GEORGE M. McKAY

Behavior and Ecology of the Asiatic Elephant in Southeastern Ceylon

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ABSTRACT

McKay, George M. Behavior and Ecology of the Asiatic Elephant in Southeastern Ceylon. *Smithsonian Contributions to Zoology*, number 125, 113 pages, 63 figures, 22 tables, 1973.—This paper reports on a three-year study of the behavior and ecology of the Asiatic elephant (*Elephas maximus maximus* L.) in the Gal Oya and Ruhunu National Park areas of Ceylon. The study area in eastern Ceylon is in a zone which shows a gradation in climate from moist to arid. This gradient is correlated with gradients in the distribution of plant species and of vegetation types.

Two populations were studied in detail. The first, in the area around the Gal Oya National Park, contained an estimated 260–300 elephants. A second population, in the area around Lahugala Tank, was estimated to contain about 150 individuals. An analysis of population structure is reported and the behavior patterns involved in locomotion, resting, feeding, drinking and bathing, rubbing, elimination, and thermoregulatory flapping of the ears are described. Movement rates while feeding were measured and mechanisms of visual communication are described, including two threat displays, nine vocalizations, and several nonvocal means of auditory communication.

Composition and structure of herd organization, seasonal movements, and variation in home ranges are discussed. Movement patterns of solitary adult and subadult males in relation to food availability and dominance roles are also considered.

Elephants make use of the full variety of vegetation types available to them. Food plants of 88 species were identified, the majority being trees and shrubs. Several important food plants were analyzed for caloric density, and chemical analyses of 8 species showed higher percentages of protein for shrubs as opposed to grasses.

Recommendations for management of the elephant within the park and the establishment of a buffer zone between the park and areas of intensive cultivation are made.

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The creation of elephants was holy, and for the profit of sacrifice to the gods, and especially for the welfare of kings. Therefore it is clear that elephants must be zealously tended.

The egg from which the creation of the sun took place—the Unborn took solemnly in his two hands the two gleaming half shells of that egg, exhibited by the Brahmanical sages, and chanted seven samans at once. Thereupon the elephant Airavata was born and seven other noble elephants were severally born, through the chanting.

Thus eight elephants were born from the eggshell held in his right hand. And from that in his left hand in turn eight cows were born, their consorts. And in the course of time those elephants, their sons and grandsons, [etc.], endowed with spirit and might, ranged at will over the forests, rivers and mountains of the whole world.

And the noble elephants went to the battle of the gods and demons, as vehicles of the lords of the quarters, Indra, Agni and the rest. Then in fright they ran away to Virinca [Brahma]. Knowing this, the spirit of Musth was then created by Fate; when it had been implanted in them, infuriated they annihilated the host of the demons, and went with Indra and the rest each to his separate quarter.

NILAKANTHA*

Introduction

Wherever elephants and men have coexisted, interaction has been inevitable. The cave paintings of Europe and North Africa amply demonstrate the importance of proboscideans as prey for preagricultural man (Carrington, 1958). The rock paintings in southern Africa are all that remain to indicate that elephants were hunted by the bushman, but elephant hunting traditions still survive among a few African tribes (Sikes, 1971).

To agricultural man the elephant assumed new significance. He became a beast of burden, an instrument of war, an object of reverence, an agricultural pest, a status symbol, and a resource to be exploited for the beauty of ivory. Until European settlers began invading the African continent in the last two centuries there was little contact between agricultural man and elephant on that continent. The Carthaginians undoubtedly used and trained native African elephants for warfare (Sikes, 1971) and the Kushites of Meroe may also have used indigenous elephants, Shinnie's (1965) argument to the contrary is not convincing, being based on the supposed intractability of this species.

It is in Asia that elephants and humans have been in prolonged and intensive contact, and it is there that the significance of the elephant to man has become the most complex.

The earliest date at which elephants were tamed in India is not known, but it is certain that elephants were in well-established use before the invasion of the Greeks. Elephants appear on plaques dating from the Indo-Sumerian period (5000–1000 B.C.) in the Sind Valley (Coomaraswamy, 1917).

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* From Matanga-Lila. In Edgerton, *The Elephant Lore of the Hindus: The Elephant-Sport of Nilakantha.* New Haven: Yale United Press, 1931.

From the time of the Aryan invasions and the advent of Sanskrit writing there have been numerous written references to elephants including the *Matanga-Lila* by Nilakantha. Stracey (1963) gives a brief summary of the history of elephant domestication in India, and Armandi (1843) reviews the use of the elephant in war. In India elephants were captured from the wild using a number of different methods. All are described in detail by Stracey (1963) including the khedda or stockade method popularized by G. P. Sanderson of the Mysore Civil Service (whose own account of the method appears in Sanderson, 1878). During the period of British occupancy of India, the capturing and training of elephants passed from the hands of private individuals to the government departments. Several books, written by civil servants concerned in khedda or logging operations, appeared, which combine, often in a charming manner, ancient elephant lore with modern veterinary medicine. Foremost among these are Steel (1885), Evans (1910), and Milroy (1922).

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Taxonomy

Ellerman and Morrison-Scott (1951) list two subspecies of *Elephas maximus* from Ceylon, equating *E. m. maximus* Linnaeus with *E. m. vilaliya* Deraniyagala (sensu Deraniyagala) and accepting *E. m. ceylanicus* Blainville as the elephant inhabiting most of the island. McKay (n.d.) proposes that *E. m. vilaliya* represents no more than a few extremely large individuals in a highly variable population and considers that it should be placed in synonymy with *E. m. maximus*. For the purposes of this paper I will consider that the island of Ceylon is inhabited by one subspecies.

Anatomy and Physiology

Frade (1955) presents a comprehensive summary of the literature concerning the anatomy of both living species of elephant. The only point on which further discussion is necessary concerns the structure of the stomach. Tennent (1867) discussed the work of earlier anatomists concerning the enlarged and folded cardiac portion of the stomach. He likened the folds to the so-called water cells in the stomach of the camel, and concluded that they must serve for storage of water. Sikes (1971) treats this problem (in *Loxodonta* where the structure is identical) only slightly. One potential function for the folded cardiac region might be to allow greater expansion than if it were not so corrugated. I have frequently observed elephants, feeding in lush grassy areas such as Lahugala Tank (p. 58), to look quite slender as they begin feeding; but after as few as five to six hours of intensive feeding, these same individuals have extremely bulging bellies. It would appear reasonable that if the rate at which an elephant can ingest food greatly exceeds the rate at which the intestines and caecum can process it, there would be a distinct advantage to the possession of a very elastic stomach. In the absence of more detailed anatomical data, one can do no more than speculate; it is a possibility worthy of further investigation.

Benedict (1936) conducted a series of experiments to examine several aspects of the physiology of elephants, using particularly one adult female *Elephas*. Details of his findings relevant to this work will be discussed in the appropriate places in the text. More recently, Sikes (1971) has summarized the available data on physiology of *Loxodonta* and provides interesting comparisons with the data of Benedict.

Behavior and Social Organization

Many accounts of elephants have been written by persons connected with forestry in India or by civil servants and planters who indulged in "sport" during their leave. Books, such as Baker's (1855), are more concerned with the "sport" of shooting elephants than with the lives of the quarry. Such accounts as Williams (1950) and Stracey (1963), on the other hand, give not only a vivid account of the intricacies of logging and elephant-capturing operations but provide, in addition, many insights into the behavior of the elephants. In particular Williams' (1950) descriptions of the social behavior of elephants, especially with regard to sexual behavior, parturition, and the participation of females in the care of the young, reflect careful observation and interpretation. Sanderson (1878) gives several precise descriptions of their behavior including five vocalizations (with implied meanings) and one threat display. His observations (1878:49) on the composition of herds deserve attention:

> Herds of elephants usually consist of from thirty to fifty individuals, but much larger numbers, even one hundred, are by no means uncommon. When large herds are in localities where fodder is not very plentiful, they divide into parties of from ten to twenty; these remain separate, though within two or three miles of each other. But they all take part in any common movement, such as a march into another tract of forest. . . . Each herd of elephants is a family in which the animals are nearly allied to each other.

Tennent (1867:45) also discusses the composition of herds:

> A *herd* of elephants is a family, not a group whom accident or attachment may have induced to associate together. Similarity of features and caste attest that, among the various individuals which compose it, there is a common lineage and relationship. In a herd of twenty-one elephants, captured in 1844, the trunks of each individual presented the same peculiar formation,—long, and almost one uniform breadth throughout, instead of tapering gradually from the root to the nostril.

He also refers to a low number of males with herds, although he does not go so far in interpreting this as Sanderson (1878:49), who states that the herd is "invariably led by a female, never a male."

More recent reports on behavior of *Elephas* are few. Elapata (1969) observed in 1957 a series of copulations involving two adult females in which one of the females mated with two different bulls and one of these bulls mated with the second female. The sequence of behavior observed is very similar to observations of my own (Eisenberg, McKay, and Jainudeen, 1971). Deraniyagala (1958) reported an interaction between two adult males (observed by S. A. I. Elapata, A. H. E. Molamure, and V. Atukorale) which he termed "pseudo-combat." From his description this appears to have been a sequence similar to what I have described as "play-fighting" (p. 65).

ECOLOGY

While there are many accounts which describe the behavior of elephants, there are relatively few data on the ecology and status of populations. Sanderson (1878) mentions that females give birth every $2\frac{1}{2}$ years and says that the majority of calves are dropped in Mysore between September and November (toward the end of the rainy season). Williams (1950:39), however, states that in Burma most wild elephant calves are born between March and May which in that area is the onset of the rainy season.

Williams (1950) also estimates that in Burma approximately 25 percent of calves fall prey to tigers—the only estimate of the extent of predation on elephants I have been able to find.

Reliable estimates of populations of elephants are few. Stracey (1963:211) reports that his department removed some 900 animals from the Naga and Mikir hills in northeastern India, an operation which "almost cleaned out the elephants there." He also estimates the population for Uttar Pradesh in 1965 at 600—an increase of 350 over his estimate for 1955. Singh (1969), however, on the basis of a number of detailed surveys considers that the population for that state as of 1967 "is not likely to be more than 400 in number."

Data from Burma are poor: Stracey (1963) estimated 10,000 for 1955 but Williams (1950) estimated 6,000. The situation in west Malaysia is somewhat better known. Medway (1965) estimated a total population of 692 in 1964–1965. This number is low enough in itself, but inspection of his figure 2 shows that there are only two herds with more than 20 individuals and ten herds with 10–20 individuals. Not only are the herds small but they are widely dispersed. Stevens (1968) estimated that the 1968 population in Malaysia was 486—he maintained that Medway's (1965) estimate was too optimistic.

CEYLON'S ELEPHANTS—GAME, PEST OR HERITAGE?

Elephants have been in use by man in Ceylon for at least the past 2000 years. According to Gooneratne (1967) a detachment of elephants was a traditional part of the army of all of the ancient Sinhalese Kings. According to Deraniyagala (1955: 45) King Raja Sinha I was able to muster 2200 elephants for his attack on the Portuguese fort at Colombo in 1588. After the spread in use of cannon, the elephant apparently became less useful in battle, but Schweitzer (1682) describes the process of conditioning elephants to the sound of gunfire.

Elephants have also been traditionally associated with such ceremonial functions as religious processions. Herport (1669) refers to the King of Kandy as maintaining a stable of 100 elephants for ceremonial purposes. Knox (1681) ascribes other functions to these animals—executioners and combatants in fights, of which the King and his court were regular spectators.

Three methods for capturing elephants were in use before the Portuguese era—pitfalls, noosing, and decoying. The pitfall technique, described by Tennent (1867) and Stracey (1963) simply required the digging of a deep pit along a pathway and covering the hole in order to delude the elephant. The noosing technique which required much more skill and bravery is described by Tennent (1867). In this method the noosers approach the elephant on foot and slip a rope around one leg of the animal tying it immediately to a tree. This method was practiced extensively by men of Arabic descent who live in the east of Ceylon, and the tradition is not quite dead. The third method, described by Knox (1681) involved noosing also but the approach was made by men mounted on trained elephants. This technique (known in India as *mela-shikar*) is described in detail by Stracey (1963).

The Portuguese apparently introduced the method of capturing elephants by means of a corral (*Kraal*-Ceylon; *khedda*-India) (Tennent, 1867). By using this method large numbers of animals could be obtained in a short period of time.

According to Abeyasinghe (1966) the Portuguese maintained an annual demand of 37 elephants for export from two kraals. These produced an average revenue of 9250 Rixdollars (roughly 15 percent of the total revenue to the state). According to de Silva (1969) 1875 elephants were exported from 1863–1884, producing a revenue of Rs. 144,715. Thus even in the colonial era, the elephant was an important part of the economy as an export commodity.

But the value of the elephant was not only economic. Elephants were and still are used as draught animals—particularly in logging operations. In 1969 there were 532 tame working elephants on Ceylon (Jayasinghe and Jainudeen, 1970). Elephants still participate in ceremonial processions such as the annual Esala Perahera at Kandy, according to the ancient tradition that tenants of temple lands or lands granted by the king must participate in the Perahera (Coomaraswamy, 1956). Thus the elephant is still a viable part of the cultural heritage of Ceylon.

It is interesting to note that Knox (1681), Heydt (1744), and Abeyasinghe (1966) (who was writing about the Portuguese era) mention elephant catchers and trainers as a distinct caste, while Coomaraswamy (1956) in his list of castes does not.

The elephant can also be an agricultural pest. Knox (1681) has noted that "these Elephants do, and may do, great dammage to the Country, by eating up their Corn, and trampling it with their broad feet, and throwing down their Coker-nut trees, and often times their Houses too." Similar statements are made by Herport (1669), Schweitzer (1682), and Heydt (1744), who are discussing the areas around Kandy, Colombo, and Ratnapura—districts from which the elephant is now long gone, but where they were, at that time, abundant.

As colonial powers the Portuguese and Dutch made relatively little impression on the ecology of Ceylon. But the advent of the British brought two new limiting factors into play against the elephant —the coffee bush and the rifle, often with both in the hands of a single man. The story of the results of this has been told many times: by proponents, "sportsmen" such as Baker (1855), by contemporary opponents (Tennent, 1867), and by modern writers (de Silva, 1969). There are no records which allow one to estimate accurately the total elephant population before the 19th century onslaught. If the entire island were populated by elephants at the present-day average of one elephant per two square miles (p. 96), there could have been as many as 12,000. That there was an onslaught is well documented, however, as reported by Tennent (1867: 78), Marshall (1846), de Silva (1969), and others.

The result of shooting and land clearing was that by 1951 the total elephant population of Ceylon was estimated at approximately 1500 (Norris, 1959). For the past two decades there has been an awareness in Ceylon that measures must be taken in order to insure that some elephants will remain. Norris (1959) made the first attempt to survey the situation at that time, but concluded that more information was needed. It was because of this need for information and because of the awareness of such a need by all of the people with whom we worked in Ceylon that this study was possible.

Norris (1959) posed three questions: "(1) How many elephants do we want to keep? (2) How much country do they need, remembering their seasonal movements? (3) What land is available for them?"

The following report is an attempt to supply the answers to questions 2 and 3 for a portion of the island.

Methods and Materials

Field Observations

In the course of this study, 453 days were spent in the field over a period of 2¾ years from February 1967 to October 1969. Of these days spent in the field, 318 were in the major study area; 89 were in Blocks I and II of Ruhunu National Park and 46 were spent in other areas outside of these two. Work in Ruhunu National Park was concentrated between April and October 1967 and work in the Gal Oya–Lahugala area was conducted from February to July 1967 and from October 1967 until October 1969.

In Ruhunu National Park the observer was restricted to working from a vehicle. As a result, observations of elephants could only be made in those areas where the animals were visible from the roadway. Travel within the National Park was restricted to daylight hours (0600 to 1800 hours), and at all times the observer was accompanied by a tracker, an employee of the Department of Wild Life. As this park contained an extensive network of sandy roads, the normal daily routine began with a systematic survey of the roads within the park to determine the movements of animals over the previous night. The author and tracker began this survey at dawn, following the same route (about 65 km) every day.

Whenever tracks of elephants were encountered, the number of animals, approximate size, and direction of movement were noted on a map along with the location of the footprints. Fresh deposits of feces were also recorded as to location and number. Any signs of feeding by elephants (e.g., scarification, broken twigs, broken branches) were recorded as to location and species of plants fed upon. For those species of plants which could not be identified in the field, specimens were taken for later identification. By conducting this regular survey in the early hours of each morning, it was possible to obtain a sufficient amount of data on the movements and approximate locations of elephants within the park. During this period, the park roads were heavily used throughout the day by both visitors and park staff. As a result, any tracks laid down by elephants over night were usually obliterated within the first few hours of the morning. On an average day, the entire circuit took approximately two hours to complete and an attempt was always made to complete the circuit as quickly as possible. Whenever solitary males were encountered during this early morning circuit, their location was noted along with ongoing activity. After the circuit was completed, an attempt was made later in the day to relocate the animal that had been observed in the morning. No herds were encountered during these early morning surveys.

Following the completion of the morning circuit, the rest of the day was spent tracing animals in those areas where tracks had been sighted the previous night. Whenever solitary males were encountered, they were observed for one hour or until they moved out of sight, whichever occurred first. Whenever herds were encountered, they were observed until they disappeared from sight or until darkness made further observation impossible. If no contacts with elephants were made by midafternoon, a second circuit of the park was made. Locations of all animals sighted were marked on maps and individual characteristics of identifiable animals were recorded upon each sighting in order to provide a confirmation of identity. Animals observed in groups were classified according to comparative size classes. Observations were made with the aid of a pair of 7–power binoculars, and records were kept primarily in a field note book, although a small portable tape recorder was used for some observations. Whenever possible a photograph was taken of each animal observed.

At all times during these observations in Ruhunu National Park, care was taken to observe the animals from the greatest distance possible (usually around 100 m) in order to minimize any potential effect on the animals' actions by the presence of the observers' vehicle. No attempt was made to condition animals to the close approach of the vehicle, even though many of the animals in this area appeared to be conditioned to the presence of vehicles at a distance of 50 m.

The area in and around the Gal Oya National Park is not covered with a network of roads as is Ruhunu National Park and the location and observation of elephants in this area presented different problems from those of the Ruhunu area. In the areas outside the National Park, it was possible to travel by vehicle to places where the probability of encountering elephants was high. In some instances it was possible to observe elephants from the vehicle, as for example around the Amparai airport, but in most cases it was necessary to continue searching on foot. In 1968 the staff of the Department of Wild Life at Inginiyagala constructed a road extending from the outskirts of the town into the southeastern portion of the National Park. This allowed easier access to this area by eliminating the amount of time spent in walking to and from areas of observation. In the area immediately surrounding the Senanayake Samudra it was possible to travel from point to point by boat. From October 1967 to April 1968, a motorized launch rented from the River Valleys Development Board was used whenever available. When this boat was not available outrigger canoes were rented from local fishermen. From May 1968 until the end of the study, a 14–foot fiber glass boat equipped with an outboard motor was used.

Whether within the National Park or in the surrounding districts, the majority of observations were made on foot. When traveling on foot the observer was always accompanied by at least one other person, as a safety precaution; firearms were never carried. In working on foot within the National Park, the observer and assistant were accompanied at all times by a member of the Department of Wild Life staff for the area.

As the town of Inginiyagala lies in a central position within the area studied, headquarters were established at the rest house operated by the River Valleys Development Board. Using this central location as a base, it was possible to work conveniently in the eastern half of the National Park and in the surrounding areas to the east and south of the park. Whenever observations were being made in the western sector of the park, however, temporary camps were established at convenient points on the bank of the Senanayake Samudra or along the Gal Oya. As this study area is much larger and more difficult to traverse than Ruhunu National Park, no routine daily circuit was made; instead, regular surveys were made either entirely on foot or by driving or using the boat, as well as on foot. Attempts were made to cover as much of the study area as possible every week; but whenever a herd was located, its movements were followed for as many consecutive days as possible. Apart from our own surveys, reliable reports of sightings by villagers and by Wild Life Department staff were used extensively in helping to locate groups of animals.

When traveling on foot the observer and companions traveled in single file and an attempt was made to minimize disturbance by enforcing silence; although with some villagers who acted as guides, silence was often impossible. Whenever elephants were encountered, strict silence was enforced and every attempt was made to remain downwind. Elephants encountered on foot were never approached closer than was absolutely necessary to insure adequate observation, so that movements of the observer and mechanical noises, such as clicking by cameras, would be less likely to disturb the animals. Throughout the study no attempt was ever made to habituate elephants to the presence of the observer. By strictly adhering to these procedures, it was possible to obtain a large amount of data from animals that one can reasonably assume were unaware of the presence of an observer and therefore unaffected by his presence. Over the entire Gal Oya area elephants and man are in frequent contact and the elephants generally resorted to flight when they became aware of the presence of the observer. The patterns of responses of elephants to man are described by McKay and Muckenhirn (in prep.).

Besides observations in Gal Oya National Park, periodic visits to Lahugala Tank and the coastal strip extending south from Lahugala to the Kumbukkan Oya were made in March, July, November, and December of 1967; February, May, July, and November of 1968; and March, June, August, and October of 1969. For the most part these visits consisted of a minimum of one trip from Lahugala to the Kumbukkan Oya in order to determine the presence or absence of elephants along this route and one to several days intensive study of the usage of Lahugala Tank and neighboring tanks by herds of elephants. At Lahugala observations were made either from the banks of the tank itself or from a tree house, constructed in July 1967, on the eastern side of the tank. Observations were also made from a similar tree house constructed at the neighboring Kitulana Tank. At Lahugala it was possible, to have a view of the entire tank and, by using a telescope with 20, 25, and 50 power lenses, to follow the activity patterns of elephants throughout the daytime hours. On two visits the author, assisted by Mr. Desmond Lockhart and Mr. Anil G. Jayasuriya, was able by alternating shifts to follow the usage of the tank by elephants over several 24–hour cycles.

Whenever elephants were encountered the first data to be recorded were the time, location, and physical description, plus the number in the group. The description for each animal included sex, size class, and individually distinctive characteristics. A great deal of variability exists within the population as regards shape of ears, shape and even presence of hairs on the tail, patterns of depigmentation around the trunk base, face, ears, and shoulders, folding of the ears, and the presence of tears or holes in the ears. Besides these characteristics, many animals were also readily identifiable as individuals by the presence and patterns of cysts on the skin. Examination of several dead animals demonstrated that many of these cysts, which are visible as large bumps on the skin, were actually encysted bullets and pellets from shotguns. At the beginning of a series of observations on a herd, the group was counted a minimum of three times or until a consistent count was obtained. Counts were repeated at intervals throughout the observation period. Such repeated counts allowed a continuing check on the number of animals and revealed any shifts in grouping tendencies or movements.

Observations of solitary animals or small groups were recorded in a notebook; but for large herds frequent use was made of a portable tape recorder from which notes were later transcribed. A watch with a sweep-second hand was used for measuring intervals and durations of acts observed, although for more accurate determination, of such patterns as flapping of ears and feeding rates, a stop watch was used. A brief description with at least one photograph of every animal or group of animals was made to confirm identifications of individuals. In this way it was possible to accrue reliable descriptions for many of the animals and to minimize the possibility of confusing those of similar appearance.

Sex and Age Criteria

The most reliable determinations of sex were those where the genitalia were visible. The penis sheath of the male and the vulva of the female can frequently be seen as the animal walks, particularly if it is walking at an angle away from the observer. Genitalia become more readily visible during urination and for very young animals this is the only time at which sex can be realiably determined. Reproductively active females can also be distinguished by tumescent mammae.

The sex of adults can also be determined from the general conformation of the body. Adult males usually have a massive trunk base which protrudes as a bulge below and in front of the eyes and a second swelling around the narial opening in the skull, above the eyes. These, along with the enlarged parietals and occipitals, give the male its distinctively large and bulky head. Females, however, have a narrower trunk base and generally lack the prominent bulge above the eyes and the swelling of the parietals. The head of the female is thus more square and relatively more slender in outline. Besides these differences in the shape of the head, there is usually a sex difference in the shape of the back. The female is generally more box-shaped with a relatively straight back and vertical hindquarters, while the male tends to have a more convex back, which curves more gradually into the hindquarters.

The frequency of tusks among males on Ceylon is generally low but varies from region to region. In the Gal Oya area only one tusker was seen among more than 35 adult males—and he was seen only during November 1967. At Lahugala two tuskers were known to be among the population of twenty-five "resident" adult males and three subadult tuskers were seen on one occasion each. Many elephants, both males and females, possess tushes or incisors smaller than the typical tusk. These tushes may be either circular or oval in cross-section and sometimes protrude to 20 centimeters or more beyond the lips. The oval type, which is generally long (15–30 cm) and decurved, as opposed to the recurved tusk, was only seen in males, but the circular type, which often is broken at the gumline, was seen in both sexes. While tusks and tushes were not always helpful in sex determination, the great variety in shapes did aid in recognizing individuals.

Reliable age estimates for animals observed in the field present a problem, the solution of which is unfortunately not yet in sight. Johnson and Buss (1965), Laws (1966), Sikes (1967), and Krumrey and Buss (1968) have devised techniques based on tooth criteria which can be used to estimate the age of *Loxodonta,* but these techniques require a dead animal. Laws (1966) does give a tentative chart for estimating ages based on shoulder height but acknowledges the relative lack of reliability in this method.

Considering the scarcity of known-age skull material for Ceylonese elephants and the lack of opportunity to examine large numbers of dead ones in the field, two methods of age classification only were open. The first method is to group the animals observed into four classes based on developmental stages and reproductive status as infants, juveniles, subadults, and adults.

The criteria for an infant, other than size, that could be used in the field included long hair on head and back, short trunk (can touch ground but unable to rest the hand of trunk on the ground), frequent suckling, continuous proximity to an adult and lack of association with juveniles for long periods. Like *Loxodonta* (Laws, 1966), infant *Elephas* can walk under their mothers. The distinction between juveniles and subadults is not so easy. Juveniles tend to remain together and form play-groups when a herd is feeding in one spot, whereas subadults tend to remain with the adults. Subadult males are frequently seen away from herds. One character that is probably reliable with the males is the size of the penis. At sexual maturity (and subadults are considered here to be physiologically mature), the penis appears to become larger. This difference can only be determined during urination. Subadult females often show tumescence of the mammae.

Adult males can be distinguished by the enlargement of the head and the distinct penis sheath; adult females by the square back. Subadults of both sexes show the beginnings of differentiation into these two types of body conformation.

Using these criteria alone it is possible to determine that subadult females are undoubtedly a part of the reproductive population but subadult males, while probably capable of breeding, do not appear to be reproductively active.

The second method of estimating age, which was used in parallel with the above determinations, involved a comparison of the height of any individual with the height of a large adult female. By a visual comparison it is thus possible to distinguish nine size classes, the fixed points of which are: Class 1—an infant capable of walking under the mother, and Class 8—a large adult female. Classes 2 through 7 represent equal divisions between the two fixed points and Class 9 is any animal larger than a large female (many adult males). These nine classes can then be compared with available data on shoulder height for known-age animals.

Data on heights of Asiatic elephants are summarized by Hundley (1934), Kurt and Nettasinghe (1968), Reuther (1969), and Jainudeen and Jayasinghe (pers. comm.). Based on those data it is possible to construct the growth curves shown in Figure 1. The lines on the graphs indicate the approximate upper and lower limits. As can be seen from these growth curves, there is an initial period of rapid growth followed by a gradual decline in the growth rate. Differences in growth between the sexes appear at about 5 years. From this point the decline in growth rate is greater for females than for males. Females appear to reach

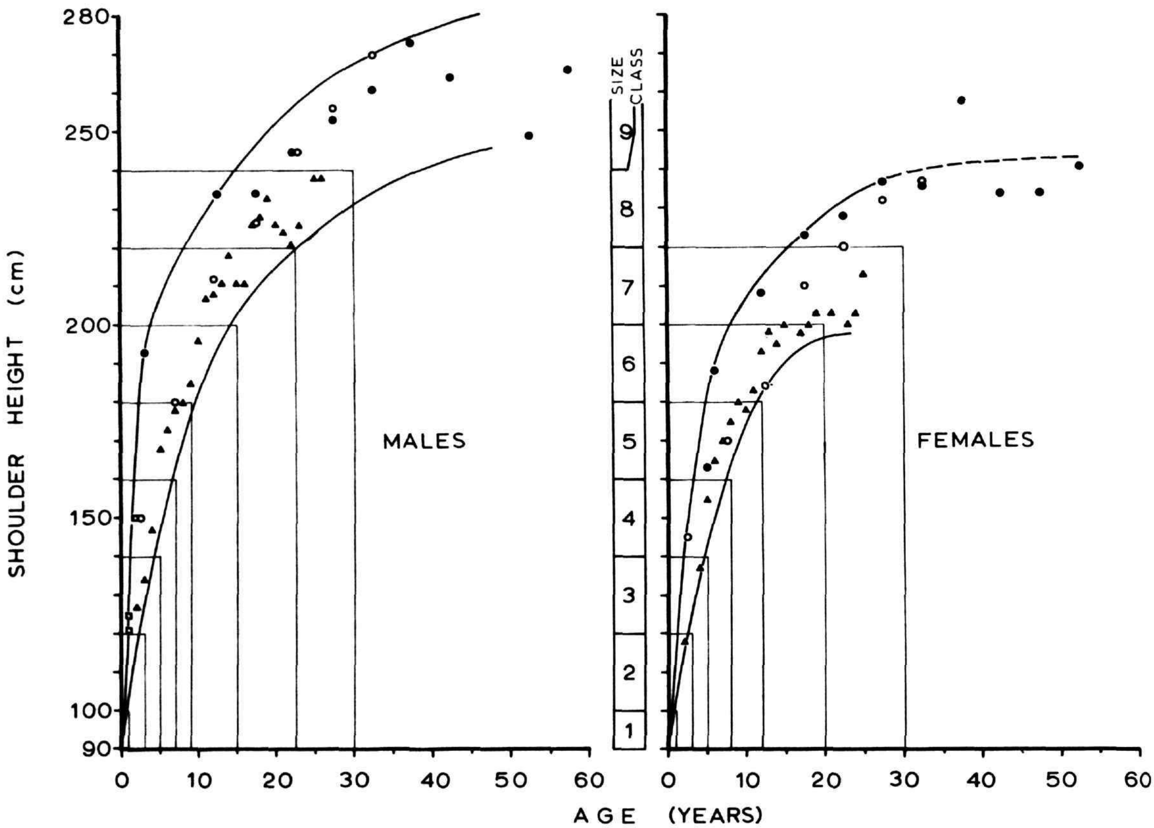


FIGURE 1.—Growth curves for *Elephas maximus*. Horizontal lines indicate the limits of size classes; vertical lines, the approximate age equivalents of these classes. Data from:
○ Kurt and Nettashinghe (pers. comm.) △ Hundley (1934)
● Jainudeen and Jayasinghe (pers. comm.) □ Reuther (1969)

a plateau somewhere between 15 and 30 years while the growth of males appears to continue, even if at a slow rate for a greater period.

As the height of an elephant at birth is about 90 centimeters (Reuther, 1969) and the plateau for Ceylon females is around 230–240 centimeters, the size classes as determined by visual comparison can be superimposed on these growth curves as shown in Figure 1. The approximate age classes, which correspond to these size classes, can be obtained by extrapolation to the abscissa as shown in the figure.

Infants of both sexes comprise Classes 1 and 2. Juveniles comprise Classes 3–5 for females and 3–6 for males. Subadults are Class 6 for females and 7 for males with adults 7–8 for females and 8–9 for males.

Maberry (1962), Evans (1910:94), and others have indicated that female *Elephas* can breed as early as 6 years and males between 6 and 7. Observations from wild elephants in Ceylon have shown that the smallest reproductively active female was an individual in Class 5 and the smallest male capable of obtaining an erection was an animal of size Class 6. This would tend to indicate, as shown in Figure 1, that puberty among wild elephants in Ceylon probably occurs between the ages of 8 and 10. As *Loxodonta* is known to have a variable age at puberty, dependent upon nutritional conditions (Laws and Parker, 1968; Laws, 1969a), it would seem probable that this apparent discrepancy could well be caused by the difference in plane of nutrition between wild elephants (and domestic animals dependent on a low plane diet) and zoo-raised animals. There is no reason to suspect that

Elephas has a fixed age of puberty. It is more likely that this will vary with plane of nutrition as in *Loxodonta.*

In field practice, elephants were classified first into the four developmental classes, then into size classes by comparison with a fully adult female. The female used for this comparison was usually the largest in the group under observation. However, since estimating the true height of an animal in the field is unreliable at best, no such estimates were made for groups not containing a fully adult female. For such groups only the developmental classes were recorded. In practice this situation arose only with groups of males where the distinctions between adult and subadult or juvenile were usually easy to make based on the shape of the head.

Laboratory Studies

A detailed description and analysis of the results of chemical analysis of food plants will be published as a separate paper (McKay, Kalpage, and Jayasinghe, n.d.); only a brief summary will be included in the present work. For a detailed description of the methods used, the reader is also referred to that paper.

The Study Area

The field work summarized in this report was all conducted in the southeastern quarter of Ceylon in an area extending roughly eastward from longitude 81° E. and southward from latitude 7° 45′ N.

Within this region of approximately 4000 square miles (10,400 km^2) three smaller areas were studied. The majority of the observations were made in an area of 720 square miles (1865 km^2) surrounding the Gal Oya National Park. This study area (Figure 2, area A) will be referred to in this report as the Gal Oya area. Secondary study areas were located in the region of Lahugala Tank (Figure 3, area B), and Ruhunu National Park (Figure 2, area C).

Extensive use is made of names of villages, rivers, tanks, and other geographical features. To aid the reader unfamiliar with the geography of the area, such names are included in maps where appropriate. A detailed map of the southeast and an annotated gazeteer are included as Appendix 1. The following list is useful in interpreting some of the names

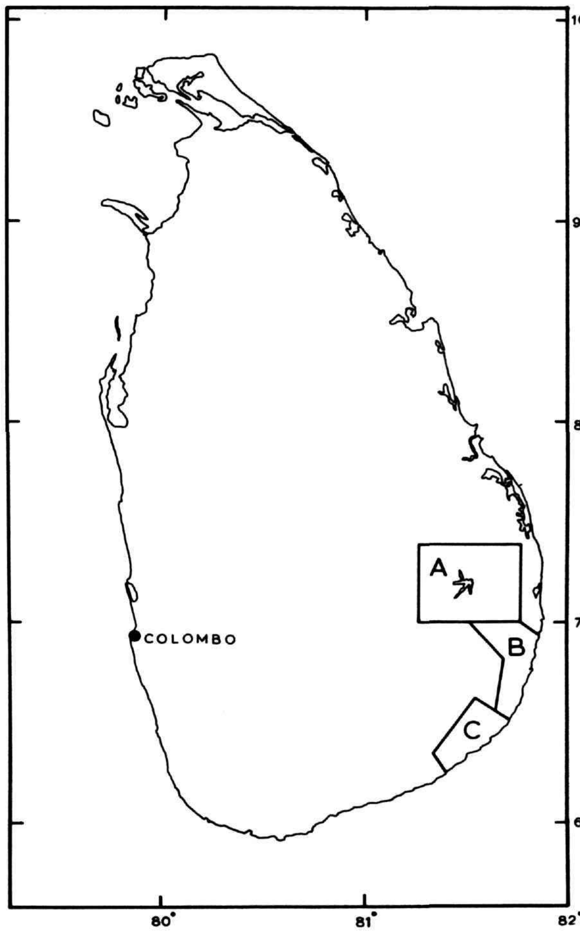


FIGURE 2.—Map of Ceylon showing study areas: A=Gal Oya study area; B=Lahugala study area; C=Ruhunu study area.

encountered: *Aru,* stream; *-gala,* rock, hill; *-gama,* village; *Ganga,* river; *-goda,* open place; *-hela,* hill; *Kulam,* tank or reservoir; *Oya,* river; *Samudra,* ocean (reservoir); *Wewa,* tank or reservoir.

Geology and Topography

Geologically, Ceylon is divided into three major zones: the highland series, the Vijayan series, and the sedimentary formations (Cooray, 1967:83). The highland series consists of khondalites, charnockites, and gneisses of Precambrian age, and granites and granitic gneisses of Upper Paleozoic age. This zone extends from the southwest of the island to the northeastern coast north of Trincomalee. The

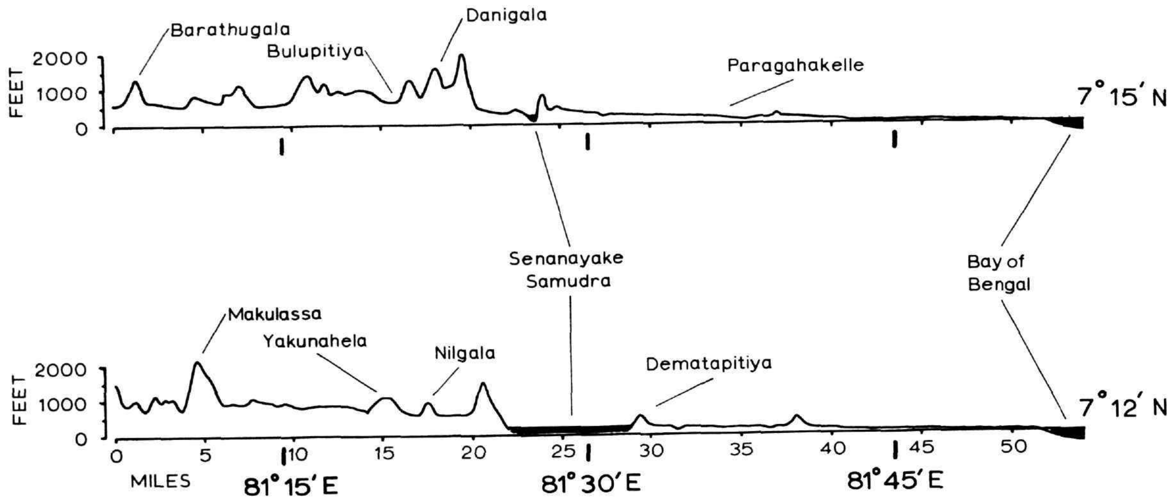


FIGURE 3.—Topographic profiles of two east-west sections at 7° 12′ and 7° 15′ N. Compiled from Nilgala and Tirrukkovil Sheets, 1:63,360 Topographic Series, Ceylon Survey Department. Vertical scale is 3.5 × horizontal scale.

Vijayan series, consisting of a variety of Lower Paleozoic gneissic rocks, flanks the highland series on the northwest and on the southeast. Sedimentary formations, mostly of Miocene and Quaternary origin, occur around most of the coastline.

In the area under consideration, the major portion consists of Vijayan series rocks. The transition zone between Vijayan and highland series follows a belt 10–15 kilometers wide running approximately between Alutnuwara, Bibile, Moneragala, and Wellawaya. This belt corresponds to the transition between the southeastern lowland and the central massif. An isolated group of hills consisting of highland series rocks occurs in the Kataragama region (Cooray, 1967:85). In eastern Ceylon the sedimentary formations, consisting of littoral sands and alluvial soils, occur as a belt 10–15 kilometers wide from Batticaloa to Pottuvil and as a narrower belt of dunes from Pottuvil to Hambantota. Between Batticaloa and Pottuvil this belt forms a flat coastal plain with no relief.

The highly eroded base rocks of the Vijayan series give rise to the topography characteristic of the eastern dry zone. The region consists mostly of a low, gently undulating peneplain with the relief being provided by erosion remnants. Erosion remnants, which have resisted erosion because of their high quartz content (Cooray, 1967), occur as solitary rocks rising from the peneplain (Westminster Abbey, Inginiyagala), as long ridges (Wadinagala), or as clusters of hills (Danigala, Amunuhela, Bulupitiyahela). In the southeastern portion of Ceylon, few of these erosion remnants rise more than 600 meters from the peneplain. Apart from these large hills there are large numbers of smaller (15–30 meters) bare rocks known as turtlebacks, formed by alternate cooling and heating and the chemical action of water (Cooray, 1967).

Within the Gal Oya region two general zones can be distinguished. To the east the peneplain is low (30–80 m) and is broken by a few solitary erosion remnants and many turtle-backs. West of a line passing approximately from Divulana via Inginiyagala to Buddama the peneplain is higher (150–250 m) and clusters of erosion fragments form the dominant relief. This difference is shown on the profiles (Figure 3) drawn at 7°12′ N and 7°15′ N from the Nilgala and Tirrukkovil sheets.

Many erosion fragments have one or more steep sides of bare rock but practically all have at least one side with a gentle, though invariably boulder-strewn, slope. These gentler slopes are usually forested.

DRAINAGE SYSTEMS

The southeastern corner of Ceylon can be divided into eight major drainage systems (Figure 4). The

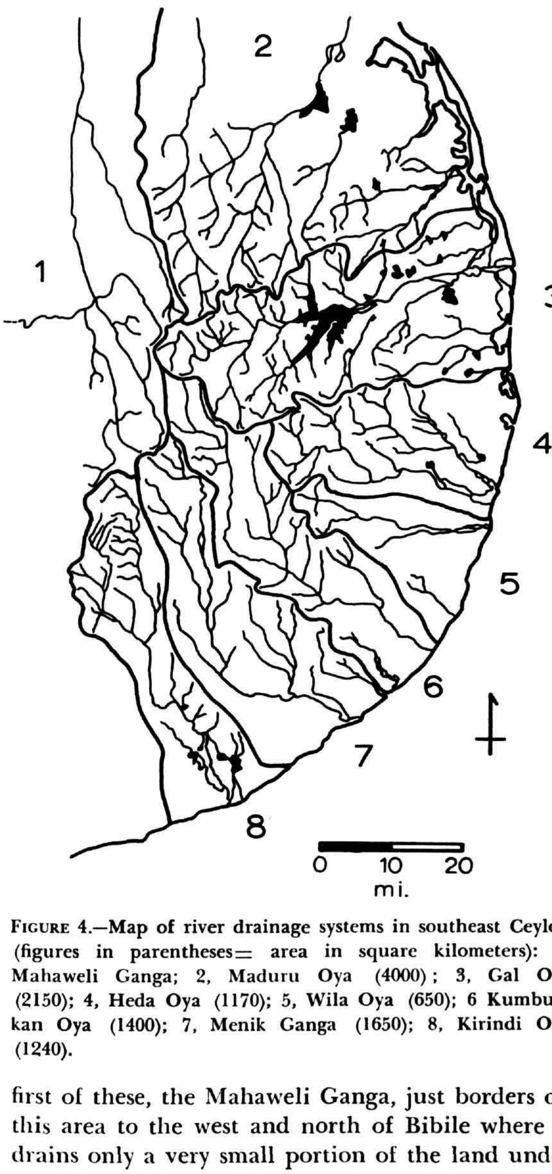


FIGURE 4.—Map of river drainage systems in southeast Ceylon (figures in parentheses = area in square kilometers): 1, Mahaweli Ganga; 2, Maduru Oya (4000); 3, Gal Oya (2150); 4, Heda Oya (1170); 5, Wila Oya (650); 6 Kumbukkan Oya (1400); 7, Menik Ganga (1650); 8, Kirindi Oya (1240).

first of these, the Mahaweli Ganga, just borders on this area to the west and north of Bibile where it drains only a very small portion of the land under consideration here. The second, consisting of nine main streams and their tributaries, drains a large area north of a line between Bibile and Kalmunai. These streams flow northeastward and northward.

The Gal Oya basin (Figure 4:3) consists of the Gal Oya and three lesser streams which flow eastward. The Gal Oya was dammed at Inginiyagala in 1948 to form a large reservoir, the Senanayake Samudra. Most of the other streams in the area have been dammed since that time.

The Heda Oya basin (Figure 4:4) also consists of one major river and several minor streams, all flowing eastward. Several small tanks (Lahugala, Kitulana, Sengamuwa, Rote) exist in this area and development schemes have been proposed for the Heda Oya and Karanda Oya. All of these river systems have some cultivation, although the Gal Oya basin is the only one extensively developed at this time.

The remaining three systems drain southeastward and, with the exception of the Kirindi Oya, have been little developed or modified.

The approximate areas of these drainage systems are included in the legend of Figure 4. The Gal Oya National Park is located entirely within the Gal Oya basin, the most extensively developed of the group. Ruhunu National Park lies along the costal edge of the Wila Oya, Kumbukkan Oya and Menik Ganga systems. Development of all these systems will be considered in a later section on agriculture.

CLIMATE AND WEATHER

Climate

The climate of Ceylon has been discussed most recently by Gaussen, et al. (1964), Fernando (1968), and Mueller-Dombois (1968). Gaussen, et al. (1964) adopt an extremely complex system of climatic subdivision in which they assign 22 types to Ceylon based on temperature, mean annual rainfall, and number of dry months. The lack of supporting data along with their map reduces its direct usefulness.

Fernando (1968:26) includes a map which shows six bioclimatic types which, although not explicitly stated in Fernando's text, are undoubtedly based on the vegetation map in the same publication (see Mueller-Dombois (1968) for critique).

Mueller-Dombois (1968) reviews all previous attempts at classification of Ceylon's climates and arrives at a compromise solution in which he portrays on a map a number of climatic diagrams showing the variation in rainfall patterns. He discusses a proposed 6–7 zonal division of the climate, but unfortunately does not include these zones on the map itself. Although his system of climatic division is the most logical of the three, the lack of sufficient climatic diagrams for the southeastern region prevents one from drawing accurate zones on his map in this area.

As a result of this lack of detailed information, I decided to compile a climatic map for the southeastern region of Ceylon. On Figure 5*a*, the open circles indicate stations from which data were obtained directly from the map in Mueller-Dombois (1968). For the remaining stations data from the Colombo Observatory Report (Ekanayake, 1964) were used to prepare climate diagrams in the same manner as Mueller-Dombois (1968). Average climate diagrams for Batticaloa, Amparai, and Bibile are presented in Figure 6, but on the map (Figure 5) only the summarized data for each diagram are presented. These data are average annual rainfall, number of rain peaks per year, and number of dry months plus arid months per year.

Criteria for classification of months as wet, dry, or arid follow those of Mueller-Dombois (1968:43–45) and Walter and Leith (1960). In this scheme of classification any month with more than 100 mm (about 4 in) rainfall is considered wet, as any excess above this amount is not normally absorbed into the soil but is surface run-off. An arid month is one where the rainfall (as plotted on the diagram) measured in millimeters is less than twice

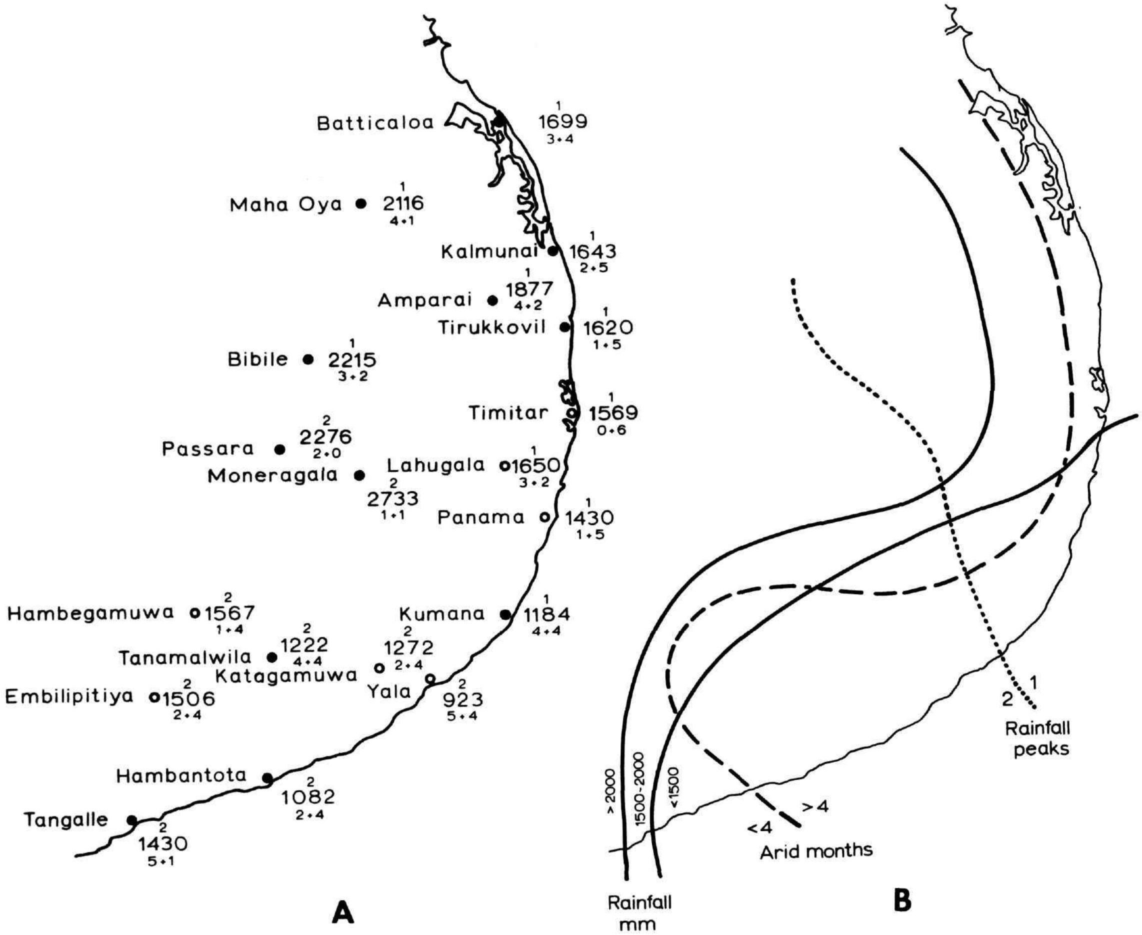


FIGURE 5.—Climatic data for southeastern Ceylon: A, Data from 19 stations showing mean annual rainfall (large central digits), number of rain peaks per year (top digits) and number of dry months plus arid months (bottom digits). Open circles indicate data from Mueller-Dombois (1968); closed circles, from Colombo Observatory Report for 1964. B, Zonation within this region based upon mean annual rainfall, number of rain peaks, and number of arid months.

the mean monthly temperature expressed in degrees Celsius. The empirical formula for determining this relationship is found in Walter and Leith (1960). Under such conditions water generally moves upward through the soil as evaporation tends to be higher than precipitation. This is, therefore, a time of stress for most plants. Any month with rainfall intermediate between this state and a wet state is defined as a dry month.

As shown on Figure 5*b*, the climatic patterns can be drawn using three criteria. The first division, based on mean annual rainfall, with boundaries set at 1500 and 2000 mm produces three zones whose best fit with any published map is the vegetation map of Gaussen, et al. (1964). The second division, based on number of peaks of rainfall produces a narrow belt with one peak (northeast monsoon) and a larger area with two peaks. The third division, based on number of arid months, shows a large southern area and narrow eastern belt with 4+ arid months and a larger area with 1–3 arid months.

At this point, I do not wish to enter the controversy of climatic zones. Rather I must agree with Mueller-Dombois' (1968:56) statement that any division of climates must necessarily depend on the reasons for that division. In the section on vegetation, I will discuss how the division of climate outlined above can be combined with vegetational analysis to provide a workable climatic-vegetational map.

Weather

The above discussion was concerned with the long-term climatic patterns, but those patterns do not imply that each year is similar or even close to the average at any station. A comparison of Figures 6 and 7 will show that, during the course of this study, the patterns were definitely not average. The only two stations for which data were available were Batticaloa and Amparai. No data were collected by the Amparai station after 1968. Data for 1967 and 1968 were obtained from the Colombo Observatory by kind permission of the Director; data for Batticaloa, 1969, were obtained from Ekanayake (1969, 1970).

During this period the rainfall pattern at Inginiyagala closely paralleled that at Amparai. A short drought in 1967 was broken by heavy rain in early October. In 1968 a brief but severe drought in February was broken by rains in March and April, followed by another severe drought which was broken by thunderstorms in July and August. At the end of the northeast monsoon in January 1969, the Gal Oya National Park area was essentially rainless (except for occasional short showers) until September.

Apart from the importance of droughts and rainy periods in determining elephant movements, the weather patterns have another important effect on the present study. Thunderstorms may occur at any time of year but data from Batticaloa (1967–1968) show that they were most frequent from April to October. Normally electrical storms are accompanied by heavy rain, but if they come after a long period of drought or if the storms are dry then the lightning can produce grass fires in the savanna areas. As most of the grass fires in this area are set by man, a discussion of fire in general will be postponed, but it should be emphasized here that lightning-started fires do occur (three were observed by the author to be started on the night of 18 June 1968 in the Nilgala area).

In the Gal Oya area, natural water holes are scarce, most free water existing either in streams or man-made tanks and irrigation ditches. During drought periods, such water holes as exist generally dry up rapidly as do many small streams. Some streams, however, retain subsurface water in sandy pockets even in the driest weather.

In Ruhunu National Park during the period of study (June to September 1967), the area was under a typical drought with occasional showers. During this time many water holes dried totally. The patterns observed at this time will be discussed more completely in considering the effects of climate and weather on elephant movements.

Soils

As with the problems of classifying Ceylon's climate, there are several opinions on classification and distribution of soil types (see Kalpage (1967), Panabokke (1967), and Fernando (1967)). Panabokke's (1967) map is the most detailed of the three and is the only one to give the source of data used in its compilation. According to him the soils of the area are predominantly reddish brown (of three subtypes) with alluvial soils along river-

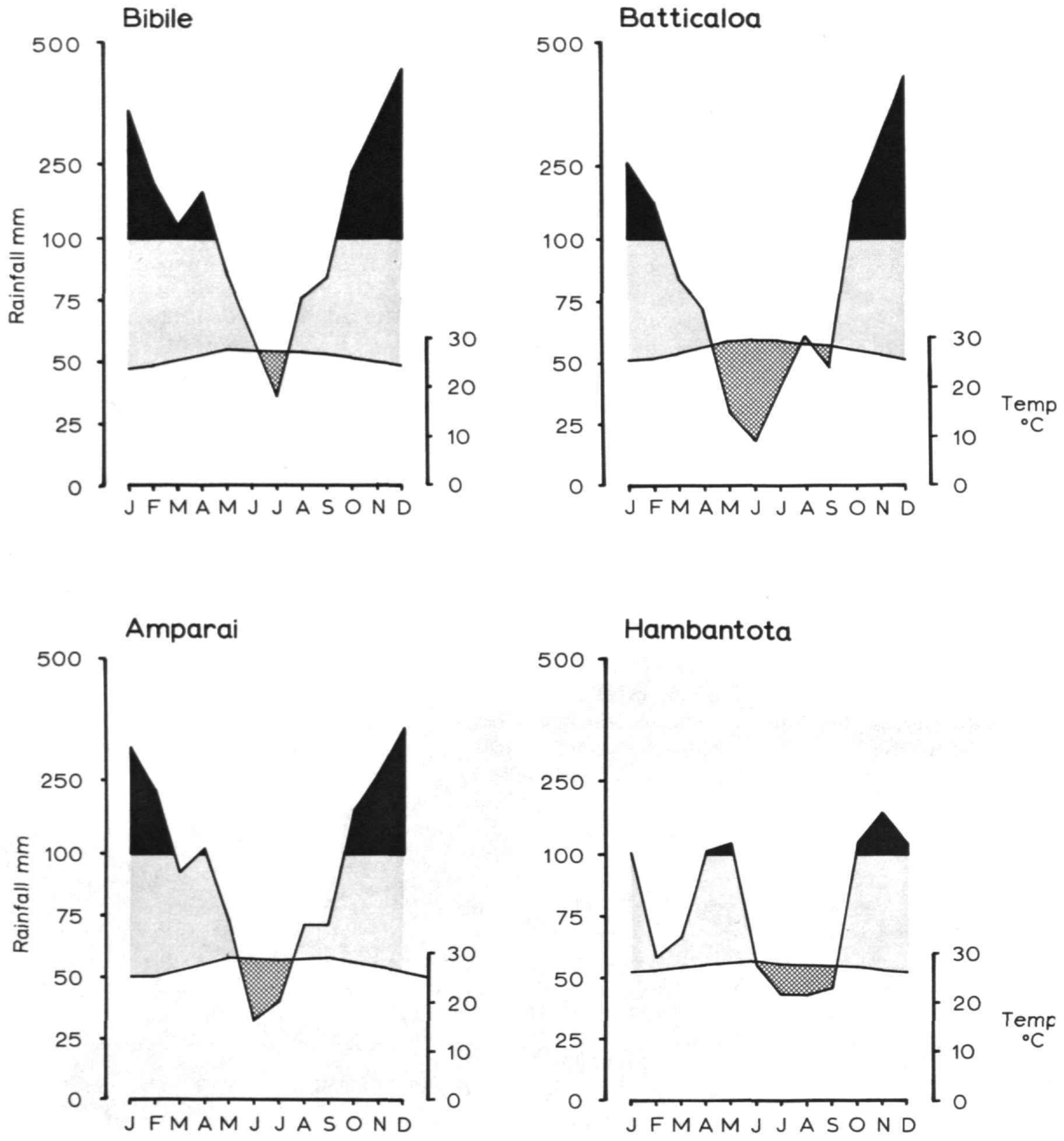


FIGURE 6.—Average climatic data for four stations in southeastern Ceylon. Data from Batticaloa, Bibile and Hambantota are based on 30 year averages (1931-1960); those from Amparai, on 10 year average (1951-1960). All data obtained from Colombo Observatory Report for 1964.

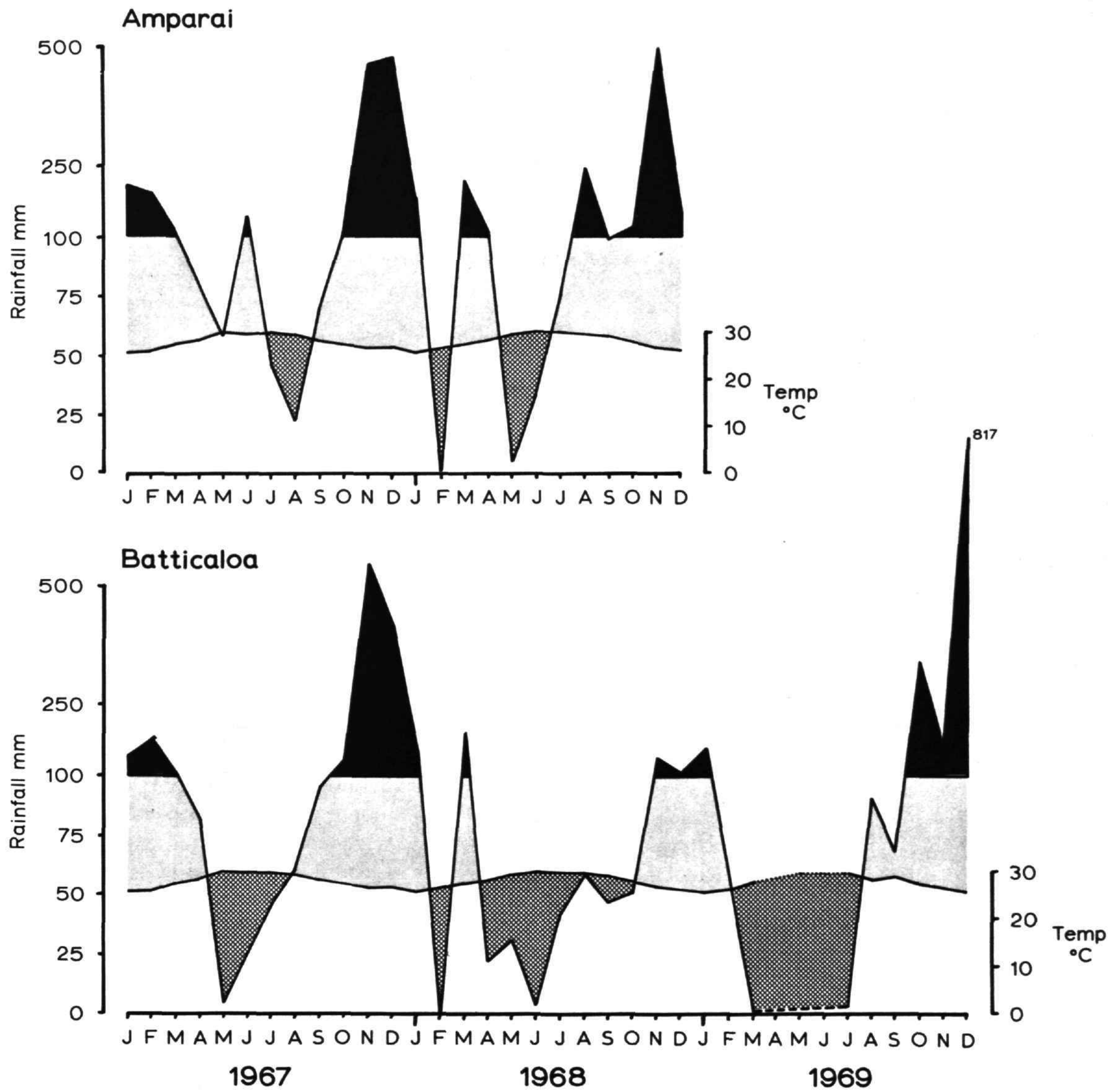


FIGURE 7.—Rainfall and Temperature Conditions at Batticaloa and Amparai, 1967-1969.

bottoms and sandy regosols along the coastal strip. The effect of soil types of vegetation in Ruhunu National Park will be considered by Mueller-Dombois (n.d.).

VEGETATION

Types and Distribution

Gaussen, et al. (1964) list three major vegetation zones for the southeast: (1) *Manilkara-Chloroxylon* series, (2) *Chloroxylon - Berrya - Vitex - Schleichera* series, and (3) *Filicium-Euphoria-Artocarpus-Myristica* Transitional series. As they do not state how they collected their data and (for the Gal Oya region at least) as *Euphoria* is a dominant in their Zone 2, their classification cannot be considered adequate.

Fernando (1968) gives a more adequate description of the forest types and their species composition. According to his map there is a small area of monsoon scrub jungle in the area of Ruhunu National Park, a wide belt of monsoon forest inland, and a narrow belt of intermonsoon forest and savanna west of the Senanayake Samudra and Moneragala.

McCormack and Pillai (1961a,b) have analyzed the composition of the forests in eastern Ceylon and by comparison of their maps with aerial photographs it would appear that their categories correspond roughly to mine:

7MD=medium stature forest; 7LD=low stature forest with emergents; 7ND=forest scrub. In these and other publications in the same series, they have divided the forests of Ceylon into three categories (wet, intermediate, and dry). Their category of dry forest includes the arid zone of Fernando (1968) and others.

It was not possible in this study to survey forest types over a sufficiently large area to make any attempt to resolve these differences for the entire area. It is, however, possible to propose a tentative classification for the region surrounding the Gal Oya National Park. Mueller-Dombois (n.d.) will provide an even more detailed analysis for the Ruhunu National Park.

From the mosiac aerial photographs published by the Ceylon Survey Department (scale 1:31680) it is possible to distinguish five major vegetation types (forest, savanna, forest scrub, scrub, grassland) as well as modified types (e.g., paddy land, chena). Vegetation maps were prepared for the area around the Gal Oya National Park, extending eastward to the coast, by outlining the areas on the mosaics and tracing onto plastic overlay sheets. These working maps were used to prepare Figures 11 and 12.

These maps can then be used as a basis for defining most of the vegetation types. In order to determine what differences, if any, existed among forests in this region, 15 plots were sampled along a 35-mile strip roughly following a 10-mile wide belt from Bulupitiya in the west of Akkaraipattu on the coast. Five of the plots were in savanna, the remainder were in forest. The dominant species in each plot sampled were recorded and samples of species unidentifiable in the field were collected for subsequent identification. Except in three savanna plots, no quantitative data on species composition and abundance were collected.

Figure 8 shows the location of plots surveyed and the distribution along the 35-mile strip of 5 grasses, 20 trees and shrubs, and 3 herbs. The grasses are those which were dominant in savannas (*Themeda, Cymbopogon, Imperata*) or man-made, tankside grasslands (*Brachiaria, Cynodon*). The first six trees are savanna species; the remainder (with the exception of *Bauhinia*), forest species. The three herbs were typical of disturbed (roadside, abandoned chena) habitats.

In the extreme west are found forest and savanna types. The forest is generally evergreen, of medium stature (30–40 m), with a dense closed canopy layer, a dense subcanopy of shorter trees and saplings and a relatively sparse shrub layer. Ground vegetation is sparse and throughout the year there is generally a layer of leaf litter 2–3 cm deep. Dominant species in the canopy and subcanopy strata are: *Artocarpus sp., Berrya cordifolia, Euphoria longana, Mangifera zeylanica, Diospyros spp.*; other species present include: *Schleichera oleosa, Pterospermum canescens, Elaeodendron glaucum,* and *Semecarpus obscura.* The shrubs and sapling layers consist of *Mallotus repandus, Polyalthia spp.,* and *Celtis cinnamomea,* among others. These forests occur as large tracts and as galleries along rivers. In the latter situation, *Terminalia arjuna* is generally present.

The western savanna (Singhalese: Talawa) is primarily tree savanna with areas of savanna woodland (Hopkins, 1965) with trees of relatively even height (10–15 m) and trunk diameter (15–30 cm dbh). Over much of the area the trees appear to be relatively evenly spaced (Figure 9) and often occur as single-species stands as illustrated by plot 2 on Table 1. Although the density of trees in this savanna is high as shown in Table 1, the crowns are sparse and nonoverlapping. Dominant species are *Terminalia chebula, Terminalia belerica, Pterocarpus marsupium;* also present are: *Butea monosperma, Careya arborea, Anogeissus latifolia,* and *Cycas rumphii.* Shrubs present are *Phyllanthus emblica* and *Zizyphus* sp. The dominant ground vegetation consists of tall, perennial grasses, the commonest of which are *Cymbopogon confertiflorus* and a *Themeda* (identified by Fernando (1968) as *T. tremula,* but from Senaratna's (1956) description appears to me to be *T. triandra*).

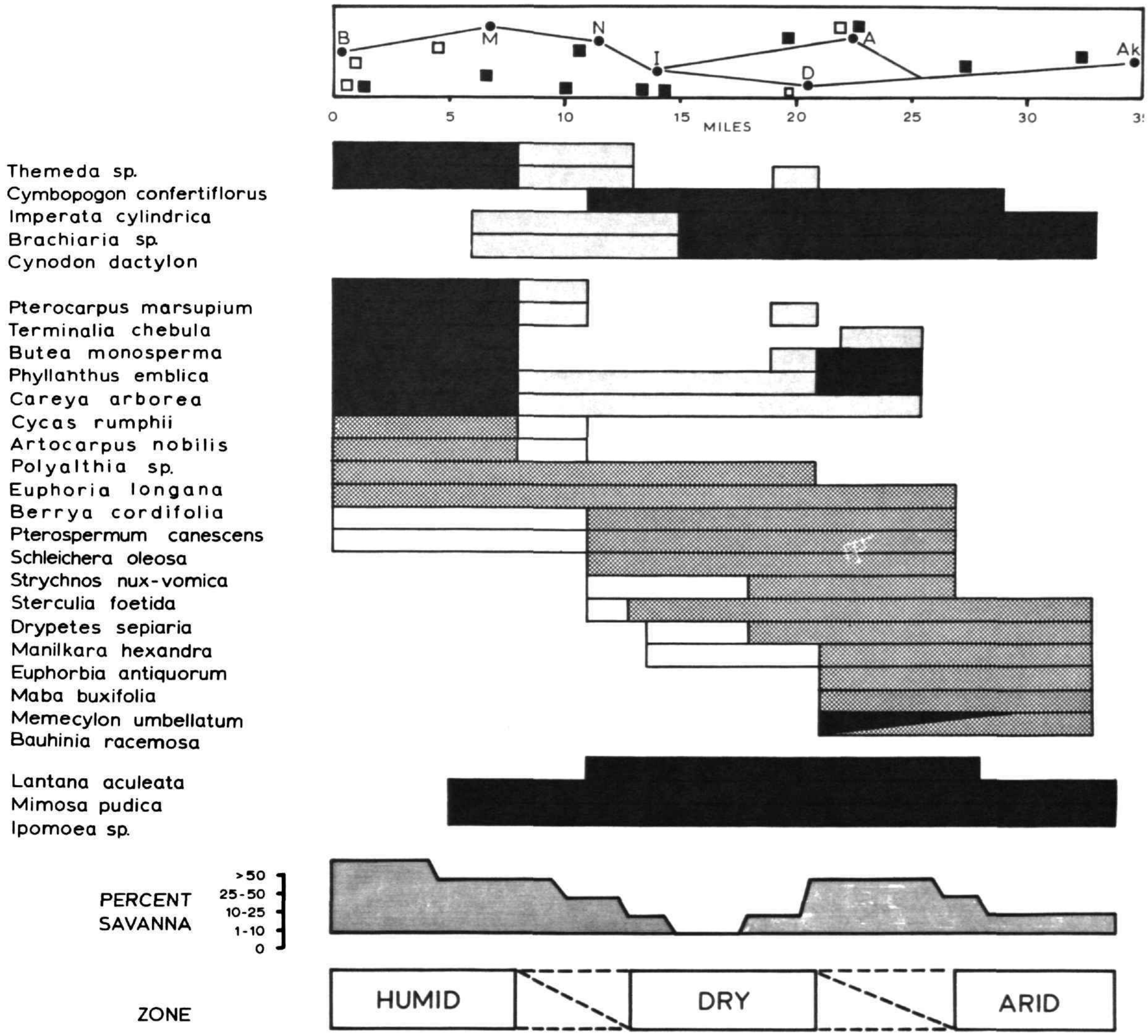


FIGURE 8.—Distribution of plants along a 35-mile strip in the Gal Oya region. For the grasses and savanna trees, the dark gray indicates presence as a dominant and white presence, but not dominant. For the forest trees the stippled area indicates presence as a dominant. The dry zone and arid zone contain relatively little savanna, while the humid zone and both ecotonal areas contain large proportions of savanna. Towns as marked from west to east are: B, Bulupitiya; M, Mullegama; N, Namal Oya; I, Inginiyagala; D, Damana; A, Amparai; Ak, Akkaraipattu.

Many other species besides those listed above occur in this area but these appeared to be the most characteristic of the Gal Oya region. Fernando (1968) lists a number of additional species, several of which were neither collected nor observed in our work.

As one moves eastward the species composition of the forest changes. Detailed surveys using quantitative techniques would be necessary to confirm the impression that the change is gradual. *Artocarpus* and *Polyalthia* become scarce east of Mullegama as do *Mangifera* and *Celtis*. East of the Mullegama–Namal Oya region the talawa becomes less extensive and occurs only as small patches or islands,

FIGURE 9.—Savanna woodland (Talawa) in western sector of Gal Oya National Park.

TABLE 1.—*Flora composition of two areas of savanna (Talawa)* (Figures in parentheses = total vegetation living and dead; other figures = living vegetation.)

Vegetation	*No. in Plot 1* *	*No. in Plot 2***
TREES (>5m)		
Terminalia chebula	33	97
Anogeissus latifolia	2	0
Pterocarpus marsupium	30	0
Careya arborea	3	0
Adina cordifolia	3	0
Phyllanthus emblica	1	0
Butea monosperma	1	0
? dead	9	19
	—	—
Total	82 (91)	97 (116)
Trees per hectare	328 (364)	388 (464)
SHRUBS (<5 m)		
Phyllanthus emblica	7	2
Zizyphus sp.	8	2
Careya arborea	0	3
Terminalia chebula	3	0
Cycas rumphii	0	3
Butea monosperma	0	2
Unidentified	0	1
	—	—
Total	18	13
Shrubs per hectare	72	52

*Plot 1: 124 m N of Gal Oya, 100 m E of road from Bulupitiya to Medagama; 100 m to nearest forest (gallery); area: 0.25 hectares (50 x 50 m).

**Plot 2: 2 km S of Bulupitiya on road to Medagama, 30 m E of road; 2 km to nearest forest; area: 0.25 hectares (50 x 50 m).

surrounded by forest.

Within this area east of Mullegama, the forest gradually becomes of lower stature (20–35 m) and contains more individuals of deciduous species as can readily be seen during the dry season. *Euphoria longana* and *Berrya cordifolia* remain common, *Pterospermum* and *Schleichera* become more common and *Strychnos, Diospyros malabarica,* and *Drypetes* appear as dominant subcanopy species. *Manilkara* and *Euphorbia* occur in rocky areas and *Sterculia foetida* appears as an emergent. At least two species of *Ficus* occur and in places may be quite common, but their distribution does not appear to be as even as that of the others.

As one moves eastward between Inginiyagala and Amparai, the species composition of the forest appears to remain stable but the character of the canopy layers changes from a dense medium stature canopy to a dense low stature canopy with emergents. Species such as *Drypetes, Pterospermum,* and *Glenniea* which form a subcanopy around Inginiyagala are in the now lower (15–20 m) canopy, 5 miles further east, and those such as *Berrya, Schleichera,* and *Sterculia* occur as emergents along with *Chloroxylon* and *Diospyros* spp. Throughout this area the shrub layer is relatively sparse, consisting mostly of saplings of *Pterospermum* and several species of shrubs.

East of Amparai the general character and composition of canopy and emergents changes little except for the addition of *Manilkara* as a common emergent. The main difference now is in the shrub layer which becomes dense, consisting of *Memecylon* spp., *Maba buxifolia,* and *Bauhinia recemosa.* Close to the coast, the number of emergents becomes less. This type can be referred to as a forest scrub (see Mueller-Dombois, n.d.).

In the area around Amparai a type of savanna, different from the talawa, exists. In this area the dominant grass is *Imperata cylindrica.* Shrubs of practically all species in the surrounding forest occur in islands within the grassland and *Bauhinia racemosa, Phyllanthus emblica,* and *Butea monosperma* occur as solitary individuals. Figure 10 shows a typical portion of this shrub savanna.

Examination of Figure 8 shows that there is a west-east gradient in the distribution of forest and savanna plant species along the 35-mile strip. These data may be combined with the climatic data presented in Figure 5*a* and 5*b* to make a tentative classification of climatic/vegetational zones.

The area of medium stature forest and talawa falls within the zone of >2000 mm annual rainfall. East of this is a zone with 1500–2000 mm annual rainfall, two or fewer arid months and 3–4 dry months. This zone corresponds to the *Euphoria-Pterospermum-Drypetes* forest (low stature with emergents) and can be considered a dry zone.

The resemblance of the vegetation between Amparai and Akkaraipattu to that of Ruhunu National Park (Mueller-Dombois, n.d.) indicates that this region should be considered an extension of the "arid zone." I hypothesize that a single peak rainfall, followed by a prolonged period of drought (1+ arid months plus 1–3 dry months) may be another factor determining the presence of arid

FIGURE 10.—Shrub savanna, three miles north of Amparai.

zone vegetation besides low rainfall per se. Certainly from the data available, it is more reasonable to extend the limits of arid zone vegetation northward along the coastal plain to some point north of Batticaloa.

While it can be seen that there are these three major types, it must also be emphasized that they are separated, not by discontinuities which can be drawn as lines on a map, but by transitional zones which in some places may be as wide as the typical "zone" itself (Figure 8).

Over large sectors of this region man has practiced a type of shifting agriculture, referred to locally as *chena* (from Sinh: "Hēn"), in which areas of forest are partially cut, burned, cultivated for a few seasons, then abandoned. In some places this activity has been extensive over a long period of time and much of the forest is actually a mosaic of small areas at different successional stages. Such areas are recognizable from the aerial photographs and are distinguished on the vegetation map (Figure 11) as "forest-chena" (Figures 11 and 12 show the results of vegetation analysis for the Gal Oya National Park and the area surrounding Amparai, respectively).

Within the Gal Oya National Park, forest is the predominant vegetation type covering 45 percent of the total area (Table 2). Forest affected by chena occupies 2.7 percent and is concentrated in the southern part of the park near the village of Baduluwela. Talawa savanna makes up 33 percent of the total area and is the dominant type in the western sector of the park.

The grassland is entirely artificial, created by logging in the bed of the reservoir and by periodic inundation of the land. The measurements in Table 2 were made from a photograph taken when the water was at a relatively low level. At extreme high water the area of grassland will be reduced drastically except in a small area south of Inginiyagala where land above the level of the reservoir was cleared.

Grassland of this type occurs around all of the tanks in this region. Except for a few small holding tanks, which are supplied by larger tanks, all of the reservoirs have a fluctuating water level, being normally high during the northeast monsoon and becoming progressively lower until the next rainy season. Grass growth begins soon after the water recedes. In lower lying areas, which are inundated for long periods annually, the common grasses tend to be annuals (e.g. *Eragrostis, Eleusine*). In the

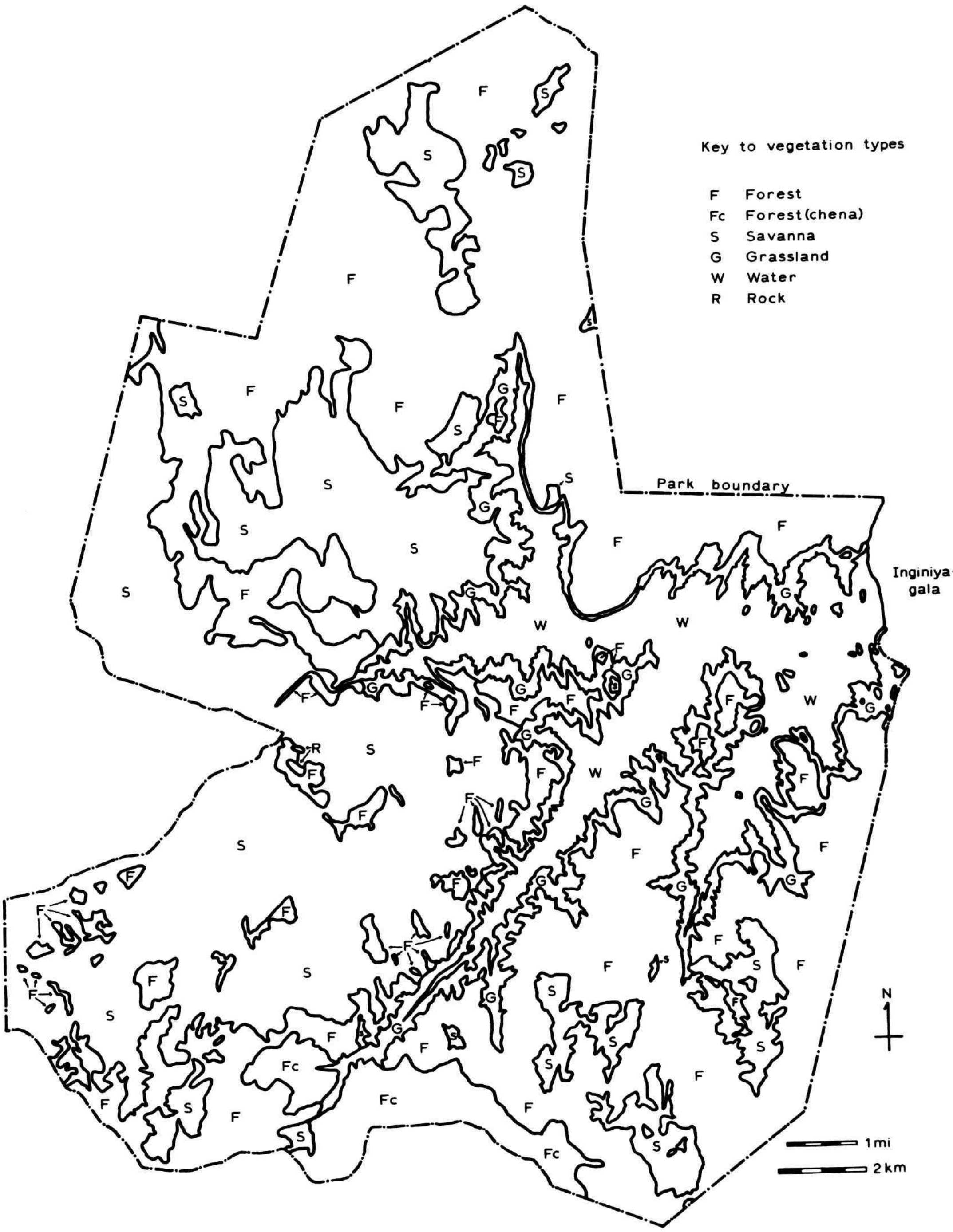


FIGURE 11.—Vegetation map of Gal Oya National Park.

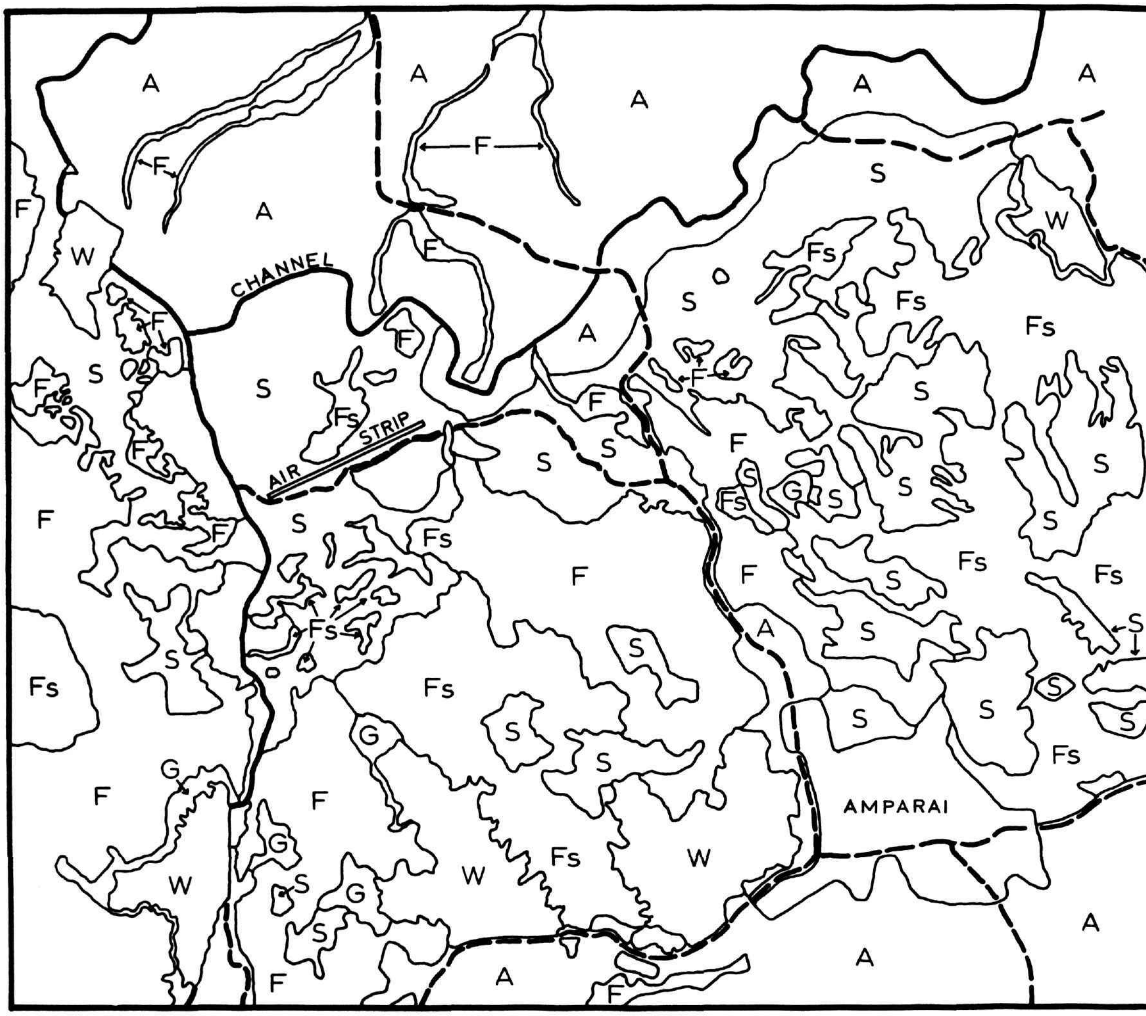


FIGURE 12.—Vegetation map of the area surrounding the Amparai Sanctuary. A=agriculture; F=forest; Fs=forest scrub; G=grassland; S=savanna; W=water.

TABLE 2.—*Composition of vegetation in Gal Oya National Park* (calculated from Figure 11).

Vegetation	*Area* mi^2	km^2	*Percentage*
Forest	62.16	160.99	45.0
Forest (chena)	3.79	9.82	2.7
Savanna (Talawa)	46.12	119.45	33.3
Grassland	12.48	32.32	9.0
Water	13.77	35.66	9.9
Bare rock	0.05	0.13	0.1
Total	138.37	358.38	100.0

higher areas, which may not be submerged every year, perennials (*Cynodon dactylon, Brachiaria sp.*) become more common. In extremely high areas of the Senanayake Samudra which are often dry for several years, other plants, such as vines (*Mimosa pudica* and *Ipomoea sp*), may become abundant and termites may move in from the forest (Figure 13).

Phenology

Although no study of phenology was made in the forests of the Gal Oya region in connection with

FIGURE 13.—Upper bank of Senanyake Samudra at Kossapola. Note the presence of a few dead trees on the upper bank. At the time this photograph was taken (1968) this section of bank had been dry for several years and termites had invaded from the forest.

this work, the data obtained by Koelmeyer (1960) and by Muckenhirn and Rudran (n.d.) show conclusively that within the drier regions of Ceylon there is a definite seasonality in the leaf fall, flushing, flowering and fruiting of many forest trees and that different species demonstrate particular patterns. The significance of these phenomena to the elephant is that not all potential food types are available in equal abundance at all times of the year.

Seasonal differences in availability are particularly apparent when one looks at the grasses. Figure 14 shows the condition of grasses in the talawa around Nilgala from late 1967 to 1969. Throughout this period of 26 months, fresh green grass was available for only 12 months.

Fire

Toward the end of the rainy periods the grass culms, which have been growing for several months, begin to die. After only a few weeks of drought these dried stems and leaves are readily ignited. Fires may be started by lightning or by man. Man-made fires observed in this particular area were started in three major ways: (1) fires set by poachers, (2) spreading of camp fires—poachers, fishermen, carters—and (3) fires set by cattle-herders who know that a fresh growth will follow with the next rains.

As most fires occur during the period of the southwest monsoon, when a dry steady wind (*kachan*)

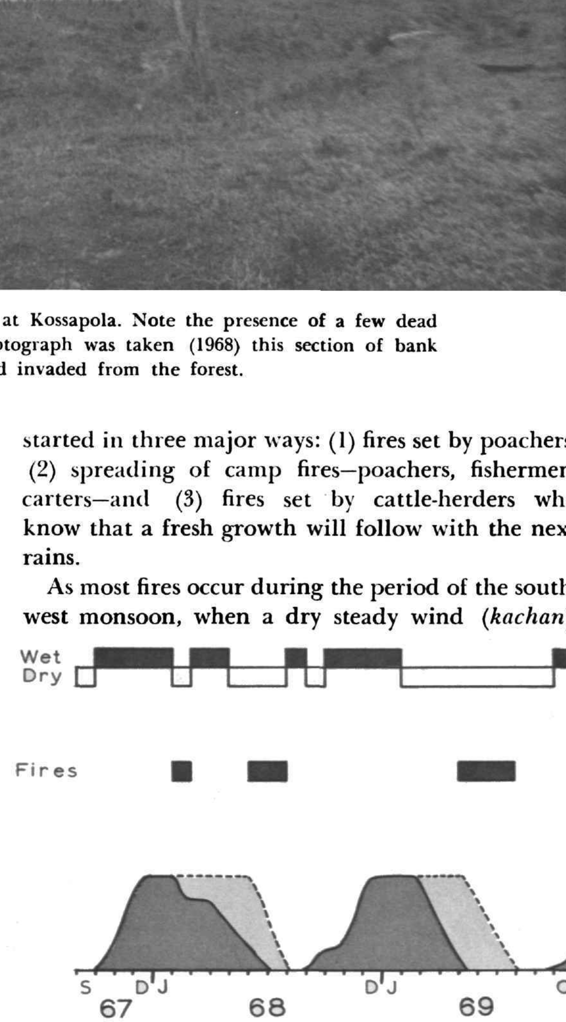


FIGURE 14.—Changes in quality of grass in relation to weather and fires. The dark-stippled area shows those periods when fresh grass was available; the lightstippled area, dry grass. Vertical scale is in arbitrary units and gives the approximate relative availabilities of fresh and dry grass.

FIGURE 15.—Savanna woodland (Talawa) after fire, September 1967.

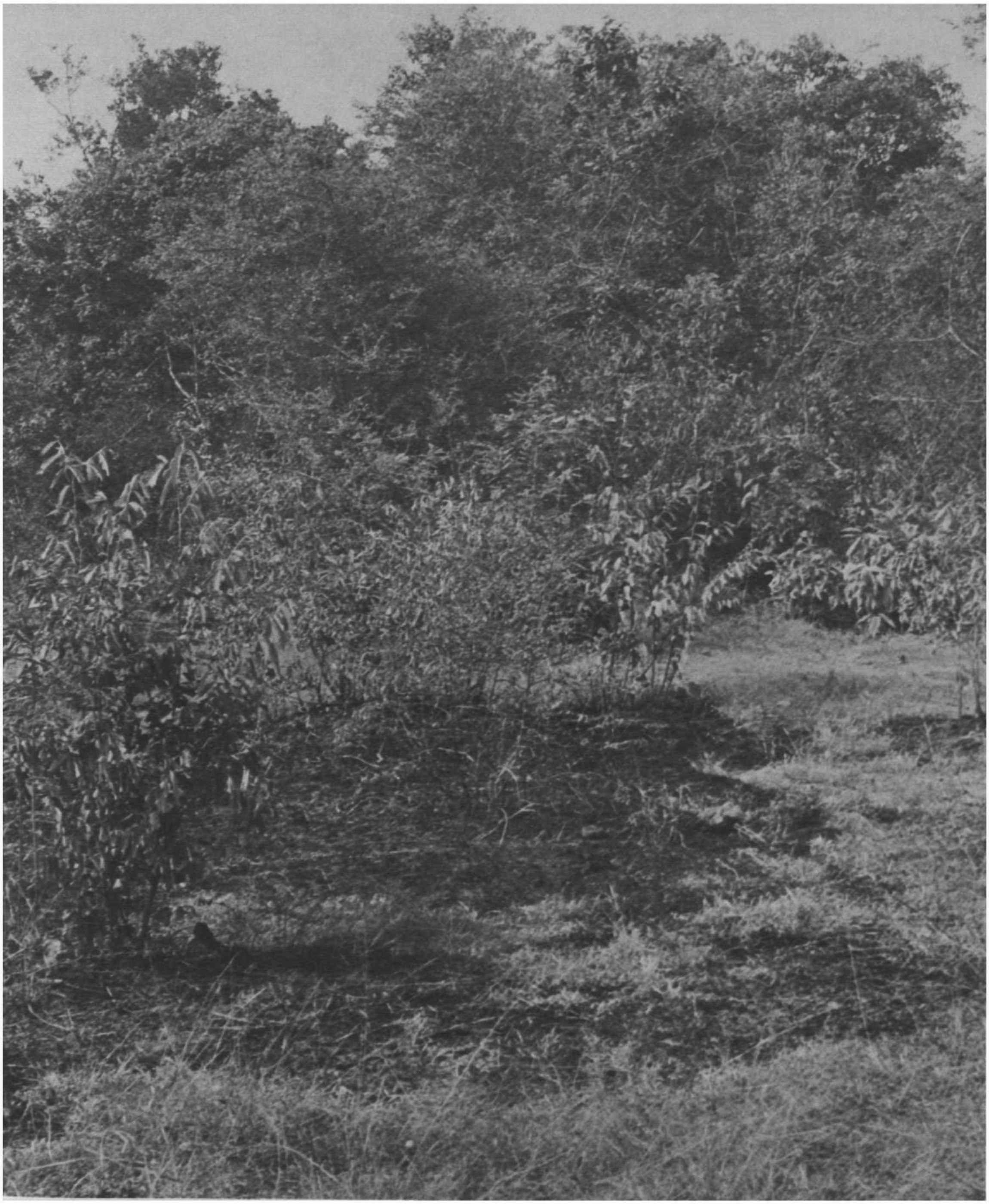


FIGURE 16.—Shrub savanna after fire, June 1969.

blows continuously during the daytime, extensive areas are burned almost every year. Approximately 50–75 percent of talawa in the region of Bulupitiya and Nilgala were burned in all three years of this study. Over most of the talawa area the fires are restricted to the savanna, the forest remaining unaffected. In only one small area (plot 2 in Table 1) were any appreciable number of savanna trees affected by the fires. In this area some 15–20 percent of the *Terminalia chebula* had burned bark and were leafless at the time the plot was sampled (about 6 weeks after burning). The shrubs, however, were apparently unaffected.

The potential effects of fire on grassland and savanna, discussed extensively by Daubenmire (1968) and Hopkins (1965), are numerous including changes in productivity, species composition, and cover type. Although it was not possible within the time limit of this study to examine any of these effects in detail it was apparent that the fast-moving fires of the talawa in general have little effect on species composition. As noted by Daubenmire (1968), a slow-moving hotter fire is capable of producing greater effects on the ecosystem. Such effects were noticeable in the savanna areas in the vicinity of Amparai, where, in the extensive fires of May and June, 1968, shrub areas bordering on the grassland were frequently burned. Shrubs as far as 1–1.5 m away from the grass died as a result of these fires. Figures 15 and 16 show the effects of fire on the two savanna types, including the affected shrubs in the shrub savanna.

History of Development

Although accurate records are not available, the ruins of a reservoir at Digavapi (east of Amparai) and remains of temples scattered throughout the region indicate that man has been present in some numbers for several hundred years and that cultivation may have been extensive during the Polonnaruwa period. Accounts by Knox (1681) and other early European visitors indicate that the town of Batticaloa remained an important population center and that the coastal strip was probably inhabited and cultivated continuously. Farmer, et al. (1970) refer to construction of an anicut and two tanks (Amparai Kulam, Kondavatavan Kulam) between 1856 and 1892 and state that by the early part of this century there were some 83,000 people living in the Gal Oya region. Of these, 79,000 were concentrated in the rice-growing land and on the coastal sandbars, with 4,000 scattered among several villages in the upper reaches of the valley, living mostly by chena cultivation.

From 1949 to 1951 an earthen dam and a concrete dam were constructed at Inginiyagala, blocking the Gal Oya and creating the reservoir known as the Senanayake Samudra. In the decade following, a series of irrigation ditches was developed along the left (north) bank and minor dams were constructed across the Namal Oya, Andella Oya, and Navakiri Aru, among others. During the 1960s work was begun on development of the right bank, including an irrigation channel from the Senanayake Samudra and minor tanks on the Pallang Oya, Ekgal Aru, Ambalam Oya, and Pannela Oya. Construction in this region is still in progress.

The population of this area has risen dramatically. In 1950–1951, 296 families were settled in the region; by 1965 the number of newly settled families was 11,936 (Farmer, et al., 1970). Data from the Ceylon Department of Census and Statistics (Yearbook, 1967) show the 1963 population of the Amparai district as 211,820. More recent figures are not available.

Agriculture

Figure 17 shows the approximate distribution of agricultural land (small areas of chena are omitted) as of 1969 and projections for future development by the River Valleys Development Board.

Agriculture in this area is of two types, intensive and shifting. Intensive agriculture may be of either the upland type (e.g., plantains, pineapples, coconut) on well-drained hillsides or of the irrigated type (sugar cane, paddy) in the bottomlands. In either case intensive agriculture involves clear-cutting of the original vegetation and maintenance of cultivated plants.

Chena farming, however, involves only partial cutting of the forest followed by burning. The land is then cultivated for one or two growing seasons with minimal disturbance of the soil, then abandoned. This land then quickly reverts to natural vegetation. The first stage, (Figure 18) in this succession generally consists of woody herbs and low shrubs (*Lantana aculeata, Ochna zeylanica,*

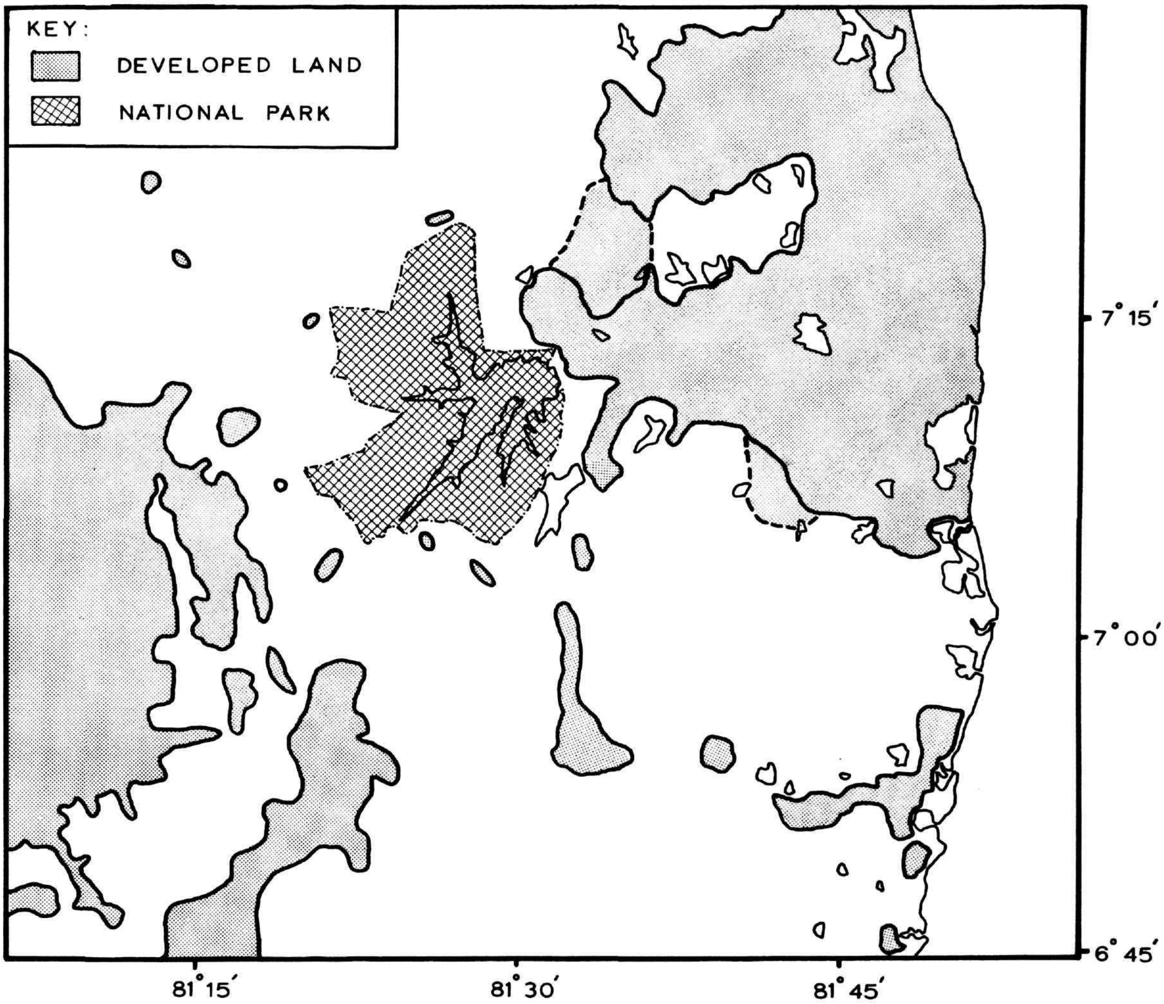


FIGURE 17.—Distribution of agricultural land in the Gal Oya region. Shaded area includes land developed as of October 1969.

and *Premna latifolia*), followed by larger shrubs and trees. During this early stage of succession such areas are heavily used by elephants.

Under the traditional methods of cultivation, discussed in detail by Wikkramatileke (1963), paddy lands generally lay close to the village. Such areas were surrounded by an expanse of relatively depauperate vegetation (due, in part, to grazing by livestock and cutting for fuel). This is, in turn, surrounded by areas of chena and forest. With this pattern of land usage, the contact between wildlife and man would be relatively slight and would be confined mostly to the chena zone. Under modern agricultural conditions, however, large areas of intensive cultivation (sugar cane, paddy) juxtapose forest land (Figure 19). This provides ample opportunity for elephants, wild buffalo, and swine to feed on cultivated crops, often causing considerable damage.

Besides cultivation, man also affects the environment through the grazing of domestic livestock. Cattle (zebu), buffalo, and goats are the principal species, and all are allowed a certain amount of freedom to forage in the forest surrounding the

FIGURE 18.—Chena land abandoned about two years previous to time photographed.

villages. In some areas cattle and buffalo may be herded into large groups. Such large herds occur in the region around the Amparai airport (cattle) and in the eastern half of the Gal Oya National Park (buffalo). Apart from the effects of grazing by the animals, the vegetation may also be altered by man, through the setting of fires to promote new grass growth.

Figure 20 shows the relationships between the various vegetation types in this region. The double arrows indicate changes that cattle-grazing and man through chena cultivation can effect on these vegetation types.

A third effect of man on the environment lies in the construction, use, and abandonment of tanks or reservoirs. When in use, a tank generally has a forested catchment area. The boundary between forest and water provides for the elephant not only a source of water, but often a source of food. When such tanks are abandoned or poorly maintained (e.g., Lahugala, Figure 21) silt accumulates and vegetation invades the tank beginning with lotus (*Nelumbium*) and a number of grasses, notably paddy (*Oryza sativa*). Such unused tanks provide a rich source of food for the elephant, particularly at the onset of the rainy season.

DEFORESTATION AND AFFORESTATION

Apart from cutting for agricultural purposes, large areas of land have been logged for commercial timber. In some areas the logging is selective as recommended for this region by McCormack and Pillai (1961a,b) but in other areas tracts have been clear-cut. Several of these areas (and some areas of grassland) have been planted with teak (*Tectona grandis*) in an attempt to provide more valuable timber. The teak trees have been planted, in

FIGURE 19.—Paddy land showing juxtaposition of cultivated area with forest.

monoculture, relatively close (3–5 m) together. Szechowycz (1953) considered that these plantations were unsuitable for the area and that the project should be halted as tree growth was apparently impaired. Few shrubs occur in the teak plantations and grasses are primarily *Imperata cylindrica* and *Cymbopogon confertiflorus*.

THE VERTEBRATE FAUNA

Terrestrial mammals known to be present in the area are listed in Table 3. Insectivorous bats are seasonally common, especially in the moister areas, but attempts to catch individuals for identification were largely unsuccessful. Fruit bats (Pteropodidae) may occur occasionally but none were observed during this study.

Of the mammals listed in Table 3, the two primates, the hare, the wild boar, the deer, and buffalo are important herbivores in addition to the elephant (see pp. 97–99).

The only large predator in the whole of Ceylon is the leopard (*Panthera pardus*), which around the Gal Oya National Park, consists of not more than three pairs. Several smaller predators are also present. Of these, the jackal (*Canis aureus*) and two species of mongoose (*Herpestes smithi* and *H. vitticollis*) feed from carcasses of elephants and other ungulates.

Comparison of Table 3 with the report for Wilpattu by Eisenberg and Lockhart (1972) shows that the total number of mammalian species present is roughly the same although the species composition of the two areas differs. Wilpattu has a higher diversity of primates and carnivores and a lower diversity of rodents than Gal Oya. In most instances these differences would appear to be due to species whose ranges are restricted to either the

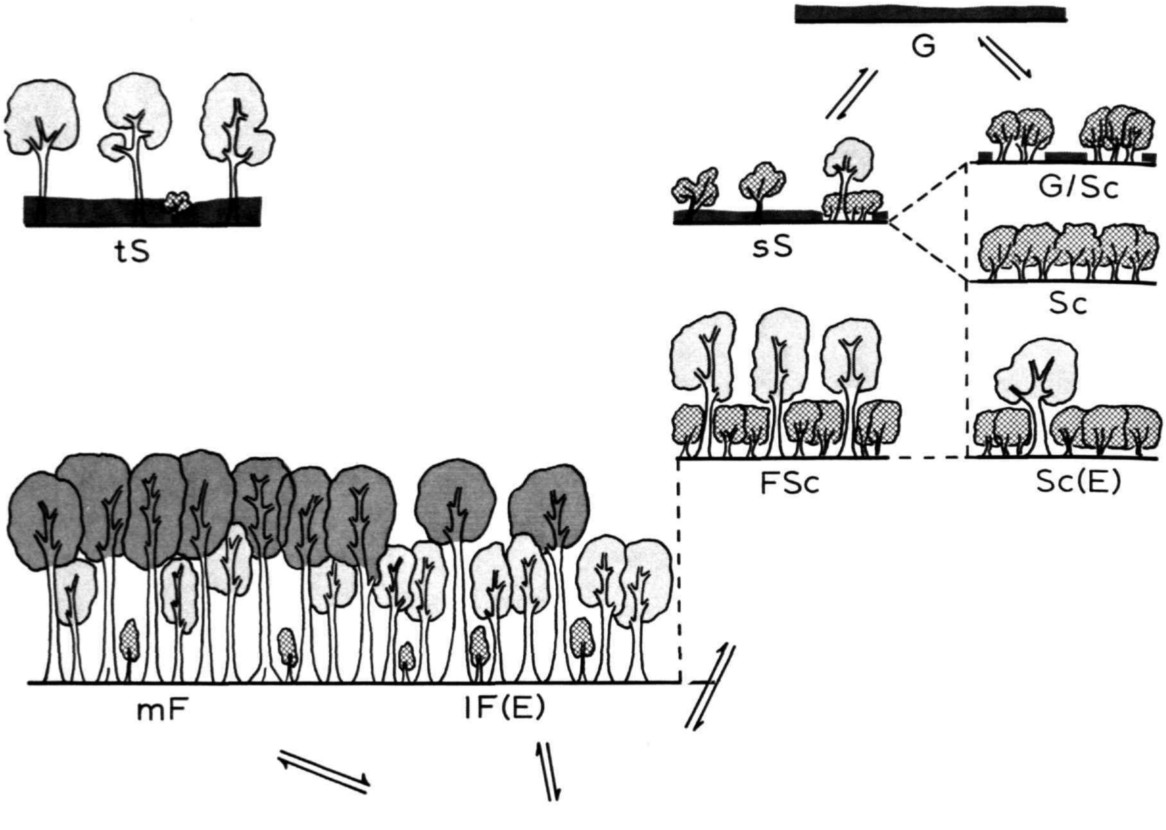


FIGURE 20.—Vegetation types in the Gal Oya region and changes due to cultivation and grazing. Chena cultivation partially clears land, which soon reverts to previous forest type. Grazing appears to have a longer-lasting effect in hindering return of the previous forest type; succession may be much slower in heavily over-grazed areas. tS=tree savanna; mF=medium stature forest; lF(E)=low stature forest with emergents; FSc=forest scrub; Sc(E)=scrub with emergents; Sc=scrub; G/Sc=grass with scrub islands; sS=shrub savanna; G=grassland.

northern or southern half of the dry zone (Eisenberg and McKay, 1970) rather than to ecological differences.

Of the more than 300 species of birds which occur regularly in Ceylon (Phillips, 1953), 150 were observed in the Gal Oya region. I do not intend to discuss these in any detail in this paper, but two ecological categories of birds deserve mention. First are the large numbers of fish-eating birds which occur on and around the tanks. Besides the numerous pelican, cormorants (three species), herons and fishing eagles (*Ichthyophaga ichthyaetus* and *Haliaeetus leucogaster*), there are large numbers of Brahminy kites (*Haliastur indus*) around the Senanayake Samudra whose food consists largely of fish.

The second group consists of such frugivorous birds as hornbills (*Tockus griseus* and *Anthracoceros coronatus*), pigeons (*Ducula aena* and *Treron* (2 species), parrots (*Psittacula* (3 species) and *Loriculus beryllinus*), and barbets (*Megalaima* (3 species)). Besides the potential effect these birds may have on dispersal of tree species, they may also have an effect as competitors with primates.

Among the reptiles present in the area, crocodiles (*Crocodylus palustris*) are locally common in tanks and irrigation ditches and the Thalagoya (*Varanus bengalensis*) is abundant in drier areas. Rat snakes

FIGURE 21.—Lahugala Tank showing dense growth of grasses.

(*Ptyas mucosus*) are very abundant but venomous snakes (*Naja naja* and *Vipera russelli*) and the python (*Python molurus*) are only locally common. Several species of gekko are found and two Agamids (*Calotes* spp.) and a skink (*Mabuya* sp.) are very abundant. Freshwater turtles (*Melanochelys trijuga* and *Lissemys punctata*) are abundant in irrigation ditches.

Amphibians include *Bufo melanostictis, Rana tigrina, Rana limnocharis, Rana gracilis,* and *Rhacophorus cruciger.*

Tanks throughout this region have been artificially stocked with fish, principally *Tilapia mossambica.*

THE INVERTEBRATE FAUNA

It would be absurd to attempt any compilation of the invertebrate fauna of this region. Only those forms of particular importance to the elephant will be mentioned.

Aquatic leeches occur in many of the tanks in this region and are particularly abundant at Lahugala. Terrestrial leeches (*Haemadipsa* sp.) occur only in moister areas around Kossapola, Baduluwela, and Bibile.

Two types (which I was unable to identify as to species) of termites occur in this region: a mound-building type which is commonest in the driest areas and a nonmound-builder which occurs in the moister forests to the west. The potential relationship between termites and elephants are discussed on page 100.

Three major groups of biting arthropods (mosquitoes, flies, and ticks) are seasonally abundant. Mosquitoes of several species and biting flies (Tabanidae) are more abundant during the wetter months, while ticks appear more commonly in the drier months.

Populations

Two terms—population and herd—will frequently be used. Population means the total number of elephants inhabiting a given geographic area. For some of the populations of elephants in Ceylon the boundaries can be demarcated by zones in which elephants apparently do not occur or are rare; for others the dividing line is arbitrary. I define "herd" as a group of elephants consisting of related adult females and their juvenile offspring who maintain a certain degree of internal organization and who do not associate over long periods of time with other such groupings. A more complete description of the herd and its social organization is given on pages 72–75.

TABLE 3.—*Mammals of the Gal Oya Region*

Family and species	*Comments*
Soricidae	
Suncus murinus kandianus	Widespread and locally abundant in moisture areas
Cercopithecidae	
Presbytis entellus thersites	Common throughout the area; higher density in the eastern half
Macaca sinica sinica	Common in eastern half of the area, sparse to the west
Manidae	
Manis crassicaudata	Sparsely distributed in the east only
Sciuridae	
Petaurista petaurista	Reported from Inginiyagala
Ratufa macroura dandolena	Common throughout the area
Funambulus palmarum ssp.	Common
Hystricidae	
Hystrix indica	Widespread but sparse
Muridae	
Tatera indica	Very abundant in open areas
Mus musculus	Common around villages
Mus cervicolor	Common to abundant around paddy fields
Mus fernandoni	Reported, but not observed during 1967-1969
Rattus blanfordi	Reported, but not observed during 1967-1969
Rattus rattus ssp.	Common around villages
Millardia meltada	Reported, but not observed during 1967-1969
Leporidae	
Lepus nigricollis singhala	Very abundant in open areas
Mustelidae	
Lutra lutra nair	Widely but sparsely distributed
Canidae	
Canis aureus lanka	Common throughout
Ursidae	
Melursus ursinus	Locally common
Viverridae	
Viverricula indica	Common
Paradoxurus hermaphroditus	Present but not common
Herpestes smithi	Locally very common
Herpestes vitticollis	Disjunct distribution, but common around Inginiyagala
Felidae	
Felis viverrina	Sparse
Panthera pardus fusca	Sparse
Elephantidae	
Elephas maximus maximus	Common
Suidae	
Sus scrofa cristatus	Locally common
Tragulidae	
Tragulus meminna	Sparsely distributed in forested areas
Cervidae	
Muntiacus muntjak malabaricus	Sparse in forest areas
Axis axis	Locally common
Cervus unicolor	Sparse but widespread throughout forested areas
Bovidae	
Bubalus bubalis	Locally common

DISTRIBUTION OF POPULATIONS

Within the southeast quarter of Ceylon there appear to be three populations. One population inhabits the area around the Gal Oya National Park; the second, from Rufus Kulam and Lahugala Tank to approximately the Kumbukkan Oya; and the third, the area around Ruhunu National Park.

Most of the data concern the first two. Within each of these two populations there is some overlap between the home ranges of their constituent herds, but a minimal overlap between populations. Figure 22 shows the distributions and sizes of the herds within the Gal Oya population and the approximate limits of the Lahugala area population. Herd ranges for this latter population are not shown on this map as it was not possible during this study to delimit these with any accuracy. As can be seen from this figure, the distribution of elephant herds is not uniform. Ranges I and III contain relatively low numbers of animals, between 15 and 25 in each; whereas areas II, IV, V, and VI contain larger numbers. Areas I and III contain approximately equivalent amounts of forest and savanna land while area II is predominantly savanna with some scattered forest blocks. The remaining areas are primarily forest. There does not appear to be any correlation between the type of vegetation predominant in an area and the numbers of elephants that will be present.

The ranges of these groups show a certain amount of overlap with the exception of area VI. It is quite probable that this spatial separation of the latter herd is due not to any traditional movement patterns but to the isolation of this area by surrounding agricultural land. The land lying

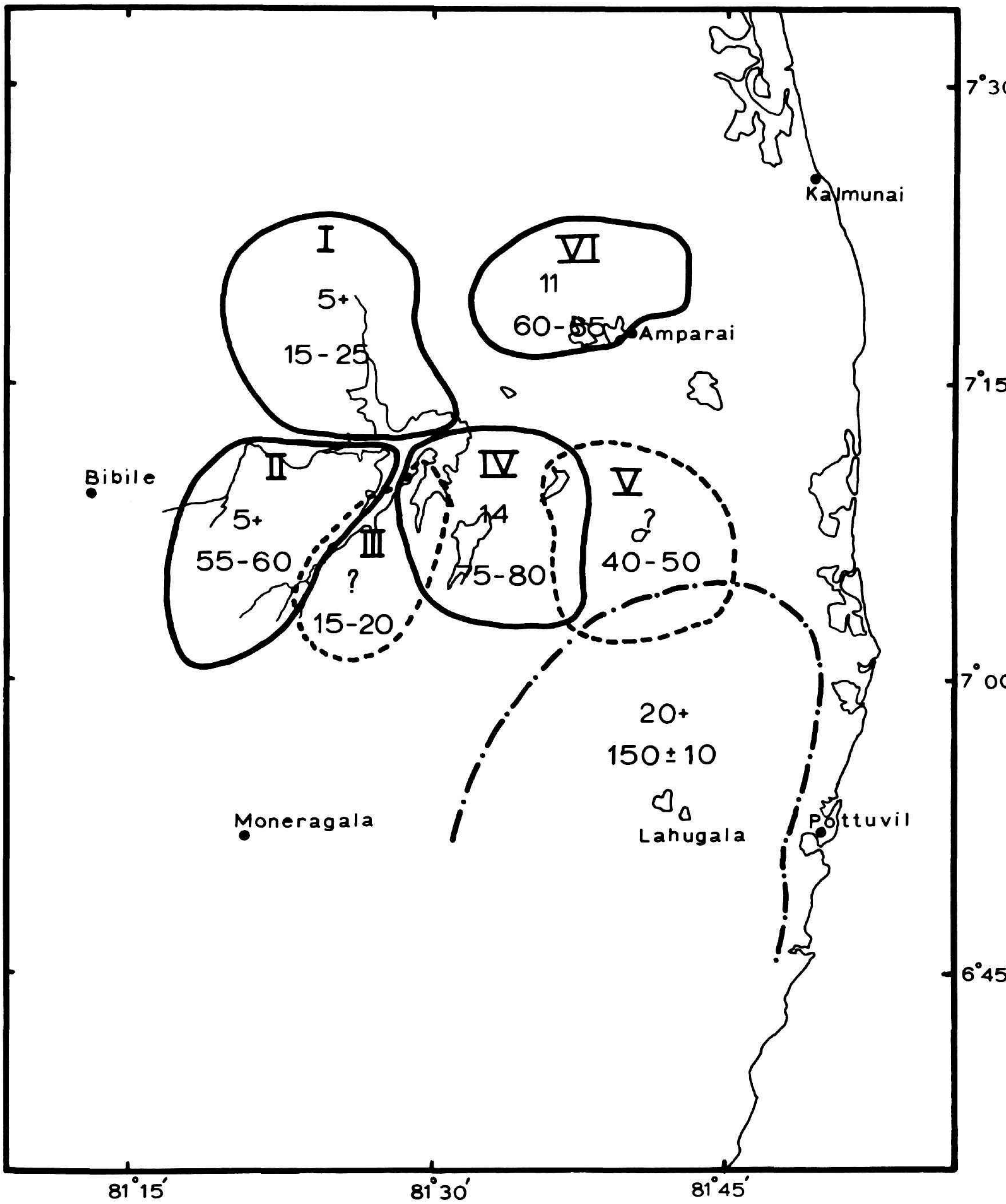


FIGURE 22.—Distribution of elephants and population sizes in eastern Ceylon. The herds within the Gal Oya population are: I Northern Park, II Talawa, III Baduluwela, IV Hatpata, V Ambalam Oya, VI Amparai. The upper digits give the estimated number of adult males living within the range of the herd; the lower digits are the estimated sizes of the herds.

between area VI and areas I, IV, and V, which is primarily cleared for agriculture, is occupied only by strays, usually adult males, although on occasions the herds from area I and area VI will invade this region of paddy land.

It is estimated that the total population in this area is between 260 and 300 elephants including adult males. The total population size for the area surrounding Lahugala Tank is estimated to be approximately 150.

Figure 23 shows the relationship of these two populations to the other populations of elephants in Ceylon with a rough estimate of the total population of the island. Estimates of any reliability are available for only four major areas: The Gal Oya and Lahugala areas included in this study, Wilpattu, Tamankaduwa, and Ruhunu National Park. Eisenberg and Lockhart (1972) have estimated that there are approximately 120 elephants in the area around Wilpattu National Park. My estimate for the Ruhunu National Park region is approximately 150. Nettasinghe (pers. comm.) estimates approximately 400 for the population in the Tamankaduwa area.

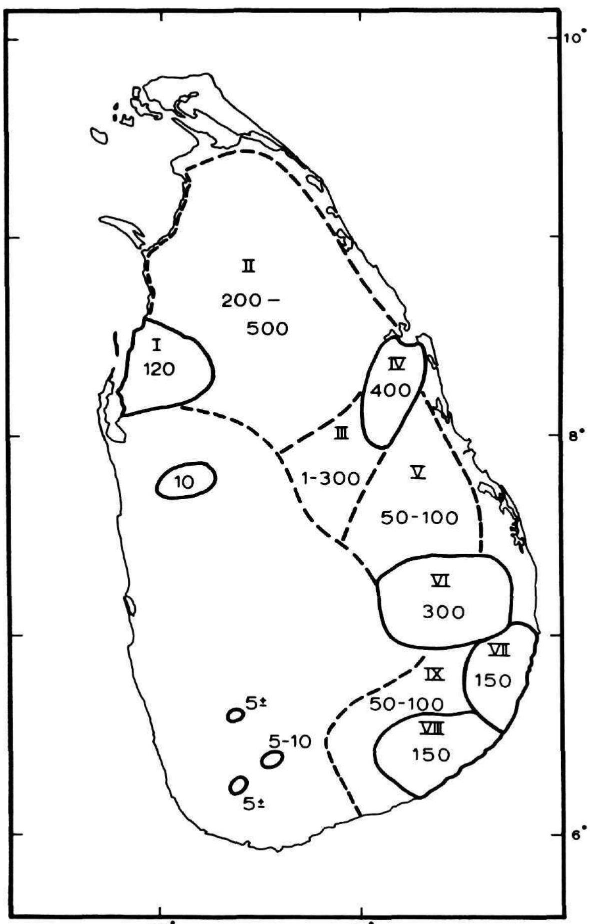


FIGURE 23.—Estimated elephant population of Ceylon, 1969 Areas with most reliable estimates are enclosed in solid lines; others in dashed lines.

The other areas shown enclosed in dotted lines on Figure 23 are not so well known. Wickremasinghe (pers. comm.) informs me that the area between Gal Oya and Polonnaruwa is relatively sparsely inhabited by elephants and observations from several trips made by the author through this area would tend to support this in that very few signs of elephants were seen when traveling through either the western or northeastern portions of this area. The reason for the relative scarcity of elephants in this area is unkown, although an examination of aerial photographs and observations made during a flight over this area in 1968 showed that this area had been subjected to quite intensive chena agriculture for some time. It appears possible that this intensive activity by man has forced the elephants out of this region. Area III lying between Dambulla on the west and Trincomalee in the northeast and including a large portion of the lower Mahaweli Ganga contains, according to Nettasinghe, (pers. comm.), about 400 elephants. It is possible that certain of the animals living to the west of Polonnaruwa do not congregate in the Tamankaduwa area closer to the mouth of the Mahaweli; therefore, this population may actually be as high as 500 to 700 animals. The relatively large area in the northern portion of the island (Figure 23: area II) was not surveyed in any detail either by myself or by Eisenberg and Lockhart (1972), although I did make two trips into this area. This region is characterized by an interspersion of forested areas and agricultural land. Several herds are known to be present around Giant's Tank, Vavuniya, and Galenbidunu Wewa. The total population in this area is probably between 200 and 500 elephants.

The areas to the north and to the west of the Ruhunu region are again characterized by interspersion of forested areas and agricultural land and probably contain between 75 and 150 elephants. The remaining four regions are relatively small isolated forested areas: in the vicinity of Hiniduma in the southwest, Deniyaya, and Adam's Peak in the central highlands and Deduru Oya in the northwest. These areas all contain isolated herds which are low in number. Thus, a minimum figure for the total elephant population of Ceylon would be between 1600 and 2200. This estimate agrees closely with that of Norris (1959), although Norris did not give any detailed account of distribution of elephants or reasons for arriving at his 1951 figure of 1500.

I cannot stress strongly enough that my estimate is only a first approximation, based upon the numbers known to be present in a few areas and, by extrapolation, the assessment of a minimum population to those areas not censused.

If the supposition of a possible elephant population of 12,000 at the beginning of the 19th century (p. 5) is correct, the present population represents about 15 percent of that one-time total. The only comparable estimates for other Asian countries are those of Medway (1965) and Stevens (1968) who show a total of about 500 elephants in 50,000 square miles (129,500 km^2)—a density much lower than that now existing in Ceylon.

Population Structure

Figure 24 shows the structure of three of the herds found in the Gal Oya area, classified according to size class, and Figure 25 the total for these three. There is definite variability between the three groups as to the proportions of the various size classes in each of the herds, but on the average there is a relatively high proportion of adult animals, i.e., females of size class 6 or larger and males of size class 8 and 9. These size classes, which are all that can be determined in the field, are not indicators of age classes (p. 10). Thus, size class 1 contains infants which are still suckling and are probably less than one year of age, whereas size class 4, for example, contains individuals which are probably between 3 and 5 years of age, and size class 5, individuals between 5 and 7 years old for males and 5 to 10 years old for females.

It is possible to treat these data in two ways. The first would be to rearrange the size classes into approximate age classes according to the data presented earlier (p. 10). This would then require combining the first four size classes as representing ages 0 to 5 years and size classes 5 and 6 for females and class 5 for males to give the next 5-year interval. Beyond this point, however, such rearrangement of the data to provide a 5-year interval would require the splitting of size classes as the size classes 7 through 9 include animals of age classes of more than 5 years. Using this method we can see that for this sample of the total population of 181 individuals, 45 would fall between the ages of 0 and 5 years and approximately 25 would be between 5 and 10 years.

A more useful method is to compare the numbers of adults, juveniles, and infants. Figure 26 shows the results of making these divisions. In each herd, as well as in each of the total populations, the number of adults is always greater than the number of juveniles which in turn is always greater than the number of infants, although the total of juvenile and infant animals may be greater than the total number of adults. For most groups, however, the ratio of adults to young is approximately 1:1.

As far as can be determined, the sex ratios among infant and juvenile animals are approximately 1:1. The sex ratios of adults, however, vary considerably. Table 4 shows the sex ratios of adults from known areas: thus, for example, the Hatpata herd contains 33 adult females whereas 14 adult males are known to be resident in the area encompassed by the range of the herd. The ratio then is 39 males to 100 females. Similarly the ratios for the other sectors of the study area are for the western savanna area 20 to 25 males per 100 females; for the Amparai area 50 males per 100 females; and for Lahugala 40 males per 100 females. The sex ratios of juveniles as mentioned earlier are approximately equal but there is a relative scarcity of subadult males. It would thus appear that the difference in sex ratios observed among adults might be caused either by a high mortality among subadult males or by

Table 4.—*Sex ratios of adult elephants in four regions*

Region	*Adult* ♂	*Adult* ♀	*Ratio* ♂:100 ♀
Hatpata	14	33	39
Western Sector	6	25–30	20–25
Amparai	11	22	50
Lahugala	20	50	40

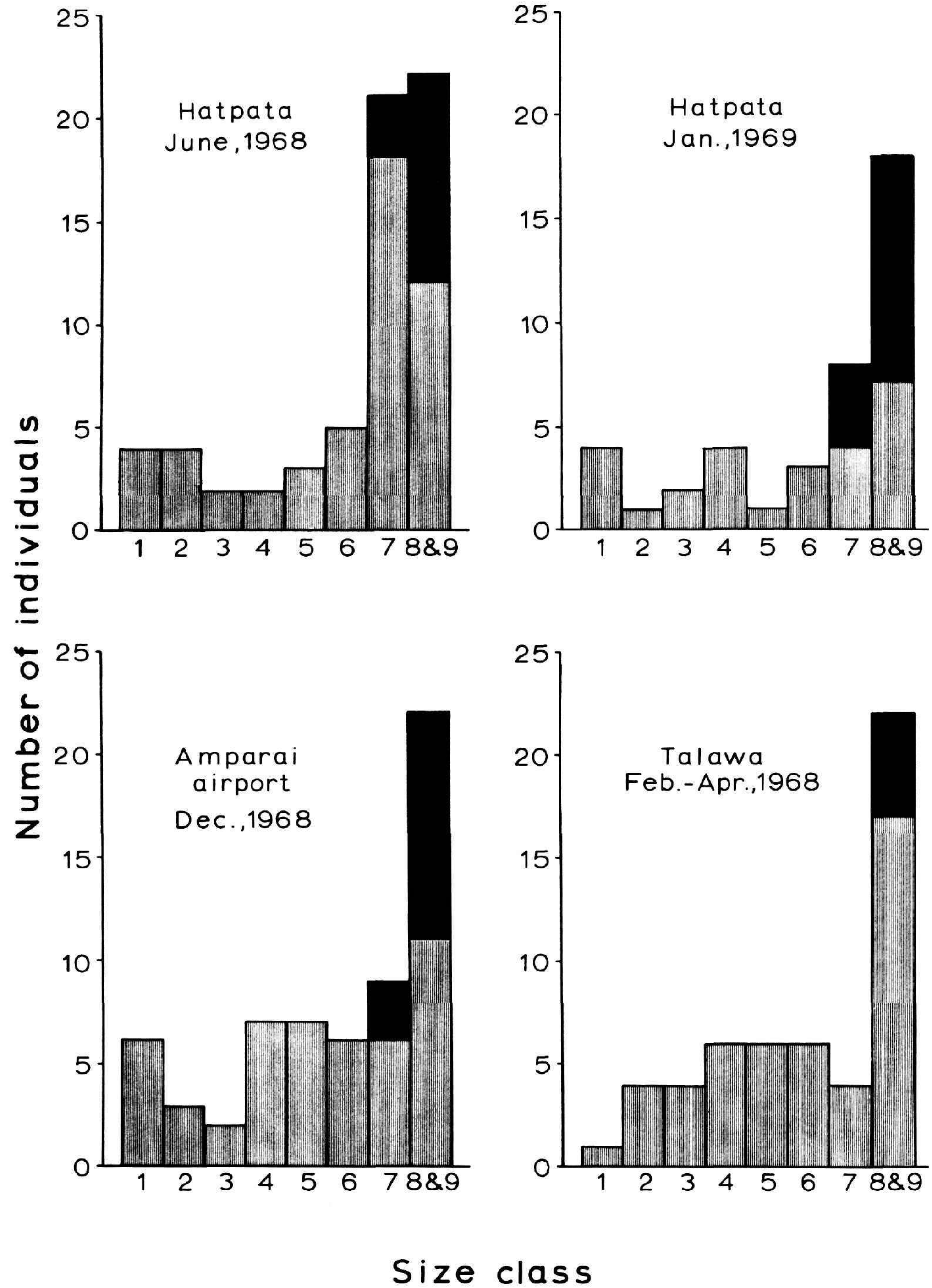


FIGURE 24.—Size class distribution for three herds in the Gal Oya population. Black=adult males.

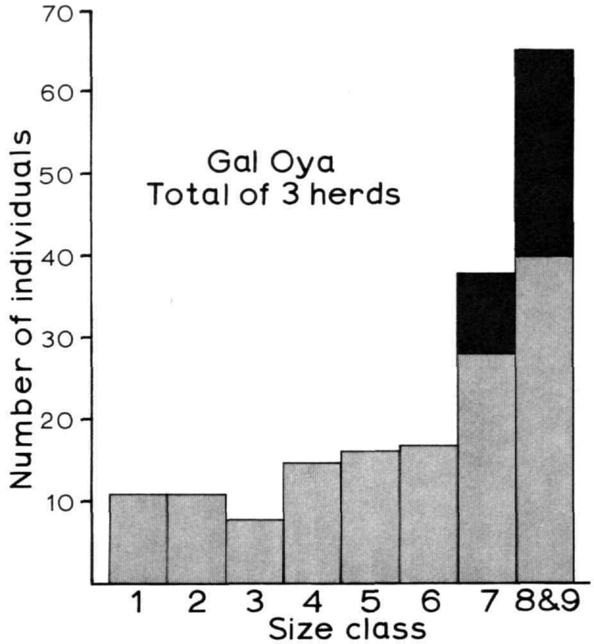


FIGURE 25.—Size class distribution of the elephant population in the Gal Oya region. Black=males.

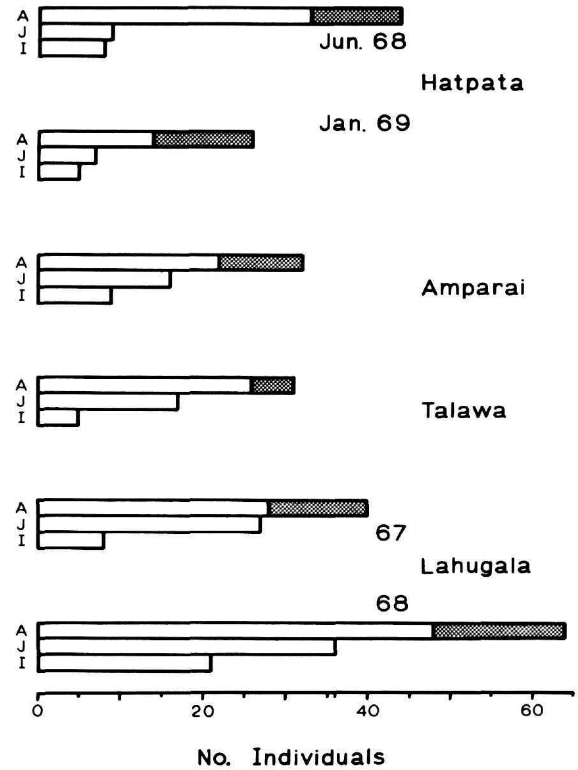


FIGURE 26.—Histogram showing frequencies of the three major age-groups (adult, juvenile, infant) in the elephant populations of eastern Ceylon. Shaded areas=adult males.

dispersion of animals in this age class. There is some evidence for a high degree of dispersion among subadult males (p. 85), but the lack of observations of these animals in the areas covered would indicate a higher mortality of animals in this age class. It would appear likely that a young male recently separated from the herd would be vulnerable not only to aggressive attack by other males through whose home ranges he was traveling but also to accidents and to being shot by cultivators. Unfortunately, we have very little data to support these hypotheses.

The data from Lahugala (Figure 27) show a similar trend to that observed in Gal Oya. The relative proportions of adults, juveniles, and infants are approximately the same as the totals observed in Gal Oya, although the proportions of infants would appear to be somewhat higher. The sex ratio of adults at Lahugala is approximately the same as that for the Gal Oya area. Figure 28 shows the breakdown of data obtained in 1967 in Ruhunu National Park (Blocks 1 and 2) and again the trend is relatively close to those of the preceding two areas except that the relative proportion of infants is much lower while the proportion of adults and juveniles remain approximately the same as do the sex ratios of adults.

Eisenberg and Lockhart (1972) report a similar age structure and sex ratio but comparable data from mainland Asia are not available.

The only data of a comparable nature from studies of the African elephant are those of Laws (1969b). He (1969b: 520-521) gives age and sex compositions for four populations within Tsavo National Park, Kenya, and for three other areas. Although the sex ratios vary between these populations there is a consistent pattern of a lower number of males than females above age 30, although the sex ratios of the age group 20–30 are near equality. Whether this difference is due to an actual difference in numbers or to male groups not counted in the surveys for one reason or another is not explained by the author.

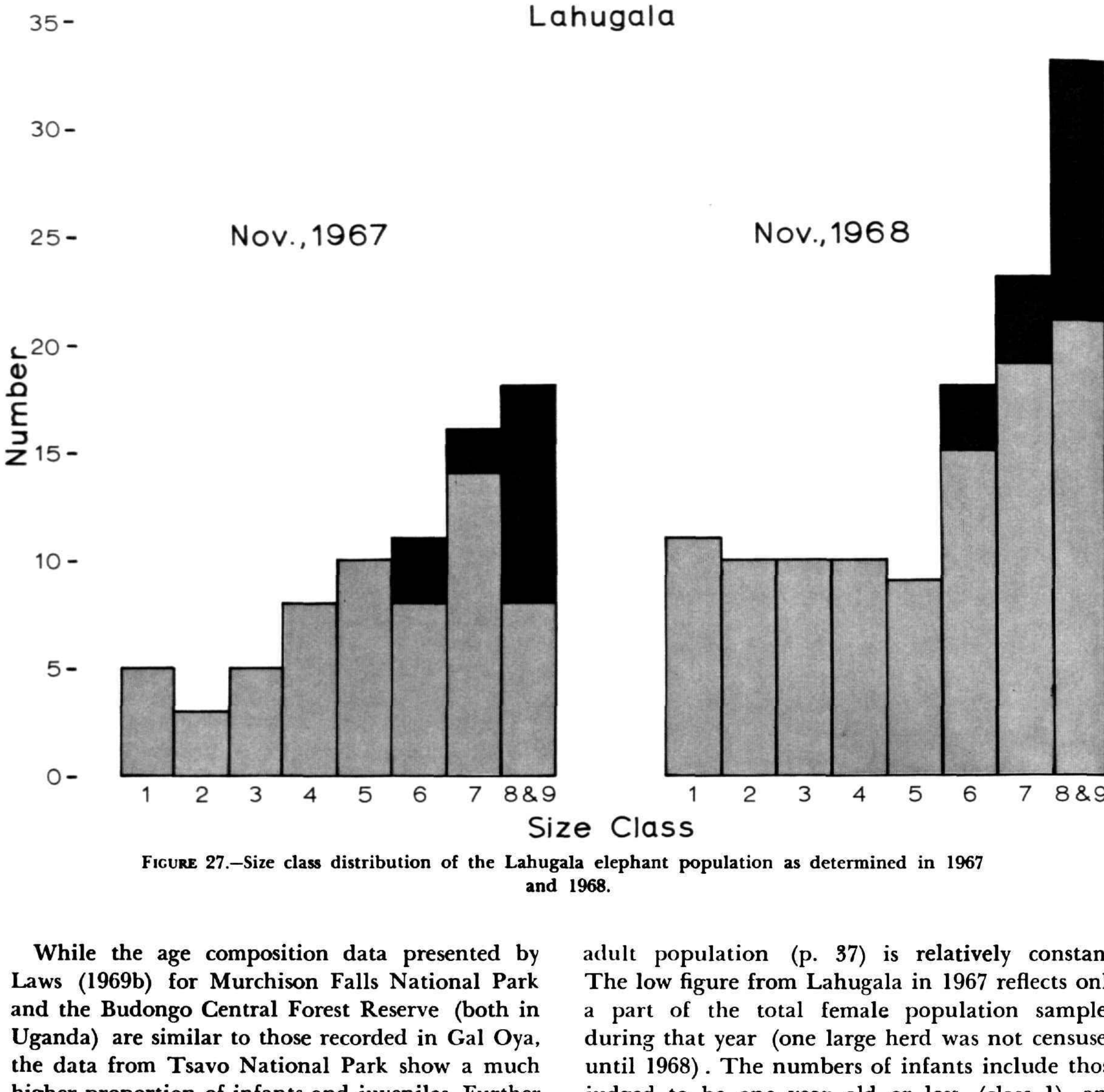


FIGURE 27.—Size class distribution of the Lahugala elephant population as determined in 1967 and 1968.

While the age composition data presented by Laws (1969b) for Murchison Falls National Park and the Budongo Central Forest Reserve (both in Uganda) are similar to those recorded in Gal Oya, the data from Tsavo National Park show a much higher proportion of infants and juveniles. Further discussion of these data relative to my own will be made in the following section as they present a valuable comparison of recruitment rates.

NATALITY

Table 5 shows the birth rates and birth intervals for three segments of the Gal Oya population during 1968 and for the Lahugala population in 1967 and 1968. The percentage of females in the adult population (p. 37) is relatively constant. The low figure from Lahugala in 1967 reflects only a part of the total female population sampled during that year (one large herd was not censused until 1968). The numbers of infants include those judged to be one year old or less (class 1) and those judged to be between one and two years old (class 2). Thus the percentage of adult females who gave birth to infants during the year preceding the actual census is only a crude estimate.

The percentages of females with young are quite variable. The factors which may be involved in causing these differences include: (1) annual seasonality in births, (2) synchronization at an interval longer than one year (thus producing a high number one year and low numbers for the

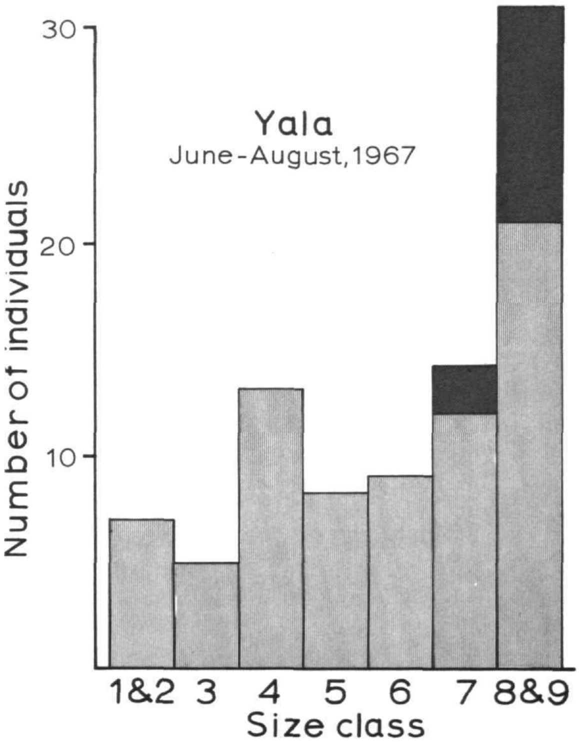


FIGURE 28.—Size class distribution of the Ruhunu National Park (Yala) elephant population in 1967.

next one or two years), (3) differences in mortality among infants, and (4) differences in mean-birth intervals between populations. Age of females at puberty can be eliminated as a potential factor since my definition of an adult was based on observable development, especially of the mammae, not strictly on size. Exact data which might point to one of these factors or a combination of two or more are unfortunately not available. This is in part due to the small sample size (compared to samples available to such workers as Laws (1969a) and in part to the duration of the study, two complete annual cycles. It is not possible to state whether there is any seasonality of births or of mating, as observed in *Loxodonta* by Hanks (1969) and others. Newborn infants were observed on only two occasions, November 1968 and January 1969. Copulation was observed only in November 1967. Interactions between animals from which it was inferred that one or more females might be in estrus were observed in March 1968, June 1968, October 1968, and in January 1969. With such sparse data I can only conclude, as did Eisenberg and Lockhart (1972) for Wilpattu, that there is no evidence for seasonality.

The numbers of infants in size class 2 would indicate that there is a distinct possibility for longer term synchronization (shown by Laws (1969a) for *Loxodonta*) or for differences in infant mortality. For example the Hatpata subpopulation and the Lahugala population show approximately equal numbers of older infants and younger ones, while the Amparai subpopulation had a larger number of younger infants, and the Talawa (western sector of the Gal Oya National Park) subpopulation, a larger number of infants one year or more. While these data indicate that one or the other factor may

TABLE 5.—*Estimates of birth rates and birth intervals*

	Gal Oya 1968			*Lahugala*	
	Hatpata (June)	*Amparai (Dec.)*	*Talawa (June)*	*1967 Nov.*	*1968 Nov.*
Total adults	47	33	32	48	68
Total adult females	33	22	26	28	48
% females (2)/(1) x 100%	70.3	66.7	81.3	58.3	70.6
Total infants <1 year (class 1)	4	6	1	5	11
Total infants 1–2 years (class 2)	4	3	4	3	10
Infants per 100 females	12	27	4	18	25
Calculated birth intervals (to nearest 0.5 year) assuming:					
no mortality	8*	4*	25	5	4*
33% mortality	5*	2.5*	16	4	2.5*
50% mortality	4	2	12	2.5	2
67% mortality	2.5	–	8	–	–

*Most reliable data.

be involved they do not provide any means of deciding which one.

In order to separate these two factors it would be necessary to know the absolute rate of mortality for each cohort of infants. In order to obtain such data it would be necessary either to census each population over a number of years or to follow all of the populations at short intervals throughout the two years of the study. In practice neither was possible for all of the populations. Detailed counts of the Hatpata and Amparai populations were made at short intervals and no infants were reported missing for the groups studied during 1968 and 1969. This would tend to indicate that for these two groups at least infant mortality is either very low or occurs during the first few weeks of life and that for the Amparai group at least there appears to be some synchronization on a cycle of at least two years. The Lahugala data also indicate that infant mortality is low, but there is either no apparent long-term synchrony or a long-term trend, only part of whose cycle was followed.

The final factor that can be examined is that of birth interval. As any calculation of birth intervals depends upon the assumptions about mortality and synchronization, it is reduced virtually to the point of speculation. Speculation, however, is worth making if only to emphasize the need for longer term studies. Based on the assumptions made above I have calculated (Table 5) a set of possible birth intervals. For the three populations with the best data available the most likely estimates are marked with an asterisk. If these assumptions are correct, it would appear that the Amparai and Lahugala groups are similar and have a relatively short mean-birth interval, while the Hatpata group has a longer one. The Talawa group presents an interesting possibility in that it must have either a very high infant mortality, a very long mean birth interval, a strong synchronization, or a combination of two or more. Whichever factor is in operation here, it is obvious that this subpopulation has a very much lower recruitment rate than any of the others.

Buechner, et al. (1963) and Buss and Savidge (1966) report data on the recruitment rates of elephants in Murchison Falls National Park, Uganda, from 1957 to 1964. They report average frequencies of infants around 8–9 percent of the total population. Assuming an adult sex ratio of 1:1 this would correspond roughly to 15–20 percent of the female population, a figure comparable to my 1967 data from Hatpata and Lahugala. Laws' (1969b) data from Murchison Falls and Budongo are approximately equivalent but data from Tsavo indicate a higher percentage of infants. Laws (1969b) concludes that there has been a steady decline in recruitment in the Uganda populations, a trend first noticed by Buss and Savidge (1966), but that some portions of the Tsavo population have continued to increase the recruitment rate. This latter trend Laws attributes mostly to the suppression of hunting. He also concludes that there is some self-regulatory cycle in the recruitment rates which account for his observations of unequal recruitment between successive cohorts. Like Buss and Savidge (1966), he (Laws, 1969b) concludes that this regulatory mechanism is density dependent but that it may well be mediated by the effects that the elephants have on their environment.

How these conclusions, based on many years of observations of large populations in East Africa, relate to the phenomena occurring in the much smaller populations of Ceylon is, at the moment, not apparent. The densities of the various subpopulations I studied (see pp. 96–97) are roughly equivalent. All groups are subject to at least some harassment and shooting by man. The most parsimonious conclusion at this time would be that with such small sample sizes, any one factor, operating over even a short period of time, might produce an apparently large effect on the recruitment of any of these populations. Thus the only way it will be possible to state with any precision what the actual status of recruitment is in these populations is to collect data over a period long enough to eliminate such short-term vagaries.

Mortality

Data on mortality are also extremely sparse (Table 6). The records from October 1966 to September 1967 were provided by the Game Ranger, Mr. Bevis Ekanayake, and indicate seven animals known to have died in his area during that period. I examined a further seven which died between September 1967 and November 1968. Of the 14 from the Gal Oya, only one was an infant, the rest were adults. These 14 deaths throughout a 2-year period can be taken as an absolute minimum estimate of the total mortality in the area. It is extremely likely that the mortality is much higher than this but as elephants that die away from cultivated areas are located only by chance, it is impossible to make an estimate of the upper limit for the rate of mortality. The structure of various size classes (Figure 25) would tend to indicate that there is a certain amount of mortality in the first 10 years of life, if one can assume that the birth rate is relatively even each year. If such an assumption concerning the birth rate can be made, it would appear that the mortality during these first 10 years of life might be as high as 2 to 3 individuals per year for the entire Gal Oya population. The causes of death are various but the majority in this area are the result of gunshot injuries (Table 6).

TABLE 6.—*Known mortality of elephants in the Gal Oya region 1966–1969*

Date	*Location*	*Sex/Age*	*Cause of death*
Oct. 66 –Sept. 67*	Gal Oya range	1 ?	Killed in self-defense
		1 ?	Gunshot injuries
		1 ?	"Apparently natural causes"
		4 ?	Unknown
Sept. 67	Nilgala	♂ A	Shot and killed by cultivator
Nov. 67	Paragahakelle	♂ A	Shot and killed by cultivator
Aug. 68	Inginiyagala	♀ A	Septic gunshot wound on leg
Aug. 68	Mahakandiya	♀ A	Multiple gunshot wounds
Sept. 68	Namal Oya	♂ I	Noosed—apparently died after capture from lack of water and/or food.
Oct. 68	Kossapola	♀ A	Unknown
Oct. 68	Ambalam Oya	♂ A	Multiple gunshot wounds

*Data provided by Mr. B. Ekanayake, Game Ranger, Inginiyagala.
? = Sex and age not recorded.

There is definite evidence of sex-specific differences in mortality as reflected in the low adult sex ratio. This has certain consequences for the social organization of the elephant (pp. 81–85). Laws (1969b) presents a survivorship curve for the Tsavo population in East Africa. He describes a fairly high mortality rate over the first 3 years followed by a fairly low rate until age 30 for males and 50 for females. The sex difference in mortality in older animals is similar to that inferred for the Ceylon populations. A lack of comparable data in the form of elephant carcasses makes any further comparison with Laws' data impossible.

Behavior Patterns

LOCOMOTION

The elephant is capable of moving either extremely slowly or quite rapidly. At whatever speed it is traveling, however, the gait is a modification of one basic gait, the rack or pace (Muybridge, 1899). In this gait, the sequence of movement of the legs is left hind, left fore; right hind, right fore. In a single stride at a slow walk, the left hind foot is raised as the right forefoot, ending the previous stride, is being placed on the ground. As the left hind foot is moved forward, the other three feet are firmly on the ground. At the same time as the left hind foot is being placed on the ground, the left forefoot is lifted. As the left forefoot moves forward, the remaining three feet again are on the ground. With the placement of the left forefoot on the ground at the end of its forward swing, the right hind foot is raised and the pattern is repeated on the other side completing the stride. In this way, three feet are on the ground for most of the stride; one foot being off the ground for a short period and two feet off the ground only for an extremely short period.

At a faster walk the forefoot is raised at the same time as the ipsilateral hind foot is being brought forward so that two feet only are in contact with the ground for a longer period of time. During the slow walk, the body and the head of the animal remain relatively stable, but during a fast walk there is a marked rolling motion of the body as the center of gravity shifts from one side to the other, accompanied by a definite bobbing of the head. This lateral motion of the body and bobbing of the head increase in amplitude as the speed of movement increases, and are extremely marked in an animal running at a fast pace.

If the animal is feeding at the same time as it is moving, the slow walk is generally used; an animal moving without feeding generally travels at a fast walk. In both the slow walk and the fast walk, the position of the trunk and tail are quite variable.

Infant and juvenile animals quite frequently move at faster speeds than the walk, i.e., when playing, chasing each other, etc., and at these times the trunk is generally held up and the tail is also arched upward. Fast movement by adult animals was observed only in cases of flight and attack. In these instances the tail is held arched upward and the position of the trunk varies, being held upward in the sigmoid pattern during flight but curled ventrally under the chin during attack. When running both adults and juveniles seem to show more arching of the back than is observed during slower locomotion.

Throughout many parts of the Gal Oya area the terrain is quite steep and rough with many large boulders. In general the elephants tend to move about in such areas along well-defined trails where it is possible for them to walk at a normal pace with a normal gait. Elephants have, however, been observed to climb relatively steep rocky areas and, in such instances, when ascending, they will occasionally make use of the elbows of the forelegs; and when descending will drop to the knees of the hind legs. In this manner, they are, when necessary, able to negotiate areas which at first sight would appear to be impossible for an animal of such large size and weight.

Elephants are quite capable of swimming and do so readily. On 7 April 1967, for example, three females were observed feeding on an island in the Senanayake Samudra at 1615 hours. At 1805 the same three were feeding on a smaller island about 50 m away from the island on which they were previously observed. As we approached in a boat, the three reacted to our presence when we were 100 m distant, moved to the side of the island closest to the first island, entered the water and swam across to the larger island where they entered the forest and passed out of sight. They covered the distance of approximately 50 m between the two islands in about 3 minutes. During this short swim we were able to maneuver our boat quite close to the animals (15–20 m) and it was possible to see that the bodies of the animals were moving with approximately the same rolling motion as would be present at a fast walk or run. Throughout the swim most of the animals' bodies remained subberged; only the tops of the heads and trunk tips being above the water.

On 9 October 1967, a herd of 28 elephants, observed by myself and Dr. Nettasinghe, were feeding on the point of land separating the Sellaka Oya arm of the Senanayake Samudra from the Kossapola arm. At 1645 hours the herd divided into two sections; a group of eleven moving off to the southeast, the remainder moving eastward toward the edge of the water. By 1658 all of the animals under observation had disappeared from sight behind an island which lay between our position and the elephants. At 1747 hours, however, one elephant appeared on land from behind the island and entered the water. At 1759 six animals emerged from the water on the near side of the arm, that is to say, the Hatpata side and by 1802 hours 14 animals had emerged from the water. Under the conditions of low water at that time, the distance covered by the animals in the water was a minimum of 200–250 m. Assuming that the rest of the herd entered the water at approximately the same time as the one that was observed to enter the water, this swim took a minimum of 12 minutes. It would, however, be more reasonable to assume that the animal observed entering the water was the last one to do so and that the length of time necessary for the swim was probably more in the order of 20 minutes or more.

Swimming is apparently common with the Asiatic elephant and is very well described by Sanderson (1878). There has, however, been considerable debate in the literature concerning the swimming ability of *Loxodonta*. Verheyen (1954) and Bourliére and Verschuren (1960) state that it cannot, but Dekeyser (1955) and Sikes (1971) have produced sufficient evidence to correct this misconception.

Resting and Sleeping

Adult elephants in the wild generally rest in a standing position. Under field conditions, it is impossible to determine whether the animals are actually asleep during these rest periods, so for purposes of this discussion, they will be considered as resting. An adult elephant may rest either standing free or touching some object such as a rock or tree. If the animal is standing free, it generally spends most of the rest period standing on all four legs with the tip of the trunk resting on the ground. Occasionally, however, one leg will be lifted slightly from the ground, and on two occasions animals were observed to alternate between lifting a hind leg and a foreleg. Occasionally these periods of resting may be accompanied by a slight bobbing of the head and body. The bobbing movement includes a lateral component and is very similar to the pattern commonly called "weaving" by keepers of captive animals. The rhythmic movements are not so pronounced as those shown by captives, and the swinging of the trunk which so frequently accompanies weaving in captives is not shown by wild elephants. When resting in contact with an object such as tree or rock, the elephant may lean against this object with its back or hind quarters or it may extend the trunk or even the chin over a low branch or over the rock.

In sitting or lying down, the elephant first goes down on the hind quarters, the forelegs being stiffly extended. The forelegs are then flexed to bring the animal to rest on its belly and elbows after which the animal then lies down onto one side. When lying asleep, the legs are generally extended and the trunk may or may not be curled inward as described by Benedict (1936) and Kurt (1960). Infant and small juvenile elephants frequently lie down to sleep for short periods but, in large juveniles and adults, lying down was infrequently observed. One male in Ruhunu National Park was observed, however, to lie down for periods varying between 20 and 75 minutes between 30 June and 8 July 1967. He rested each day in the same place on the large plain surrounding Buttuwa Lagoon. These rest periods took place in the mid-afternoon between 1400 hours and 1700 hours, and resting occurred always within a mud wallow which was used both by the elephants and by water buffalo. Adults were also observed on a few occasions to sit and rest on the elbows or even lie down completely while bathing and drinking in tanks. In these instances, however, the period of actual lying down was very short, usually less than 5 minutes. Juveniles and infants regularly lie down in shallow water when bathing.

Feeding

In feeding the elephant uses primarily the trunk, especially the terminal portion, although there may be varying amounts of usage of the feet and mouth in reducing foodstuffs to a suitable size. The patterns which the elephants show vary depending upon the type of plant being fed upon at the moment.

Grasses

The simplest pattern is that shown when elephants are feeding on grasses and other herbaceous matter of a length between 5 and 75 centimeters. When feeding on herbs of this length, the terminal 25 to 35 centimeters of the trunk (the "hand") is used to grasp a number of stems, curling around them. The stems are then pulled, generally vertically but with a slight lateral component, and put directly into the mouth. With slightly longer grasses such as those which grow in wet areas, the grasping and pulling is followed by a swinging motion in which the grass is held in the "hand" of the trunk, and the trunk is held slightly forward and swung from side to side several times. This pattern was shown mostly by animals feeding in marshy or swampy areas. After anywhere from three to ten such swings, the grass is then placed into the mouth. Roots may be bitten off and expelled, although this does not necessarily occur.

When feeding on grasses which are shorter than about 5–7 centimeters, the elephant does not seem to be able to grasp and pull with the trunk alone. In feeding on this type of material, the first action is a forward kick with forefoot which acts to scrape the surface of the ground, generally to a depth of no more than 5 to 10 millimeters. This scarifying action removes the grasses, including a certain percentage of the rhizomes, from the soil, forming a loose pile. After an area of about 0.1 square meters has been cleared in this manner, the end of the trunk is used to sweep and gather together this loose pile of grass. In this sweeping motion, the "hand" of the trunk is laid flat on the ground and curled ventrally as it is dragged across the ground. This clump of grass so formed is then picked up or gathered in the "hand" and may be either bounced on the ground several times or grasped more firmly and rubbed against one of the forelegs before being inserted into the mouth.

Shrubs

When feeding on twigs and small branches, the end of the trunk is used to grasp a twig, which is then pulled with a short, rapid, jerking motion that generally is sufficient to remove it from the larger branch. If larger branches are removed from a tree or shrub, they may occasionally be twisted in order to remove them. Usually the elephant removes from a shrub or tree a small twig, which is then placed directly into the mouth. If, however, a larger branch is removed, it is dropped and may be held with one forefoot while smaller twigs are removed from it with the trunk. Elephants occasionally feed on the bark of certain tree species, such as *Feronia*. When feeding on bark, a large branch is broken off from the tree and held on the ground with one foot while smaller portions of the branch are broken off using the trunk. These smaller sections are then grasped in the trunk, inserted in the mouth, and, by a turning motion of the trunk tip, are turned either between the molars or against a tush which serves to strip the bark from the branch. It is interesting to note that this stripping action involves rotation of the branch against the parallel transverse ridges of the molars. Richard Van Gelder (pers. comm.) of the American Museum of Natural History has informed me that *Loxodonta* uses a lateral pulling motion rather than the rotation of *Elephas,* apparently pulling the bark over the anteriorly projecting ridges on the lophs of the teeth.

When feeding from trees or bushes, it is usual for the elephant to remove either small twigs or one or more large branches, leaving the main stem of the tree untouched. Occasionally, however, trees are pushed over or perhaps pulled over. No instance of this type of behavior was actually observed, so it is not possible to say which of the two techniques is used. According to Hendricks (1971) the African elephant generally pushes the tree over using the forehead.

When feeding on certain types of very low growing shrubs, such as *Acacia eburnea,* which have very long spines projecting horizontally from the stem, the elephant first curls the trunk around the stem and, with a rapid upward motion of this curled trunk tip, breaks all of the spines without actually removing them and without removing any of the leaves. These spines can often be recovered, entire, from the feces (p. 93). After this stripping action has been performed, the stem is then grasped and jerked free from the soil. If the jerking motion fails to free the stem, then the stem will be grasped in the trunk and then kicked closer to the ground by one forefoot, thus disloding it. The stem is then placed whole into the mouth.

One interesting feature of feeding behavior in *Elephas* is the use of the forefeet in holding branches and twigs while removing smaller portions. According to Sikes (1971:76–78) this pattern is not displayed by *Loxodonta.* Rather, *Loxodonta* makes extensive use of the tusks along with the trunk to remove small portions of branches. I was unfortunately not able to obtain sufficient observations on feeding by tuskers in Ceylon to determine whether they followed the pattern shown by *Loxodonta* or that of tuskless *Elephas.* My few observations from two individuals would tend to indicate the latter is the case.

Drinking and Bathing

Although drinking and bathing are not necessarily related as functional categories of behavior, they are included together in this discussion as they often tend to occur simultaneously. When drinking, the elephant sucks water into the trunk then raises the trunk inserting the trunk tip into the mouth, accompanied by a slight raising of the head as shown in Figure 29. This allows the water to drain into the throat. Young elephants generally tend to drink in the same manner as adults, although on a few occasions juveniles, estimated to be about 5 years old, were observed to immerse themselves up to the level of the mouth and drink directly without any involvement of the trunk. When drinking and bathing occur during the same visit to water, drinking generally precedes bathing.

Elephants may drink from small bodies of water, such as pools in the ground or in crevices in rocks, or larger more permanent water sources such as streams, rivers, and man-made reservoirs. The elephant stands either at the edge of the water or in shallow water. Although surface water is generally used for drinking, there are times during extreme drought when surface water is not available in many areas. At such times elephants frequently tend to concentrate around particular sections of streams which have a sandy bed. The elephants then dig holes in the sand in order to reach the sub-surface water which remains in such pockets. The holes in the sand are excavated by a forward

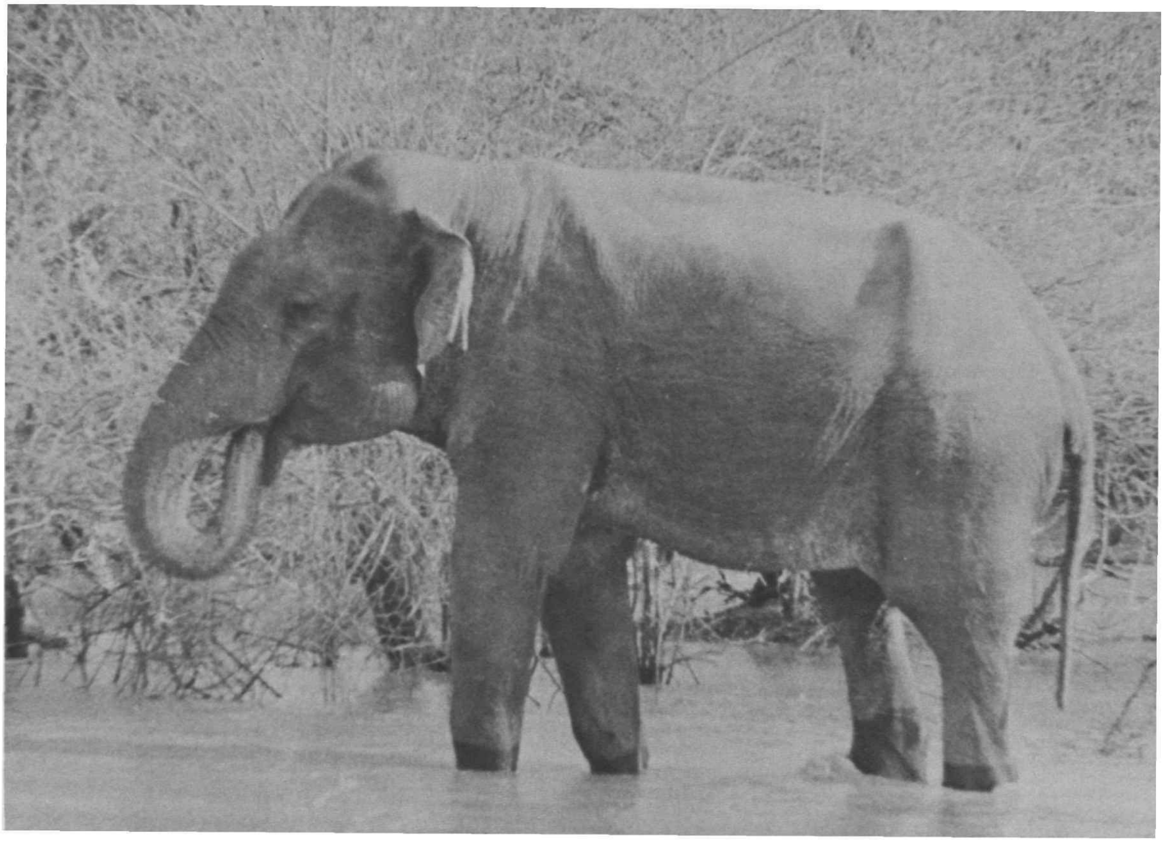


FIGURE 29.—Photograph of male elephant drinking, showing typical posture of head and trunk.

kicking movement of the forefoot which results in the formation of a hole with one sloping side and one steep side, as figured by Tennent (1867). The shape of the hole is a result of the means of digging rather than any attempt by the elephant to prevent caving in of the walls as postulated by Tennent.

Elephants appear to have traditional drinking spots, both water holes and sandy stream beds (p. 85). When bathing an elephant sucks water into the trunk in the same manner as when drinking and then sprays the water onto the body. In spraying the water, the trunk is swung forward slightly, then swung backward either laterally, ventrally, or vertically over the top of the head, releasing the water in a spray over the body. There does not appear to be any general pattern or order of spraying the various parts of the body. Some individuals appear to spray the sides and ventrum and dorsum in rotation while others will spray first one side and then the other, then the belly, etc. Young elephants generally tend to bathe by immersing themselves totally rather than by spraying, frequently lying down and rolling in the shallower portions of waterholes and tanks. Occasionally an adult will be observed to lie down and roll in the water, although the occurrence of this is infrequent.

Tennent (1867) described elephants apparently regurgitating water and spraying it via the trunk onto the body. No instance was observed among wild elephants in Ceylon where water was sprayed other than when bathing at a water hole. At a government khedda conducted near Kakankote, Mysore, India, in January 1968, a number of elephants confined without water in the roping stockade were seen to perform a series of actions which appeared like those described by Tennent. Several animals, standing in a group in the center of the stockade were seen repeatedly placing the trunk tip into the mouth. Following removal of the trunk tip from the mouth they would swing the trunk in the typical manner of an animal bathing, releasing a spray of some liquid over the head and back.

Whether this action involves regurgitation as suggested by Tennent, is impossible to say from these observations. Other alternatives might be salivation or condensation of water in the trunk. Bannikov, et al. (1961:16) have suggested that the expanded nose of the Saiga (*Saiga tatarica*) may serve to condense water vapor. A similar mechanism might well occur in the elephant. In arid areas this would undoubtedly act to conserve water from exhaled air. Under conditions of extreme heat stress and lack of free water this condensate could then be used to help promote heat loss by spraying it on the body.

Mud-and-Dust Bathing and Rubbing

Besides bathing with water, elephants also frequently cover the body with mud or dry soil. Bathing with mud may occasionally take the form of wallowing or lying down and rolling in a mud hole. This pattern, however, was observed infrequently and only with solitary males, never with females or young. The more usual pattern is for the animal to collect mud with the trunk tip by curling the terminal portion of the trunk around a bolus of mud and then throwing it onto the body dorsally, ventrally, and laterally. A similar manner of collecting by curling up the trunk tip is used when throwing loose soil or dirt onto the body. In the latter case, the soil is generally loosened prior to collecting by the same kicking motion of the forefeet which is used in loosening short grasses. Covering of the body with mud generally appears to occur independently of bathing in water (either as an alternative to bathing in water or as a totally independent phenomenon). Covering the body with soil on the other hand appears to occur most frequently after bathing in water although frequently elephants are observed to cover themselves with dirt without having bathed immediately prior to this.

After bathing with either water, mud, or soil, elephants frequently rub the body against some object such as a tree or rock. A typical sequence is for an animal to leave the water hole after bathing, stand for a few minutes on the bank, cover the body with dirt, then move toward some tree in the general neighborhood of the water hole and proceed to rub against it. This pattern was observed frequently among males at Lahugala Tank where animals upon leaving the tank would generally dust bathe and rub against a tree before entering the forest.

In rubbing the animal generally approaches the tree frontally and commences to rub the forehead and trunk base against the stem of the tree, then rubbing the sides of the head and the neck, followed by rubbing of the sides of the body and lastly the rump and perineal region. If the tree should have a low branch or if a rock is used rather than a tree, the elephant will frequently also rub the chin. Certain trees appear to be used regularly and such trees as that shown in Figure 30 are obviously used extensively. The lower portions of these trees become covered with a layer of mud and the bark often tends to become smooth. Besides rubbing the skin against the tree, an elephant will often at the same time rub the tusks or tushes against the bark often producing the elongated gashes in the bark (Figure 30).

Occasionally trees are found with gash marks from tusks or tushes in the bark without any evidence of rubbing. Eisenberg and Lockhart (1972) have postulated that this may be a form of marking, particularly if the tree so marked were to have an odorous sap. Within the Gal Oya area, the two species of trees most frequently marked with gashes from tusks were *Pterocarpus marsupium* and *Careya arborea,* both of which have a sap that has a slight odor and for *Pterocarpus marsupium* a faint pink coloration. Regardless of the odor of the sap exuding from the wound in the tree, the odor of elephant is always present at such sites. How long the odor of elephant remains at such a rubbing site is unknown but on the 10th of September 1968 we followed the path of an elephant, apparently solitary, moving northward 2 miles south of the Gal Oya near Nilgala. This elephant had broken down 29 stems of *Terminalia chebula,* all within the 15–30 centimeters dbh class, and marked with the tusks a further 18 trees of the same size and species. There was, incidentally, no evidence of feeding from any of these trees. We guessed that

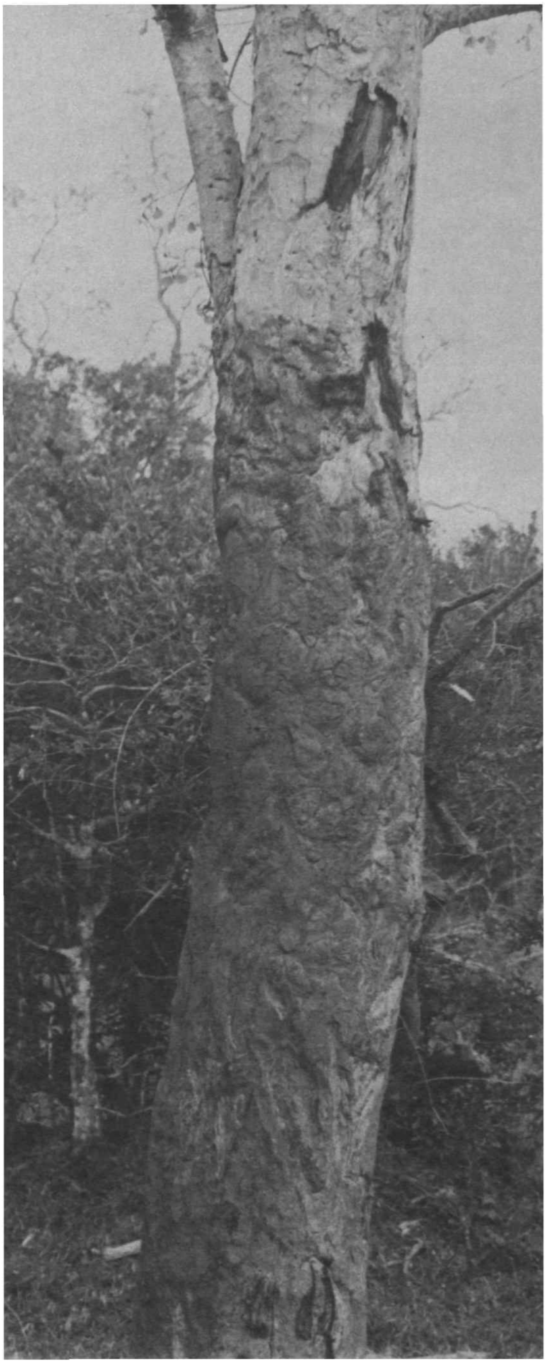


FIGURE 30.—Frequently used rubbing tree showing mudcovered area and gash-marks caused by tusks.

the probable cause of this activity was either displacement or redirected aggression after some disturbance (possibly by loggers who were working nearby) along a nearby road.

The condition of the leaves on the trees which had been killed and the condition of the pile of dung found along the trail indicated that this activity had occurred not less than one and not more than two days previously. The odor of elephant was distinctly noticeable on all of the affected trees.

Besides rubbing against objects, the elephant will also use its own trunk and tail to rub various parts of the body. The trunk tip is frequently curled and used to rub the region around the eyes and the region of the neck, throat, chin, and behind the ears. The tail is used to rub the perineal region and between the legs in the region of the external genitalia. Also one foot may be used to rub the contralateral foot. Although captive zoo elephants have been observed by the author to pick up objects such as sticks or twigs in the trunk and use them to rub the body, no instance of this was observed during field observations in the Gal Oya area. In all cases the various organs of the body were used directly or the body was rubbed against some stationary object.

DEFECATION AND URINATION

During both defecation and urination, the animal generally stands in a normal resting posture, although young animals were observed to squat occasionally upon urination and females often tend to spread the hind legs apart somewhat. This spreading of the hind legs was observed in a male only once. During defecation the tail is usually raised to a horizontal position. When a male urinates, the penis is partially erected to the point that the glans is directed backwards. In the female the clitoris may also be erected somewhat at urination. Urination may occur without defecation but a defecation is almost invariably followed by urination.

Elephants may frequently urinate and defecate when moving, leaving the feces and urine on the trail along which they have been moving. No evidence was found for any site specificity in either urinating or defecating but this does not in any way prove that the urine and feces are of no value to the elephant as a chemical signal. Whenever an animal approaches reasonably fresh urine or feces deposited by another elephant, it generally extends the trunk tip towards it. On several occasions males were observed, after extending the trunk towards the urine or feces of another elephant, to insert the trunk tip into the mouth. This action has been described by Eisenberg, McKay, and Jainudeen (1971) in the context of sexual behavior and it was concluded that this is probably, in part, homologous to the flehmen response of many other mammals.

Observations show that elephants generally defecate on the average of every one to 1½ hours or approximately 18 to 20 times per day. From 4 to 7 boluses are passed at one time, the average being 5. For an adult, each bolus may weigh between 1 and 3 kilograms upon deposition. A sample of 20 boluses from freshly deposited feces contained 45–75 percent water by weight.

Exploratory Behavior

Whenever elephants are moving and even when standing still, the trunk is generally constantly in motion. The trunk tip is frequently extended directly ahead of the animal and towards the ground as an animal moves along. In this way the elephant appears to be sampling its olfactory environment as it walks. Whenever the elephant encounters such objects as the feces of another elephant or even of other animals, or sign of man such as footprints, the trunk will be extended towards such objects.

At frequent intervals during locomotion the animal may stop and the trunk will be raised in a sigmoid curve, extended outward away from the animal and moved from side to side. This action appears to be analogous to the pattern of raising the head with a lateral movement shown by many other ungulates: in other words, a means of testing for potential scent in the wind. This pattern is frequently accompanied by an extension of the ears. When the elephant has apparently picked up some indication of the presence of man or some other species in the vicinity, the responses may include these latter components of the extension of the trunk and of the ears and may also include rotation of the entire body axis, as well as a variety of other responses. For further discussion of the responses of elephants to other animals including man see Muckenhirn and McKay (n.d.).

Small objects that the elephant encounters are frequently picked up with the end of the trunk and, especially with plant material that can be considered potential food, placed into the mouth before being discarded.

Flapping of the Ears

Based upon the observations of Kuhme (1963) made upon captive *Loxodonta*, it was postulated that elephants might be able to thermoregulate by means of inducing a flow of air over the ears. Frade (1955:757–758) has described the large veins and arteries connected by an extensive capillary bed for the ear pinna of *Loxodonta africana*. Although the pinna of *Elephas* is comparatively smaller with relation to body size, there is a comparably large supply of blood vessels. Examination of two recently dead elephants from Ceylon showed that the blood vessels of the ear lie particularly close to the skin on the inner or posterior surface of the pinna, the skin of the anterior surface being somewhat thicker.

Between 19–23 July 1967 and 12–19 December, observations were made on the ear-flapping rates of seven adult males and three subadult males at Lahugala Tank. The animals were observed through a telescope with a 25 magnification ocular lens and the number of flaps in a particular bout was recorded. An interval is measured from the last flap of a bout to the onset of the first flap of the next bout. The number of flaps in the bouts following the timed interval were subsequently recorded. Intervals were timed to the nearest 0.1 second using a stop-watch with an accuracy of ± 0.5 seconds. For each set of observations, 10 such combinations of bout-interval-bout were timed and the averages computed. Such data were recorded under varying conditions of overcast and wind velocity. Throughout all of the observations, the animals were feeding in the tank and were completely away from any potential shade. Under such conditions the concept of temperature in the shade is relatively meaningless and the relative amounts of heat stress to which the elephant is subjected will depend more on the amount of direct radiation from the sun and on the cooling effect of the wind.

The data obtained are shown in Appendix 2 and Figures 31 to 34. As shown by Figure 31, the number of fans of the ear in a bout preceding the measured interval approximately equaled the number in the bout immediately following that interval. Since this equation satisfies all observations, the first bout only will be considered in the presentation of subsequent data.

Figure 32 shows the relationships of the mean number of flaps per bout to the prevailing weather condition. During overcast conditions, the number of flaps per bout was greater in the absence of wind than with a light wind for both adults and subadults, although the difference was greater. Under sunny conditions, however, the number of flaps per bout was greater under a strong wind than under a light wind. As shown by Figure 33, the average interval between bouts of flapping was longer the higher the wind for both overcast and sunny conditions. For the two sets of observations where the wind velocity was classified as light (Force 1 on the Beaufort Scale), the interval between bouts of flapping was slightly longer with an overcast sky than with direct sunlight. Figure 34 shows a summary of the relationships between the number of flaps in a bout, the duration of the interval, and the varying weather conditions. As shown earlier the interval between bouts increases with increasing velocity of wind and decreases with the increased direct sunlight for any particular wind condition. The number of flaps in a bout, however, decreases with an increase in wind velocity and to a certain extent decreases with increase in direct sunlight, but this decrease occurs only up to a certain point. At the same time, the factors of increasing wind velocity and change in overcast or direct sunlight influence a change on the inter-bout interval and it appears that as the inter-bout interval gets longer, the number of flaps per bout increases slightly. The reason for this change is not apparent.

Under higher wind velocities the adult males tend to keep the ears extended during intervals between bouts of flapping. The subadult males did

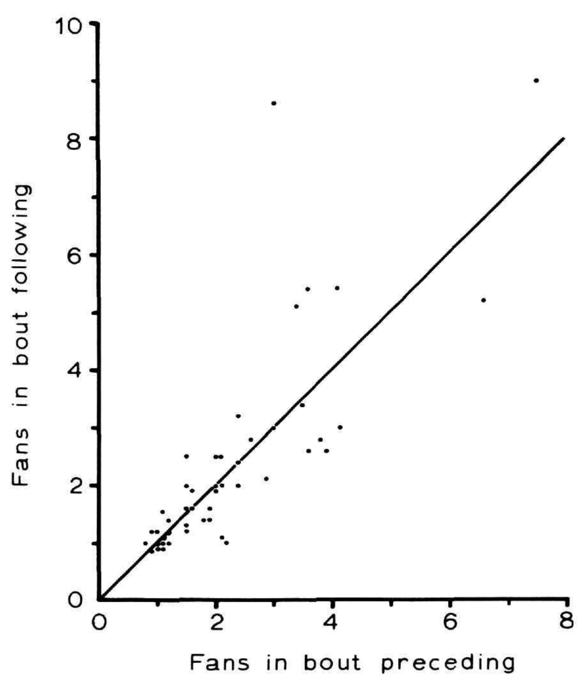


FIGURE 31.—Relationship between number of ear fans in bout preceding and following measured interval.

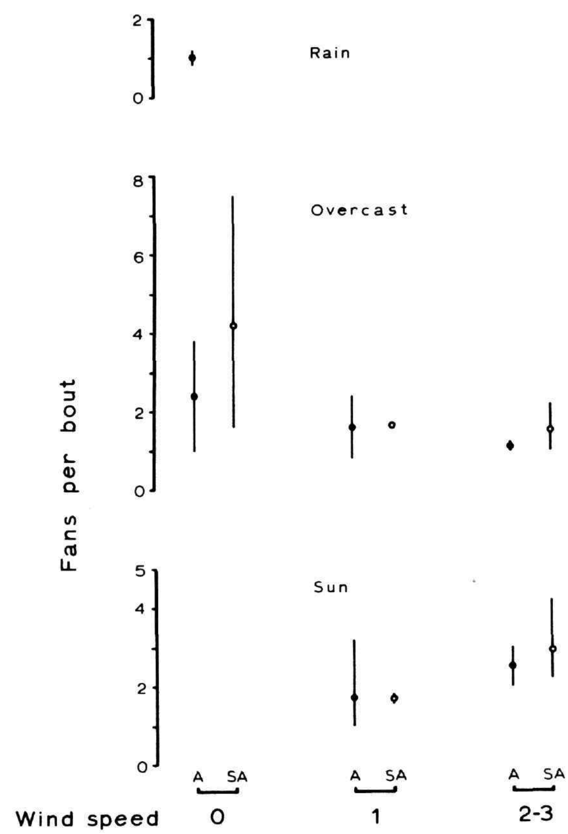


FIGURE 32.—Relationship of number of fans per bout to different conditions of wind velocity and overcast. A=adult; SA=subadult; wind speed on Beaufort scale; means and ranges indicated on graph.

not show this pattern. This pattern would definitely allow greater flow of air over the ear surface.

Thus a decrease in cloud cover or a decrease in wind velocity, both of which would tend to increase the stress of heat on an animal standing in the open, tend to result in an increase in the intensity of flapping of the ears. This increase in intensity could perhaps also be measured by timing the number of flaps per minute but the data collected would tend to indicate that the number of flaps in a bout and the intervals between bouts may be varied independently. Buss and Estes (1971, fig. 3) timed simple flapping rates (flaps/minute) for *Loxodonta*, which show a similar trend in that at higher temperatures some of the elephants kept their ears extended rather than increasing the flapping rate.

Thus it would appear that flapping of the ears does serve a thermoregulatory function and is not "merely a nervous reflex" as Benedict (1936:159) believed. Ear flapping is not, however, the only thermoregulatory device employed. Others include bathing with water (evaporation), mud, or soil (providing a layer of lighter colored dirt which will reflect more light energy than the elephant's black skin).

Another aspect that may be considered is ear flapping as a social signal. Kuhme (1963) considered that the social status of the individual affected its (thermoregulatory) ear-flapping rate. Since all but six observations of *Elephas* were made of solitary individuals the social status factor appears minimal. It would be interesting, however, to compare ear-flapping rates for animals at varying distances from their nearest neighbors, but unfortunately I did not record this information.

A further interesting observation is that on windy days the pattern of holding the ears extended was

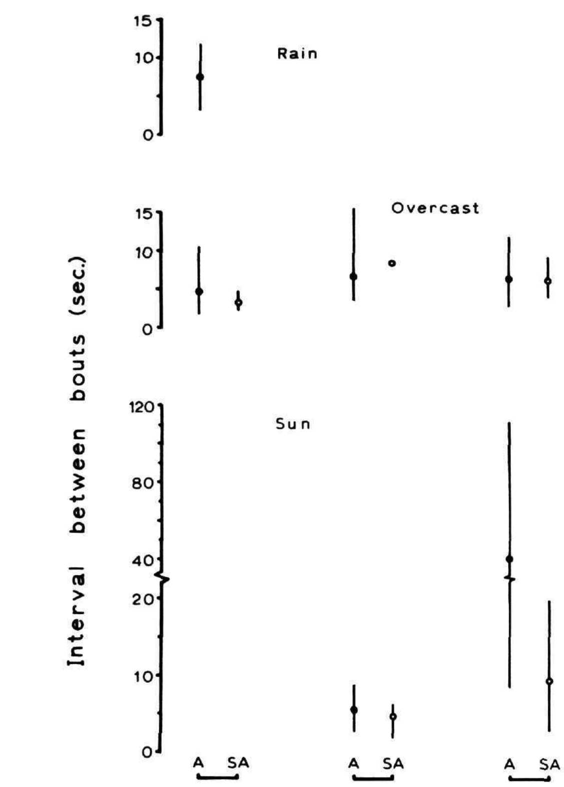


FIGURE 33.—Relationship of interval between bouts to varying conditions of wind velocity and overcast. See Figure 32 for meaning of symbols.

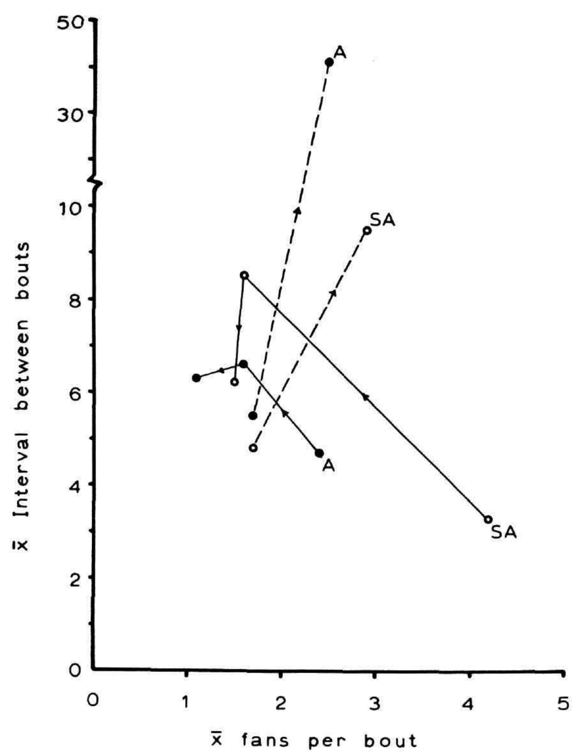


FIGURE 34.—Relationships between number of fans per bout and intervals between bouts. Solid lines=overcast conditions; dashed lines=sunny conditions; arrows=increasing wind speed; A=adult; SA=subadult.

displayed by adult males only, not by subadults. One might hypothesize from this that young animals who have not yet established a dominance order, or at least an "acquaintanceship" with all other males (p. 84) might refrain from using this pattern in thermoregulation as it might be "misinterpreted" as an aggressive gesture.

Short-term Activity Patterns

Several studies have been made of the activity patterns of both *Loxodonta* and *Elephas* in captivity. Kuhme (1963) reports on the activity patterns and cycles shown by three captive *Loxodonta.* He found that the three animals were distracted to a large degree by visitors to the zoo throughout the day and that social interactions were predominant around the early hours of the evening after visitors had departed. He also described the resting patterns of these three individuals including recumbent sleep, which occurred for periods varying from 3 to 7 hours throughout the night.

Benedict (1936:64–73) reports on the activity patterns of one particular female and several animals that belonged to circuses. He acknowledges that some of the data may be biased by the fact that these animals were used for performance and therefore their activity routine was somewhat artificial. Assuming, however, that the basic patterns were normal and would probably be displayed by animals in the wild, Benedict maintains that the elephant in the wild is probably nocturnal and that the diurnal cycle has been imposed upon the elephant by its captors. He also notes the sleeping patterns of animals in circuses, mentioning that they are generally fed after the last performance of the day at around 11.00 P.M. and, after feeding, then lie down to sleep.

Kurt (1960) also studied captive Asiatic elephants in circuses, with particular attention to the sleeping patterns. He found that the animals generally tended to lie down to sleep at one particular time and inferred that there was some social facilitation involved.

In considering the above data it should be remembered that much if not all of the routine of a captive animal is determined by its keepers rather than by its own biological clock. This is especially marked in relation to feeding where captive animals are generally presented with a relatively concentrated supply of food at one particular spot and often at the same time each day.

The Daily Activity Cycle

Times of Activity

Figure 35 summarizes the times of observation for all animals observed in the Gal Oya National Park region including the area of the Amparai Sanctuary. There are, however, two biases introduced in the data. The first bias is the activity pattern of the observer. In Ceylon dusk generally falls between 1815 hours and 1830 hours depending upon the season, and dawn comes between 0545 and 0600 hours. On a few occasions it was possible to obtain some data from animals that had been under observation prior to sunset for a further one to two hours but only a few attempts were made to locate animals prior to dawn. As a result the decrease in the number of observations after 1800 hours and the scarcity of observations prior to 0600 hours does not in any way reflect the activity of the elephants themselves. The other bias is the ease of observing elephants at a greater distance in open habitat, such as grassland surrounding tanks and in the savanna areas. As a result, the number of contacts made with elephants was greater for these open habitats than for forested areas. It is this bias which undoubtedly accounts for the relatively low frequency of observations around the midday hours, which on sunny days are the hottest hours, as the sun is very close to the zenith throughout much of the year.

Keeping these biases in mind, there is an interesting trend with regard to the times of observed activity of males and of female herds. The males tend to show one peak of activity around 0800 hours followed by a decline around noon with a second peak of activity between 1600 and 1700 hours. Female herds, on the other hand, tend to show a later peak in the morning around 1000 hours with a second small peak between 1300 and 1400 hours followed by a very large peak between 1530 and 1800 hours. When these data are compared to Figure 36, which shows a similar analysis for observations in Ruhunu National Park from April to October 1967 and January and February 1968, it can be seen that the males in Ruhunu National Park show a pattern very similar to those in Gal Oya National Park. Female herds in Ru-

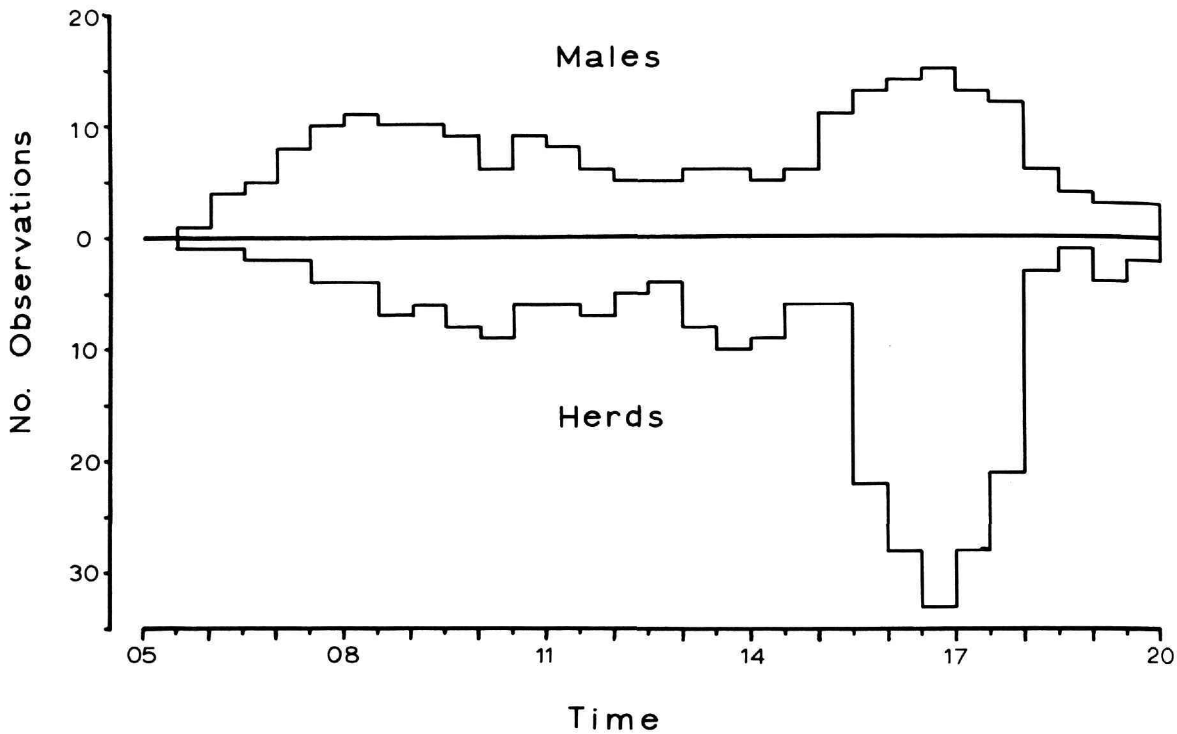
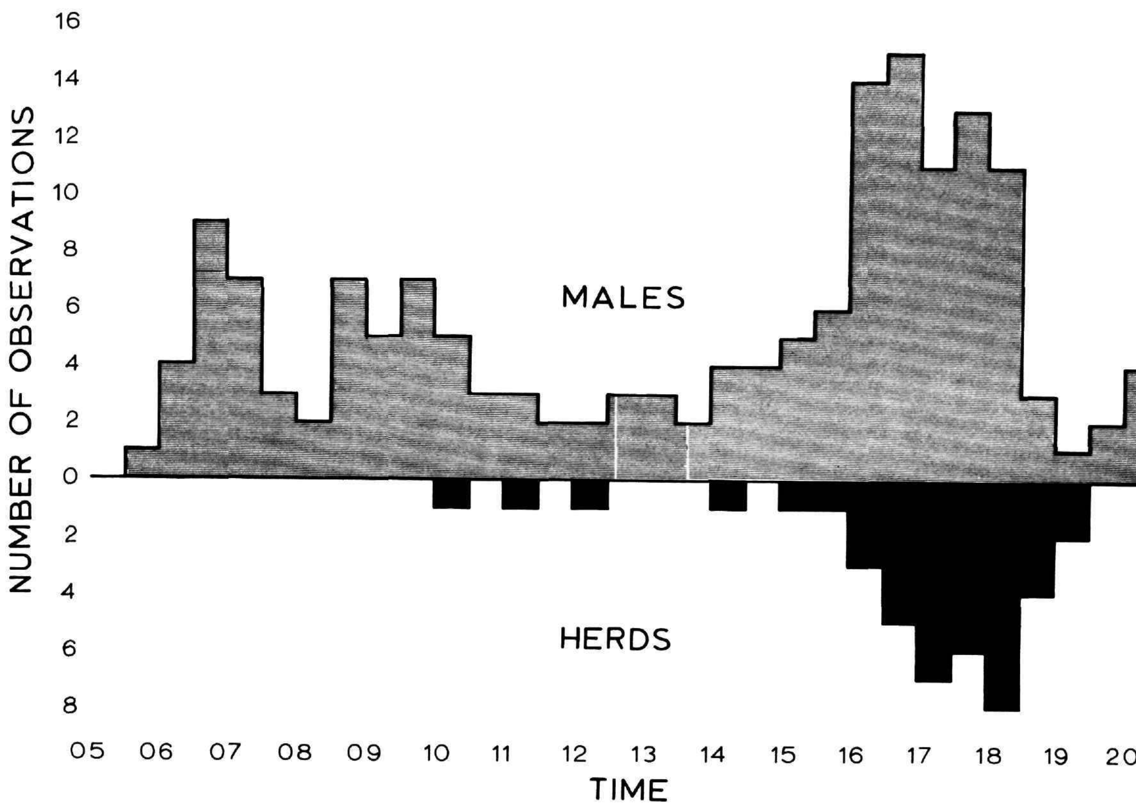


FIGURE 35.—Times and numbers of observations of elephants in the Gal Oya region.

hunu National Park, however, do not appear to show the peak of activity in the morning hours or early afternoon hours; instead the observations of herds in Ruhunu National Park showed a peak around the hours of dusk.

A possible reason for these differences in time of activity of herds in the two areas might be found in the patterns of drinking and bathing (Figure 37). The drinking and bathing times for males tend to be distributed throughout the day for both areas with no apparent peak times. For the herds, however, this is not true. Herds in Gal Oya were observed to come to water for drinking and/or bathing between the hours of 1030 and 1630 whereas herds in the Ruhunu National Park were observed drinking and bathing only after 1730 hours. Although not all observations of herds in open areas included periods of drinking or bathing in either area, most of the observations in Ruhunu National Park were made in open areas which surrounded water holes frequently used by elephants. It seems likely, therefore, that the bias towards the early evening hours in Ruhunu National Park is caused not so much by the inherent activity of the elephants themselves but by disturbance from numerous tourist vehicles moving along the roads in the park (and these roads generally pass by and connect the open areas, especially in the coastal strip). As the females inhabiting the area of Ruhunu National Park are much less tolerant of vehicles and people than are the males resident in the same area, this would appear to be the most reasonable explanation.

Figure 38 shows the times of activity of elephants at the Lahugala Tank, expressed as number of elephant-hours per hour for the months of March, July, October and December of 1967 and February of 1968. It summarizes nine days of observation in March, six days in July, three days in October, eight days in December, and three days in February. For all months the same trend is present in that very few animals are out in the tank before 0700 to 0800 hours when they emerge from the forest. The general trend then is for the number of animals present in the tank to build up to a peak some time between 1500 and 1600 hours. In



FIGURES 36.—Times and numbers of observations of elephants in Ruhunu National Park.

March and December the number of elephants present in the tank continued to increase right up until dusk, but in the other three months the number of animals began to decline after 1700 hours. Figure 38 shows only the data collected during daylight hours. Data collected by observers working in shifts throughout the night in both December 1967 and February 1968 showed that for five nights of observations at least, the number of animals in the tank began to decline more rapidly between 2000 and 2400 hours and that most of the animals were gone by 0200 to 0300 hours. On only one occasion was a single male present in the tank throughout an entire 24-hour period and this was an old-looking and emaciated male who had remained in one particular area bordering the tank and just at the edge of the tank for a period of four days.

The differences between the months December, February, and March, which show a large number of elephants present in the tank, and July and October, which show a relatively small number, are due to the fact that elephants use this particular tank for feeding. Lahugala Tank is very shallow, and during the growing season (which begins with the onset of the rains in late October and November) contains a lush growth of grasses. It is these grasses on which the animals feed. By July the tank is relatively dry and the growth of grass has died back somewhat.

Patterns of Activity

Figures 39 and 40 show typical observations of the types of activity patterns displayed by males and herds, respectively. Figure 39, for five solitary males and two male groups, shows the typical pattern of alternation between periods of feeding and walking. The lengths of feeding bouts are variable, but periods of walking without feeding are generally quite short. Feeding includes some locomotor components, as an elephant generally tends to feed

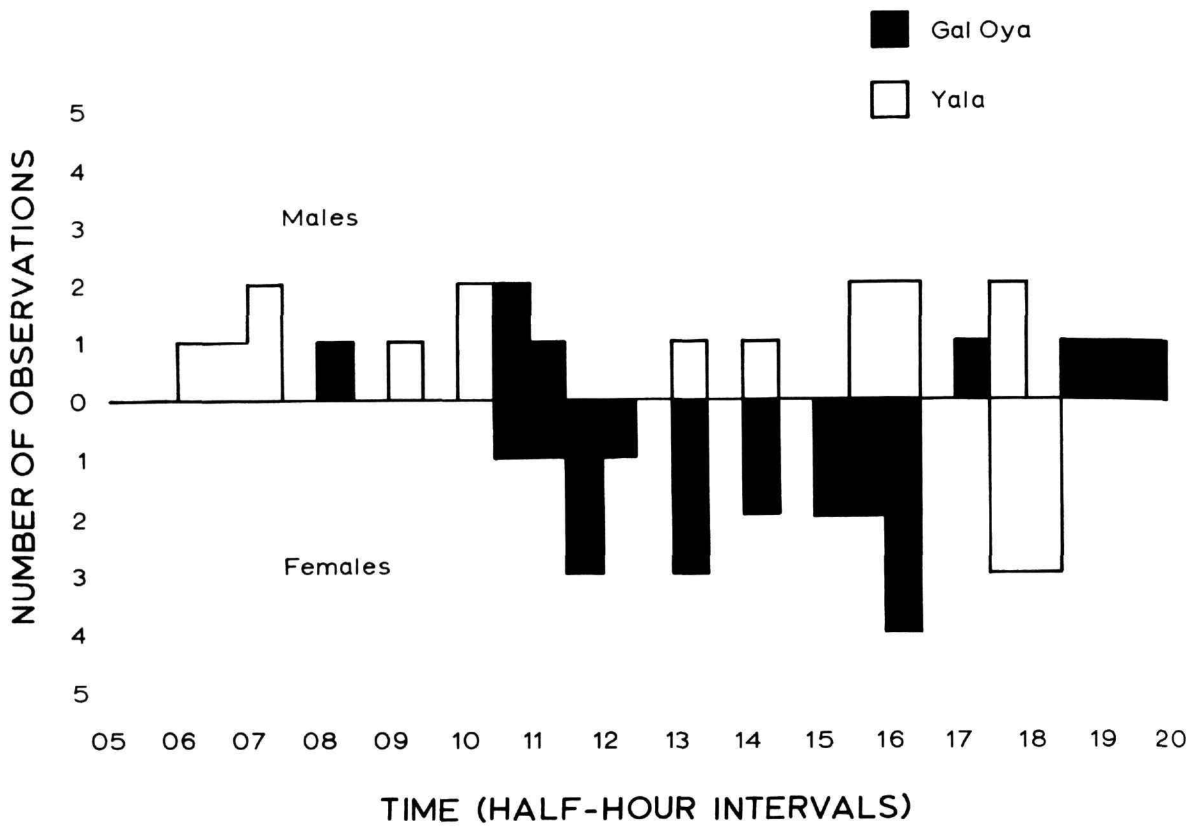


FIGURE 37.—Times and numbers of observations of drinking and bathing by elephants in the Gal Oya region and in Ruhunu National Park.

at one spot for only a few minutes. He then moves one to several steps and begins to feed again.

The data obtained for herds shows a similar trend of alternation. All of these protocols but the last (Figure 40:5) show a high degree of synchronization between the members of the groups, although there are slight exceptions. For example in the second observation one female only stopped to drink and bathe at a waterhole while the others walked past. Similar exceptions are found in example 3 where one infant lay down three times (each time in the shade of its mother) and two males also lay down for a few minutes. This incidentally, was the only occasion on which adults associated with a herd were observed to lie down (see p. 45). In the fifth example the subadult male began following the juvenile (presumed to be a female) and was attempting to rest his trunk along her back (typical precopulatory behavior) as they disappeared into the forest.

FEEDING PATTERNS

Table 7 summarizes a number of observations of the rate of feeding by both males and females. The elephant, when feeding, takes a relatively small portion of food with each mouthful. Several samples were collected of food or potential food that had been dropped by the elephant and other attempts were made to simulate elephant feeding by collecting what appeared visually to be a similar amount of a particular type from which an elephant had been feeding (p. 95). The average weight of such a mouthful is about 150 grams. Therefore, to take in the required daily input of 150 kilograms or perhaps more, a large number of mouthfuls must be taken during every 24-hour

TABLE 7.—*Feeding rates of elephants*

Date and type of food	*Sex/Age*		*Number of mouthfuls*	*Time* (min:sec)	*Rate* (mouthfuls/min.)
GRASS					
3 Mar. 67	♂	A	6	6:00	1.0
3 Mar. 67	♂	A	13	15:00	0.9
3 Mar. 67	♂	A	15	15:00	1.0
22 Apr. 67	♂	A	13	30:00	0.4
2 July 67	♂	A	5	10:00	0.5
2 July 67	♂	A	3	1:30	2.5
2 July 67	♂	A	4	2:15	1.8
1 Aug. 67	♂	A	7	5:00	1.4
1 Aug. 67	♂	A	21	27:00	0.8
5 Aug. 67	♂	A	14	10:00	1.4
10 Aug. 67	♂	A	10	10:00	1.0
10 Aug. 67	♂	A	8	4:00	2.0
11 Aug. 67	♂	A	4	2:00	2.0
11 Aug. 67	♂	A	8	4:00	2.0
SHRUBS					
30 June 67	♂	A	7	10:00	0.7
8 July 67	♂	A	5	3:30	1.4
8 July 67	♂	A	5	2:45	1.8
8 July 67	♂	A	5	2:15	2.3
11 Aug 67	♂	A	17	9:00	1.9
SHRUBS and GRASS					
2 July 67	♂	A	21	17:00	1.2
4 Aug. 67	♂	A	14	12:00	1.2
FRUIT					
30 June 67	♂	A	30	10:00	3.0
GRASS					
9 Aug. 67	♀	A	9	5:00	1.8
9 Aug. 67	♀	A	12	5:00	2.4
9 Aug. 67	♀	A	10	5:00	2.0
11 Aug. 67	♀	A	4	2:00	2.0
11 Aug. 67	♀	A	6	3:00	2.0
11 Aug. 67	♀	A	6	4:00	1.5
9 Aug. 67	♀	J	2	5:00	0.4
9 Aug. 67	♀	J	5	5:00	1.0
13 Mar. 69	♀	A	3	3:00	1.0
13 Mar. 69	♀	A	7	10:00	0.7
14 Mar. 69	♀	A	7	5:00	1.4

period. The rate of food selection, however, is not uniform. The rate of feeding may be as low as one mouthful every 2 minutes yet may be as high as 2.5 mouthfuls per minute when feeding on grasses or shrubs. The single observation of 3 mouthfuls per minute was of an animal which was feeding on tamarind (*Tamarindus indica*) fruits picked from the ground under the tree, and each mouthful consisted essentially of one or perhaps two fruits. The majority of observations fall between 0.5 and 2.0 mouthfuls per minute, although the distribution tends to be relatively bimodal with peaks around one-half to one mouthful per minute and again around 1½ to 2 mouthfuls per minute. Figure 41 shows a more detailed analysis of feeding for three adult males where the differences in feeding rates are not necessarily a reflection of the type of food being used but rather are a manifestation of alternate periods of relatively intensive and more relaxed feeding. As described earlier (p. 46), feeding, especially when feeding on such plants as low-growing shrubs or grasses, is not necessarily a simple operation but actually involves a relatively complex sequence of movements.

Table 8 summarizes 15 observations each of

TABLE 8.—*Distances moved and average rate of movement of elephants while feeding*

Date	*Time observations begun*	*Length of observation* (min)	*Distance moved* (m)	*Average rate* (m/hr)
MALES				
25 May 68	0547	25	100	120
12 Nov 67	0630	540	100	10
8 Oct 67	0700	53	600	720
10 Jun 68	0750	30	75	150
10 Oct 67	0930	270	100	20
10 Jun 68	1350	30	20	40
15 Jul 68	1420	60	500	500
5 Aug 67	1505	25	150	360
12 Aug 67	1533	60	500	500
3 Mar 67	1600	210	250	70
29 Oct 67	1602	50	120	150
12 Aug 67	1625	12	250	1500
1 Aug 67	1647	35	120	220
28 Feb 67	1650	30	150	300
28 Feb 67	1650	15	100	400
FEMALE HERDS				
19 Jun 68	0635	30	20	40
19 Jun 68	0755	60	100	100
8 Apr 68	0855	170	25	10
24 May 68	0937	25	100	240
10 Oct 67	0930	270	100	20
16 Mar 68	0955	50	50	60
10 Apr 68	1015	240	1200	300
6 Jul 68	1115	45	50	60
14 Feb 68	1140	120	250	125
15 Feb 68	1320	60	100	100
6 Jul 68	1323	60	250	250
18 Mar 68	1420	100	120	70
15 Jun 68	1445	120	250	125
17 Jun 68	1520	90	350	230
7 Apr 68	1633	30	150	300

Mann-Whitney U test; $U = 60$ *

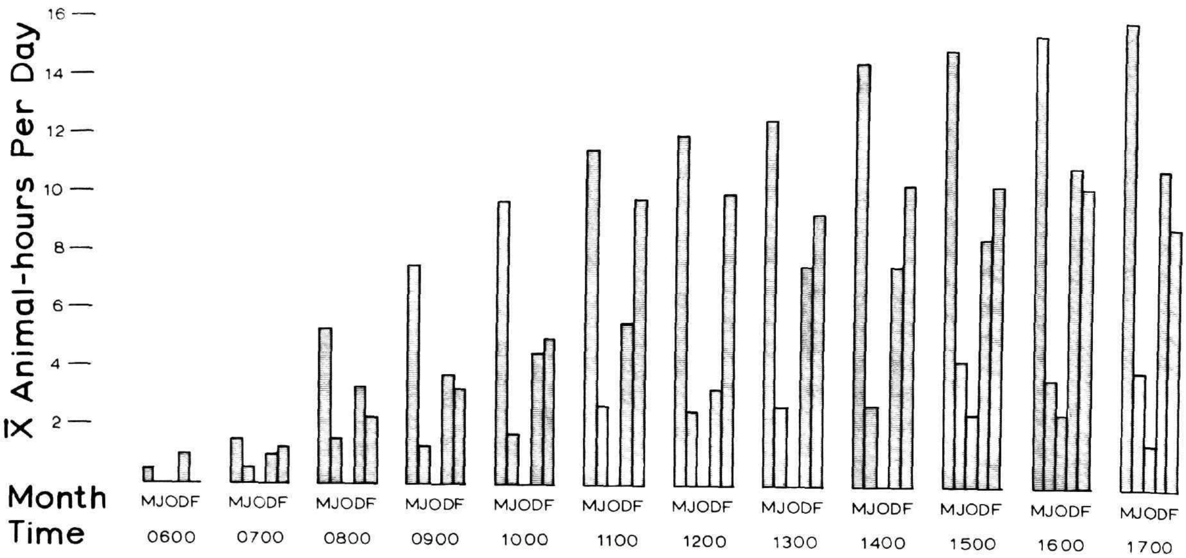


FIGURE 38.—Times of activity of elephants at Lahugala Tank. MJODF=May, July, October, December, February, respectively.

males and female herds where it was possible to measure or estimate with relative accuracy the distance moved by animals during a period of feeding. The distances moved and average movement rates are quite variable, from as low as 10 meters per hour to as high as 1.5 kilometers per hour. There does not appear to be any correlation between the movement rate and the type of food being utilized nor is there any apparent correlation with the time of day. There is, however, a significant difference between the movement rates while feeding between males and females with young, the latter feeding and moving at a slower rate.

TIME AND ENERGY BUDGET

As can be seen from the examples of protocol which were outlined above (Figures 39, 40), it is not possible to assign a particular time and energy budget which will apply to all individuals or all groups; rather, the amounts of time that an animal or group of animals will spend in any particular activity will vary from day to day. Certain general trends, however, can be drawn from these data. For example, the five protocols of herds where observations were recorded in detail for all individuals plus a further two, which were not included in Figure 40, give a total of 185 animal-hours of observation. Of this total, 167.5 animal-hours or 91.1 percent were spent in feeding, including locomotor components of feeding. The next largest category was that of locomotion or walking without feeding which occupied 9.6 animal-hours or 5.4 percent. The remaining 3.5 percent was divided between resting (1.4%), bathing (1.8%), drinking (0.1%), and all other activities combined (0.2%).

A similar estimate based on a much smaller sample size of 15 animal-hours for solitary males (Figure 39) gives 87.1 percent feeding, 10.1 percent walking, 2.0 percent resting, and 0.9 percent for all other activities combined. A much larger sample from Lahugala Tank for males is presented in Table 9 for daytime hours only, which include data from four observation periods over a total of over 108,000 animal-minutes or 1600 animal-hours. Of

TABLE 9.—*Time and energy budget for male elephants at Lahugala Tank*

Activity	*Total animal-mins*	*Percent*
Feeding	101,223	93.5
Walking	2,091	1.9
Contact-promoting	52	0.3
Play/Aggression	3,593	3.3
All other	1,052	1.0
Total	108,011	100.0

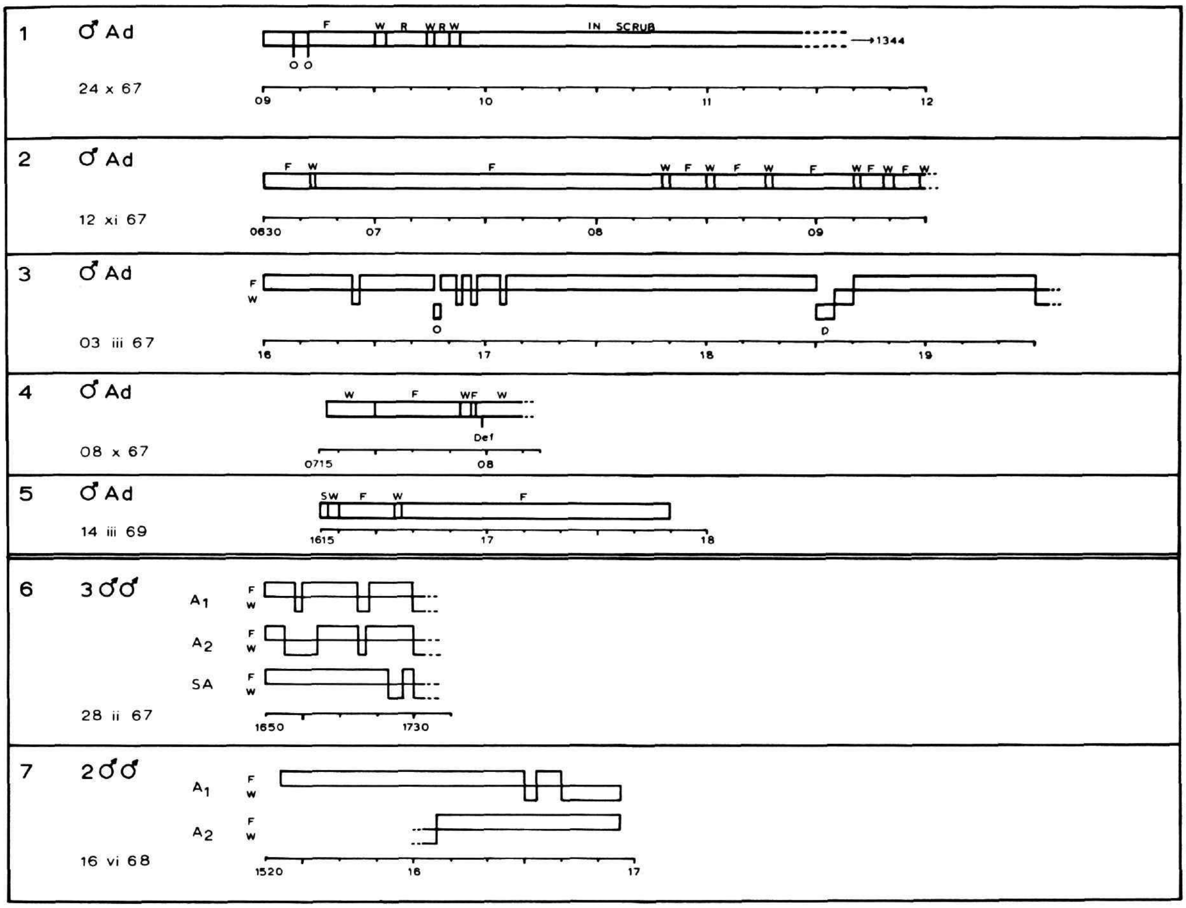


FIGURE 39.—Observations of activity patterns for five solitary males and two male groups. D=drink, Def=defecate, F=feed, O=orient toward observer or other stimulus, R=rest, S=stan· W=walk.

this total, feeding occupied 93.5 percent, movement 1.9 percent, play and agonistic behavior 3.3 percent, and all other activities combined 1.3 percent.

Within those 24-hour periods when it was possible to observe animals during the night, the relative proportions of resting or sleeping to feeding or other activities did not vary significantly from the daytime hours. Even if an elephant were to sleep for two hours during the night which appears to be much longer than would be expected, the total time spent in feeding would still be in the order of 80 percent. Several factors can, however, influence the percentage of time spent in various activities for given individuals. For example, two animals, both males, which were observed frequently for short periods were undoubtedly ill. The first of these was the male mentioned on page 55 who was observed for a period of several days at Lahugala Tank. He spent approximately 20 to 30 percent of his time, depending on the day, in resting (often leaning against a tree). Another male, at Amparai, had been shot by cultivators and for a period of slightly more than a week was observed every day resting in the tank. On one typical day, for example, he spent approximately two hours standing and resting in the water and only a half hour, of the total 2½ hours observations, feeding.

Social interactions can also occupy fairly large proportions of time for particular individuals. For example, Figure 42 shows the relative amounts of

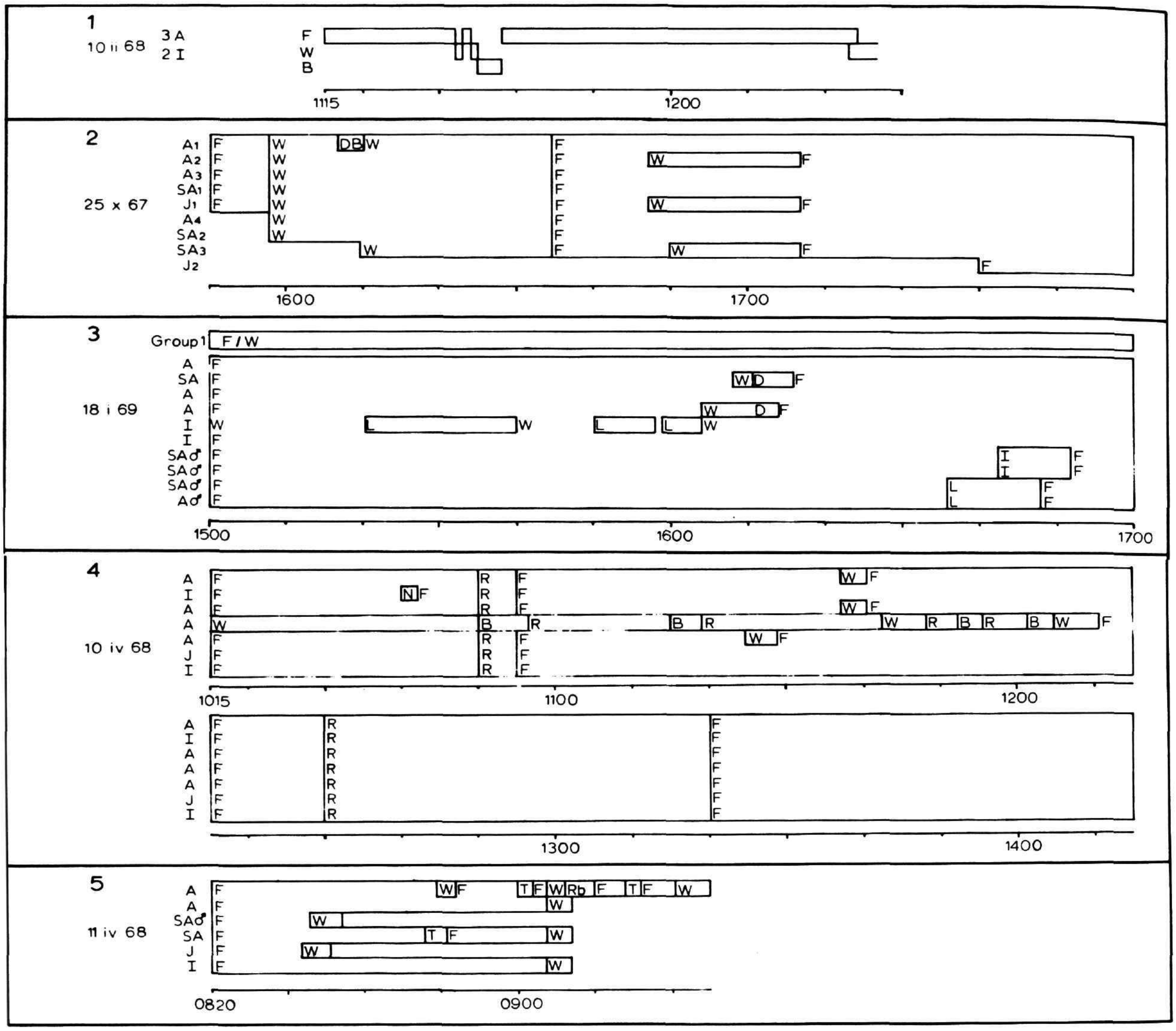


FIGURE 40.—Observations of daily activity for five herds. A=adult; B=bathe; D=drink; F=Feed; I=infant; J=juvenile; L=laying down; N=nurse; R=rest; Rb=rub against tree; T=throw dirt on back; W=walk.

time spent in various activities by one particular subadult male for a period of six days. On the first, third, and sixth days of these observations he spent a relatively large proportion of time in interactions with other individuals in the area. The other days he spent primarily feeding. A further record of time spent by an individual during social interactions was of a male who was associated with a herd containing one or possibly two females in estrus at Lahugala during 1967. This was reported by Eisenberg, McKay and Jainudeen (1971:215). Of 100 minutes of observation, 23.35 were spent in sexual behavior, 18.35 in contact-promoting behavior, and 58.3 in feeding and other activities not connected with his interactions with females. Of the 58.3 minutes, 45.9 were spent actually feeding.

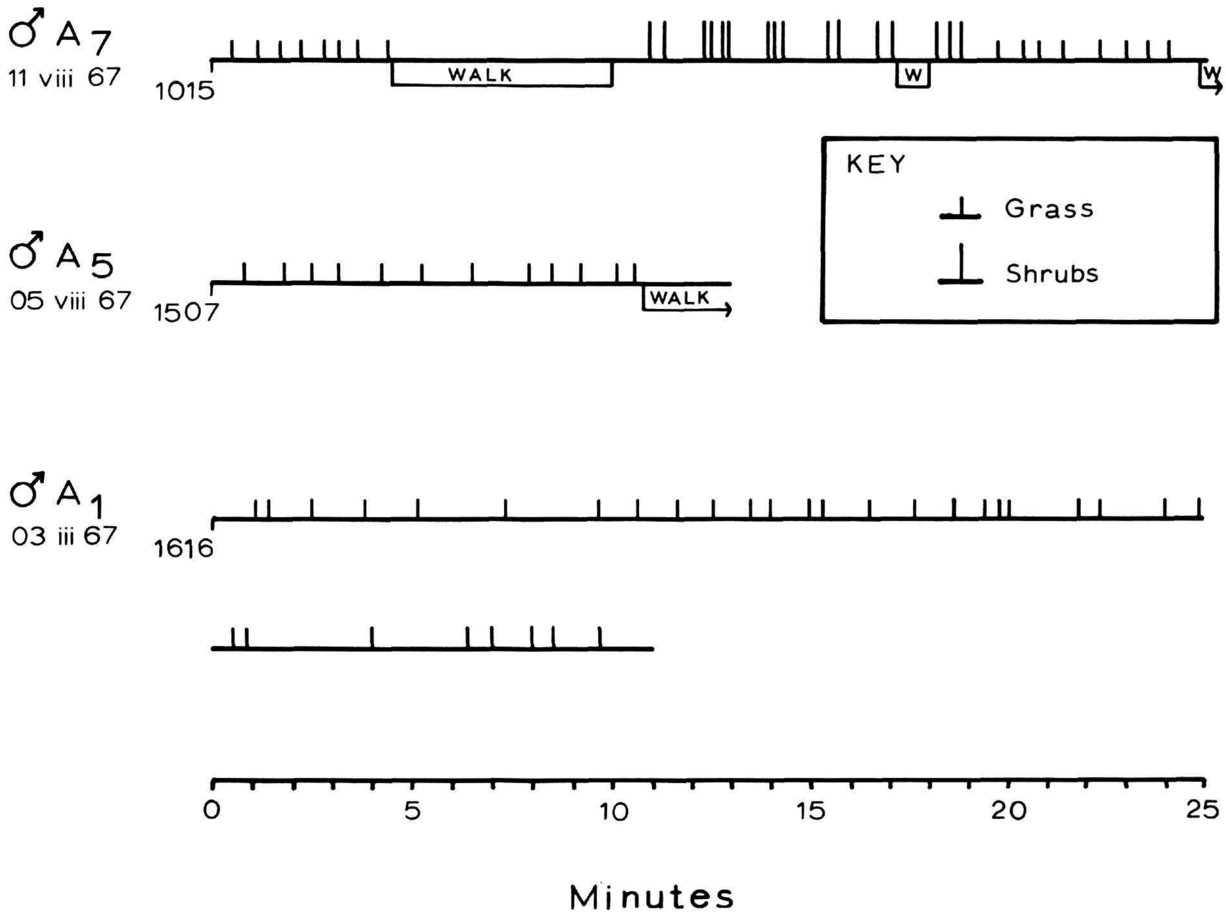


FIGURE 41.—Detailed analysis of feeding for three adult males showing alternation between periods of intense and more relaxed feeding.

From these latter observations it would appear that even though social interaction is indeed important to the elephant, a large percentage of time still must be spent in feeding regardless of the necessity for interaction with other individuals.

Data on the activity rhythms of *Loxodonta* are not as yet available. Data such as those presented by Blood (1963:91) for the bighorn sheep (*Ovis canadensis*) show a pattern typical for a largely diurnal ruminant, i.e., three peaks of activity (movement versus nonmovement) with intervening periods of inactivity.

The most interesting data available for comparison are those of Clough and Hassam (1970) for the warthog (*Phacochoerus aethiopicus*), for which they establish five classes of activity and present in their figure the relative proportions of each per-hour of daytime observation. Their data for the warthog show several similarities to mine for the elephant in that there is on the average an apparent alternation of types of activity rather than specific peaks. The warthog also shows a predominance of feeding followed by walking as the major activity types.

Schenkel and Schenkel-Hulliger (1969) discuss the activity patterns for the black rhinoceros (*Diceros bicornis*) but do not make any attempt to construct a time-energy budget. They do point out one facet of rhinoceros behavior which contrasts with the elephant—the black rhinoceros apparently

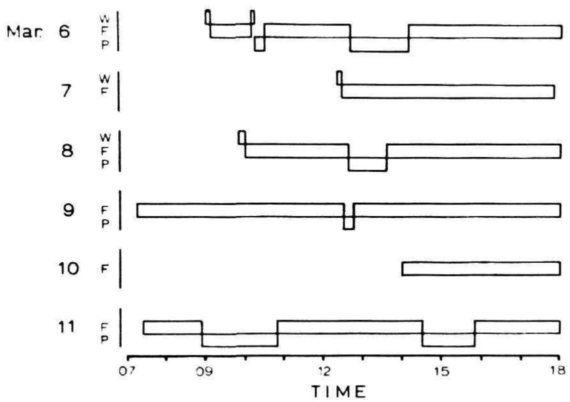


FIGURE 42.—Activity pattern of a subadult male over a period of six days (Lahugala Tank). W=walking; F=feeding; P=play-fighting; time scale=hours of day.

comes to water only at two to three day intervals, as opposed to one or more times per day for *Elephas.*

Social Behavior

INITIAL ENCOUNTER

Whenever two elephants are in the same vicinity, the first indication that one has become aware of the presence of the other is generally the extension of the trunk by one or both in the direction of the other. This is generally followed by orientation of the body axis towards the other animal, often accompanied by an extension of the ears. On at least two occasions, however, in Ruhunu National Park, two males were observed to be moving at approximately the same time over an open area and the only noticeable reaction was the extension of the trunk totally unaccompanied by any other response. This initial response may be followed by either approach or avoidance by either one or both of the animals involved.

When one elephant approaches another, the trunk is generally extended forward towards the animal being approached. The ears may or may not be held extended depending upon the situation, and the head is generally held in the normal position or may be raised slightly. Initial contact between two animals generally involves mutual examination by both animals; the trunk tip is extended towards the other individual, the most frequent areas of contact being the ear, mouth, eyes, temporal gland, tail, anus, feet, and genitalia. The neck and head region are also examined on occasion as may be the mammae, if the animal is a female. Occasionally examination of the genitalia and anal region may be followed by insertion of the trunk into the mouth (p. 65).

PATTERNS OF INTERACTION

Following initial contact, the responses of the interacting animals are highly variable. Some of the potential response and interaction types, are considered under separate categories of interactions with little or no contact and interactions with extended or repeated contact.

Interactions with Little or No Contact

The following four examples are taken from field notebooks and represent typical male-male interactions.

1. 24 September 1967, Yala, Heen Wewa, 1643 hours: A large male which has visited the tank on the previous day walks down the roadway, crosses over the bund with his penis partially erect, walks down into the water and wades to the far side, a distance of approximately 50 meters. About 2 minutes later a second male approaches from the same direction as the first one. The second male comes up onto the bund and stands facing the water. The second animal now goes down across the bund; the first turns and faces the second as the latter enters the water and begins to drink. After drinking, the second animal throws water over the sides and back. The first animal now begins to move across the water toward the newcomer. As the first male approaches the newcomer, the second male turns sideways presenting his side to the first animal.

At about this time, a third male appears on the far side of the tank approximately 150 meters away from the two under observation. As the first male approaches the second, the penis of the second is partially erected. Both animals extend the trunks toward each other but there is no contact between them. The first animal has now come up out of the water and is standing on the bank. The second animal also moved out onto the bank and the two stand side by side facing the same direction. During this time, the third animal has approached the tank and is standing in the water. The third animal has not been observed to react to the presence of the first two nor have the first two shown any response to the third.

2. 5 November, 1967, Kitulana Tank, 1725 hours: A large adult male comes out into the northwest corner of the tank and another large adult (a tusker) enters the tank from the eastern side. The two begin moving: the first tuskless male

moving along the edge of the tank towards the east and the tusker crossing the tank moving towards the west. At 1740, the two meet and begin to move towards the east, coming out into the tank. Both stop to feed at the edge of the tank, then continue on eastward feeding occasionaly until at 1750 they disappear at approximately the same point where the tusker came out of the forest. During the entire period of observation, there was no actual contact between the two animals.

3. 14 November, 1967, Lahugala Tank: A large male has been feeding out in the tank since 1050. At 1200 hours a second male comes out and moves towards the first. At 1203 the second animal stops about 150 meters away, standing facing the first animal, but not showing any signs that it is aware of the presence of the first animal. Three minutes later, the newcomer begins to walk out into the tank moving toward the south; the wind at the present moment is from the northeast and the original animal is to the east of the newcomer. After walking for about 1½ minutes, the newcomer turns and faces the first animal (they are now about 20 meters apart). The newcomer begins feeding and continues moving towards the first one. As they come to within about 5 meters, the first animal raises its trunk in the direction of the newcomer; the second animal also raises his trunk and as they make contact there is mutual trunk to mouth contact. The animals then walk past each other and at 1209 continue feeding. By 1245 they have moved approximately 200 meters apart and by 1345 they are about 500 meters apart.

4. 4 November, 1967, Kitulana Tank, 1745 hours: A large adult male who is in musth is feeding in the tank along with a herd of females and juveniles. At 1751 another adult male comes out on the opposite side of the tank. The male in musth orients towards the newcomer, extending his trunk, and then begins to approach. After the male in musth has gone 100 meters the new male turns and begins to move away. The male in musth breaks into a fast walk and the newcomer increases his pace to a run. As the new male disappears into the forest, the male in musth turns and walks back and rejoins the herd of females.

As these examples demonstrate there can be a wide range of responses on the part of an animal once he becomes aware of the presence of a conspecific. There does not need to be any contact between animals in order to have an interaction as is amply demonstrated by example 4.

The animals involved in examples 1 and 3 were seen together on other occasions besides the ones described here. For all of the first three examples, one can reasonably conclude that the interacting animals were familiar with each other. The fourth example, involving an aggressive chase, is not intended to imply that males in musth are constantly aggressive. This same animal tolerated the presence of a third male. For a further discussion of musth, see Jainudeen, McKay, and Eisenberg (n.d.).

Interactions with Extended Contact

In encounters between two adult females, there is seldom any interaction beyond the initial contact which includes investigation with the trunk of the portions of the body mentioned earlier. More complicated interaction patterns are observed, however, between adult males and adult females and between juveniles of both sexes. The following three examples will illustrate the variety of interactions observable.

1. 23 July, 1967, Lahugala Tank, 1615 hours: A group of two adult females, three young, and a subadult male tusker enters the tank and begin feeding. At 1655 two subadult males of the same size as the subadult tusker appear at the edge of the tank about 75 meters away from the group. The two new males approach the group and one of them extends his trunk towards the genitalia of the larger adult female; he then turns and puts his trunk to his mouth. By 1702 the group has moved slightly to the northwest and the two new males are following behind. At 1708 the two young males moving together approach the subadult tusker. The tusker backs off swinging his trunk. The two newcomers turn and run towards the bank, one of them actually leaving the tank and going up onto the bank. The subadult tusker follows this animal, rushing head on toward it with his ears extended. He rams the side of the other male with the base of his trunk, not with his tusks, and then as he backs off he swings his trunk in the direction of the male. He then repeats this rush and butting a further two times. Between charges, he gives one of the threat displays which involves the kicking of dirt, throwing the dirt over his own back, and swinging the trunk in the direction of the other male. After the third attack, the newcoming male dashes into the forest; the young tusker follows him into the brush and about 30 seconds after he disappears from sight there is the sound of squealing from the area where the two disappeared.

2. 12 February, 1967, Lahugala Tank 0910 hours. Four adult males are feeding in the tank and two others are standing on the north bank. Two of the adults engage in typical contact-promoting behavior but soon continue feeding, moving toward the center of the tank, in a loose group. At 1018 one of the animals which had been in the tank the longest time (which I shall call *A*) approaches the larger of the two new males (B) and begins to rub his trunk base against the forehead of *B*. *B* then extends his trunk around the trunk base of *A*. *A* now turns and they stand side by side. He then takes a step backward, lifts the head up and with the mouth open extends the trunk over the back of *B*. As *B* turns now to face *A*, *A's* trunk and mouth are over *B's* neck. They break and *A* moves around approximately 180° to a position behind *B* and extends his trunk along *B's* back. *B* now moves away; *A* follows extending the trunk along the back again with the mouth open this time. Again

B moves away. *A* follows and again puts the trunk along the back with the mouth open. *B* continues moving and *A* follows with his trunk along the rump of *B*. After they have gone about 20 meters, *A* breaks away and both animals begin feeding. They feed for 5 minutes with *A* standing side by side with *B*. Then at 1024 *A* extends his trunk to the anal region of *B*, then puts his trunk up over the back of *B* and pushes *B* down into the water. *B* gets up and *A* pushes with his trunk base against *B's* rump but this time *B* does not go down, instead he remains standing with his flank towards *A*. *A* continues pushing with the base of the trunk, then raises his trunk over *B's* back and pushes downward. *B* goes down into the water again. *A* now has his head down below the level of the grass butting at *B*; *B* gets up again. *A* again pushes against *B's* rump with the base of his trunk and forehead. This again results in *B* falling down into the water but this time when *B* rises he faces directly toward *A*. *A* now lifts his trunk and head over *B's* head and presses downward forcing *B* into the water a third time. *B* gets up and moves away about 3 meters. *A* then turns to a position behind *B* and mounts him with forelegs extended along *B's* back and during the mount which lasts about 30 seconds he is hitting *B's* head with his trunk. *A* dismounts as *B* moves away. *B* turns and stands facing *A* with trunk extended and ears forward. This same type of pattern continues with two more attempted mounts and with continual butting and extension of the trunk over the back until 1051 when both animals begin feeding.

3. 30 June 1967, Ruhunu National Park, Gonagala: Two males are standing in the tank; one is a large adult male, the second is the subadult with crossed tusks. At 1745 the larger moves up onto the bund. At 1750 the tusker follows, feeds from a small shrub and then stands scratching the inside of his left forefoot with the right forefoot and with his trunk resting on his tusks. He then turns, touching the side of his head with his trunk tip, and begins pawing with the left forefoot at the dirt. The larger male is now moving. The tusker follows, moves along side the larger male, and they make trunk to trunk contact. The tusker then backs away. Time is now 1757. The larger male approaches the tusker who continues to back off. They stand about 10 meters apart for 2 minutes, then the larger male again approaches the tusker. The tusker kicks at the dirt with his left forefoot and they make trunk contact again. Both animals now turn and begin to move away to the north. The tusker passes the larger male; they both stop and again make trunk contact as they stand side by side. The larger male now extends his trunk towards the temporal gland region of the tusker and both extend their trunks over the neck of the other. The tusker suddenly lowers his head and then raises it rapidly pushing his tusks up under the jaws of the larger male who then faces the tusker. The large male is now standing with his hind feet spread apart somewhat. Both animals again extend their trunks to the head of the other and the large male jerks his head upward attempting to throw his trunk over the head of the tusker. The tusker again rams his tusks under the jaws of the larger male, then turns and the two are now standing side by side. They again make trunk tip contact and the larger animal swings his trunk up over the neck of the tusker. The tusker turns so that he is now facing the side of the larger male and the two animals begin pushing; the larger one with the forehead and the tusker with the side of his right tusk. They break and turn standing to face each other. The tusker then swings his head and trunk toward the large male who backs off slightly, also raising his head. The tusker then backs off two steps, stops, turns, rubs the side of his head with his trunk, then rushes at the larger male swinging with a lateral motion of the tusks, hitting the larger one on the side of the head. The larger animal keeps pressing forward and the tusker delivers two more lateral blows with the right tusk. The larger animal continues pushing and the tusker turns to move away raking his tusk along the side of the larger male. The larger male then moves away. The tusker turns, approaches him, and the larger one continues moving, stops, and then backs up rapidly hitting the side of the tusker with his rump. The tusker then backs up and abruptly the interaction is over. Time is now 1808 hours and both animals begin to feed.

Clearly the first example is an aggressive response. The third example would also appear to be primarily aggressive. The second, however, poses a number of problems; there are not only patterns which would be associated with aggression, as outlined in the other two examples, but also patterns which are more frequently encountered during sexual behavior as described by Eisenberg, McKay, and Jainudeen (1971). Two other patterns have been observed which did not occur during any of the three encounters; these are the grasping of the tail of the second animal, putting it into the mouth, and biting, and kicking with one of the hind feet after backing into an animal.

All of the patterns described above, including the last two, have been observed, not only between adult males but between juvenile animals of both sexes. Juveniles, and to a certain extent infants, play among themselves for quite extended periods and during these episodes of play, the patterns described above which could be grouped into contact-promoting, sexual, and aggressive are displayed quite regularly. These observations thus raise two questions. First, is the play of juvenile elephants a mechanism for developing and practicing motor patterns which will eventually be displayed under particular discrete motivational states in the adult; and second, is it possible to define a discrete motivational state in the adult except under particularly extreme circumstances? In other words, do complex motivational states exist in the adult which result in complex patterns of behavior resembling the play of the juveniles?

With field observations of this nature, it is impossible to answer these questions adequately without detailed experimental studies on animals of a known social background. In these field observations, we have been dealing with animals whose previous history is totally unknown and two males who are observed as adults interacting in an aggressive manner for at least part of the interaction may have been raised together as juveniles or at least may have known each other as individuals since attaining puberty. It could be hypothesized that under such circumstances an interaction which begins as an aggressive interaction could become complicated by the fact that the two animals are known to each other, having shared some previous social experience, and from this a conflict could arise between aggression and contact-promoting behavior. For these reasons I have termed all interactions of this sort "play-fighting," not to imply any functional significance but simply to emphasize the similarity between the behavior of adults and juveniles. Other evidence from the spacing and grouping of males would tend to support the above hypothesis (pp. 82–85).

Interactions between Males and Females

Example 1 (p. 63) illustrates a frequently observed series of acts which occur when a male approaches a herd of females. The response of the females to such initiation of contact by a male varies. The female may apparently ignore the male but more frequently will respond by extending her trunk toward the male's head. Such contact-promoting behavior may lead eventually to sexual behavior should a female be in estrus as was observed on 14 November 1967 (Eisenberg, McKay and Jainudeen, 1971:214–215) at Lahugala and on one other occasion, 11 April 1968, at Inginiyagala.

On one occasion an adult female was observed to react aggressively to a male who approached her group. On 13 June 1968, at Hatpata, a number of groups were feeding in the open in the mid-afternoon. At 1715 one male, who was also feeding in the same area, approached one of the groups. He made trunk to genitalia contact with one female and moved on toward another. As he moved toward the center of the group, the largest female in the group (an animal we had named Big Fanny) turned and rushed toward him. The male turned and moved at a fast walk toward the forest, Big Fanny following. After about 75 meters Big Fanny returned to the group. Five minutes later the male returned to the group and again Big Fanny ran toward him, chasing him about 150 meters.

Such aggressive interactions between males and females were not observed frequently. No instance of aggressive interaction was observed between females.

Communication

Tactile and Chemical

As the external organ of olfaction and the primary organ of tactile sensation in the elephant are combined in the trunk, it is appropriate to consider the two together. Examples have already been discussed of the manner of deployment of the trunk in picking up scent presumably from objects in the environment and from the wind, and further discussion on this point is unnecessary.

Particular mention should be made, however, of the action of placing the trunk tip into the mouth following the sniffing at an object, especially of urine. According to Eales (1926), the African elephant, *Loxodonta*, has a jacobson's organ with a patent opening into the buccal cavity. Examination of the mouths of two Ceylonese elephants showed that *Elephas* also has a visible jacobson's organ. Whether this organ is functional in *Elephas* is unknown but from the behavior of the animals it would appear likely. Potential chemical signals in the elephant include feces, urine, odors from the body rubbed off onto trees, secretions from the temporal gland of the male, and of the interdigital glands. During contact behaviors the trunk tip, as mentioned previously, is extended to various parts of the body of the second animal and during such contacts it is impossible to say whether chemical information or tactile information is the more important.

Visual Communication

Although Rensch (1959) has shown that the visual acuity of the elephant at close distances is good, it would appear that its acuity at greater distances is poor or at least that elephants rely very little on vision for obtaining information about their environment. As long as one remains silent and downwind, one can move about to a certain extent in the vicinity of elephants as close as 10 meters without attracting their attention. Rapid movement or movement over a large distance will, however, draw their attention. Also on two occasions, the elephants under observation approached very close to the observers and would undoubtedly have blundered into them had not the observers reacted.

Nevertheless, it would appear that visual signals may occasionally be used in interactions between the elephants. One example would be the aggressive approach in which one animal approaches the second with the head raised somewhat and the ears extended forward or rather laterally. The position of the trunk and head may also give a certain amount of information to other animals in the group about the motivational state of a particular individual. Kuhme (1963) has attempted to describe postures for the African elephant which could be related to certain motivational states, ranging from the normal position of the head through 19 variations depending upon the angle of the head, and position of the ears and trunk. From my own observations, the postures (or to be more correct, movements) of the various organs of the head are as follows: In mild arousal or excitement, the ears are extended at a 90° angle from the body axis and the trunk is generally extended towards the stimulus causing the arousal. As lateral mobility of the head is limited, the body axis is usually realigned so that the animal faces the stimulus. In a mild or perhaps confident aggressive approach, the animal approaches the stimulus with the head raised and ears extended; the trunk is extended toward the stimulus.

Three other patterns containing aggressive components also occur. The first two can be considered threat gestures. In one threat gesture, the animal stands facing the stimulus. Dirt is kicked with one foot, using the same motion as in scarifying for feeding, although this action often appears to be more exaggerated. The dirt is then collected in the "hand" of the trunk and thrown over the back and then the trunk is brought slowly down and held for a few seconds in the direction of the stimulus. Throughout this display, which is undoubtedly entirely visual, the ears are held extended.

The first display is very similar in some of its components to the pattern of throwing dirt on the back (always repeated) often seen after bathing. It is, however, more exaggerated in the movements of the trunk and foot. The foot may be kicked forward to a 45° angle to the body during this display, whereas during normal scarification it is generally halted close to the ground and almost vertical. It would seem possible that this display may have evolved by a process of classical ritualization (Tinbergen, 1952) from a displacement activity.

In connection with this particular threat display it is instructive to look at one of the techniques used by certain trackers to deter an elephant from approaching too close. Piyadasa, a tracker at Ruhunu National Park, told me of a favorite charm used by many old jungle men which, besides the verbal component (spoken, not shouted, incidentally), involves picking up a handful of dirt and throwing it up in the air, leaving the arm briefly in the raised position. Piyadasa who himself demonstrated this charm for me on several occasions was apparently unaware that he was mimicking the actions of the elephant.

In the second display which is described both by Tennent (1867) and by Sanderson (1878), the elephant faces the stimulus with head lowered slightly and the ears extended. The trunk is held resting on the ground, raised slightly, and bounced hard on the ground. As the trunk hits the ground the animal exhales through the trunk producing a snort and the combination of the snort plus bouncing of the trunk tip on the ground produces a booming sound which can be heard for a great distance. The effect of this threat is primarily auditory. During attack, the head is lowered, the ears are held back against the side of the neck, and the trunk is curled ventrally. If the object of the attack is another elephant, the atack generally culminates in butting with the head of the attacker against the side of the animal being attacked. An animal presumed to be submissive generally turns away from one displaying the aggressive posture. The postures or movements described by Kuhme (1963) as being defensive are typical movements displayed by an animal which could be considered to be in a conflict situation between a tendency to attack and a tendency to flee.

Auditory Communication

Elephants have a relatively large repertoire of vocalizations (Table 10; Figure 43). Muckenhirn (1967) has shown that mammals can modify certain basic sounds in a variety of ways (i.e., by changing the amplitude, temporal patterning, or stressing of overtones), thereby producing a relatively large repertoire of noises using a relatively small number of basic sounds. This same pattern appears to be true for the elephant. The various sounds of the elephant differ markedly in amplitude, some being of low volume and audible only at close range, others being extremely loud and audible for several miles. The temporal patterning can also be changed. The elephant can also emit sounds through the mouth or the trunk, which appears to act as a resonating chamber changing the subjective quality of the sound emitted.

If we take, for example, the low amplitude growl, which appears to be a short distance contact call, and resonate this sound through the trunk it becomes more of a rumbling growl with a clearly resonant quality. This growl appears to be employed primarily during mild arousal. The same growl can be increased in amplitude without any apparent resonance through the trunk to produce the roar. This roar is a long distance contact call used primarily by juvenile animals who have been separated from their groups, but also used by adults. By apparently lengthening the time between pulses and increasing the amplitude, the elephant produces the long distinctly pulsed roar which can best be described as similar to a small motorcycle. This latter call has only been heard used by females answering their young who were roaring. All of these calls appear to be essentially pulsed calls and of a relatively low frequency as measured by stress on the lower harmonic.

The other basic vocalization of the elephant is a squeaking call which appears to have the stress primarily on higher harmonics. Two variations of this have been heard and recorded. The first is a series of short squeaks ("chirping," Figure 43) which was heard in a variety of contexts and the actual significance of which is uncertain. Sanderson (1878) describes this as being a pleasure call. I have recorded this call given by a captive animal at the National Zoological Park, apparently as a greeting to the keeper when the keeper enters the cage. This call has also been heard in the wild in Ceylon, but in each instance the animal giving the vocalization was in a state which could be described as conflict between attack and flight. The same basic call when given as a single protracted sound of extremely high amplitude becomes the scream or trumpet which is given generally at the time of initiation of flight. This was most frequently heard when elephants had been startled by the observer or some other human, but was heard once during an aggressive interaction between two males. Both of these calls appear to be resonated through the trunk to some degree, although the correlation between these calls and resonance through the trunk is not certain. Eisenberg and Lockhart (1972) mention an instance of a trumpeting sound being given immediately prior to attack. I have also observed the trumpet to be used in such a situation only once. A captive female *Loxodonta*

TABLE 10.—*Vocalizations of* Elephas maximus

Basic sound	*Modified by*	*Resulting sound*	*Context*
Growl	1. None	Growl	Short-distance contact
	2. Resonate in trunk	Rumble	Mild arousal
	3. Increase amplitude	Roar	Long-distance contact
	4. 3. + change pulse rate	"Motorcycle"	♀ response to 3.
Squeak	1. None	—	Not heard in wild
	2. Multiple short squeaks	Chirping	Conflict ?
	3. Lengthen, increase amplitude	Trumpet	Extreme arousal
Snort	1. None	Snort	Change in activity
	2. Increase amplitude	Snort	Mild to strong arousal
	3. 2. + bounce trunk-tip on ground	Boom	Threat display

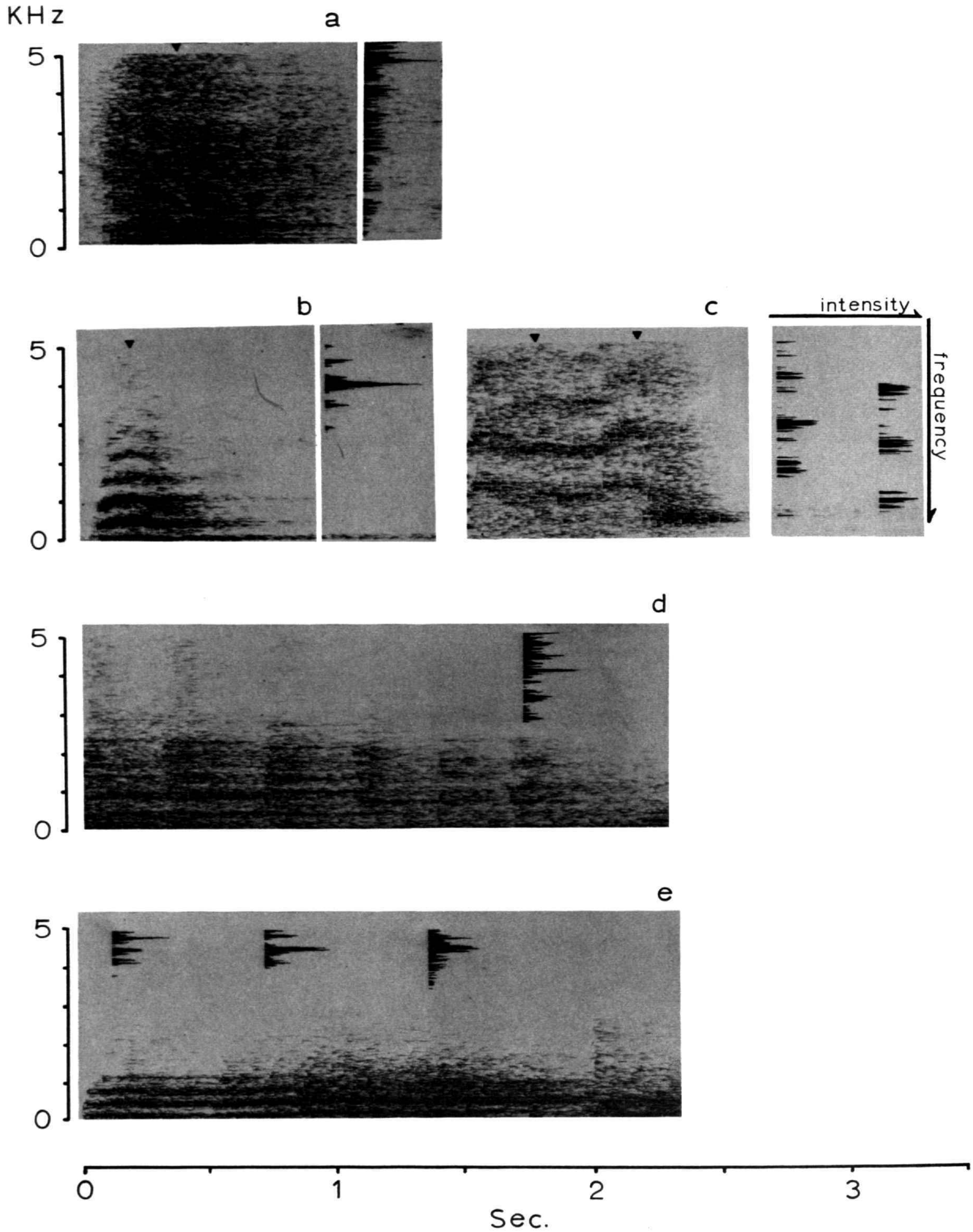


Figure 43.—Sonograms of sounds made by *Elephas maximus*. *a*, snort; *b*, *c*, trumpet; *d*, chirping; e, roar. Inverted frequency scales show intensity at different frequencies.

at the National Zoological Park was recorded using a similar trumpet-like call when aggresively approaching her male cagemate. It is quite conceivable that such a call indicates not specifically aggressiveness but rather a general phenomenon of extreme arousal.

Elephants also make a snorting noise, which although not strictly vocal is an audible sound produced by exhaling rapidly through the trunk. The low intensity snort was heard several times in the field. This can only be heard by the human observer at very close distance, less than 20 meters, and appears to indicate that the rest of the group should follow the action of the animal giving the call. It can be used either to stop the group or to start the group moving again, or to cause a change in direction of movement of the group. It is thus similar in apparent function to the rumble, although the rumble is used simply to indicate a mild arousal whereas the snort can be used both to indicate arousal and to elicit a response in the nearby animals. The louder snort is often heard when animals are surprised. The snort can also be amplified extensively during the threat display described above where the tip of the trunk is bounced on the ground at the time of exhalation. This produces an extremely loud sound which can be heard for a distance of a mile.

Frade (1955:754) has described a perforation in the septum of the trunk near the tip, in approximation with two cartilaginous valves. This structure has not been described by any of the early anatomists, nor has its existence been confirmed by the author. Should it exist, however, it could provide a mechanism for controlling and varying resonance through the trunk. Regardless of the presence of such a structure, it has been noted that when captive elephants utter calls that appear to be resonated there is a pronounced swelling of the bump of the trunk base.

Besides these vocalizations, there are a number of other sounds, such as flapping of the ears, noises associated with feeding, flatulation and eructation which have the potential of containing two signals. The first of these would be a simple short-distance contact sound, which could be of importance when a herd is feeding and moving through dense scrub. The second possibility is that the sudden cessation of such sounds, which occurs when a herd is disturbed by man, could indicate disturbance to a member of the group who might be somewhat separated without the need for any vocalization.

On several occasions we encountered groups of elephants in forest too dense to see them. On most of these occasions a vocalization (either the snort or rumble) was heard, but in a few instances there were none. For example on 16 February 1968, Anil Jayasuriya, Gomis, and I were walking along an elephant trail west of Inginiyagala. We halted upon hearing the sounds of ear-flapping somewhere to our right. After about 45 seconds all sounds stopped. Looking through the brush I could see one elephant who stood at a distance of about 20 meters. He faced us for a few seconds before turning and walked silently away. Anil saw at least one other. As on several other occasions the retreat of the elephants away from us was completely silent; not even the sound of rustling branches could be heard.

Maternal and Infant Patterns

When nursing, the female stands in a normal resting posture and the infant approaches her from one side, putting his head against the axillary region, then raises his trunk up along the side of the mother, grasps the nipple in his mouth and begins to suckle. Small infants generally tend to spend most of their time in close association with an adult, even if there are juveniles present in the group. Sanderson (1878) observed two calves suckling from one female at the same time. This was not observed during my field work but on 11 April 1968, at Inginiyagala, a small infant was observed to suckle from his own mother and from another adult female which was also in the same group.

In a group containing infants, there are frequently more adult females than infants. In such instances, all females appear to share equally in the care of the young. Whenever the group of females is feeding in a relatively stationary position, older infants frequently stray from them and indulge in fairly extensive play behavior. Whenever the group is moving, however, the infants tend to remain very close to the females and, if any disturbance is present, the adults form a group with the infants in the center. At such times, and also at other times, the infants are frequently restrained from straying by the adults who will extend their trunks around an infant that is about to move away and pull it back.

The converse frequently happens when the adults are feeding while the infants play around their feet. It has been observed several times on such occasions that the adults will kick the infant, often sending him sprawling onto the ground. As the infants get older and begin taking solid food, they frequently feed along side the head of the mother. When the mother is feeding on grass, at least, quite often the infants are allowed to take food from the handful that the mother has collected.

Organization of Elephant Groups in Time and Space

Group Sizes

Figure 44 includes all of the observations made in the Gal Oya area from 1967 to 1969, including multiple observations of particular individual males and particular herds of females. Individual animals were frequently observed in groups of various sizes. For example, a particular female might on one day be with two other animals and the following day in a group of eleven. Similarly, with males, an animal which may be solitary on seven or eight observations is occasionally seen in company with another male. Therefore, these data are not to be interpreted as an indication of stable group sizes, but rather as an index of the relative amounts of time that an elephant will spend in a group of a particular size. These data include all observations where it is reasonably certain that the total number of elephants present in the group had been counted. Brief observations of one or more elephants under conditions of poor visibility (such as animals seen moving away from the road as the vehicle or observer on foot approached) are omitted, as it was not possible under such conditions to estimate the size of the group.

Figure 44 is divided into two sections, one being those groups that contained at least one adult female, and the other, those groups that consisted of one or more males with no females present. The total number of observations is 120 for groups containing females and 99 for those containing only males. The majority of the groups containing females was small: Of the total observations 50 percent were of groups of 6 or fewer individuals; 75 percent were of 9 or fewer; and 90 percent of 14 or fewer individuals. Groups of 15 or more individuals comprised only 10 percent of the total observations. For the males, 80 of the 99 observations were of single animals and 14 were of 2 adult males. The groups of 3 to 5 individuals made up only five observations out of the 99 or approximately 5 percent. Data for Yala (Tables 11, 12) show a similar trend where, for groups observed between February and September 1967, 14 out of 30 observations were of groups between 1 and 5; 7 were of groups between 6 and 10; 6 were of groups between 11 and 15; and the remaining 3 groups consisted of between 16 and 25 individuals. Males for Ruhunu National Park also show a trend similar to Gal Oya, in that, of 123 observations 101 were of solitary animals, 20 of pairs, and there were only single observations of a group of 3 and a group of 4 adult males. Sizes of male groups for Lahugala Tank (Table 11) were noted as they were seen to emerge from the forest to enter the tank. Of 170 such observations, 103 were of solitary males; the remainder being made up of groups from 2 to 7 in size. These Lahugala data differ quite markedly

Table 11.—*Composition of elephant male groups*

Number in group	Gal Oya Σ	Yala Σ	Gal Oya and Yala	Lahugala Wet season	Lahugala Dry season	Lahugala Σ
1	80	101	181	89	14	103
2	14	20	34	31	6	37
3	3	1	4	16	1	17
4	1	1	2	3	1	4
5	1	0	1	3	0	3
6	0	0	0	1	0	1
7	0	0	0	5	0	5
> 7	0	0	0	0	0	0
Σ	99	123	222	148	22	170

TABLE 12.—*Composition of Elephant herds*

Number in group	Gal Oya			↑	Lahugala		
	Wet season	*Dry season*	Σ	*Yala*	*Wet season*	*Dry season*	Σ
1–5	30	23	53	14	5	0	5
6–10	29	13	42	7	2	3	5
11–15	9	5	14	6	2	0	2
16–20	3	1	4	2	2	0	2
21–25	2	1	3	1	0	1	1
> 25	3	1	4	0	12	0	12
Σ	76	44	120	30	23	4	27

from the observations of Gal Oya and Yala in that only 62 percent represented solitary individuals as opposed to 80 and 82 percent, respectively, for the other two areas. Using the average percentages of the Gal Oya and Yala distributions as the expected distribution and applying a Chi square test to the Lahugala data shows that the difference between Lahugala and the other two areas is significant at the .001 level. A similar difference was also found between Lahugala and the Gal Oya and Yala areas with regard to the sizes of herds containing females (Table 12). At Lahugala 12 out of a total of 27 observations consisted of herds of more than 25 individuals. This difference is also significant at the .001 level.

The effect of season appears to be relatively slight with regard to the males at Gal Oya but appears to be somewhat important at Lahugala (Table 11). The seasonal effects at Gal Oya for female herds are slightly more apparent than for the males. Eight observations of groups larger than 15 were obtained in the Gal Oya region between the months of November to April as opposed to only 3 for May to

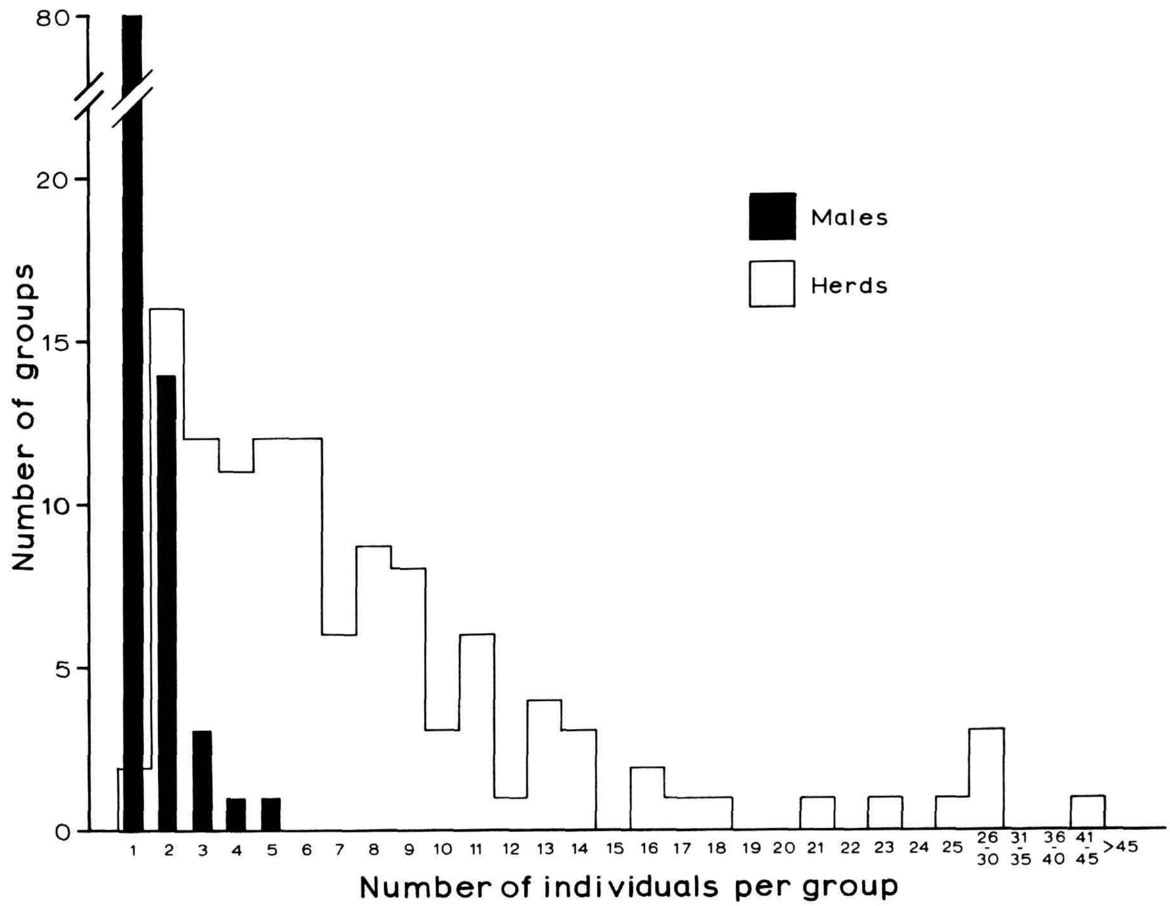


FIGURE 44.—Frequency of observation of groups of elephants in the Gal Oya study area.

October. There is, however, little noticeable difference in the sizes of groups in the Gal Oya which could be attributed to seasonality. Of the total 27 observations of groups, 12 groups containing more than 26 individuals were seen between the months of October to February at which time such large groups were observed twice as frequently as groups of 15 or fewer.

The distribution of group sizes is similar to that reported for Wilpattu by Eisenberg and Lockhart (1972). Data for *Loxodonta* (e.g., Laws, 1969b; Buss and Savidge, 1966) also show a high frequency of small groups.

To explain the observed differences in grouping tendencies between males and females and between the different areas requires a more detailed analysis of the composition of the groups.

Composition of Groups Containing Females

Of the total 120 observations of herds containing females, 73 were of sufficient duration to distinguish the size and sex classes of a significant number of animals. Those groups which consisted of 15 or more individuals always contained adults, subadults, juveniles, and infants. Groups which contained fewer than 15 individuals, on the other hand, did not always contain members of all four developmental classes. Table 13 shows the breakdown of 53 groups which contained 2 to 15 individuals. This table is divided into four major columns on the basis of the presence or absence of subadult and juvenile individuals. In the first of

Table 13.—*Frequency of composition for 53 small groups*

Herd Age Structure					
Juveniles	0	0	1	1+	
Subadults	0	1+	1+	1+	
Adults	1+	1+	1+	1+	
No. of Infants In Each Structural Type					Σ
0	0	3	6	7	16
1	7	5	7	5	24
2	3	3	1	2	9
>2	0	2	2	0	4
↓ Σ	10	13	16	14	53 Σ_{Σ}

these are the groups which contained only adult females and infants. In the second, groups which contained adult females plus one or more subadults and infants; the third column contains those observations where subadults and adults were present plus one juvenile, and the fourth column, subadults and adults plus two or more juveniles. The rows in this table list the number of infants present in these different catgories. As can be seen from this table, 3 of the 53 groups contained only adults, i.e., sexually mature animals, and 13 contained adults and juveniles only with no infants. On the other hand, 20 groups contained only sexually mature females and infants with no juveniles. A further 10 groups contained sexually mature females with one or more infants plus a single juvenile and the remaining 7 groups consisted of a mixture of mature females, 2 or more juveniles, and one or more infants. If these data are treated as a 2×2 contingency table:

	No juveniles	*Juveniles*
No infants	3	13
Infants	20	17

and tested using the Chi square test, the result is a significant difference at $p<0.05$.

These data show that there appears to be a division between those groups that contain juveniles but not infants (and which I shall term "juvenile-care" units) and those groups that contain infants but no juveniles (which I shall term "nursing" units). The following examples should help to illustrate this difference.

These observations are taken from one particular herd of elephants which inhabited the area of the eastern portion of the Gal Oya National Park. This herd was seen from March to June 1968 and again intermittently from October 1968 through April of 1969. For the moment I will tentatively refer to a herd of approximately 40 individuals from which the animals mentioned in this section form a part. In June of 1968, the herd was observed all together at Hatpata on three successive days after which time they moved to an area inaccessible by road and were not observed again until late in October.

On the 25th of October, two adult females accompanied by a subadult male, two juvenile males, and an infant were observed at Hatpata. One of the females was readily identifiable by a cyst on her right shoulder and the second was identifiable by a group of cysts on her right rump. The infant apparently belonged to the latter female as determined by the fact that he spent most of his time with this female plus the similarity in the shape of the ears and of the hairs at the tip of the tail. On the 28th of October, the two adult females and the infant were observed again at the same place.

The group was not observed again until the 7th of November when one of the two females, that with the cyst on the shoulder, was observed in company of two other adult females, one of which had an infant, the same subadult male, and a juvenile. The other adult female from the previous observations with her juvenile were observed feeding separately from this group with the extremely large male-looking female which we had named "Big Fanny." On this day it was possible to observe the animals and it was noticed that the female with the infant accompanying Big Fanny had a fairly large hole in her left ear. As the result of this she was then named "Hole Ear" in order to distinguish her from the other female who was termed "Cysty."

On the 8th of November, Big Fanny, Hole Ear, and her infant were at the same place. They were not seen on the 9th of November but on the 10th, the three were seen again feeding and Cysty was out feeding with the same females she had been with on the 7th, plus several other animals for a total of 8. These groups were not observed again for approximately a month but on the 7th of December Big Fanny, Cysty, and her infant were joined by Hole Ear.

During this period, other members of the herd were in the area including a group containing juveniles and a female who had only a single left tush, a small notch in her left ear, and very long, backward folding ears. Up to December, this female had not been accompanied by an infant but when observed on 16 January 1969, she was accompanied by a very small infant which still showed traces of the lanugo on the head and back. Both this adult female, known as "Lefty," and her infant had the same pattern of ear lobes including the backward fold and a similar twist of the hairs at the tip of the tail. On 16 January, Lefty was observed with her new infant and with a juvenile, size class 4, which had the same ear pattern and twisting of the tail. They were also accompanied by another adult female. Three other adult females accompanied by three other juveniles were present and feeding about 150 meters away.

On the following day Lefty, her infant, and the same juvenile were observed with Big Fanny. On the 18th, Lefty, her infant, and Big Fanny were seen with Cysty and her infant, while the juvenile had joined another group consisting of three adult females and three juveniles. One of the other juveniles had the same pattern of the ear lobes and tail as did Lefty and her presumed daughter. The two groups were observed feeding separately as they emerged from the forest at approximately 1500 hours, but by 1630 hours both groups had moved together and the two juveniles that resembled Lefty had moved over in advance of the rest of the group to join Lefty and her infant. On the 19th and 20th, these animals were not observed but on the 21st of January, the entire group was out feeding together, including Big Fanny, Lefty, Cysty, and Hole Ear plus several other females and juveniles for a total of 32 in two groups, one of 23 and one of 9. On 22 January, Lefty and Hole Ear were seen with their infants while the group containing adults and juveniles fed in a separate section of the bay. Big Fanny and Cysty were the only members of the group which were not observed on this occasion. They were not observed again until 13 March when Big Fanny, Hole Ear with her infant, Lefty with her infant, and Cysty with her infant were observed with a juvenile.

Similar observations from the herd of elephants occupying the area around the Amparai airport also showed divisions of animals into groups of these types. What the data from the Hatpata herd show is that the adult females with their infants tend to remain together in one or two groups, while the other females form a group with the majority of juveniles, some of which are the daughters of the females with infants. These two groups usually feed separately, but they do come together at least while feeding in an open area near the water.

Assuming that this is a general pattern for all herds (although it cannot be proved for lack of observation), it can be postulated that the females within the herd form two classes of groups: females with their nursing infants and females with juveniles. A mixture of juveniles and infants within a single group (Table 13) occurs when the two groups come together, such as seen on 18 January 1969, where Lefty and her new infant were joined by Lefty's daughters.

The tendency to form two different types of groups is caused by the propensity for females with infants, who cannot obviously travel at any great speed or for any long distance, to remain in association with each other and, on the other hand, for juvenile elephants to remain with other juveniles. Therefore, it can easily be seen how two different types of groups can emerge, for each kind moves at different rates, often in different directions.

Thus, for the Hatpata herd during this six months period of observation there existed two major subdivisions, one including Hole Ear, Lefty, Cysty, and another female with an infant and the other group consisting of five other adult females plus a number of juveniles. The two major divisions came together frequently while at Hatpata but were usually observed separately. The only observed transfer of a female from one type of group to the other was the case of Lefty who appeared and joined an infant group after the birth of her infant some time between December and January. Juveniles moved back and forth between groups several times during this period, particularly those juveniles which apparently were the daughters of Lefty but who remained most of the time with the females without infants and other juveniles.

Within each of these two types of groups, however, the number and composition of individuals varied. On some occasions Lefty was observed in the company of Hole Ear and on others Hole Ear was observed with Big Fanny. Although Hole Ear was most frequently seen with Big Fanny, she was also seen in the company of the other females with infants. Similar transfers between members of juvenile care groups were also observed. Thus the structure of an elephant herd (Figure 45) may be divided into a "nursing unit" and a "juvenile

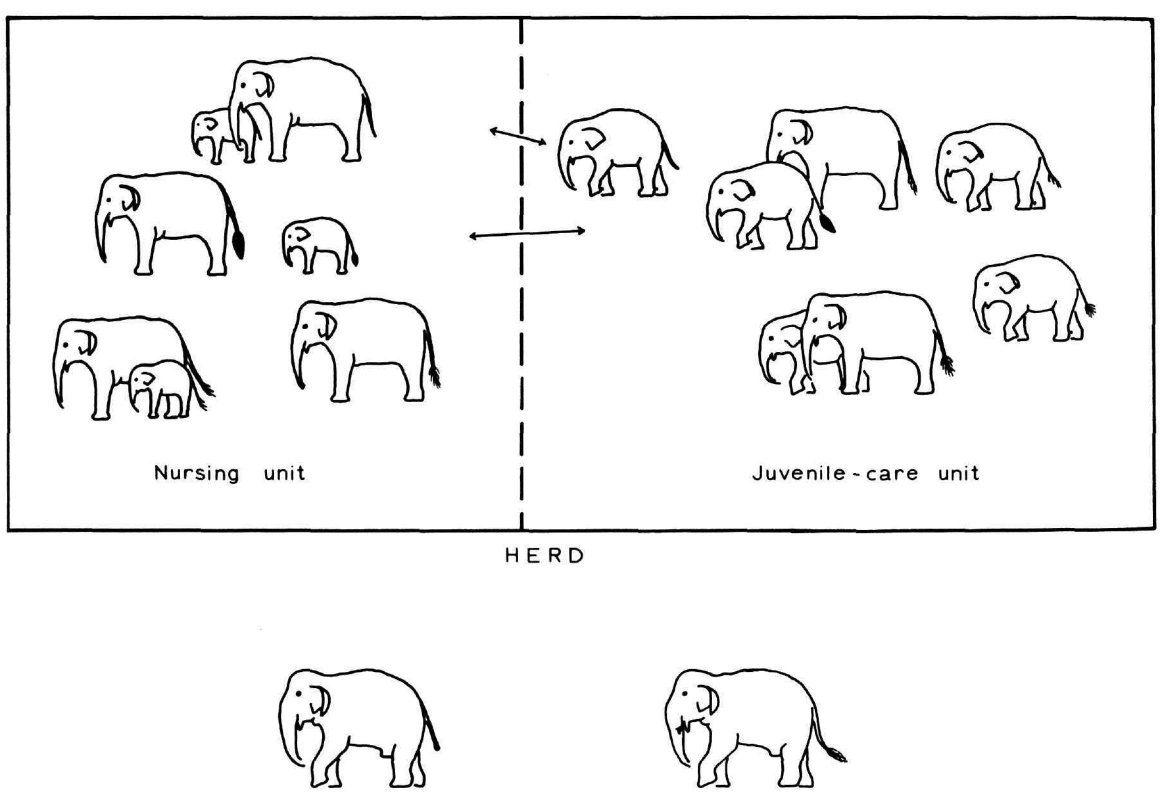


FIGURE 45.—Hypothetical internal organization of an elephant herd.

care unit." Within these two groups, there is a certain flexibility in which females may associate together at any one time and depending upon the size of either type of unit it may subdivide frequently into two or perhaps even three subunits. These subunits and units remain in relatively close contact with each other and there is potential interchange on a short-term basis for juveniles and on a longer term basis for adults (dependent upon their status as lactating or nonlactating).

The totality of the unit members is what I will term a herd, which shares a common range. The ranges of herds appear to overlap, sometimes extensively, but transfer of individuals between herds does not appear to occur even when two herds happen to be in the same area at the same time.

At the moment there are not sufficient data available for *Loxodonta* to state whether a similar phenomenon occurs in that species also. The data of Laws and Parker (1968) would tend to indicate that small groups consist of mothers with their daughters—but it must be remembered that their data are obtained by shooting and examining an entire group, not by observing the grouping and subgrouping tendencies over a long period of time.

Data for other ungulates show a gradation from solitary female with infant (*Diceros bicornis;* Schenkel and Schenkel-Hulliger, 1969), to family group (*Equus burchelli;* Klingel, 1969), to family group within a herd (*Cervus elaphus;* Darling, 1937), to a relatively amorphous herd (*Connochaetes taurinus;* Talbot and Talbot, 1963). This same pattern of specialized subgrouping tendencies has not been described for other ungulates. This would appear to be due in part to the long developmental and growth phase of the elephant and in part to the differences in mobility between infants and older juveniles (and the fact that this difference is present for long periods of time).

Medium-term Organization of Groups

The data presented above for the Hatpata herd showed that for periods of one to several weeks the organization of a herd, as evidenced by the compositions of its various subgroups, tends to be somewhat flexible. As previously mentioned, there is a definite tendency for units and subunits of a herd to remain in fairly close proximity to one another. Figure 46 shows the movements and approximate area (approximately 10–20 square kilometers) covered by the Hatpata herd during November 1968 to February 1969. The units remained in fairly close approximation throughout the entire period although there was some spatial separation; the total herd was seen together on only three occasions, although most of the members of the herd had contact with each other by switching back and forth between subunits.

The foraging distances and areas covered appear to be somewhat different for infant-nursing groups and juvenile-care groups. Unfortunately the number of observations from which it is possible to extract these types of data are few, but it would appear that the nursing groups cover a smaller area within any given unit of time than do the juvenile-care groups as shown on Figure 46. This would appear to be reasonable in view of the differences in mobility between young infants and juveniles. Since juveniles have a tendency to stay together and move with females unaccompanied by infants and assuming that the infant groups are less mobile than the juvenile care units, the division of the herd into these two unit types would appear to be somewhat advantageous to the group; such divisions would tend to reduce possible competition for food between the more sedentary nursing females and the other more mobile members of the herd.

Figure 47 shows the movements of a group of 14 elephants which constituted part of a herd inhabiting the Ruhunu National Park from 25 July–12 August 1967. During this 18-day period they stayed within an area of about 25 square kilometers moving on the average less than 5 kilometers per day. This group consisted of one nursing unit and one juvenile-care unit which appeared to remain together most of the time. Whether they foraged separately is not known but they certainly came together at water holes on each day of observation. This shows that the temporal and spatial separation of units of the herd need not always be so marked as at Hatpata. The system is undoubtedly subject to variation depending on such factors as availability of water. It is possible that the scarcity of water in Ruhunu National Park during this period accounted for their remaining together in the vicinity of water holes.

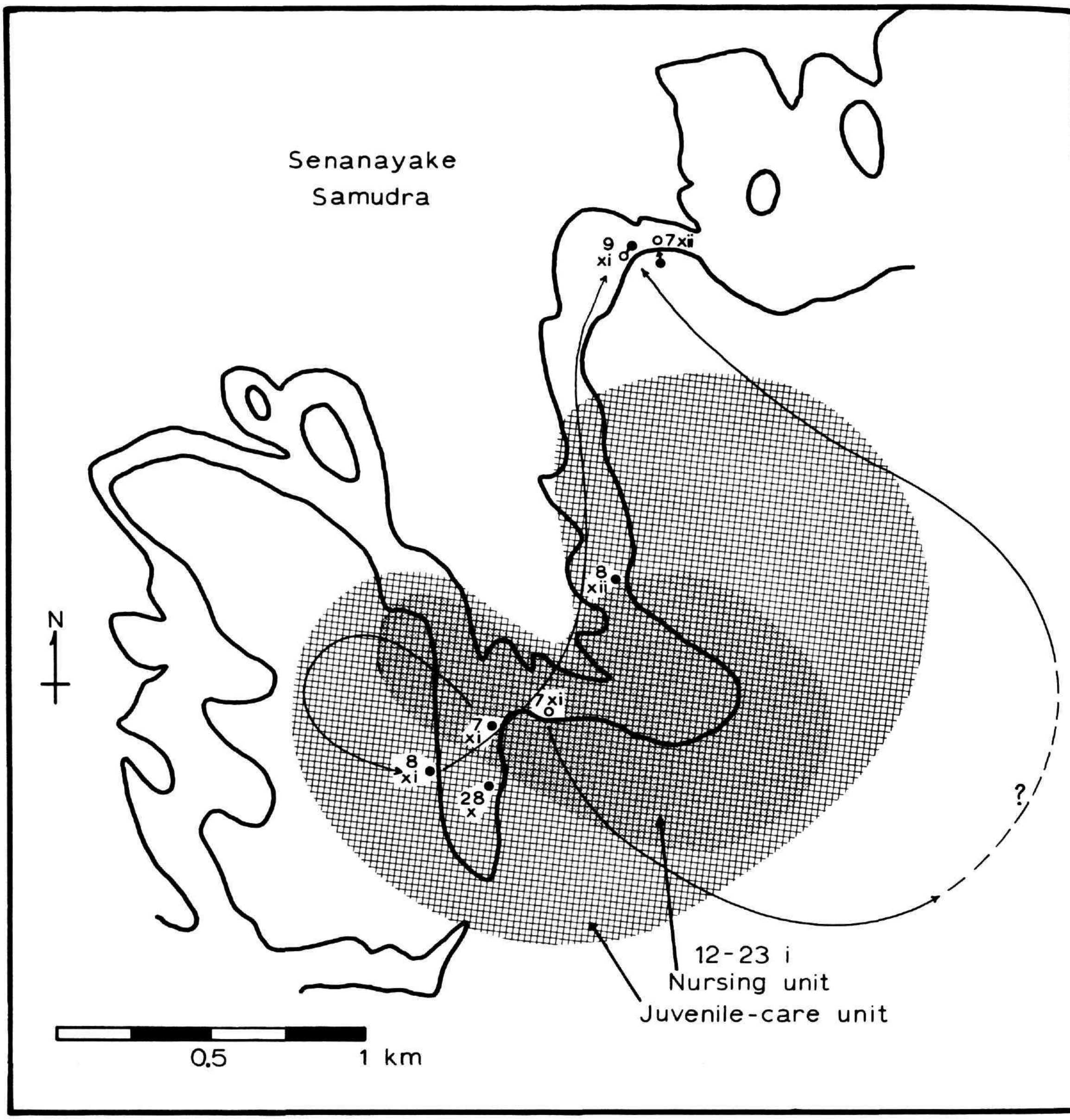


FIGURE 46.—Movements of Hatapa herd groups between November 1968 and February 1969. Dots=nursing units; circles=juvenile care units.

LONG-TERM ORGANIZATION OF THE HERD

Figures 48 and 49 show the movements and areas covered by two herds, the Hatpata herd and the Amparai airport herd over periods of one year each. As can be seen from both of these maps, each of the herds remained in a particular area for a period of 2 to 6 weeks, although the Hatpata herd did remain primarily in the Hatpata region itself for the period extending between October 1968 and April 1969. From March to June 1968, the

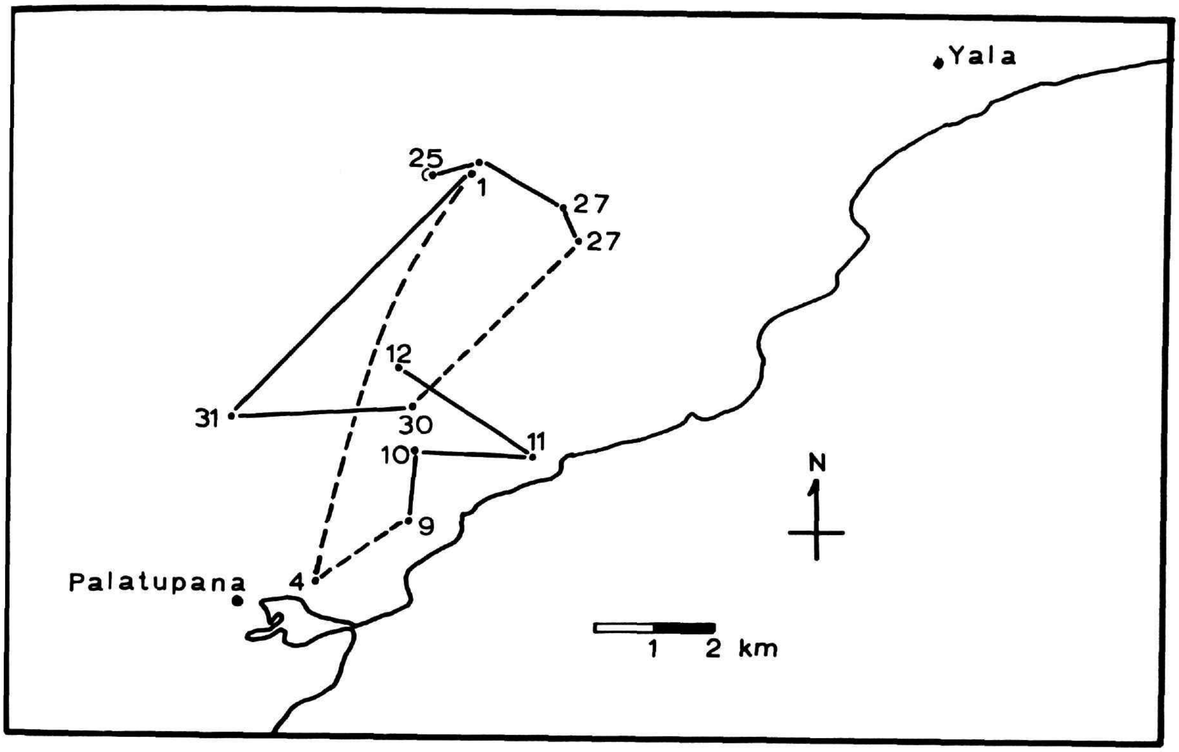


FIGURE 47.—Movements of a group of 14 elephants in Ruhunu National Park, 25 July–12 August 1967.

animals were moving fairly regularly and covered an area of approximately 40 square kilometers throughout this period. In June they were observed making a long movement into an area east of Jayanthi Wewa where they remained between July and October. It was unfortunately not possible to follow the group in this area during the dry season so it is not possible to compare their movements during this time. The movements of the Amparai airport herd (Figue 49) were somewhat similar in that the animals used only small areas of their total range for periods of one to three months.

The entire Hatpata herd was seen together in June 1968 and again in January 1969. From 10 to 13 June 1968, they were observed feeding in Hatpata Bay on four consecutive days, in association with another herd, which also shared this region as part of its total range. The subsequent movements of the Hatpata herd between the 14th to 16th of June, indicated that the herd had gathered for the purpose of making a relatively long movement to a geographically separate subsection of their total range. A similar movement of a large group of 28 was recorded in October 1967. It would appear that when herds are present in a particular area for any length of time they tend to remain dispersed, but when they are moving from one sector to another they gather together and move as a group. If this is the case, then these movements will account for the majority of the observations of groups larger than 15 in the Gal Oya area.

The situation for the Amparai airport herd, however, seems to be somewhat different as does that for the herds in the region of Lahugala. The Amparai airport herd lives in an area that is surrounded by agriculture. When making major movements the herd appeared to move in subgroupings, but when observed as a whole—December 1968—it gathered at one particular spot, which was an area of abandoned paddy fields. This gathering appeared to be more of a concentration or aggrega-

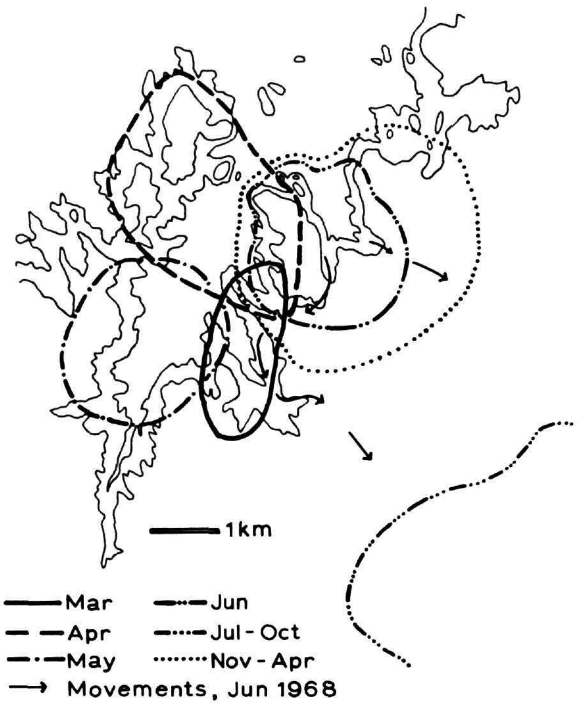


FIGURE 48.—Movements of the Hatpata herd 1968–1969.

tion at a particular food source rather than a gathering associated with movement.

It might be postulated at this point that the reason for this difference between this herd and the herds of the Gal Oya National Park is that the airport herd has a relatively small and compact home range in which the various subsectors that the animals use are not geographically separated by any large distance as is the case for the herds in the Gal Oya National Park.

The movements of the Gal Oya National Park groups are definitely seasonal. Figure 50 shows this seasonality in range utilization for three of the herds from which such data were obtainable. The movement of the herds was away from the National Park during the dry season and was correlated with the concurrent relative unavailability of grasses within the national park (pp. 88–90).

Similar seasonality is also observed in the appearance of herds at Lahugala Tank. Large herds were not observed at Lahugala throughout most of the year, small groups only being present during the months of February to September. During the months of November to January, however, large groups were observed in both 1967, 1968, and 1969. The reason for these congregations of herds at Lahugala (Table 11) would appear to be the seasonal increase in availability of swamp grasses which are preferred foods. During 1967–1968 three herds were congregated in the area and during

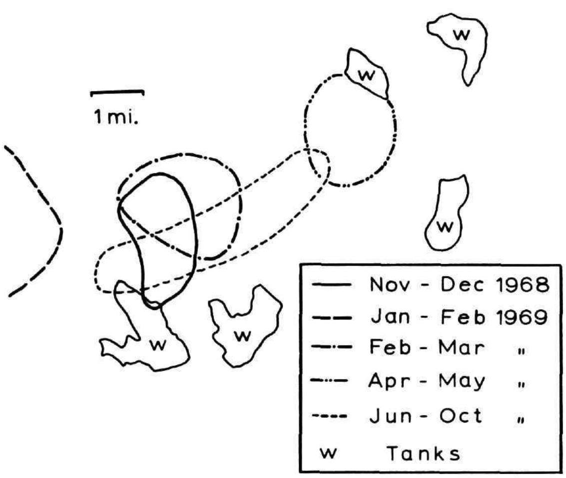


FIGURE 49.—Movements of the Amparai Airport herd 1968–1969.

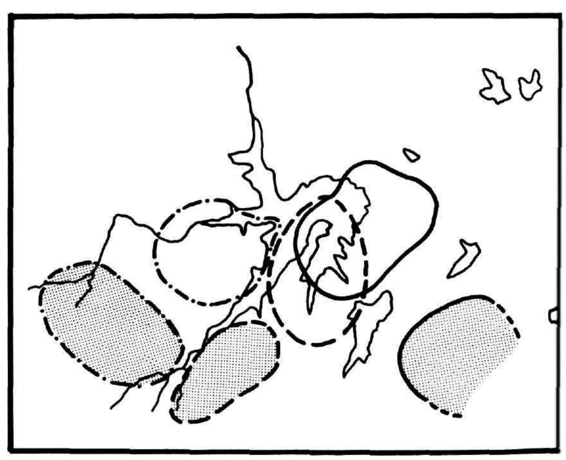


FIGURE 50.—Seasonal ranges of three herds (Hatpata, Baduluwela and Talawa) in the Gal Oya study area. Dry season ranges are shaded. Note overlap during wet season.

1968–1969 five herds were at the tank. These herds always entered the tank from the forest as a complete unit, not as subunits. On eight occasions when two or more herds were present, each herd maintained its integrity without transfer of individuals. Figure 51 shows two herds over a period of approximately one hour, during which time they were feeding and moving. These photographs show how the herds approached each other, fed in close proximity for a short period of time, then began to move off in different directions. This was particularly noticeable on 14 November 1967 when two herds were under observation at Kitulana Tank. The herds maintained relative integrity over a very large area of the tank, covering approximately 40 percent of the tank's breadth. At 1710 hours, however, the animals were alarmed by the appearance of a jeep. Upon sensing its presence, they clumped and ran off toward the forest reforming into the same two tight formations in which they had originally emerged from the forest.

From all of the above observations, the following conclusions can be drawn regarding the long-term organization of herds. A herd, which generally consists of between 15 and 40 individuals, tends to remain distinct from all other herds which may occur in the same general area. The herd does not, however, remain together as a whole throughout any long period of time but tends to forage as units as outlined above. These units forage over relatively small areas of the total range of the herd throughout periods of varying lengths but there does not appear to be any strict division of areas of feeding between the units and subunits. Rather the differences are temporal and depend upon the movement rates of the animals making up any given unit. There is, however, a spatial distinction which can be made over a period of a year or more and this appears to be seasonally determined. Thus a particular herd uses a portion of its range during the wet season and another portion during the dry season. These then can be termed rainy-season range and dry-season range, the total of which adds up to the herd range. This could be likened to the concept of home range as applied to other animals, although it might be more accurate in this case to consider two seasonal home ranges for the majority of herds.

Ranges of herds overlap to a greater or lesser degree. There does not appear to be any strict seasonality to the tendency for home ranges to overlap; but it can be shown from the above data that the home ranges of herds in the Gal Oya National Park area tend to overlap more extensively during the rainy season than during the dry season (Figure 50). A similar trend appears at Lahugala. (For the potential factors which may cause the tendency to overlap home ranges see pages 88, 92.)

Although it is impossible with the data available to make a definite statement regarding the separation of elephant populations, Figure 22 shows the approximate total ranges of the herds in the area of the Eastern Province included in this study. From this, it would appear that two relatively distinct populations occur, one around the Gal Oya National Park and the Amparai area, and a second around the Lahugala-Ruhunu National Park area. The herd around the Amparai airport is relatively small and its distinctiveness may be due not so much to the traditional movements of the animals themselves but to the fact that they have become relatively isolated due to expansion of agriculture in this area. The two populations are relatively large, being an estimated 260–300 for the Gal Oya National Park and 150 for the Lahugala area (see pp. 34–36). The population of elephants around the Lahugala area apparently draws its member herds from the areas to the north of Lahugala and to the south, perhaps as far south as the Kumbukkan Oya. Unfortunately, I have few data for the animals in the region of the Kumbukkan Oya but the apparent movements of these animals indicates that those from Block 4 of Ruhunu National Park move northward during the latter part of the dry season and probably contribute to the herds seen around Lahugala during November. The movement patterns of elephants in Blocks 1, 2, and 3 of Ruhunu National Park—distinct from those of Block 4—tend to be more towards the west.

Similar distinct seasonal ranges were documented by Eisenberg and Lockhart (1972) for Wilpattu National Park indicating that this might be a general phenomenon for all elephant populations in at least the drier parts of Ceylon.

Singh (1969), who has studied the elephant in Uttar Pradesh, India, states that some herds, especially those in the eastern and western regions of his study area, showed distinct seasonal movements.

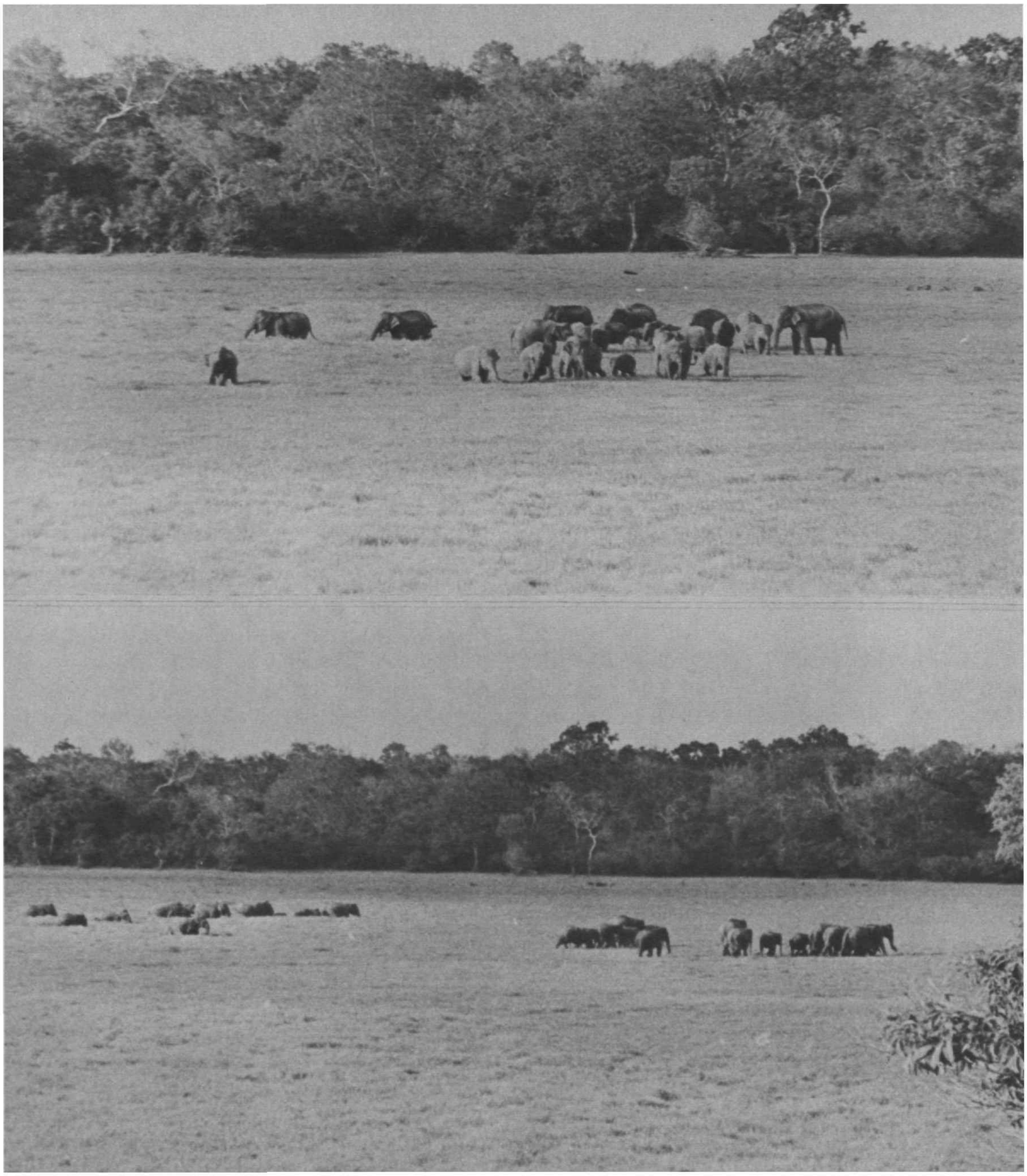


FIGURE 51.—Two herds feeding in Lahugala Tank, 15 November, 1967.

Others, such as the elephants in the Kalagarh region show little seasonal movement—a difference he attributes to the constant availability of food and water in this latter area.

Khan (1967) followed a herd of nine elephants over a period of 5 years in Perak, Malaysia. Although these animals did range over distances of 10–15 kilometers or more, there was no apparent regular seasonality to their movements.

The literature on the African elephant contains many references to long migrations of a seasonal nature (for example Sikes, 1971:105–107) but the data presented by Laws (1969b) would indicate that the seasonal shifts in home range are not so great but are consistent with the data obtained from Ceylon.

The Role of the Male

The majority of males that were observed not in association with females were single individuals (see page 70). Those data, however, do not take into account the males that were observed in association with herds (Table 14). Of the 73 counts made of herds in which sexes could be determined accurately 44 were not accompanied by males. The remaining 29 herds (or 40%) were accompanied by at least one male. The majority of such herds were accompanied by a single male, with three accompanied by two males, three accompanied by three males, and one each accompanied by 4 to 8 males. If these 29 observations of males associated with herds are added to the other 99 of males not associated with herds, it would tend to show that males are on the average in association with herds for approximately 25 to 30 percent of the time.

Table 14.—*Number of males in association with herds*

Number of males with herd	*Number of herds*
0	44
1	18
2	3
3	3
4	1
5	1
6	1
7	1
8	1
>8	0
Total	73

Table 15 shows the observations of males seen associating with the Hatpata herd (or parts of that herd) over a 5-month period. As these data show, no given male associates with the herd for a period longer than a few days. Indeed, the fact that any number of males were present only during January would seem to indicate the likelihood that one or more females were in estrus at that time.

Table 15.—*Males associating with the Hatpata herd, November 1968–March 1969*

Date	*Number of females and young in group*	*Number of males*	*Identity of males*
1968			
7 Nov.	9	0	
8 Nov.	3	0	
10 Nov.	11	0	
7 Dec.	8	1	YA–1
8 Dec.	5	0	
1969			
15 Jan.	7	1	YA–1
16 Jan.	10	2	YA–1 YA–2
17 Jan.	13	1	A–3
18 Jan.	10	5	A–4 A–2 YA–1 YA–2 YA–3
	6	2	A–3 A–5
21 Jan.	20	3	A–3 YA–1 1 unidentified
22 Jan.	23	5	A–3 A–1 YA–1 2 unidentified
8 Mar.	3	0	
12 Mar.	3	0	
13 Mar.	8	0	

A=adult, YA=young adult.

Figure 52 shows a superposition of the approximate home ranges of four adult males known to inhabit the Hatpata area on the home range of the Hatpata herd. It can be seen from this that the home ranges of males tend to be somewhat smaller than the home ranges of herds. These are, in some cases, smaller than a temporary monthly range of the herd. Not all males, however, show this particular sedentary pattern. The examples in Figure 52 were chosen specifically to show this pattern. A second pattern was recorded for two males which were marked during an experiment on tranquilization (see Gray and Nettasinghe, 1970) as well as some others which had been identified from their own physical pecularities. The patterns for the two marked males (Figure 53), demonstrate that these individuals tend to move in a manner similar to the herds, in that they spend two to several days in one locality, often covering an area of less than 1 square kilometer, then move to another area where the same pattern is repeated. Male No. 2 in particular was remarkably sedentary when in any one area but made fairly extensive movements on three different occasions. He was seen feeding primarily on *Mimosa pudica* and his movements from one section to another were, at least, unidirectional. He did not return to an area that he had just left for when he moved on the *Mimosa* from that area had been almost totally uprooted and eaten.

The home ranges of males overlap quite extensively and, in many cases completely. Correlated with this, there is no evidence of male behavior that could be described as territorial. On the other hand, it would appear that there is a great amount of tolerance between males with the possible exception of periods when a female is in estrus. Aggression between males was observed once when a female was definitely known to be in estrus during November of 1967, as reported by Eisenberg, McKay, and Jainudeen (1971), and on three other occasions where aggressive behavior was seen between males in association with a herd. In these three latter instances, the behavior of the males towards the females indicated that there might be a female in estrus in the group, although it was not possible to determine this positively. It would appear that the males remain relatively dispersed, at least throughout most of the year, and that they tend to remain restricted to relatively small home ranges. Throughout most of this longer period, they are solitary or associate temporarily in male groups.

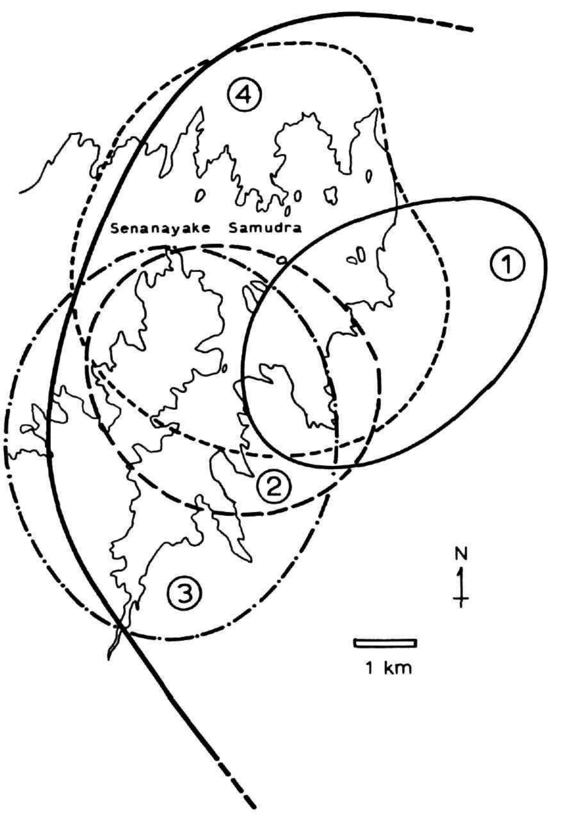


FIGURE 52.—Home ranges of four adult males superimposed on the total annual range of the Hatpata herd.

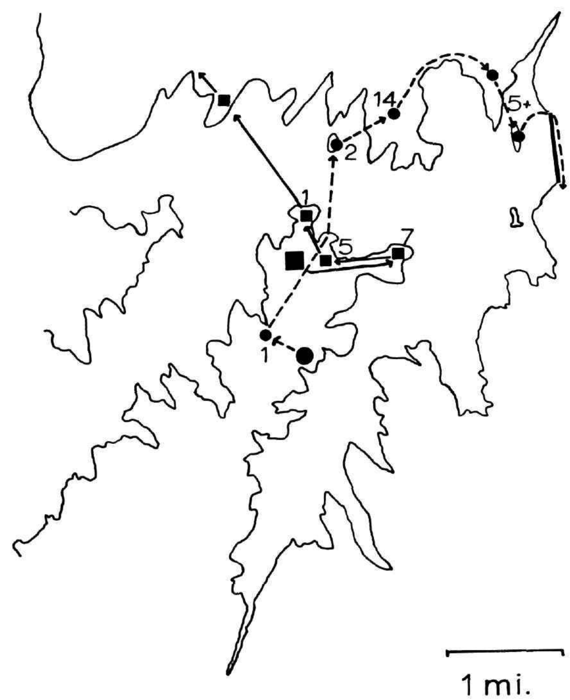


FIGURE 53.—Movements of two marked males (Nos. 2 and 3) during October and November, 1967. Circles represent No. 2; squares, No. 3. The largest circle and square indicate the site of marking; the smaller symbols, centers of activity on subsequent days. The number of days spent in any one place is indicated by the number beside the symbol.

Male groups were observed relatively rarely in the Gal Oya National Park itself, but on those occasions where groups were observed they consisted of animals which had overlapping or at least adjoining home ranges. A similar phenomenon undoubtedly occurs at Lahugala Tank where the tank apparently provides a focal point in the home ranges of a number of adult males. The fact that the lush growth of grass in Lahugala Tank provides a nutritional attraction to males would appear to facilitate the formation of groups in this area, as there is a relatively high probability of more than one animal using that particular portion of its home range at any one time. This then would appear to account for the higher frequency of male groups observed at Lahugala as opposed to those observed in the Gal Oya and Ruhunu National Park areas. Even at Lahugala, however, the groupings of males are temporary. Figure 54 shows the composition of male groups observed during March 1967. It can be seen from these observations that the members of any particular group on any particular day vary considerably.

Although there is no apparent stability in the

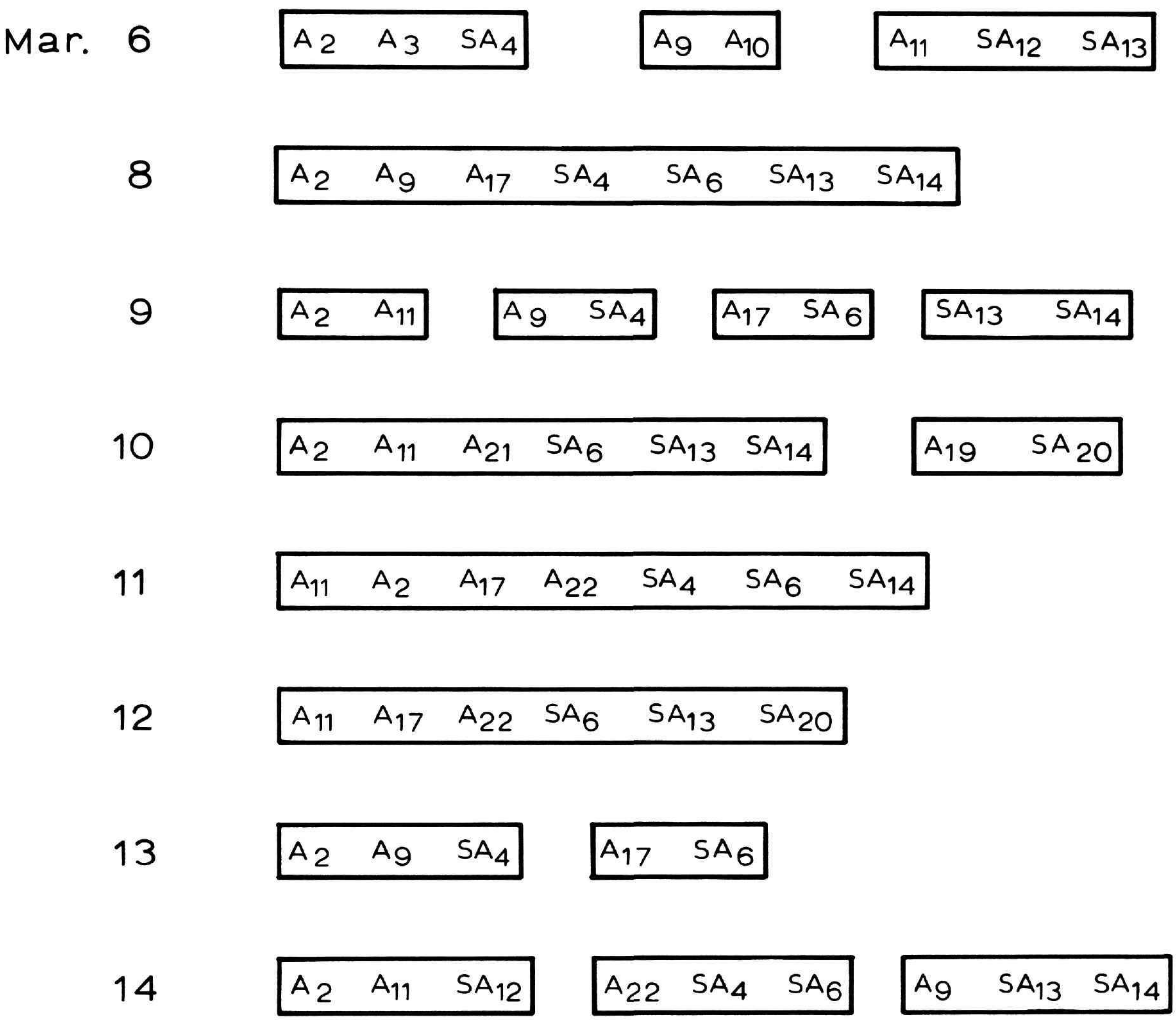


FIGURE 54.—Composition of male groups at Lahugala Tank over a period of eight days in March 1967. A=adult; SA=subadult.

composition of any particular male group, temporary organization would be dependent upon the relative dominance of the members. It is not possible to say from the data available whether there is any strict hierarchy between the animals but observations of aggressive behavior between males in groups (pages 62–65) would indicate that there is a recognized relationship between individual males. Hendricks (1971:116) found a similar situation among male groups in *Loxodonta* where group composition was constantly changing but individuals could be categorized according to their relative dominance rank. Unfortunately when one takes a short time slice out of the lives of these animals, it is impossible to know their previous social history. It would appear, however, that adult males of perhaps 30 or more years of age probably have known each other for a large percentage of that time and a dominance relationship may have been set up several years prior to any observation. This is a reasonable assumption in the light of observations at Lahugala which show a greater frequency of social interaction between subadult males than between fully adult males, especially with regard to the occurrence of play-fighting (page 65). Figure 55 indicates the amounts of time spent in play-fighting by four subadult and five adult males over a 6-day period at Lahugala in March 1967.

A similar dominance phenomenon appears to

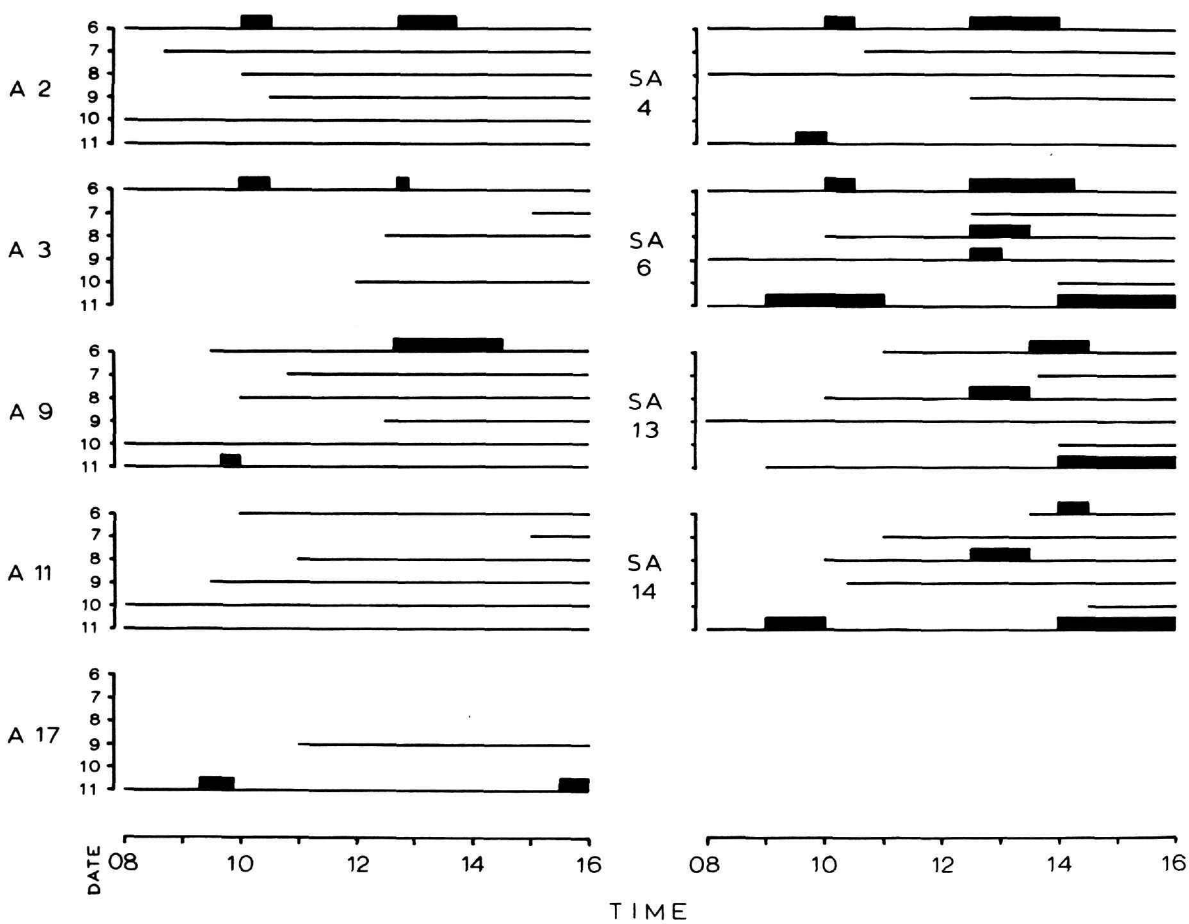


FIGURE 55.—Amounts of time spent in play-fighting by four subadult (SA) and five adult (A) males at Lahugala over a period of six days (March 1967). Lines indicate time of day (in hours) animals were observed in the tank. Black bars indicate time spent in play-fighting.

occur when males are in association with herds. For example, on 15 November 1967 a large male, which had been in association with a herd containing one or possibly two estrous females, was seen to drive a subadult male away from the proximity of those females on three occasions within a period of half an hour. A similar phenomenon was observed in June 1968 with the Hatpata herd as they were feeding at Hatpata and at Kossapola where several males were in association with the herd but one particular male was seen to interact with and chase another male which attempted to approach the herd. Also, observations of the Amparai herd on 4 December 1968 included a sequence during which a large adult male and three smaller adult males were in relatively close association with the herd. The smaller males were feeding about 30 meters away from the larger adult when two of the smaller males began to fight. As the fight progressed, the two began to move closer to the large adult. The large adult did not approach the two who were fighting but as these latter two came closer to the adult male, they broke from fighting, both moved over toward him, and initiated mutual trunk to head contact with the large adult. After the brief contact, the males all went back to feeding.

Males appear to leave the herd and become solitary at about the time of puberty. Juvenile males of size classes 5 to 6 are frequently seen feeding at greater distances from the rest of the group, often moving in advance of the main herd. On three occasions at Lahugala during November 1967, the first members of a herd to emerge from the forest and enter the tank were subadult or large juvenile males. As they get older, they appear to extend these wanderings from the herd until at some point they become solitary. Unfortunately during the period of this study, no instance was actually observed where a known juvenile left a herd.

Subadult males appear regularly at Lahugala. On a few occasions these individuals would remain in the vicinity for several days, but the majority (such as two young tuskers observed in March 1967 and a third tusker seen in July 1967) were seen on only one or two occasions, then never again. It seems probable that these were transient individuals which had not yet settled in a particular home range. For adult males, on the other hand, there were more residents than transients as shown by the following data from 1967:

	Resident	*Transient*
Adult	18–20	2–5
Subadult	2	6–8

The patterns of distribution shown by males indicate that although there is no overt territoriality, there is an effective spacing based on the relative restriction of individual males to small home ranges. There does appear, however, to be a certain amount of dispersal on the part of the males which although not definite may be greater for the younger animals. If there is extensive dispersal on the part of young males, which only studies over several years would be able to prove, this would enhance the degree of potential outbreeding for any given population. As the herds of females tend to be relatively stationary, the potentiality for outbreeding will also be enhanced by the fact that a herd in any given period of time moves over an area which includes the home ranges of several adult males. It is possible, therefore, for a herd whose constituent females apparently come into estrus at different times to be exposed to a large number of males, a significant proportion of which will be animals not related to the females.

Movement Patterns and Habitat Utilization

The Home Range

The general pattern of movement by elephants within the home range was discussed in an earlier section but there are several aspects of the use of the home range which deserve more attention. These concern various fixed points which occur within the home range of any herd.

Water

One of the most important environmental factors for the elephant is the presence of free water. Each of the ranges of the herds contains at least one river system and generally one or more small tanks or a portion of a large irrigation reservoir (Figure 50). Throughout the Gal Oya—Lahugala area, rivers and streams are abundant, and within the past 25 years many tanks have been constructed, impounding large areas of water. Water distribution in Gal Oya

National Park differs from the other two parks in Ceylon. In Wilpattu National Park, as reported in Eisenberg and Lockhart (1972), the streams and rivers tend to be somewhat localized and a large portion of the park is characterized by vertical drainage rather than lateral drainage, and in this area occur a large number of circular water holes known as villus. In Ruhunu National Park, the rivers as in Wilpattu are widely separated and with relatively few tributaries; villus are absent. There are several lagoons along the coastline of Ruhunu National Park which contain water of varying salinity and there are a large number of water holes, some permanent, some dependent upon seasonal rainfall, distributed throughout the park.

The areas used during any given monthly period by the herd at Hatpata were always close to a source of water (Figure 48). For the greater part of the year, this source of water was the Senanayake Samudra. A similar pattern is shown for the Amparai airport herd where no matter what section of the home range they were using at a particular time, they are relatively close to one of the several tanks in the area or to the irrigation channel which passes through to the north of their range. Elephants appear to move towards water and to drink and bathe once a day; as such they cannot afford to move very great distances away from water during times of feeding. Eisenberg and Lockhart (1972) have shown that the herds in the Wilpattu National Park area tend to move from one villu to another. A similar pattern is shown in Ruhunu National Park (Figure 47) where the herd moved from water hole to water hole. In some cases, it moved in a direct line; in other instances it moved over a large front through the forested areas. As such water holes are not abundant in the Gal Oya area, this particular type of movement pattern was not observed in that region. Elephants in the Gal Oya region tend to move from one stream valley to another and frequently show a pattern of moving along the streams, even along rivers, or in the case of the lower Gal Oya valley, irrigation channels.

Elephants generally do not drink at any point along the stream or channel but have particular drinking spots which they visit regularly, as well as particular crossing points. One particularly heavily

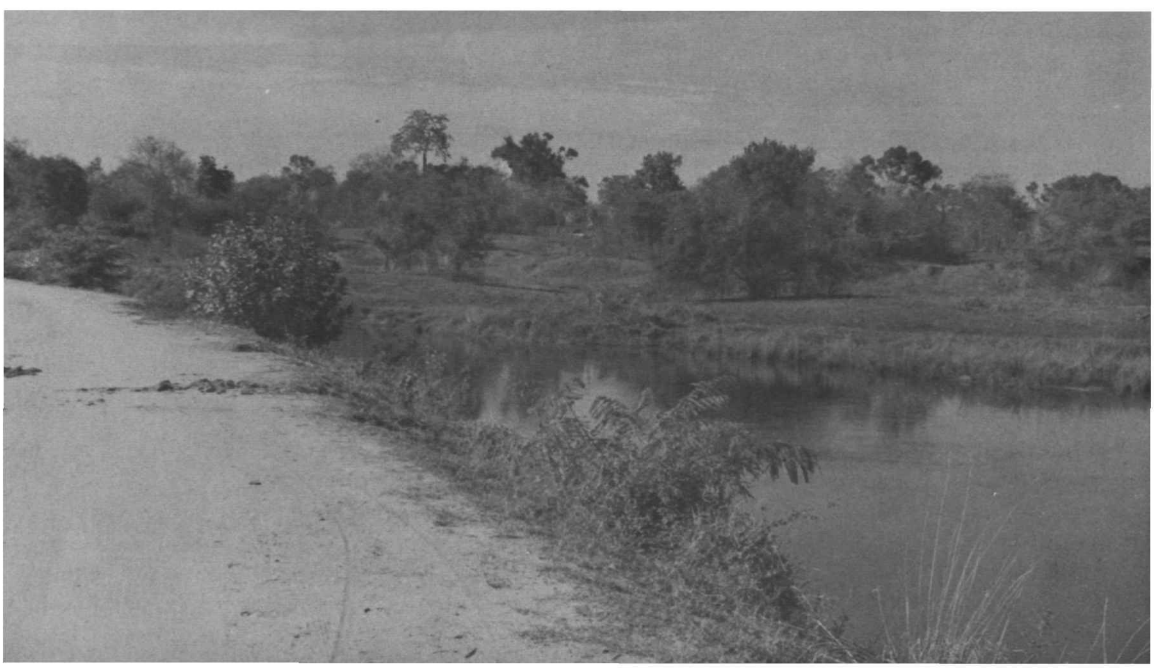


FIGURE 56.—Heavily used crossing point on left bank channel near Amparai airport.

used crossing point of the left bank channel is 3 kilometers south of the Amparai airport where the banks of the channel have been broken down by continued use by the elephants (Figure 56).

Trails

As elephants tend to move to and from particular points in their home range rather than over a broad area, there results a series of trails which undoubtedly have been built up over the years by successive generations of elephants. In grassy areas, such as the Talawa savannas of the western Gal Oya National Park, the trails occur as areas of ground which have been denuded of vegetation. Sometimes the trail is cut into the surface of the soil as much as 5–7 centimeters. In forested areas, the trails, besides being characterized by a disturbance or absence of the ground vegetation, are also characterized by the lack of undergrowth growing around the trail itself, as it would appear that elephants and other ungulates moving to and fro along these trails tend to feed while moving, thereby removing much of the new growth of saplings, etc.

"Rest Rooms"

When walking along one of the elephant trails, one occasionally encounters an area of 50 to 100 square meters where the ground vegetation is completely lacking and the shrubs have been uprooted or broken down. Occasionally branches may also be pulled from several trees in the area. This tends to give such an area an open room-like nature (Figure 57). These "rooms" often tend to occur at the intersection of two trails and are found widely spaced

FIGURE 57.—Room-like clearing used for resting.

around the Gal Oya Natioanl Park, being particularly prevalent around the periphery of Lahugala Tank. On two occasions, elephants were actually observed standing and resting in one of these rooms where there is usually a large number of relatively fresh dung piles. It would appear that they are used primarily for resting in that they provide an area relatively clear of vegetation which also provides shade from the direct radiation of the sun.

Rubbing Trees

Around any particular water hole or tank or portion of stream that is used regularly for bathing by elephants, there can be found one or more trees that are used by the animals for rubbing (p. 48). Buffalo and boar also use these trees, but the identity of the species using the tree can easily be told from the height of the mark. Around Lahugala Tank, for example, 33 trees used by elephants were found in one 700 meter segment of shoreline. Some of these trees were within the forest adjacent to the tank but most were either at the edge or solitary trees away from the edge of the forest (Figure 30). Most of the trees used for rubbing are relatively large. In fact, of the 33 examined at Lahugala, 6 had a diameter of greater than 75 cm. 10 of 50 to 75 cm, 16 of 25 to 50 cm, and only one had a diameter of less than 25 cm. As was also mentioned earlier, these trees are often marked with the tusks or tushes as well as being used for rubbing and of the 33 examined at Lahugala, 24 were rubbed only, 5 were marked with the tusks only, and 4 were used for both purposes.

The importance of such fixed points in the home ranges of animals has been discussed in detail by Hediger (1951) and further discussion of the primary function of each type of fixed point is not necessary here. There is, however, a secondary function which I believe to be quite important for the elephant. These fixed points facilitate regrouping by members of a herd who have been foraging alone or as small units. Water holes appear to be especially important in this regard. With few exceptions, whenever various subgroups of a herd were observed coming together this took place in the vicinity of a frequently used watering place.

Seasonality of Movements

Figure 50 shows the home ranges of three of the herds in the Gal Oya area for which details were known of their seasonal movements during 1968. As mentioned earlier (page 26), large areas of the savanna land in the western portion of the national park and surrounding areas were burned during June and July of 1968. Up to the beginning of July of that year, the southwestern herd was resident in the northern portion of its range (Figure 50). The Talawa in that area was burned between the 5th and 10th of July of that year and following which, tracks of elephants known to be there were found heading towards the southwest. Later in the month, the herd was located in the vicinity of Baduluwela further upstream along the Sellaka Oya. A portion of this herd or more likely the herd to the north moved during this same period along the Gal Oya down toward the region of Kotabowa. The movement of the Hatpata herds, which took place in June, has been described earlier (Figure 48) and was from the area of Hatpata towards the area east of Jayanthi Wewa. Similar seasonal movement patterns took place in 1969, but earlier than in 1968, as conditions of drought began in March and April and continued throughout the normal dry season due to the failure of the rains which normally fall during the spring intermonsoonal period.

In each of these movements. the relative amounts of available water in either half of the home range were approximately equivalent; thus, availability of water can be effectively eliminated as a potential factor in causing these movements. For the herds which reside in the western portion of the national park and to a certain extent for the herd around the Amparai airport, it is quite likely that the major factor influencing the movement was the availability of grass. In other words, after the burning of extensive areas of grassland in parts of their ranges, they moved to a separate area where fires had not been so extensive; in the case of the one herd in the southwest portion of the national park, it moved to an area which was primarily forest.

The movements of the Hatpata herd can also be explained by a change in the abundance of grass as a food. During the growing season of early 1968, the banks of the Senanayake Samudra in the area of Hatpata and Kossapola contained large areas of grass (Figure 58*a*). By June, however, the

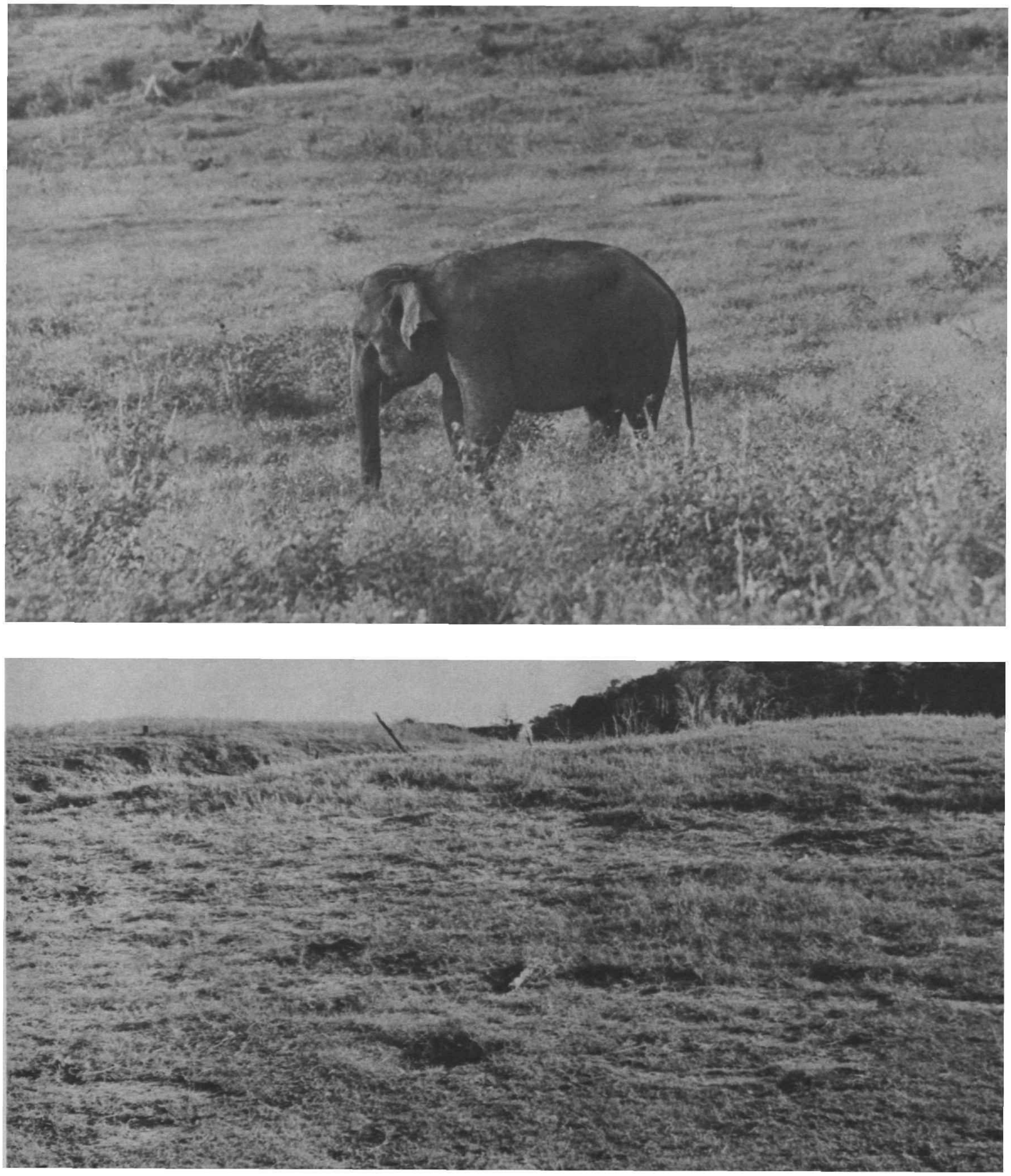


FIGURE 58.—Grassland on the banks of the Senanayake Samudra: top, during growing season; bottom, after cropping by buffalo and scarification by elephants.

grass over this entire area had been cropped extremely short by herds of buffalo which are grazed in this area. As a result the elephants in order to feed had to collect the remaining grass by scarifying with the forefeet. This resulted in large bare areas (Figure 58*b*). Grass is a very important constituent of the elephant's diet. Although the grass was not unavailable in quantity, the relative scarcity of the grass may have been one factor in determining the movement of elephants out of this area.

Seasonal movements in Wilpattu National Park (Eisenberg and Lockhart, 1972) appear to be influenced by availability of both food (wet-season movements to the large grassy villus in the West Sanctuary) and water (dry-season movements to the permanent water in the center of the park).

The factors causing seasonal movements by African elephants appear to include both food and water. Buss (1961) mentioned concentrations of elephants around Lake Albert and the Victoria Nile during the dry season. He also mentions animals moving to forested areas but concludes this is primarily for shade. More recent data (Wing and Buss, 1970) have shown that the forest areas are extremely important as a source of food. Buechner, et al. (1963), working in the same area, considered that the most important factor in elephant movements was the availability of food, particularly grass. As the availability of grass is affected in turn by the season (and by fires during the dry season), and as the weather is seldom the same from one year to the next, it is not surprising that there is no strict annual cycle. There is rather a varying cycle depending on the weather and grass conditions in any one year. Thus there is a great similarity between the types of movement patterns shown by both species, the main feature of which is the ability of both to move long distances when necessary. That this response appears to be triggered by proximate factors rather than an annual (photoperiod or whatever) cycle is particularly adapted to the variable climates in which they live.

Use of Habitat Types

Table 16 shows the total numbers of hours of observations for both males and herds in the Gal Oya area classified according to the habitat type in which the animals were seen. A large percentage of the observations were made in grassland or other open habitats such as the ecotone between forest and grassland, or savanna lands. While these data do not indicate an accurate representation of the total time spent by elephants in different habitats, they do point out a few interesting facts.

TABLE 16.—*Observations of elephants in Gal Oya habitat types*

Habitat type	*Total hours of observation*	
	Males	*Female herds*
Forest	18.0	8.0
Forest (chena)	0	0.5
Forest-scrub	7.0	0
Scrub	9.5	0
Savanna woodland	3.0	10.0
Shrub savanna	0.5	14.0
Grassland	50.5	35.5
Water	6.0	1.0
Agricultural land	2.0	0
Forest/Grassland ecotone	15.5	35.5
Total	112.0	104.5

First, elephants, both males and herds, tend to spend a relatively large amount of time at interfaces between forest and grassland. There are two possible explanations for this. First, they are able to feed on grasses without venturing too far from the relative safety of a forested area and, second, by moving and feeding in an ecotone area, they have available a greater variety of potential food plants during any given feeding period than they would were they in the forest or further out into the grassland. Another interesting fact to come out of this is that elephants, especially herds, are seldom encountered in agricultural land during the daytime. In the area around the Gal Oya National Park their depredations on paddy lands and on sugarcane generally take place at night (see pages 102–103).

Figure 59 shows the times of observations of elephants feeding on grasses or shrubs in half-hour intervals throughout the day. The peaks of feeding show the same patterns as the general times of activity for both males and female herds (Figure 35) although the morning peaks for both males and females for feeding on grasses are earlier than those for feeding on shrubs. The explanation for this would appear to be that elephants are more liable to be found in open areas in the cooler hours of the early morning than the later hours around noon.

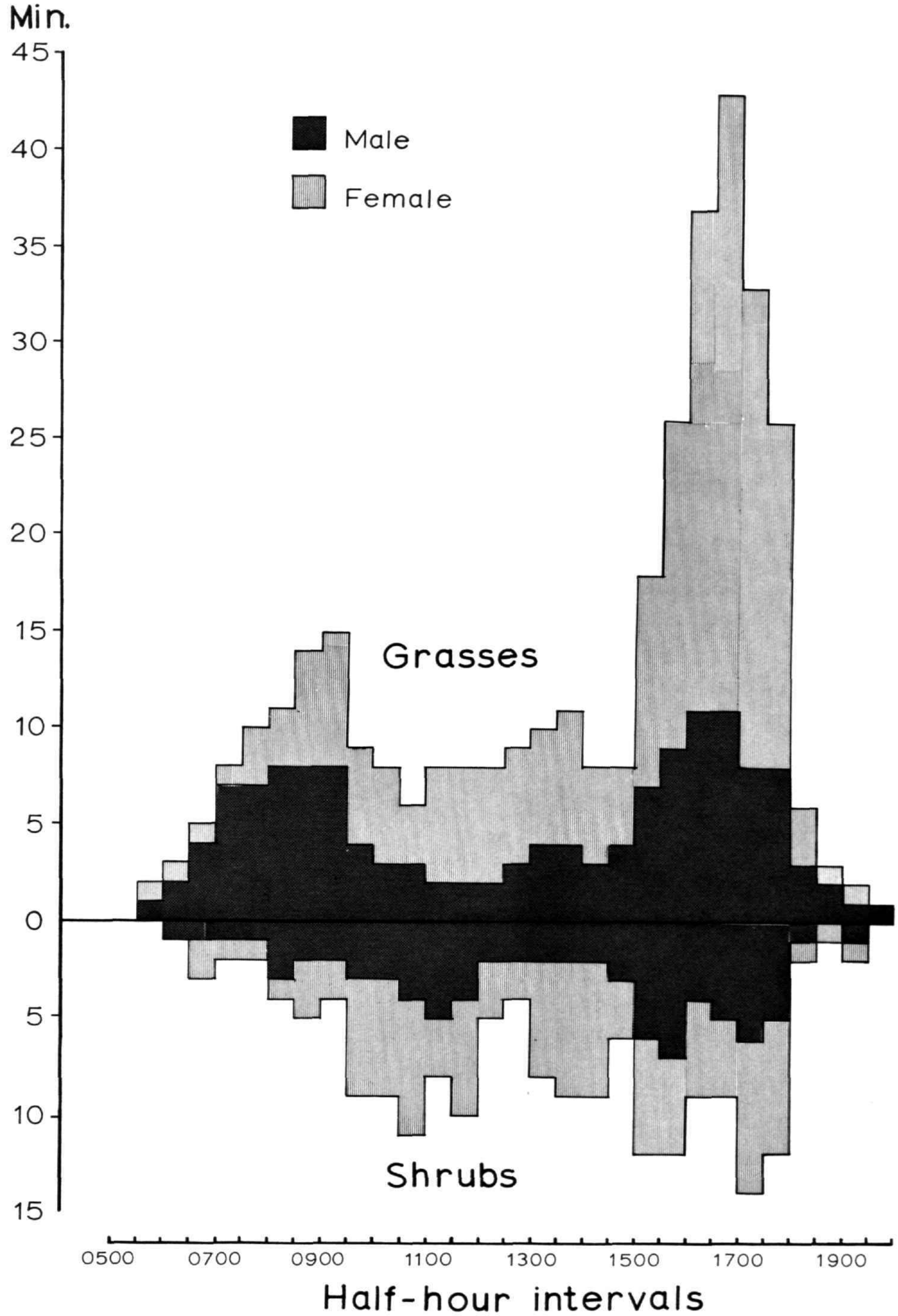


FIGURE 59.—Times at which elephants were observed feeding on grasses and shrubs in Gal Oya.

Table 17 shows the results for observations of elephants in Ruhunu National Park during 1967, classified according to different habitat types. As in Gal Oya, observations were more frequent in open habitats than in closed ones. Lahugala Tank (Figure 38) was more heavily used during the growing season than during the dry season. Since the major difference between the two seasons in the habitat is the lush growth of grass, which follows the onset of the northeast monsoon in November, it is obvious that the major attraction of Lahugala Tank for the elephants is the abundant supply of food. Similarly concentrated food supplies were found in an area of abandoned paddy land immediately south of the Amparai airport and during November and December of 1968, the entire herd from that area congregated in this one spot to feed for a period of three weeks, coming in every evening to the paddy.

TABLE 17.—*Number of elephants observed in various habitats of Ruhunu National Park, 1967*

Habitat type	*Males*	*Herds*	*Total*
Riparian forest	12	0	12
Medium-stature forest	2	0	2
Scrub with emergents	26	6	32
Scrub	3	4	7
Savanna	31	2	33
Grassland	32	7	39
Dunes	0	0	0
Water (tank, lagoon)	10	3	13

The important fact to keep in mind is that the elephants have a variety of vegetation types within this region of Ceylon and that they make use of all of them. Wing and Buss (1970) have reviewed the literature concerning the food habits and habitat utilization of *Loxodonta* and have concluded that the optimum habitat for that species is one which contains an interspersion of forest and grassland or savanna types. Their own study area contained 60 percent forest and 40 percent grassland—a ratio they considered to be close to the ideal. They (Wing and Buss, 1970:66) concluded that the declines noted in some East African elephant populations (e.g., Buss and Savidge, 1966; Laws and Parker, 1968) can be attributed to an imbalance in this ratio: "an increase in grassland probably favored the elephant population until browse reduction reached a threshold below which elephants ate grass in excess of their optimal nutritional requirements." They also state that under the optimal conditions, such as those present in their own study area, the elephant populations appear to be in equilibrium with their environment and no significant destruction of woody vegetation (as reported by Laws, 1970) occurs.

Thus it would appear that existing conditions in the Gal Oya region are very similar to those judged to be optimal in Africa. (For further similarities between my own data and those of Wing and Buss (1970), see page 96).

FOOD PLANTS

Table 18 lists the plants occurring in the Gal Oya area which were known to be used for food by the elephants (nomenclature after Abeywickrama, 1959). This is an extremely long list and includes a relatively large proportion of the total plants found in this area. Grasses were used extensively; the most important being *Brachiaria, Cymbopogon, Cynodon, Eleusine,* and *Imperata.* Most species of the genus *Cyperus* were not used but a relatively large-sized one abundant at Lahugala Tank was eaten extensively.

Bananas (*Musa*), paddy (*Oryza*), and sugarcane (*Saccharum*) were the three cultivated crops fed upon most frequently. The bananas and paddy are planted widely throughout the area, but the sugar is concentrated in one large plantation south of Amparai.

Of herbaceous plants other than grasses the most important is *Ipomoea* (Convolvulaceae). This genus includes several species which grow as herbaceous vines in the dry zone of Ceylon. *Ipomoea* is especially abundant in abandoned chenas, at ectones between forest and grassland and particularly in the drier areas of the banks of the Senanayake Samudra and other man-made tanks. *Mimosa pudica,* which is also heavily used by the elephant, is also abundant in these disturbed habitats.

Woody vines or lianas, such as *Hugonia* and *Cissus,* are occasionally eaten. With these plants the elephants generally pull down a large section of vine and eat the bark and stems rather than the leaves. The bark of *Feronia limonia* is frequently eaten during the dry season; that of *Pterospermum,* only occasionally. *Calamus,* a small shrub which grows along the banks of the Gal Oya, of which

TABLE 18.—*Plants eaten by elephants in the Gal Oya region.*

Family	*Species*
HERBACEOUS	
Gramineae	*Digitaria* sp.
	Brachiaria sp.
	Panicum repens
	Oryza perennis
	Oryza sativa
	Imperata cylindrica
	Saccharum officinarum
	Ischaemum sp.
	Cymbopogon confertiflorus
	Themeda sp.
	Cynodon dactylon
	Eleusine indica
	Eragrostis sp.
	Paspalum sp.
Cyperaceae	*Cyperus* sp.
Convolvulaceae	*Ipomoea* sp.
Leguminoseae	*Mimosa pudica*
	Crotalaria sp.
VINES	
Linaceae	*Hugonia mystax*
Loranthaceae	*Loranthus* sp.
Vitaceae	*Cissus quadrangularis*
TREES AND SHRUBS (Bark, roots, etc.)	
Rutaceae	*Feronia limonia* (bark)
Palmaceae	*Calamus* sp. (roots)
Musaceae	*Musa paradisiaca* (stem)
Sterculiaceae	*Pterospermum canescens* (bark)
TREES AND SHRUBS (Leaves and smaller stems)	
Ulmaceae	*Celtis cinnamomea*
Moraceae	*Fiscus* spp.
Anonaceae	*Polyalthia longifolia*
	Polyalthia persicifolia
Lauraceae	*Alseodaphne semecarpifolia*
Cappardiaceae	*Crataeva regiliosa*
	Capparis grandis
Leguminoseae	*Butea monosperma*
	Pterocarpus marsupium
	Cassia fistula
	Cassia roxburghii
	Bauhinia tomentosa
	Bauhinia racemosa
	Dichrostachys cinerea
	Acacia eburnea
	Acacia planifrons
Erythroxylaceae	*Erythroxylon moonii*
Rutaceae	*Glycosmis pentaphylla*
	Pleiospermium alatum
Meliaceae	*Aglaia roxburghiana*
	Chukrasia velutina
Euphorbiaceae	*Phyllanthus emblica*
	Drypetes sepiana
	Mischodon zeylanicus
	Bridelia retusa
	Macaranga peltata
	Dimorphocalyx glabellus
Anacardiaceae	*Mangifera zeylanica*
Celastraceae	*Elaeodendron glaucum*
Sapindaceae	*Lepisanthes trichocarpa*
	Glenniea unijuga
	Euphoria longana
Rhamnaceae	*Zizyphus oenoplia*
	Zizyphus xylopyrus
Tiliaceae	*Pityranthe verrucosa*
	Berrya cordifolia
	Grewia polygama
	Grewia tiliaefolia
Malvaceae	*Thespesia populnea*
Sterculiaceae	*Helicteres isora*
	Pterospermum canescens
Flacourtiaceae	*Hydnocarpus venenata*
Datiscaceae	*Tetrameles nudiflora*
Lecythidaceae	*Careya arborea*
Combretaceae	*Terminalia chebula*
	Anogeissus latifolia
Myrtaceae	*Syzygium aromaticum*
	Syzygium cumini
	Eugenia sp.
Melastomaceae	*Memecylon* sp.
Sapotaceae	*Mimusops elengi*
	Manilkara hexandra
Ebenaceae	*Maba buxifolia*
	Diospyros ovalifolia
	Diospyros oocarpa
	Diospyros malabarica
Longaniaceae	*Strychnos nux-vomica*
	Strychnos potatorum
Apocynaceae	*Carissa spinarum*
Boraginaceae	*Cordia domestica*
Verbenaceae	*Premna latifolia*
Rubiaceae	*Randia dumetorum*
	Ixora parvifolia
	Morinda tinctoria

only the roots and lower stems are eaten is occasionally uprooted. In areas such as the lower Mahaweli Ganga basin, where this palm is more abundant it is heavily used (Nettasinghe, pers. comm.). When elephants feed on the banana or plantain (*Musa*), they generally discard the leaves and outer portions of the stem, eating only the central part.

Several of the plants eaten by elephants (*Acacia*, etc.) have large spines. These may be broken before ingestion but are not removed from the stem. From a sample of 33 boluses collected in Ruhunu National Park during August 1967, 19 contained large numbers of *Acacia eburnia* spines, indicating heavy usage of this species.

The diet of the elephant includes a large proportion of twig and leaf material gathered from shrubs and smaller trees. Table 18 includes more than 60 species belonging to 30 families. This list is not intended to be a complete catalog of the plants used by the elephant, even in this region. Undoubtedly, a closer examination would reveal that elephants consume at least small amounts of most of the plants found in the area. The significant point is that the elephant is not a restricted feeder. It is capable of using many if not most of the tree species available to it. This does not imply that all plant species are eaten with equal frequency. Certain species, such as *Cassia fistula, Bauhinia racemosa, Euphoria longana, Helicteres isora,* are heavily used wherever they are abundant.

Fruits are occasionally eaten but, except in one instance when an animal was observed eating Tamarind (*Tamarindus indica*) fruits, these were generally consumed along with the leaves and twigs of the plant. It would thus appear that the majority of fruits are eaten accidentally in this way.

Table 19 shows the caloric densities determined for some of the more important food plants. The majority of these plants have caloric densities which vary between 3–4 Kgcal/gm. The grasses generally have a lower caloric value than the shrubs. This difference between caloric values of grasses and shrubs is probably due to the differences in chemical constituents (fats and proteins). These factors will be considered in more detail elsewhere (McKay, Kalpage, and Jayasinghe, n.d.).

TABLE 19.—*Caloric densities of selected food plants*

Part used	*Species*	*Kgcal/gm*
Leaves	*Celtis cinnamomea*	4.60
	Polyalthia persicifolia	4.85
	Polyalthia sp.	4.25
	Drypetes sepiaria	3.84
	Berrya cordifolia	4.30
	Grewia tiliaefolia	4.10
	Hydnocarpus venenata	3.79
	Careya arborea	3.88
	Diospyros oocarpa	4.29
	Ixora parvifolia	4.46
Leaves and Stem	*Digitaria* sp	3.01
	Cymbopogon confertiflorus	
	new	3.38
	green	3.87
	dry	3.75
	Cynodon dactylon	3.34
	Eleusine indica	3.59
	Eragostis sp.	4.18
	Carex sp.	2.96
Stem	*Loranthus* sp.	4.02
Bark	*Pterospermum canescens*	3.74

Chemical compositions were determined for eight species (4 grasses and 4 shrubs) at bimonthly intervals during 1969. The compositions of four grass species showed little variation throughout the year but *Cynodon* and *Brachiaria* had a relatively higher proportion of nitrogen-free extract to fiber than did *Imperata* and *Cymbopogon*. All of the shrubs sampled had a consistently higher proportion of protein in their leaves than did the grasses.

Four other species were examined, but not at regular intervals. Three (*Mimosa pudica, Bauhinia racemosa,* and *Phyllanthus emblica*) were legumes and contained a higher (2×) proportion of "crude protein." This figure was undoubtedly biased by the non-protein nitrogen present in members of this family. The fourth, *Eleusine indica,* a grass, resembled *Cynodon* in its composition. For further discussion of the differences in chemical composition of these plants the reader is referred to McKay, Kalpage, and Jayasinghe (n.d.).

FEEDING BEHAVIOR

An elephant, when feeding, seldom spends much time feeding on one particular plant species. The major exceptions to this are instances where the animals come out into the short grass zone of the banks of the Senanayake Samudra or other irrigation works in the area, which consists primarily of *Cynodon, Brachiaria,* and *Eleusine*. The other major exception noted to this was the animal marked as No. 2 (p. 82), who spent long periods of time feeding on *Mimosa pudica*. Otherwise, the general feeding pattern is to alternate between two or more different types of food (Figure 41). Table 20 shows a typical set of observations recorded from Ruhunu National Park of the time spent by elephants feeding on different types of food. These were recorded during 1967 and are expressed in animal minutes. As can be seen from this, the greatest amount of time spent was on feeding on short grasses including leaves, stems and roots. The

TABLE 20.—*Time spent feeding on various types of vegetation, Ruhunu National Park, 1967*

Food type	*April-May*	*June-July*	*July-August*	*Total*
Long grasses	62	28	18	108
Short grasses	1410	44	1110	2594
Leaves/twigs	29	12	40	81
Whole twigs	10	192	56	258
Fruits	0	10	1	11
Total	1511	286	1228	3025

next highest category was feeding on branches of trees or shrubs followed by feeding on long grasses. Figure 59 shows the amounts of time spent by elephants in the Gal Oya National Park feeding on herbaceous vegetation and shrub vegetation and again the majority of the observations are of feeding on grass.

Elephants take in relatively small amounts of food with each mouthful. These are gathered in the trunk, inserted into the mouth, and chewed prior to swallowing (page 45). On several occasions it was possible to collect handfuls of food that an elephant had dropped for one reason or another prior to inserting it in the mouth and when these were weighed it was found that the wet weight of such mouthfuls of vegetation, whether grasses or shrubs material, varied between 100 and 200 grams. I also collected, by visual comparison, bunches of grass and twigs which were estimated to be approximately the same size as those taken by elephants when feeding on different types of plants and these also weighed approximately 100 to 200 grams each. Based on Benedict's (1936:159–167) data on the food intake of Asiatic elephants and on observations made in Ceylon on captive animals, an adult elephant appears to have a daily food intake of approximately 150 kilograms wet weight per day. At an average weight of 150 grams per mouthful, this would mean that the elephant would have to take in approximately 1000 mouthfuls of food during a day's feeding. If the elephant were feeding steadily at the rate of one mouthful per minute, this would take approximately 17 hours or at two mouthfuls per minute 8.5 hours. Elephants vary the rate of feeding, but time spent in actual feeding would, by extrapolation from these data, be approximately 12 to 14 hours per day. As there are other locomotor components involved in the feeding, this time can then be expanded appropriately and it would appear that the calculations based on required food intake do not differ greatly from those of observations of time spent feeding (p. 58).

Using the average daily intake of 150 kilograms (wet weight) per day and allowing for the water content of the food (most plants measured averaged 40% dry matter, 60% water), the intake is approximately 60 kilograms of digestible material.

Using an average value for caloric density of 4 Kgcal/gm (see Table 19), this amounts to a daily caloric input of 240,000 Kgcal/day. With a digestive efficiency of 40 percent, according to Benedict (1936), this produces an estimate of digestible energy of 96,000 Kgcal/day. Benedict (1935:265) measured the resting metabolic rate of one large adult female *Elephas* and found an average of 65,000 Kgcal/day. Comparing these estimates it can be seen that if the data extrapolated from field observations is correct the elephant, in the wild, is existing on a daily caloric input only 50 percent greater than the resting metabolic rate.

From similar calculations, based on studies in Africa, Petrides and Swank (1965) have concluded that the elephant is a relatively inefficient herbivore in that it produces much less growth for the amount of plant biomass consumed than do voles, deer, or cattle, despite its larger standing crop. If, however, the elephants maintenance requirement is only 50 percent higher than resting requirement as opposed to 100 percent for ruminants (Crampton and Lloyd, 1959), it would appear that the elephant is more efficient with respect to maintenance. The significant point here, I feel, is that the stratagem of the elephant is to put energy into maintenance of a high standing crop (at the expense of rapid growth) while that of the ruminant is to put energy into growth and reproduction. Both are efficient for the maintenance of a population. In fact one could state that the elephant is more efficient in that it has a lower ratio of forage consumed to animal biomass than do the ruminants (Petrides and Swank, 1965) but I do not think it legitimate to compare the efficiency of maintenance of a standing crop to the efficiency of growth.

When feeding on shrub or tree vegetation particularly, the total amount of plant matter which is removed from the tree is not ingested. In fact a relatively large proportion is dropped to the ground. When feeding on some types of plants, this amount may be quite low but when feeding on others, a relatively large proportion of plant biomass may be discarded and not eaten. This occurs especially when the animals are feeding on bark, when they tear off an entire branch and consume only the bark of that branch. If then we consider the foraging efficiency of the animal to be the ratio of plant biomass eaten to the plant biomass removed but not ingested, this would appear to be on the average about 50 percent when feeding on the leafy matter of shrubs and trees. It will be higher, probably in the order of 80 percent, when feeding on grasses and much lower, in the order of 20 to 25 percent, when feeding on the bark of such plants as the wood apple (*Feronia limonia*).

The other factor which must be considered in connection with feeding behavior is the number or proportion of trees from which the elephant feeds. Detailed counts were not made of all trees fed upon in any of the plots sampled (page 18) but estimates were made using the scale: <5%, 5–10%, 10–25%, 25–50%, >50%. In all savanna plots sampled the amount of feeding on trees was estimated to be in the lowest category. In forest plots the relative amounts of feeding were estimated to fall within the second and third categories. Thus it would appear on the average that the elephants, although they eat a large percentage of the species present in an area, feed from only a small percentage of the individuals.

The feeding habits of the elephants in the Gal Oya study area show a remarkable similarity to those reported for *Loxodonta* by Wing and Buss (1970) both in the manner of feeding and in the types and amounts of food taken. That this differs from the observations of Buss (1961) and Buechner and Dawkins (1961) who found a great deal of destructive feeding and a diet consisting almost entirely of grass is attributed by Wing and Buss (1970) to greater elephant densities and habitat destruction by man-made fire in the areas studied in these earlier works.

It would appear then that under optimal conditions, both species show a variability in their diet, taking both herbaceous and woody material. Also they crop only a relatively small percentage of the plants in any area. That deviations from this norm can be ascribed to the influence of man now seems apparent. These latter factors are of great importance in any consideration of conservation of the elephant (pp. 101–105).

Density and Biomass

Considering now an area of 720 square miles which constituted the major study area, the overall density of elephants in this area is 0.43 animals per square mile (0.17/km²). If we consider only the undeveloped land, that is, leaving out agricultural land, village sites, and tanks, this amounts to a total area of 515 square miles. The density then is approximately 0.60 elephants per square mile (0.23/km²). Since some portions of the agricultural land are used by the animals especially at the onset of the rainy season, a more correct estimate of crude density would probably lie somewhere between these values, estimated to be in the region of 0.49 to 0.50 animals per square mile (0.19/km²).

Based on weights recorded for tame elephants by Kurt and Nettasinghe (1968) and allowing for the frequencies of different size classes, it is estimated that the average weight per elephant is about 4000 pounds (1800 kg). Using this estimate as a base, the total elephant biomass for the area is 600 tons and the average biomass density is 1.2 tons per square mile. As was demonstrated in Figure 22, however, the distribution of elephants within this area are not uniform and the crude density, which has been estimated above, does not necessarily apply to any particular area; these densities and biomass estimates will differ for each of the areas concerned. Density and biomass of elephants are highest in the regions around the Amparai airport and in the Hatpata area. Even breaking down the density and biomass on this basis does not give a true picture for any one time but simply the overall average for an annual period. As was discussed previously (pages 75–78) elephants spend relatively long periods of time in very small areas, so for any given day or week the effective density in any given area may be as high as 30 animals per square mile giving a biomass density of 50 tons per square mile.

The observed overall density of elephants in the Gal Oya region is similar to that reported by Eisenberg and Lockhart (1972) for Wilpattu (0.12/km²) and probably represents the average for Ceylon. Comparable estimates for other parts of Asia are not available but one can extrapolate from the data of Hislop (1961) and Stevens (1968) that the density in Taman Negara, Malaysia, an area of 1677 square miles (4300 km^2) with an estimated elephant population of 23 must be very low indeed.

Comparisons of estimates of densities reported for *Elephas* and *Loxodonta* are shown in Table 21.

TABLE 21.—*Comparison of biomass density estimates for* Elephas *and* Loxodonta

Region	*Density/km²*	*Authority*
Elephas		
Gal Oya, Ceylon	0.19	McKay (herein)
Wilpattu, Ceylon	0.12	Eisenberg and Lockhart (1972)
Uttar Pradesh, India	0.39	Singh 1969)
Loxodonta		
Albert National Park, Congo	0.2–3.36	Bourlière and Verschuren (1960)
Bunyoro, Uganda	3.43±1.00	Laws, et al. (1970)
Tsavo, Kenya	ca. 1.1	Laws (1969a)
Murchison North, Uganda	1.5	Laws (1969a)
Murchison South, Uganda	2.2–4.0	Laws (1969a)
Mkomasi, Tanzania	<1.0	Laws (1969a)

With the exception of the lowest estimate by Bourlière and Verschuren (1960) (which was only for one small part of Albert Park), all of the estimates for East Africa show densities 5 to 20 times greater than those existing in Ceylon. All of these areas censused have been in some way affected by man. Bourlière and Verschuren (1960) attribute the large elephant population of Albert National Park to immigration from surrounding areas. This view is supported by Hubert (1947) who reports an increase in the elephant population of a 1200 square kilometer sector of the park from 150 in 1931 to 500 in 1940. Similar increases are reported for other areas (Laws, 1970). These increases, and the problems they have caused, are at least in part a result of man's intervention (see page 42).

While the elephant is certainly the most important terrestrial herbivore in the Gal Oya National Park, it is not the only one. There are large populations of water buffalo (*Bubalus bubalis*), particularly in the eastern portion of the park and of wild boar (*Sus scrofa*) particularly on the eastern fringe of the park (Figure 60). Two species of deer also occur, the sambar (*Cervus unicolor*) and the axis (*Axis axis*), which are relatively thinly distributed throughout the entire region. Table 22 shows the estimates of the densities and biomasses of all the herbivores in the Gal Oya National Park and its immediate surroundings, a total area of 450 square kilometers, as determined during the wet season of 1968. During this period, it was estimated that an average of 100 elephants were using this area at any one time. The data for the other species are estimated of the total populations for these species within the intensively studied area. The elephant contributes almost one-half of the total herbivore biomass of this area during this period. The only other herbivore with a biomass density in the same order of magnitude is the water buffalo, the remaining herbivores contributing only about 20 percent of the total biomass. One fact should be mentioned at this

TABLE 22.—*Density and biomass of elephants and other herbivores in Gal Oya National Park and environs* (175 mi²)

Species	*Estimated total population*	*Mean weight (lb)*	*Numerical density (animals/mi²)*	Total biomass (lb)	*Biomass density* lb/mi²	kg/km²
Elephas maximus	100	4,000	0.6	400,000	2,280	405.0
Bubalus bubalis	470–500	600	2.6–2.9	280,000–300,000	1,600–1,820	282.0–320.0
Cervus unicolor	175–250	300	1.0–1.4	52,500– 75,000	300– 430	52.8– 75.7
Axis axis	250–300	100	1.4–1.7	25,000– 30,000	145– 170	25.5– 29.9
Sus scrofa	200–250	60	1.2–1.4	12,000– 15,000	72– 84	12.0– 14.8
Lepus nigricollis	2,650–3,500	5	15.0–20.0	13,250– 17,500	75– 100	13.2– 17.6
Presbytis entellus	1,500–2,000	10	9.0–12.0	15,000– 20,000	90– 120	15.8– 21.1
Macaca sinica	200–250	8	1.2– 1.4	1,600– 2,000	10– 11	1.8– 1.9
Total	5,545–7,850		32.4–41.4	799,350–859,500	4,752–5,015	808.1–886.0

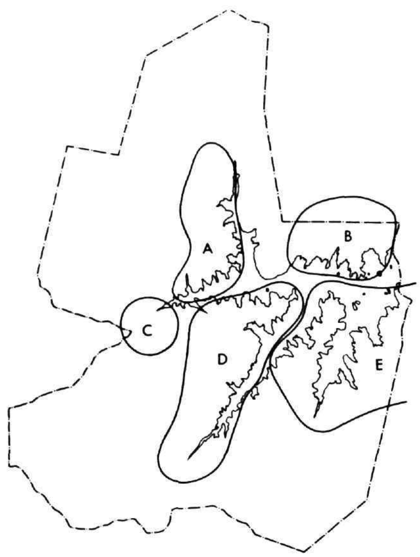


FIGURE 60.—Distribution of buffalo herds and wild boar in the Gal Oya National Park. A=50 buffalo; B=100 buffalo; 25-50 boar; C=10±buffalo; D=50-75 buffalo; E=250-300 buffalo; 100-125 boar.

time—more than half of the buffalo in the eastern sector of the National Park are tame animals that are herded by villagers from Dewalahinda and other surrounding villages and grazed in the national park.

These data give an indication of the relative effects of the different herbivores on the vegetation. The elephant is a generalized feeder, feeding on ground vegetation and on woody vegetation up to a height of approximately 10 feet. The buffalo is primarily a grazer although it does take some browse and the wild boar is partially a grazer but feeds mostly on the roots and tubers which it digs up out of the ground. The axis and sambar within this area are almost totally browsers; they seldom come out into the grassy areas to graze. The hare (*Lepus nigricollis*) is a grazer and the gray langur (*Presbytis entellus*) is an arboreal herbivore which would be considered a browser in that it feeds quite extensively on the leaves of trees and shrubs although it does occasionally come down to the ground where, among other things, it feeds extensively on the flowers of *Mimosa pudica*. Considering the relative biomasses of these various herbivores, the competition with the elephant for browse is relatively slight, whereas the competition from the buffalo for grass is quite heavy (page 90).

Table 23 shows a comparison of the biomass densities in Gal Oya with those in Wilpattu as reported by Eisenberg and Lockhart (1972). The total biomas at Gal Oya is only slightly larger than that at Wilpattu. The major difference between these two areas is not in the presence or absence of certain species but in their relative abundance. Buffalo are more numerous in Gal Oya while all species of deer are more numerous in Wilpattu.

TABLE 23.—*Comparison of biomass densities (kg/km²) in Gal Oya and Wilpattu National Parks*

Species	*Gal Oya*	*Wilpattu* *
Elephas maximus	405.0	217.2
Bubalus bubalis	282.0–320.0	73.4
Cervus unicolor	52.8– 75.7	157.9
Axis axis	25.5– 29.9	262.8
Muntiacus muntjak	**	5.9
Tragulus meminna	**	1.9
Sus scrofa	12.0– 14.8	8.1
Lepus nigricollis	13.2– 17.6	14.9
Hystrix indica	**	5.3
Presbytis entellus	15.8– 21.1	19.0
Macaca sinica	1.8– 1.9	**
Total	808.0–886.0	766.4

*Data from Eisenberg and Lockhart (1972).
**Not estimated.

The reasons for this difference in the abundance of deer would seem to be in the suitability of the habitat. The low scrub vegetation in Wilpattu is probably capable of supporting more of these browsers than is the forest of the Gal Oya region with its relatively sparse understory. Mr. C. S. Wickremasinghe, Divisional Game Ranger, Inginiyagala, has stated (pers. comm.) that deer have always been scarce in the Gal Oya region and there is no evidence to show that any disturbance or shooting during construction of the dam at Inginiyagala caused a decline in numbers. More detailed studies of the deer (primarily *Axis*) will be needed to attempt to answer this question.

The only comparable data from mainland Asia are those of Schaller (1967) from India. He found biomass densities of wild ungulates in Kanha National Park to be in the order of 600–700 kg/km². With domestic stock added the total biomass density for this area is 2400–2500 kg/km². Without the domestic stock, his data are comparable to ours from Ceylon.

Spillett (1966) estimated the numbers of ungulates in the Kaziranga Sanctuary, Assam. Using his data it can be estimated that the biomass density of herbivores in that region is about 3800 kg/km^2. As his figures for elephant seem unusually high, probably representing a seasonal concentration, a more reasonable estimate would be in the order of 2000–2500 kg/km^2.

The literature on biomass densities of ungulates in Africa is quite large and includes several reviews (e.g., Bourliére, 1963a, b; DeVos, 1969), but as emphasized by Talbot (1964) the variety of means by which various authors arrived at their estimates makes any meaningful comparison difficult. An adequate treatment of this subject would require more space than can reasonably be included in this discussion. As such it is necessary to only emphasize that a wide variety of biomass densities have been reported (see Bourlière, 1963a), the variety of which is influenced by many factors including the influence of man and his domestic animals (DeVos, 1969). Some communities appear to be able to support a larger standing crop of ungulates than others but, as DeVos (1969) adequately emphasizes, more detailed research is necessary before we can understand the factors causing such differences.

If the situation in Africa is unclear, the situation in Asia is moreso. We do not at the moment have sufficient data to make meaningful comparisons between habitats within that continent. Without such data, and without a more detailed study of the primary and secondary productivity of areas such as Gal Oya, it is not possible to assess what the carrying capacity of an area like Gal Oya should be.

Effects on the Habitat

The elephant produces several effects on the habitat which, besides affecting the plant communities themselves, can affect other animals living in the same area.

Water Holes and Trails

Elephants frequently dig holes in sandy stream-beds during the dry season (see page 47). Mongooses were observed in the vicinity of such water holes and it seems likely that they will also be used by deer, monkeys, and other mammals.

Trails which are used and maintained primarily by elephants are regularly used by other terrestrial mammals. A list of species encountered by us along such trails includes: buffalo, sambar, boar, leopard, and mongooses. Man, of course, also makes use of thes trails.

Effects Associated with Feeding

In general an elephant when feeding on a tree or shrub does not tear down the entire plant; rather it tends to remove small twigs, and for certain species, entire branches. In the plots surveyed around the Gal Oya area (see page 18), the relative proportions of trees and shrubs fed upon by elephants were found to vary between 10 and 25 percent of the total trees in the area (see page 96). This would appear to be somewhat lower than those data obtained by Eisenberg and Lockhart (1972) for Wilpattu and Mueller-Dombois (n.d.) for Ruhunu National Park. As discussed by Mueller-Dombois (n.d.), the patterns of feeding by the elephant can in some instances alter the shape and form of the tree. This is particularly true of low growing trees and shrubs where the elephant has access to the crown rather than simply to the lower branches. Species which are particularly affected in this way are *Feronia limonia* and *Dichrostachys cinerea*. As was mentioned, a few species of trees may be broken down completely. One species in the Gal Oya area that is particularly broken down in this manner is *Bauhinia racemosa*. Several instances were found where the elephants had broken this tree down but the tree remained growing in an almost horizontal position (Figure 61). This species of plant seemed particularly resistant to total destruction by the elephant whereas some other species which were broken completely, such as *Terminalia chebula* and *Anogeissus latifolia*, died after being broken.

The amounts of food which an elephant consumes must have an effect on the plant community. Based on the estimate made earlier of a daily food intake for a mature (4000 kg) elephant of 150 kg/day the annual consumption of food will be 55,000 kilograms. Correcting this value for the average size of elephants in this population gives a value of 27,500 kg/animal/yr. At the observed

FIGURE 61.—*Bauhinia racemosa* shrubs broken down by elephant, Amparai, August 1969.

density, and with an average feeding efficiency of 50 percent, the plant biomass "used" by elephants will be approximately 27,500 kg/mi^2 (approximately 10,500 kg/km^2).

As mentioned earlier, not all the plant material pulled from a tree is eaten by the elephant. Buss (1961), Buechner and Dawkins (1961), and others have described how various ungulates may browse upon branches removed from trees and left on the ground, thus gaining access to material which otherwise would not be available to them. No instances of this were observed during my study, but the possibility cannot be denied. Besides providing these potential symbiotic relationships, the removal of branches by elephants could make them potential competitors with primates. Struhsaker (1967) in his study of the vervet monkey in East Africa found that the greatest competitor for food was the elephant. Regardless of their usefulness to other mannals these broken branches are readily used by termites.

The effects of feeding do not end with ingestion. As stated previously (page 50), an adult elephant defecates approximately 18 to 20 times a day, producing some 180–200 kilograms of feces. These feces are fed upon by a variety of insects. In Ruhunu National Park especially, and in most of the drier areas of Ceylon, dung beetles (Carabidae) are extremely common and at least three species of these carabids were observed to feed upon the dung of the elephants. Another insect which was found to feed on elephant dung was termites. The termites frequently invade a bolus of feces and on two occasions were observed over a period of days to begin construction of a nest beneath a pile of feces. On both of these instances, the feces were in a roadway of dry compacted earth. One of them unfortunately was destroyed at a relatively early stage by vehicular traffic but another one on an infrequently traveled road grew to the size of a typical termite mound. Although there are very few data to support this, it would appear that the elephant dung deposited on trails is very frequently used by termites in establishing new colonies. Several instances were observed where termite mounds occurred in the pathway used by elephants. After the termite mound has grown, the elephant pathway is diverted around the side.

A further effect that the elephant can have on the environment is in the distribution of plants by ingesting the seeds when feeding on branches. Observations from feces collected in Ruhunu National Park and in the Gal Oya area during 1967 and 1968 showed that seeds were present in anywhere from 40 to 80 percent of the samples of feces. In most of these instances, the seeds were entire, the seed coat not having been broken and it seems quite possible, as discussed by Hladik and Hladik (1967), that these seeds would remain viable although no tests of the viability were made. In this way the elephant can act as a potential distributing agent for many of the species which it feeds upon.

The final effect of elephant on habitat is crop-raiding, which is as much the effect of man as of the elephant. (For further discussion of this aspect see pages 102–103).

Elephant and Man

The Current Problems

Agriculture and Movements

As was mentioned in the description of the study area, the Gal Oya valley has been subjected to rapid agricultural development over the past 25 years. Figure 17 shows the distribution of agricultural land in the vicinity of the Gal Oya study area as of 1969 and projected areas of expansion for the 1970s. As can be seen from this map, the greatest amount of agricultural development has been concentrated along the coastal strip and in the vicinity of Amparai, with a second major block of paddy land between Amparai, Namal Oya, and Inginiyagala. Smaller blocks already developed exist in the region along the irrigation canal coming from Jayanthi Wewa and in the vicinity of Ekgal Aru. Development plans call for a further extension of agricultural development in the areas north of Amparai and south and east of the present limits of agriculture between Inginiyagala, Ekgal Aru, and Ambalam Oya. The development areas around Ambalam Oya were already under construction in 1969. At the moment concrete plans for development are in existence only for the drainage of the Gal Oya valley, although plans without any definite timetable also exist for development of the Heda Oya which drains past Lahugala Tank towards Pottuvil on the east coast. Smaller isolated patches of agriculture exist around Buddama, Baduluwela, Bulupitiya, Mullegama, Siyambalanduwa, and a few other small villages. The Gal Oya region is bounded on the west by agricultural land in the vicinity of Bibile and Moneragala. The land around Bibile itself is developed primarily for paddy although as one moves west from Bibile into the hills, tea becomes predominant, while around Moneragala the primary crop is rubber.

The herd that inhabits the areas surrounding the Amparai airport, north of the town of Amparai, is at present almost completely surrounded by agricultural land. The Hatpata herd, which inhabits the southeastern sector of the Gal Oya National Park, while not completely surrounded by agriculture, is affected by the presence of paddy cultivation along the Pallang Oya and around the Jayanthi Wewa reservoir. Considering this latter herd first, it was observed during the period of this study that the various groups that constituted this herd did tend to move directly eastward from the National Park area itself into that section of land which has been slated for development lying between Inginiyagala and Ekgal Aru. At the time of this study, the elephants were known to raid the paddy fields of the Pallang Oya development area and the cultivated areas of an agricultural settlement area which was established at Ekgal Aru. It seems highly probable that with increased expansion of agricultural land in this particular area the amount of crop raiding by this herd will increase and the numbers of elephants in this herd will probably be reduced by shooting on the part of the cultivators.

Considering now the Amparai airport herd, Figure 62 shows the eastern portion of the home range of this herd with the areas of agricultural land and natural vegetation demarcated. The dashed arrows on this map indicate the commonest routes of movement between sectors of the home range used by the elephants during 1968 and 1969. These, as can be seen, pass through two narrow necks of natural vegetation between areas of agriculture and one actually passes through a narrow belt of agri-

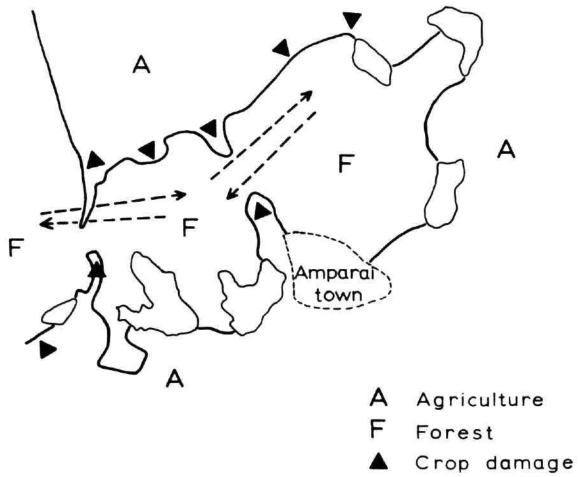


FIGURE 62.—Movements of the Amparai airport herd in relation to agricultural land. Triangles indicate sites at which crop damage occurred during 1968-1969.

culture along the irrigation canal. In this latter area, the land on the eastern side of the channel was only opened for agriculture during 1967 and 1968 and by the end of 1969 the elephants were still using this newly opened land as a regular pathway. The presence of men in this area did not appear to deter the elephants at all from moving through.

According to observations made by Mr. Bevis Ekanayake, the Game Ranger from Inginiyagala, and Mr. Joe Pereis, the Public Relations Officer for the River Valleys Development Board at Amparai, the members of this herd were at one time accustomed to move towards the south along the narrow belt of forest between Kondavatavan Kulam and Amparai Kulam, the two tanks which are situated to the west of Amparai town. In the early part of the 1960s the land to the south of these two tanks was developed in part for paddy and in part as a sugarcane plantation and for several years after the initiation of these projects, the elephants would move southward through this neck of forest in order to feed in the paddy and sugarcane. Several attempts were made during the 1960s to discourage the elephants from coming down in this direction including an attempt to drive the elephants toward the west, and the erection of an electric fence running along a line between the two tanks about a half mile north of the main road. According to Mr. Ekanayake, the drive was without result, but after several years of operation, the electric fence has proved to be a sufficient barrier and the elephants are no longer a problem in the fields to the south of this region. During the period of this study, no movement of elephants into this area was observed. A second stretch of electric fence was constructed between the western edge of Kondavatavan Kulam and the limits of the village of Paragahakelle, approximately two miles to the west, in a further attempt to limit the southward movements of this herd. As far as limiting the movements of the herd, this particular fence would seem to have been effective, but between 1967 to 1969 sectors of the fence were broken down on three occasions by solitary males who inhabit the area around Kondavatavan and Himidurawa Tanks.

Further experiments with electric fences have been made by the River Valleys Development Board including the erection of a fence around the sugarcane in the vicinity of Ambalam Oya and along the Namal Oya to the north of the town of Inginiyagala. These two fences have met with varying success in that herds were frequently known to break them down in order to pass through during 1967 and 1969.

Crop Raiding

Except for those few observations outlined above, the majority of times that elephants were known to come out into agricultural land were for purposes of feeding rather than for movement through the agricultural land. As one example from the Amparai airport herd, the black triangles in Figure 62 show the locations of crop damage by these elephants during 1968 and 1969. The areas where crop damage occurred were distributed on both the north and south sides of the range of this herd although the most severe damage was incurred in the three westernmost areas on the north side around the Amparai airport itself. The westernmost of these was in the region of the Youth Scheme agricultural area at Mahakandiya on the western side of the Left Bank irrigation channel. The second was a small development area immediately to the south of the airstrip; this particular village was abandoned by the villagers in 1968 as a direct result of the continued depredation on their crops by the elephants. The villagers then moved to the area to the south of Mahakandiya directly along the Left Bank channel which is right in the center of the main migratory path of this herd. The results of this unfortunately short-sighted move will undoubtedly be evident even by the time of this writing.

Unfortunately no data exist on the financial loss caused by these crop raids and no such records are kept by the River Valley Development Board, but my own observations during 1968 indicated that approximately 350 to 400 acres of paddy land were either disturbed or rendered unproductive by the elephants constituting this single herd.

Crop raiding by elephants in the Gal Oya area is not restricted to this one particular location. It occurs also in the areas around Paragahakelle, Namal Oya, Ekgal Aru, and the Pallang Oya development. In all of these locations, the animals known to come out and feed on the crops consisted of both solitary males and herds. Such raids by elephants on paddy land invariably occur at night and a variety of devices used by the villagers to attempt to frighten the herds including fires, noisemakers of various kinds, shouting, and the discharge of firearms, often prove to be ineffective especially towards solitary adult males. One particular adult male terrorized the villagers in the region of Pallang Oya during March and April of 1969. Whenever the cultivators from this village attempted to frighten the animal off by shouting or flashing lights, he would respond by attacking and over a three week period damaged approximately 25 buildings on the outskirts of the village.

In many parts of this region, the defenses taken by cultivators towards the depredations by elephants are not restricted to fires or noise-making devices. In fact, as is indicated by the large number of elephants throughout the area who carry visible cysts and wounds on the body and the observation that 8 out of 14 elephants known to have died in the area died as the result of gunshot injuries, it is obvious that shooting of elephants is widespread throughout the region. It would appear that, until more adequate nonlethal devices are in general use for deterring elephants from invading paddy land, the high mortality from gunshot injuries will continue for some time.

At the time of this study there were no herds in the Gal Oya area which did not come into contact with agricultural land and cause at least some crop damage.

Competition from Domestic Stock

There are some 200 domestic buffalo being grazed within the Gay Oya National Park (see pages 97–98). These animals quickly reduce the grass on the banks of the Senanayake Samudra to the point where elephants must scarify the ground in order to feed on the short grass.

In the Amparai sanctuary there are large numbers of domestic stock which compete in a similar manner for the grasses there. If the trends observed during 1967–1969 continue in this area, the combination of heavy grazing and frequent fires will probably lead to a degradation of this savanna type by reduction in the abundance of shrubs and replacement of native grasses by the less palatable *Imperata cylindrica*.

THE OUTLOOK

The problem faced at the moment has two aspects: How to maintain a population of elephants, and how to maintain an ecosystem?—neither of which can be considered alone. As the human population of Ceylon is increasing, more food, and thus more agricultural land, is required annually. As the production of food for human consumption and the maintenance of natural ecosystems are competitive there is an urgent need for the assignment of priorities. Decisions must be made concerning the amount of land that can reasonably be preserved in a natural state. As emphasized over a decade ago by Norris (1959), these decisions must be based on a knowledge of the various factors affecting the ecosystems under consideration.

Rapid, unplanned agricultural expansion can result in the destruction not only of the land "developed" but of land intended to remain under natural conditions. That such has happened in East Africa has been well documented by Glover (1963), Laws 1969b, 1970), and Laws, et al. (1970). A combination of factors, including the forced movement of elephants into reserves as a result of agricultural expansion along with man-made fires and suppression of poaching, have resulted in large increases in the elephant populations of many East African reserves. In many of these (especially Tsavo and Murchison Falls) the increasing pressure from the elephants has resulted in drastic degradation of the plant community, reducing savanna and even forest to grassland. There is evidence to show that the elephants may be capable of responding to such changes by regulating their population increases (Laws, 1969a, b) and even evidence that there may be a long-term cycle of which the present trend is only a part (Boughey, 1963; Laws, 1969a); but as reserves get smaller the probability of such habitat degradation leading to the extinction of entire faunas increases.

The question then is how can Ceylon benefit from the experiences of Africa? With regard to the elephant, the first approach to this question is to determine what size of population is to be maintained. Once this has been determined the next step is to delimit an area known to contain one or more herds approximating that number and containing their entire annual ranges and securing such an area as a park or other reserve. It would be extremely naive to assume that this is all that must be done. These are only the first steps in a continuing process, but as the present urgent need is rapidly becoming a crisis these are measures which must be taken immediately. The often-heard plea of "let us not do anything until we know everything" (see Harthoorn, 1966) has no place when an approximate solution can at least allow time to investigate the finer details (Laws, 1969b).

The following recommendations are, admittedly, approximate, being based on a preliminary study. The data reported in this study represent little more than two years observation of elephant ecology in the Gal Oya region. That continued research is needed, particularly on the seasonal movement patterns, food utilization, and effects on the plant community, cannot be overemphasized. Nevertheless, it is my opinion that, if certain measures are taken as soon as possible and if research is continued to augment and revise these plans, then a population of elephants and a unique ecosystem can be maintained in the Gal Oya valley.

RECOMMENDATIONS

1. No herd of elephants spends the entire year within the present boundaries of the Gal Oya National Park (Figure 22). The boundaries of the park must be extended or some measure taken to halt the expansion of agriculture into the dry season ranges of the herds that are to be maintained. If all four herds which currently use the park are to be maintained, then the park boundaries must be extended to the north, west, south, and southeast. As the land to the north is generally unsuitable for agriculture, such an extension might be limited to the west, south, and southeast with little danger to the northern herd.

2. A buffer zone should be established between the park and areas of extensive agriculture. Within this buffer zone the only form of agriculture which should be allowed is the chena. Restricted chena rights within this zone could be given to those villagers already resident in the areas around Baduluwela, Buddama and Bulupitiya. The buffer zone should be outside the normal home ranges of the herds or at least on their fringes. Some crop-raiding within this zone will be inevitable but the presence of the buffer itself should cut down or eliminate raids on paddy fields outside the zone.

3. If crop raiding should continue beyond the buffer zone into areas already settled and in areas where such a zone is impractical (Pallang Oya, Namal Oya), further experimentation should be made with the use of electric fences which have proven effective as long as they are regularly patrolled and maintained.

4. All grazing of domestic stock within the park (and the buffer zone) must be stopped. Grazing by domestic buffalo was the only adverse effect recorded in the park and other than this measure no other form of control over potential competitors is immediately necessary.

5. No attempt should be made at the present time to suppress fires in the Talawa savanna. Research should be undertaken on the optimum frequency of burning so that in the future, productivity can be maintained at an optimal level. But until such information is available, the present conditions should be allowed to prevail.

Burning of areas other than the Talawa should be suppressed. The fishermen who use the Senanayake Samudra should not be permitted to remain ashore and light fires in the short-grass zone.

6. Unless all further agricultural expansion within the Amparai sanctuary is halted the herd inhabiting the area around the airport is doomed. Two alternatives are open.

a. Halt all further agriculture within this area and relocate the villagers who have already settled along the Left Bank channel. In this way the herd will be able to maintain its normal movement patterns. In addition, the presently large herds of domestic cattle grazed in the area must be reduced. These steps will not eliminate the crop damage caused by these animals but they will ensure survival of the present level of interaction.

b. If expansion of agriculture in this area cannot be halted and eventually reversed to provide even a narrow buffer zone, then the elephants should be removed. This population is so small and has no other refuge so further interaction will inevitably be detrimental to both the elephants and man. A kraal should be held under supervision of the Department of Wild Life Conservation and the animals, once tamed, sold at auction. No attempt should be made to drive these animals into the National Park.

7. Further research is needed, but the suggestion made by Norris (1959) for an "elephant corridor" between Ruhunu National Park and Lahugala Sanctuary should be examined seriously as this may well afford protection to a further population of about 150 elephants. If this is to be done, the Lahugala Sanctuary itself should be expanded and elevated to the status of National Park.

At the time of this study the populations of elephants and other mammals in the Gal Oya National Park and surrounding areas were in a relative state of equilibrium. A certain amount of poaching on sambar and buffalo existed but the Department of Wild Life staff were already in the process of attacking the problem. If at least the first five recommendations listed above are considered and followed, this equilibrium can be maintained. The Gal Oya National Park offers more than a unique ecosystem, worthy of conservation for that reason alone. The lake, surrounded by abrupt, rugged hills, the ever-changing distant view of the central mountain range, the sunsets which each day are never the same, the immense flocks of water-birds, all combine to make any visit, however short, to this area a unique esthetic experience. Perhaps it is this view, rather than the coldly ecological one of the need to provide a habitat for one spectacular species which will ultimately prove the more important argument for the preservation of this area. If the elephant should be a symbol for both views, its continued existence here will be essential and must be assured.

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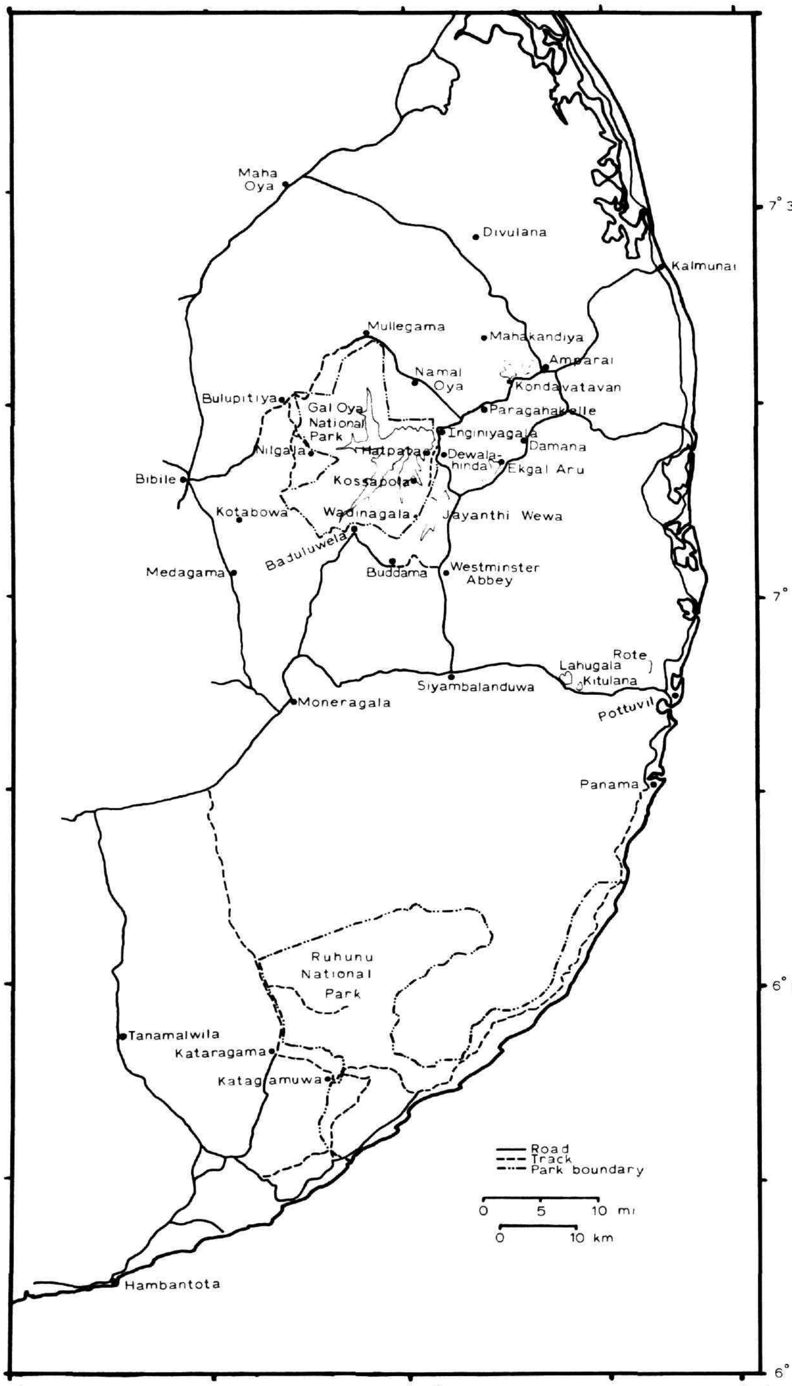

FIGURE 63.—Map of southeastern Ceylon showing some place names used in text.

Appendix 1: *Gazetteer of Place Names Used in Text*

Name	*Latitude* °	′	*Longitude* °	′	*Name*	*Latitude* °	′	*Longitude* °	′
Akkaraipattu	07	13	81	51	Kossapola	07	09	81	30
Alutnuwara	07	19	80	59	Kotabowa	07	06	81	17
Ambalam Oya	07	10	81	46	Kumana	06	31	81	42
Amparai	07	17	81	40	Kumbukkan Oya	06	30	81	42
Amunuhela	07	17	81	19	Lahugala	06	54	81	42
Andella Oya	07	28	81	43	Maduru Oya	07	52	81	31
Baduluwela	07	05	81	43	Mahakandiya	07	21	81	34
Batticaloa	07	43	81	42	Maha Oya	07	32	81	21
Bibile	07	10	81	13	Mahaweli Ganga	08	27	81	13
Buddama	07	12	81	29	Medagama	07	02	81	16
Bulupitiya	07	15	81	20	Menik Ganga	06	22	81	31
Bulupitiyahela	07	15	81	19	Moneragala	06	52	81	20
Damana	07	12	81	39	Mullegama	07	20	81	27
Daniagla	07	15	81	23	Namal Oya	07	16	81	31
Dewalahinda	07	10	81	34	Navakiri Aru	07	28	81	43
Divulana	07	28	81	35	Nilgala	07	11	81	22
Ekgal Aru	07	15	81	42	Palatupana	06	17	81	24
Embilipitiya	06	20	80	51	Pallang Oya	07	07	81	32
Gal Oya	07	18	81	46	Panama	06	45	81	48
Gal Oya National Park	07	11	81	29	Pannela Oya	07	08	81	47
Gonagala	06	20	81	27	Paragahakelle	07	15	81	36
Hambantota	06	07	81	07	Passara	06	56	81	09
Hambegamuwa	06	32	80	57	Pottuvil	06	52	81	50
Hatpata	07	10	81	32	Rote Kulam	06	55	81	48
Heda Oya	06	50	81	46	Ruhunu National Park	06	21	81	27
Heen Wewa	06	21	81	26	Senanayake Samudra	07	11	81	29
Himidurawa	07	17	81	36	Sengamuwa	06	54	81	46
Iginiyagala	07	13	81	32	Siyambalanduwa	06	54	81	33
Jayanthi Wewa	07	08	81	33	Tanamalwila	06	26	81	08
Kalmunai	07	25	81	49	Tangalle	06	01	80	48
Karanda Oya	06	55	81	45	Timitar	07	01	81	52
Katagamuwa	06	24	81	24	Tirrukkovil	07	07	81	51
Kataragama	06	25	81	20	Wadinagala	07	07	81	32
Kirindi Oya	06	12	81	18	Wellawaya	06	44	81	06
Kitulana	06	53	81	23	Westminster Abbey	07	02	81	32
Kondavatavan Kulam	07	17	81	38	Wila Oya	06	46	81	48
					Yala	06	22	81	31

Appendix 2: *Data on Flapping of Ears*

Weather	*Animal*	*Date*	*Time*	*Fans/Bout* ($\bar{x}$ *of 5*) *before/after*	*Interval* (*sec.*) ($\bar{x}$ *of 5*)	*Ears extended* *
RAIN	Ad-D	121267	1430	1.2/1.3	8.1	–
				1.0/1.0	3.1	–
	Ad-L_{13}	191267	1100	0.8	11.7	–
	$\bar{x}$			1.0	7.6	
OVERCAST Wind=0	Ad-ht	210767	1510	1.5/1.6	5.0	–
	Ad-ht	210767	1600	2.1/1.2	7.3	–
				1.5/2.0	5.6	–
				1.2/1.0	5.3	–
	Ad	210767	1510	1.4/1.2	2.5	–
				2.6/2.8	1.8	–
	Ad	210767	1600	3.8/2.8	2.2	–
				2.4/3.2	2.8	–
	Ad-L_{10}	191267	1300	3.6/5.4	3.4	–
	Ad-L_5	191267	1300	1.0/1.2	10.4	–
	Ad-L_6	191267	1300	1.4/1.2	5.8	–
	$\bar{x}$			2.4	4.7	
	SA	210767	1510	3.5/3.4	2.2	–
				7.5/9.0	2.2	–
	SA	210767	1600	3.8/2.6	3.3	–
				6.6/5.2	2.5	–
	SA-T	210767	1600	2.0/2.4	3.8	.
				1.6/2.4	3.5	–
	SA	210767	1130	4.2/5.4	4.8	–
				3.4/5.1	3.7	
	$\bar{x}$			4.2	3.25	
OVERCAST Wind=1	Ad ht	190767	1545	1.2	7.5	–
				1.4	15.4	–
	Ad	190767	1545	2.0	3.6	–
				1.9	4.2	–
	Ad	210767	0825	1.8/1.6	5.9	–
				0.9/1.2	3.3	–
	Ad	210767	0830	2.4/2.4	4.8	–
				2.0/2.4	5.5	–
	Ad-D	121267		1.2/1.0	4.0	–
				1.2/1.2	5.9	–
	Ad-L_8	121267		1.9/1.4	13.6	+
				0.9/0.9	5.4	+
	$\bar{x}$			1.6	6.6	
	SA-t	190767	1545	1.7	8.8	–
				1.6	8.2	–
	$\bar{x}$			1.65	8.5	

Appendix 2:—Continued

Weather	Animal	Date	Time	Fans/Bout ($\bar{x}$ of 5) before/after	Interval (sec.) ($\bar{x}$ of 5)	Ears extended *
OVERCAST						
Wind=2–3	Ad-ht	190767	1705	1.1	11.9	–
		230767	1600	1.0/1.0	2.9	–
				1.2/1.0	4.0	–
	Ad	230767	1600	–	–	Stands with ears extended 10 min.
	$\bar{x}$			1.1	6.3	
	SA-T	190767	1705	1.2	5.3	–
				1.7	4.0	–
	SA-T	230767	1600	1.0/1.0	9.2	–
	SA-t	190767	1705	2.2	6.4	–
	$\bar{x}$			1.5	6.2	
SUN						
Wind=1	Ad=ht	190767	1110	3.2	4.8	–
	Ad-ht	230767	1100	1.6	3.8	–
				1.1/1.6	7.0	–
				1.1/1.1	6.2	–
	Ad	230767	1100	2.0/2.0	2.8	–
				2.4/2.0	5.8	–
	Ad-pt	230767	1100	1.0/1.2	4.9	–
				1.2/1.0	7.9	–
	$\bar{x}$			1.7	5.5	
	SA-T	230767	1600	1.6/1.4	2.0	–
	SA	230767	1550	1.6/1.6	6.4	–
				1.8/1.4	6.1	
	$\bar{x}$			1.7	4.8	
SUN						
Wind=2–3	Ad	230767	0755	2.2/1.0	19.7	+
				2.0/1.9	8.6	+
	Ad-ht	230767	0820	3.0/3.0	112.0	+
				2.8/2.2	25.5	+
	$\bar{x}$			2.5	41.4	
	SA-T	190767	1035	2.2	3.1	–
				2.2	3.3	–
	SA-T	230767		2.2/2.0	19.9	–
				3.6/2.6	18.3	–
	SA	230767		3.0	8.6	–
				4.2	3.0	
	$\bar{x}$			2.9	9.5	

* + = yes; – = no.

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