ELEPHANTS OF THE MASAI MARA, KENYA: SEASONAL HABITAT SELECTION AND GROUP SIZE PATTERNS

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ABSTRACT

This study ascertained that habitat selection and group formation by elephants in the Masai Mara National Reserve (the Mara) fit the general pattern observed in other African elephant populations. Both sexes preferred habitat types with large quantities of nutritious grasses during the wet season and both tended to select browse vegetation in the dry season. In addition, average group size was larger in the wet season for most habitats. Seasonal differences in herd size were not the result of random aggregations in preferred habitats, but were more likely because bulls joined cow-calf herds to breed during the rains. The formation of larger groups in the wet season, when food is not limited, probably allows elephants to interact, to determine dominance hierarchies and to re-establish bonds.

INTRODUCTION

The differential use of habitats by elephants can alter significantly the structure of affected plant communities (Laws, 1970; Field, 1971; Thomson, 1975). Utilisation patterns are influenced by forage preference and availability (Leuthold & Sale, 1973; Western & Lindsay, 1984; Thouless, 1995) as well as by external factors such as extreme weather conditions (Corfield, 1973), human settlement and cultivation (Lamprey *et al.*, 1967; Laws, 1970; Western & Lindsay, 1984; Lamprey, 1985), and poaching activity (Dublin & Douglas-Hamilton, 1987). Over the past 25 years, these external factors have led to the concentration of the majority of Africa's elephants in protected refuges in many parts of their range (Cumming, *et al*, 1990; Said *et al.*, 1995). It is necessary to know the habitat utilisation patterns of elephants within parks and reserves, such as the Mara, in order to understand their impact and to make decisions on local management.

This paper describes the seasonal changes in habitat selection and group size of the elephants within the Mara. Habitat selection is discussed as it relates to changes in feeding patterns between the seasons. The possible functions served by elephant aggregations are examined as well as the constraints placed on group size by food availability.

STUDY AREA

The Mara lies on Kenya's southwestern border with Tanzania and forms the northernmost extension of the 2S,000km^2 Serengeti-Mara ecosystem. In 1974, over 1,700km^2 were formally gazetted for the Reserve but, following more recent boundary modifications, only 1,510km^2 remain. The area to the north and east of the Mara is now permanently settled by pastoralists and large-scale agricultural schemes (Douglas-Hamilton *et al.*, 1988). To the west, the Mara is bordered by the Siria Escarpment, which rises 100-300m above the plains below, which have a mean elevation of approximately 1 ,600m. To the south lies the Serengeti National Park in Tanzania. The Mara river, the largest perennial river in the Serengeti-Mara ecosystem, drains the northern Serengeti and Mara region and flows into Lake Victoria some 100km to the west.

In the late 1970s the Serengeti provided elephants with a safe refuge from poaching pressure which was high at that time both inside and to the north of the Mara. Throughout the 1980s, the situation was reversed and poaching pressure mounted on the Serengeti side, thus cutting off this escape route to the south. Throughout the 1980s and early 1990s, elephant seasonal movements in and out of the Mara were curtailed severely. Today, approximately 1,500 elephants utilise the Mara and its adjacent pastoral lands all the year-round and their impacts on the remaining woodland habitats are pronounced (Dublin *et al.*, 1990; Dublin, 1995).

Climate

Rainfall in the Mara is bimodal, with short rains falling in November-December and long rains occurring from April-May (Masai Mara Ecological Monitoring Programme reports, 1982-1995). The Mara also has a pronounced east-west rainfall gradient with the east side averaging approximately 800mm/year and the west side approximately 1,200mm/year (Norton-Griffiths *et al.,* 1975; Epp & Agatsiva, 1980; Stelfox *et al.,* 1986), with an overall average of 1,000mm/ year. Minimum and maximum daily temperatures in the Mara average 14.8˚C and 28.l˚C.

Habitat types

In addition to the differences in annual rainfall patterns, the east and west sides of the Mara are also characterised by differences in habitat types. The eastern portion of the Mara has more area covered in woody vegetation along river courses and on hilltops. All trees and shrubs were classified according to Dale and Greenway (1961) and all grasses and herbs according to Edwards and Bogdan (1951).

Relict thickets are widespread and diverse, containing seedlings of trees and shrubs and coppicing rootstocks of many species. These include: *Acacia brevispica, A. gerrardii, A. hockii, A. senegal, Albizia amara, A. ptrersiana, Boscia angustifolia, Commiphora africana, C. trorhae, Cordia ovalis, Dichrostachys cinerea, Grewia spp., Lippia javanica, Ocimum americanum, Ormocarpum trichocarpum,* and *Solanum incanum.* The majority of plants are less than one metre high. Standing dead trees are commonly seen in this community.

The *Acacia gerrardii* woodlands occur as highly clumped stands frequently found in association with the relict thickets mentioned above (Herlocker, 1976). Although Trump (1972) did not distinguish this as a distinct community type, Lamprey (1985) documented the rapid increase of A. *gerrardii* woodlands in many areas of the Mara over the past decade. This proliferation is largely attributed to its fire-tolerance (Glover & Trump, 1970; Spinage & Guinness, 1972; Dublin, 1995). Individual plants persist through time by sprouting new shoots from underground rootstocks following burning or browsing; it is, therefore, difficult to assess their true age. A variety of seedlings and root coppicing species are commonly found in this community. These include: *Acacia senegal, Commiphora spp., Dichorostachys cinerea,* and *Ormocarpum trichocarpum* which all remain under one metre high in areas where burning is frequent or severe.

Many ridge tops, small hills, and seasonal drainage lines in the Mara are covered by discrete islands of *Croton* thickets which are unique to the northern Serengeti and Mara region. Though *Croton* dominates the species composition in these thickets, species diversity remains high. While most species fall below the four to five metres *Croton* height class, species such as *Haplocelum foliolosum, Olea africana, Tarenna graveolens,* and *Teclea rrichocarpa* attain heights up to six and seven metres. In the lower layer *Acacia brevispica, Cordia ovalis, Grewia trichocarpa, Rhus natalensis* and *Strychnos henningisii* are found. This community is frequently marked by one or more adult *Gardenia jovis-tonantis* trees which occur 10-15m from the thicket edge and are never found inside the thickets proper.

Balanites aegyptiaca woodlands occur only in the far western section of the Mara. This community, also referred to as *Balanites - Acacia seyal* woodland (Herlocker, 1976; Lamprey, 1985), is prevalent on the open, grassy, park-like expanses of the Mara 'Triangle" area. A reported decline in the density of *Balanites* stands in this area was attributed to heavy browsing by giraffes (Glover & Trump, 1970; Pellew, 1981) and still is apparent today. The majority of remaining adult trees are well above the browsing reach of giraffes and elephants and regeneration may be limited both by seed predators (Lamprey *et al.,* 1974) and browsers (Belsky, 1984).

The Mara comprises of a combination of edaphically-derived and fire-induced grasslands dominated by the perennial grass, *Themeda triandra,* "red oat grass". Following the long rains other tall grasses such as *Digitaria macroblephara, Hyparrhenia filipendula, Pennisetum mezianum,* and *Setaria phleoides* also flower in these grasslands. The overall grass productivity is high, ranging from 7,000 - 8,000kg/ ha/yr (Sinclair, 1975). The migratory zebra and wildebeest may remove 80-90% of the standing crop biomass (McNaughton, 1976; Stelfox *et al.,* 1986; Onyeanusi, 1989) each dry season. The short-cropped plains they leave behind then permit the growth and flowering of other, less competitive grasses such as *Aristida adoensis, Eragrostis tenuifolia, E. racemosa, Harpachne schimperi* and *Sporobolus stapfianus.*

METHODS

Habitat selection by elephants was determined using two independent techniques. The first, total aerial counts, was used to distinguish selection only on a wet and dry season basis, whereas the second, monthly census circuits, allowed an analysis of habitat selection both by season and by sex.

Wet and dry season total counts of elephants

Two aerial total counts of elephants, one dry season and one wet, were conducted in the northern Serengeti National Park, and the entire Mara, in 1984 and 1985. Herds were counted and mapped by habitat type. Densely wooded areas were searched more intensively than open areas to correct for the relative visibility of elephants in different habitats.

To test the hypothesis that elephants were randomly distributed in the available habitats, the total number of elephants observed in each habitat type was compared to an expected frequency distribution. This expected frequency distribution was derived from a photo mosaic produced from an aerial survey of the area in early 1982 by the Kenya Rangelands Ecological Monitoring Unit. These photographs, at a scale of 1:50,000, were large enough to distinguish habitat types. All habitat types distinguished on the photographs were checked on the ground using a :50,000 topographic map of the Mara to re-locate the areas. Thirty line transects were drawn on the photographic mosaic and analysed for the proportions of different habitats. These proportions provided the theoretical random distribution for elephants showing no habitat selection (Table 1). For the purpose of analysis these expected distributions were converted to numbers, based on the observed sample size. Chi-square analysis was then used to compare the observed versus the expected numbers across all habitat types.

Table 1. The percentage of each habitat type measured from aerial photography of the Mara flown in 1982 and monthly census circuits. These percentages were used to calculate the number of elephants to be expected in each habitat under a random distribution.

Habitat type	Aerial photography (%)	Monthly circuits (%)
Grassland (GR)	41	43
Relict thicket (RT)	29	34
Acacia woodland (AW)	8	4
Croton thicket (CT)	6	6
Balanites woodland (BW)	4	7
Swamp (SW)	4	0
Other (OT)	8	6

Monthly census circuits

A 152km circuit was established in the Mara. Initially, the entire circuit was driven and the habitat types which intersected this circuit were mapped to the nearest 0.1km. The cumulative length of each habitat type was then expressed as a proportion of the total circuit length. From these proportions a random frequency distribution for elephants by habitat type was produced (Table 1). Using the observed sample sizes of elephants, this frequency distribution was then converted to numbers which allowed a comparison of expected with observed numbers of males and females in each habitat type for each month.

This circuit was driven once each month over a two-year period (from 1983 to 1985) comprising two dry seasons and two wet seasons. All elephants observed from the vehicle were recorded by age, sex, and the habitat in which they were seen. Visibility from the circuit was excellent and the chance of sighting elephants in the different habitats was assumed to be equal. Chi-square analysis was again used to compare the observed numbers of males and females by habitat types to the expected numbers for both the wet and dry seasons and to compare the sexes within each season.

These same circuit data were used to calculate mean group sizes for all-bull herds, mixed-sex herds and cow-calf herds both by season and by habitat. These means were then tested against one another between seasons, habitats and herd type using a Kruskal-Wallis analysis-of-variance test.

RESULTS

Habitat selection

Seven hundred and eighty-five elephants were counted in the dry season and 912 in the wet season. Elephants surveyed during the aerial counts were not distributed randomly with regard to habitat type in either season (seasonal c^2 values: wet = 126.3, dry = 347.7, d.f. =6, P<.001). They showed distinct habitat preferences (Figure 1): in the wet season elephants selected grasslands, *Croton* thickets and swamps more than expected by random use, with 48.3% frequenting grassland. A substantial proportion of elephants (27.7%) were also found in relict thickets in the wet season but less than expected by chance alone. In the dry season *Croton* thickets were selected significantly more than expected. Although frequency of habitat selection remained relatively high for grassland (33%) in the dry season, there was a clear shift in habitat preference, with 39.9% selecting *Croton* thickets as opposed to only 8.8% in the wet season.

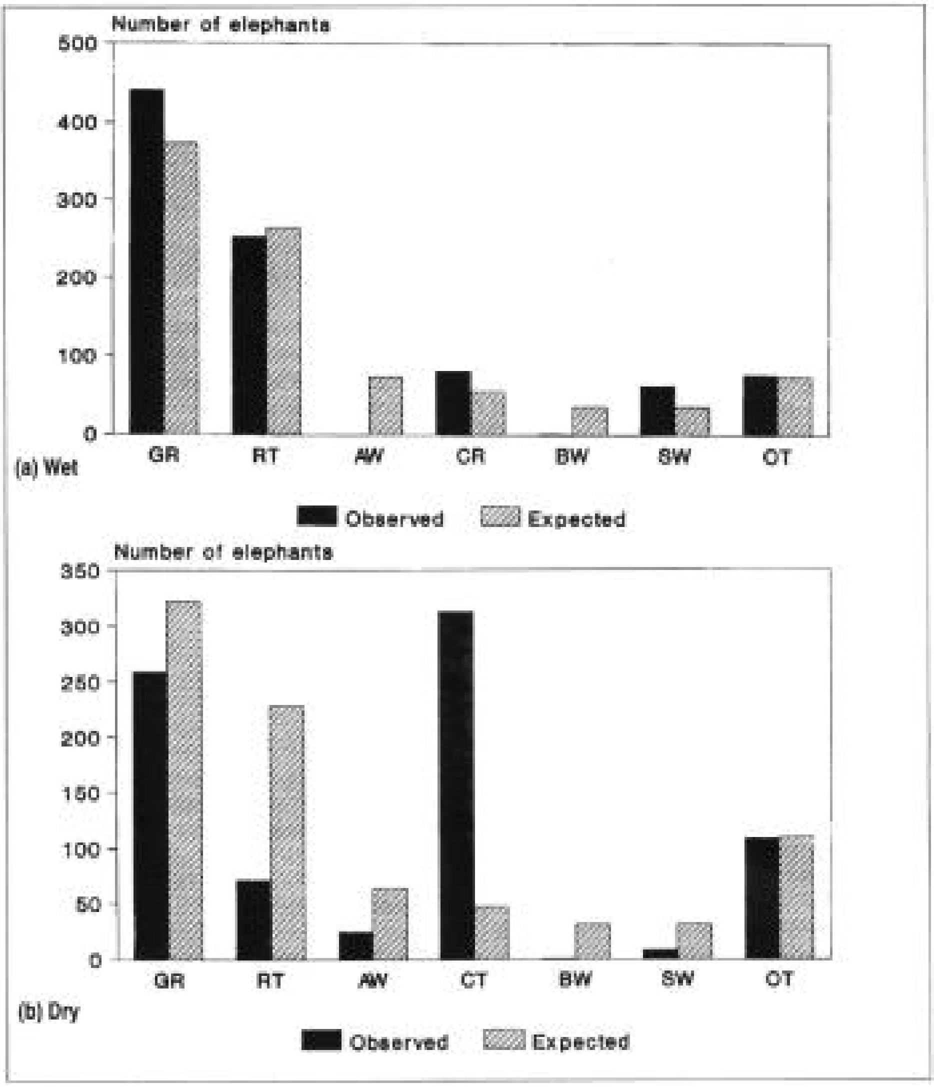

Figure 1. The habitat preferences of elephants in the Mara in the (a,) wet season and (b) dry season. The xpected values are calculated from a breakdown of the Mara by habitat type using the 1982 aerial photography. The observed numbers were taken from aerial counts flown in both seasons.

These patterns were similar to those recorded on the monthly census circuits. Both sexes showed non-random use of habitats in both seasons (c^2 values for males: wet = 11.5, number of males (n) = 111, P<.05, dry = 14.3, n = 25, P<.025, d f = 5,c^2 values for females: wet = 13.9, n = 247, P<.025, dry = 38.9, n = 116, P<.001, d.f. = 5). Females selected grasslands and *Croton* thickets in the wet season more than expected whereas males selected grasslands and relict thickets (Figure 2). In the dry season males and females both selected *Croton* thickets more than expected **by chance alone** (Figure 3) Males and females did not differ significantly in their distributions in either the wet (c^2 = 8.0, d.f. = 5. n.s.) or dry season (c^2 = 4.9, d.f. = 5, n.s.). Seasonal differences were significant for males (c^2 = 33.2, d.f. = 5, P<.001) and females c^2 = 58.7, d.f. = 5, P<.001).

Group size

Seasonal variation in group size was calculated from aerial count data, excluding all-bull groups. The average herd size seen from the air was 19.0 individu-

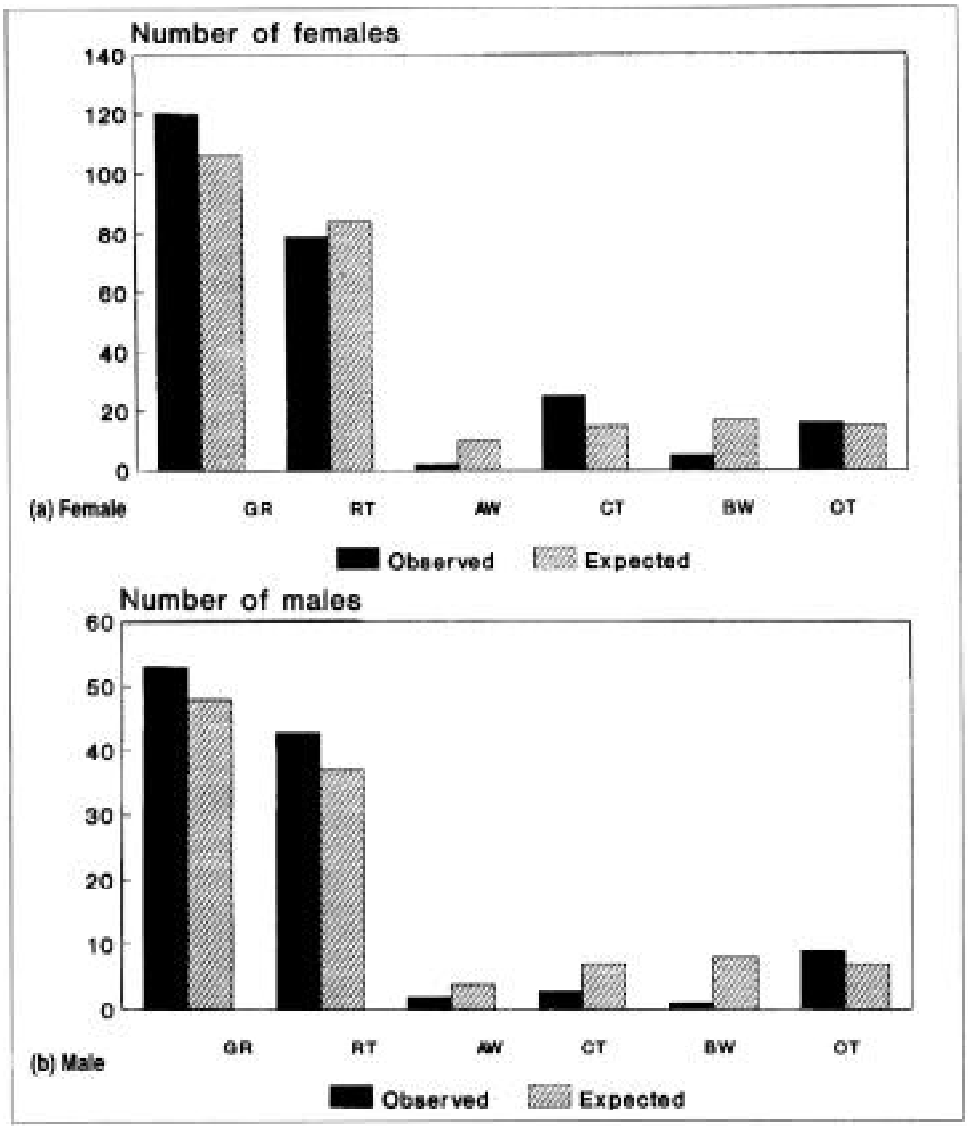

Figure 2 Wet season habitat preferences of (a) female and (b,) male elephants in the Mara. The expected values were calculated from a breakdown for the monthly. circuit by. habitat type. The observed numbers were derived from censuses driven on this circuit each month.

als/group in the wet season and 13.2 individuals/group in the dry season. These seasonal averages differed significantly (t = 2.58, d.f. = 107, P<.0l). The monthly circuit data allowed a further comparison broken down by the three diffetent herd types (Table 2). This analysis compared favourably with the results of the aerial-count data. Cow-calf groups accompanied by males (mixed-sex herds) were significantly larger than cow-calf herds in both the wet (t = 4.68, d.f. = 215, P<.0005) and dry (t = 3.34, d.f. = 172, P<.001) seasons. Mixed-sex herds further showed significant increases in mean size between the seasons (t = 2.77, d.f. = 111, P<.005) with wet season aggregations being larger than dry. Cow-calf and all-bull herds did not differ significantly in mean size between seasons. Even the largest wet season herds in the Mara never reached numbers such as the 700 recorded in seasonal aggregations in Tsavo (Laws, 1969) or the 400 in Amboseli (Western & Lindsay, 1984) National Parks. The largest wet season aggregation recorded during this study was 158 animals and the largest dry season group only 40.

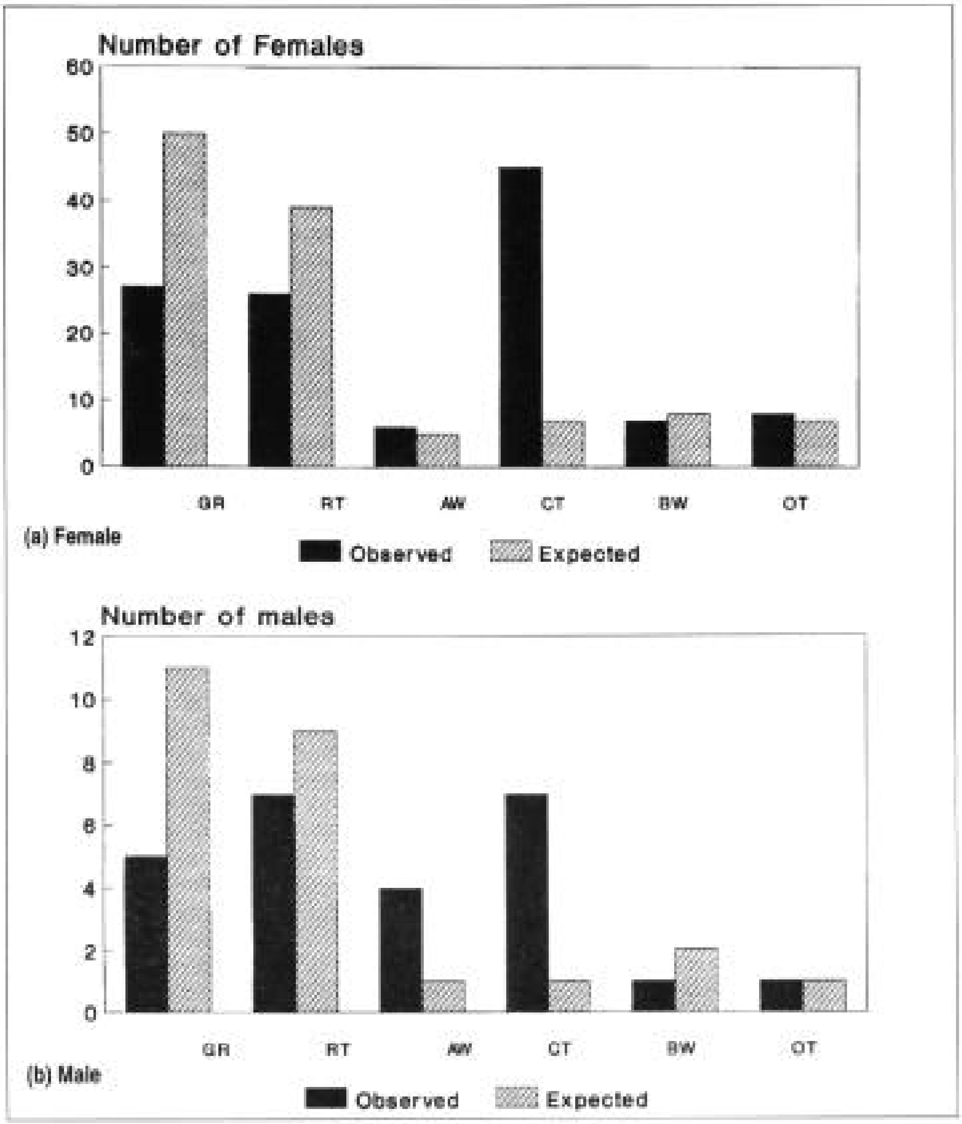

Figure 3. Dry season habitat preferences of (a,) female and (b) male elephants in the Mara. The expected valves were calculated from a breakdown of the monthly circuit by habitat type. The observed numbers were derived from censuses driven on this circuit each month.

Table 2 Mean herd size by. season and year-round for all-bull herds, mixed-sex herds and cc w-calf herds. The number in parentheses is the number of each herd type observed by season during the monthly census circuits.

Type of herd	Wet	Dry	Year-round
Mixed-sex	16.1 (85)	12.9 (28)	14.8
Cow-calf	7.4 (132)	7.7 (146)	7.5
All-bull	1.9 (113)	2.0 (78)	1.9

Mean size for each herd type did vary between seasons and between habitats (Table 3). In general all herd types tended to be larger in the wet season than during the dry season across the major habitat types. However, this seasonal difference was only significant for cow-calf groups accompanied by males $\underline{H}_{2,222} = 8.32$, P<.0l). Mean herd sizes between habitats within a season did not differ significantly regardless of herd composition (all H-values were not significant).

Table 3. Mean herd sizes by habitat type for mixed-sex herds, all-bull herds and co w-calf herds by season (w= wet; d= dry). The number in parentheses is the number of herds observed in each habitat type during the monthly census circuits summed over the entire season.

		Grassland Thicket	**Relict Woodland**	***Acacia* Thicket**	***Croton***	**Swampy**	**(n)**
Mixed-Sex	w	18.8 (14)	19.0 (31)	12.2 (10)	14.8 (20)	10.7 (10)	85
	d	12.9 (7)	8.6 (5)	10.4 (6)	14.5 (10)	- -	28
Cow-Calf	w	8.3 (20)	8.2 (65)	10.7 (13)	6.2 (21)	9.2 (13)	132
	d	8.0 (39)	7.9 (41)	6.0 (25)	7.9 (33)	7.6 (8)	146
All-bull	w	1.6 (21)	2.0 (55)	4.0 (5)	2.2 (18)	3.6 (14)	113
	D	1.7 (21)	1.7 (19)	1.8 (21)	1.8 (12)	2.6 (5)	78

Aerial count data also showed no significant correlation between average herd size and numbers per habitat type for either the wet (rs = 0.43, n = 8, n.s.) or dry season (r_s = 0.54, n = 8, n.s.). The largest groups were seen in relict thickets and grasslands in the wet season.

Photo credit: Holy Dublin

A female elephant browsing in the Mara

DISCUSSION

Habitat selection

The study revealed that during the rains, when forage of all types was abundant, Mara elephants were primarily grazers, like those in other populations (Field, 1971; Field & Ross, 1976; Guy, 1976; Barnes, 1982; Western & Lindsay, 1984). This is consistent with the idea that forage quality is the determining factor in habitat choice because the new grasses and sprouting seedlings growing in these areas are highly nutritious. Although new browse leaves may have higher absolute crude protein levels than new grasses (Dougall, 1963; Dougall & Glover, 1964; Dougall *et al.,* 1964; Field & Ross, 1976; McNaughton *et al.,* 1985), they may also contain high levels of secondary compounds such as tannins which may interfere with feeding (Coley, 1983; Sukumar, 1985; Jogia *et al.,* 1989). For the most part, the habitats selected during the wet season were dominated by grasses.

Unlike Amboseli elephants (Lindsay, 1982), Mara elephants followed a dry season foraging pattern more like that reported for elephants in other seasonal areas such as Queen Elizabeth and Kidepo Valley National Parks, Uganda (Field, 1971; Field & Ross, 1976), Sengwa Wildlife Research Area, Zimbabwe (Guy, 1976), and Ruaha National Park, Tanzania (Barnes, 1982). They switched to a predominantly browse diet in the dry season (Dublin, 1986). Even among those elephants remaining in grassland during the dry season, there was an observed shift to more “shrubby” grassland, where they foraged on small seedlings among the grasses. Dougall et al. (1964), Field (1971) and Barnes (1982) pointed out that woody species maintained higher crude protein levels relative to grasses during water-limited times. The nutritional quality of grasses declines rapidly as they begin to age in the dry season. Habitat choices in the dry season may reflect these forage preferences.

Facing an already reduced availability of browse forage and shade trees (Dublin, 1991), elephants concentrate their time within the *Croton* thickets. With the significant loss of other woodland habitats in the

Mara over the past three decades, these thickets now provide one of the last wooded refuges available to elephants. Here they are able to find shade, and also to forage on woody species, and herbs which thrive in the moist, shady conditions under the canopy of these thickets.

This constant use of *Croton* thickets for food and shade has caused severe damage to their internal structure and opened large pathways through the vegetation (Dublin, 1991). In subsequent rainy seasons, these light gaps grow thick swards of grass. Most grazers avoid the risk of hidden predators in thickets so the grass is frequently left to dry. When fires occur it burns very hotly, so that the nearby trees and bushes are also destroyed. As the years progress the thickets become increasingly fragmented.

The general tendency for elephants to under-utilise grasslands in the dry season may be a direct consequence of competition with the migratory wildebeest which are present in the Mara throughout that time. The sheer numbers of wildebeest present in the dry season displace elephants from both *Themeda triandra* grasslands and the more highly preferred but more limited *Cynodon dactylon* patches (Dublin, 1995).

Leuthold and Sale (1973) suggested that elephant habitat selection in Tsavo National Park was limited mostly by the quantity of food available and may be constrained further by the distribution of permanent water sources which are critical to their survival, particularly during the dry season (Corfield, 1973). The findings of Western and Lindsay (1985) in Amboseli partially supported this idea. In the dry season, Amboseli elephants utilised the swamps most heavily. These swamps were the lowest in crude protein (quality) but the highest in forage biomass (quantity). However, elephants used the bush-grassland habitat to a similar extent in the dry season. This bush-grassland habitat was lowest in available forage biomass but significantly higher than swamps in available crude protein. From this evidence and from the findings in the Mara, it seems likely that elephants may select primarily on the basis of forage quality but may be limited in their choice by the amount of food available within their range. The relative importance of quality versus quantity may be mediated by local elephant densities. In areas of high density, elephants may be more restricted by the absolute quantity of available food, regardless of the nutritional value of the type of forage eaten or habitat in which it is found. At the time of this study, when elephant densities were not considered to be very high in the Mara. their choice of habitats may have been influenced to a greater extent by forage quality than quantity as they appear to be in Amboseli, where local densities are much greater.

Group size

It is possible that elephants form aggregations as a direct consequence of the numbers in a habitat. However, the data do not support this hypothesis. In fact, there was no correlation between elephant numbers in specific habitats and average group size in these same habitats. Group size appeared to be determined by factors other than random aggregations based on habitat preference. In general, average herd size was correlated with season, with larger herds forming in the wet season when availability of preferred forage is greater. This was particularly true for cow-calf groups accompanied by bulls.

Such seasonal variation in herd size may be attributed to the seasonality of mating and birth peaks. In a number of populations, mating occurs during or slightly after the peak of the long rains (Hanks, 1969; Dublin, 1983; Moss, 1983; Western & Lindsay, 1984). At this time males temporarily join cow-calf herds to gain access to oestrous females. Births then occur just before or during the rains (Dublin, 1983; Hanks, 1969). Variations in the size of Mara elephant herds are consistent with this hypothesis. The average size of herds containing adult males was considerably larger than exclusively cow-calf groups and this was particularly significant during the wet season when breeding was observed.

Douglas-Hamilton (1972), Moss and Poole (1983) and Western and Lindsay (1984) have all suggested that additional social benefits provide a strong impetus for herd formation. For example, elephants may aggregate on a periodic basis as a means of maintaining and strengthening bonds or establishing dominance hierarchies within kin groups. These relationships may last throughout their long lives.

Findings by Poole *et al.* (1988) demonstrate that the low frequency sounds associated with certain behavioural patterns among elephants may actually be exchanges of information on levels previously unrecognised. Periodic aggregations would provide an opportunity for such exchanges between individuals and herds. Laws *et al.* (1975) cited predation on elephants as a basis for aggregation. Western and Lindsay (1984) discussed the possible foraging benefits which larger groups may accrue through the exchange of information or through facilitation but emphasised that there is currently no hard evidence to support these ideas.

Untangling the relative contributions of various factors to group formation and tenure is a difficult task. For a variety of possible reasons larger herds seem to be desirable but are possible only when local food supplies are not limited. For an animal as large as an elephant, this condition could restrict formation of very large groups to the rainy season only.

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