NATIONAL ZOOLOGICAL PARK

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January 8, 1975

Dr. George J. Jacobs
Chief, Earth Resources Survey Program
NASA Headquarters, Room 254
Washington, D. C. 20546

Dear George:

This letter will constitute my final report on "Satellite Animal Tracking Feasibility Studies" (NASA Grant NGR 09-015-163 to the Smithsonian Institution) which terminated on 31 December 1974. Previous reports by myself, Howard A. Baldwin, James C. Maxwell, and John J. Craighead have maintained information up-to-date.

During the past two and a half years, the project concentrated on aerial and ground testing of radio transmitters for tracking elephants in Tsavo National Park, Kenya, to develop systems for satellite tracking. A proposal was submitted for the Nimbus F experiment; NASA first authorized the experiment as part of the Numbus F program and later withdrew approval (letter from David L. Winter to me dated 5 August 1974).

A preliminary report of the results of radiotracking elephants was published by Walter Leuthold and John B. Sale in the East African Wildlife Journal in 1973 (copy of article enclosed). Additional transmitters and receivers (some also purchased by the World Wildlife Fund through a grant to the Smithsonian Institution) were provided for further elaboration of the study of movements by elephants throughout the year in relation to rainfall and food supply. Techniques were perfected for capturing and fitting radio collars to elephants (including matriarchs), the transmitter and antenna design was greatly improved, and vertical orientation of the antenna was maintained by placing the transmitter at the base of the collar and deploying the antenna between layers of the machine-belting of the collar.

The studies are continuing and publication of the results will be forwarded to NASA. It is hoped that the background of aerial and ground tracking will provide the basis at some point in time for satellite tracking of elephants in various parts of Africa.

(NASA-CR-141134) SATELLITE ANIMAL TRACKING FEASIBILITY STUDIES Final Report, 31 Dec. 1974 (Smithsonian Institution) 16 p HC $3.25 CSCL 06C

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I continue to be interested in satellite tracking of free-living animals, and I would appreciate being kept informed of new developments and new opportunities for research in this area at NASA. If I can be helpful as a consultant on matters concerning satellite tracking of wildlife, please feel free to call on me.

Sincerely yours,

Helmut

Helmut K. Buechner
Senior Ecologist

HKB:wmh

E. Afr. Wildl. J., 1973, Volume 11, pages 369–384

Movements and patterns of habitat utilization of elephants in Tsavo National Park, Kenya

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Grant NGR 09-015-163

Summary

Following the 1970–71 drought, which resulted in heavy elephant mortality, a long-term study was initiated in Tsavo National Park to determine movements and home ranges of individual elephants and their relations to overall distribution patterns and environmental factors such as rainfall. The preliminary results presented show the post-drought situation but it is recognized that they may not represent normality. Methods used were radio-tracking and observations of visually identifiable individuals. Two aerial counts provided data on overall distribution.

Two bulls and two cows were radio-tagged in Tsavo West and two bulls and four cows in Tsavo East, providing home range and movement data. Home ranges in Tsavo West (mean = 350 km^2) were considerably smaller than in Tsavo East (mean = 1580 km^2).

The differences between Tsavo West and Tsavo East are probably related to habitat quality, Tsavo East receiving less rainfall than Tsavo West. This view is supported by the fact that the 1970–71 mortality was largely confined to Tsavo East.

The movements of individuals were useful in interpreting relatively major shifts in elephant distribution that occurred within a 4-month period.

The following preliminary conclusions emerge from the results obtained so far:

(1) Elephants in the Tsavo area, particularly Tsavo East, were more mobile during the study period than was assumed from earlier studies, undertaking long-distance movements in fairly direct response to localized rainfall.

(2) A subdivision of the overall population into locally distinct units may exist during the dry season but did not obtain after significant rainfall, when the elephants ranged over wide areas and came into contact with animals from other dry-season units.

(3) Circumstantial evidence suggests that food is the primary proximal factor governing movements and distribution of elephants in the area. Food availability, in turn, is determined largely by the spatial and temporal pattern of rainfall.

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Introduction

In Tsavo National Park, elephants (*Loxodonta africana* (Blumenbach)) concentrate near permanent water supplies in the dry season, utilizing other areas primarily during and after periods of rainfall, when the vegetation is green and surface water is widely available. Little is known, however, of the details of the elephant movements involved or the factors governing them. Information on these aspects of elephant biology is needed, both in the context of a study on food habits being undertaken by one of us (J.B.S.) and from the point of view of park management.

The spectacular elephant mortality in the park during the 1970–71 drought (Corfield, 1973) highlighted these questions specifically, against the background of the long-standing 'Tsavo Elephant Problem' (Glover, 1963; Bax & Sheldrick, 1963; Laws, 1969; Glover, 1972; Sheldrick, 1972). Circumstances surrounding the mortality suggested that prolonged drought conditions lead to severe depletion of food resources in the dry-season concentration areas, causing the deaths of many elephants of certain sex and age categories. It was observed, however, that elephants died of starvation in some localities, whilst the vegetation appeared to be in considerably better condition only 10–20 km away in areas not occupied by elephants (Sheldrick, Corfield, personal communication). It was puzzling that the elephants did not move to other areas apparently offering a better food supply. These observations may suggest a strong attachment of elephants to certain localities, inhibiting them from moving elsewhere, an interpretation more or less in line with the hypothesis advanced several years earlier that the Tsavo elephant population was subdivided into about ten 'unit populations' occupying discrete ranges and undertaking only limited seasonal movements (Laws, 1969). Alternatively, it is possible that the immobility was imposed by weakness due to the cumulative effects of poor nutrition and thus represents an effect of the drought itself, rather than a normal phenomenon.

Against this background, the present study was initiated to investigate relevant aspects of the social and spatial organization of the Tsavo elephants. The immediate objective was to determine home ranges and movements of individual elephants and their relationship to overall distribution patterns within the Tsavo population during the post-drought period. The ultimate aim is to relate these and later results to environmental conditions, in particular the rainfall regime, and eventually to obtain a clearer picture of long-term habitat utilization by elephants and of the factors influencing it.

This preliminary report covers the period from December 1971 to March 1973; the study is continuing.

Study area

Tsavo National Park (*c.* 20 000 km^2) is situated about halfway between Nairobi and Mombasa in south-eastern Kenya, in a semi-arid zone of 'nyika' vegetation (mainly *Acacia-Commiphora* woodland). The Park is divided into two administrative units of unequal size: Tsavo West (TsW, area *c.* 7000 km^2), to the south and west of the Nairobi-Mombasa road and railway line (Fig. 1), and Tsavo East (TsE, area *c.* 13 000 km^2) to the north and east of the railway.

The Tsavo climate is characterized by alternating dry and rainy seasons: a long dry season from June to October, 'short' rains in November–December, a short dry season from January to March and 'long' rains in April/May. However, this pattern is quite variable and often modified by 'out-of-season' rains or dry spells.

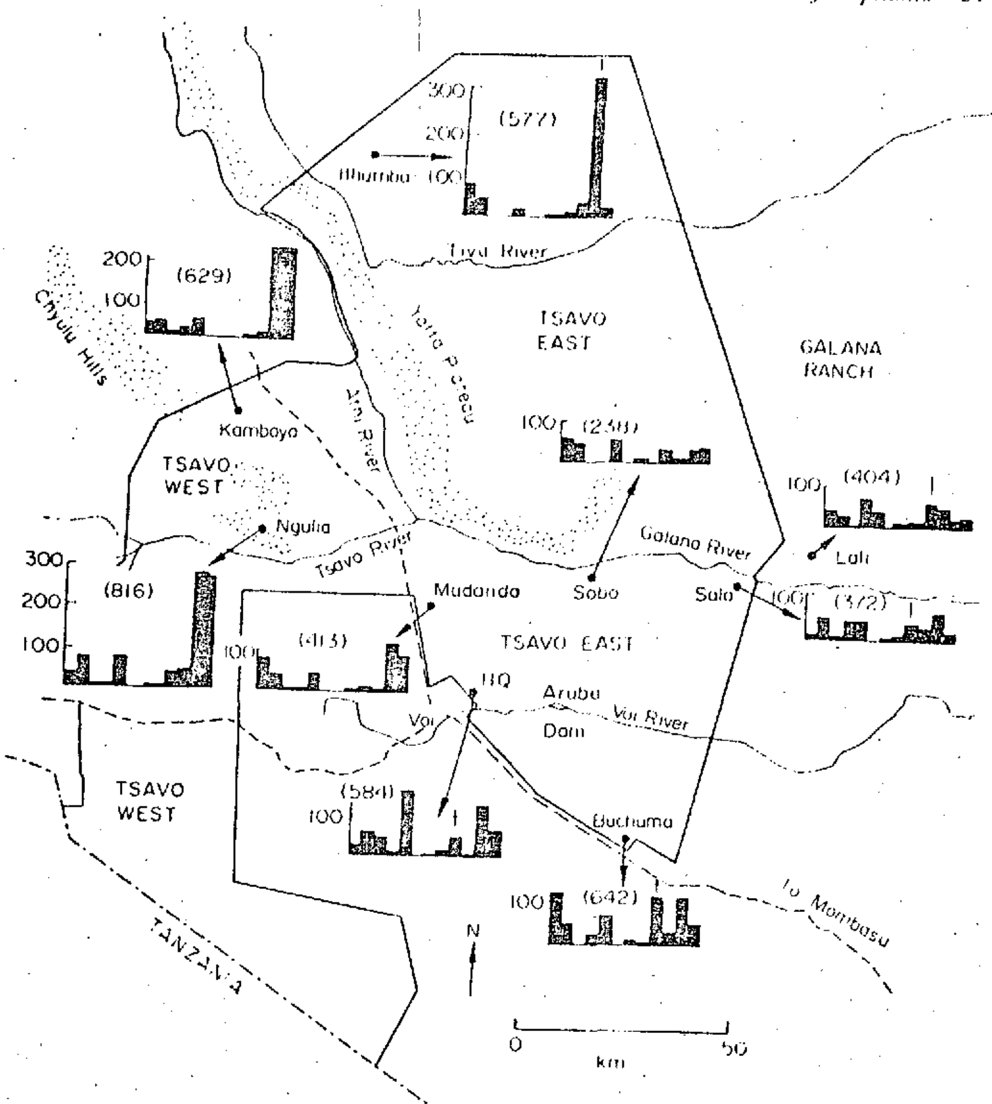

Fig. 1. Map of study area. The monthly rainfall totals for January to December 1972 are indicated for selected localities mentioned in the text. Columns marked with † show unusual rainfall (very high or out of season). Figures in parentheses total rainfall (in mm) for 1972. Solid line Tsavo National Park boundary. Broken line road and railway line.

Rainfall (Fig. 1) in TsW is generally higher and usually less erratic in spatial and temporal distribution than in TsE. On a regional scale, this is evident from the rainfall probability map, where a 'drought-prone' zone (annual rainfall less than 250 mm at least once every 10 years) envelops most of TsE, while TsW lies outside it (see Fig. 7b in Corfield, 1973). This is, at least partly, a consequence of the higher altitude and more broken topography in the region of TsW, including the Chyulu Hills and the Ngulia Range which reach 1800 m a.s.l. TsE on the other hand is mostly flat (300–500 m a.s.l.) except for the low Yatta Plateau and a few isolated granitic hills, less likely to 'trap' occasional rainstorms than the more massive ranges in and near TsW. The Chyulu Hills are additionally important by providing a virtually continuous water supply to springs along the periphery of several recent lava flows (e.g. Mzima Springs). The lava flows themselves, particularly the older ones, support largely evergreen woodlands of a type not occurring elsewhere in the Park. These apparently provide an important dry-season food supply for elephants, as can be inferred from seasonal concentrations of elephants in them.

Compared with TsW, in TsE, apart from rainfall being lower and more erratic, edaphic conditions are more uniform, water is more geographically restricted in the dry season, and the vegetation is more severely degraded in many areas, particularly along rivers where elephants tend to concentrate during the dry season (e.g. Galana, Tiva, Voi Rivers and Aruba Dam, Fig. 1).

Thus, environmental conditions can be characterized as being generally harsher and undergoing more extreme fluctuations (high probability of severe drought every 10 years) in TsE than in TsW.

Adjoining the eastern boundary of TsE is the Galana Ranch (Fig. 1), an area of fairly open *Acacia* savanna, merging into evergreen coastal bush on the eastern side. A scheme of mixed land-use is in operation there, under which wild animals are conserved for limited commercial exploitation. Elephants have unrestricted access to most of the area and freely cross the boundary between the Park and the ranch. For this reason, the western part of the latter was included in the study area. The rainfall regime is similar to that in TsE (Fig. 1).

Environmental conditions during the period of study

As one of the aims of this study is to determine the influence of rainfall on movements and distribution of elephants, a brief account of the rainfall pattern in 1972 follows (see Fig. 1).

After the 1970–71 drought, large portions of the Park, mainly in TsE, were almost completely denuded of vegetation. Rainfall in December 1971 produced green vegetation over wide areas and an immediate end to elephant mortality. However, total rainfall was less than in earlier years and did not enable the vegetation to recover fully from the drought. During the first 5 months of 1972, a fair amount of rain fell in various places, but it was very irregularly distributed, so that, just after the 'rainy season' in May/June, only 50–70% of the Park was green. No rain was in fact recorded in June, and only little in July and August. By early August, the Park was very dry throughout and more elephant mortality was anticipated. However, further large-scale mortality was averted by substantial out-of-season rainfall in early September. Most of this rain fell in the eastern and south-eastern parts of TsE and on the adjacent Galana Ranch (see Buchuma, Sala and Lali in Fig. 1). In those areas the vegetation turned lush and green, while most of the remaining areas received less rain and produced a moderate green flush at best. October brought only little additional rain and the vegetation started drying out again. More rain came in November, with exceptionally heavy falls in the northern areas of TsE (Ithumba 333 mm in November) and TsW (Fig. 1). Rain was also widespread in December so that, by the end of the year, very few areas were still dry (e.g. around Sobo, Fig. 1).

Methods

Methods of study were three-fold: tracking of radio-tagged individuals from an aircraft, visual identification of known elephants on the ground, and plotting of population distribution by aerial counts over the entire study area.

(a) *Radio-tracking*

Capturing and tracking methods will be treated in more detail in a later paper; they can be summarized as follows: Radio transmitters and receivers used were of the types commercially available from AVM Instrument Co., Champaign, Ill., U.S.A. (W. W. Cochran), each transmitter having its own frequency. Transmitters and batteries were embedded in dental acrylic and attached to a collar made of machine belting. Elephants were immobilized with M.99 (etorphine hydrochloride, Reckitt & Sons Ltd.), administered with standard 'Capchur' equipment (Palmer Co., Douglasville, Ga., U.S.A.). Tracking was done from a Piper Super Cub aircraft, using an AVM receiver with a single Yagi antenna mounted on a wing strut, pointing forward.

Radio collars were successfully placed on two bulls and two cows in TsW between 22 December 1971 and 5 May 1972. In TsE, two bulls and four cows were radio-instrumented between 14 June and 5 July 1972. Tracking and location of each individual was attempted at least once a week. On almost all occasions, the instrumented elephant was visually identified, by the collar, once its location had been established through radio contact. This permitted concurrent recording of size and composition of the group in which it occurred. In a few cases, damage to or malfunction of the transmitters and/or their aerials resulted in temporary or total loss of radio contact. This caused a number of gaps in what was intended to be a continuous record of each individual's movements, but sufficient information has been obtained to warrant publication of this initial report.

(b) *Ground observations*

Elephants showing irregularities of tusks, cuts or scars on the ears or other parts of the body were photographed and their pictures were mounted on punched cards taken into the field for quick reference. About 100 individuals were identified in this manner. Date, time, location, group size and composition were noted each time a known individual was sighted. Due to the size of the park and the rough terrain, ground observations were restricted to the area south of the Tsavo and Galana Rivers in TsE (Fig. 1), an area of about 4000 km². Initial searching was done from a vehicle travelling on park roads. This, plus the number of elephants present in the area (6000–7000), rendered the rate of repeat sightings of known elephants low. Nevertheless, some valuable data were eventually obtained by this method, complementing those gathered through radio-tracking.

(c) *Aerial counts*

Total aerial counts were carried out in the entire Park and some adjacent areas in September 1972 and January 1973. In these total counts, the area was covered visually as thoroughly as possible, with four aircraft participating, and numbers of elephants were recorded directly on to 1 : 250 000 maps. Figures 4 and 5 present a summary of the distribution obtained by these aerial counts.

Results

(1) *Home range*

Data on home range size and movements of individual elephants were obtained from both the radio-tracking and the ground observation of distinguishable individuals. Figure 2 presents data from the radio-tagged animals, showing the period over which

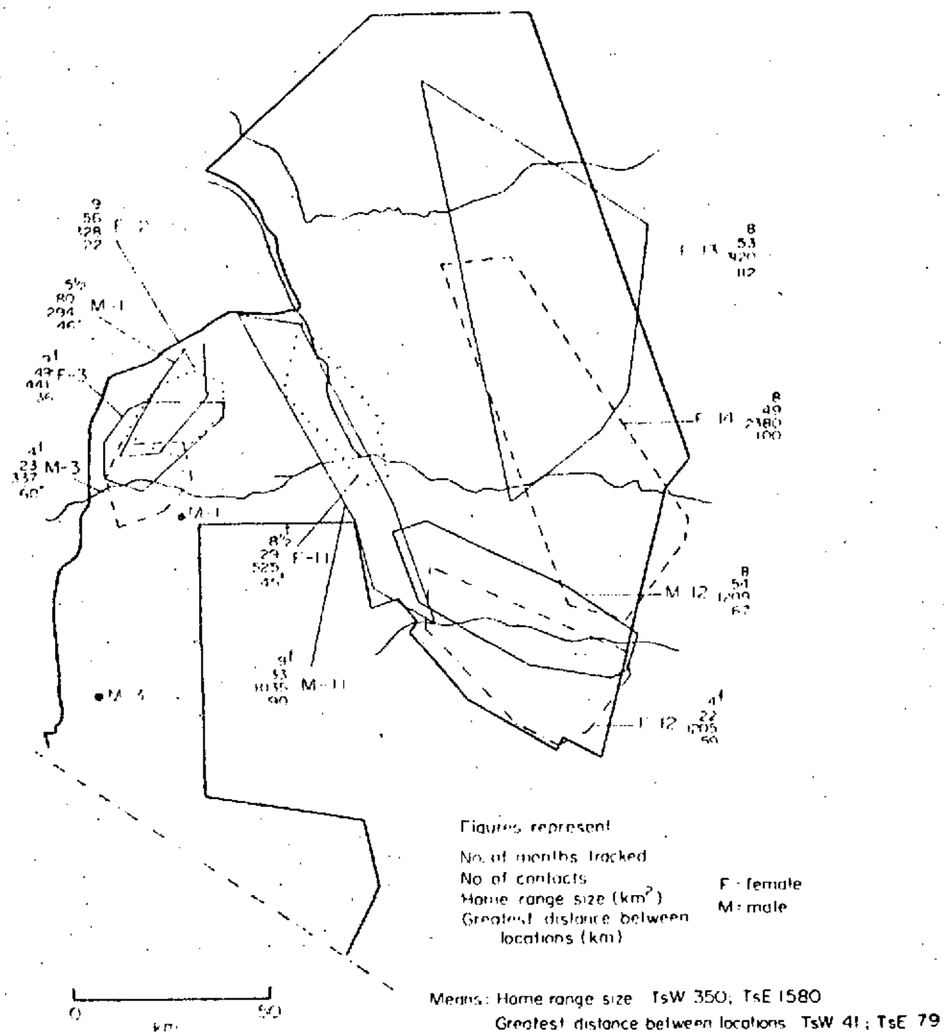

Fig. 2. Map showing individual home ranges of ten radio-tagged elephants in Tsavo. Period of observations, number of contacts, size of home range and the greatest distance between two locations are also indicated for each animal. * including one observation (shown) outside the home range; † tracking record discontinuous, one or several gaps; ‡ not including movement immediately after capture which is considered abnormal (see text).

they were obtained, the total number of radio contacts, maximum linear distance between contact locations and area of home range. The latter was calculated by joining the peripheral contact points on the map with straight lines and measuring the area thus described.

The four animals tracked in TsW inhabited fairly compact home ranges (mean = 350 km²) extending over little more than 40 km in one direction, except for a single recorded trip by each bull to well outside his 'normal' home range. Since these single contacts were greatly isolated from the main area of these bulls' activities they have been arbitrarily and tentatively excluded from home-range calculations. It is, however, possible that longer term data will reveal bulls to have larger home ranges than cows.

The movement of M-3 is particularly remarkable, as it is generally assumed that there is little or no exchange between the elephant populations of the northern and southern parts of TsW (E. C. Goss, personal communication; Laws, 1969; Parker & Archer, 1970). Unfortunately, we were unable to obtain more detailed information on this animal at the critical time.

The six elephants monitored in TsE had very much larger home ranges (mean = 1580 km²) and moved over substantially greater distances, producing a mean for the area of 79 km, almost twice that for TsW.

Considering Tsavo as a whole, there is a marked gradient of home range size and distance moved, both of which decrease from east to west.

The results to date of the ground observations in the southern sector of TsE form a useful comparison with the radio-tracking data and provide some means of checking that the radio-tagged animals are behaving normally. It has to be borne in mind, however, that numbers of re-locations are low compared with the radio-tagged animals and that any movements out of the area will not be detected. Results may therefore be taken to represent minimal rather than maximal movements. Between February 1972 and March 1973, 100 elephants (forty-one bulls, fifty-nine cows) were individually identified and catalogued. Of these, twenty-one bulls (51%) were re-sighted at least once, the highest number of records per individual being seven, while thirty-five cows (59%) were re-observed up to six times. Movements recorded so far are summarized in Table 1. The largest distance between sightings of the same individual was 67 km for an adult bull and 55 km for a cow. A substantial proportion of the animals re-sighted (27%) moved over more than 30 km within a year or less.

Table 1. Summary of observations on visually identified elephants

Sex	Distance between extreme sightings (km) 0–20	20–40	40–60	> 60	Total Number
Male	10	7	2	2	21
Female	18	13	4		35

It is conceivable that capture and radio-instrumentation could disturb elephants sufficiently to upset their normal reaction to environmental stimuli and thus their patterns of movement. However, the results obtained by radio-tracking on one hand, and ground observations on the other, suggest that this is probably not the case. For example the maximum distances for movement by a bull (67 km) and a cow (55 km) obtained by ground re-sighting compare well with radio-tagged M-12 (67 km) and F-12 (59 km) (Fig. 2) in the same part of TsE. Similarly the direction and distance of movement of ♀-30 between September 1972 and January 1973 is in good accord with F-12 and M-12 (Fig. 6).

In one instance (F-11) there was direct evidence of initial disorientation after fixing of the radio collar which resulted in the animal's losing contact with its family group. All of the other five cows rejoined their original group within a few days after capture, as far as this could be ascertained through aerial observation (from size and composition of group). Thus, the observations on the radio-tracked elephants probably reflect spontaneous movements in response to environmental factors and can be considered as representative of conditions prevailing during the study period.

(2) *The pattern of individual movements*

Movement patterns, particularly in TsE, tended to be somewhat spasmodic, an individual remaining within a given area for some time, then suddenly moving over a considerable distance, staying again for a while, and so on (e.g. M-11 and F-13, Fig. 3). This produced very irregular patterns of habitat utilization, with large areas being utilized little or not at all by the individuals concerned. For instance, there is a

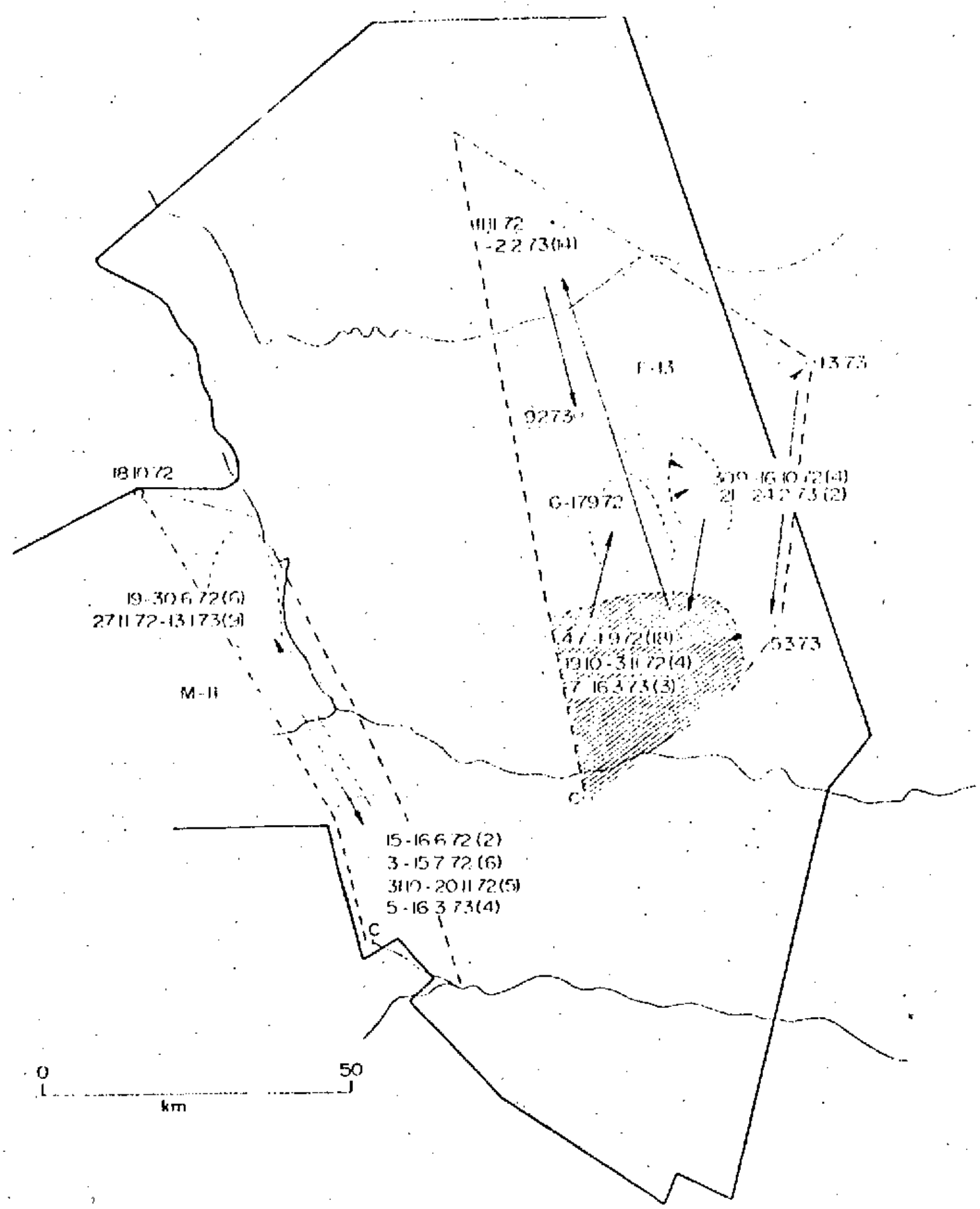

Fig. 3. Patterns of movement within their home ranges of a cow (F-13) and a bull (M-11) radio-tracked in Tsavo East. Possible 'dry season range' of F-13 is shaded; seasonally occupied areas are bounded by feint dotted lines. Dates and numbers of contacts (in parentheses) are given for each temporary range. Arrows indicate major movements. C site of initial capture.

zone of 30 km diameter with no records of M-11 between the two areas in which he was generally found. This may be due to chance to some extent but, in several cases, these patterns can be related to rainfall and the state of the vegetation, as is shown by the following example.

Cow F-13 spent most of the dry season (early July to mid-September 1972) in what appears to be her 'dry-season range' near the Galana River and the eastern end of the Yatta Plateau (Fig. 3). After the rainfall in early September, she suddenly moved some 25 km to the north-east, towards the Park boundary. After the vegetation there had dried up, she re-appeared in her former range (four records between 19 October and 3 November). On 11 November she was located well above the Tiva River, some 80 km north of the previous locality, following the heavy rainfall in that area (*cf.* Ithumba, Fig. 1). She remained near the Tiva River until 2 February 1973. From 9 to 24 February she was recorded about halfway between the Tiva and Galana Rivers and presumed to be on the way back to the dry-season range. However, on 1 March she appeared outside the Park on the Galana Ranch in an area where a local rainstorm had produced a green flush of vegetation, some 30 km NNE of the previous locality. Finally, on 7 March she was back within the area in which she had spent most of the preceding dry season, and was recorded there two more times until 16 March.

Similar movement patterns were obtained for three other radio-instrumented individuals, offering further support for a relationship to rainfall. F-11 and M-11 deviated somewhat from the picture just outlined in that there was no clearcut relationship between their movements and rainfall. However, these two animals occupy the westernmost part of TsE where rainfall is generally higher and less erratic than in the eastern parts, with conditions almost approaching those in northern TsW. F-11 shows by far the smallest home range of all six animals in TsE (Fig. 2).

In the cases of three cows in TsE (F-12, F-13, F-14) observations on group size and composition indicated that, even during large-scale movements, they remained within their family groups. Thus the long-term integrity of cow-calf elephant groups, as opposed to the loose and temporary grouping of bulls, is confirmed (Buss, 1961; Douglas-Hamilton, 1973; Laws, 1969). F-11 lost contact with her original group immediately after capture (see above) but later remained with a group she then joined near the Tsavo/Athi River junction.

(3) *Changes in overall distribution of elephants*

Results of the aerial counts conducted in 1972–73 are summarized in Table 2. We are not concerned with actual numbers in the present context; the good agreement in

Table 2. Results of elephant counts in Tsavo National Park and vicinity in 1972–73

Area	September 1972 count	January 1973 count
Tsavo West	4319	8294
Tsavo East, south of Tsavo/Galana Rivers	6633	3955
Tsavo East, north of Tsavo/Galana Rivers	6620	9925
Total Tsavo Park	17572	22174
Galana Ranch (western part)	3835	*c.*520*
Other areas adjoining Park	*c.*1800	*c.*1100†
Total overall	(*c.*) 23200	(*c.*) 23800

* 10% sample count.

† = mostly recce flights only.

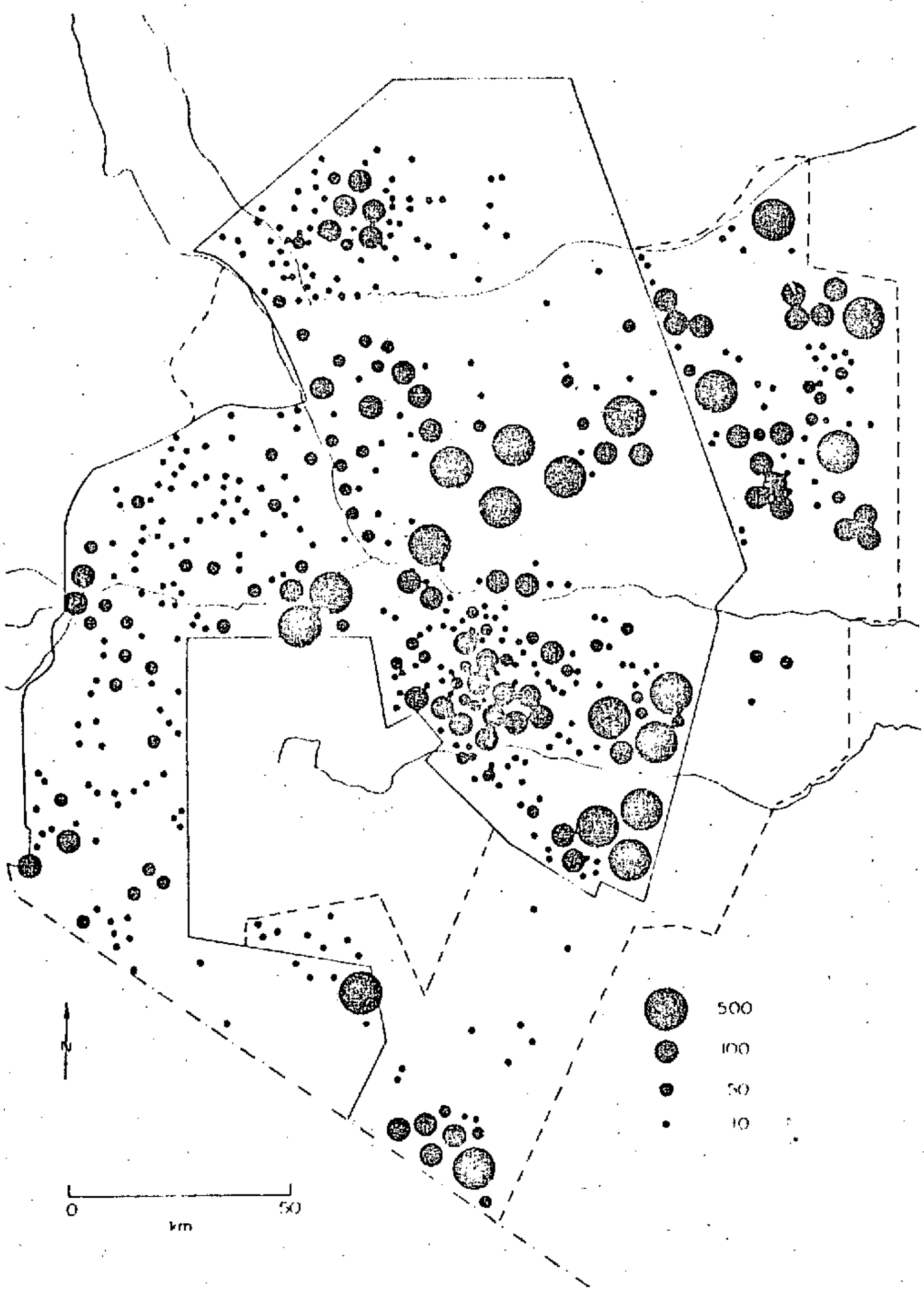

Fig. 4. Distribution of elephants in the study area in September 1972. Broken line shows areas counted outside the National Park boundary (solid line). Dots do not indicate herd sizes but simply total numbers in each area, derived from original count maps.

overall figures suggests that similar degrees of relative accuracy were attained in the two total counts (September 1972 and January 1973). The results indicate that substantial shifts of large numbers of elephants took place between the two counts, not only within the Park but also between the Park and adjoining areas. This is illustrated by the actual distribution patterns recorded in the two counts (Figs. 4 and 5). The following differences stand out:

(a) Well over 3000 elephants were concentrated in the south-eastern corner of TsE in September; all but a couple of hundred had moved away by January. This area received the first and some of the heaviest rain in early September (Sala & Buchuma in Fig. 1). Grass grew quickly and in large quantities, but by November most elephants had moved elsewhere, presumably in search of fresher green food (see c below). Neither the vegetation nor the waterholes had actually dried up by mid-January.

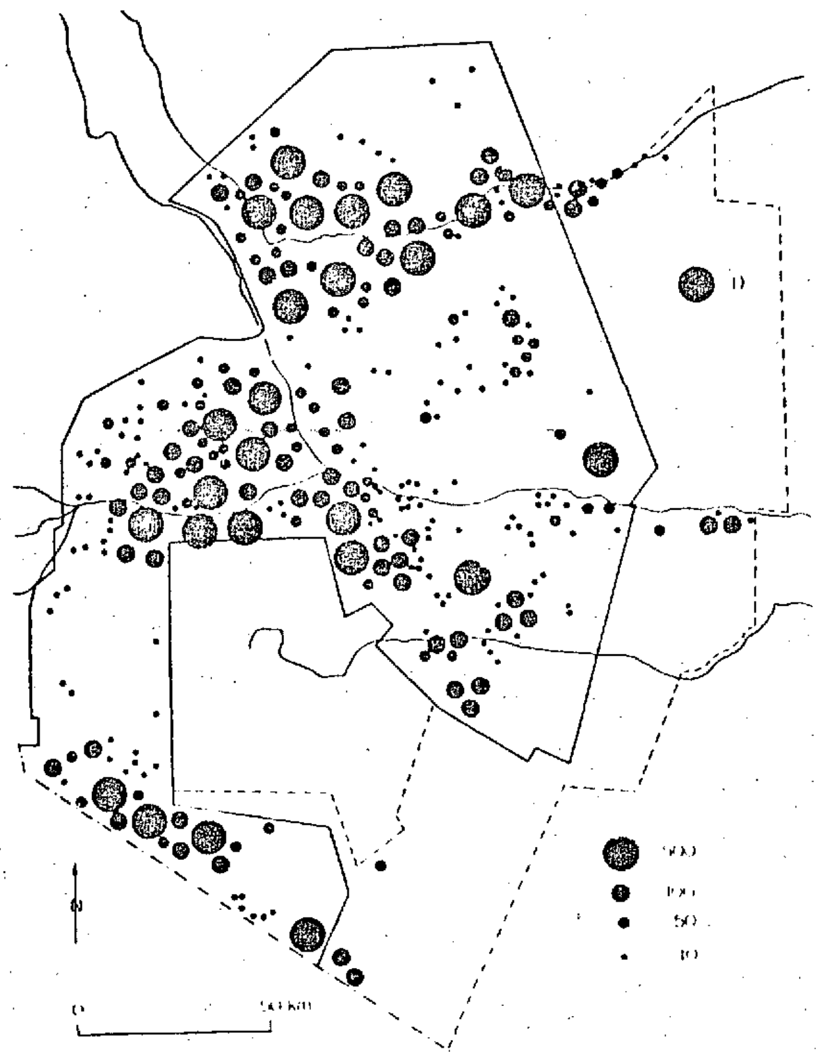

Fig. 5. Distribution of elephants in January 1973. * Represents total number only (derived from 10% sample count), not distribution pattern.

(b) A large concentration midway between the Galana and Tiva Rivers in TsE in September had largely disappeared from the area by January, when a heavy concentration had formed along both banks of the Tiva River. It seems possible that much of the September assemblage had moved northward, following the heavy rain around Ithumba in November (Fig. 1).

(c) Some 4000 elephants were counted on the western portion of the Galana Ranch in September, whereas a 10% sample count in January indicated only about 500. In September, almost the entire area was green, following recent rainfall (cf. Lali in Fig. 1) but in January most of the Ranch was dry, with little or no standing water. In the absence of any other evidence, the likeliest assumption is that the majority of the elephants recorded on the Galana Ranch in September had moved into the northern part of TsE (Tiva River area) by January, following the heavy rainfall there.

(d) While only relatively small numbers of elephants occupied the north-eastern part of TsW in September, a heavy concentration had formed there by January, again in the wake of recent rainfall (cf. Kamboyo in Fig. 1). One explanation is that considerable movement of elephants may occur between this area and the northern part of TsE, although little evidence is available to confirm this possibility. An alternative explanation, supported by the home range position of M-11 (Figs. 2 and 3), is that there is movement of elephants between the southern sector of TsE and north-eastern TsW. Elephants are commonly seen along the Nairobi-Mombasa road, which separates the two parks, and not infrequently cross both road and railway line, a fact in accord with both the above explanations.

(e) In January 1973, large numbers of elephants were concentrated in the area around Mudanda Rock in TsE where no unusual aggregation had been recorded in September 1972. This area had received substantial rainfall late in December (97 mm, Fig. 1), so that probably the youngest green vegetation anywhere in the Park was available there in January. Evidence from radio-tagged animals suggests that much of this concentration had moved from the south-eastern corner of the Park (see a above and Fig. 6 below).

Discussion

We recognize that data derived from little over 1 year's study of a few known individuals permit only a tentative interpretation of the observed phenomena.

(1) *Differences between TsW and TsE*

Considerable differences in the size of individual home ranges and the extent of movements were found between TsW and TsE (Fig. 2). In TsW, home ranges were almost one-fifth the size of those in TsE. These differences can be related to the environmental conditions described earlier, TsW providing generally more favourable conditions than TsE. This permits some of the elephants there to remain within relatively small areas the year round, with only minor seasonal movements. In particular, the evergreen woodlands on the lava flows south of the Chyulu Hills apparently provide a suitable and sufficient dry-season food supply, as can be inferred from the fact that both radio-instrumented cows in TsW spent most of their time during the dry season (June–October 1972) in such areas.

By contrast, conditions in TsE are less favourable and subject to greater fluctuations and irregularities. Dry-season concentration areas near permanent water supplies cannot support the elephant population throughout the year. These circumstances apparently force the elephants in TsE to be generally more mobile and to cover greater distances in search of food. This interpretation of the causes underlying the different habitat utilization patterns of elephant in TsW and TsE is supported by the fact that elephant mortality during the 1970–71 drought was almost entirely confined to TsE (Corfield, 1973).

Large seasonal differences in elephant density in the north-eastern section of TsW (see 3 d above) suggest that this area is ecologically allied to TsE, a fact supported by its topography and vegetation.

(2) *Individual movements in relation to overall distribution*

For most of the changes in overall elephant distribution between September 1972 and January 1973 (Figs. 4 and 5), we can only speculate about which concentration in one count corresponded to which in the other. However, for some instances in TsE the radio-tracking data, as well as some observations of visually identified elephants, provide clues as to how to interpret the distributional shifts. The relevant observations are shown in Fig. 6.

Four of the five animals referred to were located within the large (3000 |) elephant concentration in the south-eastern corner of TsE (Fig. 4) at or near the time of the September count. All of them had moved considerable distances (85 km in the case of F-14) to the north-west by January. F-12, M-12 and ♀-30 were in or near the Mudanda concentration (Fig. 5) in January, whereas F-14 was on the southern fringe of the Tiva River concentration (Fig. 5). F-13, which had been just north of the Galana River in September (Fig. 3) was at the Tiva River in January, having gone even considerably to the north of it in November, following the heavy rains in that area.

All these observations indicate a general movement of elephants within TsE in a north-westerly direction between September 1972 and January 1973, consistent with the presence of large concentrations at Mudanda and on the Tiva during the January count. It appears that the south-eastern concentration of September (Fig. 4) broke up later and that the elephant groups composing it moved to different areas, some (possibly those south of the Voi River) towards Mudanda and some (from north of the Voi) across the Galana River to the Tiva.

This is the first time that it has been possible to interpret movements of large numbers of elephants in Tsavo National Park by reference to observations of individually known animals.

(3) *Relationship of elephant movements to rainfall*

A consideration of both the pattern of movements of individuals within their home range and overall changes in the distribution of the elephant population points to a definite relationship between elephant movements and the pattern of localized rainfall in Tsavo. Whether elephants move in direct response to rain in a distant area or whether the rapid growth of vegetation after rain constitutes the cue is not clear from the present data. More detailed studies of the exact timing of elephant movements in relation to rainfall are needed, as well as studies of the detailed nature of the vegetation changes that follow rain.

The fact that individual elephants of both sexes and groups moved considerable distances to fresh food sources in this study points to the likelihood of the lack of such movements in certain cases during the 1970–71 drought being abnormal and probably due to an inhibiting effect of the drought itself on elephant movements.

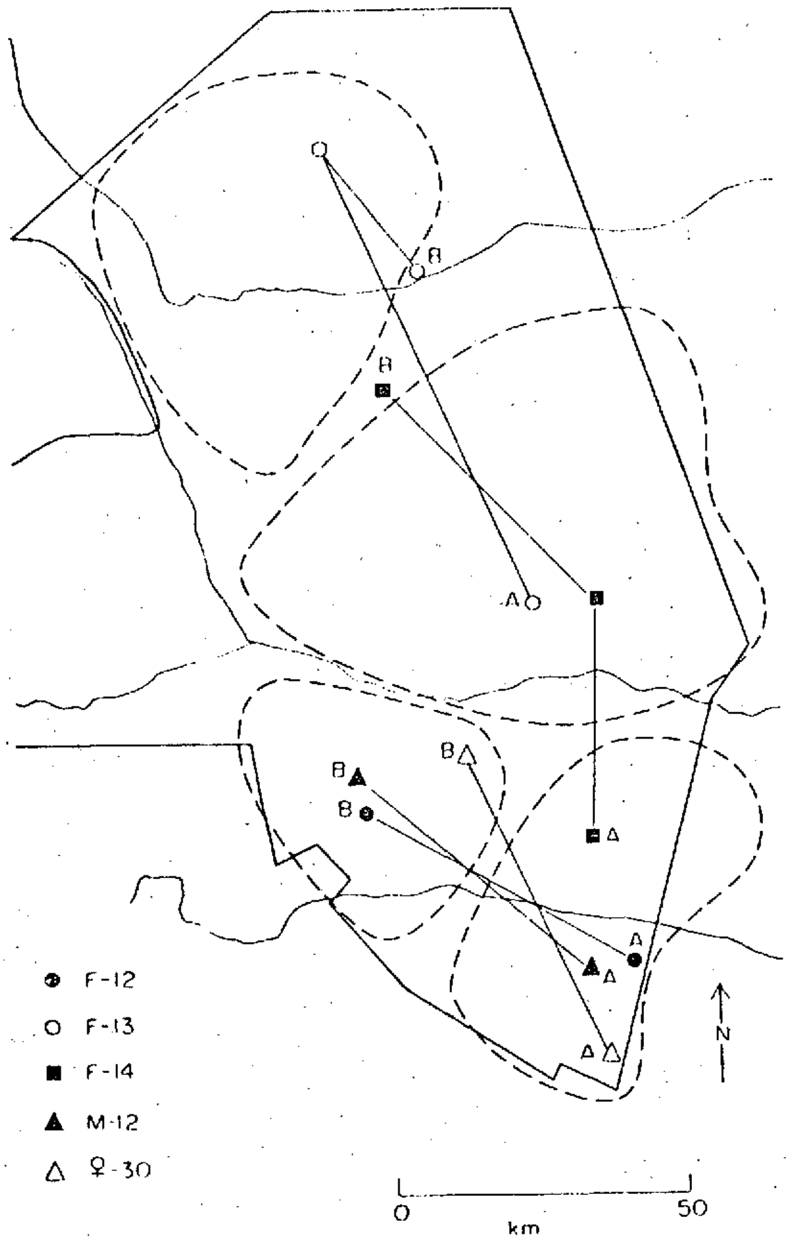

Fig. 6. Movements of four radio-instrumented (M-12, F-12, F-13, F-14) and one visually identified (♀-30) elephant between September/October 1972 ('A' positions) and January 1973 ('B' positions). Broken lines indicate the presumed ranges of the unit populations postulated by Laws (1969).

(4) *Comparison with earlier studies*

Our radio-tracking data on home ranges and individual movements in TsE (Figs. 2, 3 and 6), and observed changes in overall distribution (Figs. 4 and 5), are difficult to reconcile with Laws' (1969) hypothesis that 'there are a number of localized unit populations . . . that make limited seasonal movements' thought to involve no more than 20–30 km. All six radio-instrumented animals in TsE and one out of four in

TsW moved across the boundaries of the presumed ranges of the 'unit populations' postulated by Laws (Fig. 6). The same applies to some of the visually identified animals in TsE (e.g. ♀-30 in Fig. 6).

Laws' field work covered only a year (1967–68) and coincided with a period of high rainfall. Thus, his observations probably represent a temporarily stable situation in which food was plentiful and elephants had little cause to move over more than 20–30 km. In addition, Laws' conclusions were based on large-scale aerial surveys in which gross distribution patterns and population composition were recorded without reference to movements of known individuals or groups. Our present results show that both methods need to be combined over prolonged periods to permit a sound interpretation of elephant movements.

Although not conclusive, our data do not provide support for Laws' concept of permanent discrete subdivisions of the Tsavo population. However, the fact that several of the radio-tagged animals (e.g. F-13, Fig. 3) each returned to a definite area during dry periods suggests the possibility of spatially fixed 'dry-season ranges' for individuals or groups, a concept in accord with Laws' (1969) Text-fig. 1. While such behaviour may result in temporary sub-division of the population into distinct units, our observations show that animals from several areas congregate in regions of green vegetation during the rainy season. Hence F-13 and F-14 had both made their way to the Tiva River area by January, 1972 from the Galana and Voi River areas respectively. Similarly F-12 and F-14 which were captured 60 km apart during the dry season, were only 10 km apart near the eastern park boundary after the early September rainfall. It must be borne in mind that the situations described in this paper arose in the wake of the 1970–71 drought, under conditions that might be described as unusual. Laws' observations, on the other hand, may represent the opposite extreme, realized under especially favourable circumstances. It is possible that the propensity for long-distance movements was more pronounced after the drought than it would be under 'normal' conditions. However, we still do not know enough about what is 'normal' in Tsavo and what is not. Conditions within the Park are rather disparate (cf. differences between TsW and TsE discussed above). In TsW the model proposed by Laws may well apply, but for TsE it apparently needs to be modified and made more flexible, to accommodate the substantial fluctuations in environmental conditions and the apparently considerable ability of the elephants to cope with them.

Conclusions

The main conclusions emerging from the data and discussion presented above concern the mobility of Tsavo elephants, the question of localized sub-populations, and the influence of rainfall and food supply on distribution and movements of elephants and ultimately on population regulation.

Results of both radio-tracking and ground observations indicate that the elephants in at least part of the Tsavo area are more mobile than has been assumed earlier. Individuals and, by inference, large numbers of elephants may move over considerable distances (80 km or more) in response to localized rainfall.

An organization of the population into localized units may exist in the dry season, brought about by individual adherence to restricted dry-season ranges near permanent water. In the rainy season it may break down, at least partially, especially when rainfall is low and irregularly distributed. In such situations, localized rainfall may trigger off fairly extensive movements leading to large concentrations in areas of green vegetation.

On the basis of circumstantial evidence, we assume that the primary factor governing such movements is the food supply, specifically the flushes of green vegetation brought out by local rainstorms. This, in turn, suggests that the food supply was a crucial and probably limiting factor for the population concerned (mainly in TsE) under the conditions prevailing during the study. This view is supported by the large-scale mortality during the 1970–71 drought, the principal cause of which is thought to have been malnutrition (Corfield, 1973).

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