Mary: Your copy - Hermann Remmert will also edit it. Many thanks for your input Hu. 90/2/21

MOSAIC-LIKE EVENTS IN ARID AND SEMI-ARID NAMIBIA

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INTRODUCTION

The mosaic-cycles hypothesis, originally proposed by Aubreville (1938), has been recently reviewed by Remmert (1987). In essence, Aubreville's hypothesis predicts that if a tree or group of trees dies in a natural, tropical forest, the empty space will be occupied by new pioneer plants which will be replaced by a succession of vegetation phases ending in the original "climax" vegetation. In this manner cycles of varying "mosaic" phases are created. Remmert (1987) extended this hypothesis to all natural systems and posed, *inter alia*, the following questions:

1. "What agents drive the cycles? Is it the longevity of the key organisms or have we to look for fungi, microbes and animals?"
2. "What is the size of the mosaic stones and what determines the size?"

Apart from the study by Weiner and Gorecki (1982) on rodents in the arid steppe of central eastern Mongolia, apparently the mosaic-cycles hypothesis has not been considered in the context of desert and semi-desert environments. We address Remmert's (*op cit*) questions *via* two case histories, involving relatively long-term data sets and anthropogenic influences in arid and semi-arid Namibia.

Our case histories are based on the behaviour of large mammals and the ostrich *Struthio camelus* and the influence of modern man over periods of up to 30 years in the arid Namib-Naukluft Park and in the semi-arid Etosha National Park. We briefly describe these two areas and then organize the narrative under primary driving events for, and primary effects of, the selected biota, interpreting these features in the context of the mosaic-cycles hypothesis.

STUDY AREAS

Namibia

Our observations were made in Namibia (17^{o} - 29^{o}S, 12^{o} - 21^{o}E) in south-western Africa. Namibia covers some 824 000km^2 of which 28% can be classified as arid (<150 mm/annum) and 69% as semi-arid (150-600 mm/annum) (Tinley 1975). This paucity of rainfall (Fig. 1) is a consequence of two major factors: a South Atlantic high-pressure atmospheric cell is the dominant, off-shore, climatic feature, producing "subsidence inversion" which limits convection (Preston-Whyte *et al.* 1977); and, in the Benguela Current region, cold, upwelled and nutrient-rich, coastal waters enhance the stability of the lower air layer and limits its moisture capacity. Furthermore, precipitation by rainfall is sporadic and unpredictable, resulting in accompanying fluctuations in plant and animal abundance.

Namib-Naukluft

The Namib-Naukluft Park is located in the central Namib desert, and includes the Namib Research Institute which has stations at Gobabeb (23^{o}34 S, 15^{o}03 E) and Ganab (23^{o}09 S, 15^{o}33 E) (Fig. 2). The coastal, gypsum-gravel plains of the Namib desert are usually devoid of vegetation, except for a few hardy perennial plants in the dry watercourses and a diverse lichen flora accompanied by scattered dwarf shrubs on the gypsum surfaces (Seely 1987). This zone falls within the fog belt, which extends inland from the Atlantic Ocean to a distance of more than 100 km (Lancaster *et al.* 1984). Rainfall increases from 15 mm/annum on the coast to 65 mm/annum 110 km inland, and the vegetation is characterized by intermittent annual grassland with perennial plants largely restricted to watercourses (Seely 1978).

Two major moisture sources dominate this region: fog and rain. Whereas fog is a relatively regular, predictable phenomenon, which precipitates sufficient moisture (31 mm/annum at Gobabeb) to ensure survival of the greatest diversity of invertebrates in any desert in the world, rainfall is rare and unpredictable (Pietruszka and Seely 1985; Seely 1987). Significant rainfall events may be viewed as erratic pulses of water which result in brief flushes of highly nutritious ephemeral grasses in a desert whose barren nature normally limits the populations of large herbivores (Seely and Louw 1980).

Etosha

Etosha National Park lies within the 300 mm isohyet in the west and the 500 mm isohyet in the east (Fig. 3). Rainfall is the only measurable form of precipitation at Etosha. Three climatic periods have been identified during the year: wet and hot (January - April), dry and cool (May - August) and dry and hot (September - December) (Berry 1980). One of the park's major physical features is a vast (4 690 km^2) salt-pan that has been described as "Saline Desert with Dwarf Shrub Savanna Fringe" by Giess (1971) in his sub-division of the major vegetation zones of the country. It is on the fringe of this salt-pan that a sweet, short grassveld on calcareous soil attracts abundant populations of large ungulate grazers following good rains (Berry and Louw 1982). Fire does not play a significant role in the maintenance of these short grasslands, although it is a regular feature in the surrounding savanna vegetation (Siegfried 1981).

PRIMARY EVENTS AND EFFECTS

Namib-Naukluft

The rainfall records at Gobabeb, measured since 1962, show a 13-year period (1962-75) in which 15.4 mm/annum was the average (Fig. 4), which is lower than the long-term mean of 19.8 mm. An exceptional rainfall of 106.7 mm was measured in 1976 followed by 84.4 mm two years later. The subsequent 11 years (1978-89) were dry, with an an average of only 12.0 mm/annum. At Ganab, rainfall since 1967 has followed a sequence similar to Gobabeb: the annual precipitation averaged at least 183 mm (measurements incomplete) in the three-year period 1974-76), with a peak of at least 160 mm in 1974 and at least 355 mm in 1976 (Fig. 5). This is considerably higher than the long-term mean of 70.4 mm. Similarly to Gobabeb, Ganab's rainfall decreased sharply thereafter, averaging only 47.2 mm/annum for the 13-year period 1977-89.

The effect of unusually high rainfall events on the abundance of the area's four principal large herbivores in the gravel-plains' grasslands is obvious (Figs 4 & 5). These animals are the ostrich, springbok *Antidorcas marsupialis*, gemsbok *Oryx gazella* and Hartmann's zebra *Equus zebra*. At both Gobabeb and Ganab, peaks in large herbivore populations were reached three years after the high rainfall of 1976. Subsequently, as rainfall decreased, herbivore numbers fell sharply over a period of 10 years. This reduction was promoted by mortality, when an average of nine fresh carcasses per day were found (Nel 1980), recruitment failure, and movement away from the area as these large, mobile animals retreated to areas of more stable productivity (Boyer 1988). The one large predator of any consequence in this area is the spotted hyaena *Crocuta crocuta*. However, only a small fraction of its diet consisted of prey taken from the plains; the overwhelming majority being from the adjoining Kuiseb river-bed and the sand-dune fields in the south (Tilson *et al.* 1980). Consequently, neither predation nor disease had a significant effect on the abundance of large herbivores during this period.

Of the four herbivorous species considered here, the ostrich increased more rapidly after the increase in rainfall; springbok, gemsbok and Hartmann's zebra requiring two and three years, respectively, to reach peak numbers (Fig. 6). All four species decreased with equal rapidity. Linear regressions of these population curves were drawn against rainfall measured at Ganab, where the majority of animals congregated. The regression for the ostrich confirmed the species' predictable response to rainfall as shown in Figure 7. ($y = 9.21x + 576.92$) with a good fit to the data $r = 0.91$. The regressions for springbok, gemsbok and zebra, however, were much weaker due to their lagged responses and the coefficients of determination in all cases ($r = < 0.1$) gave a poor fit to the data. When the numbers of the four species were totalled, the regression showed no predictable linear relationship against rainfall ($y = 81.22x + 5650.33$) and the fit to the data was unacceptable ($r = 0.23$) as shown in Figure 7.

If rainfall was the single natural primary event or agent for the biotic changes reported here, then, the influence of fences and artificial waterholes should also be examined. Four borehole-fed waterholes were established on the desert plains after the eastern perimeter of the Namib-Naukluft Park was fenced in 1967. When food demands by herbivores exceed the desert's ephemeral ability for primary production, mobility to alternative feeding sites or drought-induced mortality are the only alternatives (Hamilton *et al.* 1977). Fencing and artificial water supplies probably increased the mortality of herbivores by retarding their emigration. Weak individuals began dying in the vicinity of waterholes and those animals which attempted to emigrate were hindered by the fence. However, the fence is not completely effective and cases do occur in which animals find or force their way through it (J Lenssen 1989).

In summary, the immediate consequence of the primary agent driving the observed "cycle", namely rainfall, was a widespread, but brief, "explosion" of nutritious ephemeral grass on the gravel plains, followed by herbivore immigration and production. The standing crop of the grass is positively correlated with rainfall (Seely 1978). Subsequently, food stocks were depleted, causing high mortality rates among the animals, whilst an unknown portion of the surviving populations emigrated across the park's eastern fence or southwards into the sand-dune fields.

Etosha

The rainfall record, kept at Okaukuejo in the Etosha National Park since 1956, fluctuated greatly around the annual mean of 354 mm (Fig. 8). From 1956 to 1965 precipitation averaged 320 mm/annum which is 10% below the 33-year mean. Subsequently, the period 1966-79 was a "wet" phase, with annual precipitation averaging 417 mm (18% above mean) and reaching a maximum of 678 mm (92% above mean) during 1976. The period 1980-89 was comparatively dry, with annual precipitation averaging 297 mm (16% below mean) and decreasing to 223 mm (37% below mean) during 1981. In spite of the clear wet and dry periods, we were unable to find significant statistical correlations between amounts of rainfall and any of Etosha's large mammals.

Prior to 1970 the large mammalian herbivores and probably their attendant predators migrated away from Etosha during the eight-month dry season each year. They returned briefly for the four months (January-April) in which rainfall is sufficient to produce the highly nutritious annual grasses which constitute their preferred grazing (Berry 1980). In 1970 the 850-km perimeter of Etosha National Park was fenced to a height of 2.5 m, effectively curbing the movements of most large animals, with the notable exception of the elephant *Loxodonta africana*. The animals remaining within the park were further subjected to two other artificial factors in the form of 54 waterholes, and several hundred borrow pits for gravel used in road-building. The artificial waterholes facilitated the expansion and stabilization of the lion *Panthera leo* population, whilst the latter apparently created favourable conditions for anthrax *Bacillus anthracis*, the most viable and virulent bacterium known (Turnbull 1989), and a disease fatal to herbivores (Ebedes 1977; Berry 1981). (Most of the waterholes have subsequently been closed by the park's managers; the number of operative artificial waterholes being 19 in 1989.).

Anthrax was probably accidentally introduced into Etosha *via* infected domestic livestock during 1955-60 and rapidly became epidemic (Ebedes 1977). Ebedes suggested that this had occurred mainly through optimum conditions created by the alkaline nature of the gravel pits used in road-building. Subsequently, it has been proposed (Turnbull *et al*. 1989) that waterholes and gravel pits are not sites of propagation of anthrax. Nevertheless, whatever the source of infection, anthrax has been established as a major cause of mortality in herbivores at Etosha (Turnbull 1989).

Anthrax outbreaks appear to be predictably linked to the wet season in the case of wildebeest *Connochaetes taurinus* and zebra *Equus burchellii* (Ebedes 1977), whereas elephant mortalities resulting from anthrax occur in the the dry season. This apparent paradox may be explained by the observation (Berry, unpublished data) that elephants browse *Acacia* species during dry periods. Thorns may cause lesions in their mouths, making them particularly susceptible to the passage of anthrax when drinking from infected waterpoints. This susceptibility may also be enhanced by the nutritional stress which elephant are prone to in dry conditions.

The combined effects of fencing, artificial waterholes and abnormal levels of anthrax resulted in dramatic changes in several species. For example, wildebeest decreased from 25 000 in 1954 to 2 500 individuals in 1978, staying at approximately that level until the present. Similarly, zebra decreased from 22 000 in 1969 to 5 000 individuals in 1988. Whilst these two herbivores appear to have been adversely affected by reductions in rainfall and increases in man's influence, the lion population has responded differently (Fig. 8). The lion population increased steadily from 200 to 500 individuals between 1954 and 1979. The increase in lion abundance led to an abnormally high predator-prey ratio (1:150) in Etosha (Berry 1981). Thereafter, the population decreased to 200 individuals by 1986. Since then it has again increased: the most recent (1989) estimates include a minimum of 266 and a maximum of 341 lions (Stander 1990).

One reason for the lion's resilience is its ability to behave as a predator or a scavenger with equal ease. Furthermore, lions have developed an immunity to anthrax (Turnbull *et al*. 1989), which herbivores have not, and so are able to feed on anthrax carcasses without any adverse effects. In Etosha, this phenomenon resulted in a decrease in the incidence of the lion's hunting, while the reduced migration of herbivorous prey enhanced the carnivores' recruitment. The presence of permanently available artificial waterholes throughout the park facilitated the lions' colonization of large new areas.

The advent (*ca* 1980) of the worst drought in recorded history in Etosha caused the already reduced wildebeest and zebra populations to shift from the then unproductive grassy plains into the adjoining bushland. This in turn forced prides of lions to shift their territories into finite areas, where living space was limited. Since lion-pride territories disperse animals (Schaller 1972), the displaced lions of Etosha were wedged between a drought-stricken plains system and adjoining cattle farms. Inevitably, lions began trespassing onto farmland and killing large numbers of domestic livestock (one male was responsible for killing more than 100 head of cattle, horses, donkey and goats in two years before being shot). At least 317 lions were destroyed on farms in 10 years, representing a significant proportion of Etosha's population (Table 1). During the same period, a total of 20 lion carcasses was found inside Etosha but, because freshly dead lions are seldom located, the cause (rabies) of death could only be determined in three of these.

In summary, as in the Namib-Naukluft case, the primary agent driving changes, and perhaps cycles, in Etosha's populations of large herbivores is sporadic rainfall. Superimposed on this there is a significant anthropogenic influence which affects interactions between the large herbivores and their predators. As large herbivores decreased in the system, lions and anthrax bacteria flourished quasi-symbiotically. The bacteria promoted a greatly increased supply of food for the lions which, in turn, aided the dispersal of anthrax by carrying its sporulated form in their mouths, claw sheaths and other body parts to infect new sources. The favourable phase for lions was, however, short-lived, and as their food supply diminished in response to prolonged drought and reduced productivity of the grassland, they were forced onto farmland with fatal consequences.

DISCUSSION

Both of the case histories we have presented have certain predictive capabilities for the mosaic-cycle hypothesis, but most of the predictions cannot (yet) be demonstrated statistically. In the arid Namib-Naukluft area "wet" phases may be of relatively brief duration (possibly two-three years) and dry phases may last at least 11-13 years, based on present knowledge. To speak of quasi-regular, alternating cycles of "wet" and "dry" periods in this area would be premature. It is, however, clear that it is the presence or absence of significant rainfall that primarily drives the system and shapes its phases. These phases, in terms of size, duration, structure and functioning, could be analogous to "mosaic stones" (*sensu* Rem mert 1987).

In Etosha rainfall is probably also the primary agent driving the system, with successive wet and dry phases of 10-14 years on record. Although Tyson (1986) identifies an oscillation of nine years between dry and wet periods in southern Africa, it is not possible at present to say whether the rainfall in Etosha fits this pattern or not. Despite years of good rainfall and grass production, sustained, spectacular decreases of wildebeest and zebra are still continuing. These decreases are being promoted by anthrax, predators and fences. In contrast, anthrax and lions are still flourishing in Etosha, the former by expanding its hosts to include elephant and black rhinoceros *Diceros bicornis* (Turnbull *et al.* 1989) and the latter by shifting prey preferences to springbok, gemsbok and other species (Berry, unpublished data). The relationships between rainfall, herbivores and predators in Etosha, where natural causative factors and anthropogenic influences have combined, are too complex to make possible long-term predictions at present.

Although anthrax outbreaks in wildebeest and zebra at Etosha can be predictably linked to the rainy season in both wet and dry phases, it has yet to be established whether the overall number of herbivores dying from anthrax varies significantly or is greater during a wet phase than during a dry phase of a "cycle". Factors which may mask this are the very small proportion of anthrax infected carcasses which is actually found and recorded in an area the size of Etosha (Turnbull 1989), the different levels of susceptibility between herbivore species (Turnbull *et al.* 1989) and the continuing changes in total abundance of each herbivore species.

In the light of the above, Remmert's (*op cit*) first question, *viz*, "What agents drive the cycles...?" can be answered more-or-less satisfactorily if, indeed, cycles are involved in our case histories. In the arid Namib-Naukluft area rainfall is the primary driving agent, but in the semi-arid Etosha area the system is additionally driven and made more complex by disease which is largely a consequence of anthropogenic factors. It may well be that the "mosaic" in Etosha is changing from a state dominated by long-lived large mammalian herbivores to one in which conditions are favourable for small organisms whose generation time is relatively rapid.

The second question posed by Remmert *(op cit)* concerns the size of the "mosaic stones" and what determines their size. From our two case histories, it appears that in arid and semi-arid areas the "stones" may cover areas of several hundred square kilometres, which is far greater than in tropical forests where mosaics can be measured in hectares (Remmert 1987). Size determination of natural mosaics in Namibia may be governed by the primary agents which drive the systems. Since rainfall is probably the most important but patchy agent in this territory, the size of mosaics will be accordingly varied and as yet unpredictable.

The effects of rainfall are likely to be especially dramatic in the hyper-arid to arid situation where primary production and herbivore numbers rapidly achieve maximum potential before decreasing to their previous low levels. The implications of this for practical nature conservation are manifold, and special care needs be taken to ensure that Namibian conservation areas are large enough to sustain vital ecological processes.

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Berry & Siegfried Ms - captions for figures

Fig 1: Isohyetal map of Namibia (Source: Weather Bureau, Windhoek, 1980).

Fig 2: Map of the Namib-Naukluft Park, giving combined densities of ostrich, springbok, gemsbok and Hartmann's zebra during an aerial census in October 1982. The area of greatest animal density in the vicinity of Ganab corresponds with the open gravel plains.

Fig 3: Map of the Etosha National Park. The hatched zones indicate major areas for lions, wildebeest, zebra and anthrax

Fig 4: Rainfall records (histogram) for Gobabeb (1962/63 - 1988/89), in the Namib-Naukluft Park, calculated from 1 July to 30 June each year, in relation to total numbers of four herbivore species (ostrich, springbok, gemsbok, Hartmann's zebra) for the period 1972-88

Fig 5: Rainfall records (histogram) for Ganab (1967/68 - 1988/89), in the Namib-Naukluft Park calculated from 1 July to 30 June each year, in relation to total numbers of four herbivore species (ostrich, springbok, gemsbok, Hartmann's zebra) for the period 1972 - 88

Fig 6: Numbers of four large herbivore species (ostrich, springbok, gemsbok and Hartmann's zebra) and rainfall (histogram) in the Namib-Naukluft Park (1967/68 - 1988-89)

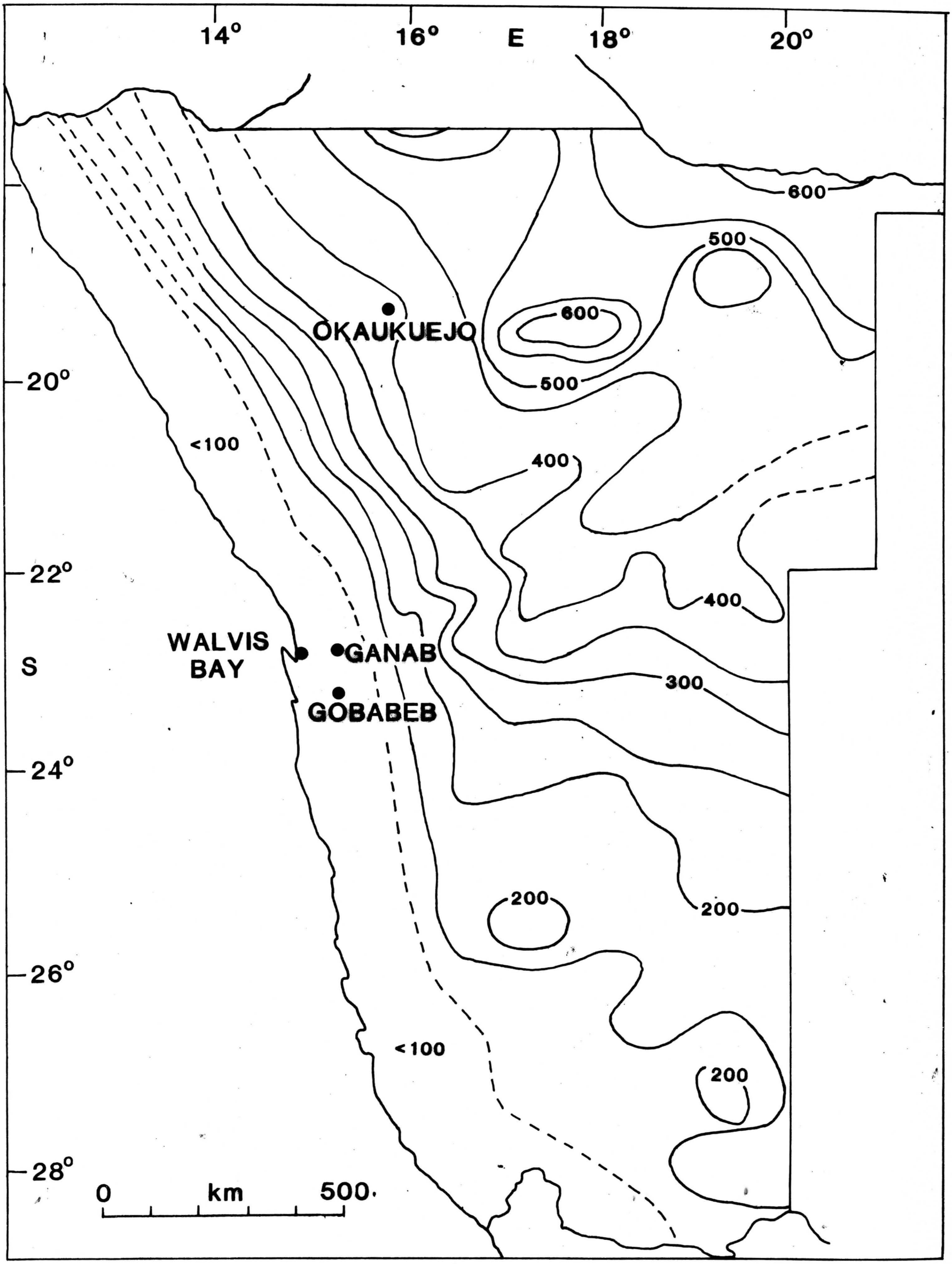
Fig 7: Relationships between the combined total populations of four herbivore species (ostrich, springbok, gemsbok and Hartmann's zebra) and rainfall, and ostrich and rainfall in the Namib-Naukluft Park (1967/68 - 1988-89)

Fig 8: Rainfall records (histogram) for Okaukuejo (1956/57 - 1988/89) in the Etosha National Park, calculated from 1 July to 30 June each year, in relation to numbers of lions (on the rainfall axis) and wildebeest-zebra (on the right-hand axis)

Table 1. Minimum number of lions reported destroyed while trespassing on farms adjoining Etosha National Park (1978-87) according to Berry (1987)

Year	Population in park	No. trespassers destroyed	Percentage population destroyed
1978	400	37	9
1979	500	11	2
1980	500	25	5
1981	450	42	9
1982	400	84	21
1983	300	39	13
1984	270	31	11
1985	230	25	11
1986	200	12	6
1987	220	11	5

FIG. 1:



14°
16°
E
18°
20°
600
500
600
OKAUKUEJO
500
20°
<100
400
22°
400
WALVIS BAY
GANAB
S
300
GOBABEB
24°
200
200
26°
<100
200
28°
0
km
500

FIG. 2:

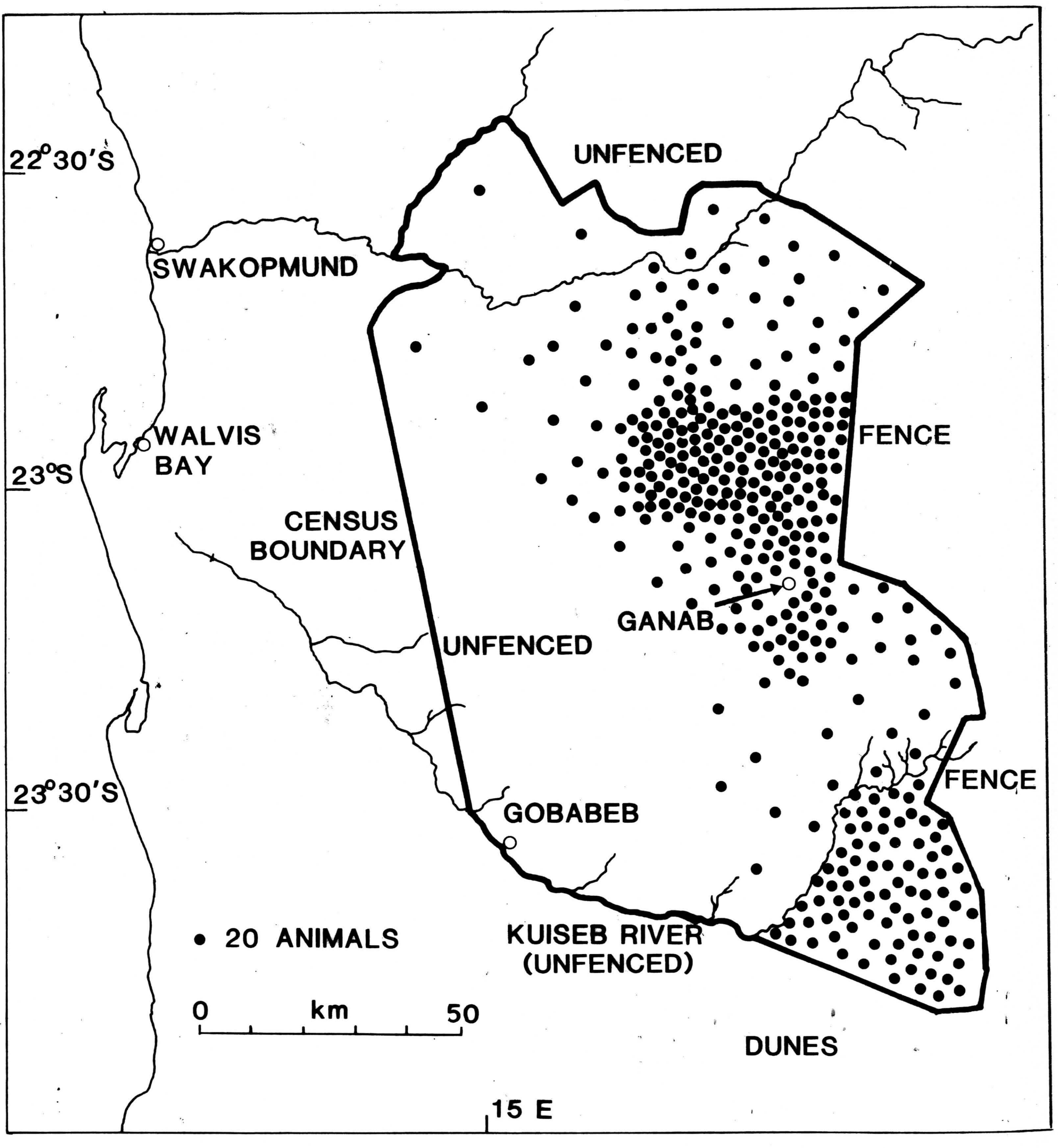

22°30'S
UNFENCED
SWAKOPMUND
WALVIS
BAY
23°S
FENCE
CENSUS
BOUNDARY
GANAB
UNFENCED
23°30'S
FENCE
GOBABEB
KUISEB RIVER
(UNFENCED)
• 20 ANIMALS
0
km
50
DUNES
15 E

FIG. 3:

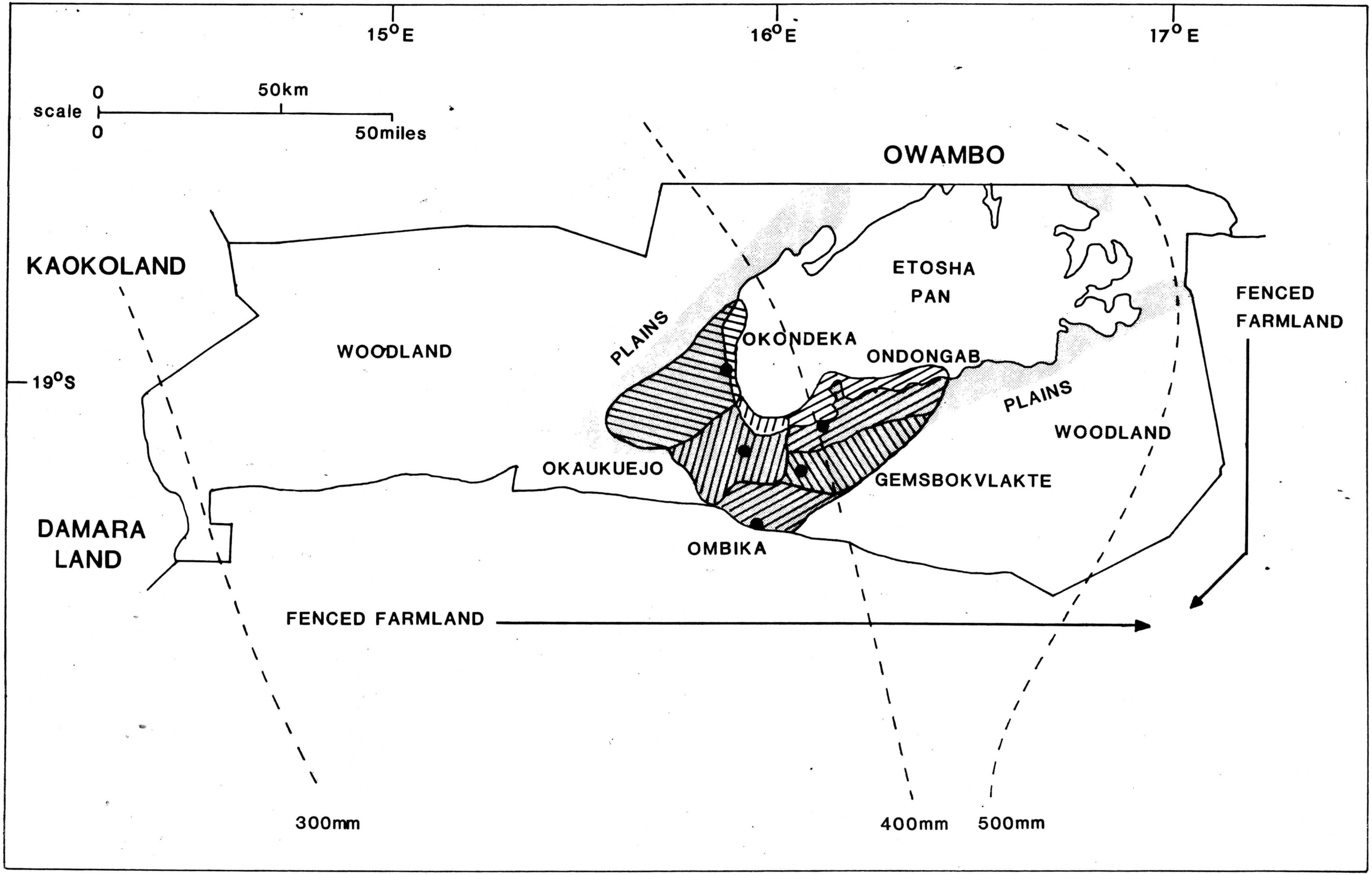

15°E
16°E
17°E
scale
0
50km
0
50miles
OWAMBO
KAOKOLAND
ETOSHA
PAN
FENCED
FARMLAND
PLAINS
OKONDEKA
ONDONGAB
WOODLAND
19°S
PLAINS
WOODLAND
OKAUKUEJO
GEMSBOKVLAKTE
DAMARA
LAND
OMBIKA
FENCED FARMLAND
300mm
400mm
500mm

FIG. 4:

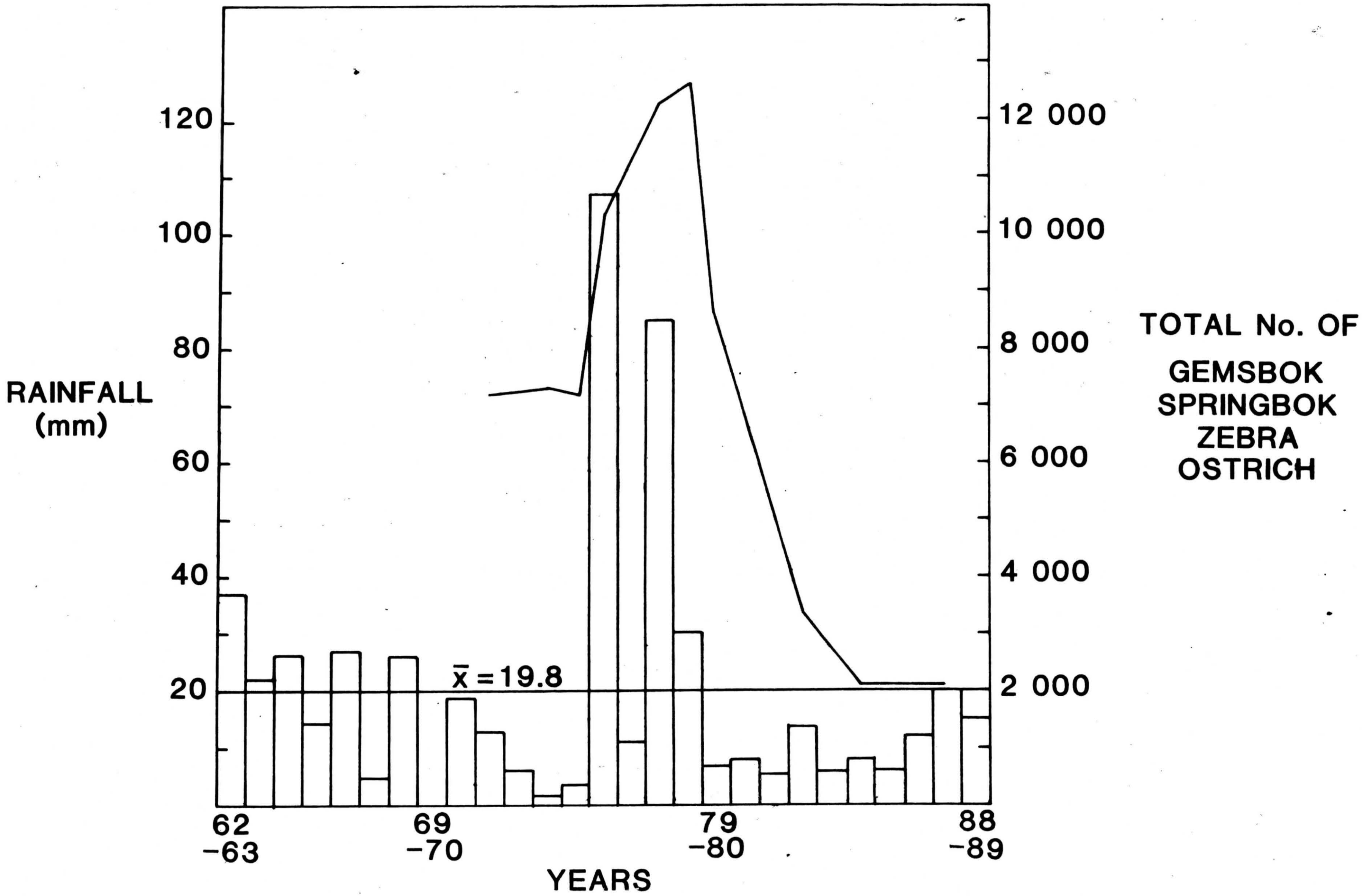

120
100
80
60
40
20
RAINFALL
(mm)
12 000
10 000
8 000
6 000
4 000
2 000
TOTAL No. OF
GEMSBOK
SPRINGBOK
ZEBRA
OSTRICH
x̄ = 19.8
62
-63
69
-70
79
-80
88
-89
YEARS

FIG. 5:

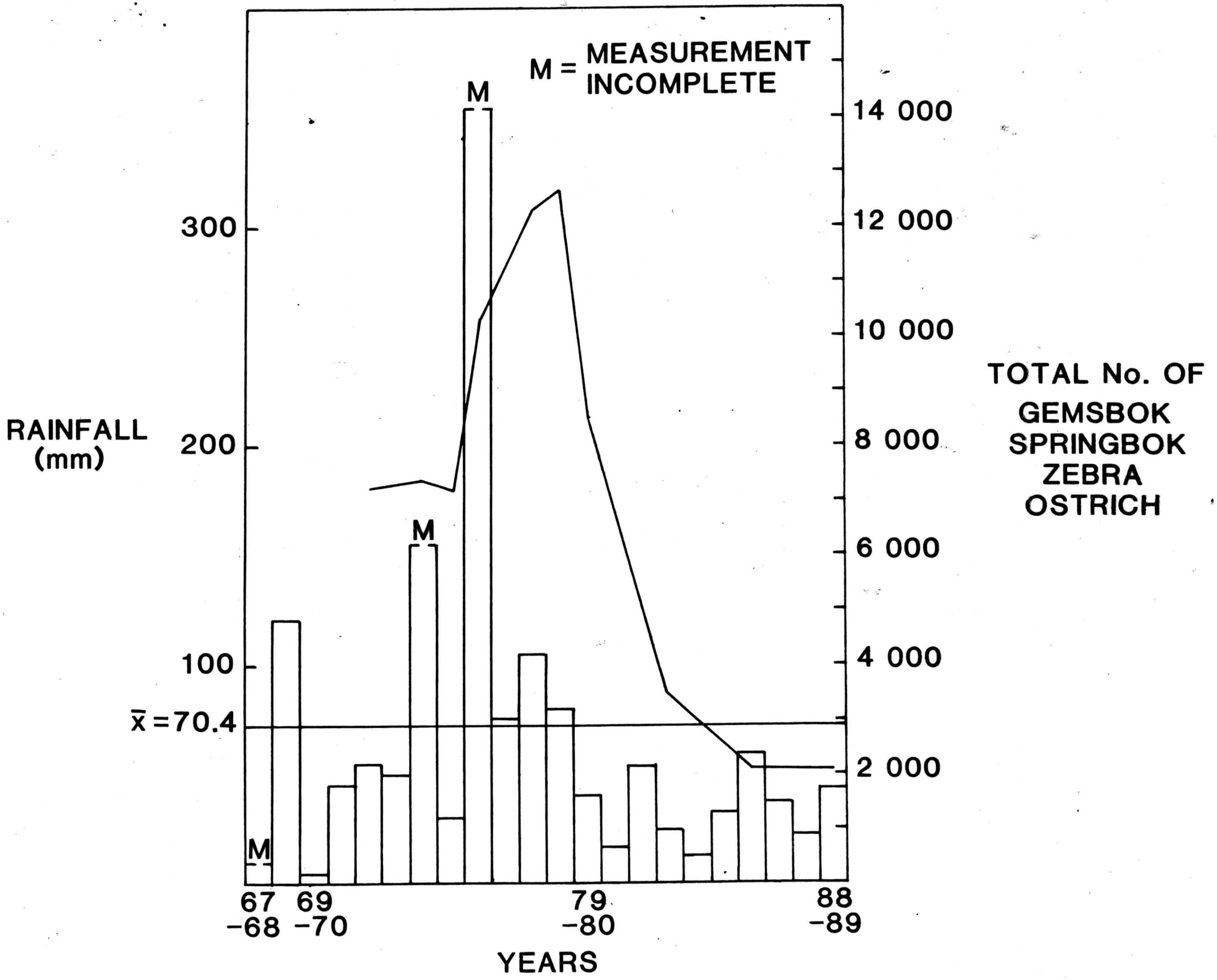
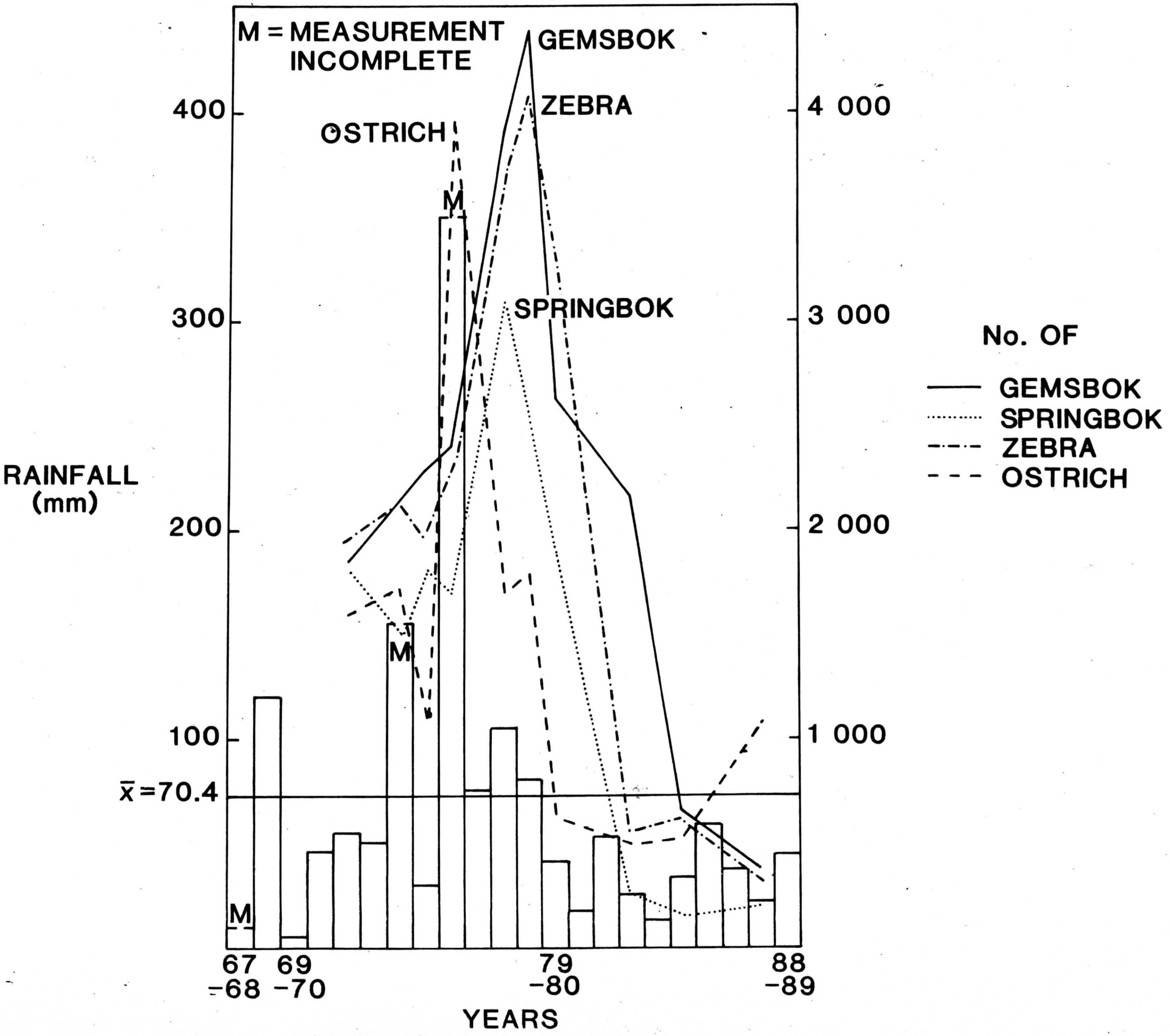
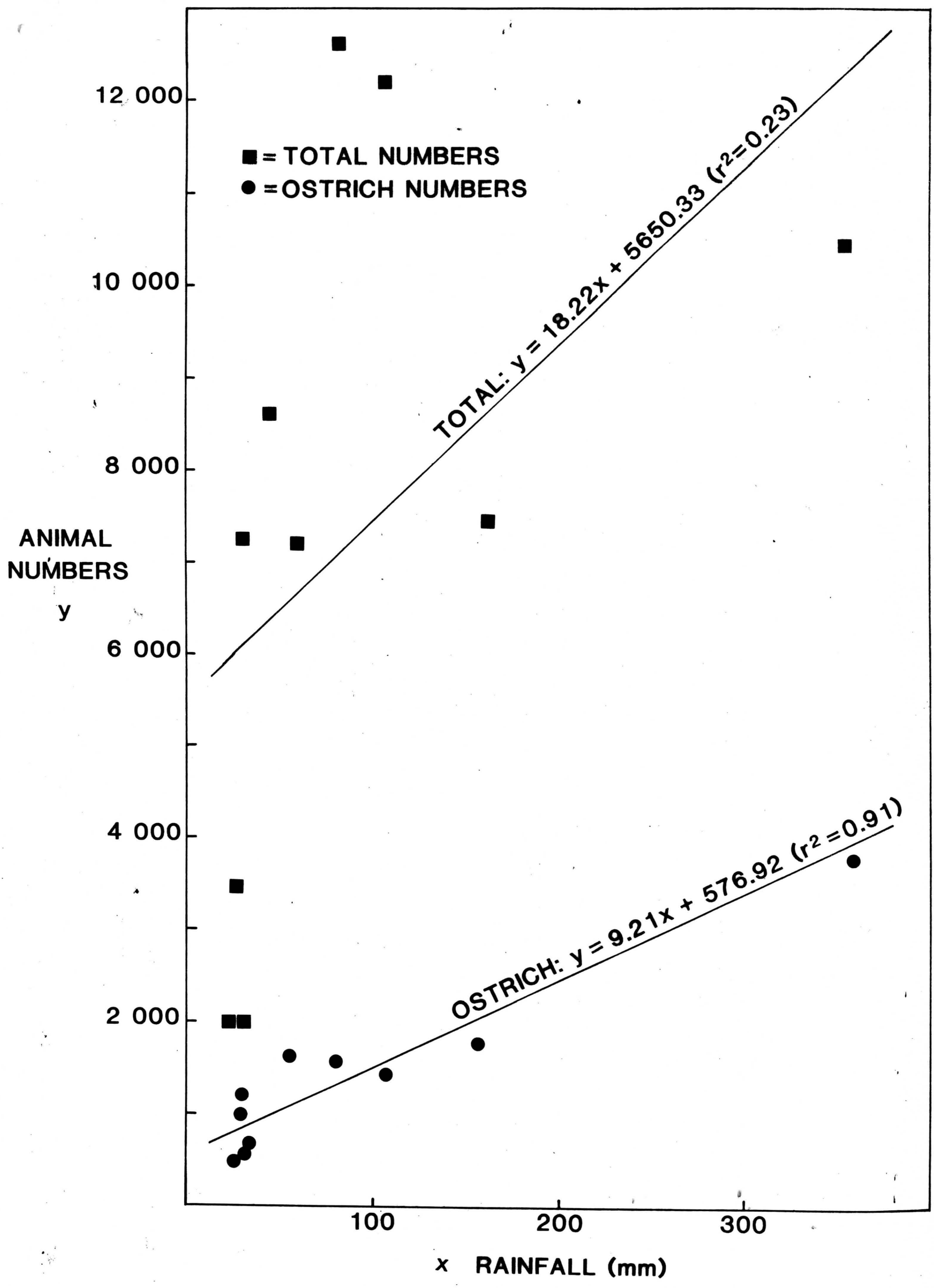

M = MEASUREMENT INCOMPLETE
M
M
M
RAINFALL (mm)
300
200
100
x̄ = 70.4
14 000
12 000
10 000
8 000
6 000
4 000
2 000
TOTAL No. OF GEMSBOK SPRINGBOK ZEBRA OSTRICH
67 -68
69 -70
79 -80
88 -89
YEARS

FIG. 6:



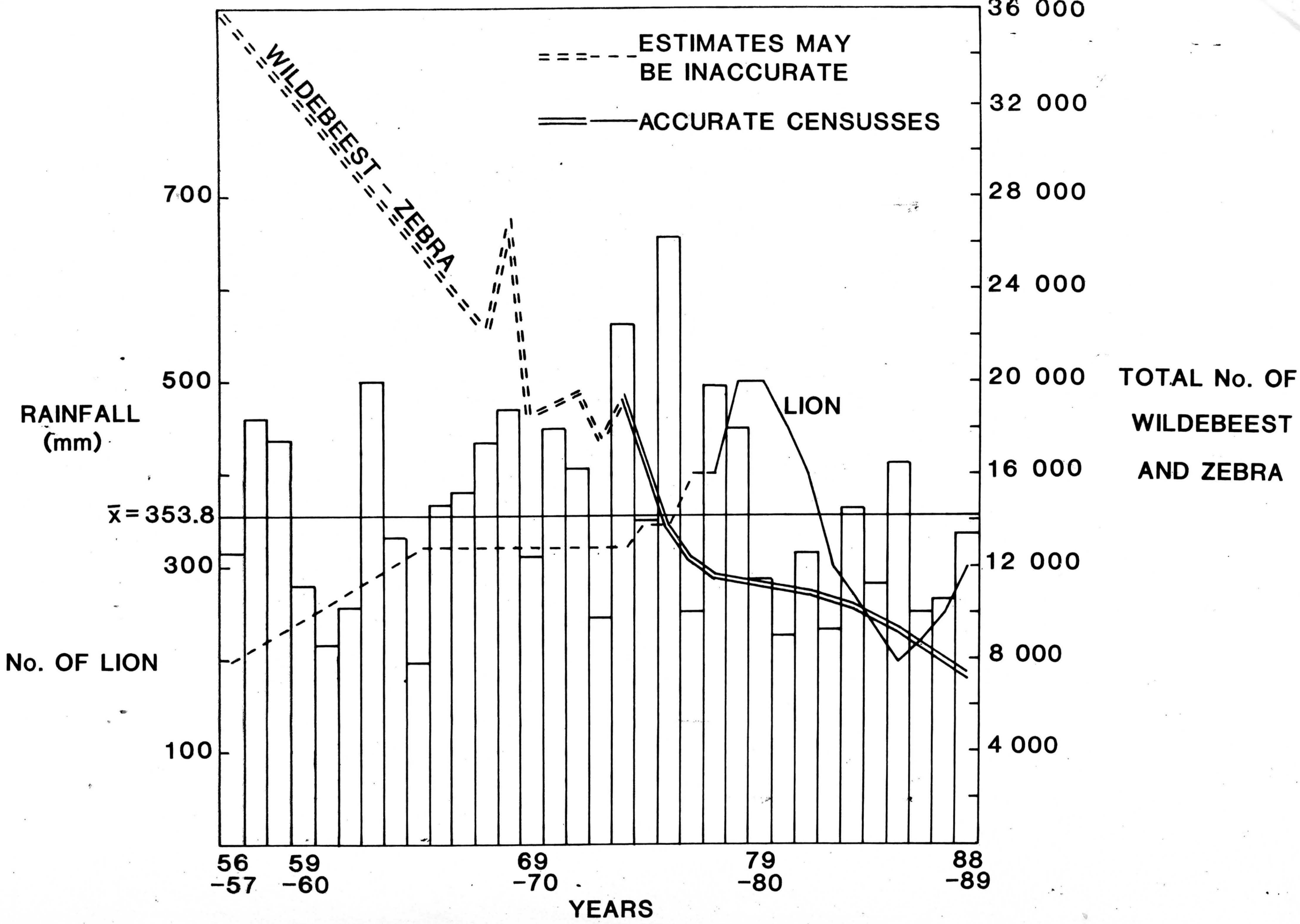
M = MEASUREMENT INCOMPLETE
GEMSBOK
ZEBRA
OSTRICH
SPRINGBOK
M
M
M
400
300
200
100
x̄ = 70.4
4 000
3 000
2 000
1 000
RAINFALL (mm)
No. OF
GEMSBOK
SPRINGBOK
ZEBRA
OSTRICH
67 -68
69 -70
79 -80
88 -89
YEARS

FIG. 7:



12 000
10 000
8 000
6 000
4 000
2 000
■ = TOTAL NUMBERS
● = OSTRICH NUMBERS
TOTAL: y = 18.22x + 5650.33 (r2=0.23)
OSTRICH: y = 9.21x + 576.92 (r2 =0.91)
ANIMAL NUMBERS y
100
200
300
x RAINFALL (mm)

FIG. 8:


ESTIMATES MAY BE INACCURATE
ACCURATE CENSUSSES
WILDEBEEST – ZEBRA
LION
RAINFALL (mm)
No. OF LION
TOTAL No. OF WILDEBEEST AND ZEBRA
700
500
300
100
x̄ = 353.8
36 000
32 000
28 000
24 000
20 000
16 000
12 000
8 000
4 000
56 -57
59 -60
69 -70
79 -80
88 -89
YEARS