso Ancho	F	6	5	11
6) Carimagua, Río Muco	F,C	10	11	21
7) Caño Limici	D,F	17	25	42
8) Ca anare	C,D	4	8	12
TOTALS		108	105	213

[a] Site numbers for El Tuparro correspond to those in Figure 8.
[b] Site numbers for El Porvenir correspond to those in Figure 9.
[c] C = in canoe; F = on foot; D = with dog

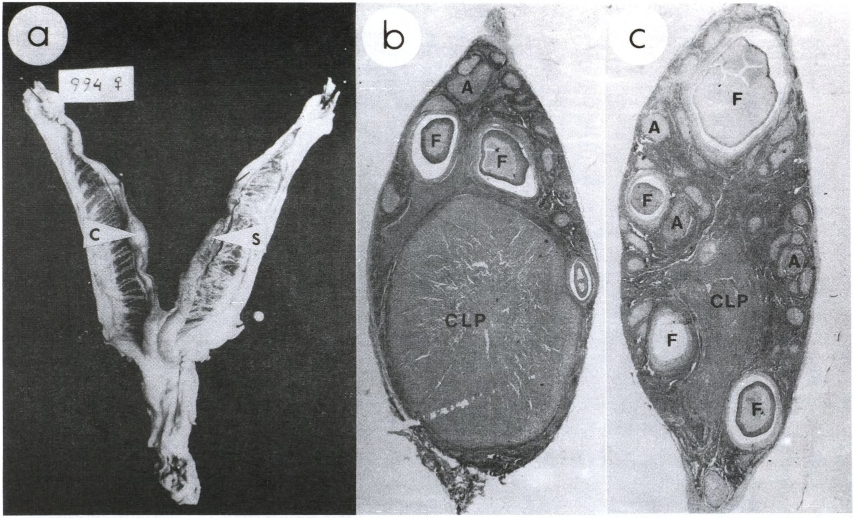
these, 42 were pregnant. Twelve pregnant and 27 non-pregnant individuals showed placental scarring of the uterus. Three of the 12 females that were both pregnant and recently parous were also lactating. One of 5 females each of which was collected together with her offspring was pregnant. This female had a conceptus measuring 17 mm in diameter and was lactating. Her young (a male) weighed 1.8 kg, which indicated that it had been born three to four weeks previously (see Appendix B). The parous horn of the uterus was distinctly wrinkled and had a maximum diameter of 23 mm, which suggests that the less-distended but distinctly wrinkled uteri observed in other specimens enable detection of a parous condition for a minimum of five to six weeks post-partum. The conspicuous conceptus in this same female indicated that she had conceived approximately two weeks after giving birth. Thus a post-partum estrus is possible, and lactation does not necessarily inhibit subsequent conception. From observations on 31 births by captive pacas, Matamoros (pers. comm. 1980) concluded that estrus occurs shortly after birth and again toward the end of the period of lactation.

Only 21 of the 39 females with placental scarring were lactating, including 3 that were also pregnant. Six of those that were not lactating had large (>40 mm) wrinkled uteri indicative of recent parturition, suggesting that early mortality of neonates had occurred in those six cases. No lactating female was collected that did not still show uterine evidence of parturition, implying that lactation does not exceed the period of regression of the parous horn of the uterus, which apparently may take five to six weeks. No evidence of intrauterine mortality was found.

Examination of sections of ovaries provided additional indications of post-partum estrus. In addition to a large corpus luteum of pregnancy (CLP) in the ovary of the pregnant horn of the uterus, numerous small accessory corpora lutea (ACLs) were found in both ovaries of all pregnant females. The CLPs of females in early pregnancy were composed entirely of large glandular cells while the ACLs were beginning to develop from unovulated follicles by a thickening of the theca interns. The ACLs of late pregnancy were irregular and had thin thecal layers, and the CLPs were large. Maturing follicles were seen in the ovary of the non-pregnant horn. Large vesicular follicles such as these were not seen in the ovary of the pregnant side, even for near-term pregnancies. The CLP of the parous horn was persistent for females that were lactating, while the ACLs were degenerating. For these females, the cells of the CLP were large and vacuolar with small nuclei and could be distinguished readily from the cells of the CLP during pregnancy. For non-lactating parous females, the CLP was irregular and degenerating, with a loss of the thecal layers. Mossman (1966) described similar differences between luteal cells for lactating parous squirrels Tamiasciurus husonicus. In none of the 36 females with placental scarring did the condition of the ovaries indicate the presence of a new pregnancy in the parous horn. Study of the ovaries and uteri revealed no pregnancies that had not been found by gross examination alone.

The genital tract and ovaries of a female that was both pregnant and parous are presented in Figure 10, where (a) is a ventral view of the uterus showing the presence of a new conceptus in the right horn (left side of the figure) of the uterus and marked wrinkling of the

Figure 10. Uterus and ovaries of a pregnant parous paca. (a) Ventral view of uterus. C = conceptus, P = placental scarring. (b) Thin section of left ovary. (c) Thin section of right ovary. Both sections 7 μm, ×10. Symbols explained in the text.


a
994 ♀
C
S
b
A
F
F
CLP
c
F
A
F
A
A
CLP
F
F

left horn. Sections of the ovaries of the parous and of the pregnant side are shown in (b) and (c), respectively. The parous ovary contains numerous irregular, small ACLs and the large CLP of the previous pregnancy, all of which have lost their thecal layers. Four luteinizing follicles (LF) are also seen, with the dark follicle cell layer regressing from the thickening thecal layer indicating that these follicles are in the process of becoming the ACLs of the new pregnancy. These features are also seen in the ovary of the pregnant side horn in (c), where the large CLP is seen to be completely filled with luteal cells.

The ovaries in Figure 11 (a) and (b) are from a female in the fourteenth (near-term) week of pregnancy. The large CLP is seen in the ovary of the pregnant side (a) along with numerous ACLs. The ovary of the non-pregnant side (b) contains ACLs and also maturing follicles (MF) which were not seen in the ovary of the pregnant side. Apparently, after parturition ova can be shed by the ovary of the non-pregnant horn but not by the ovary of the newly-parous side. A functional asymmetry of ovaries that is suggestive of this situation has been described for the porcupine Erethizon dorsatus (Mossman and Judas 1949), a species closely allied to the caviomorphs.

The seasonal distribution of reproductive activity for all females 6.5 kg or heavier is shown in Figure 12 for pregnant females (a) and for females with placental scarring (b). Although sample sizes are small and varied, as indicated at each point in (b), both pregnant and parous females were collected in ten of the thirteen four-week intervals of the year. The three exceptions are for samples of only two, three, and five animals per interval, and so should not

Figure 11. Thin sections of paca ovaries. (a) Ovary of pregnant side for a female in the fourteenth week of gestation. CLP = Corpus luteum of pregnancy. A = accessory corpus luteum. (b) Ovary of non-pregnant side for the same specimen. F = maturing follicle. (c) Left ovary of adult paca that evinced no reproductive activity. F = atretic follicle. All sections 7 μm, ×10.

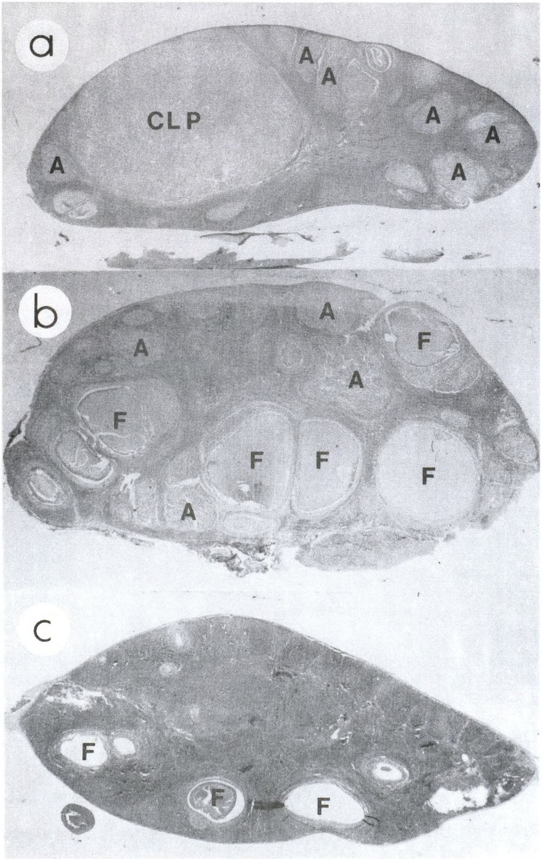
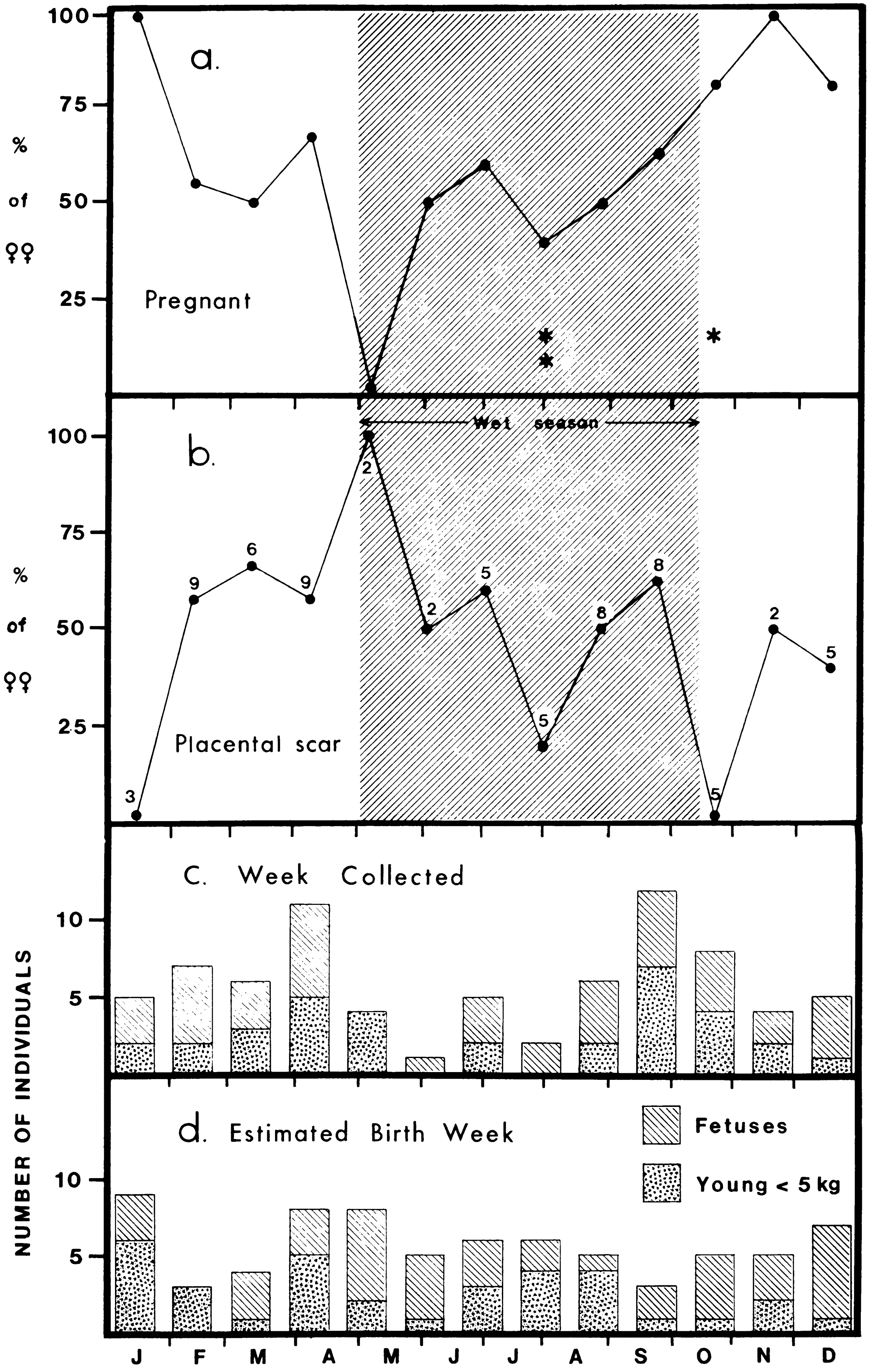

a
A
A
CLP
A
A
A
A
b
A
A
F
A
F
F
F
F
A
c
F
F
F

Figure 12. Seasonal distribution of female reproductive conditions and of estimated births. (a) Percent of adult (⩾6.5 kg) females pregnant. (b) Percent of adult females with placental scarring of the uterus. Numerals indicate the number of adult females for each four-week interval. (c) Numbers of pregnant females (diagonals) and young less than 5 kg (stipple) collected in each four-week interval. (d) Estimated times of birth for the specimens presented in (c).


a.
Pregnant
% of ♀♀
100
75
50
25
*
*
*
Wet season
b.
Placental scar
% of ♀♀
100
75
50
25
3
9
6
9
2
2
5
5
8
8
5
2
5
C. Week Collected
d. Estimated Birth Week
NUMBER OF INDIVIDUALS
10
5
Fetuses
Young < 5 kg
J
F
M
A
M
J
J
A
S
O
N
D

be taken to indicate temporal peaks of one condition or the other. Only 3 of the 69 females large enough to be considered potentially reproductive showed no sign of reproductive activity. These are indicated by the asterisks in Figure 12(a). One of the two collected in August was less than one year old, and the specimen from October was a yearling. Both of these had thin (<6 mm) uteri indicative of a nulliparous condition. Only one fully-adult female, a five-year-old collected at Caño Caviona in August of 1978, was neither pregnant nor recently parous at the time of collection. A section of the left ovary of this individual is shown in Figure 11(c). Only a few follicles in various stages of atresia are seen. The absence of corpora lutea suggests that this individual had not conceived for some time. The right ovary is virtually identical in these respects.

The gestation period of the paca is on the order of 116 days (Eisenberg pers. comm. 1977, Lander 1974, Kleiman et al. 1980). Since gestation is so long, the presence of fetuses at all times of the year does not rule out the possibility of a seasonal clustering of births. To test for such a possibility, the times when pregnant females and young pacas (<5 kg) were collected are graphed in Figure 12(c), and the estimated time of birth (see Appendix B) in Figure 12(d). No seasonal pattern is evident. Indeed, at least three birth estimates fall into each of the thirteen four-week intervals.

The occurrence by age of the various female reproductive conditions is presented in Figure 13. Again, no particular pattern is evident other than that virtually all adults are reproductively active. A higher proportion of simple pregnancies seems to occur in the younger age classes, but inference is limited by the small sample

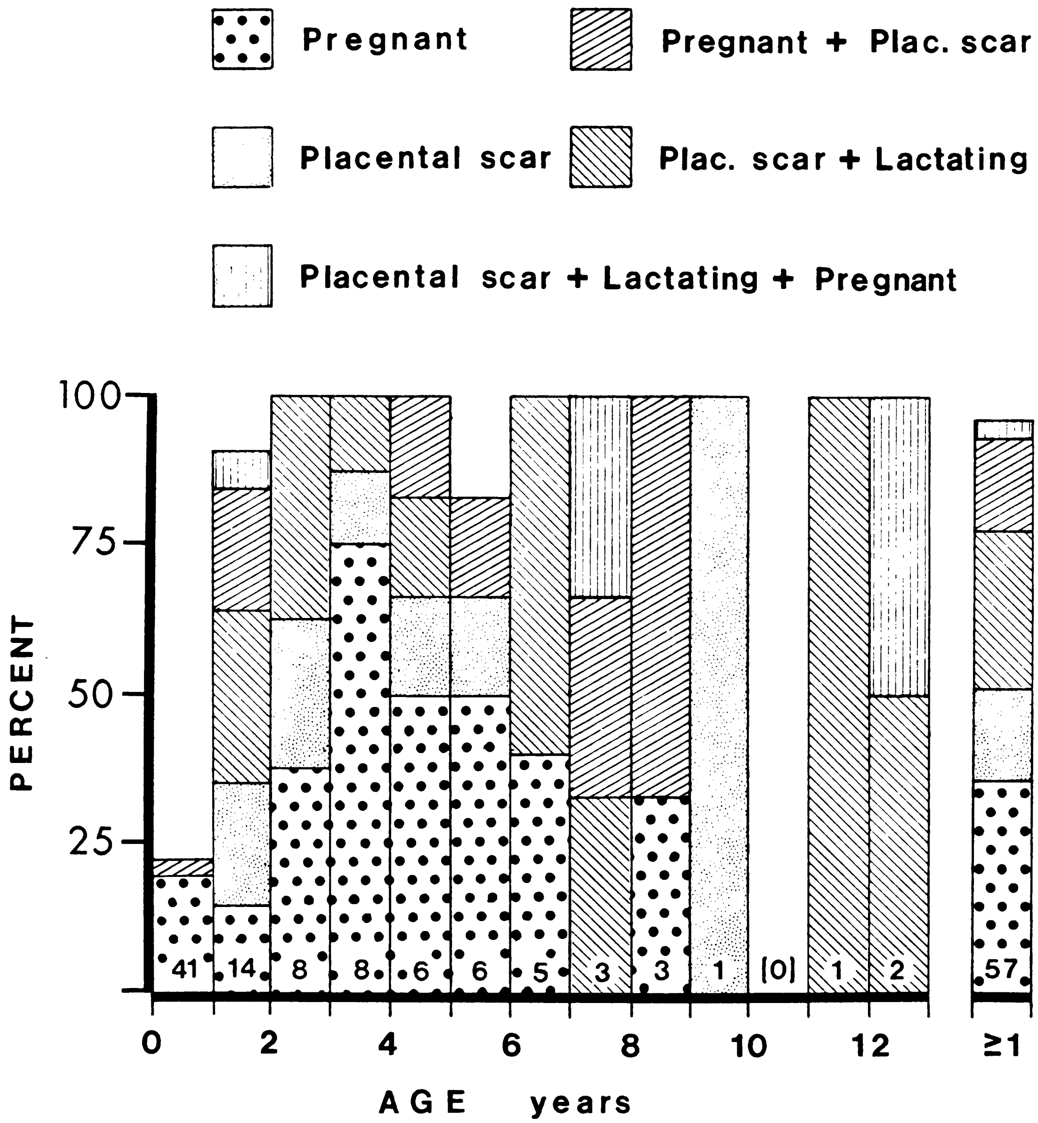


Figure 13. Distribution by age class of female reproductive conditions. Numbers above the abscissa represent the number of females in each age class. The column at right is for ages 1 through 12 combined.

sizes. Tests of the z-transformed normal approximations of the proportion pregnant in each age class (irrespective of placental scarring) against the overall proportion of 42 pregnant and 27 non-pregnant adults showed no adult age class to be different from the overall proportion ($P > 0.2$). It is noteworthy, however, that only 1 of the 9 reproductively active females less than one year of age is parous, versus 11 parous females out of 14 in the one-to-two-year age class. This suggests that in general, females first give birth at approximately one year of age.

Male Reproduction

For all males one year old or older, mean testis length and mean estimated testis volume (calculated as $(4\pi/3)\times(\text{length}/2)\times(\text{width}/2)^2$) were determined for each four-week interval of the year, as presented in Figure 14(a). Testis size appears to be slightly smaller during much of the dry season (December through April) than during the wet season, but pairwise t-tests of the differences between means showed no significant differences between months ($P > 0.2$). Although sample sizes are again small, no seasonal variation in testis size is indicated. Figure 14(b) indicates means for each age class of testis length and testis volume, ignoring obviously immature specimens (less than 5 kg). Note that testis size is essentially constant after one year of age. The length of the seminal vesicle was highly correlated with length of the testis, and so provided no additional information. Apparently, male reproductive activity begins at approximately one year of age, which is slightly older than the age of the youngest pregnant females seen, and remains constant thereafter.

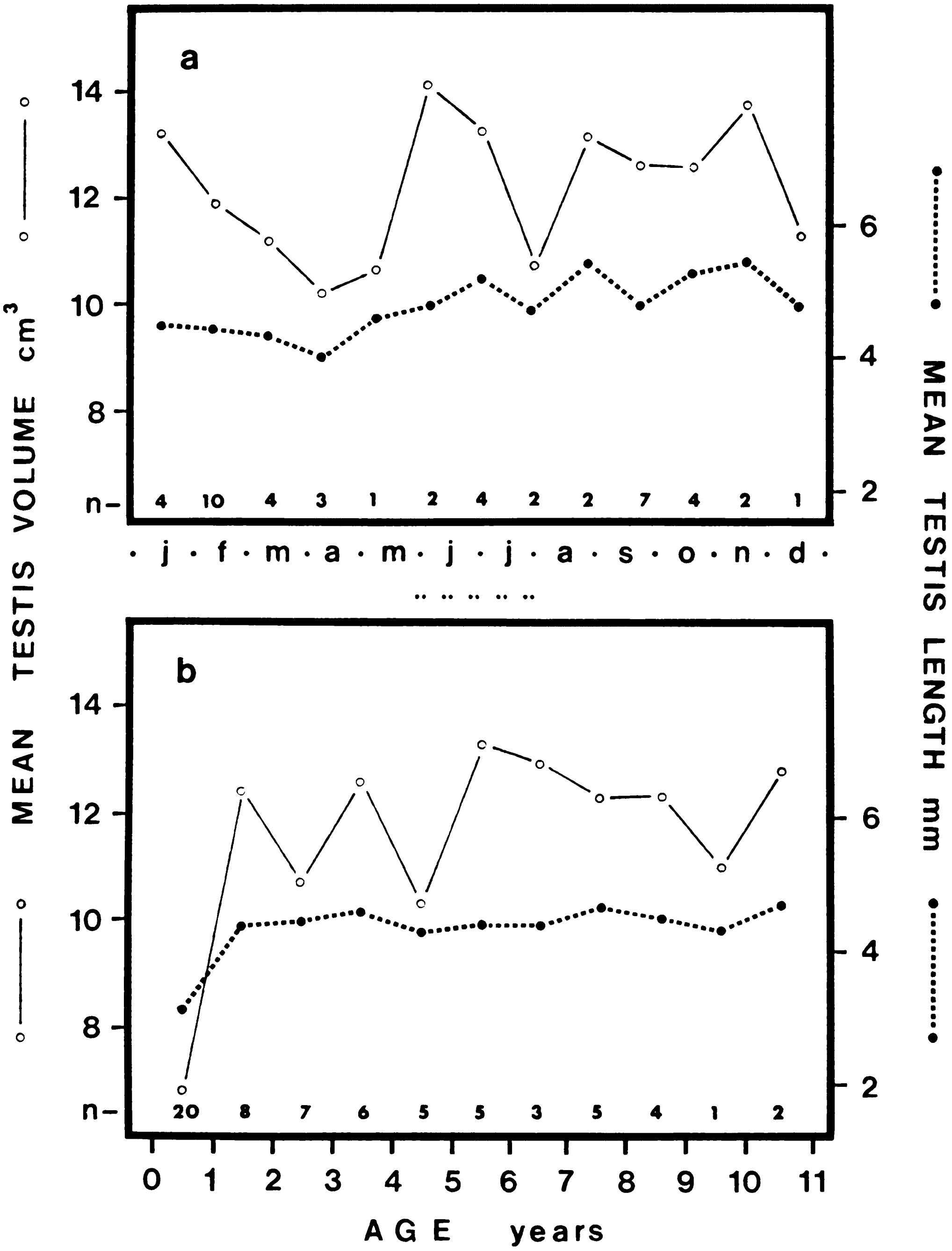


Figure 14. Variation in estimated mean testis volume (open circles) and mean testis length (solid circles). (a) By four-week sampling intervals. (b) By age class. Sample sizes are indicated above the abscissas.

The age of reproductive maturity for male pacas was also examined histologically. Sections were prepared of testes from 27 specimens, collected in ten of the twelve months of the year. Eighteen of these, representing eight different months, contained mature sperm in the seminiferous tubules. On the basis of cementum annulations, these 18 were all classed as one year old or older. None of the remaining 9, all less than one year old, contained sperm, even though the largest of these (7.9 kg) was heavier than the smallest (7.4 kg) of the pacas with sperm. The smallest testis with sperm measured 39 mm, versus 33 mm for the largest immature testis. (These were from the same 7.9 kg and 7.4 kg specimens.) All males one year old or older had testes measuring 38 mm or longer, and so can reasonably be judged reproductively mature.

Annual Fecundity

Since reproductive effort appears to be constant for all females one year old or older, irrespective of season, an estimate of overall fecundity can be derived from values for litter size, interbirth interval, and the sex ratio at birth. Since fecundity is expressed in terms of female offspring born per breeding female per year, the zero-to-one-year age class can for practical purposes be ignored since only one of 41 females in my sample of that age class had actually given birth.

For all pregnancies observed in this study, a single fetus was present. Furthermore, all hunters in the Llanos whom I queried reported having seen only single fetuses.

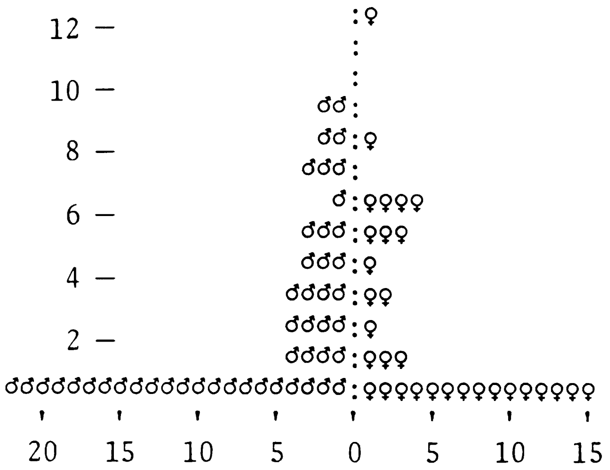
The interval between births is a function of the gestation period and the proportion of females pregnant. If 42/69 or 60.9 percent of the adult females are pregnant, it follows that the average adult female is pregnant 60.9 percent of the time. The gestation period thus represents 60.9 percent of the interval between births. Using 116 days for gestation period (see Appendix B), the best estimate of the interval between births is (116)×(69/42) = 191 days.

Of the 87 pacas less than one year old, 44 were males and 43 were females, suggesting that equal numbers of male and female offspring are born into the population. Mean annual fecundity thus becomes (litter size)×(number of births per female per year)×(proportion of young that are female), or (1)×(365/191)×(0.5) = 0.95 female offspring per female per year. This is general for all age classes beginning with the yearling class when females first give birth.

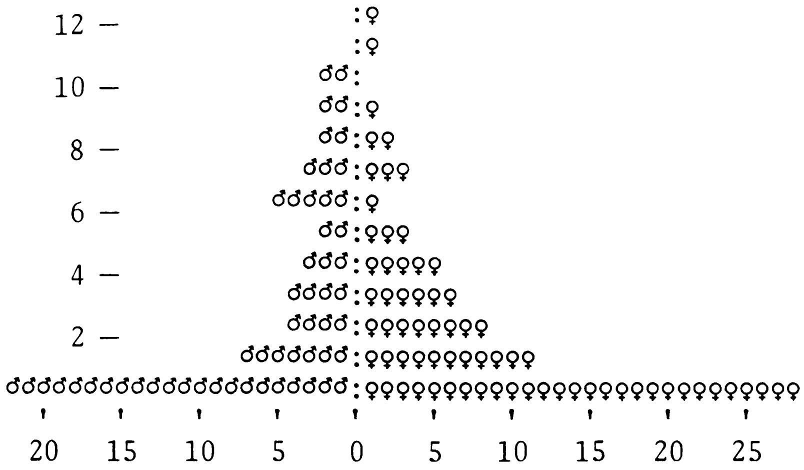
Crude confidence limits for the fecundity estimate can be obtained from the confidence limits of the binomial proportion of 42 pregnant: 27 non-pregnant adult females. The 95% confidence interval for 42/69 is 0.609 ± 0.135, or approximately 47.7 to 74.4 percent. Combining these values with the high and low observed gestation periods of 122 and 109 days reported by Lander (1974), a reasonable range of mean adult fecundity values would be 0.799 to 1.250 female offspring per adult female per year.

Age Structure

Age and sex distribution for the El Tuparro and El Porvenir paca samples are presented in Figure 15. The El Tuparro sample contains fewer young-adult females (two to five years old) and many more males



EL TUPARRO



EL PORVENIR

Figure 15. Age pyramids for the samples of pacas from the El Tuparro and El Porvenir study areas. Each row represents an age class, with age in years represented by the numbers in the vertical columns to the left. Each symbol represents an individual male (♂) or female (♀). Numbers of each sex in each row are indicated by the horizontal scales.

than females, while the El Porvenir sample has a good representation of younger females and relatively equal numbers of both sexes. These differences raise the question of whether or not the specimens that were collected adequately represent the age structure of the population; that is, whether the age distributions of Figure 15 are a random sample of the original standing age structure. This question was addressed by testing homogeneities among intuitively-defined *a posteriori* subsamples for (a) sex ratios and (b) within-sex regressions of numbers of age.

Within the two study areas, subsamples large enough to be statistically tractable were created on the basis of several *ad hoc* criteria. For the El Porvenir study area, the three watersheds in which the collecting sites were located formed three rather natural assemblages of sizeable subsamples: (a) the Muco River (sites 6 and 7), (b) Caño Caviona (sites 1 through 4), and (c) the floodplains and northern tributaries of the Meta River (sites 5 and 8). Such convenient geographical groupings of the El Tuparro sample tended to result in small subsamples, and so the study area was divided into heavily-hunted versus relatively unhunted sites. The former (sites 2, 5, 6 and 7) are those streams most suitable for hunting by canoe which are located on the lower portions of the Tomo and Tuparro Rivers, and thus are highly accessible to hunters living nearby along the Orinoco. The latter (sites 1, 3, 4, 8 and 9), widely separated geographically, are the smaller or more remote streams identified by local hunters as having been infrequently visited. The difference in hunting pressure between the two groupings has undoubtedly been pronounced for at least several years.

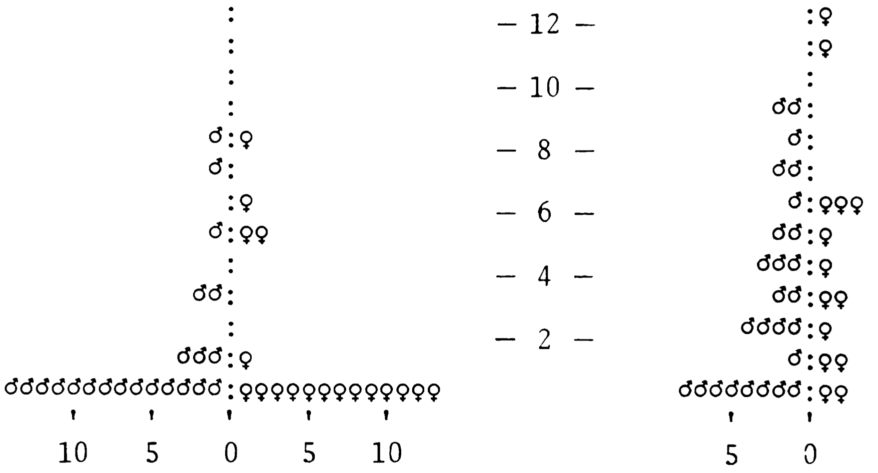
Finally, the combined sample was divided into three groupings on the basis of how the specimens were obtained: (a) by canoe, (b) on foot, or (c) with tracking dogs. Grouping by collecting methods necessarily combined the two study areas since all but 17 of the El Tuparro pacas were obtained by canoe versus only 11 so obtained from El Porvenir.

Age pyramids for the three categories of subsamples are presented in Figures 16 and 17.

Homogeneity of Sex Ratios

Since the overall sex ratio (104 males:101 females) was not different from 1:1 ($P = 0.463$), for each subsample, the exact probability was calculated of drawing the observed numbers of males and females from an infinite population with equal numbers of each sex. Probabilities were also calculated using juveniles only and using all ages greater than or equal to one year. A liberal critical value of $P = 0.2$ was chosen for distinguishing subsamples differing from the expected 1:1 ratio, since the purpose of the exercise was to avoid combining subsamples which might be different (probability of Type II error), as opposed to rigorously minimizing the probability of falsely concluding that there is a difference (Type I error). Ratios significantly different from 1:1 ($P < 0.2$) are underlined in the results presented in Table 2.

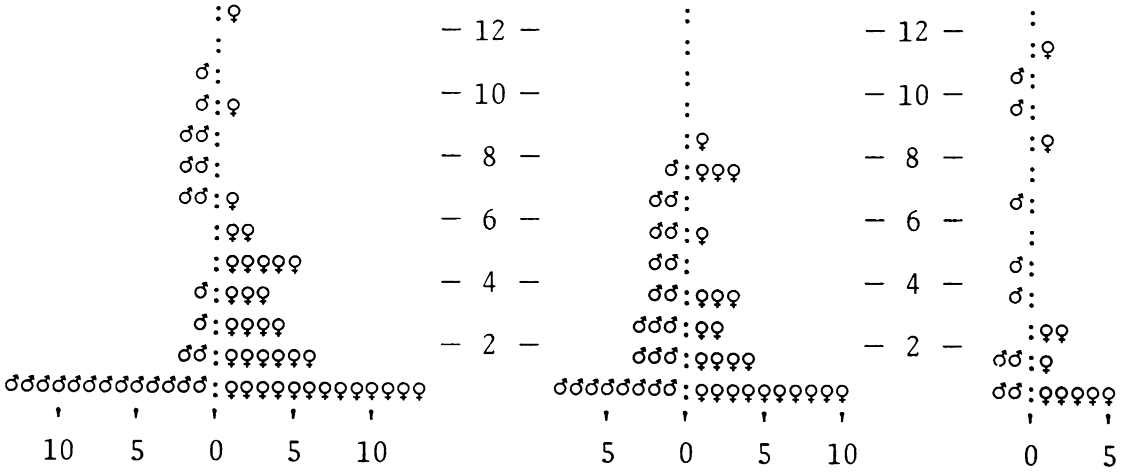
The pronounced bias in favor of males in the overall El Tuparro sample was primarily due to juveniles of the unhunted subsample, although males were more numerous (but not significantly so) than females in the hunted subsample. Females, on the other hand, were



Hunted

Unhunted

EL TUPARRO



Río Muco

Caño Caviona

Río Meta

EL PORVENIR

Figure 16. Age pyramids for subsamples of pacas from El Tuparro and El Porvenir, as defined in the text. Symbols as defined for Figure 15, page 57.

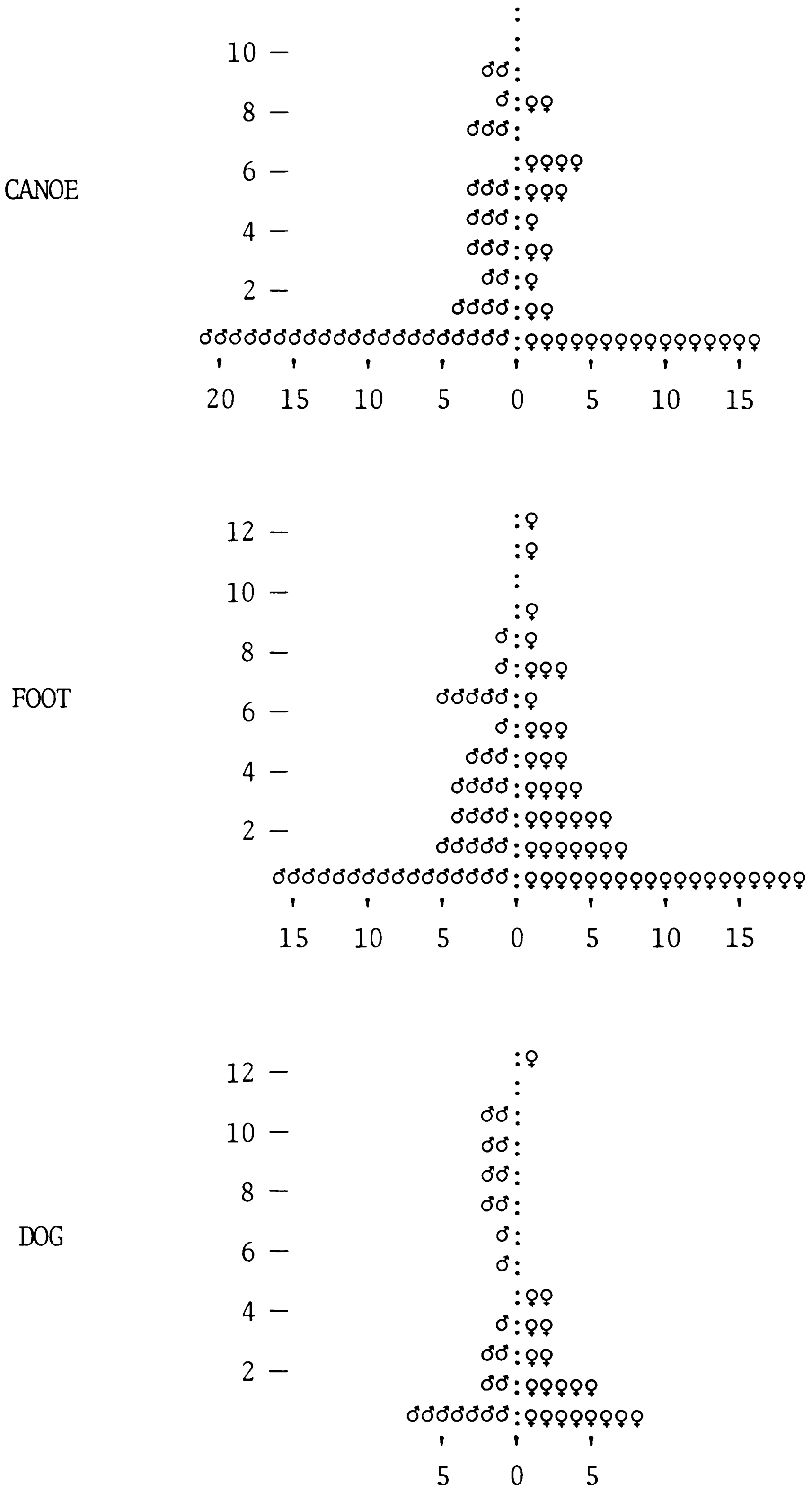


Figure 17. Age pyramids for paca subsamples grouped by collecting method. Symbols as defined for Figure 15, page 57.

TABLE 2. Sex Ratios[1] of Subsamples and Samples of Pacas

I. Within Study Areas

	El Tuparro		El Porvenir		
	Hunted	Unhunted	Muco	Caviona	Meta
<1 year	14:13	** 8:2	13:13	7:10	2:5
≥1 year	8:5	*18:11	12:23**	15:14	7:5
All ages	22:18	**26:13	25:36*	22:24	9:10

II. By Collecting Method

	Canoe	Foot	Dog
<1 year	21:16	16:19	7:8
≥1 year	21:15	24:31	15:12
All ages	*42:31	40:50*	22:20

III. Sample Totals

	El Tuparro	El Porvenir	Combined
<1 year	*22:15	22:28	44:43
≥1 year	**26:16	34:42	60:58
All ages	**48:31	56:70*	104:101

---

[1] Exact binomial probabilities were calculated to test the null hypothesis that the proportion in the smaller class is 0.5. Significant ratios are underlined.

* Probability < 0.2

** Probability < 0.1

Asterisks appear on the side of that sex which is the larger proportion.

significantly favored among adult specimens from the Río Muco watershed. The analysis by collecting methods only partially explains different sex ratios in different categories within the two study areas. The bias in favor of males for the sample from El Tuparro was only partially reflected in the overall ratio of specimens collected by canoe, most of which were obtained from El Tuparro. Adult females were significantly more numerous in the combined El Porvenir sample, where most specimens were collected by hunting on foot. The preponderance of females from the Río Muco was not evident in the ratio for specimens collected using tracking dogs. Despite the heterogeneity of sex ratios among subsamples, biases appear to cancel out when the two study areas are combined.

Homogeneity of Age Structure

It is apparent from all of the age pyramids presented that the zero-to-one-year age class is much larger than all older classes, but that numbers in each age class gradually decline with increasing age beyond one year. In order to test the homogeneity of age distributions among subsamples, least-squares regressions of animal numbers on age were performed within each subsample, with the zero-to-one-year class excluded. The model used was the log-linear form

$$ln\ (\text{NUMBER} + 1) = a - b(\text{AGE}) \qquad (1)$$

where a and b are the intercept and slope, respectively. The midpoint of each age class (age = 1.5, 2.5,...12.5) was used as an approximation appropriate to species with aseasonal reproductive patterns (the "birth-flow" population of Caughley 1966). One was added to the number in each age class in order to include classes with zero individuals (*ln*(0) being undefined), up to the oldest age class in which one or more individuals was actually present in that subsample. Adding one had the disadvantage of rotating the slope of regression (increasing *b*), roughly in inverse proportion to the size of the subsample, but for samples large enough to result in a significant regression the change in *b* was minor. A perfect log-linear fit would result from the simplest of survivorship functions -- a uniform probability of any individual alive in any adult age class surviving to enter the next older age class -- for a stable population (Caughley 1977, and see Discussion). Smaller values of slope *b* indicate more individuals in the older age classes. Differences between subsample slopes for each sex within each of the three subsample categories were tested by pairwise *t*-tests of significance between regressions (Steele and Torrie 1960:173). Differences between combined El Tuparro versus El Porvenir sample slopes were also tested. A critical value of P = 0.2 was chosen, again reflecting the concern for Type II error probabilities. Slopes, within-subsample correlation coefficients, and significant differences between slopes are displayed in Table 3.

The most notable feature of Table 3 is that in only seven of the sixteen subsample regressions are numbers significantly correlated with age (within sexes). Thus tests were performed for possible differences between pairs of regressions which were not in themselves meaningful regressions. For El Tuparro, with only one significant subsample correlation (unhunted males), no differences were detected between hunted versus unhunted subsamples. Nevertheless, the results for both sexes indicated that there were differences between subsamples from the three watersheds of the El Porvenir study area, with

TABLE 3. Tests of Homogeneity of Regression.

Subsample:	El Tuparro		El Porvenir			Methods		
	Hunted	Unhunted	Muco	Caviona	Meta	Canoe	Foot	Dog
Males								
b[1]	.121	.124	.020	.216	.064	.165	.222	.051
r[2]	.368	$\underline{.584}$	.145	$\underline{.850}$	.299	$\underline{.606}$	$\underline{.723}$	.177
n[3]	8	18	12	15	7	21	24	15
t-test[4]			———	———	———	———	– – –	———
							———	———
Females								
b	.043	.090	.265	.183	.064	.123	.191	.041
r	.069	.301	$\underline{.913}$	$\underline{.569}$	.218	.361	$\underline{.882}$	.433
n	5	11	23	14	5	15	31	12
t-test			———	– – –	———		———	———
				———	———			

[1] Subsample regression coefficent (slope) estimated from Equation (1). All coefficents were negative (sign omitted here).

[2] Subsample correlation coefficient. Underlined values are significant ($P < 0.05$). All correlations were negative (sign omitted here.

[3] Number of adults (⩾ 1 year) in each subsample.

[4] Pairwise comparisons of subsample slopes within each category. Lines connect subsamples with significantly different slopes.

significantly older males from the Río Muco and younger females from the Rio Méta. The analysis by hunting methods showed that significantly older males were obtained using dogs versus either by canoe or by foot. Using dogs also yielded significantly older females than did hunting on foot, while females obtained by canoe were not different from those obtained by the two other methods.

Pairwise testing of subsample slopes showed that in addition to differences in sex ratio, significant differences in the age structures of subsamples may be related to factors of collecting sites and hunting techniques. This poses the problem of selecting a combination of subsamples that could with confidence be taken as a random sample of the populations. To some extent, the use of different methods in different areas resulted in biases in opposite directions. Indeed, t-tests of slopes for combined samples from El Tuparro versus combined samples from El Porvenir indicated no difference, whether for males or for females. All four within-study-area correlations were significant ($P < 0.05$).

The differences demonstrated between subsample slopes may have meaning to the exploitation of the population, especially regarding age- and sex-specific differences in susceptibility to different hunting techniques. However, inference is extremely limited due to the lack of significant correlations, resulting from the small sizes of many samples, between numbers and age. One is obliged to ignore for the time being the observed heterogeneity of a partitioned sample and accept with caution the regression parameters of the combined sample. In the linear domain, the coefficient of the age term of the log-linear model becomes a coefficient p of annual adult survivorship from the relationship $p = e^b$ (see Discussion). For males, the estimate of p is 0.867 and the limits of the 95% confidence interval are 0.823 to 0.915. The estimate of p for females is 0.800 and the interval is 0.746 to 0.858. Tested in the logarithmic domain, the slopes for the two sexes are not different ($P > 0.2$). The age pyramid for the combined sample is presented in Figure 18.

Alternative Age Structure Regressions

The log-linear model of age structure used in the above analysis of homogeneity is useful because it describes the parsimonious situation of constant mortality for a stationary population. To examine its validity for describing the data presented here, it was tested against two competing models, (a) linear, and (b) log-quadratic.

The linear model,

$$\text{NUMBER} = a - b(\text{AGE}) \tag{2}$$

was chosen as a null condition. For statistical purposes, it is identical to the log-linear model in that it has the same number of terms. However, its biological meaning is minimal since a perfect fit would imply a complex function of increasing mortality with age, again assuming a stationary population. If the log-linear model does not explain statistically the variation in the observed data better than does the linear model, the parsimonious explanation of constant mortality must be rejected.

The log-quadratic model,

$$ln(\text{NUMBER}) = a - b_1(\text{AGE}) \pm b_2(\text{AGE})^2, \tag{3}$$

was chosen because it uses a higher-order term which can indicate (assuming that the population is stationary) whether mortality is an

```
     12 -                :♀♀
                         :♀
     10 -              ♂♂:
                     ♂♂♂♂:♀
      8 -            ♂♂♂♂:♀♀♀
                   ♂♂♂♂♂♂:♀♀♀
      6 -          ♂♂♂♂♂♂:♀♀♀♀♀
                    ♂♂♂♂♂:♀♀♀♀♀♀
      4 -          ♂♂♂♂♂♂:♀♀♀♀♀♀
                 ♂♂♂♂♂♂♂♂:♀♀♀♀♀♀♀♀
      2 -        ♂♂♂♂♂♂♂♂:♀♀♀♀♀♀♀♀♀
              ♂♂♂♂♂♂♂♂♂♂♂:♀♀♀♀♀♀♀♀♀♀♀♀♀♀
♂♂♂♂♂---♂♂♂♂♂♂♂♂♂♂♂♂♂♂♂♂♂:♀♀♀♀♀♀♀♀♀♀♀♀♀♀♀♀♀---♀♀♀♀
    '     '    '    '    '    '    '    '     '
   40    15   10    5    0    5   10   15    40
```

Figure 18. Age pyramid for the pacas from El Tuparro and El Porvenir combined. Symbols as defined for Figure 15, page 57.

increasing or decreasing function of age. Equation (3) is a parabola in the logarithmic domain, with its curvature relative to the straight line of the log-linear model being determined by the sign of the $(\mathrm{AGE})^2$ term (Caughly 1977 and see Discussion). For a stationary population, the sign of the coefficient b_2 implies either an increasing (b_2 negative) or a decreasing (b_2 positive) probability of death with increasing age.

Since all sample age classes except for ten-to-eleven-year-old females contained specimens, the natural logarithm of the actual number of pacas present in each class was used instead of adding one as before, and the missing female age class was ignored. Least-squares regressions of each of the three models and F-tests of the significance of regression were performed within sexes. Correlation coefficients were tested by approximate t-transformations. All equations obtained by least-squares fit were used to generate expected age distributions, which were then compared to the observed distributions of Chi-squared tests of goodness of fit. The significance of adding the quadratic age term was also tested by computing F for the reduction in sum of squares due to the quadratic term alone. Results are presented in Table 4.

Although all values of F are significant, the log-linear model did not provide an increase in F compared to the linear model, whether for males or for females. Examination of the fitted equations against the original data revealed that this was due to differences in the distributions of errors in the linear versus the logarithmic domains. Observed numbers in each age class tended to lie above the fit of the linear model for younger and older age classes, and below

TABLE 4. Tests of Three Models of Regression for the Combined Sample of Paca Age Structure.

		Males	Females
I. Linear	r	-.9409*	-.9182*
	F^a	69.514 *	43.592 *
	df	(1,9)	(1,10)
	χ^2	2.819	17.032
II. Log Linear	r	-.8522*	-.8960*
	F^a	23.878 *	40.696 *
	df	(1,9)	(1,10)
	χ^2	1.509 *	3.086
III. Log-Quadratic	r	.9170*	.9037*
	F^a	21.131 *	20.044 *
	df	(2,8)	(2,9)
	F^b	46.386 *	3.431
	df	(1,8)	(1,9)
	χ^2	.803 *	1.498 *

F^a Test of significance of overall regression.
F^b Test of significance of adding x^2 term.
χ^2 Chi-square sum of goodnes of fit, with 9 to 11 degrees of freedom in each case.

* $P < .05$

the line for classes of intermediate age, whereas deviations were more uniformly distributed above and below the exponential curve of the log-linear fit. The Chi-squared test of fit was thus a better model for comparing these models because it could be performed in the linear domain in every case. The log-linear model, both for males and for females, resulted in major reductions in Chi-squared relative to the linear model.

For females, the major source of Chi-squared error was attributable to the 12-to-13-year-old class. If the two individuals in this class had been deleted from the analysis, the Chi-squared sums for females would have been only 5.102 and 1.862 for the linear and log-linear models, respectively. The latter value would be statistically significant ($P < 0.05$). Thus when statistical variation was tested in the linear domain, the log-linear model resulted in a significantly better fit for both males and females than did the linear model.

For males, the best fit of the log-linear model was

$$ln(\mathrm{NUMBER}) = 2.555 - 0.142(\mathrm{AGE}). \qquad (4)$$

The addition of a quadratic term resulted in a significant improvement in F over the log-linear model, as well as a major reduction in Chi-squared. The value of F for the addition of the quadratic term in age was highly significant. The predictive equation was

$$ln(\mathrm{NUMBER}) = 2.044 + 0.147(\mathrm{AGE}) - 0.025(\mathrm{AGE})^2. \qquad (5)$$

The negative sign of the coefficient of the quadratic term in age implies that for the males of this population, mortality was an increasing function of age. The positive sign of the linear term, however, means that the axis of the parabola falls to the right of the

the origin, indicating that the maximum number of individuals is predicted to occur in some age class greater than zero. Solving for the zero value of the second derivative of Equation (5) shows that in this population, maximum numbers would occur at AGE = 2.94 years. Under the restrictive assumption of a stationary population, this would imply the impossible situation of survivorship values greater than unity for the age classes of 1.5 and 2.5 years. This is clearly unrealistic, since survivorship values must always be less than unity. Figure 19 shows the transformations of the fitted curves of the log-linear and log-quadratic models of age structure for adult males, together with a histogram of the observed age structure. Although the log-quadratic model has greater precision in describing the male age distribution statistically, its application does not provide a meaningful interpretation of survivorship of a decreasing function of age if the population is assumed to be stationary. The implication of an aberrant survivorship pattern must, however, be taken into account.

For females, the addition of a quadratic term in age to the log-linear model produced no significant increase in F (taking into account the loss of one degree of freedom in the numerator). The value of F for the quadratic term alone was not significant ($P > 0.1$). There was, however, a reduction in Chi-squared.

The least-squares fit of the log-quadratic model for females is

$$\mathit{ln}(\mathrm{NUMBER}) = 3.193 - 0.313(\mathrm{AGE}) - 0.008(\mathrm{AGE})^2 \qquad (6)$$

versus the log-linear fit of

$$\mathit{ln}(\mathrm{NUMBER}) = 2.852 - 0.223(\mathrm{AGE}). \qquad (7)$$

Linear transformations of Equations (6) and (7) are superimposed on a histogram of the observed female age structure in Figure 20.

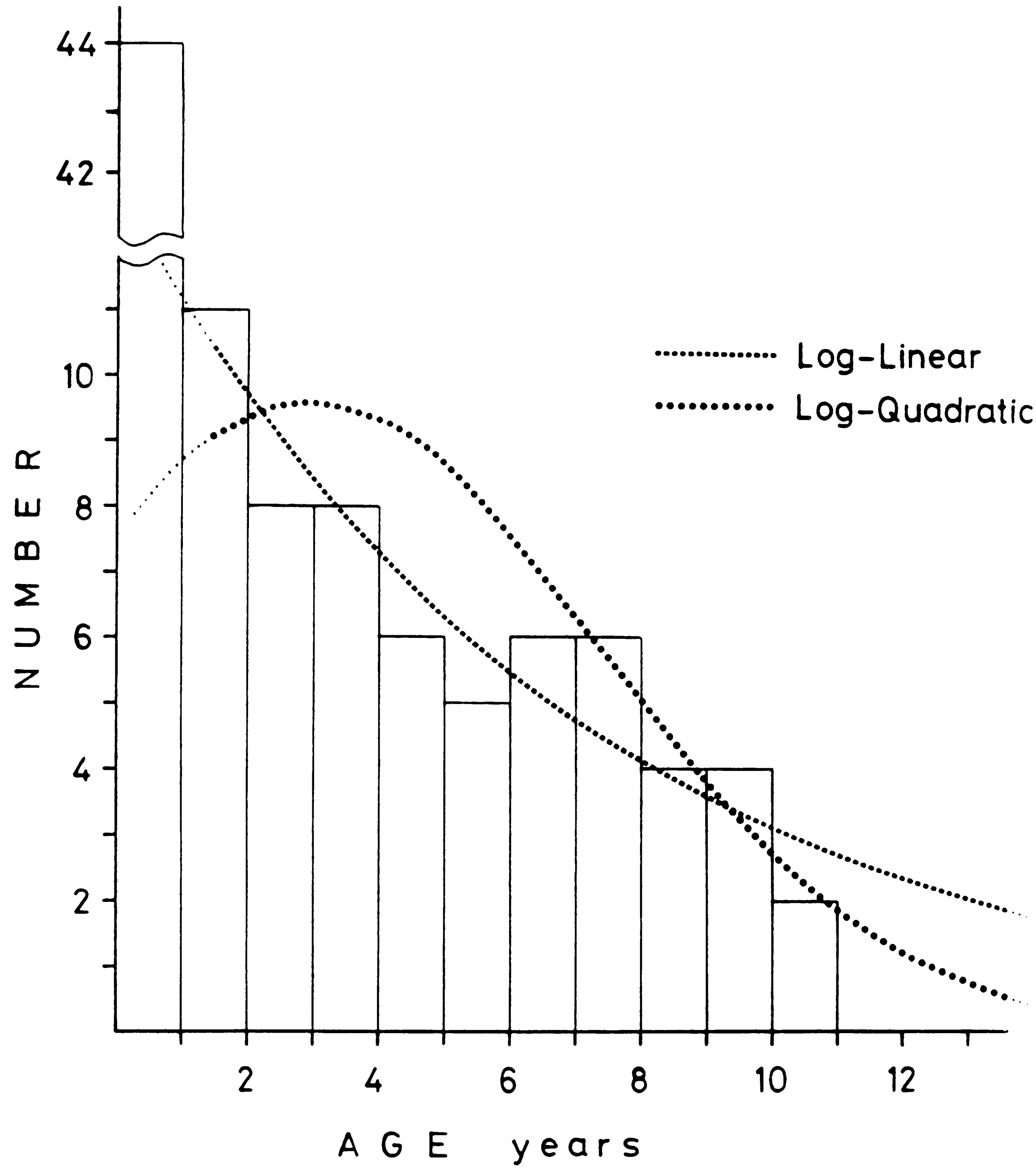


Figure 19. Curves of the log-linear and log-quadratic models for males, superimposed on a histogram for the observed age distribution to which they were fitted.

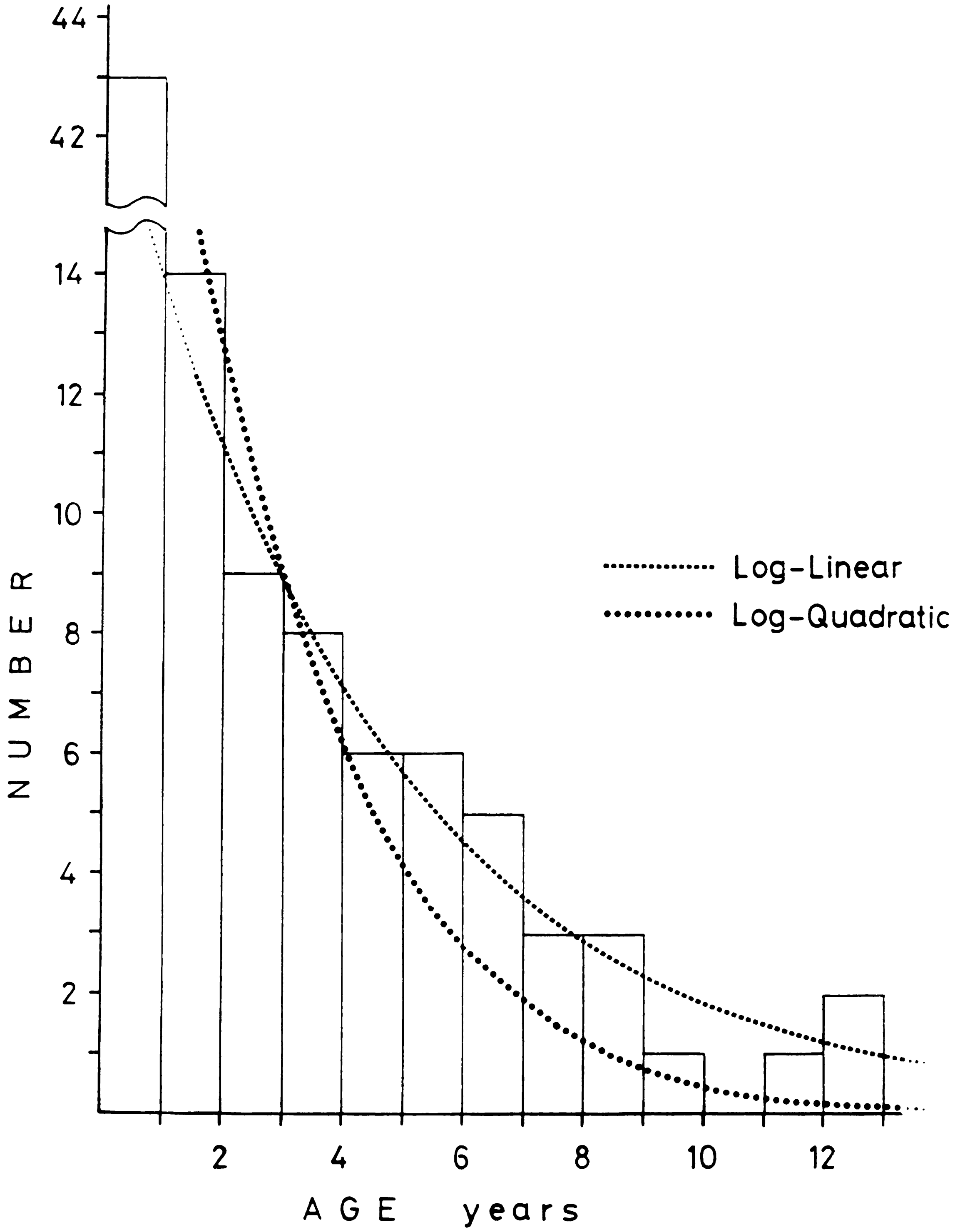


Figure 20. Curves of the log-linear and log-quadratic models for females, superimposed on a histogram of the observed age distribution to which they were fit.

Although in the linear domain the quadratic term results in a better fit to the original data, its effect is seen to be modest due to the relatively small least-squares estimate (0.008) of its coefficient. for the 12.5-year age class, the difference between the values predicted by the two models is only 1.2 individuals. I conclude that the analysis does suggest the possibility of slightly decreasing mortality with increasing age for females, but not to a degree sufficient to warrant adopting the log-quadratic rather than the log-linear model.

Disregarding problems of sample size and collecting bias, the thrust of the foregoing analysis is that all individuals older than one year have relatively the same likelihood of surviving into the following age class. In other words, all adult pacas experience approximately the same annual probability of death. Again, the entire analysis depends on the assumption, to be dealt with in the following discussion, of a stationary population.

Abundance

Estimates of the number of adult (one year old or older) pacas per km^2 of forest and of all pacas per km^2 of forest are presented in Table 5. The estimates are based on the numbers of specimens collected at those three sites that were exhaustively hunted. Numbers of pacas from each site include only specimens from discrete galleries that were thoroughly and repeatedly hunted over a relatively short period of time. The periods of hunting effort varied, but relative hunting effort was approximately comparable at these three sites. It must be assumed that none of the individuals removed by hunting effort was replaced through immigration during each of the collecting periods.

TABLE 5. Estimates of Abundance.

SITE	Sampling Period[a] (days)	Number of Pacas		Forest Area (km^2)	Number/km^2	
		Total	Adults[b]		Total	Adults
El Tuparro -- Caño Rana	26	9	4	0.105	86	38
El Porvenir -- Puente Gloria	89	10	6	0.108	93	56
El Porvenir -- Caño Limici	90	36	22	0.429	84	51

[a] Dates for each collecting period are as follows:

Caño Rana: 4 October through 29 October, 1976.
Puente Gloria: 7 July through 4 October, 1978.
Caño Limici: 8 July through 4 October, 1979.

[b] Adults are one year old or older.

This problem was more likely to inflate density estimates for the two sites of the El Porvenir study area than for the El Tuparro site (Caño Rana), where hunting occurred over a much shorter period of time.

The total area of forest in the vicinity of each of the two study areas was estimated for 50×50 km (2500 km^2) areas carefully located to represent an area readily accessible to hunters living near each study area. The mean of estimates of the percent of ground cover occupied by forest at four representative localities of the El Tuparro study area, using the transparent grid technique, is 8.04%, implying that there are approximately 201 km^2 of forest in the 2500 km^2 area readily accessible to hunters. The densitometer estimate of forest cover for a 2500 km^2 area centered on Carimagua is 4.60%, or 115 km^2 of forest. By the estimates of Table 5, then, at El Tuparro the number of adult pacas available to hunters is approximately 7,638 in 2500 km^2, versus 5,865 to 6,440 for the vicinity of El Porvenir. The estimated numbers are 17,285 and 10,695 respectively if juveniles (less than one year old) are included.

ADDITIONAL OBSERVATIONS

This section reports findings on the paca's feeding habits, behavior, use of habitat, and burrows. This information was gathered primarily in conjunction with hunting efforts. The methods used are biased toward those aspects of the species' habits which have a bearing on hunting success or are at least amenable to study in the course of hunting. Ideas and observations provided by local hunters raised several questions for testing in the field. Where pertinent, specific findings are contrasted here with those of published accounts. Discussion of the significance of these factors to the life-history pattern of the population, especially in relation to hunting, will be considered later in connection with the modeling of demographic parameters.

Foods

Evidence gathered in the Llanos indicates that pacas feed almost exclusively on fruits. Specific food items utilized by pacas were identified using three types of evidence: (1) The presence of identifiable food parts in the stomach or mouth of a collected specimen; (2) the presence of distinctive grooves, attributable to the incisor teeth of pacas, in partially eaten fruits found in the field; and (3) direct observations of what foods and animals were eating at the time of collection.

Several important food fruits could be identified from stomach contents on the basis of characteristic scales or fibers (e.g., *Mauritia*, *Syagurus*) or color and texture of fruit pulp (*Rheedia*, *Attalea*). Pacas and several other common mammals use the incisor teeth to scrape off and eat the soft pericarps of several fruits that have hard seed coats (*Spondias*, *Attalea*, *Syagurus*, *Bactris*, and *Oenocarpus*). Grooves made by an adult paca's incisors, which are 4 mm wide or wider, were readily distinguished from the narrower grooves which would be made by the other frugivorous mammals present (*Didelphis marsupialis*, *Dasyprocta fuliginosa*, *Potos flavus*, *Cebus apella*, *C. albifrons*, *Proechimys* spp., and several smaller marsupials and rodents).

Direct observation was relied upon in cases of soft fruits (e.g., *Bursera*, *Protium*) which would not show distinct incisor marks in partially-eaten fruits or characteristic parts in stomach contents. Observations by local hunters were accepted only if given without prompting on my part and if the hunter could show me where his observations had occurred and thus demonstrate that the food was available.

Twenty-three plant species were identified as being eaten by pacas. Table 6 lists these foods by the months in which the source was available, by the study area in which their consumption by pacas was observed, and by the plant parts eaten. Virtually all of the food items that were identified were fruits or fruit parts. Of the 116 stomachs examined, 112 contained only fruit parts. An adult female collected at Puente Gloria in February of 1978 also had parts of the flowers of a nearby *Cochlospermum* tree in the stomach. Leaf parts were found in three cases: (1) in the stomach of a female collected

TABLE 6. Food Items Utilized by Pacas.

FAMILY Scientific Name	Local Common Name	Parts Eaten[1]	Area Observed[2]	Months Available[3] J F M A M J J A S O N D
ANACARDIACEAE				
Spondias cf. *mombin*	hobo, jogo	Pc	T	------
ANONACEAE				
Anona sp.	anon	F	P	----*******---
AREACEAE				
Attalea regia	cucurita	Pc	T,P	----****************----
Bactris spp.	cubarro	Pc	T,P	------************------
Mauritia flexosa	moriche	F	T,P	---*******************--
Mauritiella sp.	moriche macho	F	P	--------
Oenocarpus mino	seje, pusuy	Pc	T,P	--------------
O. cf. *polycarpa*	seje	Pc	T	------------
Socratea spp.	araco, shuapo	Pc	T,P	----**********------
Syagurus inajai	churrubay	Pc	T,P	----************--------
BURSERACEAE				
Bursera sp.	aguacatillo	F	P	---------
Protium sp.	nispero	F	T,P	--------
CHRYSOBALANACEAE				
Licania sp.	guaray	F	T,P	------
Unknown	pendare	F	T,P	-----------------

[1] Pc = Pericarp; F = Whole fruit; S = Seeds; I = Inflorescence.
[2] T = El Tuparro; P = El Porvenir.
[3] Asterisks are months during which the parts eaten are generally available. Dashes are months of limited or local availability.

TABLE 6 (continued)

FAMILY Scientific Name	Local Common Name	Parts Eaten[1]	Area Observed[2]	Months Available[3] J	F	M	A	M	J	J	A	S	O	N	D
COCHLOSPERMACEAE															
Cochlospermum sp.	barbascal	I	P		--	--									
GUTTIFERAE															
Rheedia madrunno	madrono	F	T,P		--	--	--	--							
Lecythidaceae															
Eschweilera sp.	coco de mono	S	T				--	--							
Gustavia sp.	tejo	F	T		--	--	--	--							
LEGUMINOSAE															
Dipteryx sp.	serrapia	S	T,P	--									--	--	--
Unknown	tapir	S	T	--	--	-								--	--
MELIACEAE															
Guarea sp.	cedo	F	T		-	--	--	--	--	--					
MORACEAE															
Ficus sp.	matapalo	F	T		--	--	--	-							
Ficus sp.		F	P			--	--	--	--						

---

[1] Pc = Pericarp; F = Whole fruit; S = Seeds; I = Inflorescence.

[2] T = El Tuparro; P = El Porvenir.

[3] Asterisks are months during which the parts eaten are generally available. Dashes are months of limited or local availability.

in February 1976 from the upper Río Tuparro, (2) in the mouth and stomach of a juvenile female from La Arepa taken in November of 1978, and (3) in the stomach of an adult female collected in January of 1979 at Rincón Masato. No animal remains were ever seen in the stomachs examined.

Smythe (1970a, 1978) has suggested that pacas are unable to manipulate and open some hard-shelled fruits (e.g., the nuts of Spondias and Attalea) which are readily opened by the more dexterous agouti (Dasyprocta punctata). Smythe concluded that pacas browsed foliage when soft fruits were not available, a habit for which I found very little evidence. Dasyprocta and Myoprocta are known to bury caches of hard seeds (a behavior termed "scatter hoarding" by Morris [1962]) and then feed on these provisions when fruitfalls become scarce. I can find no evidence, either from the literature (Kraus et al. 1970, Smythe 1970a, Lander 1974) or from my observations in the field, for scatter hoarding by pacas. A correlate of Smythe's model is that the pacas he captured late in the wet season were fat. Smythe believed that this represented a mechanism by which pacas prepared for the limited availability of fruits during the upcoming dry season. In the Llanos, all pacas collected during the dry season were lean, even those from November and December. Fat deposits in the inguinal and retroperitoneal regions, which were prominent in all specimens collected during the wet season, were not apparent in specimens collected between December and March. Evidently, fat deposits respond quickly to seasonal change, and are not sufficient to supply energy reserves throughout the dry season. Nevertheless, the disappearance of these reserves early in the dry season does suggest that food sources are less abundant at that time.

Inspection of Table 6 reveals that the availability of some common fruits at all times of the year enables pacas in the Llanos to rely almost exclusively on frugivory. The fruits of two common palms, *Attalea* and *Mauritia*, are available at most times of the year. The importance of *Mauritia* is due to its occurrence in low-lying areas within major galleries. In the seasonally-flooded morichales of the headwaters of most gallery streams, *Mauritia* may fruit abundantly only in the wet season, but fruit-bearing individuals of this palm may be found at any time of the year in those portions of mature galleries where saturated soil conditions persist through the dry season. This was particularly evident at Caño Caviona, where *Mauritia* fruits bearing the marks of paca incisors were found in all twelve months of the year. *Attalea* has a protracted season of fruit production, and apparently individual trees produce fruit for periods of three or four months. There are also broadleaf species which bear fruit during the dry season (e.g., *Rheedia*, *Gustavia*). Seasons of fruit availability may also be expanded somewhat by the activity of arboreal frugivores, such as *Didelphis*, *Potos*, *Cebus*, and parrots, all of which drop partially-ripened fruit in the course of their feeding and thus make it available to terrestrial frugivores such as the paca.

In a quantitative study of fruitfall on Barro Colorado Island, Smythe (1970b) found that at all times of the year, there were some species of fruit that were ripening. Although the quantity of fruit that fell varied markedly between seasons, some fallen fruit was always available. The same situation applied to the Llanos, and is evident in the almost total lack of nonfruit items in paca stomachs.

Smythe's observations concerning the inability of pacas to eat the seeds of stony fruits were supported by my observations, but pacas did eat the softer pericarps of these fruits. Seeds of Spondias, Attlea, Oenocarpus, Bactris, and Syagurus were all found to have been eaten by Dasyprocta, as indicated by grooves less than 3 mm wide in the stony endocarps of these seeds that had been opened. The pericarps of these same fruits comprised a major portion of the contents of at least 46 of the 116 paca stomachs that I examined.

Several fruits appeared to be only locally important in the diet of pacas. These were identified chiefly as a result of their being known to local hunters as food items preferred by pacas, especially Spondias, Rheedia, Oenocarpus, pendare, and Bursera. It should be noted that the preference of hunters for forests containing fruiting trees of these species undoubtedly resulted in these fruits being disproportionately represented among my observations on feeding habits. Conversely, many less-conspicuous or little-known fruits must have been neglected. Hunters also reported having collected pacas that were feeding on cultivated crops such as mangos and corn. Captive pacas have been observed to eat almost anything presented to them, including table scraps, raw meat, various cultivated fruits and vegetables, lizards, and insects (Smythe 1970a, Lander 1974, Kraus et al. 1970, present study).

Apparently, pacas are not discriminating in their choice of fruits. Most fruits large enough and firm enough to show distinct tooth markings were found to have been utilized by several mammals,

including pacas, wherever I encounterd their fruitfalls. There were many fruits, however -- especially soft berries and hard legumes -- that never had tooth markings because they were either too small, too soft, or too brittle. More detailed observations on the behavior of pacas in the wild should greatly extend the list of foods begun in Table 6.

In the Llanos, food *per se* does not seem to be in critically short supply at any time of the year as far as pacas are concerned. Seasonal variation in the distribution and abundance of principal food sources does appear to affect the physiology and behavior of pacas, since they contain less depot fat, and do occasionally utilize atypical food sources such as leaves, during the dry season.

Behavior

Activity

Pacas appear to be almost exclusively nocturnal. I saw no pacas during daylight hours other than those that were frightened from their burrows by tracking dogs. However, three local hunters recalled a few occasions when they had encountered pacas in the forest during daylight. Using automatic cameras activated by tripwires, Smythe (1970a) showed that adult pacas were sometimes active during the early morning and late afternoon, and that juveniles were on rare occasions active during mid-day. The vast majority of his observations of pacas, however, were recorded at night. It is also worth noting that I made little effort to detect pacas during the day.

Local hunters always took the phase of the moon into account when planning their hunts. Persons in the Llanos believe that pacas remain in their burrows during moonlit nights, and thus are not available for hunters. In consequence, it was difficult to evaluate the effects of moonlight on paca activity since most observations were made on dark nights as a result of hunter prejudice. Nonetheless, 19 pacas were collected under conditions of bright moonlight, and many more were seen at such times but not collected. Therefore, it is not possible to distinguish between restricted activity of pacas during bright nights versus decreased hunting success possibly due to pacas being better able to detect and avoid the hunter when there is more light in the forest. Seasonal avoidance of moonlight has been demonstrated for the nocturnal rodent Dipodomys spectabilis (Lockard and Owings 1974). It would be interesting to test Smythe's automatic camera data for a correlation between paca activity and moonlight.

I noticed a tendency for hunting success to increase markedly after moonset on nights when hunting during the waning phase of the moon. During the dry season, no such relationship was apparent, but then hunting success as a whole was lower during the dry season. Local hunters suggested that food sources were more abundant during the wet season and so the pacas limited their foraging to short periods during almost total darkness, whereas during the dry season, the pacas foraged longer and more widely for more scattered food sources. However, if pacas are active longer during the dry season, they should be more frequently encountered by the hunters at that time, which was not the case.

Response to Hunters

Upon detecting the presence of the hunter, pacas responded with a wide range of behaviors, from apparent disinterest to rapid flight. Most animals that were collected were easily shot once encountered because they either "froze" or calmly gazed in the direction of the hunter. The majority of the pacas that I saw responded in ways more appropriate to their survival, the most frequent reaction being to run rapidly toward the nearest stream or toward dense cover such as patches of *Bactris* or marantaceous plants. A barking vocalization always accompanied head-long, bounding flight, and occasionally this avoidance reaction was preceded by a quiet, low-pitched growl. Often, however, the animal's movements were more controlled and no vocalizations were heard, resulting in little noise as the paca moved rapidly but calmly away. On several occasions, the animal was seen to continue on its path, apparently undisturbed by, or unaware of, the presence of the hunter.

Particularly wary individual pacas were sometimes encountered, notably at several of the Caño Caviona sites. On eight consecutive nights during January of 1979, I heard barking flight response at the same point along my hunting trail at the La Arepa collecting site. I presume that the same individual was involved in all eight encounters, although I saw the animal only twice and never collected it. My notes record 26 instances of fleeing pacas heard but not seen. These observations suggest to me the possibility that pacas may learn to avoid hunters. If such behavior is common and age-dependent, it implies a serious bias in favor of older (therefore more experienced) pacas avoiding capture.

Flight to water was one of the most common responses observed. Upon reaching the bank of the stream, the paca would leap into the water with little or no hesitation, even from as high as four meters above the water level. I observed pacas swimming both at night and during the day. Pacas swim well. They submerge and dog-paddle at a speed of approximately 0.5 m/sec, occasionally pushing off against the bottom with the hind feet. On those occasions when the animal's progress could be followed, it invariably sought brushy cover at the waterline, remaining submerged until such a refuge was reached. There it would rise until only the eyes and nostrils emerged above water, and remain still. During my experiences with tracking dogs, at least twenty pacas escaped capture in this manner. One individual was collected approximately 80 m upstream from where it had entered the main stream of the lower Río Tuparro, having covered this distance in only three to four minutes.

Feeding Behavior

On ten occasions, I was able to observe solitary pacas for several minutes while they fed on various fruits (*Attalea*, *Protium*, *Rheedia*, *Mauritia*, and *Licania*). They never attempted to lift the fruit, either with the incisors or using the forefeet, and so did not accumulate a supply to be consumed in one spot as Mondolfi (1972) suggests they do. (I did, however, observe this behavior in *Dasyprocta fuliginosa*.)

On two of these occasions, pacas were observed to feed on fruits being dropped or otherwise made to fall from the canopy by arboreal mammals (a group of *Cebus apella*, which may have been aroused by my presence, feeding on Rheedia and a Didelphis feeding on Attalea). In another four instances, two pacas were seen to be feeding together. Two adult males were collected at Puerto Alegre while they fed together. Of the three remaining instances, one involved two adults, of which a female was collected, and two involved an adult female with young. Two of the hunters with whom I worked would occasionally construct a simple platform up in a tree, and drop stones or fruits in hopes of attracting pacas by imitating the sound of falling fruit. In some cases, they were successful. More experienced hunters considered this technique to be ineffective, but my observations of pacas feeding on fruits dropped by Cebus and Didelphis lend some plausibility to the method.

Communication

From observations of a captive male paca, I was able to identify two forms of communication that I had not observed in the wild: foot stamping and tooth grinding. When approached, the captive would usually stamp his hind feet in a manner reminiscent of the thumping of rabbits. This was usually preceded by a low-pitched growl that lasted for one or two seconds, increasing in volume and ending in a sharp barking sound which coincided with the stamping of the feet. The impact of the hind feet on bare ground produced a surprisingly loud noise. After approximately two weeks in captivity, however, this animal would occasionally lower his head and produce a rhythmic, rumbling sound much lower in pitch than the growls heard in response to hunters. The rumbling sound consisted of three to seven pulses each approximately 0.2 to 0.4 seconds in duration. The animal remained virtually immobile while producing this sound. While attempting to record the rumbling, I was able to observe a forward-and-back motion of the jaw, with a forward stroke coinciding with each pulse of sound. Evidently, the rumble is produced by the animal grinding the upper and lower molariform teeth against each other. Eisenberg (1974) reported that pacas produced a variety of growling and barking vocalizations, but made no mention of tooth-grinding. Smythe (1970) briefly mentions a sound produced by tooth-grinding.

Previous to obtaining the captive male, I had on three occasions heard rumbling sounds while probing burrows that had been located by tracking dogs. In each case, the hunters took this as confirmation of the presence of a paca, and indeed a paca was obtained from each of the three burrows. This is reminiscent of Hershkovitz's (1955) accounts of encounters with pacas in burrows.

Hershkovitz also heard barks and growls produced by captive pacas, and concluded that the rumbling sounds produced by pacas in their burrows were the same growls. Furthermore, he believed that the function of the zygomatic pouches was to enable the skin of the cheeks to be stretched into a reverberating membrane. This membrane could then either amplify a vocal sound or could be made to vibrate by strong exhalations and thus produce a sound. My observations of jaw movements coincident with the rumbling sound seem to refute the mechanism proposed by Hershkovitz. In particular, the skin of the cheek was not seen to be stretched under the zygomatic pouch when rumbling sounds were produced. I do not know whether or not the zygomatic pouches have a role in the amplification of the sound produced by tooth grinding, but my impression of the volume of the rumbling sound leads me to believe that such a function is possible and deserves further study.

Several hunters living near the El Tuparro study area were familiar with the tooth-grinding sound and when hunting, they often imitated it by scraping the side of the prow of their dugout canoes with a fingernail. They said this technique could induce a paca to approach again after it had fled. I was never able to attract pacas in this manner, even when using a tape-recording of tooth-grinding sounds elicited from my captive male.

Imitation of the tooth-grinding sound may account for the preponderance of males in the El Tuparro collection, most of which were obtained by hunting from canoes. The most proficient hunter with whom I worked at El Tuparro, an Indian who for many years had been earning his living as a market hunter, relied heavily on the canoe-scratching technique. Of the 40 pacas collected by him 26 (65%) were males. This ratio (26:14) is significantly different from 1:1 ($P < 0.05$), but I do not know which of these specimens were obtained as a result of the hunter mimicking the tooth-grinding sound. This hunter said that he generally obtained approximately twice as many males as females.

Social Behavior

Of the 108 encounters with pacas that are recorded in my notes, 86 involved pacas that were alone insofar as I could determine. My notes are not complete for such encounters. On 21 occasions, I observed two pacas in close proximity (less than 5 m) of each other, but in only four of those instances was I able to collect both individuals. Only once did I see three pacas together; two adults (presumably a male and a female) and a young paca which I estimate weighed less than 2 kg. These three animals were all within touching distance of each other, but I was unable to collect any of them. On another five occasions, local hunters collected two pacas foraging together. Finally, at least six times, my attempts at collecting one paca prompted a flight response by a previously-unseen paca nearby. No noteworthy intraspecific behaviors were observed during any of these encounters, which usually lasted for thirty seconds or less before the animals either fled or were shot. Thus data on social behavior are limited to the sexes and ages of those pacas that were seen with conspecifics and actually collected.

Of the nine instances of two pacas collected together, five involved a female with young, three were an adult male with an adult female (one of these involving two individuals just less than one year old), and one case of two adult males feeding within 3 m of each other. In nine other cases, an adult was seen with a small young paca and either an adult female or the young was collected. A lactating female and her young were found in the same burrow on four occasions, the only instances of cohabitation found in the sample obtained using tracking dogs. Local hunters recounted rare occasions when they had seen three, four, and by one account, six pacas foraging together at preferred food sources such as fruitfalls of *Rheedia*. I saw no such large aggregations of pacas. Evidently, pacas are solitary in their foraging habits, with most of my few encounters of more than one together involving an adult female with her lactating young.

Smythe (1970a) states that pacas defend territories as mated pairs. His automatic cameras recorded several instances of two adults

foraging together or of a male and female together with the young. He also noted, however, that most of his observations of pacas involved lone individuals. I found no evidence of pair formation. Males and females were rarely seen to forage together, yet two males were seen together with no sign of agonistic behavior, and any combination was possible among the sightings of animals seen together but not collected. Adults were never seen to occupy the same burrow, although only eleven burrows were examined. In light of the possibility of a post-partum estrus, the occasional presence of an adult male together with a lactating female and her small offspring is perhaps better explained by the opportunity for copulation rather than by any role for the male in caring for the young. Indeed, several instances of lethal attacks on captive young pacas by their male parents have been brought to my attention (Eisenberg pers. comm. 1977, Lander 1974, Aquino Yarihuaman pers. comm. 1979, and see also Smythe 1970a:75).

Pacas, agoutis, and acouchis all possess eversible scent glands located just inside the anus (Pocock 1922). Smythe (1970a) observed wild agoutis dragging the everted glands against various substrates and concluded that agoutis used the secretions produced by these glands to mark territories. Smythe's automatic cameras produced several photographs of pacas that had the anal glands everts, but he did not observe pacas dragging the glands against substrates in the environment. Kraus _et_ _al_. (1970) stated that their captive pacas urinated in all parts of the periphery of their enclosures as a way of scent-marking. I observed neither anal glands everted by the pacas I maintained in captivity, nor the use of these glands by wild pacas. My captive pacas consistently urinated and defecated in a particular corner of their individual cages, but any scent-marking behavior may have been suppressed due to the small size (2 to 4 m^2) of the enclosures I used. It is quite possible that the anal glands or urine are used to mark territories, but whether these territories are defended by individuals, by mated pairs, or by any combination of individuals, cannot be determined on the basis of the evidence available.

Use of Habitat

Hunting efforts were focused on accessible gallery forests that were known by local hunters to contain pacas. Some time was also spent looking for pacas or their sign in habitats that were not suitable for hunting or not known *a priori* to contain pacas. Signs such as tracks and partially-eaten fruits were found in virtually all forest habitats examined, including *morichales*, swamps, dense second growth not amenable to hunting, and the mesic forests of the lower *tepuís* rock formations near the Orinoco. Tracks were found in open savanna on only three occasions. These instances (Centro Administrativo, Caño Hormiga, and Upper Caño Caviona) were all recorded in January and February, the driest period of the dry season. The only sightings I ever made of several species of mammals (puma *Felis concolor*, bushdog *Speothos venaticus*, and otter *Lutra annectans*) that ordinarily inhabit forest also occurred in the savanna during the dry season. I also saw a howler monkey (*Alouatta senicula*), ordinarily an arboreal animal, crossing the savanna near El Tapón in February of 1977. Apparently several forest mammals cross savanna between gallery forests primarily, if not only, during the dry season.

The paca tracks found in savanna were all between adjacent galleries of the same stream system, although movement over greater distances cannot be ruled out. Nevertheless, pacas ordinarily inhabit only forest or second-growth habitats, occupying a wide variety of forest types. This is borne out by their broad geographic and elevational range (see Figure 2, page 6, and Mondolfi 1972). I also found paca tracks among cultivated crops (corn, mangos, and plantain) planted adjacent to forest habitats in the immediate vicinity of the village of El Provenir.

When hunting at night, I usually encountered pacas as they walked along conspicuous trails in the leaf litter and vegetation of the forest floor. An elaborate network of these trails was seen during the wet season, but trails became less apparent during the dry season even though the amount of leaf litter was much the same. Trails were found at all times of the year near stream banks and swamps. Most terrestrial forest mammals could also be encountered on these routes, with Didelphis, Dasyprocta, Proechimys, and the armadillo Dasypus novemcinctus being most frequently seen. Hunters on foot often arranged their hunting trails to coincide with these signs of mammal traffic. I saw nothing to indicate that pacas actively built or maintained trails in the forest, and I presume that the occurrence of the trails is a consequence of repeated traffic of several species of mammals.

Local hunters attribute the partial disappearance of the trails during the dry season to a need on the part of the animals that use them to forage more widely for the fewer, more scattered food sources available at that time. Conversely, the animals may limit their activity to a few direct routes to and from the concentrated food sources which are abundant during the wet season. Although quantitative data are lacking for the Llanos study areas, a general paucity of concentrated fruit sources during the dry season seems to support the reasoning of the hunters.

The gallery forests of Caño Rana become completely inundated by water from the Río Tuparro during June, July, and August. The amount of nearby gallery forest that is permanently dry is so limited that pacas captured at Caño Rana must have been seasonally transient, taking up residence there after the water level receded in September and October.

Burrows

In the Llanos, pacas spend the daylight hours in subterranean burrows. These are difficult to locate because the occupants carefully conceal the entrances with wads of leaf litter. One burrow was located when its occupant emerged shortly after dark from an entrance in the middle of my campsite. Ten more burrows were located in the course of hunting with tracking dogs. These eleven burrows were partially excavated, measured, and sketched. Portions not dug up were carefully probed for side passages. The known occupants, numbers of entrances, total tunnel lengths, and distances from the nearest stream, of the eleven burrows are listed in Table 7, and their shapes are sketched in Figure 21.

Most of these burrows were located near streams only because that is where the hunters with whom I worked preferred to search. However, paca burrows may be found almost anywhere in gallery forest habitats.

TABLE 7. Characteristics of Eleven Paca Burrows.

Collecting Site	Distance From Stream (m)	Occupant	Number of Entrances	Length (m)
1) Puerto Alegre	2	Male	3	5.0
2) Lower Río Tuparro	3	Unknown	3	6.1
3) Caño Hormiga	3	Male	5	4.6
4) Caño Hormiga	15	Female with young	2	5.7
5) Caño Hormiga	4	Female with young	3	6.1
6) Caño Carimagua	35	Unknown	5	9.0
7) Caño Hormiga	18	Male	1	2.8
8) Lower Caño Caviona	13	Unknown	3	7.4
9) Caño Limici	25	Female with young	4	5.2
10) Caño Limici	20	Male	4	6.0
11) Caño Limici	ca. 100	Female	3	5.7

Figure 21. Sketches of the paca burrows examined. Numbers correspond to those listed on the left in Table 7. Solid lines indicate tunnels that were dug up. Dotted lines are tunnels that were probed but not dug up.

Indeed, the burrow found farthest from water (ca. 100 m) was only 15 m from the edge of the savanna. Two of the burrows (1 and 7) were located such that they would be completely under water for much of the wet season. Three burrows had horizontal entrances located just below the upper faces of steep stream banks. All eleven were located in relatively open, mature gallery forest with minimal understory vegetation, which may have been a result of the tracking dogs simply avoiding denser ground cover.

All but one of the eleven burrows that I examined had two or more entrances. None of the burrows were connected to hollow trees, logs, rocks, or any substrate other than soil, although there are reports in the literature of pacas living in hollow trees or among rocks (Mendez 1970, Mondolfi 1972). All burrows examined where shallow, the greatest depth being approximately 1.5 m below ground level. Most tunnels were approximately 0.3 to 0.8 m below gound at their floors, and roughly 0.2 m in diameter.

Varying amounts of leaf litter were found in all of the burrows examined, but no nests, sleeping chambers, or middens were found. Captive pacas have been observed to construct elaborate nests when provided with a simple box and suitable materials such as leaves and excelsior (Kraus _et_ _al_. 1970). In general, leaf litter debris formed a layer less than one cm deep all along the various tunnels of each burrow, with more debris being found just inside one of the entrances (presumably the entrance most frequently used). Cockroaches, spiders, scorpions, earthworms, and miscellaneous small insects were always found among the leaf litter in the burrows, but none of these seemed to have any commensal relationship with the resident paca.

The burrow that had only one entrance (Figure 21[7]) contained almost no leaf litter and was also the deepest below ground. The hunters accompanying me believed that the paca we dug out of this burrow, an adult male, did not ordinarily live there but had fled from its usual abode in an effort to elude the dogs. We were unable to locate any other burrows nearby, but the hunters stated that all pacas maintained these "secondary" burrows as refuges from danger.

In the Llanos, it is commonly believed that pacas adapt and modify the diggings of armadillos (*Dasypus novemcinctus* and *D. kappleri*) rather than excavate entire burrows by themselves. Armadillo diggings were certainly ubiquitous in the gallery forests of the Llanos. Three of the burrows that I examined (Figure 21 [3, 6, 10] were located in what obviously had at one time been colonies of leaf-cutter ants (*Atta* spp.). On numerous occasions, I encountered *Dasypus* digging into *Atta* colonies to feed on these ants.

Pacas may occupy extensive burrow systems. Dalquest (1953) found a paca living in a burrow some 30 m long. Lander (1974) maintained several pacas in pens constructed on bare soil and provided with concrete tubes for use as shelters, but does not mention any attempts made by those animals to dig burrows.

DISCUSSION

Three generalizations were made concerning the data obtained from the sample of pacas that I collected. First, relatively few of the young born into the population survive to enter the one-to-two-year age class, whereas numbers in each age class beginning at the age of one year were seen to decline only slightly with increasing age. Second, the age distribution of adult females in the combined sample was adequately described by the log-linear fit of Equation (7). Third, fecundity was zero before the age of approximately one year and was apparently constant at 0.95 female offspring per female per year for all age classes beginning with the one-to-two-year class. These observations can be combined to describe the demographic pattern of the paca. A model is presented below and is used to interpret the sensitivity of the pattern to disturbances such as exploitation by man and also to suggest proximate mechanisms of the behavior of the species by which the pattern might be maintained.

Demographic Parameters

Changes in the size of a population result from differences between the birth rate and the death rate. For the population of pacas in the Llanos, an estimate of the birth rate was derived primarily from the proportion of females of breeding age that were pregnant. The death rate, however, was not directly observable. For long-lived species, death rates may be calculated directly from observations of natural mortality, from the rate of disappearance from the population of marked individuals of known age, or from the ages of individuals found dead (Caughly and Birch 1971), but can be inferred only indirectly from a standing age distribution such as that for the pacas I collected. Because I have no data regarding immigration and emigration, which are functionally equivalent to birth and death in their effects on changes in population size, I must assume that these factors were equal and so had no net effect on the general demographic pattern. It is not unusual for immigration and emigration to be ignored in population studies, but in many species the emigration of subadults is a critical aspect of the life-history pattern (e.g., marmots Marmota spp., Barash 1974). Also, differences in the ages of immigrants versus emigrants can have marked effects on the rate of population change even when their numbers are equal (Pollard 1973).

For long-lived species, birth and death rates are related by the characteristic equation of Lotka (1907a,b), which in discrete terms takes the form

$$1 = \sum_{x=o}^{\omega} \lambda^{-x} l_x m_x, \tag{8}$$

where x is age, l_x is the probability of an individual born at time $(t - x)$ surviving to be alive at time t, ω is the maximum lifespan, and m_x is the number of offspring expected to be produced during the interval x to (x + 1) by an individual of age x. λ is the finite rate of increase, equivalent to the change in population number during one interval of x in the case of a population that has attained a stable age distribution. For continuously-breeding populations, Equation (8) is approximated by using l_x and m_x estimated for the midpoint of each interval of x. Thus for analyzing the data for pacas, the values of terms within the summation must be determined for ages x = 0.5, 1.5, 2.5,...12.5 years. The equation is generally used only for females, for whom fecundity can be determined readily, and the parameters for males are assumed to be equivalent.

A fundamental problem in considering the data for the pacas I collected is that although the observed age structure is a product of the survivorship process l_x, age structure reflects survivorship probabilities only under certain conditions. As Caughley and Birch (1971) have shown, for a population that has attained a stable age distribution, the proportion S_x of the population of age class x is the survivorship l_x divided by the rate of increase to the power of the number of years (the age, x) over which the population has been increasing or decreasing in relation to the cohort of age x. Using S_x in Equation (8) yields

$$1 = \sum_{x=o}^{\omega} \lambda^{-x}(S_x\lambda^x)m_x, \tag{9}$$

which results in the product $\lambda^x\lambda^{-x}$ necessarily reducing to unity irrespective of the value of λ. Thus, a standing age distribution can be used as a survivorship schedule only if one assumes that $\lambda = 1$, which is the only value for λ that would not be lost in the tautology of Equation (9). In order for $S_x = l_x\lambda^{-x}$ to apply for all age classes, the population must also have attained a stable age distribution (Sharpe and Lotka, 1911). These conditions define a stationary population.

A General Model

The pattern of constant adult fecundity and constant adult survivorship for female pacas can be used to reduce Equation (8) to a general demographic model in five terms if it is assumed that the pacas I collected are a random sample from a stationary population. Let l_α be the probability at birth of a female surviving to begin reproductive life in the α age class, and let p be the probability of a female in any age class x surviving to appear in the next $(x + 1)$ age class after one year, up to the oldest age class $x = \omega$. From the definition of p, survivorship for adult females can be expanded as a geometric series,

$$l_x = l_\alpha p^{(x-\alpha)} \Big|_{\alpha \leqslant x \leqslant \omega.} \tag{10}$$

The summation of Equation (8) can be divided into a juvenile (pre-reproductive) portion having zero fecundity, and an adult portion having constant expected annual fecundity $\bar{m}$. Factoring constant terms out of the summation yields

$$1 = (0) \sum_{x=0}^{\alpha-1} \lambda^{-x} l_x + \bar{m} l_\alpha \sum_{x=\alpha}^{\omega} \lambda^{-x} p^{(x-\alpha)}. \tag{11}$$

The first summation is zero, and the second can be rearranged to yield

$$\frac{p^{-\alpha}}{\bar{m} l_\alpha} = \sum_{x=\alpha}^{\omega} (p/\lambda)^x. \tag{12}$$

For the present, we assume that $\lambda = 1$ and use p derived from the regression of S_x instead of from l_x. From Equation (12), the demographic pattern of a stationary population of female pacas can be described by five parameters: (1) α, the age class in which females first give birth; (2) ω, the maximum longevity; (3) $\bar{m}$, expected annual fecundity for all females; (4) p, annual adult survivorship; and (5) l_α, juvenile survivorship.

Parameter Values for the Sample of Pacas

The age at which pacas first reproduce was seen to be approximately one year, with eight of fourteen females in the one-to-two-year age class actually having given birth. Therefore, α is the midpoint of that class, or 1.5 years. The oldest observed age for females was twelve to thirteen years, so that $\omega = 12.5$. A larger sample from the Llanos might well have included individuals estimated to be older than 12.5 years. Pacas surely do not live much longer than twelve years because by that age, their teeth are almost completely worn out. Walker et al. (1975) reported that a paca kept at the U. S. National Zoo lived for fifteen years, which suggests to me that 12.5 years is not an unreasonable estimate of their maximum longevity in the wild.

Annual adult fecundity $\bar{m}$ was estimated to be 0.95 females/female/year, with 95% confidence limits of 0.799 and 1.250. The confidence interval is based on the variance of the proportion of females that were pregnant and on the range of estimates for gestation period as reported in the literature. Litter size and sex ratio at birth were also involved in calculating $\bar{m}$. Hingston (1932), Smythe (1970a), Mondolfi (1972), and Lander (1974) all have reported instances of pacas carrying twins, but I observed only single fetuses. In the absence of an estimate based on data, I have assumed that the sex ratio at birth is 1:1.

An estimate of adult survivorship p is provided by the least-squares estimate of slope b of the log-linear model of age structure for females. In the linear domain, the log-linear model is a continuous exponential function, equivalent to a discrete geometric series. Thus p is estimated as e^{b}. For females, the estimate of p is 0.800, with 95% confidence limites of 0.746 and 0.858.

The juvenile survivorship parameter l_α cannot be estimated directly from the data: Equation (13) becomes a single equation with two unknowns, l_α and λ (implicit in p). The difference in numbers of individuals in the 1.5-year versus the 0.5-year age classes is not an appropriate measure of survivorship since many young individuals were obtained while foraging with the mother, and therefore are probably over-represented in the sample. All 43 of the females that are less than one year old must be considered to be 0.5 years old for the purposes of the model. I have no way of directly evaluating survivorship from birth to 0.5 years. An expected value for l_α can be determined from estimates of the other parameters by rearranging Equation (12) to solve for values of l_α that meet the original assumption of a stationary population for a variety of combinations of p and $\bar{m}$ as suggested by their respective variances. Equation (12) thus becomes

$$l_\alpha = 1/(\bar{m} \sum_{x=\alpha}^{\omega} p^{(x-\alpha)}) \Big|_{\lambda=1.} \qquad (13)$$

Figure 22 presents curves for the estimated mean and for the ±95% confidence limits of $\bar{m}$ as a function of p and l_α when $\lambda = 1$. Within these limits, the shaded area is bounded to the left and right by the ±95% confidence limits of $p = 0.800$ (solid triangle). Combining these limits predicts the value of l_α with 95% confidence given all of the underlying assumptions:

1) Sex ratio is 1:1 at birth;
2) Litter size is always one;
3) Gestation period is between 109 and 122 days;
4) $\alpha = 1.5$ years;
5) $\omega = 12.5$ years;
6) Annual survivorship of adults is p for all $x | 1.5 \leqslant x \leqslant 12.5$;
7) Adult fecundity is $\bar{m}$ for all $x | 1.5 \leqslant x \leqslant 12.5$;
8) $\lambda = 1$.

These tenuous limits are bounded by the broken line in Figure 22. The predicted value of l_α is 0.228 (open triangle), with 95% confidence limits of 0.132 and 0.325.

An additional assumption is implicit in the entire study. That is, the data are assumed to have come from a single population. This possibly is not the case. It would have been preferable to have sampled over a much smaller area, perhaps using only a single method of hunting. Nevertheless, since gallery forest habitats are essentially continuous -- albeit irregularly distributed -- in the Llanos, I feel justified in dealing with a large global population considering the difficulties encountered in obtaining the sample.

Validity of the Assumptions

Assumptions 1), 2), and 3) above cannot be elaborated upon because I have no data concerning them. 4) and 5) depend primarily on the accuracy of the techniques used to determine age (see Appendix A), but in fact the model is relatively insensitive to errors in

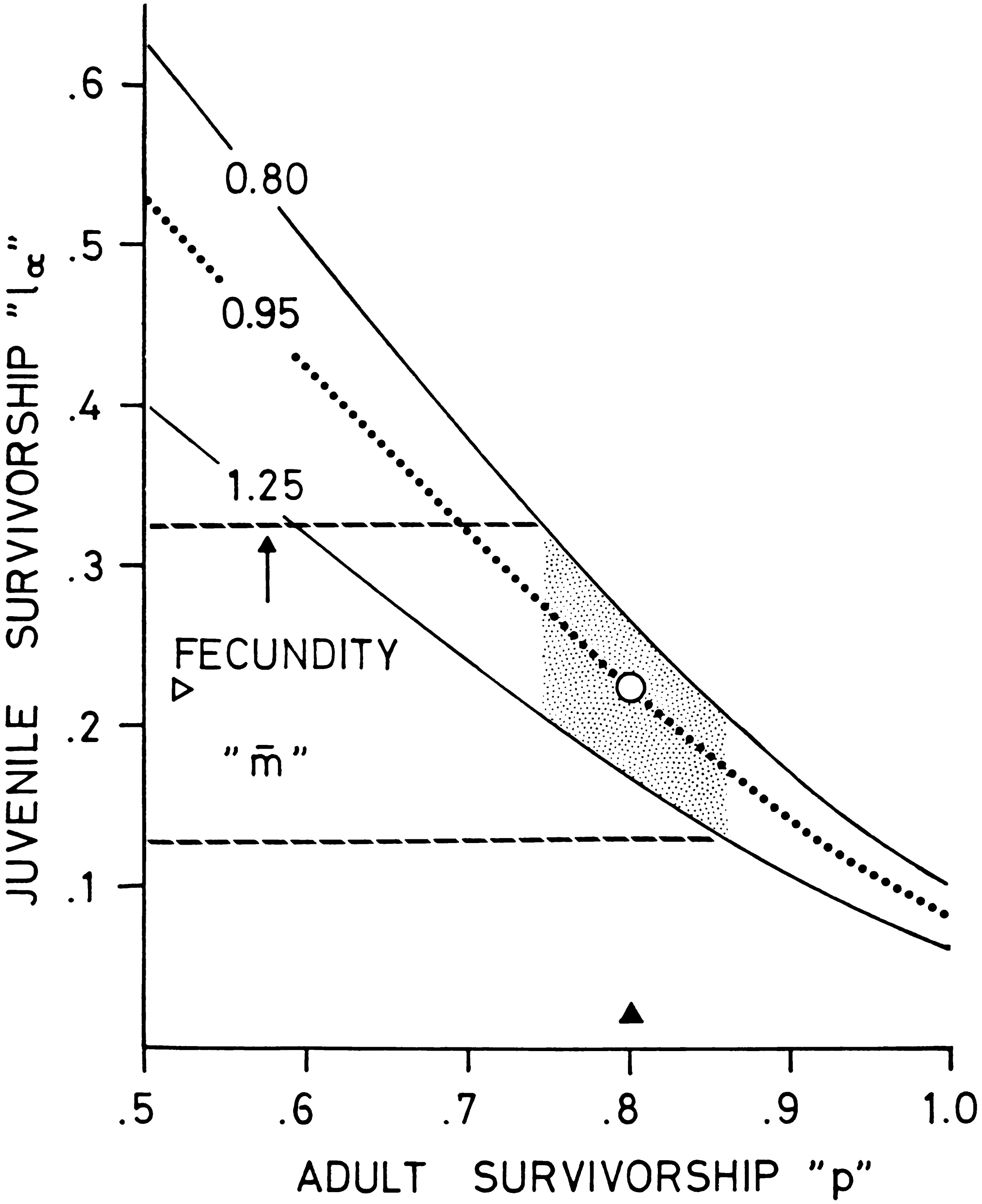


Figure 22. Prediction and confidence limits for juvenile survivorship. Symbols explained in the text.

estimating α and ω (see below). Assumptions 6), 7), and 8) require considerable clarification.

The variance of p was estimated from the log-linear regression of numbers on age must be applied with caution. Age structure is a multiplicative function of p operating over the lifespans of all individuals, so that

$$S_x = \lambda^{-x} \prod_{y=0}^{x} p_y \tag{14}$$

Clearly p determined by regression provides an estimate of the mean of p for the interval of time when age structure was observed (in this case, the interval was four years), but not of p as a composite of the effects of p_x for the lifespans of the individuals in the sample. In order to estimate p properly, one would need direct estimates of survivorship. Also, in obtaining subsamples from various sites, one introduces differences in habitat and history of hunting pressure among the various sites. This underlying variation was lost because regression was performed on the combined sample. I must assume that these local effects balance out when considering the entire population. Changes in demographic characteristics have been found over small distances for contiguous populations of long-lived species even when considered over much smaller distances than those between my collecting sites (Dapson et al. 1980).

Annual adult survivorship p as estimated from the coefficient b of the log-linear model was higher for males than for females. If a stationary condition is assumed, this implied that adult males experience a lower annual probability of death $(1 - p)$ than do females. Non-rejection of the log-quadratic model of age structure implies that for adult males, p_x decreases with increasing age. Inference regarding the l_x schedule is limited since the log-quadratic fit based on S_x predicts the impossible situation of $l_x > 1$ for some real values of x.

The estimated fecundity value of 0.95 must be used for all age classes $1.5 \leqslant x \leqslant 12.5$ in order for Equation (12) to apply. For populations of continuously-breeding species, this is often assumed to be true in the computation of instantaeous birth rates (see Lotka 1956: 115), although approximations using Equation (8) have also been used to show that the age-specific intensity of natural selection varies with age as an increasing function of age-specific differences in fecundity (Emlen 1970). Although I detected no differences between adult age classes in the proportion of females pregnant, there was a tendency for the older age classes to include more individuals that were both pregnant and parous (see Figure 13, page 52). This trend was not tested since it involved only twelve individuals.

Analyses of real populations by Schaffer and Tamarin (1973), Ricklefs (1977), and Siler (1979) suggest that the parsimonious assumptions of constant adult survivorship and constant fecundity may be applicable to a variety of long-lived species. The relationship of Equation (13) has been applied to pelagic birds by Goodman (1974), who found the basic assumptions to be reasonable. It is often acknowledged (Deevey 1947) that for many species of birds and mammals, adult survivorship is nearly independent of age.

The assumption of a stationary population is onerous but not unreasonable in the case of a long-lived species in a relatively stable tropical environment. The popular concept of *r* and *K* selection

(MacArthur and Wilson 1967) has its roots in Dobzhansky's (1950) observation that populations in the tropics are much less subject to variation in environmental factors that can cause fluctuations in numbers than are temperate populations. *K*-selection refers to a life-history strategy geared toward maximizing efficiency of utilization of resources as opposed to maximizing the production of progeny (Pianka 1970, 1972). The paca has several characteristics of *K*-selected species, such as low reproductive rate and maternal care of the young.

The concept of rate of increase has been a source of confusion in the literature. Reviews of the various definitions and restricted meanings are found in Davis (1973) and Slade and Balph (1974). One must bear in mind that those populations which have attracted the most attention from population biologists are of *r*-selected species such as pests, populations being manipulated to maximize yield such as fish stocks, or populations undergoing relatively unrestricted growth, such as man. A strong bias in population thinking has resulted from over-emphasis of the logistic model (Pearl and Reed 1920) (upon which the concept of *r* and *K* selection is based), which is demonstrably unrealistic (see Pielou 1977:35).

Some authors have considered many natural populations to be at or near a stationary condition (e.g., Goodman 1974), and in considering the models of Goodman and of Ricklefs (1977), Green (1980:295) posits, without elaboration, that "it is useful to bear in mind that many animal populations are quite stable." In reality, actual evaluation of λ is not possible without large bodies of data which are difficult to collect, yet the estimate obtained may not be very accurate. Tait and Bunnell (1980) have shown by computer simulation that even large samples drawn at random from an infinite population with idealized age structure may yield widely-disparate results in replicated trials. The cumulative effects of sampling errors are thus a major problem in analyzing limited sets of data by means of traditional life tables or projection matrices.

The greatest stumbling block to the present study is the possibility of λ being consistently less than one, resulting, for example, from the population having been heavily overexploited for some years. Although a stable age distribution may be apparent from a smoothly-declining sample age distribution, S_x could still depart significantly from l_x consistently for all x. As Equation (12) shows, a geometric series results from constant annual survivorship as (p/λ), whether or not λ is actually 1.0 as assumed.

While the assumption of $\lambda = 1$ cannot be directly demonstrated from the data, it can readily be invalidated. For a rapidly declining population, some age classes may be larger than younger ones, a condition for which $\lambda = 1$ would imply the impossible situation of an increase in numbers in a birth cohort, when only mortality is operating. Fluctuations in λ through fluctuations in any of the parameters will produce an irregular age distribution departing significantly from the stable distribution predicted by constant adult survivorship. As has been shown previously (see Figure 20, page 74), the observed age distribution is quite regular.

The effect of a particular deviation in λ away from the stationary condition can be evaluated by solving Equation (12) for the relationship between juvenile survivorship and adult survivorship using a variety of values for λ while $\bar{m}$ remains constant at the estimated value. Figure 23 presents curves for $\bar{m} = 0.95$ as a function of l_α and p given several values for λ. The shaded area is the same set of ±95% confidence limits presented earlier. A vertical distance between the line of $\lambda = 1$ and a line for any other value of λ thus represents the error in estimating l_α due to $(p - p/\lambda)$ assuming that p is accurate, and a horizontal distance is the error in estimating p for the value of $\lambda \neq 1$ given that all of the other parameters are accurate. Thus confidence in the model's prediction of the value of l_α has a precision equivalent to assuming $\lambda = 1$ when the actual value of λ may be as low as 0.93, even given that the remaining assumptions are true. If indeed $\lambda = 0.93$, the population would be declining by 50% every ten years. Without an independent estimate of λ or of l_α, interpretation of the model in terms of $\bar{m}$ and p is seriously restricted.

That the population is approximately stationary can be shown from the data by generating an artificial estimate of juvenile survivorship. Fifty-eight females of reproductive age were collected. If each is expected to produce 0.95 female offspring in the course of one year, an artificial birth cohort expected from one interval of x would consist of 55.1 females. From the fit of the log-linear model for females (see Equation (7), page 72), 12.39 of these newborn would be expected to survive to age $\alpha = 1.5$ years, giving $l_\alpha = (12.39/55.1) = 0.225$, as the model predicts when λ is assumed to be 1.0. No assumption was made concerning λ in generating the artificial birth cohort: Estimating l_α in this way shows that the observed age structure expresses a net death function equal in magnitude to the observed net birth potential, the situation which defines a stable population.

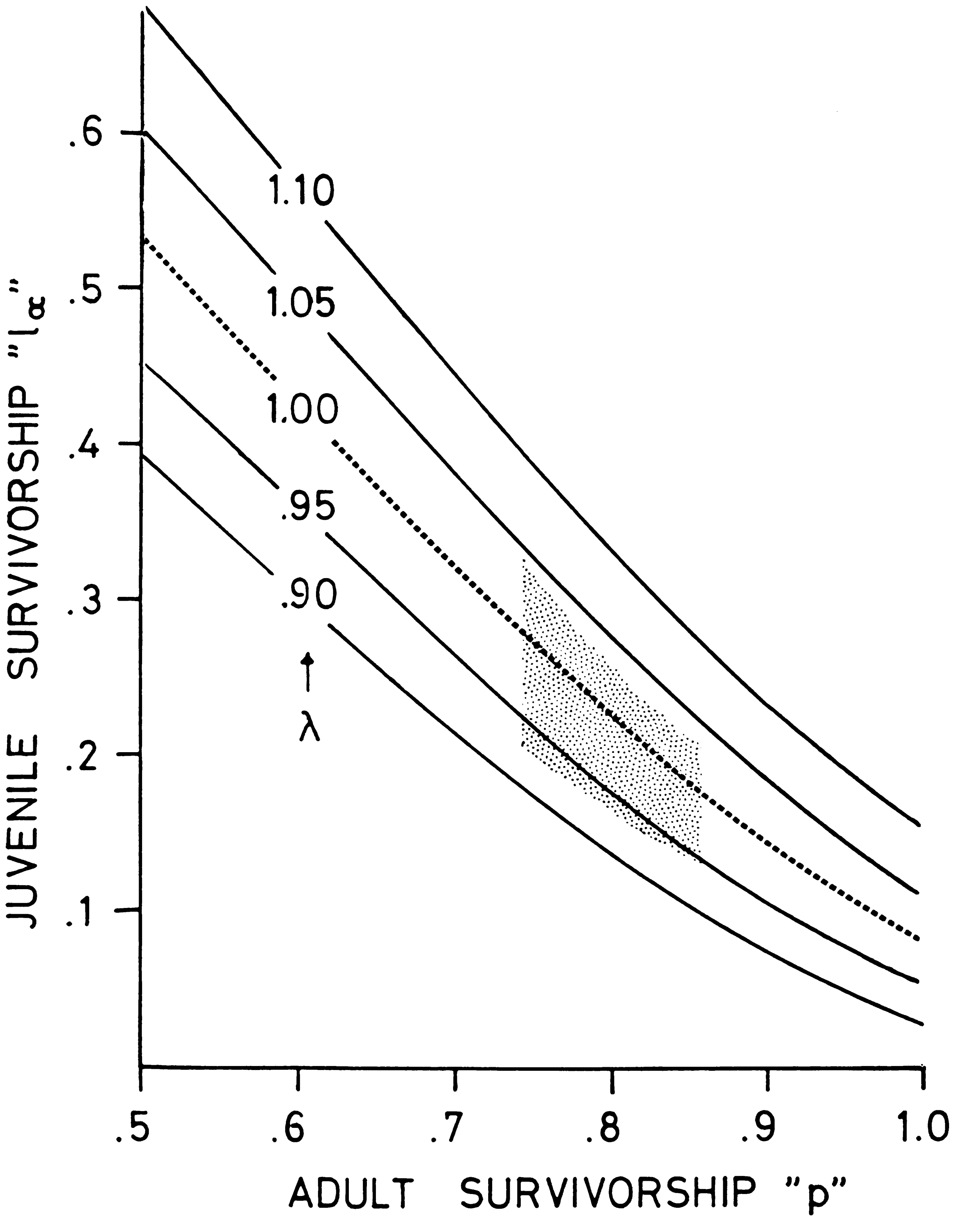


Figure 23. Curves for $\bar{m}$ = 0.95 for different values of λ, assuming α = 1.5 and ω = 12.5 in each case. The shaded area is the ±95% confidence areas for *p* and $\bar{m}$ when λ = 1.0.

There are two critical flaws in this line of reasoning. First, it is circular in that l_α is not estimated independently of p and $\bar{m}$. Second, it evaluates observed data from a time-specific or "vertical" life table as if it were obtained from a time-composite or "horizontal" life table. The two computational forms are equivalent only if (1) the population has attained a stable age distribution, and (2) λ is constant for the time interval represented by the composite case (see Caughley 1977:119-20), which is 12.5 years for these data. The regular form of the observed age distribution suggests that these assumptions have not been violated. Thus estimated juvenile survivorship can be obtained indirectly whether or not the population is assumed to be stationary, although difficult assumptions are involved in either case. When λ is not assumed to be 1.0, the estimate obtained is virtually 1.0. This is equivalent to obtaining a net replacement rate (R_0) of 1.0.

Michod and Anderson (1980) have shown that λ and the schedule of l_x can be jointly calculated if l_α, the age distribution, and the fecundity schedule are known. Letting n_x be the number of individuals in age class x, values for each l_x are calculated as $l_x = l_\alpha \ (n_x/n_\alpha)$. From the artificial birth cohort, let $n_0 = 55$ and from the observed age distribution (see Figure 20, page 74) let $l_\alpha = 14/55 = 0.225$ and $l_x = 0.255 \ (n_x/14)$. I used the above to solve Equation (8) for λ by iteration, letting $m_x = 0.95$ for all x 1.5, and found $\lambda = 1.001$. Solutions using the limits of l_α predicted in Figure 22 gave a range for λ from 0.88 to 1.06. Thus assuming only $m_x = \bar{m}$ suggests that λ is indeed in the neighborhood of 1.0. Even when m_x is calculated for each x according to the proportion pregnant in each age class, the range for λ is from 0.86 to 1.04. WIth an independent estimate of l_α, the value of λ could be calculated more precisely.

To summarize, the data cannot be used to evaluate λ directly, but they do indicate that λ has been relatively constant for some years at approximately 1.0. The validity of the original assumption is supported in that:

1) The age distribution is regular (see Figure 20, page 74);
2) the range of λ (as p/λ) in Equation (12)) that could have resulted in the 95% confidence interval of p as estimated from age structure (see Figure 23, page 115) is not large ($0.93 \leqslant \lambda \leqslant 1.11$);
3) juvenile survivorship estimated from the net fecundity of the collected females and from the size of the α = 1.5-year age class indicates that $\lambda = 1$ independently of the original assumption involved in estimating adult survivorship from age structure; and
4) if λ is assumed to be constant (i.e., vertical and horizontal life tables yield equivalent solutions for λ), and then is estimated jointly with age structure using the range of l_α as predicted by the model of Equation (13), the range of estimates for λ is again small ($0.86 \leqslant \lambda \leqslant 1.06$).

Of the several lines of reasoning, the most rigorous is the method of Michod and Anderson, in that no assumption concerning the value of λ was made in conceding that l_α cannot be estimated independently of the remaining parameters. Provided that fecundity is indeed constant over age classes and the techniques used to determine age are accurate, the smooth form of the observed age distribution is the most intuitively satisfying indication that the size of the population has not fluctuated noticeably for at least the twelve years represented by individuals in the sample. Small fluctuations in λ in the past may account for the small irregularities in the histogram of Figure 20, but given the small sample size involved, the observed regularity could only have been produced by a population that had been stable for those years. If this stable age distribution is accepted as implying constant λ, then the assumptions involved in generating the artificial birth cohort must be valid enough for confidence in accepting the value of $\lambda = 1.0$ indicated by the resulting estimate of l_α. It is reasonable that a population of such a long-lived species, experiencing relatively low annual mortality, would be essentially stationary. Such is often assumed for large mammals, and suggests that for the paca there do exist mechanisms, involving intraspecific communication (e.g., scent marking and tooth grinding) and defense of territory, which may function in the intrinsic regulation of the population.

Factors Affecting Demographic Parameters

It is beyond the scope of the present descriptive study to test the immediate effects of potentially-limiting factors such as hunting, use of space, food, or predators on the demographic processes of the population of pacas in the Llanos. Nevertheless, inferences can be made regarding mechanisms inherent in the natural history of the species which might have effects on population size. The observations I made in the field and comparable observations reported by other authors can be examined in relation to demographic parameters as defined by the simplified model above. While the mechanisms mediating any changes in demographic parameters cannot yet be identified, such speculation should serve to generate hypotheses for testing in the field.

Sensitivity of the General Model

A rigorous analysis of the sensitivity of the model (see Appendix C) showed that for the range of parameter values as estimated from the data, rate of increase λ is more sensitive to small changes in juvenile survivorship l_α than to equal changes in adult survivorship p or annual fecundity $\bar{m}$. Whether λ is most sensitive to juvenile survivorship or to adult survivorship depends upon both the estimated value of $\bar{m}$ and on maximum observed longevity. The analysis may not be directly applicable because absolute changes in one parameter potentially may be much greater than is likely for another parameter. For example, adult survivorship may always be 0.75 or greater for a given population whereas juvenile survivorship may vary from 0.75 to 0.25 between good and bad years. Similarly, annual fecundity may be more variable within the limits of the species' reproductive physiology than is either survivorship parameter. A more realistic approach would be to evaluate the variability of the three parameters l_α, $\bar{m}$, and p for several populations under identifiably different environmental conditions.

Survivorship parameters perhaps are treated more logically in terms of mortality. The annual probability of death for an adult female would be $(1 - p)$ or approximately 0.20, and the probability of a newborn female dying before age $\alpha = 1.5$ years would be $(1 - l_\alpha)$ or approximately 0.77. To approximate in terms of annual death rates, let l_1 be l_α (1.5/1.0) $\approx$ 0.35. This means that on an annual basis, the mortality rate is approximately 65% for juveniles versus only 20% for adults.

Hunting

One of the principal reasons for beginning field studies at Territorio Faunístico El Tuparro was that as a national park the area was *de jure* closed to hunting, ostensibly providing for a large, undisturbed population to study. This soon proved not to be the case, primarily because the limited resources of INDERENA could not provide for control of access to the park by nearby hunters. Indeed, early successes in obtaining specimens were a direct result of the occasional collaboration of a local poacher who made the major part of his living by hunting pacas and other large vertebrates to sell in nearby Venezuela. Since hunting is this intensive in what is supposedly a remote and protected area, it surely represents a significant management problem in areas adjacent to villages where market hunting is legal or otherwise tolerated.

The estimated densities of 38 to 54 adult pacas per km^2 for the three intensively-hunted sites in the Llanos agree with figures reported by other authors for other populations. Over a period of 60 days, Lander (1974) identified nine resident pacas in an area of 15 ha, for an estimated density of $60/km^2$. Eisenberg *et al*. (1980) reported a tentative estimate, based primarily on track frequency, of 25 pacas/km^2 for Fundo Agropecuario Masaguaral in the Llanos of Venezuela. On the basis of seven years' live-trapping data, Smythe *et al*. (in press) estimated the density of adult pacas on Barro

Colorado Island, Panama, at 70 adults/km^2. None of these estimates is based on large numbers of animals, either captured or observed, and I believe that all are somewhat low because of trap-shy or otherwise wary individuals, but their close agreement suggests that 40 to 70 adult pacas/km^2 of suitable forest habitat is a reasonable figure for estimating the abundance of pacas in the Llanos. Since hunters rarely shoot obviously young pacas (i.e., less than 5 kg), I will discuss abundance in relation to hunting mortality only in terms of adult pacas.

Discussions with poachers, park officials, and other local residents produced estimates of the number of pacas removed by hunters from the eastern portion of the El Tuparro Park ranging from 200 to 600 per year. This is not an unreasonable figure in view of the successes obtained when I worked with these skilled hunters. If my estimate of 7600 adult pacas in an area of 2500 km^2 (which represents the portion of the park and surrounding areas that is accessible to hunters) is accurate, hunters could have been removing from 2.6% to 7.9% of the adult population year year. If adult pacas experience an annual mortality rate of $(1 - p) = 20\%$ (for females, less for males, assuming $\lambda = 1$) from all causes, then these figures suggest that hunting could account for approximately 13% to 40% of adult paca deaths. The latter figure seems extreme, and perhaps is due to underestimating the total population on the basis of only three small areas. Nevertheless, hunting surely is a significant source of mortality in the El Tuparro study area.

Hunting pressure in the El Porvenir study area was more difficult to quantify since no organized commercial poaching existed there.

Residents of the many ranches in the area regularly hunt pacas for food. Hunting is undoubtedly the principal cause of death for pacas in the few accessible gallery forests near human settlements. As a result, the effects of hunting are not distributed uniformly over the variety of forest habitats occupied by pacas. Since all forest habitats comprise only about five percent of the Llanos, the paca population is small in relation to the level of hunting even in areas where conditions for hunting are less than optimal.

Several features of hunting by canoe may serve to ameliorate the impact of hunting on the population. Small, particularly suitable sites are visited only about once a year, the timing of the hunting trips being determined primarily in relation to the annual cycle of the level of the river. If only a small portion of a forest gallery is hunted, even intensively, pacas from adjacent areas may move into the hunted area from adjacent forests during the intervening year before the next hunt. Of 17 pacas collected at Caño Alto on the upper Río Tuparro, nine were in the 4.5- or 5.5-year age classes. This is intriguing because the poacher who collected these specimens had told me that he had not been so far upstream on the river for several years. The pacas were all collected from a single gallery during four nights of hunting by canoe. Perhaps the majority of the pacas available at the time of my visit were recruited into the population as dispersing juveniles becoming established in territories made vacant by my companion's activities on his last visit.

Obviously, hunting is not the only factor affecting adult survivorship. I obtained no direct information on predators or other natural sources of mortality. The jaguar, Felis onca, and the ocelot,

F. pardalis, are acknowledged predators of pacas (Mondolfi 1972), but both have long been hunted in the Llanos for their skins and are presently rare there. The bushdog, Speothos venaticus, which is not hunted for skins but is known to prey on pacas (Tate 1931; see also Bates 1964) is present in the Llanos but is not common (D'Alessandro et al. in press). Increases in adult survivorship resulting from removal of natural sources of mortality such as predators may more than offset losses due to hunting (e.g., deer [Odocoileus hemionus] in California, Taber and Dasmann 1958). Decreased adult survivorship can result in an increase in the productivity of a population, either by (1) increasing the number of females in the younger age classes because of higher juvenile survivorship (Beddington and Taylor 1973), or (2) by increased fecundity or decreased age of reproductive maturity due to the resulting net increase per capita in environmental resources. The sensitivity of λ to changes in demographic parameters shows that, for pacas, factors which increase juvenile survivorship would be the most efficient means of increasing population numbers.

Use of Space

Scent-marking, using urine or anal-gland secretions, could perhaps indicate that pacas define and defend territories, but there have been no definitive observations of this or any more overt forms of territorial behavior by the species. Ralls (1971) has suggested that scent-marking may be used to show dominance without marking space for exclusive use. Furthermore, an exclusive territory may comprise only a small portion of the area an individual uses as a home range, as Ewer (1968) has emphasized.

Smythe *et al*. (in press) suggested that high disappearance rates for juvenile pacas live-trapped on Barro Colorado Island were an indication that the population was regulated by the supply of suitable territories. If individual pacas occupy exclusive territories, then a mechanism by which juvenile survivorship can increase as a direct response to adult mortality is that the removal of adults increases the availability of suitable territories for subadults entering the breeding population. Agoutis (*Dasyprocta punctata*) on Barro Colorado defend territories as mated pairs, with the territories fairly uniformly distributed with considerable overlap of activity (Smythe 1978). Although maturing agoutis may remain in the maternal territory even while a subsequent litter is being raised, subadults eventually are forced to leave by harrassment from the territorial adults. It seems likely then that the related paca would use a similar system of territorial behavior. Smythe (1970a) reported on limited observations of agonistic encounters between captive adult pacas introduced simultaneously into a neutral arena.

Many rodents that are dependent on burrows are highly territorial, either as individuals (e.g., pocket gopher, *Thomomys bottae*, Howard and Childs 1959) or as larger social groups (e.g., marmots, *Marmota* spp., Barash 1974), in excluding conspecifics from the burrow and its immediate vicinity. In the Llanos, pacas and agoutis differ in this respect in that agoutis use shallow scrapes and small burrows (Smythe 1970a) in contrast to the extensive burrows used by pacas. The acquisition of a suitable vacant burrow, or of a site for the establishment of a burrow, may be a critical factor for the recruitment of young pacas into the breeding population.

The tooth-grinding sound mimicked by hunters to attract pacas when hunting by canoe may have a territorial function. Hershkovitz (1955) and Smythe _et al_. (in press) have ascribed loud sounds produced by pacas as responses to a perceived threat, but this would not account for a paca's approaching when the sound is heard. It is interesting that the analysis of homogeneity of sex ratios indicated that more males than females were obtained when hunting by canoe. Perhaps the rumbling sound is related to defense of the territory against comspecifics or even to courtship behavior. The contexts in which this sound is produced by pacas in the wild should give some indication of its function.

Experimental removal from a relatively undisturbed area of large numbers of adult pacas could enable the identification of both the types of individuals that replace those removed and of the essential elements of the environment that determine what a suitable territory is. If the major source of juvenile mortality relates to failure to secure a territory after leaving the place of birth, then replacements would be mostly juveniles. If however there exist non-territorial adults in the area of removal, or if pacas are not very territorial to begin with, then immigrants might be of any age class, entering the area from adjacent territories or in the course of movements not related to territory. For birds, the existence of non-territorial individuals or "floaters" has been demonstrated by removal of territory-holders (e.g., tits, _Parus major_, Krebs 1971). A more homogeneous, contiguous forest environment would be more appropriate for testing hypotheses concerning the use of space than the smaller, more heterogeneous forests of the Llanos, where the density of pacas relative to the width of the gallery forests may result in an essentially linear arrangement of territories in an irregular habitat. It seems likely to me that the dispersion of paca territories in the galleries would reflect local variations in habitat more than intraspecific interactions.

Direct observations of the intraspecific behavior of the paca, both in the wild and in captivity, would clarify a number of questions raised by the demographic analysis. In particular, to what extent do pacas limit the use of space and food resources by conspecifics? Is there a particular stage in juvenile development when a subadult paca must leave its place of origin? Do interactions between members of the breeding population and immigrating juveniles determine whether or not such an immigrant survives to reproduce? A major deficiency of the present study was the inability to document the role of immigration and the ages of immigrants. Since my samples came primarily from small areas that had long been subject to hunting without the local populations becoming depleted, immigration surely must have been a factor in replacing pacas removed by hunters. For most vertebrates, there exists a stage of development when subadults disperse from the site of their birth and rearing (Howard 1950). If survivorship is high until the age of dispersal, the availability of suitable vacant space is more likely to be of importance than if other sources of mortality limit the numbers of potential recruits.

It is possible that in the Llanos, the ubiquitous diggings made by armadillos provide a surplus of potential burrows for use by pacas. The spatial distribution of paca burrows in relation both to each other and to the diggings of armadillos could furnish an indication of the importance of these ready-made burrows to dispersing juveniles and to the apportionment of surrounding habitat by their occupants. If territorial behavior necessitates a uniform dispersion of burrow sites whereas armadillo diggings are found to be randomly dispersed or clumped because of the distribution of resources of importance to armadillos, then the perceived surplus of burrows would be more apparent than real. The rarity of encounters with two pacas foraging together might be a function of their territories being uniformly spaced, but the position of the burrow within that territory might not be related to the spacing of territories. This would be difficult to test in the heterogeneous, thin gallery forests of the Llanos.

Food

The availability of suitable fruits at all times of the year indicated that food was not a limiting factor for pacas in the Llanos. Smythe *et al*. (in press) proposed that the population of pacas on Barro Colorado Island was regulated by the supply of suitable foods, in the authors' context actually by the supply of territories with suitable foods. They also found that the paca population was less affected by seasons of abnormally low fruit availability than were populations of agoutis or arboreal frugivores. This suggests that pacas are not as exclusively frugivorous as my observations indicated. Animals on Barro Colorado are protected from hunting, and so presumably pacas and their competitors are more abundant there than in the Llanos. Perhaps at higher densities, food supply operates as a limiting factor by reducing either fecundity or early juvenile survivorship during the dry season. In the Llanos, reproductive activity did not seem to be reduced during the dry season.

Comparisons with Other Mammals

The paca has both a longer gestation period and a smaller litter size than is typical of most myomorph and sciuromorph rodents, but this is true of caviomorphs in general (Kleiman *et al*. 1980). Several caviomorphs have even longer gestation periods than the paca (e.g., pacarana, *Dinomys branickii*, Collins and Eisenberg 1972). As Bourliere (1973) has mentioned, the analogies between caviomorphs and Old World ecological equivalents among the primitive tragulid ungulates extend even to reproductive characteristics, and presumably to survivorship patterns as well. Such data are lacking for the chevotain *Hyemoschus*, although Dubost (1965) has found that it does live for over six years.

It would appear that the life-history strategy of the paca, involving low fecundity and high adult survivorship is more typical of the demographic patterns of many ungulates than of most rodents. Fleming (1975) in summarizing the available demographic data for a number of small tropical rodents, reports fecundity values ranging from 2.2 to 12.8 females/female/year and a maximum annual survivorship of 0.36 (for the spiny rat *Proechimys semispinosus*). In reviewing data for small mammals in general, French *et al*. (1975) concluded that fossorial types tended to have low fecundity and high survivorship. The paca is not truly fossorial, but like many rodents living in extensive burrows does exhibit high survivorship. For the marmot *Marmota flaviventris*, a colonial burrow-dwelling species, annual adult survivorship is typically 0.75, with fecundity on the order of 1.5 females/female/year and maximum longevity of approximately seven years (Armitage and Downhower 1974). Unfortunately, data are lacking for larger rodents, particularly for tropical species. Even the capybara, however, at over 50 kg, the largest of the rodents, typically bears litters of five and experiences high mortality of juveniles (Ojasti 1973), as does the large (ca. 3 kg) cane rat, *Thryonomys swinderianus*, of Africa (Aisbey 1974). These latter two species are also hunted by man for their meat, but present quite different management problems than does the less-fecund paca.

The survivorship patterns of several tropical ungulates have been studied (Spinage 1972), but as Eisenberg (1966) has pointed out, the conspicuous ungulates that are well-studied are found in more open environments, where they tend toward increasing social organization (see also Jarman 1974). For the impala *Aepyceros melampa*, the smallest ungulate for which Spinage (1972) reports survivorship data, females may live for up to 12 years and typically experience annual survivorship rates of 0.64 to 0.95, with considerably higher survivorship in the younger adult age classes. Spinage further suggests that juvenile survivorship is 0.50 or less for many smaller African ungulates. Although precise fecundity data are often lacking, the example of the impala indicates somewhat lower fecundity than for the paca, which has relatively lower survivorship.

Conclusion

Particular differences in demographic parameters between populations existing at different densities or experiencing different levels of exploitation may reveal how the populations respond to different levels of adult mortality. Surveying several populations would amount to replication of the present study in order to evaluate the variability of fecundity and survivorship, especially in relation to environmental factors, whereas the present study was limited to evaluating the precision of estimating demographic parameters for a single population.

There is great potential for obtaining estimates of adult survivorship and fecundity data from teeth and genital tracts of pacas sold in established meat markets. Commercial hunting, on a scale sufficient to provide adequate samples over a period of several years, is undoubtedly practiced at several sites in Brazil (Wetterberg _et_ _al_. 1976), at Iquitos in Peru (Aquino Yarihuaman pers. comm. 1979), or at any large but remote concentration of people such as Leticia or Mitú in the Amazon lowlands of Colombia. Such a study would incur ethical and legal problems since commercial hunting is officially discouraged by most national governments out of concern for depleting wildlife resources. Such concern is justified, judging from Smythe's (1978) experiences in developing rural areas in Central America where pacas and agoutis have been rapidly depleted. Nevertheless, if such exploitation is occurring, the concerned conservation biologist would do well to attempt to evaluate its impact.

Without an appropriate method of directing estimating juvenile survivorship, the model presented above is limited to predicting juvenile survivorship from observed combinations of fecundity and adult survivorship. Providing that patterns of constant fecundity and constant adult survivorship hold true under differing conditions, consistent application of the model can serve as a test of the paca's ability to withstand exploitation. More generally, it serves to summarize my findings concerning the demographic parameters of a single population sampled only with difficulty. Such a general approach has been criticized by Murray (1979:184) with considerable justification, since it represents an attempt to describe in static generalities what is traditionally thought of as a dynamic system. I must agree that censusing over time or direct evaluation of l_x and m_x schedules would yield more information and would certainly go beyond the present study in describing variation in population numbers. Nevertheless, it is not yet practical to census pacas or to live-trap them on a meaningful scale, and perhaps never will be.

It remains entirely possible that in the absence of the influence of man, the demographic characteristics of the paca would be rather different, involving a more pronounced breeding season or a different pattern of age-specific survivorship. In the Llanos of Colombia, however, pacas experience relatively constant mortality as adults and produce approximately 1.9 offspring per year without a birth season. Between birth and reproductive maturity at the age of about one year, they experience approximately 77% mortality. The accuracy of the parameter estimates I obtained and the generality of their application to the species as a whole remain to be demonstrated by methods involving fewer (or at least more tractable) assumptions.

APPENDICES

APPENDIX A

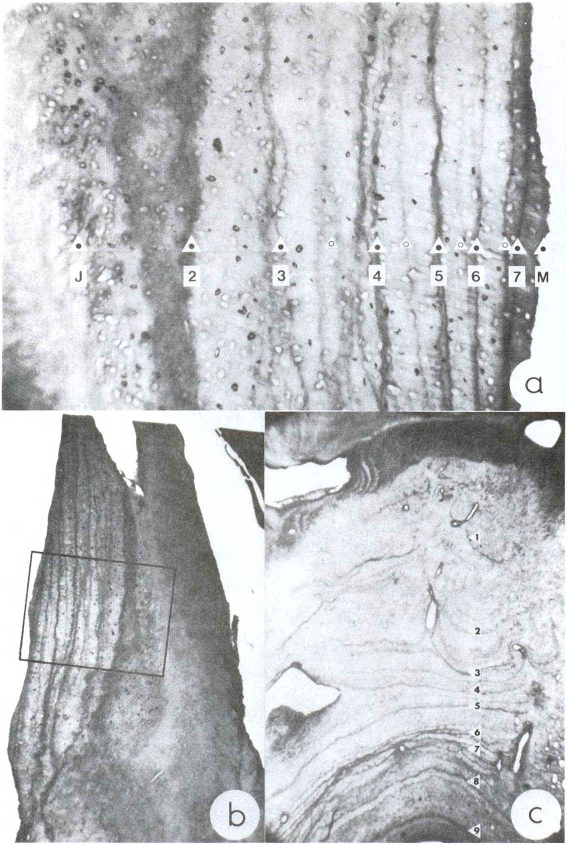
METHODS USED TO ESTIMATE AGE

Examination of the tooth sections revealed that annulations were present in the cementum tissue of upper first molars (M^1) of most specimens which were clearly adult, but that in young specimens these teeth were virtually devoid of cementum tissue. Thus in order to evaluate the age at death of all individuals, multiple criteria had to be considered and the relationship between numbers of cementum annulations and actual age had to be established. The system finally adopted depended upon characteristics of tooth eruption in addition to cementum annuli.

In order to evaluate the ages of those specimens with annuli, it was first necessary to determine the interval of time represented by each annulus and to estimate the age of appearance of the first annulus. I suspected that the thin, dark-staining annuli were being deposited during the dry season, when food fruits were of limited availability. I selected forty-five specimens having three or more annuli that were regular in shape and sufficiently distinct as to permit measurement. The ratio of the width of the outermost light-staining region to that of the previous complete light-staining region was determined and graphed against the time of the year (by weeks) in which the specimen was collected. At first, the results were ambiguous, with dark-staining annuli occurring outermost in specimens from both the dry season and from the latter part of the wet season. Broad light-staining regions occurred outermost for most of the year. Eventually, it was realized that secondary dark annuli, staining less densely than those of the dry season, were being deposited during the brief dry period ("veranillo") occurring in the middle of the wet season, especially in the El Porvenir study area. Upon re-examination of the specimens, examples were found with a very consistent alternation between very dense and less-dense annuli. The principal features of the annular cementum patterns are clearly seen in the micrographs of two specimens which are presented in Figure A1.

The ratios of the widths of the two outermost light-staining regions were calculated again for the same 45 specimens mentioned above, ignoring the less-dense-staining annuli in those specimens with dark annuli of alternating staining density. As an example, for the specimen in Figure A1(a), the ratio would be the distance between point 7 and M, divided by the distance between points 6 and 7. The results of the measurements are graphed in Figure A2. Apparently, then, annuli with very dense staining properties represent periods of slow deposition of cementum tissue during the dry season (November through March). The darker staining properties of dry-season cementum are attributable to a higher proportion of proteinaceous material (Morris 1978). During the wet season, cementum-growth is rapid and calcite is abundantly deposited, resulting in a broad region with light staining characteristics. A thin annulus of intermediate staining density may be produced during the "veranillo" period. A

Figure A1. Micrographs of thin sections of upper first molars of pacas. All sections 12 μm, haematoxylin and eosin. (a) Portion of upper root near alveolus, seven-year-old male. *J* is the junction between dentine and cementum. Numbers indicate the years of life represented by each dense-staining dry-season annulus. Open circles indicate mid-wet-season annuli. *M* is the outer margin of the cementum. ×200. (b) Low-magnification (×40) view of the same specimen. Rectangle indicates the postion of (a). (c) ×40 view of cementum in the crotch between the roots of M^1, nine-year-old male. Numbers as in (a) above.


J
2
3
4
5
6
7
M
a
b
1
2
3
4
5
6
7
8
9
c

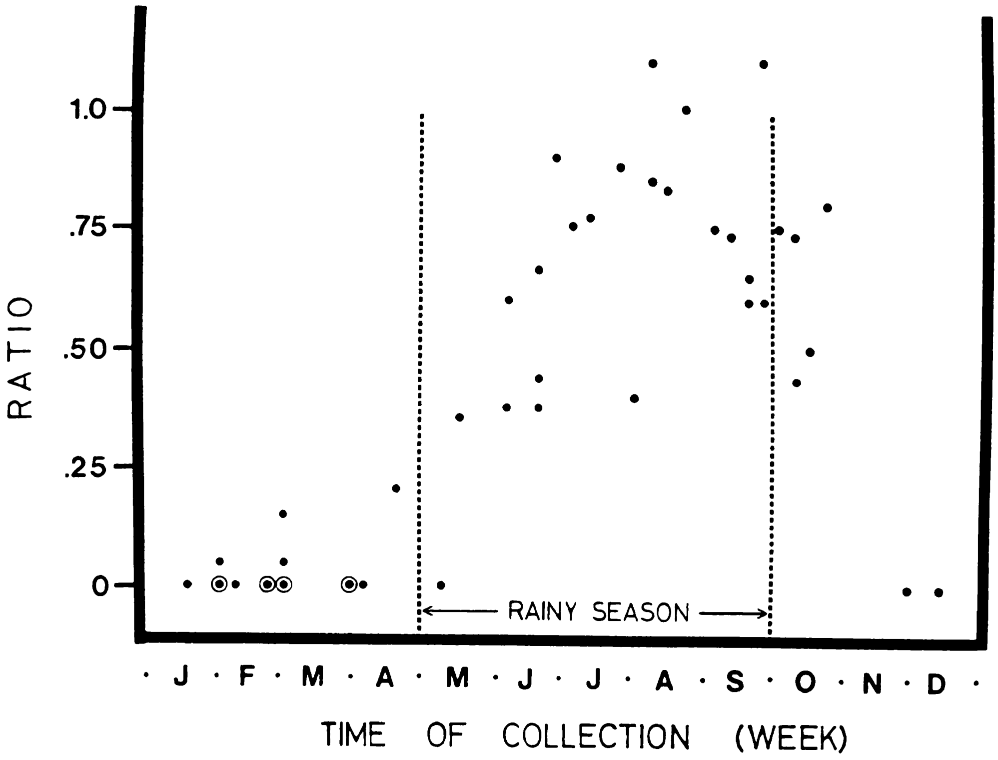


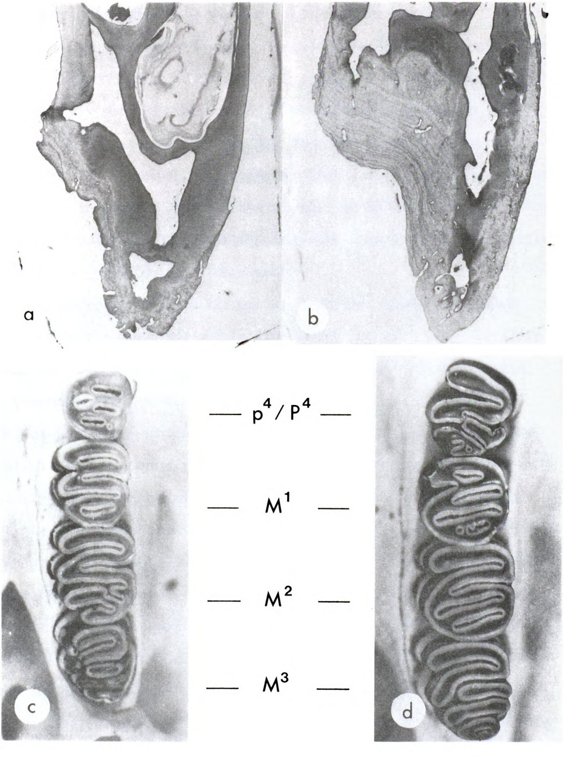
Figure A2. Variation by weeks of the year in the amount of light-staining cementum in the outermost portion of the root of M^1 for 45 adult pacas. RATIO is the width of the outermost staining region divided by the width of the adjacent light-staining region.

similar pattern of two annuli per year was found in African ungulates experiencing similar climates (Spinage 1970).

Cementum tissue is not found in specimens with incomplete dentition; that is, with the third molar (M^3) either not erupted or not fully occluded and before the deciduous premolars (p^4) have been replaced by permanent premolars (P^4). Light-staining cementum is present around the developing roots, and especially in the crotch between the two roots, in those specimens with complete but relatively unworn dentition. The first dark-staining annulus may appear anywhere in the thick (> 100 μm) layer of cementum which begins to fill in the apertures of the root canals, but generally does not extend along the outside of the upper part of the root to the region of the alveolus. The extent of these early cementum layers is shown in the section of M^1 from a one-to-two-year-old paca presented in Figure A3(a). Subsequent annuli extend along the root up to the vicinity of the alveolus, where they are thin but usually distinct. In each older specimen, the root has been extended by proliferation of much greater cementum than is found on the lateral margins of the base of the crown, as shown in Figure A3(b). The area in which annular layers are seen can therefore be divided into root-crotch and alveolar regions. The root canal becomes a narrow extension of what was a large (> 2 mm) aperture in the newly-erupted tooth. Any annuli seen along these root canals are highly irregular.

Thus the earliest dark annulus to be deposited appears only on the lower root, being especially conspicuous in the crotch between the two roots, and is not represented in the region of the alveolus. The upper alveolar region seen in Figure A1 (a) and (b) therefore has

Figure A3. Distribution of cementum tissue, and crown patterns of molariform teeth. (a) Section of M^1 of one-year-old female paca. (b) Section of M^1 of nine-year-old male. Both sections 12 μm, ×10. (c) Occlusal view of left upper molariform teeth of female paca classed as slightly less than one year old. Note that only the anterior half of M^3 is occluded. (d) Occlusal view of male paca classed as slightly older than one year. M^3 is fully occluded. P^4 = permanent premolar, p^4 = deciduous premolar, M^1, M^2, M^3 = first, second, and third molars, respectively.


a
b
c
d
— p^4 / P^4 —
— M^1 —
— M^2 —
— M^3 —

no "first year" annulus; the dark stripe nearest the junction between dentine and cementum is labeled (2). The view of the crotch region in Figure A1(c) shows how the first dark-staining annulus is limited to the region between and around the primitive root canals and in the crotch between them. Indeed, for all specimens for which sufficient cementum was seen in sections of M^1, the number of annuli in the crotch region was generally one more than the number seen in the region of the alveolus. For eight specimens, there were two more dark annuli in the crotch, and for three pacas, there were three more, than in the alveolar region. This suggests that late in life, very little cementum is produced near the alveolus.

In order to estimate the age at which the first dark annulus appears in the cementum, and in fact to distinguish first-year (less than one-year-old) from yearling (one- to two-year-old) individuals, a generalization had to be made on the basis of very little information concerning convenient developmental criteria. A female paca raised by me in captivity from the age of approximately one week was sacrificed at the age of seven and one-half months, shortly after termination of the work in Colombia. At that age, the third molar was not present. Observations on the development of the same animal had revealed that the second molar had begun to erupt at approximately four and one-half months of age. Since wild pacas weighing less than two kg (i.e., less than one month of age -- see Appendix B) have only the deciduous premolar (p^4) and an emerging M^1 present, it would appear that several months are required to complete the eruption and full occlusion of a molar. I assume that it would have taken an additional four to five months for the captive-reared individual's M^3 to form, erupt, and wear down into a fully-occluded condition. For most specimens, p^4 is replaced either at or shortly after the time of attainment of a fully occluded M^3. On the basis of this and no other information, I presume that fully-occluded M^3 and/or the presence of P^4 indicate that a paca is approximately one year old or slightly older. Figure A3 (c) and (d) shows occlusal views of the upper toothrows of specimens judged by these criteria to be slightly less than (c) and slightly more than (d) one year of age.

Of 48 specimens classified as being less than one year old by the above criteria, 39 had no cementum tissues in sections of M^1. Only relatively thin (< 100 μm) caps of cementum were found in the remaining nine first-year pacas, always located around the openings of the broad primitive root canals and in the crotch between them. Twenty-five pacas classed as older than one year had teeth with rather broad (> 100 μm) areas of light-staining cementum in the crotch but no cementum around the alveolus. For eighteen of these, a dense-staining dry-season annulus was found at a variable position within the crotch cementum. Five animals, all collected between July and October, had no annuli, and the remaining two, collected in December and March, had dark-staining cementum at the margins of the crotch area.

As determined in the text, pacas give birth at all seasons of the year. If, as Figure A2 suggests, proliferation of cementum is largely restricted to the wet season, one can expect that the age at which the dark-staining dry-season cementum begins to appear depends as much on the season of birth as on the age of the animal. For pacas born during the wet season, cementum begins to develop before the age of one year, and the first dark-staining annulus will be deposited during the dry season in the middle of the second year of life. For pacas born in the dry season, the first wet season may pass without much deposition of cementum taking place, but the first dry-season annulus will be deposited at just about one year of age. I conclude that the appearance of the first dark-staining annulus occurs sometime during the second year of life and each subsequent dark-staining annulus corresponds to an additional year of life. The final criteria used to estimate the ages of pacas are therefore as follows:

1) Pacas with deciduous premolars (p^4) present and with M^3 not fully occluded are less than one year old;
2) Pacas with permanent premolars (P^4) and/or fully occluded M^3, and having no more than one dense-staining (dry season) annulus in the cementum of the crotch of the roots of M^1, are between one and two years of age; and
3) For all older specimens, the age in years is taken to be the number of dense-staining (dry-season) annuli seen in the crotch of M^1, or one less than the number of annuli in the region of the alveolus. In cases of a discrepancy between the numbers of annuli in the two regions, the value for the crotch region is used. Thus, a specimen with one (in crotch) and two (in alveolus) dry-season annuli, respectively, is placed in the 3- to 4-year age class.

Of 205 pacas examined (eight others were excluded due to missing skull or damaged dentition), 106 were classed on the basis of tooth eruption (often taking into account the amount of light-staining cementum in M^1) and 99 on the basis of the number of cementum annulations. In only four cases was the age estimate based on annuli in the alveolar region alone.

This system is of course subject to error, especially since no known-aged adult animals were available for study. The potential error in discriminating first-year from yearling pacas is at most several months (probably two or three). Furthermore, greater errors are likely in simply determining age on the basis of cementum from a single tooth, since counts of annuli may differ for teeth from opposite sides of the same individual, at least in the case of *Odocoileus virginianus* (Rice 1980). There is a tendency also for the boundaries of older age classes to overlap as a result of the aseasonal breeding pattern of the paca. For example, an older paca that was born in the wet season would have dark-staining annuli representing the midpoints of chronological years of life. If collected in the wet season, the broad outermost light-staining region might represent nine months of life since the appearance of the last dark-staining annulus. For such a specimen, age would be underestimated by approximately three months, and the age class to which it is assigned would be in error by one year. Such a shift in estimated age, if consistent for all older age classes, need not have any effect on the survivorship values obtained from the slope of regression of the resulting age distribution.

APPENDIX B

METHODS USED TO ESTIMATE TIME OF BIRTH

Growth of Young Animals

Age in weeks was estimated from body weight for relatively young specimens as a means of estimating the week of their birth. Growth data were obtained from four specimens raised in captivity; two of unstated sex born at the U. S. National Zoo in 1972 and 1973 (J. Eisenberg pers. comm. 1977), and one male and one female purchased in August of 1979 from a fisherman living near El Porvenir, obtained at approximately three weeks and one week of age, respectively. Gross body weight was taken from the latter two individuals at variable (generally weekly) intervals. In fitting a growth curve, the ages when first obtained of the El Porvenir captives were estimated using the data provided by Eisenberg. All data were combined and fitted by the least-squares methods to a growth equation of the form

$$\mathrm{AGE}_{\mathrm{weeks}} = a - b(ln(\alpha - \mathrm{WEIGHT}_{\mathrm{kg}})) \qquad \text{(B1)}$$

with a and b being the intercept and slope, respectively, and α being an appropriate adult weight toward which the curve converges asymtotically. Trial values of 7, 7.5, and 8 kg were used for α, the best fit being obtained using $\alpha = 7.5$ kg. The resulting equation is

$$\mathrm{AGE}_{\mathrm{weeks}} = 36.74 - (19.11)(ln(7.5 - \mathrm{WEIGHT}_{\mathrm{kg}})). \qquad \text{(B2)}$$

The standard error of the estimate is 1.76 weeks. The fitted curve is plotted together with the original data points and 90% confidence limits in Figure B1.

As the figure shows, the data are concordant at least up to a weight of approximately five kg. The curve was used to estimate the age in weeks of specimens less than this weight, and thus to estimate the weeks in which they were born.

Due to the vagaries of regression, the confidence limits suggest less precision in the first few weeks of life than is likely to obtain. Birth weight is surely constrained by the reproductive structure of the mother to a range of 500 to 800 g and one cannot conceive of a newborn quadrupling in weight in the first two weeks of life. One suspects that more data, especially if replicated to permit evaluation of residual variation at each week of age, would reduce the error limits considerably. The limiting value of 5 kg used in estimating age, which is somewhat larger than the maximum weight of the El Porvenir male before he escaped, is thus somewhat arbitrary.

Since the animals used for the data provided by Eisenberg were born to pacas obtained from Panama, there is some need for caution in combining these data with that obtained from the El Porvenir animals. Also, some circularity was introduced in using Eisenberg's data to estimate the ages of the El Porvenir animals when they were first obtained and then combining the two sets of data to derive the predictive curve. In any case, caution is in order whan applying data obtained from captive animals to specimens collected in the field. It should be noted, however, that such data are difficult to obtain. Indeed, three other young pacas were captured at El Tuparro in the

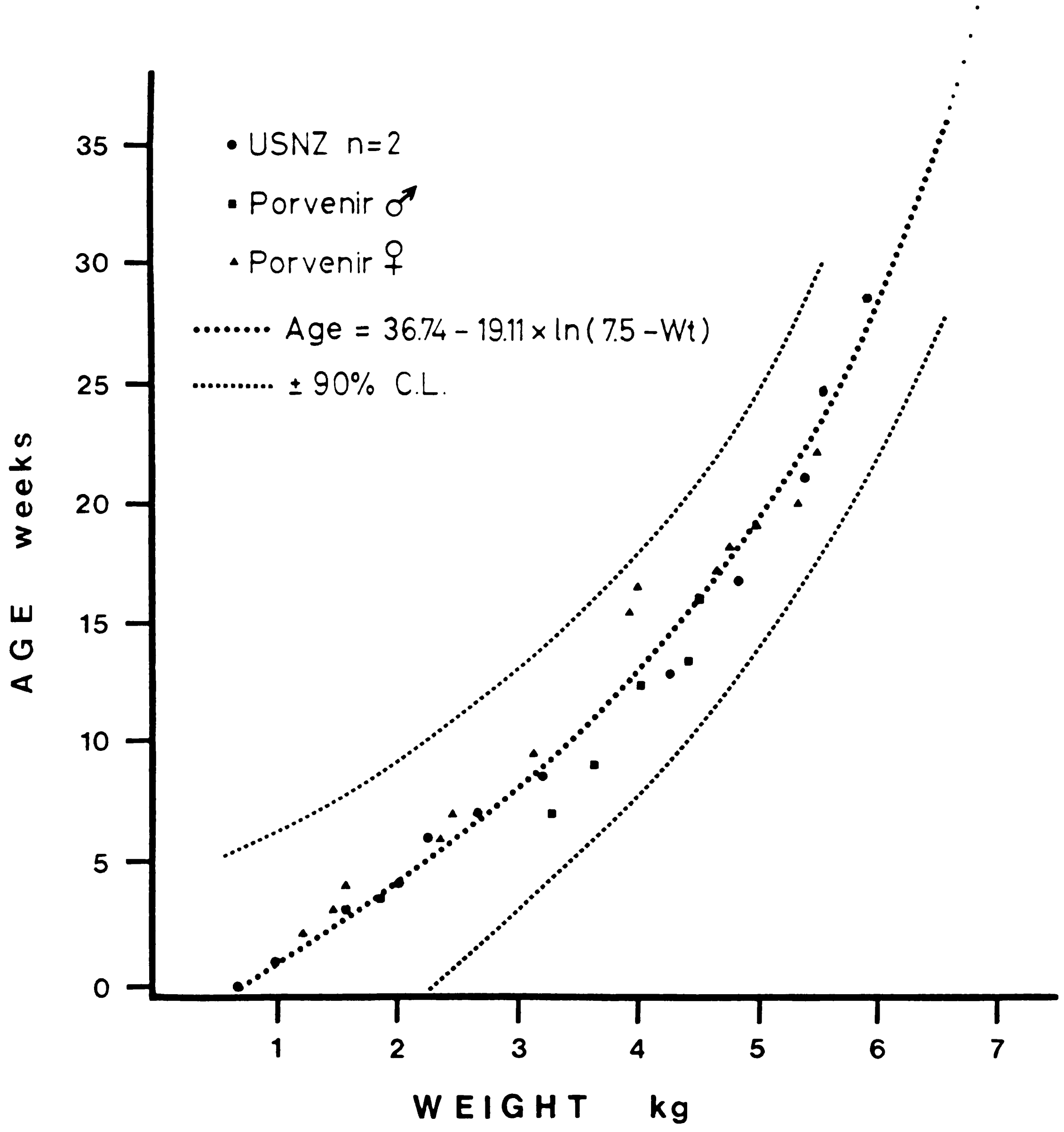


Figure B1. Growth curve for four pacas raised in captivity.

course of hunting with dogs. These three animals showed abnormal development due to nutritional deficiency and/or inadequate housing, and in fact ceased to grow beyond 2.9 kg (the largest specimen, sacrificed after seven months). The curve does demonstrate, at any rate, that growth is similar for both Panamanian and Llanos pacas at least under laboratory conditions.

Fetal Growth

The studies of Huggett and Widdas (1951) have shown that fetal growth follows the relationship

$$(\mathrm{WEIGHT})^{1/3} = \alpha(t - t_o) \tag{B3}$$

where t is the time elapsed since conception, t_o is a period of time after conception and before the cubic growth function of fetal weight on age applies, and α is a fitted coefficient, termed "specific fetal growth velocity" by Huggett and Widdas. An equivalent relationship for the paca can be derived using the estimates, taken from the literature cited previously, for the gestation period and the birth weight, and by solving for α at the time of birth.

For the guinea pig (like the paca, a caviomorph rodent), t_o was found to be 23% of gestation period (Huggett and Widdas 1951). Applying this figure to a gestation period of 116 days for the paca, t_o is approximately 28 days. Using the weight of the largest fetus observed in the field (750 g) as an estimate of birth weight, Equation (B3) becomes

$$(750)^{1/3} = \alpha(116\text{-}28) \tag{B4}$$

at birth, which gives a specific fetal growth velocity of .103. Converting to weeks and solving for age yields

$$\text{AGE(weeks)} = (\text{WEIGHT})^{1/3}/0.73) - 4. \qquad \text{(B5)}$$

Equation (B5) was used to estimate the time of gestation to the nearest whole week from the weight of each fetus. The twelve conceptions with microscopic embryos, which represent fetuses in the period of t_o, were placed into weeks one through four on the basis of the diameter of the sphere of fetal membranes. Based on the observed sphere diamter of 46 mm for a 6 mm fetus and on observations on the three females that were simultaneously pregnant and parous (see Figure 10, page 45), assuming post-partum conception, intuitive limiting values for sphere diameters of less than 15 mm, 15 to 25 mm, 26 to 35 mm, and greater than 35 mm were assigned to gestation weeks one through four, respectively. The fetal age obtained was subtracted from the gestation period of 16-1/2 weeks and the difference added to the week in which the specimen was collected to give the estimated birth weeks shown in Figure 12(d) (page 50).

APPENDIX C

SENSITIVITY ANALYSIS

Since demographic parameters are ultimately defined in terms of birth and death rates, the effect on the general model of a given change in any parameter can be interpreted in terms of the effect on λ, the difference between the birth rate and the death rate, relative to the effects on λ of equal changes in the other parameters. Thus the following sensitivity analysis asks the questions: Which parameter produces the greatest effect on rate of increase for the smallest adjustment in the value of that parameter? By considering the case of $\omega = \infty$, Goodman (1980) described the relative sensitivities of the parameters of Equation (12) using implicit differentiation. Goodman's analysis is as follows:

The summation of Equation (11) can be expressed as the sum for all age classes, minus the sum for those age classes not yet reproducing, or

$$1 = \bar{m} l_\alpha p^{-\alpha} \left[\sum_{x=0}^{\infty} (p/\lambda)^x - \sum_{x=0}^{\alpha-1} (p/\lambda)^x \right] . \qquad \text{(C1)}$$

Since

$$\sum_{x=0}^{\infty} y^x = \frac{1}{1 - y} \quad \text{and} \quad \sum_{x=0}^{i-1} y^x = \frac{1 - y^i}{1 - y}, \qquad \text{(C2)}$$

Equation (C1) reduces to

$$1 = \bar{m} l_\alpha p^{-\alpha} \left[\frac{1 - (1-(p/\lambda)\ )}{1 - p/\lambda} \right] \tag{C3a}$$

or

$$1 - p/\lambda = \bar{m} l_\alpha \lambda^{-\alpha}. \tag{C3b}$$

Multiplying by λ^α yields

$$\lambda^\alpha - p\lambda^{\alpha-1} - \bar{m} l_\alpha = 0. \tag{C3c}$$

Differentiating implicitly for l_α, p, $\bar{m}$, and α, with respect to λ given that λ is assumed to be 1.0 (see page 104 above),

$$\left.\frac{\partial\lambda}{\partial\bar{m}}\right|_{\lambda = 1} = \frac{l_\alpha}{p + \alpha(1 - p)}, \tag{C4a}$$

$$\left.\frac{\partial\lambda}{\partial p}\right|_{\lambda = 1} = \frac{1}{p + \alpha(1 - p)}, \tag{C4b}$$

$$\left.\frac{\partial\lambda}{\partial l_\alpha}\right|_{\lambda = 1} = \frac{\bar{m}}{p + \alpha(1 - p)}, \tag{C4c}$$

and

$$\left.\frac{\partial\lambda}{\partial\alpha}\right|_{\lambda = 1} = 0. \tag{C4d}$$

Thus with infinite longevity, whether λ is more sensitive to a small change in l_α or to an equal change in p depends on the value of $\bar{m}$, and since l_α is necessarily less than 1.0, λ is less sensitive to changes in $\bar{m}$ than to equal changes in either l_α or p. The relative sensitivities of λ to p or l_α can be shown graphically. When $\omega = \infty$ and $\lambda = 1.0$, different values of $\bar{m}$ as solutions to Equation (12) are represented to the Cartesian plane of $(p,\ l_\alpha)$ by straight lines radiating from the point ($p = 1.0$, $l_\alpha = 0.0$), so that the slope of a line indicates the change in l_α for a given change in p for that value of $\bar{m}$ (see Figure C1). When $\bar{m} = 1.0$, the slope is -1.0, and a given small increase in the survivorship of all adults has the same effect on λ as increasing the survivorship of juveniles by the same amount. When $\bar{m} > 1.0$, a greater increase in λ results from increasing juvenile survivorship, and when $m < 1.0$, as was the case for pacas in the Llanos, increasing adult survivorship has the greater effect.

As Goodman has indicated, the apparent insensitivity of λ to changes in α is an artifact of the assumption of $\lambda = 1.0$. The partial derivative of $p\lambda^{(\alpha-1)}$ is lost when transforming to obtain α in ordinary form, since when (λ) is assumed to be 1.0, $ln(1) = 0$. For even minor deviations from a stationary condition, the age of onset of reproduction can have a marked effect on population growth. In the simplified model, however, sensitivity to changes in α is still minor. The effect is one of shifting the net maternity function ($l_x m_x$) along the age axis, while replacement rate (the area under the curve, $\Sigma l_x m_x$) remains constant. Changes in rate of increase obtain from changing the area under the curve. Thus the model is not sensitive to changes in α alone, particularly in Goodman's analysis where $\omega = \infty$, but rather is sensitive to changes in the net length of reproductive life, or ($\omega - \alpha$).

Figure C2 plots curves of the estimated constant fecundity value of 0.95 as a function of combinations of l_α and p which satisfy the conditions defined by Equation (14). Each curve represents solutions for a different value of ω, assuming that $\alpha = 1.5$ in each case. Clearly, the model is sensitive to the length of reproductive life

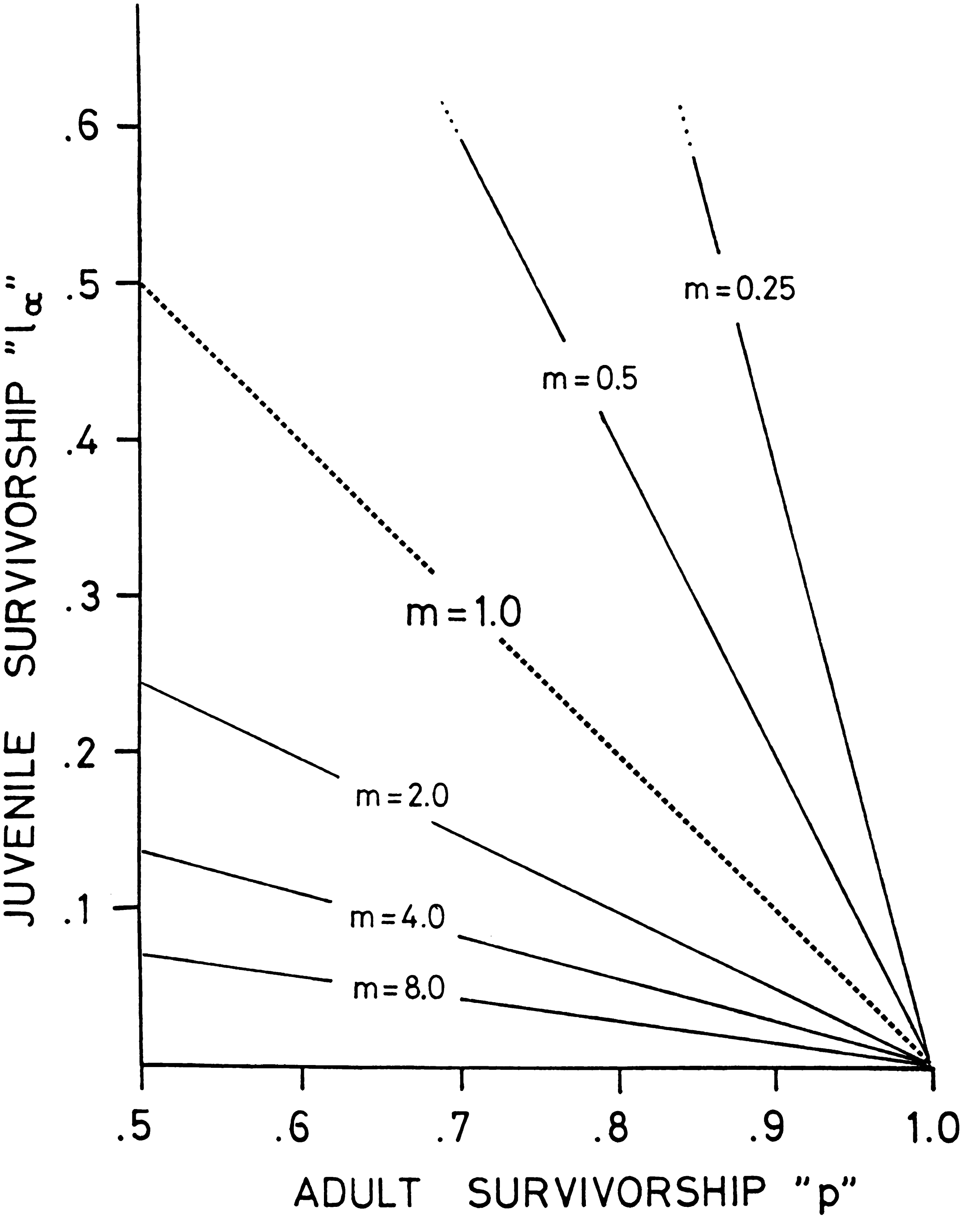


Figure C1. Sensitivity of λ to changes in l_α and p when $\omega = \infty$. The sensitivities are equal when $\bar{m} = 1.0$ (broken line).

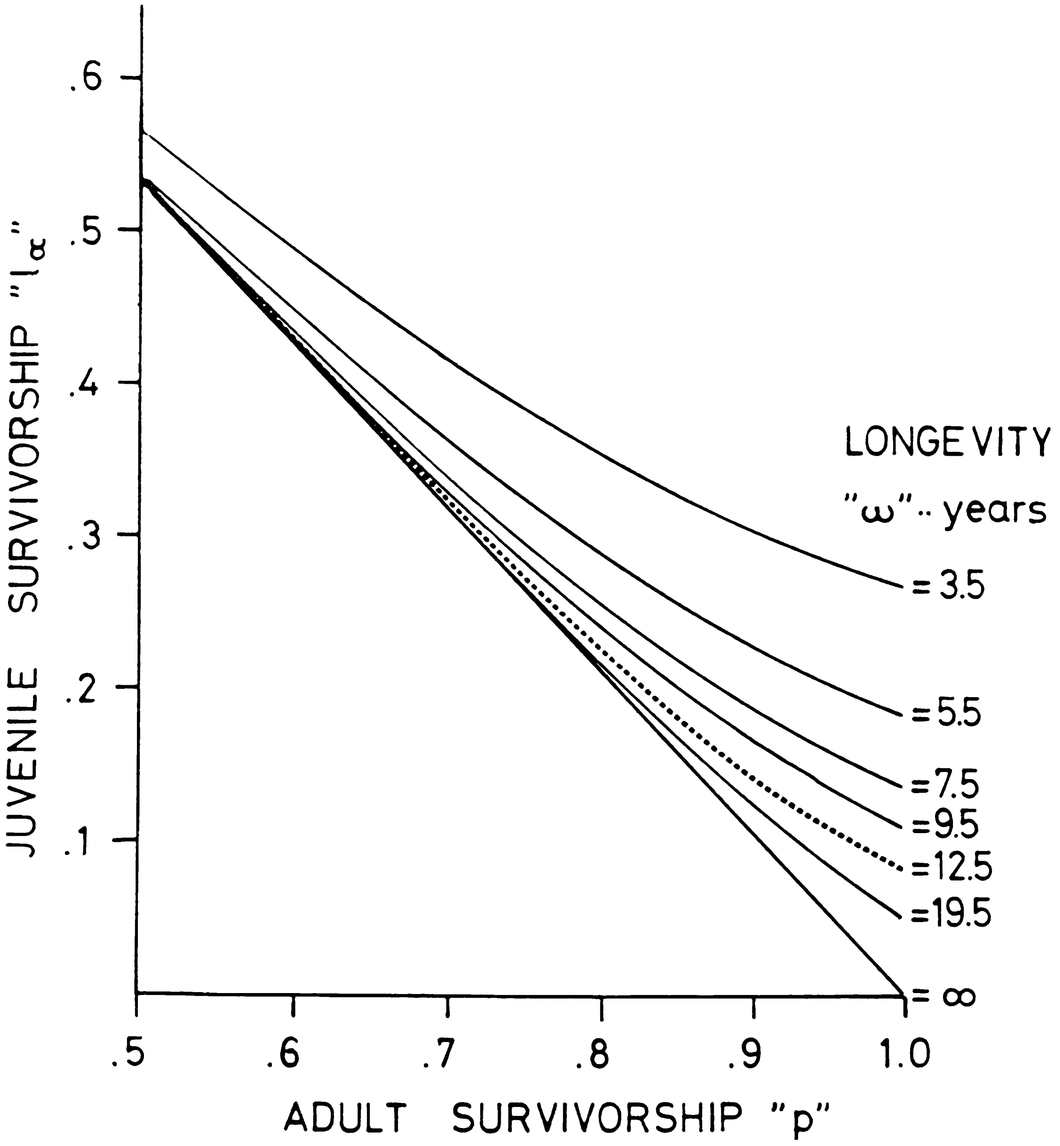


Figure C2. Curves showing the relationship between juvenile and adult survivorship using different values for maximum longevity in solving Equation (14), assuming $\alpha = 1.5$, $\bar{m} = 0.95$, and $\lambda = 1$.

expressed as variation in ω, especially as p approaches 1.0, but the effect of decreasing ω from infinity to the observed value of 12.5 is equivalent to a change of less than three percent in the value of l_α when p is in the neighborhood of the estimated value of 0.8. Furthermore, α is subsumed in l_α, so that survivorship to the first reproductive age class enters the model without regard for the length of time represented by α. Decreasing α (hastening the onset of reproductive life) would have the effect of increasing the difference $|\lambda - 1|$, and increasing α would decrease $|\lambda - 1|$. When p is 0.8 and λ is 1 ± 0.1, the relationship between l_α and p is affected by less than four percent when $\omega = 13.5$ and α is as large as 3.5. Thus, although it is important to estimate the value ω, the model is robust even for improbably large deviations in ω and/or α.

To incorporate $\omega << \infty$ into the analysis of Equation (12), Equation (C1) is modified by subtracting summations to account for the range of $\omega + 1$ to ∞, so that

$$1 = \bar{m} l_\alpha p^{-\alpha} \left\{ \left(\sum_{x=0}^{\infty} (p/\lambda)^x - \sum_{x=0}^{\alpha-1} (p/\lambda)^x \right) - \left(\sum_{x=0}^{\infty} (p/\lambda)^x - \sum_{x=0}^{\omega} (p/\lambda)^x \right) \right\} . \qquad \text{(C5)}$$

Using the definitions of Equation (C2) and rearranging superscripts,

$$1 = \bar{m} l_\alpha p^{-\alpha} \left\{ \frac{(p/\lambda)^\alpha - (p/\lambda)^{\omega-1}}{1 - (p/\lambda)} \right\} , \qquad \text{(C6a)}$$

or

$$1 - (p/\lambda) = \bar{m} l_\alpha \lambda^{-\alpha} - \bar{m} l_\alpha p^{-\alpha} (p/\lambda)^{\omega+1} . \qquad \text{(C6b)}$$

Multiplying by λ^{α} gives

$$\lambda^{\alpha} - p\lambda^{\alpha-1} - ml_{\alpha}(1 - (p/\lambda)^{\omega-\alpha+1}) = 0. \tag{C6c}$$

The relevant partial derivatives are

$$\left.\frac{\partial\lambda}{\partial\bar{m}}\right|_{\lambda = 1} = \frac{l_{\alpha}(1 - p^{(\omega-\alpha+1)})}{1 - p(\alpha-1) - \bar{m}l_{\alpha}(\omega-\alpha+1)p^{(\omega-\alpha+1)}} , \tag{C7a}$$

$$\left.\frac{\partial\lambda}{\partial p}\right|_{\lambda = 1} = \frac{1 - \bar{m}l_{\alpha}(\omega-\alpha+1)p^{(\omega-\alpha)}}{1 - p(\alpha-1) - \bar{m}l_{\alpha}(\omega-\alpha+1)p^{(\omega-\alpha+1)}} , \tag{C7b}$$

$$\left.\frac{\partial\lambda}{\partial l_{\alpha}}\right|_{\lambda = 1} = \frac{\bar{m}(1 - p^{(\omega-\alpha+1)})}{1 - p(\alpha-1) - \bar{m}l_{\alpha}(\omega-\alpha+1)p^{(\omega-\alpha+1)}} , \tag{C7c}$$

$$\left.\frac{\partial\lambda}{\partial\alpha}\right|_{\lambda = 1} = 0 , \tag{C7d}$$

$$\left.\frac{\partial\lambda}{\partial\omega}\right|_{\lambda = 1} = 0 . \tag{C7e}$$

Equation (C6c) is identical to Equation (C3c) except that the product $\bar{m}l_{\alpha}$ is now weighted by a factor of approximately $(1 - p^{\omega})$ since $\alpha = 1.5 \simeq 1.0$ for the present purpose). Since p is necessarily a fraction, the weighting factor becomes vanishingly small as p becomes small or as ω becomes large, giving partial derivatives for p and α equivalent to Equations (C4b and d). When p is large and ω is small, as in the case of the pacas, l_{α} and $\bar{m}$ have smaller effects on Equation (C6c) and so the sensitivity of λ to small changes in them is increased over the infinite longevity model by a function of p, α, and ω. The partial derivatives relative to α and ω are again intractable when λ is assumed to be 1.0

When length of reproductive life is included in the model (i.e., $\omega << \infty$), fecundity as a function of l_α and p is not a straight line and the critical fecundity at which λ is equally sensitive to l_α and p is no longer a unique value. As p becomes large, the critical fecundity becomes lower, the relative sensitivities of λ to l_α and p are defined in terms of both $\bar{m}$ and $(\omega-\alpha)$, and the slope of the curve for a given value of $\bar{m}$ does not define these sensitivities. Line (a) in Figure C3 locates the set of combinations of l_α and p for which λ is equally sensitive to both, using the observed values of $\alpha = 1.5$ and $\omega = 12.5$. Line (b) is the line for $\bar{m} = 0.95$ as before, and line (c) is where sensitivites to l_α and p would be equal for $\omega = \infty$. The open circle shows the position of the estimated values of $\bar{m} = 0.95$ and $p = 0.80$, and the shaded area defines the ±95% confidence limits as before. Notice that taking length of reproductive life $(\omega-\alpha)$ into account reverses the sensitivities to l_α and p. If maximum longevity is 12.5 years, a greater increase in the number of pacas will result from increasing juvenile survivorship than from increasing survivorship for all adults by the same amount. As before, even less is to be gained from increasing fecundity by the same amount. As the shaded area indicates, the higher sensitivity to l_α holds true for virtually the entire range of confidence for the estimates of $\bar{m}$ and p.

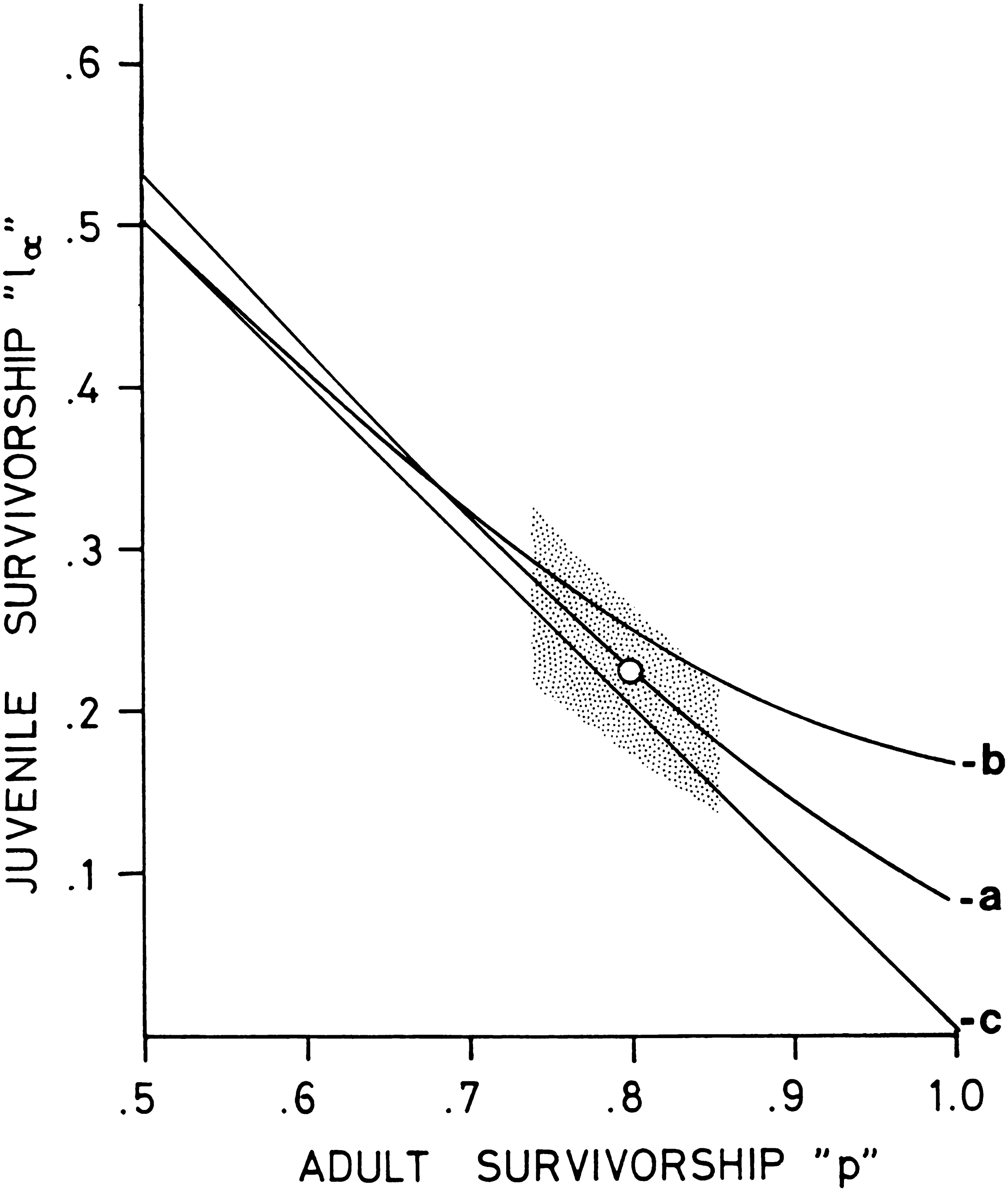


Figure C3. Demographic parameters for the population of pacas (line (a) and open circle) in relation to values for equal sensitivity of λ to l_α and p for the finite (ω = 12.5, line (b)) and infinite ($\omega = \infty$, line (c)) longevity situations.

LIST OF REFERENCES

LIST OF REFERENCES

Aisbey, E. O. 1974. The grasscutter, Thryonomys swinderianus Temminck, in Ghana. Symp. Zool. Soc. Lond. 34:161-170.

Alvarez del Toro, M. 1977. Los mamíferos de Chiapas. Tuxtla Gutierrez, Universidad Autón. de Chiapas, 147 pp.

Aquino, Yarihuaman Rolando, personal communication. 1979. (Ministerio de Agricultura y Alimentacion, Proyecto de Asentamiento Rural, Iquitos, Peru).

Armitage, K. B., and J. F. Downhower. 1974. Demography of yellow-bellied marmot populations. Ecology 55:1233-1245.

Barash, D. P. 1974. The evolution of marmot societies: A general theory. Science 185:415-420.

Bates, M. 1964. The land and wildlife of South America, by Marston Bates and the editors of Life. New York, Time Inc., 200 pp.

Beard, J. S. 1953. The savanna vegetation of northern tropical America. Ecol. Monogr. 23:149-215.

Beddington, J. R., and D. B. Taylor. 1973. Optimal age-specific harvesting of a population. Biometrics 29:801-809.

Blydenstein, J. 1967. Tropical savanna vegetation of the Llanos of Colombia. Ecology 48:1-15.

Bourliere, F. 1973. The comparative ecology of rain forest mammals in Africa and tropical America: Some introductory remarks. Pp. 279-292 in: B. J. Meggers et al. (eds.), Tropical forest ecosystems of Africa and South America. Washington, D. C., Smithsonian Institution Press, 438 pp.

Brisson, M. J. 1762. Regnum animale in classes IX distributum. Leiden, Theodorum Haak, 296 pp.

Brunnschweiler, D. 1972. The Llanos frontier of Colombia. Environment and changing land use in Meta. Latin American Studies Ctr. Monograph 7, Mich. St. Univ., 71 pp.

Cabrera, A. 1961. Catálogo de los mamíferos de América del Sur. Rev. Mus. Arg. Cienc. Nat. Cien. Zool. 4:1-625.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47:906-918.

Caughley, G. 1977. Analysis of vertebrate populations. New York: John Wiley and Sons, 228 pp.

Caughley, G., and L. C. Birch. 1971. Rate of increase. J. Wildl. Manag. 35:658-663.

Charnov, E. L., and W. M. Schaffer. 1973. Life-history consequences of natural selection: Cole's result revisited. Amer. Natur. 107: 791-793.

Cole, L. C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol. 29:103-139.

Collins, L. R., and J. F. Eisenberg. 1972. Notes on the behavior and breeding of pacaranas, _Dinomys_ _branickii_, in captivity. Internat. Zoo Yb. 12:108-114.

D'Alessandro, A., R. L. Rausch, G. A. Morales, S. Collett, and D. Angel. In press. _Echinococcus_ infections in Colombian animals. Amer. J. Tropical Med. and Hygiene.

Dalquest, W. 1953. Mammals of the Mexican state of San Luís Potosí. Louisiana St. Univ. Studies, Biol. Ser. 1:1-224.

Dapson, R. W., P. R. Ramsey, M. H. Smith, and D. F. Urbston. 1980. Demographic differences in contiguous populations of white-tailed deer. J. Wild. Manag. 43:889-898.

Davis, D. E. 1973. Comments on _r_. Bull. Ecol. Soc. Amer. 54(3):14-15, 26.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22:283-314.

Defler, T. R. 1979. On the ecology and behavior of _Cebus_ _albifrons_ in eastern Colombia: I. Ecology. Primates 20:475-490.

Dobzhansky, T. 1950. Evolution in the tropics. Amer. Scientist 38: 208-221.

Dubost, G. 1965. Quelqes traits remarquables du comportement de _Hyaemoschus_ _aquaticus_ (Tragulidae, Ruminantia, Artiodactyla). Biologia Gabonica 1:282-287.

Dubost, G. 1968. Les niches ecologiques des forets tropicales sud-americaines et africaines, sources de convergences remarquables entre rongeurs et artiodactyles. La Terre et la Vie 22:3-28.

Eisenberg, J. 1966. The social organization of mammals. Handbuch der Zoologie 10(7):1-92.

Eisenberg, J. 1974. The function and motivational basis of hystricomorph vocalizations. Symp. Zool. Soc. Lond. 34:211-247.

Eisenberg, John F., personal communication. 1977. (United States National Zoo, Front Royal, Virginia).

Eisenberg, J., and G. McKay. 1974. Comparison of ungulate adaptations in New World and Old World tropical forests with special reference to Ceylon and the rain forests of Central America. Pp. 585-602 in: V. Geist and R. Walther (eds.), The behavior of ungulates and its relation to management, Vol. 2, IUCN Publ. 24.

Eisenberg, J., M. O'Connell, and P. August. 1980. Density, productivity, and distribution of mammals in two Venezuelan habitats. Pp. 187-207 in: J. Eisenberg (ed.), Vertebrate Ecology in the Northern Neotropics. Washington, D. C.: Smithsonian Institution Press.

Eisenberg, J., and R. W. Thorington, Jr. 1973. A preliminary analysis of a Neotropical mammal fauna. Biotropica 5:150-161.

Ellerman, J. R. 1940. The families and genera of living rodents. Volume I. Rodents other than Muridae. London: British Museum, 653 pp.

Emlen, J. M. 1970. Age specificity and ecological theory. Ecology 54:588-601.

Ewer, R. F. 1968. Ethology of mammals. New York: Plenum Press, 418 pp.

FAO. 1965. Reconocimiento edafológico de los Llanos Orientales, Colombia. Vol. I. Los suelos de los Llanos Orientales. United Nations Food and Agriculture Organization, 528 pp.

Fleming, T. H. 1975. The role of small mammals in tropical ecosystems. Pp. 269-298 in: F. B. Golley, K. Petrusewicz, and L. Ryszkowski (eds.), Small mammals: Their productivity and population dynamics. International Biological Programme 5. Cambridge: University Press.

French, N. R., D. M. Stoddart, and B. Bobek. 1975. Patterns of demography in small mammal populations. Pp. 73-102 in: F. B. Golley, K. Petrusewicz, and L. Ryszkowski (eds.), Small mammals: Their productivity and population dynamics. International Biological Programme 5. Cambridge: University Press.

Goodman, D. 1974. Natural selection and a cost ceiling on reproductive effort. Amer. Natur. 108:247-268.

Goodman, D. 1980. Demographic intervention for closely managed populations. Pp. 171-195 in: M. Soule and B. Wilcox (eds.), Conservation biology: An evolutionary-ecological perspective. Sunderland, Mass.: Sinauer Assoc.

Green, R. 1980. A note on *K*-selection. Amer. Natur. 116:291-296.

Haffer, J. 1974. Avian speciation in tropical South America. Publ. Nutall Ornithol. Club 14:1-390.

Hershkovitz, P. 1955. On the cheek pouches of the tropical American paca Agouti paca (Linnaeus, 1766). Saeugetirk. Mitteil. Muenchen 3:67-70.

Hershkovitz, P. 1969. The recent mammals of the Neotropical region: A zoogeographic and ecological review. Quart. Rev. Biol. 44:1-70.

Hingston, R. 1932. A naturalist in the Guiana forest. London: Edward Arnold and Co., 285 pp.

Hopwood, A. T. 1947. The generic names of the mandrill and baboons, with notes on some of the genera of Brisson, 1762. Proc. Zool. Soc. Lond. 117:533-536.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midland Natur. 63:151-162.

Howard, W. E., and H. E. Childs. 1959. Ecology of pocket gophers with emphasis on Thomomys bottae mewa. Hilgardia 29:227-358.

Hugett, A. St. G., and W. F. Widdas. 1951. The relationship between mammalian fetal weight and conception age. J. Physiol. Lond. 114:306-319.

Instituto Geográfico Agustín Codazzi. 1973. Atlas de Colombia, 3rd edition. Bogotá, Colombia, 269 pp.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 58(3):171-209.

Kleiman, D. 1974. Patterns of behaviour in hystricomorph rodents. Symp. Zool. Soc. Lond. 34:171-209.

Kleiman, D., J. Eisenberg, and E. Maliniak. 1980. Reproductive parameters and productivity of caviomorph rodents. Pp. 173-183 in J. Eisenberg (ed.), Vertebrate ecology in the northern neotropics. Washington: Smithsonian Institution Press.

Kraus, C., M. Gihr, and G. Pilleri. 1970. Das Verhalten von Cuniculus paca (Rodentia, Dasyproctidae) in Gefangenschaft. Revue Suisse de Zoologie 77:353-388.

Krebs, J. R. 1971. Territory and breeding density of the Great Tit, Parus major L. Ecology 52:2-22.

Lacépède, G. 1799. Tableau des divisions, sous-divisions, ordres, et genres des mammiféres. In: Buffon, G., Histoire naturelle. [Vol. 14, Quadrupes.] Paris: P. Didot L'Aine et firmin Didot.

Lander, A. 1974. Observaciones preliminares sobre lapas Agouti paca (Linn. 1766) (Rodentia, Agoutidae), en Venezuela. Univ. Central de Venezuela, Fac. Agronomía, Inst. de Zoologia Agrícola, Maracay, 104 pp.

Laws, R. M. 1969. Aspects of reproduction in the African elephant, Loxodonta africana. J. Reprod. Fert., Suppl. 6:193-217

Leopold, A. S. 1959. Wildlife of Mexico. Berkeley: Univ. of California Press, 568 pp.

Lewontin, R. 1965. Selection for colonizing ability. Pp. 77-91 in: H. Baker and G. L. Stebbins (eds.), The genetics of colonizing species. New York: Academic Press.

Linnaeus, Carolus. 1766. Systema naturae. 12th edition, revised. Stockholm: Laurentii Salvii, 824 pp.

Lockard, P., and D. Owings. 1974. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. J. Mamm. 55: 189-193.

Lotka, A. J. 1907a. Relationship between birth rates and death rates. Science 26:21-22.

Lotka, A. J. 1907b. Studies on the mode of growth of material aggregates. Amer. J. Sci., Ser. 4, 24:199-216.

Lotka, A. J. 1956. Elements of mathematical biology. New York: Dover Publications, 465 pp.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biography. Princton Univ. Press, 203 pp.

Marcgrave, J. 1648. Historia naturalis brasiliae. Tras. J. procopio de Magalhaes. Ed. Museu Paulista de Sao Paulo, Sao Paulo 1952.

Matamoros, Yolanda, personal communication. 1980. (Universidad National, Heredia, Costa Rica).

Méndez, E. 1970. Los principales mamíferos silvestres de Panama. Privately printed, 283 pp.

Michod, R. E., and W. W. Anderson. 1980. On calculating demographic parameters from age frequency data. Ecology 61:265-269.

Mondolfi, E. 1972. La lapa o paca. Defensa Natur. Venez. 2(5):4-16.

Moro, M. 1976. Utilization of wild species in human nutrition in the tropics. Pp. 55-63 in: VIII Inter-American Meeting on Foot-and-Mouth Disease and Zoonoses Control. PAHO Sci. Publ. 316.

Morris, D. 1962. The behavior of the green acouchi (Myoprocta pratti) with special reference to scatter hoarding. Proc. Zool. Soc. Lond. 139:701-732.

Morris, P. 1978. The use of teeth for estimating the age of wild mammals. Pp. 484-494 in: P. Butler and K. Joysey (eds.), Development, function and evolution of teeth. New York: Academic Press, 523 pp.

Mossman, H. W. 1966. The rodent ovary. Symp. Zool. Soc. Lond. 15: 455-470.

Mossman, H. W., and I. Judas. 1949. Accessory corpora lutea, lutein cell origin and the ovarian cycle in the Canadian porcupine. Amer. J. Anat. 85:1-39.

Murray, B. G. 1979. Population dynamics: Alternative models. New York: Academic Press, 212 pp.

Ojasti, J. 1973. Estudio biológico del chiguire o capibara. Caracas: Fondo Nacional de Investigaciones Agropecuarias.

Ojasti, J., and G. Padilla. 1972. The management of capybara in Venezuela. Trans. 37th North American Wld. Nat. Res. Conf. 37: 268-277.

Pearl, R., and L. J. Reed. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc. Natl. Acad. Sci. U.S.A. 6:275-288.

Pianka, E. 1970. On r and K selection. Amer. Natur. 104:592-597.

Pianka, E. 1972. r and K selection or b and d selection? Amer. Natur. 106:581-588.

Peilou, E. C. 1977. Mathematical ecology. New York: John Wiley and Sons, 385 pp.

Pierret, V., and M. Dourejeanni. 1966. La caza y la alimentacion humana en las riberas del Río Pachitea, Perú. Turrialba 16: 271-277.

Pierret, V., and M. Dourejeanni. 1967. Importancia de la caza para alimentación humana en el curso inferior del Río Ucayali, Perú. Rev. Forest. Perú 1(2):10-21.

Pine, R. 1973. Mammals (exclusive of bats) of Belém, Pará, Brazil. Acta Amazonica 3(2):47-79.

Pocock, R. I. 1922. On the external characteristics of some hystricomorph rodents. Proc. Zool. Soc. Lond. 25:365-427.

Pollard, J. 1973. Mathematical models for the growth of human populations. London: Cambridge Univ. Press, 181 pp.

Ralls, K. 1971. Mammalian scent marking. Science 171:443-449.

Rice, L. A. 1980. Influences of irregular dental cementum layers on aging deer incisors. J. Wildl. Manag. 44:266-268.

Ricklefs, R. 1977. On the evolution of reproductive strategies in birds: Reproductive effort. Amer. Natur. 111:453-478.

Rowlands, I. 1974. Mountain viscacha. Symp. Zool. Soc. Lond. 34: 131-141.

Rowlands, I. W., and B. J. Weir (eds.). 1974. The biology of hystricomorph rodents. Zoological Society of London Symposium 34, 482 pp.

Sarmiento, G., and M. Monasterio. 1975. A critical consideration of the environmental conditions associated with the occurrence of savanna ecosystems in tropical America. Pp. 223-250 in: F. B. Golley and E. Medina (eds.), Tropical ecological systems. New York: Springer Verlag.

Schaffer, W., and R. Tamarin. 1973. Changing reproductive rates and population cycles in lemmings and voles. Evolution 27:111-124.

Sharpe, F. R., and A. J. Lotka. 1911. A problem in age-distribution. Philos. Mag. 21:434-438.

Siler, W. 1979. A competing-risk model for animal mortality. Ecology 60:750-757.

Slade, N. K., and D. F. Balph. 1974. Population ecology of Uinta ground squirrels. Ecology 55:989-1003.

Smythe, N. 1970a. Ecology and behavior of the agouti (Dasyprocta punctata) and related species on Barro Colorado Island, Panama. Ph.D. dissertation, University of Maryland, 201 pp.

Smythe, N. 1970b. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. Amer. Natur. 104: 25-35.

Smythe, N. 1978. The natural history of the Central American agouti (Dasyprocta punctata). Smithsonian Contribs. Zool. 257:1-52.

Smythe, N., W. Glanz, and E. Leigh, Jr. In press. Ecology and population regulation in pacas and agoutis. In: E. Leigh, Jr. (ed.), Seasonal rhythms and long-term changes in a tropical forest. Washington, D.C.: Smithsonian Institution Press.

Spinage, C. A. 1970. Incremental cementum lines in the teeth of tropical African mammals. J. Zool. Lond. 178:117-131.

Spinage, C. A. 1972. African ungulate life tables. Ecology 53: 645-652.

Stearns, S. C. 1976. Life history tactics: A review of the ideas. Quart. Rev. Biol. 51:3-47.

Steele, R., and J. Torrie. 1960. Principles and procedures of statistics. New York: McGraw-Hill, 481 pp.

Stolzmann, J. 1885. Description d'un nouveau rongeur du genre Coelogenys. Proc. Zool. Soc. Lond. 1885 VI:161-167.

Taber, R. D., and R. F. Dasmann. 1958. The black-tailed deer of the chaparral. Bull. Calif., Dept. Fish and Game 8:1-163.

Tate, G. H. H. 1931. Random observations on habits of South American mammals. J. Mamm. 12:248-256.

Tait, D., and F. L. Bunnell. 1980. Estimating rate of increase from age at death. J. Wildl. Manag. 44:296-299.

Vincelli, P. In press. Estudio de la vegetación del Territorio Faunístico El Tuparro. Cespedesia (Cali), 1980.

Walker, E., F. Warnick, S. Hamlet, K. Lange, M. Davis, H. Uible, and P. Wright. 1975. Mammals of the world. 3rd edition, revised by J. Paradiso. Baltimore: John Hopkins Univ. Press.

Weir, B. 1974a. Reproductive characteristics of hystricomorph rodents. Symp. Zool. Soc. Lond. 34:265-301.

Weir, B. 1974b. The tuco-tuco and plains viscacha. Symp. Zool. Soc. Lond. 34:113-130.

Wetterberg, G., M. Ferreira, W. dos Santos Brito, and V. C. de Araújo. 1976. Amazon fauna preferred as food. Brazil, PRODEPEF Field Document No. 23, UNDP/FAO/IBDF Project for Forestry Development, 17 pp, (mimeograph).

Wood, A. E. 1955. A revised classification of rodents. J. Mamm. 36: 165-186.