JOHN F. EISENBERG
and MELVYN LOCKHART

An Ecological Reconnaissance of Wilpattu National Park, Ceylon

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY NUMBER 101

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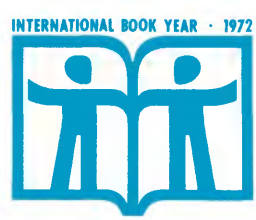

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ABSTRACT

Eisenberg, John F., and Melvyn Lockhart. An Ecological Reconnaissance of Wilpattu National Park, Ceylon. *Smithsonian Contributions to Zoology,* number 101. 118 pages 76 figures, 16 tables. 1972.—The results of this study are based on a 14-month survey in Wilpattu National Park, Ceylon, covering an area of some 580 square kilometers in the lowland dry zone scrub jungle. Special attention was paid to the major ungulate species and data concerning abundance, seasons of reproduction, and feeding patterns are discussed. Although the elephant (*Elephas maximus*) exhibits the lowest numerical density, it accounts for the second highest biomass, exceeded in biomass only by the axis deer, which is also the most numerically abundant ungulate in the lowland dry zone of Ceylon. Special attention was paid to the role of the elephant in the dry zone ecosystem. Composition of social groupings, seasonal habitat utilization trends, general behavior patterns, and population structure are discussed for the elephant *(Elephas maximus)*, water buffalo *(Bubalus bubalis)*, axis deer *(Axis axis)*, sambar *(Cervus unicolor)*, muntjac *(Muntiacus muntjac)*, wild swine *(Sus scrofa)*, and mouse deer (*Tragulus meminna*). Certain aspects of the behavior of the major predators are also discussed, including the general biology of the golden jackal (*Canis aureus*) and the Ceylon leopard (*Panthera pardus*). Social organizations of the ungulate species are compared with special attention given to the mode of antipredator behavior exhibited by ungulates. Habitat utilization trends and comments on competition and ecological separation are included together with an estimate of numerical abundance and biomass for the major ungulate species. Recommendations for management of the park system are discussed.

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Introduction

Although the study here reported was addressed primarily to the problem of conserving Ceylon's elephant population, it has been necessary to survey all the major ungulate populations in the National Park in order to assess such subtle effects as competition and cooperation among the various populations of large mammals. Special attention was directed towards censusing the populations of large ungulates resident in the parks and to gather data concerning the seasonal movement patterns with respect to the distribution of food and water. Methodology was carried out in a classic pattern. Two types of censusing operations were conducted, including a jeep survey of the major water holes and river areas where actual counts of the animals could be made, or indirect counts based on tracks. Certain parts of the park were subjected to a walking survey, especially in the West Sanctuary area where jeep trails have not been constructed. Indirect estimates of animal activity were routinely conducted in certain areas of the park; plots were set up and pellet counts were carried out on these plots for a period of some six months (see Eisenberg, Santiapillai, and Lockhart 1970). In addition, transect walking permitted an estimate of habitat utilization employing a check sheet designed by Dieter Mueller-Dombois. For actual discussion of the methods employed, see Appendix A.

A map of Wilpattu National Park and the surrounding sanctuary and intermediate zones is portrayed in Figure 1. In our survey, we intensively studied the West Sanctuary, parts of the North Sanctuary, and the major park area including the old south intermediate zone which last year was included in the park itself. Two camps were established: a temporary camp on the banks of the Moderagam Aru, which forms the north boundary of the park, and a permanent camp at Marai Villu on the border between the West Sanctuary and the park proper. The park and northern portion of the West Sanctuary were surveyed in their entirety on a quarterly basis employing the major jeep trails and walking trails as indicated on the maps in Figures 75 and 76. This also included portions of the river systems: the banks of the Kala Oya, the banks of the Moderagam Aru, portions of the Pan Ella, and the Eerige Ella. The total area which was surveyed quarterly included some 745 square kilometers. Monthly surveys were executed in the northern portion of the West Sanctuary and the central or villu area of the park up to the Moderagam Aru; this included an area of approximately 320 square kilometers. Intensive surveys of ten to fourteen days duration were carried out monthly in an area from the Moderagam Aru to the seacoast including the north portion of the West Sanctuary and the western villu area; this area included some 266 square kilometers. Surveys in

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the park began in July 1968 with a preliminary check for campsites. In August 1968 the intensive surveys were begun and continued until October 1969. The study thus covers fourteen months and includes two drought periods.

ACKNOWLEDGMENTS

The study reported in the following pages was part of a team effort to investigate the behavior and ecology of the Ceylon elephant. The team surveying the National Parks of Ceylon was organized and coordinated by the Smithsonian Institution.

In 1966, The Wild Life Protection Society of Ceylon and the Ceylon Department of Wildlife sent a request to the Smithsonian Institution for advice and/or help in the organization of an elephant study program. Dr. Helmut K. Buechner, then Head of the Office of Ecology, invited Dr. John A. King from Michigan State University to survey the possibilities for a research project. Dr. King filed a report with several recommendations but was unable to follow up as a principal investigator on the project. On the basis of King's report, Dr. Buechner and Dr. John F. Eisenberg, Resident Scientist at the National Zoological Park, wrote a grant request and formed a team for elephant research. The study was projected to extend from 1967 to 1969, concentrating in three dry zone national parks: Ruhunu, Gal Oya, and Wilpattu. At the same time, Dr. Raymond Fosberg of the Smithsonian Institution formed an Ecology Project built around a botanical reconnaissance which was under the field direction of Dr. Dieter Mueller-Dombois of the University of Hawaii.

Throughout the course of this three-year investigation there was continual cooperation and exchange of information among the team members. The primary responsibility for the survey of Ruhunu National Park fell to Dr. Fred Kurt of Switzerland, who conducted his studies from 1967 through 1969. Dr. Eisenberg initiated and directed the survey of Wilpattu National Park from 1968 through 1969 and Mr. George McKay of the University of Maryland conducted extensive studies in Gal Oya National Park from 1967 through 1969. The authors are indebted to McKay, Kurt, and Mueller-Dombois for their assistance and for exchange of information.

The Smithsonian teams were aided by many individuals in Ceylon. In particular we may mention the efforts of Mr. Th. Hoffman, Secretary of the Wildlife Protection Society of Ceylon; Mr. Max Hemple, former editor of "The Loris"; and Mr. Lynn de Alwis, Director of the Zoological Gardens at Dehiwala and Warden of the Wild Life Department of Ceylon—without the aid, assistance, and encouragement of Mr. de Alwis, the project could not have achieved success. Throughout the survey, we were aided by members of the faculty of the University of Ceylon, Perideniya. In particular we wish to thank Professor Hilary Crusz of the Department of Zoology, and Professor P. Senivaratne, Drs. J. B. Jayasinghe, and M. R. Jainudeen, of the Faculty of Veterinary Medicine at the University of Ceylon, Perideniya. Helpful assistance in the initial phases was provided by the former President of the Wildlife Protection Society of Ceylon, Mr. T. E. Norris. The cooperation of Mr. Percy de Alwis, Divisional Game Ranger, who is responsible for the supervision of Wilpattu National Park, is deeply appreciated. Able assistance in the survey operations came from Mr. Desmond Lockhart, Mr. Anil Jayasuria, Mr. A. P. W. Nettasinghe, and Mr. Charles Santiapillai.

Assistance in data collection was also supplied by members of the Smithsonian Primatological Survey; in particular we are indebted to Miss Nancy Muckenhirn for making her observations on leopards available to us and for undertaking a primate survey in the western part of Wilpattu Park. Helpful comments were also forthcoming from Dr. Suzanne Ripley, Dr. Gilbert Manley, and Mr. Wolfgang Dittus.

Useful discussions concerning vegetation and productivity came about through frequent interchange of information with Dr. Marcel Hladik and his wife, Annette, who jointly carried out a survey of productivity in the western part of Wilpattu. Identification of plants and discussions concerning the physiognomic classification of the flora were forthcoming with Dr. Dieter Mueller-Dombois and his assistant, Mr. Ranjit Cooray. To all of these people we are indebted for comradeship, inspiration, guidance, and cooperation; and, although at times there may have been certain points of stress, the results which we are about to jointly present could not have been achieved without the interaction of trained observers.

The research was supported by Grants No. SFC-7-0059 and No. 7428 from the Smithsonian Foreign Currency Program, and Grant No. 258 from the World Wildlife Fund to Drs. Buechner and Eisenberg. Two landrovers were donated by the World Wildlife

Fund and Fauna Preservation Society through the Wildlife Protection Society of Ceylon.

Logistic support while in the field, as well as technical support during the preparation of the manuscript, was provided by the National Zoological Park-Smithsonian Institution. The authors are indebted to the enthusiasm, support, and encouragement provided by Drs. T. H. Reed and H. K. Buechner.

Assistance in the reduction of the primary data to tabular form was performed by Miss J. Block. Preparation of the figures was carried out by G. McKay. McKay also read the entire text and offered useful criticism. The text was prepared by the senior author who spent one hundred twenty-one days in the field engaged in the survey operations. The junior author spent some two hundred and sixty days in Wilpattu and was responsible for the continuing census operations aided by several trackers from the staff of the Ceylon Wildlife Department. The manuscript was typed and edited by Mrs. W. Holden.

The Environment

Physical Description of the Park

Ceylon is located in the northern tropics off the southern tip of India, lying in the main between 5° and 9° N latitude. It is approximately 430 kilometers long and 221 kilometers wide, with an area of some 67,400 square kilometers. Although Ceylon is divisible into a highland, a midland, and a lowland area, the highland area has a peneplane of some 1830 meters elevation, and the major land mass is below 762 meters. Wilpattu Park itself is located in the lowlands. All of the land contained within the park is below 152 meters elevation and the majority of park land is less than 91 meters above sea level. The park and sanctuary are located in the northwest corner of Ceylon. The west boundary of the sanctuary area includes Portugal Bay. The north boundary of the park is set by the Moderagam Aru and the southern boundary by the Kala Oya (see Figure 1).

Several geological considerations are pertinent to an understanding of Wilpattu's ecosystems. The West Sanctuary area is characterized at its western margin by littoral sands with some dune formation which overlays sandstone. The western portion of the park itself is dominated by the so-called Jaffna limestone formations which extend up to the northwestern portion of the island into the Jaffna Peninsula; this extensive limestone bed permits the capillary uptake of water from underground streams and results in extensive depressions formed by a gradual sinking of the land. At such places the soil surface is thin over the limestone and water can percolate to the surface through capillary action, thus forming a small pond or lake with no visible source or external drainage. Such water is often of a permanent nature and such bodies are referred to as "villus." The central portion of the park is dominated by a series of such lakes or ponds which form the major water reservoir through the drought period for the game species. Approximately 24 kilometers from the coast, the rocks change in character from the Jaffna limestones to the so-called Vijayan series which is a complex conglomerate of supercrustal rocks, including crystalline limestone and granitic gneiss. These same rock formations are gen-

FIGURE 1.—Map of Wilpattu National Park showing the major river systems and villus discussed in the text (See also Figures 74, 75, and 76.)

Major villus and water holes

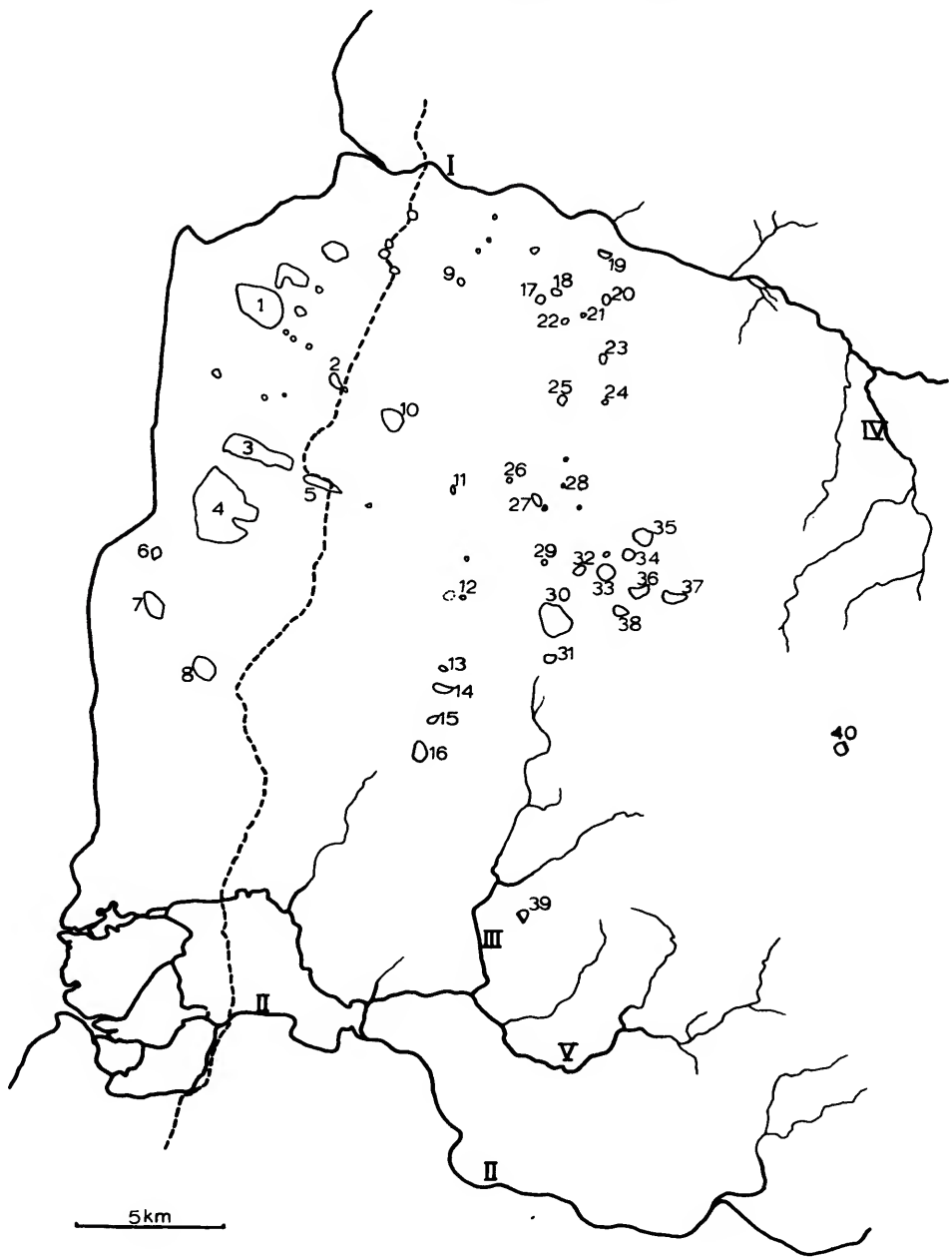
1. Mail
2. Marai
3. Periya Naga
4. Periya
5. Maduru Odai
6. Sinna Uppu
7. Periya Uppu
8. Atha
9. Marikaram
10. Kali
11. Kanjuran
12. Eranapola
13. Allam
14. Pannikar
15. Kombonsanchi Pooval
16. Tala
17. Uduppu
18. Sengapadu
19. Katakandal Kulam
20. Namada
21. Herathamy Wala
22. Katarampu
23. Kara
24. Kaya Motai
25. Mana
26. Kumuttu
27. Manikepola
28. Illande Motai
29. Kuruttu Pandi
30. Kokarre
31. Nelun
32. Kudapatessa
33. Mahapatessa
34. Demata
35. Luna
36. Timpiri
37. Borupan
38. Kumbuk
39. Peddiveli Wewa
40. Maradan Maduwa

Rivers and tributaries

I Moderagam Aru
II Kala Oya
III Denigaha Ella
IV Eerige Ella
V Pan Ella

erally overlain with reddish brown earth (Cooray 1967).

The soils of Wilpattu Park may be considered in a series from west to east. At the extreme edge of the West Sanctuary, the soils are littoral as a result of sand deposition from wave action. After passing the dune barrier and into the first depression, the soils are typically of a saline nature and some of the water



sources here are strongly saline, hence the name Sinna Uppu and Periya Uppu[1] for two of the southern, low villus. The rest of the West Sanctuary is characterized by red-yellow latosols which are slightly acid, low in organic material, and also low in phosphate, calcium, potassium, and magnesium. These are in general very poor soils and support a scrub-type jungle. These soils are intermittently characteristic of the western portion of the park until approximately the level of Mana Villu. From Mana Villu to the east, the soils are more frequently characterized as reddish brown earths. These soils have a rather good fertility being high in phosphorous, calcium, and magnesium. Along the banks of the major river systems and their tributaries, the soil types are characteristically alluvial deposits resulting from upstream erosion.

In areas of former cultivation within the park, especially Mail Villu and Periya Naga, and the series of abandoned tanks along the Moderagam Aru and the Eerige Ella down to Maradan Maduwa, the soils are characteristically clay-type. These clay soils show a rapid uptake of water but very soon dry out in the drought period forming a cracked hexagonal pattern on drying. These former tank areas support mostly scrub vegetation and are prime feeding areas for elephants and other game. For more detailed considerations of soils and their characteristics, the reader is referred to Panabokke 1967.

[1] Sinna=little; Uppu=salt; Periya=large.

Climate

The reconstruction of Wilpattu's climate is based upon the long-term records taken at the station at Pomparippu. The average annual temperature is 27.2°C and the average precipitation is approximately 1,000 millimeters. According to the climate analysis published by Mueller-Dombois and Sirisena (1968) and Mueller-Dombois (1968), the Wilpattu area is generally characterized by two drought periods. There is a brief drought period of variable duration in January and February, followed by moderately heavy rains in March and April with an average peak of 100 millimeters rainfall in March. An extensive drought period then begins in May, lasting through August to the beginning of September. During the height of the drought, rainfall is less than 10 millimeters per month. The major rainy season commences in September, rising to a peak in October, November, and December. During October and November rainfall typically ex-

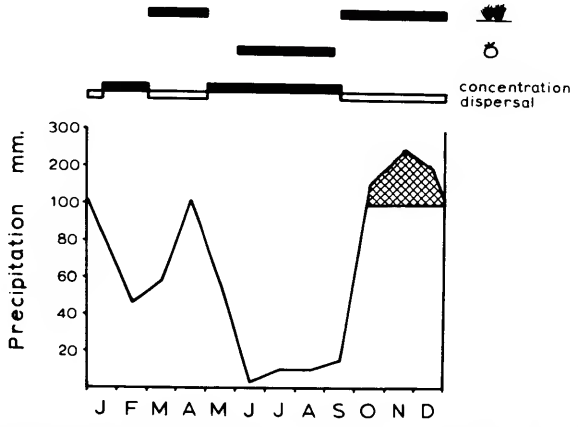


FIGURE 2.—Interrelationship of ungulate habitat utilization, rainfall, and grass growth. Precipitation for 1968-1969 taken from the station at Pomparipu. Dispersal refers to the time when ungulates utilize the grassland in the vicinity of permanent water to the least extent. Concentration refers to increasing utilization of grassland in the vicinity of permanent water by ungulates. Black bars above the concentration dispersion indicator line refer to times of maximal fruit production and new grass growth. The shaded area within the rainfall curve defines the autumnal monsoon period.

ceeds 100 millimeters per month. There is a slight difference between the West Sanctuary area, which is characterized as hot arid lowland tropical, and the easterly portion of the park, which is characterized as hot dry lowland tropical (Fernando 1968).

Figure 2 portrays the average annual flux in rainfall and correlates the appearance of new grass growth with the behavior of the resident ungulate populations. In general, there is a renewal of moderate grass growth during the rains of March and April. During the period of June-July-August, fleshy fruits which fall from the trees are abundant but very little new vegetation growth can be observed. New grass growth commences again in September and persists well into January. During the months of June, July, August, and into September, there is a concentration of the mobile species of game near permanent water sources, either in the villus or on the two major river systems. With the onset of rains in the two periods, October-November-December and March-April, the mobile game species generally disperse into the forest or into seasonal grazing areas, such as those provided by parts of the West Sanctuary. These two factors then, the growth of grass and its control by the onset of rain and the abundance and distribution of permanent water, are the determinants of distribution patterns for the larger ungulate species within the park system.

Flora

The flora of Wilpattu Park may be divided into three categories: (1) the littoral vegetation, including salt grass and low scrub immediately adjacent to the beach sand, rapidly grading into (2) monsoon scrub of a very low stature, which imperceptibly grades into (3) monsoon forest including tall emergents, such as *Manilkara* and *Chloroxylon*. This monsoon forest and monsoon scrub division is discussed in detail by Fernando (1968). The monsoon scrub classification of Fernando roughly corresponds to the vegetation zone A of Gaussen, et al. (1964). Fernando's monsoon forest vegetation type roughly corresponds to Gaussen's vegetation zone B, characterized by *Chloroxylon, Berrya, Vitex,* and *Schleichera.*

For the purposes of our animal census surveys and in an attempt to correlate animal activity with different vegetational types, we adopted the plan of discussing the vegetation in terms of physiognomic or structural types as proposed by Mueller-Dombois. In his published vegetation map of Wilpattu National Park, Mueller-Dombois and Fernando (1970) have divided the park into three ecological zones which are in general in agreement with our own observations. The first zone, or villu zone, has two subtypes: subtype A with perfect vertical drainage and characterized by the underlying Jaffna limestone and the small permanent lakes, and subtype B with locally impeded vertical drainage characterized by low lying masses of water which do not persist throughout the drought period. In general, villu zone subtype B corresponds to the major portion of the West Sanctuary. The third ecological zone is the Ara zone which shows lateral surface drainage and restricted vertical drainage; this includes the borders of the Moderagam Aru and its tributaries, including the Eerige Ella, thus encompassing the eastern portion of the park and the northern boundary.

FIGURE 3.—Typical alluvial forest on the banks of the Moderagam Aru. The prominent Kumbuk (*Terminalia arjuna*) characterizes this vegetation form.

We have employed the same classification of vegetation as proposed by Mueller-Dombois with three major cover types: forest cover, scrub cover, and herbaceous cover types. The forest cover type includes low to medium stature forest and forest scrub islands. The scrub cover type includes vegetation less than two meters in height which may be either discontinuous or clumped. Herbaceous cover types include grasslands, herbs, and forbs, divisible into short grass or tall grass.

Although Mueller-Dombois' vegetation map does not cover the total area of the park which we surveyed, it covers sufficient area to be representative and to characterize the habitat. The sheets include some 54,429 hectares. The Ara zone, including the river systems and their tributaries, comprises 17,894 hectares; the West Sanctuary (villu zone B) 13,005 hectares; and the villu zone A 23,532 hectares. Villu zone A has 96 percent of its area in the forest cover type classification, only .3 percent in scrub cover, 3.1 percent in herbaceous cover, and .6 percent includes open water. Villu zone B, lying in the main in the West Sanctuary includes 89 percent forest cover type, .7 percent scrub cover type, and approximately 10 percent herbaceous cover type, with only .2 percent open water. The Ara zone is 87 percent forested, 9 percent scrub cover, and 3 percent herbaceous cover. Most of the scrub and herbaceous cover types lie in areas of former cultivation or in the flood channel areas periodically scoured when the Moderagam Aru or Kala Oya overflow their banks (Figures 3, 4, and 5).

Although the three major physiognomic categories are useful, it should not be concluded that less than 10 percent of the park supports grasses and forbs. The latter plant forms persist in open forest and open scrub. When one calculates the areas of the park which exhibit discontinuous forest or scrub cover, then 27

FIGURE 4.—Typical short grass and forb carpet surrounding a villu in Wilpattu. The isolated trees are Palu (*Manilkara hexandra*). Low stature forest with emergent trees can be seen in the background. Such a grazing area can be heavily utilized during the drought.

FIGURE 5.—Flood channel area near the Moderagam Aru. Such an area may be flooded during the autumnal rains at irregular intervals. Scrub and scattered herbaceous undergrowth characterize the high ground.

percent of the park supports adequate grasses and forbs for sustained ungulate grazing and only 73 percent of the park is characterized by dense scrub or forest with a minimum of herbaceous undergrowth.

A species list for the dominant plants within each of the physiognomic vegetational classes is included in Appendix B. According to the floristic analyses done by Koelmeyer (1959), the period of maximum fruiting for the low altitude dry zone forests lies between May and August. January to May are poor fruiting months which follow on the autumnal rains; however, at this time flowering is maximal and may provide a food resource for arboreal species. Of course, some tree species may fruit almost throughout the year; a notable example being *Vitex pinnata* which will fruit in January, February, and March, as well as in August through December. Dominant fruit plants that provide a feeding substrate for terrestrial forms at the time of fruit fall include *Chloroxylon swietenia, Schleichera oleosa, Manilkara hexandra, Vitex pinnata,* and *Drypetes sepiaria.*

The Mammalian Fauna

The terrestrial mammalian fauna of Ceylon consists of 109 forms (including subspecies). These 109 forms are distributed in the seven major vegetational zones of Ceylon as defined by Gaussen, et al. (1964). Gaussen's zone A or the lowland dry zone does not exhibit the same level of faunal diversity as that displayed by zone D-1 or the lowland wet zone. Exclusive of the Chiroptera, thirty-two forms are found in the lowland dry zone compared with forty-eight forms for the lowland wet zone. If the Chiroptera are included, there are forty-five recorded forms on the lowland dry zone and seventy for the lowland wet zone. Faunal diversity is also low in the highland wet zone where some twenty-four mammalian forms are recorded exclusive of the Chiroptera and only thirty if the Chiroptera are included.

The mammalian faunal diversity parallels the floral diversity and both are highest in the lowland wet zone; but diversity is inversely related to the numerical density of any one species. Diversity of the Chiroptera and nonvolent forms when considered separately show the same trends. When individual Orders are considered, the following trends are noted. The Insectivora are reduced in diversity to almost virtual absence in drought areas such as the lowland dry zone. The Chiroptera are least favored at high elevations but seasonal aridity has little overall effect except to induce seasonal movement patterns in the bats which utilize the lowland dry zone. The present Artiodactylan diversity is maximum in the more open vegetation zones of the lowland dry areas. Trends in carnivore diversity parallel those of the Artiodactyla. Rodent diversity is favored in the highland wet zone and they make their maximum contribution to faunal diversity there. For other comments, see Eisenberg and McKay 1970.

Table 1 provides a species list of the mammalian fauna noted for Wilpattu National Park. Since collecting was not carried out on any large scale within the park, the species of bats and rodents are imperfectly known for that area, although collection in adjacent areas would indicate that at least a dozen or so species are present in the park itself but not recorded during our reconnaissance (Eisenberg and McKay 1970).

In general, the alluvial forest habitat with its associated dry washes carrying scrub and herbaceous cover are favorable to most of the dominant species within the park. The forest itself can be utilized by the elephants and to some extent by sambar *(Cervus unicolor)*, but the forested habitat over great tracts of Wilpattu Park is certainly not favorable to high numerical density of any one species. Rather the forest margins grading into scrub and open grassland in the West Sanctuary and in the areas bordering the villus and drainage systems within the center of the park are most favorable to faunal diversity and intensive ecological densities. Further discussion of these problems will be taken up in the section titled "Numerical Abundance and Biomass," pages 101-103.

THE ELEPHANT *(Elephas maximus)*

Description and Aging Criteria

The Asiatic elephant, *Elephas maximus*, is the largest terrestrial mammal in Asia. The Ceylon subspecies is the forma typica, *E. maximus maximus* L. (for a discussion of synonomy see Deraniyagala 1955). Adult weights range from 3,950 to approximately 4,000 kilograms and the average height of cows is approximately 2.0 to 2.46 meters. The height of adult bulls ranges between 2.46 to 3.00 meters (Kurt and Nettasinghe 1968). Height increments as a function of age have been treated in the literature by a variety of authors, including Hundley (1934), Rzasnicky (1939), and summarized in Frade (1955). Recently Reuther (1969) has summarized the early growth increments for captive elephants and has suggested that aging criteria for many published accounts could well be in error. Table 2 summarizes our field criteria for average growth increments based in part on the data from the literature cited previously and the data from Kurt and Nettasinghe (1968).

Criteria for Age Classes

The animals are approximately 90 to 95 centimeters in height at birth and increase their height to approximately 130 centimeters by two years of age. At three

TABLE 1.—*Mammalian fauna of Wilpattu**

Species	*Comments*
CHIROPTERA	
Pteropus giganteus	Seasonally abundant
PRIMATES	
Loris tardigradus	Not abundant
Presbytis entellus	Abundant in vicinity of permanent water
Presbytis senex	Moderately abundant in riverine habitat
Macaca sinica	Moderately abundant in riverine habitat
PHOLIDOTA	
Manis crassicaudata	Rare
RODENTIA	
Funambulus palmarum	Abundant in vicinity of permanent water
Ratufa macroura	Abundant in vicinity of permanent water
Hystrix indica	Thinly distributed
Tatera indica	Extremely abundant
Rattus rattus	Abundant in tall forest
Golunda ellioti	In eastern portion of park especially near cultivation
LAGOMORPHA	
Lepus nigricollis	Moderately abundant in scrub and grassland
CARNIVORA	
Canis aureus	Thinly distributed
Melursus ursinus	Thinly distributed
Viverricula indica	Locally abundant near permanent water
Paradoxurus hermaphroditus	Locally abundant near permanent water
Paradoxurus zeylonensis	Near permanent water; rare
Herpestes edwardsii	Thinly distributed
Herpestes fuscus	Locally abundant in northwest
Herpestes smithii	Abundant
Felis rubiginosa	Rare
Felis chaus	Rare
Panthera pardus	The dominant carnivore in the park; estimate less than 20 resident animals
PROBOSCIDEA	
Elephas maximus	Estimated 75 to 80 resident animals
ARTIODACTYLA	
Sus scrofa	Locally abundant
Tragulus meminna	Thinly distributed
Muntiacus muntjac	Locally abundant
Axis axis	Extremely abundant
Cervus unicolor	Moderate distribution
Bubalus bubalis	Moderate distribution

* Species seen or collected. Many species of Rodentia or Chiroptera are undoubtedly present but intensive collecting was not carried out in the park. For comments on distribution and nomenclature, see Eisenberg and McKay, 1970.

TABLE 2.—*Field age criteria for* Elephas maximus

	Adult	*Subadult*	*Juvenile*	*Calf*
MALE	9+yrs	40 mos–9 yrs	14–40 mos	≤14 mos
Height (shoulder)	>2.1 m	>1.5 m≤2.1 m	>1.2 m<1.5 m	.91 m≤1.2 m
Track (circumference)	>119 cm	>76 cm≤119 cm	>61 cm<76 cm	>45 cm≤61 cm
FEMALE	7+yrs	40 mos–7 yrs	14–40 mos	≤14 mos
Height (shoulder)	>1.83 m	>1.5 m≤1.8 m	>1.2 m≤1.5 m	.91 m≤1.2 m
Track (circumference)	>91 cm	>76 cm≤91 cm	>61 cm<76 cm	>45 cm≤61 cm

years of age, the animal may be from 150 to 160 centimeters at the shoulder; at four years of age, most males are between 175 to 190 centimeters at the shoulder. At six years of age, shoulder height may vary between 180 and 200 centimeters; hence, the growth rate is much more rapid than had been previously supposed.

We consider males to be in the subadult category from approximately four to nine years. They are capable of reproduction from six to seven years on but, from the age of approximately eighteen to twenty-four years, they show an increased spurt of growth in shoulder height and begin to consistently show the phenomenon of musth, which first manifests itself at fourteen to fifteen years. This is a transition phase to full adulthood in a sociological sense which extends from approximately fifteen to twenty years of age. We refer to adulthood in terms of sociological age because, although males can reproduce at an earlier age, within a normal herd structure males under eighteen years of age are probably prevented from mating due to their lower dominance position with respect to older cows, as well as being dominated by the fully adult males living in the population. With the preceding discussion in mind, we wish to point out that in censusing we considered males greater than 2.1 meters at the shoulder as "adults"; thus we do not separate males older than nine years into sociologically functional categories.

Females may under the best nutritional conditions come into their first estrus as early as seven years of age (Evans 1910, Seth-Smith 1932). This is in reasonable agreement with age at onset of first reproduction cited by Buss and Smith (1966) for the African genus, *Loxodonta*. Since the gestation is twenty-two months, the age at first parturition for many cows will be approximately nine years. Much variation exists in the literature concerning the age at first estrus in cows and this has been summarized by Dittrich (1967) and reviewed by Kurt (1971).

With these criteria in mind, we established a field age criteria for *Elephas maximus* and employed it in our censusing. Since we included both track data and actually observed data in our tabulations, we include our track criteria as well. According to Kurt and Nettasinghe (1968), a reasonably close relationship exists between the circumference of the track and shoulder height. Table 2 includes the field age criteria for *Elephas maximus* as employed throughout this study.

CRITERIA FOR DISTINGUISHING THE SEXES

After some experience with adult elephants, it is not too difficult to distinguish the sex of the animal even without seeing the external genitalia. The male in general has a broader face and a more bulging nasal bump. Less than 10 percent of the males on Ceylon bear tusks, so the possession of tusks is not an adequate criterion. The male frequently releases his penis from the sheath especially when moving into new areas or crossing from one habitat type into another. The exact significance of this will be speculated on in the section on behavior. Suffice to say that absolute determination of sex can generally be made when the full animal is

in view and moving from, for example, the scrub into the open. Without the protrusion of the penis, the sex of the animal can still be determined since the position of the penis in the male can be noted even when retracted into the body as a distinct bulge from the sheath opening to the anus. Sex determination in animals younger than five years is difficult but not impossible by employing the same genital criteria as for adults. The only problem is that the frequency of penis protrusion in the younger animals, as well as its visibility, is somewhat reduced.

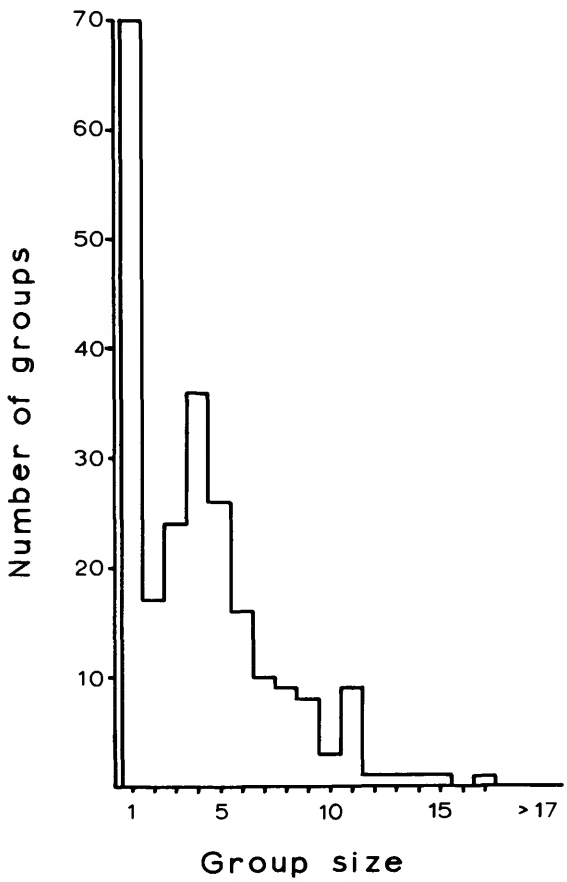


FIGURE 6.—Frequency of sightings for elephant groupings of various sizes. Over 90 percent of all solitary sightings were of adult males. The usual grouping of four or five is a subunit of a larger herd consisting of some eleven to seventeen individuals.

Social Groupings

Some 233 sightings and track determinations were made of elephants in the twelve-month survey at Wilpattu; seventy of these records were of solitary individuals. Almost invariably the solitary individuals are subadult or adult males. The remaining sightings were for the most part groups of females with their young or partially grown young. The most frequent grouping was four individuals recorded thirty-six times. Notations of three and five individuals were recorded twenty-four and twenty-six times, respectively (Figure 6).

In general one can say that the adult males are semisolitary, utilizing a given home range for prolonged periods of time. Shifts in home range utilization by males generally accompany shifts in the availability of water and are determined by the length and severity of the drought period. Figure 7 illustrates the positions of solitary males in the park with home ranges for individuals which were known.

Females and young, including males up to the age of approximately eight to ten years, comprise the majority of the social groupings exceeding two in number. One herd which we consistently observed in this area included eight adult females, three subadults, four juveniles, and two calves. Frequently this herd was split into two subgroups consisting respectively of four adult females, two subadults, one juvenile, and one calf; and four adult females, one subadult, two juveniles, and one calf. A second herd utilizing this same area consisted of seven adult females, three subadults, two juveniles, and one calf. Within this same study area were four adult males and four subadult males; thus giving a total population of thirty-eight animals, three of which were calves less than one year old. It is not uncommon for the individuals comprising a given herd to split up in order to feed in groups of three to five. In general the female with a small calf will be accompanied by at least one other female; hence, the groups of females having the smallest calf in it will generally be the larger groups.

Subadult animals are prone to be more individualistic, to wander in pairs or, in the case of young males, in a solitary fashion. The total herd will assemble in order to drink or graze at choice sites, coming together in the early part of the evening and perhaps remaining together for several hours before once again dividing into subgroups. The maximum extended herd size counted in Wilpattu Park consisted of seventeen ani-

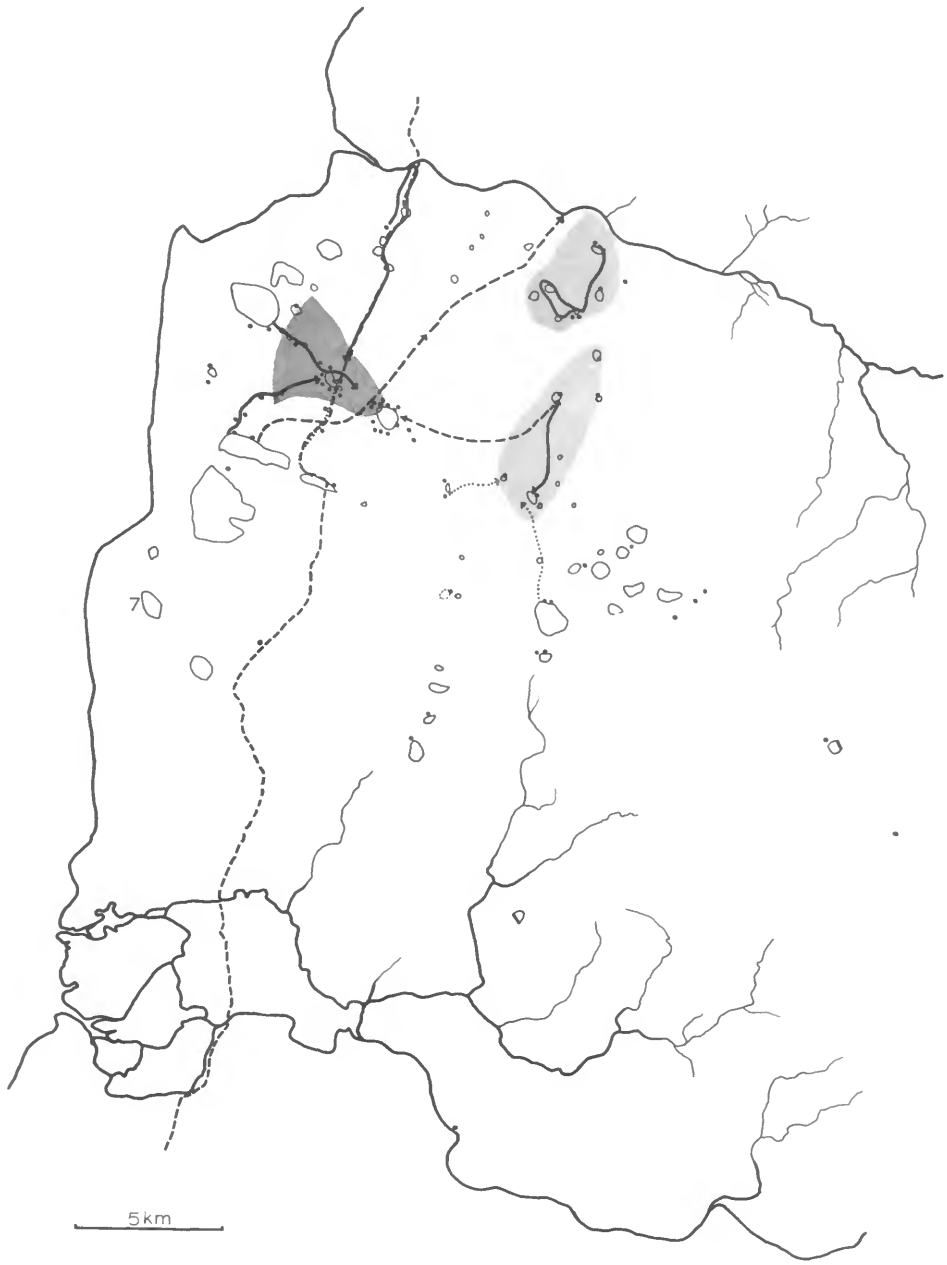


FIGURE 7.—Locations where adult male elephants were sighted throughout the annual cycle. Black dots=individual males; shading=home ranges for three known males; dashed lines=movements for known males during dry seasons; solid lines indicate movements during the rains. Dotted lines=movements of males whose ranges were imperfectly known. Except for the excursions, the ranges of adult males remained remarkably constant for the better part of the year.

FIGURE 8.—Distribution of cow herd activity in Wilpattu Park during the rainy season. Heaviness of shading indicates relative intensity of habitat utilization; lines and arrows indicate movements of individual herds at the onset of rains. The solid black lines indicate the movement cycle of the "villu herd" (see Figure 9) during a two-month period (November-December 1968).

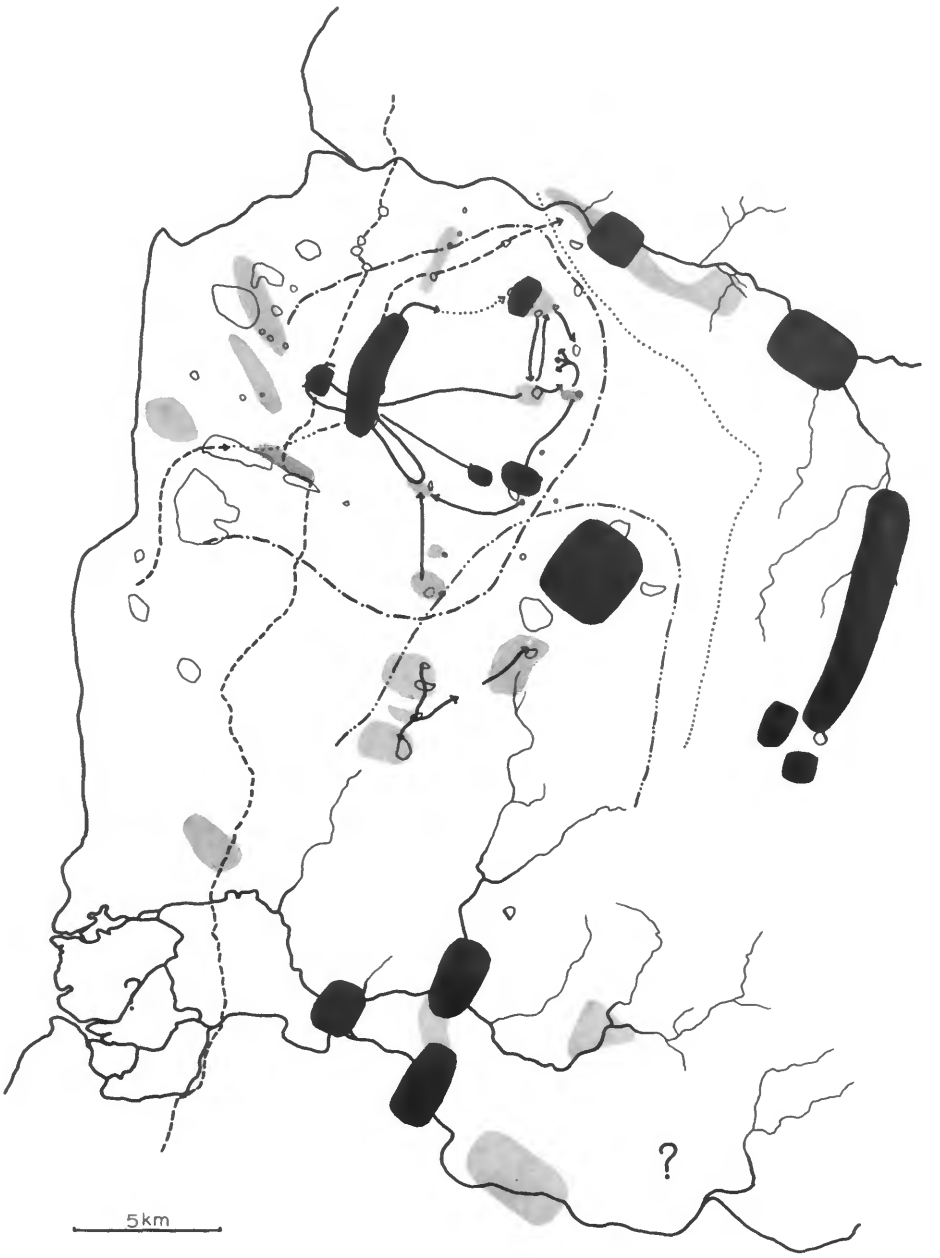


FIGURE 9.—Distribution, intensity of activity, and movement patterns of cow herds during the drought season. Compare with Figure 8. Movements at the onset of the drought to areas of permanent water are indicated and the ranges of three separate cow herds are delineated with dashed and dotted lines for the duration of the June-August drought. In general the cow herds maintained a separate habitat utilization pattern in contrast to the more extensive range overlap illustrated in Figure 8 during the rainy season. Question mark designates total extent of range undetermined.

mals; however, at least four adult and two subadult males were associated off and on with this herd, thus raising the total count for the extended "villu herd" to twenty-three animals. Other large groupings composed of the smaller subunits included sizes of eleven animals nine times and one sighting each for herds of twelve, thirteen, fourteen, fifteen, and seventeen. The latter series really represents sightings of the same maximum group of seventeen broken into various fractions with the absence of from two to five animals. In March of 1970 two herds (the west herd and the villu herd) assembled jointly at Mail Villu, but such an aggregation of over thirty animals is only temporary.

Essentially the most permanent social grouping appears to be related to cows and their offspring. This social structure is virtually identical to the herds described for the African elephant by Laws and Parker (1968).

Distribution in the Park

Figures 8 and 9 indicate the distribution of elephants within the park for the two rainy periods and the dry season. As can be seen, as the drought proceeds, the animals aggregate either in the center of the park including the freshwater villus or near the banks of the two permanent rivers, i.e., the Moderagam Aru and Kala Oya. There is a pronounced shift at the onset of rains to feeding activity in the West Sanctuary. This includes movements of herds from the Kala Oya as well as movements from herds that have been utilizing the central villus to the West Sanctuary. The bulls move widely at the onset of rains, dispersing from areas of concentration, and returning to more stable home ranges (Figure 7).

Movements within the park may be considered from two standpoints. The extent of movement is dependent on the available forage and the location and size of the water hole. When small water holes are visited with very little grassland in the near surroundings, the herd may spend only one evening, or at the most two, moving on to a neighboring water hole at a distance of approximately 4.8 kilometers. Thus, there is a shifting or rotation from one small water hole to the next. This is a characteristic movement pattern during the drought period; however, at the onset of rains, when the vast expanses of low lying areas are inundated in the West Sanctuary and grass growth is encouraged, herds may remain in the vicinity of these water holes for a week at a time before shifting. Nevertheless, the pattern is for utilization at one locus and re-utilization at a new locus after a period of several days. The duration of the stay at any one given water hole is determined in part by availability of water, grasses, and the amount of disturbance to the elephants.

Seasonal movements in the western part of Wilpattu involve major shifts in the intensity of utilization from the villu area to the large temporary villus which support a luxuriant grass growth during October through January. Figure 10 illustrates the frequency of movement across the Mannar Road during the shift from the drought period to the rainy season and back during the short drought from January through March. As can be seen there is a pronounced seasonal shift in frequency of movement by individual elephants across the Mannar Road.

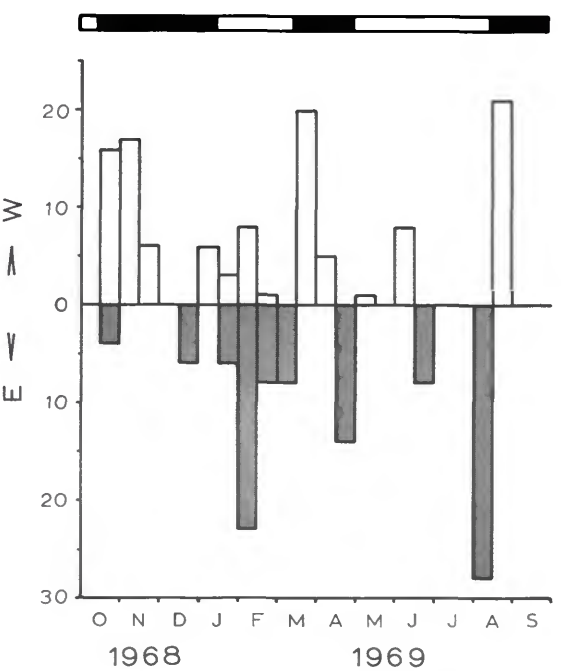


FIGURE 10.—Movement across the Manar Road for the drought and rainy seasons. At the onset of the rains, movement to the west increases; movement to the east, or villu area, increases at the onset of the drought, through both periods of rainfall and drought in the annual cycle of Wilpattu. Stretch of road surveyed was from Moderagam Aru to Maduru Odai. Black areas in bar above graph indicate periods of rainfall. Ordinate indicates number of animals crossing for each fortnight.

There are no long-range migrations on the part of the park elephants, at least with respect to the cow herds. The longest movement by any single bull recorded was slightly in excess of 24 kilometers. The longest single linear movement by any cow herd was slightly under 6 kilometers. Rather, with respect to the cow herds, one can see from Figure 9 that there is a constant shift in the intensity of habitat utilization and even during the drought period the western feeding areas are sometimes visited by the cow herds, but they do not remain for long at one locus. The onset of rain and sustained rain seems to synchronize the assembling of the cow herds in the West Sanctuary area.

Habitat Utilization

The animals appear to drink at least once a day. Generally clear, nonsaline water is taken. Those villus that exhibit a pronounced salinity, such as Kokarre Villu, Luna Villu, Sinna Uppu, and Periya Uppu, do not show evidence of being utilized by elephants for drinking, although the animals may graze in the vicinity of these villus. Drinking behavior during daylight hours is generally brief. If the animals are quite calm, they may engage in bathing but, if they are in any way disturbed, the drinking will be furtive and swift. Sporting in the water, spraying, and bathing generally take place in the latter part of the evening or during the hours of darkness. Example from field notes:

> 11 September 1968, 1810 hours. Three elephants emerged on the west side of Kali Villu, two females and one juvenile. After remaining in the fringing forest, they moved down to drink at 1814; they drank for four minutes without interruption and then stood until 1825. The juvenile sprayed the smaller of the two females. We departed before the elephants.

When river beds are dry, it is not uncommon for the elephants to dig by kicking forward and backward with their forefeet and subsequently removing sand from the riverbed with their trunk thus creating a small depression into which the groundwater will seep. Example from field notes taken in Ruhunu Park:

> The Menik Ganga is dry. We went into the river bed and observed where an elephant had dug a hole and water had seeped up. Later that same afternoon, we observed an elephant come to the pool to drink [see Figure 11].

Feeding is typically carried out throughout the day and night. Exact rhythm of feeding activity is treated in analyses by McKay (1971) and Kurt (1971).

In utilizing trees as a food resource, the animals can reach a height of approximately 3½ to 4 meters. The animal will approach a tree, orientate toward a branch overhead, and then extend his trunk to reach directly overhead toward the branch. It can grasp the branch tip and exert a twist and pull to snap merely the tip of the branch off without breaking the whole branch.

The animal can snap the branch by exerting two different stresses on it with its trunk. Curling its trunk around the branch and pushing down with its trunk tip the branch is braced against the rest of its trunk which exerts an upward pressure. In this manner, the elephant can effectively break off the terminal portion of branches. Leaves may be stripped off the branches themselves. Stripping involves holding the branch stationary with the foot while sliding the trunk and exerting slight pressure along the length of the branch. The leaves can be retained in the trunk and, by rolling the trunk up and down, a small bolus can be formed. The coiling and uncoiling movement results in pressing the leaves into a ball, which is then inserted into the mouth. Bark can be removed from branches by inserting the branch into the mouth and rolling it against the molars. Larger branches may be broken off and split into thinner lengths for mastication and then be discarded. Splitting of larger branches is generally accomplished by employing the forefoot or, if the animal has tushes or tusks, the branch may be brought into close proximity with the tush or tusk tip. Utilizing the trunk musculature and exerting pressure against the tusk tip, splitting can be effected.

The Use of Tall Grass Villus

Here follows a description of elephant use at Atha Villu made on 21 December 1968:

> Elephants have fed here about three days ago for an extended period of three to four days. There is an area of free water where drinking takes place and there are at least three different points on the tall grass villu that show where the elephants have fed on three different occasions, probably on successive nights. About 10 to 30 percent of the new grass is cropped in the first of these areas. Wherever the elephants have gone into the water, the villu grass is stomped down and disturbed. I estimate one area of feeding is 48 hours old, one 36 hours old, and the other greater than 72 hours. There is a calf track associated with the herd that is less than 15.3 cm in diameter. Grazing activity is spotty and not necessarily consistent. In the vicinity of this water hole there are several trees with permanent leans from animals rubbing against them, showing that these trees have been habitually used for rubbing for many years. I note that some of the tall grass is

torn up by the elephants and dropped, being not eaten. This all appears to be of the same species. The *Cymbopogon* is fed on heavily. There are at least two types of grasses, with the *Cymbopogon* and the tall grass growing on higher ground. Perhaps one-fifth of the prime grasses have been already fed upon and suffered some physical damage from the elephants' feet.

Short Grass Feeding

Where the herbaceous cover is extremely short, including not only short grasses but also a variety of forbs, the animals employ the forefeet to scrape or scuff the grass from the substrate. Here follows a description of a cow herd made on 31 January 1969:

All animals feeding are scraping grass with the forefeet. Clouds of dust are raised on the plains by the sustained effort of several elephants. The grass scraping includes scuffing with the forelegs. The motion is slightly idiosyncratic, that is, the stroke may be forward and backward, or to one side. This appears to vary from individual to individual. As grass is scuffed up, the trunk is employed to gather it into a pile which gradually increases in size in front of the animal. The temporal patterning of this activity is (given 40 seconds total time): scuffing for approximately 10 seconds, gathering 3 seconds, scuffing 5 seconds, gathering 3 seconds, scuffing 15 seconds. The complex gathering movement includes not only bringing the grass together into a pile but seizing it in the trunk and then stroking it on the leg to remove the earth. When the pile is of sufficient size, it is seized in the trunk and rolled up and down the outer face of the leg. The earth is thus thoroughly scraped before it is inserted in the mouth. Only after this earth removal is the grass inserted into the mouth. When adults feed in this fashion, they are spaced out at anywhere from 9.1 to 91 meters. Young calves may take food from an adult's pile but juveniles may be kicked if they approach too near an older animal's food pile. [Figure 12.]

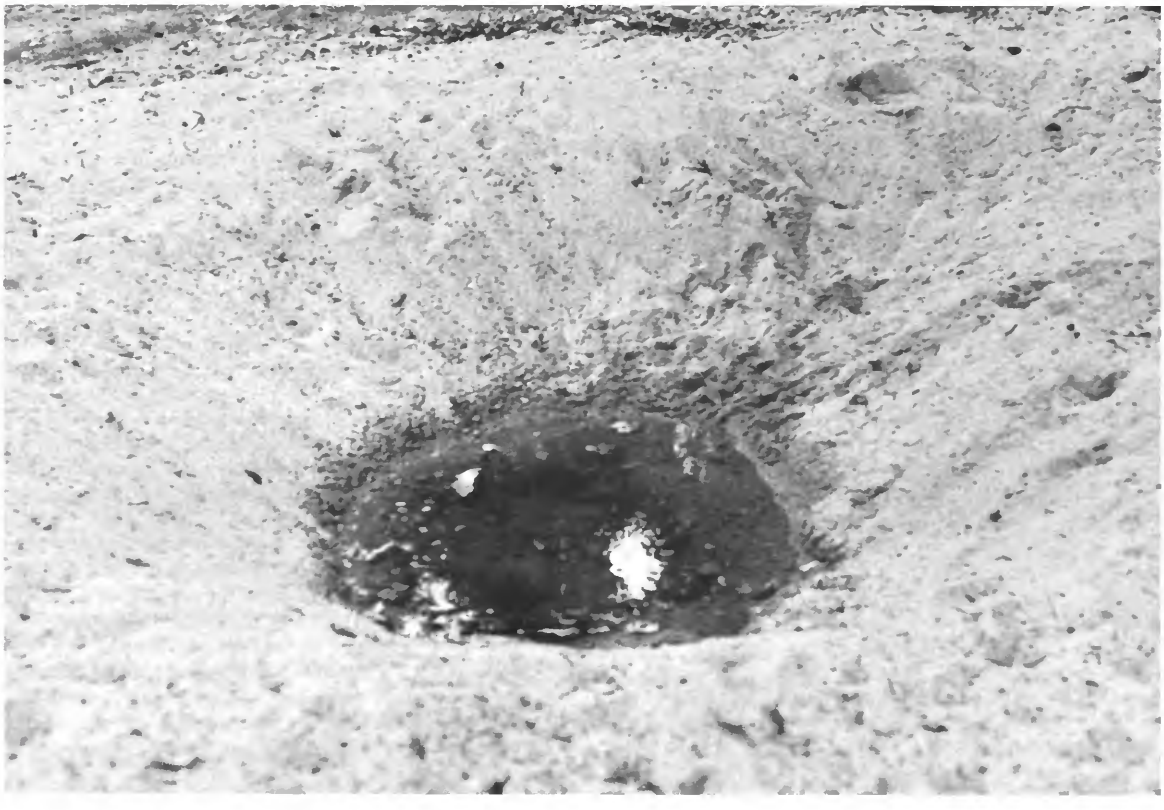


Figure 11.—Hole dug in dry river bed by elephant seeking water.

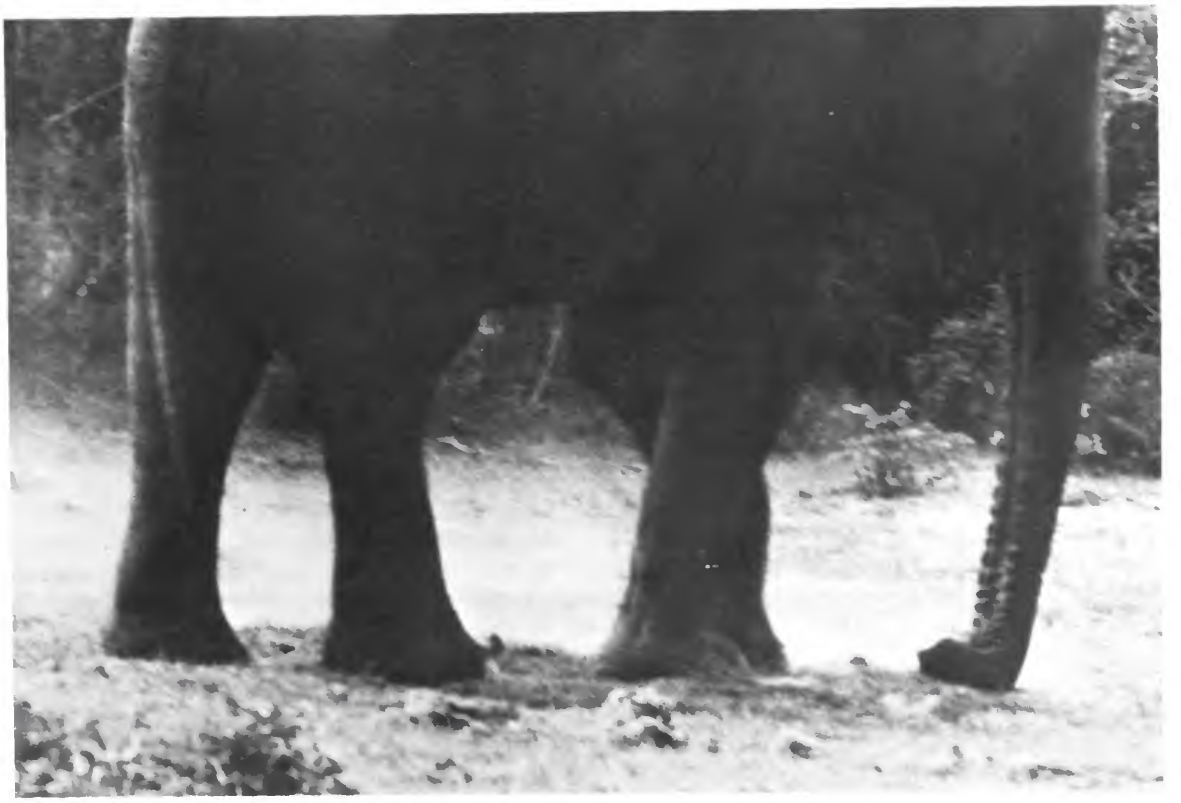


FIGURE 12.—Elephant scuffing short grass, creating bare areas of earth during the height of the drought.

TRAIL UTILIZATION DURING A LONG MARCH

Here follows an account of an elephant herd's activities on a march from the night of 19 to 20 October 1968:

We noted where an elephant march had begun from Kali Villu in the general direction of Mannar Road. After passing down the road from Kali Villu for about 2 kilometers, we noted that twelve elephants had crossed since 1700 hours yesterday. We began back-tracking on the herd of twelve toward Kali Villu. The following comments are noteworthy. The dung passed by the animals on the march has already been destroyed in part by the scarab beetles. The whole trail length exceeded 4 kilometers; thirty-three dung piles had been deposited during that time which would mean two defecations per animal during the march. On the trail itself, after 35 meters, we came to a digging spot where the whole herd had apparently gathered and engaged in dust-bathing before proceeding to cross the Mannar Road itself. The total number of branches broken along the trail included eight. The number of scuffiings with feeding areas included only one. One rubbing tree showed recent use and only one sandy spot showed recent use. The group had moved in a direct fashion with adults leading and subadults following. There was very little indication of feeding other than noted above. The animals stopped to defecate and mill about three times on the trail, always at forks in the trail.

Returning to the Mannar Road junction, we then proceeded to follow the elephants toward their ultimate destination which was Periya Naga Villu. The total length of this portion of the trail was slightly in excess of 1.6 kilometers. There was one trampled spot where perhaps the calf had rested while the herd milled around. Immediately adjacent to the open area of grass surrounding Periya Naga Villu, three rubbing trees had been used during the march and there was hardly any evidence of feeding. The elephant trail itself may be only 41 to 46 centimeters wide in spots. They step one foot in the other track so that a 61 centimeter wide area of bare earth is the only indication of the trail; but the

trees are set back far enough so that the animals can slide through easily, although the hanging creepers give an impression that the trail is almost impenetrable.

Tree-Pushing Behavior

Trees may be pushed down or broken off at the base by employing the forehead, shoulder, or one forefoot and the trunk, depending on the diameter of the tree itself. Tree breaking was noticeable during the height of the drought and may be related to obtaining access to branches which for the young juveniles are out of reach. In addition to pushing over trees for obtaining branches for feeding or to expose roots for chewing on, the males engage in tree-pushing behavior that seems to be unrelated to feeding at all. At Marai Villu we had a tuskless male elephant visiting us on a regular basis. In October he pushed down a 7-meter tree about 92 meters south of Marai Villu on the Mannar Road. Thereafter we kept a record of his tree-pushing behavior. On 13 February 1969, the sketch reproduced in Figure 13 was made. This indicates that the male tended to push trees down at interfaces between trees and grassland or in what looks to be a new rest area that he was creating immediately to the east of our camp. This is indicative of route stereotypy since the old male used the same path over and over again, and furthermore he tended to show the same activities at the same places.

In Figure 13, we have indicated a tree A that was knocked over in October 1968; a tree B in November 1968; a tree next to tree A pushed over in November; and another tree near tree A pushed over in January 1969. These trees are C and D, respectively. Tree E was knocked over in December 1968 and tree F in early January 1969. All of these trees were pushed over by a single animal throughout the time period indicated. Very little feeding was evident on these fallen trees and the reason for this is not at all clear. We have other cases of tree pushing where an animal had eaten a piece of root and a second case where one branch had been taken and fed upon. Most often this tree pushing by males involves no feeding whatsoever.

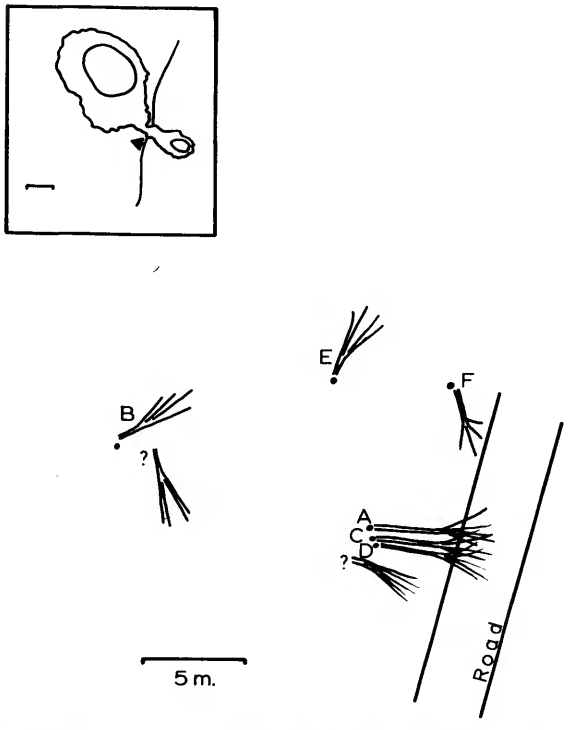


Figure 13.—Trees pushed over by adult male in the vicinity of Marai Villu (see text for discussion). Inset shows study plot location at the edge of Mannar Road and outline of Marai Villu.

Description of River-Crossings

In an area extending 1.2 kilometers along the course of the Moderagam Aru we found three elephant crossings. Each crossing point is characterized by having a low gentle bank. The terrain is fairly open with no dense cover and the water is reasonably shallow. At one crossing a low branch on a Kumbuk tree of approximately 1.8 meters above the ground showed two tush gouges on the branch.

Elephant Sign in the Habitat

Typical sign around a water hole is rather easy to note. If the soil is sandy or moist clay, the tracks are evident; the fecal piles are quite distinctive (Figure 14). Elephant males possessing tushes or tusks will scarify the bark of trees. These tush marks may range anywhere from 20 to 30 centimeters apart. They are about 1.8 to 2.1 meters above the ground level depending upon the height of the elephant. The animal bears its weight against the tree and leaves two gouges and very often sap runs out of the gashes (Figure 15).

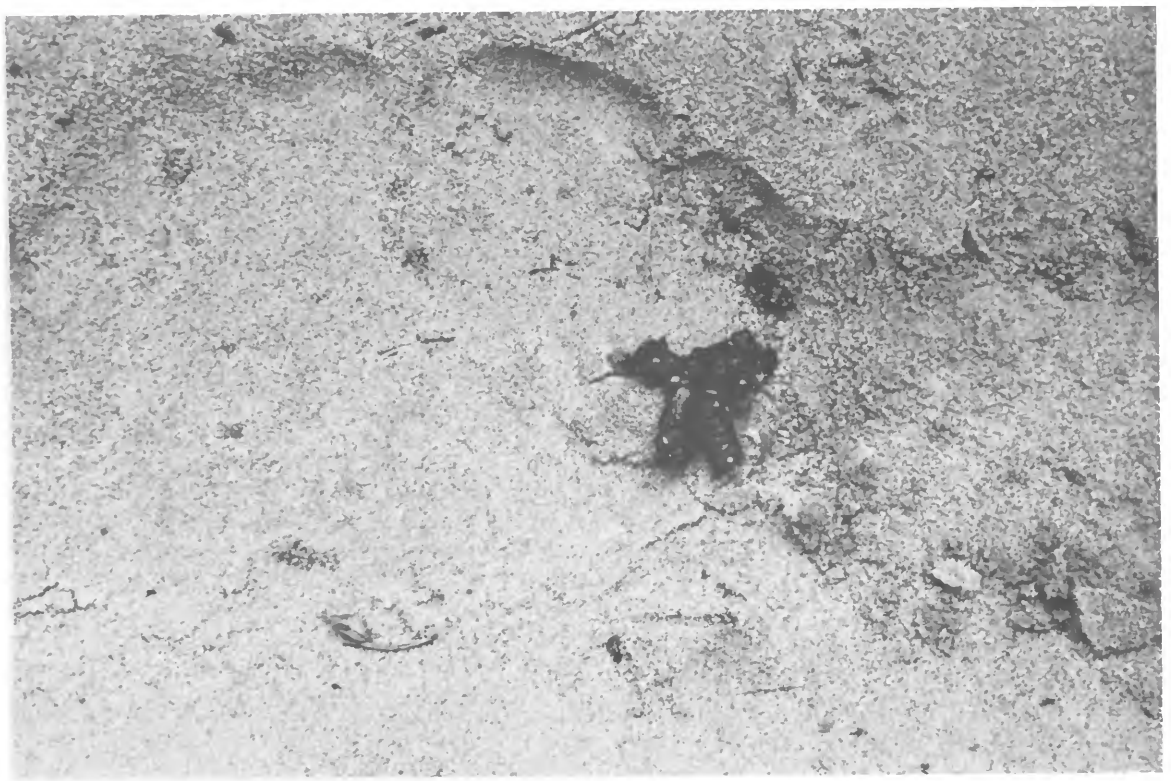


FIGURE 14.—Elephant track. The pile of feces in the track was deposited by a civet, *Viverricula indica*.

Branches that have been twisted off and partly debarked are characteristic of elephant feeding activity. If they are not debarked, the branches are often defoliated. Mud is often rubbed on trees from the sides of the animals or on fallen logs. The inference is that the animals stand over and straddle the logs to rub their bellies. Elephants will scarify the earth by kicking it either to obtain dust for throwing on their backs, or kicking it to loosen short grass during short-grass feeding (see p. 19). Well-used rubbing trees may show tush marks or gouges and rubbing spots on the bowl and on the branches where they start to emerge from the bowl of the tree. The highest point of rubbing spots is usually from 1.8 to 2.3 meters above the ground .

Male elephants may be prone to mud-bathe even during broad daylight. Generally, these mud holes are shallow and small. They may be on the edge of a larger body of water or may be located at some distance away (Figure 16).

Concluding Remarks on Habitat Utilization

The elephant has the highest reach of any terrestrial mammal in the Indian subcontinent. As a result, it can utilize both forested and scrub land vegetation as well as the grasses. A habitat survey in Wilpattu Park executed in September revealed that areas of grassland, mixed scrub and grass, and even dense scrub were heavily used by elephants for foraging. No sample plot showed the absence of elephant feeding; however, the forest plots showed the least intense feeding by elephant herds. This would indicate two features: First, that the elephant is able to utilize a wide variety of habitats within the park but, on the other hand, the

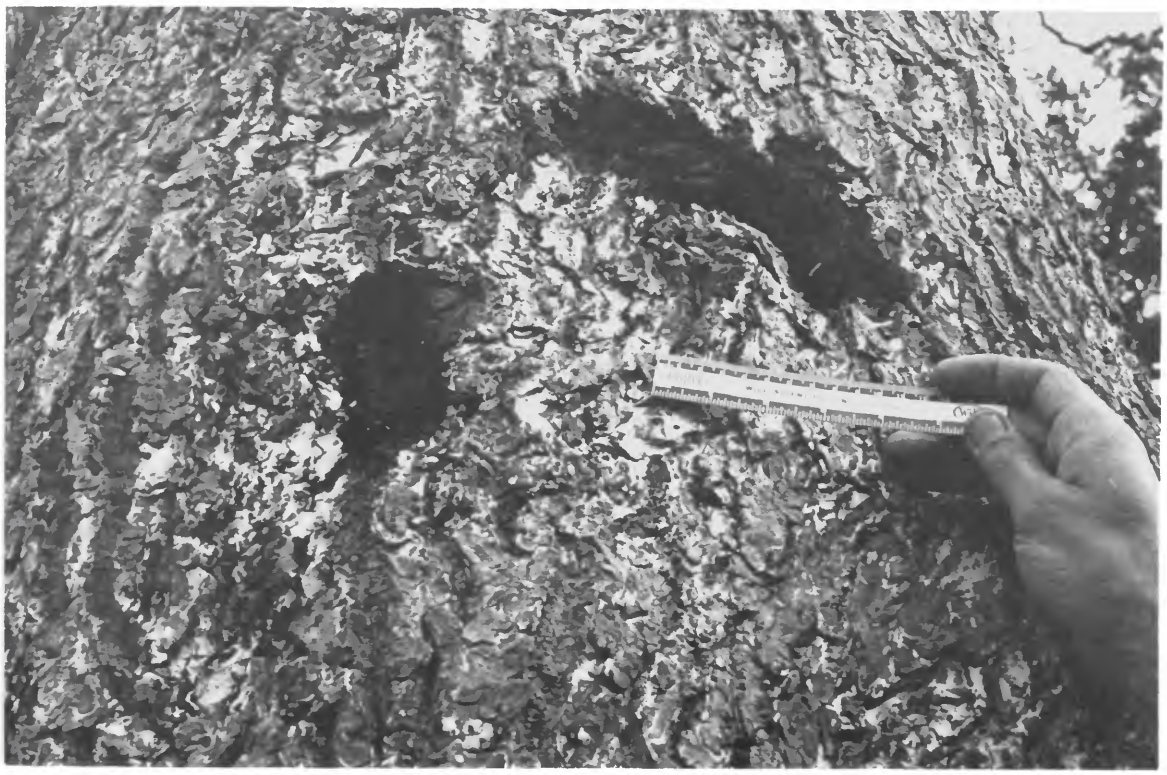


FIGURE 15.—Tush marks on tree trunk at approximately 2.3 meters above the ground.

feeding of cow herds and bulls is favored in the mixed scrub grassland areas when these vegetation forms are compared with the forest (Figure 70).

Summary of Elephant Behavior Patterns

ACTIVITY

The elephants in Wilpattu are quite secretive and shy, coming out in the open to graze or bathe in the afternoon or at night. A great deal of long range movement is also carried out nocturnally. Feeding is intermittent throughout the 24-hour period; in excess of sixteen hours are spent in feeding activities. Branch feeding or feeding on apical tips of shrubs is generally carried out during the daylight hours when the animal can be partially concealed. Tall grass feeding, as well as short grass scuffing, is almost invariably carried out in the early evening or through the dark hours. Drinking is typically an activity of the early evening and just before daybreak; however, during the drought season, it is not uncommon even for cow herds to venture into the open at noon for water.

PATTERNS OF SOCIAL INTERACTION

Communication or the transfer of information from one elephant to another is generally accomplished utilizing all the major sensory modalities. The sounds produced by elephants are employed in a variety of contexts and are rough indicators of the elephant's mood and intent. A long drawn-out, undulating roar is produced for distance communication between two elephants or among individuals of two separate herds. This apparently can serve to bring animals into the same location and perhaps can also serve to maintain

FIGURE 16.—Male elephant lying in small mud hole at mid-day.

spacing when two herds are very close to one another and are not attempting to unite. Calves produce a roaring bawl when separated from their mothers which apparently serves a similar function in maintaining vocal contact and promoting an encounter for reuniting two separated individuals. When frightened, elephant calves will squeal, and the adults when frightened will generally trumpet shrilly and sharply. An aggressively motivated animal will give a low trumpet blast that is quite different in tonal qualities from a frightened one.

Tactile communication is employed when two individuals come together. Females generally touch males in the vicinity of the temporal gland, with both sexes touching in the vicinity of the genitalia. Touching in the vicinity of the mouth or mutual mouth touching is a frequent greeting ceremony.

The role of olfaction during tactile communication is only partly understood. Certainly piles of feces, as well as urine spots, are frequently sniffed and, during mutual contact at genital orifices or the mouth, olfactory signals may play a role in information exchange.

Visual communication appears to be involved to a limited extent. Dominant animals stand quite tall with the head up; subordinates typically turn away and lower the head. [A more detailed analysis of elephant communication is included in the publication by Eisenberg, McKay, and Jainudeen 1971.]

BEHAVIOR DURING AGONISTIC ENCOUNTERS

When an elephant is aroused by an alien stimulus, such as the odor of man, it may exhibit a variety of ambivalent behaviors, which include standing and orientating toward the danger source, trumpeting, flapping of ears, or touching its own temporal gland, especially if it is

a male. Redirected activity, such as directing aggression toward the environment by tearing off a branch and perhaps throwing it into the air is shown in thwarting contexts. Similarly displacement behavior, such as scuffing sand with its feet, picking sand up in its trunk and throwing it on its back may be demonstrated by ambivalent individuals. Such ambivalent behaviors can alternate with alert or attentive behavior toward the source of irritation. This involves spreading the ears while extending the trunk and scenting in the direction of the danger source. Depending on the strength and quality of the alien stimulus, the elephant can show flight behavior. Typically during flight, the elephant will turn and while trumpeting shrilly, begin to walk rapidly away with the tail up and the trunk partially coiled. Aggressive behavior is often accompanied by a low trumpet blast while rushing toward the offending object. The trunk may be partially curled as it approaches and just preceding contact with the offending object the trunk is frequently curled tightly out of danger. The attacked object will generally be kicked with the forefoot. We have observed such behavior with respect to jackals and pigs.

Antipredator Behavior

Naturally the flight behavior or attack behavior may be shown toward potential predators or unknown stimuli in the environment; however, a herd can take unified action by forming a "cluster." In the formation of a cluster, the adults will turn toward the source of danger either scenting or threatening while the younger animals align themselves either between two adults or behind the adults. If the source of disturbance can-

FIGURE 17.—Cluster or star pattern assumed by cow group, juveniles, and calves when threatened by an alien stimulus. The older female is preparing to advance.

not be localized, the adults may even form a star pattern with the youngsters in between them or in the center (Figure 17). Young animals attempting to pass an adult will be restrained by the trunk. Two examples are quoted:

Seventeen elephants are being observed on 11 March 1969 at Mana Villu. At 1800 hours only 14 animals were in sight. A low rumble preparatory to moving into the forest was emitted by an adult female. At 1815, two adult females, two subadults, and three juveniles were still feeding in the water. At 1820, a jeep came by on the nearby trail causing all the animals to wheel and withdraw from the water. Some of the cows emitted a low growl. They immediately turned toward the oncoming jeep and formed into a cluster with the adults facing outward and the small juveniles behind them or between them. As the jeep passed, they then turned in a synchronous movement and moved away with the juveniles still between the adults. They entered the edge of the forest, paused, turned to the jeep again, picked up sand and tossed it on their backs; then after a few minutes continued to move into the brush. A low growl was uttered again.

On 1 February 1969 the following notes were made:

About 183 meters away from the main herd, a small subgroup of elephants was gathered near a water hole. The oldest cow was up wind. Behind her is a class 6[2] male, then a male approximately 1.2 meters high, then a very small calf approximately .92 meters high; 27.4 meters away are three adult females, one with a calf and a satellite subadult; two more animals are in the brush nearby less than 13.7 meters away and are only partially visible. A crocodile resting near the water hole suddenly moves causing the younger animals to become frightened. They immediately turned toward and moved rapidly in the direction of the class 6 male. The male himself started to turn away; however, there were no large elephants in the immediate vicinity, so he wheeled and oriented toward the crocodile while the youngsters aggregated around him.

As a generalization, animals from 1.5 meters at the shoulder on down tend to move near the largest elephant in the immediate vicinity. In the previous case the 1.8-meter male turned but, upon seeing he was alone, he then faced the source of potential danger and stood. Thus, he served as the nucleus for a cluster or star formation. There is a moment of turning and milling before the pattern is set. The large male also reached out with his trunk and held back a younger animal from straying forward. This restraining movement may spring from the tendency to react negatively to any disturbing stimulus or slight stimulus contrast to either side of the body when the attention is directed forward.

[2] Class 6 refers to estimated height (in feet) at shoulder and the term "class" is occasionally employed in this sense throughout the text.

Female-Young Relationships

The mother of a calf and, indeed, all adult females appear to be rather solicitous of the young animal. Females will guide the movements of their calves by urging them to move ahead of them with the trunk; they will restrain the movements of a calf when the female is attentive to potential danger by holding the calf back or pushing the calf to one side with the trunk. Adults will interpose their body between the youngster and a source of potential danger. Often when a road is to be crossed, an adult female will lead, the calves will follow in the middle, and another adult female or male will bring up the rear (Figure 18).

"Nursery behavior" is quite common in the elephant. It would appear that when a calf gets beyond six months of age it is prone to stray from its mother's side and to be especially attracted to other calves of approximately the same age class or slightly older; thus, play groups will form. In general a female who loses her calf when it strays to a play group will take little note of this and move on feeding independently. On the other hand, a female will not desert calves deliberately and any adult or adults that happen to be in the vicinity of the nursery group will remain with it until an opportunity is provided for feeding on their own. As a "nursery" female feeds and, as she tends to move away from the nursery group, some of the younger animals will attempt to keep up with her thus maintaining the integrity of the "nursery." There appears to be a reciprocity in the formation of the nursery unit in part resulting from the attractiveness of young animals to each other and an attractiveness for a large adult. At the same time, there is some reluctance on the part of the adult to stray from the vicinity of the play group. Voluntary joining on the part of a youngster, however, does not necessarily involve a movement of the mother to the play group. Any adult female will respond to the distress cry of a calf by approaching rapidly and in a threatening manner toward the source of danger.

Sexual Behavior

The sexual behavior patterns of the elephant have been outlined in detail in another publication (Eisen-

FIGURE 18.—Elephant group crossing the Kala Oya. The male with tusks brought up the rear. Crossing in and out of the park on the north and south bounding rivers is extremely common.

berg, McKay, and Jainudeen 1971). The stable unit of social organization within an elephant population appears to be a group of related females and their progeny. The leadership role of such a herd belongs to an old cow. From time to time cow herds come together in traditionally preferred feeding grounds to form larger aggregates of 70 to 100 animals. This interpretation of social organization is compatible with the extensive data for the African elephant (*Loxodonta africana*) presented by Laws and Parker (1968.)

Young males remain with the cow herd until the onset of puberty when they begin to contest for dominance status with the older cows in the herd. At this time the young males are generally prone to wander, remaining in the periphery of the cow herd or attaching themselves temporarily to solitary, older males. Eventually the maturing male establishes a home range which he uses in conjunction with other males, but they may regulate their behavior so that definite preferences for specific male companions are favored. A mature male passes through a period of increased aggressiveness about once or twice a year. This condition termed "musth" is characterized by an increased secretory activity by the temporal glands and at this time they are impelled to join and remain with the cow herds. In the domestic elephant population, musth frequency shows two peaks both coinciding with the lowland wet zone monsoon peaks to which the domestic population is subjected (Eisenberg, McKay, and Jainudeen 1971, Jayasinghe and Jainudeen 1970).

The period of musth appears to aid the male in

overcoming the aggressiveness of the older herd cows while at the same time the musth bull can generally dominate other non-musth bulls in the same area. Although a bull can breed whether in musth or out of musth the condition of musth is clearly related to the male's ability to achieve a high dominance status on an annual basis. Gradually through the years a given bull may establish a relationship of familiarity with specific cow herds and a definite position of dominance within the population of males. The periodicity of musth as it occurs in the domestic population tends to lead us to believe that the same increased frequency of musth may be shown in the wild population; however, our data are too sparse to permit this generalization. If, however, wild males tended to come into musth during the rainy reason, we would anticipate that a birth peak would be shown on the average a month or so before the onset of the rains.

Cows come into estrus once every twenty-four to twenty-eight days. The period of attractiveness to the male lasts some four to five days. Peak receptivity on the part of the female and presumptive ovulation occur during the last two days of estrus. Details on the estrous cycle and determination of estrus in domestic elephants is included in the publication by Eisenberg, McKay, and Jainudeen (1971).

Mating behavior involves the establishment of a contact relationship between a cow and a bull. Continuous courting by the bull persists until the peak of receptivity on the part of the female when she will tolerate being mounted. Thus, several bulls may be in attendance on a cow herd at the time that a given female or females are coming into heat. A male may mount a female several times within the course of two or three hours. Mount duration is less than half a minute; intromission time is less than ten seconds. Several males may make attempts to mate with the same cow over a three- or four-day period; however, during her period of maximal receptivity it may well be that a dominant male in the vicinity has precedence in mating with the female (Kurt 1971).

Behavior Patterns of Different Age and Sex Classes

From birth until approximately four years of age, the calf elephant shows very little role differentiation in its behavior. At approximately four years of age, young males can begin to manifest a more independent habit of movement, showing less cohesion and attachment to the cow herd itself. At the age of six to seven years, the female elephant in areas of adequate nutrition may experience her first estrus and, if she conceives during this interval, she can have her calf as early as nine years of age. Young males begin to show incipient sexual behavior from the age of approximately three years on, but mature patterns of sexual behavior do not appear until approximately the seventh year. Young males, however, have very little opportunity to mate due to the appearance of older dominant males at the time of estrus in the cows comprising their herd. Young males frequently receive aggressive action from older females when the male attempts to mount young females in proestrus and when they redirect thwarted sexual activities toward younger animals. As a consequence, younger males begin to spend less and less time with the cow herd and either form a subgroup on the periphery or attach themselves as satellites to older bulls.

Male associations are certainly not as cohesive as those found within the cow herd itself. The role of leadership for the cow herd generally falls to the oldest cow. The role of the adult male seems to be transient; he exerts some influence on the movements of cows when he is with them and especially if he is in musth. At other times of the year, however, the male moves quite independently of the cow herds and is attracted to them only if a female is in estrus.

Interspecific Social Relations

The elephant herds at Ruhunu are quite habituated to the presence of human visitors in the park and show a minimum amount of fear. Those segments of a cow herd with very small calves frequently are more wary and circumspect in their movements even in Ruhunu. The elephants at Wilpattu, on the other hand, frequently come into contact with village planting outside the park and are occasionally shot at. As a result they are quite wary of man.

In interaction with other species of game in the park, we have seen young male elephants chase buffalo, pig, and jackal. Only in one instance did we witness an encounter between a leopard and an elephant herd.

12 March 1969, Kaya Motai, 1720 hours: Elephant herd in the forest and at 1725 a very old female elephant greater than thirty years of age proceeded out of the forest followed by a class 3 animal, a class 4, a class 7, a class 5 with tushes, and a class 5 cow. At 1726 they passed very close to where

a leopard was lying at the edge of the forest. As the leading female got to within approximately 6.1 meters of the leopard, she tossed her trunk to one side in the direction of the leopard and expelled air noisily and continued on her way. The leopard stood and slowly walked into the forest.

Population Structure

The elephant population in Wilpattu Park is estimated to be somewhere in the neighborhood of seventy resident animals. This includes residents only. In addition, at least forty to fifty animals utilize the park on a part time basis, foraging during other seasons of the year either to the south or north of the two bounding river systems. With such a small sample, it is impossible to obtain accurate data on the age structure but suffice to say that our total inventory would indicate that of the population counted approximately 10 percent were calves less than one year of age. This is in keeping with the more extensive censuses performed by Nettasinghe on the Maheveli Ganga system, McKay in Gal Oya and Lahugala, and Kurt in Ruhunu and Lahugala. Furthermore, Kurt (1969) notes that, with respect to sex classes, the male-female ratio is equal until the adult class is reached whereupon there are only 8 percent males compared to 31 percent females.

This ratio is not in agreement with the data submitted by us in Table 3; however, we have defined our age classes more broadly (see page 11). Our adult male category includes three of Kurt's more restricted age classes. When allowance is made for our different criteria, the data are still somewhat different, since males exceeding twenty years of age in Wilpattu comprise some 13 percent of the population. This may mean that older males in Wilpattu are less prone to raid cultivated plots and thus are less subject to wounding by cultivators. On the other hand, the discrepancy may be an artifact resulting from our small sample size.

It was impossible for us to detect any season of reproduction in the herds at Wilpattu. It would appear that calves may be dropped during any quarter of the year but a birth peak may be demonstrated with continued censusing operations. Referring again to Kurt's paper (1969), it would appear that mortality is high at the time of weaning or two years of age, and then mortality increases in the male population as they pass from juvenile status to subadults.

As indicated previously the bulls are typically solitary, occupying individual home ranges that show some overlap especially at water holes or rivers (Figure 7). The cow herd's home range is much more extensive than a given bull's and may cut across the home ranges of several bulls. Bulls may join the cow herds when they are in the area at watering places, whereupon some interaction may take place and it is at this time that, if a cow is in estrus, courting and attempts to mate may be noted (Eisenberg, McKay, and Jainudeen 1971).

We estimate the numerical density of the elephant in Wilpattu Park to be approximately .12 animals per square kilometer; however, the ecological density for the elephant may be as high as 1.0 to 1.2 animals per square kilometer in areas of optimal habitat or during periods of concentration at the height of the drought. Elephant biomass calculations at the crude density of .12 per square kilometer works out to 217.2 kilograms per square kilometer. At ecological density, the elephant biomass may reach 1,800 to 1,955 kilograms per square kilometer.

TABLE 3.—*Population structure of* Elephas maximus

Populations	*Adult* ♂	♀	*Subadult* ♂	♀	*Juvenile* 2	*Juvenile* 1	*Calves*	→ Σ
Maradan-Maduwa	1	1	–	2	2	–	1	7
Tala-Nelun	1	4	–	3	2	2	–	12
Villu Herd	4	8	2	3	2	2	2	23
West Herd (Part)	–	7	2	3	–	2	1	15
Miscellaneous males	4	–	–	–	–	–	–	4
Total Number	10	20	4	11	6	6	4	61
Total Percentage	16	33	7	18	10	10	7	
Grand Total Percentage	49		25			27		

THE WATER BUFFALO *(Bubalus bubalis)*

Description and Aging Criteria

The wild water buffalo is the largest member of the Bovidae found in Ceylon. It is the second largest bovine found in peninsular India being exceeded in size only by the gaur *(Bos gaurus)*, which has been extinct on Ceylon since late Pleistocene times (Deraniyagala 1958). The bulls may be 1.53 meters at the shoulder and 2.7 to 3 meters head and body length. The weight of mature bulls can exceed 450 kilograms. The cows are slightly smaller (Phillips 1935). The wild type animals show a distinctive color pattern. The bulls are typically black with white on all four feet extending to the wrist or hocks. The females tend to be slightly lighter in color but the adult age class stands in marked contrast to the juveniles which are a reddish brown and to the calves which are a tan to reddish color.

For censusing work, we distinguished four classes of animals based on age: adult, subadult, juvenile, and calf. The calf may be easily distinguished by the absence of horns and its color pattern. Horn growth begins at approximately six months of age when they are still considered juveniles class 1. The coat is shed from the long tan hair to the reddish color and they may be considered juveniles on through approximately fifteen months of age. It is possible to discriminate a juvenile class 2 when the horns are conspicuous and approximately 15 centimeters long; the color still being a reddish brown. Molt to adult pelage involves passing through a grayish black phase. This molt begins at approximately eighteen to twenty months of age, and defines the subadult class.

Females typically conceive anywhere from twenty to twenty-four months of age and may then be considered adults. Males are considered subadult until the horn growth begins to show a pronounced curvature when they are arbitrarily designated as adults for the purposes of censusing, although they still may not be adult in terms of sociological status. Young bulls probably begin to breed at around four years of age and, although they could breed at an earlier age, they are prevented from doing so by the presence of more mature adult males.

Social Groupings and Habitat Utilization

The frequency of group size showed several peaks (Figure 19). Solitary individuals were sighted the most

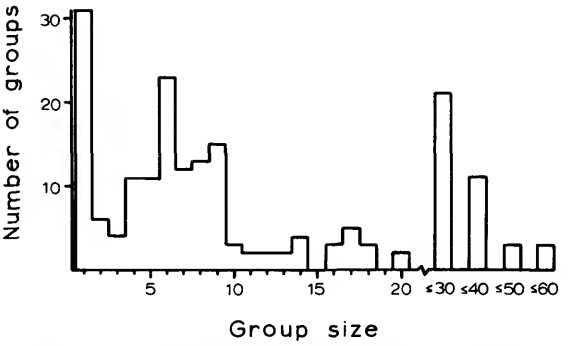


FIGURE 19.—Frequency diagram indicating grouping tendencies for water buffalo. Most of the solitary sightings were of adult males. Forest buffalo tend to be organized in groups of six to nine. The villu buffalo occur in larger herds or subgroupings of sixteen to forty.

frequently and, in over 90 percent of the cases, these were adult males. The next most frequent group size was six individuals, followed by thirty individuals, followed by nine individuals. Some explanation is necessary at this point in order to interpret these data. The size of the buffalo herd very much depends on the habitat in which it is living. Furthermore, we have found that there are two herd types characterized by two subpopulations of buffalo in the park. The so-called "forest buffalo" utilize the central villus or rivers in the central and northeastern portion of the park. On the other hand, we have the "villu buffalo" which habitually use the large tall grass villus in the West Sanctuary during the wet season and then migrate into the permanent central villus during the dry season. The villu buffalo are more diluted with domestic blood and the more nearly wild-type buffalo are those in the central and northern portions of the park. Herd size in the forest buffalo ranges between six and nine individuals whereas herd size in the villu populations runs consistently from thirty to fifty.

Distribution in the Park

As discussed in the introductory section, three ecosystems can be discriminated within the park, the Ara or river system, the villu system including permanent central villus, and the western villu section including the large grassland areas which are periodically inundated during the monsoons. As indicated in the pre-

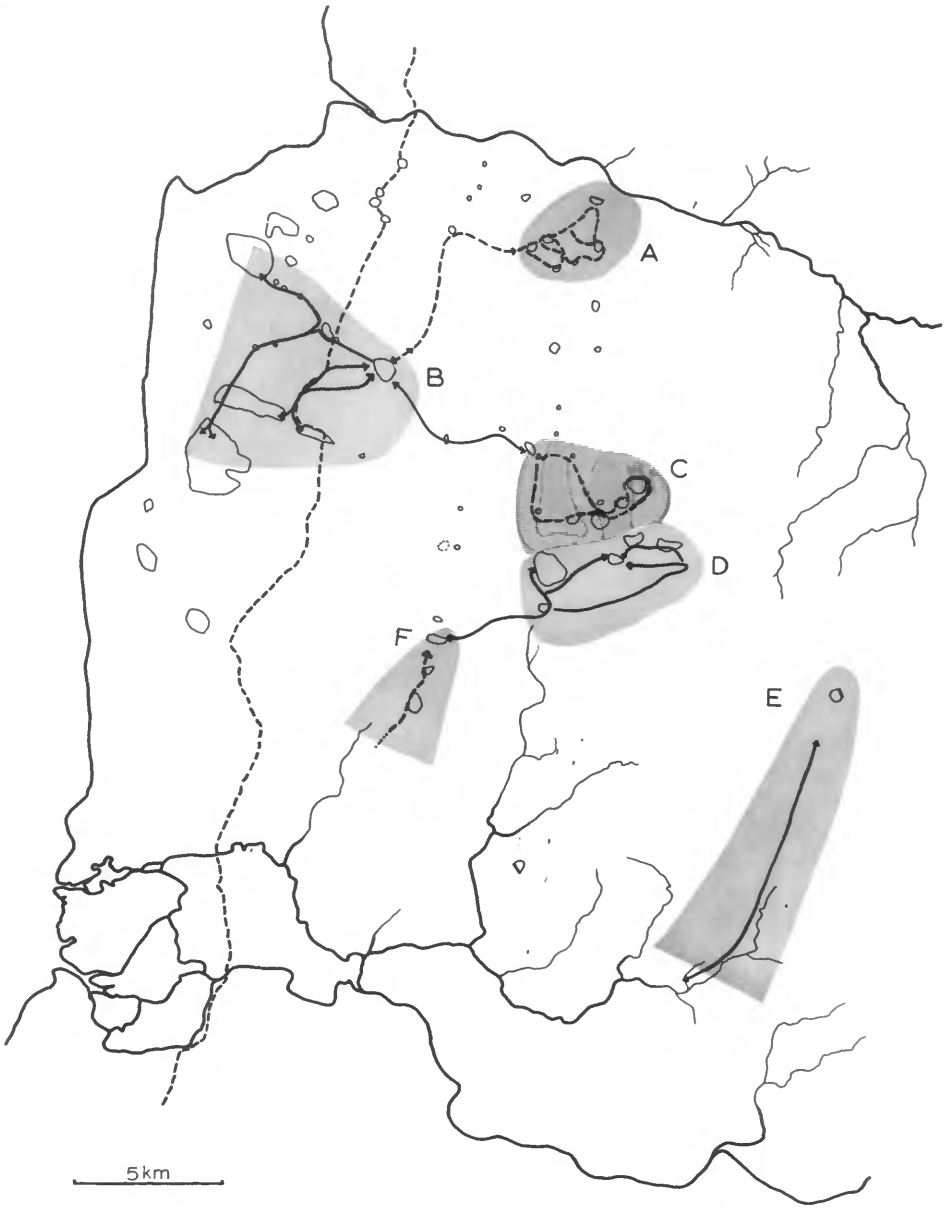


FIGURE 20.—Patterns of habitat utilization by forest buffalo and villu buffalo. Only six herds are portrayed including their movements during the annual cycle. The movement patterns of the large western villu herd (B) are similar to those displayed by the elephant cow herds, see Figure 9. The herds of forest buffalo (A, C, and D) are more consistent in their habitat utilization patterns and do not exhibit such long range movements. Forest herd A made one long range excursion to Kali Villu in the 1968 drought (dashed line) but during the 1969 drought it remained in Katakadal Kulam which had been repaired in 1968 and held water in 1969. The Tala Villu herd (F) made an excursion to Pannikar Villu in the 1969 drought; and in the same period herd B made an unprecedented trek to Manikepola Uttu and back. Buffalo were also present on the Eerige Ella and Pan Ella systems (E) but their ranges were imperfectly known.

vious section, two herding types may be found utilizing the three systems. The larger herds seasonally utilize the West Sanctuary villus and the central villus; the small herd types and more true "wild type" utilize the eastern river systems and the central villus. Hence, discussion of movements of the buffalo naturally must make a distinction between the two ecological types which we have designated.

Movements

Forest herds remain resident in the vicinity of permanent water for prolonged periods of time. This is especially true of the cow herds. During the rutting season, the bulls, especially the younger bulls, may be prone to wander over considerable distances; however, the cow herds are remarkably stable in the forest populations. As the villus begin to dry out and as the available forage diminishes during the drought, there may be some shifting on the part of the forest populations (Figure 20), but the return to the original home range with the onset of the rains is the rule. The site attachment shown by the forest buffalo is similar to the observations made in Australia by Tulloch (1969).

On the other hand, the larger herds characteristic of the western villu population rotate their pasture areas over a considerable period of time. An inspection of Figure 20 indicates one such herd which remained resident alternating between three areas with residences ranging from a week to ten days at each of three points. This pattern of cyclic movement is reminiscent of elephant herds.

Seasonal movements as a function of the drought and monsoon are not as pronounced as in the case of the elephants. Indeed, the large western villu herds of buffalo will continue to show cyclic oscillation between dried pasture and more favorable areas throughout the drought period. In part this is due to the fact that the buffalo apparently has a higher tolerance for drinking saline water. Dependence on clear water appears to be much less than is the case in elephants.

The buffalo does have a shade requirement and during the height of the drought will spend much of its time browsing in the forest. The buffalo will always seek out some form of water for bathing and plastering itself with mud. This undoubtedly is related to its thermoregulation problem, as well as to protect it from insect bites.

Habitat Utilization

As has been mentioned previously, the buffalo appears to have a high tolerance for saline water and will drink in areas where elephants will not. This is especially true of Kokarre Villu where, as the drought season progresses, the salinity of the water becomes higher and higher. Very few animals other than the buffalo appear to have such a high tolerance for saline water. Even so, the buffalo did not drink from Luna Villu which appears to be the most saline of all water sources in the park.

In addition to water requirements for drinking, the buffalo spend no inconsiderable amount of time lying about in the water during the heat of the day. Where extensive tracts of water are not available, the buffalo will make use of very small water holes or pot holes as long as some water remains and the buffalo can churn the substrate to a muddy consistency. As such wallowing areas dry out during the drought, the buffalo will then seek out new bathing spots.

The buffalo is typically a grazer but it makes considerable use of browse during the drought season spending much time in the forest browsing on small trees and shrubs within reach of its tongue. A survey of habitat utilization made in September indicates that the buffalo is strongly associated with grass, grass scrub, and discontinuous forest areas. Utilization of the forest itself by buffalo is very low, lower than that shown by the elephant and sambar (Figure 70). Nevertheless, in forest tracts with associated dry washes near the rivers, sparse populations of forest buffalo may be found throughout the drought period (Figure 20).

Buffalo show a very extreme form of trail stereotypy utilizing traditional routes over and over again even when these routes cut across shallow water (Figure 21). Access to water along rivers together with trail stereotypy results in the formation of rather deep cuts in the banks of rivers where buffalo habitually trek down to water.

Aside from trail formation, the buffalo make an impact on the habitat in the formation of wallows. This is especially true in the vicinity of smaller villus where, as the water level falls, the buffalo in aggregating in the vicinity of these villus will churn up the surrounding terrain into a veritable quagmire. Buffalo are responsible for fouling some of the water pools especially when a small herd remains in residence through the drought period. When the water has been used by buf-

FIGURE 21.—Trail utilization by Periya Naga herd of buffalo in crossing Periya Villu. Note the route stereotypy in that the same path tends to be used over and over again in crossing the villu.

falo for several weeks, it is generally unacceptable to elephants for drinking (see also Kurt 1969).

Buffalo are prone to rub on trees in the vicinity of water holes after mud bathing characteristically leaving a strip of mud with some hair adhering to the trunks of trees in the immediate vicinity of the wallow.

General Observations on Behavior

Buffalo feed and move during the early part of the evening and the early morning hours. Grazing is also heavy in the early morning and late afternoon. Typically at midday, the buffalo lie up in the water or in mud wallows (see also Ullrich 1966).

The social groupings of buffalo are quite cohesive and the most cohesive unit is the cow herd with calves and juveniles. Subadult males and adult males typically are solitary or form into temporary all-male herds which do not show nearly the same degree of cohesion as is the case with cow herds. During the rut, the males become exceedingly aggressive toward one another and actively defend an area against intrusion by other adult males. At the time of rut, when a cow herd passes into the territory of a male, he will actively investigate the cows and attempt to breed any that are in estrus.

In Wilpattu the density of buffalo is not nearly as high as that found in Ruhunu Park. As a consequence, the adult males tend to be spaced out and no formal territorial phenomenon can be observed as is the case where the males are concentrated in restricted areas and in great numbers, which one finds in Ruhunu. There the territories of individual males may be very small and closely packed around available water with definite boundary defense easily observed. In Wilpattu such a manifestation of territoriality is not to be seen because of the more dispersed condition of the population. In Wilpattu, if a cow herd has a number of estrous females in it, the male may move away from

FIGURE 22.—Calf buffalo nursing. Note that the calf approaches the female from the rear inserting his head between her hind legs.

his residential area and follow the cow herd. In addition, subadult males may attempt to join the cow herd with adult males already in attendance. At this time genuine fights can be observed. We offer the following quotation from our field notes:

10 March 1969: The buffalo males are becoming more and more aggressive the last few weeks and fighting behavior is noticeable. Today at Kali Villu, two males were associated with a cow herd and one male threatened and chased away a smaller one. The threat involves approach with head up, ears extended and nostrils flaring. A male may turn broadside to an opponent, then may turn to and approach with head still up, only to lower the head and make a rush. If the buffalo are going to fight, the opposing male will lower his head and lead the rush with the horns clashing. Otherwise, if he is very subordinate, he will turn and flee immediately.

13 March 1969: Note a second sequence of male conflict at Kali Villu. The sequence is as follows: Approach by the dominant male with the head up and the lip curled almost in a "low-stretch posture" as defined by Geist (1968b). The subordinate will lift his head and toss but eventually flees. Male aggressive behavior is so intense now at the buffalo herd that a juvenile male has been chased from the herd and has fled over 1.7 kilometers to Marai Villu where he is grazing alone.

It would appear that the frontal approach to another animal is almost an immediate threat; indeed, we have observed when calves approach a female frontally it induces the female to lower her head and then gently prod with her horn thus turning the calf to one side. Older calves typically do not approach the mother from the front in order to nurse but approach from the rear and nurse between her hind legs (see Figure 22).

The female buffalo will generally retire away from the herd at the time of parturition. In the western villu herd, females at the onset of parturition would remain in the vicinity of Periya Naga Villu for at least

FIGURE 23.—Cow herd of buffalo orientated toward an enemy. Note that the calves and juveniles are either between the cows or to the rear. Such a cow herd, when advancing toward a potential predator, such as a man on foot, can cause flight behavior on the part of the predator (see text, page 36).

two weeks while the calving took place. The females at this time were extremely wary. Even though the calf can accompany its mother within 24 hours after birth, the newborn calves are generally given every opportunity to rest in a secluded spot. Within two weeks or so, the females with new calves will form again into a regular herd.

As the calves become more mature, there is a tendency to form nursery units. Mothers may graze more individualistically while the calves are congregated together in a group generally with one or two females and juveniles in attendance. Example from field notes:

13 February 1969, 1123 hours, Kali Villu: There is a herd of buffalo including sixteen females, three juveniles, and one subadult male in one subgroup and another subgroup consisting of six calves, one juvenile, and one adult female. The subadult male is actively courting one of the cows and attempts to mount her. The herd was doing some grazing but most were lying in the water. In response to our approach the females became restless and a low grunt by the females plus jostling by the juveniles or calves with the nose or horns induces movement on the part of the young in a direction away from our approach.

There is a marked tendency to form subgroups. One should note that within a herd the most cohesive unit is a female and her calf; nevertheless, not withstanding the fact that nursery groups are formed, it would appear that mothers recognize the call of their calf individually and perhaps the calves learn to recognize the voice of their mothers. It is easy upon inducing a disturbance to see the nursery group begin to break up at the approach of the mothers and a definite segregation into mother-calf units resulting.

When moderately threatened the cow group will

form a defensive front to an enemy, with the calves between and slightly behind the mothers and the mothers facing out toward the threat of danger (see also Ullrich 1966). Females are prone to charge offending objects that come too close; this includes jackals and leopards (Figure 23). The following example is from field notes taken by G. McKay:

12 June 1968, Gal Oya National Park, Hatpata Bay (2½ miles south of Inginiyagala), 1505-1800: Herd of elephants and herd of buffalos feeding in grass zone. 1625: Growling heard from direction of buffalo herd. Entire buffalo herd runs toward a large clump of rocks about 75 meters from where they were feeding. Distance from our position about 500 meters. With telescope can see a leopard (fairly large adult) moving slowly among the rocks. As buffalos approach leopard freezes. Buffalos stand near rocks orienting toward leopard. When leopard begins to move entire buffalo herd chase. Leopard crosses open area about 100 meters and enters forest. Herd of buffalos stops at edge of forest orienting to place where leopard entered but one adult female continues on into forest. 1638: Adult female returns after about one minute. Herd begins to move away from forest edge.

Population Structure and Dynamics

The age structure through the annual cycle for the buffalo of Wilpattu are presented in Figure 24. As can be seen, the proportion of calves shifts markedly reaching a peak in December with a secondary peak in April. This is indicative of two parturition periods, one in November-December and the other one in April. The sex ratio in the calf and juvenile classes appears to be approximately equal. Adult males evidently suffer a heavier mortality than is the case for females since the ratio of adult males to females in the population is less than one to eight (Table 4).

There are two periods of reproduction in the Wilpattu population; one in February-March and the other in late May-early June. The February-March peak is by far the more pronounced and at this time the males are exceedingly aggressive. The conception peak corresponds very well with the birth peak. It is known from the literature that the females generally come into the estrus two months after calving. The duration of estrus is approximately two to three days with a 22-to 28-day interval between estrous periods.

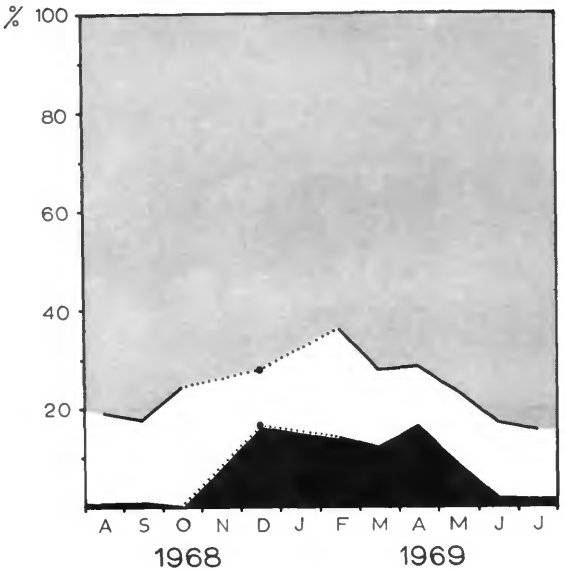


FIGURE 24.—Breeding season for water buffalo is indicated by the peaks for calves (black area) born during the months of December and April. Two breeding periods are suggested. The juvenile precentages (white area) reflect recruitment from the calves born during the two peaks. Calf counts are lower than expected since the mothers with newborn calves are more wary and secretive. Census taking during November and January was inadequate since the herds were dispersed. Ordinate expresses percentage of total population for calves and juveniles.

TABLE 4.—*Population structure of* Bubalus bubalis*

Total Count	*Adult* ♂	*Subadult* ♂	*Adult* ♀	*Subadult* ♀	*Juvenile*	*Calves*
February, 141	7	3	74	7	31	20
June, 112	11	7	66	9	17	2
August, 77	4	2	55	–	15	1

* Partial tabulation of known herds.

Gestation is ten months and typically a single calf is born (Ishaq, in Asdell 1964).

We estimate that approximately 160 buffalo are resident in Wilpattu Park giving an overall density of .27 animals per square kilometer. Attempting a biomass calculation based on the typical age structure of a population, we find that crude density biomass levels are at approximately 73.4 kilograms per square kilometer. During the maximum concentration of game at the time of the July-September drought, the density per square kilometer of buffalo may reach 1.5, with a biomass of 408 kilograms per square kilometer.

The significant causes of mortality in the buffalo population seem to be from three sources: (1) predation on the calves by leopards, (2) indiscriminate poaching of adults in the West Sanctuary and along the Moderagam Aru, and (3) mortality of males induced by fighting at the time of rut. In commenting on the last statement, two males are known to have been severely injured and to subsequently have died of injuries as a result of fighting at the time of rut.

THE SPOTTED DEER (Axis axis)

The spotted deer of Ceylon and India is the most abundant game animal of the lowland dry zone. It is not adapted to wet zone habitats and on peninsular India the low, wet jungles are occupied in part by the hog deer (*Axis porcinus*), its close relative. Although the hog deer was believed to have been introduced by the Dutch (Phillips 1935) on Ceylon, its numbers in the lowland wet zone have declined greatly in recent years, and it is now found only in small numbers in the extreme southwest delta country. The Ceylon axis is a medium size deer with males weighing up to 74 kilograms and females averaging about 46 kilograms. Stags may reach 145 centimeters at the shoulder while does are about 12 to 15 centimeters shorter (Phillips 1935).

The young males grow antlers at one year of age and females come into estrus at approximately the same age (that is, from 12 to 24 months). Gestation is believed to be about seven months; thus a female may be as young as eighteen to nineteen months old at the birth of her first fawn. Typically a single fawn is produced. (See Schaller 1967 for a discussion of reproductive data.)

For the purposes of censusing, we established the following aging and sexing criteria: Fawns were defined as the smallest size class characterized by their longer hair. Animals of about six to twelve months show glossy coats and were designated juveniles. Yearlings were classified as to sex. Male yearlings begin to show antler growth and the yearling females are about 12 to 15 centimeters shorter than the adult females. Typically yearling females have more rounded abdomens. Adult males and females were arbitrarily defined as animals judged to be in their third year or older.

Yearling males were classed with respect to whether their antlers were in the velvet or not. Adult males were further broken down into shed-antler, velvet, and hard antler classes. Throughout a twelve-month period, 3,067 axis were censused with respect to age and sex classes at selected water holes. In addition, rough counts without aging and sexing were maintained throughout our study area.

Social Groupings

Axis typically move in small groups which subsequently assemble at various times during the diel cycle to form a herd. The term herd thus refers to a gathering of smaller groups and is the social formation most often seen grazing near water holes or in park country. Such an extended herd generally exceeds twelve animals and over seventy have been counted within the same continuous grouping. Figure 25 presents a frequency diagram representing grouping tendencies.

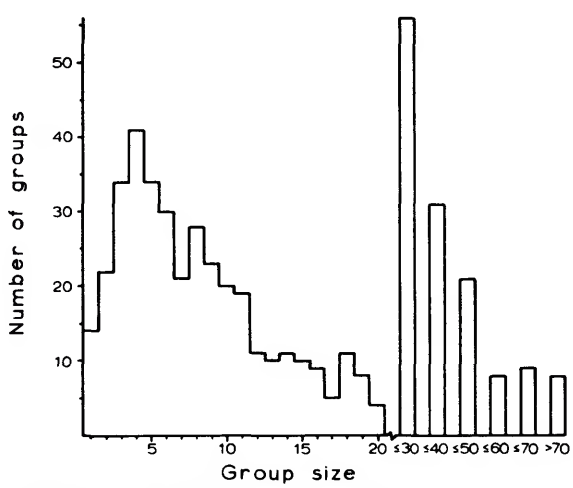


FIGURE 25.—Frequency diagram indicating group size for axis deer. Note the rarity of solitary sightings. The basic social unit includes some three to six individuals. The higher counts reflect a melding of these units during open country grazing.

Considering all groups of less than twenty animals, only fourteen out of 365 sightings were of solitary individuals or less than 4 percent; 38 percent of our sightings included groups of three to six individuals. In the main, these small units are composed of a doe, her fawn, and a yearling female with or without a fawn. Hence, the axis is quite gregarious, seldom moving alone, with a basic sociological unit consisting of a female and her probable descendents. Within the extended herds and even within the smaller groupings, there is some tendency for unisexual subgroup formation; such that, the males will tend to form all male groups and, of course, the does will tend to segregate out into groupings of does and their progeny. As an example of such subgroup formation, we cite the following from field notes:

Mahapatessa Villu, 1315 hours: Forty-four axis are grazing. Eight of these are males with antlers. The distribution in space is as follows: One male far to the left, then a string of females and juveniles extending almost linearly for a distance of approximately 92 meters. Two males are sparring in about the center of the line. Two other males are left of center grazing, and at the extreme right end are three antlered males together and slightly detached from the female-juvenile group.

The question of herd integrity may well be asked since the small subgroups come together periodically during the 24-hour cycle. One wonders how consistent the larger assembly is in its structure. This question is rather difficult to answer since the animals composing a given herd were not generally identifiable as individuals. In some cases, however, individuals could be identified; when we kept track of such individuals, it was found that a given animal, especially a doe, generally spent most of her time within an area of approximately 2.5 square kilometers. In particular, we might cite the example of the white doe at Kudapatessa. This individual was observed throughout the year grazing generally in the evening near the same water hole. The evidence from observing this individual and at least two other animals that could be identified with reasonable certainty has led us to the conclusion that does are extremely consistent in their use patterns. Although they may not emerge from the forest to graze at the same time on a given day, in general one can say that the composition of the extended herds is relatively constant.

The bucks seem more prone to wander and those herds which habitually utilized water holes that dry up during part of the annual cycle will undertake movements of 2.4 to 3.2 kilometers. We quote from Eisenberg's field notes:

Summary of herd structure at Marai Villu at the onset of the rains, 22 October 1968: There are four discernible herds of axis at Marai Villu. These herds form at different points around the villu before grazing and advancing to water. They form from small subgroups of approximately four individuals, generally a doe and her offspring of several years. The time of morning drinking is approximately 0730 to 0800 hours and they come out to drink and then retreat. Group 2 generally comes out first, group 3 somewhat later, and group 4 last of all. Groups 3 and 4 are frequently seen to mix with one another. Group 1 is from the neighboring villu which is now dry and seems to be the most inhibited in its activity. Groups 2, 3, and 4 would appear later on in the afternoon from 1600 hours on but sometimes earlier depending on the nature of the current rainfall and the overcast. Overcast tends to result in earlier emergence. Estimated numbers of the groups: Group 1, twelve animals. Group 2, approximately twenty. Group 3, approximately sixty-five. Group 4, about thirty-two. Group 1, as previously noted, is obviously attached to the dry villu behind the camp and is more nocturnal and restricted in its movements at Marai and apparently only uses Marai Villu for water during the extremely dry periods. As noted before, emergence is often done in small groups of three to six in rapid succession. Often in the morning the younger axis show much activity, bounding and chasing down to the water's edge.

As indicated in the preceding field notes, the extended herd which makes its appearance is formed by an assembly of smaller units which tend to emerge as subgroups. Following is an example from field notes:

14 February 1969, Marai Villu, 1500 hours: Axis are beginning to emerge to drink and to feed. A group of five are out and then a group of three at the opposite side of the villu emerges. At 1600 hours, two groups of four each have assembled at the forest edge and now proceed together toward the water in a line splitting off into two groups of four and going to different points of the pond to drink. At 1603 hours, more axis are appearing from the forest.

19 February 1969, Marai Villu, 1500 hours: Composition of social units of axis emerging: Adult male and female emerge together; three females and three juveniles emerge; female and a juvenile emerge; two females and one yearling emerge; a yearling and an adult female with a juvenile and a fawn emerge as a unit. All of these groups converge together to graze between 1500 and 1520 hours.

Distribution in the Park

Figures 26 and 27 indicate the approximate numerical densities as estimated for the axis populations in both the drought and rainy seasons of 1968. Sampling and density calculations are discussed in a previous publica-

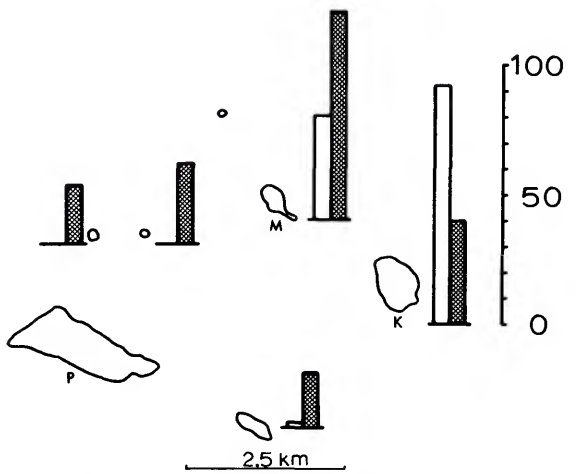


FIGURE 26.—Numerical density of axis for drought and rainy periods in the intensive survey area (see Figure 76). At the onset of rain, there is a tendency for dispersal away from concentration at certain selected villus toward villus which have been dry during the drought period. The relationship between Marai Villu (M) and Kali Villu (K) is rather complicated, since Marai Villu tends to dry out more rapidly and concentration increases at Kali only to fall at the onset of rain with a restoration toward more intensive grazing at Marai. This pattern may alter from one year to the next depending on the extent of habitat utilization. Shaded bars refer to the wet season; white bars refer to the dry season. Numbers refer to the average highest evening count. The total high counts for the wet season are higher than for the dry season. This reflects both an increased duration of grazing activity at the onset of the rains and an increasing tendency to remain in the open during daylight when the cloud cover increases. The counts reflect intensity of utilization for each villu but do not parallel density (see Eisenberg, Santiapillai, and Lockhart, 1970). P=Periya Naga.

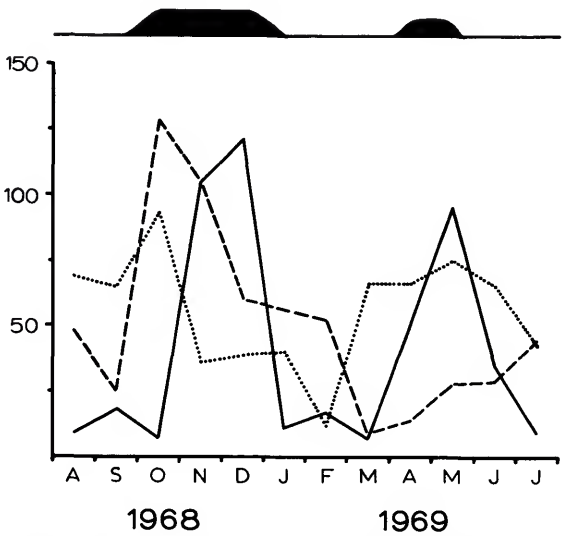


FIGURE 27.—Average maximum monthly concentrations of axis grazing near three villus: Kali (dotted line), Marai (dashed line), and Kokarre (solid line). Line above graph indicates periods of rainfall. Concentration at the brackish water Kokarre is later and more restricted than is the case for Kali and Marai, indicating grazing on grass growth initiated by the rainfall and little utilization during the drought when its salinity increases. Concentrations at Kali and Marai increase as the drought proceeds only to fall after the sustained onset of rains, indicating return to other grazing areas and more intensive grazing in the forest. The relationship between Kali and Marai Villus is in part reciprocal, as indicated in Figure 26.

tion (Eisenberg, Santiapillai, and Lockhart 1970). During the drought interval, the axis feed less in the forest and utilize the grasses bordering on the permanent villus. As the smaller villus dry up there is a general movement to the neighboring nearest permanent water source (ibid.). Movements are not extensive and no long-term migrations are discernible. Herds in the vicinity of permanent villus probably occupy home ranges of less than 2 square kilometers; however, stags may move more widely (see also Schaller 1967).

Habitat Utilization

A survey of animal activity during September in Wilpattu clearly indicated that the habitat utilization displayed by axis is in the main limited to grassland or scrub. Forest utilization by axis is high only when the forest borders on open grassland or scrub areas (Figure 70). Adult male axis utilize browse to a maximum height of roughly 2 meters. The average axis can forage only at about 1.5 meters. Browsing on apical tips and shoots shows an increase after the onset of rains when the new shoots are developing. During the height of the draught, axis are prone to supplement their diet with fallen fruit or even bark. Browsing and grazing in the forest or open scrub leads to trail formation. The deer opportunistically utilize elephant trails and use common trails with *Bubalus, Sus,* and *Cervus*. When one maps game trails in the vicinity of water holes, it is easy to discern convergence of many smaller separate trails into larger trails of a more unidirectional character which again split at the forest edge (Figure 28).

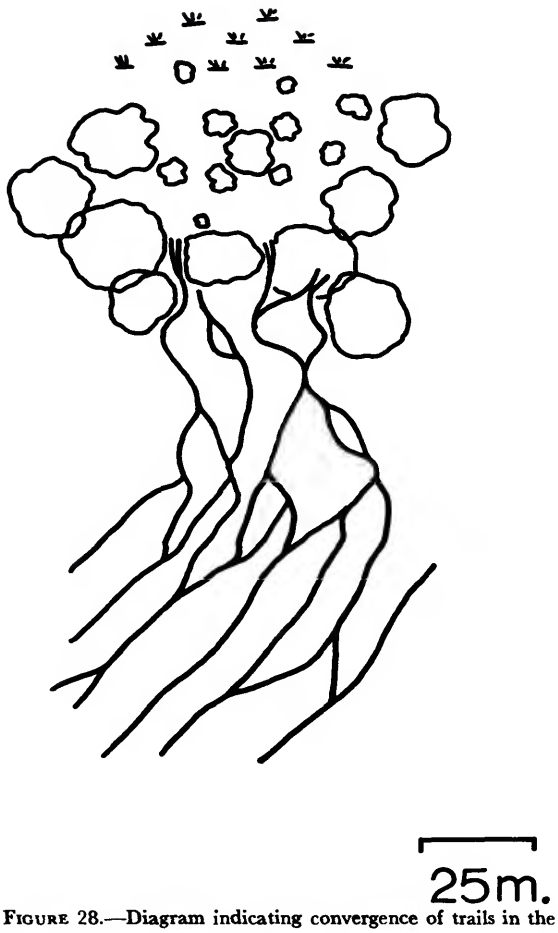


FIGURE 28.—Diagram indicating convergence of trails in the vicinity of water hole only to break up into numerous smaller trails in the area where browsing is concentrated. Breakup of trails generally occurs at the interface between forest and scrub. Survey made at Kali Villu plot.

Axis do not wallow in contradistinction to sambar *(Cervus unicolor)*, buffalo, and swine. The axis do leave many traces of their passage in the habitat. Feces are deposited without a bias resulting from a predisposition to "mark" the habitat; nevertheless, feces may accumulate in areas where the animals are prone to rest or stand for long periods.

One of the more consistent features in the habitat resulting from the activities of antlered bucks are low shrubs which have been in part debarked. Hard antler males will rub their antlers on the bark of low saplings or shrubs and, in fact, a definite preference for certain species may be shown in some habitats, e.g., *Cassia fistula* in Wilpattu. Occasionally bucks will rise on their hind legs under low-hanging foliage and trample around in a tight circle, thus leaving an area of tramped ground with disturbed fragmented vegetation immediately above it. This behavior, termed "preaching" (Schaller 1967), is frequently shown during rut.

Behavior Patterns

The behavior of axis has been described in some detail by Schaller (1967). In general, we have found no major differences in the behavior of the Ceylon axis. The reader is referred to Schaller's work for more detailed descriptions.

Activity Rhythms and Group Behavior

The amount and type of activity displayed by the axis is very much a function of the ambient temperature, extent of cloud cover, and the presence or absence of rainfall. Considered in the reverse order, the rainfall induces the axis to move in the open; indeed, the highest population counts can be made during such weather. Quotation from field notes:

> 12 November 1968: The axis are spending less time in the open and more time in the forest; however, when it rains most of the animals will leave the forest and come out into the open. Either the dripping water from the leaves of the trees is distracting to them or they are made uneasy by the fact that they cannot hear well with the pattering of the rain. But whatever the cause, the axis are very much driven into the open when it rains heavily. The herbaceous undergrowth in the forest is dense and green as the result of the rain; fecal pellets are disintegrating rapidly; termite activity is at an all time high.

Cloud cover which ameliorates the effect of direct sunlight can encourage grazing in the open during midday. During the drought when water is at a premium, the axis may drink at midday as well as in the evening and morning, but open-country grazing will be reduced (Figure 29). During the rainy season, the growth of grass, forbs, and branches (new leaves, etc.) stimulates much browsing in the forest itself with grazing in the open confined to the late afternoon and evening. Conversely, all things being equal, there is more nocturnal utilization of the open grassland around water holes during the drought period than is the case during the rains.

Drinking times are dependent upon the season of

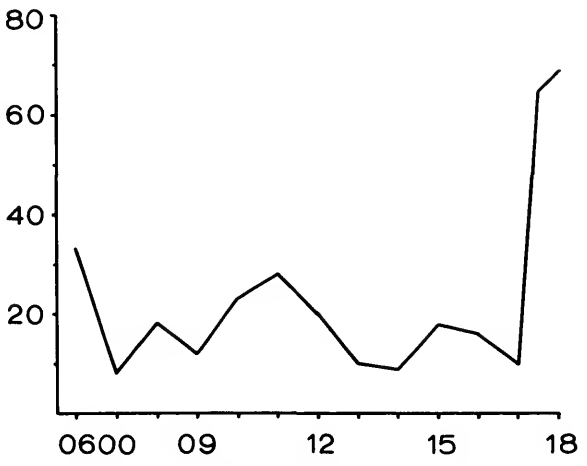


FIGURE 29.—Diurnal activity of axis. In both the wet and dry seasons, maximum build-up of axis for grazing in the open occurs in the late afternoon. These data are computed from average maximum counts at Kali Villu during the August drought.

the year with an increase of frequency of visits during the drought. Typically the groups emerge in three's and four's, pausing at the forest edge before trekking to the water hole itself. Following quote from field notes:

12 October 1968, 0700 to 0730 hours: I have been watching the axis take their early morning drink. They drink rapidly and graze little. The group sizes are four and six; in other words, it appears that axis are split into the basic social unit during the early morning hours. These small groups emerge from the forest with very little grazing and make their way rapidly to the water's edge to drink. They generally run from the forest to the water, drink rapidly, then turn. The juveniles may play slightly as they canter back toward the forest itself.

During the assembly of the herd at the water hole, social interaction is intensified as the small units converge and interact. Activity continues through the night and often about midnight the animals bed down as groups in the open.

7 December 1968: Around 2100 hours, I made the following observations on the axis deer at Marai Villu: Four are lying down, sixty-seven are grazing near the camp. At 0300 hours, the small herd of axis was lying down near the camp. It would appear that intermittent resting and grazing take place at night in the open following the evening drink which occurs anywhere from 1630 on to 1800 hours.

18 January 1969: Axis are not visible in the open this morning. Last night they bedded down in the open, gathered into small herds or groups near the villu edge. After the evening feeding session from around 1700 to 2000 hours, they rested for some hours in small groups before recommencing feeding and gradually retiring to the forest at dawn.

Resting may involve a synchrony in behavior. During the day, virtually the whole herd will lie in the shade but still be visible, for example at Kumbuk Villu. At other villus, such as Marai, the herd breaks into subgroups which rest intermittently, concealed from view within the forest. As mentioned before, nocturnal resting typically involves the formation of an extended group bedding down in the open. A similar synchrony in grazing behavior may be easily observed as the small subgroups unite to form the typical herd.

12 October, Marai Villu: There is a tendency to align body axes parallel when grazing. There are deviations from this but for any given subgroup within a larger aggregation of deer, there is a strong tendency for the members of the subgroup to align their body axes in a parallel fashion and to be facing in a similar direction. In a total herd or aggregation, however, animals may be facing in various directions depending on the distribution of the subgroups and their spacing.

COMMUNICATION MECHANISMS

A profound influence on the behavior patterns of *Axis* deer is noted at the onset of the rut. Although the rut is not as sharply demarcated in *Axis* as is the case for *Bubalus,* the buffalo, there are definite birth peaks and differences in the intensity of sexual behavior. Before proceeding to a discussion of differences and changes in social interaction, it would be useful to review communication mechanisms in axis.

Auditory communication involves two classes of sounds; those sounds made by the animal's body itself and true vocalizations. The axis typically stamp when startled and may stamp with either the forefeet or the hind feet. Hind foot stamping generally accompanies a spring away from an offending object.

Vocal communication involves the following call types:

The alarm cry.—This cry is sharp and repeated and is given in response to the sight of a predator such as a leopard or in some cases to human beings. While the cry is given, the animals may show some pilo erection. The tail is often held upright and the animal is generally oriented toward the source of the disturbance. The alarm cry of the buck is generally deeper in tonal quality that that of the female.

The challenge call or long call of the buck.—This is a high pitched repeated note given in a burst of about six or seven. It is generally given by a buck in full rut as he emerges from the forest to approach a doe herd.

The growl.—This type of cry is sometimes produced by the buck. It is very low and not heard unless one is quite close to the animal. The buck is generally exhibiting aggressive behavior.

The scream note.—This is produced by an animal that is either extremely terrified or has been recently captured by a predator and not yet killed.

The bleat.—This is produced by the fawn when attempting to contact its mother which is either out of view or not in the immediate vicinity. It is a high pitched repetitive call with an undulating quality to it. The does may respond with a similar bleat which is deeper in quality and not repeated as frequently. Does may produce this sound when moving from the herd to the forest thus inducing the fawn to follow.

Patterns of display in the axis have been reviewed by Schaller (1967). It would appear that the low-stretch posture during approach by bucks to females has some communicatory significance. Furthermore, the head up and head nod are employed by bucks during aggressive encounters. Turning away is apparently a submissive gesture.

Chemical traces left in the environment include the urine of bucks, the urine of does at estrus, and perhaps secretions from the pedal glands in the hind feet when the animals are frightened. The function of such odors has been reviewed in part by Schaller (1967). Males in rut may also rub their pre-orbital glands or brows on branches or tree trunks (Figure 30).

Patterns of Social Interaction

Male-Male Interactions.—Male interactions are very much governed by their reproductive state. When the males are not rutting there is a marked tendency to form unisexual subgroupings or bachelor groups. Some of these groups may show a consistent composition over a period of several months, as for example, the group at Kanjuran Villu, consisting of five animals, including three adult males and two spike males. During the rutting period hard antler males will spar and actively attempt to court females (Figure 30). Younger males are generally subordinate to the three and four-year old males. They may, however, actively follow older males and, although not challenging them, they may secondarily participate in courting activities.

14 February 1969, Marai Villu, 1603 hours: Suddenly an adult male gives a challenge call and is seen pausing at the forest edge. He holds his head up and then proceeds to the females and juveniles. He "lip-curls" as he approaches with his neck held low in the "low-stretch" posture, and then sniffs a female's flank. He nudges the female with his head and, as she moves off, her fawn follows. Meanwhile a young two-year old male with hard antlers approaches the spot where the adult male had emerged. The young male rises on his hind legs and thrashes his antlers in the overhead foliage. He repeats. This is "preaching." The old buck has been moving around the villu pausing to sniff each of the adult females in turn. When he approaches the females, his penis is unsheathed. Two males of approximately three years of age are fighting. During fighting, their penises are also unsheathed, and they are about 30 feet away from the older adult male. He ignores them.

Male fights generally involve males of equivalent age; spiked males are always subordinate to the two and three year olds.

13 March 1969, Marai Villu: A three-year old male with hard antlers and a male of approximately the same size but antlers in the velvet are exhibiting challenges. The challenge involves an approach with the head up and held at about 45 degrees to the ground. The challenger bobs his head up and down. If responded to by the second animal, they will begin to spar gently by opposing their antlers and pushing. Alternatively, they may not lock antlers but merely push with their foreheads. The subordinate male (in this case the one with antlers in velvet) will break off to graze with his head down or will turn his head away and give a jump to one side. This generally causes the dominant hard-antlered one to desist momentarily; but the hard-antlered male will continue to approach and head-bob and it seems that the velvet male can hardly resist the challenge and will then begin to push foreheads. I think the velvet-antlered male definitely is attempting to avoid contacting his soft antlers with those of the hard-antlered male.

Male-Female Behavior.—During the nonrutting phase, the males appear to ignore the females, although occasionally they may join in with a female subgroup and follow. Some social facilitation appears to be involved. During the rut, the males will approach and flehmen, as has been described in the previous section. Typical male-female interaction may be characterized by the following notes:

12 September 1968, Mana Villu: While observing an axis herd, I noted an antlered male sniffing at the urine of a female. He raised his head and curled his upper lip back thus exposing his lower teeth while slitting his nostrils. This is a typical flehmen reaction. Another adult male with

FIGURE 30.—Typical activity by axis males. An adult male marks with his pre-orbital gland on the tree to the right. Two males in the two-year age class are sparring, while two females in the foreground take little notice.

antlers, while walking along, paused suddenly to prong at the earth with his horns thus stirring up the ground; then he lay down.

13 March 1969, Marai Villu: An adult male with hard antlers of at least three years of age was observed chasing a female in the open. He continued to follow her with his tongue protruding and when he was close enough he licked at her rump. He mounted once, then continued to drive her for a period exceeding two minutes until they both entered the forest. At one point, a spiked male began to follow the pair at a distance of approximately 15 to 20 meters.

Female-Female Behavior.—As indicated in the previous sections on social tendencies, the females are quite gregarious and it would appear that the small subgroups showing the most cohesion may well be extended mother families, including an old doe and her related female offspring and occasionally yearling males. At the time of parturition, a female is prone to retreat from the main herd and becomes somewhat aggressive toward her own offspring. The fawn is generally delivered in a very secluded place and, for the first ten days of its life, the fawn is unable to follow the mother. After approximately ten days, however, the fawn will begin to accompany her and at this time the small subgroupings of females and their descendents, as well as the extended herd groupings are reformed; hence, there is a temporary break-up in herd structure at the time of parturition.

Female with Young.—As noted in the previous section, the newborn fawn is born in a very secluded spot. The fawn is unable to accompany the mother continually on her grazing forays during approximately the

first week to ten days of life and, as a consequence, the mother must return to it in order to nurse it. Some observations were made on the behavior of a tame female axis deer and her fawn which were resident at the rangers' headquarters at Maradan Maduwa. Here follows a synopsis:

After approximately ten to twelve days of age, the fawn would begin to accompany the mother on her grazing forays. Even at this time, however, the fawn was prone to rest in secluded thickets while the mother grazed unaccompanied by it. What resulted was the creation of certain meeting spots based on a learned tradition between the fawn and its mother so that even well into the fawn's second month of life it could graze somewhat independently of the mother and return to either its own resting place or other meeting spots where it would maximize its probability of encountering the mother.

There apparently is a synchrony in the temporal patterning of movements by the female and her fawn as well as a memorization of certain key places in the environment where the fawn and the mother can meet. On one occasion the fawn came to a spot where it habitually was nursed by the mother and the mother was not present. The fawn began bleating and then moved off continuing to bleat and ceasing after about five minutes when it disappeared in the forest. Approximately fifteen minutes later, the mother arrived at the spot only to find that the fawn was not there. The mother then initiated a few bleats and began to move off apparently toward the next spot where eventually they must have made contact.

We envision thus that there develops out of a pattern of resting and nursing some sort of consistent usage of the space by the mother and her fawn. The fawn need not necessarily be in continual attendance with the mother in order to guarantee contacting her again. This would be especially useful in forested areas. In general, however, from approximately the tenth day on, the fawn is prone to accompany the mother when she grazes in the open and may stay rather close to her. Although even at this time the fawn is prone to rest in tall grass while the mother grazes often 4 to 7 meters away from it.

Antipredator Behavior

A startled axis will generally leap suddenly to one side, stamp and/or give an alarm bark, and then run rapidly for cover, whereupon it will turn and regard the place of fright, sometimes continuing to emit alarm barks. The stimuli initiating the response are not often obvious.

21 October 1968, Marai Villu: An antlered male emerges from the forest and walks alone through the grass toward the water. He tosses his head up and down as he walks. He passes near the jackal family. The male jackal who is walking deflects his walk to avoid intersecting with the stag. The stag pauses, faces the forest, flaps his ears, the skin on his rump twitches, his tail twitches, and then he holds perfectly motionless. He stamps; then he leaps suddenly and trots off, thus startling one of the jackals which faces the forest and moves on. The first stag has now entered the forest. A second stag now leaves the forest and approaches the pool. He drinks at a small pond around 3 meters from the villu edge. He has hard antlers also. Suddenly he tosses his head, drinks, flips his tail, ripples his skin and twitches his ears—the flies are apparently extremely bothersome. Then the second stag trots toward the spot where the first stag was frightened. Upon reaching this spot, he jumps and runs to the forest edge, pauses there, then slightly wrinkles his nose. At the forest edge the stag bolts again and runs to enter at a second point. Possibly both stags were frightened by the smell of blood since the spot where they took flight from was very close to where the jackals had been chewing on bones and strips of skin from a hare that they had killed the evening before.

Upon perceiving a leopard, axis may respond in a variety of patterns. If an axis is startled by a leopard at close quarters, it will generally make an immediate escape response; e.g., a jump followed by a rapid gallop away from the vicinity of the leopard. On the other hand, if it is not startled but the leopard can be perceived at a distance, then the axis' next act is dependent upon what the leopard does. If the leopard is at a reasonable distance and resting, the axis will orientate toward the leopard, may show pilo erection and a raised tail and, depending upon the distance, will generally maintain its orientation and emit a warning bark. If the leopard remains resting in the open, the axis will approach with the head down and in an elongate posture. If the leopard still does not move and if there are several axis gathered together, the axis will actually exhibit a mobbing response, often inducing the leopard to get up and move.

12 September 1968, Kali Villu, 1755 hours: A herd of axis consisting of approximately eleven females including older females and yearlings plus two obvious juveniles and one fawn. A leopard is lying down in the open approximately 70 meters from the forest edge. The axis were to the west of it and at a distance of about 140 meters when they noticed the leopard, orientated toward it, with ears directed forward and stiff body postures, tails erect, and all hairs on the tail erect, thus presenting a white patch. They began barking

while more and more members became oriented toward the leopard. After three to four minutes the deer began to advance, led by an old doe. During the advance the doe's neck was stretched out very elongate in what could be called an elongate posture. The barking continued and the whole group advanced, led by the doe and followed by some of the younger females with the older females scattered throughout. The group advanced on the leopard continually until the leopard stood, turned away from them, and walked into the forest. All deer then stopped to sniff at the spot where the leopard had lain while some still remained oriented toward the forest where the leopard had entered and continued to bark. From within the forest new barks could be heard from deer that evidently had spotted the leopard as it entered. Eventually the doe herd ceased sniffing at the spot while still manifesting varying degrees of pilo erection and tail erection. They then commenced grazing, glancing from time to time at where the leopard had entered the forest. This group behavior we have termed "mobbing."

If the leopard is moving slowly at a reasonable distance of approximately 100 meters, let us say, and moving away from the deer, the same sort of response can be shown and the deer will often move toward the leopard but may not exhibit full mobbing. If the leopard moves toward the deer, the mobbing response is not shown but they will reman oriented toward the leopard, barking. When he comes within approximately 45 meters, they will move away to a safer distance, then orientate again, still continuing to bark. It is believed that the mobbing response occurs when there is a balance between the tendency to approach and the tendency to flee with the approach tendency slightly exceeding the flight response. A concerted mobbing effort by axis can lead to the movement of the leopard into the forest.

Interspecific Relationships

The relationship between axis and leopard has been referred to in the previous section. Suffice to say that, with respect to predators, axis are generally tolerant of jackals but a female with a fawn may definitely show attentive behavior and may even be forced to attack the jackals if the jackals show an interest in the fawn. Jackal predation on fawns will be discussed in the section under jackals (page 63).

Concerning the relationship between axis and langurs, it is a well-known fact in Ceylon and in southern India that langurs and axis may form a feeding association (Champion 1927, Schaller 1967); see also Figure 31. During the dry season when langurs are feeding on fruits, they frequently drop fruits and leafy branches to the forest floor after having fed on parts of them. The axis can then have access to browse and fruits which would be out of their reach. For this reason it is not uncommon for traditional patterns of association to be set up locally between an axis herd and a langur troop. There may be a distinct survival advantage inherent in the association between langurs and axis, not only from the axis benefitting from food but also from the standpoint of antipredator behavior; the langurs will respond to the sight of leopards by warning whoops and a display involving vertical leaping and jumping about in the branches of trees. In addition the warning barks of the axis may serve to focus the langurs' attention on a potential predator such as the leopard which may not be immediately visible to them in the trees.

Population Trends

In an unmarked population with only a few individuals readily recognizable, one has difficulty in obtaining an absolute census. Similarly the tendency to fractionate into small subgroups of three to five and the unpredictable nature of herd formation tends to obscure complete counts. Very often complete assembly of a population in the evening grazing unit proceeds after dusk; hence the full count cannot be made during daylight hours. These difficulties coupled with the seasonal shifts in intensity of open-country grazing all prevented the establishment of an absolute census although the resident populations at Kumbuk, Kali, and Marai villus were relatively easy to work with. Even so, during several months of the year, some inaccuracies were inevitable, especially in the determination of sex and age class ratios. This resulted from the propensity of females to restrict their movements when giving birth and the relative shyness of males which had recently shed their antlers. In spite of these fluctuations, the ratio of adult males to adult females remained relatively constant at approximately one male to two females (Table 5).

Seasons of Birth and Mating

Although fawns may be born in almost any month of the year with the possible exception of July and August, most fawns are born in September and October and later in December and January. Assuming a seven-month gestation, one could expect maximum

TABLE 5.—*Population structure of* Axis axis

Total Count	*Males*					*Females*	*Juv.*	*Fawns*
	Adult (h)	*Adult* (s)	*Adult* (v)	*Yr* (h)	*Yr* (v)	*Adult+ Yr*		
August, 169	50	2	2	2	–	90	23	–
October, 88	21	–	1	1	–	37	20	8
December, 322	40	2	5	15	7	195	39	19
February, 142	21	3	5	9	–	56	40	8
April, 264	33	6	38	17	5	116	32	17
June, 502	73	5	51	15	11	295	41	11

h=hard antlers; s=shed antlers; v=velvet antlers; yr=yearling.

FIGURE 31.—Langur and axis associated at Kali Villu. In the above photograph the langur (arrows) are foraging on the ground with the axis.

breeding in June, July, August, and January to February. This implies breeding at the end of the drought periods and births at the onset of rains (Figure 32 and Table 5). Furthermore, it would appear that most males shed their antlers at the end of the January-February rut with over 50 percent of the adult males showing velvet antlers in April and May. Hence, there is a partial synchrony in the reproduction shown by

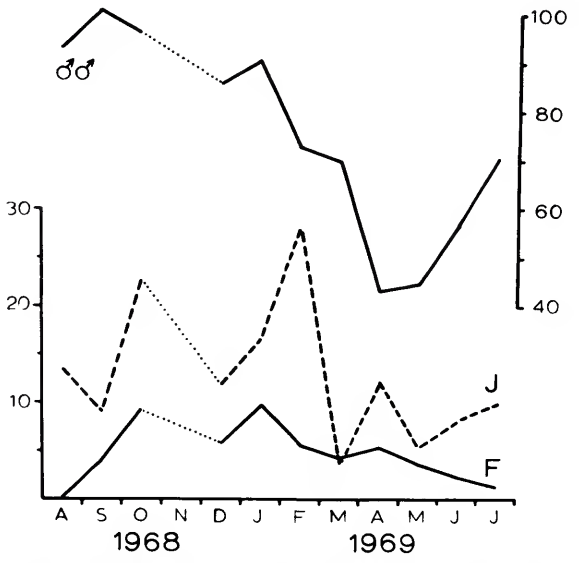


FIGURE 32.—Breeding season data for axis. Trends throughout the annual cycle clearly indicate that the number of antlered males reaches a maximum in August and September then declines with a corresponding increase in the percentage of males with shed antlers or antlers in velvet (top line). Fawns show two peaks in occurrence, one in October and the other in January (solid line). Juveniles peak slightly later than the fawns as the fawn groups are recruited into the juvenile class (dashed line). Fawn counts remain artificially low since they are not easily seen during approximately the first month of life. November census figures were rejected as too low resulting from the dispersal of deer and increased feeding in the forest. Percentages for fawns and juveniles are based on the total population. Percentage scale for males (right ordinate) refers to male population only.

the axis of Wilpattu and this synchrony is tied to the rainfall. Just after the height of the major birth season in February, the ratio of fawns and juveniles to adult females was thirty-three to thirty-nine or approximately all adult females were accompanied by young less than six months old.

MORTALITY AND BIOMASS

Significant mortality appears to occur after the first year of life with only a 10 to 15 percent loss during the first year. The principal predators are the jackal and the leopard (see pages 63, 66). If up to 1,500 young are produced annually and the average weight for the first year animal is taken at 23 kilograms, then 30,400 kilograms of biomass are produced annually. If predators take 80 percent of the crop, then 24,300 kilograms of meat are available which could support twenty leopards alone (see pages 68 and 69).

We estimate (Eisenberg, Santiapillai, and Lockhart, 1970) that approximately 3,500 axis are resident in Wilpattu (exclusive of the West Sanctuary.) This yields a crude density of 5.8 deer per square kilometer or 263 kilograms per square kilometer crude biomass. Ecological densities were estimated during the July-September drought for the study area indicated in Figure 76. Densities may reach twelve per square kilometer for a biomass of 544 kilograms per square kilometer.

The axis are the most numerically abundant of all ungulates in the Park and account for the greatest biomass. Only the hare (*Lepus nigricollis*) approximates the same numerical density, although its biomass is 7 to 8 percent of the axis. The numerical density of elephants is much less than that for axis yet at crude density the elephant almost approximates the axis in biomass. At ecological densities, the elephant may exceed the axis in biomass by a factor of three (see pages 101-103).

THE SAMBAR (*Cervus unicolor*)

Description and Age Classes

The sambar is the largest member of the family Cervidae found on Ceylon (Figure 33). It has a wide tolerance for different habitat types being found from the Horton Plains at 1,800 meters elevation down to sea level in the lowland dry zone. Stags are almost 150 centimeters at the shoulder, does are about 30 centimeters shorter. Stags may weigh up to 216 kilograms, does generally average slightly less than 136 kilograms (Phillips 1935). The young fawn is generally somewhat paler in color that the adult and does not exhibit spotting as is the case with so many young of the Cervidae.

For the purpose of our censusing, we distinguished the following age and sex classes: Adult females were individuals approximately 120 centimeters high at the shoulder. Individuals less than 120 centimeters were classified as juveniles. Fawns were small individuals less than 90 centimeters high at the shoulder.

The following classes were distinguished in the males: Adult males were those considered to be three years and older, exhibiting three pronounced tines on

FIGURE 33.—Sambar deer, *Cervus unicolor*. Adult male entering his third year with hard antlers. Villu habitat.

their antlers. We divided these into three subclasses, those with hard antlers, those with shed antlers, and those with antlers in the velvet. Two-year old males or prong bucks were again divided into the classes with antlers, with velvet antlers, and with shed antlers. Spike bucks or bucks between twelve and twenty-four months of age were classified as either velvet or hard antlered individuals.

Grouping Tendencies

In one year 250 sambar individuals were sighted. Of these 230 were classified with respect to age and sex classes, with 60 percent of all sightings being of solitary individuals. Out of 145 groupings, 88 were solitary individuals. Group sizes ranged from two to eight in descending frequency (Figure 34). Of all adult females sighted 82 percent were accompanied by another individual whereas only 45 percent of all adult males, exceeding three years of age, were accompanying or accompanied by a second animal. This species appears to move and feed alone except for the female and an attendant juvenile or fawn. The fawn, during the first three months of its life, does not consistently follow the female but appears to rest alone. The female returns to the fawn at set intervals; however, the following tendency by the three-month old fawn is rather pronounced and indeed the "family group" does not appear to split up for at least two years.

Assemblies of sambar can occur at restricted places, apparently based on a traditional habitat use pattern. Water holes are places where the sambar population in a given area comes together in the late evening to form temporary aggregates before dispersing to feed. There is no evidence for territorial behavior on the part of bucks. The social gatherings are potentiated at known

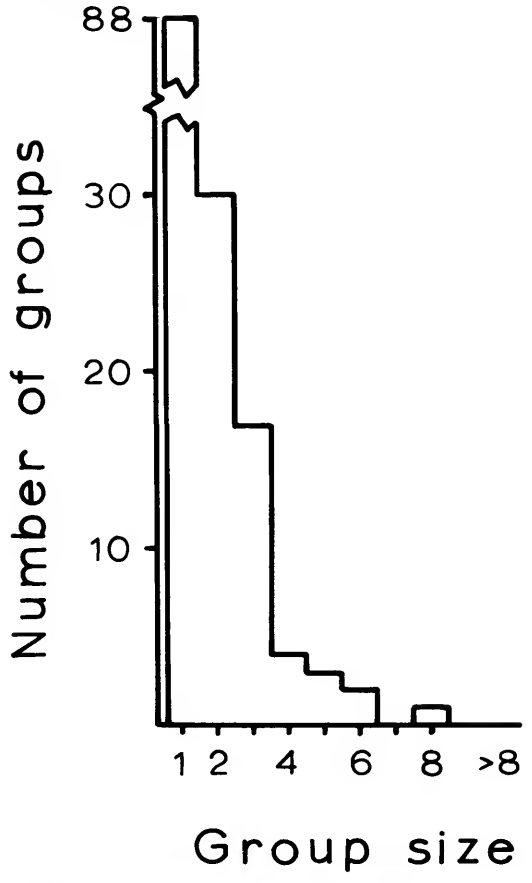


FIGURE 34.—Frequency diagram indicating grouping tendencies for the sambar. Sambar are not nearly as social as axis and the most consistent grouping is the mother and her young, although solitary sightings far outweigh grouped sightings. At certain times of the day and seasons of the year, Sambar may aggregate at water holes. Individuals comprising such a group seem to be known to one another.

areas within the overlapping home ranges. After an assembly the bucks return to solitary foraging unless accompanied by a two-year old or juvenile male. The does typically forage accompanied by a juvenile and/or a fawn of the year.

Habitat Utilization

Our September survey of habitat utilization trends indicated that the sambar do utilize open grassland and scrub areas but generally only at night. In contradistinction to the axis, the sambar will utilize forested areas to a considerable extent; hence, sambar utilization patterns are broader than those of the axis and the sambar show a wider range of habitat types which it can and does utilize consistently. The general pattern of the sambar feeding activity is to browse in the forest during the morning hours, to rest during mid afternoon generally in a shaded, secluded spot, and then to browse again emerging into the open scrub land for grazing at night.

The animals utilize consistent trails much in the manner of axis and as noted in the preceding section assemblies seem to occur daily at preferred watering spots. The male sambar are prone to wallow in the mud or in the shallow water at the edge of the lakes. This is especially true during the drought season when the sambar stags spend a great deal of time in the water. They prefer villus that support a tall grass growth where they can lie in the tall grass and still remain concealed. During the height of the drought, when it is impossible for them to seek water without exposing themselves to the direct sunlight, the males are prone to lie in shaded resting places in the forest which they may use over and over again for as much as six weeks. Such a resting spot becomes well demarcated and fecal deposition often accumulates in such an area over a period of time. In its wallowing behavior, the male sambar differs markedly from the axis, muntjac, and mousedeer; and although the sambar have a high water requirement and appear to drink daily, their large size and mobility gives them a wider foraging radius away from a permanent water source than is the case with the axis.

Social Behavior

The female and her attendant yearling or fawn of the year comprise the most cohesive social unit. Indeed, it would appear that the family group persists for at least two years. Example from field notes:

17 January 1969: On the drive from Panikkar Villu to Borupan Junction, I saw three sambar just short of the junction. This group consisted of an adult female, a female approximately two years old, and a yearling male. This was undoubtedly a family group. This argues strongly for the persistence of the family group in *Cervus* which runs in direct opposition to the tendency found in the North American moose (*Alces*) and is reminiscent of the wapiti (*Cervus canadensis*). It appears that the female makes no attempt to drive away her calf of the previous year when she has a second young.

Although the animals tend to forage as either a mother-family or as a single individual, they do come together habitually at the water holes and temporary groupings of individuals who are known to one another can thus be constituted. Courting behavior and male-male interaction can and do occur at this time.

12 December 1968, approximately 1600 hours, Timpiri Villu: An adult male sambar was observed courting a female. The male had hard antlers and the long hair on his neck was quite evident. He was observed to approach the female in a low stretch posture, sniff at her urine, lift his head, show a flehmen response, and then follow the female, running along side and driving her. Full mating was not observed.

The differences in behavior patterns expressed by juveniles and the more attentive behavior of the female may be illustrated from the following example where a mother accompanied by a yearling male approached a water hole. The young male boldly went forth to drink as the mother remained behind apparently catching my scent. Eventually she gave a warning bark which caused the young male to retreat with her into the forest.

13 March 1969, 1810 hours, Mana Villu: A male sambar yearling with spike antlers in the velvet was accompanied by an adult female presumably his mother. They came to drink. The young male was advancing toward the water; the female following some 9 meters behind. The female stopped short of the water hole and directed her attention toward my blind. The young male continued on and drank but the female did not approach the water, continuing to face me with her tail up, hairs erect, and the white rump patch quite evident. Her ears were fully extended. Then the female turned and trotted at an angle to me while the male finished his drink and started to follow her. The female then stopped, faced me, and gave a warning bark. Immediately she stamped, turned, and trotted off accompanied closely by the young male.

Antipredator Behavior

The foregoing example also indicates the alarm behavior exhibited by *Cervus unicolor*. Alarm behavior includes orientation toward the offensive object, distending the ears maximally, raising the head, raising the tail while spreading the white hairs on the rump, and then either barking or barking, stamping, and moving away or fleeing. The bark is quite distinct from that of the axis being repeated two or three times and quite explosive. As with the axis, the bark of a doe can be distinguished from that of a buck.

Population Trends

An examination of the population data (Table 6) indicates that females probably breed once every two years or 50 percent of the females breed every twelve months. Fawns are probably dropped during the rains in November and are first seen during censusing in December, January, and February. Fawns may be dropped well into March or April. This would indicate that intensive rut probably takes place in December and January following the monsoons.

TABLE 6.—*Population structure of* Cervus unicolor

	Males					
	Adult		*2 Yrs + Yr*		*Females*	*Juveniles*
Selected Counts	(h)	(v)	(h)	(v)	*Adult*	*+ Fawns*
August	–	2	1	–	9	1
October	3	–	–	–	5	1
December	4	4	1	–	6	3
February	15	2	3	–	12	4
April	12	2	–	–	2	1
May	6	–	1	–	22	7
July	1	2	1	–	10	1
Total Counts for 12 months	81	13	12	3	86	26

h=hard antlers; v=velvet antlers; Yr=yearling.

Although leopards have been known to prey on adult sambar (see pages 69-70 on *Panthera pardus*) most of the mortality seems to be inflicted on the juveniles. An inspection of the age classes would indicate that mortality in the males and females is heaviest during their first year and from two years on there is probably insignificant mortality. One could estimate then, between birth and the attainment of two years of age, that slightly in excess of 50 percent of the recruited population dies. We estimate that this effect is inflicted by the leopard.

With an animal that is so shy and nocturnal in its habits, we had great difficulty in achieving an accurate census. Estimates of the number of sambar in the park were based in the ratio of sambar to axis feces recovered in our sample plots (Appendix A). For the whole of Wilpattu Park, we estimate that there could be 700 sambar. This would give a crude density

of 1.17 sambar per square kilometer or a biomass of 158 kilograms per square kilometer; however, a more conservative estimate would be some 400 animals yielding a crude density of .7 animals per square kilometer and a biomass of 93 kg/km^2 (see Appendix A). At ecological densities during the maximum concentration of game during the July-September drought in an area of 24 square kilometers, we estimated that there were twenty-four sambar giving a density of 1.0 per square kilometer and a biomass of 135 kilograms.

THE MUNTJAC OR BARKING DEER

(*Muntiacus muntjac*)

The muntjac is the smallest of the true Cervidae found on Ceylon (Figure 35). The adult males are less than 60 centimeters high at the shoulder and weights range from 15.4 to 20 kilograms (Phillips 1935). The young show spotting until approximately three to six months of age. We distinguished the following age and sex classes: (a) juveniles which still exhibit faint spots, (b) adult females, and (c) adult males which were broken into two classes: subadult males that were obviously in their first year and showing some antler growth in the velvet, and adult males, either with hard antlers or velvet antlers. During the twelve-month survey a total of ninety-two muntjacs were seen of which seventy- nine were classified. Males were sighted forty-nine times, females twenty-eight, and juveniles were sighted only twice.

The mobility of the muntjac is not at all high and the greatest population densities appear to be in the vicinity of permanent water. The animals are quite secretive and could best be seen in the evening when emerging from the forest to graze or drink. Best counts could be obtained during the drought when they may

FIGURE 35.—Muntjac or barking deer. During the height of the drought the deer will continue to use villus which have virtually dried out.

come out at midday to seek water. The animals both browse and graze but no estimate of the extent of habitat utilization could be made.

Of all sightings, 83 percent were of solitary individuals. The largest temporary grouping observed consisted of three individuals. An adult male and yearling male were sighted together four times. Of other double associations, seven consisted of a male and a female and one sighting was a female with a juvenile. Observations at the National Zoological Park suggest that the juvenile or fawn does not accompany the mother during her foraging trips but remains concealed and spends much of its early life resting alone; hence, the ability to see juveniles is vastly reduced under field conditions.

The muntjac is termed the barking deer because of its characteristic warning cry when it is startled. Typical responses of the muntjac subjected to an alien stimulus include tensing the body, orientating toward the disturbance, extending the ears, raising the tail, and erecting the white hairs on the rump; it then springs or runs rapidly away. At a fast walk the animal locomotes by using a pacing gait but it can spring and bound if greatly frightened. When mildly aroused, it may flee while uttering low growls. Generally the bark is not delivered until the animal stands and orientates to the potential disturbance; then it is in a more secure position. They are loathe to come out in the open during daylight hours and are very wary at that time. The bark is long and quite loud, very reminiscent of a hound's bark. It may be repeated several times.

13 March 1969, 0945 hours, Kumuttu Villu: Three axis are grazing at the villu edge. An adult female muntjac is in view approaching the water and a young adult male is near the water hole also in the open. As the female moves toward the water, she apparently becomes aware of my presence because I am standing slightly up wind. At any rate, she becomes startled, erects the hair on her tail, raises the tail, and orientates toward me. Suddenly she bounds away and, as she leaps, she gives a series of low growls. Then in the forest she gives three very loud barks, much like the bark of a dog. At the moment she started to flee, it caused a similar reaction on the part of the young adult male who ran into the forest in a different direction. Interestingly enough, the axis do not flee and do not seem to take very much notice of the warning cry of the muntjac other than to raise their heads.

Our data do not permit an analysis of population trends. We can only estimate the numbers of muntjacs by estimating the numbers utilizing permanent water sources and then multiplying the known permanent water sources by this estimate. We arrive at a figure of 264 muntjacs as a park population with a density of .44 per square kilometer and a crude biomass of 13.5 kilograms per square kilometer.

THE MOUSE DEER (*Tragulus meminna*)

This is the smallest Artiodactylan found on Ceylon, being slightly under 60 centimeters in length with field weights ranging to 4 kilograms (Phillips 1935). The male is characterized by a set of protruding upper canine teeth, a feature shared in common with the buck muntjac. No antlers are present. The basic ground color of the coat is brown; the ventrum is light yellow; the dorsum is marked with a series of spots and stripes on the neck with a broken spotted pattern on the sides and back (Figure 36).

In censusing we attempted to separate males, females, and juveniles; however, we contacted only eighteen mouse deer in the course of our operations. Since the animal is nocturnal in its habits and quite secretive, we were unable to determine the age and sex of the specimens which were sighted for brief intervals, and as a result, no general conclusions concerning the population or sex ratios can be made.

All sightings were of solitary individuals. The mouse deer's small size, nocturnal habits, and color pattern are shared by unrelated mammals occuping similar ecological niches in the Old World and New World tropics. These include the caviomorph rodent, *Cuniculus paca*, and the closely related water chevrotain, *Hyemoschus aquaticus* (Dubost 1968).

When we were making foot surveys around large water holes, mouse deer were frequently encountered but seldom seen as they ran off in the underbrush. They have a typical warning cry when startled which is a sort of reedy grunt repeated two or three times while they are running. In traversing areas around water holes, we have come to the conclusion that several individuals utilize a water hole and the surrounding brush area for foraging. It would appear that they are organized in a small "community" and, although they move alone in the forest, they must surely come together for breeding purposes and the female-young unit must persist at least through the lactation period. It would appear that individuals have a rather consistent home range. A female near our camp was sighted on several occasions; however, we cannot say to what extent given home ranges overlap.

FIGURE 36.—Mouse deer, *Tragulus meminna*. Note the striped and spotted coat present in the adult characterizes this nocturnal ungulate. (Photo by M. Hladik.)

The enlarged canines of the male mouse deer are useful in defensive behavior. When we caught a live mouse deer in Yala and attempted to restrain it, it jerked its head suddenly to one side laying open the finger of the handler. The hoofs are also quite sharp and by kicking the animal can deliver a rather nasty wound.

From the work of Davis (1965) on *T. javanicus*, it is known that the female becomes sexually mature at 4½ months of age. Breeding season in captivity appears to be nonexistent since births occur in almost every month of the year. The litter size for this species is invariably one. The females come into a postpartum estrus within a few hours and can conceive at that time. Gestation is around 155 days or slightly over 5 months. If these figures prove correct for the species *T. meminna*, then conceivably a female could produce two young in a given year.

Little can be said concerning the population dynamics of this species. We have noticed that during the drought the animals apparently suffer from a lack of water and, during drought seasons in Wilpattu and Ruhunu Parks, three individuals were captured in an advanced state of emaciation due to dessication. Such a small mammal probably has a limited mobility; hence, we can be reasonably sure that permanent home ranges of this species are in the main confined to areas around the permanent villus and the rivers. Utilizing the same assumptions for the calculation of the muntjac density, we estimate that there may be up to 350 mouse deer within the park boundaries, giving an overall crude density of .58 per square kilometer and an average crude biomass per square kilometer of 1.9 kilograms.

SUMMARY STATEMENT ON THE SMALL FOREST UNGULATES

At this time, we would like to summarize some of our thoughts concerning the behavior patterns of the smaller forest ungulates, i.e., the muntjac and mouse deer. Unless otherwise specified, the following remarks apply to both of these species. A glance at our census data will indicate that these animals are generally seen alone. We tend to think of them as solitary in their habits. They feed, drink, and rest separately from other members of their species. It is evident, however, that the animals do come together at appropriate seasons of the year for mating and that some continued contact must be maintained between the mother and her young during the lactation phase. It would appear that, in the early life of the fawn, it is left in a secure resting place and the mother returns to it to feed it. Following on the part of the fawn probably starts at the age at which the youngster can escape on its own if necessary. It would seem that the male and female home ranges overlap so that the male can contact the female at the time she comes into estrus. Overlap of home ranges probably takes place at water holes and here we have noted male muntjacs attempting to court females.

In the case of the muntjac, some sort of spacing among males is carried out. This has been well described for *M. reevesi* (Dubost 1970). Although yearling males may associate with adult males, we have not seen two adult males in hard antler condition associating together. It is entirely possible that the males are aggressive toward one another and they may indeed mark their territories with secretions from their preorbital glands (Dubost 1970) in a manner reminiscent of the duiker as reported in the literature for the genus *Philantomba* by Aeschlimann (1963) and *Cephalophus* (Ralls 1969). The analogy between duikers and muntjacs is probably valid since they are ecologically comparable in their habits and we would assume convergence in social behavior.

Spacing mechanisms for the mouse deer remain to be investigated. It seems reasonable to assume that the large canines of both muntjac and mouse deer are used in sexual fighting. The antlers of the muntjac are probably employed in a similar fashion.

One can conceive of these small forest ungulates as living in auditory and chemical contact with each other with the home ranges of males and females overlapping (Dubost 1970). Perhaps the home ranges of related females overlap and something similar to the extended mother-family units of the larger cervids is being maintained in a more dispersed pattern. If this is the case, then the pattern approximates the pattern shown by the small solitary cervid *Capreolus*, as reported by Kurt (1968). Indeed, our observations on the mouse deer reported in the previous section reinforce the conviction that, although these animals are dispersed, they are to some extent in auditory contact with one another. This would help to explain the role of the alarm call characteristic of the muntjac and the mouse deer which would at first sight seem to be unrelated to a social function when these animals appear to be solitary. Nevertheless, if home ranges do overlap, and the individuals in a "community" are in auditory contact, then the loud warning cries can serve to alert not only the young but neighbors.

This behavior need not be considered as altruistic since the hypothesis developed by Smythe (1970) would indicate that the original selective advantage for alarm cries and conspicuous markings, such as white rump patches, is to attract the predator's attention toward the prey and induce the predator to give chase since, all things being equal, a healthy prey animal should be able to outdistance a predator if the predator is still outside of its escape distance (Hediger 1950). For an extended discussion of this and its implications, see Smythe (1970). All altruistic derivatives of such warning barks are secondary rather than primary to the original selective advantage which remains with the individual.

THE WILD SWINE (*Sus scrofa*)

Description and Definition of Age and Sex Classes

The swine on Ceylon are quite large; males being almost 1.5 meters in length, with a height at the shoulder of approximately 91 centimeters. Females are slightly less than 60 centimeters at the shoulder, with a head and body length of about 1.37 meters. Males may weigh up to 127 kilograms; maximum weights for females are approximately 57 kilograms (Phillips 1935). In addition to the larger size, adult males are characterized by a rather longer mane down the center of the back and more well-developed canines. Adults are generally a shade of black to gray in color; younger animals appear to be more brown. The very young animals have a rather well-developed coat of hair, being basically a light brown color with longitudinal stripes of yellow-brown on the sides. The stripes are lost at approximately two and a half months of age.

We distinguished the following age and sex classes: Striped young or infants were considered to be less than ninety days of age. A transition class of approximately 70 to 110 days of age exhibit faint stripes. Subadults, both males and females, were identified on the basis of their smaller size. Adult females were those approximately 60 centimeters at the shoulder and/or lactating. Adult males were estimated to be in excess of two years of age and were distinguished by their large size. Males may easily be distinguished from females in both the subadult and adult classes by the presence of the scrotum.

Social Groupings

Over 1,216 animals were counted during the twelve-month census, although many of these counts were of the same individuals, and 184 "groups" of less than 20 were recorded of which 70, or 38 percent, were solitary individuals. Of the solitary sightings, 74 percent were adult or subadult males. The next most frequent group size was in the range of four to six individuals. Larger groupings exceeding ten individuals are rearing groups or "sounders" composed of four to eight adult females and their collective progenies (Figure 37).

To summarize, young males become more solitary from approximately one and a half to two years on. Fully adult males are much more independent of

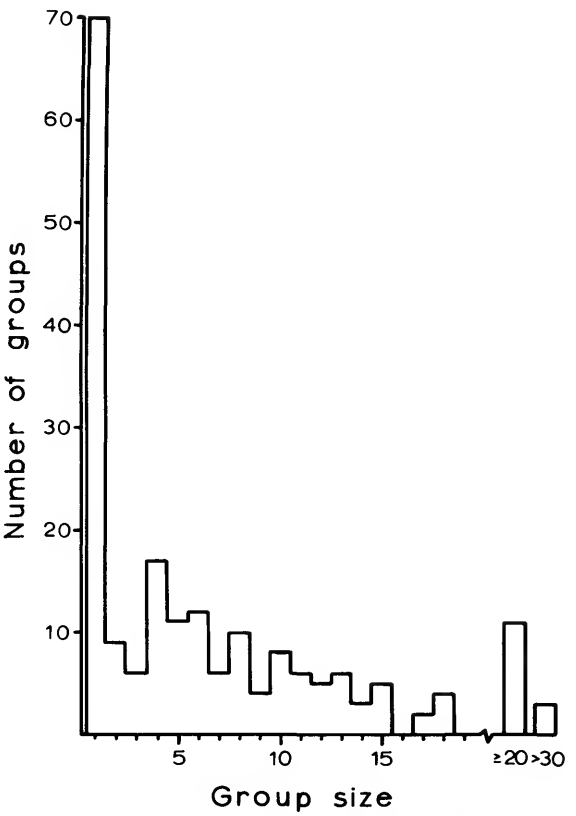


FIGURE 37.—Frequency diagram indicating average grouping tendencies in swine. Adult males account for most of the solitary sightings (see page 55).

sounders and join when the females are approaching estrus. Females become solitary when they give birth but reform into consistent units, thus establishing a rearing group or sounder. Because the young within a sounder are of approximately the same stage of development, we believe that there must be some estrous synchrony in a group of females which travel around and forage together; hence, conception among the females of a sounder is within a few days of one another and the births are generally synchronized.

Reproduction

The female swine has an estrous cycle of about twenty-one days; heat duration is two to three days. The gestation period is approximately four months and the number of young produced varies depending upon the

nutritional state of the female and the actual geographic locality. In Ceylon it would appear that females have from four to six young (Hatt, in Asdell 1964, Phillips 1935).

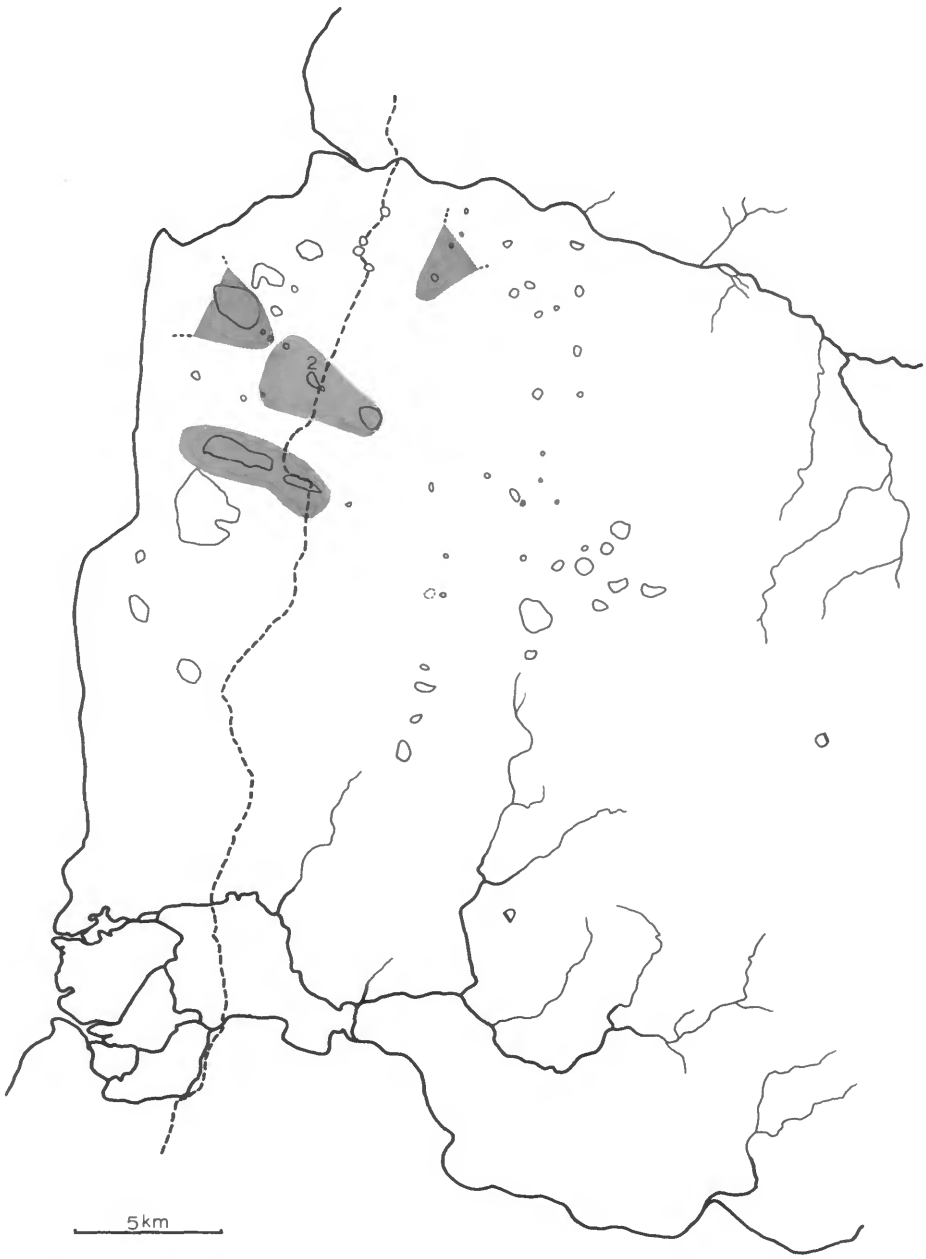


FIGURE 38.—Home ranges for four swine sounders. Home ranges contract and expand depending on rainy or dry season but in general a sounder is quite consistent in its space utilization pattern. This sketch does not indicate the distribution of swine for the entire park.

Distribution in the Park

There is a tendency for pigs to collect and concentrate their activity in the vicinity of permanent water during the dry season. The pig has a considerable mobility and its home range is quite large; however, the home ranges are stable during the drought and they may include several water holes (Figure 38). The pig is definitely dependent on water for drinking and wallowing. Wallowing behavior may be quite brief but seems to be necessary to plaster the skin with mud as added protection against flies. Soaking in water may also serve to aid in thermoregulation at midday during the drought. In the vicinity of a water hole utilized by pigs, one will find rubbing trees characterized by a strip of mud left from the pigs' activities. Pigs will approach such a tree after wallowing and lean against it, rubbing the length of their sides, sometimes pausing to move back and forth. In addition to rubbing the sides, pigs also may mark with their tusks in the bark of trees. Such marks are quite characteristic.

7 December 1968: On the way back from Periya Naga Villu, we stopped at Salamba and examined some bark gouging apparently done by a large pig. Three marks were noted in the bark of a tree approximately 60 centimeters above the ground. There were pig tracks at the base of the tree and the bark below the gouging marks showed evidence of rubbing.

Feeding

Pigs are quite omnivorous in their diet and throughout the annual cycle definite seasonal shifts in their habitat utilization can be noted. With the onset of rains, fungi are prone to grow in the forested areas and the pigs feed on these to a considerable extent, often rooting for these fungi which are subterranean. During the dry season, as we have mentioned before, there is a considerable fruit-fall, especially in the months of July and August. At this time the pigs are very dependent on fruit which falls from the trees.

Swine are able to dig extensively utilizing their mouth and nose to acquire tender roots, especially during the rainy season. They also may root for tubers in the vicinity of water holes leaving a virtual ring around a water hole where the growing plants have been uprooted. As the water retreats during the drought season, such rings may be progressively extended inward, thus giving some index of successive pig activity as the water hole continues to dry up.

In addition to roots, fungi, and fruit, pigs are also prone to eat grass, especially certain species of sedge and the tall grass growing in the vicinity of villus. Grass feeding seems to be particularly common during the rainy season and the grass blades may be picked up almost intact in pig feces at this time.

Pigs will also utilize other vertebrates for food. Small turtles may be fed upon as well as turtle eggs. The habit of rooting up turtle nests on beaches is well known in Ruhunu Park. Although we have no direct evidence, we have no doubt that ground-nesting birds' eggs and rodents are eaten if the pigs can find them. Pigs are also prone to eat carrion and, when a large carcass has been abandoned by other predators, pigs will feed on it until it is reduced to bones. Thus, the pigs, mongooses, and jackals together with the monitor lizards comprise the scavenger component in the community.

Habitat Utilization

Pigs utilize trails in common with deer and with elephants but are by no means confined to trails in moving from one water hole to the next. Very often they depart from a well-worn trail after some hundred feet from the water hole and begin to forage on the forest floor. An examination of the intensity of habitat utilization by swine indicates that it parallels that of elephants. Pigs show a great deal of activity in the vicinity of water holes and in open scrub country. Activity by swine in forested areas is vastly reduced but in the vicinity of riverine forests with associated scrub habitat, pig activity is quite high. Such an intensity of habitat utilization pattern is in conformity with the distribution patterns as outlined in Figure 70.

Summary of Swine Behavior

The discrete behavior patterns of swine have been reviewed in part by Hafez, et al. (1962). Further reproductive data on swine is included in the recent publication by Fraser (1968). Rather than reiterate the general outlines drawn in the main from domestic swine, we will proceed with an examination of those behavior patterns which we observed in the park, urging the reader to make reference to the data from the domestic swine, since it would appear that wild *Sus scrofa* do not depart very radically in their behavior patterns from those exhibited by their domestic relatives.

Activity

Pigs generally show periods of activity both during the day and the night, although diurnal activity predominates. Activity during the daylight hours extends on until about 10 o'clock when the pigs are generally inactive. Depending on the extent of cloud cover and the season of the year, pigs may become active during midday. During the drought period, pigs very often come to water at midday and may wallow at that time frequently before retreating to the shade of the forest. During the rainy season pigs may feed intermittently during the midday if the cloud cover is sufficient. Pigs generally rest in the late afternoon exhibiting increased activity as night approaches and quite a bit of activity takes place in the early evening hours. The extent of their activity during the total dark period is poorly understood.

Patterns of Social Interactions

For a detailed discussion of postures and sounds produced by pigs during social interactions, the reader is referred to Hafez, et al. (1962) and Gundlach (1968).

In general pigs employ chemical marking, auditory communication, and to some extent visual communication in their interactions. During aggressive arousal, a pig generally stands rather erect with the mane extended. The small tuft of hairs in the sacral region of the back may be raised independently of the dorsal crest during mild arousal (Figure 39). An aggressive pig will champ its jaws together causing the tusks to clack. Loud explosive grunts may be given and, if the pig suddenly becomes frightened, it will emit a loud snort, stamp, and wheel to run away. Pigs mark chemically in the vicinity of their wallow by dragging the

FIGURE 39.—Typical sounder of *Sus scrofa* composed of several females and their collective progeny. Note the tendency for the young to collect in the center with adult females in the forefront and rear of the formation. (Photo by M. Hladik.)

per.neal region along the ground, which we have termed the anogenital rub. Also during wallowing they can leave traces of their own body secretions behind during a brief wallow which consists of a side rub, lying on the side, and extending and flexing on alternate sides.

13 December 1968, 1414 hours: Female pig with six young still showing faint stripes emerges from the forest. Female rests in the mud for 95 seconds, then gets up and moves off. While lying on her side in the wallow, the young flock around her and attempt to suckle. Before lying down in the mud for the 95-second period, the female, at the approach to the edge of the villu, paused to rub her anogenital area in the mud and then to rub alternately her left side and her right side.

Male-Male Interaction.—Subadult males may associate together within the same sounder but fully adult males are generally solitary. Aggressive attacks by an adult male toward subadult males are rare but may manifest themselves when there is competition over females in estrus. It would appear that subadult males, even though traveling with the sounder, have a limited opportunity to breed, since at the time the females come into estrus, an adult male is usually in attendance.

14 January 1969, Kali Villu: Two males are in association with five large adult females, four subadult females, and one immature male. The two adult males show frequent aggressive interaction with each other. One large adult male with tusks was attempting to court a sow and periodically chased off the second adult male. The second adult male will approach the female but if too close to the estrous female, the first adult (Alpha) male will orientate toward him, approach, and suddenly chase for about 9 to 12 meters only to stop and then turn broadside to the male. At this time his mane is raised and his whole appearance in size is increased; generally the subordinate male will hold his position or withdraw further. Adult boars such as these two fighting males are easily distinguished from subadult males. Although subadult males have large descended testes and run with the herds, their tusks are poorly developed and they are much more slightly built than the fully adult males.

Male-Female Behavior.—As indicated in the previous section, subadult males will travel with sounders and, although they attempt courtship, they are not usually successful because of the presence of fully adult males. An example of sexual behavior demonstrated by an adult male toward an estrous sow is given.

14 January 1969, 1400 to 1530 hours, Kali Villu: At the north shore of the villu, there are two large adult male pigs, five large adult females, four subadult females, and one immature male; divided into two subgroups. One adult male with tusks was attempting to court a sow and periodically chased off a second adult male. The estrous sow raises her mane, squats, and urinates in a mud hole, slightly dipping her hind quarters and rubbing her ano-genital region as she moves away. The adult male standing behind her sniffs the urine, raises his mane, then follows the female. This adult male attempts to follow the female from time to time and stands near her. Such courtship continues with attempts on the part of the adult male to mount the female.

Female-Female Behavior.—As indicated under the section on "social groupings," females will retire to give birth to their young but then reform into a sounder or a group of females which apparently acts in common to defend their young. The young begin to follow the female at approximately two weeks of age and that is the time that we first note their presence. There appears to be no strict leadership in the sounder although older sows are often seen to take the initiative in moving. There appears to be little discrimination on the part of a sow with respect to her offspring; hence, whenever a sow lies down most of the youngsters in the vicinity will attempt to nurse. Thus, there is some cooperative nursing effort on the part of sows in a sounder which is reminiscent of what one observes among elephant cow herds.

Adult-Young Relationships.—The young pigs, when they begin to follow the female, have to be very independent in their movements. Most of the social interaction within a sounder, aside from the nursing, takes place among the youngsters and juveniles.

15 August 1968: A group of pigs is under observation at Timpiri Villu. The group consists of a male, a female, and one juvenile. The adults are rooting in the soil near the edge of the water hole. The juvenile keeps dashing around the adults and attempting to join them in their rooting behavior. He is definitely pushed away by a head toss on the part of one of the adults. While rooting the pigs are kneeling on their wrists with the hind legs extended. The male walks over to a small depression near the edge of the water and rolls on his side. The juvenile approaches and lies down beside him; then both get up and move off to join the female.

When a sounder is moving with young pigs associated, very often several sows will take the lead followed by the piglets with a sow or a subadult male bringing up the rear or moving to one side of the young (Figure 39).

13 August 1968, 1315 hours, near Kumbuk Villu: Observed seven adults and approximately ten young. The band consisted of three males and four females. During movement the animals were strung out in a line with the three adult males in the lead, the young in the middle, and the four females bringing up the rear. One of the females, however, was walking parallel to the group of youngsters.

At other times, however, if a lone female is with a group of young, she will usually bring up the rear.

13 December 1968, 1410 hours, Marai Villu: As the sounder begins to leave, consisting of a female and six young with faint stripes still visible, the female moves slightly up wind with the youngsters ahead of her. The youngsters are moving along in a group and she is following behind and seemingly guiding them to some extent and nudging them with her snout. This is a case of a single female moving with a group of almost juvenile young. She does not lead but rather encourages them to move ahead of her while she brings up the rear.

Nursing is very brief in the sow, rarely lasting over a minute in duration. At the time that a sow lies down, the young will immediately group around her and attempt to nurse (see page 59).

Interrelationships of Young Pigs.—It may be useful to quote from an extended set of field notes concerning the behavior patterns of young swine when a sounder is feeding near a water hole.

14 March 1969, 1240 hours, Marai Villu: A sounder of pigs enters the cleared area immediately in the vicinity of the villu. There are eight adult females, all lactating, and twenty-four to thirty striped young, three juveniles, and one subadult male in the transition age class. The adults drink and root. After approximately 10 minutes of observation, most of the adults have now rubbed their ventrum and perineum in the mud at the water's edge. One sow finds a dead turtle and carries it by the hind foot to the water's edge. The young show continued motivational shifts; they root, run, attempt to suckle, mount each other, mock fight with each other including headbutting, chasing, and biting at each other, rolling and tumbling together, and then they will break off, attempt to suckle, or root—there is continuous activity. Two young have risen on their hind legs and are tussling with their forefeet around each other; they toss their heads, batter with their heads, and chase one another. At one point, there is a confusion effect as the adult sows form two subgroups and begin to move in opposite directions. Piglets run back and forth as the sows split. One sow lies down and immediately the young in the vicinity approach her and begin to suckle for about one minute. This is at the water's edge.

A detailed analysis of the behavior of young swine is discussed by Gundlach (1968).

Antipredator Behavior

When surprised by a predator, such as a leopard, the sounder may immediately begin to disperse in various directions, running rapidly, creating a confusion effect. A predator, however, may be confronted by a pig and the pig will show a direct aggressive behavior, especially if it is an adult, including mane erection, champing of the jaws, and even short rushes. This may be shown in response to jackals and, indeed, it seems that an adult pig might well be a match for a leopard. An interesting piece of antipredator behavior was recorded with respect to crocodiles:

14 March 1969, Marai Villu: The same sounder [referred to above] is present. While a sow is nursing the young, a crocodile begins to move up close to her. It appeared for a moment as if the crocodile intended to grab one of the piglets but suddenly the crocodile makes a slash with his head only to grasp a dead turtle. As he did this, the male and one sow noticed the crocodile and immediately oriented toward him. The male lip-curled and champed his tusks together. The nursing female rose and moved away followed by the piglets.

Interspecific Relationships

Responses to predators will be discussed in the following section. Pigs in general give way to elephants and there is very little interaction between pigs and buffalo, or pigs and deer. The cleaning of pigs by mynahs is of some interest.

15 February 1969, 1505 hours. A male pig has finished feeding and is lying down near the water. Two mynahs light on his back. After about two minutes, one mynah remains clinging to his left hind leg apparently cleaning ticks from the vicinity of his scrotum. On the third minute, he lay on his left side. The mynah continues to clean. At 1509 hours the male pig continues to feed and the mynahs have left him.

Population Trends

Table 7 presents a summary of the age class and sex class distributions of pigs throughout the annual cycle. It is rather difficult to arrive at a consistent population figure for the swine since they breed over a broad period of time and have reasonably large litters. Furthermore, the mortality is rather high during the first two months of life; hence there is a continual fluctuation in numbers. Breeding appears to take place during the rainy season of October, November, and December and again during February, March, and

TABLE 7.—*Population structure* of Sus scrofa *for central villa area*

Quarterly Counts	*Adult* ♂	*Subadult* ♂	*Adult* ♀	*Subadult* ♀	*Juvenile*	*Young* * f-st	*Young* * st
Aug.–Oct.	1	8	8	–	9	10	–
Nov.–Jan.	2	6	15	2	7	–	6
Feb.–Apr.	9	7	28	2	4	8	27
May–July	12	5	51	7	12	20	21

* Values alter during three-month survey, see Figure 40; numbers recorded indicate the high count.

f-st=faint stripes, st=stripes.

April. Most intensive breeding probably occurs during the fall rains (Figure 40). Mortality is extremely high and up to 50 percent of newborn pigs are lost within the first month of life. Table 7 indicates that mortality may continue at a diminished rate through the first year of life but that the adults are relatively invulnerable to attack from predators. We have estimated the crude density of pigs within Wilpattu Park to be at approximately 180 individuals or .30 individuals per square kilometer. This would yield a crude density biomass of 8.1 kilograms per square kilometer. At ecological densities during the drought concentration, the crude density per square kilometer may reach 1.16 with an average biomass per square kilometer of 31.3 kilograms.

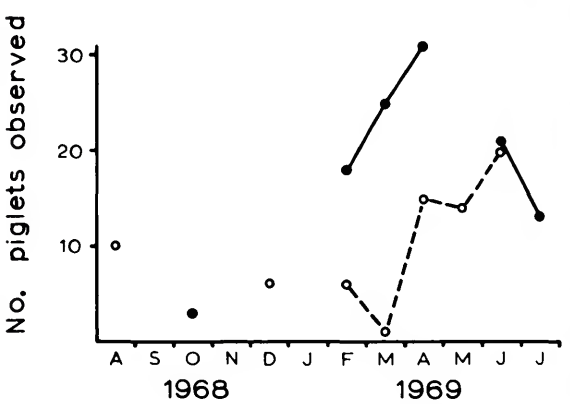


FIGURE 40.—Young swine may be born during any month of the year but there appears to be a peak production from February to May. Mortality is high, as is indicated by the lower dotted line which shows the number of juveniles losing their stripes, being recruited in from the population produced in the preceding months. Black dots=young less than six weeks of age; open circles=young from six to ten weeks of age.

THE JACKAL (*Canis aureus*)

Description and Social Organization

The golden jackal of Ceylon is the size of a medium dog. Adults are about 122 centimeters long from the tip of the nose to the tip of the tail and stand approximately 61 centimeters high at the shoulder (Figure 41). Weights can reach up to 9 kilograms (Phillips 1935).

Jackals are organized into social units based on a pair bond which persists throughout the annual cycle.

FIGURE 41.—Female *Canis aureus*, the Ceylon jackal.

Some eighty-four jackals were counted in the park and this count avoids duplication of the same individuals. Jackals are generally seen in groups and the most frequent grouping is a pair or three individuals. Most of the remarks for the rest of this discussion are based on the observations we made with two families; one family at Marai Villu and the other at Pannikar Villu.

The group at Marai Villu was first contacted in July 1968 and at that time consisted of two adults and two juveniles. The juvenile animals were a male and a female. The young male disappeared from the group between December and January. The old female exhibited lactation in March, and in June the two juveniles of the year were brought forth into the group giving a total of five animals at Marai. In July and August the younger female disappeared reducing the Marai Villu group to four again. Hence, it would appear that in Wilpattu Park the average social group consists of a bonded pair and their offspring of the year. Apparently daughters may stay with the parental group for at least one annual cycle but young males appear to disperse early.

Distribution in the Park

An inspection of Figure 41 demonstrates that jackals tend to be localized in the vicinity of permanent water holes. It would appear that only a single family group occupies a given home range. The spacing is reminiscent of a territorial pattern. The home range of the Marai Villu group included Kali Villu on the east and Salamba Villu on the west. The extent of the home range then exceeded 4 kilometers. One got the distinct impression that the male jackal was able to cover the whole range at least once in twenty-four hours.

Behavior Patterns

From about 1000 to 1400 hours, jackals are not particularly active. They commence hunting activity from approximately 1600 hours on. Howling was heard only after dusk. During midday jackals will rest in the shade, or if cloud cover is heavy, they will rest in the open near the villu edge. We have hypothesized that the moist soil may have some cooling effect for the animals and by keeping its fur moist the jackal may promote thermoregulation through evaporation of water from the body fur.

Male jackals mark throughout their home range depositing urine in a typical dog-like fashion. After dark, contact may be maintained among jackals of the same group through howling.

7 December 1968, 1920 hours: Jackals howled tonight but not simultaneously. There are two or three preface notes which are groan-like in their tonal quality and then a wail which varies in pitch. There was one call from approximately 137 meters to the north of the camp, two calls about 46 meters north of the camp, and one call some 68 meters south of the camp. These were apparently emitted in response to one another and indicated the current position of the calling animals.

The interaction patterns are quite dog-like in their form. For example, a greeting ceremony between an adult male, a lactating female, and a second female:

15 March 1969: Both adult animals roll in the grass and are joined by their daughter. At first interaction the second female crawls toward the pair on her belly. The old male urine marks twice between bouts of rolling on the ground. The second female sniffs the spot where the male urinated and then exhibits an open-mouth with tongue extended, looking around. This is reminiscent of the flehmen response of female cats to male urine.

Interactions between an adult male and an adult female may vary in their form.

Male approaches female, nose to nose with her. Male runs off as female bares her teeth at him. Male walking with fluffed tail carried upright at an angle; walks to a grass tuft, cocks his leg and urinates. Female approaches male. Male lip-curls with his muzzle tense, he moves away. Female sniffs the urine spot then sits and licks her ano-genital area. The two young jackals are circling the villu and return to the opposite side where the parents are located. All four now rest together except for the young male who remains approximately 18 meters from the three other animals.

A further example of encounter behavior:

Adult male approaches adult female who is lying down. The male flops on his side with forelegs extended and his lips curled; tilts his head back in front of the second animal. The second animal, the old female, begins to groom on the head and neck of the male. Male then rolls on his back with his forepaws crossed on his chest; second animal licks on his neck, chin, and chest. Then the second animal stretches and presses its nose on the ground and rolls its shoulder in the earth, stretching and sliding on its side, thus marking on the grass or perhaps impregnating its body fur with an odor trace present on the grass.

A further example between an adult male and one of his juvenile offspring:

Adult male turns to approaching juvenile. The juvenile moves away with his tail down, then the juvenile turns and approaches; they touch nose to nose and begin to engage in typical dog-like play; that is, rushes and snapping at each other, and short chases. The adult male approaches the adult female and grooms her on the nape of the neck and side of the neck while the female sits upright. The male extends his grooming to the neck and chest. The male goes over to a pile of bones which are the remains of a carcass and approaches the adult female with a piece from the carcass; he drops the food before the female and both commence to eat. One juvenile approaches the feeding pair but does not feed while the adults are occupied with the bones.

The social structure and interaction patterns of the jackal are typical of many canids which form family groups. The general trends conform to the review presented by Kleiman (1967).

Predation Behavior

The jackal is an opportunistic feeder, hunting ground-nesting birds, rodents, hares, and utilizing the remains of leopard kills. The jackal, however, should not be underestimated as a predator since it will attempt to hunt the fawns of axis and does this with considerable success. They generally hunt in pairs or the whole family group can participate in cooperative hunting. For purposes of illustration, we quote from field notes on hunting behavior.

8 December 1968: Forty-three axis are feeding to the northwest of the camp. A jackal entered the subgroup of females and fawns. The females and their young immediately exhibited the raised tail and orientated toward the jackal. As the jackal continued to approach them, individual females with their young would move away. Suddenly a group of females and young ran. Two more jackals emerged from the forest and joined the first in trotting after the fawn. Females and fawns entered the forest. No further action was noted. At 1345 hours, however, the jackal initiated a chase with a fawn which was detached from its mother. The fawn began to run toward the forest edge when it was intercepted by the second jackal waiting near the forest. This second jackal made an attempt to snap at the fawn but the young deer leaped to one side and continued to run to the safety of the forest. While this was going on, the remainder of the herd took no notice of the jackals. Around five minutes later when the jackals approached the deer herd and lay down, no warning or attentive postures were shown by the deer.

Marai Villu: All four jackals running along the forest edge by the villu until suddenly one of the four deflects and moves toward the water's edge while the others disperse in the forest. The three remain almost concealed in the forest shifting back and forth while oriented toward the fourth jackal which is now near the edge of the villu. This animal employs a zigzag walk oriented laterally toward the villu edge, as it approaches a feeding lapwing. The lapwing begins to move away from the jackal and the jackal does not attempt to pursue but rather herds it slightly until the lapwing is walking away from the water and directly toward the spot where the other three jackals are waiting in ambush. Suddenly the fourth jackal begins to chase the lapwing which runs rapidly toward the edge of the forest and then starts to fly at the last minute as one of the three jackals in the forest breaks cover and attempts to catch it. All jackals then come together and touch noses with tails wagging. They move together as a group of four when, all of a sudden, an individual detaches and heads toward the edge of the villu and the whole ambush process is repeated.

Population Structure and Dynamics

It would appear that a given jackal family breeds once a year. Breeding seems to take place in December or January. An inspection of Figure 42 will give some idea of the patterns of habitat usage by the families. We estimate that there are less than 120 jackals in the park. This is a much lower density than one encounters in Ruhunu Park and perhaps the low density is effected through the predatory activities of the leopard.

THE SLOTH BEAR (*Melursus ursinus*)

The sloth bear is the only member of the family Ursidae found in south India and Ceylon. It is a rather small bear with adult weights seldom exceeding 113 kilograms (Phillips 1935). Sloth bears were only encountered twenty-four times by the survey team. In general, its distribution in the park conforms to the same trends as outlined for the jackals; that is, the sloth bears are found within a reasonable distance of permanent water (Figure 42). Although the sloth bear may be active in the morning and late afternoon, it is also active throughout the early hours of the evening and two of our encounters were with animals after dark.

An inspection of the feces of the sloth bear indicated that they fed heavily on termites and fruit. During August when the palu tree (*Manilkara hexandra*) drops fruit, sloth bear feces contained large quantities of these seeds. In a similar fashion the seeds of the vira (*Drypetes* sp.) may be noted in the feces during the fruiting season.

When the sloth bear is feeding on termites, it seems oblivious to any observer. The bear will move along

with its nose to the ground continually sniffing and pausing from time to time to extend its lips and suck rhythmically at insects which have been exposed by tearing open a log or a termite mound.

The sloth bear apparently does not prey on any of the larger game species. We have seen bears feed approximately 4.2 meters away from axis and the deer in no way seemed disturbed by the bear's presence.

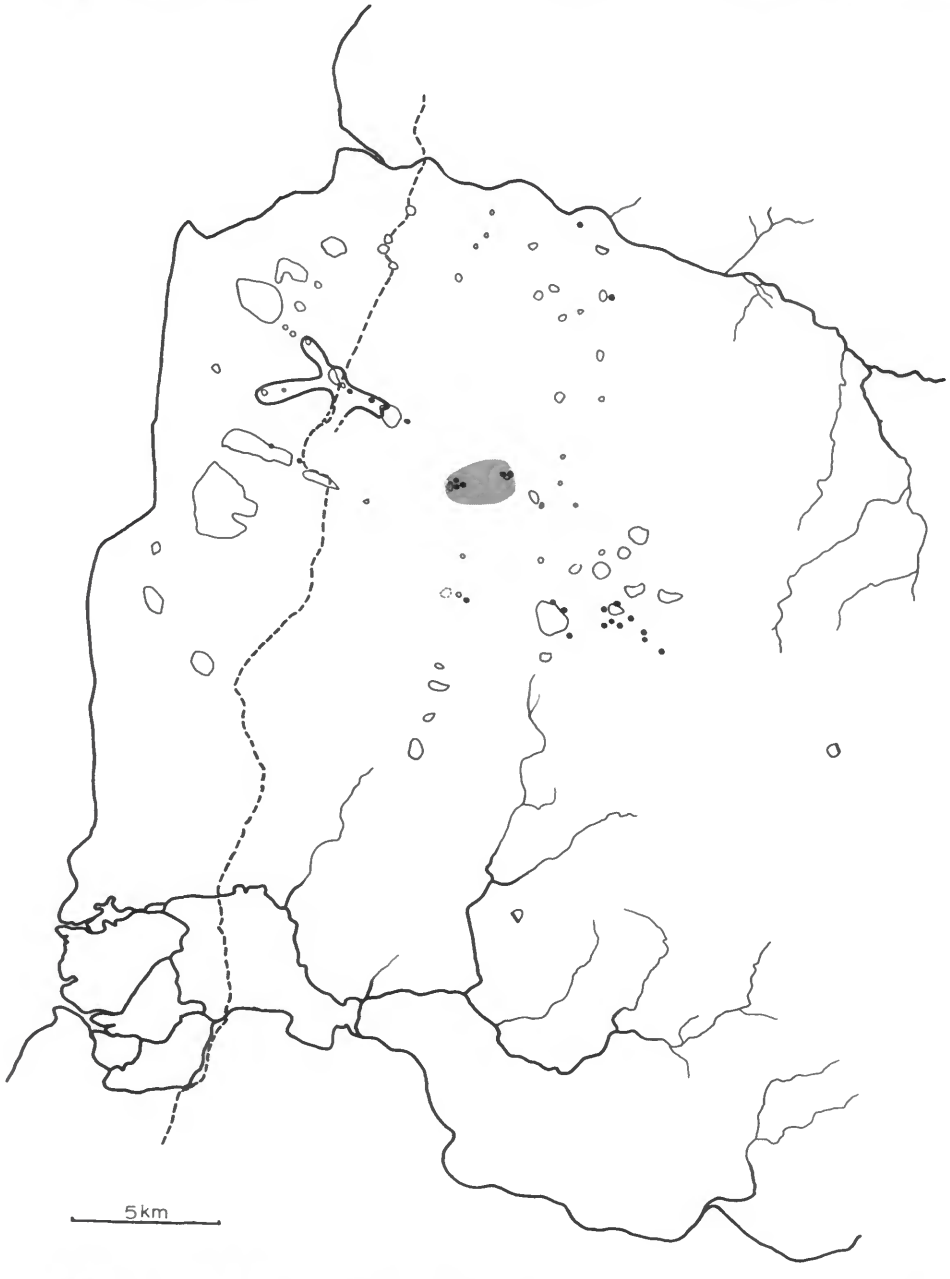


FIGURE 42.—Home range for one jackal family (black lines) and a female sloth bear with young (shaded area). Dots indicate sightings of other sloth bears within the monthly survey area.

FIGURE 43.—*Melursus ursinus*, the sloth bear.

During the course of our study, one female gave birth to a cub which accompanied her throughout its first year of life. The mother and cub seemed to have a home range which included Kumuttu and Kanjuran villus (Figure 42).

This mother-young unit which was also observed in Ruhunu Park seemed to be the only permanent social grouping that the sloth bear exhibits. The female sloth bear will carry the young on her back until it is approximately six months of age. The female has a rather heavy pad of fur between the shoulders which seems to serve as a place of attachment for the young. Carrying the young in this manner seems to be unique among bears, and we have noted the same phenomenon for the two births of *Melursus* at the National Zoological Park (Figure 43).

THE LEOPARD (*Panthera pardus*)

The leopard was observed frequently in Wilpattu Park and during a twelve-month period 113 animals were contacted in the course of 96 separate encounters. Approximately 700 minutes of direct observation were logged, averaging slightly less than 10 minutes with each contact.

Ceylon would appear to offer a unique opportunity for studying the leopard, since it is the largest carnivore on the island and is in no direct competition with the tiger and lion, which is often the case in other parts of its range in southeast Asia and Africa. As a consequence the leopard on Ceylon is much bolder. It spends a good part of its time on the ground and stalks about in the open in a manner more reminiscent of a small lion (Figure 44). Solitary leopards were

FIGURE 44.—*Panthera pardus*, the leopard. Young adult male utilizing a jeep trail as a route from the vicinity of Kali Villu to Kanjuran Villu.

sighted seventy-eight times; eighteen sightings included two individuals in each sighting. Of the couplets observed, ten observations were made on adult male-female combinations; four were of adult females accompanied by a juvenile, and four others were not classified with respect to age and sex classes. All sightings of leopards were made during the daylight hours with the exception of three instances. Of the ninety-six sightings, ninety-three were of animals traveling on the ground and only three were of animals in trees.

As indicated in the introduction, the park may be divided into two rather separate ecosystems; the riverine system and the villu system. In the villu situation

we were able to make rather good observations on the movements of leopards and their distribution in space and most of the remarks made in this section refer to the population living in the villu habitat.

Home Range

In the villu habitat, the home range of a given leopard is rather small. For four individuals we have recorded home ranges of less than 8 square kilometers and the maximum was 10 square kilometers in area. Within its home range the animal may move almost from one end to the other within a twenty-four-hour period. The greatest linear movement determined for a leopard during twenty-four hours was approximately 5.5 kilometers and that was recorded for a young male (Table 8).

TABLE 8.—*Leopard home ranges*

Animal	*Sex and Age*	*Greatest Dimension* (km)	*Minimum Estimated Area** (km²)
A	♀ – 2 cubs	2.5	?
B	♀ – 1 cub	3.5	8
C	♂ and ♀	4.0	10
D	♂ solitary adult	5.5	9

* Home range shifts can alter the total area traversed.

The quality of a leopard's home range varies considerably depending on the nature of the small lakes or villus contained within it. If the home range contains one of the larger villus with a circumference exceeding 4.8 kilometers, there will be a large number of deer utilizing the habitat and an excellent food supply for the leopard so that it can feed repeatedly around the perimeter of the lake without causing too much disturbance to the resident game animals. On the other hand, if the home range contains a number of smaller villus with circumferences of less than 800 meters and with corresponding lower densities of game, it is generally the habit of the leopard to move from one villu to the next within its home range making a circuit; staying at one villu for three or four days, then shifting to the next for perhaps two days, and then shifting again, gradually coming back to its starting point (Figures 45 and 46).

The question may be raised as to whether a home range of 8 or 10.5 square kilometers will support a leopard and, in order to answer this question, we offer the following evidence: The crude density and biomass of the various herbivores resident in Wilpattu Park has been calculated based on our twelve-month census. The biomass expressed in kilograms per square kilometer for the park is on the average 766. If we delete the elephant and the adult buffalo from the biomass calculation which are generally not available to the leopard and if we assume a 10 percent cropping rate by the leopard, then approximately 47.6 kilograms of animals per square kilometer would be available (Table 10). If we assume from our data on captives at the National Zoo that 950 kilograms of meat are needed to support one leopard for a year and if we further assume that 1,360 kilograms of meat killed will furnish 950 kilograms for the leopard with 400 to 500 kilograms for

TABLE 9.—*Leopard predation analysis*

Prey Species	*Attempted Kill*	*Actual Kill*	*Feces*			*Total*
			Skeleton	*Bone*	*Hair*	
Axis	3	1	7	2	1	14
Sus	–	–	6	2	–	8
Cervus	–	1	–	–	–	1
Presbytis	1	–	–	–	1	2
Lepus	–	1	–	–	1	2
Hystrix	–	–	1	–	–	1
Bubalus (calf)	–	1	–	–	–	1
Total						29

TABLE 10.—*Theoretical minimum biomass available to leopard per square kilometer* (assuming a minimum of 10 percent cropping at crude densities; buffalo calves are not included)

Species	*Number*	*Kilograms*
Axis axis	.58	26.3
Cervus unicolor	.12	15.8
Sus scrofa	.03	.8
Muntiacus muntjac	.04	.6
Tragulus meminna	.06	.2
Hystric indica	.06	.5
Lepus nigricollis	.4	1.5
Presbytis entellus	.28	1.9
Total		47.6

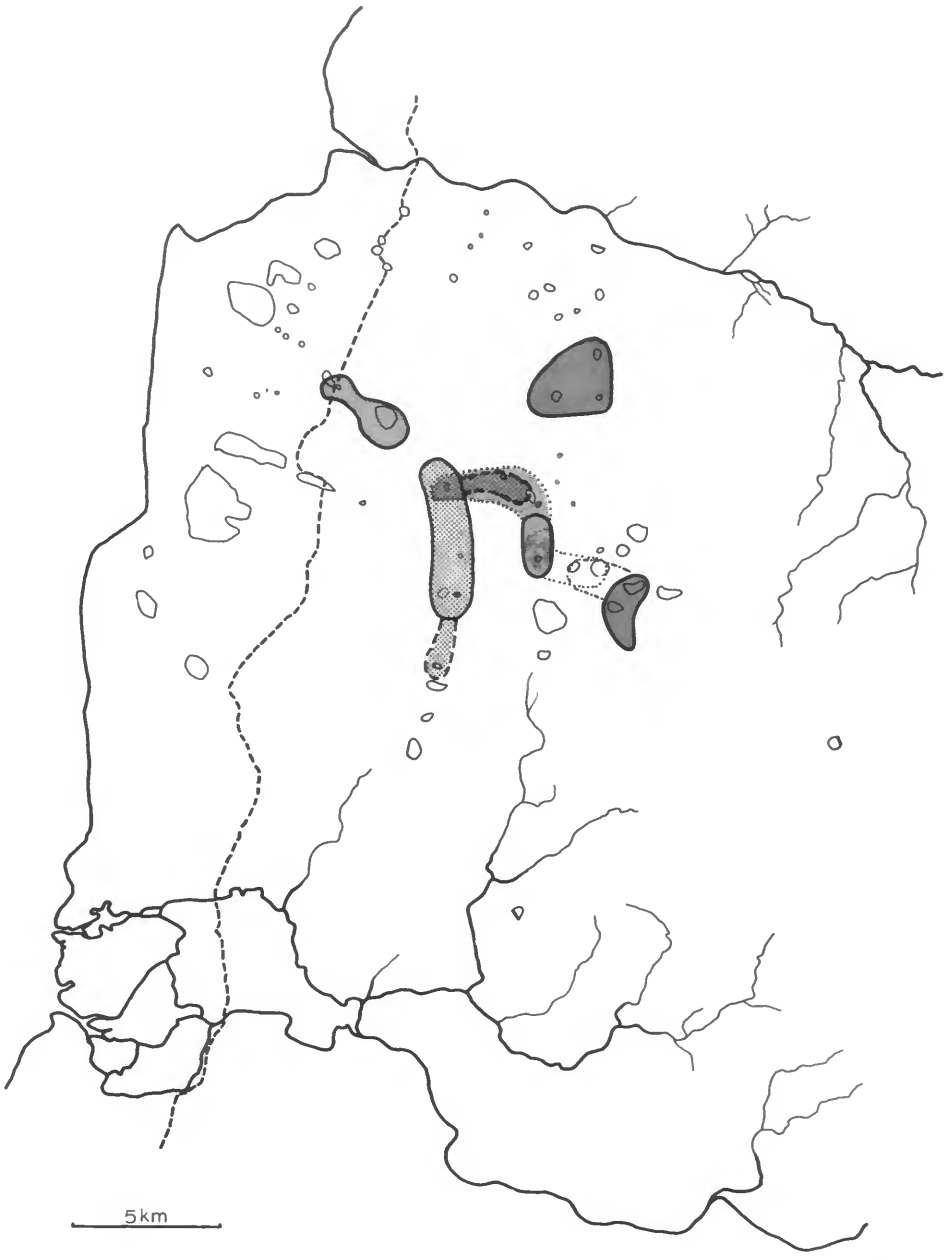


FIGURE 45.—Core areas of home ranges of five adult male leopards (August 1968–June 1969). Little overlap can be noted; however, there may be pronounced shifts in home range as indicated by dotted lines. One such shift is indicated by the center male which moved quite far to the east when his eastern neighbor moved west to utilize part of his range for a month period. Upon returning to his home range, this center male or Kanjuran male then extended his range to the south. (Home range boundaries are approximate and based upon tracks and actual sightings hence these areas represent centers of activity rather than the limits of movements.)

scavengers, then the leopard's home range at crude densities would have to be at least 29 square kilometers. Since the old park was roughly 600 square kilometers, we can assume that overall there could be no more than approximately 20 resident leopards utilizing the park on a year long basis; however, these figures are based on crude densities. Ecological densities, that is, the actual density of game in a given microhabitat,

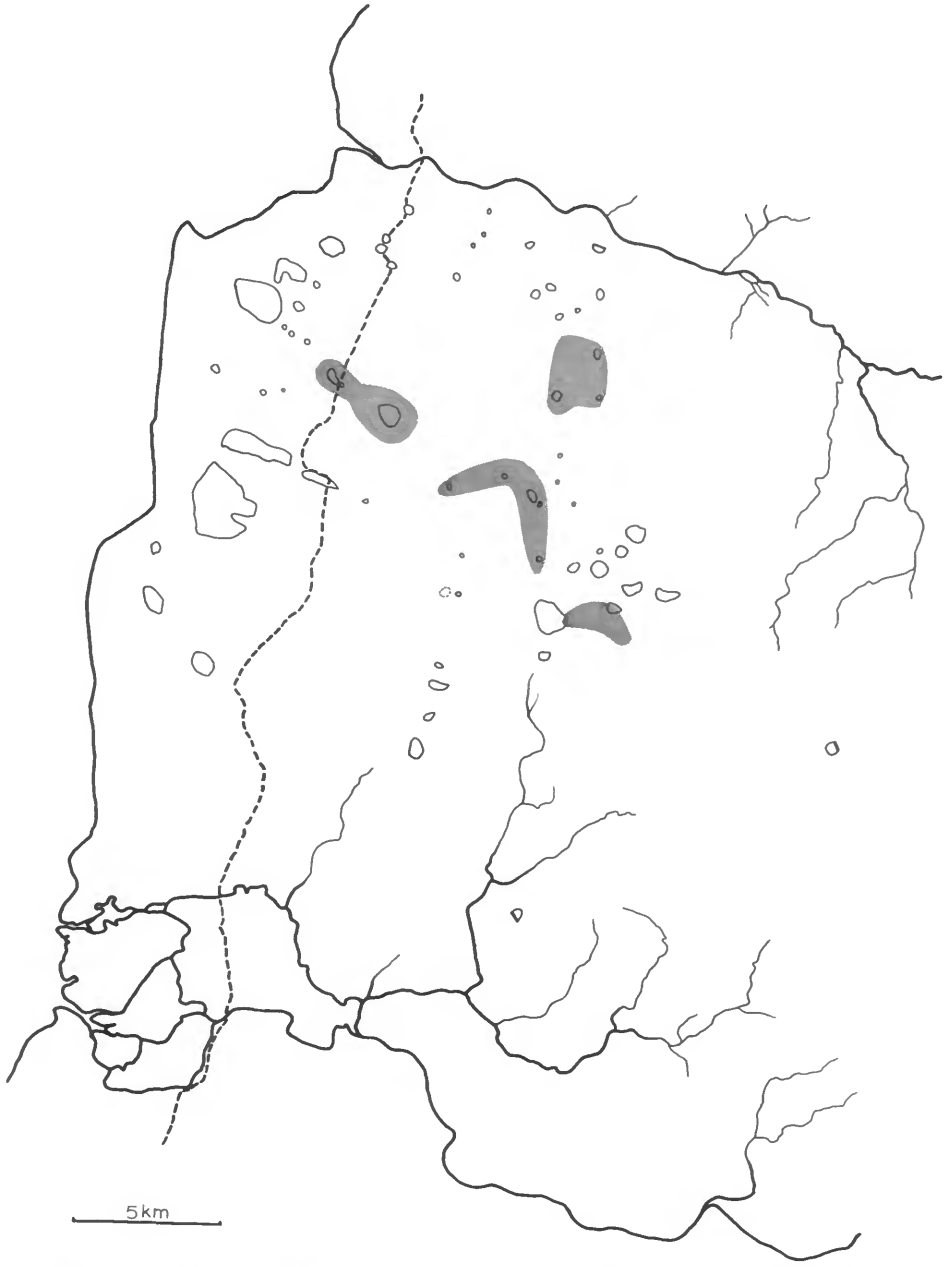


FIGURE 46.—Estimated home ranges for four selected female leopards. Compare with Figure 45. Overlap between male and female ranges is almost complete. (Dates comparable to Figure 45.)

average two to five times that of the crude density depending on the season. Thus, the actual home range of the leopard can be as small as 8 to 10 square kilometers within the villu habitat during the dry season and still support him with a reasonable amount of food (Tables 9 and 10, see also Tables 14 and 15).

Considering our census efforts, we find that the theoretical maximum of twenty leopards is quite realistic for the park and, in fact, we can delineate partial ranges for some eighteen animals within the park. For those animals in the villu habitat that we are discussing, however, the home ranges are smaller and the concentration of leopards per unit area is higher than it is in some of the less favored areas of the park.

Activity

Leopards were sighted more frequently during the early morning hours from 0600 to 1000 hours. Leopards were seldom sighted between 1100 and 1400 hours. They were again sighted frequently and often engaged in hunting from 1500 hours until darkness at approximately 1830 hours. Nocturnal activity of leopards could be inferred in part from their calling. Peak frequencies of calling occurred at 1900 hours and at 0500 hours. Scattered calling could be detected during almost every hour of the night but with a much lower frequency than during the period just following darkness and just preceding dawn (Figure 47).

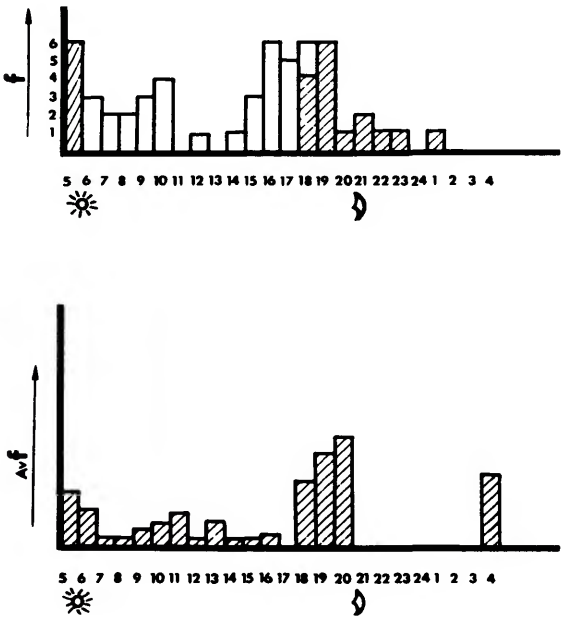


FIGURE 47.—Frequency of calling and frequency of movements by leopards throughout the 24-hour cycle. Calling rates (shaded bars) show a peak frequency in the evening and just prior to dawn. Leopard activity (white bars) is moderately high in the early morning and late afternoon but shows a minimum during midday. Lower graph portrays calling frequency in zoo animals. Again note the bimodal calling peaks at dusk and at dawn; however, captive individuals show some calling prior to feeding time.

Stalking and Predation

Although the leopard may turn scavenger and feed on buffalo and elephant carcasses, in Wilpattu leopards are primarily hunters. If we put aside elephants and adult buffalo as prey animals for the leopard, this leaves, listed in order of numerical abundance, axis, hare, langur, sambar, mouse deer, porcupine, swine, and muntjac. Buffalo calves are taken rarely because of the vigilance of the cows. On one occasion we observed a leopard catch a turtle in one of the shallow villus (Figure 48).

It would appear that the sambar is somewhat difficult for the leopard to bring down. Of twenty-nine kills based on all evidence including actually observed kills, attempted kills, skeletons, and bones and hair retrieved from the feces, we find that axis and swine are taken with the highest frequencies, with axis accounting for over half of all inferred kills (Table 9).

When hunting langurs (*Presbytis entellus*), the leopard may approach by stalking a troop which is in a tree. Upon being sighted, the leopard often makes little attempt to conceal itself and actually may walk directly under the tree looking up at the langurs. The langurs frequently respond with low barks and the adult males give vent to loud barking or warning calls. The adult males are prone to leap about in the tree often providing a distraction while the females with young will gradually move away quite secretively to neighboring trees. Subadult langurs, especially subadult males, become quite excited whooping and jumping about and on occasion may slip and fall. This is much to the leopard's advantage and, if he is quick, he can catch the langur before it can get up into a neighboring tree.

An alternate method of hunting langurs consists of lying in partial or total concealment near a villu edge. During the height of the dry season between the rains,

FIGURE 48.—Leopard catching turtle at Kanjuran Villu.

the langurs generally gather at the edge of the villu and proceed in small groups to drink. The whole troop never goes down at one time. Some individuals remain sitting at the forest edge quite vigilant, while others remain up in the trees. Eventually small groups of two or three venture across the open grass to the water's edge to drink. Here ambush is quite possible if the leopard can conceal itself at a point near to where the langurs emerge.

The stalking of deer is again a matter of concealment. Where the low scrub provides some cover near the grassland edge, the leopard can lie in ambush or, if there happens to be a stand of rather tall grass (about 60 centimeters high), the leopard can conceal itself almost completely. The leopard will generally wait until the deer are quite close before making a rush. To give a typical example: At a small water hole which was part of a leopard's home range, three kills were made between December and April. The kills included a two-year old axis buck and two wild swine, one subadult and one adult which was probably a female. The exact location of the kills could not be determined since the carcasses were dragged or perhaps killed some 11 to 12 meters back from the edge of the forest. The leopard will attempt to drag its kill to some concealing cover if it is in the open.

In all our water hole analyses of killing tendencies on the part of leopards, we have seen no case where the kill has been placed in a tree. The kill, if moved, was not dragged very far from the grass at the edge of the forest; however, it should be noted that Kurt has recorded an instance where a young sloth bear was killed by a leopard and the leopard did indeed drag it into the lower branches of a tree (Kurt and Jayasuriya 1968). Perhaps the tendency to drag prey into a tree is in part a function of the density of jackals. In Wilpattu jackals were not abundant and the leopards did not seek to drag their prey into tree branches; however, in Ruhunu the jackals were quite numerous and, indeed, aggregated into larger hunting packs than was the case in our particular study area. This may be a significant correlation.

Reproduction

It is known from the work of Sadleir (1966) that the leopard has an estrous cycle corresponding to the following pattern: The mean inter-estrous interval is 45.8 days with a range between 25 and 58 days, highly suggestive of a lunar cycle. The estrous period itself averages 6.7 days or approximately one week.

Turning to the reproduction data from the National Zoological Park, based on seventeen litters and thirty-five cubs, we find a range in litter size from one to three with an average of two. The sex ratio of young which survived in these litters and were not devoured was 11 males to 18 females or .6 males to 1 female. This is rather interesting since, based on our observations, we find that males were sighted in the wild twice as often as females. This may, however, not be indicative of a difference in sex ratio but rather of greater boldness on the part of the males.

At the National Zoological Park, litters were born during all months except February, October, and November; however, June, July, and September are peak birth months at the zoo. Gestation lies somewhere between 90 and 100 days. In Wilpattu two sets of cubs four months of age were noted in July and August of 1969. This implies breeding in December or January.

Social Behavior

General Comments on Sociability

The leopard must be classified as an animal living essentially a solitary life. Since it moves alone and generally hunts alone, the only cohesive social grouping seems to be a female and her cubs and the cubs appear to stay with the mother until almost one year of age. The only other social grouping observed, showing any degree of cohesion at all, is that formed between a male and female presumably when the female is in estrus. Nevertheless, these animals do make frequent contacts with each other through various communication mechanisms. An examination of our home range

data shows that there is considerable overlap when home ranges are compared especially between the home ranges of males and females. The home range of adult males shows little overlap and when it does occur it usually involves the displacement of one male, though this displacement might be only temporary. These observations on spacing are in agreement with the results reported by Hornocker (1969) for the North American puma (*Felis concolor*) and by Schaller (1967) for the tiger (*Panthera tigris*). This brings us to a consideration of communication among leopards.

Communication Mechanisms

Scratching Trees.—Several trees have been observed within home ranges of leopards which show that the leopard repeatedly visits them to scratch with its claws and perhaps urinate at the base of the tree. In all instances these trees show a decided lean or are trees that have a very large limb approximately 1.8 to 2.4 meters above the ground. Upon approaching such a tree, a leopard will sniff at the base and then climb rapidly up it, pausing to sniff at the previous scratch marks, digging in its claws to scratch backward with its hind feet, or claw with its forelegs while bracing with the hind legs. The leopard continues to pause from time to time to sniff at the bark especially where fresh and old scratch marks still remain. No doubt this could have some communicatory significance. Not only is urine often sprayed around the base of such a tree but perhaps exudates from the paws are left or odor from the animal's body as it stretches or reclines its ventrum on the bark. In addition, the tree is rendered attractive or noticeable by the visual appearance of the scratch marks as well as the sap that exudes from the wounds made in the tree bark. In the course of lying on the tree and scratching, the leopard may exhibit several incipient marking movements including reclining at full length on the branch and rubbing the chest or perineal region on the limb, and rubbing the cheeks apparently on points which bear odor traces (Figure 49).

Urine Marking.—Both males and females urine mark, although males show the pattern most often. While walking along trails they will occasionally pause to sniff at the undergrowth near the trail edge. They will then pause and urinate backward when flexing the tail dorsad. In males the urine stream will be directed at a height of approximately 61 centimeters

Figure 49.—Leopard marking in scratching tree. (Photo by N. Muckenhirn.)

against the vegetation bordering the trail. When marking in this fashion, females are not capable of directing the urine as far or as accurately. Whether marking is induced by the odor on the vegetation or the odor of the vegetation itself we cannot at present say.

Scrapes.—Male and female leopards also prepare scrapes. During the rainy season when the soil is reasonably moist, one frequently finds evidence that the leopard has scraped soil back with his hind feet. Sometimes this scraping is accompanied by the emission of urine on the vegetation or earth immediately behind the scraped spot. Occasionally urine is deposited on the spot which has been scraped. Feces may be found near the scrape but this is extremely rare. Scrapes are noticed during the wet season because the earth is soft and lends itself to scratching. The length of the scrape is approximately 61 centimeters and usually there is a clear imprint of both hind feet at the end of the scrape.

Calling.—A leopard call consists of a repeated pattern of strokes sounding much like the sawing of wood. The number of strokes in a given call is highly variable and may have a range from two to thirty. At our Marai Villu camp, where two leopards frequently called, the number of strokes in a call had on the average thirteen to sixteen beats; the range, however, was

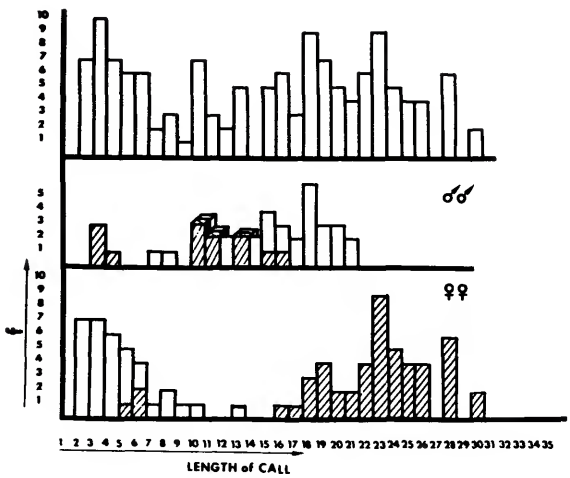


FIGURE 50.—Length of calls (in number of strokes per call) for captive male and female leopards. Top graph indicates frequency for different call lengths for the total captive leopard population. Middle graph indicates the males; the bottom graph, the females. Note the tendency for different individuals to call on the average with different call lengths. Different individual distributions are represented by differential shading.

from five to twenty. Records of calling at the National Zoological Park, including five individuals, give a range from two to thirty with two peaks; one individual called with an average of three strokes per call and a second individual showed a peak at twenty-three strokes per call.

At present it is not possible to say to what extent an individual leopard has a fixed call length. We do not have enough identifiable data from the field to substantiate this point. We believe, however, that there is some truth to it, since the evidence from the zoo indicates that individuals can be roughly characterized by the number of beats to a call. Our female, Goldie, called on the average with twenty-three beats per call. Our female, Pattie, called on the average at approximately four beats per call. This is quite a difference; in fact, you do not have to see the two animals to realize which one is making the call. There is no overlap between the calls of the two females at the zoo. Whether we can generalize this to a wild situation or not, we are not prepared to say at the moment. There are certainly other characteristics of the call which might give information concerning the individual's identity. These would not be merely the number of strokes per call but the rate of delivery and perhaps even the pitch. Furthermore, it may well be that motivational differences can lead to modifications in the length of the call itself as determined by stroke duration or stroke frequency (Figure 50).

When a solitary individual commences calling in the evening, the interval of time between calls ranges from approximately one to ten minutes. The average interval between calls in a wild population for a single individual calling was six minutes. In the zoo the average interval was three and a half minutes (Table 11, p. 87).

A phenomenon was noted in the wild which cannot readily be confirmed in the zoo which we have termed "dueting." Duet calling generally occurs on the boundary between the home ranges of two males. It could, of course, occur under other circumstances but the only situation we studied was the apparent dueting between males. In dueting, the movement patterns of the two animals are regulated in such a way as to avoid one another and the interval between calls is less than one and a half minutes. Furthermore, there

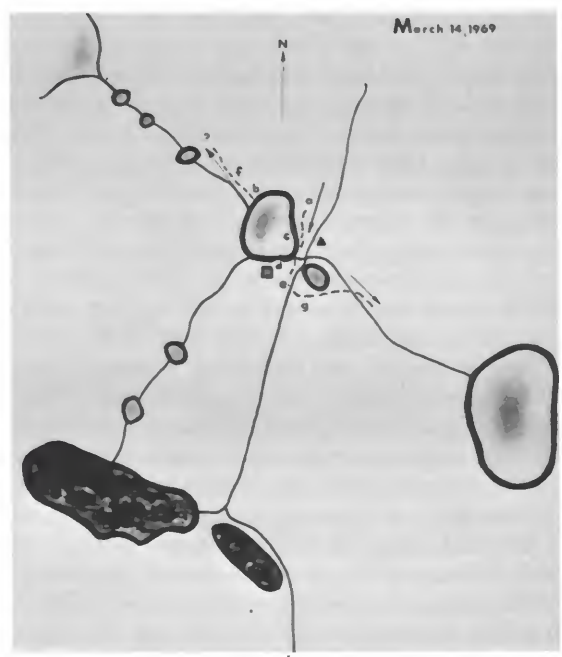


FIGURE 51.—Dueting situation between two male leopards at Marai Villu. Note the tendency to remain spaced while calling. Letters refer to sequence of calling.

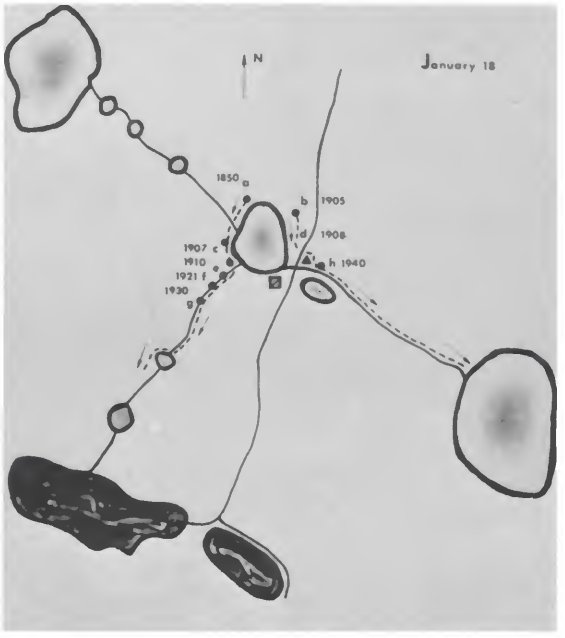


FIGURE 52.—Second set of duets (see Figure 51). The time of calling is included.

is some suggestion that the animal that is deviating from its original course as a result of the dueting curtails the length of its call until it seems to pass into a more secure situation. We indicate this phenomenon by reference to Figures 51 and 52. These figures portray two different duets involving, we believe, the same two individuals. This is not to imply that this is the only circumstance under which dueting occurs, but it is merely to point out that it can occur and may be indicative of a spacing function.

We would like to infer from consideration of these figures that leopards are able to maintain their spacing and avoid one another by means of roars. These calls may, however, serve to bring two individuals together, such as a male and a female. Indeed the rate of calling per unit time by a female increases during estrus (Muckenhirn 1971). This process would be greatly facilitated if individual leopards could recognize another individual's call. We have little evidence of dueting in our zoo colony but this is not surprising since the animals occupy stable caging situations and are probably so familiar with one another's voices that they do not respond in the way wild free-moving animals would.

REVIEW OF SOCIAL ROLES

Based on our observations we find that a female and juveniles associate together for almost a year. The youngsters will hunt with the mother and, when they are about six months of age, will stay with her almost continually, even when she is moving in the open. The female indulges in a great deal of typical cat-like play patterns with the young involving chase, mock fighting, etc. Male-female relationships were noted from time to time. In one instance not recorded by us, a tracker noted two males in association with one female, but the usual case would appear to be one male associated with a female. In one case the duration of association during our period of observations was seventeen days. We have one record of an adult male chasing a subadult male from a kill.

We have recorded two instances when a young male (the Kanjuran male) was temporarily displaced from his normal home range by the appearance of, in one case, an adult male and, in the second, an adult male and female (Manikepola pair) who had been resident at a neighboring villu.

Case I.—On 23 March 1969 the Manikepola pair was noted at Kanjuran Villu, the normal home range of the subadult Kanjuran male. Later the same day this pair was located some 3 kilometers to the south, still in the Kanjuran male's home range. On 24 March the Kanjuran male was noted at Kumuttu Villu for the first time in an area some 2 kilometers east of his normal range. He was moving west and by the end of the day was noted at Kanjuran Villu at his usual resting place. The Manikepola male was noted in his normal home range at Kuruttu Pandi on 24 March and the pair was again noted at the same villu on 8 April 1969.

Case II.—The second displacement of the Kanjuran male was less clear cut. On 13 June 1969 the Kanjuran male suddenly appeared at Manikepola at 0900 hours. He was sighted at Manikepola again on 16 June and on 27 June. At the same time, on 27 June a strange male was sighted at Kumuttu Villu that had not been seen there before but was identified as the male generally resident at Manikepola and Kuruttu Pandi. On 28 June the pair which had been resident at Manikepola previously suddenly appeared at Manikepola about half a mile to the north and subsequently the Kanjuran male was then seen again on 10 July resident in his own home range, this time at Kumuttu Villu, and on 19 July he was seen 6.4 kilom-

FIGURE 53.—*Viverricula indica*, the lesser Oriental civet. (Photo by M. Hladik.)

eters south at Allam Villu, giving an extension to his former home range area (Figure 45).

One gets the impression that the Kanjuran male very much biased his movements depending on his awareness of the presence of other residents in the near vicinity. During September to February the Kanjuran male went almost every week to within half a mile of Kali Villu only to turn back. There was a resident male and female at Kali during this time. The Kanjuran male's favorite marking tree was on the presumptive boundary between the Kali Villu pair's home range and his own.

Some leopards would appear and then not be seen again. We can only conclude that these were transients. We hypothesize that leopards can move through the home ranges of others if they do not attempt to settle. Leopards were often noted on the dry water courses near the northern river boundary but it was impossible to keep track of these individually and we do not know how often they crossed to the other side. Hence, as we noted in the introduction, our conclusions regarding home ranges and movements apply only to the central villu population.

Biomass of Prey and Home Range Occupancy

If we consider the five adult animals that we know best, we have a situation with a male and female showing overlapping home ranges, concentrating their efforts around Kali Villu with excursions to Marai Villu; a single subadult male of approximately two and a half years of age patrolling three villus regularly, and a fourth patrolling intermittently to the northeast of him; while another pair occupied the large rich villu, Manikapola, as well as three other subsidiary villus as hunting areas (Figures 45 and 46). An estimate of the biomass of prey throughout the annual cycle for three home ranges indicates that for the young male less than 50 percent of the biomass was available to him in a home range of approximately 9.3 square kilometers whereas the average biomass available to the two adult pairs which shared

adjacent home ranges was more than twice as much as that available to the younger lone male.

THE SMALLER CARNIVORES

The Mongooses (*Herpestes*)

Three species of mongooses have been noted in Wilpattu, *H. smithi, H. fuscus,* and *H. edwardsi.* The last mentioned species was seen the least frequently and was noted near the borders of the park adjacent to cultivated fields on several occasions. *H. smithi* is by far the most numerous mongoose in the forested areas of the park and is generally found in the vicinity of permanent water. *H. smithi* is active during the day and may extend its activity period to the evening as well. It is a rather effective predator on small birds, rodents, reptiles, eggs, and various invertebrates. Most sightings of *H. smithi* were of single animals or a mother with an immature. Temporary pairings of males and females were noted on occasion but it definitely does not forage in a group. *H. fuscus* is somewhat rare in the park but in its feeding habits and activity periods resembles *H. smithi. H. fuscus* may be a bit more gregarious, since the frequency of sighting pairs or trios was more common.

The mongooses appear to have a rather restricted home range and the same individuals could be seen day after day, especially where we were permanently camped.

The Civets (*Viverricula* and *Paradoxurus*)

The lesser oriental civet *(Viverricula indica)* was noted near permanent water sources in the park but it was active only at night. The animals could be called to an observer by imitating a "squeaking" sound and often would approach to within 3 meters or so. Three animals, two males and one female, were resident at the Marai Villu camp. One male died during our twelve-month sojourn there but the other two animals could be seen on occasion in the evening near the camp (Figure 53).

Two species of palm civet (*Paradoxurus*) were noted in Wilpattu including the toddy cat (*P. hermaphroditis)* and the golden palm civet *(P. zeylonensis).* Both species were strictly nocturnal and were most often sighted in trees. *P. zeylonensis* is by far the rarer of the two species and was sighted only twice. It would appear that *Paradoxurus* has a limited home range, foraging arboreally, and preying upon small rodents, birds, and insects. Fruits are certainly taken during the fruiting season. In their niche exploitation, *Paradoxurus* are the arboreal complements of *Viverricula,* although *Viverricula* appears to be the more carnivorous of the two genera.

The Smaller Cats

Because of their shyness, the smaller cats were seldom seen. Both *Felis chaus* and *Felis rubiginosa* were resident in the park; the latter was noted only once.

THE PRIMATES AND OTHER MAMMALS

The Primates

The Indian gray langur (*Presbytis entellus thersites*) was well distributed throughout the park (Figure 54). Figure 55 portrays the distribution of the three primate species in our intensive study area. A detailed study of the ecological separations displayed by the three diurnal primate species resident in Ceylon was conducted by Muckenhirn within Wilpattu and the

FIGURE 54.—Gray langur, *Presbytis entellus,* sitting on the ground. This species is the most terrestrial of all members of the genus *Presbytis.* (Photo by G. McKay.)

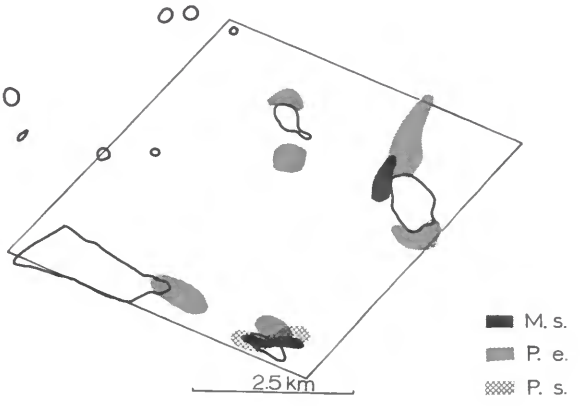


FIGURE 55.—Distribution of primate troops within the intensive survey area. Note the gray langur (P.e) tends to be associated with all bodies of permanent water. The purple-faced langur, *Presbytis senex* (P.s.), is more restricted to areas with large trees. The macaque, *macaca sinica* (M.s.), is most thinly distributed in this portion of the park. The diamond-shaped survey area is depicted in Figure 76. Each side is approximately 4.9 km in length.

results of this work will be published under separate cover (Muckenhirn 1971). In general, *Presbytis entellus* is organized into troops of varying size which include within their home ranges some permanent water. Troops are spaced regularly along both the Moderagam Aru and the Kala Oya. Their distribution throughout the villu portion of the park is closely associated with water. During the height of the dry season, the animals seem to derive a great deal of moisture from the larger fleshy fruits; however, they were seen repeatedly to descend to the ground and drink during the daylight hours. (For an extended study, see Ripley 1965 and 1970).

The gray langur was sufficiently abundant to warrant a biomass estimate. We estimate a crude density for Wilpattu of 2.8 langurs per square kilometer yielding a biomass of 19.0 kilograms per square kilometer (Figure 72 and Appendix A).

The purple-faced langur (*Presbytis senex*) (Figure 56), although distributed in reasonable numbers along the river systems, was very rare in the park itself. A small colony was located in the vicinity of Maduru Odai and Periya Naga and was the subject of investigation by Miss Muckenhirn.

The toque macaque (*Macaca sinica*), although somewhat abundant along the bounding rivers, was very scattered in its numerical distribution within the park. In the eastern portion of the park, the so-called ara ecosystem seemed to support reasonable numbers of macaque troops, but in the villu portion of the park macaques were quite rare, except in the vicinity of Nelun Villu, Kumbuk Villu, Maradan Maduwa, and Maduru Odai. A detailed report on *P. senex* will be published separately by Dr. G. Manley, and *M. sinica* will be the subject of a special report by W. Dittus.

The loris (*Loris tardigradus*) is distributed throughout Wilpattu. At least two animals were noted in the vicinity of our camp at Marai Villu. The status of the loris and its social organization is discussed for the lowland dry zone in the publication by Petter and Hladik (1970).

FIGURE 56.—The purple-faced langur, *Presbytis senex*. Note the conspicuous white hairs on the chin and cheeks. This species prefers larger trees and is far more arboreally adapted than is *P. entellus*.

Comments on Other Mammals

By far the most abundant rodent in Wilpattu Park is *Tatera indica*. The Indian gerbil is active at night, living in burrows either of its own construction or opportunistically using natural crevices and cracks in termite mounds. *Rattus r. kandiyanus,* the jungle rat, is also nocturnal and seems to be confined to areas near permanent water in contrast to *Tatera* which seems to be able to occupy quite arid situations. *Rattus r. kandiyanus* is very arboreal and does a considerable amount of foraging in the trees or in the rafters of bungalows.

Two species of squirrels are to be found in reasonable abundance and both are diurnal. The palm squirrel (*Funambulus palmarum*) is found in reasonable densities in the ara ecological zone. It may be locally abundant in the vicinity of the large villus, such as Kali, Manikepola, and Kumbuk. The rock squirrel *(Ratufa macroura)* is quite abundant along the rivers and seldom seen in the villu zone of the park. In our intensive study area, several pairs were known to us, both at Marai Villu and at Maduru Odai.

The porcupine (*Hystrix indica*) is widely spread throughout the park but at rather low densities. It would appear to utilize both open habitats and forested habitats, digging for roots, feeding on fruits and grazing on tall grasses when available.

The hare (*Lepus nigricollis*) was reasonably abundant only in the open habitats showing a fairly good growth of grass interspersed with scrub (Figure 57). Relative abundance of hares, as a function of habitat type as assayed indirectly through feces counts, are portrayed in Figure 70.

The biomass of the smaller mammals is generally insignificant when compared with the biomass of the ungulates; however, the porcupine and hare do form important parts of the diets of predators and were sufficiently abundant so that we attempted an estimate. Crude density estimates for *Hystrix indica* yield an average density of .58 per square kilometer with a biomass of approximately 5.3 kilograms per square kilometer. Crude density for the hare works out to approximately 4.7 per square kilometer with a biomass of 14.9 kilograms per square kilometer.

FIGURE 57.—The Indian hare, *Lepus nigricollis.*

Comments on the Nonmammalian Fauna of Wilpattu

The Avian Fauna

Although we made no attempt to conduct systematic studies or censusing operations with the avifauna of Wilpattu Park, some mention should be made of the dominant species. The black crow (*Corvus macrorhynchos*) is abundantly distributed in the park. These birds are quite versatile, serving as scavengers in the vicinity of camps and forming a loose symbiosis with some of the larger ungulates, since the crows will pick off ectoparasites, such as ticks. This symbiotic tick-cleaning function is also practiced by the common mynah (*Acridotheres tristis*) which can serve as a "cleaner" for even smaller species of game, such as swine and deer; Schaller (1967) made the same observation in India.

The tall forest and scrub forest in the vicinity of either the river systems or the larger villus is populated by a wide variety of birds; among the more dramatic are the racket-tailed Drongo (*Dissemurus paradiseus*) and the Ceylon paradise flycatcher (*Tchitrea paradisi ceylonensis*). Some of the more conspicuous vocalizing birds of the forest include two species of barbets, the crimson-breasted and the green barbet (*Megalaima haemacephala* and *Megalaima zeylanica*).

Of great interest are the Malabar hornbills (*Anthracoceros coronatus*). At Marai Villu there were two groups of hornbills which would call every evening but generally spaced themselves out at opposite ends of the villu. Malabar hornbills seem to pair for life, travel in pairs, and assemble in the evening to call in a tall tree. The larger assemblies might be composed of several generations of offspring from the original pair.

Conspicuous in the scrub country is the Ceylon hoopoe (*Upupa epops*) which is one of the more colorful birds commonly seen. In the vicinity of the villus, the bee-eaters are conspicuous and so are their ground nests, which they excavate themselves. Both the Ceylon bee-eater (*Merops orientalis*) and the blue-tailed bee-eater (*Merops superciliosus*) were noted.

In the vicinity of streams, the Ceylon kingfisher (*Alcedo atthis*) was noted. These birds appear to be quite territorial and well spaced. During night patrols we frequently came across the night jar (*Caprimulgus macrurus*) and on several occasions made observations on the brown fish owl (*Ketupa zeylonensis*); however, the bird was most easily localized by its call which is easily recognized. The common coucal or crow-pheasant (*Centropus sinensis*) was not at all common in the drier western portion of the park but readily seen in the eastern or ara region. Similarly, the parakeets seemed to confine their distribution to the river system, being represented by the rose-ringed parakeet (*Psittacula krameri*).

Although several species of doves were present in the park, the spotted dove (*Streptopelia chinensis*) was the most common. In the vicinity of the villus, terns were commonly noted feeding, including the white-shafted little tern (*Sterna albifrons*) and the crested sea tern (*Thalasseus bergii*). Also common in the vicinity of villus, especially the larger ones such as Kali Villu, were the great stone plovers (*Esacus recurvirostris*). Black-winged stilts (*Himantopus himantopus*) could be noted, especially in the central villus, including Mahapatessa and Kumbuk. By far the commonest plover-like bird in the vicinity of villus is the Ceylon red-wattled lapwing (*Lobivanellus indicus*).

The Galliformes were well represented by the bustard quail (*Turnix suscitator*), the pea fowl (*Pavo cristatus*), and the jungle fowl (*Gallus lafayettii*). Bustard quail are rarely seen and were observed most frequently in the ara zone. Pea fowl are not at all common in Wilpattu in contrast to Ruhunu Park where they are easily seen in numbers. In general the pea fowl could be noted in parts of the West Sanctuary, along the upper reaches of the Moderagam Aru, and in the vicinity of Maradan Maduwa. The jungle fowl, however, were extremely abundant in both the scrub jungle and the taller ara forest. Although no attempts were made to calculate it, the biomass of the jungle fowl is probably significant and may be double that of the hare.

The most commonly seen raptorial birds included the Ceylon crested serpent-eagle (*Spilornis cheela*),

the white-bellied sea eagle (*Haliaetus leucogaster*), the Ceylon crested hawk-eagle (*Spizaetus cirrhatus*), and the Brahminy kite (*Haliastur indus*).

Winter visitors included ducks, especially the Garganey (*Anas querquedula*) and pintail (*Anas acuta*). The whistling teal (*Dendrocygna javanica*), however, is resident throughout the year in the park.

The larger wading birds are well represented in the park, especially in the central villu areas of Kumbuk, Mahapatessa, Borupan, and Kudapatessa. These include the spoonbill (*Platalea leucorodia*), the white ibis (*Threskiornis melanocephala*), the adjutant stork (*Leptoptilos javanicus*), the open-billed stork (*Anastomus oscitans*), the painted stork (*Ibis leucocephalus*), the large white egret (*Egretta alba*), the cattle egret (*Ardeola ibis*), and the eastern purple heron (*Ardea purpurea*). The Indian darter (*Anhinga melanogaster*) is also abundant in the vicinity of those villus which support a fish fauna.

It is interesting to comment in passing that many of the villus have no inlet or outlet and thus support no fishes. Those bodies of water which were former tanks or have had some connection with the tributaries of the Moderagam Aru or the Kala Oya do have fish faunas, such as Maradan Maduwa Wewa. Most of the feeding by waders and terns in larger land-locked villus apparently involves the crustacean fauna present in the villus and the larvae of aquatic insects.

The Reptile Fauna

The breeding status of the sea turtles that were present off the coast of Wilpattu is not assessed. The most conspicuous reptiles in the park included three species of Testudinata; one lizard, the monitor (*Varanus bengalensis*); the crocodile (*Crocodylus palustris*); and two snakes, the rat snake (*Ptyas mucosus*) and the Indian python (*Python molurus*).

The pond turtle (*Melanochelys trijuga*) and the soft-shelled turtle (*Lissemys punctata*) are resident in most of the larger permanent villus in the park. When villus dry out these turtles are not at all averse to going overland as much as a mile to the nearest water and, during the rainy season, there is often a tremendous movement of turtles between bodies of water.

The star tortoise (*Testudo elegans*) may be noted in the grassy areas in the western part of the park and is spottily located in other suitable habitats throughout the ara zone and in the central villus. No attempt was made to estimate the biomass of this tortoise, which is primarily a grazer.

The crocodile (*Crocodylus palustris*) is a significant predator on small game both along the Moderagam Aru and in the larger central villus. At the Marai Villu camp, we counted five resident crocodiles at the end of the dry season which were approximately 1.3 to 1.5 meters long. They were prone to sun themselves in the early morning and retired to the water around 0900 hours. On overcast days they may remain out almost all day. At night they lie at the water's edge.

Crocodiles reaching a much larger size up to 3.6 meters could be noted at Kali Villu. Like the pond tortoises, pond turtles, and soft-shelled turtles, crocodiles are prone to move between one villu and the next, traveling over land both at the onset of the rainy season and during the height of the dry season.

Rat snakes (*Ptyas mucosus*) were frequently seen in the vicinity of the larger villus, but the python (*Python molurus*) was only noted in the vicinity of Moderagam Aru. The python is known to be a significant predator on fawns of *Axis axis*, but its relative density and effect as a predator could not be estimated in this study.

The monitor lizard (*Varanus bengalensis*) is probably the most abundant large reptile in the park. It is a versatile feeder, utilizing termite nests and feeding after sloth bears have fed. It also is an effective scavenger of carcasses and can be a predator in its own right. We observed one individual run down and attempt to catch a jungle fowl cock one evening.

A Consideration of the Termites

No attempt was made to assess the density or diversity of insect fauna in this park; however, some mention should be made of termites. Termites of the genus *Trinervitermes* probably account for the most significant biomass of all invertebrate fauna within the park. Figure 58 portrays the density of termite nests as a function of habitat and the area of termite nests for varying habitat types. Termites are consumers of cellulose in the form of wood fiber or from soft plant parts and are able to utilize effectively the standing crop of forested material within the bounds of the park. As such, they represent no small contribution to the biomass of the park and are in turn fed upon by the monitor (*Varanus*), the sloth bear (*Melursus*), and the pangolin (*Manis*). Termites are only utilized by other forms to a limited extent and would seem to

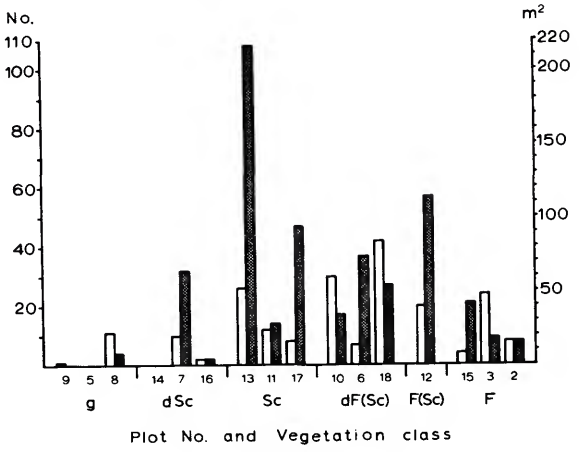


FIGURE 58.—Total area occupied by (shaded bars) and number of termite mounds (white bars) on plots of varying vegetation form. Note that grass plots (g) without the presence of scrub show little termite activity except for termite tunnels which are built to utilize feces. Termite activity reaches a peak in scrub (Sc) and forest-scrub(F(Sc)) and seems to be somewhat less in tall mature forest (F). Termite activity is virtually absent from Plot 14 because this plot is periodically inundated and the substrate is clay, a substrate which is not conducive for termite utilization. Method of censusing is described in Appendix A. dSc = discontinuous scrub; dF(Sc) = discontinuous forest scrub.

represent a rather stable food-producing unit in the above outlined food chain which can be exploited only by some mammals exhibiting extreme specializations. In all parts of the world, termites have been exploited and, in every case, are exploited only by mammalian forms which have undergone morphological specializations for the art of opening termite nests and extracting the termites from their tunnel systems.

Termites are also very important in the dung cycle by reducing to its basic constituents the undigested woody particles in the dung of the ungulates. The dung cycle may be thought of as beginning with the plant food itself, grasses, forbs, leaves, barks, fruits, etc., ingested by herbivores and passed out in a partially digested form. The dung is then further reduced by termites and the termite dung is reduced by bacteria.

The dung may be used by dung beetles and become scattered by the activity of these insects as they form it into balls for nourishing and maintaining a moist environment for their larvae. Dung beetles will bury the balls of dung containing their eggs where it again may be reduced by bacteria at the conclusion of the larval hatching. Dung beetles provide food for sloth bears, numerous species of birds, mongooses, and monitor lizards. The termites, as stated before, provide a largely untapped food source for certain specialized feeders, such as the sloth bear and the pangolin.

Synthesis and Comparisons

TRENDS IN THE EVOLUTION OF SOCIAL BEHAVIOR AS EXEMPLIFIED BY UNGULATES

Review of Ungulate Evolution

The "ungulates" in the broadest sense[3] exhibit an old and diversified lineage within the class Mammalia. We can discern three large radiations within the ungulates; one, the Paenungulata giving rise to the Sireneans (sea cows), hyraxes, and elephants. The second major radiation gave rise to two subdivisions, the first being the Perissodactyla including the horses, tapirs, and rhinoceroses; whereas the second or Artiodactyla gave rise to the deer, mouse deer, camels, giraffes, swine, and bovine-like mammals (Thenius and Hofer 1960, Gregory 1951).

The evolution of the ungulates has been paralleled in part by a complementary radiation within the order Carnivora. In the main the history of the carnivores is written in attempts to perfect methods for overcoming diverse prey animals and a large component of prey animals for the Carnivora is derived from the ungulates. On the other hand, the ungulate evolution has its history written in attempts to escape predation by its ever-present symbionts, the carnivores, and in the evolution of adaptations permitting it to utilize plant cellulose in varied habitats as a food resource.

Plants may be utilized for food with little modification of mammalian gut morphology if only the starch, protein, and simple sugars stored within the plants are utilized by the animal. This is especially true for the phloem portions of plant stems, the parenchyma of plant leaves, the fruits, and other reproductive structures, as well as roots, especially those roots specialized for starch storage. The vast majority of plant carbohydrate, however, is locked in the form of the complex polysaccharide cellulose. Cellulose or plant starch is formed by linking glucose molecules, together with a so-called beta linkage which differs structurally from the alpha linkage characteristic of both plant and animal starch. No vertebrate animal possesses a self synthesized enzyme capable of breaking the beta linkage; such enzymes are readily present in many bacteria (Hungate 1960).

Bacterial symbionts in the gut of many mammals aid in the breakdown of plant cellulose and provide amino acids and vitamins when the bacteria are digested or the byproducts of bacteria are absorbed. In order to efficiently utilize cellulose, herbivorous mammals have evolved modifications of the gut. One refinement permitting the breakdown of cellulose by bacteria has been to add a caecum to the gut, thus enhancing the action of symbionts. Another evolutionary solution was to develop a chambered stomach with one chamber for the fermentation of plant cellulose by bacterial symbionts. Both methods have been evolved within the ungulates with the Perissodactyla and Paenungulata utilizing a caecum as the primary place for bacterial symbionts to break down cellulose, whereas the Artiodactylans, with the exception of the hippopotami and swine, have evolved a chambered stomach where bacterial symbionts assist in the breakdown of cellulose to simple sugars which then can be absorbed by the gut.

Thus the trend in the utilization of foodstuffs within the class Mammalia began with an unspecialized mammal utilizing a high energy food source such as an insect, another animal's body, fruit, or grain. Through natural selection, mammalian species departed from this omnivorous way of life giving rise to specialists on insects or ants, specialists as carnivores or frugivores, and finally specialists as exemplified by the ungulates for utilizing the readily available but less easily metabolized food resources of plants and plant parts, including cellulose.

The ability to digest cellulose has had tremendous consequences for the ungulates. As a result, their teeth have become modified from low crowned grinding organs, for the reduction of plant parts into smaller particles, to high crowned, rootless, ever-growing teeth. Finally, the modifications of the gut including a caecum or, alternatively, a chambered stomach with a rumen has permitted efficient activity by bacterial symbionts. With the ability to utilize grass as a food source, ungulates were able to evolve away from dependency

[3] Ungulates is here used as equivalent to the Protungulata, Paenungulata, Artiodactyla, and Perissodactyla.

on forested habitats and indeed by their activities have contributed to the reduction of forested habitats to grasslands, thus promoting in a way their own food resources.

Within the living ungulates, one can find a spectrum of morphological types ranging from those forms that are somewhat omnivorous, such as the swine, utilizing both forest and open habitats and dependent on readily available energy food resources, to animals such as buffalo, deer, and elephants capable of utilizing grasses and inhabiting the open plains. The history of grass evolution is tied to the evolution of ungulates and one can correctly say that these two biological assemblages have evolved together.

Understanding the evolution of social organizations within the ungulates and correspondingly interpreting the social organizations of carnivores against a parallel evolution with their prey necessitates a thoughtful consideration of the preceding paragraphs which concern themselves with the utilization of food substrates by the evolving ungulate groups. We will now turn to a consideration of evolutionary trends in social structure and communication mechanisms by considering the alternative consequences of adaptation to a forest life versus adaptation to the utilization of open grasslands.

Adaptation to Open Country

Many ungulates still utilize the forest. For noncellulose feeders, such as swine, the forest provides many forms of food including roots, fallen fruits, and various invertebrates and vertebrates. The vast majority of highly evolved ungulates, however, are adapted for browsing either on the forest edge utilizing shrubs or feeding out in the grasslands themselves. The grassland is a uniform habitat not necessarily offering very much cover for hiding by the grazing ruminant, which is a potential prey animal.

The proximity of forest cover can be utilized as a refugium, but complete adaptation to open grasslands necessitates other forms of antipredator behavior. This is especially true of ruminants which have tended to become larger, thus becoming more conspicuous and not able to use tall grass as a hiding place in itself. Increase in size is also correlated with increase in speed. In fact, as Howell (1965) points out, some morphological trends in the evolution of ungulates have been in response to predator pressure. To increase size serves two functions: (1) it can make a prey animal less vulnerable to a smaller predator, and (2) it can increase the potential speed of the prey animal. In any event, becoming large reduces inconspicuousness so one of the primary modes of antipredator behavior (that is, remaining immobile and inconspicuous) is lost to a large mammal grazing in open grassland habitats.

The primary modes of antipredator behavior, outside of remaining inconspicuous or camouflaged, involve the ability to either spring away quickly coupled with some rapid method of running and/or to be able to sustain a swift run when being chased by a predator. Much of the color patterning, especially in forest-dwelling ungulates, is related to camouflage for rendering the animal inconspicuous (Cott 1957) and the need for speed in locomotion has keynoted the evolution of limb structure in ungulates (Howell 1965).

Another characteristic of ungulates has been the evolution of horns or hornlike structures. Paradoxically the evolution of such structures is not necessarily tied to antipredator behavior but rather the primary selective force would seem to be sexual selection resulting from male combat during the breeding season. This is not to say that some of the horns, tusks, and hornlike weapons have not evolved as antipredator devices; this certainly has had some influence in selection especially where the structures are retained by both sexes. But where the structures are the exclusive property of males and where there is no evidence that the males actively participate in defense of female groups, we must assume that the primary selective force has been the competition of males for access to females during the breeding season. (For an extended discussion of the evolution of horns and hornlike organs, see Geist 1966).

Of course, within the ungulates, we have seen several times the evolution of such a large body size that speed is no longer of importance in antipredator behavior but rather the ungulates themselves, by virtue of the large size and armament, can successfully withstand attack by even the largest predators (e.g., elephant and rhinoceros). The rise of man as a socially organized hunter, however, has profoundly affected the utility of many ungulate defense mechanisms. Wholesale extinctions of species in the last 15,000 years seems to have been caused by early man (Martin and Wright 1967).

The Social Organizations of Ungulates

Two very strong trends in social organization may be noted within the ungulates. The first trend is the ex-

tended mother-family, that is, the mother and her immediate descendents, constitutes the most cohesive social unit, and all other social groupings are formed out of such units. The second major trend is for a consistent division of habitat utilization between males and females whenever possible. Although in some migratory grassland species differential habitat utilization is not pronounced, nevertheless, in many species one can detect a tendency for adult males and adult females to form, except for the breeding season, unisexual herds which forage independently of one another, or, if not manifest to that extent, then at least unisexual subgroupings within an extended herd. Although this is a very old tendency, probably reflecting processes and mechanisms of affiliation already operative at the level of primitive mammalian systems, such a separation can and often does result in great benefit to the female and the young in that direct competition between males and females for food resources in short supply is reduced markedly. Such a trend can be noted for elephants and buffalo in Ceylon as well as for the mountain goats and mountain sheep of North America (Geist, 1964, 1968a, 1968b).

In addition to these two basic trends, we can, as we turn to a consideration of habitat utilization patterns, distinguish two broad classes of social organization based on the mode of habitat utilization. In general, utilization of a forested habitat makes the coordination of cohesive groupings more difficult, especially if the forest animal is large. Hence, one of the major features observed with ungulates utilizing forested habitats is that they tend not to form into large social aggregations but rather the minimum social unit, i.e., the extended mother-family.

If the forest ungulate is very small and vulnerable to predation, it would seem that inconspicuousness is the best defense and hence an almost solitary state can be observed. Referring to the muntjac, however, we may note that to be solitary does not imply the absence of social life; indeed, the home ranges of given males and females may overlap and their descendents may utilize the same home range until reaching adulthood. Nevertheless, they tend to move alone. On the other hand, if the ungulate can defend itself well, such as swine (*Sus scrofa*), it may form into small troops generally based on several "mother-families" which band together.

In contradistinction to the smaller social groupings or more solitary way of life characteristic of forest-adapted ungulates, the utilization of grassland, especially by migratory species, has resulted in the formation of large herds. At the time of mating, we may note the evolution of very complicated mating systems and ceremonies involving male territoriality and male defense of specific areas to which females come and are bred. (For extended discussions, see Leuthold 1966; Eisenberg 1966; and DeVos, Brokx, and Geist 1967).

Ungulate Social Systems and Antipredator Behavior

To clarify the preceding discussions, we will review the social behavior of several species previously discussed in the text; these include the muntjac (*Muntiacus muntjac*), the wild swine (*Sus scrofa*), the axis (*Axis axis*), the water buffalo (*Bubalus bubalis*), and the Asiatic elephant (*Elephas maximus*).

The Muntjac or Barking Deer

These animals are generally sighted moving alone and we can think of them as solitary in their feeding, drinking, and resting. It is also evident that muntjacs do come together at appropriate times of the year for mating and that some continued contact must be maintained between the mother and her young during the lactation phase. During the early stages of growth by the young, it is left in a secure resting place and the mother returns to it in order to feed it. Persistent following by the young generally begins at the age at which it can escape on its own if necessary.

The male and female home ranges overlap to some extent, thus the male can service the female when she comes into estrus. The greatest overlap in activity takes place at water holes and indeed this is the place at which we have noted the male and female muntjac together. Some sort of spacing must be maintained especially among adult males and to a certain extent among adult females. Yearling males can and do associate with adult males. It is thought that the males mark their territories with glandular secretions and actively defend their home ranges against other males by ritualized combat with their antlers. The rather pronounced canine teeth of the male may be involved in combat as well.

The small forest ungulates live in auditory and chemical contact with each other, with the home ranges of males and females overlapping. Perhaps the home ranges of related females overlap to some extent also, approximating the extended mother-family units of the larger more social Cervidae.

The muntjac possesses an alarm call which sounds very much like the bark of a small dog and may be repeated two or three times when the animal is startled. The role of the alarm call would at first sight seem to be unrelated to a social function especially when these animals appear to be solitary; however, if the home ranges do indeed overlap, then the individuals in a given "community" are in auditory contact and the loud warning cries can serve to alert not only the young but neighbors.

The Wild Swine

As indicated in the section on swine, social tendencies show a marked change throughout the annual cycle. Swine typically show the pattern of females associating together in a sounder which travels about within a known home range. Females appear to become impregnated at roughly the same time, perhaps with estrous synchrony being induced by the presence of a male. Female swine will move to individual areas to give birth and when their young are approximately ten days old will begin to rejoin former female companions to form an extended rearing group composed of anywhere from two to five females with their progeny. This extended "sounder" then moves together for several months until the young have reached the stage of independence; even then the primary foraging group may remain together.

Adult males take no part in the rearing of the young and are typically solitary. Younger males may associate with the female groups until approximately two years of age but seem to participate in very little breeding since, at the time of estrus, an older boar will generally take charge and drive off any younger males who attempt to mate with estrous females.

Wild swine are not ruminants and apparently cannot utilize cellulose in their diet. They are omnivores, feeding on carrion, vertebrates, invertebrates, fallen fruit, and the roots and soft parts of plants containing starch and simple sugars. The home range of swine is typically quite large. The female rearing group serves as a defensive unit for the young against small predators. If surprised by a larger predator, the sounder may scatter leaving the young quite vulnerable to being attacked singly. Adult swine, however, are more than a match for most predators and indeed, after suffering an initial heavy mortality during the first three months of life, the chances of swine survivorship increase dramatically. It is on record that adult swine can effectively defend themselves against the attack of a tiger, cheetah, or leopard (Schaller 1967, Eaton 1970). We have observed subadult swine falling prey to the leopard on Ceylon so the generalization is not absolute; however, it seems safe to say that the chief antipredator defense of the swine is the communal rearing unit of several adult females and attached older progeny. Our observations on the social behavior of swine are completely consistent with the observations of the European swine by Gundlach (1968).

The Axis Deer[4]

The axis is a social cervid spending the better part of the diel cycle in company with a great number of its own kind. The axis typically move singly or in small groups of two or three while in the forest. These small units subsequently assemble at various times during the diel cycle to form a herd in the open. A given herd is the result of the gathering of small groups and is formed most often at grazing areas in the vicinity of water holes. The most frequently observed grouping assembling at the forest edge is from three to six individuals. In the main, these small units are composed of a doe, her fawn, and a yearling female with or without a fawn. The basic social unit presumably consists of a female and her descendents. The axis is quite gregarious and extended herds are formed from these smaller groupings. Even within the extended herds there is some tendency for unisexual subgroup formation so that the males will tend to form all-male groups and the does tend to segregate into groupings of does and their progeny.

The quality and form of male interaction is very much influenced by their reproductive state. Although the rut is not totally sychronized within the axis populations of Ceylon, nevertheless, there is a pronounced rutting trend toward the end of August and into September.

When males are not rutting, there is a marked tendency to form a unisexual subgroup or bachelor group which is not completely consistent in its composition but may maintain itself over a period of several months. During the rut, males with hard antlers will spar and actively attempt to court females. Younger males are almost always subordinate to the three or four-year old males; however, they may actively follow older males and, although not challenging them, they may secondarily participate in courting activities.

[4] For an extended treatment, see Schaller 1967.

During the nonrutting phase, the males appear to ignore the females although occasionally they may join in with a female subgroup and follow it. During the rut, the males will approach and actively court females. There is no permanent pair bonding.

The females are quite gregarious and indeed it would appear that the small subgroups showing the most cohesion are extended mother families. At the time of parturition, the female is prone to retreat from the main herd and becomes somewhat aggressive toward her own offspring. The fawn is generally delivered in a very secluded place and, for the first ten days of its life, the fawn is unable to consistently follow the mother; however, after approximately ten days, the fawn will begin to accompany her. At this time the small subgroupings of females and their descendents, as well as the extended herd groupings, are reformed. Although the fawn is unable to accompany the mother on her grazing forays during the first week or ten days of its life, the mother nevertheless maintains contact with it by remembering the place at which she left it. Furthermore, contact between a fawn and mother may be facilitated by the bleating call of the fawn and a similar bleat produced by the female.

When startled axis will generally leap to one side, stamp and/or give an alarm bark and then run rapidly for cover, sometimes continuing to bark. Upon perceiving a leopard, axis may respond in a variety of patterns. If an axis is startled by a leopard at close quarters, it will generally make an immediate escape response, a jump followed by a rapid gallop away from the vicinity of the leopard. On the other hand, if it is not startled but the leopard can be perceived at a distance, the axis' next act is dependent upon what the leopard does. If the leopard is at a reasonable distance and resting, the axis will orientate toward the leopard, may show pilo erection and a raised tail, and, depending on the distance, will generally maintain its orientation and emit a warning bark. If the leopard remains resting in the open, the axis will approach with the head down and in an elongate posture. If the leopard still does not move and if there are several axis gathered together, the axis will generally exhibit a *mobbing* response, often inducing the leopard to get up and move. If the leopard moves toward the deer, the mobbing response is not shown but they will remain orientated toward the leopard, barking. When he comes within approximately fifty yards, the axis will move away to a safer distance and then orientate again and continue to bark.

The Water Buffalo

Except at the time of the rut, adult male water buffalo are almost always seen in a solitary state. Subadult males and occasionally adult males outside the rut may form into temporary loose bachelor groups. In contradistinction, the cows are very cohesive, forming herds which remain together throughout the better part of the annual cycle with the exception of parturition time when individual cows may leave the herd to give birth. The size of the buffalo herd very much depends on the habitat in which it is living. Two ecologically different populations of buffalo may exist in the same area. Herds being locally adapted to forest generally form smaller groups, whereas herds utilizing more open grasslands form into larger groupings of twenty to thirty.

During the rut the males become exceedingly aggressive toward one another and actively defend an area against intrusion of other adult males. At the time of rut when a cow herd passes into the territory of a male, he will actively investigate the cows and attempt to breed any that are in estrus. At high-population densities where water resources are restricted, many adult males may congregate in the vicinity of the same water hole. At this time, the males will actively defend an area including a portion of the water hole and adjacent grazing grounds; hence, clustered territories may be shown by bulls at this time. Where the habitat densities are lower, the bulls may be spaced out so that such overt territorial behavior is not apparent (Kurt 1971).

The female buffalo leaves the main herd at the time of parturition and is extremely wary. The calf can accompany a female within twenty-four hours after birth, although slowly. Within two weeks or so, the females are generally again formed into a regular herd. As the calves become more mature, there is a tendency to form nursery units. Mothers may graze more individualistically while the calves are congregated together in a group generally with one or two females and juveniles in attendance. There is a sustained tendency to establish subgroups. One should note that within a herd, unless a nursery group is formed, the most cohesive unit is that displayed by the female and her calf. Nevertheless, notwithstanding the fact that nursery groups are formed, it would appear that mothers can recognize the call of their calf individually. When threatened by a predator, a cow group will form a defensive front with the calves between and slightly behind the mothers and the mothers facing out toward

the threat or danger. Females are prone to charge offending objects that come too close, including jackals and leopards.

The Asiatic Elephant

As in all of the preceding examples, the most cohesive social unit shown by the elephant is a given female and her descendents. Because of the great age to which an elephant attains, there is a maximum possibility for generation overlap. Hence, a female of thirty-five years of age may have up to seven descendents accompanying her at the same time. This leads to a series of core mother-families related by descent, which constitute the extended herd of from twenty to thirty individuals. Individuals within the herds seem to be recognized as such. In fact, when two herds come together and mix, they generally separate intact with the same composition.

Adult males generally do not accompany the cow herds but forage independently, joining the cow herds at water holes, and especially at the onset of rain when many cows are in estrus and mating occurs. There would appear to be a dominance hierarchy among males established by tradition and maintained over time through ritualized combat or in exceptional cases by actual combat. The males typically exhibit a more consistent home range pattern. Females have a much larger habitat utilization radius with marked seasonal shifts depending on the availability of grass and the rainfall patterns. Bulls may shift in company with cow herds during major seasonal changes in habitat utilization trends.

Because the members of the cow herd live together for such an extended period of time and because of the extensive generation overlap, there is a great deal of mutual care for infants with several emergent properties. First of all, the auntie phenomenon is well known within elephants. A female with a newly born calf is generally accompanied by at least one female who assumes maternal roles with respect to the calf when the mother must feed, and otherwise occupy herself. As a derivative of this, it is not uncommon for females in late pregnancy or older females that have given birth many times, to begin lactation after several days when in the company of young calves. This is noted in zoological gardens and confirmed in the field (Kurt 1969).

A second emergent property in the social behavior of females is the cluster formation as a part of anti-predator behavior. This is similar to the linear formation of the buffalo herd when facing a predator, but it is more integrated. The larger cats in the mainland of Asia are significant predators upon elephant calves, although the adults are relatively invulnerable. Nevertheless, the adults exhibit cluster formation related to calf protection even toward smaller predators or toward man when flight is prevented. Elephants have lived with man for thousands of years and man may well be considered a natural predator upon the elephant.

Although flight or attack behavior may be shown toward potential predators, including man under appropriate circumstances, the cluster formation is definitely an adaptation to reduce predation on calves. In the formation of a cluster, the adults will turn toward the source of possible or actual danger while the younger animals align themselves either between two adults or behind them. If the source of the disturbance cannot be localized, the adults may even form a star pattern with the youngsters in between them or in the center. Young animals attempting to pass an adult will be forcibly held back by the adult's trunk. Animals of five feet or less at the shoulder tend to move near the largest elephant in the immediate vicinity. Thus even a juvenile may serve as the nucleus for a cluster or star formation if larger adults are not in the area. Such a defensive cluster may break up if an older individual sets out to attack or the older individuals may hold positions while the younger ones gradually move away in twos or threes into the protecting forest. (For more details, see McKay 1971.)

Mating behavior involves the establishment of a contact relationship between a cow and a bull. Continuous courting by the bull persists until a peak of receptivity on the part of the female. Cows come into estrus once every twenty-one to twenty-eight days and the period of attractiveness to the male may last some four to five days; however, peak receptivity on the part of the female occurs during the last two days of estrus. Several bulls may be in attendance on a cow herd at the time that a given female or females are coming into heat; however, precedence ih mounting generally goes to the largest male or the male that happens to be in musth. Musth is a condition exhibited by males which is equivalent to rut in deer although musth in the male population is not necessarily synchronized (see also Eisenberg, McKay, and Jainudeen 1971).

Young males have very little opportunity to mate due to the appearance of older dominant males at the

times of estrus in the cows comprising their herd. Young males in their persistent attempts to mount females in pro-estrus frequently receive aggressive action from older cows. As a consequence younger males begin to spend less and less time with the cow herd and either form a subgroup on the periphery or attach themselves as satellites to older bulls. Male associations in the elephant are certainly not as cohesive as those found within the cow herd itself. The role of leadership for the cow herd generally falls to the oldest cow.

Relationship of Social Organization to Antipredator Behavior

It is perhaps useful at this point to summarize some of the information we have tried to impart in the preceding review. In general, an ungulate species has two major problems, to feed itself and to avoid being fed upon. Eight intergrading adaptive responses may be discerned for response to predators:

1. Sight the predator and either sneak away or freeze, keeping the predator in view. If it would appear that the predator has spotted the prey, then give an alarm call and prepare to flee.
2. Give an alarm call and flee from the predator.
3. Move, thus increasing the conspicuousness, while remaining orientated to the predator and give a repeated alarm call.
4. Give an alarm call while displaying some conspicuous color pattern such as erecting the tail or rump hairs which may be white and further enhance conspicuousness.
5. With tail erect and perhaps emitting an alarm call, to move in a zigzag fashion or "stot" to induce the predator to chase (see Smythe 1970 for an extended discussion). All things being equal, a healthy prey animal should be able to out-distance a predator still outside its flight distance. In any event, the alarm call serves to attract attention to itself and induces a chase. Should the predator chase and fail to capture the prey, then chances are the prey will not be molested again. Secondarily, the warning call and movements serve to alert the other members of the community or herd.
6. If the animal be a herd animal and if in a state of motivational balance between the tendencies to attack and withdraw with approach tendencies slightly exceeding, then a mobbing by the herd can initiate either a direct chase by the predator which would be futile assuming the predator is outside the flight distance of the prey animal, or the mobbing activity may serve to drive the predator away.
7. Forming into a cluster and actively advancing on the predator with perhaps one or two individuals showing attack on the predator. This is possible only if the species is large enough and with sufficient armament to damage the predator.
8. Whether alone or in a group, to outright attack the predator. This is possible only subject to the qualifications indicated in (7) above.

Table 12 summarizes these trends for the several species of Ceylonese ungulates with respect to the leopard as a potential predator. The predator must be specified since small predators, such as the rusty-spotted cat, will be responded to differently when all of these presumptive prey animals are considered as a group. In addition all ungulates subjected to human hunting pressure will respond to the odor or sight of man by exhibiting response types (1) through (3).

Forming into a defensive cluster and actively advancing on a predator or, if alone, to outright attack a predator, is an adaptive response which is open only to animals large enough and possessing weapons that can serve to intimidate or injure the presumptive predator. The mobbing response on the other hand is an additional option open to herd or community-dwelling

TABLE 11.—*Average intervals (minutes) separating a series of leopard roars*

Subject	*N*	*Range*	*Average*
Wild single animal	6	3-9	6.0
Captive single animal	36	1-10	3.5
Wild duets	6	1-2	1.5

TABLE 12.—*Potential antipredator responses by ungulates to leopards*

	Response Types *							
Species	1	2	3	4	5	6	7	8
Tragulus	X	X	–	–	–	–	–	–
Muntiacus	X	X	X	X	X	–	–	–
Cervus	X	X	X	X	X	–	–	–
Axis	X	X	X	X	X	X	–	–
Bubalus	X	X	Na	Na	Na	X	X	–
Elephas	X	X	Na	Na	Na	X	X	X

* The numbers correspond to response types 1 through 8; see page 87.

X=potential response; –=response type not shown; Na=not applicable (see p. 87-88).

animals and is shown with resepct to a potentially dangerous predator. Although certain aspects of ambivalence suggestive of mobbing behavior may be seen in a solitary animal and may be referred to as "individual mobbing" behavior, mobbing as a group phenomenon is only possible within the context of a herd or if recruitment from neighbors is a possibility.

Giving an alarm call while displaying some conspicuous color pattern and employing a gait which induces the predator to chase is a strategy open only to animals which can easily outdistance their predator; hence, they must attract the predator at a sufficient distance to have an advantage allowing a certainty of escape, i.e., the escape distance (Hediger 1950, 1951), or they must be swift enough or have enough alternative escape mechanisms, such as dodging, to permit effective escape with respect to a swift predator.

Freezing, sneaking away, or direct flight are options open to all presumptive prey animals when they spot a predator or are startled by one. These options, however, are the standard forms of response by small relatively defenseless solitary prey animals and although warning cries may accompany escape maneuvers, in general, these are the only options open to a presumptive prey animal which is relatively weak with respect to its predator (Table 12).

One point to bear in mind is that until we get to response types 6 and 7, the forms of antipredator behavior are in the main individualistic. Even in the case of mobbing, the activities of the individuals composing the group are primarily carried out as individual activities and, indeed, mobbing is an emergent property coming out of group or community life. Many individualistic responses to predators, such as attracting attention, giving warning cries, etc., secondarily serve to protect the young. Indeed, the selective advantage inherent in some antipredator behaviors must surely be related to the overall increased survivorship of the young and add a selective bonus on the behavior. In addition, such forms of antipredator behavior in general increase the individual performer's survivorship. It is from the interaction system of the mother-young and the development of patterns which favor the survivorship of young that so-called altruistic behavior emerges as a property of those ungulates that dwell in extended mother-family herds. Hence, in such cases as the elephant and buffalo, where cluster formations are set up with the juveniles somewhat protected, there is not only a response benefiting individual survival but also a response of direct benefit to the young.

Communication Mechanisms and the Evolution of Social Organizations

As outlined under the species description, the communication systems of ungulates involve visual signals including various postures and movements sometimes augumented by the presence of antlers or horns, olfactory signals involving chemical marking, and auditory signals including various classes of sounds. Tactile communication through licking and various other forms of body contact are generally reserved for female-infant interaction and the interactions of adults during the breeding season. It has been conjectured that more complex, social organizations require more complicated forms of integration, hence a richer repertoire of signals for the exchange of information among the constituent members. This would seem to be a reasonable hypothesis; but the lack of detailed ethograms for many of the species effectively prevents a meaningful comparison for all categories of potential communication. If we consider one channel of communication, namely auditory communication, and compare the signals for a semisolitary forest-dwelling species, such as the muntjac, with the more social living elephant and axis, perhaps some trends can be elucidated.

We can consider various functional classes of sounds, such as contact calls which promote the cohesion of groups and the integration of inter-individual activity. Generally contact calls can be broken down into close-range calls, which are very often confined to the female-young unit, or long-range calls, for communicating distance information to members of a group which are separated.

Closely related to long-range contact calls are advertisement calls, which are indicators of the presence of an individual and potential indicators of its age and reproductive state. In this functional category we can include the vocalizations by adult males in rut.

A third functional class of vocalizations includes those sounds accompanying fighting which may be termed agonistic calls and generally form a graded series related to the intensity of arousal on the part of the vocalizing animal.

Feeding calls are generally functional in primate societies for indicating the presence of foodstuffs to scattered members of a foraging band. Warning calls are quite common and functionally serve to either attract the attention of a predator and secondarily to influence the behavior of the young or associated individuals. Pain cries are common to all animals and

are generally noisy intense vocalizations uttered by an injured individual.

If we examine these classes of calls, we can note that no specific feeding call can be discriminated within any of the species of ungulates; however, both types of contact calls, advertisement calls, aggressive calls, warning calls, and pain cries can be discerned for many species. A superficial comparison of the muntjac, axis, and elephant demonstrates that no long range contact call is present in the muntjac and axis repertoire and no advertisement call can be noted on the part of the male muntjacs. Rather, for the muntjac, longe range communication of presence and advertisement of presence seems to be carried out through the modalities of chemical communication. Elephants do utilize a long range call for maintaining contact among group members dispersed in the forest, although axis do not. A modified advertisement call which is a derivative of the long range contact call may be shown by elephants and axis males do emit a "challenge" call; hence, dramatic differences in the vocal repertories of ungulates are not apparent at this stage of the analysis. It may well be that there are finer gradations in the vocalizations of elephants when, for example, their calls are compared with those of the muntjac; but at this stage we may assume this to be in part conjectural (Table 13).

Discerning the significance of intergrades among call types as to their communicatory function is often very difficult and sometimes suspected differences are more apparent than real. Indeed, it would appear that for most mammals, the basic components of communication are remarkably similar and when differences do occur, it is through the ritualization of intermediate forms of vocalizations which may occur in the repertoires of even the most primitive forms. Ritualization of intergrade forms of signals can give rise to the so-called richer vocabulary of the more highly evolved forms (Eisenberg and Gould 1970: 116-123).

TABLE 13.—*Comparisons of auditory communication in three species of ungulates*

	Species		
Functional Class of Sounds	*Muntiacus*	*Axis*	*Elephas*
Close range contact calls			
Mother young	+	+	+
Group integration	−	+	+
Long range contact calls (advertisement of location)			
Challenge (adult male)	−	+	?
Group advertisement	−	−	+
Mother young separation	+	+	+
Agonistic cries (roar, growl)	+	+	+
Feeding calls	−	−	−
Warning calls	+	+	+
Pain cries	+	+	+

+ = response noted; − = response not noted.

Summary of Other Social Mechanisms Manifest in Ungulate Groupings

With the preceding considerations in mind concerning antipredator behavior and communication systems, it is time now to rapidly review other social phenomena typically exhibited within ungulate groupings. First of all, feeding is an individualistic matter. The location of food, ingestion, digestion, especially with respect to grasses and leaves, is an individual activity. Although the selection of appropriate foodstuffs by the young animals may be potentiated through following and participating with the mother in feeding, there is no sharing of food nor is there any collection and storage of food stuffs for future use.

The mother is responsible for primary parental care by returning to the infant to nurse it, maintaining contact with the infant, and by showing protective responses in the presence of danger. There is no cooperation in parental care involving the male and little care involving unrelated females. The only possible qualification to this preceding statement would be the cooperative maternal care shown by elephants, where the social unit is based on an extended mother grouping and where transferred maternal behavior may be shown on the part of adult females to groups of young. The auntie phenomenon is an emergent property of such extended kinship groups (Eisenberg 1966).

The male role in rearing the young or in the protection of female groups is practically nonexistent, unless the male happens to be associated with the female group during rut and redirects aggressive behavior, normally exhibited toward other males, toward intruding members of other species. Male activity toward other males of the same species, however, may secondarily reduce competition on food resources with respect to the female-young unit. In short, even in the solitary species where adult male spacing is the rule, a given male keeps clear an area that he shares in common with a female and her young. Thus he effectively reduces the competition of other adult males for the female and the young with respect to the same resources.

FIGURE 59.—Scrub vegetation, Wilpattu National Park. This photograph was taken in August when many deciduous species have shed their leaves.

This phenomenon, however, is by no means confined to the ungulates (see pages 62, 67-68 on the leopard and the jackal).

Differentiation of roles is in part promoted by maturational and hormonal processes within the infant and the mother. One of the first critical phases in the life of the maturing juvenile is the breaking of the close bond with the mother when she comes close to parturition with her next young. The degree to which the "old baby" is rejected differs markedly when various species of ungulates are compared (Altmann 1960, 1963). For example, in the case of the moose (*Alces americana*), the maturing juvenile is openly repulsed from contact with the mother. In contrast, the more social wapiti (*Cervus canadensis*) female is similar to sambar and axis in that, after an initial rejection, her yearling is allowed to remain in the vicinity and to accompany her when the "new" baby is older.

Further differentiation of roles is potentiated by the formation of bisexual or unisexual juvenile subgroupings so commonly seen in the ungulates. The creation of "play groups" is instrumental in integrating relevant activities at the appropriate developmental stages. The fact that yearling females tend to remain associated with their mothers even if it is a loose kinship group and further that yearling males gradually take up with adult males or other yearling males promotes the differentiation of roles. Such processes are reviewed by Altmann (1963).

TRENDS IN HABITAT UTILIZATION

As outlined in the introduction, our survey operations were carried out with respect to defined physiognomic classes of vegetation according to the scheme developed by Mueller-Dombois. This classification system groups vegetation types by the presence of grasses, shrubs, or trees, and the relative degree of continuous

FIGURE 60.—Savanna habitat, Wilpattu National Park. This photograph was taken in August at the height of the drought. The trees are of low stature. Such a habitat type is very rare in Wilpattu.

cover between the dominant plant forms; hence, at one extreme one may consider short grass cover near open water without the presence of any woody vegetation. From short grass, the next step in complexity is grass with scrub islands; followed by scrub islands or clumped scrub blending into open scrub with scattered trees, followed by forest scrub islands, open forest scrub, discontinuous forest scrub, discontinuous low to medium stature forest, low stature forest without emergents, and low to medium stature forest with emergents.

To what extent these physiognomic classes of vegetation represent stages in plant succession, we cannot at this moment say. It seems reasonable to assume, however, that given land cleared through the activities of man there will be a succession of stages from grass and forbs through grass with scrub to scrub with emergent trees and finally to a continuous forest situation as a climax form.

Discontinuous forest with grass interspersed or a savanna condition is perhaps a special case of climax type which can remain relatively stable with the periodic burning of undergrowth. Such savannas or talawas did not occur frequently in Wilpattu although they were characteristic of certain parts of the Gal Oya survey area. Similarly dense scrub may perhaps be a climax form or subclimax form under certain conditions of soil and drainage. Bearing in mind that the hypothetical stages of succession are not firmly established for the vegetation zones of Ceylon, it is nevertheless useful to think of a potential series of successional forms of vegetation with dense scrub as one climax (Figure 59), savanna as another subclimax (Figure 60), mature forest with emergents as the typical climax (Figure 61), and perhaps tall grass areas subject to periodic inundation as a relatively stable subclimax form which does not exhibit typical succession

FIGURE 61.—Mature forest with emergents, Wilpattu National Park. The grassy area in the foreground represents a drainage area sloping down to the channel of the Moderagam Aru.

as a result of periodic flooding in low lying areas (Figure 62).

The grazing and browsing activities of ungulates certainly have an effect on the rate of recovery of cleared areas and indeed it is an open question to what extent elephants and buffalo have had an influence on the orderly processes of succession in those areas of Wilpattu Park which were once formerly cultivated. In the ara region of Wilpattu are many abandoned tanks indicative of cultivation carried out up to 300 years ago (Figure 63). Many of the former tank sites are completely silted in with a characteristic clay soil supporting a scrub vegetation (Figure 64). It would appear from the intensive utilization patterns by elephants in this area that normal growth of some of the plant species is seriously retarded. This is especially true of trees, such as *Feronia*, which are actually stunted and distorted through the grazing activities of the elephants in this area (Figure 65). It is useful then to think of ungulates as retarders of successional rates. To clarify our assumptions with respect to this, Figure 66 develops the hypothetical retardation effect by elephants upon orderly succession of tree growth in the lowland dry zone when cleared areas are no longer kept open through the activities of man.

By utilizing standard plots, we were able to make indirect estimates of animal activity and estimate the relative intensity of animal activity with respect to the

FIGURE 62.—Tall grass villu during the rainy season with elephants feeding. (Mana Villu, March 1969.)

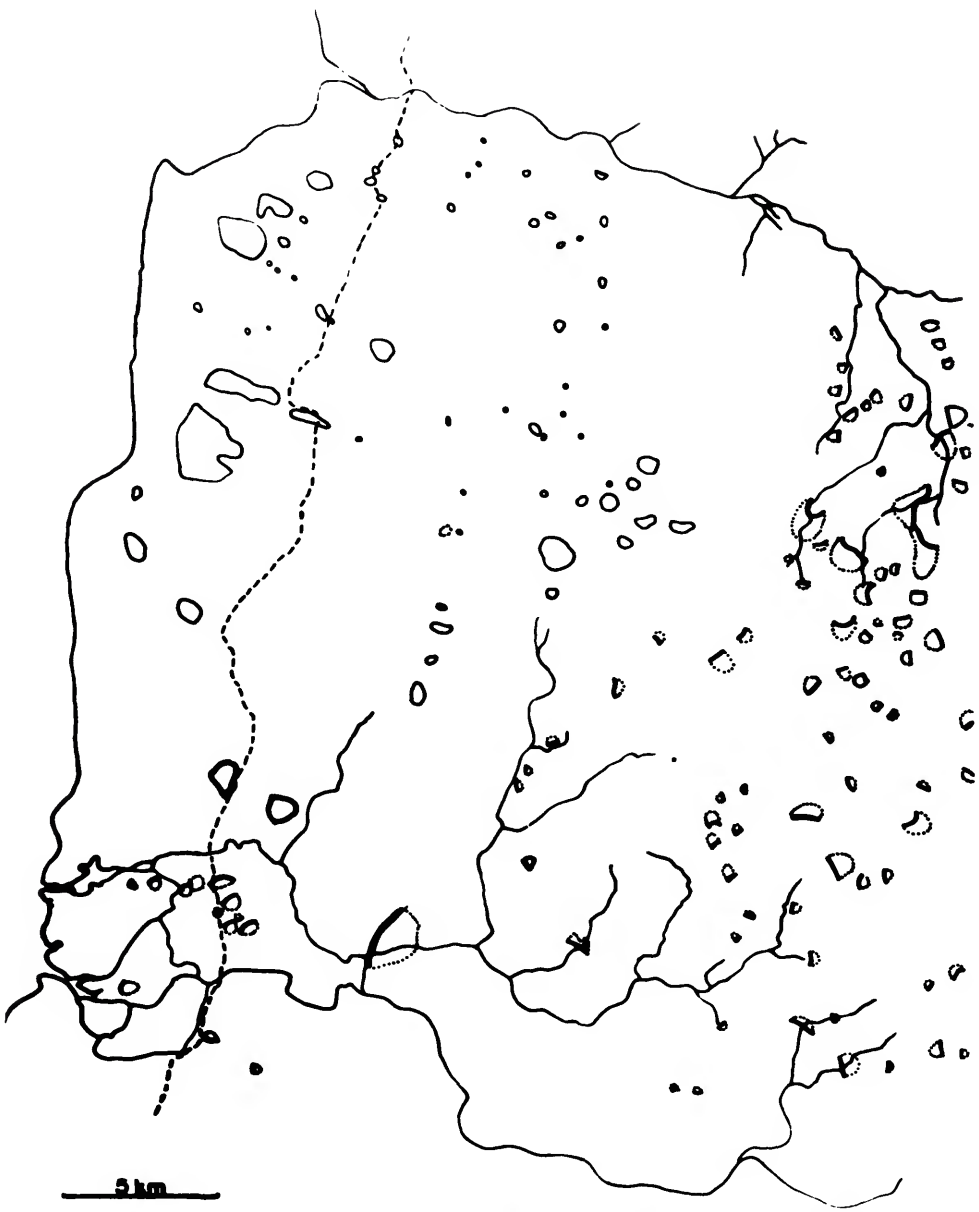


FIGURE 63.—Map indicating the regions where abandoned tanks occur (dotted lines). Sites of tanks which are now silted-in with broken bunds are areas supporting clay soil type and open scrub vegetation. These are prime feeding areas for all varieties of ungulates. Compare Figure 63 with the distribution of feeding by elephant cow herds in Figure 8 and 9.

FIGURE 64.—Open scrub on clay. This tank bed is partially inundated as the result of flooding. (Katakandal-Kulam, December 1968.)

different physiognomic classes of vegetation. In addition, relative productivity of different vegetational classes was also estimated by Dr. C.M. Hladik of the Laboratoire d'Ecologie Générale (Muséum). (See also Appendix A.)

One of the simplest indicators of long-term utilization by animals is the presence of game trails. Figure 67 illustrates an analysis of the amount of animal activity inferred by counting the number of trails present on one half hectare plots. An inspection of this figure will indicate that, as the vegetation becomes higher or as we proceed through a seris of plots toward pure forest, the number of game trails decreases markedly; hence, areas of discontinuous scrub or areas of discontinuous forest with scrub show much more animal activity than pure stands of forest or dense scrub. Dense scrub itself (plot number 17), although low enough for most animals to browse upon, is nevertheless by virtue of the sheer vegetation density not utilized as readily as stands of vegetation showing some discontinuity.

Utilizing the same series of sample plots, one can consider the proximity of the plot to water and its effect on animal activity. Figure 68 shows that within any vegetational type proximity to water has a profound influence. Plots that are within one mile (1.6 kilometers) of permanent water show consistent heavy use compared to plots that are in excess of two miles (3.0 kilometers) from permanent water which show relatively little use. The data suggest that, when there is an interspersion of scrub and grassland in close proximity to water, succession may well be retarded but, when such a condition is distant from water, the growth of trees may actually be encouraged.

On the basis of this analysis, we considered the relative animal activity data for a series of plots and eliminated those plots which appeared to be of a sufficient distance from permanent water to bias the utiliza-

FIGURE 65.—Stunted or distorted trees as the result of long-term ungulate feeding. (Giants Tank, February 1969).

tion patterns. In this estimate, it was important to consider the relative mobility of the species in question. Some species showing a high mobility could be studied in plots which were quite distant from permanent water sources. On the other hand those species showing very little mobility could have their activity analyzed with respect to plots within 2 to 3 kilometers of a permanent water source.

Roughly speaking the elephant, buffalo, and sambar show the greatest potential and actual mobility, closely followed by the swine. Although axis have a reasonably high potential mobility and have been known to undertake movements in excess of 1.6 kilometers, in reality they show very little mobility and exhibit a strong site attachment. Smaller species such as the hare, porcupine, muntjac, and mouse deer have a much lower potential mobility and were only censused with respect to permanent water sources.

The inevitable conclusion then is that for an interpretation of density and habitat utilization patterns, the interspersion of resources must be considered which includes proximity of water and availability of browse or grazing material to the species in question. Figure 69 illustrates the feeding height of the major herbivorous species with respect to the average heights of scrub and forest. As can be seen from an inspection of this figure, the elephant, sambar, and buffalo can carry out some forest grazing although scrub is more easily accessible for browsing. Axis, muntjac, mouse deer, and hare are restricted with respect to forest utilization. If the forest shows some discontinuity and a reasonable growth of herbaceous material, then some forest grazing can be carried out; however, in dense, continuous forest with reduced herbaceous undergrowth, effective habitat utilization by the smaller herbivores is retarded. The exceptions, of course, are those forms which can dig for tubers and roots, such as the porcupine and swine.

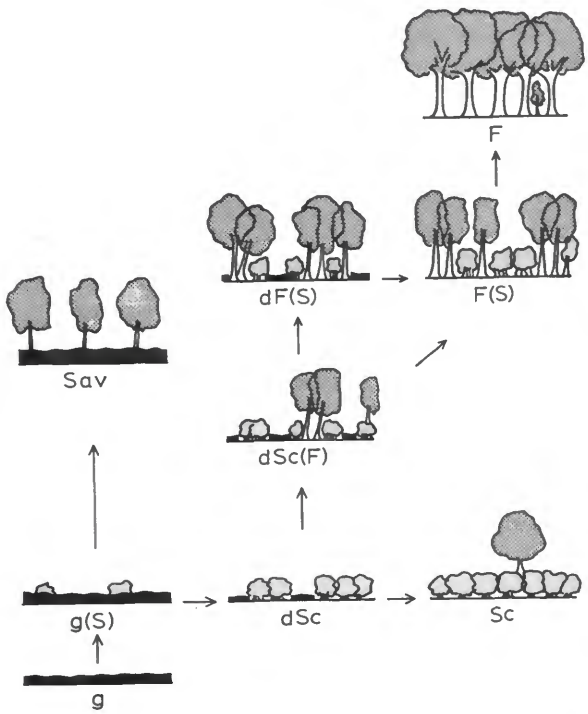


FIGURE 66.—Hypothetical stages of succession in the lowland dry zone. The savanna (Sav) and dense scrub (Sc) may be considered as edaphic climax forms which occur under appropriate conditions. The savanna is maintained mainly through grazing activities of ungulates and burning resulting from electrical storms. Scrub is the dominant vegetation type where ground-water levels appear to be too low to support tree growth. Grassland (g) itself may be considered a climax form in the vicinity of villus if the villus indeed are sink holes and are possibly increasing in size. Periodic inundation may prevent colonization by trees. Disregarding the three exceptional cases of subclimax forms then, all things being equal, vegetation should proceed toward forest (F); however the activities of elephants may help to promote retardation from growth to forest and sustain discontinuous (dSc) or open scrub formation (g(S)) in some areas. See also the discussion by Boughey 1963, and Buechner and Dawkins 1961. Intermediate stages are discountinuous scrub with forest (dF(S)), and forest scrub (F(S)).

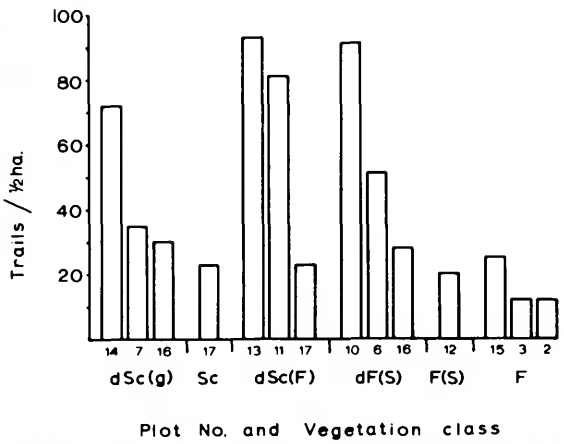


FIGURE 67.—Indication of animal activity by trail counts as a function of height of vegetation. Forest areas (F) show the least overall activity by game in comparison to areas of scrub (Sc) and forest scrub (F(S)). See also Agnew 1966 and Figure 68.

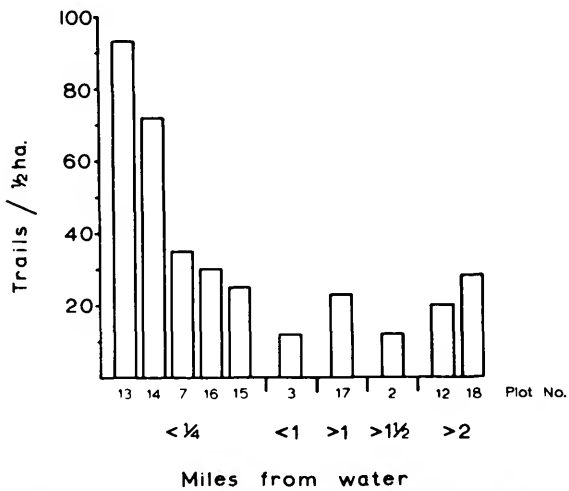


FIGURE 68.—Proximity to water has an effect on animal activity, as indicated in the above diagram. The closer to water the more activity regardless of the vegetation class; even so, forest vegetation shows less utilization than scrub when equally close to water. Compare plot numbers in this figure with numbers in Figure 67.

All species exhibiting any reasonable mobility can make use of fallen fruits in the forest at the appropriate seasons of the year. Although the productivity of the forest is higher than that of the grassland (C. M. Hladik, in preparation), terrestrial herbivores cannot effectively utilize the productivity of the forest itself. (For an extended discussion of this phenomenon in semi-arid habitats of North America, see Chew and Chew 1970.) Only an arboreally adapted herbivore can effectively utilize the productivity of the forest itself and, in the case of the lowland dry zone of Ceylon, this would appear to be the gray langur (*Presby-*

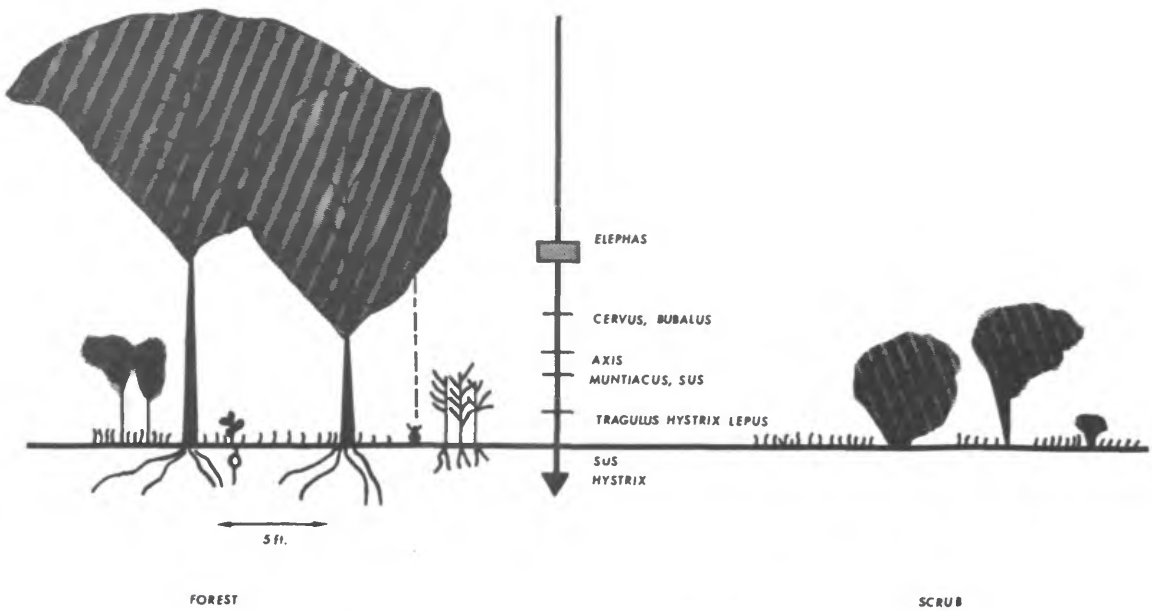


FIGURE 69.—Feeding heights of major herbivores. The elephant has the tallest reach and can utilize forested habitats to a greater extent than any other ungulate. All things being equal, grazing ungulates are favored by discontinuous forest or discontinuous scrub and least favored in a continuously forested habitat with maximal shade and a minimum of herbaceous vegetation.

tis entellus). Depending on the water requirements of *Presbytis*, its distribution in the lowland dry zone would seem to be limited only by access to fruits bearing sufficient moisture to sustain them during drought periods. In the absence of such fruits, the langur probably must drink; hence, its distribution will be tied somewhat to water. Nevertheless, aside from the elephant, the langur probably represents the largest biomass component in the forested habitat.

All of the foregoing discussion leads us to believe that the maximum densities of game can and will be achieved only where water, herbaceous growth, and scrub are at a maximum and with the exception of the langur these predictions are amply confirmed and illustrated in Figure 70. This figure illustrates that the maximum utilization of habitat by the herbivorous species in the park occurs in vegetation zones including grass, grass with scrub, discontinuous scrub with grass, and discontinuous scrub with tree emergents. Dense scrub itself shows very little activity with the exception of the elephant, whereas the savanna situation shows reasonably high activity.

An inspection of Figure 70 shows that the elephant is able to utilize a wide range of habitat types although it is favored by a discontinuous forest situation. The elephant may be considered as a grassland-dependent form and in this respect does not differ markedly from the African elephant (Wing and Buss 1970). The langur is very much confined to the forested situation although some activity can be noted in the scrub areas in the vicinity of forests. The hare is very much confined to the discontinuous scrub or grassland situation. The swine, in its habitat utilization trends, is definitely favored by the discontinuous scrub or grassland, but can and does utilize the forest. To an extent the porcupine appears to parallel the swine in its utilization patterns. Although the sambar does utilize the discontinuous open habitats to a great extent, its activity is extended into the forest and makes a major contribution to habitat utilization in the forested areas. By contrast, the axis makes very little contribution to the utilization of forested areas and in the main is favored by an open or discontinuous vegetational pattern. The buffalo likewise is favored by a discontinuous pattern of vegetation although the buffalo can browse in the forest and traces of buffalo ac-

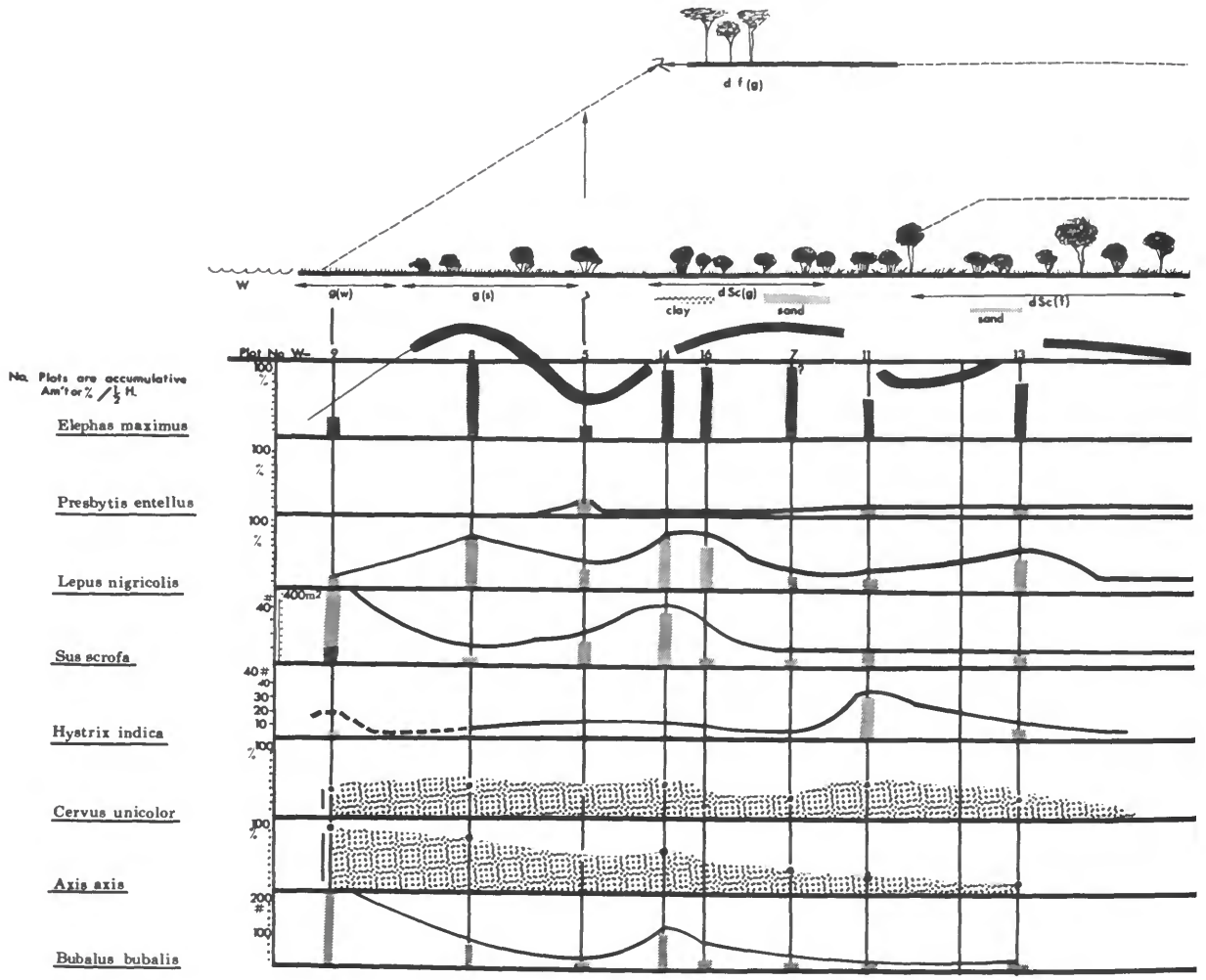
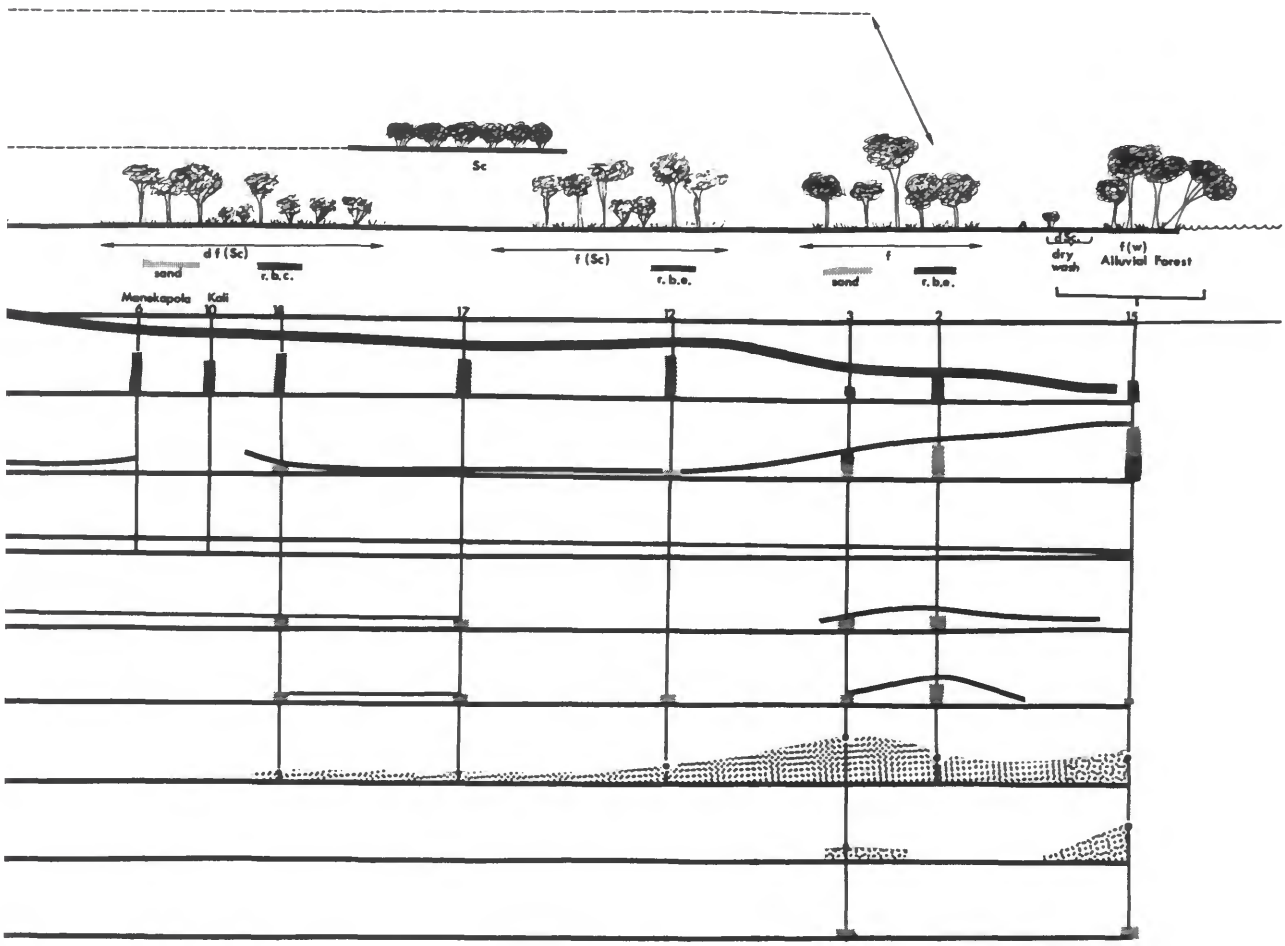


FIGURE 70.—Habitat utilization trends as indicated by intensity of habitat utilization for a series of vegetation types. Intensity of habitat utilization was measured according to procedures outlined in Appendix A. Note that the elephant shows the broadest habitat utilization; *Presbytis* is confined in the main to forested area; *Lepus* is confined mainly to open scrub; *Axis* is more restricted in its form of habitat utilization to open scrub than is *Cervus*. The buffalo, *Bubalus*, parallels the axis in favoring open habitats. With the exception of the alluvial forest region, forested areas do not favor high densities of herbivores. Only the elephant and the sambar utilize

tivity can be ascertained in forested areas which are in the vicinity of good grazing areas.

COMPETITION AND ECOLOGICAL SEPARATION

The foregoing discussion indicates that the intensity of habitat utilization by the various grazing species is in part dependent on season as well as the physiological capabilities of the species in question. Axis utilize the grassland and scrub-grassland interfaces. Although axis will enter the forest and browse, their ability to utilize the forest is in part dependent on the maturity of the stand since the axis cannot reach above some 1.5 meters. Although it is true that when pressed, axis will browse by rearing up on their hind legs, in general, the return from this mode of browsing is ap-



the forest to any appreciable extent. Percentages for *Presbytis, Lepus, Cervus, Elephas,* and *Axis* refer to number of 5 m^2 plots out of 140 which were found to contain feces of the species in question. Numbers for *Hystrix, Sus,* and *Bubalus* refer to the total number of fecal piles counted on a half hectare plot. Plots 6 and 10 were not plotted for *Presbytis, Lepus, Hystrix, Cervus, Bubalus,* and *Axis* because they were examples of forest pockets in association with villus, thus utilization trends were biased. Similarly Plots 12 and 18 were not plotted for *Axis, Bubalus,* and *Lepus* because of their distance (>3 km) from water (see Appendix A).

parently not high enough in quality to make it a predominant feeding mode except under times of extreme deprivation.

The taller sambar deer, the adult at least, can browse to a height of approximately 1.8 meters. The sambar, although utilizing open grasslands, is more nocturnal than the axis, rarely grazing in the open during daylight hours, and in addition spends a great deal of its time in more discontinuous forest areas where it can remain in the shade, browse to a reasonable height on the vegetation, utilize the herbaceous plant growth forming the understory in forested areas, and in general make much more effective use of the forested habitat than does or can the axis.

The buffalo, although browsing to some extent in forested areas, is very much dependent on grass and

water, especially standing water. A good part of each day is spent lying in the water probably to protect itself from biting insects and also to regulate its body temperature. The buffalo is far more grass dependent than is the sambar deer and its habitat utilization patterns parallel that of the axis.

The elephant is in part grass dependent, which is a function of age and sex. Lactating females and their young utilize the herbaceous growth to a far greater extent than do adult males (McKay 1971). Nevertheless, the elephant can and does browse a great deal and because of its extreme reach can utilize the forest by reaching into the lower branches. The height of reach of an adult elephant is approximately 4 meters. The elephant has one additional advantage in that it is capable of pushing down small trees, thus making the crowns available for browsing by younger animals and also making browsing a simpler process. Furthermore, when a tree is pushed down, the elephant has access to the roots of the tree without having to dig for them.

The elephant is quite versatile in being able to utilize short grass even when it is too short to be conveniently grasped by its trunk, for it will then kick up the turf to form a pile of uprooted grasses and, after scraping the soil from the roots, commence feeding. Although this method of feeding is not particularly efficient, the elephant is so dependent on herbaceous growth that during drought periods it will aggregate and feed on short grass in the vicinity of the small lakes or villus. In terms of the intensity of habitat utilization then, although the elephant does not utilize the forest to the same extent that it does the scrub area, it nevertheless seems the least restricted by physiognomic classes of vegetation with respect to its intensity of utilization. Although our analyses were not as controlled as those conducted by Wing and Buss, we conclude that the Asiatic elephant is remarkably similar to the African form with respect to diet and habitat preferences (Wing and Buss 1970).

Wild swine are, of course, not adapted to grazing but will devour quantities of herbaceous growth at certain seasons of the year. Instead, swine are broadly adapted to feeding on a variety of vegetable and animal foodstuffs. The movement patterns of sounders are very much determined by the local abundance of fruit which has fallen to the ground and by the seasonal growth of tubers and fungi in the forest. So versatile is the swine that it is impossible to discuss its feeding habits in a meaningful comparison with the feeding habits of the ruminants.

The muntjac is primarily a dweller at the forest edge utilizing the forest for cover and grazing in the evening or browsing on low shrubs in the open. The muntjac is extremely limited with respect to the height of its browsing ability as is the mouse deer. The mouse deer is somewhat more versatile in its feeding habits, in that it takes quantities of fruit and even the eggs of ground-nesting birds; however, it is similarly restricted in its browsing height and, in general, is distributed at the edge of the forest or at a forest interface between mixed scrub and grassland.

The porcupine (*Hystrix indica*) does graze on grass and equally well digs for roots and tubers. It is thinly distributed in the vicinity of permanent water. The hare is apparently not as water dependent, but it is primarily a grazer. It can also convert to browse and bark feeding during the drought period. The hare appears to be less restricted with respect to water but is almost entirely restricted to the scrub and mixed scrub grassland types of vegetation and does not utilize the forest to any extent.

The gray langur (*Presbytis entellus*) utilizes fruit and leaves. The langur has a sacculated stomach and is capable of utilizing cellulose as a carbohydrate substrate (Bauchop and Martucci 1968). During the maximum abundance of fruit, the langur feeds heavily on this food and during the nonfruiting season, the langur apparently can rely on flushing leaves and buds for its dietary intake. The langur obviously is able to utilize the crowns of forests and has a cellulose resource which removes it from any direct competition with the terrestrial ungulates during drought periods.

If we can consider a provisional classification of lowland dry zone vegetation based on a hypothetical series of successional forms from grassland through scrub to forest, it is appropriate to speak of the axis deer as an intermediate successional species, the sambar as a late intermediate successional species, the muntjac and mouse deer as intermediate successional species, the hare as an early successional species, and the langur as a climax adapted species.

The differences in food preference exhibited by the swine, mouse deer, and porcupine virtually eliminate them from any general competition with the other dominant members of the Ceylon fauna. Differences in ability to feed on forest vegetation in part remove the elephant from direct competition with the buffalo.

Differences in habitat preference shown by axis and sambar ameliorate competition between them; however, all of the species to some extent compete for grass when it is available. Since availability of grass is in part seasonally determined, each of the species must to some extent have alternative sources of food when the abundance of grass decreases. To this extent, then, the only two critical times of potential competition occur during the two drought periods when fresh, growing grass becomes restricted. During the drought there is some competition for low-stature shrubs and competition with respect to the utilization of water. The great mobility of the elephant removes it in part from competition with the sambar and axis; however, the equal mobility of the villu buffalo sometimes creates competition for unpolluted water sources (Kurt 1969). Buffalo have a tendency to foul water holes when large numbers lie in the water for several days at a time—defecating and churning up the mud bottom. This appears to render the water unpalatable for elephants but appears to be a serious problem only in Ruhunu Park, where a large percentage of available water is in small, shallow water holes.

NUMERICAL ABUNDANCE AND BIOMASS

Our censusing operations and calculations are discussed in Appendix A. It should now be obvious from a close reading of the preceding section that certain compensations had to be made for each species in estimating their density within the park. Details for estimating the numbers of each species are included in Appendix A. An extended consideration of the utility of pellet-count techniques versus actual visual-counting techniques for the axis deer is considered in the publication by Eisenberg, Santiapillai, and Lockhart (1970).

Two types of calculations are presented here: crude density and ecological density. Crude density and biomass include estimates without reference to the discrete habitat utilization patterns of the species in question. The crude estimates are based on a consideration of Wilpattu Park as a total habitat (exclusive of the West Sanctuary and the recently added South Intermediate Zone); hence, the calculations are based on an area of only some 600 square kilometers. Table 14 includes the crude density estimates and Figures 71 and 72 compare crude density and biomass for the dominant species. Our crude estimates of biomass worked out to 766 kilograms per square kilometer.

TABLE 14.—*Crude density and biomass of herbivores in Wilpattu Park* (area: 580 square kilometers)

Species	*Number*	*Density (km²)*	*Average wt./ animal* (kg)*	*kg/km²*
Elephas maximus	70	.12	1810.0	217.2
Bubalus bubalis	160	.27	272.0	73.4
Axis axis	3,500	5.84	45.0	262.8
*Cervus unicolor***	700	1.17	135.0	157.9
Sus scrofa	180	.30	27.0	8.1
Muntiacus muntjac	264	.44	13.5	5.9
Tragulus meminna	350	.58	3.2	1.9
Hytrix indica	350	.58	9.1	5.3
Lepus nigricollis	2,800	4.67	3.2	14.9
Presbytis entellus	1,700	2.84	6.7	19.0
Total				766.4

*Adjusted with respect to percentage of age and sex classes for larger ungulates.

** This may be taken as the maximum value; see Appendix A. If we assume 400 sambar as a minimum then the sambar biomass equals 93.1 kg/km² and the total biomass is reduced to 702 kg/km².

Since in the main Wilpattu Park is a forested habitat, the biomass is considerably lower than those biomass estimates calculated for steppe and savanna country in East Africa, being almost one sixth of the biomass

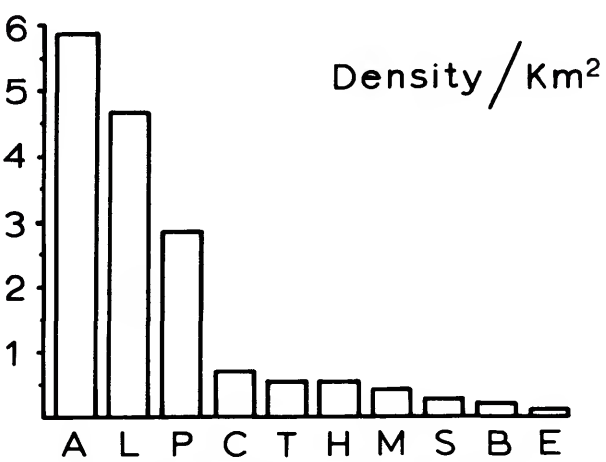


FIGURE 71.—Crude density of major herbivores in Wilpattu National Park were ranked in the order of numerical abundance. A=*Axis*. L=*Lepus*. P=*Presbytis*. C=*Cervus*. T=*Tragulus*. H=*Hystrix*. M=*Muntiacus*. S=*Sus*. B=*Bubalus*. E=*Elephas*.

estimate calculated in 1958 by Grzimek (in Bourliére 1966) for the Serengeti and falling considerably below the high biomass estimates of up to 31,000 kilograms per square kilometer quoted in the tabulation by Bourliére in 1966 (see also Bourliére and Verschuren 1960). Nevertheless, we feel that this is a fair estimate of the crude density and biomass pattern for our forested habitat.

It is interesting to note that ranked in order of greatest numerical abundance axis deer are first followed by hare, langur, sambar, and then at low densities by the mouse deer, porcupine, muntjac, and swine. Buffalo and elephant show the lowest density of individuals per square kilometer. On the other hand, when biomass is considered, elephants almost equal the first ranked axis followed by sambar, buffalo, langur, hare, and then in insignificant amounts swine, muntjac, and mouse deer (Figures 71 and 72).

To supplement the crude density and biomass calculations, we offer ecological density calculations from an area of 24 square kilometers including all major habitat types (Figure 76). During the drought in July and August, rather large congregations of game can occur for periods of up to seventy days. Censusing at this time we can define a maximum biomass figure for a given time interval. During the rainy season, dispersal of buffalo, elephant, and sambar causes this maximum biomass value to drop to a value still exceeding the crude estimates by almost 100 kg/km.[2]

Tables 15 and 16 compare and contrast the ecological densities for the drought season and the rainy season. During the drought biomass can reach 3,000 kilograms per square kilometer only to fall by 60 percent during the wet season when the elephants and buffalo may be dispersed into other areas. Hence, ecological densities can reach a critical maximum for this area and the figure of approximately 4,000 kilograms per square kilometer may be taken as an extreme value. At maximum densities, our 24 square kilometer survey showed up to two sloth bears, four jackals,

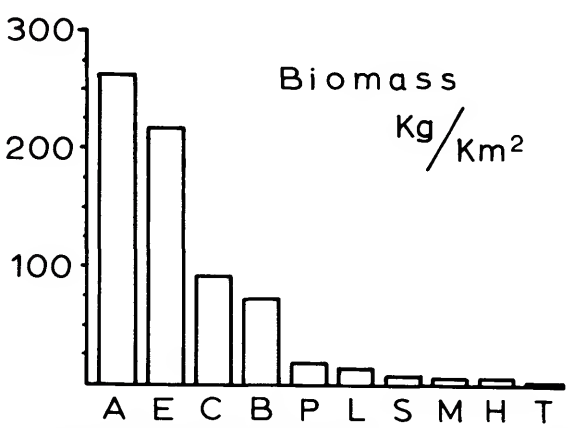


FIGURE 72.—Crude biomass expressed as kilograms per kilometers squared. Animals listed in order of decreasing biomass contribution. Note that, although the elephant is the least in numerical density, it is second only to the axis in its contribution to crude biomass (see Figure 71.)

TABLE 15.—*Ecological density calculation.**

Species	*Number*	*Density (km²)*	*Average wt./ animal*** *(kg)*	*kg/km²*
Elephas maximus	24	1.00	1810.0	1810.0
Bubalus bubalis	36	1.50	272.0	408.0
Axis axis	290	12.09	45.0	544.0
Cervus unicolor	24	1.00	135.0	135.0
Sus scrofa	28	1.16	27.0	31.3
Presbytis entellus	68	2.82	6.7	18.8
Total				2957.1

* Estimate made during the maximum concentration of game at the time of the July-September drought. Area: 24 km². Habitat: villu type (three permanent water holes). Physiognomic class of vegetation: forest cover 91-92 percent, scrub cover 4 percent, herbaceous cover 3 percent.

** Adjusted with respect to percentage of age and sex classes for larger ungulates.

TABLE 16.—*Ecological density calculation.**

Species	*Number*	*Density (km²)*	*Average wt./ animal (kg)*	*kg/km²*
Elephas mavimus	3	.13	1810	235.3
Bubalus bubalis	5	.21	272	57.1
Axis axis	240	10.0	45	450.0
Cervus unicolor	15	.62	135	83.7
Sus scrofa	17	.71	27	19.2
Presbytis entellus	50	2.10	6.7	14.1
Total				859.4

* Estimate made during the minimum concentration of game during the October–November rainy season. Area: 24 square kilometers. See Table 15.

three leopards, four troops of langurs, one troop of *Presbytis senex*, perhaps two troops of *Macaca sinica*, varying numbers of buffalo averaging around thirty, up to twenty-four elephants, approximately three hundred axis, anywhere from twenty to thirty sambar, and three sounders of swine which varied in composition from less than twenty to almost thirty individuals.

When our data from Wilpattu Park are compared with the population density and biomass calculations presented by Schaller (1967) for Kanha National Park in Madhya Pradesh, India, we seem to be in reasonable agreement with respect to pounds per square mile for wild game; however, in Schaller's study area considerable domestic cattle and buffalo were grazed, so in effect his biomass calculation comes to approximately three times the level we have estimated when the domestic livestock is added in. This suggests that the Kanha forests and meadows show an overall higher productivity and that the domestic stock are providing very strong competition for the wild species resident in his particular study area (Schaller 1967).

Surveys in the wet lowlands of Assam yield higher biomass estimates for elephant and other ungulates (Spillet 1967) and, until further surveys are conducted in tropical dry zone forests with seasonal drought, we cannot evaluate the extent to which the carrying capacity is being approached here in Wilpattu. Further biomass calculations are considered in the report of McKay (1971).

Recommendations for Management

Clearly our studies indicate that the West Sanctuary is an integral part of the villu ecosystem and should be included within the park proper. All domestic cattle grazing and agriculture currently being carried out in the West Sanctuary in the vicinity of Mail Villu and south near Pomparippu should be discontinued and, if necessary, the human populations dependent on these areas be relocated. The old Mannar Road is used by carters and by some automobiles for communication between Puttalam and Mannar. The use of this road should be restricted and only daylight travel should be allowed. If it were at all possible, the park should be bypassed completely and the use of the old Mannar Road be discontinued.

The Ceylon Department of Wildlife has been attempting to include the West Sanctuary within the borders of the park proper and every effort in this direction is to be encouraged. Residency of elephants in the West Sanctuary could be prolonged and more effective utilization of the grassland areas around Atha, Periya, Periya Naga, and Mail villus could be promoted if the water were supplied throughout the drought period. The possibility occurred to us that wells could be bored in the vicinity of these large villus and by installing windmills and pumps a continuous supply of fresh water could be delivered to the low-lying villu areas. Windmills and pumps would be a very cheap method of supplying water throughout the drought period to the West Sanctuary region. This would encourage the growth of grass and increase the carrying capacity of the West Sanctuary area considerably. In addition, it would reduce the pressure on habitat utilization in the vicinity of the permanent villus which suffer greatly from earth scarification by elephants during the drought period when they are forced to scuff up short grass and herbaceous ground cover. This is especially true in the vicinity of Tala, Kali, Marikaram, Marai, Mana, Katarampu, Mahapatessa, Kudapatessa, Borupan, and Kokarre villus.

A word of caution should be added, however. Since we have a very poor knowledge of succession in the dry zone, experimental plots should be set up to assess the quality of changes induced by permanent water in these areas. It may well be that long-term grazing and permanent water could promote succession of less palatable grasses.

Some success was achieved during 1968-1969 by the reconstruction of the bund at Katakandal Kulam. Thus water was retained throughout the 1969 drought period in this area and the migration of the buffalo herd observed during the drought of 1968 did not occur with retention of water at Katakandal Kulam. The utility of this repair system is readily demonstrable and it remains only to be extended to other ruined tank areas in the central villu system.

As indicated on pages 94-95, it is the degree of interspersion of resources that determines the quality of the habitat. Water, grass, and scrub must be interspersed in an appropriate balance to insure uniform grazing habits by the resident herbivores. Currently the elephant population in the central villu portion of the park is forced to move extensively and also forced to destroy much herbaceous cover in the vicinity of permanent water during the period of prolonged drought. Increased productivity of the West Sanctuary and subsequent relaxation of pressure on the central villus could be insured by the establishment of wells and pumps in the low lying temporary villu areas of the West Sanctuary itself.

A consideration of the mortality trends and predation habits by the leopards and jackals, as outlined under the species sections, gives no indication of overpredation on the part of the leopard. Rather there is every indication that the axis and sambar populations are increasing. Buffalo populations appear to be increasing as well, and a close watch must be kept on the trends within the buffalo populations lest buffalo density reach a critical level as it already has in Ruhunu Park. At present Wilpattu Park is in fairly good balance and during the years that we studied it, the park was experiencing severe droughts without serious degradation of the habitats themselves. With the very heavy rains in late 1969, the over-utilization trends in the vicinity of the larger villus should be in part reduced and if the drought cycle is broken at this point the park may come into even better balance within the next two or three years.

FIGURE 73.—Wounded male elephant at Katarampu Villu, Wilpattu National Park, August 1968.

Poaching is still a serious problem in parts of Wilpattu. Some poaching is carried out in the West Sanctuary by the resident populations who cultivate and also by fishermen who visit from across Putallam Bay. Evidence of poaching was noted in the vicinity of Atha Villu, Periya Uppu, Periya Villu, Periya Naga, and Mail Villu. Shooting blinds were located north of Marikaram Villu along the banks of the Moderagam Aru. Actual cases of poached buffalo came to our attention twice during 1968 and 1969 and how many cases went undetected we cannot say.

Two wounded elephants, both bulls, were noted in Wilpattu during the 1968-1969 survey, apparently having suffered gunshot wounds from cultivators while foraging across the Moderagam Aru (Figure 73). One of the primary problems in reducing elephant shooting by cultivators is to induce the elephants to remain within the park boundaries. Improvement of the habitat within the park could contribute to this. In addition, the buffer zone of the north sanctuary on the north bank of the Moderagam Aru should be extended and its status changed from sanctuary to full national park status. Both banks of the bounding rivers—the Kala Oya and Moderagam Aru—should be buffered not by sanctuaries alone but rather by full portions of the National Park. In view of the settlement at Marichchukkadi, such an extension of the park to the north would be extremely difficult without radical relocation of the resident human population; nevertheless, one cannot overstress the importance of buffering both banks of the river system to insure adequate protection of the game animals which use the river. Elephants do cross rivers and will continue to do so as long as there is attractive forage on the opposite bank.

In Ruhunu Park, the Manik Ganga runs through the park itself and hence both banks are secure for elephants and other game species. Unfortunately the situation in Wilpattu is not so easy since in both cases the south bank of the Kala Oya and the north bank of the Moderagam Aru are experiencing sporadic cultivation and are not parts of the park proper. Until such time as both banks are secured and given full

protection, one can only anticipate that the wounding of elephants will continue as they seek to cross and inevitably begin to raid cultivated plots.

Wilpattu Park is certainly one of the most beautiful natural areas in the lowland dry zone. The series of lakes in the central portion provides not only beauty for the eye of the human observer but an extraordinarily interesting habitat situation with the dispersed pure-water resources spaced so uniformly within the forest. Extending the park boundaries to include the West Sanctuary and portions north and south of the bounding rivers would greatly enhance the value of the park as a reservoir of Ceylon's native fauna. More strict patrolling to reduce the incidence of poaching and regular censusing to determine long-range population trends should be executed. Only by continually monitoring the population trends within the park can adequate predictions be made with respect to the extent of habitat utilization and the degree of competition for critical resources.

In a park as small as Wilpattu, supporting as it does such a varied and dense fauna of ungulates, a rather continuous check on the extent of habitat utilization and a rather continuous estimate of the degree to which the carrying capacity is being exceeded must be made. Indeed, the balance of the park may well have to be adjusted many times over the years. Buffalo populations, in the absence of any more effective predator than the leopard, may reach critical values within this park during the next fifteen to twenty years and serious competition with the elephant will then result in a manner reminiscent of the situation at Ruhunu Park. Selective shooting or selective round-up of buffalo for selling to cultivators may become a necessity. Indeed, within the next twenty-five years, the elephant population may similarly have to be cropped either by employing a round-up technique or by actually shooting excess animals.

The managers of these park areas are certainly aware, and the general public must be made aware, that an area of this size needs to be managed. It cannot be left to the animals to control their own habitat utilization trends. A park of this size cannot manage itself but must be treated as a garden and, as a garden, must be cultivated.

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Appendix A

METHODS EMPLOYED IN CENSUSING

Figure 74 illustrates Wilpattu National Park and its associated intermediate zones and sanctuaries. At the time of planning the study, the park itself consisted of the unshaded area in the map bounded by solid lines. This comprised approximately 580 square kilometers and, although the former south intermediate zone (area 3 in Figure 74) was subsequently added to the park, this area remained relatively inaccessible and was not included in our normal survey; thus, crude density and crude biomass estimates were made with respect to the original national park boundaries.

Referring again to Figure 74, area 1 or the North Sanctuary comprises some 6.3 square kilometers; area 2 or the east intermediate zone consists of approximately 281 square kilometers. The former south intermediate zone includes some 71 square kilometers and the West Sanctuary or area 4 includes roughly 214 square kilometers. Crude density and crude biomass calculations were based on a map area with the old national park boundaries of approximately 225

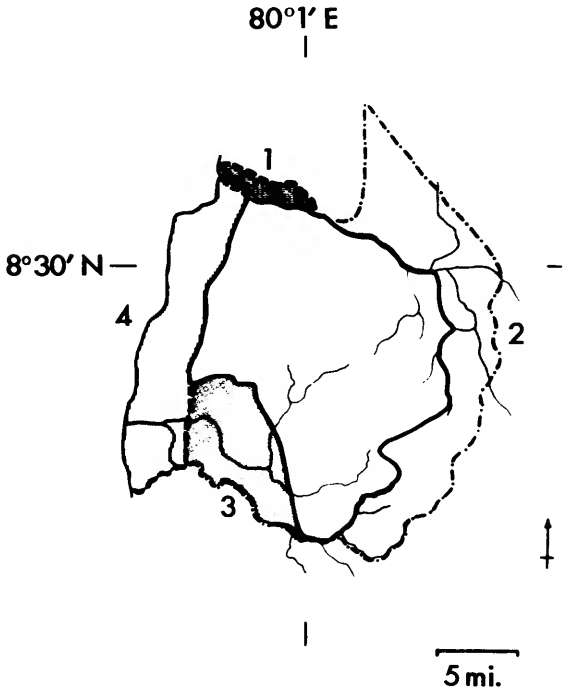

FIGURE 74.—Map of Wilpattu National Park and associated intermediate zones and sanctuaries. In 1967 when the study was planned, the area of the National Park comprised the unshaded portion of the map bounded by solid lines. All references in text to the National Park refer to this area even though area 3 was included within the boundaries of the National Park during 1968. Because of difficulty of access, area 3 was surveyed only sporadically; therefore, crude density and crude biomass estimates refer to the old boundaries of the National Park itself. Area 4, the West Sanctuary, was surveyed extensively however, but when referred to in the text is so designated.

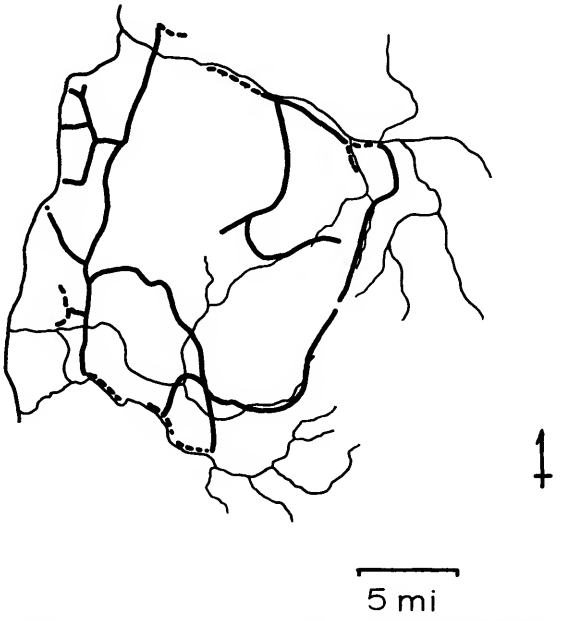

FIGURE 75.—Survey routes employed for estimate of habitat utilization during the quarterly survey. As can be seen, portions of the West Sanctuary, as well as the boundaries of the National Park itself, and the river systems were surveyed on a quarterly basis. Dotted lines refer to foot surveys.

square miles or 580 square kilometers. The total area of national park and associated sanctuaries and intermediate zones include in excess of 1,118 square kilometers; hence, our estimates of crude biomass and density refer to approximately one-half of the area currently under total or partial protection.

Figure 75 indicates the survey routes employed during the quarterly circuits of the park. We were able to survey portions of the Kala Oya, Moderagam Aru, and the West Sanctuary. By employing the feces-count technique, we were able to get a rough estimate of the intensity of habitat utilization by elephants in these park boundary areas. We were not, however, able to monitor movements or get absolute counts of the elephant herds in these peripheral areas. The quarterly circuit did allow us to gain some insight into the intensity of habitat utilization by elephant herds not directly associated with the central park itself.

Figure 76 indicates the survey routes employed in taking the census in the park proper and in interpreting the relationship of the West Sanctuary habitat utilization patterns to those of the national park itself. The monthly survey and censusing included some 190 square kilometers of national park area and roughly 127 square kilometers of the West Sanctuary. Intensive censusing operations were carried out in the 24 square kilometer area indicated by the diamond pattern on the map.

Locations of twenty-two study areas are indicated by dots on the map in Figure 76. At these locations, standard plots were established for studying habitat utilization patterns by the various ungulate species; twenty-nine plots were included within the twenty-two locations and ten of these plots were used for our pellet-count monitoring (Eisenberg, Santiapillai, and Lockhart 1970). The monthly survey and plot locations permitted us to compare and contrast habitat utilization trends through the wet and dry seasons for the major villus in the park and the Moderagam Aru.

Surveys on the study plots involved two techniques.

1. In September of 1968, together with the botanists under the direction of Dr. Dieter Mueller-Dombois, seventeen plots were surveyed. An area 100 by 50 meters was surveyed by seven people walking linear transects parallel to one another, being equally spaced and surveying some twenty stations along the 100 meter transect, noting such characteristics as fecal piles, evidence of branch feeding, height of branch feeding, extent of cover, presence or absence of game trails, location and size of termite mounds, tracks, and presence or absence of ground disturbance as the result of digging, flat scarring, resting, or wallowing. The results of this September survey were employed in preparing Figure 70 which illustrates relative intensity of habitat utilization by the major herbivores. The seventeen plots were selected with respect to differences in physiognomic classes of vegetation. Further details of this method of animal activity analysis and its application will be included in a forthcoming publication by Mueller-Dombois for Ruhunu National Park (*in preparation*).

2. Ten plots were studied for seven months by measuring the number of fecal piles and weights of feces for axis, sambar, hare, buffalo, and elephant. These plots were located in pairs at three water holes and along the Moderagam Aru. Each plot equalled roughly 450 square meters or 5,000 square feet. Pellet groups were counted and weighed once every 30 days. Estimates of intensity of habitat utilization based on the pellet count paralleled actual visual counts of animals. Our visual counts, however, do not necessarily represent the maximum number of animals utilizing a given area and appropriate corrections in censusing were made. For a further discussion, see Eisenberg, Santiapillai, and Lockhart, 1970.

As indicated in the previous paragraphs, a 24 square kilometer area was set aside for intensive survey, including Marai Villu, Kali Villu, and parts of Maduru Odai. This area allowed us to check our crude density and biomass estimates against figures based upon counts which were as near accurate as possible. We chose two periods for intensive censusing, one during the maximum dispersal phase of the ungulates during the rainy season and the other during an interval of maximum concentration of game in the dry season. Since the elephants and water buffalo in this sector moved widely, the maximum estimate gives only a temporary concentration value; however, such a density may be achieved several times during the annual cycle (see pp. 101-103, Tables 14 and 15).

Because the elephant and buffalo move widely within the park, it was necessary to employ long-term tracking techniques in order to ascertain actual movement patterns. Some of the movement patterns for elephant and buffalo with respect to the park and the West Sanctuary are portrayed in Figures 7, 8, 9, and 20.

Although we feel quite confident concerning the biomass and density estimates for our intensive survey areas and the areas in which the monthly counts

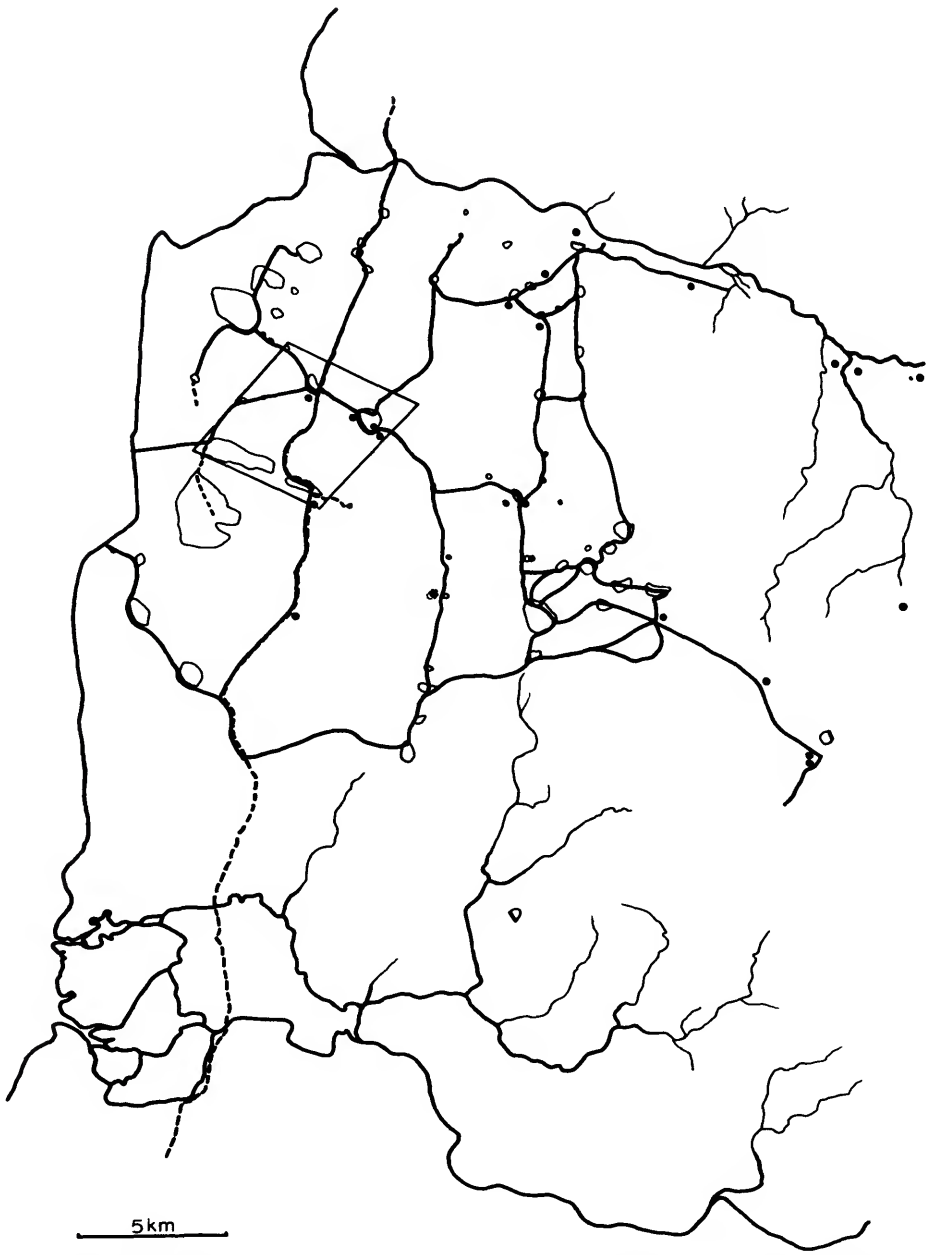

FIGURE 76.—Monthly survey routes employed during the censusing operations. Dots indicate location of some 22 areas where study plots were located; 29 plots located within these 22 areas, 10 of which were studied consistently for intensity of habitat utilization by employing the pellet count technique, see Appendix A. The diamond shaped area of some 24 km^2 is that area referred to in the text as the area of intensive survey and is the location in which the ecological density calculations in Tables 14 and 15 were made. One side of the diamond-shaped area is approximately 4.9 km.

were carried out, it is necessary to outline here our procedure in estimating crude density and biomass for each of the species.

The population estimates for the 580 square kilometers area took into consideration the mobility of the species in question and its dependency on water. The mobility of sambar, buffalo, and elephant is high. Although axis deer have a high potential mobility, they seem to move only short distances of up to 1.5-2.0 kilometers. The other species show a limited mobility; hence, the three largest contributors to the biomass can and do move around a great deal when water resources become restricted during the dry season. Adequate allowance must be made for migration and the high counts made during times of maximum concentration must not be taken as indicators of the average biomass for a given area. The smaller species, such as muntjac, mouse deer, and hare, must be considered as animals being both dependent on water and restricted to areas of permanent water. Hence, all biomass estimates were made with respect to eight permanent villus of a large size, twenty smaller but permanent villus supporting perhaps half the population of the larger villus, and a riverine system allowing for a strip of approximately 0.8 kilometers on either side, giving an area of 38.8 square kilometers. By allowing for the movements of the larger species and considering the presence or absence of permanent water as an important regulator of density, we have arrived at a reasonable approximation to the actual densities and biomasses for the major herbivorous species within the park.

Elephant (*Elephas maximus*)

We were able to ascertain the movement patterns for one major herd within the park system. Two other herds which were reasonably well known to us had their ranges partially mapped whereas the fourth could only be surveyed sporadically. Table 3 portrays the counts from those herds for which we have the best data. Three of the four herds spent at least part of the time in the West Sanctuary. We counted sixty-one individual animals and we estimate that roughly seventy animals, including some bulls that we may have missed, utilize the core national park area throughout most of the year. If we include the other protected areas, such as the entire West Sanctuary, the newly incorporated south intermediate zone, and the east intermediate zone, a reasonable figure for the total elephant population within the national park boundaries and associated protected areas would be at least twice as large or 140 to 150 elephants. In addition an unknown number of elephants in the vicinity of the south bank of the Kala Oya do cross over into the park and its associated intermediate zones and sanctuaries; hence, the overall population of elephants dependent in part on Wilpattu Park may be close to 200 animals.

Buffalo (*Bubalus bubalis*)

For the national park itself our estimate of 161 animals is based on counts of known herds as is the case for the elephants. In addition, at least one of the herds spends part of its time in the West Sanctuary. If we include the other associated areas, including the old south intermediate zone, the eastern intermediate zone, and the West Sanctuary, some 300 to 400 buffalo are probably dependent on the park for the better portion of the year.

Axis deer (*Axis axis*)

As outlined in a previous publication (Eisenberg, Santiapillai, and Lockhart 1970), visual counts were correlated with pellet-count techniques utilizing the study plots. On the basis of our counts, we assume that the average density of deer at major villus was in the neighborhood of 115 animals per square mile or 68 axis per square kilometer. Since the axis are dependent on permanent water sources and since there are 8 major villus each supporting up to 100 deer and 14 minor villus retaining permanent water each of which may support up to 20 deer, then some 1,080 axis deer are associated with the major permanent villus in the national park itself. Considering riverine habitats, if we assume that at best density there may be 150 deer per square mile or 57.9 deer per square kilometer, and if we further calculate the density of deer based on a 38.8 square kilometer area along the river system within the national park or bounding the park, then some 2,240 deer may be considered to be in association with the bounding rivers and their tributaries. This would mean that approximately 3,320 animals comprise the axis population for the area included within the old national park boundaries. We settled on a figure of 3,500 as a safe estimate for the axis deer population.

The Sambar (*Cervus unicolor*)

Feces counts on the study plots indicate deposition by

sambar equal to 10-15 percent that of axis. If we assume an equal defecation rate for axis and sambar and equal habitat utilization, then the population of sambar may lie between 350 and 525. We know, however, that sambar graze less in the open and when they do graze in open country it is generally at night. Hence, there is less than half the opportunity to drop feces in open parkland than is the case for axis. Therefore, there could be twice as many sambar or up to 700. Our known count, based on the monthly census, for approximately 190 square kilometers is 170 sambar or slightly less than 0.9 sambar per square kilometer. If we extrapolate for the 580 square kilometer area taken as the base for our census area, then roughly 520 sambar may be present. The riverine population, however, may be higher and, once again, we are faced with considering up to 700 sambar as a maximum for the park itself; hence, in the presentation of our crude density and crude biomass data, we have set 700 as a maximum and 400 as a minimum.

Wild swine (*Sus scrofa*)

Tabulation for the national park is based on actual counts at the major villus and an estimated density for the riverine system based on inference from the highest counts at the major villus which are utilized by the swine. This gave us overall an estimate of 180 animals for the 580 square kilometer area; however, litter sizes are large in the swine and there may be dramatic fluctuations in actual count of animals throughout the annual cycle.

Muntjac (*Muntiacus muntjac*), Mouse Deer (*Tragulus meminna*), Porcupine (*Hystrix indica*), and Langur (*Presbytis entellus*)

Estimates for these species were based on counts made at Kali Villu and Marai Villu and we assumed that the density for these two major villus would be equivalent for the remaining six larger villus within the park. Populations for smaller villus were estimated to be at half that for larger villus and the average density per unit area of usable habitat at the larger villus was set at the density estimate for our 38.8 square kilometer area of riverine habitat. Since these species are not particularly mobile, we considered them to be more or less bound to permanent water. Therefore, their total density estimates are based on considerations similar to those for the axis.

Hare (*Lepus nigricollis*)

The hare is exceedingly difficult to census directly. On the feces plots, the weight of hare feces correspond to roughly 10 percent that of the axis. If we assume equivalent habitat preferences between axis and hare and if we allow for the weight difference since the hare averages less than one-tenth the weight of an axis, then the hare density might be considered to be almost equivalent to that of axis deer. Axis, however, would seem to have a broader habitat tolerance than the hare which does not seem to be particularly abundant in the vicinity of the rivers. Thus, we arbitrarily set the estimate for hare density at 80 percent that of the axis, realizing that this may be slightly low. Hare density, however, can fluctuate vastly from year to year and any estimate we make can be taken only as an approximation.

Appendix B

LIST OF SOME DOMINANT PLANTS OF THE LOWLAND DRY ZONE

(Nomenclature and classification from Fernando 1968)

Trees and Tree-like Plants

Ara Zone

Adina cordifolia
Alphonsea selerocarpa
Alseodaphne semicarpifolia
Berrya cordifolia
Cassia fistula
Cassia marginata
Chloroxylon swietenia
Cordia domestica
Diospyros ebenum
Diospyros ovalifolia
**Drypetes [=Hemicyclia] sepiara*
Elaedendron glaucum
Euphorbia antiquorum
Ficus glomerulosa
**Ficus parasitica*
Gleniea zeylanica
Grewia polygama
**Manilkara hexandra*
Nephilium longana
Pleurostylia wightii
Pterospermum canescens
Sapindus emarginatus
Schleichera trijuga
Sterculia foetida
Strychnos nux-vomica
Syzygium cuminii
Vitex pinnata
Walsura piscida

West Area

**Acacia leucophila*
Acacia planifrons
Cassia timorensis
**Ferronia elephantum*
Fragerea zeylanicus
Limonia crenulata
Nephelium gardneri
**Phoenix zeylanica*
**Salvadora persica*
Sapium insigne
Vitex negundo
**Zizyphus jubata*

Shrubs

Ara Zone

Allophyllus cobbe
Croton aromaticus
Ehretia buxifolia
Glycosmis pentaphylla
Ixora arborea
Mallotus sp.
Memycylon sp.
Murraya koenigii
Phyllanthus sp.
Polyalthia korotoni
Randia dumetorum
Stenosiphonium cordifolium
Tarana asiatica
Webera corymbosa

*Indicates intensive feeding by elephants (Norris 1959, McKay 1971).

West Area

*Acacia eburnea
Azima tetracantha
Cassia spinosum
Cissus quadrangularis
Gardenia coronavia
Grewia orientalis
Plumbago zeylanica
Sanseviera zeylanica
Wrightia zeylanica

Grasses and Forbs

Ara Zone

Aliscarpus vaginalis
*Amphilophis pertusa
Apcopis wightii
Aristida setaceae
*Bracharia reptens
Celosia argentea
*Chloris barbata
*Chloris inflata
*Cymbopogon confertifloris
Cyrtococcum trigonum
Dactyloctenium aegyptium
Desmodium heterophyllum
Desmodium triflorum
Digitaria marginata
Echinochloa colonum
Eragrostcella hitaria
*Eragrostris coramandeliana
Euphorbia geniculata
Indigofera achinata
Ipomoea angustifolia
Leptochloa neesii
*Paspalum conjugatum
Phaseolus trilobus
Ruellia ringens
Syndrella nodiflora
Tridax procumbens

West Area

Acanthospermum hespidium
Aristidia depressa
*Cynodon dactylum
Enteropegon monostachys
Lopholepus ornithocephala

*Indicates intensive feeding by elephants (Norris 1959, McKay 1971).

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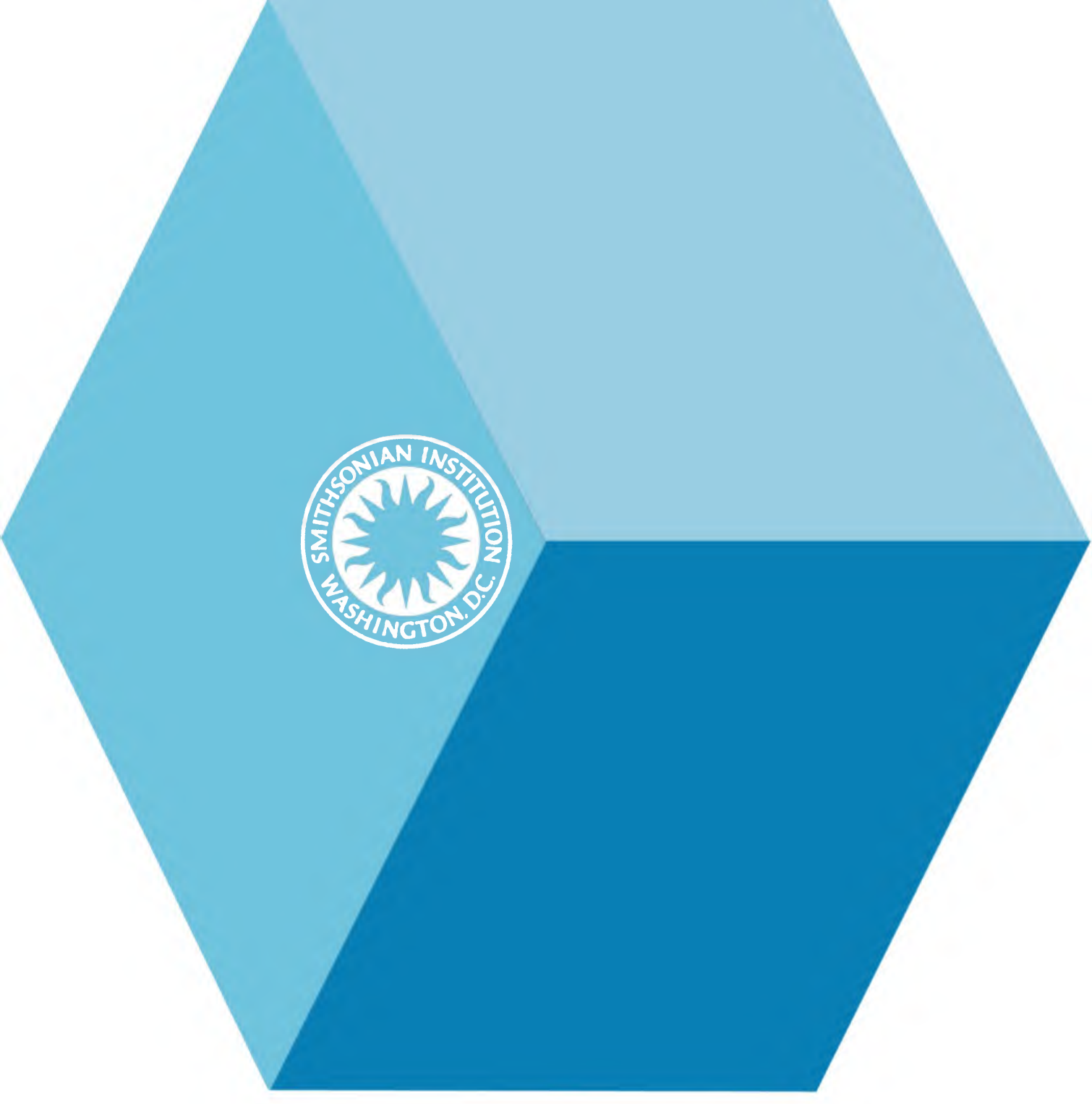
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