

HABITAT SELECTION AND SOCIAL GROUP DYNAMICS
OF AFRICAN ELEPHANTS IN AMBOSELI, KENYA

by

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ABSTRACT

The selection and use of habitats by African elephants were examined in relation to vegetation abundance and elephant social grouping patterns. I conducted the study in the Amboseli basin and surrounding semi-arid bushlands in southern Kenya from November 1978 to October 1979. Elephant habitat distributions in the basin in 1978/79 were monitored in a series of 88 ground surveys, while data from 54 aerial counts from 1975 to 1980 were examined for a longer term view. Plant density and biomass were monitored in permanent vegetation plots located in different habitat types in the Amboseli basin and bushlands.

Habitat types were defined, described, and compared. Herbaceous (grass/forb) biomass was more abundant than browse (twig/leaf) biomass at all times within habitat types, but in the dry season, the woody layer of some habitat types, such as the swamp edge woodlands and dense bushlands, was more abundant than the herb layer of other habitats, such as the open grasslands. Bushlands and woodlands had highest diversity of herbaceous and woody biomass. Biomass production was significantly related to wet season rainfall in all habitats. The herb layers of swamp edge habitats consistently had the highest biomass and lowest nutritional quality (exemplified by crude protein content), and were abundant well into the dry season. Woodland and bushland habitat types had herb layers which were only seasonally abundant, but of higher protein content through the year.

Elephants preferred woodlands (and, in drier years,

bushlands) in the wet seasons and swamps in the dry seasons. Elephant numbers in the woodlands and grasslands were positively related to monthly rainfall and herb layer biomass, and numbers in the wet swamps and in the swamp edge grasslands and woodlands were negatively related to the same variables. There was a large amount of variance associated with these relationships. The ranking of habitat use by elephants was significantly correlated with the ranking of herb layer biomass across habitats in the dry season, but not in the wet season, when less abundant, but more nutritious, vegetation was available in the woodlands and bushlands. There were no clear relationships between elephant numbers and browse biomass or percent woody cover across habitat types.

Groups of cows and calves were larger in the the rainy seasons, and in years with higher rainfall, and smaller in low rainfall seasons and years. Bachelor bull groups showed some similar patterns but group sizes and the range of variation were always fairly small. There was an apparent shift by the larger cow/calf groups to the high biomass habitats, and possibly more open habitats, with changes in plant abundance in the dry season. The number of large groups was not correlated with elephant density in habitat types. This supports the hypothesis that large social group size is maintained by habitat selection, rather than random encounters of groups. The larger bachelor bull groups did not shift habitats in this way.

Although their habitat use patterns were similar overall, bachelor bulls used the wet swamps and open woodlands more in

the dry season while cow/calf herds preferred the open woodlands more in the wet seasons and swamp edge grasslands more in the dry seasons. Explanations of these differences relating to physiological and social differences between the gender classes were offered.

Elephant habitat selection strategy appears to consist of a "stable element" centered on the predictable dry season habitats and an "opportunistic element" in less predictable, but more profitable, wet season habitats.

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CHAPTER 1 INTRODUCTION

Elephants are dominant herbivores in many savannah ecosystems of East Africa, and can cause significant changes in the vegetation by their feeding activities (Laws 1970). This study is concerned with one aspect of the foraging process in African elephants, their selection of feeding habitats. The setting of my study was the semi-arid Amboseli region of southern Kenya. This work is an initial part of a broader study of the foraging behaviour of elephants in relation to their biotic and social environments, and its possible application to population level processes.

The interaction of elephant populations with their habitats in east, central, and southern Africa has been the subject of discussion and controversy in scientific and management circles for many years (Agnew 1968, Beuchner and Dawkins 1970, Caughley 1976, Glover 1963, Hanks 1979, Laws 1970, Laws et al. 1975, van Wyk 1969). The controversy centers on the apparent damage that elephants inflict on woody vegetation. A central question concerns the nature of population regulation by elephants: are elephant populations capable of self-regulation, or is there need for management intervention to "save" the elephants or their habitats from extinction?

Some researchers (notably Laws et al. 1975) have concluded that woody plants are the critical dry period food source of

elephants, and that elephant populations at high density inevitably destroy this resource through over-use. They argued that in areas with large elephant populations, the woodland destruction seen will reduce the long term carrying capacity of the environment. Under this model, the growth of most large African elephant populations was being limited by density-dependent feedback mechanisms operating through age of females at puberty and calving interval (Laws 1969), but these were acting too slowly to prevent elephant population crashes and irreversible habitat damage. Elephant culling was prescribed for all elephant populations, with some areas requiring urgent action.

Other scientists (Caughley 1976, Cobb 1980, Harris and Fowler 1975, Norton-Griffiths 1979) felt that the tree/elephant dynamics may include more components, and could possibly involve long term plant/herbivore cycles, climatic cycles, or other interactions driving the systems in less straightforward ways. Norton-Griffiths (1979) suggested that the dynamics of plant/elephant systems may be complex, and specific to local conditions of climate and habitat composition. It seems likely that habitat modifying factors such as the presence of other large herbivores, the extent and timing of rangeland fires, and the effects of other human activities are also important in the ecosystem dynamics. For example, in Uganda, where annual rainfall is relatively high, elephants which consumed slow-growing woody vegetation had alternate food available in the abundant herb layer that could carry them through periods of low

woody cover. Ugandan elephant populations had significantly reduced woody cover in their habitats, and density-dependent mechanisms were apparently acting slowly to reduce elephant population growth (Laws 1970). However, Laws felt that this process was still too slow to prevent a population crash and habitat destruction. Norton-Griffiths (1979) predicted a different outcome: slow decline in elephant numbers with the vegetation maintained in an open grassland state for a long period until woodland regeneration could occur at low elephant densities.

The population consequences could be more abrupt, but not necessarily catastrophic, in a system where little alternate food was available in the herb layer. In the semi-arid Tsavo ecosystem of central Kenya, the herb layer is relatively sparse and the woody vegetation much reduced by heavy elephant use; large-scale mortality of several thousand adult females and their young occurred in the 1971 droughts (Corfield 1973), which resulted in a sharp decrease in the population size.

In order to understand the workings of specific elephant/habitat systems, and of elephant populations in general, we need more information on the nature of elephant foraging patterns and population dynamics in areas of different habitat structure and composition, and of the dynamics of the vegetation in those areas. As yet, there are few data available on the nature of elephant-habitat interactions. Feeding studies that have been done (Buss 1961, Field 1971, Field and Ross 1976, Guy 1976b) have not considered the relative abundance of

different habitat types, or food types within habitats, and their relative use. Most workers report a foraging shift from grazing in the rainy seasons to browsing on woody vegetation in the dry season, and cite anecdotal evidence that woody plants are of higher quality in the late dry period. However, there have been few analyses of the plant parts consumed and avoided by elephants to document these statements, and no evidence to show the relative abundances of grass and browse at different times of year, or between different habitats. For example, Guy (1976b) reported that elephants in Zimbabwe browsed on shrubs more, but spent less total time in feeding activity, than did Ugandan elephants (as reported by Wyatt and Eltringham (1974)). He suggested that this was due to habitat differences between the study areas, but offered no comparative vegetation data to test this hypothesis. Similarly, most of the surveys of elephant numbers and distributions (Beuchner et al. 1963, Caughley and Goddard 1975, Eltringham 1977, Laws et al. 1975, Watson et al. 1969) did not evaluate their results with reference to quantitative estimates of plant abundance (but see Cobb (1976)).

Most vegetation-based studies of woodland use by elephants (Anderson and Walker 1974, Laws et al. 1975, van Wyk 1969) were not done with reference to elephant habitat use and food selection patterns. Evaluation of the results of such studies, and comparison between results from different areas and time periods is therefore difficult, if not impossible. In the cases where some of these factors have been considered, as by Croze

(1974a,b), the conclusion is often that elephant use of woody vegetation is not the ultimate cause of woodland decline.

The foraging behaviour and habitat use strategies of elephants are interesting from a theoretical viewpoint, as well as from the conservation/management perspective. As the largest of present-day terrestrial animals, elephants represent an extreme example of the large generalist herbivore. Much of the field work in foraging theory until fairly recently has focussed on small predators, and large herbivores have been neglected. An additional dimension in foraging behaviour is the interaction of the social and physical environments to produce compromises in foraging activity. Elephants have a structured and dynamic social organization (Douglas-Hamilton 1972, Moss 1981), which should provide an opportunity to examine social effects on, and consequences of foraging.

With a few exceptions (Belovsky 1978, Glander 1981), most research in foraging theory has been done with predators (Krebs et al. 1981), seed-eaters (Reichman 1981), or nectar-feeding specialists (Gass and Montgomerie 1981). Many of the findings in this area are currently too simple or artificial for application to wild populations of generalist herbivores, which may need to obtain a balance of nutrients or avoid toxic compounds in their choice of a diet (Freeland and Janzen 1974, Westoby 1974). Empirical results from field studies of large herbivores are clearly needed to improve existing models, or to replace them, if necessary, with a different approach.

A hierarchical approach may be the most reasonable way to

approach the study of foraging processes (Dawkins 1976, Gass and Montgomerie 1981, Johnson 1980). For example, a given animal species is distributed across its geographical range, a specific population of the species occupies a region of land, individual members of the population have home ranges, and within those home ranges, choose habitats in which to spend time. For a foraging herbivore, there are further levels of choice: what food type to select, which individual plant species, and what specific plant parts. These choices may be made on the basis of relative "profitability" -- rate of nutrient intake per unit cost -- of food items (Krebs 1978), and of the relative abundance and dispersion of profitable food items in different habitat patches, which may change seasonally in predictable or unpredictable ways.

Most of the models which have been developed in the theory of habitat "patch" selection (Charnov 1976, Levins 1968, Rosenzweig 1979), involve optimality criteria, and often deal with coexisting competitive species. The models developed are simplistic and ignore potentially critical complicating factors such as learning and sampling other habitats (Werner et al. 1981), the risk of predation, or social interactions (Myers et al. 1981). Fretwell and Lucas (1970) put forward a theory of habitat selection based on the "suitability" of habitat types. They defined "suitability" as the availability of resources such as food or mating opportunities in a given habitat, relative to the density of animals in that habitat and in the population. The theory predicts that habitats will be colonized in order of

suitability, with suitability declining as the animal density increases in each habitat in turn. The prediction that habitats are colonized in order of suitability with increasing population density was tested and supported for minnows by Fraser and Sise (1980). They suggested that food abundance might be the resource which defined habitat suitability for the minnows.

In this study, I will examine food availability as a major cue for elephant habitat selection. Elephants have a large absolute requirement for food, estimated at about six percent of their body weight per day (Laws et al. 1975), and are bulk feeders which need to process large quantities of food -- about 150 to 200 kg, fresh weight, per day (Guy 1975). They feed for large parts of the day -- some 50 to 75 % of the total day length (Guy 1976a, Wyatt and Eltringham 1974). I will ask two questions: which habitat patches (vegetation communities) are chosen, and why those particular ones? My proposed explanation is that relative food availability is of central importance in elephant habitat selection.

Social considerations could possibly affect the use of habitats by elephants. As Alexander (1974) noted, group membership generally confers an automatic cost of feeding or reproductive competition to individual members. For an individual, the benefits derived from joining a group -- for example, safety from predators, increased reproductive success, improved foraging ability -- must outweigh these costs. Rubenstein (1978) reviewed theories and empirical evidence of the costs and benefits of group living. In some of the examples

he discussed (largely dealing with birds), foraging success was improved by social grouping, and larger groups formed in periods of food scarcity or under certain types of resource patchiness. However, in large African ungulates, bigger social groups generally form when food resources are widespread and abundant (Leuthold 1977a).

It would appear that competition in feeding -- either interference competition and supplantation from localized food sources, or exploitation competition by neighbouring group members (Post 1981) -- could be an important factor in causing social groups to split up during food scarcity or patchiness. As well, when a group is feeding on clumped food items or in dense cover, it may be difficult for individuals to maintain contact with other group members, or to keep up with the group's movement. It is possible that in some large herbivores, feeding habitats are chosen so that social groups will not be forced to break up (Jarman and Jarman 1979). In this case, other benefits of group living, such as protection from predation, will be retained and the costs of feeding competition reduced.

Elephants have complex levels of social interaction between individuals and different degrees of social grouping, from small bachelor bull groups and matrilineal family units of females and juveniles, to large aggregations (Douglas-Hamilton 1972, Moss 1981). The tendency to group is seasonally dynamic: Leuthold (1976) found that group size in elephants was positively related to rainfall, as were their movement patterns (Leuthold and Sale 1973). I suggest that the tendency of elephants to form social

groups is important in modifying their habitat selection.

The differences in size, reproductive biology, and social organization between male and female elephants suggests that there could be differences in their respective use of habitats. Clutton-Brock et al. (in press) demonstrate that the survival and reproductive strategies of male and female red deer are markedly different and that this results in observable differences in foraging patterns. Differences between the habitat preference patterns shown by bachelor bull and female/juvenile herds of African buffalo were noted by Sinclair (1977). Because of the strong sexual dimorphism in body size and social organization seen in elephants, I expect that there should be similar differences in habitat selection by bull and family unit herds.

To summarize, the main questions that I ask in this study are:

1. What habitats are used by elephants? Which are selected and which avoided?
2. Are habitat choices related to the abundance of herb layer and/or woody layer food in those habitats?
3. Do elephant family units and larger aggregations shift habitat use to maintain large group size in the face of changing food abundance?
4. Are there differences in habitat use between bachelor males and the matrilineal family units?

My approach will be exploratory, but I will use general

hypotheses as a framework for my analyses.

This thesis is divided into sections which deal separately with the composition and dynamics of habitat types (Chapter 3), habitat use and selection by elephants (Chapter 4), and the dynamics of elephant social groups in relation to habitat use (Chapter 5). In Chapter 2, I will describe the study area and context, while in Chapter 6, I will summarize and the main points of the study and present my conclusions and speculations.

CHAPTER 2 THE STUDY AREA

A. Introduction

The study was conducted in Amboseli National Park and its environs in south-central Kenya, East Africa. The structure, seasonal dynamics, and long term changes of the Amboseli ecosystem have been summarized by Western (1975) and Western and van Praet (1973), and described in detail in Western (1973).

In this chapter, I will briefly describe the physical, climatic, and biotic characteristics of the study area, with special reference to the elephant population. I will conclude by defining the temporal and spatial scale of the current study.

B. Ecosystem Structure and Seasonal Dynamics

Western (1973) sets the spatial boundaries of the Amboseli ecosystem at the extremities of large herbivore (chiefly wildebeest) migrations. This area comprises an ecological unit of some 3000 sq. km., including the central Amboseli basin, which covers about 600 sq. km., and surrounding bushlands (see Figure 1). The name "Amboseli" is the Maasai word for "salty soil", which describes the saline lake bed of the basin. In this thesis, I will follow Western's practice of applying the name to the entire system. The ecosystem as defined lies between $2^{\circ}15'$ and 3° S. latitude and $36^{\circ}50'$ and $37^{\circ}45'$ E. longitude, and while the bulk of the area is found within Kenya,

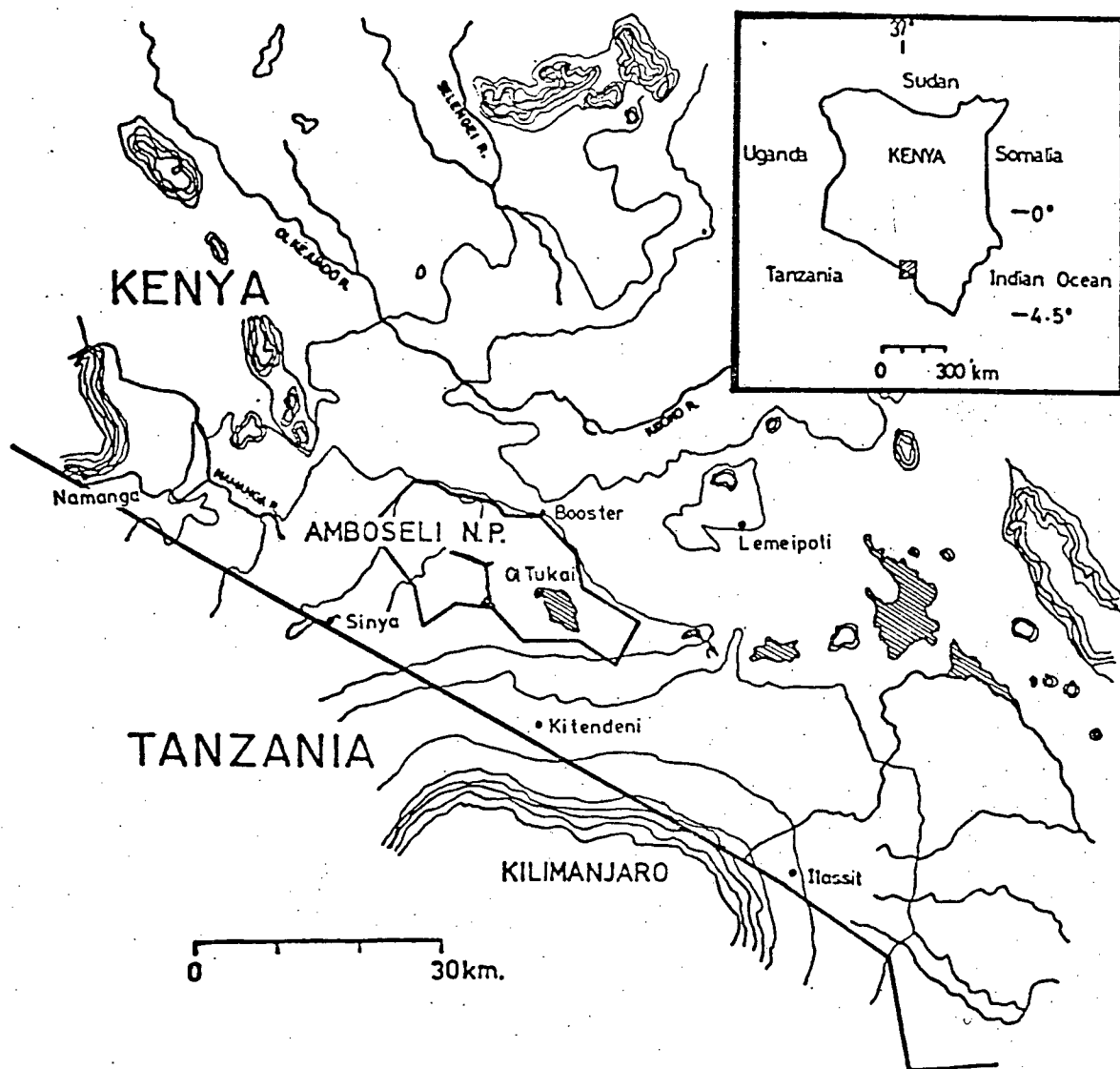


Figure 1. Amboseli National Park and the surrounding bushlands. The major seasonal rivers are noted, as are the locations of rainfall stations. Principal swamps are indicated by shading. Contour lines represent intervals of approximately 65m., and the elevation of Ol Tukai is roughly 1170 m.

the southern limits of the system reach up the slopes of Mt. Kilimanjaro, a few kilometres across the border in Tanzania.

1. Geology, soils, and hydrology

A variety of geological and hydrological processes have shaped the physical and chemical structure of the Amboseli landscape, producing a pattern of great diversity within a fairly small area (Western 1973).

Precambrian metamorphic rock underlies the entire area, and has remained exposed to physical and chemical weathering at the surface in the north and northwest. The soils which developed in these areas are reddish, well-drained laterites on the hills and ridges, and dark, sandy clays in the drainage lines.

The Kilimanjaro volcanics emerged in the late Pliocene and early Pleistocene, creating the mountain massif and ash falls and basaltic lava flows across the metamorphic surface. Volcanic-derived soils are either well-drained dark clays, often overlain with lava boulders, or finer drainage clays; both have a high mineral content.

The Kilimanjaro lava flows diverted and then blocked a large, ancient river system, which formed Lake Amboseli as a closed drainage basin, some 40 km. north of the mountain. The lake periodically dried and flooded until its final desiccation at the beginning of the Recent Epoch. Since that time, the former lake basin has been dry, except for a low western portion, the present "lake bed", that may hold shallow surface water during periods of high rainfall or high water table. The

basin has gradually accumulated sediments from both the volcanic and metamorphic systems, creating a complex pattern of alluvial and lacustrine soils. Saline and alkaline lake bed soils border the shallow alkaline soils of the central plains, and deeper alkaline soils, with salinity increasing towards the basin center, are transitional with the southern volcanics. Mildly alkaline dark soils have developed around permanent water sources.

Rivers in the region are seasonal; surface water flows only during and shortly after rainy periods, but subsurface flow may continue for considerably longer. A number of underground springs from the Kilimanjaro watershed emerge in the Amboseli basin and in isolated bushland areas to the east, and here water flows for short distances across the surface on a more or less continuous basis.

In rainy seasons, surface water is widespread, in drainage lines and sumps, rivers, and pools, but the Kilimanjaro springs are the only natural permanent water sources in the entire ecosystem. Borehole development in the 1940's has provided a number of permanent water sources for livestock in the bushland areas.

2. Climate

Rainfall is possibly the single most important climatic factor in this semi-arid region (Pratt and Gwynne 1977). Annual rainfall recorded in the Amboseli basin averages 350 mm. or less (Western 1975), although both the amount and timing of

rainfall can vary from year to year. This regime is typical of large areas of central East Africa; Amboseli is included in Ecological Zone V, Semi-Arid bushed grassland, by Pratt, Greenway, and Gwynne (1966) in their East African rangeland classification.

Most of the rain falls between November and May; in an "average" year there is usually a period of low rainfall in parts of January, February, and March. This "mid rains" or "short dry season" separates the "short rains" (November, December) from the "long rains" (March, April, May). In wetter years, such as 1977 to 1979, the short dry season may not appear, and the short rains, mid rains, and long rains merge into one long wet season. A long dry season occurs from May or June until October or November during which little or no rain falls.

East African rainfall patterns are highly variable, and different authors have suggested regimes of regularly cyclic (Phillipson 1975, Wood and Lovett 1974), or merely random (Pennycuick and Norton-Griffiths 1976) fluctuation. While the latter authors found that variance obscured all but annual, and possibly, 5-year cycles, in the rainfall of Serengeti (in northern Tanzania), they suggested there might be a more widespread tendency in East Africa towards cyclicity in specific localities. Anecdotal evidence suggests possible 5- and 10-year drought cycles in Amboseli, but records are too limited to allow firm conclusions.

Rainfall is also spatially variable. The slopes of

Kilimanjaro receive more rain than the lower elevations; the Amboseli basin and nearby bushlands are in the "rainshadow" of Kilimanjaro. As well, rainstorms are typically very localized and one area may receive over 70 mm. of rain in one day while an area less than a kilometre away receives none (pers. obs.).

3. Vegetation

A mosaic of vegetation communities has developed on the complex substrate of soil, hydrology, and rainfall patterns of Amboseli. I will describe the vegetation structure and dynamics in greater detail in Chapter 3, but will give a brief introduction here.

Western (1975) recognized seven broad vegetation types in Amboseli: lake bed and alkaline plains grasslands, sparse and dense woodlands, swamp, and sparse and dense bushlands. "Sparse" and "dense" are relative terms: "sparse" vegetation types have a woody cover of 1 - 2% or less, while "dense" types generally run from 5 - 20% woody cover. The grasslands, woodlands, and swamps are largely restricted to the Amboseli basin, while bushland types occur on the surrounding ridges and slopes.

Because of the high alkalinity and/or salinity of its soils, the flora of the Amboseli basin is fairly simple. Grasses tend to be salt-tolerant perennials, while the few woody species are largely evergreen shrubs or Acacia trees. The bushlands, by contrast, have greater variety in both herbaceous

and woody vegetation (Western 1975).

The bushland pastures are generally of higher nutritional quality and similar biomass when compared with most of the salt-tolerant basin swards, and may respond more quickly to the onset of rainfall (Western 1975). My casual observations suggested that woody plants respond to seasonal rainfall in a manner similar to herb layer species, but with productivity and green leaf retention extended longer into the dry periods due to deeper root systems. Swamp edge vegetation is in leaf and productive for most of the year (Pellew 1980, pers. obs.).

4. Fauna

The large mammal community of Amboseli is abundant and diverse: hippopotamus, rhinoceros (now becoming rare), elephant, 16 species of wild ungulates, four large predators, and several species of primates. Two migrant ungulate species, wildebeest and zebra, dominate the wildlife community in both numbers (the populations of both species include approximately 4000 animals) and biomass (Western 1975).

Domestic livestock -- cattle, sheep, goats, and donkeys -- of the indigenous pastoralists, the Maasai, constitute a major proportion of the large mammal biomass; as much as 75% in recent times. The people and their livestock have long been an important component of the ecosystem, in evident coexistence with the wild fauna for thousands of years (Western 1973).

Western (1975) has categorized the large herbivores as

either dependent or independent of surface drinking water. The most common water-dependent herbivores -- wildebeest, zebra, and Thomson's gazelle -- concentrate in the basin in the dry season and migrate outwards to bushland areas with the rains. Western hypothesized that this expansion/concentration ranging pattern allows the migrants to make use of higher quality bushland grasses when surface water is widespread, and to return to the poorer pastures near permanent water in the dry seasons. The Maasai livestock follow a similar seasonal movement pattern, although their dry-season range has been somewhat extended into the bushlands by water development. Other water-dependent species -- impala and waterbuck for example -- rarely leave the vicinity of the swamps, while water-independent herbivores such as eland and oryx are found in low densities throughout the ecosystem at all times of year.

5. The elephants

The Amboseli elephant population size has been estimated at 580 animals (Poole and Moss 1981), and the majority of individuals have been identified and monitored since 1974 (Moss 1980). The population has been fairly stable for at least the last 12 years, with a recent birth pulse under favourable habitat conditions. The elephants' seasonal movements are similar to those of the other water-dependent migratory species. They are generally seen in the dense bushlands, woodlands, and swamps, and in the latter most commonly (Western 1975).

The only predator which seriously threatens African elephants is man, and in Amboseli this threat is not severe at present (see below). When compared with other populations, the Amboseli elephants can be considered fairly "natural" and undisturbed.

C. Long Term Changes

Western and van Praet (1973) discuss long term habitat changes in Amboseli. They described a dramatic decline in the Acacia xanthophloea, or fever tree, woodlands from 1950. Over 90% of the trees had disappeared within 17 years, a process which is continuing at the present day. Initially blamed on Maasai livestock overgrazing and/or elephant damage, the woodland decline was correlated to a rise in the water table and the release of soluble salts to the trees' sensitive root systems. Soil salt content was positively associated with tree death and with the spread of a salt-tolerant bush, Suaeda monoica. Elephant damage has merely accelerated the woodland die-off. The fever tree decline has meant a loss of habitat for woodland-dependent animal species such as monkeys, certain antelopes, and leopard.

This kind of habitat change is not unique historically. Early reports by European explorers described a high water table with extensive swamps, few trees, and widespread S. monoica in the Amboseli basin in the late 1800's (Thomson 1887, von Hohnel 1894). By the 1930's, dense young fever tree stands were found

in the Amboseli basin (Johnson 1935), and healthy mature stands were widespread in the 1960's when the recent decline was first noticed. Western and van Praet (1973) suggested that the water table fluctuations and the retreat and expansion of the fever tree woodlands could be periodic in nature, a consequence of possible long term rainfall cycles.

The Amboseli elephant population may have been affected by the long term habitat changes. The early explorers made no mention of elephants in the Amboseli area. They recorded most of the other large game species now seen in Amboseli, and noted elephants in other localities, so it seems likely that elephants were less conspicuous residents of the Amboseli basin in the late 1800's. Stigand (1909) stated that elephants could be found on the slopes of Kilimanjaro and in the marshes of the Amboseli basin in the early 1900's, while some years later, Percival (1924) talked of elephants migrating from the basin swamps to northern bushland areas. Elephants were seen in Amboseli basin swamps and woodlands by Johnson (1935) and in the northern bushlands near the Selengai River by de Watteville (1935), concurrent with the spread of fever trees in the basin.

The verbal history of the Amboseli Maasai tells a similar story (Western 1973). They say that fever tree woodlands were limited and elephants rare in the basin at the turn of the century, but that both have increased since that time. However, it is unclear whether the apparent correlation between the extent of fever tree woodlands and elephant numbers in the Amboseli basin is causally connected or merely coincidental (see

Spinage's comments below).

If Western and van Praet's (1973) hypothesis of periodic habitat and faunal changes linked to long term climatic cycles is correct, then the structure of the Amboseli ecosystem could be continually changing rather than stationary at a stable equilibrium. In this case, change should be considered a "normal" feature of the area, instead of an unusual perturbation.

D. Human Influences

Human influences on the Amboseli system have come from two sources: the indigenous Maasai herdsman, and Arab and European colonists and visitors.

As noted previously, the Maasai and their predecessors have long been an integral part of ecosystem dynamics. Since they hunt wildlife exclusively for sport or self-defense, except during severe droughts, their direct impact on the wild herbivore populations has been fairly limited. The aggressive nature and military skills of the Maasai have kept other tribal groups from the area, and their own numbers had, until recently, been limited by disease, drought, and practical considerations of domestic livestock husbandry. Conditions were such that the biomasses of wildlife and livestock were roughly equal. However, water development, medical services, and famine relief have allowed both human and livestock populations to increase sharply since the 1940's. The wild herbivore populations have

not yet suffered, but competition between livestock and wildlife for forage could now become critical during severe drought periods when the habitats of the Amboseli basin are the last food source for both groups.

Wildlife management authorities have attempted to reduce this conflict by separating the dry season ranges of wild and domestic stock. A small livestock-free zone in the central Amboseli basin formed the nucleus of a larger game reserve in the area from 1947. In 1977, a project to provide financial compensation, more water, and alternate grazing for livestock was completed, and the Maasai agreed to remain outside a 400 sq. km. area of the basin gazetted as Amboseli National Park (Western 1977).

European man has affected the ecosystem indirectly through the impacts of development on the Maasai lifestyle as noted above, and more directly through hunting and tourism.

Hunting pressure on elephants was reportedly intense in the mid to late 1800's and populations may have been drastically reduced over huge areas of East Africa in an extensive Arab ivory trade, which was accelerated, then curtailed, by the arrival of British (Spinage 1973). Spinage suggested that widely reported increases of elephant populations since the turn of the century could be a result of the collapse of the ivory trade and the release of elephant populations from the heavy hunting mortality. The Amboseli elephants may have been affected in this way. More recently, government controlled hunting blocks in the northern seasonal range removed small

numbers of elephants and other Amboseli wildlife, but this source of mortality probably had a limited impact on the animal populations. Hunting of elephants was banned in Kenya in 1973, and of all wildlife in 1977. Elephant poaching in Amboseli occurred for a short period from 1974 to 1976, reducing the population slightly. This activity has now been virtually eliminated, through effective anti-poaching enforcement and cooperation with the local Maasai.

The impact of large numbers of tourists -- more than 80,000 annually -- on the ecosystem has been surprisingly small (Western 1977). The major effect has been to create a large economic incentive for wildlife conservation, especially since the Maasai began to receive benefits directly (Western and Henry 1979).

E. Context of the Study

My study took place during 1978 and 1979, a period of high rainfall following a drought in 1976. In my analysis, I make use of longer term habitat and elephant data collected by Western from 1975 through 1980; I helped in this data collection during my stay in Amboseli. Because the Amboseli basin is the focus of the elephant population's ranging activity, and for logistical reasons, I concentrated my research efforts on this relatively small area.

CHAPTER 3 HABITAT STRUCTURE AND DYNAMICS

A. Introduction

In this chapter, I will describe the habitat types of Amboseli, their composition and seasonal dynamics. An animal species' "habitat" was defined by Fretwell and Lucas (1970, p. 17) as "any portion of the surface of the earth where the species is able to colonize and live". They further defined habitats as areas which are "essentially homogeneous with respect to the physical and biological features which we believe to be most relevant to the behavior and survival of the species". Sinclair (1977, p. 53) defined habitats for African buffaloes as vegetation types which provide for the basic needs of the animals -- needs such as food, water, protection from climatic extremes, and protection from predation. I will use the term "habitat type" synonymously with "vegetation community" in all discussion that follows, for although elephants rarely colonize and live within a single plant community, a distinct vegetation community could be considered internally "homogeneous" in terms of such biological features as food type abundance, composition, and quality, relative to other communities. Western's (1973) studies and my own initial casual observations suggested that the plant communities of Amboseli differ considerably in their structure, biomass standing crop, and seasonal dynamics.

In my study of elephant habitat selection as a level of foraging choice, I want to examine the abundance of plant

material in each habitat which is available as potential food for the elephants. I assumed that all herb layer plants, mainly grasses and forbs, were available, while the availability of woody browse required a more specific definition. From the results of other workers (Guy 1976a, Laws et al. 1975, Wing and Buss 1970) and my own observations, it appeared that elephant browsing of woody plants is concentrated on leading twigs and their leaves. Croze (1974b) estimated the maximum feeding height for elephants on woody vegetation to be 6 m. I therefore considered the twig-plus-leaf biomass of all woody species below that height to be potentially available as elephant food. Bark is another major food type found on woody plants, but, for practical reasons, I did not attempt to estimate bark biomass in the present study. Elephants also eat the fruits and flowers of shrubs and trees (pers. obs.), but these are relatively scarce and ephemeral, and I did not attempt to monitor their abundance.

The seasonality of food availability is an important aspect of the foraging options faced by elephants. Rainfall is a critically important climatic factor affecting vegetation productivity and biomass in semi-arid regions (Phillipson 1975, Whittaker 1970), such as Amboseli. Direct quantitative relationships between rainfall and grass production were noted in Serengeti, Tanzania, by Sinclair (1977). I would therefore expect to find that the primary production of herb layer vegetation in Amboseli during a time period is closely related to the rain falling during or immediately preceding that period. Other factors that could modify the relationship between

rainfall and herb layer productivity are the site conditions -- species composition and abundance of the vegetation, physical and chemical soil characteristics -- , past history, and the effect of disturbances such as fire and herbivory.

I compare how the different plant communities with different local soil, hydrological, and floral conditions respond to the same seasonal rainfall regime. Western's long term habitat data will be analysed to compare the results from my study period to those of periods with different rainfall patterns, to get a longer term perspective on habitat dynamics. I did not attempt to examine the effects of disturbance on the vegetation. Fire did not affect any of the areas I was concerned with during the course of my study, and while I did make note of herbivore consumption on a rough presence/absence scale, I did not approach this question quantitatively.

My discussion of habitats includes the composition and abundance (standing dry mass) of the herb and woody (shrub and tree) layers of the defined communities. I also discuss the dynamics of some herb layer characteristics -- the standing crop biomass of green (photosynthetic) plant material and all plant material (green plus structural) -- through the seasons and between years. Shrub and tree phenology and productivity are more complex and were considered beyond the scope of this study. The density and biomass of all but the most prolific woody plants were taken as constant during the one-year period of my field work. Woody plant density and biomass were not monitored in other periods.

The hypotheses I use as a framework for describing Amboseli vegetation dynamics are:

H1: The standing crop biomass of both the herbaceous and woody layers differs between habitat types in Amboseli.

H2a: The production of herb layer biomass in the different habitats is positively related to the amount of rainfall received.

H2b: This relationship will differ between habitat types, and between different climatic periods.

B. Methods

The task of vegetation sampling can be overwhelming, and even with techniques currently available, is often tedious and time-consuming. As with any system of sampling, a compromise between time and energy expended and the level of accuracy and precision required must be achieved. For the purposes of comparison between habitats in the current study, and within logistical limitations, I used a fairly broad level of approximation. In general, a standard error of 10 % of the mean was considered acceptable for most of the vegetation measurements taken.

1. Rainfall records

Rainfall has been recorded with a Kenya Meteorological Department raingauge near the Park headquarters at Ol Tukai in the center of Amboseli basin on a continuous daily basis since 1974. Various other gauges distributed around the area have operated sporadically and less reliably for varying periods. I attempted to verify the operation of a number of these during 1978 and 1979, for an examination of the spatial variability in rainfall patterns.

For the purposes of site comparison and herb layer dynamics, I consider a "rainfall year" to begin in October/November with the onset of the short rains after the long dry season.

2. Definition and mapping of habitat types

In his comprehensive study of the Amboseli ecosystem and its grazing herbivores, Western (1973) defined 28 unique vegetation types based on an analysis of floristic abundance. Basing my classification on the dominant species of the woody canopy and herb layers, and on physical characteristics, such as the presence of surface water, I took Western's original 28 plant communities and grouped them into 14 habitat types. In general, I lumped together a number of vegetation types which Western considered separate on the basis of more subtle differences in herb layer species composition. I recognize the subjective nature of this method of community definition

(Whittaker 1970), but I feel that the sharp boundaries between different geological and hydrological conditions which occur in the Amboseli basin and its environs are reflected in differences in the floral composition of those areas. An additional check on my community definitions was provided by Lee (1981). In a cluster analysis of woody species composition in Amboseli woodlands, she found associations of plant species which were very similar to my more subjective definitions of habitat types.

Western (1973) had mapped the vegetation of central Amboseli at a scale of 1:50,000, using an aerial photomosaic, and adjusting community boundaries on the ground by "successive approximation" (Poore 1962). I used the same technique to update Western's map. Because of habitat changes due to water table fluctuations -- alterations of swamp courses and the boundaries of swamp edge habitats, and the shrinking of the fever tree woodlands -- and herbivore consumption of woody plants, some of the previously defined communities had disappeared, changed, or had shifted their distributions by the time of my study. I incorporated these changes in the vegetation map used for the present study.

3. Habitat description and monitoring: Herb layer

I located permanent vegetation plots in each habitat type (except the young fever tree swamp edge woodlands -- see below) by driving to subjectively defined "representative areas" of each habitat type, tossing a marker, and then locating the plot center at a point a random distance and direction from the

marker. Western had established 13 such plots in 1976; I retained 12 of these, and added 16 more for the period of my study in 1978/79, giving me a total of 28 plots. Since the herb layer of the young fever tree woodlands was essentially the same as the swamp edge grasslands (Seg), and since the two habitat types were generally closely associated in locality, I used herb layer data from the latter to describe the young fever tree habitat type. The number and location of plots in habitat types were selected as a compromise between the extensive coverage of large areas under limitations of time and travel costs, and the accurate reflection of the structure and changes of the habitat types. The distribution of plots in habitat types can be found in Table 2 (see below).

The herb layer species composition, relative abundance and diversity were estimated at each permanent plot by a slanting pin frame method (McNaughton 1979a, D. Western pers. comm.). These attributes were determined at the time of high green biomass, in January 1979. A frame with five slanting pins was placed at sixteen regularly spaced locations around the center of each plot, giving a total of 80 pins per plot. The number of "hits" per species -- points where plants were intercepted by a slanting pin -- was recorded for each pin at a given frame location. A regression derived from clipped quadrats related hits-per-pin to dry biomass in g/m^2 (see Appendix 1). The relative abundance of a plant species was calculated as the proportion of total biomass that was estimated for each individual species. Diversity of the herb layer was estimated

by the Shannon-Weaver index (Pielou 1966). Plant species were identified with a reference collection of Amboseli flora which I updated and maintained. The original plant identifications were made by the staff of the Herbarium of the Kenya Agricultural and Forestry Research Organization in Nairobi.

Herb layer biomass was estimated, for monitoring purposes, by a different method. At each permanent plot location, a circular area 20 m. in diameter was sampled according to a method devised by D. Western (pers. comm.). Measurements were made of leaf height and percent ground cover -- the latter estimated with a 10-pin vertical frame as percent of the pins intercepting a plant. Sixty paired measurements were made per plot at regularly spaced intervals along radii from the plot center. This generally gave mean values of height and cover with acceptable standard errors. A calibration regression based on clipped quadrats related the product of height and cover to total dry biomass in g/m^2 (see Appendix 1). This method of biomass estimation gave similar results to the slanting pin method described above, but was quicker and more precise. The S. consimilis grasslands were monitored on only three occasions at widely spaced intervals -- both green and total biomass changed very little during the course of my study.

The biomass of green herb layer vegetation was estimated with a hand-held spectrophotometer; the theoretical background and practical use of this machine are described elsewhere (McNaughton 1979a, Pearson et al. 1976). Basically, the machine measures light reflected by photosynthetic pigments at

two wavelengths, and the ratio of these two measures is linked through a calibration regression to the dry mass, in g/m^2 , of green vegetation present (see Appendix 1). Although some reservations have been expressed concerning the repeatability of measurements under varying light, shade, soil, and plant conditions (F. Bunnell, pers. comm.), my results appeared consistent between similar plots on the same day and within the same plot at subsequent measurement. Ten measurements were made per plot; this generally gave an acceptably low standard error. I did not attempt to monitor green mass in the wet swamps, because the meter was vulnerable to water damage; when necessary for some analyses (see Chapters 4 and 5), I made crude estimates of the green mass.

Visual estimates of the percent of plant matter removed by grazing herbivores were also made at each plot by separate observers. Inter-observer agreement was high, and generally a single observer's estimate was recorded.

I measured total and green herb layer biomass, and estimated consumption at the permanent plots at intervals of roughly 4 - 6 weeks; sampling intensity was increased during periods of more rapid change in the rainy seasons.

Western's original 12 plots have been monitored from April 1976 up to the present, while the plots I established during my study were monitored from November 1978 to October 1979.

In addition to biomass dynamics of the herb layer, I am also interested in the dynamics of forage quality. I did not collect data on herb layer nutrient contents during my field

work, but D. Western (pers. comm.) has provided the results from proximate analyses of herb layer samples from his 12 plots during 1977. I will present and evaluate a summary of these data.

4. Habitat description: Woody vegetation

Techniques for the estimation of the biomass standing crop of woody vegetation are still at an early stage of development (Rutherford 1979). Most current techniques operate in two stages: an estimate of plant density is coupled with estimates of the dry mass of individual plants based on dimension/weight equations (Stanek and State 1978, Whittaker and Marks 1975). I used this two-stage method, at a fairly crude level of approximation.

For the estimation of plant density, I used a modified Bitterlich stick or "occlusion quadrat". The technique was described by Cooper (1957, 1963). The method involves sighting along a calibrated stick with a crossbar as it is swung horizontally through 360° around the observer, and recording all individuals of each species with canopy diameters that appear wider than the crossbar. A "cover percentage factor" based on gauge geometry gives the percent ground cover for each species considered.

I extended a modification of this technique (Cooper 1963) to allow estimation of plant density in stems per hectare. I measured a large number (generally about thirty-four) of individual plants, chosen at random, of each of 36 of the more

common woody species in Amboseli. Canopy diameter, height, and depth were measured for each individual. Species mean values generally had an acceptably low standard error, since stands of many species appeared to be fairly even-aged. For species with wider variance in size, I subdivided the species into two or more broad size classes and made additional measurements for each class. Using mean values of canopy diameter, I calculated the circular ground area covered by the "mean individual" of each species (or species size class) and from this, a "computation factor" relating gauge count to plant density in numbers/hectare (see Appendix 3). Cooper (1963) cautioned on the use of this modified technique; error can enter into the method when small differences in canopy measurement result in proportionally larger changes in density estimates, especially with the smaller shrubs.

For the second stage of biomass estimation, I used regression analysis of woody dry mass on plant dimensions to estimate the biomass of individual plants. Since I was interested in the woody plant material available as elephant food, I derived a regression for twig-plus-leaf dry mass on measurable plant dimensions.

Taking the dimension figures (canopy diameter and height) I had collected for each shrub and tree species, I located approximately "mean individuals" of 22 species, and then measured, harvested, dried, and weighed them. The harvesting of the few deciduous woody species in Amboseli was done at maximum leaf flush, generally in the rainy seasons, while evergreen

plants were taken during other times of year as well.

All plant samples were separated into flowers and fruit, leaf, leaf-bearing twig, and woody stem (branches and mainstem) fractions which were then oven-dried and weighed.

With small shrubs, the entire plant was collected, while for larger plants subsampling approximations were used. In the latter case, two observers, myself and an assistant, estimated the proportion of canopy occupied by a selected large branch. This branch was collected, and, since observer agreement was good, was weighed as a fractional sample of the whole plant.

The dimension and dry mass values for the 22 species sampled (see Appendix 2) were subjected to regression analysis (Whittaker and Marks 1975), and the resulting best-fit equations were applied to all the woody species of known mean dimensions. Canopy diameter gave the best estimate of twig/leaf dry mass in the multi-species regressions (see Appendix 1). The twig/leaf biomass of the mean individual of each species or size class within a species was then estimated for the measured mean individual of each of the 36 species and the size classes within species. (see Appendix 3). Values for twig/leaf biomass density, in kg/ha, were calculated by multiplying plant density by dry mass values of each species in the community.

Woody plant percent cover, numerical density, and biomass density were estimated at each of the permanent plot locations at the same time as the herb layer species composition sampling. In addition, a number of extra "temporary plots" were added on a random basis in some of the habitat types (including the young

fever tree woodlands) of the Amboseli basin for the purpose of woody plant measurement.

I did not attempt to record seasonal changes in woody biomass for most habitat types because my extensive approach and the approximations employed would not pick up any but the grossest changes in woody dry mass. Since I did not notice any marked changes in woody plant densities, through casual observations, in the year of my field work, I felt this approach was justified. Most of the woody species in the Amboseli basin are evergreen, so that twig/leaf mass was probably fairly constant through the seasons, for basin habitats, at least. In the swamp edge community, shrub growth was dramatic and density changes were recorded at intervals, but for all other habitats, woody biomass was taken as constant for the period of the study. This is undoubtedly an oversimplification, and further work on woody plant phenology in these semi-arid areas is clearly needed.

Shannon-Weaver diversity was calculated for woody species on the basis of available biomass contribution (ie., twig plus leaf, below 6 m.).

I calculated mean values of herb and woody layer characteristics at the vegetation plots for each habitat type, and used the mean values in all subsequent analyses.

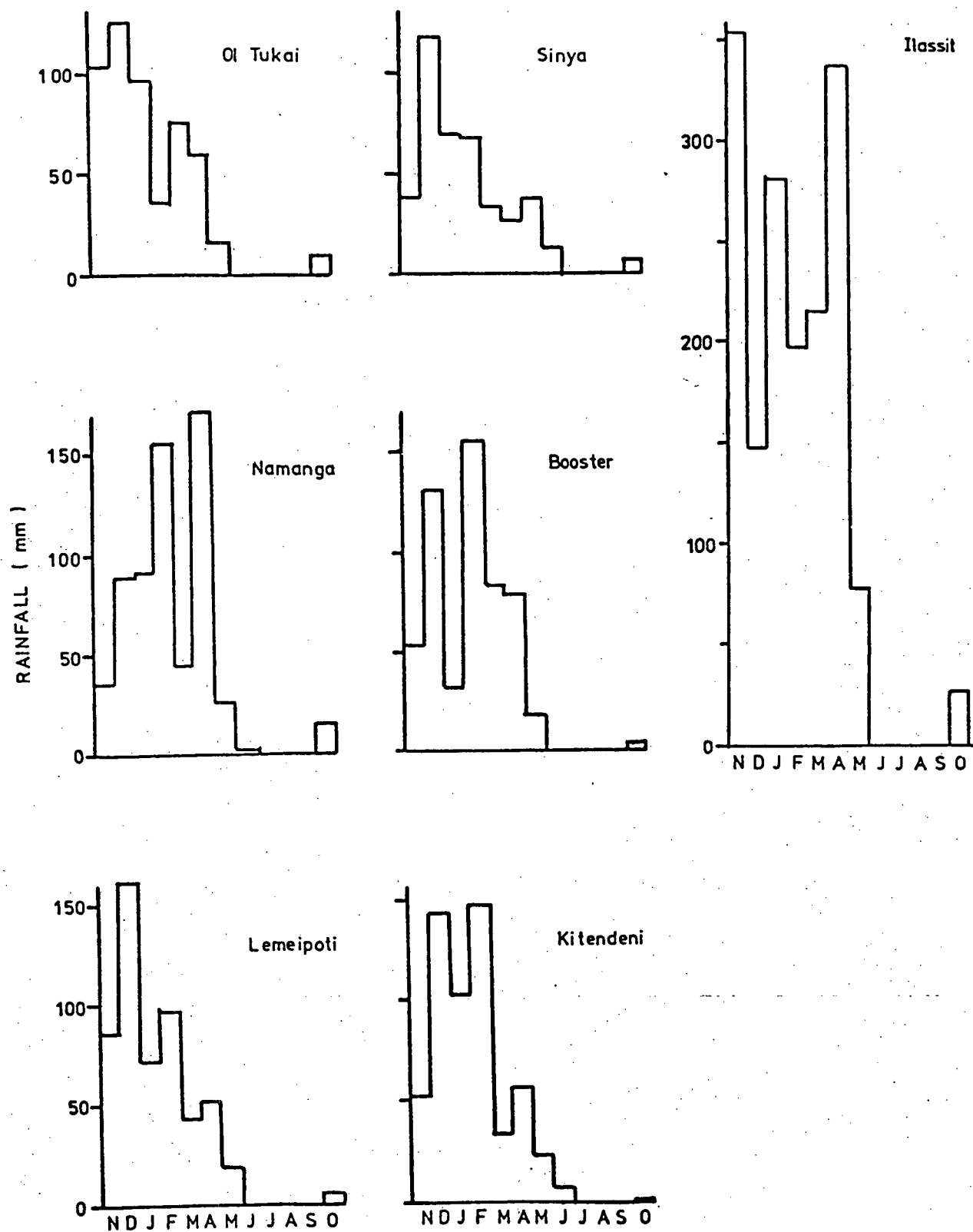
C. Results

1. Rainfall patterns

Rainfall is variable in Amboseli in both space and time. Figure 2 shows monthly rainfall recorded at sites around Amboseli from November 1978 to October 1979, the '78/'79 "rainfall year". The general seasonal pattern was similar for the various localities: rainfall began in late October or early November and continued until May or June with weak nodal peaks in December/January and April/May and a long dry period from June to September. However, Table 1 shows that correlations between monthly rainfall at Ol Tukai and at other sites ranged from good (at Lemeipoti, $r=.854$, $p<.01$, $n=12$) to fair (at Namanga, $r=.509$, n.s., $n=12$). The degree of correlation varied in a manner not simply related to the distance of sites from Ol Tukai ($r_s=-.029$, n.s., $n=6$, Spearman's rank correlation (Siegel 1956)). When I compared daily rainfall records for 1978/79 from Ol Tukai and nearby Sinya Mine, the correlation was low ($r=.457$, $p<.01$, but $n=365$), indicating that short-term (ie., daily) rainfall patterns can be quite different over fairly small distances, while over a longer time interval, such as a month, the differences can tend to even out.

Rainfall patterns also vary markedly through time, as revealed by analysis of longer term rainfall data from Ol Tukai. Annual rainfall at Ol Tukai for the last seven years fell into three periods (see Figure 3). A fairly dry period from 1974 to 1977 with an mean of about 230 mm. total annual rainfall

Figure 2. Monthly rainfall patterns in 1978/79 at Ol Tukai and six other stations in the surrounding bushland (locations given in Figure 1). Note the variability in rainfall pattern between the different localities.



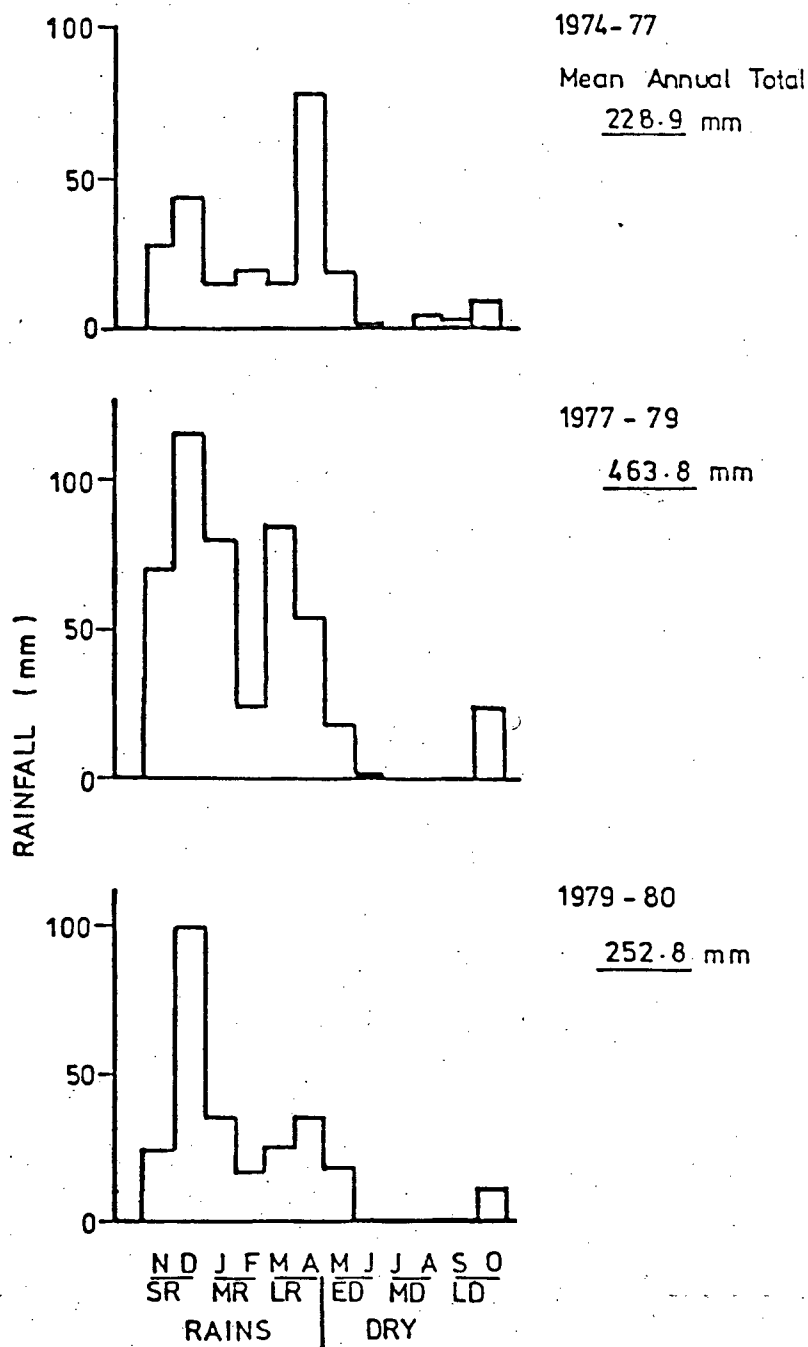


Figure 3. Mean monthly rainfall at Ol Tukai in three periods: Dry1- Nov. 1974 to Oct. 1977, Wet- Nov. 1977 to Oct. 1979, and Dry2- Nov. 1979 to Oct. 1980. Note the differences in the amount and temporal patterning of rainfall between periods. In the Wet period, mean annual rainfall was much higher, and almost unimodal, when compared with the lower, bimodal pattern of the two Dry periods. Seasons are defined as: SR- short rains, MR- mid rains, LR- long rains, ED- early dry, MD- mid dry, LD- late dry.

Table 1. Rainfall at various stations around Amboseli from October 1978 to October 1979.

Rainfall Station	Total Annual Rainfall(mm)	Correlation with Ol Tukai(r)	Distance from Ol Tukai(km)
Ol Tukai	551.0	1.000	0
Sinya Mine	405.1	0.757 **	27
Namanga	630.1	0.509 n.s.	55
Booster Pump	595.9	0.601 *	10
Lemeipoti	572.6	0.854 **	28
Kitendeni BH	565.7	0.659 *	15
Ilassit	1640.8	0.747 **	50

Significance levels of Correlation with Ol Tukai (r):

* $p < 0.05$

** $p < 0.01$

Spearman's rank correlation of r

with Distance from Ol Tukai: $r_s = -0.029$, n.s., $n=6$

included a drought which culminated in October 1976. The following two years (which included my study period during 1978/79) were much wetter by comparison, with an annual mean total of 465 mm., while more recently in 1979/80, a dry year (255 mm. total) was recorded. The distinctly bimodal pattern -- short rains, short dry season, long rains -- of the earlier dry period was replaced by a more clustered, almost unimodal pattern in the wet years, and the bimodal pattern had not completely returned by the more recent dry period. This was, in effect, a natural experiment in soil water availability for plant growth. The low rainfall pattern is apparently more "typical" of Amboseli climate -- it has a short recurrence interval (Western 1973).

2. Habitat types defined, mapped, and described

The habitat types I defined for this study are listed in Table 2 with the approximate area of the Amboseli ecosystem

Table 2. Amboseli habitat types: Approximate areas in the Amboseli ecosystem, and the number of fixed vegetation plots in each.

Habitat Type	Area(km ²)	Number of plots
GRASSLAND		
Alkaline grassland	130	3
Lake bed grassland	120	2
<u>S. consimilis</u> grassland	31	1
WOODLAND		
<u>A. tortilis</u> woodland	43	3
Fever tree woodland	43	1
<u>Salvadora/Suaeda</u> shrubland	33	2
Palm/Fever tree woodland	5	1
Young Fever tree woodland	4	-
SWAMP		
Swamp edge grassland	10	6
Permanent swamp	15	1
BUSHLAND		
Bushed grassland	725	1
Open bushland North	1000	1
Open bushland South	700	1
Dense bushland North	100	1
Dense bushland South	120	2
<u>A. drepanolobium</u> bushland	20	2

covered by each. The distribution of the habitat types of Amboseli can be seen in the vegetation map, Figure 4, which focuses on the Amboseli basin. The spatial complexity of habitat distribution reflects the mosaic nature of soil and hydrological conditions in the Amboseli environment. A

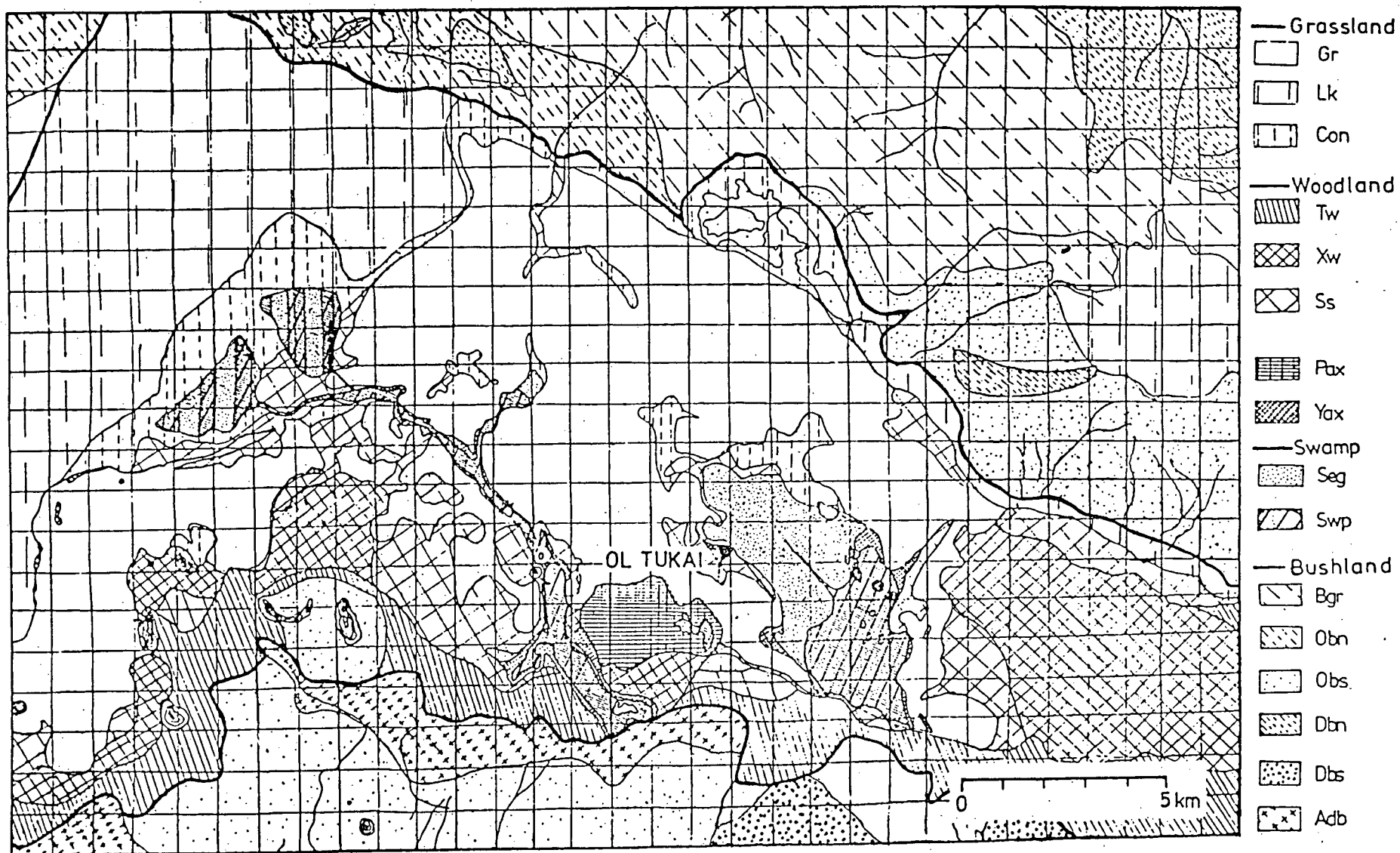
Figure 4. Map of the habitat types of the Amboseli basin and nearby bushland areas. The margin of the basin is indicated by the solid dark line. The abbreviations used for habitat types are defined as in the text, and will be used throughout the thesis:

Basin habitats

Gr	Alkaline grassland
Lk	Lake bed grassland
Con	<u>S. consimilis</u> grassland
Tw	<u>A. tortilis</u> woodland
Xw	Fever tree woodland
Ss	<u>Salvadora</u> / <u>Suaeda</u> shrubland
Pax	Palm/Fever tree swamp edge woodland
Yax	Young fever tree swamp edge woodland
Seg	Swamp edge grassland
Swp	Permanent wet swamp

Bushland habitats

Bgr	Bushed grassland
Obn	Open bushland, North
Obs	Open bushland, South
Dbn	Dense bushland, North
Dbs	Dense bushland, South
Adb	<u>A. drepanolobium</u> bushland



consequence of this complexity is that a great variety of habitat conditions can be encountered within fairly short distances, especially in the vicinity of the basin. A brief description of each habitat type follows.

Grassland habitat types

Alkaline grassland, Gr

With virtually no woody cover, these grasslands are dominated by perennial Sporobolus spp. grasses and include a few seasonally ephemeral forbs on the shallow alkaline soils of the central Amboseli basin.

Lake bed grasslands, Lk

This vegetation type occupies the present lake bed of the Amboseli basin, parts of which are seasonally inundated with rain water. At different sites on the lakebed, one finds a single salt-tolerant grass species, (Psilolemma jaegeri), a dense, mixed species grass community, or a surface barren of vegetation, depending on local soil chemistry and water regime.

Sporobolus consimilis grassland, Con

Generally found in dense, single species stands of the tall (1 to 2 m.), coarse grass, Sporobolus consimilis, this habitat type is located in fairly small, scattered sites of poor drainage on clay soils at grassland/swamp, grassland/lake bed, or grassland/woodland transition zones.

Woodland habitat types

Acacia tortilis woodlands, Tw

This vegetation type occurs along the southern edge of the Amboseli basin on transitional volcanic/lacustrine soils. The woody layer is dominated by mature Acacia tortilis, the "umbrella tree", with a variety of woody shrubs and herbs, mostly evergreen, in the understory. A. tortilis canopy cover is variable, but averages around 4 - 5 percent. The palatable and productive grass, Cynodon plectostachyus, dominates the herb layer, which also includes Sporobolus spp. and a number of annual grasses and forbs, which are found directly under the shade canopy of the umbrella trees.

Acacia xanthophloea woodlands, Xw

Much reduced in extent (as I described in Chapter 2), the remaining Acacia xanthophloea, or fever tree, woodlands survive on the deeper alkaline soils of the eastern Amboseli basin and in isolated patches near water in the central and western basin. Although similar in many ways to the A. tortilis woodlands, the fever tree woodlands have fewer herb and shrub species, a Sporobolus-dominated herb layer, and a tree layer composed exclusively of A. xanthophloea in varying states of size and health, which averages a canopy cover of about 2 percent. The salt bush, Suaeda monoica, now occurs as a major understory species over much of this habitat type.

Salvadora/Suaeda shrublands, Ss

These shrublands represent areas of the central and western Amboseli basin formerly occupied by A. xanthophloea woodland, but now devoid of all but the occasional seedling fever trees, and currently dominated by the shrubs, Salvadora persica and Suaeda monoica. The herb layer is similar to that of the A. xanthophloea woodlands, although species composition and biomass may have changed somewhat since the disappearance of the canopy trees.

Date palm/fever tree swamp edge woodlands, Pax

Occurring in a small, isolated area around a cluster of swamp sources in the central Amboseli basin, this habitat type has a woody layer composed of low-growing Phoenix reclinata, or date palms, and fever trees. Canopy cover, including date palms and fever trees, averages about 20 percent. The growth of large woody herbs -- especially Abutilon mauritianum -- has been prolific in recent years, while the grass/herb layer is typical of swamp edges (see below).

Young Acacia xanthophloea swamp edge woodlands, Yax

This type occurs in scattered patches along the margins of swamps in the Amboseli basin. It is basically swamp edge grassland (see below), with a fairly dense (about 15 percent) cover of young and maturing fever trees, which flourish in these areas of low soil salinity and year-round ground water supply. The palm/fever tree woodlands and the young fever tree woodlands

could be considered as both woodland and swamp edge habitat types.

Swamp and swamp edge habitat types

Swamp edge grassland, Seg

Swamp edge grasslands occur along the edge of permanent swamps in the Amboseli basin, where water flows below the soil surface for much of the year. The herb layer is dominated by a dense layer of Cynodon dactylon, or Bermuda grass, with a few creeping herbs found at ground level. Woody herbs and shrubs develop localized thickets in areas of high soil moisture, especially in the large Olokinya swamp in the east-central basin.

Permanent swamp, Swp

In the areas of spring sources where water flows over the soil surface in pools or channels, tall coarse sedges, such as Cyperus immensus and C. papyrus, and succulent creeping herbs have developed in dense mats of floating vegetation. The distribution and extent of this habitat type is somewhat variable, depending on the output of spring water and the direction and volume of water flow as affected by Park managers.

Bushland habitat types

Bushed grassland, Bgr

Extensive areas of the lateritic ridges north of the basin are covered by seasonally arid bushed grassland. It is sparsely wooded (less than 1 percent cover) with Balanites spp. and Acacia mellifera , or wait-a-bit thorn, shrubs. The low, but productive, herb layer is a mixture of Sporobolus spp. and other annual grasses, and a number of annual herb species.

Open bushland, north, Obn

This diverse type which is found on transitional soil types and drainage zones in the ridges and valleys north of the Amboseli basin, is characterized by a variety of woody shrubs -- A. mellifera , Cordia spp., Commiphora spp., Balanites spp., and others -- which combine to make up a canopy cover of about 10 percent. The herb layer is composed of a variety of annual and perennial herbs and grasses.

Open bushland, south, Obs

The southern open bushlands occur on the volcanic ridges and lava boulder fields to the south and east of the basin. Shrub cover, mainly A. mellifera , amounts to less than 2 percent, but low woody herbs such as Triumfetta and Hibiscus spp. are abundant. Both annual and perennial herbs and grasses are common.

Dense bushland, north, Dbn

In drainage areas and localities of higher rainfall near hill ranges northeast of the basin, fairly dense (over 15

percent cover) mixed stands of A. mellifera , S. persica , and Abutilon spp. are found. Grasses are a patchy mixture of tall, coarse perennials and short palatable annuals. Annual and perennial herbs are fairly abundant.

Dense bushland, south, Dbs

Areas of transitional volcanic soils south of the Amboseli basin woodlands host fairly dense -- cover about 15 percent -- stands of A. mellifera and A. nubica with other smaller shrubs in the understory. The herb layer is dominated in patches by Cynodon plectostachyus , and in other patches a mixed community of annual and perennial herbs and grasses is found.

Acacia drepanolobium bushland, Adb

In poorly drained areas at the southern basin margin, isolated stands of fairly dense Acacia drepanolobium , or whistling thorn, mixed with Balanites glabra are found. This habitat type has a diverse and productive herb layer with a variety of annual grasses and herbs.

The woody and herbaceous biomass of the different habitat types, as of January, 1979, are compared in Figure 5. The highest values of herb layer biomass (range: 20,000 to 30,000 kg/ha) were in the swamp (Swp), swamp edge grassland (Seg), and swamp edge woodland (Pax, Yax) habitats. Also abundant at that time of year, the mid rains, were the herb layers of the fever tree and A. tortilis woodlands (Tw,Xw) (17,000 to 20,000 kg/ha),

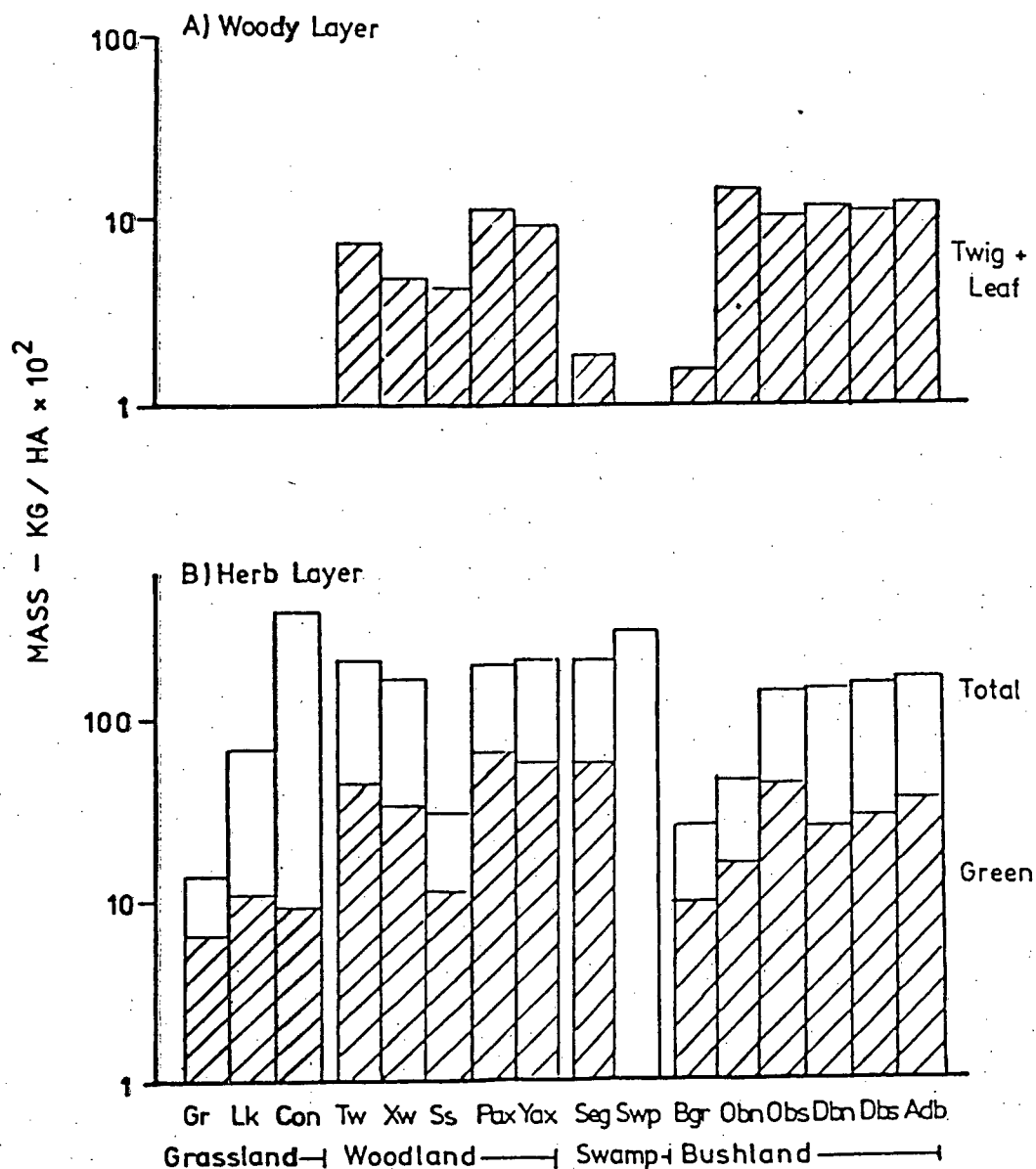


Figure 5. Standing biomass (dry weight) of the woody (twig+leaf) and herbaceous (green matter and total dry mass) vegetation in the habitat types of Amboseli in January 1979. Note that the scale is logarithmic. There are marked differences between habitats in available plant biomass. In all habitats, herb layer biomass (both green and total mass) is higher than twig/leaf mass. Note that green mass was not measured for the Swp plot.

and the denser bushlands (Dbn, Dbs, Adb) and the open southern bushlands (Obs) (about 15,000 kg/ha). The S. consimilis (Con) grassland patches had a high total biomass (40,000 kg/ha), but very low green mass (900 kg/ha), indicating that much of the plant biomass in this habitat was dry "standing hay" and structural material, even during the rains. This was also the case, at a lower biomass level, in the lake-bed grasslands (Lk). The alkaline grasslands (Gr), Salvadora / Suaeda shrublands (Ss), bushed grasslands (Bgr), and open northern bushlands (Obn) had relatively lower total biomass in the herb layer (1500 to 4500 kg/ha), with green mass making up a higher proportion of the total. For these latter habitats, the herb layer appeared to have more photosynthetic material and less structural material per unit of plant biomass.

Twig/leaf biomass was most abundant in the swamp edge woodlands (Pax, Yax), where young fever trees contributed much of the mass (about 1000 kg/ha), the A. tortilis woodlands (750 kg/ha), where understory shrubs were abundant, and all bushland habitats (1000 to 1500 kg/ha), except for the bushed grassland (170 kg/ha). Twig/leaf biomass was low (190 kg/ha), in the swamp edge grasslands (Seg), and absent from all other grasslands (Gr, Lk, Con) and the wet swamps (Swp). In all habitats, available twig/leaf mass was considerably less than the total dry mass on offer in the herb layer, during the mid rains. In some bushland communities, (Obn, Dbn, Dbs) twig/leaf mass was fairly high, almost comparable to herb layer green mass, but not total dry mass.

When diversity of available biomass in habitats is compared (as in Figure 6), the woodland habitats (Tw, Xw, Ss) and all bushland habitats appeared to have high diversity of woody species, while the bushlands also had relatively high herb layer diversity. Overall, the bushlands had a greater diversity of plant species in both the woody and herb layer available as potential foods for the elephants during the rains.

3. Dynamics of the herb layer in different habitat types

Figures 7 and 8 summarize the dynamics of green and total biomass of the herb layer of the different habitat types of the basin and bushlands for the 1978/79 period. The swamps (Swp), swamp edge grasslands (Seg), and swamp edge woodlands (Pax, Yax) maintained high green and total dry mass through the year, while drier habitats of the Amboseli basin and some bushland types showed wider fluctuations. The lake bed grasslands had a high total mass, and low, fluctuating green mass throughout the year. The alkaline grasslands and Salvadora / Suaeda shrublands showed similar changes in both green and total mass, dropping to low values (less than 500 kg/ha) in the dry season, although the latter maintained higher biomass throughout. The A. tortilis woodlands showed wider fluctuations, rapidly developing green and total mass early in the rains, and dropping back down to fairly low levels (900 kg/ha total biomass) by the late dry season. The fever tree woodlands had a fairly high total biomass (8000 to 15,000 kg/ha) throughout.

The denser bushland habitats maintained a high total dry

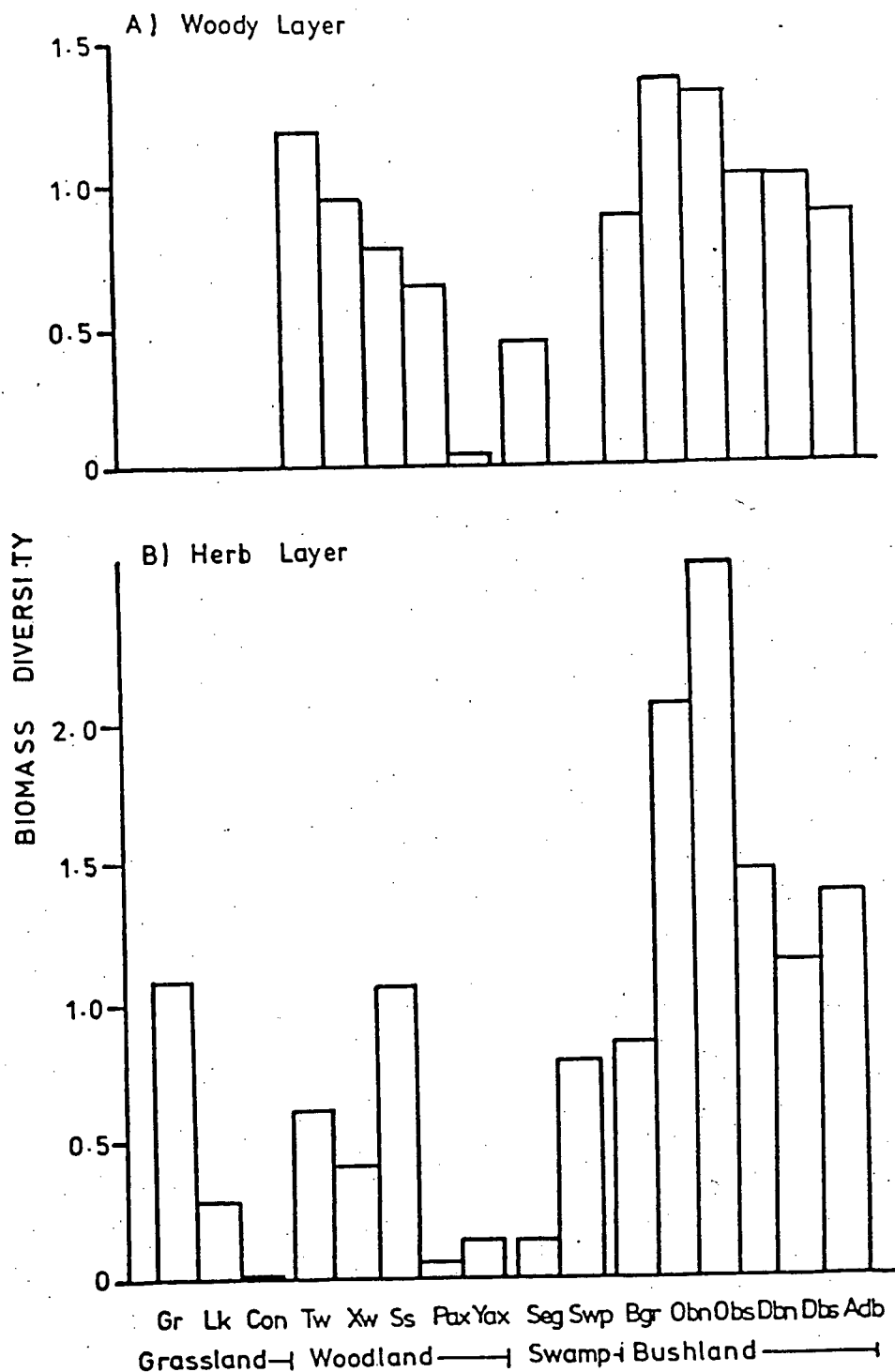


Figure 6. Diversity (Shannon-Weaver index) of available plant biomass in the woody and herb layers of Amboseli habitat types in January 1979. The bushland types had high diversity in both woody and herb layers, while the basin woodlands (Tw,Xw,Ss) were also fairly diverse.

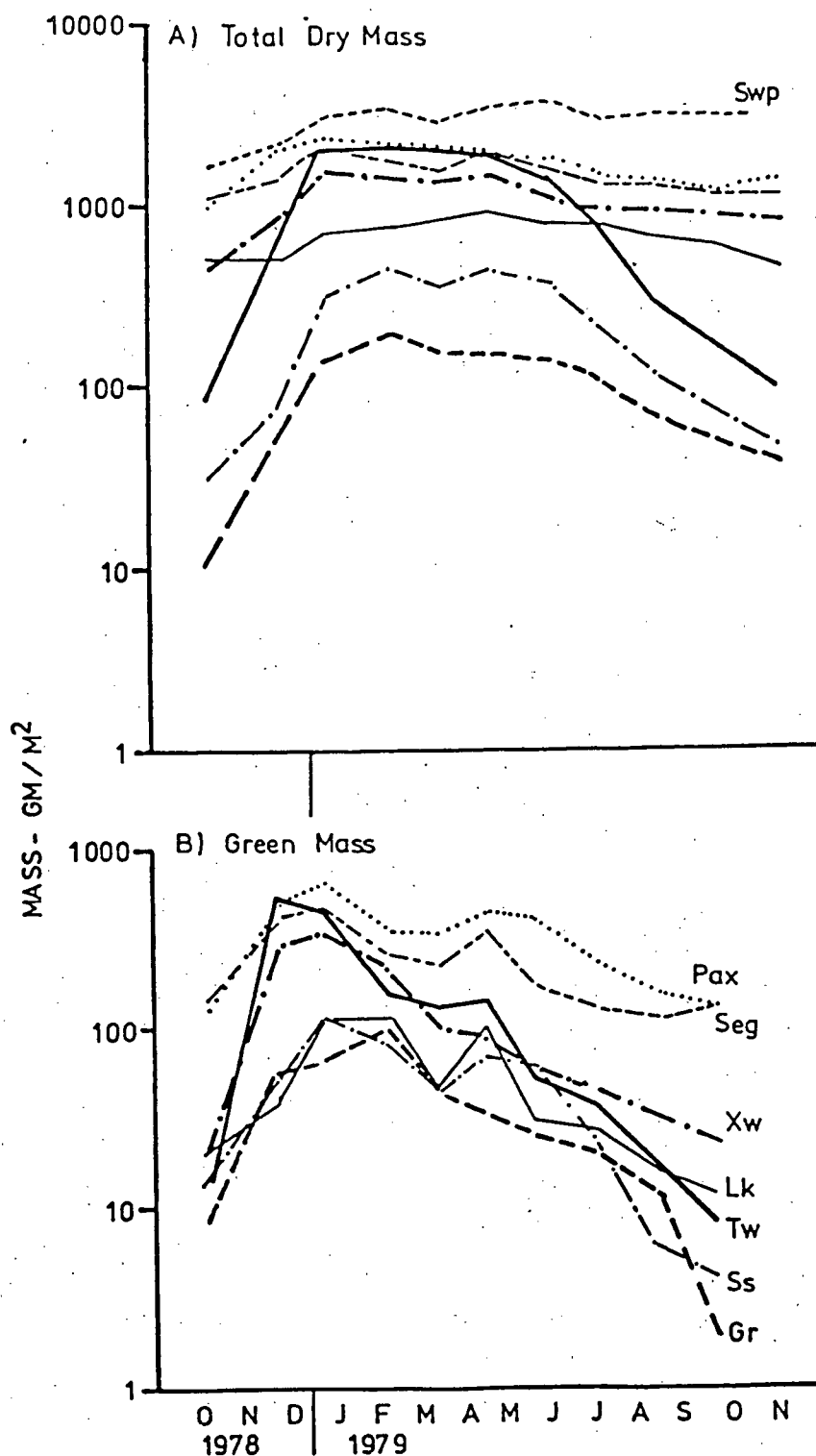


Figure 7. Dynamics of total biomass and green biomass of the herb layer of Amboseli basin habitats in 1978/79. The scale is logarithmic. Peak biomass for most habitats was reached in January/February 1979. The biomass of green vegetation declined more quickly than the total biomass. Note that the swamps and swamp edges (Pax, Seg) maintained high total and green biomass throughout the year.

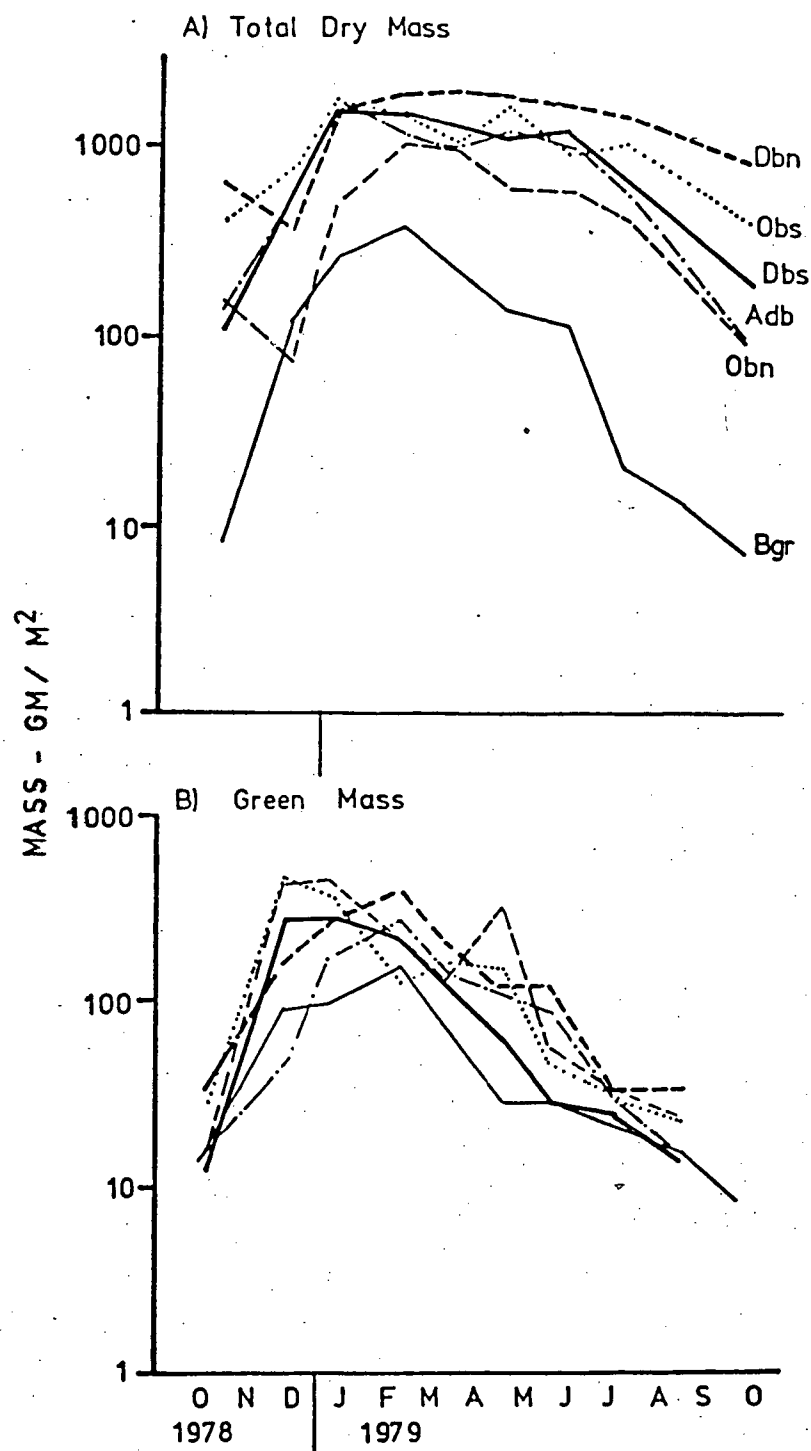


Figure 8. Dynamics of total biomass and green biomass of the herb layer of Amboseli bushland habitats in 1978/79. As with basin habitats, peak biomass was reached in January/February 1979. Most bushland types showed a sharp biomass increase with the rains and a gradual decline in the dry season.

mass through the year, while the bushed grassland (Bgr) had the most widely varying biomass of the bushland habitat types, decreasing to low levels (70 kg/ha) in the late dry season. Two of the northern bushland types, the open (Obn) and dense (Dbn) northern bushlands, actually showed a decline in herb layer dry mass with the onset of the short rains, largely because dry standing grass from the previous dry season was knocked down with the first rains. Green mass showed a steady increase with rainfall in these habitats.

Most habitats reached peak green mass in December or January; some bushland habitats (Bgr, Dbn, Adb) peaked later in February. This appeared to represent the maximum point of herb layer growth, apparently related to the phenological changes of leaf flush, flowering, and subsequent seed-set. After this point, the green mass declined. Total grass/herb biomass plateaued at roughly this time, but remained high for some months to follow in most habitats. At this point, the grasses were slowly drying out, and, presumably, translocating nutrients to their root systems (McNaughton 1979b). The total biomass of the herb layer in most habitat types remained fairly high until the dry season, when consumption by elephants and the migrant grazing herbivores (wildebeest, zebra, and livestock) began to reduce biomass levels. In the bushed grasslands (Bgr), consumption by domestic livestock reduced total biomass levels promptly after the rains. The migrant herbivores moved to bushland areas during the rains (as described in Chapter 2), and used the basin habitats extensively in the dry season, in a

sequence from alkaline (Gr) and lake bed (Lk) grasslands through the woodlands (Tw, Xw) and Salvadora / Suaeda shrublands (Ss) to swamp edge grasslands (Seg) and woodlands (Pax, Yax). They reduced the herb layer biomass substantially in the grasslands and woodlands as the dry season continued, although during my study period, they did not venture deeply into the swamp edge habitats.

The longer term data from Western's monitoring (see Figure 9) of his permanent plots shows how seasonal herb layer dynamics can vary under different rainfall regimes. During the drought period leading up to 1977/78, the herb layers of all habitats, including the swamps, fluctuated dramatically, reaching low levels by the end of the dry season as the large herbivores made extensive use of all the basin habitats. In subsequent wetter years (1977 to 1979), oscillations in biomass were damped somewhat and occurred at a higher level. The swamp edge habitats (Pax, Yax, Seg) were used less by the plains grazers during the dry seasons, and these habitats built up a biomass "capital" during this period. In the recent period of low rainfall in 1980, green and total biomass values dropped back down in all habitats except the swamp edges, which retained the biomass capital developed during the years of higher rainfall.

I analyzed the relationship between rainfall and a simple estimate of herb layer biomass production in different habitats by plotting total dry mass measured in the late dry season and early to mid rains -- the growth phase -- against cumulative rainfall at Ol Tukai from the onset of rains to the date of

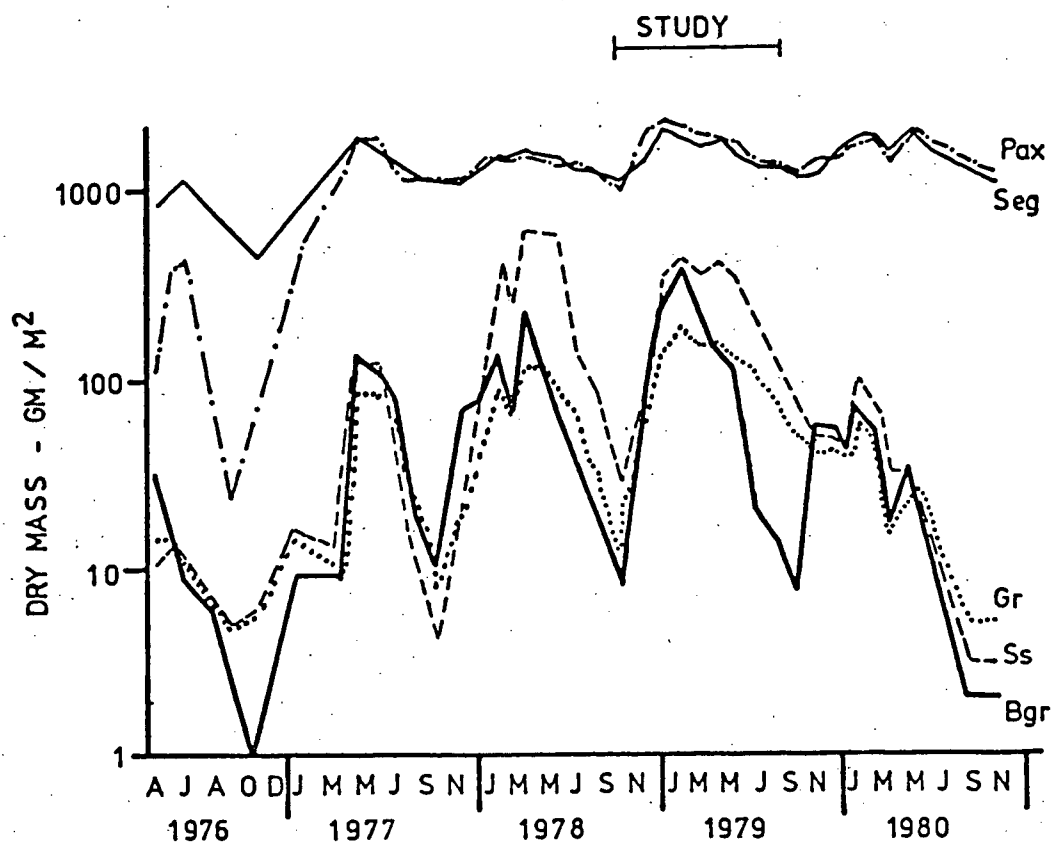


Figure 9. Long term dynamics of total herb layer biomass in some Amboseli habitat types. During the dry period before Nov. 1977, the biomass in all habitats was fairly low, and showed wide fluctuations during the rains. In the Wet period, 1977/79, herb layer biomass increased in all habitats, and fluctuations were at a higher level. In subsequent dry year, 1979/80, biomass was reduced again in the grasslands, woodlands, and bushlands, but has remained high in the swamp edges (Pax, Seg).

vegetation sampling. These regressions were based on only a few data points (only three to five measurements at the plots before peak biomass), and the rainfall records from only one station. Even so, many of the regressions were significant, and the coefficients of determination were generally high (see Table 3). There were marked differences in the slopes of the regressions between rainfall and dry mass in the different habitats during 1978/79. The bushlands (Obn, Obs, Dbn, Dbs), woodlands (Tw, Xw), and swamps (Swp) had a high rate of biomass growth with rainfall, while the bushed grassland (Bgr) and Salvadora / Suaeda shrublands (Ss) increased at a more moderate rate, and the alkaline and lake-bed grasslands (Gr, Lk) and swamp edge habitats (Seg, Pax, Yax) had a fairly slow response to rainfall.

The relations between herb layer growth in many habitats and rainfall appear to be different in the longer term data from before and after 1978/79 (see Table 3). The seasonal dynamics of the alkaline grasslands (Gr) and bushed grasslands (Bgr) remained fairly similar through the different rainfall periods, with some increase in the slope of the rainfall/growth relation in the wet years. Swamp edge grasslands (Seg) had the steepest response to rainfall in the drier periods, when biomass fluctuations were more extreme. Herb layer growth in the woodlands, represented by the Salvadora / Suaeda shrublands (Ss), showed a marked increase from the early drought (pre 1977) to the wet years (1977-1979), and a subsequent decrease in the dry period of 1979/80. It appears that the current state of herb layer vegetation can have a strong influence on its

Table 3. Relationship of herb layer biomass growth to rainfall rainfall, showing regression coefficients of total biomass vs. Cumulative rainfall from the start of the short rains until peak growth, in different habitat types and different years (in g/m /mm rainfall). r^2 is given in parentheses, with significant regressions noted.

HABITAT TYPE	RAINFALL YEAR			
	1976/77	1977/78	1978/79	1979/80
GRASSLAND				
Alkaline	0.48(.731)	0.34(.929)**	0.60(.960)	0.42(.896)
Lake bed	1.71(.994)*	0.26(.956)**	1.06(.876)	-1.14(.455)
WOODLAND				
<u>A. tort.</u>	- -	- -	5.77(.718)	- -
Fever	- -	- -	2.85(.542)	- -
<u>S/S shrub</u>	0.83(.781)	1.94(.927)**	1.54(.947)	0.46(.852)
<u>Palm</u>	9.77(.999)**	1.32(.859)*	0.27(.034)	4.52(.899)
SWAMP				
Edge gr.	7.63(.972)	2.11(.940)**	1.25(.302)	4.43(.525)
Swamp	- -	- -	5.56(.906)	- -
BUSHLAND				
Bush gr.	0.87(.759)	0.50(.631)	1.14(.984)*	0.93(.782)
Open N.	- -	- -	4.22(.999)**	- -
Open S.	- -	- -	3.27(.675)	- -
Dense N.	- -	- -	6.49(.870)	- -
Dense S.	- -	- -	4.08(.601)	- -
<u>A. drep.</u>	- -	- -	2.74(.257)	- -
n =	3	5	3	3

Significance of r^2 : * $p < .05$
 ** $p < .01$

potential for growth with rainfall.

4. Herb layer nutrient dynamics

Data collected by D. Western in 1976 (pers. comm.) show the dynamics of herb layer crude protein content for some habitat types (see Figure 10). Woodland (Ss) herb layer had the highest protein content all through the year, and varied substantially through seasonal changes in phenology: 23 to 12 percent crude protein (% C.P.) from long rains to late dry season. The protein content of the herb layers of both the alkaline grasslands (Gr) and bushed grasslands (Bgr) was fairly high, and also decreased, although less dramatically, in the dry season: 18 to 8 % C.P. The lake bed grasslands (Lk) and, especially, swamp edge grasslands (Seg) had low, fairly constant protein content through the year: 8 to 5 % C.P.

D. Discussion

The habitat types I defined for Amboseli fall into two broad categories: those with ground water and more or less continuous, though seasonally varying, potential for primary production, and those dependent on seasonal rainfall for the soil water necessary for plant growth. The first group includes the swamps (Swp), swamp edge grasslands (Seg), and swamp edge woodlands (Pax, Yax), and the second group includes the A. tortilis (Tw) and fever tree (Xw) woodlands, the alkaline (Gr) and lake bed (Lk) grasslands, and the semi-arid bushlands.

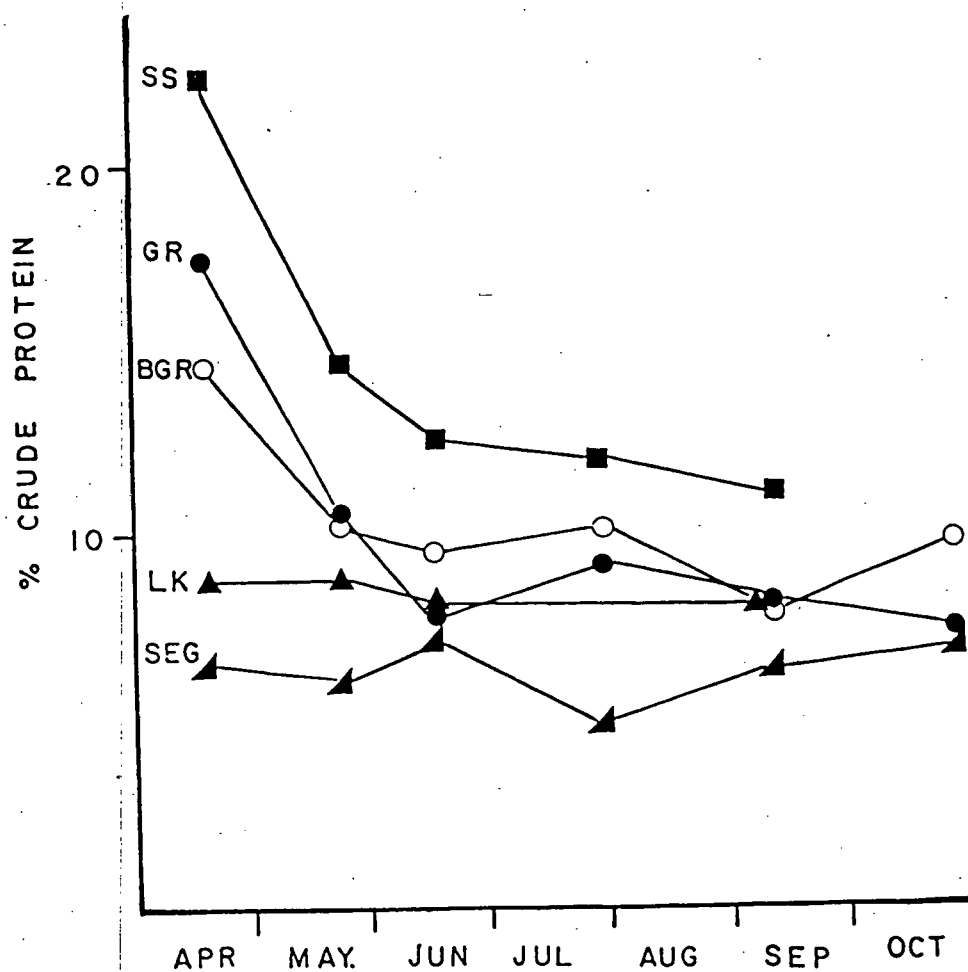


Figure 10. The dynamics of herb layer crude protein content in certain Amboseli habitat types in 1977 (after Western (pers. comm.)). The woodlands, represented by the *Salvadora/Suaeda* shrublands, SS, had high herb layer protein content in the rains, which dropped in the dry season to moderate levels. The herb layer of alkaline grasslands, GR, and bushed grasslands, BGR, showed similar, but lower level, seasonal crude protein content. The lake bed grasslands, LK, and swamp edge grasslands, SEG, had low protein content throughout the year.

The latter "rain-dependent" habitats have herb layers with relatively lower biomass and higher protein content than the former ground-water habitats. In the rain-dependent habitats, biomass and quality were more directly linked to rainfall patterns (see below), and thus were more variable on a seasonal or longer term basis. The bushland habitats were more productive in the rains, and had more diverse and nutritious plant material on offer than most of the basin habitats, except for the A. tortilis and fever tree woodlands during wet years.

There were marked differences in overall structure and herb layer dynamics between the habitat types of Amboseli. Total biomass of the herb layer was greater than or equal to twig/leaf biomass within habitats at all times of year during 1978/79. At peak herb layer biomass, this difference was greater than an order of magnitude in all habitat types, except the Salvadora / Suaeda shrublands (Ss) and the open northern bushlands (Obn). However, in the late dry season of 1979, there was greater biomass in the woody layer of the more densely wooded habitat types -- the bushlands and swamp edge woodlands -- than in the herb layer of other habitats -- the alkaline grasslands, Salvadora / Suaeda shrublands, A. tortilis woodlands, and bushed grasslands. During low rainfall years, when the herb layer abundance in many plant communities is reduced to very low levels by herbivore consumption, the twig and leaf material in wooded habitat types could have greater relative importance.

The crude protein of twigs and especially leaves of woody plants can be relatively high; values range from 10 to over 30

percent crude protein has been reported by various authors (Dougall et al., 1964, Field 1971, Pellew 1980) for different parts of woody plant species found in Amboseli. This material, when sufficiently abundant, could provide a valuable food source for elephants.

It appears that herb layer vegetation in the rainfall-dependent habitats (grasslands, woodlands, and bushlands) of Amboseli is potentially productive only during the rainy season months of November to May, with little or no production during the rest of the year, when there is no rainfall. This contrasts with the situation seen in the grasslands of Serengeti (McNaughton 1979a,b) which receive light rainfall in the dry seasons, and are potentially productive, especially when grazed, at most times of year. It is also clear that grass biomass and production varies considerably between habitats and between years, and is affected by both the fluctuating rainfall, which stimulates biomass production, and consumption by the different herbivores in the system, which reduces the herb layer biomass. The quantitative values of these relationships are currently under study (D. Western, pers. comm.).

CHAPTER 4 ELEPHANT HABITAT USE AND PREFERENCE

A. Introduction

In this chapter, I will examine elephant habitat use with reference to seasonal changes. The approach will focus on the Amboseli basin and its mosaic of habitat types.

Elephants use the whole range of basin habitats in a given season, month, or even on the same day. A central assumption I make is that all areas and habitat types in the Amboseli basin are available to elephants at all times of the day and year. I make a further assumption that my perception and definition of separate "habitat types" is congruent with the way elephants perceive and use them. The first assumption is most probably valid, in that all areas of the Amboseli basin are potentially free for elephant use. The second assumption is more arbitrary, and less likely to be true -- my position in this case is that my definitions were based on broad-level structural and floristic differences between specific sites that I could identify and measure (see Chapter 3).

In the following sections, I will identify the habitat types selected and avoided by elephants. Elephants spend a large proportion of their time feeding; a range of 50 to 75 percent of total daily activity has been reported in the literature, and reviewed by Guy (1976b). With this in mind, I will examine food, or plant material available as food, for elephants, as a potential basis of their habitat selection. Habitat occupancy by elephants will thus be examined with

reference to vegetation abundance in the different habitat types.

Many studies of elephant distribution (Caughley and Goddard 1975, Eltringham 1977, Lamprey 1963, Leuthold and Sale 1973, Norton-Griffiths 1975) found that the populations were non-randomly distributed, with respect to geographical features or broad habitat categories. The work of Leuthold (1977b), which linked movements and habitat use strategies to seasonal rainfall, suggested that the vegetation available in habitats might be an important determinant of elephant movements. Leuthold showed that within populations, bulls and family units had apparently different habitat use strategies, although he did not suggest reasons for these differences. In this chapter, I will test the general hypotheses that:

- H1. Elephant habitat distribution is nonrandom.
- H2. There are significant relationships between elephant numbers and the biomass of the herb and woody layers in the different habitat types.
- H3. There are differences in habitat use between bachelor bull and cow/calf herds.

In the discussion, I will use my observations to suggest a general strategy of habitat selection by the elephants.

B. Methods

Survey counts were the basic tool I used in evaluating elephant habitat distribution in the Amboseli ecosystem. The survey data were collected in two ways: I made a series of intensive ground-based counts in the year November 1978 - October 1979, while D. Western has done aerial total counts as part of his extensive monitoring programme of the Amboseli ecosystem since 1975. I collaborated in the collection and analysis of the latter dataset.

The aerial and ground count data were collected in different ways: I will analyse them differently and use them for different purposes. Basic conclusions about elephant habitat use will be derived using the ground count data, while the aerial count data will give an historical perspective.

Total counts of elephants in the Amboseli basin were attempted because other researchers who used sample count estimates of elephant population size had encountered problems of accuracy and precision. Because elephant populations have low densities and contagious distributions (Eltringham 1977), sample estimates are usually of questionable accuracy and have wide confidence intervals (Croze 1972, Watson et al. 1969) unless the sampling fraction is large or the counting effort is stratified into many regions of different elephant density. As well, the actual number of animals counted is usually low, making finer scale analysis of habitat distribution dependent on only a few sightings. On the other hand, total counts suffer the disadvantage of a biased tendency to underestimate, and lack

confidence limits to indicate the precision of the estimate (Norton-Griffiths 1978). However, if the total counts are done under the same conditions in a series of counts, the values obtained can be compared with each other, to indicate trends at least, with some degree of assurance. Surveys were focussed on the Amboseli basin since it is a fairly small area of the ecosystem where elephant use is concentrated through much of the year; in effect, this was a stratification of survey effort.

In addition to survey counts, I made casual observations of elephant movements, feeding behaviour, and individual group identity on an opportunistic basis, throughout the study area and period. Cynthia Moss has been observing the social behaviour and monitoring the demography of the Amboseli elephant population since 1974. She has identified all the individual members of the population, and continues to record the status of individuals as members of stable cow/calf family units, or as independent, freely associating adult bulls. I assisted her in this work in 1978/79, and I include some of her published and unpublished results, with her permission.

In this section, I describe the methods I used to monitor and analyse elephant habitat distributions.

1. Counting methods

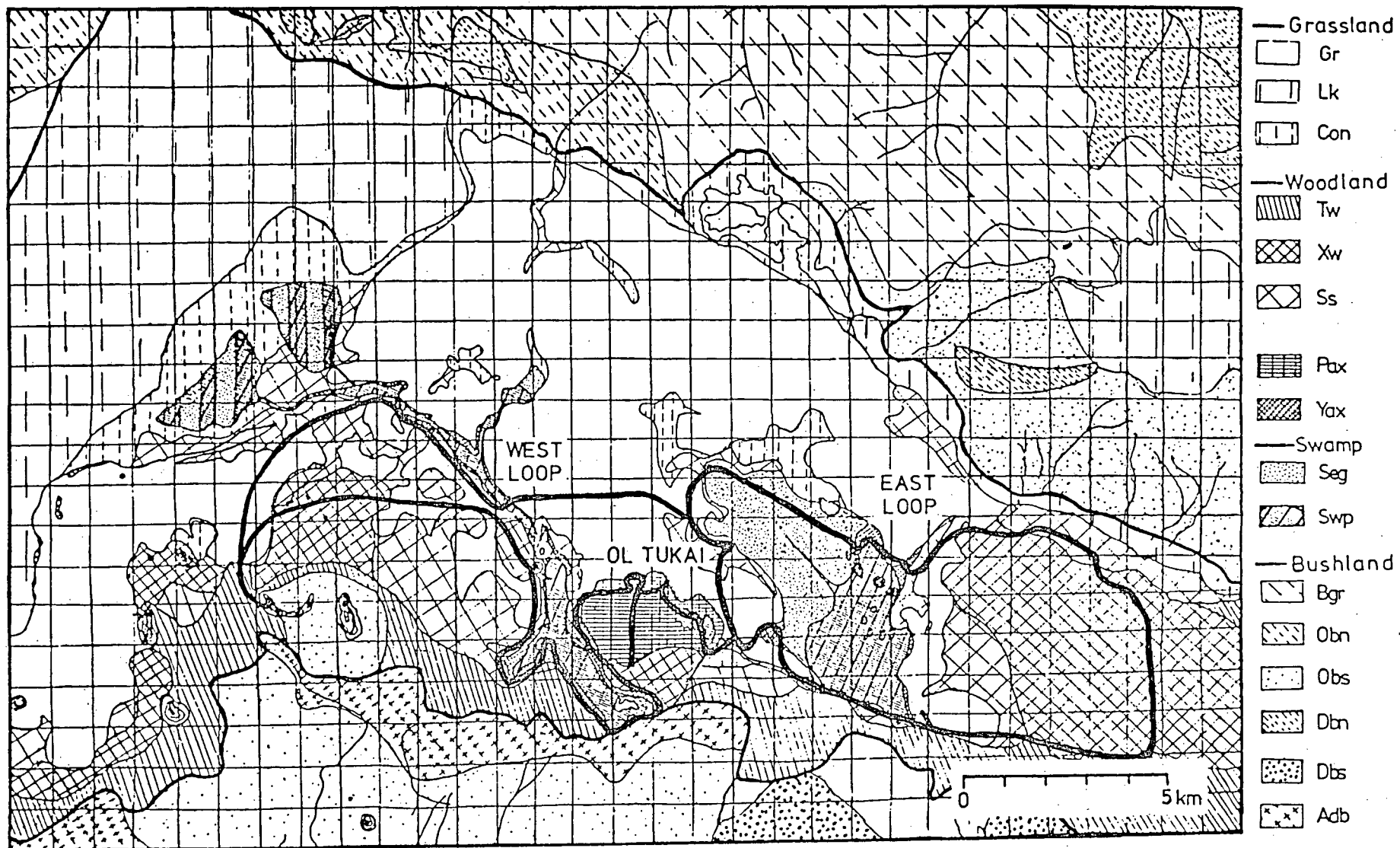
a. Ground counts

In the ground surveys, I tried to obtain total counts as far as were possible from a ground-based vehicle; a Suzuki four-wheel drive "jeep" was the vehicle I used for most of the ground counts. I designed the surveys to cover each area and habitat type of the Amboseli basin in each part of the day at least once a month, so that total daytime use of the basin by elephants would be sampled.

I attempted to complete eight survey circuits of the Amboseli basin in each month. Each circuit consisted of an eastern (three hours travel time) and a western (three-hour) loop (see Figure 11). Either loop could be travelled two ways, "clockwise" or "counter-clockwise" as viewed on the map. This meant there were four possible six-hour routes which could be done in either the morning or the afternoon, or a total of eight possible circuits in the full daylight period of 6 am. to 6 pm. I arbitrarily divided the daylight hours into four equal time blocks: TBlk1 - 6 am. to 9 am., TBlk2 - 9 am. to 12 noon, TBlk3 - 12 noon to 3 pm., TBlk4 - 3 am. to 6 pm.

Visits would thus be made to every area of the Amboseli basin twice (once in each of two directions) per month in each time block. Surveys were done at roughly 3 to 4 day intervals; the order of survey routes was chosen at random in each month. Night-time survey counts were not possible, but I attempted to observe elephant activities and movements after dark by

Figure 11. Routes of ground-based surveys of the Amboseli basin, showing the West and East Loops of the six-hour circuit.



following family units through a number of moonlit nights.

Counts were done each month of the rainfall year from November 1978 to October 1979. I was principal observer on counts until mid-September, but occasionally I had an extra observer as a spotter. A co-worker, Michael Milgroom, completed counts for me in September and October; we had compared separate counts of elephant groups for the month of August and observer agreement was high. For various reasons, some surveys were missed in three months: only four counts were done in November 1978, seven in December, and five in October 1979. A total of 88 from a possible 96 counts was successfully completed.

In designing routes, I made use of roads, dirt tracks, and cross-country driving, when necessary. The vehicle was stopped at regular intervals along the route and the surrounding area scanned from the roof with binoculars. I made use of two low hills in the western basin as lookout points which greatly increased the detectability of elephants in the surrounding areas. Elephant groups located, but too far away to count accurately, were approached and counted; I returned to the survey route after recording the group. In the more open habitat types, such as the alkaline, lake-bed, and S. consimilis grasslands, fever tree woodlands, S. monoica shrublands, and swamp edges, visibility was virtually unrestricted and the whole habitat area was considered surveyed. In habitats with dense woody cover -- the A. tortilis woodlands, date palm/fever tree and young fever tree swamp edge woodlands -- or tall sedges, as in the permanent swamps, I estimated the "visibility profile"

(Norton-Griffiths 1978) of the "transect" represented by the survey route with a stereo rangefinder. In these latter habitat types, a subset of the total habitat area was observed (see Table 4 for areas of habitats surveyed), but I do not consider

Table 4. Areas of habitat types surveyed in aerial and ground counts of the Amboseli basin. The proportion of the total area surveyed in ground counts which was occupied by each habitat type is shown, including and excluding the lake bed grasslands.

HABITAT Type	AERIAL COUNTS		GROUND COUNTS	
	Area(km ²)	Area(km ²)	P. of Total (inc. Lake)	P. of Total (exc. Lake)
GRASSLAND				
Alkaline	130.6	130.6	0.3559	0.4648
Lake bed	85.9	85.9	0.2342	-
<u>S. consimilis</u>	30.5	30.5	0.0830	0.1084
WOODLAND				
<u>A. tortilis</u>	42.9	20.7	0.0564	0.0737
Fever tree	43.2	43.2	0.1177	0.1537
S/S shrubs	33.1	33.1	0.0902	0.1178
Palm/Fever	5.2	2.1	0.0056	0.0074
Young Fever	4.2	3.5	0.0096	0.0126
SWAMP				
Edge grass.	10.0	10.0	0.0271	0.0354
Swamp	14.6	7.4	0.0201	0.0263
Total	400.2	367.0	0.9998	1.0001

this a statistically valid sample of those habitat types, for reasons I discuss below.

During each survey, every separate elephant group encountered was recorded. Definition of "separate" groups was arbitrary: groups (including single animals) more than about 50

m. apart were considered "separate". This is probably a reasonable, functional definition of separate foraging groups, since the distance between elephants within groups was generally only a few metres. For each group I noted: time block, location, habitat type, activity -- feeding, or one of seven non-feeding categories -- of the majority of the group, group type, and group size. If the group was a cow/calf herd, I attempted to count the number of associated adult bulls, but it was not always possible to distinguish the small- and medium-sized independent bulls from cow/calf group members, especially in large aggregations.

I estimated group size by counting the group several times until I reached a consistent figure. For a small proportion of the 656 cow/calf groups encountered (15%), an accurate count was clearly not possible because of habitat structure (11 %) -- high grass or shrubs which hid smaller juveniles -- or because the elephants were standing in a tightly bunched group (3 %) which also hid immature animals from view, or both (1%). In these cases, I counted the visible elephants and a note was made for bias correction in later analysis (see "Corrections for bias" below).

Two additional sources of bias affected the counting of elephants in different habitats. The survey routes were not chosen at random and avoided certain areas where vehicle travel was difficult, but where elephants may have been present or absent in a nonrandom way. The effect of this bias is unclear, but may have led to an underestimate of elephant numbers in the

denser habitats. A second source of bias was that the relative detectability of small groups or single individuals in the denser habitats would have been lower than for large, more conspicuous groups. This would tend to reduce both the total number of elephants seen, and the relative representation of small groups (see Chapter 5). It was not possible to correct for these two biases.

b. Aerial counts

Western used a small fixed-wing aircraft, usually a Cessna 185, in the aerial counts, acting as both pilot and primary observer. A search pattern of parallel lines was flown over the woodlands, grasslands, and swamp courses of the basin, at an altitude above the ground of about 300 ft. Elephant visibility in virtually all habitats was good to excellent. Woody cover approached 20 % in only a few small and scattered areas of woodland, so that canopy cover did not hide many elephants from view, and the areas of all habitat types overflown were considered to be surveyed completely (see Table 4). All the counts were flown in late morning, generally between 10 and 11 a.m., and took about one hour of flying time. Occasionally, additional observers were used as spotters and recorders -- I served in this capacity for many of the flights in 1978 and 1979.

On each count, the location of every separate elephant group was recorded on an airphoto or vegetation map of the basin. The type of group -- bachelor bull or cow/calf "breeding

herd" -- was also noted. Western began the aerial counts in April 1975, and surveyed at fairly regular intervals (almost monthly) from October 1975 to the present; counts up to December 1980 were considered in the present analysis. In some of the early counts, only total elephant numbers were recorded, without separation into group gender type or, in some counts, separate groups. Of the total of 61 counts since April 1975, 54 were considered "classified counts" for use in the present analyses.

An inevitable bias was built into both the ground and aerial survey programs. Because surveys could be done in daylight hours only, the results were biased towards those habitats that elephants used in the daytime. Wyatt and Eltringham (1974) noted that elephants fed extensively at night, and not necessarily in the same places as they did in the daytime. Any relationships between daytime habitat occupancy and vegetation characteristics which are derived in the present analysis are thus only part of the total picture of elephant habitat use, and must be viewed with this bias in mind.

2. Analyses

The basic statistics calculated for the ground count data were monthly total numbers of elephants seen across all times of day. In each month, there were (or should have been) the same number (eight) of counts, so that monthly totals were used as comparable units of population distribution. For ground count analyses, seasons were strictly defined as equal-sized two month periods: short rains - Nov./Dec., mid rains - Jan./Feb., long

rains - Mar./Apr., early dry - May/June, mid dry - July/Aug., late dry - Sept./Oct. For some analyses, counts were pooled as seasonal sums of monthly totals, derived from 16 counts each, or as seasonal means of two monthly totals per season.

The aerial counts were each taken as an "instantaneous" total count of the basin taken at a specific time of day, the late morning, and thus individual counts were directly comparable. They can be divided into three groups reflecting three rainfall periods : Dry1 - April 1975 to November 1977 (n=19 classified counts), Wet - December 1977 to October 1979 (n=20 counts), and Dry2 - November 1979 to December 1980 (n=15 counts). The number of counts in each season, or in each year or rainfall period, was not always the same.

All of the following analyses were done separately for bachelor bull and cow/calf groups.

a. Corrections for bias and missing counts

In my analysis of the ground count data, I made an attempt to correct for the underestimation of numbers in cow/calf group records that I knew were biased because of habitat structure and/or group bunching (see Counting Methods, above). I also attempted to "fill in the gaps" for those months with missing surveys.

An accurate record was kept of the numbers, age structure, and demography of the whole, or at least a very large segment of the whole, Amboseli elephant population (C. Moss 1980, pers. comm.). It was possible to estimate the proportion of different

size classes that could be found in the cow/calf population on a monthly basis, and therefore the proportion of animals that could be hidden by shrubs and grass of known height, or by elephants in different size classes. The correction factor for each habitat in each month could then be derived as follows:

$$\begin{aligned}
 \text{if} \quad N(\text{total}) &= N(\text{seen}) + N(\text{hidden}) \\
 \text{then} \quad 1 &= N(\text{seen})/N(\text{total}) + N(\text{hidden})/N(\text{total}) \\
 \text{and} \quad N(\text{seen})/N(\text{total}) &= 1 - P(\text{hidden}) \\
 N(\text{total}) &= 1/[1 - P(\text{hidden})] * N(\text{seen}) \\
 \text{and} \quad \text{Correction Factor} &= 1/[1 - P(\text{hidden})],
 \end{aligned}$$

where $N(x)$ = Number(x), and $P(x)$ = Proportion(x). For counts of individual groups which I had recorded as potentially biased by hidden animals, I multiplied the number actually seen by the appropriate Correction Factor for the habitat and month of the count record, and rounded the product up to the nearest whole number.

The correction factors were derived from population statistics, and would not necessarily reflect the proportions of animals in different size classes which actually occurred in every individual group encountered, especially if the group was a small sample of the population. However, as a correction for the "possible" number of animals missing from the observer's view in any given group, the error in estimation should be randomly distributed across the group sizes corrected in this way, with no consistent bias (unless groups with many small

calves were more likely to be found in shrubs and dense grass). I did not attempt to check the accuracy of this correction factor technique.

Correction factors for the number of animals in a group which might be hidden by dense grasses or shrubs were calculated for each habitat type (see Appendix 4). I used the average height of dense grass or shrubs within habitats to estimate which size classes of elephants would be hidden. This allowed me to calculate the appropriate Correction Factors for each habitat in each month, as outlined above.

Correction factors for bunching, also found in Appendix 4, were calculated for each month, as above. The assumption was made that in a tightly bunched group of elephants, approximately one quarter of all animals with shoulder heights of about 200 cm. or less (mean adult female shoulder height is approximately 250 cm., Laws et al. 1975) would be located behind, not to either side or in front of, adults, and would not be visible to a ground-based observer. Croze (1972) followed similar reasoning when he corrected calf number estimates in a Ugandan elephant population. This correction may still underestimate numbers in larger, tightly bunched herds, since many of the small animals could then be hidden in the middle of the group. In a very few group records, correction for both habitat structure and bunching was necessary. In this case, I calculated the proportion hidden by shrubs and grass first, then the additional proportion hidden by other elephants, and summed the two. Since there were only a few instances of this double

bias occurring, I calculated Correction Factors for the necessary habitats and months (see Appendix 4).

For months with missing surveys, count figures were corrected upwards in the appropriate time blocks depending on the specific -- morning or afternoon -- routes missed. Monthly sums in the time blocks with missing counts were multiplied by the inverse of the proportion of completed counts in the time blocks. For example, in December, one morning count was missed, or three of a possible four counts were completed. The monthly sums for the morning time blocks, TBlk1 and TBlk2, were multiplied by $4/3$, and rounded up to the nearest whole number. The sums from all the time blocks, including the "corrected" ones, were added together to give a corrected monthly total number of elephants observed. This was done separately for cow/calf and bull monthly totals. The corrected values for elephant numbers are used in all the following analyses.

b. Comparison of ground and aerial counts

The results from aerial and ground counts, as noted earlier, may not be directly comparable. The ground counts were indices rather than absolute population estimates, and monthly totals reflected elephant occupancy of the basin across the entire daytime period, while aerial counts reflected basin occupancy at a specific time of day, and were done less frequently, though for a longer period.

To examine the similarity of results from the two survey methods, I calculated the product-moment correlation of seasonal

means from aerial surveys with ground-based seasonal sums for the whole day and for the late morning time block (TBlk2), the time when aerial counts were flown.

c. Large scale habitat preference

Large scale habitat choice -- bushlands vs. basin -- in 1978/79 was examined by analysis of variance of monthly total numbers in the basin across the seasons. I looked at the pattern in other years by ANOVA of aerial counts across seasons. The relationships between total numbers in the basin and rainfall, and total biomass and green biomass in the herb layer of individual habitat types were assessed by linear regression. For ground counts, I used total rainfall for the month preceding the count month, while for aerial counts, I calculated cumulative rainfall for different lag periods (5, 10, 15, 20, 30, 40, 50, 60, 70, 80, and 90 days) preceding the count date. Western (1975) used a similar technique, and found that livestock and wild grazer numbers in the Amboseli basin had the strongest (negative) correlations with rainfall over the preceding 40 to 50 days. Herb layer biomass values -- mid-month for ground counts and date-of-count for aerial counts -- were interpolated from the running record of permanent plot measurements (Chapter 3).

d. Habitat use and preference in the Amboseli basin, in relation to vegetation and climatic variables

Habitat use and preference by elephants, as seen in the ground count series, was analyzed with a goodness of fit chi squared technique, combined with a "family" of confidence intervals (Neu et al. 1974). For each season, I compared the frequency distribution of elephants observed in habitat types with an expected random distribution. Assuming that all areas surveyed were equally available to all elephants, a random distribution would have elephant numbers occur in habitats in proportion to the area of the habitats. I calculated the expected random distribution for ground counts by multiplying the total number counted in the whole basin in a given season by the proportion of the basin area surveyed which occurred in each habitat type (see Table 4). Bonferroni normal statistics (Miller 1966) were used to construct simultaneous confidence intervals about the individual observed proportions in habitats for comparison with expected proportions. Selected and avoided habitat types were identified as expected values for habitats in each season fell outside the confidence limits about the observed values.

I compared the distribution of bachelor bull and cow/calf numbers across habitat types in each season using Spearman's rank correlation (Siegel 1956).

Habitat distributions as seen in the aerial count series are presented for comparative purposes, but not subjected to the above analyses. The aerial count data probably do not reflect

fine scale habitat use very accurately because of their low sampling intensity and the great variance in daily elephant habitat distributions.

The relationships between numbers observed on ground counts and herb layer biomass within habitat types were examined through linear regression. Monthly total numbers in habitats were analysed using linear regression on total rainfall of the preceding month, and mid-month herb layer total dry mass and green mass values interpolated from the permanent plot record. I compared the distribution of elephant density with the distribution of plant biomass density -- total and green herb layer dry mass, woody twig-plus-leaf dry mass, and herb layer plus woody biomass -- across habitat types in each season using Spearman's rank correlation.

C. Results

1. Comparison of ground and aerial counts

The correlations between ground and aerial seasonal basin counts are shown in Table 5. Correlations were poor between aerial counts and ground counts for all time blocks pooled; the correlations were better when ground counts in time block 2 alone were compared with aerial counts, and but were still not significant at $p=.05$. It appears that the aerial counts were not an accurate sample of total daytime occupancy of the Amboseli basin by elephants, but were biased towards the time of day when they were collected. The ground counts may give a more

Table 5. Correlations of aerial seasonal means and ground-based seasonal totals of bachelor bull and cow/calf numbers in 1978/79, showing low correlation when all time blocks are considered, and higher correlation when the late morning time block alone is used. No correlations were significant at $p=.05$, $n=6$.

TIME BLOCKS	CORRELATION COEFFICIENTS	
	Bachelor bull numbers	Cow/calf numbers
All time blocks	0.2510	0.6777
Time block 2 (late morning)	0.6042	0.7864

complete picture of total daytime habitat use, for the 1978/79 study period, at least. However, the aerial counts remain useful for comparing the long term patterns and differences in habitat use.

2. Large scale habitat choice

a. Bachelor bulls

Seasonal mean ground counts (the means of two monthly totals per season) of 1978/79 are shown in Figure 12, along with the results of ANOVA comparisons of numbers in the basin between seasons. These show that total numbers of bulls in the basin differed significantly (exact $p=.014$) between seasons, and that there was a trend for bull numbers to increase in the mid and late dry season. If the late morning time block (TBlk2) alone was considered, no significant difference ($p=.283$) between seasons was found.

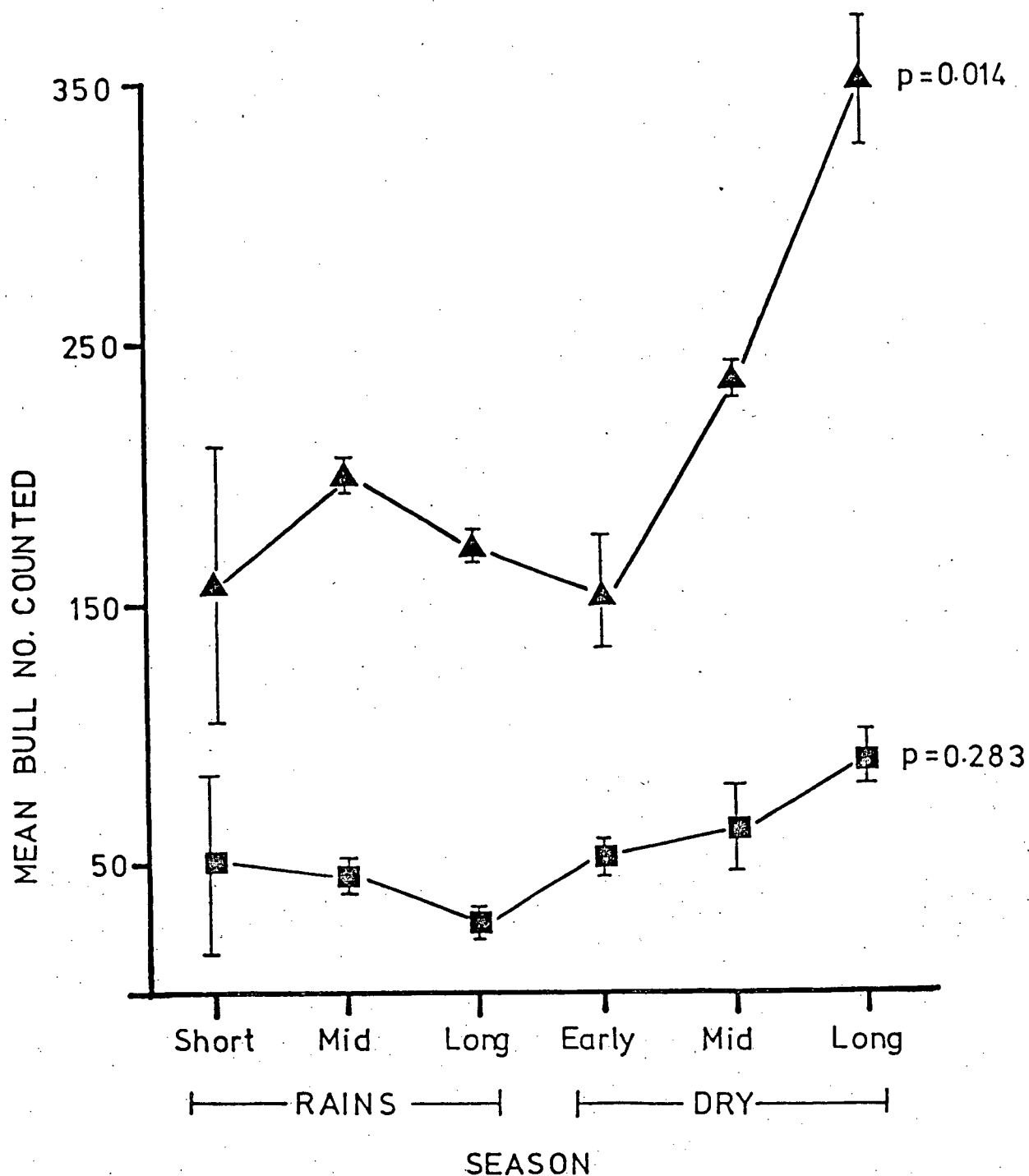


Figure 12. Seasonal means of monthly totals of bachelor bulls counted in ground counts of the Amboseli basin in 1978/79, over the whole daylight period, ▲, and in the late morning time block, ■. There was a significant difference between seasonal means when the whole daylight period was considered -- more bulls were seen in the later dry season -- but there was no significant difference when late morning time block alone was used. Vertical bars indicate ± 1 standard error of the mean.

The situation was somewhat complicated by the changing tendency of bulls to associate with cow/calf groups at different times of year (Poole and Moss 1981). The observed changes in the bachelor bull population may have resulted from an increase in the absolute number of bulls entering the basin, or from a relative increase in the number of bulls joining bachelor herds, instead of cow/calf groups. Figure 13 shows that the latter argument is unlikely: the numbers of both young/medium and large adult bulls associating with cow/calf groups apparently increased from the rains to the late dry season, suggesting an absolute increase in numbers. This result may be due, at least partially, to a counting bias: I may have underestimated the numbers of bulls -- especially young and medium bulls -- associating with large cow/calf herds in early, rainy season counts because of a lack of experience in differentiating the bulls from adult females. The numbers of bulls with cow/calf groups was, however, always fairly small.

The analysis of aerial count data (see Figure 14) shows that there were non-significant ($p=.053$, ANOVA) seasonal differences in basin occupancy by bachelor bulls in the Dry1 period, no seasonal differences ($p=.328$) in the Wet years of 1977/79, and significant differences ($p=.040$) in the Dry2 period. The pattern of seasonal differences was similar in the Dry1 and Dry2 periods: low numbers in the rains, with increases in the dry season. The same pattern was seen in the full-day ground counts of 1978/79.

The relationship between basin occupancy by bull herds and

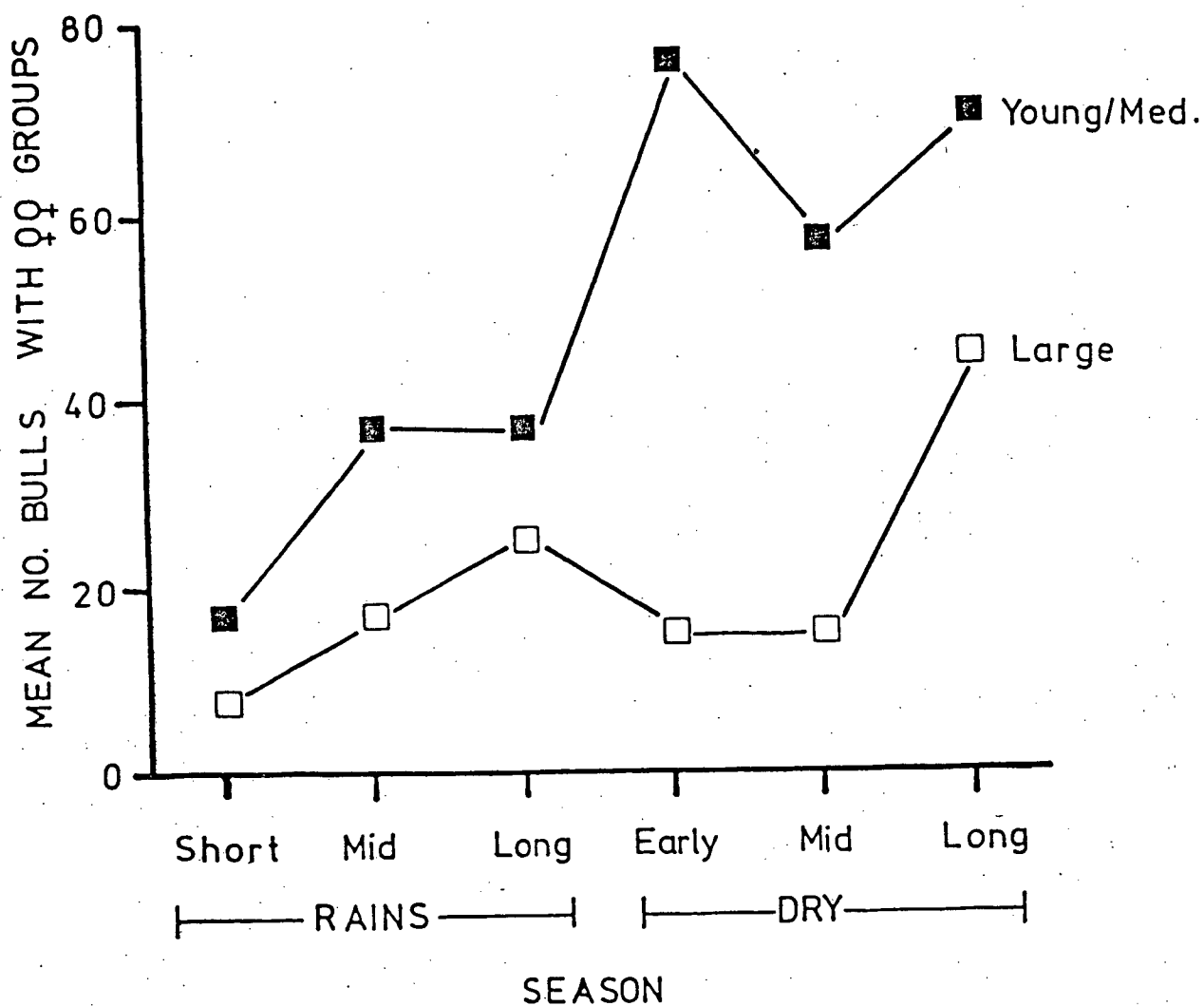
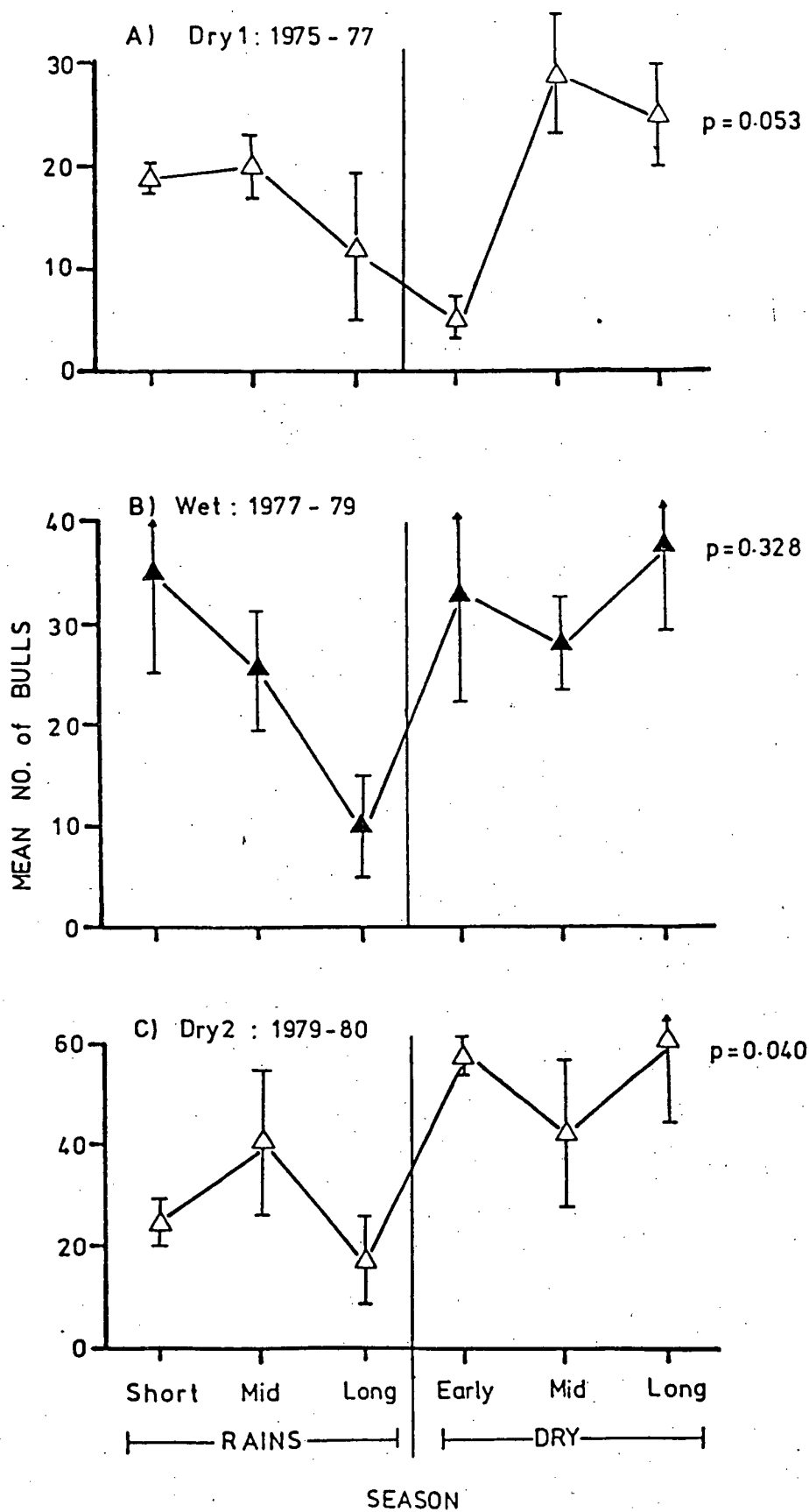


Figure 13. Seasonal means of monthly total numbers of bulls associating with cow/calf herds. The numbers of both young/medium, \blacksquare , and large, \square , bulls seen associating with breeding herds increased towards the late dry season.

Figure 14. Seasonal mean numbers of bachelor bulls seen in aerial counts of the Amboseli basin in the three rainfall periods. Note the nearly significant seasonal differences in Dry1 period, non-significant differences in Wet period, and significant differences in Dry2 period. Vertical bars indicate ± 1 standard error.



rainfall in the Dry1 years is shown in Figure 15; bachelor bull numbers were most strongly, and negatively, related to cumulative rainfall over the 90 days preceding the counts ($r^2=.39$, $p<.01$, $n=19$). Regressions with rainfall for other lag periods were also significant, but less strongly so. The regressions were not significant with the other variables, such as herb layer biomass in habitat types, in Dry1 period, or between bull numbers and rainfall or habitat variables in other time periods (Wet, Dry2). No significant relationships were found between the number of bachelor bulls seen in the basin during ground counts and rainfall or herb layer biomass.

b. Cows and calves

Figure 16 shows seasonal mean (means of two months per season) cow/calf numbers in the basin in ground counts. Mean numbers in the basin did not vary significantly between seasons in 1978/79 ($p=.600$, ANOVA), with no apparent seasonal trend. If ground counts for time block 2, the time of aerial counts, are compared, there was still no significant difference ($p=.146$), nor apparent trend, although the mid rains count was low, and numbers were higher in the late dry season.

Seasonal means from the aerial counts (see Figure 17), were significantly different between seasons during the Dry1 ($p=.044$) and Wet ($p=.005$) periods, but no significant differences appeared during Dry2 period ($p=.942$). The pattern of seasonal change in cow/calf numbers during Dry1 period paralleled the bull situation, with numbers low in the short and long rains,

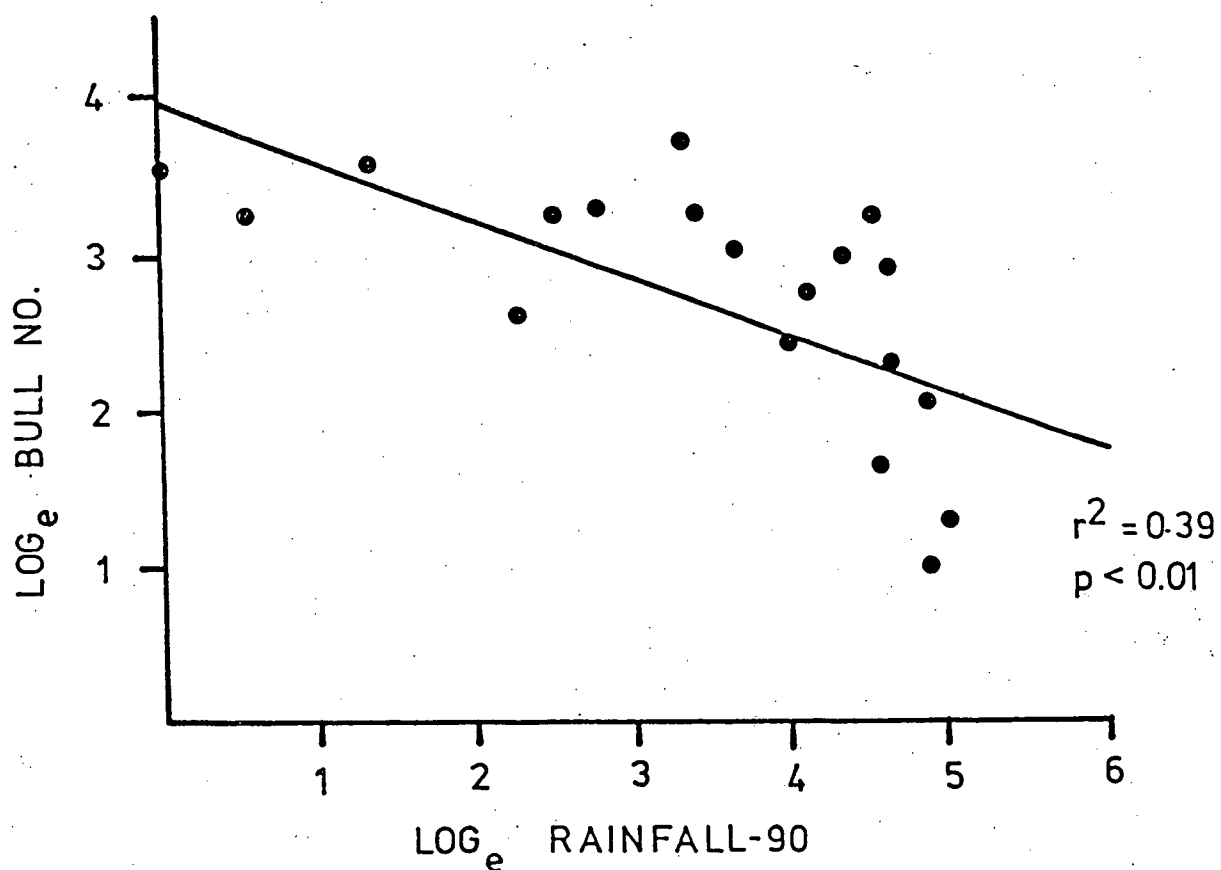


Figure 15. Log_e Bachelor bull numbers in aerial counts of the Amboseli basin were negatively related to Log_e Cumulative rainfall over the 90 days preceding each count, during the Dry1 period, 1975-1977.

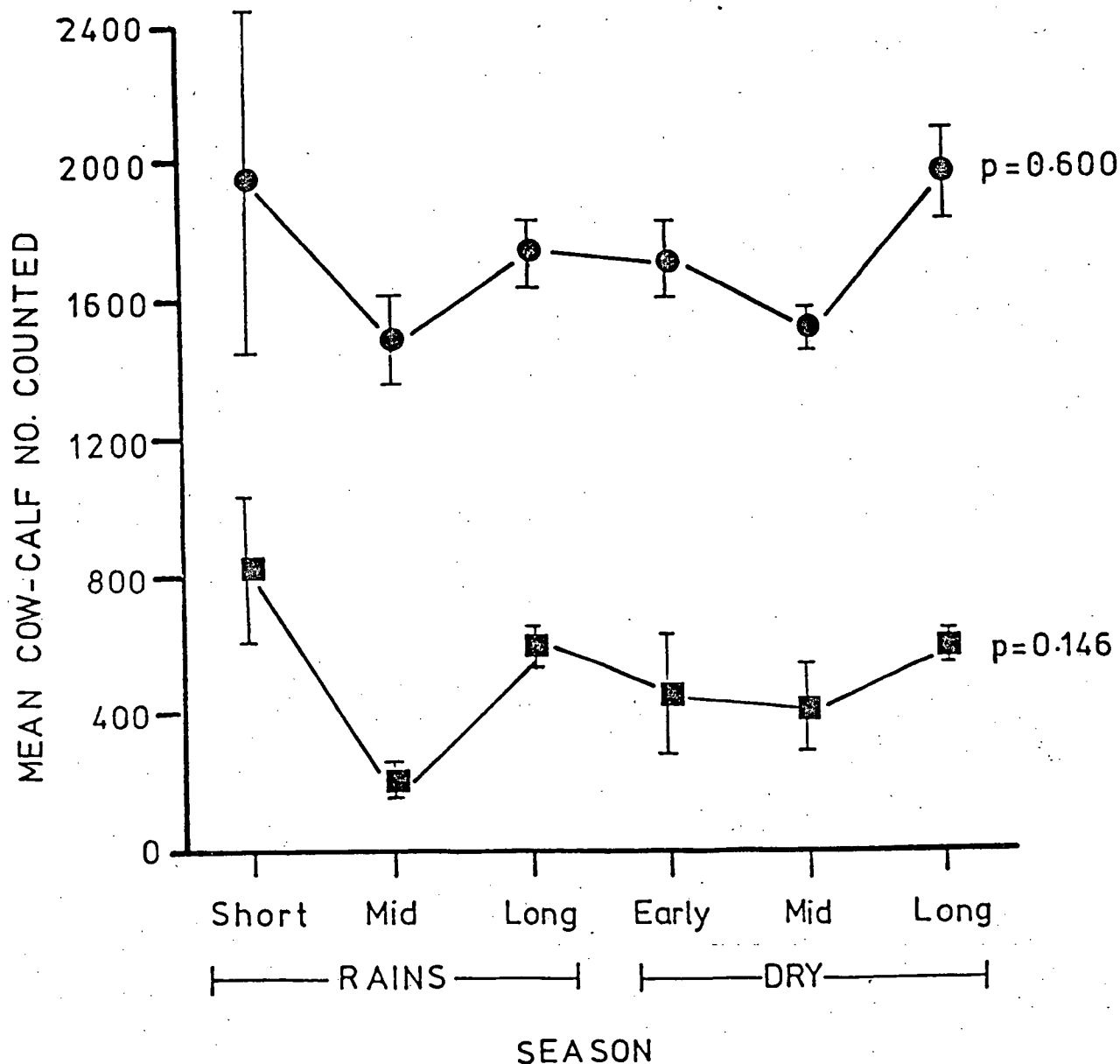
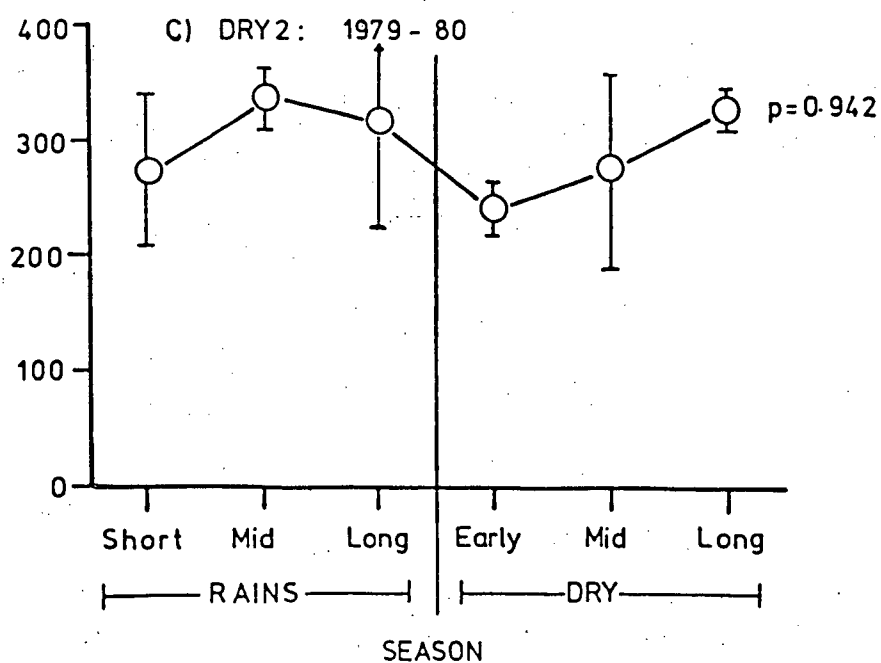
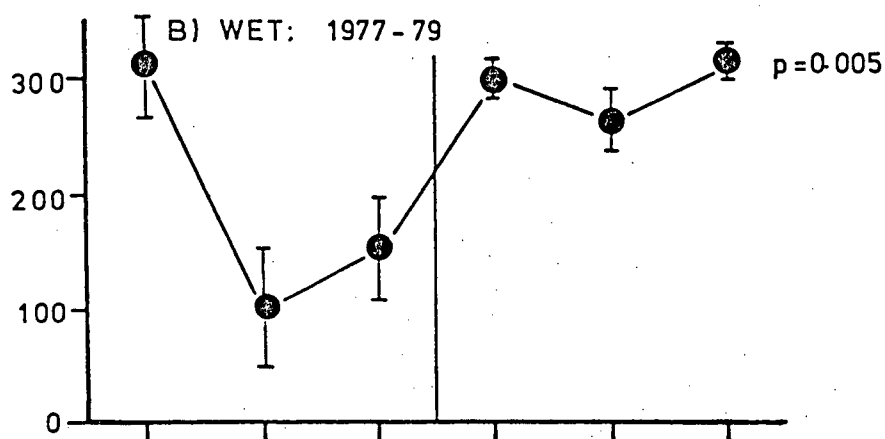
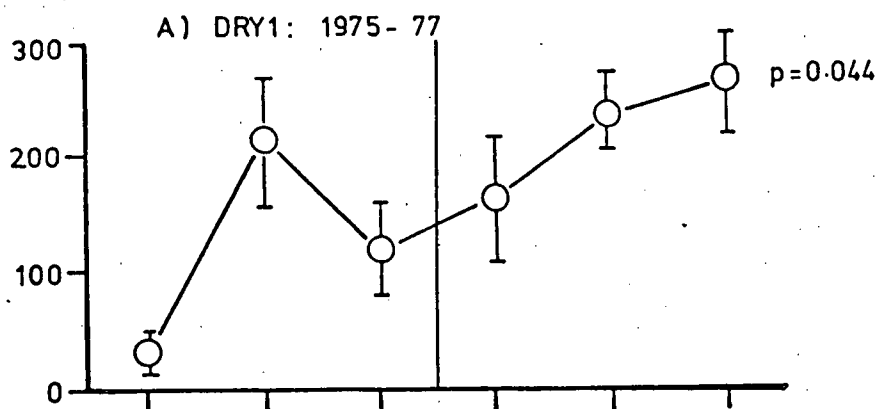


Figure 16. Seasonal means of monthly totals of cows and calves seen in ground counts of the Amboseli basin in 1978/79, over the whole daylight period, ●, and in the late morning time block, ■. There were no significant differences between seasonal means in either case. Vertical bars indicate ± 1 standard error.

Figure 17. Seasonal mean numbers of cows and calves seen in aerial counts of the Amboseli basin in the three rainfall periods. There were significant differences between seasonal mean numbers in the Dry1 and Wet periods -- more cows and calves were seen in the basin during the dry season than during the rains. There were no such differences in the Dry2 period. Vertical bars indicate ± 1 standard error.

MEAN NO. of COW-CALF COUNTED



and higher in the late dry season. In the mid rains, which in Dry1 period was actually a short dry season, relatively high numbers of cows and calves occupied the basin. In the Wet period, the pattern was somewhat different, with relatively low cow/calf numbers in mid and long rains, and high numbers at all other times. High cow/calf numbers were observed in aerial counts of the basin through all seasons of the year in the Dry2 period, 1979/80. These patterns may apply only to the late morning time block, as discussed above.

The relationship between rainfall and cow/calf occupancy of the basin in aerial counts during the Dry1 period is shown in Figure 18. Cow/calf numbers were most strongly related to cumulative rainfall over the preceding 15 days in the Dry1 period ($r^2=.54$, $p<.001$, $n=19$). Regressions with rainfall for different lag periods were also significant, but less strongly so. No significant relationships between cow/calf numbers and rainfall were found for the Wet and Dry2 periods. Other regressions between cow/calf numbers in aerial counts and herb layer biomass were not significant. Total cow/calf numbers in ground counts were not significantly related to either rainfall or herb layer biomass.

3. Habitat use and preference in the Amboseli basin

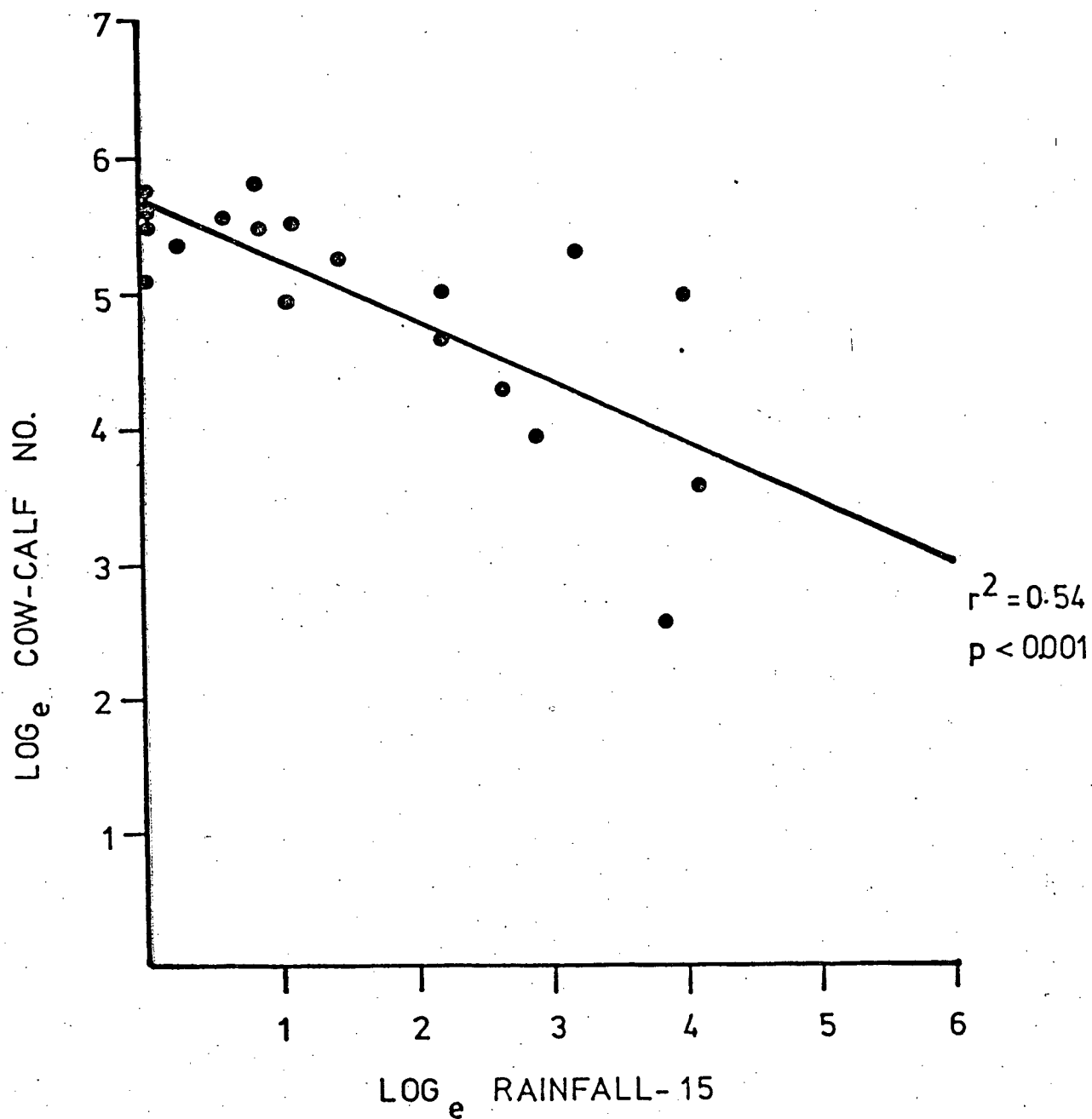


Figure 18. Log_e Cow/calf numbers in aerial counts of the Amboseli basin were negatively related to Log_e Cumulative rainfall total over the 15 days preceding each count, during the Dry1 period, 1975-1977.

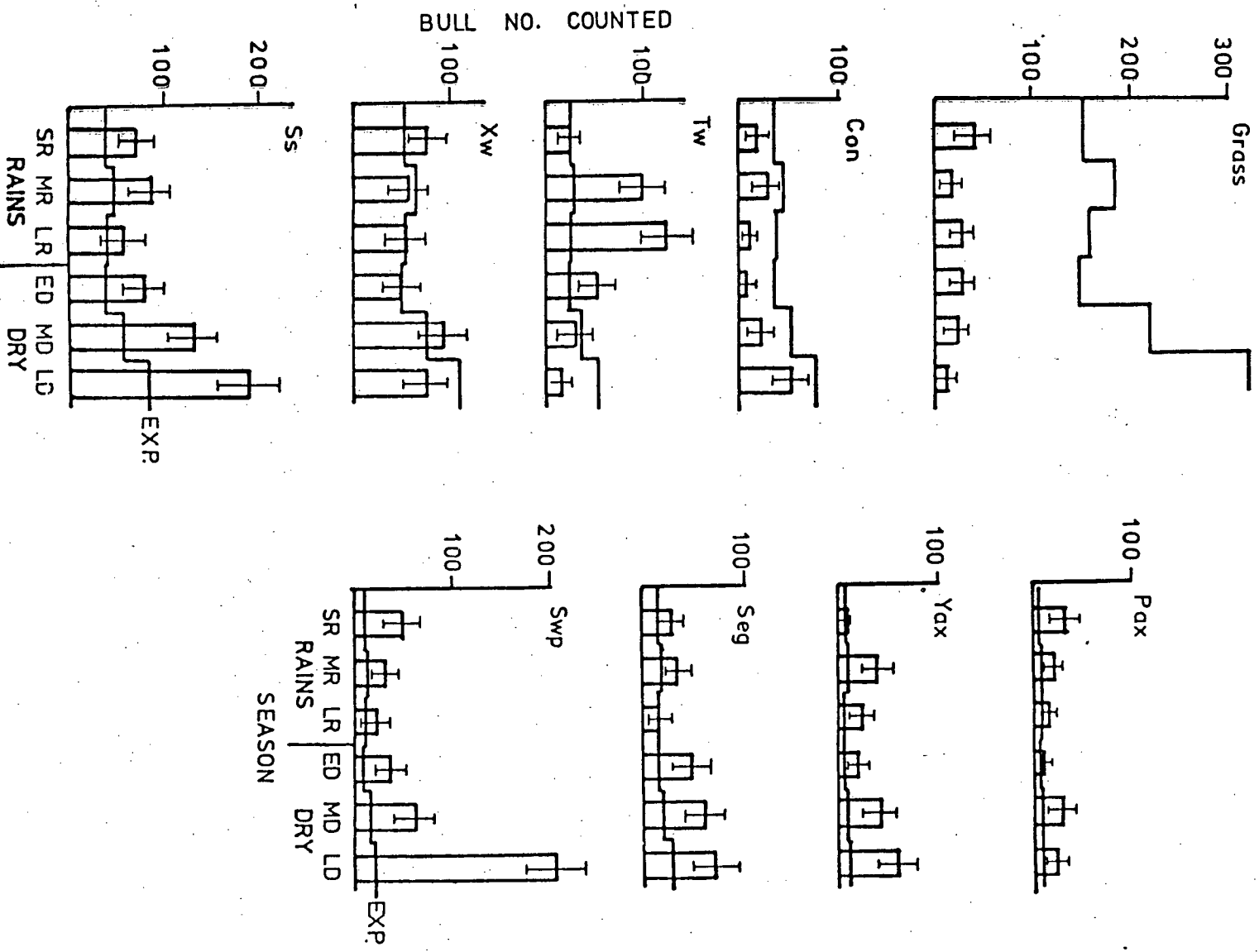
a. Bachelor bulls

The numbers of bachelor bulls seen in the different habitat types in each season of 1978/79 (ground counts) are shown in Figure 19. Monthly count densities (number counted per month / km²) in each habitat averaged over the whole year are shown in Figure 20. No elephants were ever observed on the lakebed grassland, so only nine habitat types were considered in initial analysis. The expected distributions based on occupancy proportional to habitat area are also plotted in Figure 19, as are the 95 percent simultaneous confidence intervals about the observed values. Habitats significantly preferred or avoided are found when the expected value falls outside the confidence limits about the observed.

In the S. consimilis grasslands, the main activities of bulls and breeding herds were standing and walking. Elephants were never seen feeding there, which could explain the low density noted in Figure 20. Casual observations suggested that patches of this type were commonly used as midday rest areas by the elephants. Elephants fed in all the other habitats, so I examined elephant distributions with respect to food availability in those eight habitat types only. Values for overall chi square goodness of fit with the expected random distribution are shown with and without the S. consimilis grasslands in Table 6. The observed habitat distributions were significantly non-random in all seasons.

Alkaline grasslands, although used to a small extent, were avoided at most times. The woodlands (Tw, Xw, Ss), especially

Figure 19. Total numbers of bachelor bulls counted in each habitat during ground counts in each season of 1978 /79. The horizontal lines represent expected numbers based on a random distribution proportional to the area of each habitat type. The vertical bars represent 95% simultaneous confidence intervals about the observed numbers. Significant preference or avoidance of habitat types is indicated when the "expected" line falls outside the confidence intervals. Grasslands were always avoided. Woodlands (Tw, Xw) were preferred in the rains and avoided in dry season, while swamp and swamp edges were more strongly preferred in the dry season and used to some degree throughout the year.



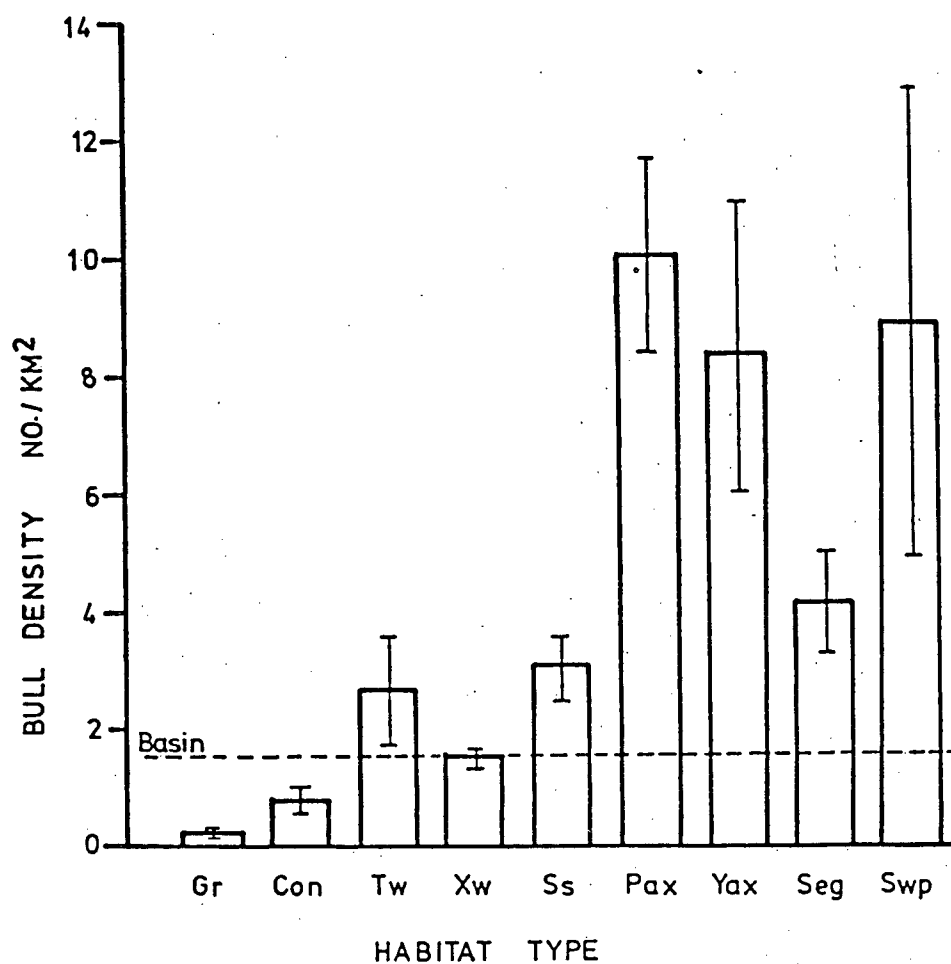


Figure 20. The yearly mean of monthly count densities (total numbers divided by area) of bachelor bulls in habitat types in 1978/79. The horizontal line indicates the overall mean density of bulls in the Amboseli basin, while vertical bars represent ± 1 standard error of the mean (note that preference or avoidance was not tested here). Bull densities in the swamps and swamp edges were always relatively high.

Table 6. Goodness of fit chi squared values of observed bachelor bull habitat distributions vs. an expected random distribution based on the areas of habitat types. These were calculated for the distribution across nine habitat types (including S. consimilis grassland), and eight habitat types (excluding S. consimilis grassland) in each season. All distributions were significantly non-random with $p < .001$.

CHI SQUARED VALUES FOR	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
9 Habitat types (inc. <u>S. consimilis</u>)	652	696	660	462	955	2822
8 Habitat types (exc. <u>S. consimilis</u>)	605	662	586	396	872	2716

at $p = .001$, with 8 df, chi squared = 26.1
with 7 df, chi squared = 24.3

A. tortilis woodlands, were preferred in the rains and, except for the Salvadora / Suaeda shrublands, avoided in the late dry season. The Salvadora / Suaeda shrublands (Ss) were preferred at all times, especially during the rains. The swamp edge woodlands (Pax, Yax) and grasslands (Seg) and swamps (Swp) were preferred in the dry seasons and were less preferred or even avoided in the rains. The wet swamps were used by some bulls throughout the year, but were especially preferred by bulls in the late dry season. Bull densities (see Figure 20) in the swamp edge woodlands (Pax, Yax) and the swamps (Swp) were high at all times; these habitat types cover small areas and received a proportionally large amount of use.

Similar patterns were seen in the long term aerial survey data, Figure 21, although there is a large amount of variability

in these results. Dry season use of the swamps and swamp edges was more pronounced in the Dry1 and Dry2 periods, while in the Wet period the elephants used the swamps less overall. In Dry1, rainy season woodland use was low, presumably because the bulls had left the basin entirely for the bushlands.

b. Cows and calves

The monthly numbers and overall mean count density of cows and calves in different habitats are shown in Figures 22 and 23. In Table 7, I show chi squared values comparing observed and expected numbers across habitat types, including and excluding the S. consimilis grasslands. The distribution of cow/calf groups across habitats was significantly non-random in all seasons, and most strongly so in the late dry season. The pattern of habitat use by cow/calf groups was generally similar to that of bachelor bulls. They showed preference for the woodlands (Tw, Xw, Ss) during the rains, and for the swamps (Swp) and swamp edges (Pax, Yax, Seg) during the dry season.

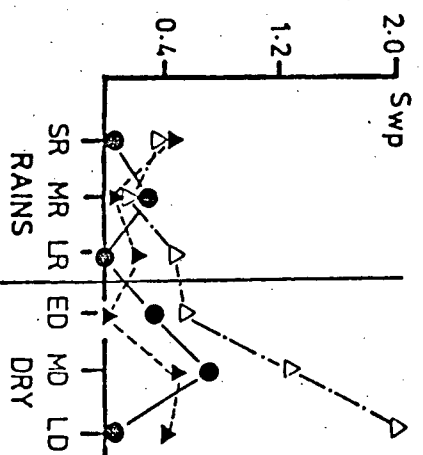
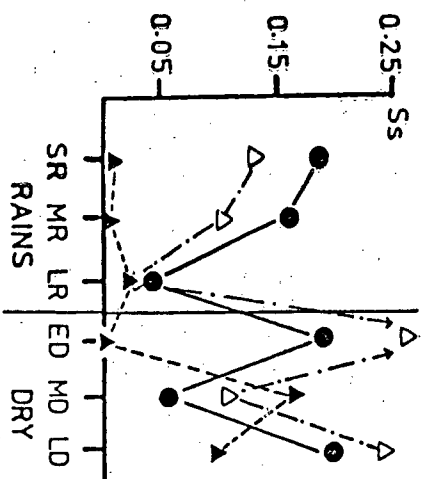
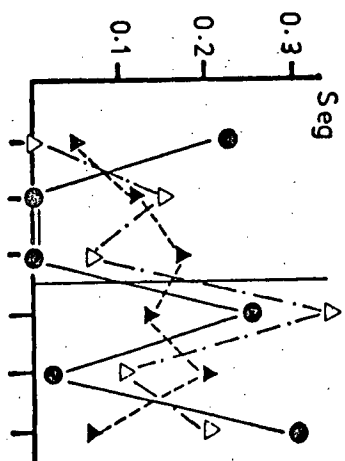
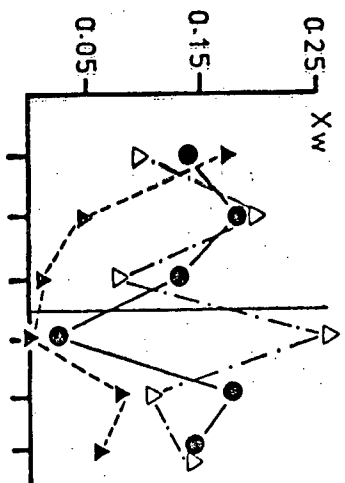
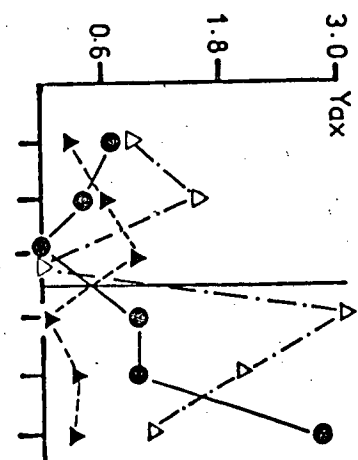
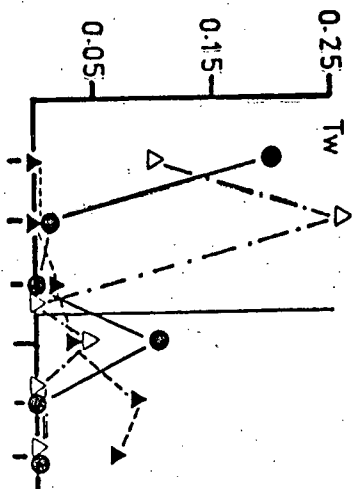
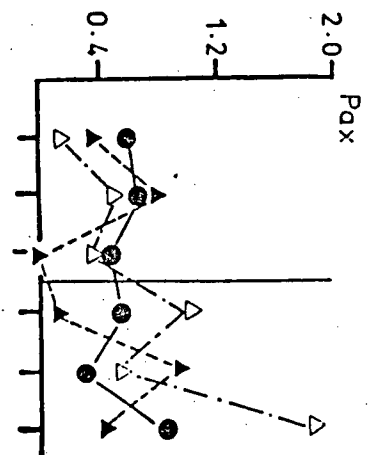
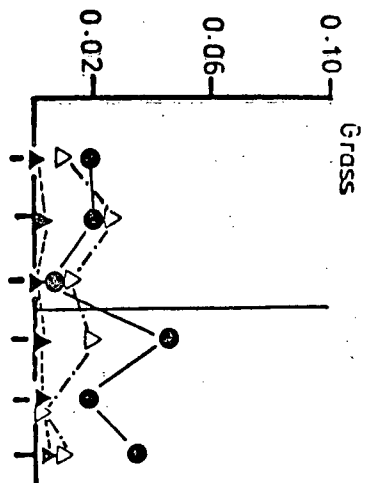
The distribution of bachelor bull numbers across habitat types was significantly correlated with the distribution of cow/calf numbers in the same habitat types in the mid and long rains and mid dry season (see Table 8). The correlations were lowest in the short rains and late dry season.

The use of habitats by cow/calf groups differed from the bull pattern in a number of ways. Individuals in the breeding herds were distributed more contagiously, ie. their numbers were more concentrated in specific habitats in each season than

Figure 21. Seasonal mean densities of bachelor bulls in habitat types as seen in aerial counts during the three rainfall periods:

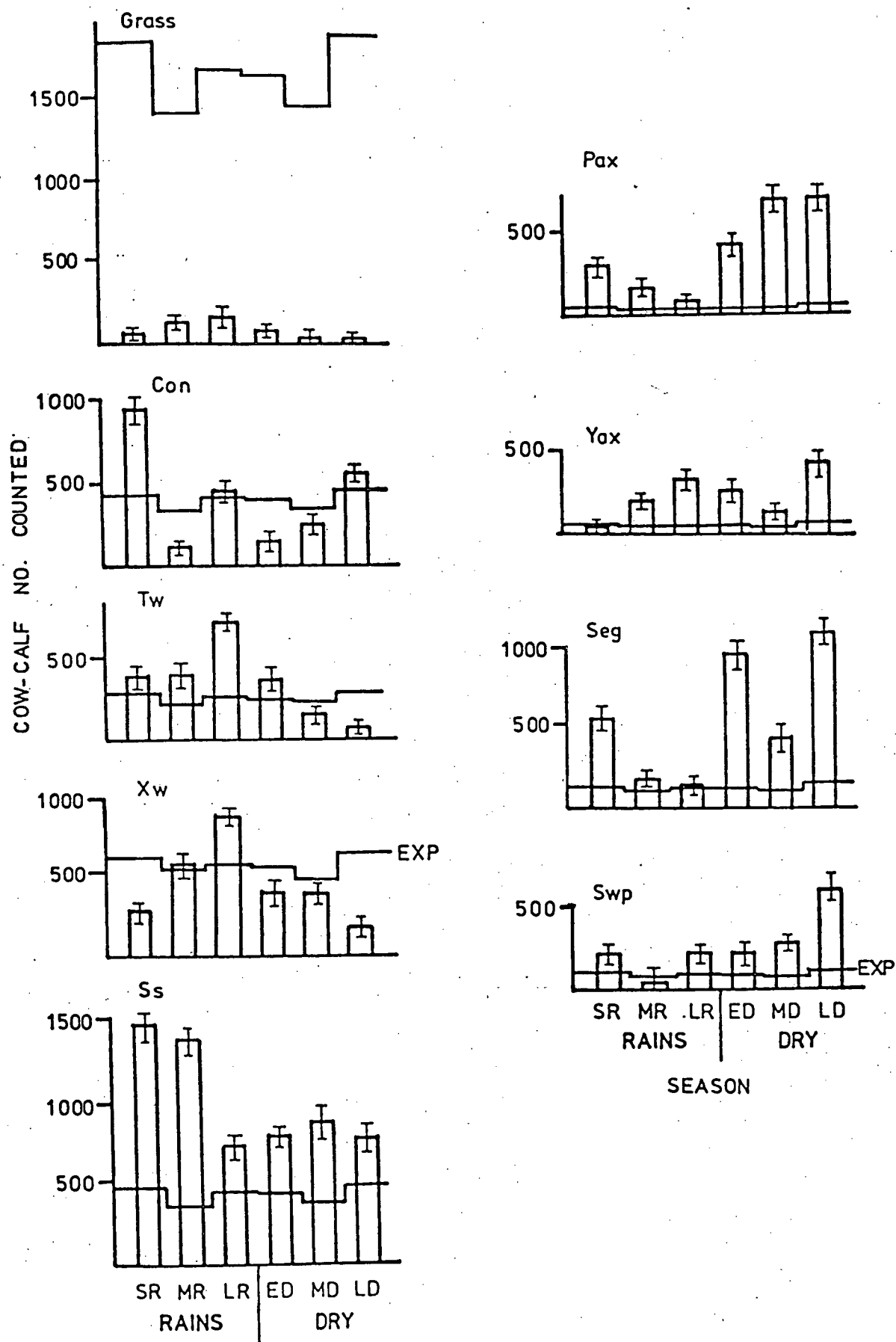
- ▲ Dry1 -- 1975-1977
- Wet -- 1977-1979
- △ Dry2 -- 1979-1980.

Bull densities were low in most habitats during the rains of Dry1 period, as many had left the basin (see above). In general, woodlands were used in the rains and swamps during the dry seasons. Use of the swamps and swamp edges appeared greatest in the Dry2 period.

BULL DENSITY NO./ KM²

SEASON

Figure 22. Total numbers of cows and calves seen in each habitat type during ground counts in each season of 1978 /79. Preference or avoidance of habitat types is indicated when the expected value (horizontal line) falls outside the 95% simultaneous confidence intervals about the observed numbers (see Figure 19). Grasslands were always avoided. Woodlands (Tw, Xw, Ss) were preferred most strongly in the rains, while swamps and swamp edges were most strongly preferred in the dry season.



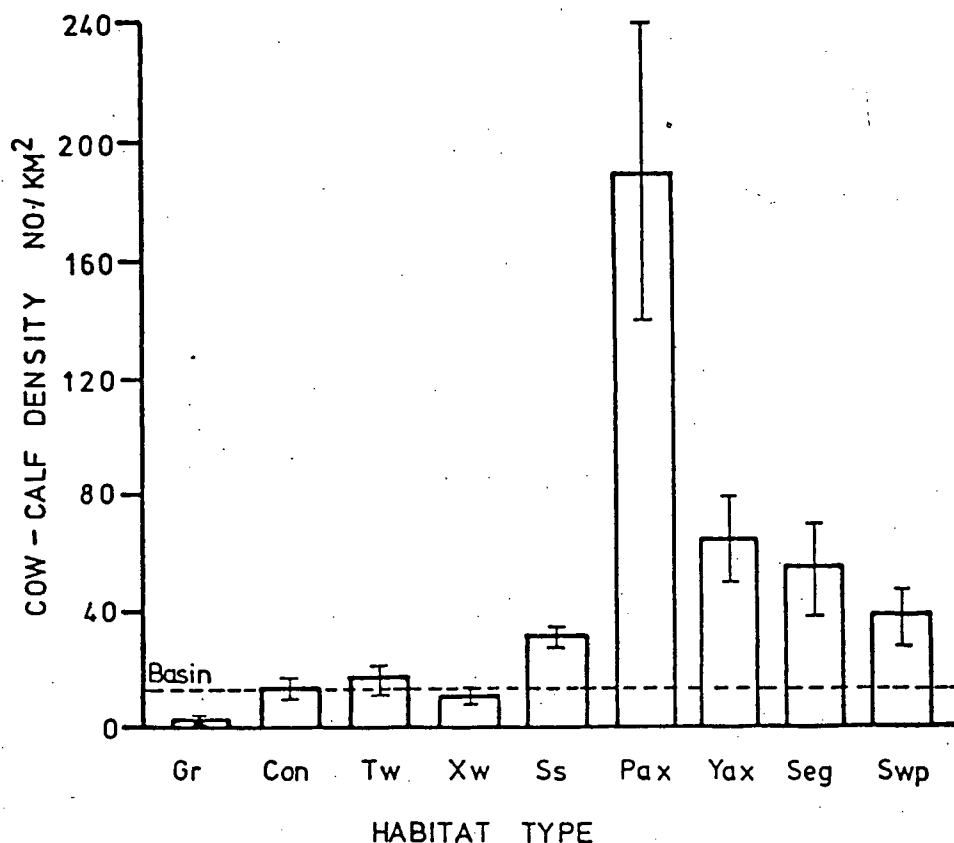


Figure 23. The yearly mean of monthly count densities of cows and calves in habitat types in 1978/79. As for bachelor bulls (see Figure 20), the horizontal line indicates overall mean density of cows and calves in the basin, while the vertical bars represent ± 1 standard error. Cow/calf density was always fairly high in the swamps and swamp edges, and highest in the palm/ fever tree swamp edge woodlands (Pax).

Table 7. Goodness of fit chi squared values of observed cow/calf habitat distributions vs. an expected random distribution based on the areas of habitat types. These were calculated for the distribution across nine habitat types (including S. consimilis grassland), and eight habitat types (excluding S. consimilis grassland in each season. All distributions were significantly non-random with $p < .001$.

CHI SQUARED VALUES FOR	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
9 habitat types (inc. <u>S. consimilis</u>)	.7840	5839	4501	13374	21956	25429
8 habitat types (exc. <u>S. consimilis</u>)	8340	5212	4542	12218	21151	25838

at $p = .001$, with 8 df, chi squared = 26.1
with 7 df, chi squared = 24.3

Table 8. Correlations (Spearman's rank) of bachelor bull and cow/calf numbers in habitat types in different seasons, showing significant correlation in the mid and long rains, and mid dry season.

	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Spearman's r_s	.070	.754*	.647*	.585	.685*	.568

Significance of Spearman's r_s (n=9): * $p < .05$

was the case with the bulls; therefore, their overall chi squared values were much higher. The cow/calf family units used the S. consimilis grasslands more (although irregularly), and

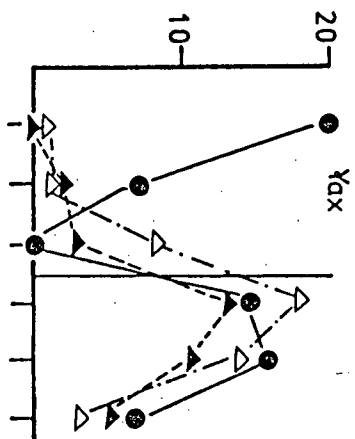
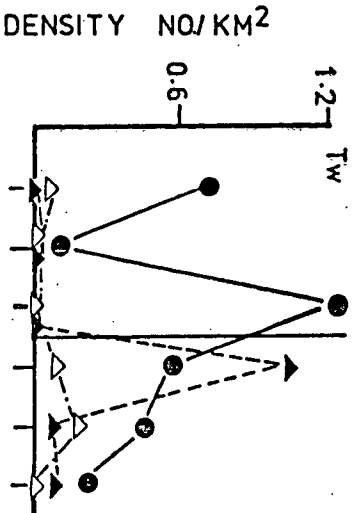
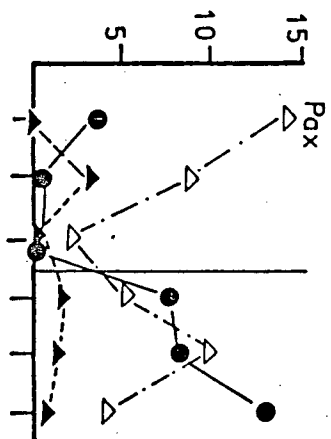
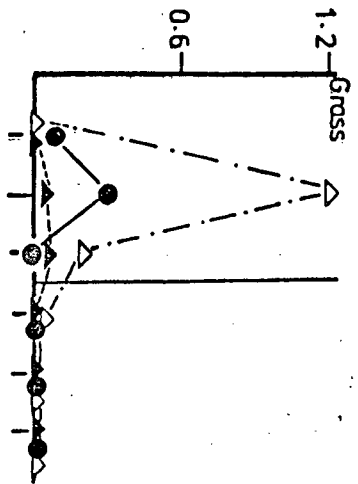
made more use of the more densely wooded habitats (Pax, Yax), especially during the late dry season. They showed a stronger preference for the open Salvadora / Suaeda shrublands during the rains, but less during the dry seasons, when bull preference for this habitat type increased. Cow/calf groups preferred the wet swamps (Swp) in the dry seasons, to a lesser degree than did the bulls, and made greater relative use of the swamp edge grasslands (Seg).

The habitat use patterns of cow/calf groups seen in aerial counts (see Figure 24) from different rainfall periods were somewhat similar to the 1978/79 ground count picture with a large amount of variability. In the Dry1 period, most family units left the basin in the rains and returned to the woodlands and swamps in the dry season. The Wet period pattern was similar to that found in the ground count analysis -- woodland use was high in the rains, with a dry season shift to the swamps. As with the bulls, there were some differences in specifics of cow/calf habitat use between the ground and aerial count results for this period that may have resulted from the difference in counting methods. The pattern in Dry2 period was different; less use was made of the A. tortilis woodlands and more use of the swamps and swamp edges throughout the year, especially during the dry season.

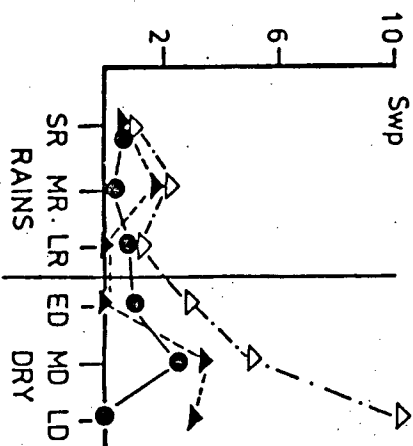
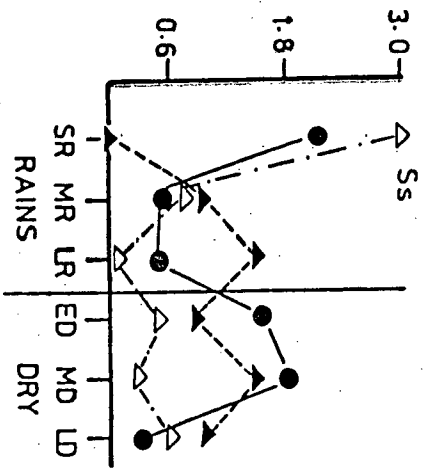
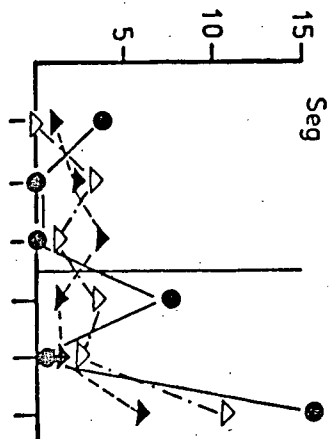
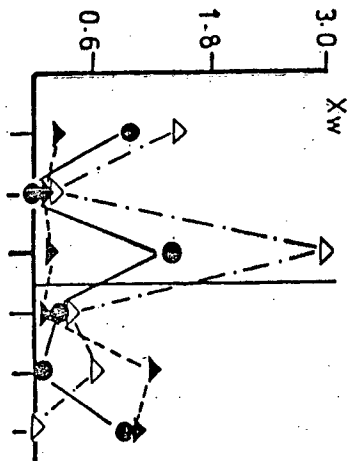
Figure 24. Seasonal mean densities of cows and calves in habitat types, as seen in aerial counts during the three rainfall periods:

- ▲ Dry1 -- 1975-1977
- Wet -- 1977-1979
- △ Dry2 -- 1979-1980.

Cow/calf densities were low in most habitat types during the rains of the Dry1 period. In general, woodlands were used more in the rains, and swamps more in the dry seasons. The swamps and swamp edges were used more by cow/calf groups in the Dry2 period.



COW - CALF DENSITY NO/KM²



SEASON

4. Habitat use in relation to climate and vegetation

a. Bachelor bulls

Linear regression plots of bachelor bull numbers in ground counts against total rainfall of the previous month, herb layer total dry mass, and herb layer green mass are shown in Figures 25 to 27. There are some clear trends in these data, although there is also a great deal of variance. Bull numbers were positively related to rainfall and herb layer biomass, in the grasslands and the A. tortilis woodlands, and, in general, inversely related to swamp and swamp edge herb layer biomass. The fever tree woodlands and Salvadora / Suaeda shrublands were used by many bulls at all times of year, and the latter especially in the late dry season. Hence, use of these habitat types was negatively related to seasonal rainfall and biomass. The only regression that was significant was bull numbers vs. total biomass in the A. tortilis woodlands (see Figure 26). The relation of bull numbers to green mass in habitats was generally less strong than was the relation to total herb layer biomass.

The results of rank correlation of bull densities with plant biomass density across habitat types are shown in Table 9. Significant correlations of bull densities with herb layer total biomass and green biomass occurred mainly in the dry seasons; the correlations with total and green mass were about equally significant overall. Woody biomass alone was a poor predictor of bull density, but when combined with herb layer biomass, especially total herb layer biomass, it produced significant

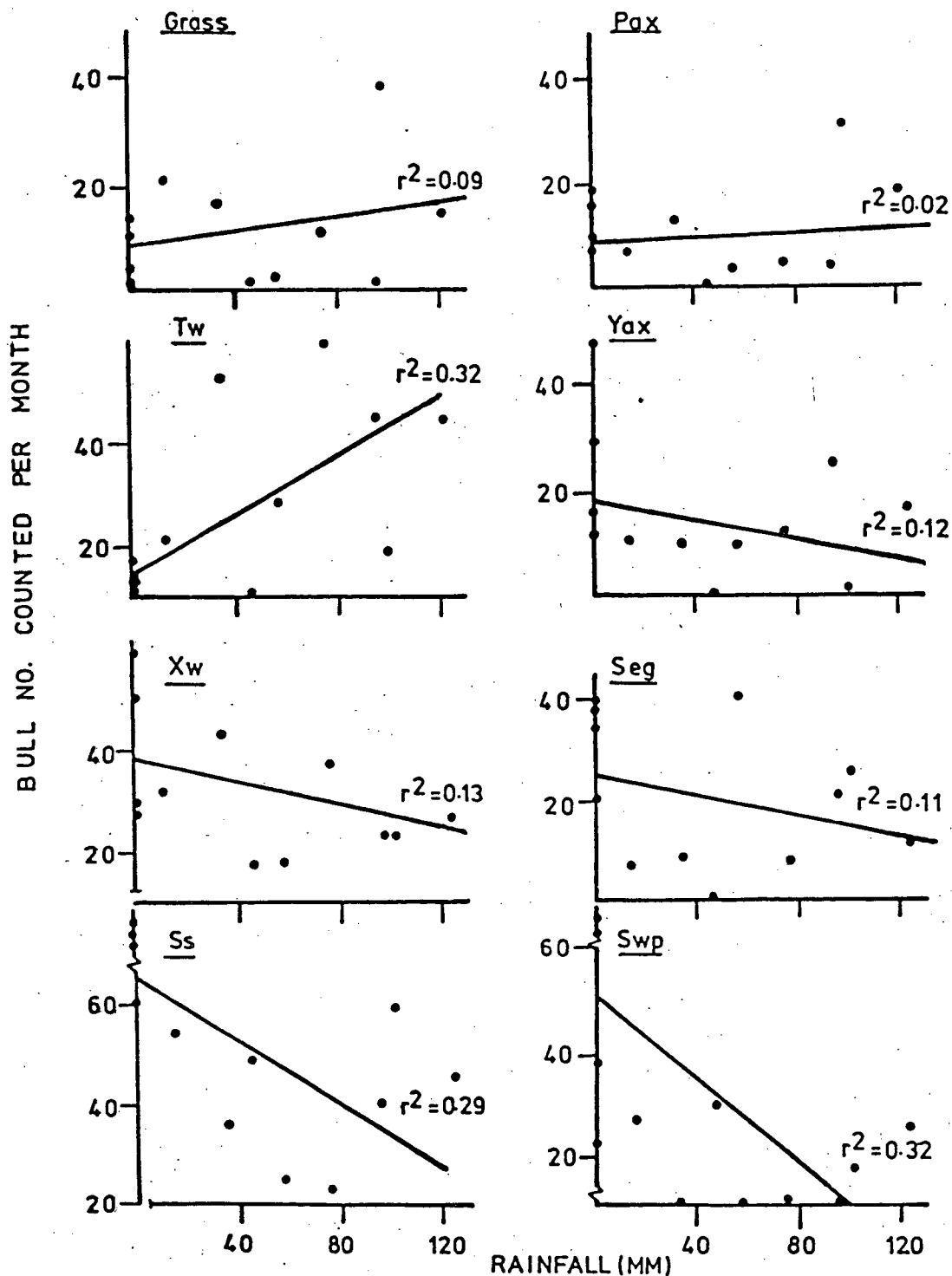


Figure 25. Linear regressions of monthly totals of bachelor bulls seen in habitat types in ground counts in 1978/79 vs. total rainfall of the preceding month. Slopes are positive for alkaline grasslands, *A. tortilis* woodlands, and palm/fever woodlands, and negative for other woodlands and the swamps and swamp edges. No regressions were significant.

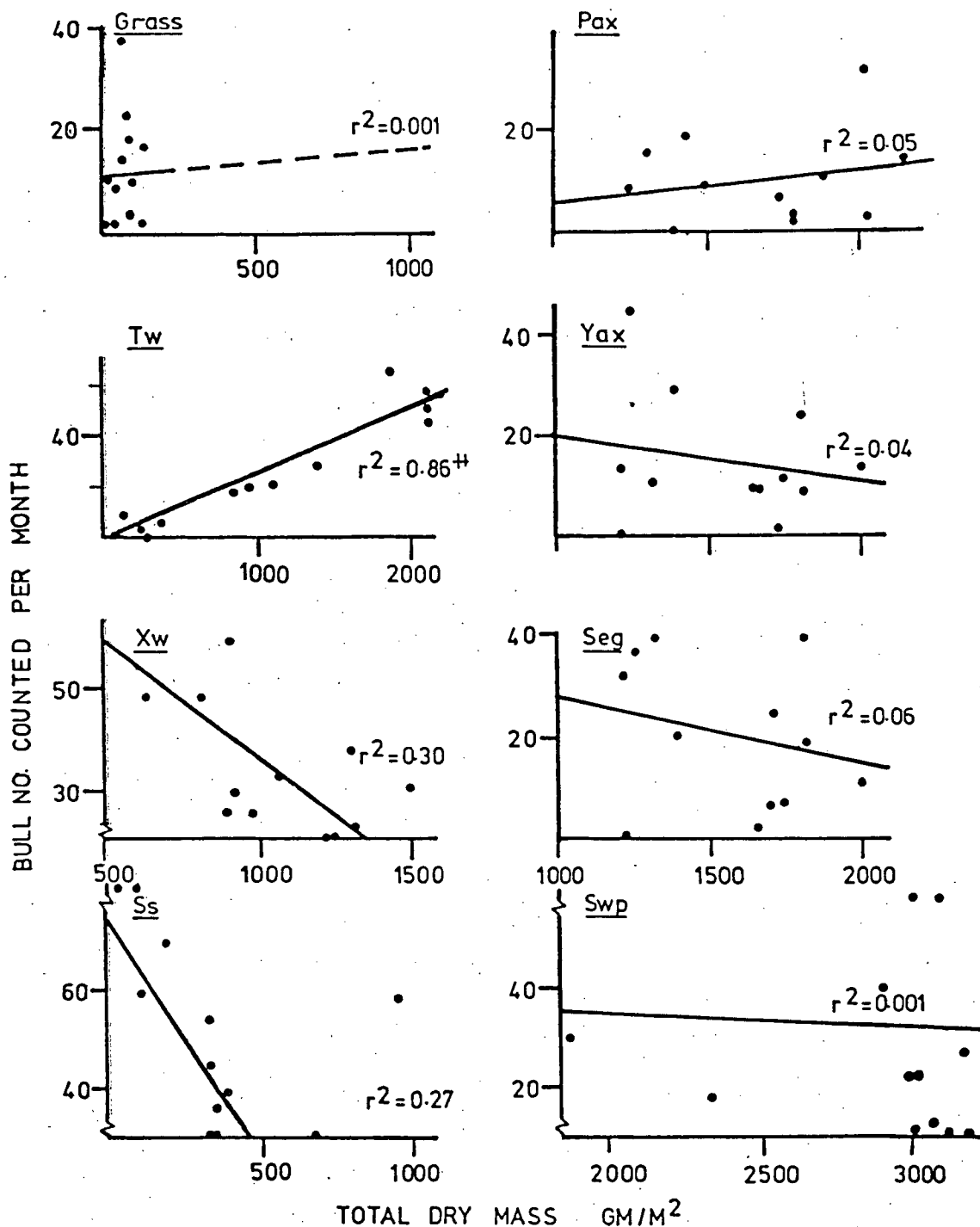


Figure 26. Linear regressions of bachelor bull monthly totals in habitat types vs. total herb layer biomass in the middle of the current month. Slopes are positive for alkaline grasslands, *A. tortilis* woodlands, and palm/fever woodlands, and negative for other woodlands and swamps. ++ indicates a regression significant at $p < .01$, for the *A. tortilis* woodlands. No other regressions were significant.

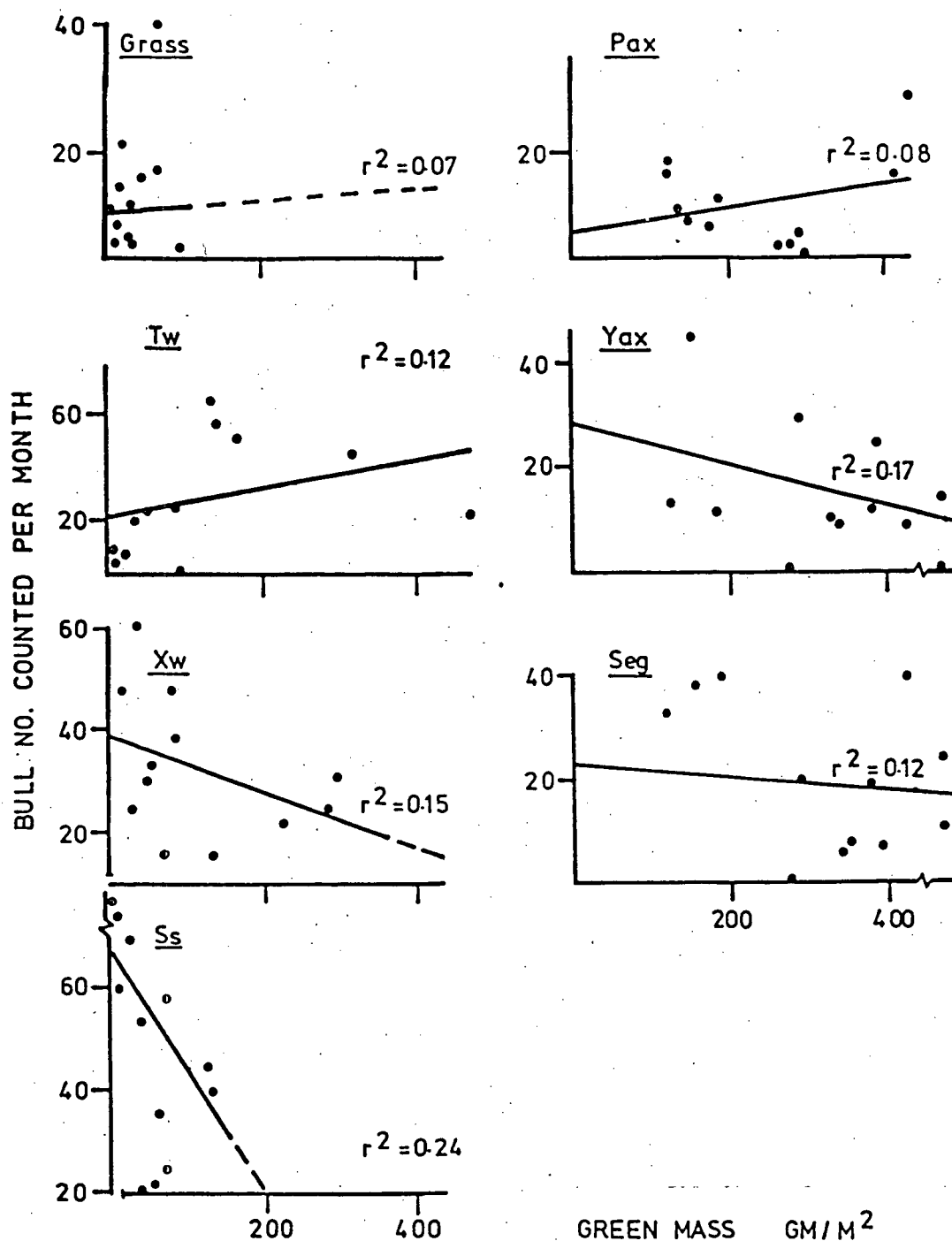


Figure 27. Linear regressions of bachelor bull monthly totals in habitat types vs. green herb layer biomass mid-month. Slopes are positive for alkaline grasslands, *A. tortilis* woodlands, and palm/fever woodlands, and negative for other woodlands and swamps. No regressions were significant.

Table 9. Correlations (Spearman's rank) of bull densities with total mass and green mass of the herb layer, and twig/leaf mass and % cover of the woody layer across habitat types in different seasons in 1978/79. Significant correlations with herb layer biomass occurred in the dry season. Correlations with twig/leaf mass alone were generally not significant, but were significant when twig/leaf mass was added to herb layer biomass. Bull density did not correlate with % woody cover.

SPEARMAN'S Rs: BULL DENSITY VS.	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Herb layer total biomass	.613	.720*	.637	.780*	.839**	.887**
Herb layer green biomass	.304	.577	.470	.845**	.673*	.976**
Woody layer twig/leaf mass	.042	.530	.673*	.375	.375	.065
Total herb + twig/leaf mass	.548	.762*	.690*	.762*	.810*	.857**
Green herb + twig/leaf mass	.524	.619	.429	.881**	.786*	.857**
% woody cover	-.006	.601	.601	.232	.494	.185

Significance of Spearman's r_s (n=8):

*	p < .05
*	p < .01

correlations across habitats in the long rains and dry season. There were no significant correlations between bull density and percent ground cover by woody shrubs.

b. Cows and calves

Regressions of monthly cow/calf numbers in habitat types as seen in the ground counts against total rainfall in the month preceding the counts, herb layer total biomass, and green biomass are shown in Figures 28 to 30. Cow/calf numbers in the alkaline grasslands and woodlands (both A. tortilis and fever tree woodlands) were positively related to rainfall and herb layer biomass (both total and green mass), and, in general, negatively related to herb layer biomass in the swamp edge habitats (Pax, Yax, Seg). The relation of cow/calf numbers in the Salvadora / Suaeda shrublands to rainfall and green mass was positive, but to total mass, weakly negative. The only regressions which were significant were between cow/calf numbers in the swamp edge palm woodlands (Pax) and the wet swamps (Swp) and rainfall (see Figure 29), and between cow/calf numbers in the A. tortilis woodlands and total herb layer biomass (see Figure 30).

Rank correlations of cow/calf count densities with vegetation variables across habitat types, Table 10, were also similar to the bachelor bull results. Cow/calf density was significantly related to herb layer biomass in the dry season only, when the animals were using the swamp and swamp edge habitats. It appears that both herb layer total biomass and

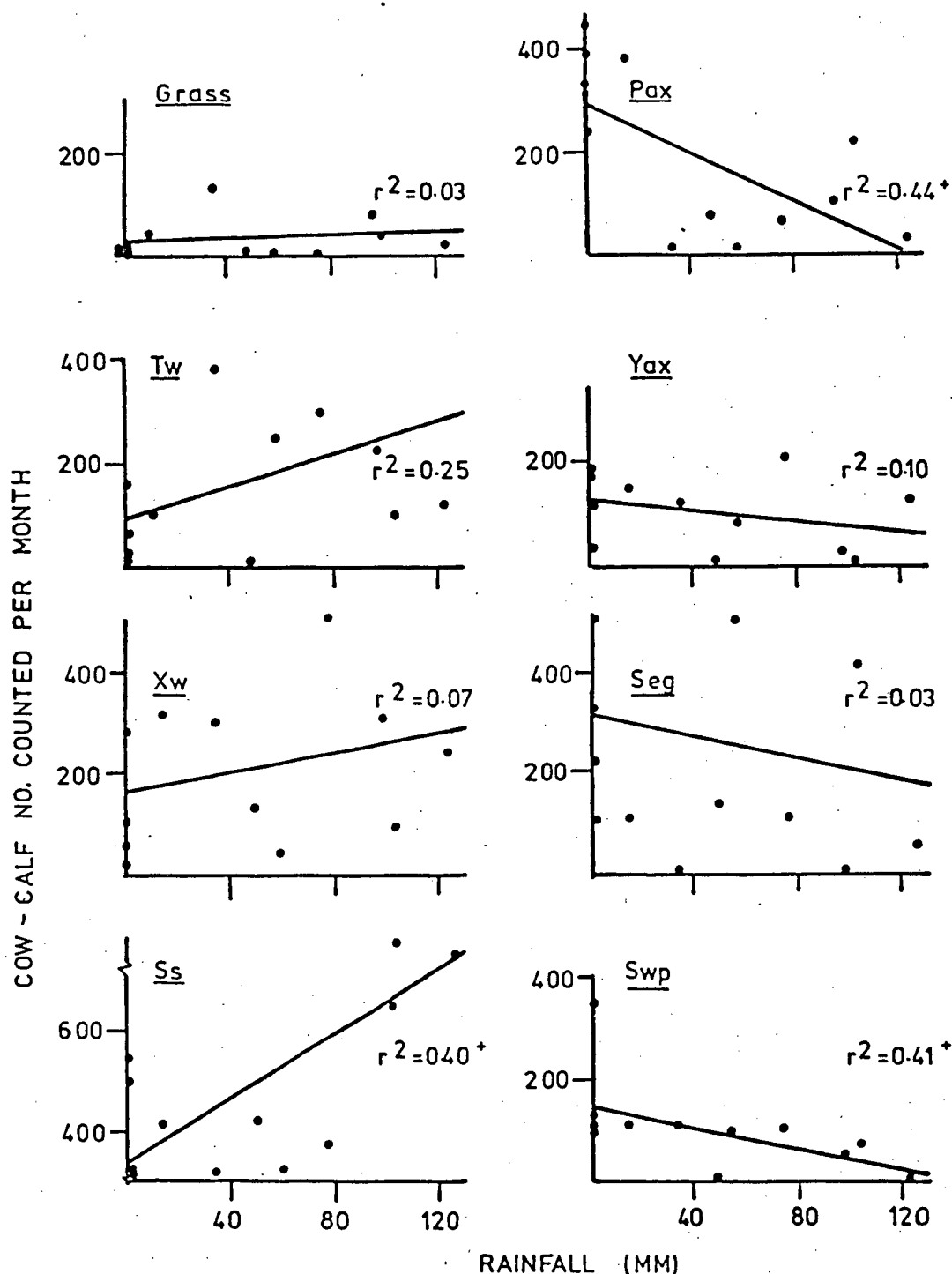


Figure 28. Linear regressions of cow/calf monthly totals in habitat types vs. total rainfall of the previous month. Slopes are positive for alkaline grasslands, *A. tortilis* woodlands, Fever tree woodlands, and *Salvadora/Suaeda* shrublands, and negative for swamps and swamp edges. + indicates regressions significant at $p < .05$, for the *Salvadora/Suaeda* shrublands, palm/fever woodlands, and wet swamps.

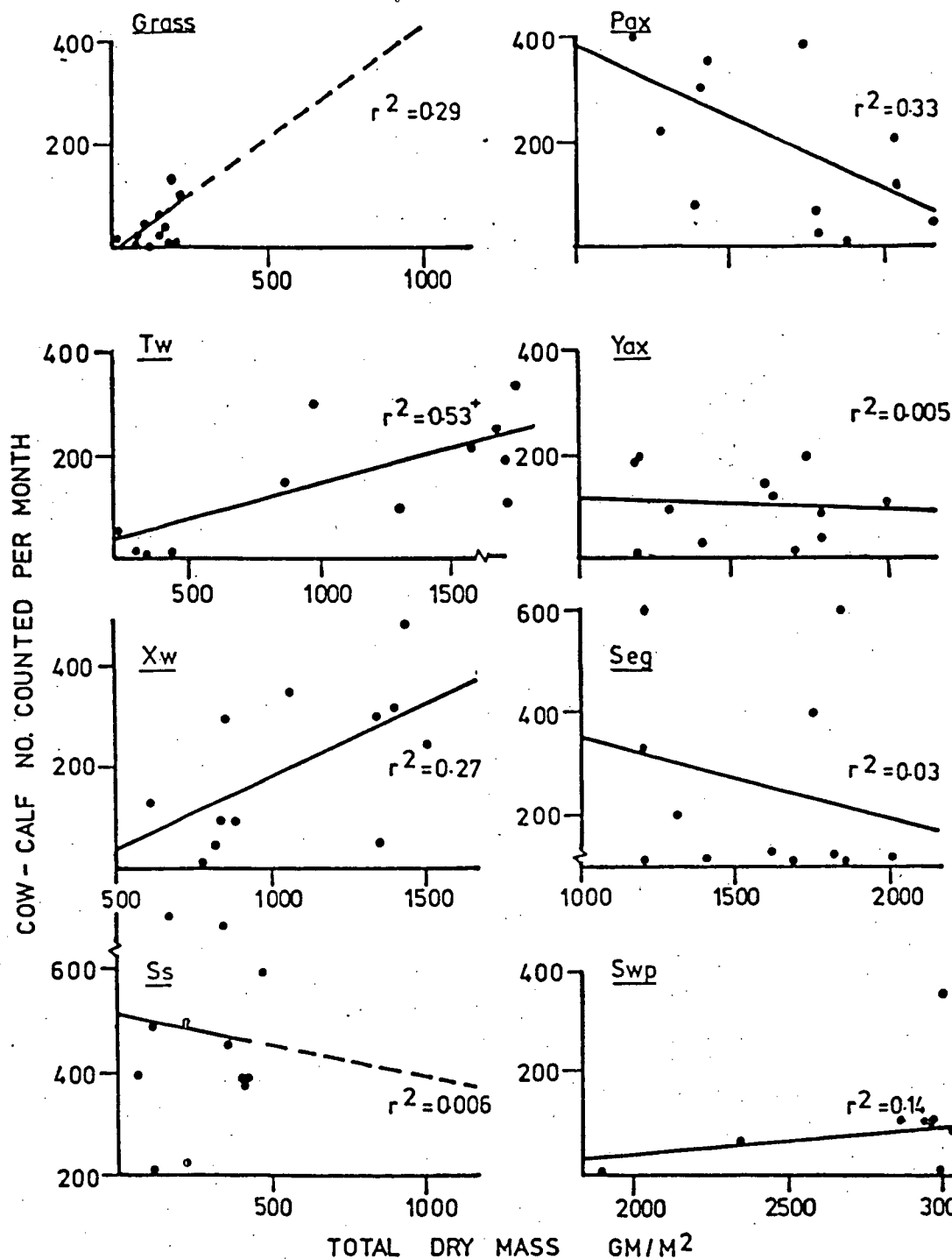


Figure 29. Linear regressions of cow/calf monthly totals in habitat types vs. total herb layer biomass mid-month. Slopes are positive for alkaline grasslands, *A. tortilis* woodlands, fever tree woodlands, and wet swamps, and negative for *Salvadora/Suaeda* shrublands and swamp edge habitats. + indicates a regression significant at $p < .05$, for the *A. tortilis* woodlands.

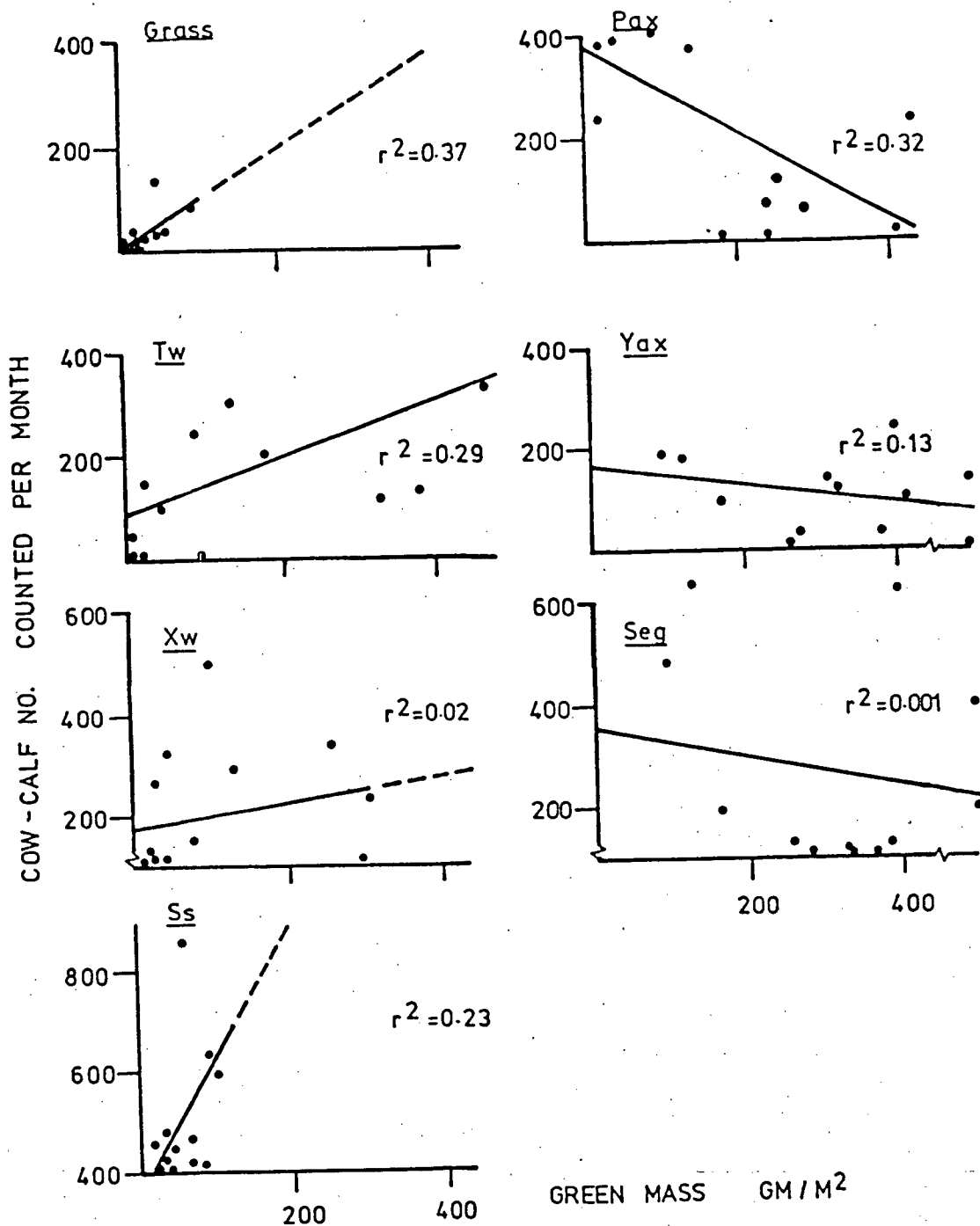


Figure 30. Linear regressions of cow/calf monthly totals in habitat types vs. green herb layer biomass mid-month. Slopes are positive for the alkaline grasslands, *A. tortilis* and fever tree woodlands, and *Salvadora/Suaeda* shrublands, and negative for the swamp edge habitats.

Table 10. Correlations (Spearman's rank) of cow/calf densities with total and green mass of the herb layer, and twig/leaf mass and % cover of the woody layer across habitat types in each season of 1978/79. Significant correlations with herb layer mass occurred mainly in the dry season. Correlations with twig/leaf mass alone were generally not significant, but woody mass + herb layer mass correlations were significant. Correlations with % woody cover were significant in the mid and long rains, and late dry season.

SPEARMAN'S Rs: COW/CALF DENSITY VS.	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Herb layer total biomass	.494	.399	.577	.780*	.780*	.756*
Herb layer green biomass	.232	.232	.482	.738*	.637	.810*
Woody layer twig/leaf mass	.292	.696*	.506	.577	.506	.554
Total herb + twig/leaf mass	.429	.452	.524	.786*	.786*	.726*
Green herb + twig/leaf mass	.452	.262	.405	.714*	.762*	.738*
% woody cover	.196	.720*	.696*	.411	.435	.649*

Significance of Spearman's r_s (n=8): * $p < .05$

green biomass correlated about equally well with cow/calf densities in habitat types, with slightly stronger relationships with total dry mass. Woody biomass alone correlated significantly with density in the mid rains only, but in contrast to the bull situation, the correlations were not improved by combining twig/leaf biomass with herb layer biomass. Cow/calf density correlated positively with percent woody cover in habitats in the mid and late dry season.

5. Observations of individual movements

Casual observations of known individuals and cow/calf family units suggested that movement patterns were quite different for different individuals and family units, and that they also varied considerably between seasons. In the general diurnal foraging pattern of many cow/calf herds and, to a lesser extent, bachelor bulls, in the Amboseli basin, a group of one or more individuals or family units entered the basin at its northern or southern edge in early to mid-morning. The group then fed in woodlands or swamp fringes, working its way towards the vicinity of permanent water in the central basin by midday. In late afternoon, the group began moving back towards the basin edge, and remained in basin edge woodlands or moved farther out into the bushlands, where the elephants spent the night feeding and sleeping. The pattern of entering the basin habitats during the day and leaving at night might be repeated in following days, or the elephants might spend a day or more feeding in bushland areas before returning to the basin.

Individual family units appear to have fairly specific and distinct, but often overlapping, dry season home ranges (Moss 1980, 1981), which cover differing portions of the Amboseli basin, and which might alter the basic pattern described above. Some family units were rarely seen in the basin during the dry season, and apparently foraged in the semi-arid southern bushlands most of the daytime, visiting the basin swamps at night. Other groups periodically entered the basin during the day, while still others used specific areas of the basin on a very regular basis. The structure of home ranges changed dramatically during the rains, when elephant family units from all parts of the basin and its peripheries mixed together and moved across all areas of the basin and over large areas of bushland.

The movement patterns of individual bulls are less well documented. Bulls appear to have specific home ranges which may overlap with those of other bulls, and these may change on a seasonal basis (C. Moss, J. Poole, pers. comm.). However, the bulls' ranging patterns are apparently altered during periods of reproductive activity, when they may associate with cow/calf herds. Ranging and grouping behaviour may also change with the age of bulls, as they are apparently more gregarious when they are younger, and might have different home ranges (J. Poole, pers. comm., in prep.). The ranging patterns of individuals and groups of both bulls and cow/calf family units needs further study to examine the causes and consequences of individual differences.

D. Discussion

Studies of resource preference, whether the resource is food, a place to feed, or some other objective of value, generally involve a comparison of use and availability. However, as Jacobs (1974) noted, most indices of preference are based on the implicit, but often unrecognized, assumption that all items on offer are of equal abundance. If the items are available in unequal proportions, it is difficult to realistically demonstrate preference of items which are relatively common (unless use is very high), or avoidance of items which are relatively rare (unless use is very low). Johnson (1980) echoed this point, and added a further caution for the study of habitat or diet preference. He suggested that it is better to regard use and choice as relative decisions between the number of different items found on offer at a particular time and place, rather than as absolute preference. The definition of "different" resources such as habitat types, can be arbitrary or variable, yet can influence the outcome of an analysis which compares use and availability on an absolute scale. He recommended that ranked use and availability be averaged for individuals in a sample, and that selection or rejection be evaluated on the basis of difference between ranks.

In the current study, I did not record the use of habitats by individual elephants, but rather by the elephant population as a whole. Habitats were not all equally abundant -- the areas occupied by different habitat types differed greatly (see Table 4). I used rank comparisons in looking at the distribution of

elephant numbers with plant biomass across habitats, and I viewed the observed differences between habitat use by elephants and availability as relative preference between the defined habitat types.

1. General pattern of seasonal habitat preference

It would appear that, as a general rule, elephants select habitats for the most profitable foraging opportunities, within limits imposed by their requirements for surface water.

Western (1975) and Leuthold(1977b) showed that the availability of surface water restricted the number of habitats available to elephants in dry seasons. Elephants concentrate in the vicinity of permanent water sources in the dry seasons, and can venture farther afield during rainy periods. The survey data analyzed in the current study supported these observations in the Amboseli ecosystem, notably in the pre-1977 drought years. During that period, the cow/calf groups responded very strongly to short term rainfall (over two weeks), by moving out of the basin habitats in a preference for the diverse and productive bushlands, and returning promptly after the rains. The bachelor bull herds appeared to respond to rainfall by emigration, and to drought by immigration, over a much longer term (three months) -- however, this result may be a spurious statistical artefact, since the effects of rainfall, desiccation, and herbivore consumption on both surface water and herb layer biomass abundance would change considerably during such a long period (Western 1975). The large scale movement

patterns of bachelor bulls may be complicated by their seasonal association with cow/calf groups.

During the years following the 1977/78 rains, the elephants stayed close to the Amboseli basin for much of the year (all areas of the Amboseli basin are within a few kilometres of water). This "natural experiment" suggested that limitation of water availability alone was not sufficient to explain the large scale habitat use patterns, and that the relative availability of herb layer vegetation (which is most responsive to short term rainfall) in different habitats, was also important.

Herb layer vegetation may be the most profitable food source for elephants within habitat types through much of the year. Some preliminary studies of elephant feeding behaviour (Guy 1976, Wyatt and Eltringham 1974), suggested that elephant feeding rate may be higher on herb layer vegetation than on woody browse. Woody plant material is often of higher quality than the grasses of the herb layer, but it is also much less abundant in most habitat types, at most times of year (see Chapter 3). For an animal like the elephant, which needs to maintain a large and fairly constant rate of nutrient intake, the herb layer of most habitat types would probably provide the best foraging opportunities through much of the year, unless its abundance is too low to allow a high intake rate, or its quality is too low for a net gain in nutrients. Profitability would be highest in habitats where the herb layer is of the highest quality, and where it is sufficiently abundant to allow a high intake rate. I have no data on the feeding rate of elephants at

different herb layer biomass levels, and this is an area which needs further work.

In Amboseli, herb layer quality is not necessarily directly related to plant greenness per se. The relationships between elephant numbers and herb layer biomass were more significant for total biomass in the herb layer, than green mass, suggesting that the greenness of vegetation was less critical as a feeding cue. This contrasts with the reported importance of green grass to other large herbivores, such as the African buffalo (Sinclair 1977).

In the general pattern, elephants use the woodlands or bushlands in the rains when their herb layers, which have the highest nutrient content, are abundant enough for profitable foraging. When the herb layer of these habitats becomes reduced through consumption in the dry season, or, in the case of the bushlands, surface water also becomes limiting, they concentrate in the ground water habitats -- swamp (Swp), swamp edge (Seg), and swamp edge woodlands (Pax,Yax). In these habitats, the herb layer biomass is high, but of lower quality. It may become profitable to feed on woody plant material at this time.

In the extended period of low rainfall in the Dry1 period prior to 1977, elephants travelled out to northern bushland areas for rainy season feeding, and returned to the woodlands and swamps in the dry season. In such low rainfall periods, herb layer production in rainfall-dependent habitats is relatively low and biomass falls to low levels under herbivore consumption in the dry season. Swamp edge biomass was also

fairly low by the end of the dry season. Bushland herb layers appear to respond to the early rains more quickly than the basin habitats, and would be relatively more attractive under these conditions.

In the years of higher rainfall, 1977 to 1979, most of the elephants moved much less in the rains; they stayed in the vicinity of the basin through much of the year. I suggest that this was because of the increased abundance of high quality woodland herb layer (relative to food quality in the swamps). They did not have to travel to the usual bushland habitats in the wet season. In the low rainfall year of 1979/80, the cow/calf groups did not resume the movement pattern of the previous drought, possibly because of a conservative habitat use strategy, or because the swamps and swamp edge herb layers were still abundant and relatively more attractive as feeding sites than the distant bushlands. I would predict that after a longer period of extended drought, when basin swamp, swamp edge, and woodland herb layers are significantly reduced by the end of the dry season, the elephants would return to a basin/bushland large-scale movement pattern. Leuthold (1977b) noted that in areas of higher rainfall within the Tsavo ecosystem, cow/calf home ranges were smaller, and he speculated that this may have been due to greater local food availability. This system might also operate between years of different rainfall in the same area, such as in Amboseli.

The difference in distribution across habitat types between bachelor bulls and cows and calves was greatest in the early

rains and late dry season. The early rains were times when the cow/calf groups were using the Salvadora / Suaeda shrublands and S. consimilis grasslands much more than the bulls. During the late dry season, the cow/calf groups used the swamp edge grasslands much more than did the bulls, while the bulls used the swamps more than did the family units. Differences in habitat use by bachelor bulls and breeding herds could be due to metabolic differences in food requirements between the sexes (see Chapter 6, General Discussion), or to differences in social behaviour (see Chapter 5). Habitat distributions of the bulls and cow/calf groups were similar through much of the rest of the year.

Bachelor bull herds showed some degree of large-scale movement to bushlands during the wet season in all climatic periods. Their eventual dry season concentration in the basin was probably dictated by water availability. Over the whole gender class, bulls were less selective of habitats than the cow/calf herds. It is likely that Amboseli bulls are more mobile than cow/calf groups, and have larger home ranges than do family units. Leuthold and Sale (1973) and Leuthold (1977b) described this for elephants in the nearby Tsavo West National Park. Family unit mobility and habitat selection might be affected by the presence of small calves or other slow-moving individuals in the groups.

Average patterns of habitat use shown by the population may not accurately reflect habitat use by individual groups of cow/calves or bulls. Cow/calf groups (and possibly bull groups)

remain within specific home ranges in the dry season, and tend to avoid each other (Douglas-Hamilton 1972, Leuthold 1977b, Moss 1981). Partitioning of the Amboseli basin and its surroundings into home ranges allows access for some groups and precludes access for others to the Amboseli basin. The "availability" of habitats to certain groups may be decided by their choice, or lack of choice, in home ranges.

More work must be done on the movements of individuals and family units, and the underlying causal mechanisms of the apparent partitioning of the ecosystem. The development of models which are more sophisticated than simple linear relationships may be needed to explain more of the variance in elephant habitat use patterns.

2. Departures from the general pattern

Some habitats with substantial herb layer biomass were not visited (lake bed grasslands), or were not used for feeding ()u S. consimilis grasslands). Others were used for foraging, yet had low biomass (alkaline grasslands, Salvadoria / Suaeda shrublands).

Lakebed grasslands had a low quality herb layer, fairly low biomass density, and they are located some distance away from permanent water sources (see Figure 4). They are not near any woodlands nor the traditional diurnal foraging routes from bushlands to swamps. They were apparently not worth a "special trip" for foraging elephants, and were even given little attention during rainy season movements.

The S. consimilis grasslands are somewhat of a special case, but one which may point to the relative nature of habitat preference. I never saw elephants feeding in this habitat type, yet occupancy, especially by cow/calf groups, was fairly high in the early rains. The tall, coarse grass, S. consimilis, undoubtedly has a high fibre and low protein content, and is likely to be an unprofitable food plant. I would have expected elephants to avoid this habitat for feeding. Yet, according to other observers (D. Western, C. Moss pers. comm.), elephants fed here during the drought years before 1976, when the tall, abundant grass may have been more attractive than the greatly reduced herb layers of nearby plant communities. I can only speculate on the reasons why elephants, and particularly cow/calf groups, would use the areas for midday rest periods, since they offer neither shade nor surface water during much of the year. Patches of this habitat type are generally found near swamp edges or woodlands and are thus near favoured feeding habitats. Tall grass may afford some cover to smaller individuals of cow/calf groups when they are resting. I occasionally observed disturbed cow/calf herds run to patches of S. consimilis where they halted and gradually calmed down, suggesting that the elephants felt somehow "safer" in those areas than in other places.

The alkaline grasslands consistently had the lowest herb layer biomass density (it never rose above 200 g/m²) and its grasses were of low to intermediate nutritional quality. The alkaline grasslands were probably the least profitable habitat

used by elephants for foraging. My casual observations suggested that the only areas where elephants ventured out onto the alkaline grasslands were adjacent to woodlands, Salvadora / Suaeda shrublands, or swamps, and there may have been a "boundary effect" (Lamprey 1963) taking place.

The Salvadora / Suaeda shrublands were preferred through most of the year by family units and bulls, yet had a relatively low herb layer biomass density. One possible reason for the high amount of use of this habitat could be its location towards the center of the basin (see Figure 3) near the midpoint of the general daytime foraging path described in Section 4.3.4 above. This location could increase the likelihood of the daytime counting bias described in the Methods section; central basin habitats might be used less over the whole 24 hour day, yet be more represented in my daylight-biased survey counts. It may also be that the open, lightly wooded nature of this habitat type is genuinely attractive to cow/calf herds for social reasons of group cohesion, as I will describe in Chapter 5. Another possibility is a "boundary effect"; many patches of this habitat type are adjacent to swamp areas which elephants used for drinking in the rainy season and for feeding and drinking in the dry season.

CHAPTER 5 ELEPHANT SOCIAL GROUP DYNAMICS AND HABITAT USE

A. Introduction

In the preceding analysis of elephant habitat selection, I treated all the individuals in the population as if they chose habitat types independently of the presence of other animals. However, the social organization of elephants is highly structured (Moss 1981), and social structure has been suggested as potentially important in affecting the use of space and habitats in other animals (Fairbanks and Bird 1978, Fretwell and Lucas 1970, Hoffmeyer 1973). One aspect of social organization is the formation and splitting of groups of individuals at different times of year. These processes have been discussed for hamadryas baboons (Kummer 1968) and gelada baboons (Dunbar and Dunbar 1975), and related to their feeding ecology and habitat use, with larger groups forming in times and places of food abundance. Sinclair (1977) discussed seasonal group fission in African buffalo herds. He suggested that females and their young remain in large herds to reduce the impact of predation, and that the herds may break up in the dry season when food becomes distributed in patches so small that entire large herds cannot feed in them. Leuthold (1976) found that group size in elephants was positively related to seasonal rainfall, as in other large herbivores (Leuthold 1977a). He also proposed that high woody cover acts to reduce group cohesion, as food items would be patchily distributed, and the individuals feeding on these localized food sources would

therefore be unable to maintain contact with a large, mobile group.

Jarman and Jarman (1979) suggested that it is important for female impalas attempt to maintain social group cohesion at all times, possibly as a response to the constant threat of predation. However, feeding competition as food items become scarce and patchy in the dry season could act to divide these social groups. The impalas appear to shift their habitat use to stay in areas where they can maintain large group size. When they reach the last habitat with abundant food sources, and resources decline there, group members become more widely separated, then break up into smaller groups.

Under an alternate approach, the foraging success of individuals or family groups could be considered of greater importance in habitat selection than other benefits derived from the formation of large groups (as reviewed by Alexander 1974, Bertram 1978, and Rubenstein 1978). In this view, larger groups would be expected to form when individuals or small groups randomly encounter each other while foraging in the same area, or congregating at favored food sources, at any time of year. Group encounter rate should be proportional to animal density in the habitat, which might be inversely related to the habitat area. Large groups would be less likely to form where the habitat area was large, the relative density of animals was low, and the chances of encountering another group was also low. At any time when individual foraging efficiency was compromised by group membership, as when food items became relatively rare or

patchy and feeding competition within the group increased, the group would be expected to break up.

Elephants are gregarious and their social organization is matrilineal. The basic unit in elephant society is the cow/calf family unit, of one or more adult females with their juvenile offspring (Douglas-Hamilton 1972). The adult females in a family unit are thought to be closely related; the females are mothers and daughters, half-sisters (or possibly, in some cases, full sisters (Dublin in press)), and half- or full cousins. Males leave the family units at about the age of puberty, and become members of adult bull society. The adult bulls have a more loosely structured system of short term associations (Croze 1974a), although longer term social ties may be present (Poole in prep.). Juvenile females remain in the family units, where they eventually raise their own young. When family units become large, they apparently divide to form two or more distinct units, which retain social bonds, and which associate together frequently. This division of large family units into separate groups is thought to be the origin of "extended family units" (Douglas-Hamilton 1972) which are often seen in foraging aggregations. I will use the more conservative term of "bond group" (Moss 1981) to describe family units which are regularly seen together, until their kinship ties have been clearly established.

Elephant family units, and the potentially related "bond" groups, reportedly form large herds in the rainy seasons in some semi-arid regions. Examples of this seasonality in group size

have been reported for localities in Uganda (Laws et al. 1975), Kenya (Leuthold 1976), and Tanzania (A.R.E. Sinclair, pers. comm.) while in other areas of Tanzania and Uganda, elephant herd size was not significantly different between seasons (Douglas-Hamilton 1972, Eltringham 1977).

In this chapter, I will attempt to distinguish between two general alternative hypotheses as I examine the potential effects of social organization on habitat selection by the Amboseli elephants:

H1a: Elephants have a tendency to form large aggregations at all times, and choose habitats that allow them to maintain large group size. Under this hypothesis, the number of large groups should remain high through the seasons, and they should move to habitats with abundant herb layer biomass and low woody cover to permit the lowest feeding competition. The proportion of animals forming large groups should remain fairly constant through the seasons, until food sources become limited during the dry season. Then, in their final habitat, group size should decline as the food supply dwindles. Group size should not be directly related to elephant density in habitat types; large groups could form where density is either high or low.

H1b: Elephants are primarily concerned with foraging efficiency and have a secondary tendency to

aggregate when they encounter other elephants, if foraging efficiency is not sacrificed. In this case, there could be a correlation between elephant density and large group numbers in habitats, when food density is also high in those habitats. Large groups should not form where the density of elephants is low; small groups could be found in habitats with either high or low elephant density. This hypothesis predicts no clear trend in large group numbers across seasons: habitat shifts should not maintain large group size, but should be provide the best foraging opportunities for individuals or family units.

These hypotheses will be examined separately for bulls and cow/calf groups.

B. Methods

For analysis of elephant social structure, I used the same set of data as in Chapter 4: the ground and aerial survey counts. In this chapter, the data of interest are the sizes and habitat distribution of elephant groups. The analysis is concentrated on ground count data, but some aerial count data are presented for longer term comparison. All analyses were done separately for bull and cow/calf herds.

1. Analyses

a. Corrections for bias in ground count data

The figures I used for group size were corrected for biases due to habitat structure and group bunching, as in Chapter 4. I did not consider it valid, or necessary, to make corrections for months with missing counts, since I wanted to compare the relative distribution of the observed group sizes, not absolute numbers of animals. Each observation of an elephant group was taken as a separate independent record, and in most cases, observations in each season were pooled for analysis of group size patterns. Sightings of 1027 bull groups and 656 cow/calf groups were recorded in the ground surveys of 1978/79, while a total of 492 bull groups and 524 cow/calf groups were recorded in the aerial survey series from 1975 to 1980.

b. Group size distribution

I examined the relative distribution of group size in ground counts across the whole Amboseli basin in different seasons as a series of cumulative percent frequency distributions which I compared with the Kolmogorov-Smirnov two-sample test (Siegel 1956). I then calculated the arithmetic mean of bull and cow/calf group sizes (MGS) in each season across the basin and within each habitat type for both ground and aerial counts. In the Dry1 period aerial counts, the absolute number of elephants using the basin, especially

cow/calf groups, was low in the rains (see Chapter 4), and mean group size (MGS) values for the rainy season in this period should be viewed with this reservation in mind.

The variance associated with MGS values was in most cases very high, especially for cow/calf groups. For this reason, I calculated statistics reflecting the distribution of cow/calf group size in a more meaningful way: the percent of groups larger than 25 and larger than 50 in the whole basin and in each habitat type. These were calculated as the percent of all basin groups >25 and >50 which were seen in each habitat, and also the percent of the groups counted in each habitat which were >25 and >50. I chose these values since the largest cow/calf family unit in the Amboseli population included about 25 individuals, while the largest "bond group" (of potentially related family units) had about 45 members (C. Moss pers. comm.). Groups containing more individuals than these values were most likely aggregations larger than family units in the first case, and larger than "bond groups" in the second. The distribution of bull and cow/calf MGS in habitat types were compared to elephant density, herb layer and woody layer biomass, and percent woody cover in habitats by Spearman rank correlation. The percent of all cow/calf groups >25 and >50 which occurred in each habitat were correlated with cow/calf density and herb layer and woody layer total biomass in comparisons across habitats, while the percent of the groups in each habitat which were >25 and >50 were correlated with percent woody cover within habitat types.

C. Results

1. Group size distribution in the Amboseli basin

a. Bachelor bull groups

At all times, the frequency distribution of bull group size was strongly skewed to small groups (Figure 31). Fifty percent of all sightings were of one to two animals, while 75 (short rains) to 90 (early dry) percent of all sightings were of groups of four animals or less. The general pattern seen across the cumulative percent distributions of different seasons was the tendency for groups to be smaller and the distribution more strongly skewed in the dry seasons. However, this general pattern did not vary consistently and sequentially through all seasons; for instance, the early dry season distribution was more skewed than those of the mid and late dry seasons. There was a significant ($p < .05$, Kolmogorov-Smirnov test) difference between the frequency distributions for the short rains and the early dry seasons, but all other distributions were not significantly different from each other.

Bull mean group size (MGS) across the whole basin in different seasons can be seen in Figure 32. Also shown are the group sizes which included 50 and 90 percent of the bulls recorded. An analysis of variance showed that MGS differed significantly ($p = .0002$, $n = 1027$ groups) between seasons, although the actual range of values was not very great (ie. 1.8 to 3.4). After an initial decline from the short rains to early dry

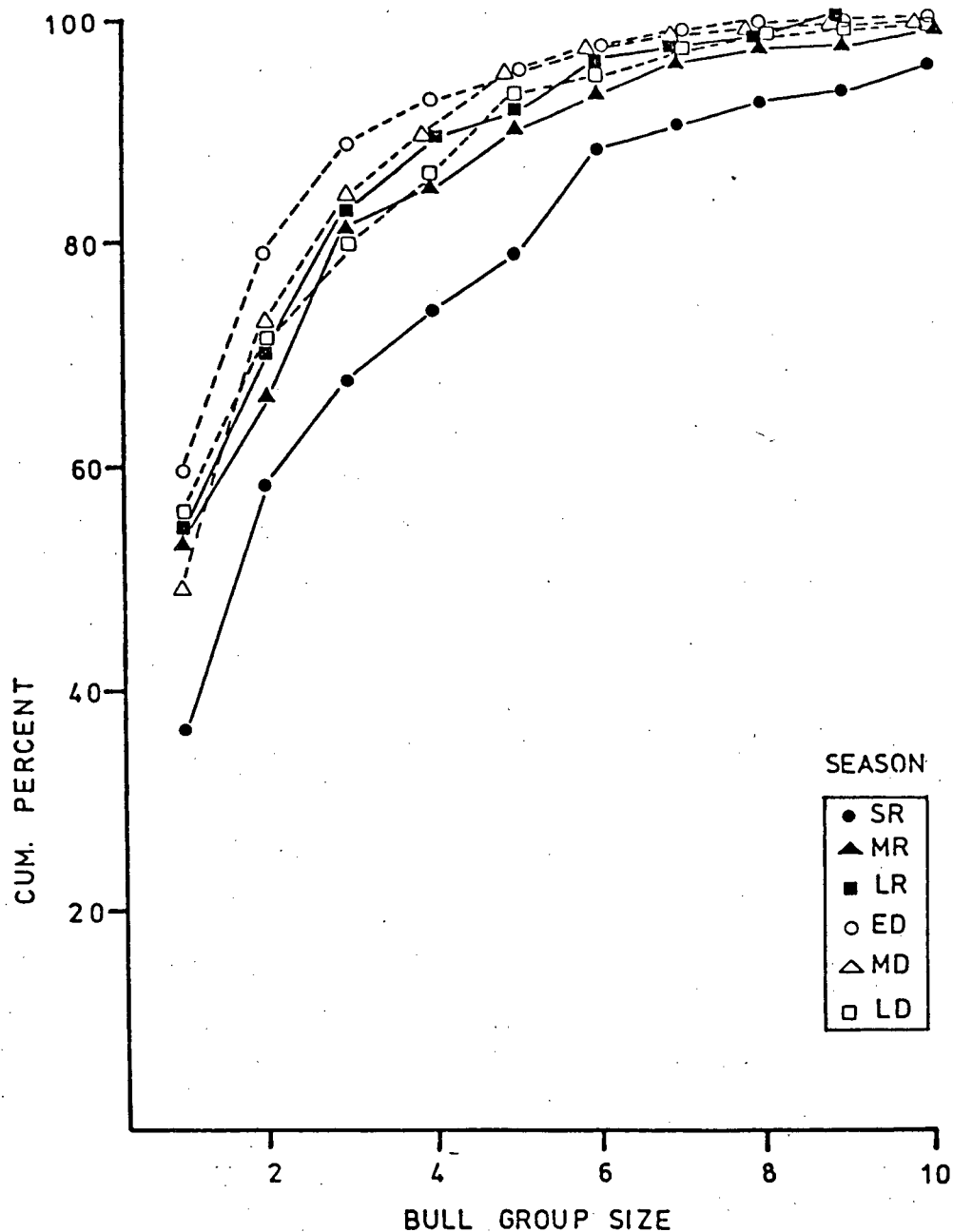


Figure 31. Cumulative frequency distribution of bachelor bull group size as seen in ground counts of the Amboseli basin in each season of 1978/79. There was a trend, however inconsistent, for groups to be smaller the dry season, although bachelor bull groups were fairly small at all times.

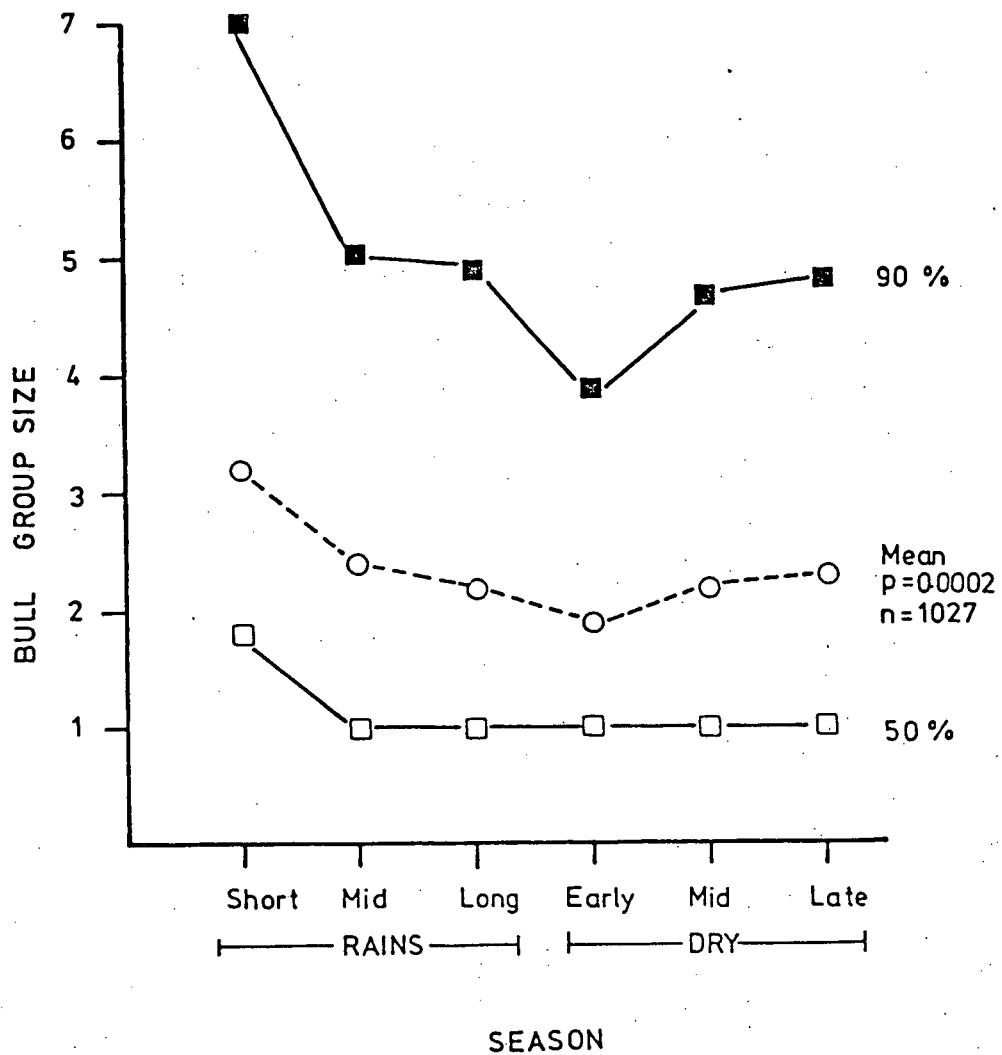


Figure 32. Bachelor bull mean group size, ○, and group sizes which included 50%, □, and 90%, ■, of all bulls sighted during ground counts in 1978/79. Note that mean group size was significantly different between seasons, although the range of values was small. There was no apparent trend in bull MGS through the seasons, after an initial decrease from short to mid rains.

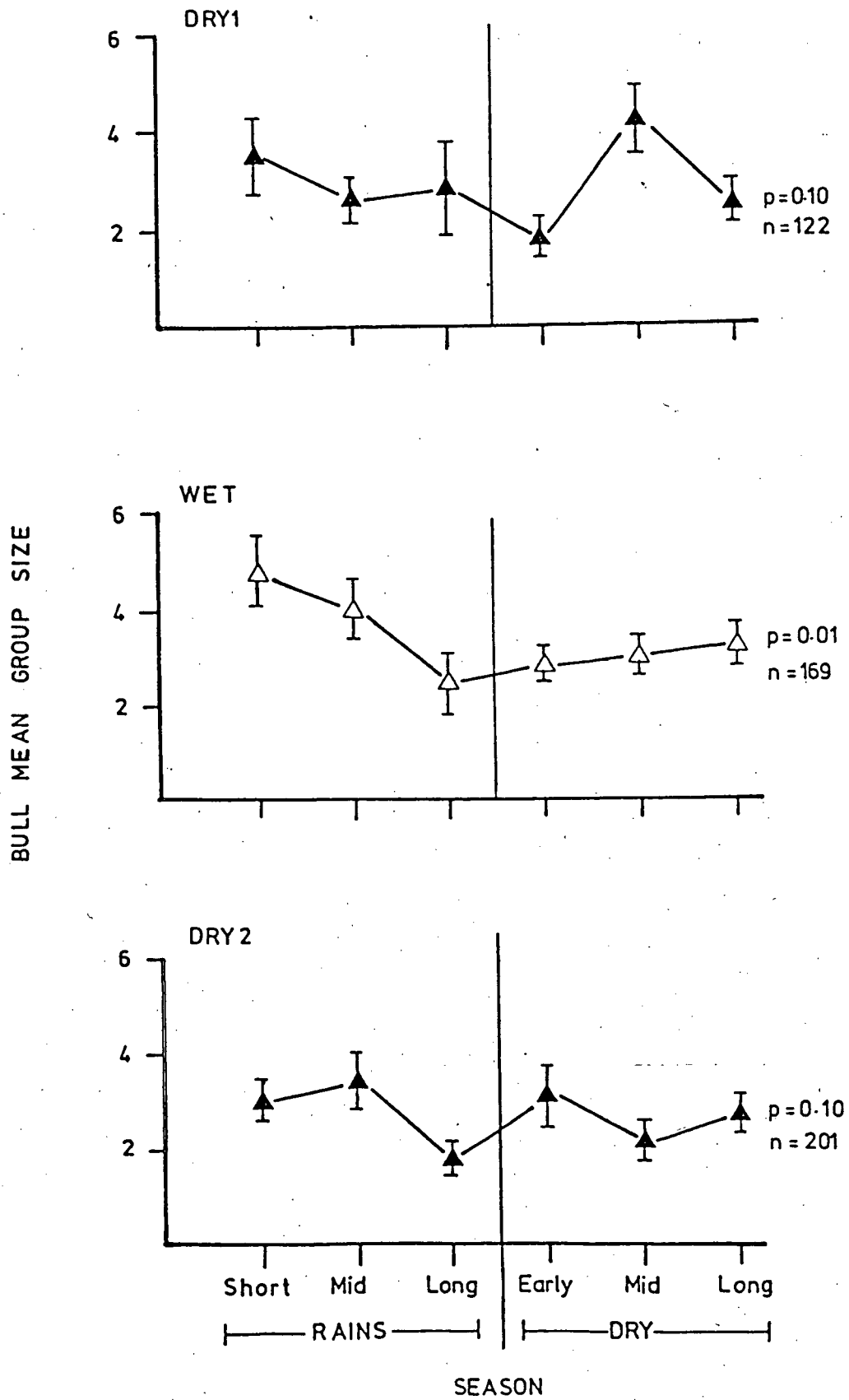
season, bull MGS increased slightly towards the late dry season.

Analyses of the aerial survey data (Figure 33) show that bull MGS did not vary greatly between seasons and rainfall periods, with fairly large associated variance at all times. The Wet period (1977 to 1979) aerial counts have a similar pattern to the ground count results: a decrease in bull MGS from the short rains followed by an increase towards the late dry season. An analysis of variance revealed significant differences ($p=.01$ $n=169$ groups) in bull MGS between seasons for this period. The two low rainfall periods (Dry1, 1975 to 1977, and Dry2, 1979 to 1980) both had irregular, non-significant seasonal patterns, and their MGS values were somewhat lower than those of the Wet period.

b. Cow/calf groups

The cumulative percent frequency distributions of cow/calf group size in different seasons are shown in Figure 34. Fifty percent of all sightings were of groups of 20 animals or less, while cow/calf groups of 50 or less made up 75 (short rains) to 90 (late dry) percent of the group sightings. The seasonal distributions, like those of the bull groups, were strongly skewed towards smaller groups, with skewness increasing in the dry season. However, the seasonal trend of increasing group size skewness was more regular for the cow/calf groups than it was for the bulls. Small groups became increasingly more common from the short rains through to the late dry season. No comparisons between frequency distributions were statistically

Figure 33. Bachelor bull mean group size seen in aerial counts during the three rainfall periods. Vertical bars indicate ± 1 standard error of the mean. There were significant differences between means in the Wet period only, and the range of values was never great. Group sizes were slightly higher in the Wet period, 1977-1979.



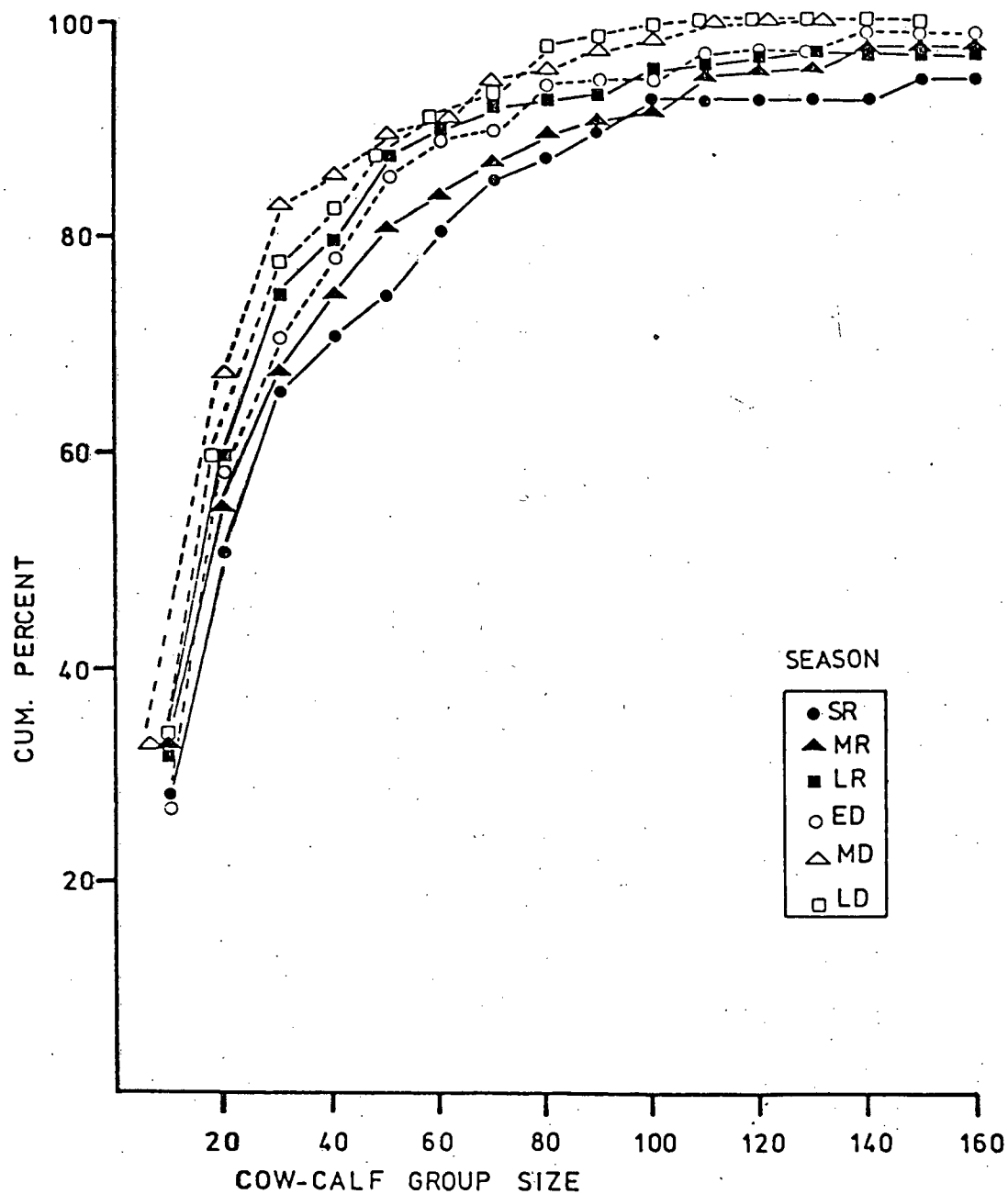


Figure 34. Cumulative frequency distribution of cow/calf group size seen in ground counts in each season of 1978/79. There was a consistent trend for groups to be smaller from rains to late dry season.

significant.

The trend of cow/calf MGS in ground counts (Figure 35) was a steady, significant ($p=.012$, $n=656$ groups) decrease from the short rains to mid dry season, with a slight increase in the late dry season. The group sizes which included 50 and 90 percent of the observed cows and calves showed a similar seasonal decline. In the aerial count data, cow/calf MGS decreased from the short rains to the mid and late dry season in both the Wet and Dry2 periods (Figure 36). In the Dry1 period, the rainy season counts recorded small MGS values; this result appeared because most of the cow/calf herds had left the Amboseli basin entirely in the rains during this period (see Chapter 4). The variance associated with the cow/calf MGS values was high at all times, and seasonal differences were significant in analysis of variance ($p=.01$, $n=199$) only in the Dry2 period. Note that cow/calf MGS in the dry season was generally lower in both the Dry1 and Dry2 periods than in the intervening Wet period.

Figure 37 shows that across the basin, the proportion of large aggregations, (those larger than 50 animals), declined sharply from the early rains to mid rains and then decreased more gradually towards the late dry season. The proportion of groups larger than family units (more than 25 individuals) declined in a similar, though less significant, fashion, and remained at a higher level than % of groups >50 throughout the year. The mean number of groups recorded per count increased steadily through the same seasons.

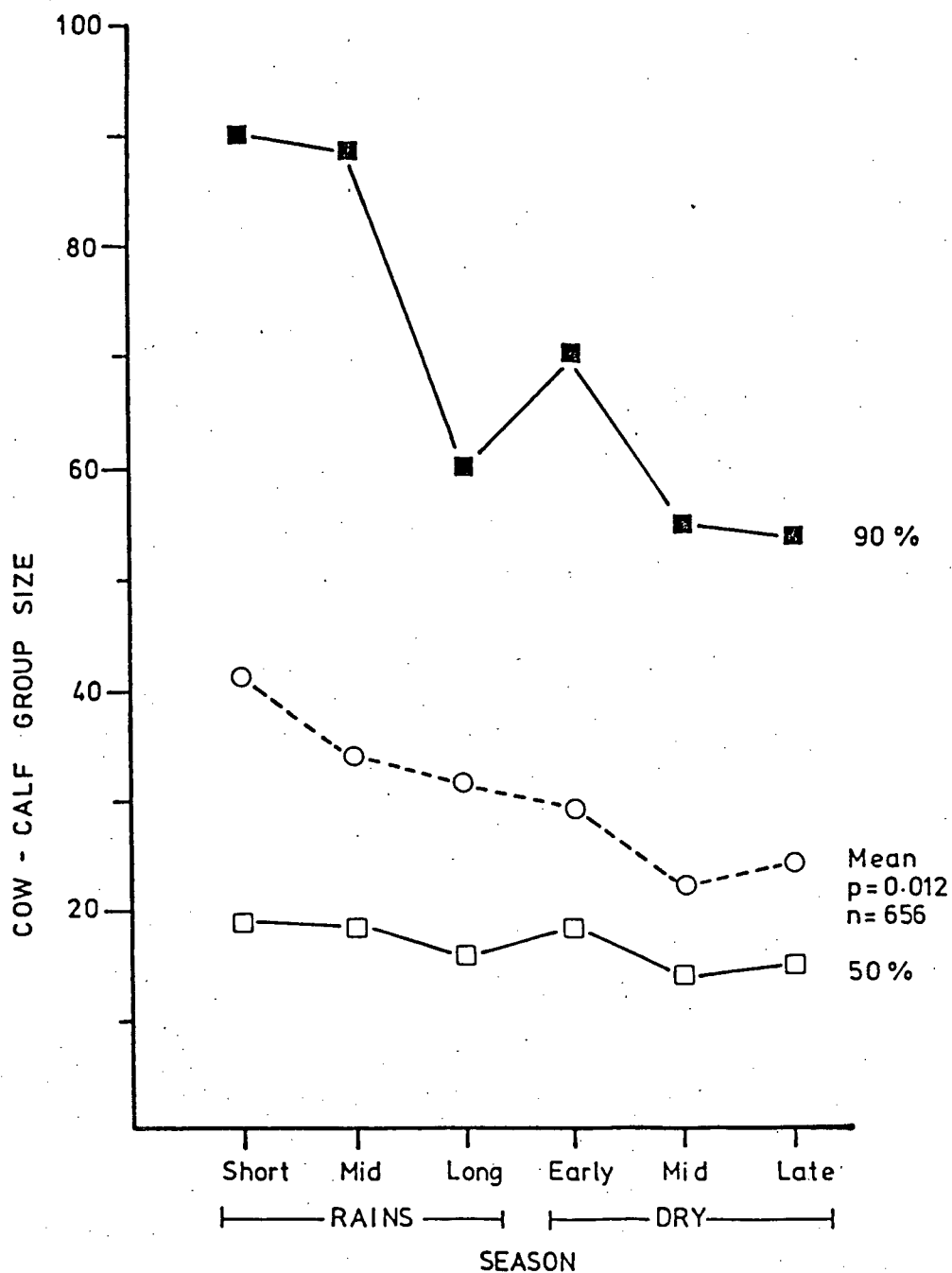
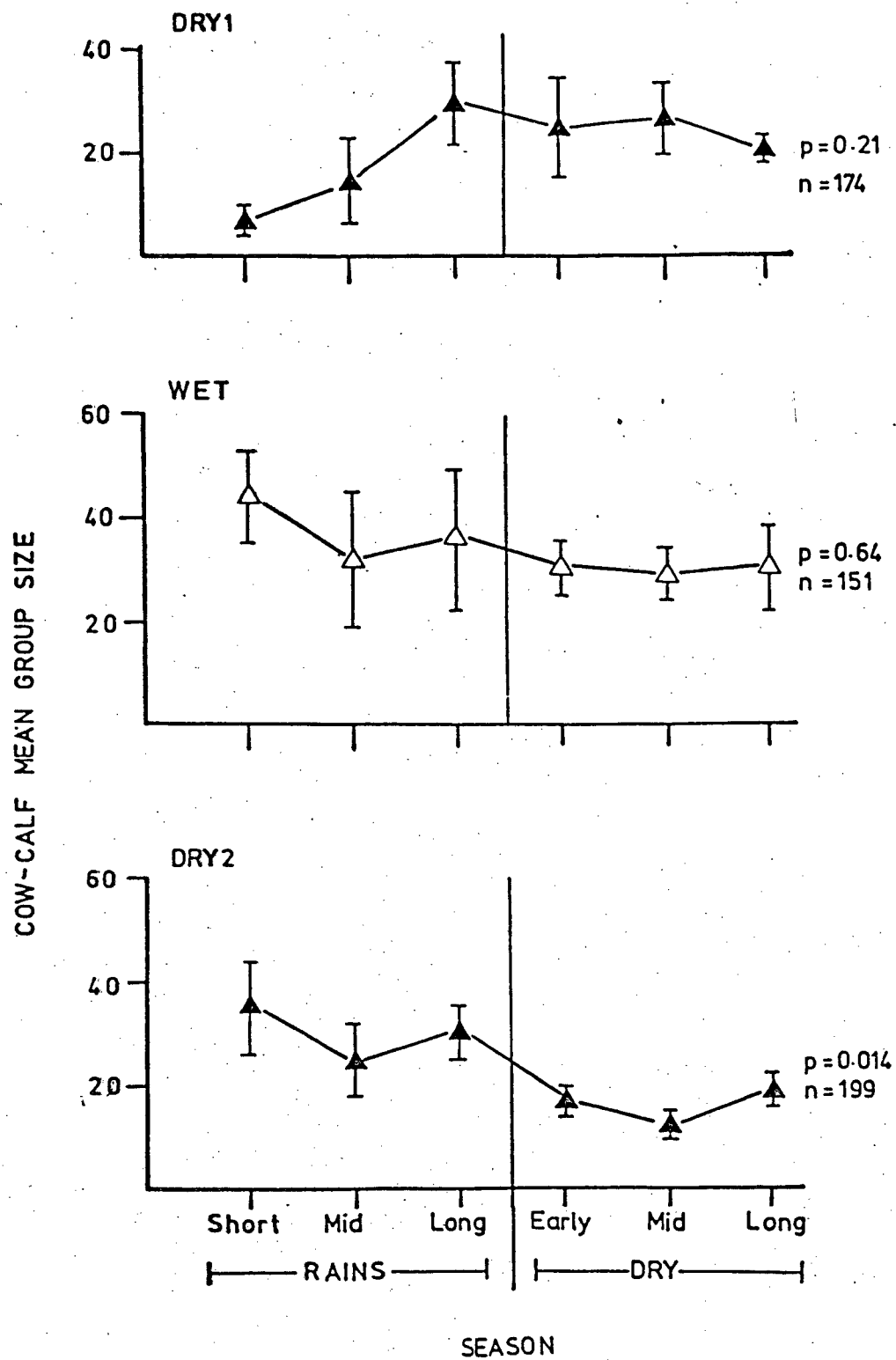


Figure 35. Cow/calf mean group size, ○, and group sizes which included 50%, □, and 90%, ■, of all cows and calves sighted during ground counts 1978/79. Mean group size was significantly different between seasons, with a consistent trend of decreasing MGS towards the late dry season.

Figure 36. Cow/calf mean group size as seen in aerial counts over the three rainfall periods. Vertical bars indicate ± 1 standard error. There were significant differences between means in the Dry period only. In Dry1 period, group sizes were small during the rains, probably because there were few cow/calf groups using the basin at this time (see Chapter 4).



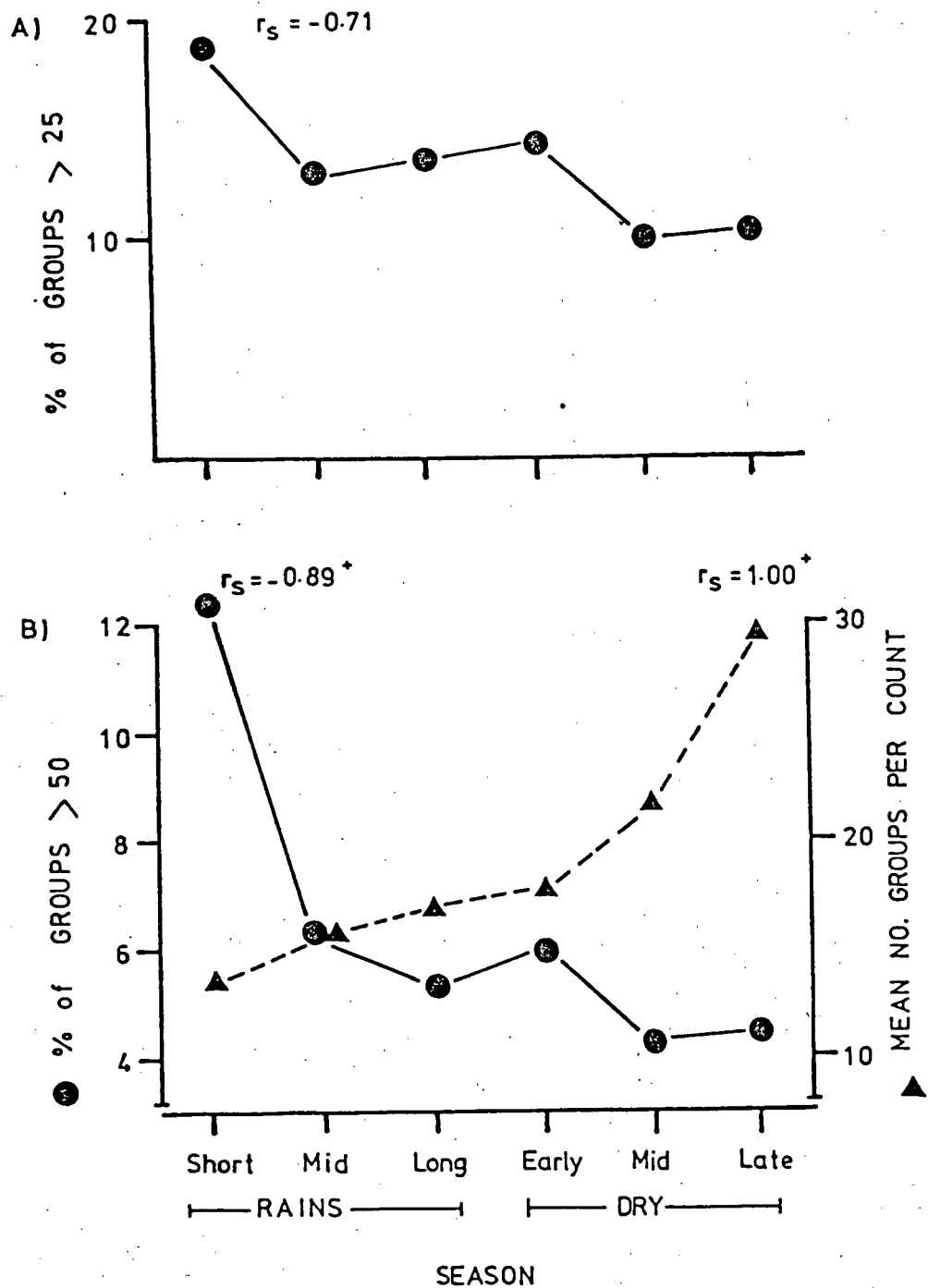


Figure 37. The percent of cow/calf groups > 25 and > 50, and the mean number of groups per count, as seen in each season in ground counts of the Amboseli basin. The trend of decreasing % of large groups was significant at $p < .05$ for groups > 50, but not for groups > 25. The trend of increasing numbers of groups seen per count was highly significant.

2. Habitat distribution of elephant group size

a. Bachelor bull groups

The overall distribution of bull MGS across the habitat types of the Amboseli basin (see Figure 38) was fairly even; larger bull MGS was found in the A. tortilis woodlands (Tw) while lower MGS occurred in the swamp edge grasslands (Seg), and permanent swamps (Swp).

Table 11 shows the seasonal rank distribution of bull MGS across habitats. There are few consistent patterns in these

Table 11. Ranking of bachelor bull MGS across habitat types in each season (read vertically in columns). Ranks were assigned as for Spearman's correlation, with low MGS values having low ranks. Average values were given to tied ranks. There was no consistent pattern in the ranks of bull MGS across habitats between seasons.

RANK ACROSS HABITAT TYPES	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Alkaline grass.	7	2.5	8.5	5.5	4	1.5
<u>S. consimilis</u> gr.	3	5	3	5.5	9	5.5
<u>A. tortilis</u> woods	9	8	7	9	8	1.5
Fever tree woods	6	2.5	5.5	8	5	8
<u>S/S</u> shrubs	8	4	4	5	6	4
Palm/Fever woods	5	7	8.5	1	3	7
Young Fever woods	1	9	5.5	3	2	9
Swamp edge grass.	4	1	2	4	7	5.5
Swamp	2	6	1	7	1	3

results. Bull MGS was both large and small in the grasslands, woodlands, and swamp edges in both rainy and dry seasons, with no clear trends visible. The only consistent result was that

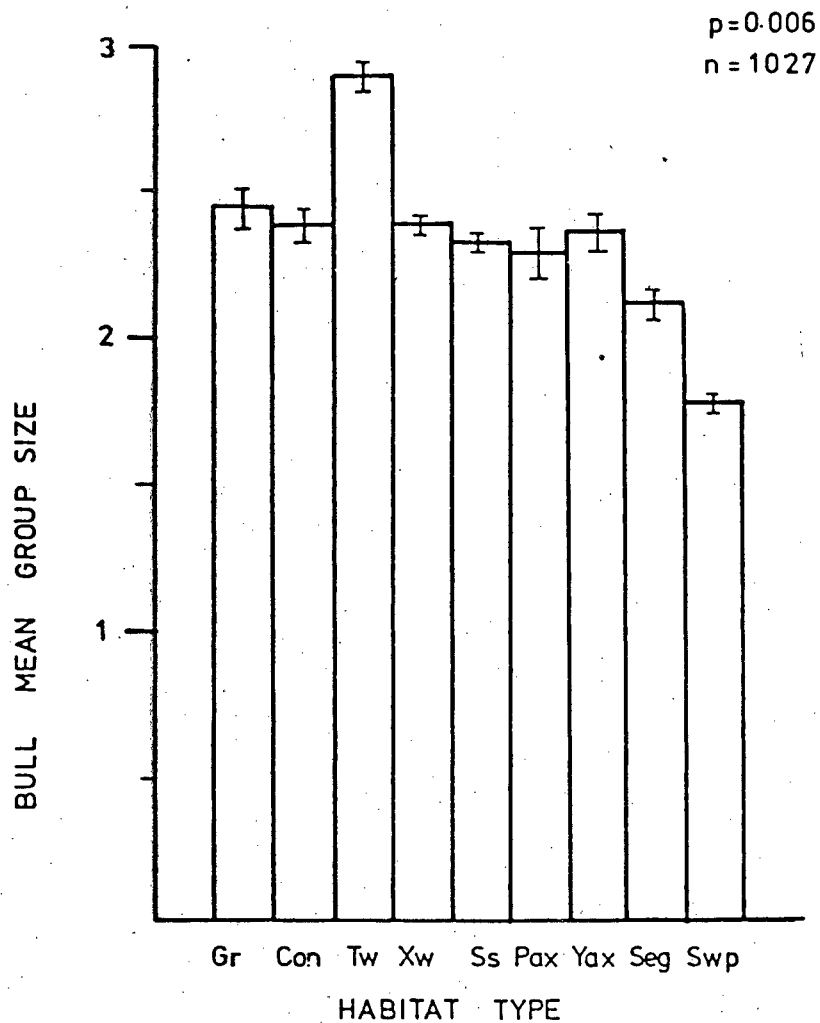


Figure 38. The yearly mean size of bachelor bull groups seen in habitat types in ground counts. Differences were significant, although the range in group size was low. Vertical bars indicate ± 1 standard error. The largest groups were seen in the A. tortilis woodlands, and the smallest were seen in the wet swamps.

bull groups were generally smaller in the permanent swamps. This echoes the year-round result shown in Figure 38. Because of the variability, there was no significant correlation between bull MGS and such habitat characteristics as herb layer total biomass or percent woody cover.

Bull MGS in habitat types was positively correlated with the density of bulls in the same habitats only in the mid rains (see Table 12). MGS was negatively correlated with bull density

Table 12. Correlations (Spearman's rank) of bachelor bull density with MGS across habitat types in each season. There is no consistent pattern in these correlations.

SPEARMAN'S Rs	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Bull Density vs. MGS	.033	.754*	.232	-.628*	-.617*	.445

Significance of Spearman's r_s
(n=9, ties corrected): * $p < .05$

in habitats in the early and mid dry season. Thus, there were no clear correlations between bull MGS and density across habitat types at most times of year.

b. Cow/calf groups

The year-round distribution of cow/calf MGS across the basin habitats is seen in Figure 39. There is some suggestion that cow/calf group size was inversely related to the woody

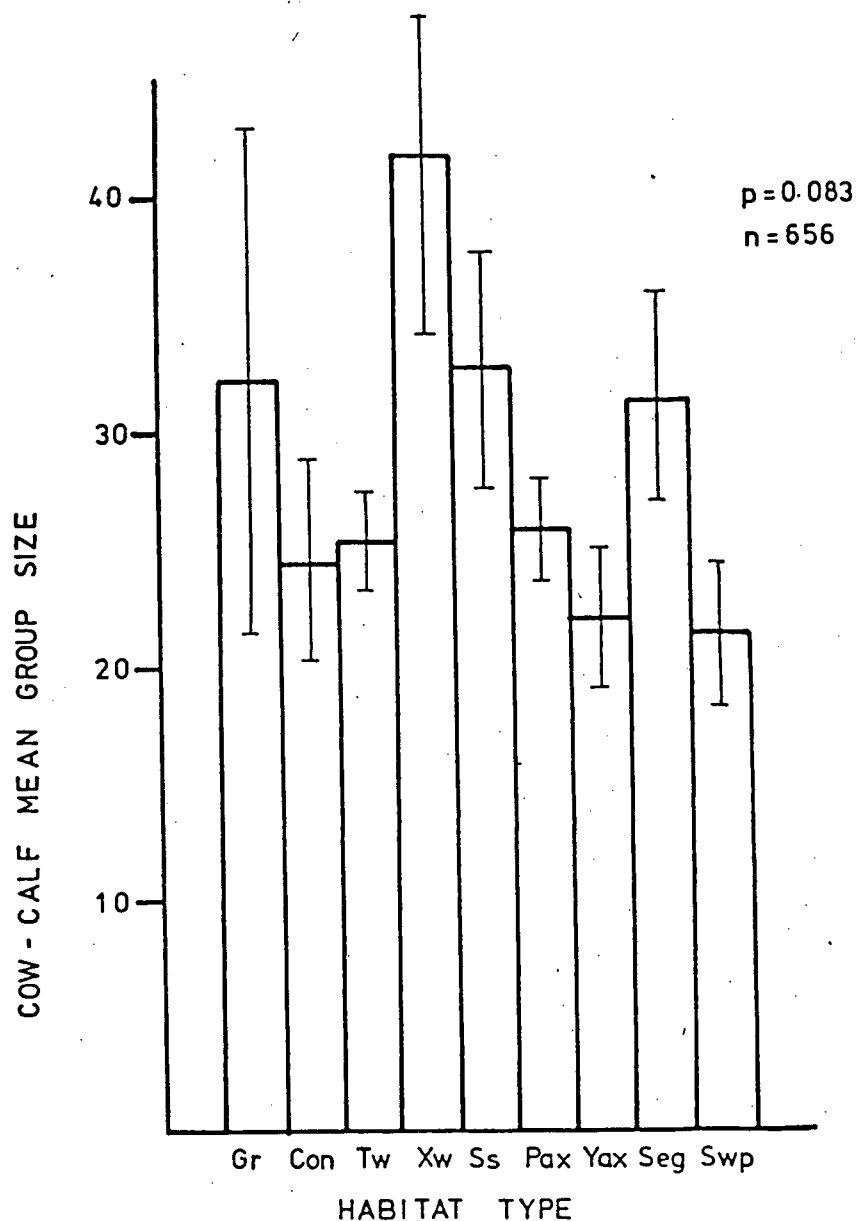


Figure 39. The yearly mean size of cow/calf groups seen in habitat types in ground counts. Vertical bars indicate ± 1 standard error. Differences were not significant, and the range of values was high. Generally, the largest groups were seen in the alkaline grasslands, fever tree woodlands, Salvadora/Suaeda shrublands, and the swamp edge grasslands.

cover of habitat types. Some of the habitats with low woody cover, such as the fever tree woodlands, Salvadora / Suaeda shrublands, and the swamp edge grasslands had relatively high cow/calf MGS on a year-round basis, while other, more densely wooded habitats -- the A. tortilis woodlands, palm / fever tree swamp edge woodlands, and young fever tree woodlands -- had smaller overall MGS values. Cow/calf MGS was also small in the permanent swamps and the S. consimilis grasslands.

The seasonal rank distributions of the percent of cow/calf groups >25 and >50 in habitats are seen in Table 13. There is a trend in the relative occupancy of habitats by large groups, which may be more clearly seen in the schematic diagram, Figure 40. Aggregations larger than 50 animals were found most often in the open Salvadora / Suaeda shrublands and fever tree woodlands, and in the A. tortilis woodlands in the rainy seasons. In the dry seasons, the large aggregations were found increasingly in the swamp edge (palm/fever tree) woodlands and, by the late dry season, in the swamp edge grasslands, while rarely in the woodlands and shrublands.

Spearman rank correlations of percent of groups >25 and >50 with herb layer biomass and percent woody cover in habitat types are shown in Table 14. Herb layer total biomass correlated positively with the percent of groups >50 occurring in each habitat in the late dry season. Other correlations with plant biomass were not significant. However, there was an interesting trend in the relationships with herb layer biomass. The non-significant correlations of percent of groups >25 with herb

Table 13. Rankings of % cow/calf groups > 25 and > 50 across habitat types in each season. The ranking system is the same as was used for bachelor bull MGS (see Table 11). There is a consistent pattern for large cow/calf groups to shift from using the woodlands in the rains to using the swamp edge woodlands and grasslands in the dry season.

A) COW/CALF GROUPS: % > 25

RANK ACROSS HABITAT TYPES	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Alkaline grass.	6.5	6	3	2	2	1.5
<u>S. consimilis</u> gr.	7.5	1.5	3	1	2	4
<u>A. tortilis</u> woods	3.5	6	9	5.5	4	1.5
Fever tree woods	5	8	7.5	7	6.5	7
S/S shrubs	9	9	7.5	8.5	9	8.5
Palm/Fever woods	6	4	1	5.5	8	3
Young Fever woods	1.5	7	5.5	3.5	2	6
Swamp edge grass.	7.5	4	3	8.5	6.5	8.5
Swamp	1.5	1.5	5.5	3.5	5	5

B) COW/CALF GROUPS: % > 50

RANK ACROSS HABITAT TYPES	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Alkaline grass.	5	2.5	2	4	2.5	1.5
<u>S. consimilis</u> gr.	7	2.5	4.5	1.5	5	4
<u>A. tortilis</u> woods	3	7	7.5	4	2.5	1.5
Fever tree woods	5	8	9	8.5	8	3.5
S/S shrubs	9	9	7.5	8.5	7	3.5
Palm/Fever woods	5	2.5	2	6.5	9	2
Young Fever woods	2	5.5	4.5	4	2.5	4
Swamp edge grass.	8	5.5	2	6.5	6	1
Swamp	3	2.5	6	1.5	2.5	4

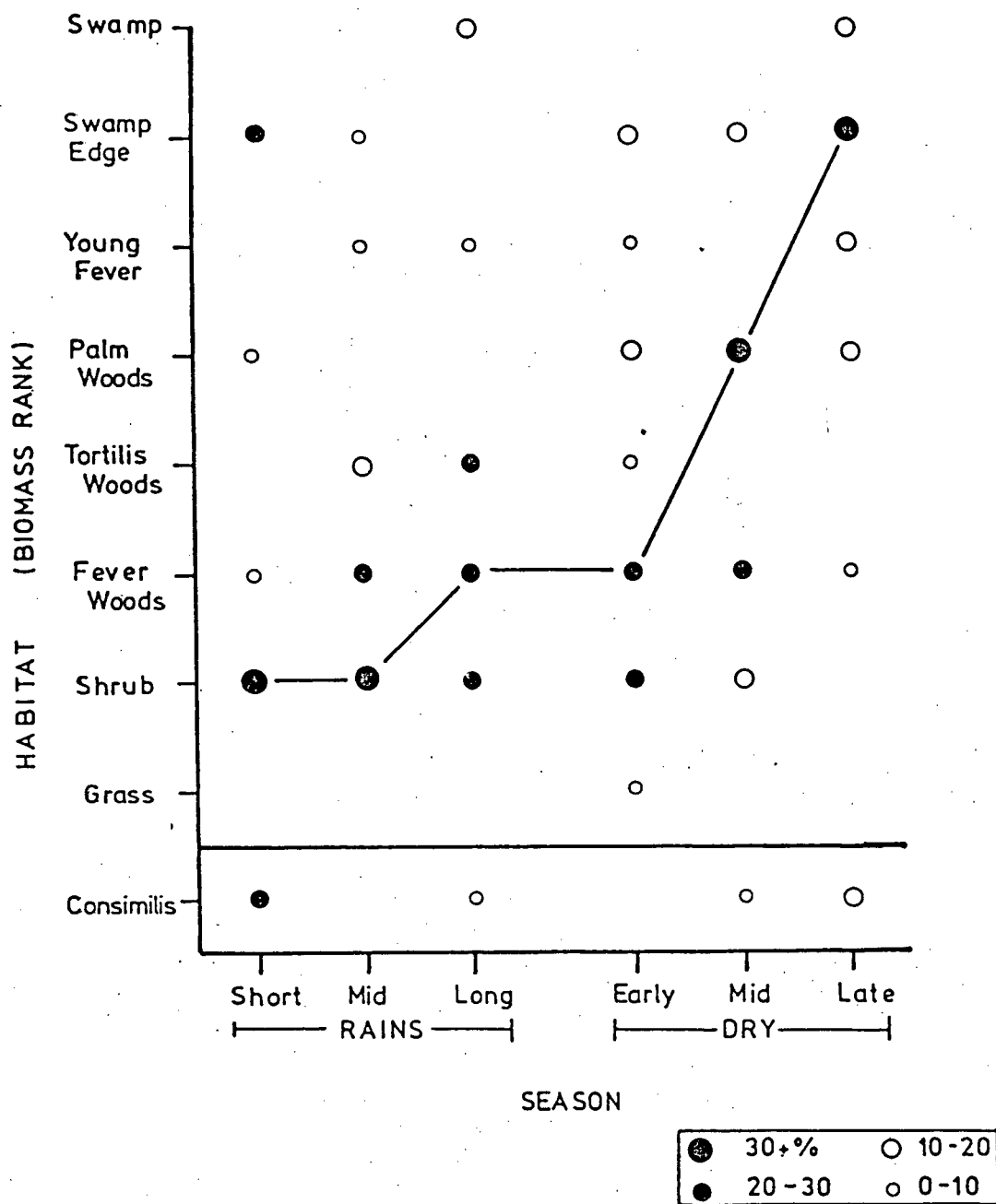


Figure 40. Schematic diagram of the seasonal habitat distribution of cow/calf groups which had > 50 individuals. The highest proportion of these large groups shifted from the woodland habitats during the rains to swamp edge woodlands (palm/fever tree) and grasslands during the dry season.

Table 14. Correlations (Spearman's rank) of % cow/calf groups > 25 and > 50 with total biomass of the herb layer and % cover of the woody layer across habitat types in each season. Few significant correlations were found, although correlations were generally more positive in the dry season.

	A) COW/CALF GROUPS:			% > 25		
SPEARMAN'S Rs:				SEASON		
% GROUPS > 25	RAINS			DRY		
VS.	Short	Mid	Long	Early	Mid	Late
Herb layer						
total biomass	-.273	-.515	-.329	-.085	.145	.307
% woody cover	.127	.428	.048	.802*	.371	.524

B) COW/CALF GROUPS: % > 50						
SPEARMAN'S Rs:	SEASON					
% GROUPS > 50	RAINS			DRY		
VS.	Short	Mid	Long	Early	Mid	Late
Herb layer						
total biomass	.077	.026	.137	.030	.406	.852**
% woody cover	.204	.494	.315	.594	.690*	.601

Significance of Spearman's r_s
 (n=8, ties corrected): * p < .05
 ** p < .01

layer biomass were negative during the rains and became increasingly positive in the dry season. Percent woody cover in habitats correlated positively with the percent of groups in each habitat >25 in the early dry season and with percent of groups in each habitat >50 in the mid dry season. There was no clear trend across the seasons.

Cow/calf density correlated positively with the percent of groups >25 in each habitat in the short rains and late dry season (Table 15), and with the percent of groups >50 in each

Table 15. Correlations (Spearman's rank) of cow/calf density with MGS, % groups > 25, and % groups > 50 across habitat types in each season. There are no consistent patterns in these results, except that density correlated with % of groups > 25 and > 50 in the late dry season.

SPEARMAN'S Rs: COW/CALF DENSITY VS.	SEASON					
	Short	RAINS Mid	Long	Early	DRY Mid	Late
Mean Group Size	.150	.266	-.033	-.383	-.417	.520
% Groups > 25	.675*	.426	.239	.422	.510	.654*
% Groups > 50	.587	.272	.194	.227	.372	.834**

Significance of Spearman's r_s
(n=9, ties corrected): * p < .05
 ** p < .01

habitat in the late dry season only. All other correlations (for example, density vs. MGS in all seasons, or % >25 and % >50 in other seasons) were not significant.

D. Discussion

1. Bachelor bull groups

Although there were seasonal differences in the size of bachelor bull social groups, there were no clear seasonal trends in group size, save that groups were apparently largest in the early rainy season, and lower during the rest of the year. Mean group size was never particularly high, ranging from one to four animals in different habitats. Bull group size was significantly related to bull density in habitat types in the mid rains, but was non-significantly or inversely related in other seasons. There was no clear seasonal shift or pattern in habitat use by large or small bull groups.

From these results, it appears that there is no general tendency for bulls to form large bachelor herds, and that their habitat selection is little affected by a need to stay in large groups with other bulls. There is a tendency for bulls to form small groups, the size of which may be somewhat larger in rainy seasons or high rainfall years. Sinclair (1977) suggested that by leaving the large female herds, male buffalo could have access to extra food resources in small patches unavailable to the larger groups. This benefit may be balanced by the threat of predation on individual animals in small groups. However, bull habitat selection may also be influenced by foraging and reproductive strategies which involve associating with cow/calf herds at different times of year (Poole and Moss 1981, J. Poole in prep.).

2. Cow/calf groups

The variance seen in cow/calf group sizes reflects the flexible, variable nature of elephant social dynamics. My casual observations indicated that herds larger than "bond groups" stayed together for relatively brief periods -- in some cases only a few hours, in other cases for a period of days -- when compared with the longer term associations of African buffalo (Sinclair 1977) or impala (Jarman and Jarman 1979) herds. It appeared that the large aggregations usually broke up in the evenings and during the course of the night, often re-forming the next day with the same or somewhat different family unit composition. Groups could also form and break up at any point during the daylight hours. When seasonal group size indices are compared, group formation should be viewed as a statistical tendency by the elephants to form large or small groups of family units, rather than as the cohesion or fission of fixed-membership groups.

The pattern of cow/calf herd formation and break up is markedly different from that of bachelor bulls. Cow/calf herds were obviously much larger than bull herds at all times of the year -- the largest breeding herd recorded in ground surveys included 335 individuals, while the largest bachelor bull herd numbered only 17 animals. The pattern of cow/calf group size distribution across seasons and habitat types showed clear trends in contrast to the bull group pattern of inconsistent variation.

Cow/calf MGS in ground counts over the whole basin declined

steadily from the rains through to the late dry season. This pattern was also seen in the long term aerial count data for Wet (1977 - 1979) and Dry2 (1979 - 1980) periods. The proportion of large (size >50) aggregations seen in ground counts dropped sharply after the early rains, and declined gradually through the dry season, while the total number of groups (which included many smaller groups) formed increased steadily. The proportion of aggregations with more than 25 members showed a more gradual seasonal decline, maintaining a higher level throughout the year. Large groups in the rainy season were seen, but not recorded in basin aerial counts, during the Dry1 (1975-1977) period, since most of the cow/calf groups left the basin entirely in the rains. It appears that large aggregations formed in the rainy seasons of all years studied. However, in the two low rainfall periods (before 1977 and after 1979), MGS dropped substantially lower in the dry season, as compared with the intervening Wet period. This supports the idea that group membership is limited by food abundance, especially of the herb layer, which I showed was sensitive to annual rainfall patterns (see Chapter 3).

Most of the large cow/calf groups formed in the savannah woodlands (Tw, Xw, Ss) in the rains and early dry seasons, and in the swamp edge grasslands and swamp edge woodlands in the mid and late dry seasons (see Figure 40). This parallels the seasonal shift in cow/calf habitat use demonstrated in Chapter 4. Group size, however, was not simply correlated with the density of animals using the habitat types through the year.

The large groups were found in the habitats with relatively low densities of elephants in the rainy season; it was only in the late dry season that density correlated with percent of large groups. The latter correlation could be a consequence of a number of large groups producing a high density in the small swamp edge habitats, rather than high densities of elephants resulting in the formation of large groups. This result supports the hypothesis that elephants generally tend to form large aggregations and shift their habitat use to allow large group formation; it does not support the alternate hypothesis that large groups form after random encounters.

Significant correlations between the percent of groups >50 and habitat characteristics such as herb layer total biomass were found in the late dry season. However, the pattern seen was similar to that of simple numerical habitat preference shown in Chapter 4. Correlations were increasingly positive towards the late dry season. It appears that large groups form where the vegetation is of high nutritional quality, as well as simply abundant. The smaller group sizes seen in the dry seasons of low rainfall years suggest that the abundance of nutritious food, or of "profitable foraging", may limit the group sizes that can form.

An inverse relationship between woody cover and group size, as proposed by Leuthold (1977a), was not clearly demonstrated in the current study. Leuthold suggested that food source patchiness in woody vegetation types would disrupt group cohesion. However, in semi-arid areas such as Tsavo, where he

worked, herb layer cover is inversely related to woody cover (Norton-Griffiths 1979, Pratt and Gwynne 1977). In the Amboseli swamp edge woodlands, high herb layer cover and high woody cover coincided. The distribution of food items for grazing animals would be much less patchy in the dense swamp edge woodlands than in semi-arid bushlands, and group size could be expected to remain large. However, the year-round pattern of cow/calf group size in habitat types did suggest that large groups were seen more often in the less woody habitats, so Leuthold's suggestion might have some degree of validity in Amboseli. My impression from casual observations was that large elephant aggregations in wooded areas were more widely dispersed and sometimes became fragmented, but that they re-formed into large well-defined herds when they emerged onto more open grasslands or swamp edges.

My results do not support the hypothesis of group formation by random encounter in areas of high density. Notably, a high proportion of the large groups formed in the savannah woodlands and shrublands during and after the rains where densities were not high compared to swamp edge habitats, but where abundant, nutritious grass was available. The hypothesis of large group formation and habitat selection to maintain large group size is more strongly supported. However, not all the predictions of this hypothesis were met. Specifically, mean group size declined evenly through the seasons, as did the percent of large groups in the basin population, instead of being maintained at a constant high level until the dry season. It may be that

habitat shifting cannot maintain the integrity of the very large and temporary aggregations, but may apply more effectively through time at the level of the intermediate-sized "bond groups". Individual family units might differ in their tendencies towards aggregation, as preliminary observations of identified females would suggest. The family units might also differ in their tendency to avoid social interactions or foraging competition with other elephants, and to return to their distinct dry season home ranges, resulting from differential success in foraging or other activities in the large groups.

The general patterns of interaction between group formation and habitat selection are suggested by the current study. However, the answers to more specific questions of individual group behaviour, and the importance of different levels of social structure in foraging and habitat selection must come from finer scale studies at the individual level.

CHAPTER 6 GENERAL DISCUSSION AND CONCLUSIONS

A. General Habitat Selection Pattern of the Amboseli Elephants

Leuthold (1977b) viewed the strategy of habitat use by elephants as a "pulsating system". This system has a "stable element" centered on dry season home ranges near water sources and an "opportunistic element" involving movements to ephemeral, localized water and food sources scattered across the bushlands in the wet season. This strategy could be observed in action at the level of large-scale shifts in the seasonal habitat distribution of the population, or at the level of seasonal movements by individual elephants. I examined habitat use by elephants at the broad level in the current study, and my results support Leuthold's hypothesis.

My broad-level explanation of habitat selection by elephants in Amboseli is that they choose the habitats where herb layer vegetation of the highest quality is sufficiently abundant to permit a high intake rate. Selection of habitats or patches with higher than average food abundance and potential for efficient foraging has been predicted by foraging theory (Pyke, Pulliam, and Charnov 1977), and found empirically in field studies of birds (Goss-Custard 1981, Royama 1970, Zach and Falls 1979).

When viewed from the level of the population, the Amboseli elephants appear to concentrate their daytime habitat use in the swamps and swamp edge woodlands of the Amboseli basin during the late dry season, the period when food resources and water

sources are most limiting (Sinclair 1975, Western 1975). These are areas where the herb layer is abundant but of relatively low nutritive value. The dry season habitats vary in their extent of woody cover: in the swamps and swamp edge grasslands, there is little or no woody cover, while in the swamp edge woodlands, the woody cover is relatively dense. The dry season habitats are thus areas of predictable, abundant, but fairly low quality herb layer food availability, and of differing twig/leaf biomass density.

During the wet season, the elephants extend their habitat use into the woodlands and grasslands of the Amboseli basin, and across the bushland areas surrounding the basin. They spend comparatively less time feeding in the swamps and swamp edges at this time. In the habitat types used in the wet seasons, the herb layer is of higher nutritional quality than in the swamps, and is productive and abundant during the rains. Woody cover in these habitats varies from open (the alkaline grasslands) to moderately dense (the dense bushlands in the north and south). The abundance and quality of herb layer biomass in the wet season areas depends largely on local rainfall, which is variable on spatial and temporal scales. The best foraging sites in the wet season are therefore more unpredictable in space and time than the ground-water swamps of the Amboseli basin. Surface water availability in the bushlands outside the Amboseli basin is also spatially and temporally unpredictable (Western 1975).

Based on the limited set of observations I made during the

course of the present study, and my analysis of Western's longer term aerial count data, I can make some tentative predictions about wet season movements. I suggest that the elephant population as a whole will tend to move farther out into bushland areas in the wet season during extended periods of low annual rainfall (250 mm. or less), and will remain in or near the basin habitats during periods of higher annual rainfall (300 mm. or more). This view suggests that the elephants have no inherent reason to make long distance migrations in the wet seasons except to search for the best foraging sites.

B. Factors Modifying the General Pattern

Any a priori definition of potential foraging profitabilities in different habitats which is based on simple measurements of herb layer biomass is probably inaccurate and overly simplistic. In a social, generalist herbivore such as the elephant, there are many possible complicating factors. These include:

1. The effects of social group formation on the foraging efficiency of individuals.
2. The effects of gender differences on the foraging efficiency and needs of individuals.
3. The difficulty of describing the "food availability" in a habitat type in general terms, such as average abundance and quality, when there are local differences in plant abundance and quality within the habitat. The need of all

animals to maintain a "nutritional balance" could mean that a large herbivore such as an elephant might have specific search patterns to search out certain plant types or avoid others found in different plant communities (Westoby 1974).

I will discuss these factors as they relate to elephant habitat selection.

1. The effects of group formation

Alexander (1974) notes that the costs to an individual of joining a group include increased competition for mates or food. The benefits from group membership must outweigh these costs. Bertram (1978), Rubenstein (1978), and Wrangham (1980) describe possible foraging benefits which could accrue through group membership. These generally involve increased success in the detection, capture, or handling of prey. They focus largely on predators, however, or other animals which exploit highly nutritious food items distributed in a patchy, unpredictable way in time and space. For large generalist herbivores, the detection, capture, and handling of their relatively low quality and widely distributed food items is unlikely to be enhanced by social group formation, and is more likely to be reduced (Jarman and Jarman 1979). Other, non-feeding benefits must outweigh the costs of this reduced foraging efficiency.

Foraging efficiency is reduced by competition with other animals in the group; either directly by interference

competition and supplantation from localized food sources (Leuthold 1977a, Post 1981), or indirectly by exploitation competition as neighbouring animals reduce the food supply for those foraging behind them (Jarman and Jarman 1979, Post 1981). As the food available for a given group of individuals decreases, the group progression rate and inter-individual distance increases. This acts to reduce the cohesiveness of the group, and makes it more likely that the group will break up.

Of the many benefits that have been suggested to favour membership in a group, I suggest that the following could be potentially important for elephants.

1. Reduced or diluted predation risk for adults and juveniles through the selfish herd concept (Hamilton 1971), or through group defense (Douglas-Hamilton 1972, Kruuk 1972). Juvenile elephants, especially smaller calves, are potential prey for large predators such as lions. More important might be the threat of predation by man, the only predator of adult as well as juvenile animals. Man has probably been a predator of elephants for tens of thousands of years (Howell and Bourliere 1964), and possibly longer (Isaac and Crader 1981). It would appear that group formation for protection of juveniles and dilution of the threat to individuals from human predation could be an evolutionary pressure promoting the formation of large groups at all times of the year.

2. Female mate choice in a strategy analogous to that shown by female elephant seals (Cox and LeBoeuf 1977), which encourages male-male competition. In semi-arid regions, oestrus

in female elephants occurs through the year, but peaks in the wet and early dry seasons. Large adult bull elephants in reproductive condition (termed "musth" by Poole and Moss (1981)), tend to associate with cow/calf aggregations and fight to control access to the oestrous females. Observations of female elephants in oestrus (C. Moss, pers. comm., pers. obs.), suggest that they might incite male competition by aggregating in a few large groups and drawing the attention of all "musth" males in the vicinity. This would improve the chances that any individual female would be mated by the "fittest" bull.

3. Benefits for juvenile offspring of increased survival and accelerated social development through allomothering, or care by non-mothers, (Hrdy 1976), and of more rapid socialization of immatures through an increased availability of play partners (Fagen 1981) could be realized if adult females with young associated with other similar adults. Allomothering of young juveniles by older but subdominant females, has been observed in elephant family units by Douglas-Hamilton (1972) and reviewed by Dublin (in press). Generally, but not always, the allomothers are thought to be kin of the infants (reviewed by Hrdy 1976).

4. A variation of the information center idea (Krebs 1974, Ward and Zahavi 1973), where group members could benefit from the accumulated experience in habitat selection of the older matriarchs, might improve the foraging success of individual group members. Individuals or family units would continue to stay with an aggregation as long as individual foraging

efficiency remained high. This reason for group formation might be expected to operate at all times of year, although the greater unpredictability of food and water sources in wet seasons might favour group formation more at that time.

With the data available at present, it is not possible to distinguish which, if any, of the various potential reasons for group formation are most important. The reasons for forming bond groups might be different from those which favour the formation of family units on the one hand, and large aggregations on the other. For example, the threat of human predation should select for large groups at all times, while under the female mate choice hypothesis, large groups should form only when many females are likely to come into oestrus. Selection for allomothering opportunities might favour the formation of family units and, possibly, bond groups, but probably not large aggregations. The reasons for group formation for females and juveniles are likely different than for bachelor bulls, and are undoubtedly different again for bulls in "musth". Bulls in musth would have a greater tendency to associate with cow/calf groups than with other bulls, and, since bulls are not involved in the rearing of young, they would not have the same incentive for group formation as adult females.

Since it appears that there are a number of potentially important reasons for elephants to form large aggregations at most times of year, it seems that elephants may need to compromise foraging efficiency to satisfy these other goals.

This situation has been reviewed for wild birds (Zach and Smith 1981). However, foraging may ultimately limit elephants' ability to form large groups at times when food resources are limited, and the non-foraging goals may have to be sacrificed. It is possible for herbivores to maintain large group size through seasonal changes by choosing feeding habitats where large groups can remain cohesive, ie., where food is widespread and abundant (Jarman and Jarman 1979). The fragmentation of large groups elephants through time may not be random; it is possible that "bond groups" may persist for a longer period into the dry season than do aggregations of groups with no obvious social ties, possibly because of their (suggested) relatedness.

My results show that there was a tendency for numbers of large cow/calf groups to form in favourable habitats on a seasonal basis, although there was also a steady decline in the number of large groups sighted through the rains to late dry season. The habitats where large groups were found changed through the seasons, from the open Salvadora / Suaeda shrublands, and fever tree woodlands in the rains to swamp edge grasslands and woodlands by the late dry season. This suggests that the formation of large groups is important to a certain segment of the cow/calf population at least, and that the elephants could be making a compromise between foraging and social considerations in their selection and use of habitats.

Bachelor bull elephants had no apparent tendency to form large groups, nor did their larger groups tend to shift habitats in a consistent way.

2. Gender differences in habitat selection

In general, habitat selection and use was similar for bulls and cow/calf groups but there are also some differences, as noted in Chapter 4. Bulls were more evenly distributed across habitats, and selected the coarse grass swamp habitats more than the female groups. These differences may have been due to displacement of the bull groups by cow/calf herds, or may have resulted from an active choice by the bulls to avoid competition with the cow/calf herds at all times of year. The differences might also be correlated with differences in the metabolism and social organization of bulls and adult female leaders of the cow/calf groups.

Demment (1978) discussed sexual dimorphism in size and reproductive function with respect to metabolism and foraging requirements in baboons. The larger male baboons have a lower metabolic energy requirement per unit of food processing capacity (based on gut volume) than females, but have a larger absolute requirement. They should, therefore, feed on the more abundant, but lower quality, plant material. Their smaller size and the additional nutritional stress of pregnancy and lactation could require females to select a higher quality diet. Clutton-Brock et al. (in press) followed similar reasoning in their discussion of red deer foraging.

In the Amboseli elephants, the coarse grasses of swamp and swamp edge were probably digested more easily by the bulls. The larger bulls needed a greater absolute intake rate, but were able to compensate by eating low quality forage. This could

explain why bulls were seen feeding in the swamps more often than the cow/calf groups.

Because their social organization is so different, the effect of the social environment on foraging efficiency should also be different between bull and cow/calf groups. Bull groups are small, and individuals within the groups are widely separated and probably not closely related. Direct interference competition would have less effect on progression and feeding rates within bull groups, since this factor may have already acted to prevent large group formation. Members of cow/calf aggregations, on the other hand, must continually move with the group in search of new food sources, and both interference and exploitation competition would affect members directly. The habitats selected by cow/calf groups which allow feeding by larger groups (ie., the sites which are more open and where food items are more evenly distributed) might be different from the areas selected by bulls. For example, cow/calf groups made greater relative use of the open Salvadora / Suaeda shrublands in the rains and swamp edge grasslands in the dry season than did the bulls.

One might suspect that when bulls associate with the matriarchal groups, they are more interested in mating than feeding, but they would be affected by the same restrictions of maintaining contact with the group as are females and juveniles.

3. Special food types

The description of habitat herb and woody layers in simple terms such as "total dry mass", or "percent woody cover" ignores the complexity of species composition and the needs of the elephants to choose specific high value food types, or avoid particularly unpalatable ones. For example, in the wet season, the swamp edge herb layer contained succulent creepers that the elephants apparently sought as a food item (pers. obs.). Similar creeping vines were found on woody shrubs in the swamp edge young fever and palm woodlands. In the mid dry season of 1979, the A. tortilis woodlands produced a mast crop of high protein seed pods, while earlier in the year, the P. reclinata palm trees produced fruit pods. The elephants were seen feeding on these relatively rare, but presumably favoured and nutritious items. Were the habitats containing them selected as foraging sites because of these items? At this level of complexity, a more detailed study of diet selection is needed to answer this question.

In a similar vein, the low palatability of certain food types which may contain toxins, digestibility reducing compounds, or physical defences complicates the description of habitat feeding options. For example, many of the plants in the shrub and tree layer of the woodlands and bushlands are evergreen, while others are deciduous. Croze (1974b) found that in general, the bull elephants he studied were not selective in most of their feeding on woody species, although a few plants were significantly preferred or avoided. I did not examine this

question in the present study, but casual observations suggested that many shrub species were fed upon while others were never or only rarely touched.

The possibility that the elephants sought different, specific food types for specific needs such as digestible energy, protein, or minerals (for example, sodium (Weir 1972)), could affect the relative value of different habitats. In Amboseli, the bark of Acacia xanthophloea, or fever tree, was apparently attractive to elephants through much of the year -- the sap is known to have a high sugar content (Hausfater and Bearce 1976) -- , although the incidence of barking seemed to increase in the dry season. These trees were found in the swamp edge woodlands and the fever tree savannah woodlands, and could have affected their selection of these habitats.

C. Some Management Implications

It appears that the Amboseli elephants could be buffered from the severe effects of long term drought by their use of the swamp and swamp edge habitats in the Amboseli basin. The dense herb layer cover in these habitats, which is productive even during dry times, might make the Amboseli elephants less reliant on woody vegetation for drought period maintenance, when compared with the elephant populations of completely arid regions such as Tsavo. As Norton-Griffiths (1979) suggests for elephant populations with a food source alternative to woody plants, the Amboseli elephants might slowly decline through reduced recruitment at high density; rather than experiencing

the major adult mortality seen in Tsavo. The elephants could probably reduce the woody cover in the basin considerably in the process, and perhaps maintain the system in an open shrub grassland condition, or follow the possibly cyclic effects of water table fluctuations on woodlands. However, this process might be modified by the large populations of zebra, wildebeest, and livestock which also depend on the swamp edges as a food source in drought periods. Exploitation competition between elephants and the other large herbivores would likely occur at this point, and it is difficult to say which population would suffer from this competition the most. More information is clearly needed on the impact of elephants and other factors on woodland and herb layer dynamics.

For the sake of the elephant population alone, I would not consider management intervention through culling or hunting to be necessary at the present time. However, other management priorities may be important, such as the maintenance of woodland areas for aesthetic reasons, or for the preservation of woodland-dependent species such as rhinoceros, certain antelopes, or monkeys. A more detailed study of elephant impact on the woodlands would be necessary, and possibly management reduction of elephant numbers might then be justified. However, any removal of elephants through cropping should be accompanied by a research program to monitor the effects of such an action on habitat dynamics and on the social structure and population dynamics of the elephants and other large herbivores.

D. Questions for Further Study

Many of the suggestions put forward in this discussion can be only tentative at this point, since my approach was at a very broad level. Some questions raised, and which clearly need further study are presented below:

1. What is the foraging efficiency in different habitats, on different food types, with differing abundance of individual elephants in separate age/gender classes?
2. What are the effects of social grouping on foraging efficiency? How do the effects differ for different age and gender classes?
3. Are there measureable differences in habitat selection and diet between individuals, or individual family units, which have different habitat use patterns? Are the different habitat use patterns of separate family units or bachelor bulls affected by social interactions such as spacing behaviour? What are the consequences of any such differences in terms of survival or reproductive success?
4. What are the direct effects on the vegetation, both woody and herb layer, of elephant feeding? Is the impact different when the elephants are in large vs. small groups?
5. What are the digestible nutrient contents of different elephant food types, in different

phenological stages? What are the minimum maintenance requirements of elephants for various critical nutrients, such as digestible energy and protein? Is there a useful indicator, such as faecal nitrogen, that could be used to estimate the nutrient content of elephant food intake?

The answers to these questions would bring us closer to an understanding of the interactions between elephants and their habitats, and would be useful from both the theoretical and practical perspectives.

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APPENDIX 1

Regressions Used for Biomass Estimation

1. Total biomass, herb layer (in g/m²): Slanting pin intercept
(D. Western, pers. comm.)

$$\text{Dry mass} = 8.630 + 67.745 * (\text{mean no. hits/pin})$$

$$r^2 = 0.882$$

2. Total biomass, herb layer (in g/m²): Circular plot
(D. Western, pers. comm.)

$$\text{Log(Dry mass)} = 1.02 * \text{Log}(\text{height} * \text{cover}) - 0.38$$

$$r^2 \text{ not given}$$

3. Green biomass, herb layer (in g/m²): Spectrophotometer
(McNaughton, 1979)

$$\text{Green mass} = 109.8 * \text{Ratio} - 83.8$$

$$r^2 = 0.956$$

4. Twig/leaf biomass, woody layer (in kg)

$$\text{Ln(Twig/leaf mass)} = 2.1177 * \text{Ln(Canopy Diameter)} - 0.7317$$

$$r^2 = 0.960$$

APPENDIX 2

Woody Species Measured for Calibration of the Biomass Estimation Regression

Tree/Shrub Species	Measured Canopy Diameter(m)	Measured Canopy Volume(m ³)	Twig/Leaf Biomass (kg)
<u>Cadaba farinosa</u>	1.86	4.89	1.787
<u>Capparis tomentosa</u>	2.57	8.82	2.480
<u>Maerua triphylla</u>	3.03	15.14	13.362
<u>Suaeda monoica</u>	2.74	5.72	4.100
<u>Sericocomopsis hildebrandtii</u>	0.96	0.33	0.364
<u>S. pallida</u>	0.91	0.33	0.678
<u>Acacia drepanolobium</u>	3.30	29.08	15.922
<u>A. mellifera</u>	6.04	77.36	22.671
<u>A. nubica</u>	3.69	20.85	8.805
<u>A. tortilis, mature</u>	16.60	2239.96	197.716
<u>A. xanthophloea, mature</u>	18.20	4032.41	136.777
<u>Azima tetraacantha</u>	2.34	6.88	2.538
<u>Salvadora persica</u>	3.06	13.97	4.115
<u>Balanites glabra</u>	2.99	24.53	42.268*
<u>Commiphora africana</u>	3.38	28.71	6.233
<u>Pluchea ovalis</u>	1.22	1.60	0.602
<u>Triplocephalum holstii</u>	1.29	1.41	0.626
<u>Lycium europaeum</u>	1.91	4.87	1.349
<u>Solanum incanum:</u>			
Canopy Diameter < 50 cm	0.28	0.04	0.029
C.D. > 50 cm	1.01	1.12	0.589
<u>Withania somnifera</u>	1.64	2.75	0.997
<u>Dicliptera albicaulis</u>	1.85	2.37	1.333
<u>Phoenix reclinata</u>	3.59	39.48	21.434*

Note:

Species indicated by * had unusually large twig/leaf biomass to canopy dimensions, and were not used in the multi-species regressions.

APPENDIX 3

Computation Factors and Estimated Twig/Leaf Mass for the "Mean Individual" of Each Woody Species

Tree/Shrub Species	Mean Canopy Diameter (m)	Computation Factor	Estimated Twig/Leaf Biomass (kg)
<u>Cadaba farinosa</u>	2.00	6.37	2.088
<u>Capparis tomentosa</u>	2.42	4.35	3.126
<u>Maerua triphylla</u>	2.96	2.91	4.790
<u>Trianthema ceratosepala</u>	1.48	11.63	1.104
<u>Suaeda monoica</u>	2.72	3.44	4.004
<u>Achryanthes aspera:</u>			
Canopy Diameter < 50 cm	0.30	282.94	0.028
C.D. > 50 cm	0.96	27.63	0.441
<u>Sericocomopsis hildebrandtii</u>	1.01	24.96	0.491
<u>S. pallida</u>	0.87	33.64	0.335
<u>Triumfetta flavescens</u>	0.78	41.86	0.284
<u>Hibiscus flavifolius</u>	0.38	176.35	0.062
<u>Abutilon grandiflorum</u>	0.48	110.52	0.102
<u>A. mauritianum:</u>			
C.D. < 50 cm	0.26	376.70	0.028
C.D. > 50 cm	1.79	7.95	1.651
<u>Acacia drepanolobium</u>	2.79	3.27	15.922
<u>A. mellifera</u>	5.91	0.73	20.713
<u>A. nubica</u>	3.82	1.75	8.220
<u>A. tortilis:</u>			
mature	16.21	0.10	0.000
young	4.28	1.39	10.458
<u>A. xanthophloea:</u>			
mature	15.27	0.11	17.862
young	6.61	0.58	23.091
sapling	4.22	1.43	10.049
seedling	0.33	233.84	0.037
<u>Azima tetracantha</u>	2.36	4.57	2.965
<u>Salvadora persica</u>	3.04	2.76	5.068

Appendix 3 continues on the next page

APPENDIX 3 continuedComputation Factors and Estimated Twig/Leaf Mass for the "Mean Individual" of Each Woody Species

Tree/Shrub Species	Mean Canopy Diameter(m)	Computation Factor	Estimated Twig/Leaf Biomass(kg)
<u>Balanites glabra</u>	2.81	3.22	42.268*
<u>B. pedicellaris</u>	2.68	3.55	34.000
<u>Commiphora africana</u>	3.55	2.02	7.165
<u>Erlangea somalensis</u>	0.69	53.49	0.174
<u>Helichrysum glumaceum</u>	0.63	64.16	0.174
<u>Dicoma tomentosa</u>	0.30	282.94	0.026
<u>Pluchea bequaerti</u>	0.80	39.79	0.300
<u>P. ovalis</u>	1.28	15.54	0.811
<u>P. sordida</u>	0.54	87.33	0.130
<u>Triplocephalum holstii</u>	1.27	15.79	0.213
<u>Lycium europaeum</u>	1.79	7.95	1.651
<u>Solanum incanum:</u>			
C.D. < 50 cm	0.28	324.81	0.032
C.D. > 50 cm	1.02	24.39	0.502
<u>Withania somnifera</u>	1.36	13.77	0.923
<u>Barleria acanthoides</u>	0.42	142.86	0.077
<u>Dicliptera albicaulis</u>	1.78	8.05	1.631
<u>Leucas pododiskos</u>	0.40	159.15	0.068
<u>Phoenix reclinata</u>	3.24	2.43	21.434*

Note:

1. Twig/leaf biomass was estimated for tree and shrub canopy available below a height of 6 m., as calculated from mean plant dimensions.
2. Species indicated with * had unusually high twig/leaf biomass relative to canopy dimensions, so actual measured twig/leaf biomass was used for these species.

APPENDIX 4

Correction Factors for Ground Counts

A) Correction Factors for Vegetation Structure

MONTH	HABITAT TYPE				
	<u>S. consim.</u> grass.	<u>A. tort.</u> woods	Fever woods	<u>S/S</u> shrub	Swamp edge gr.
November 1978	1.012	1.199	1.087	1.154	1.021
December	1.024	1.213	1.100	1.167	1.033
January 1979	1.036	1.227	1.113	1.181	1.045
February	1.048	1.241	1.126	1.195	1.058
March	1.066	1.263	1.145	1.216	1.076
April	1.078	1.278	1.158	1.230	1.088
May	1.096	1.299	1.178	1.250	1.113
June	1.115	1.322	1.198	1.272	1.132
July	1.121	1.326	1.201	1.276	1.139
August	1.127	1.333	1.208	1.283	1.145
September	1.133	1.341	1.214	1.290	1.151
October	1.139	1.348	1.221	1.297	1.157

B) Correction Factors for Group Bunching

MONTH	ALL HABITAT TYPES
November 1978	1.134
December	1.136
January 1979	1.138
February	1.140
March	1.142
April	1.143
May	1.148
June	1.149
July	1.153
August	1.152
September	1.154
October	1.153

APPENDIX 4 continuedCorrection Factors for Ground Counts

C) Correction Factors for Both Vegetation Structure and Group Bunching

MONTH	HABITAT			
	<u>S. consim.</u> grass.	<u>A. tort.</u> woods	<u>S/S</u> shrub	Swamp edge gr.
November 1978	1.182			
December				
January 1979				
February				
March				
April	1.260			
May				1.259
June		1.457		
July			1.474	
August				
September				
October				