

Eisenberg '74
McKay

Reprinted from

The Papers of an International Symposium on

The Behaviour of Ungulates and its relation to management

THE UNIVERSITY OF CALGARY,
ALBERTA, CANADA

2-5 November 1971



Union Internationale
pour la Conservation de la Nature
et de ses Ressources

International Union
for Conservation of Nature
and Natural Resources

Morges, Switzerland, 1974

Movement Patterns and Habitat Utilization of Ungulates in Ceylon

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ABSTRACT

In order to develop accurate biomass estimates for the ungulate populations resident in two of Ceylon's National Parks, special attention was devoted to the seasonal movements of the dominant species. The two study areas differed with respect to climate, vegetation and the distribution of water; hence differences in movement patterns of the two study populations could often be related to the specific patterns of resource distribution. Seasonal shifts in grazing by elephants and buffalo could give fluctuating biomasses for small sample areas ranging from 750 to 2,900 kg/km². Average biomass estimates for the study areas in Ceylon are in reasonable agreement with comparable studies in India and Java, but far lower than biomass estimates for the savanna habitats of East Africa. On the average two to three ungulate species contribute at least 70% of the total mammalian biomass in the forested habitats of Ceylon, India and Java. Although the species diversity of ungulates in African savannas may be two to three times as great as in Asia, three to five species in four African study areas account for 75 to 84% of the mammalian biomass. Ungulate species which contribute to high biomass levels are also characterized by great potential mobility and the capacity to form cohesive social groupings. Such social groupings may facilitate the development of traditions in the use of resources.

INTRODUCTION

Measurements of the density and biomass of ungulates have been used extensively to compare estimates of carrying capacity for different habitats (see for example Bourlière, 1963a, b; Sharkey, 1970; Stewart and Zaphiro, 1963). These data have been used to demonstrate such points as the differences between various habitat or community types (e.g., Stewart and Zaphiro, 1963) and the differences in productivity between wild and domesticated herbivores (e.g., Sharkey, 1970; Dasmann, 1964). Talbot (1964), while stressing the need for such comparisons, emphasized that any determination of biomass depends on (a) the numbers of animals, (b) accurate estimates of weights, (c) the unit of time, (d) the unit of area, and (e) seasonal factors such as births, growth and mortality.

As part of our study of the ecological conditions in Ceylon's National Park System, we required accurate estimates of the biomass of herbivores using the National Parks. Since the major concern of our study was to obtain an overall estimate of the status of the ungulate populations (in particular of the elephant) in the parks, the following information was required:

- (1) Population sizes and population dynamics of each species.
- (2) Relationships between species (competition, predation, etc.).
- (3) Usage of different habitat types within each park.
- (4) Adequacy of the resources available within each park for the support of each species.

In considering the latter two problems, it was necessary to study not only the density and biomass of the various ungulate species in these areas but also the movement patterns. In this paper we will consider both of these problems, especially the relationship between movement patterns and the concentration of biomass.

THE STUDY AREAS

Ceylon's three National Parks (see Fig. 1) all lie within the 'Dry Zone'—the area of Ceylon which receives < 2000 mm annual rainfall.

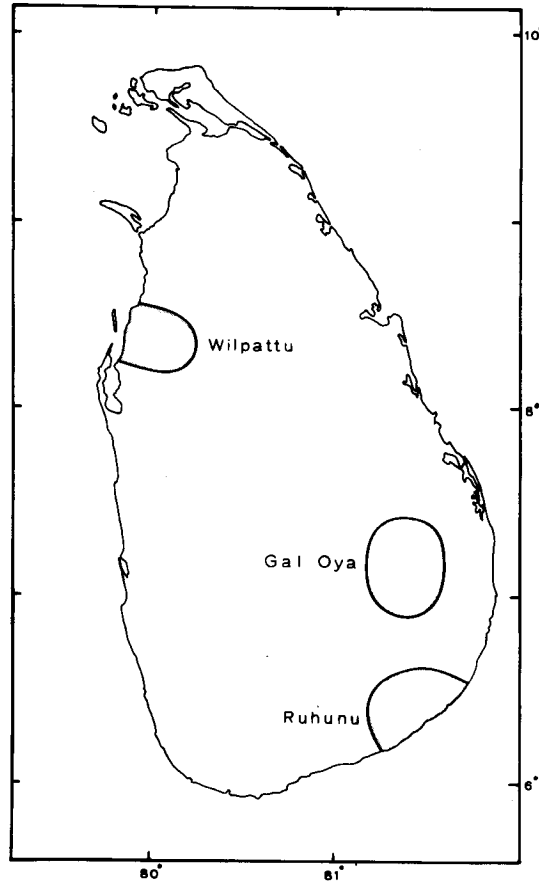


Fig. 1. Ceylon, showing the position of the three National Parks, which constituted the study areas.

Wilpattu National Park, situated on the northwest coast, is in an area with a climatic gradient, being drier to the north and west. The park is bounded to the north and south by rivers but no major river flows through the park. The western portion of the park has a limestone base and is characterized by vertical drainage. Within this portion of the park are many villus, or depressions in the limestone, which contain water. Some are seasonally dry, others contain water year round. The eastern portion of the park which has a base of gneissic rocks is characterized by horizontal drainage by seasonal streams and a lack of villus. Apart from the villus, the banks of which are covered with grass and other herbaceous plants, the remainder of the park (ca. 90%) is forest or forest-scrub (Eisenberg and Lockhart, in press).

Gal Oya National Park surrounds a large (36 km²) reservoir, the Senanayaka Samudra. This reservoir, constructed in 1948-50, lies at the confluence of a large river (the Gal Oya) with three major tributaries. These streams plus their numerous smaller tributaries give this area a water distribution pattern quite different from Wilpattu. The major vegetation types in this area are forest (48%) and savanna woodland (33%), the latter being concentrated in the western half of the park. Grassland, occurring on

the banks of the reservoir, covers 10% of the total area on an average, depending on the water level (for a more detailed description, see McKay, in press).

Ruhunu National Park, on the southeast coast, shows a greater similarity to Wilpattu than to Gal Oya. Two rivers pass through the park but have few tributaries within the park itself. Especially in the southwestern sector of the park, there are numerous water holes, some natural, others man-made; along the coast there are several lagoons of varying salinity. The vegetation of this area is scrub intermixed with grassland along the coast gradually being replaced by forest further inland (Mueller-Dombois, in preparation).

Work in Wilpattu was conducted by Eisenberg and M. C. Lockhart from July 1968 to April 1969 and continued by Lockhart until October 1969. McKay worked in the Gal Oya area from October 1967 to October 1969 and in Ruhunu National Park from June to October 1967. F. Kurt worked in Ruhunu National Park from June 1967 to March 1969. For details of methods the reader is referred to Eisenberg and Lockhart (in press), Eisenberg, Santiapillai and Lockhart (1970), and McKay (in press).

THE MAMMALIAN FAUNA

The mammalian fauna of Ceylon is derived from that of South India. A few endemic species (one primate, one viverrid, several rodents, and insectivores) occur, but all of the larger mammals are closely related to mainland forms, being at most subspecifically different (Eisenberg and McKay, 1970). Within the areas of the National Parks, the following species are important.

Elephant (*Elephas maximus*) occur throughout the dry zone. Total elephant populations around the National Parks are estimated to be: Wilpattu—120 (Eisenberg and Lockhart, in press); Gal Oya—300 and Ruhunu—150 (McKay, in press). The elephant feeds on both browse and grass showing a higher usage of the latter during the rainy season. Females accompanied by juveniles of both sexes travel as herds or as subgroupings of herds; adult males are primarily solitary (McKay, in press).

Water buffalo (*Bubalus bubalis*) occur in all three parks. Not all individuals within any park are wild. There are many recent escapees from domestication, and in Gal Oya one or more herds released there for grazing by their owners. The buffalo is primarily a grazer, although wild buffalo at least will take some browse.

Three species of deer—Sambar (*Cervus unicolor*), Chital (*Axis axis*) and Muntjak (*Muntiacus muntjak*)—occur in all three parks. The sambar and muntjak are primarily browsers; the chital feeds on both grass and browse, showing a preference for grass. One tragulid, the mouse deer (*Tragulid meminna*) occurs in this area also. This small forest dweller is primarily a browser/frugivore.

Wild boar (*Sus scrofa*) occur in all three parks. Although the boar do graze, especially in the wet season, they feed primarily upon tubers and roots dug from the ground. They also act as scavengers.

Two non-ungulates, the porcupine (*Hystrix indica*) and the hare (*Lepus nigricollis*) are also important terrestrial herbivores. The porcupine is abundant only in drier areas but the hare is common throughout the dry zone wherever there is open vegetation.

Not only do the feeding levels of these species overlap extensively; the same overlap is also shown in the species taken. Elephants use all of the browse plants eaten by the other species as well as the grasses. The elephant will, however, eat coarse grasses such as *Imperata* and *Cymbopogon* which are not used by buffalo or chital.

MOVEMENT PATTERNS

1. The Elephant

In Wilpattu the herds of elephants show a pattern of movements which is dependent upon the seasonal rains. During the rainy season, which normally lasts from October to January (a second smaller rain peak occurs in March-April), the elephants are

concentrated in the West Sanctuary. This area, which lies along the coast, has several large villus which, when wet, support a lush growth of grass (Eisenberg and Lockhart, in press). These large areas of grass are evidently attractive to the elephants as they form a concentrated supply of food with water readily available. During this time of year the elephants tend to remain in the West Sanctuary and movements are generally from one villu to another.

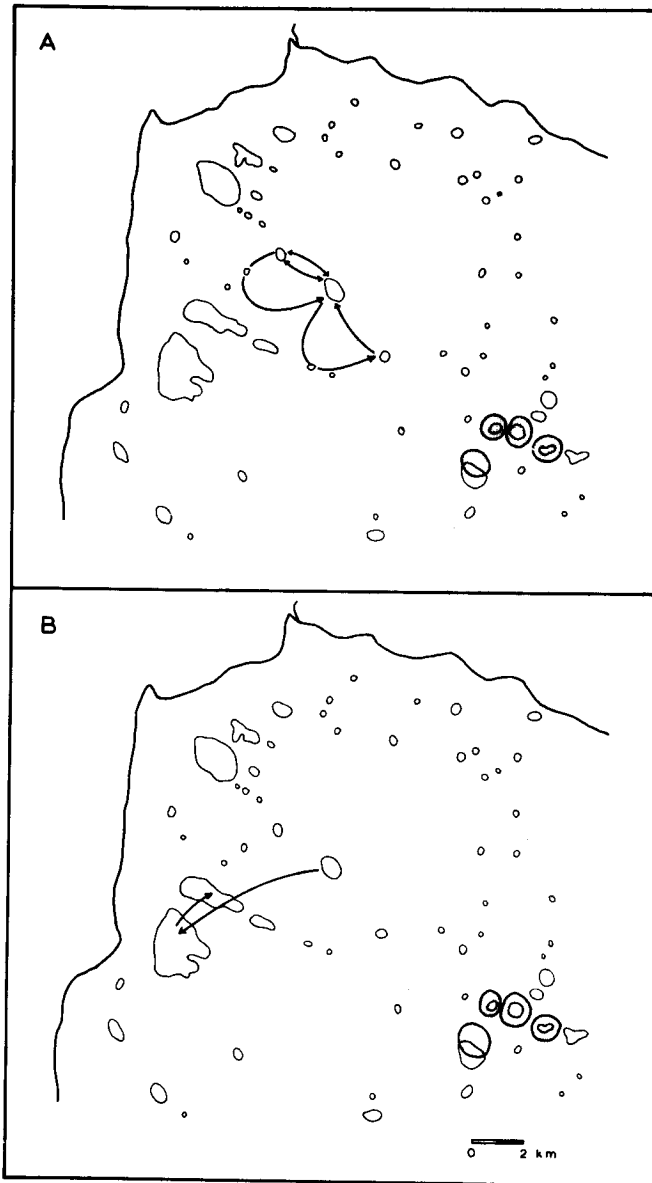


Fig. 2. Movements of a herd of elephants in Wilpattu, August 1969:

- A Movements during August 1-15 during drought;
- B Movements during August 15-31 immediately after onset of rains.

Following the rains these large villus begin to dry and the available surface water decreases. As the dry season progresses, the elephants leave the West Sanctuary and move either towards the rivers which lie to the north and south or to the villu region in the center of the park. This results in two types of movement pattern which are maintained throughout the dry season. Throughout this period the elephants forage during the day in the forest and scrub areas coming to water in the evening to drink and bathe. Those herds which spend the dry season around the rivers tend to remain in the vicinity of those rivers for foraging and their movements, from day to day, are generally parallel to the rivers.

The herds which remain in the central region of the park, however, show a different pattern. They forage in the forest areas around the villus, often remaining in the vicinity of one villu for several days. Their movements are from one villu to another and within a period of 2-3 weeks they may visit 5 or more of these water sources. Thus they tend to remain concentrated in one area around a particular source of water for one to a few days, moving at short intervals to another one.

This latter pattern is demonstrated in Fig. 2 which shows the movements of one herd of 9 individuals during August 1969. In the first two weeks of the month, the herd moved regularly between villus as shown by the arrows in A, concentrating primarily around two villus. Rains began on August 15, breaking a drought of several months. Immediately following the onset of the rain, the herd moved westward into the West Sanctuary and from then until the end of the month its activity was concentrated around three large villus in that area.

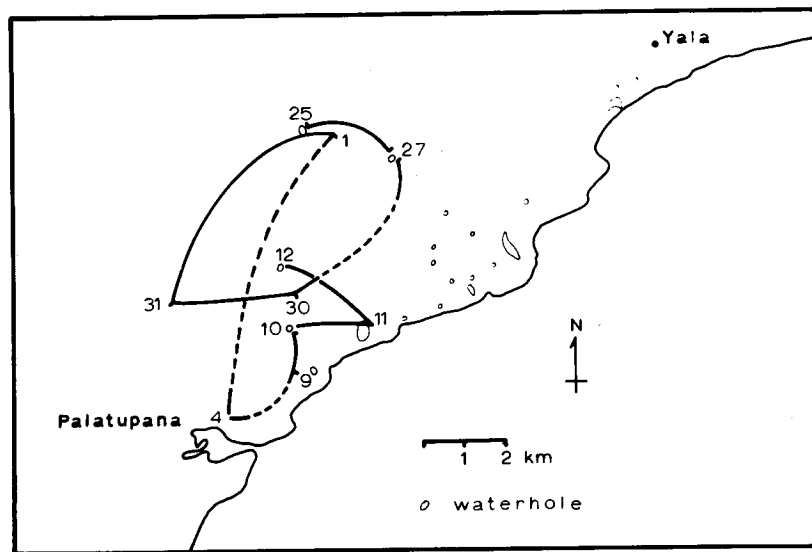


Fig. 3. Movements of a herd of 14 elephants in Ruhunu National Park, July 25-August 12, 1967. Note pattern of movement between water holes.

Movements of elephants in Ruhunu National Park are similar. Figure 3 shows the movement of one group of 14 individuals during July and August 1967 (dry season). Throughout the two weeks that movements were followed, the herd moved from one water hole to another. On three occasions they remained foraging in one area for 2-5 days but on the other days movements were relatively direct and frequent. Feeding accompanied movement between water holes on all days but July 31, when the movement was direct, following a park road. Seasonal trends in this area show a greater concentration along the coast in the wet season accompanied by little daily movement and a dispersal toward the north and west in the dry season with greater daily movement between water holes as outlined in Fig. 3.

Movement patterns shown by elephants in the Gal Oya National Park region differ from those in the other areas. As with the elephants in Ruhunu and Wilpattu National Parks, the Gal Oya elephants have a tendency to use separate parts of their total home range in wet and dry seasons, it is the movements within each of these halves of the ranges that differ. Figure 4 shows the areas covered by one herd of elephants in the eastern sector of Gal Oya National Park during 1968-69. From March to June, 1968, the herd remained in a small area to the southwest of the town of Inginiyagala. They did not, however, move throughout the entire area at frequent intervals. In March their movements were very restricted and they remained feeding in the vicinity of two small bays of the reservoir. In April they moved northward and westward, crossing one arm of the reservoir. By May they had moved south again and early in June they moved northeastward and remained in the area immediately south of Inginiyagala for about 2 weeks. Throughout this entire period (from the end of the wet season to the middle of the dry season), their daily movements were short. They fed in the forest around the reservoir and in the grass zone on the banks of the reservoir itself. They did not move more than 2 km. from the water.

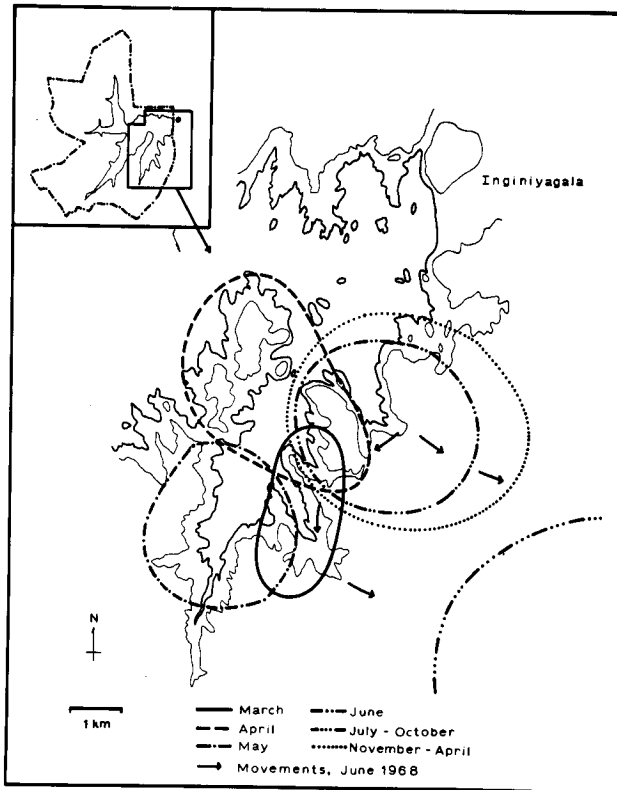


Fig. 4. Movements of a herd of elephants in Gal Oya National Park, 1968-69. Inset shows area of park on main map.

On June 13 and 14, 1968, the herd began to move out of the area they had been in for the past two weeks, part of the herd moving eastward, another part south and east. By June 15 they had left the park and they remained in an area of forest to the southeast of the park until mid-October. In October they returned to the sector of the range they had occupied in June and half of the herd at least remained in this area until April 1969. In April 1969 they again apparently followed the same paths toward their dry season range, but, unlike the previous year, these animals were not observed during the movement.

Thus, the elephants in the Gal Oya region appear to display movement patterns based on three time scales:

- (a) daily movements—associated with feeding and to and from water,
- (b) seasonal movements—between dry season and wet season home ranges, both of which are shown by the elephants in the other two parks, and
- (c) medium-term movements—between sectors of the seasonal home range.

The factors determining these movements appear to be the availability of food and water. Shortage of free water and lack of grass in the West Sanctuary of Wilpattu National Park during the dry season can readily account for the concentration of elephants in the central villu area which contains permanent water and around the rivers (Eisenberg and Lockhart, in press). The seasonal movements of the elephants in Gal Oya appear to be related to availability of food, particularly grass. This, as described by McKay (in press), is in part due to the influence of buffalo which crop the grass around the reservoir to the point where the elephants must scarify the ground in order to obtain any grass. Water does not appear to influence the movements in Gal Oya.

Daily movements are influenced by food and water in that an elephant which requires a large amount of free water daily cannot move too far from a stream or villu or other such source of water. Two patterns are possible: feeding in the vicinity of water (0-2 km) requiring only a short daily movement, and feeding away from water (> 2 km) requiring a long, often rapid, daily movement. The latter case is observed only infrequently and is not maintained for any long period.

The factors determining the medium-term movements in Gal Oya are not so apparent. There is some suggestion that availability of particular food plants may be involved, but at the moment the evidence is inconclusive.

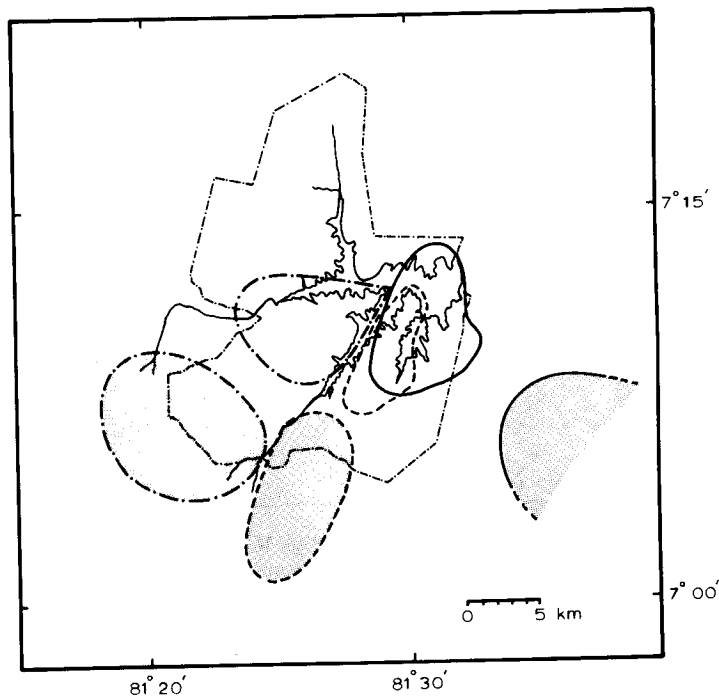


Fig. 5. Seasonal home ranges of three elephant herds in the Gal Oya region. Dry season home ranges shaded, wet season unshaded; note that dry season ranges lie mostly outside the park boundary.

One important aspect of the seasonal movements of the elephants is the relationships between such movements and the park boundaries. As shown in Fig. 5, three herds which use the southern half of the Gal Oya National Park have dry season home ranges which are partly or entirely outside the park. As these dry season ranges are in areas which are being subjected to rapid agricultural development; there is imminent danger that they will become contracted. Evidence from another herd, already surrounded by agricultural land (McKay, in press), shows that elephants appear to maintain their traditional movements even after forest land has been cleared and planted in paddy or other crops. This results in considerable damage to the crops and shooting of elephants. Because of this, it was recommended by McKay (in press) that the boundaries of the park be extended to include the dry season ranges of these herds, rather than make any attempt to restrict the movements of the elephants to a smaller home range.

The only comparable data from mainland Asia are those of Khan (1967) and Singh (1969). Khan (1967) found that a herd of elephants he followed for two years in Malaya showed periodic but non-seasonal movements. Singh (1969), working in Uttar Pradesh, India, found that some herds show seasonal movements while others do not, dependent upon the availability of food and water. Food and water (particularly the former) are responsible for movements of at least some African elephant populations (Buechner *et al.*, 1963). Movements related to rainfall were also recorded by Laws (1969) in Tsavo National Park and by Wing and Buss (1970) in the Kibale Forest Reserve, Uganda.

2. The Water Buffalo

In Wilpattu National Park there are two types of movement patterns shown by the buffalo. Some large herds tend to move from villu to villu in a manner similar to the elephants while a number of smaller groups usually remain in the vicinity of a single permanent villu. As illustrated in Fig. 6 a herd of 52 buffalo spent the period at the end of the dry season (August 1-15, 1969) in the vicinity of 5 villus in the central portion of the park, concentrating primarily around the 2 largest ones. With the onset of rains this herd, like the herd of elephants mentioned above, moved to the larger grassy villus of the West Sanctuary. Four smaller herds, toward the southeastern fringe of the villu zone, remained at the same villus they had occupied during the dry season.

Herds of both types show a seasonal shift in concentration, tending to remain more concentrated around permanent villus in the dry season and dispersing more widely into forested areas in the wet season.

The movement patterns of the buffalo in Gal Oya are shown in Fig. 7. The four groups shown on the north shore of the reservoir for August are wild animals which concentrate in this area during the dry season. They remain in the vicinity of the water making short daily movements into the neighboring forest to browse. During the wet season these herds disperse northward and westward, using temporary water holes and streams for wallowing, only seldom coming to the reservoir.

The remaining four areas outlined on each section of the map show the distributions of buffalo herds which contain large numbers of feral and domesticated individuals. The herds in this area do not maintain the same distinctiveness as do the herds of wild buffalo. Groups of animals will frequently move from one bay to another and recombine with other groups. Figure 7 shows the areas used by these animals during August and March. In both wet and dry seasons these feral and domestic animals remain mostly in the grass zone of the reservoir bank occasionally dispersing slightly into the forest. They tend, however, to remain in the vicinity of one or other of the many shallow bays. There is no seasonal variation in this pattern, the animals merely shift their center of activity from one bay to another. Daily movements are short and consist mostly of a gradual shift along the bank while feeding, occasionally moving into the forest in the early morning, followed by a return to the currently used wallow. The same wallowing site will often be used for several days to weeks.

3. The Chital and Sambar

The movements of both large deer in Wilpattu consist of concentration and dispersal. As described by Eisenberg and Lockhart (in press), the chital tend to concentrate

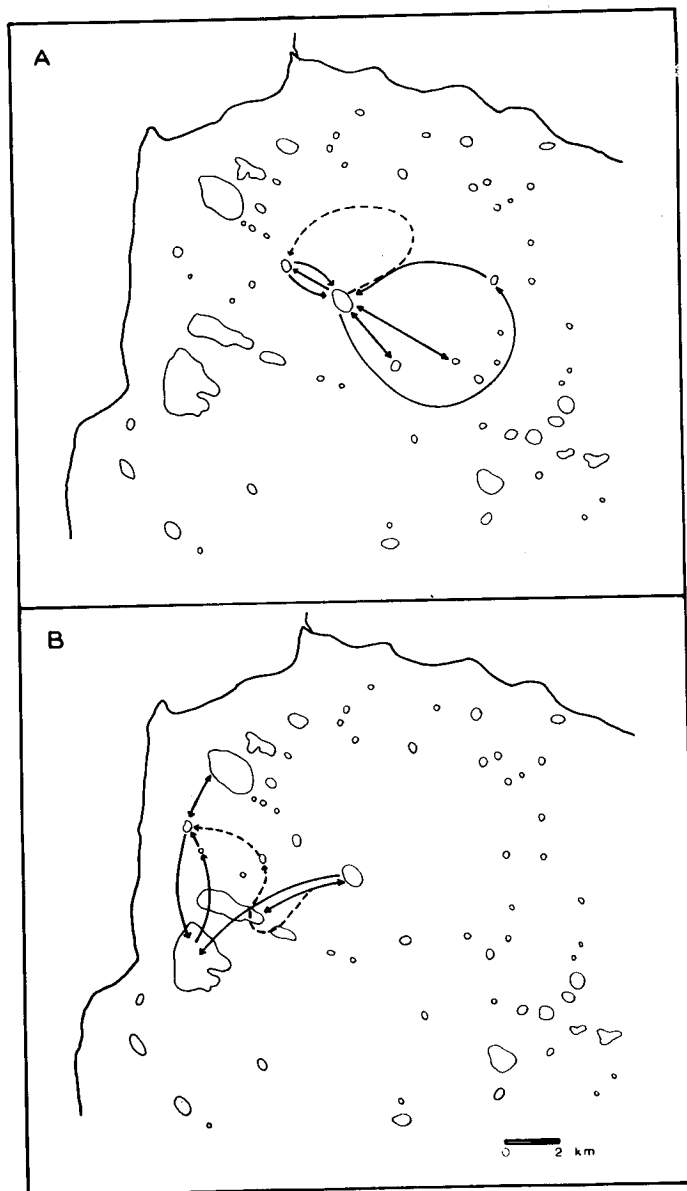


Fig. 6. Movements of a herd of 52 buffalo and 4 smaller herds, Wilpattu National Park, August 1969:

- A August 1-15: large herd moves around 5 villus in the central area;
- B August 16-31: immediately after rains large herd moves to west sanctuary, smaller herds remaining in the same areas as before.

their activity in the dry season around a permanent water hole or villu. During the daytime they forage in the forest surrounding the villu, moving out into the open again in the late afternoon to graze and drink. At this time of the year large herds form in the grassy areas around the villus. In the wet season the larger herds fragment and

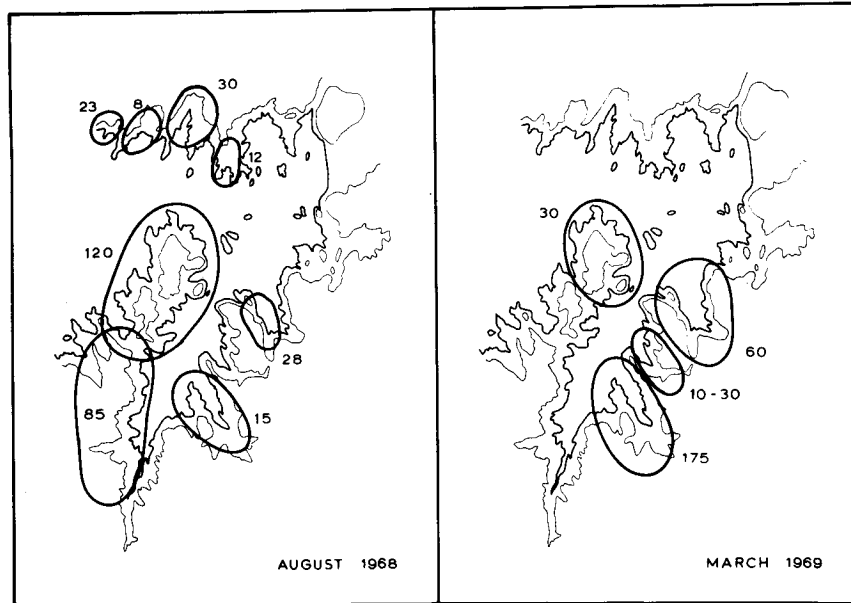


Fig. 7. Areas used by buffalo herds in Gal Oya National Park. In August (dry season) wild herds to north are concentrated by the reservoir. In March (end of rainy season) wild herds have dispersed, while feral herds remain concentrated in different areas.

small groups disperse more widely into the forest, centering their activity around smaller temporary sources of water.

Sambar in Wilpattu show less of a seasonal trend remaining dispersed in small groups whose activity centers around a villu or other source of water throughout the year. In Ruhunu National Park both species show the same patterns as in Wilpattu but in Gal Oya National Park where the numbers of chital are extremely low compared to the other two parks both species remain dispersed showing only a slight tendency to concentrate around the reservoir in the dry season.

4. The Wild Boar

Boar are, like the buffalo and elephant, highly mobile and tend to parallel those species in their movements. In Wilpattu pigs will move from villu to villu but tend to concentrate their activity around one villu during the dry season. In Gal Oya the boar show a more irregular pattern, moving from bay to bay around the edge of the reservoir and from the open areas to the surrounding forest. They do not, here at least, appear to use specific areas on any consistent basis during either wet or dry season, although there is a definite concentration around the easternmost bays of the reservoir during the dry season. This lack of specificity in foraging or wallowing areas may be related to the comparatively high availability of water relative to the home range size of individual groups.

MOVEMENTS AND THE CONCENTRATION OF BIOMASS

Densities and biomass densities were calculated for Wilpattu by Eisenberg and Lockhart (in press) and for Gal Oya by McKay (in press). In calculating biomass densities, weights for elephants were obtained from Kurt and Nettasinghe (1968) and adjusted for the size distribution of the populations. Weights for other species were taken from Phillips (1935).

TABLE I. DENSITIES AND BIOMASS DENSITIES OF TERRESTRIAL HERBIVORES IN TWO OF CEYLON'S NATIONAL PARKS

Species	Gal Oya National Park (453 km ²) ¹			Wilpattu National Park (580 km ²) ²		
	Density km ⁻²	Biomass Density kg/km ²	% Biomass	Density km ⁻²	Biomass Density kg/km ²	% Biomass
<i>Elephas maximus</i>	0. 232	405. 0	46. 9	0. 12	217. 2	29. 1
<i>Bubalus bubalis</i>	1. 119	320. 0	37. 1	0. 27	73. 4	9. 8
<i>Cervus unicolor</i>	0. 540	75. 7	8. 8	1. 17	157. 9	21. 1
<i>Axis axis</i>	0. 656	29. 9	3. 5	5. 84	262. 8	35. 2
<i>Muntiacus muntjak</i>	*	*	—	0. 44	5. 9	0. 8
<i>Tragulus meminna</i>	*	*	—	0. 58	1. 9	0. 2
<i>Sus scrofa</i>	0. 540	14. 8	1. 7	0. 30	8. 1	1. 1
<i>Lepus nigricollis</i>	7. 72	17. 6	2. 0	4. 67	14. 9	2. 0
<i>Hystrix indica</i>	*	*	—	0. 58	5. 3	0. 7
Total		863. 0	100. 0		747. 4	100. 0

¹ McKay (in press).

* Present at very low density.

² Eisenberg and Lockhart (in press).

— Numbers not estimated.

Table I shows the annual average for numerical density and biomass density of terrestrial herbivores in these two parks. While the species composition of the two areas is identical, the relative abundance of species differs markedly. Sambar and chital are more abundant in Wilpattu than in Gal Oya and elephant and buffalo are more abundant in the latter area. Wild boar are slightly more abundant in Gal Oya as are hare. In the case of the hare, this difference is undoubtedly due to the higher percentage of grassland in Gal Oya.

The data presented in Table I represent an overall average which would only be a true picture were the species involved equally and evenly distributed throughout the areas censused. When the movements and resulting concentrations of animals are taken into consideration, the maximum biomass densities are as shown in Fig. 8. For Wilpattu the maximum densities were estimated for an area of 25 km² including 3 permanent water holes during the July-September drought period. For Gal Oya the maximum densities were calculated for an area of 10 km² including 3 bays of the reservoir. The densities were not, however, all calculated for one particular time period. The maximum densities for all species but the elephant were recorded during the dry season, a time when the elephant is absent from this portion of the park.

Thus at Wilpattu the biomass density in the area censused may reach a level as high as 6930 kg/km² during the dry season. In the Gal Oya concentration area the biomass density during the same period reaches a level of 2860 kg/km²—with the elephant absent. The elephants return to this area during the rainy season and they alone contribute about 2600 kg/km² for this period. As the buffalo do not disperse widely in this portion of the park, the biomass density during the rainy season may at times exceed 4000-5000 kg/km².

Thus, when the movement patterns of the animals are taken into account, it can be seen that the effective biomass density over any given period of time can be several times higher than would be estimated were one to consider only the total annual situation. The converse is also true in that estimates of density and biomass made during periods of concentration do not accurately reflect the overall distribution on an annual or longer-term basis. In order to estimate accurately the carrying capacity and productivity of an area, as emphasized by Talbot (1964), it is essential to

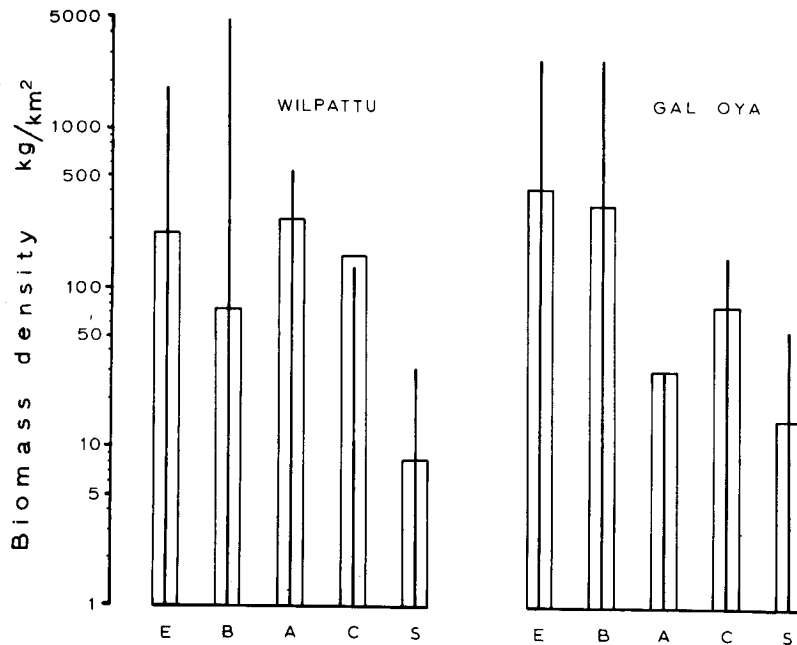


Fig. 8. Biomass densities of major ungulate species in Wilpattu and Gal Oya National Parks, 1968: bars indicate average density; lines indicate maximum concentration.

E = *Elephas*; B = *Bubalus*; A = *Axis*; C = *Cervus*; S = *Sus*.

consider both the short term and long term biomass densities. In this way it is possible to arrive at an accurate assessment of the effects of various species on the habitat.

It is unfortunate that most authors give only annual or long-term averages Bourlière and Verschuren (1960) give data from each census along 4 transect lines throughout the period of their study. Even a cursory examination of their data shows that there are not only marked seasonal fluctuations but often rather marked day to day fluctuations especially with regard to highly mobile species such as elephant or buffalo. Perhaps the most complete survey to date is that of Lamprey (1964) which includes monthly estimates over a 4-year period. On the basis of his data, he has divided the species occurring in the Tarangire Reserve into 5 categories, a number of which can conveniently be reduced to 3 major groups: (a) residents, (b) residents with partial dispersal, and (c) migrants.

Another aspect of the study of biomass densities concerns the relative proportions contributed by the different species in the community. From the data presented in Table I and Fig. 8, it is evident that only a small number of the total species are contributing a high percentage of the total herbivore biomass. Table II shows summarized results from a number of studies, giving the number of species which contribute at least 70% of the biomass. In comparing the species compositions of such studies one can see a trend in that mobile species often are among those which contribute most to the biomass. Thus for the Gal Oya study area, the elephant and water buffalo contribute 84%. In Wilpattu the sambar, chital and elephant (two which show a wet season dispersal and one highly mobile) contribute 85% of the average biomass but the elephant and buffalo (both highly mobile) contribute 90% of the biomass in the area of dry season concentration. An examination of the data presented by Lamprey (1964) similarly shows that for his east transect zebra, buffalo and elephant (all migrants) account for 78.9% of the average biomass. In his west transect these same three species account for only 58.3% as the giraffe (resident) and impala (dry season dis-

TABLE II. COMPOSITION OF TERRESTRIAL HERBIVORE COMMUNITIES

Region	Total Number of Species	Number Contributing $\geq 70\%$ Biomass (and %)	Authority
Gal Oya, Ceylon	6	2 (84.0%)	McKay, present study
Wilpattu, Ceylon	9	3 (85.4%)	Eisenberg, present study
Kanha, India	9	3 (89.6%)	Schaller (1967)
Udjung Kulon, Java	6	2 (74.3%)	Hoogerwerf (1970)
Umfoloji, South Africa	18	5 (75.4%)	Mentis (1970)
Tarangire, Tanzania—West	14	5 (83.6%)	Lamprey (1964)
Tarangire, Tanzania—East	14	3 (78.9%)	Lamprey (1964)
Nairobi, Kenya	16	4 (77.2%)	Foster and Coe (1968)

persal) are more abundant there. The same pattern is evident in the data of Foster and Coe (1968) where 55% of the biomass is contributed by 3 highly mobile species: wildebeest, hartebeest and zebra. The somewhat mobile giraffe adds a further 22%.

In discussing the movements of elephants, Buechner *et al.* (1963) (for *Loxodonta*) and McKay (in press) (for *Elephas*) have described the 'seasonal' movements of elephants as a response to proximate conditions of rainfall and food availability. This same pattern appears to be shown by a number of other large ungulates which are major components of herbivore communities. It seems reasonable to assume that the high mobility and the ability to respond to proximate environmental factors rather than be restricted to a rigid annual cycle will be advantageous in areas where rainfall (and thus plant growth) is uncertain and uneven (both temporally and spatially). This will then allow animals, such as elephants and buffalo, which have a high water requirement to maintain high densities in areas that are seasonally arid. It should also be noted that all such species are herd-forming animals. Thus the formation of large herds and, in the case of the elephants at least, a complex social organization will help to facilitate these movements by allowing and promoting the development of traditions. Such traditional use of trails, water holes, etc., is particularly evident among elephants (McKay, in press).

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