THE ECOLOGY OF THE ASIAN ELEPHANT (*ELEPHAS MAXIMUS* L.) IN SRI LANKA

By

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to

my

parents

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ABSTRACT

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The distribution, structure and habitat relations of elephant populations in areas to be developed for agriculture under the Accelerated Mahaweli Development Program of Sri Lanka were studied between September 1980 and July 1982.

Seasonal changes in high elephant-activity sites along the Mahaweli Ganga river evidently were influenced by changes in available grass. Grasslands of mixed species composition were preferred habitats and grasses were the elephant's most important foods. The Mahaweli Ganga floodplains provided a higher quality diet for elephants than that of other parts of the study area.

A higher number of adult males per adult female was observed in floodplains than in upstream habitats along the Mahaweli Ganga. Female herds seen along the same river seemed to separate into nursing and juvenile-care units during certain times of the year.

Partially flooded villus, protected croplands and the abundance of non-preferred stages of *Imperata*-grass perhaps led to increased competition between elephants and livestock on upland grazing sites during the wet season. In the dry season, floodwaters in the villus

receded, croplands were abandoned after harvest and preferred stages of *Imperata* became available following burning. Owing to such increases in available grazing sites, no dry season competition on upland grazing sites, between elephants and livestock, was evident. Possible changes in grass-species composition and ungulate densities that might lead to competition between elephants and ungulates inside national parks were discussed. The extent of browsing by elephants was assessed in this study to be lower than that reported for other study sites in and near national parks.

Economic equivalents of crop losses reported by farmers perhaps reflected their hopes for compensation. Existing and new wildlife reserves in the study area protected only parts of elephant ranges. The maintenance of existing corridors would minimise the chances of elephant populations being isolated in one or more of the reserves. The future of the Asian elephant in Sri Lanka was discussed. Other important management and research recommendations for conserving the elephant populations of the Accelerated Mahaweli Development Area, are given.

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INTRODUCTION

Human-elephant conflict probably existed from historical times in the dry zone of Sri Lanka. The tradition of irrigated agriculture in those parts of the island dates back to 3-4 A.D. (Brohier, 1974). Land area cultivated under the irrigation schemes prior to independence in 1948 rarely exceeded 5,000 ha (Brohier, 1974). The introduction of large scale river valley development to dry zone areas during the 1950's, however, intensified human-elephant conflicts. The Gal Oya Valley Development Project of those times irrigated 48,000 ha of land (Johnson and Scrivenor, 1981). The Mahaweli Ganga Development Project (MGDP), initiated in 1970, will irrigate 364,000 ha in the lowland dry zone. Of this area, 265,000 ha were, until recent times, under natural vegetation. They also comprised important habitats for about 30% of the island's elephant population (McKay, 1973).

The pace of the MGDP, originally extended over a 30-year period, was accelerated by the government that took office in 1977. About 173,000 ha of land was to be developed in six years under the Accelerated Mahaweli Development Program (AMDP). The quickening of development intensified human-elephant conflicts, and posed immediate threats to the survival of the Asian elephant in Sri Lanka. Scientific data necessary to guide the conservation and management of elephant populations that would be displaced by the AMDP were urgently needed.

Ecological studies on elephant populations have been conducted in and around the Gal Oya and Ruhuna National Parks of southeastern Sri Lanka (McKay, 1973; Vancuylenberg, 1974 and 1977; Ishwaran, 1979, 1981 and 1983). Eisenberg and Lockhart (1972) reported population data for elephants in the Wilpattu National Park of northwestern Sri Lanka. Nettasinghe (1973) provided the only data available for elephants using the Mahaweli Ganga floodplains. He identified four populations with overlapping ranges. They inhabited an area used intensively by domestic cattle and buffaloes. He also discussed possible interactions between elephants and domestic stock, and argued that there were no evident signs of competition between them.

Most of the above studies have shown that elephant distribution and movements were largely determined by the availability of grass and water. On the basis of such findings and the knowledge of experienced field personnel, the Department of Wildlife Conservation identified areas to be set aside as national parks and corridors. These areas were to provide refuges for elephants displaced by the AMDP. The main objective of this study was to provide base-line data against which such preliminary conservation measures could be evaluated. Furthermore, such data would also be useful in the inauguration of an immediate conservation and management program for elephants in the area. For the two-year study it was planned:

1) to monitor seasonal changes associated with elephant distribution in the study area with particular emphasis on the proposed corridors,
2) to assess the structure of elephant populations in terms of herd composition, herd size, sex ratio and age class composition,

3) to determine habitat preferences of elephants and to compare the quality of various occupied ranges within the study area,
4) to correlate changes in habitat use with changes in habitat quality and existing levels of human activity,
5) to investigate existing patterns of crop damage and estimate economic losses incurred by farmers,
6) to make recommendations for the conservation and management of elephants in the study area.

THE STUDY AREA

The study area (Figure 1) lies in the lowland dry zone between lattitudes 7°41' and 8°30'N and longitudes 81°31' and 81°20'E. It extends over the central and northcentral provinces of the country. This area (Figure 1) will hereafter be referred to as the Accelerated Mahaweli Development Area (AMDA).

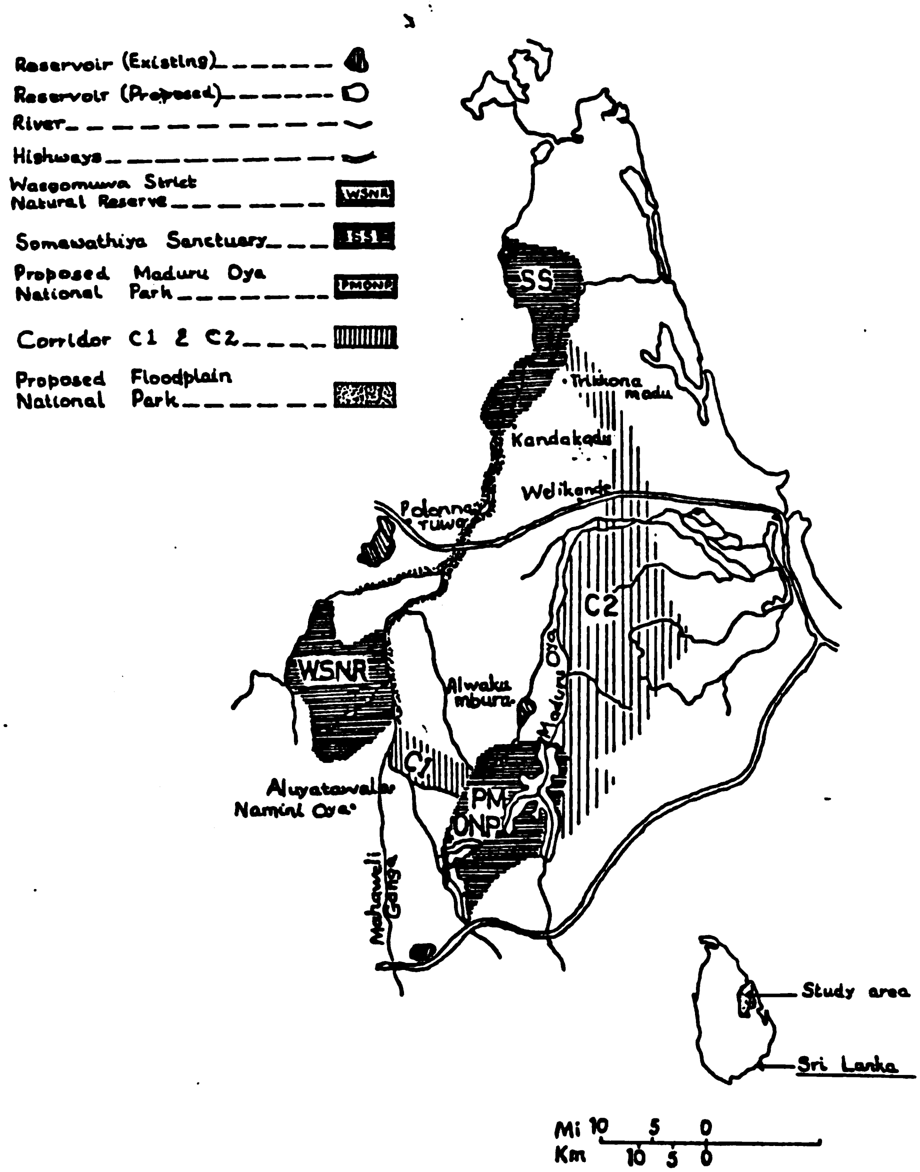
Topography and Geology

In general, the area has a gently undulating terrain. It consists predominantly of precambrian rocks (ACRES, 1979). The eastern and the southeastern parts comprise mainly gneisses and granites. In other parts metasediments including limestones and dolomites are found (Johnson and Scrivenor, 1981). Inselbergs (rocky outcrops) rising to about 500 meters are common. These are erosion remnants with a high quartz content (McKay, 1973).

Soils

In well-to-moderately drained upland sites, reddish brown earths are the predominant soil types. Non-calcic brown soils occur in certain parts of the Maduru Oya basin. Floodplain soils chiefly are alluvial, humic gley or solodized solenetz types. Recent alluvial soils occur along the river banks and narrow stretches of the Mahaweli Ganga and Maduru Oya floodplains (TAMS, 1980a).

Figure 1. Map of the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.



Reservoir (Existing)
Reservoir (Proposed)
River
Highways
Wasgomuwa Strict Natural Reserve
WSNR
Somawathiya Sanctuary
SS
Proposed Maduru Oya National Park
PMONP
Corridor C1 & C2
Proposed Floodplain National Park
SS
Trikkona madu
Kandakadu
Welikande
Polonnaruwa
C2
WSNR
Alwakalambura
Maduru Oya
C1
Aluyatawala
Namini Oya
PM ONP
Mahaweli Ganga
Study area
Sri Lanka
Mi 10 5 0
Km 10 5 0

Climate

The marked seasonality of the lowland dry zone is mostly attributed to the alternation of wind-flow patterns between the southwest and northeast monsoons (Johnson and Scrivenor, 1981). The northeast winds occur between November and March while the southwest monsoon prevails between May and September. April and October show greater variation in wind direction and are referred to as inter-monsoonal months (Johnson and Scrivenor, 1981).

The lowland dry zone receives a mean annual rainfall of 1,500 to 2,000 mm. Most of the rainfall in the study area occurs during the northeast monsoon. The southwest monsoonal winds lose most of their moisture in the southwestern lowlands and hill country. They blow across the study area between May and September as dry winds. Together with high temperatures (25-30^{o}C), these winds contribute to high evapotranspiration rates. Despite occassional rains between June and September, periods of severe drought conditions are common.

River Flow and Drainage Systems

Of the two major drainage systems in the study area, the Mahaweli Ganga (Figure 1) drains a much larger area than the Maduru Oya. The former originates in the hill country and has considerable water-flow even when drought conditions prevail within the study area; e.g. mean monthly flow in the Mahaweli Ganga ranged between 1,459 million m^3 in December to 435 million m^3 in September (NEDECO, 1979). In contrast, the mean monthly flow of Maduru Oya for the same months were only 184 million m^3 and 6 million m^3, respectively (NEDECO, 1979).

Vegetation

The semi-deciduous forest characteristic of the lowland dry zone varies in physiognomy and contiguity within the study area. It has lower canopy height and less contiguity in the eastern and northern parts of the study area than is true for the western regions. Drypetes sepiaria is the dominant tree species throughout the study area. Chloroxylon swietenia and Manilkara hexandra are abundant in the upper canopy layers. The lower shrub and tree layers are dominated by Dimorphocalyx glabellus, Polyalthia korinti, Diplodiscus verrucosa and Glycosmis pentaphylla. The herbaceous understory is sparse in the forest and is dominated by the grass Certococcum trigonum. The understory of forests surrounding the villu-grasslands of the Mahaweli Ganga floodplains has a greater variety of grass species; e.g. Digitaria sp., and Eragrostris tenella.

Open patches, that have been cleared of forests and abandoned after a few seasons of cultivation, are dominated by the grass Imperata cylindrica. Other tall-grass species, namely Panicum maximum and Themeda triandra, also occur at localized sites. Many short-grass meadows also are scattered across the study area. Species composition of such grasslands are highly variable. Dactyloctenium aegyptium , Brachiaria distachya and Digitaria marginata are common species.

The villu grasslands are unique to the study area. Most of them occur along the Mahaweli Ganga floodplains, while only a few are along the Maduru Oya. Regular inundation, at least once a year, is an important factor in maintaining this grassland community. Increased diversion of upstream waters of the Mahaweli Ganga had decreased the villu area by about 20% over the last two decades (TAMS, 1980b).

Grasses such as _Brachiaria mutica_ (the villu grass), _Sacciolepsis interrupta_, _Eichinochloa colonum_, _Paspalum metzi_ and _Oryza perennis_ and the sedges _Cyperus marginata_ and _Cyperus iria_ are abundant in areas subjected to regular inundation. In upland sites _Chloris barbata_, _Cynodon dactylon_ and _Eragrostris tenella_ are common. Improved pastures on government farms at Trikkonamadu, Kandakadu and Welikande (Figure 1) are monocultures of artificially bred varieties of the villu grass.

Human Impact

A. Land-use Categories

1. Agriculture. Cultivation in most of the study area was dependent on rain-fed water. Land preparation, plowing and sowing of paddy seeds are normally completed by mid-November. Harvesting is done in March-April. Since most farmers were Buddhists or Hindus, harvesting was done prior to their New Year on the 14th of April.

A second cultivation between May and September was only possible where water from a reservoir is available for irrigation; e.g. Namini Oya, Alwakumbura and Polonnaruwa (Figure 1). In agricultural areas adjacent to nature reserves, crops were cultivated between October and April. The traditional "chena" (slash and burn) cultivation was practiced only during this season.

2. Grazing of Domestic Stock. Most farmers owned at least one or two draft buffaloes for plowing their fields. Between October and April these animals grazed in upland grasslands of nearby reserves. After harvesting in March-April they were moved to abandoned crop-fields for grazing.

Owners of larger herds grazed their livestock in reserves during the dry season as well. The villus in Somawathiya Sanctuary (SS in

Figure 1) were grazing sites for livestock belonging to private individuals and government farms at Trikkonamadu, Kandakadu and Welikande. During the dry months, large herds comprising about 500 cattle and/or buffaloes were regularly seen to graze in the villus between 0800 and 1600 hours. As villus flooded during the wet season, livestock were moved to natural and artificial pastures in upland sites. The latter also attracted the elephant herds.

3. Nature Reserves. Wasgomuwa Strict Natural Reserve (WSNR in Figure 1) legally prohibited any human use of that area except for scientific research. Research had not been conducted there prior to this study. The southwestern parts of this reserve were opened to settlers in early 1970's for political reasons. Officials of the Department of Wildlife Conservation, however, succeeded in reclaiming this reserve and all settlers were removed out by May 1980.

A corridor permitted the use of that area for tourist visitation. Settlements, however, were not permitted. That part of corridor C2 north of the Maduru Oya river (Figure 1) was legally preserved in 1970 for protecting elephant ranges. But it has been severely encroached by villagers. As development in connection with AMDP began, exploitation of forests for commercial timber, some with government approval, increased considerably.

A sanctuary, e.g. Somawathiya Sanctuary (SS in Figure 1) legally permitted existing land-use to continue, but prevented the initiation of new ones. Villus and other grazing sites in this reserve were always used by villagers. After 1960, however, the opening of the three government livestock farms, and permitting the construction of semi-permanent dry season camps of private livestock owners, increased grazing pressures there. The private owners camping inside the sanctuary also cultivated tobacco along the banks of the Mahaweli Ganga. This practice, however, was halted by officials of the Department of Wildlife Conservation during 1981. The Buddhist temple in this sanctuary attracted many pilgrims throughout the year, with maximum visitation rates during June.

The boundaries of the proposed Maduru Oya National Park (PMONP in Figure 1) were marked so as to include parts of the catchment areas of reservoirs that were being constructed there (Figure 1). This, and the new Floodplain National Park (Figure 1; TAMS, 1980c) were also being established as additional reserves to protect the elephant and the other fauna and flora charateristic of the area. The establishment of corridor C1, and the southern extension of corridor C2 connecting SS and PMONP were considered as economically unjustifiable (TAMS, 1980d).

B. Fire

Most fires were started by villagers. Post harvest burning of croplands could begin during late April. In June, increasing dryness and the strong southwestern winds carried fires over long distances. Such fires affected wildlife habitats. Late dry season fires of September-October, when started by villagers in *Imperata cylindrica* dominated areas, was aimed at creating fresh grass for their livestock.

C. Other Activities

Many other existing and past human activities had impacts on elephant and other wildlife of the area. Construction activities at proposed reservoir sites were major impact. Elephants regularly used reservoirs and irrigation channels for drinking and bathing. Fluctuation of water-levels of reservoirs probably mimicked seasonally flooded rivers and also provided grass along the shores (Olivier, 1978; Eltringham, 1982).

Reservoirs, when abandoned owing to breached dams, accumulated herbaceous vegetation. Two such reservoirs, one in WSNR and the other near Aluyatawala, south of corridor C1 (Figure 1), were regular grazing sites for elephants. An enormous number of such small reservoirs have been discovered in the dry zone of Sri Lanka (Johnson and Scrivenor, 1981). A topographic survey of 1904 revealed 11,200 reservoirs in a single north central provincial district (Brohier, 1974).

In spite of most farmers being Buddhists, many of them poached, particularly on spotted deer (*Axis axis*), sambur (*Cervus unicolor*) and wild boar (*Sus scrofa*). Poaching increased particularly after the harvest since farmers in the area rarely cultivated a second time. Most villagers hunted for food but some sold the meat to tourist restaurants where venison was served as a delicacy to visitors. Government employees, with vehicles for official work, also hunted ungulates. Elephant was probably the only mammalian herbivore that was shot in defense of crops but not for its meat.

MATERIALS AND METHODS

Field data were collected between September 1980 and July 1982. Methods of data collection and analysis were specifically related to ecological aspects as listed under the objectives. These are described separately.

Complete randomization of data collection procedures was impossible, since all parts of the study area were not equally accessible. No intentional biases were introduced in data collection methods used in regularly accessible areas. Randomness in observations was thus assumed and statistical tests used for making inferences. Influences of likely biases were discussed whenever possible. Statistical tests in this study were used to identify important differences and major sources of associations, and not for distinguishing between predictions of alternative hypotheses. Such an objective was best achieved by minimising type II error (Bhattacharrya and Johnson, 1977). Therefore, a significance level of 0.10 was preferred over the more conventionally used 0.05 for rejecting statistical null hypotheses.

Rainfall data from three meterological stations within the study area were obtained for the period between December 1980 and December 1981. Predominant wind directions for the study area were generalised based on the maps of Johnson and Scrivenor (1981). Long-term means of monthly pan evaporation rates were obtained from TAMS (1980e). Human activities affected grazing sites available to elephants at different times of the year (Table 1). Their dependence on changing climatic conditions was therefore included as an important part of the seasonal classification scheme. The period between 15 October and 15 April was classified as the wet season. The other six months were categorised as the dry season (Table 1).

Satellite images of the year 1979, topographic maps of 1960-61, and ground surveys conducted throughout this study, were all used in mapping major areas of natural and plantation forests in the study area.

Distribution of Elephant Populations

Elephant distribution in the study area was monitored throughout the study period. Motorable jeep tracks (Figure 2) were traversed once a month by a Toyota Land Cruiser when they were passable. Many other areas were surveyed on foot for elephant activity. All signs of elephant activity, both direct (animals seen, and/or heard calling or breaking woody vegetation) and indirect (feces, foot-prints and indications of grazing and browsing) were recorded. Directions of movements, those directly observed and indirectly inferred from foot-prints, were also noted. These data were used in mapping areas of high, moderate and low activity for the entire study area during the period from December 1980 to December 1981.

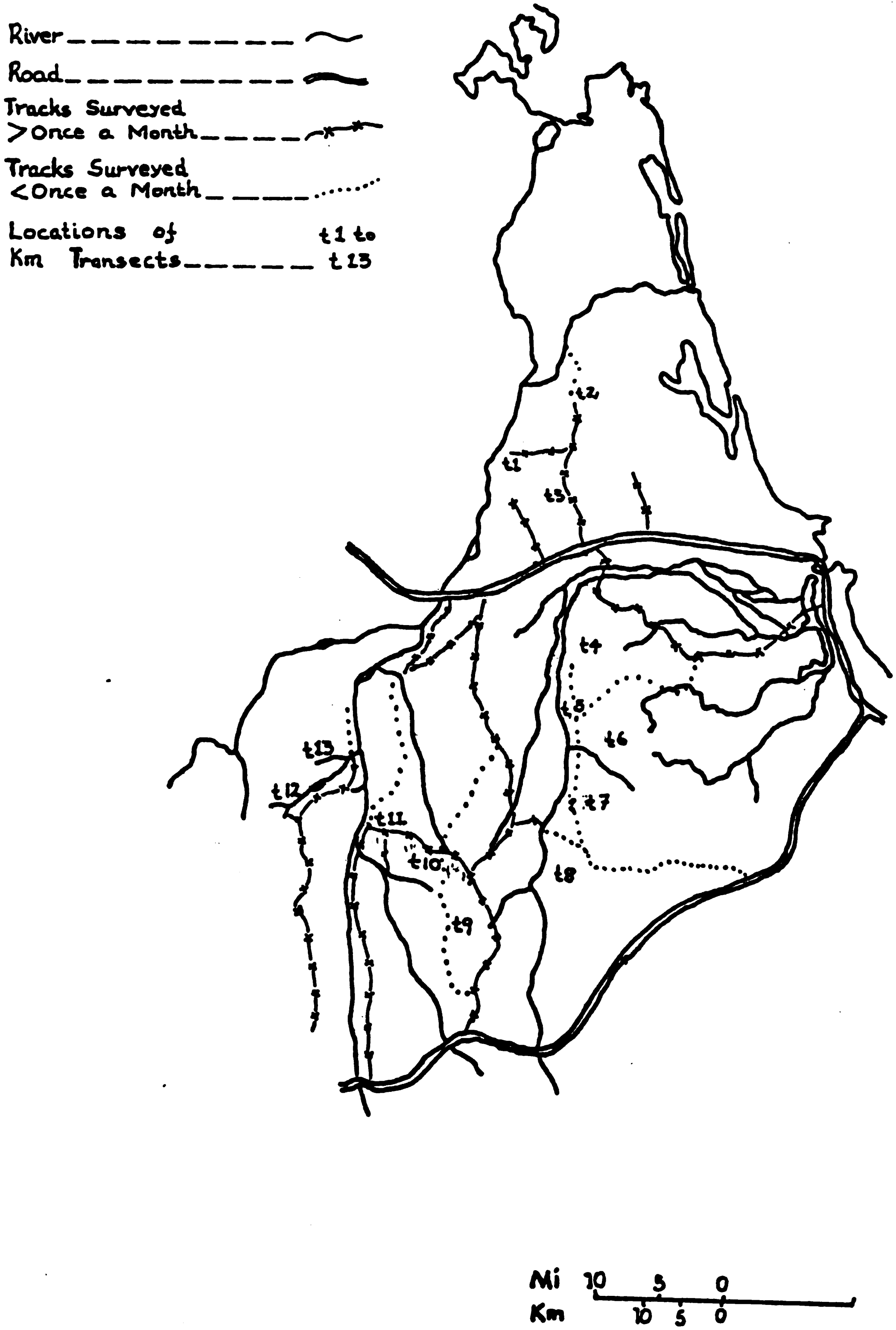
A high activity area was one where direct signs of elephant activity were detected during most visits made there. Signs of activity observed in moderate activity sites were of the indirect type. Only lone elephants, most of them males, were observed in low activity sites. Indirect signs of use by herds were very rarely seen in low activity sites.

TABLE 1 - Climatic data and human activities used in classifying wet and dry seasons for the period December 1980 - December 1981 in the Accelerated Mahaweli Development Area, Sri Lanka.

Season	Period in 12/80 to 12/81	Rainfall (in mm)			Predominant wind Direction		A		B
Wet	Dec. 15 - Jan. 15	209.9	203.3	224.5	NE	SW	Jan.	102	Cultivation season. Crop fields protected from elephants. Villus* flooded between November and February.
	Jan. 15 - Feb. 15	226.9	142.4	124.8	NE	SW	Feb.	98	
	Feb. 15 - Mar. 15	103.9	35.2	17.0	NE	SW	Mar.	131	
	Mar. 15 - Apr. 15	130.3	35.4	77.7	Variable		Apr.	122	
	Oct. 15 - Nov. 15	262.7	173.6	106.0	Variable		Nov.	95	
	Nov. 15 - Dec. 15	172.2	214.5	148.6	NE	SW	Dec.	95	
	Total	1105.9	806.4	699.4	Mainly			643	
	Mean	184.3	134.4	116.6	NE	SW		107.2	
Dry	Apr. 15 - May 15	166.3	113.3	88.5	Variable		May	153	Harvested croplands were grazing sites for elephants. Upland grasslands burnt. Upto 500 livestock grazed between 0800-1600 hours in the villus. Increased poaching on ungulates.
	May 15 - Jun. 15	21.3	0.0	4.6	SW	NE	Jun.	182	
	Jun. 15 - Jul. 15	15.9	0.0	0.0	SW	NE	Jul.	182	
	Jul. 15 - Aug. 15	190.8	93.6	49.1	SW	NE	Aug.	182	
	Aug. 15 - Sep. 15	114.8	110.4	169.1	SW	NE	Sep.	169	
	Sep. 15 - Oct. 15	49.4	129.0	91.1	Variable		Oct.	140	
	Total	558.5	446.3	402.4	Mainly			1009	
	Mean	93.1	74.4	67.1	SW	NE		168.2	

1, 2 and 3 were meterological stations within the study area where rainfall data were collected .
Predominant wind directions were generalized from maps of Johnson and Scrivenor (1981).
A - Long-term monthly means of pan evaporation rates, in mm, from TAMS (1980e).
B - Major changes in human activity that coincided with change of seasons.
*Villus - grasslands maintained by wet season flooding.

Figure 2. Jeep tracks (roads usually motorable at all times but sometimes impassable during heavy rains) surveyed for elephant activity, and the locations of 13 one km line transects used in habitat preference study carried out in the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.


River
Road
Tracks Surveyed >Once a Month
Tracks Surveyed <Once a Month
Locations of Km Transects t1 to t13
t1
t2
t3
t4
t5
t6
t7
t8
t9
t10
t11
t12
t13
Mi 10 5 0
Km 10 5 0

Study area distribution maps were prepared for wet and dry seasons. Relative seasonal distributions of high, moderate and low activity sites were indicated for the whole study area. Main population ranges of the study area were demarkated on the basis of these distribution maps. Population range maps were superimposed on the forest cover map of the study area and the percentages and total areas of forest and open habitats estimated. Grassland composition and distribution, as known from ground surveys, were used to qualitatively describe the characteristics of open habitats in different population ranges.

A certain amount of subjectivity in the description of elephant distribution for the whole study area was unavoidable owing to limitations of terrain, accessibility and the unavailability of modern radio-telemetry equipment. Elephant distributions in other study areas of Sri Lanka (McKay, 1973; Nettasinghe, 1973; Ishwaran, 1979) have also been described subjectively. Quantitative data to support the locations of high activity sites were collected in a few areas where elephants could be regularly observed. Number of feces counted in other areas was assumed to provide a reliable index of elephant activity there. Seasonal use of those areas as inferred from changes in feces counts and changes in the distribution of high, moderate and low activity sites were checked against each other for conformity.

Observations on wild (Vancuylenberg, 1977) and captive (Benedict, 1936) Asian elephants have shown that defecation occurred regularly throughout the day and night. Therefore, the deposition bias (Eisenberg et al., 1970) with respect to time and habitat was assumed to be negligible. The decay of elephant feces over time was assessed by observing the rates of disappearance of marked feces. 52 scats

(14 inside forests and 38 in grasslands) were observed from late October to December 1980. Another 48 droppings (12 in forests, 18 in grasslands and 18 in mixed habitat comprising woody vegetation and scattered grass cover) were observed for more than 100 days from January to April 1982. Although this would be the wet season during normal years, the 1982 period experienced drought conditions owing to the failure of the northeast monsoon. Hence, feces decay rates for this period was assumed to be representative of the dry season.

Feces were counted along road and foot transects in both corridor areas (C1 and C2 in Figure 1). In C1, two road transects and one foot foot transect were surveyed. One of the former extended east-west for 7.2 km. The other ran north-south for 6.1 km and was located about 4.8 km east of the Mahaweli Ganga. The road transect in C2 ran in a SE-NW direction for 22.4 km. Road transects were open paths that traversed predominantly forested habitats. All feces between the track and the forest border were counted. That border was between 5-7 m on either side of the vehicle in C1. In C2, that distance was 10-15 m. A speed of 5-10 m.p.h. was maintained while driving along all road transects. Feces along them were counted in 0.8 km blocks.

The foot transect in corridor C1 started from the end of the east-west road transect and extended 0.96 km to the banks of the Mahaweli Ganga. All feces, within 5 m on either side of the foot transect were counted. All road and foot transects were surveyed for about a year at approximately one-month intervals.

Droppings counted along all road and foot transects were classified as a) fresh b) old and c) very old. Fresh feces were less than a day old and retained most of their moisture. Old feces were partly moist and their age (probably about 2-3 days old) was less than the interval between successive counts, i.e. one month. Very old feces were either those which were deposited between counts but had dried completely, or those from the previous count that had not yet fully decayed. Comparing fresh, old and very old feces categories between successive counts for each 0.8 km block of road transects, and allowing for maximum feces deterioration rates, a minimum number of feces deposited between counts was estimated. The same procedure was also used to estimate the minimum number of feces deposited along the 0.96 km foot transect.

Since vegetation along all road transects was low and sparse, recognizing feces from the vehicle was not difficult during any time of the year. Assuming that the average transect width remained constant between seasons, the number of feces counted on each transect was compared between seasons using chi-square (X^2) tests (Bhattacharrya and Johnson, 1977).

The distribution of known elephants were mapped. Morphological features such as tusks, cysts on parts of the body, rips on ears, and depigmentation patterns were useful in identifying individual elephants (McKay, 1973). Repeated sightings of two juveniles and one adult male were mapped in WSNR. In areas east of SS, locations of 2 adult males and an adult female were mapped.

Elephants were observed regularly along the track in WSNR and also along the track leading to Trikkonamadu and Kandakadu in areas east of SS (Figures 1 and 2). All observations were made between 1400 and 1900 hours. The number of elephants seen along the track in WSNR at different distances from the Mahaweli Ganga (less than 3.2 km, 3.2-6.4 km, and greater than 6.4 km) were estimated for wet and dry seasons. Similarly numbers seen at 1) Kandakadu 2) Trikkonamadu and 3) along the track that led to those two sites were also estimated for each season. Dry and wet season counts for the period December 1980 to December 1981 were compared in all cases using X^2 goodness-of-fit tests (Bhattacharyya and Johnson, 1977).

Population Structure

Whenever elephants were seen, the number present, herd size, and time of observation were noted. A herd was defined as two or more elephants occurring together, where the distance separating any two adjacent individuals was less than 100 m (Kurt, 1974).

Four age-classes, namely infants (less than 3 ft tall), juveniles (3-6 ft tall), sub-adults (6-8 ft tall) and adults (more than 8 ft tall) were identified. Infants and juveniles could not be easily sexed. It was possible to identify the sex of sub-adult and adult individuals so long as the animal could be observed for about 1-2 minutes. Females always had tumescent mammae while males had a prominent penis sheath. Males also had a convex and sloping posterior. Females were box-shaped when viewed laterally owing to their vertical hindquarters (McKay, 1973). The male head was massive with a prominent bulge at the base of the trunk. Females had an angled forehead profile. Both sub-adult and adult females were frequently accompanied by infants.

Sex and age-classes of individuals observed in herds were used in recognizing the following herd types (Petrides, unpublished):

a. Female herds. Groups containing adult and/or sub-adult females with or without sub-adult males, juveniles and infants and where adult males were absent

b. Male herds. Groups of adult and/or sub-adult males, with or without juveniles and where adult females were absent

c. Harems where single adult male was associated with a female herd comprising two or more adult and/or sub-adult females

d. Mixed herds. Groups where two or more adult males were associated with female herds

e. Juvenile herds comprising only of juveniles

Lone elephants were considered as a separate category.

Observations made in WSNR and in areas east of SS are hereafter referred to as belonging to the WSNR and SS sub-populations, respectively. Herd structure and compositions were analyzed and described for observations made a) in the whole study area b) separately in the two areas occupied by the two sub-populations and c) during dry and wet seasons in the two areas occupied by the two sub-populations. Appropriate X^2 tests were used to compare sex and age-class compositions of herd types between sub-populations and between seasons for the same sub-population. When a significant effect was detected in a X^2 test for r x c contingency table, the procedure of Haberman (1973) was used to test the significance of the difference between observed and expected frequencies of individual cells in that table.

Herd size frequency distributions of female herds were compared between sub-populations and between seasons for each sub-population. Wilcoxon rank sum tests (Bhattacharyya and Johnson, 1977) were used for all such comparisons. Sizes of other herd types were either too variable or their samples too low for making any meaningful statistical comparisons.

Estimates of certain population parameters, e.g. sex ratio and age-class composition, were calculated from a sub-sample of daily observations, selected from observations made of each sub-population. The following criteria were used in selecting those sub-samples:

1) Days when at least 30 elephants were seen were initially selected, and were assumed to provide a representative sample of the sub-population under consideration. Since the largest size reported for any population in Sri Lanka was 400 (McKay, 1973; Nettasinghe, 1973), sample sizes of more than 30 in the present study area could have represented more than 10% of the elephants belonging to each sub-population
2) When more than 30 elephants were seen during successive days within the same area, only those observations made during that day when the largest number of elephants was observed, were included. The number of observations per day within each sub-sample was assumed to be independent of one another
3) Only those days when about 90% of the observed elephants were classified with respect to sex (of adults and sub-adults) and age-classes were included in the sub-samples

Estimates of the following were obtained for each sub-sample:

1) proportion of infants
2) proportion of females with infants assuming that all sub-adult and adult females were capable of giving birth to infants and that no twins were born
3) proportion of juveniles
4) observed sex ratio among sub-adults
5) observed sex ratio among adults
6) observed sex ratio among adults and sub-adults

Descriptive statistics such as mean and standard deviation were calculated for each of these estimates. They were compared between the two sub-populations using Wilcoxon rank sum tests. These same parameters, estimated from total observed frequencies of different sex and age-class categories, were also compared between sub-populations using tests for comparing binomial proportions (Bhattacharyya and Johnson, 1977). Results obtained by the two methods of comparisons were checked against each other and reasons for observed discrepancies discussed.

Habitat Preference and Range Quality

Habitat preference is a measure of the elephant's use of a particular habitat in relation to its availability. Indices of diet quality, extent of available preferred habitats and other incidental data obtained throughout the study period were used in evaluating the quality of ranges of the main populations.

Lack of vegetation maps for all parts of the study area and the low probability of seeing elephants in forests, limited direct appraisals of habitat availability and use. Indirect measures of both habitat availability and use were made along 13 transects each 1 km long. Those 13 transects (Figure 2) were selected so as to cover the whole study area. Elephant distribution with respect to each of these transects was assumed to be random.

The habitat available along each of the 1 km transects was recorded at every 25 m as belonging to any one of the following six categories:

1) Forests with an understory dominated by *Certococcum trigonum*

2) Forests with an understory of mixed herbaceous composition

3) Vegetation dominated by *Lantana camara*, *Eupatorium odoratum* and grasses such as *Imperata cylindrica* and *Panicum maximum* and characteristic of areas recovering from forest clearing
4) Grasslands dominated by *Imperata cylindrica*
5) Grasslands with a mixed species composition
6) Plantation forests comprising mainly of teak (*Tectonia grandis*) with a sparse understory of *Imperata cylindrica*

Distances along each of these transects were measured using a 25 m rope. Feces within 5 m on either side of the 1 km transects were counted as an index of habitat use. Low feces decay rates were observed between January and April 1982 when all 13 transects were surveyed. Hence the number of feces in a habitat was assumed to provide a reliable index of its use by elephants. Whenever dung was seen the habitat in which it was found was also noted.

On all 13 transects, the portion lying between 0-100 m, 400-500 m and 900-1000 m were surveyed for woody plant use by elephants (Wing and Buss, 1970; Vancuylenberg, 1974; Ishwaran, 1979 and 1983). All woody plants taller than 150 cm and within 2 m of the transect were enumerated. The dbh (diameter at breast height) value was recorded in six categories: 1) less than 5.0 cm 2) 5.0-10.0 cm 3) 10.0-20.0 cm 4) 20.0-40.0 cm 5) 40.0-80.0 cm 6) greater than 80.0 cm. Browsing by elephants was identified by signs such as broken branches, peeled bark, and uprooted trees. Woody plant species were identified in the field or later at the herbarium at the Royal Botanic Gardens at Peradeniya.

Information from all 13 transects was pooled. The number of times a habitat was encountered was used to estimate its proportional availability. The number of feces counted in a habitat category was used to estimate its proportional use. Proportional availability and use were also estimated for all woody plant size classes.

Observed use (of habitats or woody plant size classes) was compared with that expected on the basis of availability. X^2 tests were used for this purpose. When a significant difference between observed and expected use was detected, the Bonferroni z-statistic (Neter and Wesserman, 1974) was used to estimate confidence intervals for observed use (Neu et al., 1974). Comparisons between these confidence intervals and the respective estimates of expected use, enabled the distinction between habitats and woody plant size classes which were preferred, neglected or used in proportion to their availability.

A total of 116 fecal samples were collected between January and December 1981. When fresh fecal piles of adult elephants were seen, the largest bolus in the pile was collected for analysis. Only one sample was collected at any particular site. It was assumed that each sample represented a different animal. Each bolus was partially air-dried before being oven-dried at the University of Peradeniya. The contents of the dry fecal bolus were spread on a dissection tray and separated into grass, woody and other components. The percentage of occurrence, by volume, of each component was recorded. Percentage occurrence of food items in fecal samples have been used for identifying the major components of the African (Wing and Buss, 1970) and the Asian (Vancuylenberg, 1974) elephant's diet.

A sub-sample of each fecal bolus was used for proximate analysis (carried out by a trained technician at the Government Veterinary Center, Peradeniya) of crude protein, crude fiber and ash. These were percentages of dry matter. Based on the area of collection, the data for 116 fecal samples were divided as belonging to three different populations.

Percentage crude protein of feces and feed were found to be correlated for many species of African mammals (Arman et al., 1975). Fecal crude protein as a relative indicator of diet quality was considered suitable for large, non-ruminant herbivores with a predominantly grass-based diet, which also passed food through their intestines rapidly (Robbins, 1983). Since anatomical and physiological characteristics of the Asian elephant (Benedict, 1936; Eltringham, 1982) as well as its food preferences in this study area met these requirements well, percentage fecal crude protein was used as a reliable indicator of diet quality.

In using fecal crude protein as an indicator of diet quality, it was assumed that the digestive efficiency and the ratio between metabolic and fecal nitrogen were the same for adult animals of the different populations. Crude protein estimates within a season were compared between populations using the Kruskal Wallis test for k-treatments (Bhattacharyya and Johnson, 1977). When a significant difference between populations was found, multiple pairwise comparisons were made using the method of Conover (1982:231).

Changes in Habitat Use and Habitat Quality

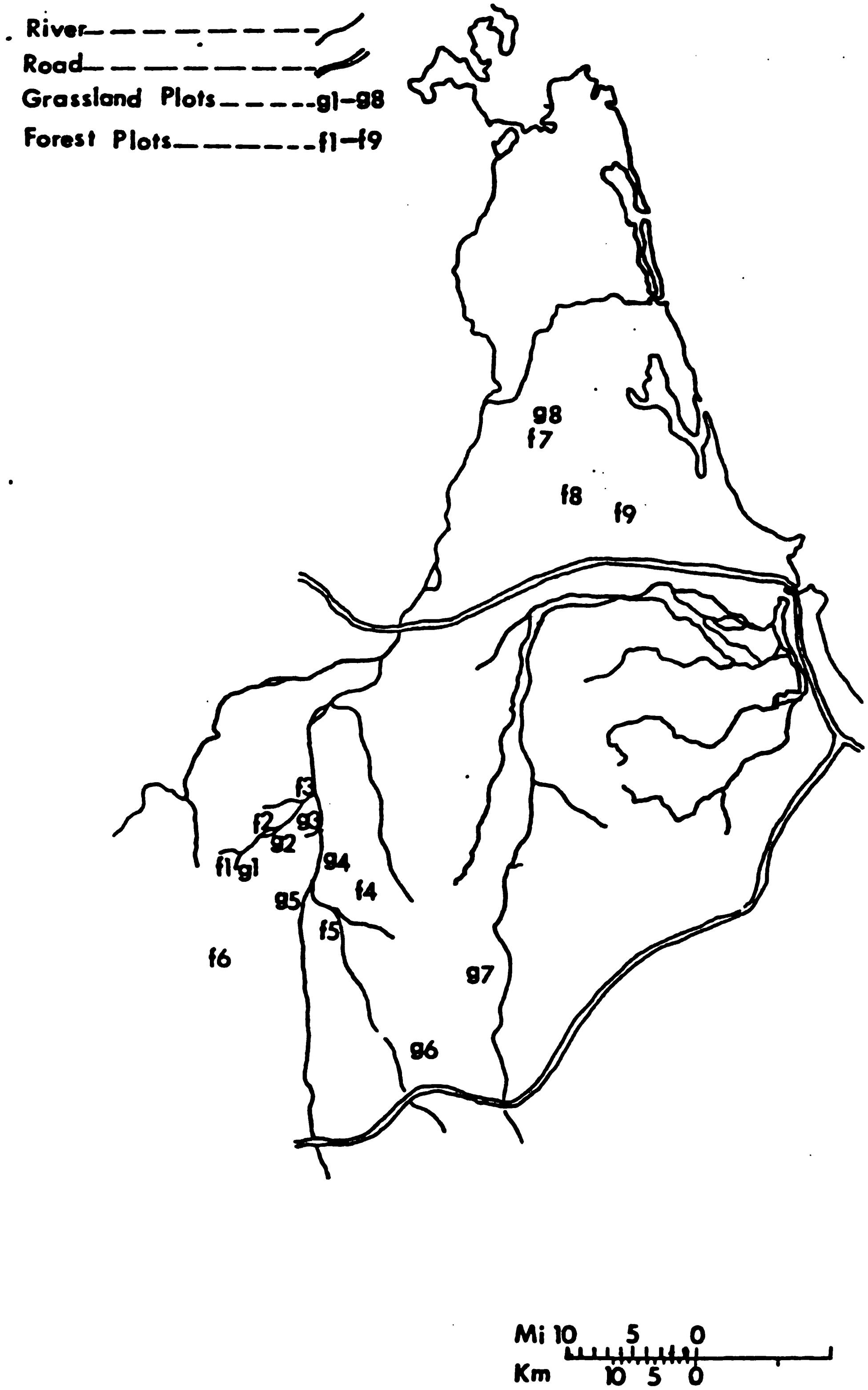
Relationship between habitat use and habitat quality were studied in fixed plots. Nine plots were located in grasslands and nine more were in forests (Figure 3). All grassland plots were 1.5 ha (100 x 150 m^2) in extent. Attempts to survey plots of similar size inside forests had to be abandoned in early 1981 owing to limitations imposed by terrain, accessibility, time and available man-power. The forest plots were all 2,500 m^2 (50 x 50 m^2) in size. Forest plot f6 was established in an area known to be regularly used by elephants for resting. Such resting sites inside forests were recognized by McKay (1973).

Grassland plots g1-g8 were surveyed between 22 November 1980 and 20 December 1981. All of them except g5 were surveyed 6 times during the wet season and 5 times during the dry season. The sixth wet season count, the last in 1981, could not be carried out in g5 because the plot was plowed for cultivation by encroaching farmers. Plot g9 was surveyed 6 times in the wet and 4 times in the dry season between August 1981 and June 1982. All forest plots were surveyed between May 1981 and April 1982, 6 times during the wet and 4 times during the dry season.

During every period of count, feces were either removed from plots or broken into small pieces. Recounting of the same feces was thus avoided. Droppings in grassland plots were systematically counted along ten strips, each of them 10 m wide and 150 cm long. Along each line, a 0.25 m^2 quadrat was placed at the 0, 50, 100 and 150 m points. For each quadrat site, the following were recorded: 1) percentage grass cover 2) percentage grass greenness 3) grass height measured as an average of 5 of the tallest stems. Hence, for each month on each plot, 40 recordings of each grassland quality parameter were made. Simultaneous recording of habitat quality variables and local animal abundance was recommended for aerial surveys in African Habitats (Western, 1976). This principle was adopted for ground surveys in grasslands of the present study area.

In each grassland plot, all feces of buffalo and/or cattle were also counted in the way described for elephant feces. Deterioration rates of buffalo and/or cattle feces were, however, unknown. Estimated

Figure 3. Locations of grassland (g1-g9) and forest (f1-f9) plots used for estimating relative elephant densities by feces count method in the Accelerated Mahaweli Development Area, Sri Lanka. November 1981 - July 1982.


River
Road
Grassland Plots g1-g8
Forest Plots f1-f9
g8
f7
f8
f9
f3
f2
g3
g2
f1
g1
g4
f4
g5
f5
f6
g7
g6
Mi 10 5 0
Km 10 5 0

densities were considered therefore, to be minimum values for the specified period of time. Other variables such as distance from forest, and distance from the nearest source of water, were comparable for the different grassland plot sites and were assumed to be constant.

Species composition of grassland plots was determined in January-February 1982 and was assumed to have remained constant throughout the period of feces counts. In all grassland plots, the cumulative number of species reached a maximum in 10-20 sites, randomly selected by throwing a 0.25 m^2 quadrat frame. Percentage relative cover of plant species was recorded at 20 quadrat sites within each plot.

Forest plots were surveyed in a similar manner. Forest quality variables that possibly affected elephant use of that habitat could not be identified from past studies. Hence, recording of such variables was not attempted.

Relative densities of elephants and livestock (buffalo and/or cattle) for periods between successive counts were estimated by the formula:

$$\text{Relative density} = \frac{\text{Total number of feces counted}}{\text{Daily defecation rate x Number of days between counts}}$$

A defecation rate of 14 per day was used for elephants (Eisenberg et al., 1970; Ishwaran, 1979). Based on information available for farm animals in the study area, a defecation rate of 10 per day was used for livestock. Defecation rates were assumed to remain constant between seasons. They were also assumed to be independent of age for both the elephant and livestock. All relative density estimates were converted to number of animals per hectare.

Wet and dry season relative elephant densities on each grassland plot were compared using Wilcoxon rank sum tests. Species composition of plots g1-g8, as recorded in 20 quadrat sites, were tabulated. In plots g2 and g6, *Imperata cylindrica* was the dominant grass. Observed frquencies of *Imperata* and all other grass and sedge species were tallied separately for both those plots. Association between the two frequencies and plot sites were tested for plots g2 and g6. Relative densities, of both the elephant and livestock, were also compared between the two plots using a Wilcoxon sign rank test (Bhattacharyya and Johnson, 1977).

In seasonally flooded villus, densities could not be estimated using feces counts. In the villu at Trikkonamadu, however, density estimates were obtained for animals seen as a) solitaries and in male herds and b) in female herds, mixed herds and harems.

For each feces count, variance estimate of each grassland quality parameter provided a measure of patchiness in the availability of that parameter; e.g. mean percentage grass cover of 70% with a variance of 500 would indicate a more patchy availability of grass than when the mean was the same but the variance only 100. Variance estimates of grassland quality parameters are hereafter referred to as measures of patchiness in available grass cover, greenness and height.

For each grassland plot, an average elephant density was obtained for 6 wet and 5 dry season counts. Grassland quality estimates were also averaged for wet and dry season counts. For each plot, average estimates were obtained for both seasons of 1) percentage grass cover 2) patchiness in grass cover 3) percentage grass greenness 4) patchiness in grass greenness 5) grass height 6) patchiness in available grass height and 7) minimum density of livestock.

The relationship between mean seasonal estimates of grassland quality variables and relative elephant densities was investigated separately for wet and dry seasons. Stepwise linear regression (Neter and Wesserman, 1974) using the MINITAB program (Ryan Jr et al., 1982) was performed, with the average relative elephant density as the dependent variable and each of the seven grassland quality parameters as separate independent variables. When none of the independent variables showed a significant regression relationship with the dependent variable, the effect of the combined presence of two or more independent variables in the regression model was tested. Those independent variables that were most correlated with the dependent variable but not significantly correlated with one another were selectively introduced into the regression model.

Wet and dry season relative elephant densities on each forest plot were compared using Wilcoxon rank sum tests. Relative elephant densities recorded in the resting area plot (f6) were compared with average relative elephant densities of forest plots in WSNR (3 plots), corridor Cl (2 plots) and areas east of SS (3 plots). The Kruskal Wallis test for k-treatments was employed for this purpose. When a significant difference was found, multiple pairwise comparisons were made using the method of Conover (1982:231).

Crop Damage by Elephants

Eleven open-ended questions were used to interview farmers on the extent of economic damage suffered by them due to crop-raiding elephants. Interviews were conducted between January and April 1982. All questions were related to crops cultivated during November 1980 to April 1981. Crop losses due to bad weather conditions were minimal during that season. Although it was planned to interview farmers with respect to the 1981-

1982 cultivation season, the drought that began in January 1982 forced many farmers to abandon their crops. Data for this cultivation season were therefore not gathered.

Farmers from the villages of Namini Oya, Trikkonamadu and Aluyatawala were interviewed. These villages were near other data collection sites which were regularly visited. Number of farmers who were expected to respond to the interview-request was also higher for each of these three villages than for other villages in the study area.

The village council and some of the older farmers and traders in each community were informed of a date for the interviews which were held at a school or shop. Farmers were interviewed individually. Farmers who voluntarily attended the interviews made up the sample in each village. Hence, the samples were probably biased towards the more highly motivated section of the farmer population (Filion, 1980), which suffered crop damage by elephants.

The following questions were asked regarding the 1980-1981 season:

1) How much land (in area) did you cultivate ?
2) How far was the nearest forest border from your cultivation ?
3) How close to your home was your cultivation ?
4) Were you able to cultivate during the dry season ?
5) What were the main crops cultivated ?
6) Assuming that climatic and other conditions were favorable, what was your expected yield/acre ?
7) Did your cultivation suffer from crop-raiding elephants ?
8) During which months did the raids occur ? At what time of the day did they occur ?
9) The crop-raiding elephants were: 1) mostly lone elephants 2) lone

elephants and groups comprising only larger individuals 3) groups which had younger and larger elephants

10) What was your final yield/acre ?

11) What measures did you take to protect crops ?

After questions were answered, the farmers were asked to state their opinions on the problems caused by crop-raiding elephants.

Paddy planted in October ideally required rainfall till January for growth and flowering. Proper seed formation was ensured if the drier conditions of February-April (Table 1) followed. Harvesting too, needed to be completed before the end of that dry period. Even when weather conditions were optimal as during the November 1980-April 1981 season, the ability of farmers to follow the proper schedule of plowing, land preparation, sowing of paddy and harvesting could be limited by many socio-economic (other conditions in question 6) factors. The influence of those factors on expected and final yields of farmers who were interviewed was not known and was assumed to be minimal for the 1980-1981 season.

The responses of farmers to the questions were assumed to be true. It was not possible to check any of the reported crop-raids since they occurred during a period 8-12 months prior to the time of interviews. This time delay perhaps introduced a recall-bias (Filion, 1980) to farmer responses. However, farmers also were likely to exaggerate their losses since they expected compensation payments. It was judged that the tendency of farmers to exaggerate their losses would be more important biasing their responses to questions 6 and 10 rather than their propensity to forget the extent of crop damage they suffered at a time 8-12 months earlier.

Information gathered from the eleven questions provided basic statistics pertaining to crop damage incurred by farmers. Loss of yield per ha per farmer was estimated from responses to questions 6 and 10. The reliability of this estimate in reflecting damage caused solely by elephants will be discussed. Assuming that these estimates within each village sample were independent of one another, mean estimates of loss and 90% confidence intervals were calculated for each village. In converting loss in crop-yield to estimates of economic loss, the value of the produce, as quoted by the Department of Agriculture, Sri Lanka, was used.

Impact of Development Program

A map of the AMDP land use plan for the study area was superimposed on the elephant population range map. Percentage loss of area to development and settlement was estimated for each population range identified in the study area. The potential of new national parks for protecting elephants that would be displaced by development activities was discussed. Recommendations for management and research were made separately.

RESULTS

Forest cover, both of natural and plantation forests, was about 32.0% of the study area (Figure 4). Natural forest cover in existing reserves, e.g. WSNR and SS (Figure 1), was about 80-90%. In PMONP (Figure 1), only 30% of the area was occupied by forest, with 18% of that cover being teak (*Tectonia grandis*) plantations.

Distribution of Elephant Populations

High, moderate and low elephant-activity sites changed seasonally (Figure 5 and 6). These changes were comparable to those inferred from quantitative data available for some areas. For example, a wet season high activity site was identified and described across the Mahaweli Ganga in the WSNR-corridor C1 areas (Figure 5). Number of elephants observed within 3.2 km of the Mahaweli Ganga, along the track in WSNR, were significantly higher in the wet than in the dry season ($X^2 = 16.2$; $p < 0.001$; 1 d.f.; Table 2). Those three observations of recognizable elephants which were closest to the Mahaweli Ganga (Figure 7) were also made during the wet season. Although higher feces deterioration rates of the wet season (Table 3) led to an underestimation of feces counts made then, wet season counts in all road and foot transects of corridor C1 were significantly higher in the wet than in the dry season (Table 4). This finding too, supported the inference that the corridor C1 probably had higher levels of elephant activity during the wet (Figure 5) than during the dry (Figure 6) season.

A dry season high activity site in and outside the southwestern boundary of WSNR (Figure 6) was identified. Areas at distances greater than 6.4 km from the Mahaweli Ganga, along the track in WSNR, were part of that dry season high activity site. Observed elephant numbers in those parts were significantly higher in the dry than in the wet season ($X^2 = 271.98$; $p < 0.001$; 1 d.f.; Table 2). All sightings of known elephants in WSNR (Figures 7 and 8), other than those three closest to the Mahaweli Ganga (Figure 7), were also made during the dry season.

In areas east of SS too, changes in seasonal numbers of elephants observed at selected sites were predictable on the basis of the location of high elephant-activity sites. Trikkonamadu (Figure 1) was located within the wet season high activity site of the Mahaweli Ganga floodplains (Figure 5) and hence number of elephants seen there was significantly higher in the wet than in the dry season ($X^2 = 14.85$; $p < 0.001$; 1 d.f.; Table 2). Similarly, Kandakadu (Figure 1) was within the dry season high activity site identified along the Mahaweli Ganga floodplains (Figure 6) and the numbers of elephants observed there were significantly higher during the dry than in the wet season ($X^2 = 188.93$; $p < 0.001$; 1 d.f.; Table 2).

Locations of wet season high activity sites along the Maduru Oya river (Figure 5) could not be checked against quantitative data since those regions of the study area were less regularly accessible (Figure 2). The road transect in corridor C2 traversed parts of the northern wet season high activity site along the Maduru Oya (Figure 5). Feces counted along that transect, however, did not differ significantly (Table 4). Since it was not possible to identify localized high activity sites during the dry season (Figure 6), the validity of the described elephant distribution along the Maduru Oya river remained low.

Figure 4. Areas of natural forests, teak (<u>Tectonia grandis</u>) plantations and open habitats in the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

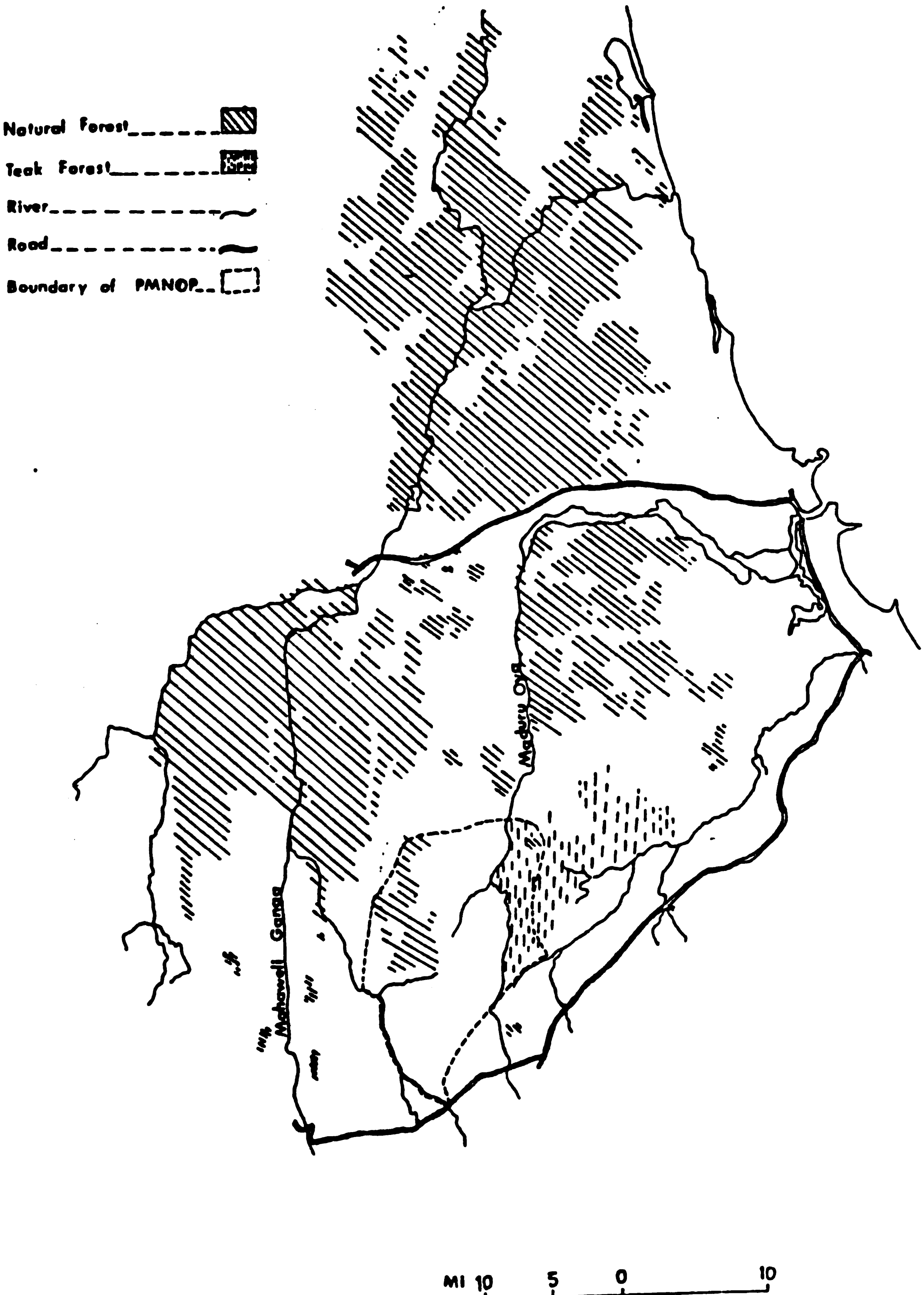

Natural Forest
Teak Forest
River
Road
Boundary of PMNOP
Maduru Oya
Mahaweli Ganga
MI 10 5 0 10
Km 10 5 0

Figure 5. Wet season areas of high, moderate and low elephant-activity in the Accelerated Mahaweli Development Area, Sri Lanka. November 1980 - December 1981.

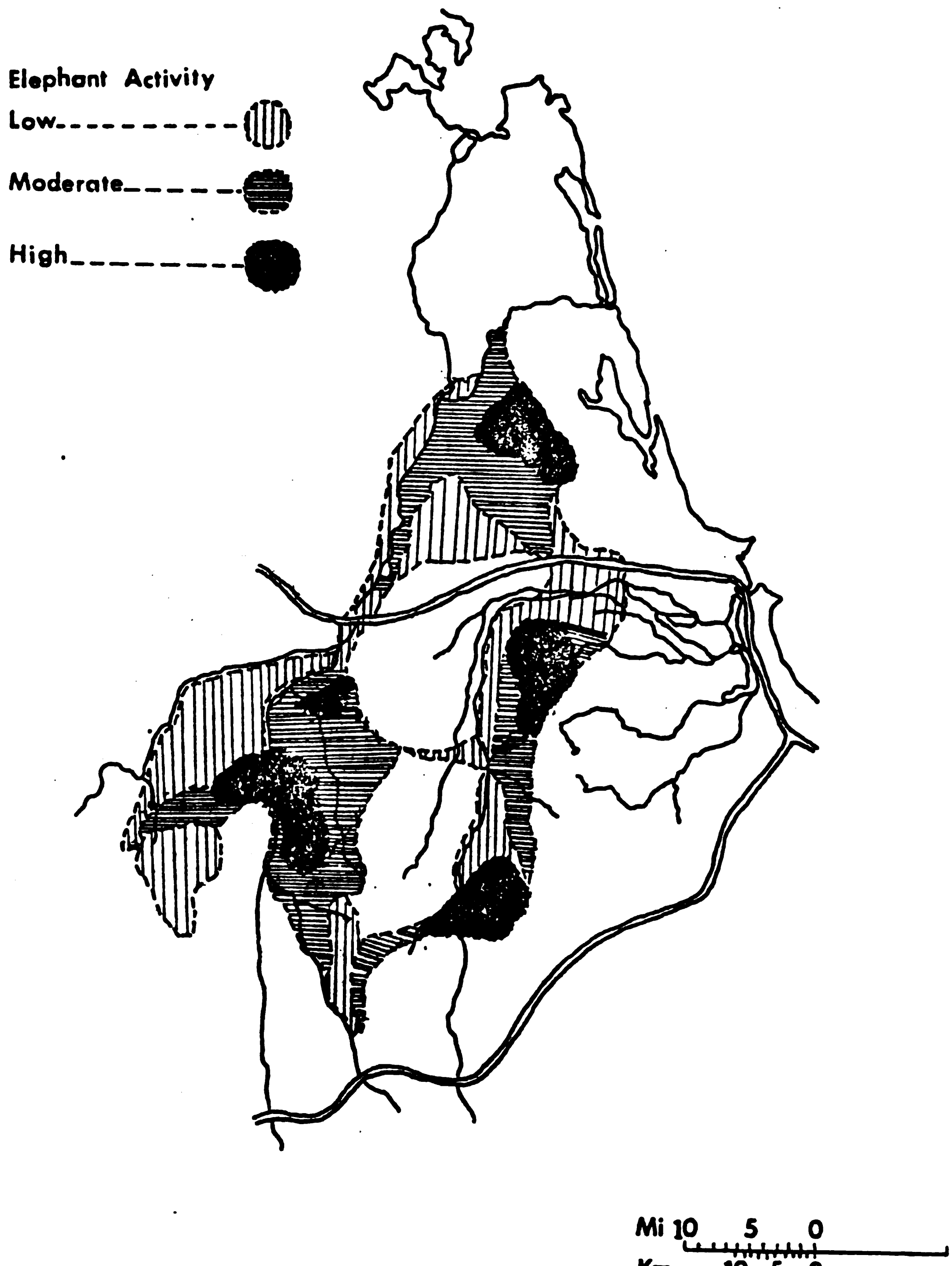
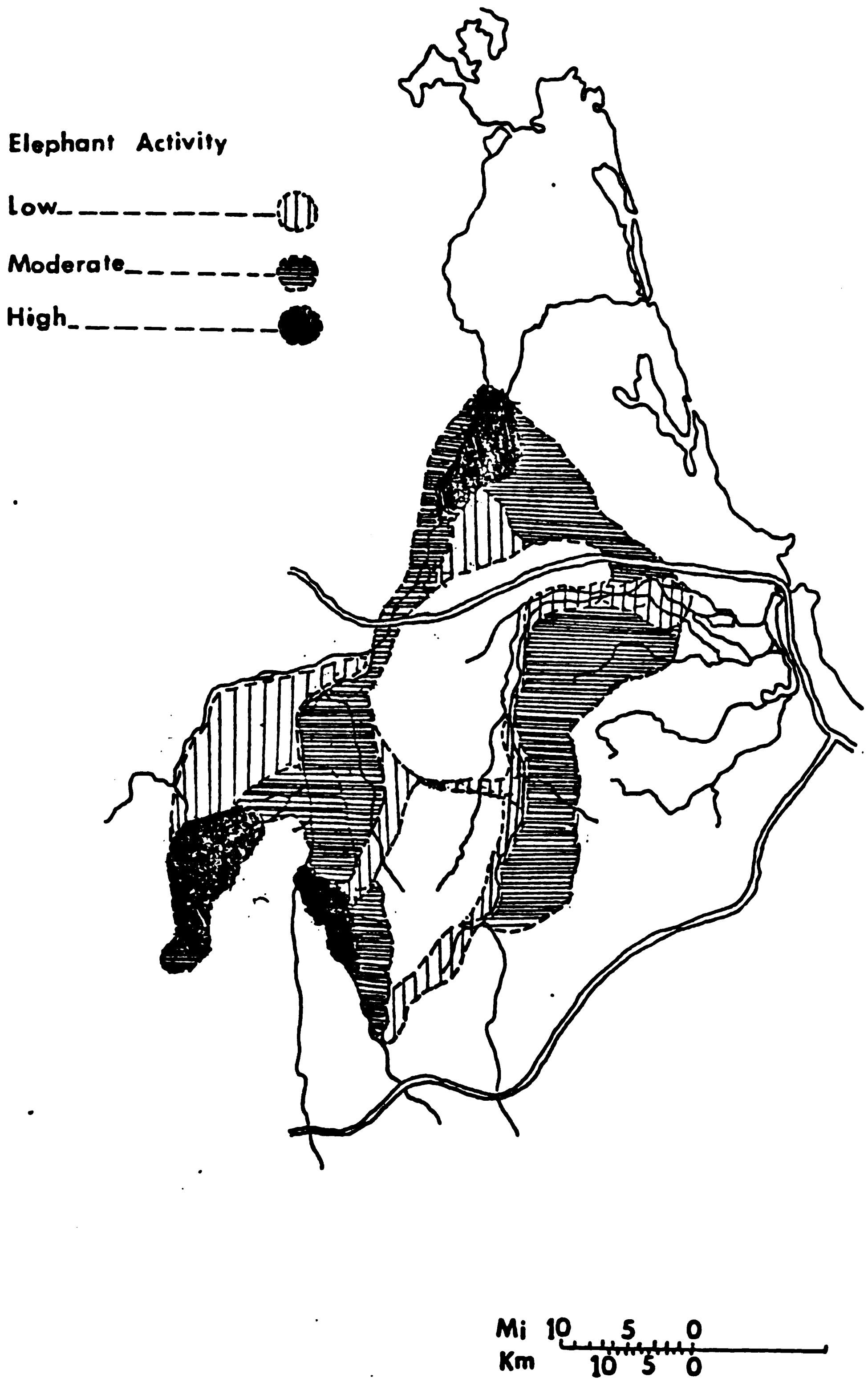

Elephant Activity
Low
Moderate
High
Mi 10 5 0
Km 10 5 0

Figure 6. Dry season areas of high, moderate and low elephant-activity in the Accelerated Mahaweli Development Area, Sri Lanka. November 1980 - December 1981.



Elephant Activity
Low
Moderate
High
Mi 10 5 0
Km 10 5 0

TABLE 2 - Relationship between seasonally observed elephant numbers during evening hours of 1400 - 1900 hrs. and those expected on the basis of frequency of visits to selected sites in the Accelerated Mahaweli Development Area, Sri Lanka. November 1980 - December 1981.

Site Description	Season	I a	I b	I c	II a	II b	II c	III a	III b	III c
Track in WSNR	Wet	69	21	50.58	73	23	90.74	114	24	373.93
	Dry	13	13	31.32	69	13	59.26	499	15	239.07
		$X^2 = 16.2$ $p < 0.001$			$X^2 = 9.6$ $p < 0.005$			$X^2 = 271.92$ $p < 0.001$		

Site Description	Season	IV a	IV b	IV c	V a	V b	V c	VI a	VI b	VI c
Areas East of SS	Wet	01	15	81.93	190	21	132	33	21	40.17
	Dry	141	11	60.07	60	14	88	32	13	24.83
		$X^2 = 188.93$ $p < 0.001$			$X^2 = 14.85$ $p < 0.001$			$X^2 = 3.35$ $p < 0.10$		

I = 3.2 km from the Mahaweli Ganga
II = 3.2 - 6.4 km from the Mahaweli Ganga
III = 6.4 from the Mahaweli Ganga
IV = Kandakadu
V = Trillonamadu
VI = Track leading to Kandakadu and Trikkonamadu

a = observed number of elephants
b = number of visits to that particular area
c = observations expected on the basis of number of visits

TABLE 3 - Observed decay rates of elephant feces in forest, grassland and mixed habitats of the Accelerated Mahaweli Development Area, Sri Lanka, for periods of high (October - December 1980) and low (January - April 1982) rainfall.

Observation Period	Total Rainfall (mm)	Habitat	No. of Feces Marked	No. recognizable After 30 days	No. recognizable When observations were halted
October to December 1980 (High rainfall period representative of normal wet season.)	1)595.9	Forest	7	4	4 after 61 days
			7	7	6 after 52 days
	2)472.4				
	3)402.3	Grassland	38	22	18 after 52 days
January to April 1982 (Low rainfall representative of normal dry season.)	1)346.9	Forest	8	8	8 after 97 days
			4	4	4 after 101 days
	2)232.1				
	3)203.9	Grassland	7	7	1 after 64 days
			7	7	7 after 98 days
			2	2	2 after 97 days
			2	2	2 after 61 days
		Scrub Interspersed with grass	18	16	15 after 98 days

1, 2, 3 represent rainfall data from three meterological stations in the area.

TABLE 4 - Relationship between seasonally observed and expected number of feces counted along transects in corridors C1 and C2 of the Accelerated Mahaweli Development Area, Sri Lanka. January 1981 - February 1982.

Corridor Description	Transect Description	Period of Study	Seasons	No. of Counts/Season	No. of days between 1st & last count	Observed Feces Count	A	X^2 & p
C1	Foot tran. 0.96 km	Jan-Feb 1981	Wet	5	149	96	57.69	47.93
			Dry	5	169	27	65.32	<0.001
	East-West road tran. 7.2 km	Jan-Dec 1981	Wet	5	149	166	141.64	7.89
			Dry	5	169	136	160.36	<0.01
	North - South road tran. 6.1 km	Feb-Dec 1981	Wet	4	116	75	60.24	6.10
			Dry	5	169	73	87.76	<0.05
C2	Southeast-Northwest road tran. 22.4 km	March 1981 to Feb 1982	Wet	5	157	386	398.4	0.74
			Dry	5	170	444	431.6	>0.10

A — Feces count expected on the basis of time interval from 1st to last count

Figure 7. Locations within and near the Wasgomuwa Strict Natural Reserve (WSNR) of the Accelerated Mahaweli Development Area, Sri Lanka, where recognizable individuals were seen repeatedly between September 1980 and July 1982.

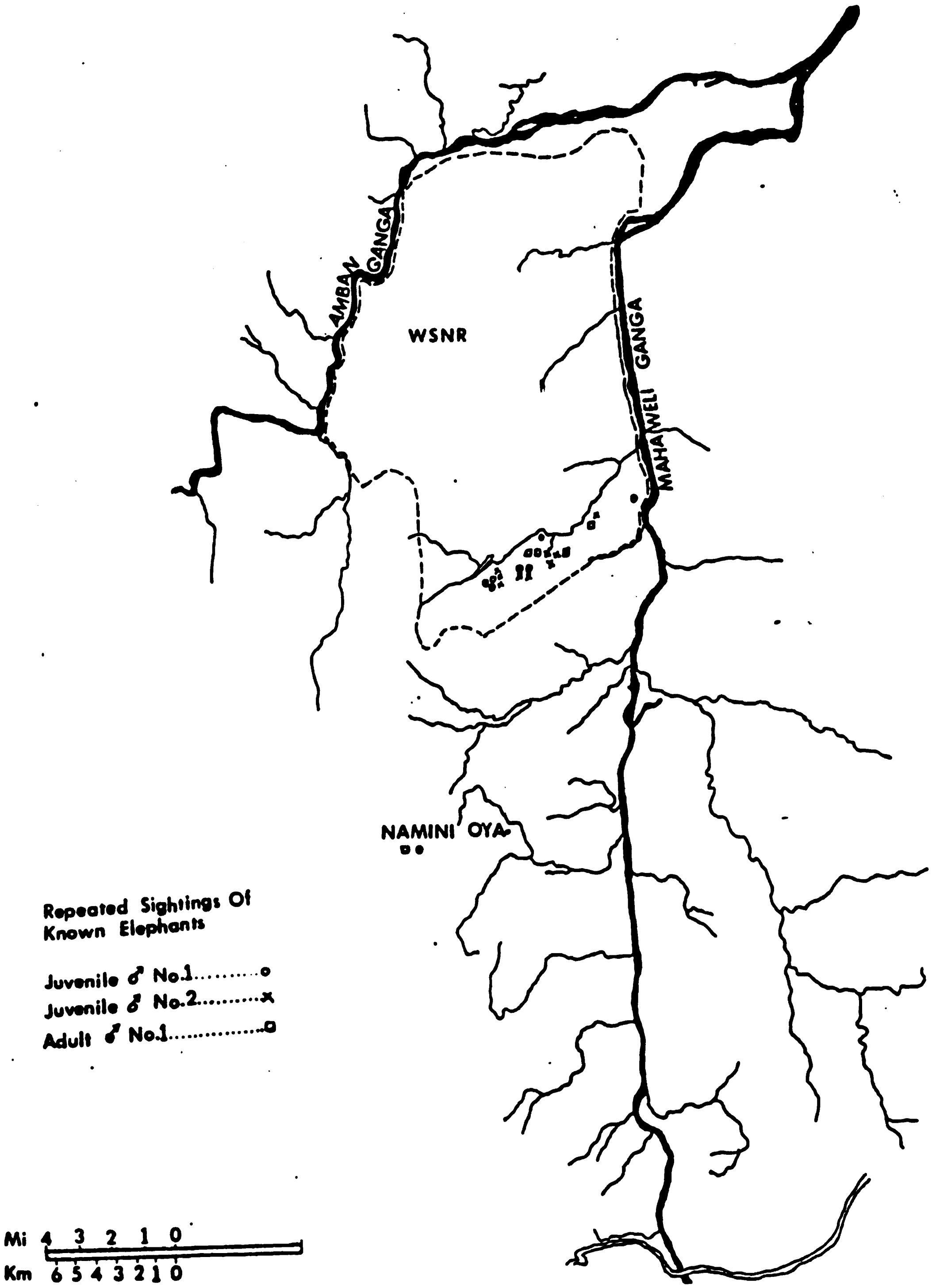

AMBAN GANGA
WSNR
MAHAWELI GANGA
NAMINI OYA
Repeated Sightings Of
Known Elephants
Juvenile ♂ No.1..........o
Juvenile ♂ No.2..........x
Adult ♂ No.1..............□
Mi 4 3 2 1 0
Km 6 5 4 3 2 1 0

Figure 8. Juvenile no. 2, a male recognized by the presence of its tusks, is shown playfighting with another individual of the same age-class in the Wasgomuwa Strict Natural Reserve (WSNR) of the Accelerated Mahaweli Development Area, Sri Lanka. September 1981.

The boundaries of high, moderate and low activity sites, as indicated in Figures 5 and 6, were subjective. Nevertheless, since quantitative data in selected sites supported the locations of high activity sites, and because more objective descriptions of elephant distributions in the area were not available, seasonally high, moderate and low activity sites along the Mahaweli Ganga (Figure 5 and 6) were assumed to provide a representative description of elephant distribution along that river.

The dry season high activity site in areas east of SS were nearer to the Mahaweli Ganga (Figure 6) than that of the wet season (Figure 5), Flooding of habitats closer to the Mahaweli Ganga, during the northeast monsoonal rains, probably forced elephants to move away from it. Flooding might have influenced elephant movements by restricting available grazing sites near the river. Even though most villus were flooded during the rains adequate grasses were available in them (Figure 9a), and hence elephants were regularly observed to feed on them. All observations made in Trikkonamadu were in and/or near the villu there, and significantly more elephants were observed during the wet than in the dry season (Table 2). Low human and livestock use of flooded villus (Table 1) could have also enabled the elephants to emerge from forests earlier in the evenings and thereby increased their chances of being observed. In the dry season when human and livestock use of the villus during the day increased (Table 1), elephants became nocturnal. Indirect signs of use of the villu at Trikkonamadu were regularly detected in the dry season. Since green grass was available only in the villus during the drier months (Figure 9b), their importance to elephants as a potential grazing area was probably similar to, or higher that of the wet season.

Figure 9a. The villu at Trikkonamadu, a site located in areas east of the Somawathiya Sanctuary in the Accelerated Mahaweli Development Area, Sri Lanka, partially flooded during the wet season. December 1980.

Figure 9b. The villu at Trikkonamadu, a site located in areas east of the Somawathiya Sanctuary, in the Accelerated Mahaweli Development Area, Sri Lanka, showing green forage available in the moist regions of that habitat in contrast to dry vegetation in upland sites. June 1981.

Heavy southwest monsoonal rains in the catchment and other upstream areas of the Mahaweli Ganga led to flooding of villus in June 1982, though the study area was experiencing normal dry season weather (Table 1). Mixed herds, comprising all three recognizable elephants of the area, seemed to move away from the river, and were seen near the east-west highway (Figure 10). All changes in weather conditions, within the study area and in other parts of the country which affected water-levels in the Mahaweli Ganga, could potentially influence elephant distribution and movement in the floodplain areas east of SS.

WSNR and corridor Cl were located in areas further upstream along the Mahaweli Ganga than SS (Figure 1). Flooding in those upstream regions was less severe and wet season high activity site in WSNR-corridor Cl areas extended across the Mahaweli Ganga (Figure 5). Dry season high activity sites in WSNR and corridor Cl areas were nearer to human settlements than the wet season high activity site (Figure 5). Croplands abandoned after harvest were important grazing areas for elephants in the dry season (Table 1). Imperata cylindrica which was fed upon only after burning in the dry season was also more prevalent in areas near human settlements. Since elephants in WSNR and corridor Cl occupied largely forested ranges, availability of those new grazing areas probably influenced their dry season movement into high activity sites in the vicinity of human settlements.

Three (A, B and C) population ranges were demarcated (Figure 11) on the basis of the distribution of high, moderate and low activity sites. The low activity overlap zone between population ranges B and C was probably a temporary effect of reservoir construction sites there (Figures 1 and 11). All the villus along the Mahaweli Ganga floodplains were included as parts of the population range A. The total of 5,090 ha of villus (Table 5) was an area of superior pastures not available in other ranges (Table 5).

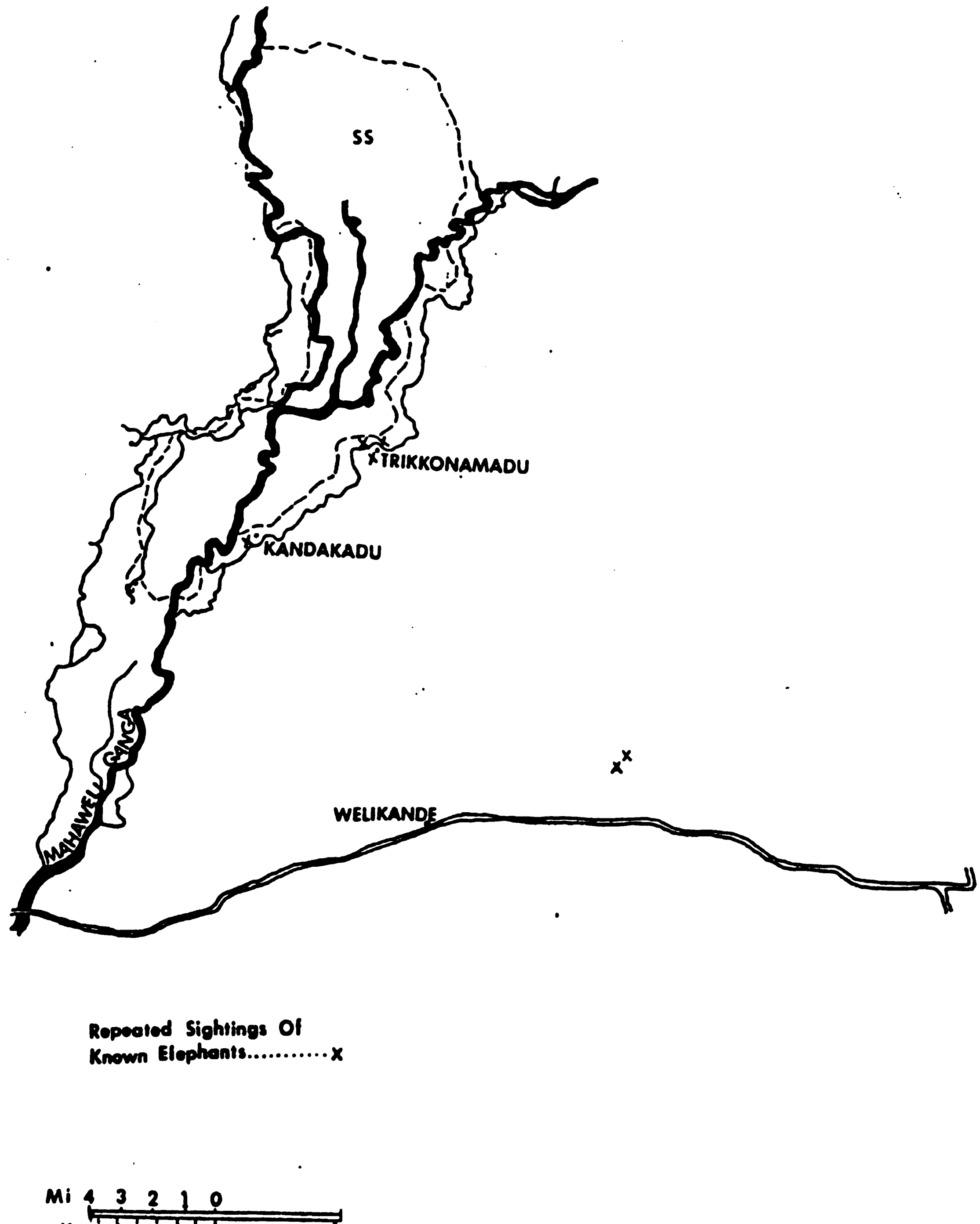
Population Structure

A total of 2130 observations was made of elephants. 87.7% of those (1870) were of elephants belonging to the WSNR and SS sub-populations. Although 24.0% of the observations were uncategorized in the wet season in WSNR, total number of observations per sub-population per season were never less than 270 (Figures 12 and 13). These samples were assumed to be representative for the purpose of describing seasonal characteristics of the two sub-populations.

Although total numbers of elephants observed in many parts of the study area probably increased during late night hours, such increases were unlikely to affect observed sex and age class composition of herd types. Within each sub-population each individual was assumed to be equally susceptible for observation. Relative visibility of sex and age class categories of the two sub-populations were also assumed to be similar.

Whether data were considered for the whole study area, or for separate seasons for the two sub-populations (Figure 12), solitary elephants (more than 95% of them males) and female herds were the most frequently observed units of elephant social organization. While solitary elephants were seen more often than female herds in the SS sub-population, female herds were the most frequently seen category in WSNR (Figure 12). Other herd categories were seen less frequently, but number of elephants seen in some of them could be higher than those in female herds; e.g. wet season mixed herds of the SS sub-population (Figure 12).

Figure 10. Locations in areas east of Somawathiya Sanctuary (SS) of the Accelerated Mahaweli Development Area, Sri Lanka, where mixed herds comprising three recognizable elephants were repeatedly seen between September 1980 and July 1982.



Repeated Sightings Of
Known Elephants..........X

Figure 11. Approximate ranges of three populations demarcated on the basis of the distribution of high, moderate and low elephant-activity areas and available grassland types in the Accelerated Mahaweli Development Area, Sri Lanka. November 1980 - December 1981.

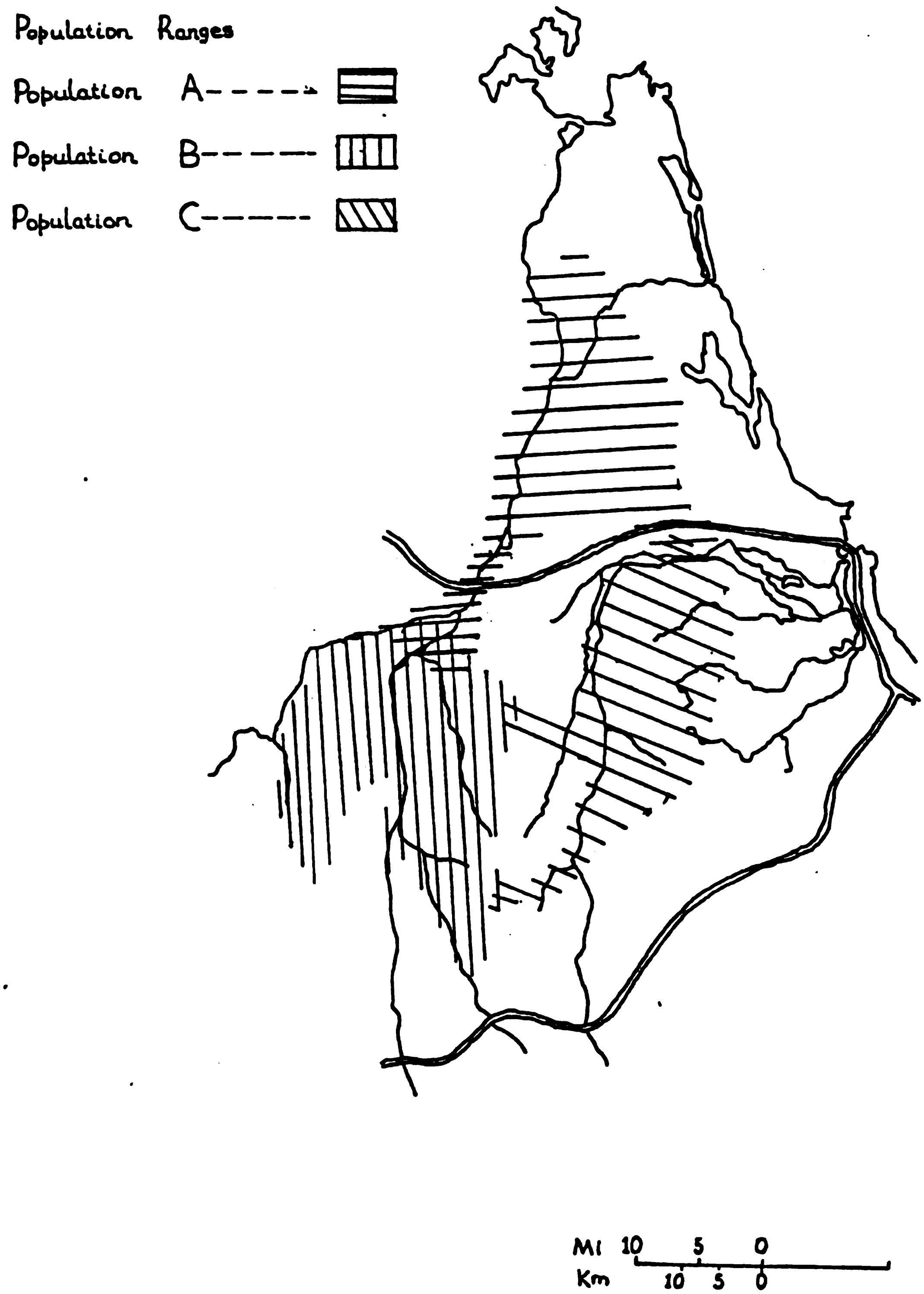

Population Ranges
Population A
Population B
Population C
Mi 10 5 0
Km 10 5 0

TABLE 5 - Total area and percentage composition of major cover types within three elephant population ranges in the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

Population Range	Total Area	Cover-type and site	Percentage Cover	Area of Cover-type	A
Population range A	1082 km^2	Forest	79.0	857 km^2	In areas surrounding villus understory comprised mixed species of grasses
		Open-habitats	21.0	225 km^2	Villu grasslands and artificial pastures of the willu grass within wet and dry season high activity sites were about 5.0% (51 km^2) of open-habitats. The rest were largely *Imperata* dominated grasslands and cultivations.
Population range B	1039 km^2	Forest	70.0	731 km^2	Most of WSNR and corridor Cl areas. Sparse understory dominated by *Certococcum trigonum*.
		Open-habitats	30.0	308 km^2	About 6.0% of open-habitats (63 km^2) were grasslands of mixed species composition which were in wet season high activity sites. The other 24.0% were mainly *Imperata* dominated areas.
Population range C	878 km^2	Forest	45.0	395 km^2	Patchy; when present understory dominated by *Certococcum trigonum*
		Teak forest	14.0	119 km^2	Sparse understory of *Imperata cylindrica*
		Open-habitats	41.0	365 km^2	Grasslands of mixed composition were about 10% and were in floodplain areas. Others were *Imperata* dominated grasslands and vegetation recovering from forest clearing

A = Comments, based on ground surveys, on vegetation, elephant-use and other aspects related to importance of cover-types.

Figure 12.. Composition of solitary animals and herds observed, and the number and percentages of individual elephants seen as solitaries and in different herds observed in the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

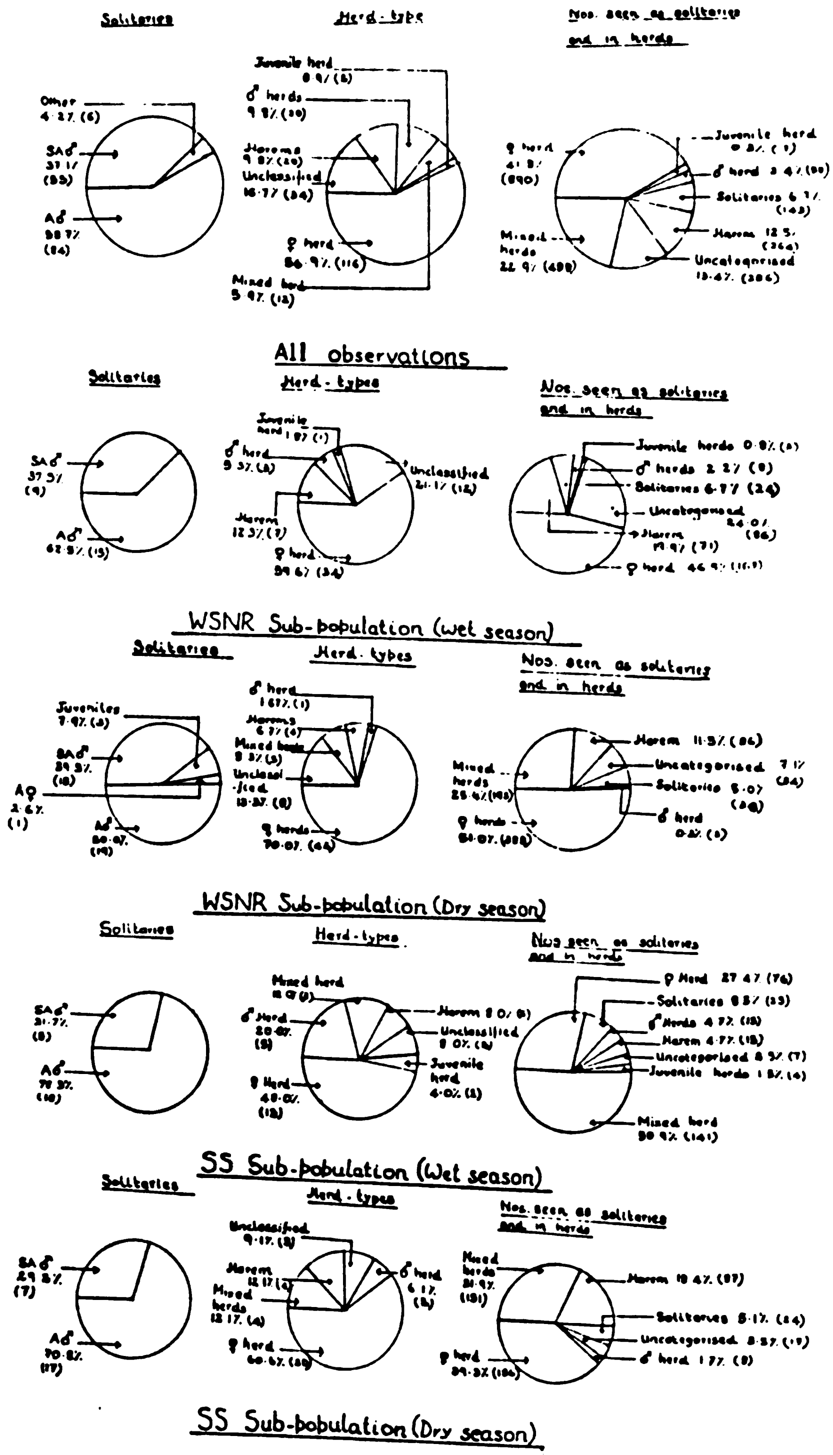
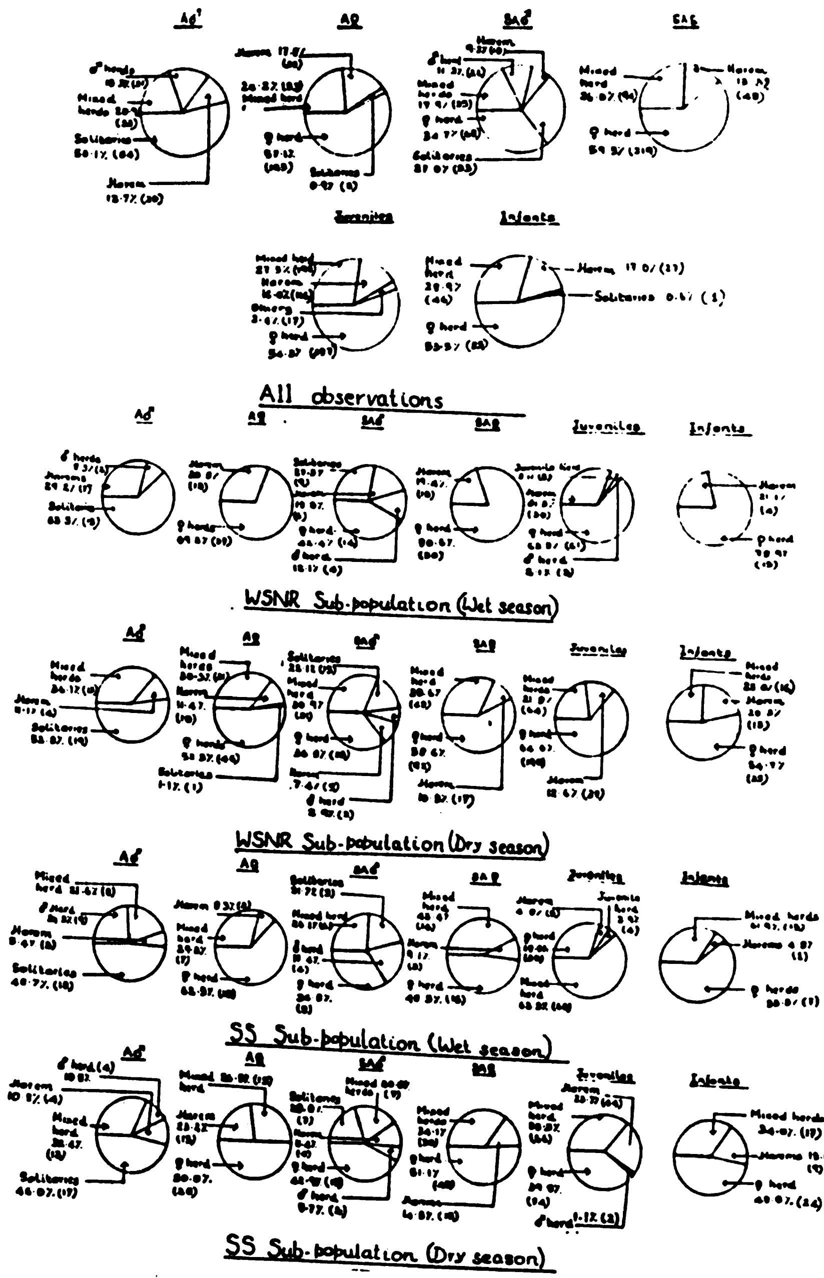

Solitaries
Herd-type
Nos. seen as solitaries and in herds
All observations
Herd-types
WSNR Sub-population (wet season)
Herd-types
WSNR Sub-population (Dry season)
Solitaries
Herd-types
SS Sub-population (Wet season)
Solitaries
Herd-types
SS Sub-population (Dry season)

Figure 13.. Percentages and numbers of adult males, adult females, sub-adult males, sub-adult females, juveniles and infants observed as solitaries and in different herd types seen in the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.


All observations
WSNR Sub-population (Wet season)
WSNR Sub-population (Dry season)
SS Sub-population (Wet season)
SS Sub-population (Dry season)

A mixed herd, by definition, had two or more males. Mean number of adult males per mixed herd did not exceed 2.86 in either of the two sub-populations. Average number of elephants seen in other sex and age-class categories varied to a greater extent among herd types of both sub-populations. Compared to female herds and harems, the number of females (adults and sub-adults) per mixed herd was higher (Table 6). Some of the older juvenile females might also be sexually mature (McKay, 1973; Eisenberg, 1981). The chances of an adult male finding an estrous female was likely to be higher in a mixed haerd than in other herd types.

Obsèrved frequencies of sex and age classes in female herds differed neither between sub-populations nor between seasons for the SS sub-population (Table 7). In WSNR, observed numbers in sex and age-class categories of female herds showed significant association with seasons ($X^2 = 8.075$; $p < 0.10$; 4 d.f.; Table 7). This significance was due to differences between observed and expected frequencies of juveniles seen during the two seasons. They were observed in higher than expected numbers in female herds of the dry season ($z = 2.63$; $p < 0.01$) but in lower than expected numbers in the same herds of the wet season ($z = -2.62$; $p < 0.01$).

Herd size frequency distributions of female herds showed similar trends. Female herd sizes (Figure 14) did not differ between sub-populations and between seasons for the SS sub-population. In the WSNR sub-population, however, dry season frequency distribution of female herds was significantly higher than that of the wet season ($W_s = 980$; $p < 0.001$). Of the 32 wet season female herds seen in WSNR (Figure 12), 31 had 3 or less number of juveniles ($\bar{x} = 1.94$; s.d. = 0.91). On the contrary, only 17 of the 42 herds seen in the dry season had less than 3 juveniles. In the other 25 dry season female herds of the WSNR sub-population, 4 or more juveniles, upto a maximum of 15 ($\bar{x}$ = 4.52; s.d. = 3.39) were counted.

McKay (1973) hypothesised that most herds of Asian elephants were divisible into two units; a nursing unit with females and their suckling infants and a juvenile-care unit with juveniles and other females. This hypothesis implied that the two units could feed and move at different velocities as well as in different directions (McKay, 1973). Assuming that the same female herds were repeatedly observed during both seasons in WSNR, changes in numbers of juveniles seen among them might support McKay's (1973) hypothesis. Physical features, such as rivers with high water-flow, perhaps selectively restricted movements of females with nursing infants (McKay, 1973). Since the WSNR elephants were known to use a wet season high activity site that extended across the Mahaweli Ganga (Figure 5), it was possible that while females with nursing infants remained within the reserve, other females and juveniles could have moved farther in their search for new grazing areas. Such grazing sites within the wet season high activity sites of the WSNR-corridor C1 areas were few and scattered throughout the predominant forest habitat there (Figures 4 and 5).

Since juveniles were the most frequently seen age class (Figure 13) significant changes in their observed numbers were perhaps easily detected. Many lactating females were probably adults. Opposing trends in the relative association of adult females and juveniles with other herd types might also provide support for McKay's (1973) hypothesis. Juveniles were seen less often than expected in the mixed herds of the WSNR sub-population seen only during the dry season ($z = -3.24$; $p < 0.01$).

TABLE 6 - Mean numbers observed in sex and age-class categories per female herd, harem and mixed herd of the Wasgomuwa Strict Natural Reserve (WSNR) and Somawathiya Sanctuary (SS) sub-populations of the Accerlerated Mahaweli Development Area, Sri Lanka. September 1908 - July 1982.

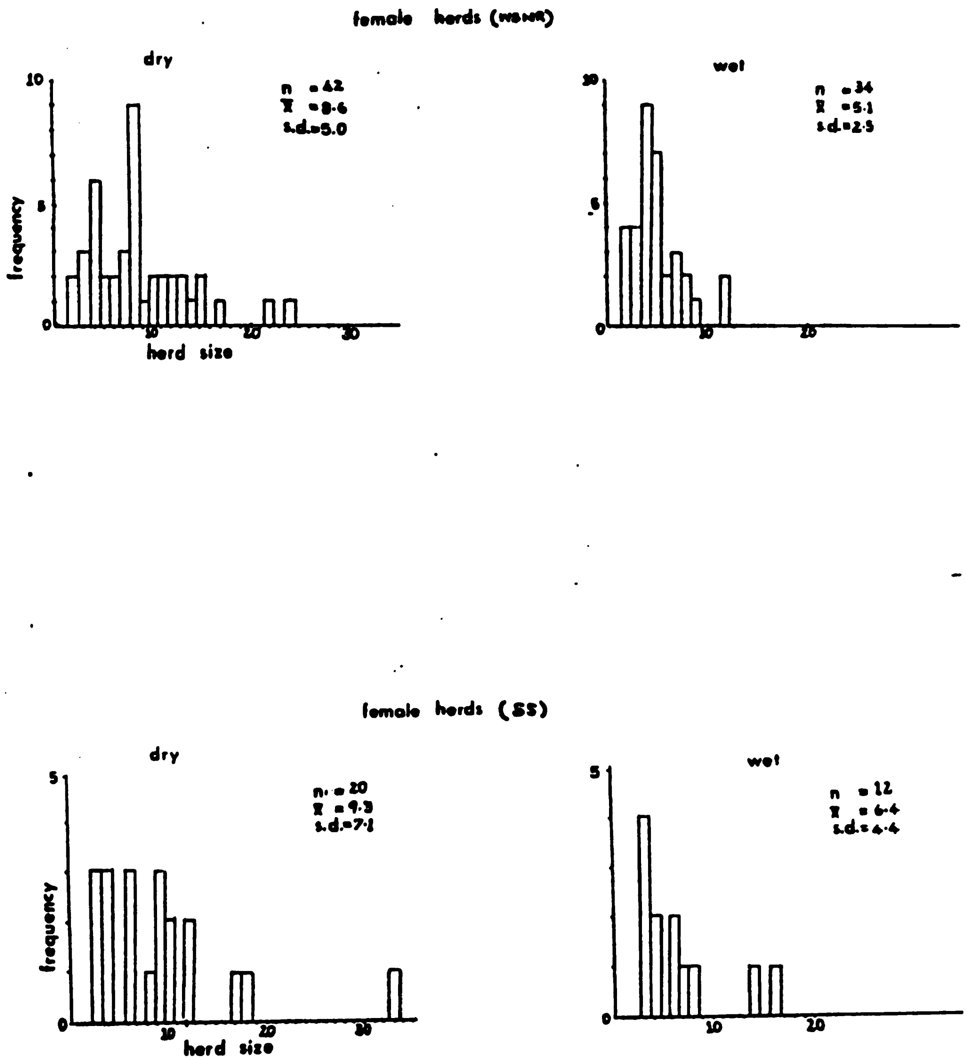
Sub-population	Herd type	Adult Male	Adult Female	Sub-Adult Male	Sub-Adult Female	Juveniles	Infants
Wasgomuwa Strict National Reserve (WSNR)	Female	--	0.96	0.51	1.87	3.30	0.66
	Harem	1.0	2.0	1.0	2.63	6.09	1.55
	Mixed	2.6	6.2	4.2	9.6	12.7	3.2
Somawathiya Sanctuary (SS)	Female	--	1.34	0.72	1.91	3.25	0.97
	Harem	1.0	2.5	0.67	2.67	8.17	1.67
	Mixed	2.86	3.14	1.86	6.29	18.71	4.29

TABLE 7 - Results of comparisons made using contingency tables between Somawathiya Santuary (SS) and the Wasgomuwa Strict Natural Reserve (WSNR) sub-populations, and between seasons within each sub-population, of frequencies of observations in sex and age class categories of female herds, harems and mixed herds of the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

Herd type	Basis of comparison	Chi-square (X^2) estimate	Degrees of freedom and probability.	A
Female herd	Between sub-populations	4.96	4 d.f. and $p > 0.10$	
	Between seasons for WSNR sub-population	8.05	4 d.f. and $p < 0.10$	Juveniles in wet season; $z = -2.69$; $p < 0.01$ Juveniles in dry season; $z = 2.68$; $p < 0.01$
	Between seasons for SS sub-population	1.95	4 d.f. and $p > 0.10$	
Harem	Between sub-populations	1.89	5 d.f. and $p > 0.10$	
	Between seasons for WSNR sub-population	6.08	5 d.f. and $p > 0.10$	
	Between seasons for SS sub-population	-	-	
Mixed herd	Between sub-populations	29.11	5 d.f and $p < 0.001$	Adult ♀ in WSNR; $z = 2.50$; $p < 0.02$ Adult ♀ in SS; $z = -2.47$; $p < 0.02$ Sub-adult ♀ in WSNR; $z = 2.10$; $p < 0.05$ Sub-adult ♀ in SS; $z = -2.10$; $p < 0.05$ Juveniles in WSNR; $z = -3.67$; $p < 0.01$ Juveniles in SS; $z = 3.62$; $p < 0.01$ Sub-adult ♂ in SS; $z = -5.21$; $p < 0.001$ Infants in SS; $z = -1.75$; $p < 0.10$
	Between seasons for WSNR sub-population	-	-	
	Between seasons for SS sub-population	5.79	5 d.f. and $p > 0.30$	

A - Individual cells, in a significant r x c contingency table, where observed and expected frequencies were found to differ significantly by the method of Haberman (1973).
Where a chi-square (X^2) estimate is not given, sample sizes were either too low or completely lacking for that herd category

Figure 14. Dry and wet season distributions of female herds observed in the Wasgomuwa Strict Natural Reserve (WSNR) and the Somawathiya Sanctuary (SS) subpopulations of the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.


female herds (WBNR)
dry
wet
n = 42
$\bar{x}$ = 8.6
s.d. = 5.0
n = 34
$\bar{x}$ = 5.1
s.d. = 2.5
frequency
herd size
female herds (SS)
dry
wet
n = 20
$\bar{x}$ = 9.3
s.d. = 7.1
n = 12
$\bar{x}$ = 6.4
s.d. = 4.4
frequency
herd size

Adult females, however, were seen in significantly higher than expected numbers in those same mixed herds of the WSNR sub-population ($z = 1.78$; $p < 0.10$; Table 8). Such trends were evident in the herds of the SS sub-population as well. Adult females were observed in significantly higher than expected numbers in the wet season female herds of the SS sub-population ($z = 2.63$; $p < 0.01$; Table 8), but juveniles seen in those herds were in significantly lower than expected frequencies ($z = -2.96$; $p < 0.01$; Table 8). In mixed herds of the SS sub-population seen during the wet season, juveniles were seen in higher than expected numbers ($z = 2.95$; $p \; 0.01$; Table 8), but adult females were seen in significantly lower than expected frequencies ($z = -2.65$; $p < 0.02$; Table 8).

Observed frequencies of sex and age class categories in harems were not significantly associated with sub-populations ($X^2 = 1.89$; $p > 0.10$; 5 d.f.; Table 7). Wet season frequencies of those categories were not significantly associated with female herds and harems of the WSNR sub-population ($X^2 = 3.88$; $p > 0.30$; 4 d.f.; Table 8). Numbers of observations of sex and age class categories in harems of the SS sub-population seen during the wet season (Figure 12) were too low to be used in contingency table analysis. Infants seen in the dry season in WSNR were the only age class that showed positive association with harems ($z = 1.92$; $p > 0.10$; 8 d.f.; Table 8). The relevance of this association was not clear.

Since adult and sub-adult females, and juveniles did not show significant associations with harems it was not clear as to how harems were formed from smaller female herds and lone males. The reproductive status of the males in harems was also uncertain except on two occassions where the harem-bull was the recognizable dominant in WSNR.

TABLE 8 - Association between observed frequencies of adult females, sub-adult females, sub-adult males, juveniles and infants and the herd type (female herd, mixed herd and harem) in which they were seen for the Somawathiya Sanctuary (SS) and the Wasgomuwa Strict Natural Reserve (WSNR) sub-populations of the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

A	B	C	D	E	F
Whole study area	1552	female and mixed herds and harems	4.22	8 d.f. and $p > 0.70$	
WSNR sub-population	871	"	13.75	8 d.f. and $p < 0.10$	Sub-adult ♂ in mixed herds; $z = 2.77$; p 0.01 · Juveniles in mixed herds; $z = -2.34$; $p < 0.03$
WSNR sub-population, dry season	650	"	16.96	8 d.f. and $p < 0.10$	Adult ♀ in mixed herds; $z = 1.78$; $p < 0.10$ Sub-adult ♂ in mixed herds; $z = 2.24$; $p < 0.03$ Juveniles in mixed herds $z = -3.24$; $p < 0.01$ Infants in harems; $z = 1.92$; $p < 0.10$
WSNR sub-population, wet season	231	female herds and hrems	3.88	4 d.f. and $p > 0.30$	
SS sub-population	596	female and mixed herds and harems	17.16	8 d.f. and $p < 0.05$	Adult ♀ in female herds; $z = 1.88$; $p < 0.10$ Adult ♀ in mixed herds; $z = -2.49$; $p < 0.02$ Juveniles in female herds; $z = -3.44$; $p < 0.01$ Juveniles in mixed herds; $z = 2.79$; $p < 0.01$ Sub-adult ♀ in female herds; $z = 1.69$; $p < 0.10$ Sub-adult ♀ in mixed herds; $z = -1.78$; $p < 0.10$
SS sub-population, dry season	404	"	7.41	8 d.f. and $p > 0.30$	
SS sub-population, wet season	181	female herds and mixed herds	13.70	4 d.f. and $p < 0.01$	Adult ♀ in female herds; $z = 2.63$; $p < 0.02$ Adult ♀ in mixed herds; $z = -2.64$; $p < 0.02$ Juveniles in female herds; $z = -2.96$; $p < 0.01$ Juvenile in mixed herds; $z = 2.95$; $p < 0.01$

A - Data category
B - Total number of observationas made
C - Herd types observed
D - Chi-square (X^2) estimate
E - Degrees of freedom and probability
F - Individual cells, in a significant r x c contingency table, where observed and expected frequencies were found to differ significantly by the method of Haberman (1973).

Assuming that elephants seen in mixed herds were the same individuals as those observed in the female herds of a sub-population, mixed herds were likely to be aggregations between whole or parts of female herds that were joined by adult males in search of estrous femaes. The two dominant males recognized in the SS sub-population were always seen in mixed herds. The large bull recognized in WSNR sub-population was also seen twice in mixed herds. These known bulls of both sub-populations were the largest individuals seen during this study. Although only one of them in the SS sub-population was observed to successively defend a female against an intruding male, all of them were probably dominant bulls.

Mixed herds of the WSNR sub-population were only seen during the dry season. Compared to observations in female herds and harems seen during that season, adult females were observed in significantly higher than expected frquencies in those WSNR-mixed herds (Table 8). Juveniles, however, were seen in significantly lower than expected frequencies in those mixed herds (Table 8). Female herds of the WSNR sub-population probably split during the dry season, and aggregations occurred between those parts comprising mainly adult females but few juveniles. When males joined such aggregations mixed herds could have been formed. Aggregations between such part-female herds might provide extra protection to calves while those adult females fed in grazing sites near human settlements.

Observed and expected numbers of sex and age class categories in female herds, harems and mixed herds of the SS sub-population did not differ significantly in the dry season ($X^2 = 7.405$; $p > 0.10$; 8 d.f.; Table 8). Aggregating parts of female herds, that attracted bulls to form mixed herds of the SS sub-population in the wet season, however, were likely to be juvenile-care units. Relative to numbers observed in female herds of the SS sub-population during the wet season, juveniles were seen in significantly higher than expected numbers in mixed herds, but adult females were seen in significantly lower than expected frequencies (Table 8). Many of the older juvenile females in such mixed herds were perhaps sexually mature and were probably inseminated by the dominant bulls which were regularly seen in those herds. In the WSNR sub-population too, juveniles were known to separate from female herds in the wet season, but whether or not they were joined by males to form mixed herds similar to those observed in the SS sub-population, however, was not known.

Among all studies done on elephants in Sri Lanka (Eisenberg and Lockhart, 1972; McKay, 1973; Kurt, 1974; Ishwaran, 1981; Santiapillai et al., 1984) the WSNR sub-population, reported here, was the only one where the predominant observation category was the female herd. In all other study areas and in the SS sub-population reported here, soiltary males were the most frequently seen type. This difference pointed to the probability of the WSNR area being one that was used by relatively more females.

The number of adult and sub-adult bulls, seen as solitary animals (Figure 13), were significantly associated with the sub-populations ($X^2 = 2.86$; $p<0.10$; 1 d.f.). A significantly higher number of lone males seen in the SS sub-population were adults ($z = 1.74$; $p<0.10$). In the WSNR sub-population, however, a significant proportion of lone bulls were sub-adults ($z = -1.72$; $p<0.10$).

The fact that there might be a fewer number of adult males in WSNR was also supported by the association shown by males of the two sub-populations towards male herds, mixed herds and harems. Observed frequencies of adult males in these three herd categories were significantly associated with the two sub-populations ($X^2 = 8.775$; $p<0.025$; 2 d.f.). Adult bulls in male herds were significantly higher than expected numbers in the SS, but lower in the WSNR sub-population ($z = 2.38$ and -2.43; $p<0.025$). Frequencies in harems were, however, significantly higher than expected in the WSNR but lower in the SS sub-population ($z = 2.44$ and -2.43; $p<0.025$). Since bulls in WSNR were significantly more often associated with females, in the absence of a second bull (i.e. in harems), fewer adult males probably competed for available females there. Observations of adult males in mixed herds did not differ from expected frequencies in both sub-populations.

Large body size was an advantage for adult bulls competing for females. One of the large amles recognized in the mixed herds of the SS sub-population was once observed (08th October 1981) to fight and chase away another smaller adult bull from approaching a sub-adult female. The larger male mounted the female 2-3 minutes later. All recognizable males in both sub-populations were most likely to be dominant bulls. Those two of the SS sub-population, though regularly seen in the same mixed herds, were never seen fighting each other. Those two dominant bulls were also never seen in harems. The known male in WSNR was in association with female herds 4 of the 5 times it was recognized. Twice, among those four times, it was the only bull in the herd. These observations, though too few to be analysed statistically, also indicated that more males probably competed for available females in SS than in the WSNR sub-population.

Male Asian elephants, relative to that of the female, showed a post-pubertal spurt in growth (McKay, 1973; Kurt, 1974; Eisenberg, 1981). Since a sub-adult was defined on the basis of its height (5-7 ft) instead of its age, relatively more older females were probably classified as sub-adults while many younger males could have categorised as adults. Apart from differences in the age-height relationships of males and females, behavioral differences between sexes also could have biased sex ratio estimates (Tables 9 and 10). Sub-adult males often dispersed from their maternal ranges (Eisenberg, 1981) and adult males were, most often, lone individuals (Figure 13). Adult and sub-adult females occurred together in groups. Female biased sex ratios (Tables 9 and 10), nevertheless, have been reported for all studies in the past, including those where several males and females were individually recognizable (Eisenberg and Lockhart, 1972; McKay, 1973; Kurt, 1974; Ishwaran, 1981).

Even though sex ratio estimates were probably biased towards the female they were still of relative importance for comparisons between the two sub-populations. Estimated number of adult male per female was significantly higher in the SS, than in the WSNR sub-population; this was true irrespective of the fact whether they were estimates calculated using total observed frequencies of adult males and females (Table 9) or those computed from selected sub-samples of daily observations (Table 10). Although sub-adult sex-ratios did not differ between sub-populations, number of male per female for adult and sub-adults combined was also significantly higher in the SS than in the WSNR sub-population (Tables 9 and 10).

TABLE 9 - Selected population parameters estimated using total observed freguencies of sex and age-class categories for the Somawathiya Sanctuary (SS) and Wasgomuwa Strict Natural Reserve (WSNR) sub-populations of the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

	SS Sub-population	WSNR Sub-population	Z value and probability
Total number of Categorized Observations	694	980	--
Population Parameter			
1) Proportion of infants	0.102	0.085	Z=1.172, $p>0.1$
2) Proportion of females (adult & sub-adult classes) with infants	0.353	0.240	Z=2.90, $p<0.01$
3) Proportion of juveniles	0.418	0.398	Z=0.76, $p>0.10$
4) Adult male per adult female	0.925	0.472	Z=5.09, $p<0.001$
5) Sub-adult male per sub-adult female	0.479	0.461	Z=0.26, $p>0.10$
6) Male per female (adult & sub-adult classes)	0.657	0.465	Z=4.36, $p<0.001$

TABLE 10 - Selected population parameters estimated as proportions of number of elephants seen per day for sub-samples of observations chosen from those made for the Somawathiya Sanctuary (SS) and the Wasgomuwa Strict Natural Reserve (WSNR) sub-populations of the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

A	B	C	Adults			Sub-adults			Adults and sub-adults	Juveniles	Infants	
			0	0	0/0	0	0	0/0	0/0		I	II
SS	08/22/81	33	0.061	0.181	0.333	0.151	0.152	1.00	0.636	0.393	0.061	0.182
	10/06/81	93	0.053	0.087	0.625	0.043	0.204	0.211	0.333	0.441	0.151	0.518
	11/06/81	45	0.067	0.067	1.000	0.067	0.133	0.500	0.666	0.600	0.067	0.333
	04/08/82	59	0.085	0.135	0.625	0.101	0.238	0.429	0.500	0.356	0.085	0.227
	05/08/82	93	0.097	0.086	1.125	0.022	0.237	0.091	0.367	0.452	0.108	0.333
	06/05/82	69	0.072	0.174	0.417	0.072	0.217	0.333	0.370	0.319	0.143	0.370
$\overline{X}$			0.073	0.121	0.688	0.076	0.197	0.427	0.479	0.427	0.103	0.327
s.d.			0.016	0.049	0.315	0.046	0.044	0.317	0.145	0.099	0.039	0.118
WSNR	11/23/80	49	0.041	0.102	0.400	0.041	0.245	0.167	0.235	0.531	0.041	0.118
	05/25/81	40	0.025	0.175	0.143	0.100	0.175	0.571	0.357	0.425	0.100	0.286
	06/26/81	32	0.063	0.125	0.500	0.025	0.157	0.200	0.333	0.500	0.125	0.446
	08/17/81	56	0.035	0.071	0.500	0.036	0.303	0.118	0.190	0.387	0.125	0.333
	09/19/81	89	0.056	0.146	0.386	0.135	0.247	0.545	0.486	0.337	0.079	0.200
	06/08/81	43	0.023	0.116	0.200	0.093	0.209	0.444	0.357	0.512	0.047	0.143
$\overline{X}$			0.041	0.122	0.355	0.072	0.223	0.341	0.326	0.449	0.086	0.254
s.d.			0.016	0.036	0.151	0.044	0.054	0.444	0.104	0.077	0.037	0.124

Comparisons between sub-populations (using Wilcoxon rank sum test) which were significant:
1) Adult sex ratios; W_s = 51 and 27; $p < 0.064$. 2) Sex ratios for adults and sub-adults; W_s = 51.5 and 26.5; $p < 0.064$.

A - Name of sub-population. B - Date of observation (month/date/year). C - No. of categorised observations.

I - Infants, as a proportion of total number of categorised observations

II - Infants, as a proportion of total number of adult and sub-adult females.

Sex ratios were the only parameters which differed between the sub-populations, irrespective of the procedures used in estimating them (Tables 9 and 10). Proportion of females with infants differed significantly when frequency data were used to estimate the proportions of the two sub-populations (Table 9), but not when those proportions were calculated from sub-samples of daily observations (Table 10). Number of infants seen, and hence the number of females with infants, were likely to be underestimated in larger elephant herds. Infants in such herds could be hidden between adult females and thus not counted. Since adult females in the two sub-populations were found to differ in their association with the different herd types (Table 8), relative visibility of infants could have been different between the two sub-populations. Estimated proportions of females with infants, when calculated from total observed frequencies of females and infants, could be biased to different extents for the two sub-populations. This difference in bias was perhaps minimized when daily observations were used to estimate those proportions of females with infants.

The associations of known bulls with females in both sub-populations were not dependent upon seasons. Frequencies of males seen a) as solitaries and in male herds, and b) in harems and in mixed herds, were also not associated with seasons in either of the two sub-populations ($X^2 = 2.13$; $p > 0.10$; 1 d.f. for the SS, and $X^2 = 1.95$; $p > 0.10$; 1 d.f. for the WSNR sub-populations, respectively). Furthermore, the number of infants per adult female also did not differ between seasons for either of the two sub-populations. Infants, however, could have been as old as 1.5-2 years (McKay, 1973; Kurt, 1974), and hence, seasonality in births, even if there was a trend, could not have been detected.

Habitat Preference and Range Quality

The observed use of habitat categories was significantly different from that expected on the basis of availability ($X^2 = 130.81$; $p < 0.001$; 5 d.f.). Grasslands of mixed species composition were preferred habitats (Table 11). Forests with a mixed herbaceous understory, which were also preferred habitats (Table 11), were mainly encountered along transects t2 and t3 (Figure 2), both of which were near villu grasslands. Elephants either preferred those forests because they fed upon grasses available within them, or due to their proximity to the villu grasslands. The latter habitat had adequate amounts of grass throughout the year.

McKay (1973) reported that ecotonal habitats, which had similar species composition as that reported here for vegetation recovering from forest-clearing, were preferred habitats. Ecotonal habitats of McKay's (1973) study site were adjacent to grasslands along the shores of a reservoir. The preference shown for ecotonal habitats therefore, could have been due to the elephant's preference of grasslands. Vegetation recovering from forest-clearing in this study was a neglected habitat (Table 11) and was patchily distributed throughout forested regions, particularly along the Maduru Oya river. Teak plantations in river basin areas of the Maduru Oya (Figure 4) were also neglected habitats (Table 11). Availability of woody plants within those plantation forests was confined to scattered patches of remnant natural forest. Most available grasslands in these plantation-areas were also dominated by Imperata cylindrica.

The grass Imperata cylindrica was rarely fed upon by elephants from November until they were burnt in early dry season. The reported

TABLE 11 - Availability, use and confidence intervals for observed use of habitat categories along the 13 - 1 km transects surveyed in Accelerated Mahaweli Development Area, Sri Lanka. January - April 1982.

HABITAT	A	B	C	D	E	
1)Forests with a sparse or Certococcum dominated understory	217	0.421	101	0.435	0.435 ± 0.092 (0.343, 0.527)	*
2)Forests with a mixed-grass understory	33	0.064	42	0.171	0.171 ± 0.069 (0.102, 0.240)	+
3)Vegetation recovering from forest clearing	122	0.235	21	0.085	0.085 ± 0.051 (0.034, 0.136)	-
4)Grasslands dominated by Imperata cylindrica	26	0.05	24	0.098	0.098 ± 0.055 (0.043, 0.153)	*
5)Grasslands with a mixed species composition	51	0.098	50	0.203	0.202 ± 0.074 (0.129, 0.277)	+
6)Teak forests	57	0.110	2	0.008	0.008± 0.016 (0.000, 0.024)	-
7)Others (bare rock, abandoned cultivations, etc.)	14	0.027	0	0	--	
TOTALS	520	1.0	246	1.0		

A = Number of times a habitat was encountered along the 13 km transects
B = Proportional habitat available (proportional area of available habitat)
C = Total number of feces counted in habitat category
D = Proportional number of feces counted in the habitat category (proportional use of habitat)
E = 90% (family-level) confidence interval for proportional use derived by the formula:

$$p_i = \sqrt{p_i(1-p_i)/n} \times Z(1-\tfrac{\alpha}{2x})$$

Where, p_i = proportional use of habitat
n = total number of feces counted
= family-velel of significance = 0.10
x = number of habitat categories

+ = preferred
- = neglected
* = used in proportion to their availability

use (Table 11) of Imperata grasslands might not have been representative of all times of the year. The predominant forest habitat which was used in proportion to its availability probably served many requirements of elephants. Scattered locations inside this forest habitat were used by elephants for resting during late-morning and early-afternoon hours (McKay, 1973). Since the area surveyed for elephant-use along each line transect was small, and also because the number of transects used in this study was few, many other habitat requirements of elephants, e.g. calving, were not properly assessed. Data on the elephant's habitat requirements with respect to its diverse needs were not available. Since it was known to spend as much as 17-19 hours a day on feeding and related movement (McKay, 1973), habitat preference, as reported here, was most likely to be related to the elephant's food requirements.

Extent of browsing, assessed from recognizable signs, was low. Percentage of woody plants browsed in any habitat did not exceed that of teak forests, namely 6.2% (Table 12). In other natural habitats, woody plant use was lower, between 1.1-1.5% (Table 12).

Observed use of woody plant size classes was significantly different from that expected on the basis of availability (X^2 = 32.87; p 0.001; 4 d.f.). Size classes below a dbh of 5.0 cm were neglected but others above it were used in proportion to their availability (Table 13). The Asian elephant's preference for woody plant size classes within a dbh range of 2.0-32.0 cm, reported for another study site in Sri Lanka (Ishwaran, 1983), was unreliable since confidence intervals for preference ratios were not calculated.

TABLE 12 - Proportions of woody-plants browsed by elephants in different habitat categories along the 13 - 1 km transects surveyed in the Accelerated Mahaweli Development Area, Sri Lanka. January - April, 1982.

Predominant Habitat-type	Forests with a *Certococcum* understory	Forests with a mixed grass understory	Teak Forests	Grasslands and vegetation recovering from forest clearing
Total number of woody-plants	3791	378	241	344
Woddy-plants browsed by elephants	43	6	15	5
Percentage use	1.1	1.5	6.2	1.5

TABLE 13 - Availability, use and confidence intervals of observed use for six size-classes of woody-plants enumerated along the 13 - 1 km transects surveyed in the Accelerated Mahaweli Development Area, Sri Lanka. January - April. 1982.

Dbh ranges of Woody-plant size-classes	A	B	C	D	E	
5.0 cm	1833	0.379	05	0.073	0.073 ± 0.08 (0.00, 0.153)	-
5.0 - 10.0 cm	1355	0.280	29	0.420	0.420 ± 0.153 (0.267, 0.573)	*
10.0-20.0 cm	754	0.156	18	0.261	0.261 ± 0.136 (0.125, 0.397)	*
20.0 - 40.0 cm	376	0.078	11	0.159	0.159 ± 0.112 (0.046, 0.272)	*
40.0 - 80.0 cm	215	0.045	4	0.058	[a]0.087 ± 0.087 (0.00, 0.174)	*
80.0 cm	299	0.062	2	0.029		
TOTALS	4832	1.000	69	1.000		

A = available woody-plants enumerated in all 13 transects
B = proportional availability of woody-plant size-class
C = woody-plants browsed by elephants
D = proportional use of woody-plant size-class
E = 90% (family-level) confidence interval for proportional use derived from the same formula as in Table 6

[a]Since expected use (total number of used woody-plants x proportional availability of woody-plant size-class) was less than 5 for each of the last two classes, they were considered together.

- = Neglected
* = Used in proportion to their availability

Low percentage utilisation of woody plants was also indicated by fecal analysis data from samples collected in the range of three different populations (Table 14-16). Maximum percentage twigs found in any fecal bolus did not exceed 20.0% (wet season sample of population B; Table 15). Mean percentages were below 4.0% (Table 14-16). Asian elephants in primary and secondary forests of Malaysia were also found to browse relatively less on woody plants (Olivier, 1978). Earlier predictions that elephants might browse to a greater extent during the dry season (McKay, 1973; Vancuylenberg, 1974) were also not supported by fecal analysis data (Tables 14-16).

Methods used in this study were likely to have underestimated the importance of browse to the elephant. Feeding on terminal twigs and branches of the taller trees would not be detected by indirect signs. 20-34% of all woody plants surveyed for the same types of signs of elephant-use as in this study, showed evidence of browsing by elephants in habitats near a national park in southeastern Sri Lanka (Ishwaran, 1983). Despite underestimation, woody plant use in this study area was unlikely to be as high. Browse components other than twigs, e.g. leaves, were probably broken down into micro-fragments which were not identifiable in feces. Nevertheless, elephants were rarely observed browsing during this study. Observations of other authors (Vancuylenberg, 1974; Olivier, 1978) however, suggested that where they were eaten in sufficient quantities, leaves and other browse items could be detected in elephant feces.

An accurate assessment of the quality of the elephant's diet would require analysis of adequate samples of stomach contents. Such data, however, might not become available for long times in the future. Percentage of crude protein, crude fiber and ash (Table 14-16) are

TABLE 14 - Percentages of grass, twigs, crude fiber, crude protein and ash for fecal samples collected in the habitats used by elephant population A of the Accelerated Mahaweli Development Area, Sri Lanka. January - December 1981.

DRY SEASON						WET SEASON					
Sample No.	A	B	C	D	E	Sample No.	A	B	C	D	E
1	99	1	35.03	7.93	17.57	1	92	8	38.60	8.70	20.0
2	98	2	29.43	9.68	26.30	2	98	2	42.75	10.58	7.97
3	97	3	38.61	9.68	21.34	3	99	1	35.54	9.03	11.88
4	98	2	41.40	7.98	13.30	4	89	11	43.78	9.64	9.02
5	99	1	43.20	9.50	12.70	5	93	7	27.60	12.50	21.70
6	99	1	43.40	9.23	13.80	6	98	2	33.70	14.70	20.40
7	98	2	46.86	8.44	14.01	7	96	4	46.80	8.50	14.90
8	97	3	42.30	7.34	13.99	8	95	5	42.80	10.60	8.0
9	99	1	32.89	6.46	32.60	9	95	5	35.50	9.0	11.90
10	98	2	42.22	8.77	14.66	10	97	3	43.80	9.6	9.0
11	97	3	46.47	7.66	11.94	11	96	4	44.33	7.95	10.46
12	96	4	44.54	8.76	23.42	12	98	2	48.66	8.93	11.45
13	99	1	39.79	8.93	13.83	13	99	1	37.76	7.10	18.80
14	99	1	35.18	7.50	21.78	14	99	1	35.16	7.11	44.86
						15	99	1	42.23	10.05	9.94
						16	100	0	27.71	13.32	25.24
						17	96	4	45.78	10.25	14.55
$\bar{X}$	98.07	1.93	40.06	8.42	17.95	$\bar{X}$	96.44	3.59	39.55	9.86	15.84
s.d.	1.00	1.00	5.28	0.98	6.22	s.d.	2.94	2.94	6.30	2.06	9.16

A = %grass
B = %twigs
C = %crude fiber
D = %crude protein
E = %ash

TABLE 15 - Percentages of grass, twigs, crude fiber, crude protein and ash for fecal samples collected in the habitats used by the elephants of population B of the Accelerated Mahaweli Development Area, Sri Lanka. January - December 1981.

DRY SEASON						WET SEASON					
Sample No.	A	B	C	D	E	Sample No.	A	B	C	D	E
1	99	1	12.92	6.42	68.98	1	99	1	37.06	8.0	17.70
2	99	1	34.31	9.92	20.61	2	99	1	37.30	7.6	15.00
3	96	4	45.19	8.30	19.55	3	96	4	33.40	7.4	19.30
4	98	2	35.38	7.94	24.08	4	95	5	19.80	8.0	14.10
5	99	1	30.13	5.87	32.49	5	99	1	35.06	6.2	21.11
6	99	1	30.63	5.93	31.67	6	98	2	32.84	11.59	22.20
7	98	2	45.16	7.87	13.62	7	96	4	43.83	10.06	12.07
8	96	4	37.50	7.50	16.20	8	98	2	35.36	7.85	18.43
9	98	2	48.30	5.80	12.30	9	99	1	40.09	9.74	15.25
10	99	1	41.90	6.30	24.90	10	80	20	40.29	5.97	20,47
11	96	4	37.40	6.20	9.00	11	92	8	40.39	8.64	16.47
12	99	1	34.10	6.00	15.90	12	98	2	43.45	8.66	23.05
13	90	10	31.40	6.50	13.70	13	99	1	46.43	6.54	12.62
14	99	1	33.63	7.45	12.34	14	95	5	46.59	10.56	11.71
15	99	1	35.72	7.03	18.06	15	98	2	51.52	7.09	11.67
16	99	1	35.42	8.68	18.28	16	98	2	35.55	8.05	12.24
17	98	2	39.28	7.55	18.98	17	90	10	39.20	11.20	24.30
18	98	2	41.35	6.45	22.36	18	94	6	46.70	7.80	18.80
19	99	1	34.57	9.76	15.44	19	98	2	32.80	11.60	22.20
20	99	1	36.13	8.98	19.94	20	97	3	43.80	10.10	12.10
21	99	1	33.29	8.56	25.90	21	98	2	40.30	5.90	20.30
22	99	1	31.08	13.03	20.68	22	99	1	34.54	6.00	31.61
23	99	1	46.03	8.07	11.52	23	99	1	44.22	6.1	12.54
24	99	1	36.08	6.58	29.42	24	95	5	51.08	8.44	11.49
25	98	2	39.40	8.43	19.13	25	99	1	38.90	6.97	22.99
26	99	1	30.81	6.03	32.34	26	99	1	37.86	8.61	19.42
27	99	1	51.16	7.56	12.06	27	99	1	40.70	8.22	14.40
						28	99	1	39.54	7.81	16.43
						29	98	2	49.46	7.71	12.68
						30	98	2	46.40	8.40	13.90
						31	97	3	35.10	6.20	21.10
						32	98	2	35.40	7.90	18.40
						33	99	1	40.10	9.70	15.30
						34	94	6	40.40	8.60	16.50
						35	98	2	38.51	6.63	25.53
$\bar{X}$	98.11	1.89	36.79	7.58	21.46	$\bar{X}$	96.77	3.23	39.83	8.16	17.53
s.d.	1.88	1.88	7.30	1.62	11.56	s.d.	3.65	3.65	6.17	1.61	4.79

A = %grass
B = %twigs
C = %crude fiber
D = %crude protein
E = %ash

TABLE 16 - Percentage of grass, twigs, crude fiber, crude protein and ash for fecal samples collected in the habitats of population range C of the accelerated Mahaweli Development Area, Sri Lanka. January - December 1981.

DRY SEASON						WET SEASON					
Sample No.	A	B	C	D	E	Sample No.	A	B	C	D	E
1	98	2	28.22	6.18	35.59	1	94	6	69.60	7.27	18.1
2	99	1	42.10	6.8	18.50	2	99	1	17.1	10.80	50.7
3	99	1	34.60	8.17	21.20	3	99	1	31.5	8.70	15.5
4	97	3	48.70	5.0	8.60	4	99	1	32.0	10.20	16.5
5	99	1	39.38	7.61	12.81	5	97	3	35.0	4.60	25.3
6	98	2	34.13	9.71	17.36	6	98	2	45.99	8.68	13.62
7	98	2	42.45	7.40	11.23	7	98	2	44.21	9.01	23.35
8	99	1	35.37	3.09	27.02	8	99	1	38.70	7.91	20.98
9	97	3	46.03	8.07	11.52	9	99	1	42.12	7.74	12.18
10	99	1	40.49	7.01	19.47	10	99	1	42.72	8.38	14.61
11	98	2	45.24	8.11	9.12						
12	99	1	39.20	6.84	13.52						
13	99	1	33.18	7.32	27.85						
$\bar{X}$	98.46	1.54	39.16	7.03	17.60	$\bar{X}$	98.1	1.9	39.89	8.33	21.08
s.d.	0.78	0.78	5.86	1.63	8.27	s.d.	1.60	1.60	13.45	1.7	11.24

A = %grass
B = %twigs
C = %crude fiber
D = %crude protein
E = %ash

the only such data available for the Asian elephants in their natural habitats. They compared well with data for captive elephants from circus companies (Benedict, 1936), but percentage crude protein estimates of several fecal samples collected in this study area were higher than values reported by Benedict (1936).

Estimates of percentage crude protein differed significantly between the three populations during both wet (Kruskal Wallis test statistic $H = 11.22$; $p<0.005$) and dry ($H = 5.38$; $p<0.10$) seasons. Multiple pairwise comparisons (Conover, 1982;231) showed that fecal samples in population range A had a higher wet season mean percentage crude protein than those in B ($p<0.01$) and C ($p<0.10$). The same was true of the dry season as well (A and B at $p<0.05$, and A and C at $p<0.02$, respectively). Mean percentage crude protein estimates did not differ between fecal samples in B and C for either of the two seasons ($p>0.10$).

Higher protein quality of the elephant's diet in population range A, in comparison to those in B and C, was at least partly due to better pastures in the villu grasslands of the Mahaweli Ganga floodplains. Flood waters of the wet seaso bring in many important nutrients from catchment and other upstream areas. Fertilisers that were released into the river by agricultural activities in upstream areas also probably reached the villus. Grasslands in the ranges of B and C, were to a large extent, _Imperata_ dominated (Table 5). Soils in other short-grass meadows were unlikely to be as productive as those in the villus which were found only in population range A.

Changes in Habitat Use and Quality

The longest period between two dry season counts was 51 days, while it was 49 days during the wet season (Table 17). Since wet season feces decay rates were higher (Table 3; Wiles, 1980), all mean wet season relative densities, in comparison to those of the dry season, were underestimates. Hence, a significantly higher dry season mean, as in plot g1 (Table 17), was unreliable. But when wet season relative elephant densities were significantly higher (plot g4 in Table 17), higher wet season use of that area could be reliably inferred. Plot g4 was located in corridor C1 (Figure 3) and its higher use provided further evidence to the earlier inference that corridor C1 was a wet season high activity area (Figure 5 and Table 4).

Since grassland plots g1-g8 were surveyed during times when climatic conditions were comparable (all surveyed 11 times between November 1980 and December 1981; Table 17), the bias due to feces decay was assumed to have uniformly affected their estimates of elephant and livestock relative densities. Plot g9 was surveyed during a different period (July 1981 to June 1982; Table 17) and hence, has not been used in any comparisons of relative densities with other plots.

The violation of the assumption regarding similar seasonal defecation rates could affect the reliability of relative density estimates. Wyatt and Eltringham (1974) and Barnes (1979) provided evidence to show that African elephants probably defecated more during the rainy than in the dry season. They attributed the difference to a greater abundance of green matter in the wet season. Wet and dry season estimates of percentage grass greenness differed

TABLE 17 - Relative elephant density estimates obtained from dry and wet season feces counts in grassland plots (g1 - g9) surveyed in the Accelerated Mahaweli Development Area, Sri Lanka. November 1980 - June 1982.

Plot No.	Period of survey		DRY SEASON A	B	C	WET SEASON A	B	C	D
g1	November		66	32	0.098	40	48	0.04	
	1980 to		85	30	0.135	04	37	0.005	
	December		68	51	0.063	20	38	0.025	W_s = 44
	1981		40	35	0.054	32	31	0.049	$p < 0.018$
			25	28	0.043	01	33	0.001	
						12	30	0.019	
		$\bar{X}$			0.079			0.023	
		s.d.			0.037			0.019	
g2	November		46	31	0.071	116	49	0.112	
	1980 to		39	31	0.051	73	37	0.094	
	December		55	51	0.051	09	43	0.010	W_s = 21
	1981		27	33	0.031	35	28	0.059	$p > 0.18$
			27	29	0.044	104	33	0.150	
						47	31	0.072	
		$\bar{X}$			0.051			0.083	
		s.d.			0.012			0.048	
g3	November		39	31	0.060	04	48	0.004	
	1980 to		17	31	0.026	100	40	0.119	
	December		05	51	0.003	87	37	0.112	W_s = 29
	1981		03	31	0.005	20	32	0.030	$p > 0.25$
			51	29	0.084	06	33	0.009	
						00	31	0.000	
		$\bar{X}$			0.036			0.046	
		s.d.			0.035			0.055	
g4	November		19	36	0.025	101	48	0.100	
	1980 to		04	30	0.006	164	35	0.223	
	December		08	37	0.010	127	31	0.195	W_s = 15
	1981		00	38	0.000	54	29	0.089	$p < 0.018$
			00	39	0.000	29	29	0.048	
						30	30	0.048	
		$\bar{X}$			0.008			0.117	
		s.d.			0.010			0.075	
g5	November		24	30	0.038	13	49	0.013	
	1980 to		25	32	0.037	00	35	0.000	
	November		26	51	0.024	77	40	0.092	W_s = 29
	1981		23	33	0.033	36	31	0.056	$p > 0.25$
			27	29	0.043	38	32	0.057	
		$\bar{X}$			0.035			0.044	
		s.d.			0.007			0.037	
g6	November		14	31	0.023	02	48	0.001	
	1980 to		16	33	0.022	02	26	0.003	
	December		16	31	0.020	00	33	0.000	W_s = 35
	1981		20	39	0.024	05	34	0.007	$p > 0.25$
			27	30	0.042	44	31	0.068	
						07	29	0.011	
		$\bar{X}$			0.026			0.015	
		s.d.			0.009			0.026	
g7	November		29	30	0.046	46	47	0.047	
	1980 to		00	35	0.000	34	26	0.062	
	December		06	35	0.008	15	33	0.022	W_s = 23
	1981		11	38	0.014	13	36	0.012	$p > 0.25$
			24	31	0.037	98	31	0.151	
						04	29	0.007	
		$\bar{X}$			0.021			0.051	
		s.d.			0.020			0.054	
g8	November		28	25	0.053	24	40	0.029	
	1980 to		09	47	0.009	06	21	0.013	
	December		06	52	0.006	34	38	0.043	W_s = 21
	1981		01	15	0.003	26	30	0.041	$p > 0.18$
			00	31	0.000	12	30	0.019	
						15	30	0.024	
		$\bar{X}$			0.014			0.028	
		s.d.			0.022			0.012	
g9	July 1981		60	37	0.077	21	28	0.036	
	to June		36	30	0.057	03	30	0.005	
	1982		26	43	0.029	00	37	0.000	W_s = 29
			02	16	0.006	01	31	0.002	$p > 0.15$
						07	29	0.015	
						03	26	0.006	
		$\bar{X}$			0.042			0.011	
		s.d.			0.032			0.013	

A - Total number of feces counted during each count
B - Number of days between successive counts
C - Estimated relative density of elephants (in number of elephants/ ha)
D - Wilcoxon rank sum of the smaller seasonal sample of counts (W_s) and the significance probability

significantly in only 3 of the 8 plots surveyed in this study ($W_s = 20$; $p<0.02$ for g1, $W_s = 15$; $p<0.018$ for g4 and $W_s = 19$; $p<0.052$ for g8; Tables 18 and 19). Villu grasslands and burnt patches of *Imperata* enhance dry season availability of green forage to elephants. Relative to the African environments, climatic conditions in this study area, even during the dry season except in June-July, were more moist (Table 1). Therefore, any differences in seasonal defecation rates which was based upon seasonal changes in available green forage was unlikely to be important for the elephant in this study area.

Feces counted were not distinguished on the basis of age classes. Coe (1972) provided evidence that indicated independence between age classes and daily defecation rates for the African species. Time of day and habitat bias in defecation rates have been shown to affect the reliability of feces counts as a method of measuring animal abundance and/or use of a habitat (Collins and Urness, 1981). But for the elephant regular intervals of defecation have been observed in the wild (McKay, 1973; Vancuylenberg, 1974) and hence those biases were assumed not to be of importance.

Plots g2 and g6, both had high percentages of *Imperata cylindrica* (Table 20). This grass species was recorded in all 20 quadrat sites in plot g6 but was found in only 13 of them in g2 (Table 20). Observed frequencies of *Imperata*, and all other grass and sedge species combined, were significantly associated with those two plot sites ($X^2 = 7.76$; $p<0.01$; 1 d.f.). The higher frequency of recording grasses other than *Imperata* in plot g2 might have been due to higher densities of elephants and livestock there (Edroma, 1981). Located in the WSNR, dry season relative densities of elephants ($T^+ = 15$;

$p<0.062$) and livestock ($T^+ = 15$; $p<0.062$) were both higher in g2 than in g6. Relative densities for the whole feces-count period of 11 months were also higher in plot g2 than in g6 ($T^+ = 66$; $p<0.018$ for both elephant and livestock).

Since elephants and livestock rarely fed upon Imperata during the wet season, mean grass height in g6 was higher than in any other plot. In g2 which was most similar to g6 in species composition (Table 20), mean wet season grass height was lower at 61.42 cm while in g6 it was 89.95 cm (Table 19). Plot g6 was also the only one which was located near a moderate and low elephant-activity site, while all other plots were near a high elephant-activity site at least during one of the seasons. Owing to these differences data from plot g6 were excluded from stepwise regression analysis performed for the two seasons using mean seasonal relative elephant densities as the dependent and mean grassland quality estimates as the independent variables.

A significant percentage of the variation in mean dry season relative elephant densities of the seven grassland plots (g1-g5, g7 and g8) was reduced by the independent variable mean grass height (R^2 adjusted for degrees of freedom = 72.7%; $F = 16.95$; $p<0.01$; Table 21). Other variables when combined with mean grass height did not effect further significant reductions in the observed variation in mean dry season relative elephant densities of grassland plots.

Mean grass heights of the seven plots varied between 23.23 and 44.78 cm (Table 18) during the dry season. In African habitats accumulation of dead matter (decreasing grass greenness) was considered to render grass as an unsuitable food for the elephant in the dry season (Laws, 1970). Percentage grass greenness in this study

TABLE 18 - Dry season grassland quality estimates for plots g1 - g8 of the Accelerated Mahaweli Development Area, Sri Lanka. Mid-April to early October 1981.

Plot No.		A	B	C	D	E	F	G
g1		94.00	91.28	81.60	64.60	57.80	269.69	0.271
		88.50	350.26	43.25	358.29	53.23	542.28	0.562
		90.11	345.50	35.38	362.24	46.80	502.32	0.107
		89.88	248.06	75.13	371.14	30.78	99.50	0.044
		88.00	121.95	65.00	410.27	35.30	214.16	0.206
	X̄	90.10	282.61	60.08	313.31	44.78	337.59	0.238
g2		93.25	162.24	48.13	180.36	62.32	475.45	0.150
		95.00	202.56	22.75	96.09	51.66	721.87	0.062
		64.50	239.44	70.50	294.62	30.43	301.23	0.120
		82.13	139.60	96.63	27.42	37.81	273.92	0.218
		85.38	208.19	83.37	203.06	38.89	419.60	0.046
	X̄	84.06	190.41	64.28	160.31	44.22	438.27	0.119
g3		58.00	562.56	47.50	489.74	54.75	272.04	0.108
		64.75	667.88	25.62	474.89	41.00	285.59	0.052
		68.15	677.88	25.25	270.89	36.10	251.22	0.000
		64.63	837.88	86.63	312.04	29.28	240.51	0.022
		66.88	512.40	76.63	472.29	28.18	224.97	0.161
	X̄	64.60	651.72	52.33	403.97	37.89	254.87	0.068
g4		91.63	235.53	76.00	182.31	51.28	387.45	0.004
		94.35	164.00	52.63	324.34	48.13	253.55	0.000
		56.60	404.34	76.75	484.04	13.88	47.86	0.009
		63.63	217.93	67.50	335.89	9.80	9.70	0.004
		69.13	207.55	61.50	419.49	15.78	56.33	0.064
	X̄	75.07	245.47	66.88	349.21	27.77	161.08	0.016
g5		87.25	397.37	70.88	216.52	62.20	290.47	0.078
		92.13	104.98	49.00	598.57	43.93	284.74	0.202
		52.13	1562.67	11.38	119.21	16.33	269.76	0.215
		80.38	204.34	91.63	96.66	18.73	636.68	0.285
		87.75	115.36	91.13	92.93	19.30	115.34	0.198
	X̄	79.93	476.88	62.80	224.78	32.10	319.32	0.196
g6		79.00	1328.46	56.50	986.27	82.05	1775.48	0.000
		37.88	294.73	51.88	581.68	20.33	91.67	0.000
		52.25	258.90	94.50	80.51	32.43	118.81	0.004
		69.63	382.55	96.50	54.10	51.20	502.33	0.010
		37.75	1433.27	24.0	681.43	33.18	1197.12	0.007
	X̄	55.30	739.58	64.68	471.99	43.84	737.08	0.004
g7		60.00	529.49	60.00	511.54	40.15	649.77	0.029
		7.25	492.24	2.50	167.95	3.10	142.35	0.004
		32.75	346.09	100.00	0.00	10.30	42.98	0.166
		75.00	415.38	99.75	2.50	19.88	147.55	0.081
		77.00	564.86	99.00	9.23	42.70	812.93	0.194
	X̄	50.40	470.61	72.25	138.24	23.23	359.12	0.095
g8		61.13	623.70	84.63	305.62	36.60	175.11	0.355
		68.00	756.15	24.50	1065.13	33.73	173.03	0.760
		71.50	882.31	26.75	693.01	30.08	316.01	0.947
		56.63	1105.63	62.88	1093.45	17.45	274.15	3.208
		48.63	1030.75	65.38	1185.11	21.58	293.08	1.194
	X̄	61.18	879.71	52.83	868.46	27.89	246.28	1.293

A - % grass cover
B - Patchiness in available grass cover
C - % grass greenness
D - Patchiness in grass greenness
E - Grass height
F - Patchiness in available grass height
G - Minimum relative density estimates (no of animals/ ha) of livestock

TABLE 19 - Wet season grassland quality estimates for plots g1 - g8 of the Accelerated Mahaweli Development Area, Sri Lanka. November 1980 to Mid-April 1981 and early October to December 1981.

Plot No.	A	B	C	D	E	F	G
	88.50	459.23	97.50	250.00	58.45	373.99	0.108
g1	68.25	676.35	79.80	567.90	55.48	429.59	0.328
	82.50	565.38	72.50	356.41	62.88	360.52	0.521
	88.50	398.37	70.38	237.68	61.90	356.81	0.204
	83.13	782.16	86.50	488.72	36.40	349.12	0.301
	83.75	386.56	91.00	275.89	33.83	178.92	0.453
$\bar{X}$	82.44	531.49	82.95	362.77	51.49	341.49	0.319
	84.38	638.57	71.75	490.86	68.38	800.90	0.042
	89.13	369.09	56.50	355.38	63.13	688.88	0.177
g2	88.38	476.14	50.25	383.27	57.10	933.58	0.102
	91.13	341.65	63.25	203.27	59.88	426.90	0.136
	88.25	146.66	95.00	29.49	56.09	367.33	0.065
	89.75	335.83	87.25	137.12	63.88	603.49	0.099
$\bar{X}$	88.50	384.69	70.67	266.57	61.42	637.51	0.104
	64.13	957.55	71.75	840.44	42.98	488.23	0.353
	62.88	981.90	57.13	851.14	43.53	427.54	0.470
g3	63.10	947.35	44.75	726.86	49.58	341.58	0.341
	57.00	944.62	59.38	610.49	45.93	223.35	0.148
	66.75	621.22	91.13	277.55	37.35	200.34	0.426
	63.25	484.04	87.87	270.37	44.50	677.59	0.105
$\bar{X}$	62.85	822.75	68.67	596.14	43.97	393.11	0.307
	92.00	134.85	83.50	275.89	50.03	216.79	0.104
	95.25	59.63	76.38	193.87	51.00	56.00	0.002
g4	93.63	70.49	81.50	300.23	49.98	207.05	0.067
	88.50	391.28	64.38	303.00	40.53	319.74	0.014
	76.38	191.00	85.25	79.42	19.80	76.78	0.030
	90.00	101.28	92.13	57.55	31.40	213.99	0.000
$\bar{X}$	89.29	158.08	80.52	201.61	40.46	181.69	0.036
	83.88	269.86	81.25	175.32	23.53	135.03	1.177
	84.12	224.21	80.25	120.44	20.65	105.31	1.693
g5	82.88	419.09	77.13	143.45	41.75	247.59	0.625
	91.13	98.06	81.25	75.32	44.95	234.24	0.611
	92.00	113.85	94.75	67.88	36.03	388.89	0.758
$\bar{X}$	86.50	225.01	82.93	116.48	33.34	222.21	0.974
	81.75	487.68	78.13	384.21	96.93	1184.07	0.001
	76.15	348.14	77.00	317.69	97.00	1389.61	0.028
g6	86.13	250.63	74.50	207.44	98.75	628.50	0.000
	91.50	164.36	73.88	213.45	100.05	407.54	0.000
	74.38	445.30	86.25	434.29	57.65	776.69	0.000
	79.63	227.42	92.38	107.68	89.83	610.53	0.009
$\bar{X}$	81.77	320.66	80.36	277.46	89.95	832.82	0.006
	68.88	919.88	80.78	689.47	45.90	504.99	0.052
	55.13	958.32	72.00	1036.92	40.20	357.45	0.131
g7	57.13	629.34	59.88	821.65	51.30	466.64	0.079
	52.88	829.34	46.38	443.57	37.13	705.39	0.013
	79.63	356.91	99.25	7.11	43.88	549.44	0.069
	55.13	923.70	97.58	16.65	47.87	519.90	0.172
$\bar{X}$	61.46	769.58	75.97	497.56	44.39	517.30	0.086
	49.25	658.91	75.75	1117.37	14.55	220.25	1.320
	39.50	788.21	79.00	809.23	18.45	115.57	0.654
g8	55.00	643.58	46.75	689.17	24.50	212.63	0.625
	55.00	947.37	79.88	871.14	28.05	195.99	0.196
	52.63	805.11	90.50	498.46	28.68	444.64	0.676
	54.13	875.50	94.88	258.31	32.05	248.56	0.367
$\bar{X}$	49.75	786.45	77.79	707.28	24.38	239.61	0.640

A - % grass cover
B - Patchiness in available grass cover
C - % grass greenness
D - Patchiness in grass greenness
E - Grass height
F - Patchiness in available grass height
G - Minimum relative density estimates (no. of animals/ ha) of livestock

TABLE 20 - Vegetative composition as determined from 20 randomly selected 0.25 m^2 sites within grassland plots (g1 - g8) located in the Accelerated Mahaweli Development Area, Sri Lanka. January - February 1982.

Plant species	Grassland plots															
grasses:	g1		g2		g3		g4		g5		g6		g7		g8	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Alloteropsis cimicina							9	8.8	8	10.5						
Brachiaria distachya			9	10.8									7	8.8		
Brachiaria mutica															4	2.3
Cenchrus echinatus			3	1.5												
Chrysopogon fulius					9	14.8	11	15.8								
Chloris barbata															14	19.0
Cynodon dactylon													1	0.3	3	1.5
Dactyloctenium aegyptium			9	14.3									15	15.8		
Digitaria marginata			6	7.5			7	4.5					2	1.0		
Eichinochloa colonum	2	1.3			1	0.3	6	3.8	8	5.8	3	2.0			1	0.3
Eleusine indica					2	0.5										
Eragrostris tenella					4	2.8	3	2.3					13	7.8	11	17.0
Eragrostris viscosa									2	4.5			2	1.5		
Heteropogon contotus											2	3.5				
Imperata cylindrica			13	45.5							20	58.8	3	3.0		
Ischaemum indicum	18	20.8			15	25.0										
Ischaemum sp.	17	26.5			1	2.0	7	5.8	14	19.5						
Iseilema laxum	10	5.8			12	21.8	20	49.5	17	12.5						
Oryza sp.									1	1.0						
Panicum typheron			3	1.5	3	1.8			1	1.0			2	2.3	2	0.8
Paspalum metzi	9	3.0							6	5.3	1	0.8				
Setaria geniculata	14	14.8							11	11.5						
Themeda triandra											3	5.5				
Themeda sp.											1	0.3				
sedges:																
Bulbostylis barbata					2	0.8										
Cyperus iria													1	0.5	5	3.0
Cyperus sp.									6	4.0	1	0.5	6	4.3	1	0.3
Fimbristylis fulcata	17	8.0			7	5.8			2	1.3	1	0.8	7	4.3		
other species:																
Cassia mimoides			2	0.8					4	2.3						
Desmodium triflorum	3	1.8			3	1.5	8	4.6	13	5.8			4	2.0	3	2.0
Melochia sp.			4	3.5					2	1.0			10	8.1	2	5.5
Mimosa pudica	11	11.8	4	2.0									19	24.8	5	2.3
Phyllanthus virgatus	5	1.8			5	1.5			3	2.0	6	3.3	3	0.8		
Polygala telephoides					1	0.3										
Sida rhombifolia									10	6.0	1	1.3	1	0.3	1	1.5
Sphaeranthus indicus															5	2.5
Tephrosia sp.					8	15.5										
Sida sp.											1	0.3				
Gomphrena celosoides													2	0.5	13	6.3
Unidentified species					3	0.8	9	2.8	2	0.8	3	1.5	3	1.0		
Bare ground	8	4.4	15	12.6	10	4.8	6	2.1	12	5.2	15	21.4	1	2.7	19	35.6

A - The number of times (maximum of 20) a species was recorded within a plot
B - Mean percentage relative cover of the species based on records made at 20 sites

TABLE 21 - Regression relationship between mean dry season relative elephant densities and mean grassland quality variables based on 5 dry season counts in seven grassland plots in the Accelerated Mahaweli Development Area, Sri Lanka. Mid-April - Early October, 1981.

Regression equation

$$y = -0.0509 + 0.0025x_1$$

y = mean dry season relative elephant density of grassland plot

x_1 = mean dry season grass height of those same plots

ANOVA Table:

SS Due to	DP	SS	MS=SS/DP	F=MS(Regression)/MS(Error)
Regression	1	0.0027482	0.0027482	16.95; $p<0.01$
Residual (error)	5	0.0008106	0.0001621	
Total	6	0.0096689		

R^2 adjusted for degrees of freedom 72.7%

was not an important predictor of relative elephant densities in grassland plots. Dry season mean grass greenness estimates were also not correlated with those of mean grass height ($r = -30.8\%$; $p < 0.10$).

None of the seven grassland quality variables significantly reduced observed variation in mean wet season relative elephant densities of grassland plots. However, the combined presence of mean patchiness in available grass cover and mean relative density of livestock resulted in the significant reduction of variation in mean relative elephant densities (R^2 adjusted for degrees of freedom = 64.4%; $F = 6.43$; $p < 0.10$; Table 22). The two predictor variables were not significantly correlated with each other ($r = 3.1\%$; $p > 0.10$). Increase in both predictor variables negatively influenced the mean wet season relative use of grassland plots by elephants.

In the wet season, villus were flooded and <u>Imperata</u> was not eaten. As several upland grassland patches were cultivated, livestock grazing pressures in the remaining patches, such as those in the seven grassland plots, increased. Despite underestimation, wet season livestock densities in four of the seven plots were numerically higher than the dry season estimates (Table 18 and 19). In plot g8, mean percentage grass cover during the rains was lower than that of the dry season (Tables 18 and 19). This too indicated that grazing in that plot might have been higher in the wet than during the dry season. Those upland grassland plots were also important grazing sites for the elephant. Point estimates of mean wet season relative elephant densities of six of the seven plots were also, despite underestimation, higher than the respective dry season estimates (Table 17).

TABLE 22 - Regression relationship between mean wet season relative elephant densities and mean grassland quality variables b ased on six wet season feces counts in seven grassland plots of the Accelerated Mahaweli Development Area, Sri Lanka. November 1980 - Mid-April 1981, and early October - December 1981.

Regression equation

$$y = 0.11832 - 0.00008x_1 - 0.059x_2$$

y = mean wet season relative elephant density of grassland plot

x_1 = mean wet season patchiness in available grass cover of those plots

x_2 = mean wet season relative livestock density of those plots

(Only when x_1 and x_2 were present together in the model was a significant regression produced.)

ANOVA Table:

SS Due to	DF	SS	MS=SS/DF	$F = \frac{MS(Regression)}{MS(Error)}$
Regression	2	0.005024	0.0025012	6.43; $p < 0.10$
x_1	1	0.0025756	0.0025756	6.62; $p < 0.10$
x_2	1	0.0024267	0.0024267	6.23; $p < 0.10$
Residual (error)	4	0.0015571	0.0003893	
Total	6	0.0065594		

R^2 adjusted for degrees of freedom 64.4%

Since available grazing patches were limited in the wet season competition between elephants and livestock was probably high. Mean livestock density was one of the two important predictor variables interacted to limit wet season elephant use of grassland plots (Table 22). Locally heavy grazing on available grass could favor the spread of non-grass increaser species. This perhaps increased patchiness in available grass cover, which also limited wet season elephant use of grassland plots (Table 22).

Rainfall conditions during the wet season were suitable for growth. Grazing too, under such favorable climatic conditions, probably stimulated grass-growth (McNaughton, 1979). Grass height was therefore not a important predictor variable limiting wet season grassland use by elephants. In national parks of Sri Lanka, decreases in grass height, during the dry season, were reported to be unfavorably influencing grazing by elephants (McKay, 1973; Kurt, 1974). This view was supported for the present study area by the significant regression relationship between mean dry season relative elephant densities and mean dry season grass heights of grassland plots (Table 21). The hypothesised role of wild ungulates in further reducing heights of grass available to elephants (McKay, 1973; Kurt, 1974) was, however, not supported for the dry season conditions of this study area. Wild ungulates in this study area were hunted and their densities were unlikely to be as high as those in national parks where they were protected from hunting. Potential grazing sites available to elephants and livestock of this study area, also perhaps increased during the dry season. As flood waters receeded larger areas of the villus become available for grazing during the dry season.

Imperata was eaten after burning in the dry season and croplands harvested and abandoned were additional grazing sites that were accessible to elephants and livestock. Hence, competition for grasses available to elephants in upland grazing sites from livestock might not have been as important as it was during the wet season.

Relative to that of the dry season, the wet season regression model was less reliable. Estimates of the dependent (mean wet season relative elephant densities) and one of the independent (mean wet season livestock densities) were biased during the rainy season. The bias of those density estimates during the dry season was perhaps less than that of the wet season. The ratio of the number of predictor variables (two) to the total sample size of observations (seven) was lower than the optimal 1:5 (Ahlgren and Walberg, 1975) during the wet season. In the dry season the same ratio was 1:7 and hence the model was considered more reliable.

Use of indirect methods, such as feces counts, for determining relative densities was not possible in regularly inundated areas of the villu. Density of males observed at the villu at Trikkonamadu ranged between 0.0019 to 0.0041 per ha, or 0.19 to 0.41 per km^2. For those individuals seen in herds (316 elephants seen during 8 of the 58 days when that villu was visited; Table 23) densities were between 0.06 to 0.6 elephants/ ha or 6 to 60 elephants/ km^2. Relative densities for upland grasslands near the same villu, as determined from feces counts in plot g8, were less variable; i.e. 0.012 to 0.032 elephants/ ha or 1.2 to 3.2 elephants/ km^2.

Number of grassland and forest plots within the range of any one population were low and relative density estimates could not be used calculate population sizes. Subjective estimates for the three ranges

TABLE 23 - Density estimates for the villu at Trikkonamadu of the Accelerated Mahaweli Development Area, Sri Lanka, calculated on the basis of number of individuals seen there per day during visits made between September 1980 - July 1982.

	Total	Number Elephants Seen	Only Males Seen	Males and other individuals seen
Number of Visits	58	31 (53.4%)	19 (32.7%)	08 (13.9%)
Total numbers observed	345	--	29	316
*Number seen per day of visit	5.95 ± 4.36	--	0.5 ± 0.18	5.44 ± 4.39
**Density (elephant/ha)	0.01 to 0.063	--	0.0019 to 0.0041	0.0064 to 0.060

*Number seen per day of visit estimated with 90% confidence

**About 80% (164.17 ha) of a total 205.21 ha. villu area was assumed to be visible would be about 200-300 elephants for population A, 150-200 for population B and 100-200 for population C. Assuming that these guesses were reliable, density of elephants within the three ranges did not exceed 0.3 elephants/ km^2.

Relative densities in individual forest plots differed between seasons in only one of the nine surveyed (Table 24). But since the dry season relative densities in plot f5 were significantly higher, statistical significance associated with that difference was not reliable. Relative densities recorded in the resting area plot did not differ from average densities estimated from forest plots in three other areas (Table 25). High variance associated with relative densities estimated from feces counts made in small forest plots could have prevented the detection of any differences. Whether or not resting sites were preferred over other forest-sites was therefore not known.

Crop Damage by Elephants

In government sponsored colonisation schemes, land ownership was similar to that in Namini Oya (Table 26). In that village farmers owned 1.03 $\pm$ 0.23 ha of paddy-land and another 0.46 $\pm$ 0.08 ha for cultivating subsidiary crops. It had been planned that settlers under the AMDP would be provided with 1.0-1.25 ha of land for cultivating paddy and other subsidiary crops. Those peasants who cultivated by cutting government owned forest lands, normally cleared a higher land area; e.g. those farmers in Aluyatawala cultivated slightly more hectare of land than others from Namini Oya and Trikkonamadu (Table 26). This enabled Aluyatawala farmers to expect reasonable yields even after allowing for damage by elephants and other wild animals.

TABLE 24 - Relative elephant densities estimated from dry and wet season feces counts in forest plots (f1 - f9) surveyed in the Accelerated Mahaweli Development Area, Sri Lanka. May 1981 - April 1982.

Plot No.	Period of survey	DRY SEASON A	B	C	WET SEASON A	B	C	D
f1	May 1981	00	30	0.000	02	30	0.019	
	to April	04	50	0.023	02	30	0.019	
	1981	00	35	0.000	00	28	0.000	W_s = 19
		00	30	0.000	02	33	0.017	p > 0.25
					02	30	0.019	
					00	32	0.000	
	$\bar{x}$			0.006			0.012	
	s.d.			0.011			0.010	
f2	May 1981	00	29	0.000	00	31	0.000	
	to April	01	50	0.005	00	30	0.000	
	1982	00	33	0.000	00	26	0.000	W_s = 20
		00	29	0.000	01	32	0.009	p > 0.25
					01	30	0.009	
					00	32	0.000	
	$\bar{x}$			0.0013			0.003	
	s.d.			0.0025			0.005	
f3	May 1981	00	29	0.000	00	31	0.000	
	to April	04	50	0.023	01	30	0.009	
	1982	06	33	0.052	01	26	0.011	W_s = 28.5
		01	29	0.009	00	33	0.000	p > 0.25
					00	30	0.000	
					00	32	0.000	
	$\bar{x}$			0.021			0.0033	
	s.d.			0.023			0.0052	
f4	May 1981	02	30	0.019	21	29	0.207	
	to April	00	37	0.000	01	31	0.009	
	1982	00	38	0.000	00	42	0.000	W_s = 18
		03	30	0.029	00	25	0.000	p > 0.25
					06	34	0.050	
					02	37	0.015	
	$\bar{x}$			0.012			0.047	
	s.d.			0.014			0.081	
f5	May 1981	01	30	0.009	00	33	0.000	
	to April	02	38	0.015	00	32	0.000	
	1982	09	51	0.051	00	24	0.000	W_s = 36
		06	24	0.071	00	25	0.000	p < 0.02
					01	34	0.008	
					00	37	0.000	
	$\bar{x}$			0.037			0.0013	
	s.d.			0.030			0.0031	
f6	May 1981	26	31	0.239	65	31	0.599	
	to April	23	49	0.134	12	39	0.118	
	1982	14	36	0.111	03	29	0.029	W_s = 24.5
		03	29	0.029	00	31	0.000	p > 0.25
					01	30	0.009	
					08	32	0.071	
	$\bar{x}$			0.076			0.138	
	s.d.			0.055			0.230	
f7	May 1981	00	46	0.000	00	31	0.000	
	to April	00	50	0.000	00	29	0.000	
	1982	00	15	0.000	00	32	0.000	W_s = 21.5
		03	32	0.027	03	36	0.023	p > 0.25
					03	36	0.023	
					01	35	0.008	
	$\bar{x}$			0.007			0.009	
	s.d.			0.014			0.011	
f8	May 1981	04	47	0.024	09	30	0.086	
	to April	03	50	0.017	01	28	0.010	
	1982	00	15	0.000	11	32	0.098	W_s = 20
		03	31	0.028	04	26	0.044	p > 0.25
					00	35	0.000	
					00	25	0.000	
	$\bar{x}$			0.017			0.040	
	s.d.			0.012			0.044	
f9	May 1981	01	50	0.006	01	31	0.009	
	to April	00	49	0.000	07	31	0.065	
	1982	00	17	0.017	01	33	0.008	W_s = 23
		04	30	0.038	01	26	0.011	p > 0.25
					00	35	0.000	
					00	25	0.000	
	$\bar{x}$			0.015			0.016	
	s.d.			0.017			0.025	

A - Total number of feces counted during each count

B - Number of days between successive counts

C - Estimated relative density of elephants (in number of elephants/ ha)

D - Wilcoxon rank sum of the smaller sample of counts (W_s) and the significance probability

TABLE 25 - Average relative elephant densities on the resting-site forest plot and those in Wasgomuwa Strict Natural Reserve (WSNR), Corridor Cl and in areas east of Somawathiya Sanctuary (SS) in the Accerlerated Mahaweli Development Area, Sri Lanka. May 1981 - April 1982.

Rest-area plot in WSNR	Other forest plots in WSNR	Forest plots in Corridor Cl	Forest plots east of SS
0.029	0.00	0.014	0.010
0.134	0.017	0.008	0.006
0.111	0.017	0.026	0.006
0.029	0.003	0.036	0.031
0.599	0.006	0.104	0.032
0.118	0.009	0.003	0.025
0.029	0.004	0.000	0.035
0.000	0.006	0.000	0.018
0.009	0.009	0.007	0.000
0.071	0.003	0.008	0.000
$\bar{X}$ 0.113	0.0074	0.021	0.016
s.d. 0.178	0.0058	0.032	0.014

Kvustal-Wallis test statistic $H = 4.20$, $p > 0.10$

TABLE 26 - Economic losses due to crop raiding elephants during the cultivation season of October 1980 - April 1981 as estimated from farmer responses obtained at the villages of Aluyatawala, NaminiOya, and Trikkonamadu. January - April, 1982.

Villages	A	B	C	D	E	F	G	H
Aluyatawala	Paddy	36	1.79±0.26	2.44±0.66	0.74±0.14	2356.53 ± 292.01	989.24 ± 148.54	1372.00±220.28 or Rs. 3443.45 to 4760.28
	Paddy	30	1.03±0.23	0.74±0.18	1.69±0.37	1810.33 ± 224.03	1267.15 ± 196.12	543.19±181.78 or Rs. 1080.25 to 2166.94
Namini Oya	Corn	25	0.46±0.08	home garden	—	597.07 ± 91.73	57.85 ± 30.11	539.23±103.07 or Rs. 1308.40 to 1926.90
	Others	21	0.46±0.08	home garden	--	425.50 ± 125.90	28.28 ± 16.82	397.21±130.04 or Rs. 1466.85 to 2901.31
Trikkonamadu	Paddy	20	1.41±0.21	1.8±0.34	0.78±0.23	3299.14 ± 546.02	998.14 ± 419.72	2301.01±500.02 or Rs. 5383.16 to 8372.28

A = main crops
B = farmers who responded to questions
C = hectares cultivated per person
D = distance (km) between cultivation & residence
E = distance (km) between cultivation & nearest forest patch
F = expected yields (kg/ha/farmer)
G = final yields (kg/ha/farmer)
H = loss in yields and economic equivalents* (Rs/ha/farmer)

*1 kg of paddy valued at Rs. 2.98
1 kg of corn valued at Rs. 3.00
1 kg of other crops (cereals, legumes, etc.) valued at an average cost Rs. 5.62
1 U.S. dollar = 25.00 Sri Lankan rupees

The paddy plant (*Oryza sativa*) is a grass. Its wilder relatives, *Oryza perennis* were eaten by elephants in the villus and in certain grasslands close to the Mahaweli Ganga in WSNR. During the wet season when there was a reduction in grazing area available to elephants, paddy cultivations within their ranges could become sites of high-quality forage availability. Raids by elephants on artificial pastures of the villu grass at Trikkonamadu, Kandakadu and Welikande (Figure 1), and on sugar cane (another grass species, namely *Saccharum officinarum*) plantations in other parts of the island, were also evidently related to the fact that those crops were preferred foods of elephants in their natural range.

The crop loss, estimated from responses to questions 6 and 10, was due to all wildlife pests. Farmers interviewed considered elephants and the wild boar as the most persistent crop-raiders of all mammalian pests. They attributed all damage to the elephant because it was the more visible of the two species, particularly during nights when most crop-raiding seemed to occur (Table 27).

An unbiased estimate of crop losses solely due to the elephant would require direct observations in the crop fields during nights. Facilities for making night time observations were limited. Furthermore, this study was done in collaboration with Department of Wildlife Conservation. Owing to the existing status of laws protecting elephants and the wild boar, farmers avoided regular visits from a wildlife officer, particularly during nights. None of the farmers interviewed confessed to shooting at the elephant or other wildlife pests. But this was because they feared prosecution by wildlife officials with whom I was constantly associated. Instances of crop damage, voluntarily brought to the notice of wildlife officials by farmers, were cases where the damage has been so extensive as to force the farmer to abandon his crops. Farmers perhaps hoped that by permitting the wildlife officials investigate such damage, their chances of receiving compensation improved.

As an estimate of total loss due to wildlife pests (loss due to climatic and soci-economic factors were assumed to be minimal), those shown in Table 26 were higher than other estimates used in the economic analysis of the wildlife component (TAMS, 1980d). All estimates shown in Table 26, except that reported for home gardens of Namini Oya, were perhaps overestimates of crop damage caused solely by elephants. Home gardens of Namini Oya were mostly raided by lone individuals and herds comprising only adults (Table 27). They were probably younger dispersing males which had come into conflicts with settlements at the periphery of their ranges. The other important mammalian pest, namely the wild boar, was shot for its meat, and was less likely to raid home gardens of farmers. Crop losses in the home gardens of Namini Oya were therefore, more likely to be entirely due to elephants. Other economic equivalents of crop losses (Table 26) might be a reflection of farmer-expectations for compensatory payments.

If elephants avoided cultivated areas until such times when natural pastures within their ranges were overgrazed, then one would expect crop raids to increase in frequency during the latter half of the cultivation season. Dates of reported crop raids supported this prediction only in Aluyatawala, where 29 of the 36 raids were during the months after January 1981 (Table 27). Farmers distinguished between larger (adults and sub-adults) and smaller (juveniles and

TABLE 27 - Characteristics of elephant raids on croplands of farmers, during November 1980 to April 1981, in the villages of Aluyatawala, Namini Oya, and Trillonamadu of the Accelerated Mahaweli Development Area, Sri Lanka. January - April 1982.

Name of Village	No. of farmers who responded to question	Time of year when crops were raided			Time of day when crops were raided			Type of herd which raided crops		
		A	B	C	D	E	C	F	G	H
Aluyatawala	36	2	29	5	8	21	7	6	11	19
Namini Oya	30									
a)paddy lands	30	9	11	10	17	3	10	1	20	7
b)home garden	25	12	13	--	22	3	--	1	23	1
Trikkonamadu	20	8	12	--	12	4	4	3	11	6
	86									

infants) elephants. Whether or not there were differences in encountering females with infants (nursing units) and juveniles with non-lactating females (juvenile-care units) in crop fields was not certain. Sex and age class composition of crop raiding elephant herds would be of interest to future researchers.

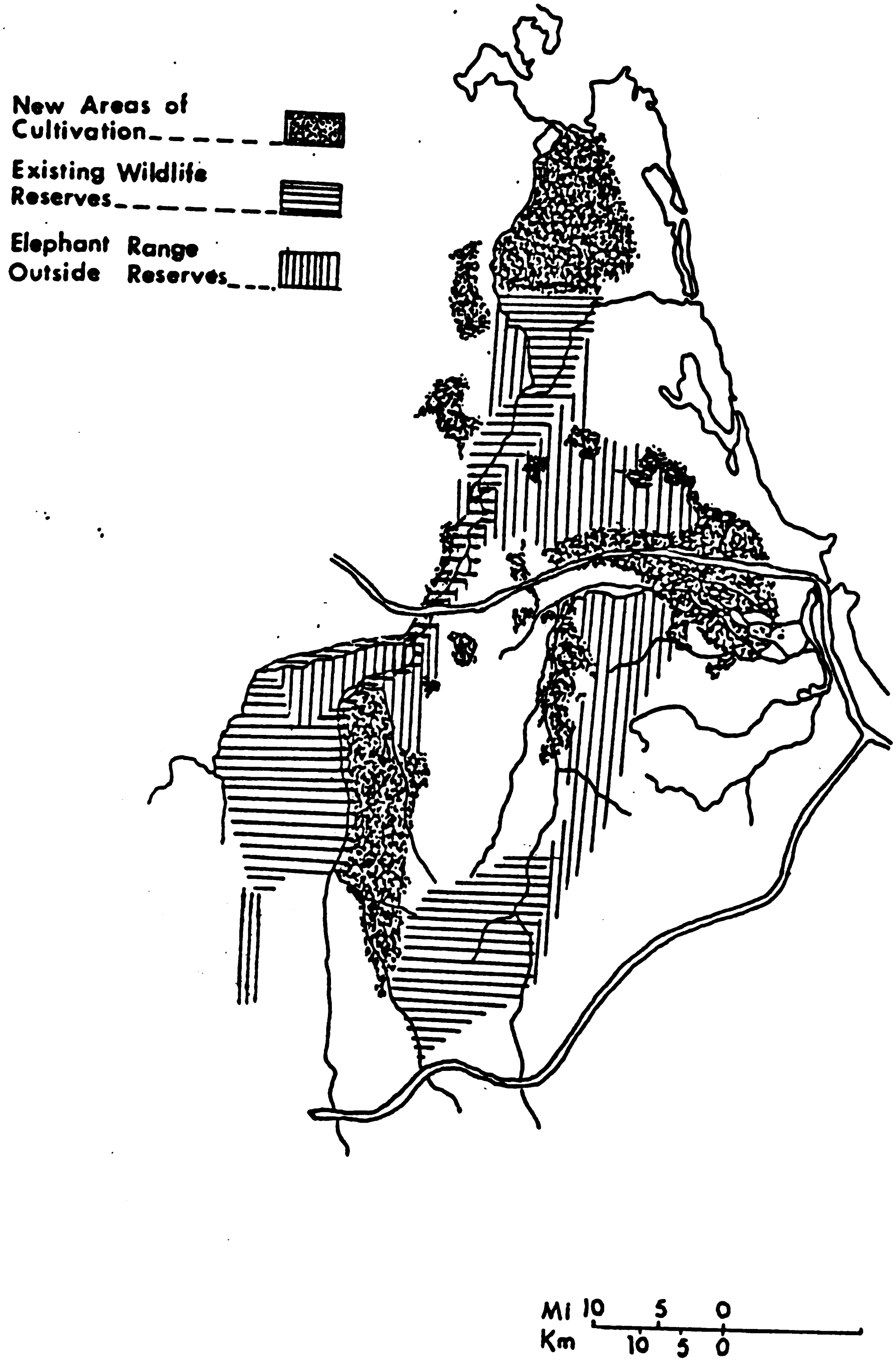
Impact of Development Programs

27.0% of the population range B will be lost to development of agriculture and settlements (Figure 15). In range A, a further 12.0%, and 9.0% in range C, will also be lost to development. As later stages of the Mahaweli Development Program are implemented, further losses of elephant ranges outside existing and new reserves (Figure 15) are inevitable.

When this study was completed, the proposed Maduru Oya National Park protected only peripheral parts of the ranges of populations B and C (Figures 1 and 11). As development intensified in areas outside reserves elephants might use PMONP to a greater extent. During the next few transitional years, when there would be changes in elephant ranges relative to the new development areas, patchy clearing of forests and subsequent creation of pocketed elephant herds (Olivier, 1978) could result in serious management problems for farmers and conservationists. Corridor C1 and the southern extension of corridor C2, both could have important roles in maintaining continuity between populations, particularly during the transitional years. Since the chances of either of these corridors being permanently established were low, it was likely that the new PMONP would eventually be isolated from the other two reserves.

The PMONP, presently had many of its grasslands under the dominance of *Imperata cylindrica*. This grass was not eaten during

Figure 15. Areas to be developed for agriculture and settlement which were parts of elephant ranges identified in the Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.


New Areas of Cultivation
Existing Wildlife Reserves
Elephant Range Outside Reserves
Mi 10 5 0
Km 10 5 0

during the rains when farmers would also be cultivating in areas adjacent to this new national park. Increased crop-raiding by elephants, in search of new grazing areas, are likely, particularly during the early years after the establishment of the national park.

Villus would be available for grazing by elephants within the Somawathiya Sanctuary (SS) and in the new Floodplain National Park. But outside of those two reserves, villus would probably be used by increasing numbers of livestock. Reduced flooding, caused by diversion of upstream Mahaweli-waters for irrigation, could result in further reductions in the surface area of the villus.

As more villagers are settled in the area, increasing human-elephant conflicts would be inevitable. The success of efforts to preserve the Asian elephant in this study area will depend on resources available for continuously updating the data base for managers, and the extent to which the benefits of wildlife conservation reaches the people resident there.

DISCUSSION

Distribution of Elephant Populations

The home range of an animal has been defined (Jewell, 1966) as the area it lives upon except during dispersal and migration. Since repeatable sightings of recognizable elephants were few (Figures 7 and 10), and was possible only in open habitats, measurements of their home ranges were not attempted. Seasonally-high elephant-activity sites in each population's range were described in locations where female herds were found to spend most of their time (Figures 5 and 6). Those observations can be checked further when radio-telemetry or other more objective methods become available for studying elephant distribution in Sri Lanka.

Elephant activity was seasonally high at certain sites (Figures 5 and 6) and it was never discontinuous within and between population ranges (Figure 11). Elephants moved from high to moderate activity sites during late-night hours. Seasonally separate ranges described for some elephant populations in national parks (Mckay and Eisenberg, 1974) could have been due to differences in seeing elephants in different parts of their range (Table 2). Owing ot their large food requirements (150 kg/ day , Vancuylenberg (1974)), and a tendency to move while grazing (McKay, 1973; Vancuylenberg, 1974), individual elephants and herds probably ranged more widely than observed during both seasons. Radio-telemetry studies in the Lake Manyara National Park, Tanzania, showed that the African elephant herds there reached all parts of their range during each month (Douglas-Hamilton, 1972).

Elephant distribution along the Mahaweli Ganga appeared to be related most to the distribution and composition of available grasslands. Wet season high activity sites near the Mahaweli Ganga in the WSNR-corridor C1 areas (Figure 5) were predominantly forested habitats with grassland patches being few and of mixed species composition (plots g3, g4 and g5; Table 20). Additional grassland patches near human settlements were of lower importance for grazing by elephants either because they were cultivated or because they were dominated by non-preferred stages of Imperata cylindrica. In the dry season, however, cultivations were abandoned after harvest and preferred stages of Imperata cylindrica became available after burning. Therefore, dry season high activity sites in WSNR and in corridor C1 areas (Figure 6) were closer to human settlements than that of the wet season.

Flooding of floodplain areas of the Mahaweli Ganga forced elephants to move away from that river. In villu habitats, however, where grass was available despite flooding, more elephants were observed in the wet than during the dry season (Table 2). The influence of flooding on elephant distribution was therefore likely to be related to its effects on available grass.

Scarcity of water did not appear to be an important factor influencing elephant distribution in the dry season. Although the dry season high activity site in the Mahaweli Ganga floodplain was close to the river (Figure 6), it was probably related to the availability of grazing sites there and not to water-shortages in other parts of that range. Long-term association between elephants and agricultural areas enabled elephants to use reservoirs and irrigation channels. Complete dependence on one perennial source of water was not a characteristic of elephants in this study area. Distances travelled to and from any river, even during the dry season, were therefore likely to be less than that reported for the African elephant (Lamprey, 1963).

Population Structure

Competition for food among individual elephants and defense against predators are reported to be important factors which determine the size of female herds (Douglas-Hamilton, 1972; Wittenberger, 1981). Since the largest predator in Sri Lanka is the leopard (*Panthera pardus fusca*), even the elephant calves are relatively free of predator threats. Humans, since they captured elephants for domestication, could have played a predatory role in the past. The larger dry season sizes of female herds in WSNR was probably attributable to the fact that elephants, during that time of the year, grazed predominantly in grasslands near human settlements. Wet season high activity sites of WSNR-elephants were close to the Mahaweli Ganga, and not near human settlements. Female herd sizes in WSNR were significantly lower in the wet than in the dry season (Figure 14). In the SS sub-population, however, changes in grass available in the villus were less variable and this probably reduced seasonal fluctuations in female herd sizes.

The wet season reduction in female herd size of the WSNR sub-population was due to decreases in numbers of juveniles seen among them (Table 7). This may support McKay's (1973) hypothesis regarding the splitting of a female herd into nursing units of lactating females and infants, and juvenile-care units of non-lactating females and juveniles. Additional support to this hypothesis might be obtained from significant associations of adult females and juveniles with herd types of the two sub-populations. Whenever affinities shown by adult females and juveniles towards a herd type were simultaneously significant, they always contrasted each other (Table 28). This also indicated that female herds could be splitting into sub-units, with adult females (many of them probably lactating) in one and juveniles in the other unit.

Specific associations between lactating females and infants, and non-lactating females and juveniles, would be detected only if sufficient numbers of females were individually recognizable. Energetic costs and benefits associated with feeding and movement would, however, be likely to be different for lactating and non-lactating females. The presence of infants would limit the movement of lactating females (McKay, 1973). Increased movement would be beneficial for the non-lactating female if it increased its chances of encountering a dominant male. Home ranges of the female Asian elephants were larger and traversed the smaller ranges of many males (Eisenberg et al., 1981). Higher food requirements of lactating females (Laws et al., 1975) would also favor continued grazing in one food patch in preference to movement between alternative patches (Krebs and Davies, 1981). Sexually-mature juvenile females, would be of similar reproductive condition as non-lactating females. Other juveniles too, owing to their exploratory nature, might also preferentially associate with non-lactating rather than lactating females.

TABLE 28 - A summary* of significant associations shown by adult females and juveniles towards different herd types of the WSNR and SS sub-populations. Accelerated Mahaweli Development Area, Sri Lanka. September 1980 - July 1982.

Sub-population	WSNR Sub-Population						SS Sub-Population					
Seasons	Dry			Wet			Dry			Wet		
Herds	A	B	C	A	B	C	A	B	C	A	B	C
Adult Females			+			⊗				+	⊗	-
Juveniles	+		-			⊗				-	⊗	+

A = female herd
B = harem
C = mixed herd

+ observed frequency significantly higher than that expected in contingency table analysis

– observed frequency significantly lower than that expected in contingency table analysis

⊗ low sample size or lack of observation of particular herd-types

Blank spaces were instances where difference between observed and expected frequencies in contingency table analysis were not significant.

* Summarized from detailed results shown in Tables 7 & 8.

More than 45.0% of all males seen in a sub-population (SS sub-population, Figure 13) were lone individuals. 32-44% of the time sub-adult males were seen, they were in female herds (Figure 13). During the period when a sub-adult or a young adult male was dispersing, it is believed that it could frequently return to its maternal herd (Croze, 1974; Laws et al., 1975). Except for those harems where the bull was certainly a dominant individual (seen only in WSNR), others might have been temporary associations between young males and their maternal herds.

Mean numbers of adult and sub-adult females per herd were nearly double in harems when compared to that in female herds (Table 6). The increase between harems and mixed herds was nearly threefold in WSNR but of a lower magnitude in the SS sub-population (Table 6). Mean number of juveniles per mixed herd was also about twice that of harems and approximately 3-5 times that of female herds (Table 6). The probability of an adult bull encountering an estrous female, belonging to adult, sub-adult or juvenile classes, was therefore considered to be highest in mixed herds.

Mixed herds were probably formed when mature bulls in search of estrous females joined aggregations formed by smaller female herds. Aggregations might be formed due to chance meetings between female herds (Laws et al., 1975; Ishwaran, 1981). Associations of sex and age-class categories with mixed herds of the SS sub-population were not significant during the dry season (Table 8 and 28). Thos mixed herds might have formed due to random aggregations between female herds and males joining the aggregations. Mixed herds of the SS sub-population seen in the wet season comprised significantly higher numbers of juveniles

(Tables 8 and 28) and hence could have been aggregations between juvenile-care units of female herds. In WSNR sub-population, adult females were seen in significantly higher than expected numbers in mixed herds of the dry season (Table 8 and 28). Those mixed herds might therefore be associations between nursing units comprising related adult females, and adult males in search of estrous females.

As in other polygamous mammals (Wittenberger, 1981), probably a few dominant male elephants inseminated most estrous females. Dominant bulls whether they were in mixed herds or in harems were likely to defend individual estrous females but not entire female herds (Barnes, 1982). Since the dominant bull in WSNR, which was twice seen in harems, was also once seen alone, apparently harem-bulls did not associate with female herds on a constant basis. If dominant bulls in one area were more frequently seen in harems than in another area it was likely to be due to differences in the ratio of dominant bulls per adult female rather than differences in the male reproductive strategy. Neither of the two known dominant bulls in the SS sub-population were seen in harems. Despite the fact that dominant bulls were seen in the same mixed herds on five occassions, aggression between them was not evident. Sample sizes of mixed herds comprising both dominant bulls of the SS sub-population was probably too low to detect such aggressive encounters.

Co-operation between bulls which reached a similar dominance status would theoretically be difficult to justify. Elapata (1969), in reporting a series of copulations between two males and two females, however, noted that one female mated with both males while the other mated with only one of them. Female choice for dominant males

(Wittenberger, 1981), with age and status in a female herd as factors influencing choice of females, is a possible reproductive strategy. Reproductive behavior and ecology of the Asian elephant, unfortunately, is an aspect that lacks quantitative data and hence requires detailed study for complete analysis.

Observed number of males per females was higher in the SS than in the WSNR sub-population (Table 9 and 10). There was evidence to indicate that protein quality of the diet in the floodplain areas were better than that in habitats further upstream in WSNR (Tables 14 and 15). Although male elephants reached physiological maturity by the age of 8-9 (Eisenberg, 1981), sociological maturity, or the ability to compete for estrous females (Croze, 1974; Laws et al., 1975; Eisenberg, 1981), was not attained till about 17-18 years (Eisenberg, 1981). Better protein-quality of diet could influence maturation rates of males in the SS sub-population relative to that in the WSNR sub-population. Since grass availability in the villus was reliable throughout the year, young males of the SS sub-population might also avoid cultivations and conflict with humans and thereby survive to older ages than those in the WSNR sub-population.

Preferred Habitats and Foods

The preferred foods of the Asiatic elephant on the study area were grasses. Browsing was relatively unimportant (Tables 12-16), though it is possible that the extent of feeding on woody plants could have been underestimated.

Earlier studies of the African elephant led researchers to classify it primarily as a grazer (Buss, 1961; Wing and Buss, 1970). Later authors (Sikes, 1971; Field, 1971; Field and Ross, 1976), however, reported higher extents of browsing. Recent problems related to tree damage caused by the African elephant (Laws, 1970; Laws et al., 1975) were probably related to habitat changes which have influenced the relative abundance of grasses and browse available to elephants.

Apart from present differences in their habitats, dietary preferences of the two living genera of elephants are probably also affected by their evolutionary histories. The African *Loxodonta* has been referred to as the more conservative genus since its tooth structure underwent little specialization after evolving in late Pliocene (Maglio, 1972). This genus is adapted to woodlands and open savannas and did not expand its range to other continents. The dental structure of the Asian *Elephas* (and of the extinct mammoths) reached a complexity similar to that of *Loxodonta* by early Pleistocene. It evolved further as *Elephas* invaded the European and Asian continents (Maglio, 1972). Competition between the many elephantids in Europe and Asia could then have led to a greater dietary specialization among its members. The higher degree of enamel-folding in *Elephas* molars may be an adaptation for feeding upon coarser food items (Sikes, 1971). Of the two living genera of elephants, the Asian form probably seeks after grass more than the African species (Eltringham, 1982). Elephants on the present study areas were at times observed to feed upon dry grass of mixed species composition available in meadows prior to burning in the dry season.

The better quality diet available to elephants in the Mahaweli Ganga floodplains (crude protein estimates of fecal samples in Tables 14-16) was at least partly due to superior pastures in villus compared to grasslands of other ranges (Table 5). Grasses were available year-long in villus (Figures 9a and 9b). The availability of these grasses to elephants, however, was restricted during both seasons. Flooding restricted the available villu areas for grazing during the rains. In the past, when Mahaweli-waters were not diverted for irrigation at upstream areas, flooding would have restricted grazing areas in the villus even during the dry season. At present, dry season grazing by elephants in the villus is time-limited since humans and livestock use that habitat during the day (Table 1).

The time available for feeding perhaps limited the size to which an elephant could grow on poor-quality foods (Wyatt and Eltringham, 1974). The government farms in Trikkonamadu, Kandakadu and Welikande were established after 1960. Since then, increasing numbers of humans and livestock tend to limit elephant-use of the villus. Artificial pastures of the villu-grass created by farms, on the other hand, formed additional grazing sites accessible to elephants. Hence, it is believed that rather than being a larger sub-species of the Asian elephant (Deraniyagala, 1955), the larger size of the Mahaweli Ganga floodplain elephant, as compared to those from other parts of the island, is more likely a result of nutritional differences.

Digestibility reducing substances might be more prevalent in woody plants than among grasses (Levin, 1976; McNaughton, 1979). Hence, the elephant, whose digestive efficiency is low (Benedict, 1936), perhaps prefers grazing over browsing under optimal conditions. Relatively low energy costs associated with preparing and feeding on grasses might also favor grazing. McKay (1973) says that, while 80% of the grasses removed from the ground might be eaten, only 50% of leaves and 20-25% of bark removed from trees and shrubs were likely to be eaten. Differences in such foraging efficiency (McKay, 1973) may also favor grazing over browsing.

Changes in Grassland Use and Quality

Imperata-dominated grassland patches, where relative densities of herbivores were higher (plot g2 in comparison to that of g6; Table 17) also had higher frequencies of other grass and sedge species (Table 20). Many Sri Lankan national parks were traditional agricultural areas at the time of their establishment and hence probably had grasslands which were dominated by *Imperata cylindrica*. As densities of grazing animals increased inside national parks, the relative cover of *Imperata* probably decreased. After the establishment of a national park there was always a time-lag in the recovery of ungulate populations. Grazing by domestic stock was legally prohibited inside national parks. Elephants, however, quickly began to use areas vacated by humans, and hence were probably important in controlling the spread of *Imperata* in newly established national parks.

In Ruhuna and Wilpattu National Parks of Sri Lanka, both of which were established at the beginning of this century (Crusz, 1973), *Imperata cylindrica* is not now a dominant species (Eisenberg and Lockhart, 1972; Kurt, 1974; Santiapillai et al., 1981). In the Gal Oya National Park, established in the early 1950's, it occurred as an understory species in the savanna woodlands (McKay, 1973; Vancuylenberg, 1974; Ishwaran, 1979). Compared to areas where tree cover has been completely removed and densities of grazing herbivores low, *Imperata* was less abundant in those woodlands (Ishwaran, 1979). The same grass species, however, is still present in many parts of the grasslands along the shores of a man-made lake in the Uda Walawe National Park, established in the 1970's.

Ungulates are not hunted in national parks and perhaps because of this, their densities increased. Illegal grazing of domestic stock might also add to existing densities of ungulates in national parks. A principal evolutionary response of grasses to herbivory is selection for prostrate rapidly growing genotypes (Stapledon, 1928). Short-grass meadows become increasingly dominant in older national parks (Eisenberg and Lockhart, 1972; McKay, 1973; Kurt, 1974; Vancuylenberg, 1974; Ishwaran, 1979). In WSNR too, grasslands near the river (g3, g4 and g5; Table 20) where elephant and other herbivore densities were probably high over long periods of time had less _Imperata_ than those closer to human settlements (g2; Table 20).

In the wet season, flooding of villus, cultivation of several patches of grasslands, and the unavailability of _Imperata_ in preferred stages, perhaps led to increased competition between elephants and livestock in remaining upland grasslands of mixed species composition. Livestock density was one of the two predictor variables which negatively influenced elephant-use of grassland plots in the wet season (Table 22). Although it has never been reported for national parks, wild ungulate densities there might play a role similar to that of livestock densities of this study area. All national parks of Sri Lanka are predominantly forested areas, and grassland availability were largely confined to the proximity of water-holes (McKay, 1973; Eisenberg and Seidensticker, 1976; Santiapillai et al., 1981).

Dry season grazing by ungulates tend to be concentrated around water-holes (McKay, 1973; Kurt, 1974). Grass height was an important predictor variable positively influencing elephant-use of grasslands in this study area during the dry season (Table 21). In national parks reductions in dry season grass heights and related decreases in grazing by elephants might be accelerated by ungulate-grazing (McKay, 1973; Kurt, 1974). In many Sri Lankan national parks elephants used a procedure called scarification (McKay, 1973) for feeding upon short, competitively-grazed dry season grasses. Scraping the low forage plants loose with their fore-feet, the elephants swept its trunk over the loosened vegetation and collected it for feeding (McKay, 1973). African elephants have been observed to use a similar method of feeding on short herbaceous vegetation (Petrides, unpublished).

Dry season elephant movement away from grasslands in national parks, towards more forested regions, was evidently because of shortages in available grass (McKay, 1973; Santiapillai et al., 1984). Although a similar movement in Wilpattu National Park was interpreted with respect to the location of the main river there (Eisenberg and Lockhart, 1972), the possible role of decreasing supplies of grass was also probably important.

Use of specialized feeding techniques, such as scarification, probably increases the energy costs of food consumption. Shorter, drier and competitively-grazed grass perhaps provide relatively low benefits per unit of energy invested in feeding. As ungulate densities increased and short-grass meadows became abundant in national parks increasing costs and decreasing benefits associated with grazing perhaps led to relative increases in the importance of browse as a food for the elephant. Woody plants in and near the Gal Oya National Park were eaten to a greater extent (20-34%; Ishwaran, 1983) than that reported for this study (Tables 12-16). Asian (McKay, 1973; Vancuylenberg, 1974) and the African (Field and Ross, 1976; Guy, 1976) elephants have been found to browse more during the dry season. African elephants were also reported to browse more in a short-grass than in tall-grass area (Field, 1976).

Crop Damage by Elephants

In crop raiding by elephants, cultivated crops evidently are preferred foods. Palms were a major food type for the elephant in the forest of Malaysia (Olivier, 1978) and oil palm estates there suffered from extensive damage by elephants (Olivier, 1978; Blair, 1980).

As cultivation increasingly limited available wild grazing sites, elephant raids on croplands will certainly become more frequent. Homogeneous stands of cultivated grasses, e.g. paddy, sugar cane etc., are ideal for elephants and probably offer higher quality food than that available in their natural range. Olivier (1979) hypothesised that creation of additional food supplies within an elephant's residual range might reduce conflicts with agriculture.

Elephants learn to avoid or surmount barriers erected against their entry into cultivated fields. Structures such as trenches and fences lost their utility during the monsoonal rains which is a characteristic feature of many Asian countries where elephants are agricultural pests (Blair et al., 1979). Mildly-charged electric fences erected at key points along established elephant tracks failed to stop crop-raiding elephants in the Gal Oya Valley Development Scheme of the 1950's (Brohier, 1974). Electric fences charged at 5,000 volts for three thousandth of a second and operated only at night have been successful in containing elephants from oil palm estates in Malaysia (Blair et al., 1979; Blair, 1980). Their usefulness in settlement schemes planned under AMDP would, be limited by economic and safety constraints.

The stated (Table 26) economic equivalents of crop-losses overestimated damage caused solely by elephants. Those exagerated economic losses might reflect farmer expectations with respect to compensation payments. Crop damage due to elephants, particularly in the early stages of development, was often higher than expected levels (Brohier, 1974). Farmers cultivating at the periphery of reserves, although suffering from heavy losses, probably buffered damage to cultivations of other farmers at greater distances from the periphery. Any crop field abandoned at the periphery would become part of the elephant's range. Since land allocated per farmer, under the AMDP, was only about 1.25 ha, anyone suffering regular crop losses might be economically incapable of continuing their efforts for long. A continuously shifting conflict-zone at the periphery of a reserve would be difficult to manage. Stabilising that zone would help, however, to limit crop losses to predictable levels.

Impact of Development Program

The attempt to establish corridors C1 and C2 demonstrated an acknowledgement of the need to maintain gene-flow between elephant populations to be protected by the reserves. Their rejection by development authorities, for economic and political reasons, was an indication of future difficulties faced by conservationists. In the early stages of the Gal Oya Valley Development Program of the 1950's, a total of 770.0 km^2 was set aside for wildlife conservation (De Silva, 1958). Although the total land area to be developed under the present MGDP was about eight times higher than that program of the 1950's, only 389.1 km^2 in PMONP were new wildlife conservation areas.

A total of 609.4 km^2 (WSNR, SS and the northern part of corrido C2) was preserved from times prior to the initiation of the MGDP. Proposals to declare WSNR and SS as national parks were ready to be approved when this study was being completed. Additional areas along the Mahaweli Ganga also would be protected in a still-to-be-defined Floodplain National Park. The loss of 100 km^2 of elephant habitats in the northern parts of corridor C2, however, seemed inevitable.

In many other parts of the island elephants moved to areas outside national parks where contiguous forest cover prevailed (McKay, 1973; Ishwaran, 1979). If all development programs planned under the MGDP were completed on schedule, elephants could become largely confined to the three reserves (WSNR, SS and PMONP; Figure 1) by the end of this century. Delays and set backs in project implementation often helped elephants to maintain parts of their ranges outside parks.

In the early years after the establishment of the reserves, minimising crop damage by elephants would be the major management problem. Effective mitigation of that problem might favorably influence farmer attitudes towards wildlife conservation. If elephants become completely isolated in reserves, other management problems related to habitat and species diversity of reserves could arise. Natural ecological processes might be ineffective in maintaining genetic diversity in small isolated reserves (Soule, 1983) and hence management of elephant and/or ungulate populations might become necessary. There has never been any active management in Sri Lanka's national parks in the past, but such a policy might not be desirable for all times in the future.

WSNR and SS would be connected through the Floodplain National Park (Figure 1) but the new PMONP would be isolated from all other reserves in the study area. Corridors could be useful in maintaining continuity between populations until such times as elephants have adjusted to their new ranges. Even the establishment of the smaller corridor Cl, an important wet season high activity site (Figure 5), would help to achieve certain amount of continuity between the reserves. If corridors were not established, PMONP would still be connected to the Gal Oya National Park, located southeast of this study area. But at the time of this study, only lone males were found to be using the range between these two national parks.

About 200-300 elephants might use habitats in and around each reserve within the study area. If isolated such small populations could be vulnerable to extinctions (Soule, 1983). Deteriorating habitat conditions resulted in delayed maturity, longer calving intervals and reduced recruitment rates for the African elephant in the Murchison Falls National Park of Uganda, Africa (Laws et al., 1975). Similar developments in the smaller populations of the Asian species in Sri Lankan reserves, would reduce its chances for survival. Assuming that the emphasis of conserving the elephant remains a long-term goal of the reserves, continuous data collection and regular evaluation of management strategies will be increasingly important in the future.

SUMMARY AND CONCLUSIONS

The following conclusions, based on their presumed order of importance, were summarized for this study:

- Grass was the most important food and grassland of mixed species composition the preferred habitat for the elephant in the Accelerated Mahaweli Development Area in Sri Lanka. Elephant-use of seasonally flooded villu-grasslands were limited to times when human and livestock use of those grasslands were low.
- As low lying villus flooded and many upland grassland patches cultivated, competition between livestock and elephants in remaining upland grassland sites increased in the wet season. The combined influence of livestock densities and patchiness in grass cover negatively affected relative elephant use of upland grassland areas in the wet season.
- Harvested croplands and villus where flood-waters have receded were additional grazing sites which perhaps helped to reduce dry season competition for grazing in upland grasslands between elephants and livestock. Relative elephant-use of such upland grassland sites was positively affected by the height of grass available in the dry season.
- Seasonal shifts in high elephant-activity sites in WSNR and corridor Cl areas were probably dependent upon the distribution and composition of available grasslands. The influence of flooding on elephant distribution in floodplain regions in areas east of SS were probably

related to its effect of inundating grasslands.

- Although the extent of browsing was underestimated, it was assessed to be lower than that reported for habitats in and around older national parks of Sri Lanka. Changes in species composition and increasing ungulate densities might interact to increase the importance of browse to elephants in national parks.
- Female herds and solitary males were the most frequently observed units of elephant social organisation. Female herds might split into nursing units with lactating females and infants, and juvenile-care units with non-lactating females and juveniles. Harems were formed when dominant bulls joined female herds or perhaps when younger adult males returned to their maternal groups. The chances of an adult male finding an estrous female were probably highest in mixed herds. When whole or parts of female herds aggregated, either by chance or based on relationship among adult females, males perhaps joined such aggergations to form mixed herds.
- Seasonality in reproductive activity was not evident. Number of males per female was higher in the SS than in the WSNR sub-population. Better pastures of the villus perhaps favored male survival rates and/or maturation rates in the SS sub-population relative to that of the WSNR sub-population. Despite differences in grassland quality within the ranges of the two sub-populations, differences in proportions of infants were not evident.
- The predominant cultivated crops, perhaps because they were grasses, were quite vulnerable to damage by elephants. Crop damage, as estimated from farmer responses to interview-questions, was higher than that reported in past analysis and probably reflected farmer hopes for compensation.

- The new PMONP protected only peripheral parts of existing elephant ranges. As development proceeded, elephants of the PMONP might be isolated from those of the WSNR and SS. The small populations that would be protected by these reserves, if isolated, would be vulnerable to extinction.

OUTLOOK FOR THE FUTURE

The proposed Maduru Oya National Park would protect only marginal portions of a wet-season high elephant-activity site along the Maduru Oya river (Figures 1 and 5). Other high elephant-activity sites (Figures 5 and 6) were also partly or completely outside protected areas. Inclusion of the corridors as part of the reserve system to be established in the area would help to protect a larger part of the present elephant range and maintain contiguity between existing elephant populations. It also should minimise losses both to humans and elephants during the next few transitional years, when elephant ranges as shown in this study (Figures 5, 6, 11 and 16), would change relative to new areas of agriculture and wildlife reserves.

The proposed Maduru Oya National Park, and other new national parks established in areas of agricultural development, are demarcated so as to protect catchment areas of reservoirs and/or located in regions where other types of land-use have not been planned. Such objectives do not seem to coincide either with existing or optimal ranges. The size of the proposed Maduru Oya National Park, namely 384 km^2, is smaller than areas now occupied by elephant populations identified in the study area (Table 5). Furthermore, if isolated from other reserves in the study area, the design of PMONP is sub-optimal for protecting elephant populations and maintaining existing levels of species diversity (Diamond, 1975).

National parks established after the independence of Sri Lanka in 1948 are all smaller than 400 km^2. At present elephant ranges between such small reserves remain contiguous with many lone males occupying areas of high human-elephant conflict. The development for irrigated agriculture is always a threat against preserving contiguity between elephant populations protected in national parks. Even the larger reserves (Ruhuna (Yala) and Wilpattu National Parks, both about 900-1000 km^2; Crusz, 1973) which were established during the early part of this century are smaller than the 10,000 km^2 area recommended for protecting diversity among large mammal communities (East, 1981).

If the reserves in this study area are included, 11-12% of Sri Lanka's 64,000 km^2 would be protected for nature conservation. This would be a commendable achievement for a developing nation with a per capita GNP of US $ 320.00 per year. Their role in protecting elephant populations, however, would largely depend upon those national parks remaining as a contiguous stretch of suitable wildlife habitats. Maintaining contiguity between national parks through corridors will be a politically difficult task. Public relations programs, aimed at stressing the importance of maintaining contiguity between national parks, would be essential if corridors were to acquire permanent legal status. Intensive management techniques possibly could aid in the conservation of elephant populations or populations of other selected species as well as in maintaining species diversity in smaller reserves (East, 1981), but they are probably no substitute for preserving adequte areas of contiguous wildlife habitats.

The religious and cultural importance of the Asian elephant (McKay, 1973; Olivier, 1978) might awaken a public desire to preserve that endangered species in Sri Lanka. Conservation of viable wild populations, however, depends on the protection of minimum areas of contiguous habitats and the adoption of necessary attitudinal changes towards resource conservation and development.

RECOMMENDATIONS

Management

- The legal status of all reserves in the study area should be changed to that of a national park. Their boundaries must be clearly demarcated. Adequate signs informing the villagers of their purpose and the nature of activities prohibited within the reserves, suould be posted.
- The establishment of the corridors, at least on a temporary basis, should be reconsidered.
- Grazing of domestic stock in any grasslands within national parks should be prohibited.
- Burning of grasslands should be restricted to Imperata dominated patches. Dry season burning of short grass meadows should be avoided.
- Development authorities and planners should be urged to compensate farmers for their crop losses. Combined patrolling of farmers and wildlife guards in conflict zones should be encouraged. Regular advice and support to farmers in order to minimise crop damage should be an important task of wildlife employees.
- National parks should encourage visitation by tourists in selected zones where wildlife could be viewed for aesthetic and educational purposes. Special programs for area residents must be encouraged. Although visitation by foreign and urban tourists could bring in much needed economic benefits, the long-term success of wildlife conservation

in the national parks of this study area would depend on communicating the conservation message to area residents.

Research

- Regular monitoring of selected climatic parameters should be initiated in all national parks
- Census and/or sample counts of elephants and the major ungulate species should be attempted preferrably on a seasonal, but at least on an annual basis.
- Population parameters such as age class composition, sex ratios, mortality and natality rates should be regularly assessed.
- Records of elephants shot in defense of crops should be maintained. Feasibility of collecting data on stomach contents and other aspects e.g. parasites of elephants, should be investigated.
- Vegetation maps must be prepared for all national parks. Species composition of grasslands should be monitored in fixed plots, and associated changes in the relative use by elephant and different ungulate species documented.
- A preliminary assessment of attitudes of farmers and nearby residents towards wildlife and nature conservation should be attempted. Such data will be useful in assessing regional needs of the people towards which a conservation program must be planned.

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