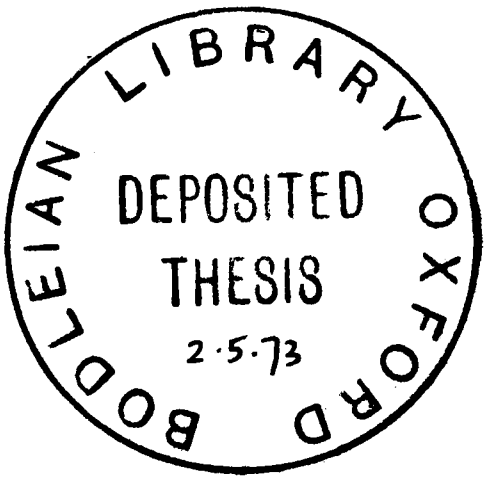
The Ecology of Serengeti Vultures.

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Abstract

The relationship between the whiteback vulture Gyps africanus, and Ruppell's griffon Gyps ruppellii and their food supply was studied in the Serengeti National Park in northern Tanzania for sixteen months during 1969 and 1970. Seven species of vulture occur in this region, although over most of their ranges each species is separated from the others ecologically and they do not compete. These two griffon vultures both specialise in taking the soft parts of carcasses and between them account for 85% of all vulture sightings in this area. In the Serengeti region both species are common, an unusual situation, and they are potentially in direct competition for the same food supply.

In the Serengeti about 80% of herbivores are migratory and the large distances covered by these herds during the year prevents their predators from increasing sufficiently to become a major mortality factor. Other causes of mortality are therefore of far greater importance and may account for perhaps 80% of all mortality in the area. However, the nature of this mortality causes seasonal fluctuations in the number of deaths, as well as the variations in distribution caused by the movements of the herds. These conditions prevent mammalian scavengers from being able to utilise the food effectively, and these may take perhaps only 5% of the total food available to scavengers. There is therefore potentially available a food supply for scavengers which fluctuates considerably in quantity and distribution through the year. This is the food supply that griffon vultures utilise. Predators are usually efficient in their feeding and vultures obtain only small amounts of food from predator kills. A large vulture population can probably only occur in areas where there is a food supply that is not effectively exploited by mammaliam carnivores.

In the Serengeti there are probably two peaks of food availability. At the end of the dry season when animals are in poorest condition and scattered widely through the northern woodlands, and a second peak at the time of wildebeest calving when herds are heavily concentrated on the eastern plains. Birds travel widely during food searching and tend to concentrate heavily in areas of large game herds, which is where most of the food is available. The Ruppell's griffon is uncommon in areas away from the migratory herds. They locate food largely by watching the activity of other birds and converging on an area where vultures are seen to be descending. In areas of moderate game density birds search at low altitudes and relatively high density so that birds congregate rapidly at any food source. However, in areas with little game, birds search at higher altitudes and may not always be within sight of other individuals, and fewer birds may be attracted to carcasses. Since birds can cover large distances rapidly, they are able to exploit the food supply despite variations in distribution through the year.

However, food also fluctuates in abundance. Captive birds were used to establish the food requirements for inactive birds. The amount of food actually obtained by wild birds was also recorded from the size of the crop of birds roosting in the afternoon, and this showed that non breeding birds during the first half of 1970 were probably able to obtain sufficient food to satisfy their food requirements. Their fat levels were high throughout this period. Birds can store fat very rapidly after a large food intake and use this to last over periods when the food supply is not adequate to satisfy the food requirements. The body temperature does not fall abnormally at night.

The food requirements of birds could be increased seasonally by

both moult and breeding. Moult is continuous throughout the birds life. Primary feather moult starts about ten months after the bird leaves the nest, and the first feather to be shed is the innermost primary. From this position primary moult proceeds in an orderly progression outwards towards the tip of the wing. Subsequent primary moults also occur as similar waves of moult activity moving outwards across the wing. Secondary moult, however, does not show a clear pattern. The innermost secondary is the first to develop, but later feather replacements occur at sites further along the wing, and although there is no fixed position for these additional growing sites, there is a tendency for replacement to occur first in three areas. Further secondary replacement does not occur by the progression of moult waves, but by the irregular growth of feathers. Subsequent secondary moults also appear to be irregular. It probably takes about three years of moult activity to complete the first feather replacement. Adult birds show individual variation in the number of actively growing feathers, but this could not be related to breeding or body condition. Feather growth accounts for perhaps 6% of the total energy intake of the bird throughout the year.

Breeding, however, is confined to a definite season. The Ruppell's griffon lays about two to three months earlier than the whiteback. In the Ruppell's griffon the food requirements for egg laying are considered to be slight, although the provision of calcium for the egg shell might be an important factor. Captive chicks were hand reared to determine their food requirements during growth and these estimates were combined with the figure for the food requirements of adult birds to determine a total estimate of food requirements for breeding birds. The amount of food actually obtained by a group of birds was recorded from the size of the crops of birds returning to the colony in the afternoon.

The comparison of food obtained and food required rough the season suggested that their may be a period during rearing when there was insufficient food available to satsify the food requirements of both chick and adult. Chicks were found to have a very high survival rate and they are not able to alter their growth rate according to the amount of food that they are supplied and presumably chick food requirements were being met. The examination of a sample of adult birds for body condition through the year showed a clear decline in the fat deposits through the breeding season, although no bird was found with seriously low protein levels. It was considered that for both species breeding is timed so that the young leave the nest at a period in the year when food conditions are good and young birds can feed with little competition from adults. However, adults have to rear young during a period in the year when food conditions are not always adequate and they have to rely on utilising fat reserves.

Introduction

Vultures are abundant scavengers in Africa in areas of game concentrations. Observations on feeding groups of birds have been made by Attwell (1963) and Petrides (1959). However, with the exception of Kruuk's (1967) detailed study of inter-specific competition for food among vulture species, little was known of their general ecology.

This study was concerned with the relationship between the food supply and griffon vulture populations and the work was initiated to consider the effect of scavenging birds on predatory mammals and their general role in the African savanna. In Section 1 the ecological isolation of the seven species of vultures found in the study area is briefly discussed. Section 11 describes the nature of the food supply of the most numerous of the vulture species, the whiteback Gyps africanus and the Ruppell's griffon Gyps ruppellii. Section 111 then considers the effect of this food supply on the birds activities by comparing their food requirements for various activities with the annual fluctuations in food availability.

This study was made in the Serengeti National Park and surrounding areas in northern Tanzania. Sixteen months of field observations were made from December 1968 to August 1969 and from January 1970 to August 1970. No observations covering the period from September to December have been made and the majority of the results presented in Section 111 were obtained from the 1970 season only.

Section 1

Ecological Isolation of African Vultures

Birds of prey specialized in feeding exclusively on carrion have evolved from separate stocks giving rise to the New and Old world vultures. Fig 1 shows that Africa now supports a larger number of species of vulture than any other continent, with up to seven species found in any one region.

Lammergeier Gypaetus barbatus, whiteback Gyps africanus, Ruppell's griffon Gyps ruppellii, lappet faced Torgos tracheliotus, whiteheaded Trigonoceps occipitalis, Egyptian Neophron percnopterus and hooded Necrosyrtes monachus are all found in the study area of the Serengeti.

The problem of possible competition for food between these species was studies by Kruuk (1967) who showed that the six common species (excluding the lammergeier) separated clearly into three pairs, as in Fig 1 , each pair showing similar bill structure and food selection. Within each pair, however, differences between species were less obvious and their feeding behaviour was often similar.

In this section the ecological isolation of the species found in the study area is briefly considered.

Lammergeier

Throughout its range the lammergeier is confined to precipitous mountain ranges, gorges and canyons. In the Serengeti region birds are uncommon and have only been seen along the eastern escarpment of the Gol mountains. Only one bird has been seen feeding; it was alone on

Figure 1

	North America	South America	Southern Europe	Asia	Africa
Large, heavy billed birds. Precipitous mountain regions.	Gymnogyps californianus	Vultur gryphus	Gypaetus barbatus	Gypaetus barbatus	Gypaetus barbatus
Large, heavy billed tearers of soft tissue from large carcasses.	–	Sarcorhamphus papa	Gyps fulvus	Gyps bengalensis Gyps fulvus (Gyps indicus) (Gyps himalayensis)	Gyps africanus Gyps rüppellii (Gyps fulvus) (Gyps coprotheres)
Very heavy billed tearers of tough tissues from large and small carcasses.	–	–	Aegypius monachus	Aegypius monachus (Sarcogyps calvus)	Torgos tracheliotus Trigonoceps occipitalis
Small birds with thin bills. Less specialised than other types.	Cathartes aura Coragyps atratus	Cathartes aura (Cathartes burrovianus) (Cathartes melambrotus)	Neophron percnopterus	Neophron percnopterus	Neophron percnopterus Necrosyrtes monachus

Species in brackets are equivalent feeders in different geographical regions.

an isolated Thomson's gazelle carcass on the plains at the foot of the mountains. In other parts of their range these birds have been reported to have two specialisations for feeding in mountainous regions; by sweeping animals off isolated ledges (Meinertzhagen 1959) and by dropping tortoises and large limb bones onto rock slabs to shatter the bone and enable the bird to feed on the tortoise or bone marrow (Huxley & Nicholson 1963, Meinertzhagen 1959). This species is therefore a scavenger and predator confined to rocky mountainous areas.

Griffon vultures

Both species of griffon vultures congregate in large numbers at kills and with their long necks can reach inside carcasses to tear off meat and viscera. The Ruppell's griffon is a considerably larger bird than the whiteback (7.4 and 5.3 kilo) and will often dominate the whiteback at any aggressive encounters while feeding. (Kruuk 1967). Both species feed exclusively off the soft tissues of large carcasses and there is no difference in the parts of carcass selected.

Percentage Composition of Crop Contents of Collected Birds.

Muscle	86%	89%
Fat	3%	5%
Skin	-	.2%
Tendon	-	-
Gut	8%	4%
Gut contents	1%	.1%
Liver	2%	-
Bone	-	-
N	28	20

Since the soft tissues of an animal form the largest proportion of food available to scavengers from a carcass, the griffon vultures are the most numerous vulture species in the Serengeti and account for about 85% of all vulture sightings. Both species locate food in the same way and congregate in large numbers at carcasses and there is a great deal of aggression between the two species (Kruuk 1967). Potentially, these two species are in direct competition for food in the Serengeti area.

However, it is not typical to find two species of griffon vultures commonly present in other areas of Africa. General distribution maps for species (Fischer 1963, Mackworth-Praed and Grant 1952) can be misleading by representing ranges which include areas of rare occurence as well as areas of common residence. Fig 2 has been compiled from the information given in the 71 regional avifaunas issued by the Percy FitzPatrick Institute of African Ornithology for the two griffon species of southern Africa. Such detailed mapping is not possible for the East African species since there is insufficient knowledge of bird distribution in East Africa. However, observations suggest a similar separation as in southern Africa. The whiteback nests in trees and is a bird of tropical lowland savanna, and occurs in these areas throughout East Africa. Ruppell's griffon (as with its ecological equivalent the cape vulture) nests on cliffs and occurs over a largely separate habitat in highland areas of Ethiopia, reaching down the rift valley into Kenya and northern Tanzania. Although the two griffon vultures travel widely in food searching and may overlap in parts of their distribution, each has a distinct geographical range which is separate from the other.

The smaller whiteback vulture is able to undertake flapping flight for distances of one mile or more and can reach food in the open plains and savanna conditions in heavy overcast weather when thermal soaring is impossible.

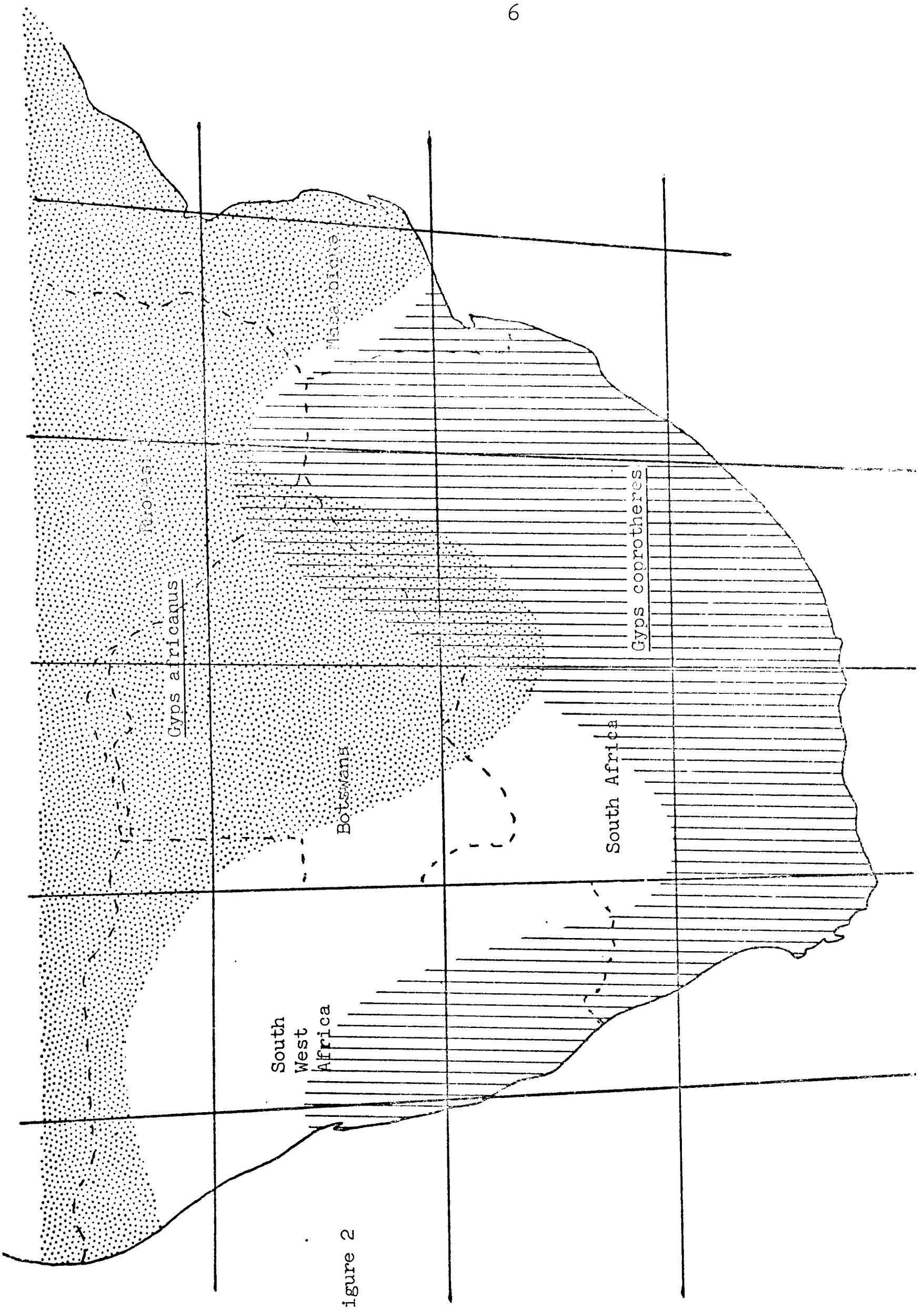

Gyps africanus
Botswana
Gyps coprotheres
South West Africa
South Africa

Figure 2

The larger Ruppell's griffon, however, cannot sustain flapping flight, and this species is adapted for highland and hill country where it can use rising air over slopes to search for food in poor weather conditions. The two griffon species therefore separate out in their ranges, although the study area occurs on the edge of the distribution of both species and at present both are abundant in this region.

Lappet faced and whiteheaded.

Both lappet faced and whiteheaded vulture (6.2 and 4.0 kilo) have deep powerful bills and specialize in feeding off the tougher parts of carcasses, pulling against their feet to tear off skin and other pieces of tough tissue from bones. Whiteheaded are usually found individually or in pairs, the lappet faced with a few individuals of its species. Neither build up into large feeding parties like the griffon vultures, and both have been suspected of killing their own prey (Kruuk 1967), although this is rare. Both are probably territorial and have to obtain their food from a restricted area, which they patrol regularly, unlike the griffon vultures which travel large distances following the migratory herds.

Kruuk's (1967) observations on feeding of these species were largely concerned with conditions at predator kills and are not typical of feeding in these species. Lappet faced are highly aggressive and congregate with griffon vultures at game carcasses. They are usually found feeding in small groups of 2 to 6 birds, and may arrive together as a group, suggesting that they may sometimes search together. They are probably territorial and on several occasions a bird has been seen to stop feeding and run to attack a new bird which has just landed some distance from the carcass. The nests are widely scattered and built in trees, both on

the plains and in woodland areas, and the same site is re-built for many years and may develop into a structure up to six feet across and five feet thick. However, during the early wet season large numbers of lappet faced vultures move out into the open plains to take advantage of the food abundance during wildebeest calving. At a large source of food caused by the drowning of many wildebeest calves in Lake Lagarja on 3rd February 1969, 76 birds were seen feeding in the same area.

They are aggressive when feeding and depose all other species, including the larger Ruppell's griffon, and dominate the feeding. In carcasses which are untouched by predators and have not therefore been opened up, it is usual for lappet faced vultures to wait until the griffon vultures have torn the skin and removed part of the soft tissues from the carcass before moving in and driving away the griffons and dominating the feeding. The lappet faced is therefore probably a territorial bird for most of the year, almost always feeding among groups of griffon vultures and dominating other species present. With large carcasses it relies on predators and griffon vultures to remove part of the soft tissues from the carcass before starting to feed.

However, the whiteheaded is a timid species nesting in trees and found only in woodland areas. It usually feeds alone, and if several griffon or lappet faced vultures arrive it will usually retreat slowly and give way. Much of the feeding is from small carcasses which other species either do not descend to or do not locate. Out of 37 feeding records (not considering occasions when birds were present but did not feed) 19% were from small carcasses such as hyrax and gazelle fawns, 43% from the remains of hyaena kills and 30% from carcasses that griffon vultures had abandoned. This species is probably territorial, living in pairs often with immature young. A pair of adults and one juvenile were frequently

seen feeding along the Seronera rivers and these birds were considerably tamer than any other whiteheaded vultures which were encountered. No other 'wild' whiteheaded were ever seen in this area.

Kruuk (1967) found that in 50% of cases the first vulture species to arrive at a predator kill was the whiteheaded, although this species forms only 3% of the vulture population. However, out of 64 complete carcasses which have on various occasions been taken and placed to observe birds feeding, this species was never recorded to arrive first and was only present later at 7 of the feeding parties. It seems very probable that this species specialises in following the movements of predators and the scattered remains of hyaena kills attract this species particularly. In the whiteheaded vulture a pair of birds probably patrol a regular territory and specialise in locating small food items which do not attract other species, and possibly they follow closely the activities of predators. This contrasts sharply with the lappet faced which feeds off the skin and tougher tissues of large game carcasses and aggressively dominates over griffon vultures.

Hooded and Egyptian

Both hooded and Egyptian are small birds (1.9 and 1.8 kilo), less specialised than the other vultures. At carcasses they peck at small scraps of meat left lying around, or on bones, and both species also take insects, dung and commonly congregate near human settlements and rubbish tips. The Egyptian will also feed off bird's eggs, breaking small eggs by throwing them on the ground and cracking larger eggs with stones (Lawick Goodall 1969). Both are general purpose scavengers which are not usually found commonly in the same area. The Egyptian is a dry country bird occuring in semi desert and very arid conditions, and

nesting on cliff ledges. In the Serengeti it is common only in the far eastern plains with a rainfall of 40 to 50 cm a year. Over the other regions of the park the hooded vulture is the common small scavenging bird and throughout its range the hooded occurs in savanna and open forest conditions, nesting under the canopy of large trees.

Ratio of Egyptian to hooded vultures recorded at feeding parties

In areas under 40 cms rain	336 Egyptian per 100 hooded
In areas over 60 cms rain	0.6 Egyptian per 100 hooded

These two species therefore separate from each other by habitat and the ranges of the two species overlap in the eastern Serengeti.

The seven species of vulture found in East Africa therefore all separate from each other either ecologically or in their ranges.

The proportion of species present in any area varies due to differences in the distribution of the species. However, to give a rough indication of the relative abundance of the species, the percentage composition at feeding parties using 6112 birds is given below.

Whiteback	70%
Ruppell's griffon	18%
Lappet faced	8%
Hooded	3%
Whiteheaded	.3%
Egyptian	.03%

The remainder of this study is concerned only with the two griffon species.

Section 11

Food Supply

The purpose of this section is to determine in general terms the nature of the food supply of griffon vultures and the way in which it is utilised.

Introduction

The Serengeti National Park in northern Tanzania covers an area of 5,600 square miles, with an average altitude of 4,500 feet, between the mountains associated with the rift valley systems in the east, and Lake Victoria in the west (1° 30' to 3° 15' south and 34° 00' to 35° 15' east). There is a rainfall gradient across this area with rainfall highest in the north west and lowest in the east. The park may be roughly divided into three vegetation zones.

a) Short grass plains in the east, with an average rainfall of about 50 cm per year.

b) Taller grasslands on the western edge of the short grass plains, with about 70 cm rain per year.

c) Open Acacia woodland, covering the northern and western areas of the park where rainfall is heaviest, 80 to 100 cm per year.

Further general details were given by Pearsall (1957) and Grzimek (1960).

Rain falls chiefly in two periods during the year, from February until June, and also scattered rain from November until January, although timing and amount are often irregular. There is therefore only one long dry season from July until October, when standing water can be found only in occasional springs and in the permanent Grumeti and Mara rivers which flow through the park. This rainfall cycle determines the movements of the migratory game species, the wildebeest, zebra, gazelle and eland. During

N

Mara river

Lake
Victoria

Ikoma
Region

Grumeti river

Kirawira

Mbalageti river

Banagi

Seronera

Soit
Aye

Gol
kopjes

Naabi
hill

Lake
Lagarja

Loliondo
Region

Gol Mountains

Sale
Plains

Lake
Natron

Rift
Escarpment

Crater
Highlands

0 20 40m

the rainy season these herds feed on the open plains in the east of the park. Towards the beginning of the dry season the herds concentrate in large numbers and move towards the west to reach permanent water. Later in the dry season the herds disperse, and move slowly north and spread widely through the woodlands, concentrating near the rivers. At the start of the long rain season the herds again concentrate and start to move south to the plains where they remain as long as rainfall is adequate to supply grazing and standing water. These migratory herds utilise large areas outside the park boundaries during their movements. There is also a resident population of ungulates in the woodland, chiefly buffalo, impala and hartebeest.

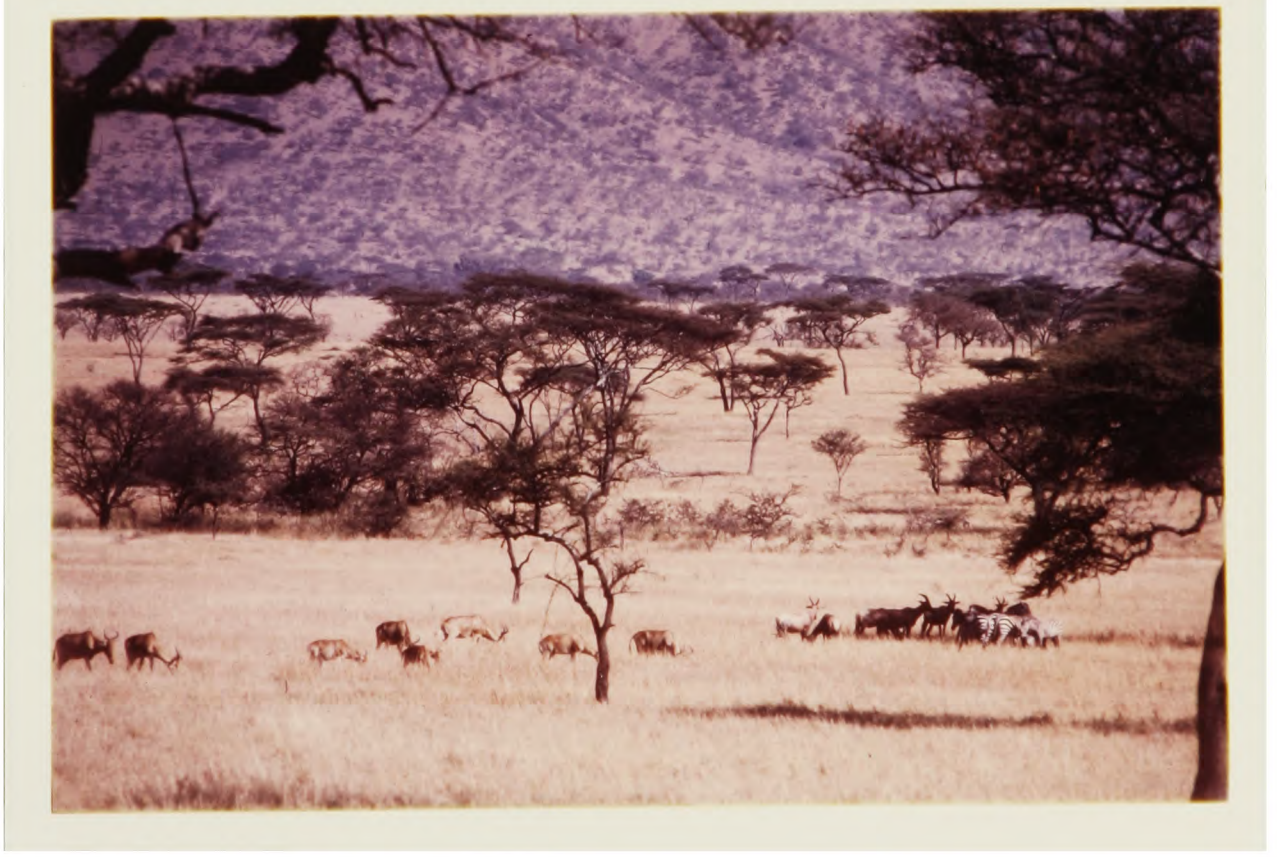
These herbivore populations supply food for both predators and scavengers, and firstly the seasonal distribution of the game and its mortality is considered.

Extent of Annual Game Mortality.

Fig 4 shows an attempt to estimate the extent of annual mortality among large mammal species in the Serengeti area. This must be considered a speculative estimate based on the limited evidence that is available. It assumes almost stable numbers for all species, although it is probable that for some species recruitment may have exceeded mortality in the period of study (buffalo and wildebeest, Sinclair 1970). Migratory species are considered as those undertaking predictable, long distance movements with the seasons. Substantial parts of the year may be spent in areas outside the park boundaries, and these populations must therefore be considered to occupy the Serengeti region of perhaps 35,000 km^2 rather than the 10,000 km^2 within the park boundaries. Resident, or non migratory, species population estimates are usually made for the area within the park boundaries



Serengeti short grass plains during wet season. Wildebeest concentration.



Woodlands in dry season. Seronera.

Figure 4

Species	Population size	Number of young born per year.	% 1st yr. mortality	Wt. of 1st yr. animals at death. v. approx.	Total wt. of 1st yrs. dying per year	% Adult mortality per year	Mean Adult Weight	Total wt. of adults dying per year	Combined wt. of adults + 1st years dying per year.	
Wildebeest	650,000	270,000	70%	50	9,500,000	12%	180	14,040,000	23,540,000	M
Thomson's gazelle	1,000,000	1,100,000	75%	5	4,125,000	20%	20	4,000,000	8,125,000	M
Zebra	170,000	70,000	70%	70	3,430,000	12%	230	4,600,000	8,030,000	M
Buffalo	114,000 (57,000)	40,000	70%	80	2,240,000	6%	600	4,800,000	7,040,000	N-M
Topi & Kongoni	100,000 (50,000)	50,000	75%	40	1,500,000	10%	130	1,300,000	2,800,000	N-M
Impala	140,000 (70,000)	70,000	75%	17	892,000	10%	50	700,000	1,593,000	N-M
Giraffe	20,000 (10,000)					7%	1,000	1,400,000	1,400,000	N-M
Eland	15,000	6,000	75%	80	360,000	10%	400	600,000	960,000	M
Grant's gazelle.	75,000	37,500	75%	15	422,000	10%	50	375,000	797,000	M
Waterbuck	4,000 (2,000)	4,000	75%	60	76,000	10%	200	80,000	156,000	N-M
Elephant	4,500					2%	2,500	225,000	225,000	M
Hippo	1,500 (1,000)					2%	1,500	45,000	45,000	N-M
Rhino	400 (200)					2%	1,000	8,000	8,000	N-M
								Total	54,719,000 kilo	

and are not therefore comparable with the estimates for migratory species. These have therefore usually been multiplied by a factor of 2 to account for comparable areas of woodland outside the park. All figures are therefore considered to be those of the region rather than the area within park limits. Although laden with approximations, such a rough breakdown does indicate the relative importance of various species. It suggests that perhaps 76% of the total food available for carnivores came from migratory species of game. One species, the wildebeest, provided about 43% of the total.

A proportion of this mortality is due to predation. Fig 5 shows another tentative calculation to estimate the amount of food taken by predators within the region. Jackal are not included here for lack of information. Although in some seasons they are major predators of gazelle and small antelope fawns, they probably usually kill animals less than two weeks old (Wyman 1967) and therefore do not compare with the larger predators in regard to total food intake. The predation pressure will vary among species due to predator selection. Overall, predators might take perhaps 20% of the estimated food available from the mortality of all species. However, some predators will scavenge as well as kill their own prey, and the extent of actual predation will therefore be less than this figure, although it will be shown later that predators do not scavenge large amounts of food. At least four fifths of deaths are therefore probably due to causes of mortality other than predation.

Figure 5

Predator	Estimated population size.	Weight of food killed per day per animal (+ wastage)	Weight of food killed per year per animal.	Total weight of food taken by predator species per year.
Hyaena	3,000[a]	3 kilo[a]	1095 kilo	3,285,000
Lion	2,400[b]	6 kilo[b]	2190 kilo	5,256,000
Cheetah	200 ?	7 kilo[c]	2555 kilo	511,000
Wild Dog	100 ?	7.5 kilo[d]	2740 kilo	274,000
Leopard	700 ?	6 kilo ?	2190 kilo	1,533,000
			Total	10,859,000 kilo

a Kruuk 1970
b Schaller pers. comm.
c Schaller 1968 adapted.
d Kuhme 1965

Origin of the Food of Griffon Vultures

The origin of the food taken by vultures was estimated by recording the cause of death for all carcasses on which birds were found to be feeding. Usually a carcass was not located until a party of birds was actively feeding and the cause of death therefore had to be deduced from the remaining evidence. If a predator was present and there were signs of a predator attack on the carcass, then death was assumed to be the result of a predator kill. Occasionally a predator kill was found abandoned, but signs of predator attack and feeding activity around the site were usually evident. If there was no sign of any predator attack, the carcass was recorded as being killed by causes other than predation. In most cases where a group of birds had almost finished feeding, it was impossible to know the cause of death, and in all cases where there was any doubt over the cause of the mortality it was recorded as unknown.

In Fig 6 the estimated causes of mortality of the carcasses used by the feeding birds is shown. This shows that predatcrs provided a relatively small proportion of the carcasses which attracted birds, although this increases at the end of the wet season.

These observations are almost entirely concerned with areas near to concentrations of wildebeest, zebra and gazelle, where most of the food is available and where it will be shown the birds concentrate heavily. From January until March observations were all made on the Serengeti plains where visibility is excellent and feeding groups of birds can be rapidly located. Almost all carcasses observed were located by watching flying birds and following individuals which descended to the ground. Since the observer was using the same method to locate carcasses as the birds themselves, it is assumed that a representative sample of feeding sites was visited. However, from May until August observations are chiefly from woodland areas where visibility is poor and carcasses are often found by locating groups of birds perched in trees, as well as following individuals in flight. Birds may wait in the area of a predator kill for a considerable time before the predators have finished feeding and an unrepresentatively large proportion of predator kills is therefore probably recorded.

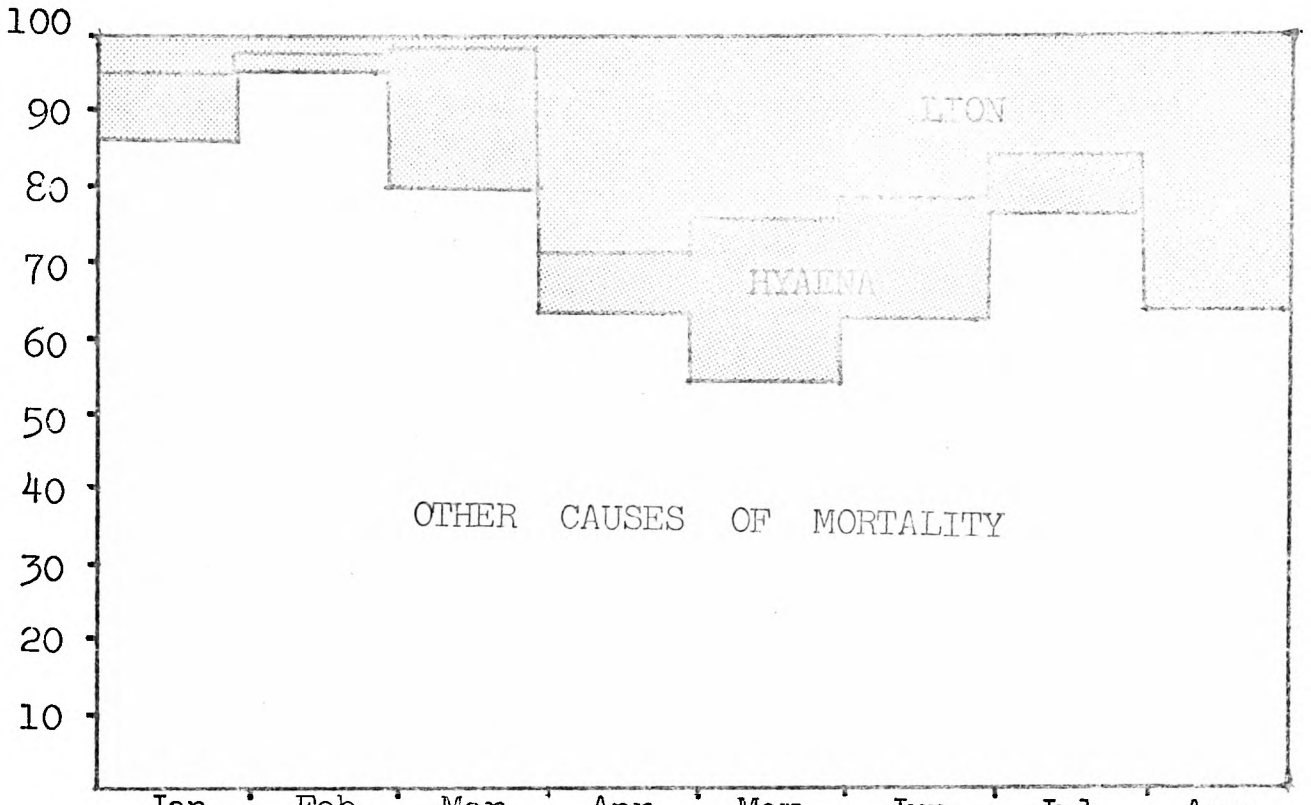
Although birds may descend to a carcass, the value to the birds depends on the amount of food they can take from it. It is therefore also necessary to consider the amount of food available from carcasses and the relationship between the predators and vultures.

Relations with Feeding Predators

The relationship between griffon vultures and predators differs according to the species of predator involved and their numbers and comparative aggression. Jackal and Hyaena are both relatively tolerant of vultures

Origin of food supply

Figure 6

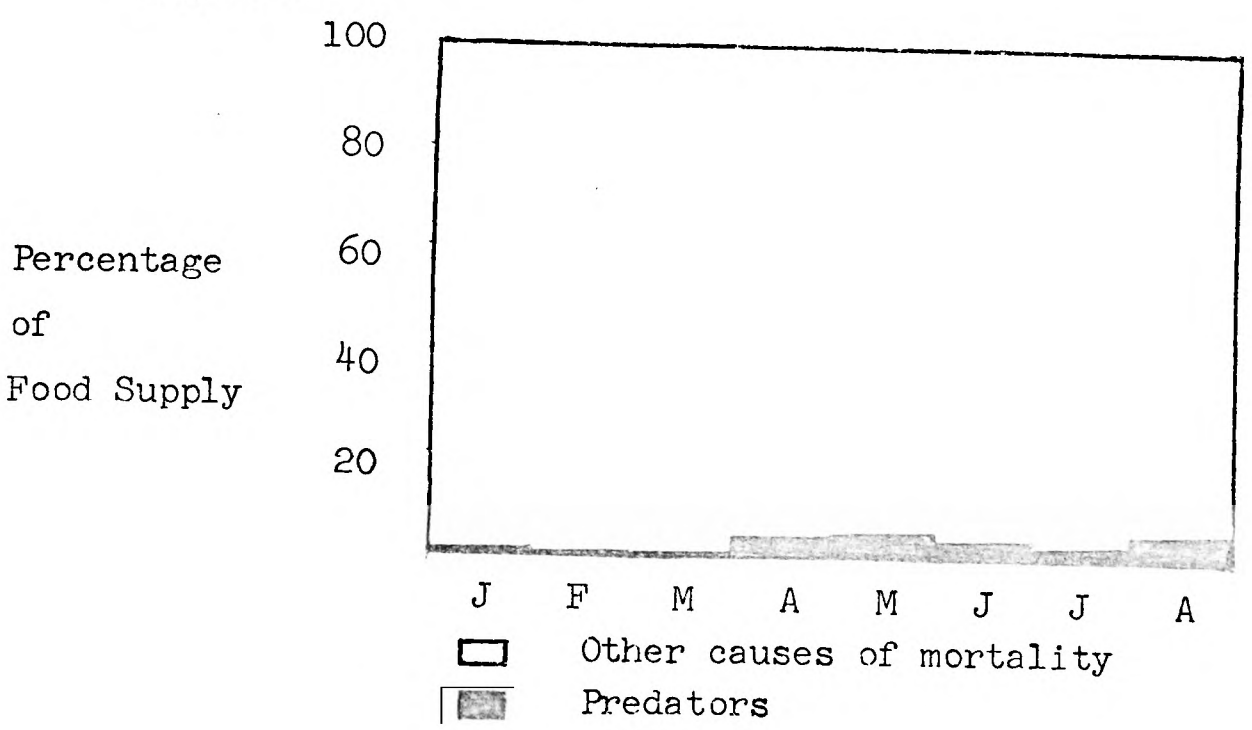


	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
Sample Size	60	376	55	32	28	37	49	17
% Unidentified	20	11	25	31	21	20	18	17

Estimate of the Proportion of Potential food available on a Carcass which was eaten by Griffon Vultures Figure 7

	Mortality Agent			
	Lion	Hyaena	Cheetah	Non-predatory mortality
Mean Proportion eaten	7%	2.5%	17%	About 85%
Number of observations.	26	42	11	144

Figure 8



if only one or two birds are present, and individuals may be allowed to feed together with the predator. However, if 3 or more birds are present, the predator will usually prevent birds from feeding by making attacks at any individual approaching the carcass, and most birds wait nearby.

Estimated minimum distances reached by whiteback vultures to feeding predator.

	Mean minimum distance. Yards	Number of observations	S.E.
Jackal (b-b)	1.8	10	.44
Cheetah	4.5	7	1.3
Hyaena	3.9	14	1.1
Lion	10.6	10	.8

If many aggressive birds gather and there are few jackal present, the birds may be able to drive the predator away from feeding, and this has been observed on seven occasions with lone jackal.

Lion, however, will not tolerate the close attention of vultures while they are feeding and will frequently attack birds which approach too-close to the carcass. Hooded vultures come considerably closer to feeding lion than griffon vultures, which remain in a group at a respectful distance from the pride. Cheetah are relatively unaggressive and birds may approach close to a feeding animal. A single cheetah has on two occasions in the middle of the dry season been seen to be driven off its kill by a large group of very aggressive birds. This is a period when food is not abundant and it seems probable that birds become more aggressive towards timid predators during poor food conditions.

All predators are efficient in their feeding and do not present opportunities for vultures to remove large amounts of their prey. The spotted hyaena usually kills in groups in the night and the prey is almost totally utilised very rapidly after killing. Hunting dogs similarly

feed immediately after killing and the prey is usually completely eaten by the pack. Lions are social predators which may not finish feeding from a large kill for several days and some pride members will usually guard the food to prevent scavengers from removing it before they have finished feeding. Leopards are solitary predators which eat small food items immediately after killing, and protect larger prey from scavengers by guarding and carrying into particularly dense trees where they are not visible from the air. Cheetah are the only large predator which regularly leave a small part of their kill uneaten, usually the digestive tract, but the number of cheetah is low, and they usually kill smaller antelope, so that this is not an important source of food to the birds.

The importance of this to the griffon vultures is shown in Fig 7 where rough estimates are given for the proportion of the potentially edible parts of carcasses from the different sources which were actually eaten by griffon vultures. The total weight of the potentially edible parts (considered to be viscera + muscle tissue) available from each prey species involved were taken from the figures given by Ledger (1968) for the body composition of East African mammals - usually 70% of body weight. The approximate amount of food that the vultures were able to obtain was estimated visually for very small quantities from the meat left after the predators had finished feeding, and for larger amounts chiefly from the size of the crops of birds after feeding (method described later). Predators will also scavenge carcasses located by vultures and prevent birds from taking all the available food, and this is considered later. In Fig 8 the results of Fig 6 and Fig 7 have been combined to give a rough indication of the relative importance of predators in supplying the food of griffon vultures. The figures for the amount of food taken from predator kills were mostly collected during March and April on the Serengeti plains and cannot be assumed to accurately represent the situation at other seasons.

There is probably considerable variation in the feeding efficiency of predators with season, habitat and food availability, and the extent to which predators scavenge carcasses located by vultures will also vary. In addition the rate of predation will be relatively constant through the year compared to the fluctuations in other causes of mortality, and the relative importance of predator kills to the vultures will therefore change through the year. However, this is unlikely to alter the overall picture and it would appear that under present conditions the remains of predator kills account for a very small proportion of the total food supply of griffon vultures.

However, the activities of vultures around predator kills are conspicuous and therefore superficially give a false imporession of their importance. Lions particularly may take a long time feeding and guarding their kill. When food conditions are abundant vultures may not descend to lion kills, presumably because relatively little food is available compared to alternative feeding sites. But when food conditions are poor, birds may wait for several hours or even days before they can start to feed. However, if there are no predators at a carcass, then feeding is very rapid. Quick feeding is important since the carcass may later be scavenged by a mammalian carnivore. The speed with which food can be removed depends on the species of carcass concerned, the number of birds and their feeding efficiency. A rough indication of the possible speed of feeding was found by taking several carcasses to areas near a wildebeest herd. The griffon vultures extracted the soft tissues from a Thomson's gazelle (20 kilo) mostly within 7 to 8 minutes (4 occasions), a Grant's gazelle (50 kilo) within about 8 minutes (1 occasion) and a wildebeest (200 kilo) in about 30 minutes (2 occasions) , although other species of vultures will remain actively feeding after this period. Zebra and larger species take them considerably longer because the thick skin cannot be torn by the birds

and they have to wait for predators to open up the carcass. In addition, most carcasses located for food are found shortly after dawn (Fig23a), indicating that animals tend to die during the night (Aschoff 1964). Since feeding is so rapid, most carcasses will be utilised within a few hours after dawn. The activities of vultures around predator kills are therefore considerably more conspicuous than for other causes of mortality, but as a source of food they are of only slight importance.

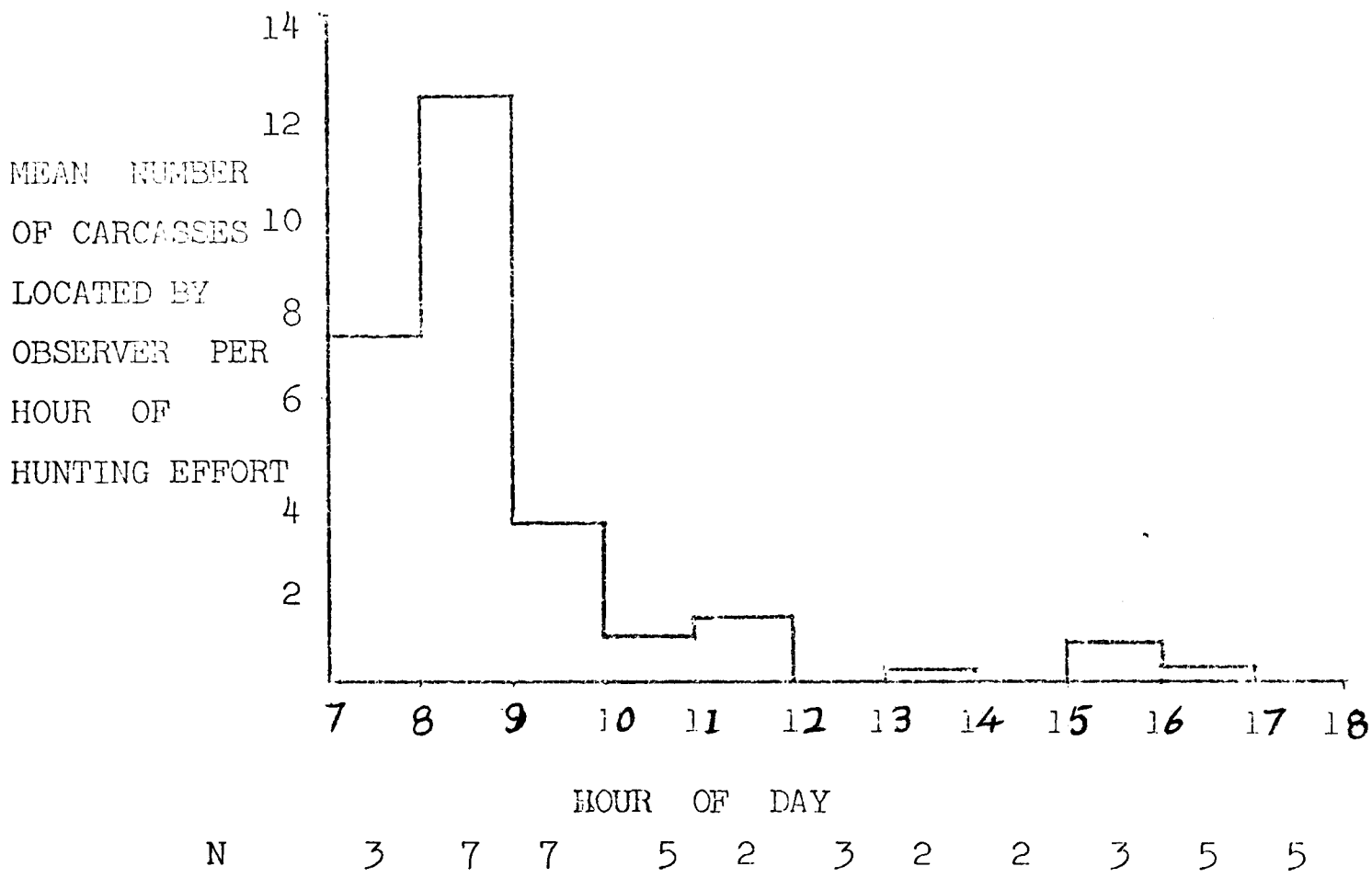
Since causes of mortality other than predation contribute the basic food supply for the vulture population, it is important to consider the nature and extent of the mortality agents operating on the game species.

Causes of Mortality other than Predation.

There is no quantitative information on the causes of mortality, other than predation, among game animals, which is unfortunate in view of the obvious importance of these factors.

Accidents account for a part of this mortality. Wildebeest seem particularly accident prone, and accounted for 99% of the 360 carcasses obviously caused by accidental death. Herds periodically stampede when crossing rivers or lakes and young or adult animals may be drowned. On 1st February 1969 a wildebeest calving herd crossed Lake Lagarja and at least 700 calves were drowned or died later after being separated from their mothers. Large scale mortality of this nature is unusual, but small scale accidental drownings of wildebeest occur frequently. On one occasion four adult wildebeest were found dead within 200 yards of each other in or beside a road drainage ditch, presumably following a group stampede in the area during the night. Broken legs are occasionally seen. However, accidents of this nature are unlikely to account for an important proportion of mortality, and presumably disease, parasite burdens, starvation

Figure 8a


MEAN NUMBER OF CARCASSES LOCATED BY OBSERVER PER HOUR OF HUNTING EFFORT
14
12
10
8
6
4
2
7 8 9 10 11 12 13 14 15 16 17 18
HOUR OF DAY
N 3 7 7 5 2 3 2 2 3 5 5

and old age are chiefly responsible.

Disease

Diseases affecting game populations may be artificially considered as highly contageous epizootic infections which spread rapidly and relatively unselectively among animals, and less spectacular enzootic diseases which are resident among the game populations and only become lethal under certain conditions.

Of the epizootic infections, rindepest has in the past caused large mortality among some species and as recently as 1963 about 85% of wildebeest calves were lost chiefly through this disease. (Talbot & Talbot 1963 However, rindepest has not been recorded in the Serengeti since 1963. Anthrax acts in a similar manner and can cause large scale mortality (Pienaar 1961 & 1967) and in South West Africa occurs in a chronic annual manner (Ebedes pers. comm.). Isolated cases of anthrax have been diagnosed from widely separated areas in the Serengeti and it is probable that this disease will prove to be responsible for a small annual toll of animals. An Allerton - typs virus has caused local small scale mortality among buffalo (Schiemann pers. comm.) but during the study period there was no evidence of epizootic infections directly causing important mortality.

Among enzootic diseases there is at present insufficient information to be able to reasonably consider their relative importance. Most diseases of this nature probably act as secondary factors leading to death in individuals in poor condition with weakened resistance. Young (pers. comm. in Sinclair 1970) found Trypanosome infections heaviest in animals of poor condition, as did Staak & Protz (Sinclair 1970) for a bacterial infection among young buffalo; in both cases the infection was

widespread and only became pathogenic when body condition was poor.

Malnutrition.

Hirst (1969) found that malnutrition was a major cause of mortality in several species of ungulates in South Africa. It seems probable that in the Serengeti malnutrition is a major factor influencing mortality. Sinclair (1970) found that 93% of buffalo 10 years and older found dead had poor bone marrow condition (N=14) and all but one of these animals were found during the dry season. However, no adult animals under 10 years were found dead. Similarly in wildebeest, no young animals were found dead with poor bone marrow condition (N=16) although 88% of animals over 9 years found dead were in poor condition (N=8), all during the dry season. We might therefore conclude that for these species malnutrition is a factor which can cause mortality in old animals during the dry season.

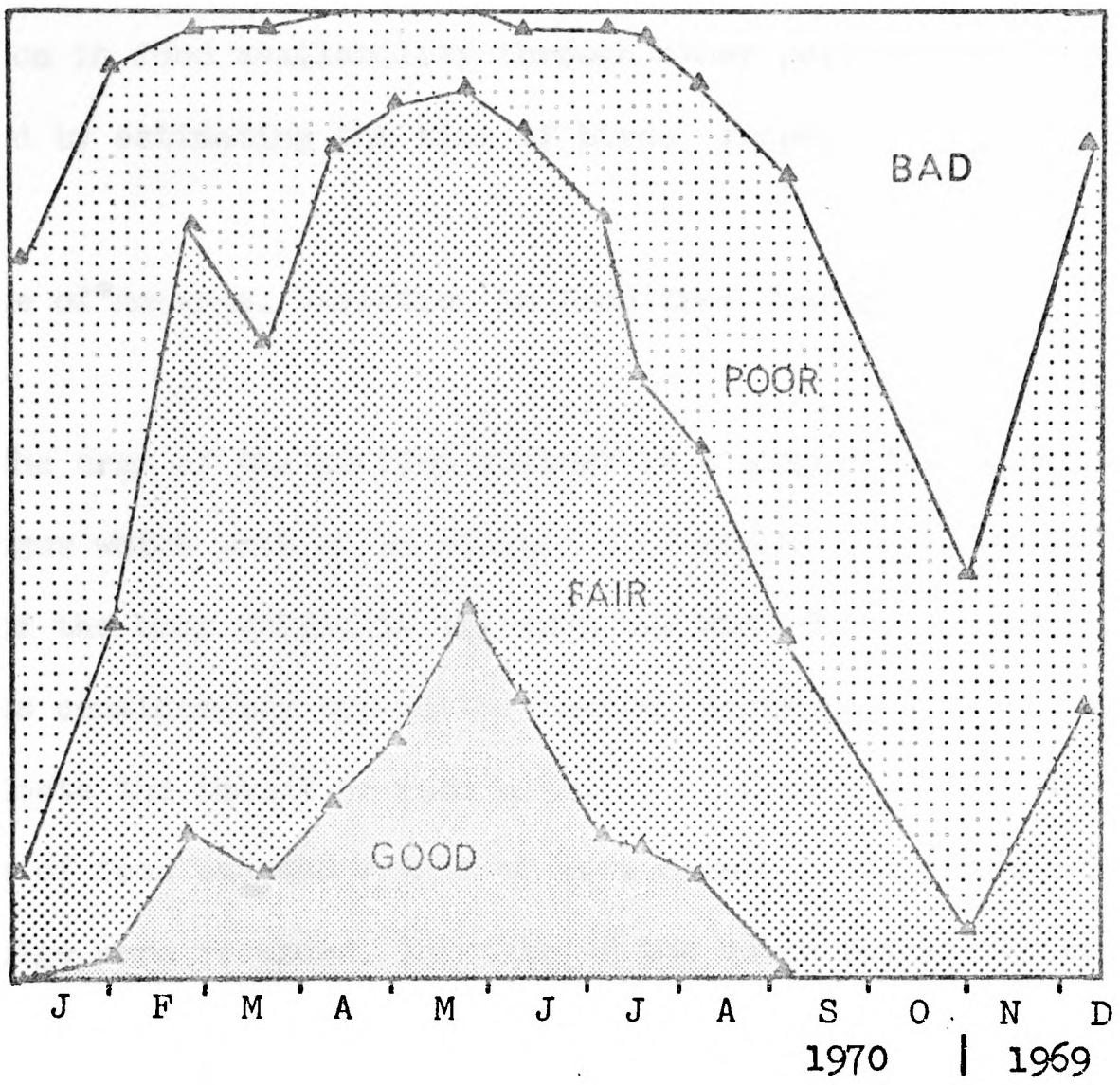
However, it is clear that all individuals are influenced by the varying quality of the grazing through the year. The protein content of grass varies through the year depending on rainfall (Field 1968). Sinclair (1970) showed that the protein content of the grass species eaten by buffalo declined during the dry season and for several months was considered below the level needed for maintainance requirements. Animals therefore presumably have to rely on body reserves during this period, and their general condition declines. Jarman (pers. comm) has made a subjective estimate of the body condition of a sample of female impala through the year, Fig 9 which shows a very clear seasonal fluctuation in body condition of all individuals and suggests a greater susceptibility to starvation or enzootic disease during the dry season.

We can therefore conclude that the major mortality agent among game

Figure 9

BODY CONDITION OF FEMALE IMPALA

Mean Sample Size 101





MONTHLY RAINFALL - SERONERA

herds was a combination of malnutrition and enzootic disease, which probably shows a strong seasonal fluctuation. Observations have not been made over the period from September to December and so the relative importance of the dry season period is unknown. However, the presence of considerable variation in food availability through other periods in the year has been recorded by estimating the size of birds' crops.

Estimate of Seasonal Variation in Food from Crop Size.

The crop of the griffon vulture is a simple diverticulum of the oesophagus which acts as an elastic food store. Birds can hold about 1/5th of the body weight in the crop and when fully bloated the crop wall projects considerably beyond the contour feathers, and this can be used to estimate the amount of food eaten. Captive birds were fed weighed amounts of food and the weight of meat necessary to produce varying sizes of crop bulge were recorded, the size of the bulge being compared to the size of the bird's head to measure size. The state of the crop of birds roosting in the afternoon could therefore be used to give an indication of the amount of food that the bird had been able to find during the day. The rate of food digestion is slow (about 24 hours to pass a crop full of food into the digestive tract in the whiteback vulture). Some food will be passed from the crop into the stomach after feeding and before observations were made, but all birds were recorded in the late afternoon after 1600 hours and so although some food will have been digested, this will presumably be constant through the year. The actual weight of food recorded may not therefore be accurately represented, but the fluctuations should show the true general trend.

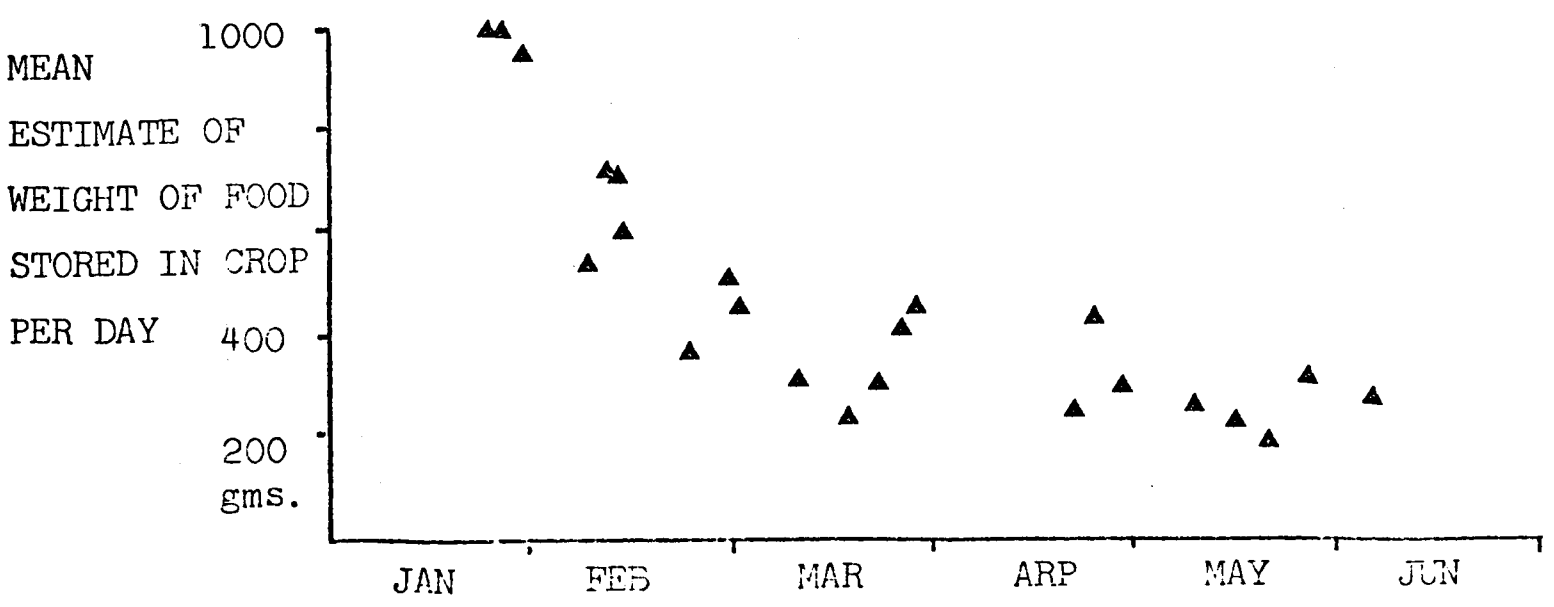
During the wet season the herds are on the open plains where there are relatively few trees suitable for roosting during the night. Isolated



Ruppell's griffon vulture with crop containing 1,000 gms of meat.

wooded areas such as Naabi Hill are therefore used by large numbers of birds from the surrounding plains. By recording the crop size of birds roosting in this area it is possible to observe a large and presumably representative sample of birds. However, in woodland areas it is difficult to obtain a representative sample. Birds can roost anywhere and if a group of birds is encountered it is probably due to a local source of food from which the birds have been recently feeding. Birds which have not fed that day are more likely to be roosting alone and less likely to be noticed. Since the important period at the end of the dry season has not been observed, Fig 10 can only be used to demonstrate that fluctuations in food availability do occur. Results are therefore shown only for birds observed on the open plains. During wildebeest calving in late January births are highly synchronised. There is considerable juvenile and adult mortality following birth and lactation. Food availability apparently declines rapidly after this to a considerably lower level, which corresponds to the period of optimum grazing conditions at this season.

Figure 10



Mean N. 31

Competition with Other Scavengers

Vultures are the only large animals which subsist entirely by scavenging. However, most predators are also opportunist scavengers, and therefore to some extent compete with vultures for their food supply. The amount of food scavenged by predators must therefore be considered.

In the Serengeti marabou stork, tawny and bateleur eagles, kite, ravens lion, hyaena and jackal are commonly or occasionally seen feeding from scavenged carcasses.

Bird Predators.

Tawny (Aquila rapax) and bateleur (Terathopius ecaudatus) eagles are resident woodland species, the two commonest eagles in the Serengeti, and both frequently feed from carcasses. During the rainy season in small numbers they move onto the open plains among the wildebeest herds. Although carrion is probably an important food for both eagle species, neither are abundant enough, compared to the griffon vultures, to compete to any important extent. Both species are often ignored by griffon vultures and they will usually feed off an isolated bone near the carcass. They usually depart if a large group of vultures starts to gather. The black kite (Milvus migrans) is an invasive species in the Serengeti which is predominently an insect feeder, and is only occasionally found at carcasses. The only bird which regularly associates with vultures at feeding parties is the Marabou stork (Leptoptilos crumeniferus).

Marabou are present in small numbers throughout the Serengeti region. This is a species which has benefited greatly from village settlements and large groups of birds are found near any rubbish tip or abattoir. Away

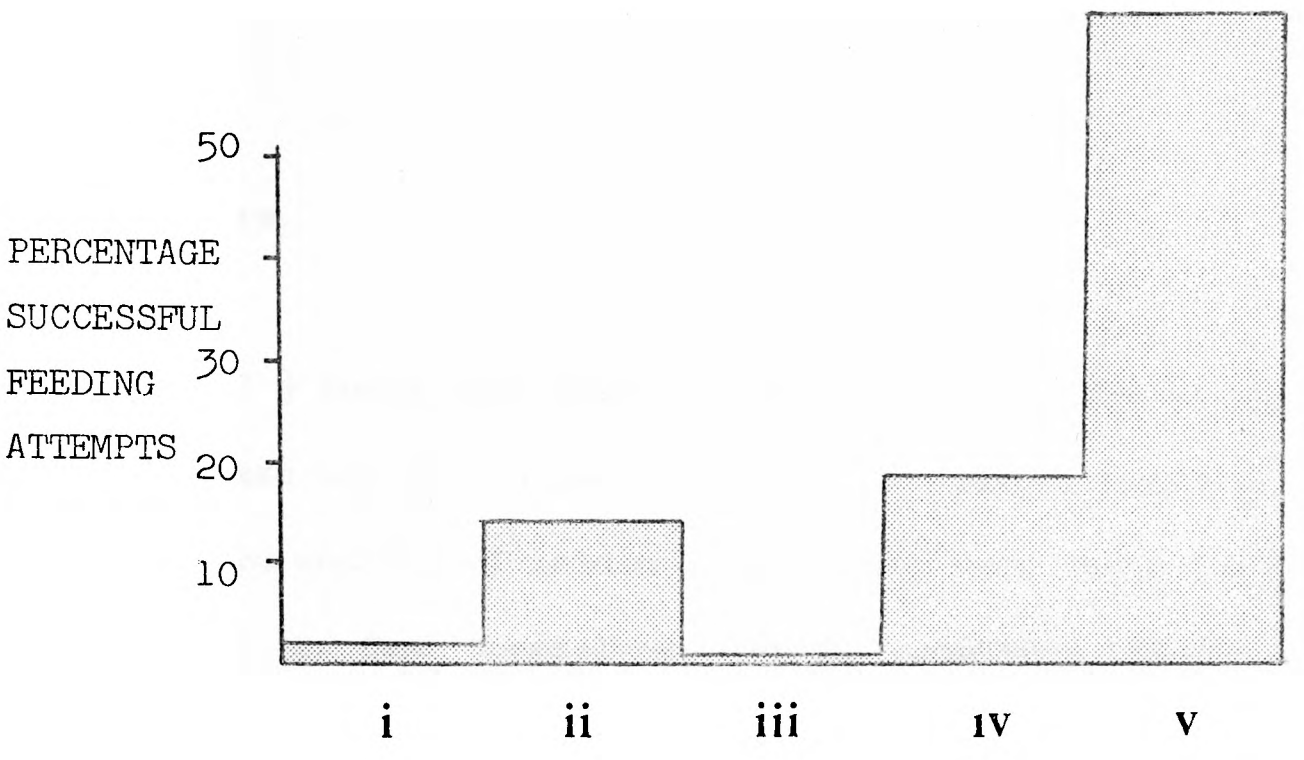
from man made sources of food they associate with vultures at carcasses and catch fish and frogs. There are few breeding sites in East Africa and there is no regular breeding in the Serengeti. Probably birds must supply fish and frogs regularly to give a calcium rich diet to the growing young, and this is not possible in areas like the Serengeti where the majority of birds feed from carcasses or out of old tin cans and where their diet is nutritionally meagre.

Birds associated with the village refuse tip are probably resident. Their numbers do not fluctuate through the year, and two recognisable individuals have been seen there, both for over six months. There is also a population of 'wild' marabou who associate with vultures at carcasses. The bill of the marabou is deep, broad and long, enabling the bird to swallow large bones, which are presumably later regurgitated, and also to make robbing attacks on vultures. The bill cannot tear meat, and this must be done by griffon vultures or predators before the bird can feed. In Fig 11 the feeding behaviour of marabou has been recorded, each score being made when the method led to the successful swallowing of an item of food. Observations were made at the site of a cropping camp and the food contained many isolated bones, and a lower proportion of swallowed bones would be recorded under normal conditions.

Marabou therefore obtain food at carcasses by robbing griffon vultures or picking up pieces of meat and bone which have been detached from the carcass by vultures or other scavengers. However, there are few marabou feeding in this way in the Serengeti. 60 marabou were marked with plastic leg rings, mostly at the site of a game cropping scheme at Soit Aye on the eastern border of the park which had attracted over 200 birds, presumably mostly from surrounding villages to which they later returned. Only 9 individuals were seen in the Serengeti, but it seems probable that these

Marabou Stork Feeding

Figure 11



i Tearing off soft tissue from carcass.

ii Picking up pieces of soft tissue left lying near carcass by griffon vultures.

iii Pecking at meat attached to bone.

iv Swallowing piece of bone.

v Attacking griffon vulture and stealing food.

birds search in the same way as griffon vultures in areas of high game density. It seems unlikely if more than 400 birds feed in this way in the Serengeti. Kahl (1966) considered an adult marabou required 500gms of meat per day, and the Serengeti marabou population may take perhaps only 72,000 kilo of meat per year.

Mammalian predators.

Wyman (1967) found that young Thomson's gazelle form an important part of black backed and golden jackal's diets. From January to April, 82% of black backed and 81% of golden jackal which were found feeding on young gazelle had killed the fawn themselves, and the remaining 18% and 17% of carcasses were scavenged from other predators. Over the year, Wyman found that the faeces consisted of only about 3% wildebeest and zebra remains and although such a figure is meaningless for evaluating food intake, it is probable that both species take predominently insects, small mammals and young fawns, and scavenging is limited and chiefly confined to predator kills (Grafton 1965).

Kruuk (1970) found that out of 919 parties of hyaenas observed feeding on the Serengeti plains, 53% of prey had been killed by hunting, 25% from scavenging dead animals and 22% carcasses were of unknown origin. These observations based on plains conditions probably do not apply in woodland where scavenging is more difficult. However, hyaena obtain an important proportion of their food during at least part of the year from scavenging dead animals.

Lion will also feed from any dead carcasses which they find, although this is also probably only important for those animals feeding in plains conditions with good visibility. Schaller (pers. comm.) found that

overall the meat scavenged from carcasses probably provided about 8% of the lion's food. 42% of their scavenged carcasses came from hyaena kills, the remainder from non predatory causes of morality.

Both of these species respond rapidly to the activity of vultures and watch their movements closely, running to any area where birds are seen to be descending. Few carcasses were watched until all food had been eaten, but on the open plains during the wet season in 1970, 11% of isolated carcasses identified as having died from some cause other than predation and which were initially located by vultures were later scavenged by lion and 7% were scavenged by hyaena before birds had finsihed feeding (N = 38). These predators will drive vultures away and take over the carcass, often before birds have been able to effectively break through much of the skin.

Of the other large mammalian predators, leopard stalk small antelope and do not normally scavenge (Kruuk & Turner 1967). Wild dog are uncommon and principally predators. Schaller (Schaller & Lowther 1969) observed 135 feeding packs and in 95% of occasions the prey had been killed by the pack, 5% scavenged off hyaena. Cheetah are also principally predators and have not been recorded scavenging (Schaller 1968).

Of the mammalian scavengers therefore only hyaena and lion regularly scavenge and both obtained a significant proportion of their food by following the activities of vultures and scavenging the carcasses they locate. However, although a large proportion of the hyaena population feed on the plains during the wet season, only about 20% of the lions take advantage of these conditions and most remain in woodland territories throughout the year (Schaller pers.comm.) Scavenging is probably less frequent in woodland conditions when herds are widely dispersed and visibility is poor. However, if we assume that these figures apply throughout the year we can

make a tentative estimate of the proportion of food taken by these predators, and from the estimates given earlier, 5% of the lion food supply might be represented by 263,000 kilo per year and 30% of hyaena supply by 986,000 kilo. The total quantity of food scavenged by predators may therefore represent perhaps 5% of the total quantity available to scavenging animals.

Competition between Predators and Vultures.

Because of extensive mortality from causes other than predation in the Serengeti, griffon vultures obtain only a small proportion of their food supply from predators. However, this does not imply that there is no competition for food between predators and vultures, or that vultures do not interefere with the feeding of predators. To the predator involved, the removal of any potential food by the large vulture population must be important. The significance of this will vary. Cheetah do not scavenge carcasses, but being a solitary hunter often in open plains conditions they cannot conceal their prey, or eat all the available food immediately after killing. The parts of their prey which are uneaten, usually about 25% of the potential food, are normally taken rapidly by griffon vultures thus preventing the animal from the opportunity of returning later. The cheetah is probably the predator which is most influenced by the activities of vultures.

As mentioned earlier, leopards, wild dogs and hyaenas do not usually have much of their prey taken by vultures.

Lion may be deprived of a part of their kill when the prey is left

unguarded. Being relatively slow feeders, they probably lose important amounts of food to vultures. Food shortage is the major cause of mortality among lion (Schaller pers. comm.)

Since both hyaena and lion scavenge carcasses, these predators and vultures are directly competing for the same food supply. In addition, the feeding behaviour of all predators is clearly designed to prevent the removal of food by vultures or other scavengers. Just as predation has caused a selective pressure in the evolution of ungulate behaviour, so the activities of vultures have clearly influenced the development of the behaviour of all predator species to minimise direct competition over the food from their prey. This indicates that there may be a strong degree of competition between predators and vultures and it is due to this competition that both can exist in the same area only by utilising basically different sources of food.

Due to the competition between predators and vultures, a large population of scavenging birds can probably be supported only in areas where there is a considerable mortality from causes other than predation, which, because of wide fluctuations in distribution or seasonal variation, the resident mammalian scavengers cannot exploit. This is the food supply that vultures can utilise far more efficiently than any mammalian scavenger. A bird has great mobility, and using gliding flight it can cover large distances rapidly with little energy expenditure. An avian scavenger also can search over large areas very efficiently from the air, while a mammal has to rely on a limited range of vision on the ground and probably depends more on the sense of smell. These advantages have enabled some birds to develop into exclusively scavenging feeders, able to utilise large areas for food searching, whereas there is no large mammal that is known to exist only be scavenging.

In competition with predators at their kills, birds will never be able to obtain large enough amounts of food to form an important food supply. In conditions where predation forms a high proportion of the total mortality there will be strong direct competition between the predators and scavengers; both for food from predator kills and also for food from any carcasses dying from other causes, which will be more frequently found by predators since the density of predators will be high and that of vultures low. It is doubtful in these conditions if many exclusively scavenging birds would be able to survive. In Ngorongoro Crater predation by hyaena could account for a high proportion of wildebeest, and probable other ungulate, mortality (Kruuk 1970), and in these conditions griffon vultures are comparatively scarse. The notable absense of any griffon type vulture from the plains of the North American continent might suggest that mammalian predators were responsible for a large part of the mortality of the plains game there.

The rainfall in the Serengeti region allows for a population of resident game species in woodland areas only, but migratory species have the advantage of being able to utilise the abundant grazing conditions on the eastern plains, which are available for only a limited period. During the study period about 83% of animals in the area were of migratory species. However, most predators are territorial or resident. Only about 20% of the lion population follow the wildebeest out onto the plains (Schaller pers. comm) and although hyaena can travel up to 100 km to reach food (Kruuk 1970) they cannot follow the herds through their migration. Predator density is therefore determined by the resident game population. In areas such as Ngorongoro Crater which supports a high density of resident game, the proportion of predators to herbivores is considerably higher than in the Serengeti and predation may be an important mortality factor. (Kruuk'70) However, in the Serengeti the number of predators resident in any area is determined by the maximum number which can be supported by the relatively

small resident game population. When a large migratory herd enters an area of woodland, the resident population of predators is completely swamped by the influx. Predators therefore probably have considerably less effect on the overall mortality of migratory species compared to that of the resident ungulates, and other causes of mortality are far more important here. Also, because of the size of the migratory herds, predators are physically incapable of scavenging all the food which occurs through the various causes of mortality, and the scavenging ability of the predators is also swamped. In these conditions, mammalian predators cannot reach a level where they become a major mortality factor on migratory species, or build up to the point where they can utilise all the carcasses available to scavengers from other causes of mortality among these migratory herds. It is in these conditions that scavenging birds can exist in large numbers because the great fluctuations in distribution and availability of their particular food source prevents effective competitions from predators.

The effect of the fluctuations in food availability on the bird's activities will be considered in Section 111. The effect of the variation in distribution of food through the year is now considered by examining the distribution, movements, food searching and food utilisation of the birds.

Species Distribution

The two griffon species.differ in their distribution in the Serengeti. Whiteback vultures are found throughout the park in all seasons, although they concentrate heavily over migratory game concentrations. Ruppell's griffon vultures however, are localised in their distribution and only occur near to large game herds.

Number of Ruppell's griffon per 100 whiteback vultures
Observations at feeding parties.

Within 10 miles of migratory game concentration	28.5	(N = 7,730)
30 miles or greater distance from game conc.	4.4	(N = 1,344)

The whiteback is typically a bird of lowland savanna and is found throughout the Serengeti region. The larger Ruppell's griffon, however, is predominently a highland bird not typically found in lowland savanna. In the Serengeti it is uncommon away from the large game concentrations and the population almost entirely exploits the wildebeest and zebra herds for food.

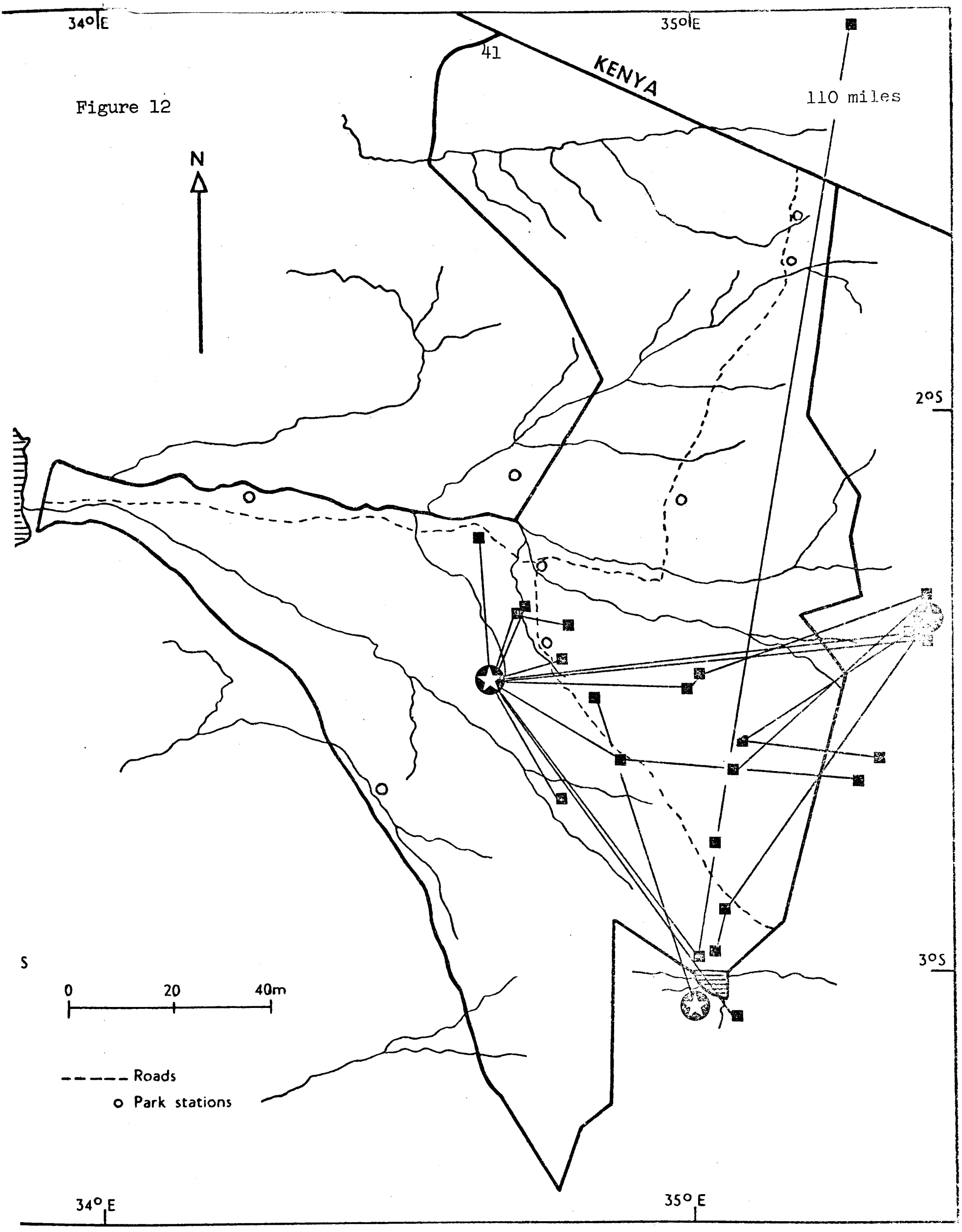
Movements.

Both whiteback and Ruppell's griffon vultures cover large distances in their search for game animals. 153 whiteback vultures and 9 Ruppell's griffon vultures were captured, mostly with a cannon net fired over bait, and marked by P.V.C. plastic rings with an engraved number so that the bird could be identified later without recapture. 22 resightings have been made of 13 individuals. If there had been an equal probability of each marked bird being resighted, then after 22 resightings, 21 individuals should have been seen. The number of individuals actually recorded is therefore significantly less than expected (X^2, $p = 0.05$) and this would suggest that either there was a heavy mortality of birds following ringing, or that birds lost their rings, or that many birds left the area. The P.V.C. rings were securely bonded around the bird's leg by a solvent plastic cement. Captive birds fitted with these rings did not attempt to remove them, and the rings remained in good condition. It is considered unlikely that rings were lost or that there was large scale mortality following ringing. It is very probable that birds regularly travel large distances and a large

proportion of marked birds later moved into areas away from the Serengeti.

The distances moved by marked birds are shown in Fig 12. Only one bird was resighted outside the park boundaries, to the north at Maji Moto. This, an adult whiteback, had been seen only six days previously in the south of the park at Lake Lagarja, 110 miles away. There was abundant food in the area and the breeding season had not yet started. Long distance movements of this kind are probably normal during food searching. Pennycuick (in press), using a glider, has recorded an average speed of 30 miles per hour for a Ruppell's griffon in straight flight for a distance of over 40 miles. Large distances can be therefore covered relatively quickly. Recoveries of ringed birds away from the park area are unlikely to be reported and there is therefore no information on the extent to which birds range over areas outside the park. However, in Fig 13 the ringing recoveries for Gyps coprotheres are shown. These birds cover considerable distances, the recovery sites probably reflecting the distribution of Europeans over the bird's range. This species is the ecological equivalent of the Ruppell's griffon in South Africa and it habits are apparently very similar. The breeding colony of the Ruppell's griffons in the Gol mountains is the largest known in East Africa and it seems probable that this species will also be found to travel large distances away from the breeding area. Both species of griffon vulture therefore probable cover large distances during their search for food.

Figure 12



Movements of marked whiteback vultures.

★ Site of Marking

■ Area of re-sighting.

Gyps coprotheres

Distribution of ringing recoveries

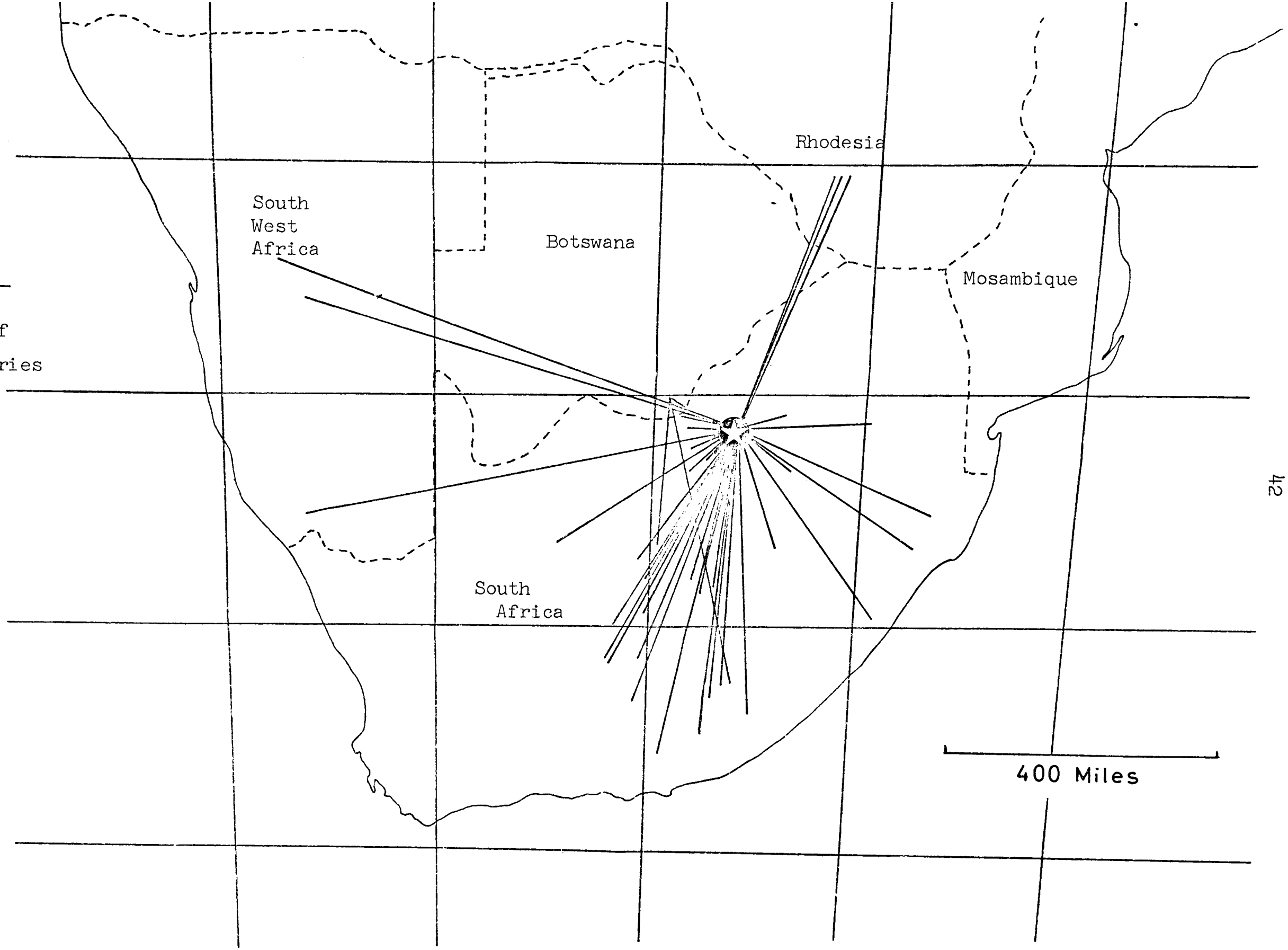


Figure 13

Food Searching

The ability of griffon vultures to locate isolated carcasses and rapidly gather in large numbers where previously they had apparently been scarse has caused various writers to suspect acute vision, smell, telepathy or divine guidance. Following the charge of the light brigade in the Crimean war so many birds gathered on the battlefields that shooting squads had to be sent out to protect the injured (Meintzhagen 1959). Tristram (1867) correctly described the birds method of food searching.

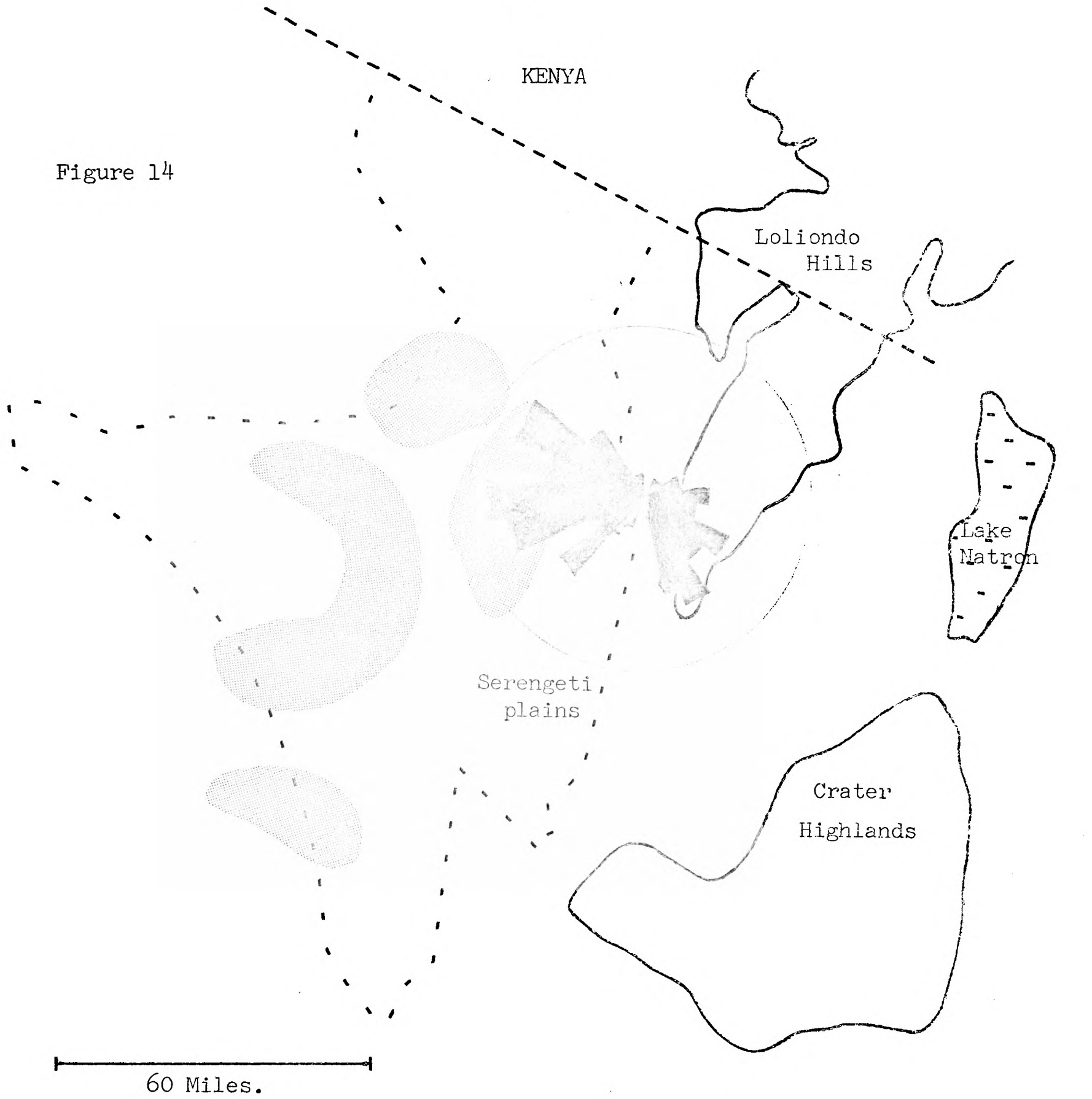
" These birds detect their food by sight, not by scent. --- The process is probably this. The griffon vulture who first detects the quarry, descends from his elevation at once. Another, sweeping the horizon at a still greater distance observes his neighbours movements and follows his course. -- He is traced by another and thus a perpetual succession is kept up so long as a morsel of flesh remains over which to consort."

In the Serengeti griffon vultures do not use the sense of smell to locate carcasses. On four occasions parts of carcasses have been placed inside perforated cardboard boxes and hauled into trees and left for five days. At the same time a similar uncovered bait was placed in a tree within one mile of the covered meat. The area had a large resident whiteback and hooded vulture population. On all occasions the uncovered food was located and eaten within the first day, although the covered food was not examined or located. After several days the smell emmited from the cardboard boxes was sufficient to attract groups of hyaena to the tree during the night. After the covering was removed from one box the food was located and eaten within one day. It would appear that, unlike some new world vultures (Cathartes aura Stager 1964), the old world vultures may not use smell to locate food. Bang (pers comm) has measured the ratio of the length of the olfactory lobe of the brain to the total hemisphere length for the whiteback 14.0 and Ruppell's griffon, 16.6. Compared to that of the new world

turkey vulture, 28.7, the olfactory lobe is small.

Food is therefore probably located entirely by vision. Griffon vultures rely on gliding flight during food searching and cannot sustain flapping flight for long periods. They can normally search over open plains by relying on thermal upcurrents of rising warm air for gaining altitude, then gliding off, slowly losing height, until they contact another thermal. Rising air on the windward side of cliffs and hills is also used for gaining height, and these are the only methods available in heavy cloud conditions, or early in the morning before there is sufficient heat to generate thermals. Both griffon species are apparently similar in their searching behaviour and cover large areas (Pennycuick in press). Once food is sighted the birds flight path changes from a wandering, slow searching flight into a direct dive towards the food. This direct flight is conspicuous and, if it persists, attracts other birds although they themselves cannot see the food. This development may be extensive. In Fig 14 the pattern of arrival to a large supply of food in an area of only moderate game density is shown. Observations were made using 5 complete zebra carcasses, plus carcasses from seven other animals. Observations were made at a game cropping camp following a period of several weeks inactivity and there were therefore no resident birds in the area dependent on a regular supply of food. The pattern of arrival of 150 birds within one hour of the food being uncovered is shown. A large proportion of birds arrive from the west and south east (compared to even distribution X^2 p = less than .001) which corresponds to the location of the nearest of the game concentrations and the breeding colonies of the Ruppell's griffon vultures in the Gol mountains. The preferences in the direction of arrival therefore reflect the pattern of bird density in the surrounding areas and birds were probably being drawn from at least 20 miles away.

Figure 14



DIRECTION OF ARRIVAL OF GRIEFON VULTURES TO BAIT AT SOIT AYE

Distribution of wildebeest and zebra herds (Skoog pers. comm)

Length of line indicates number of birds arriving from compass bearing.

The pattern of arrival in Fig 15 shows that although birds continue to land at a steady rate during the hour, the number circling overhead rises to a maximum and then starts to decline. The attraction of birds towards a source of food presumably starts to decline when birds that are arriving can see that, for the amount of food available, there are too many birds already present to justify landing. Once this stage is reached and birds begin to pass over the area and continue to search moving away from the food source, the attraction to other birds will disappear. Hence the number of griffon vulures that are attracted to a carcass roughly depends on the amount of food that is available. This is shown in Fig 16 where the maximum number of birds present at any one time at a feeding party on the ground is plotted against the estimated weight of food available (from Ledger 1968). More individual birds will feed from the carcass than shown here since birds are usually arriving and leaving during feeding. There are many other factors which will affect the number of birds that arrive at a carcass, particularly the alternative availability of food locally. If food is abundantly available, relatively few birds will be present at a large number of carcasses, however, if food is scarse then large numbers will gather at each source of food. To eliminate these effects due to changing food conditions, all the observations plotted have been made within three weeks of each other on the Serengeti plains during the wet season.

This method of food searching is not possible in heavy cloud conditions during the rainy season when thermals are not produced. Birds can then only search by short distance flapping flight, which can only be sustained by the whiteback, or by relying on the rising air over hill ranges. Fig 17 shows arrival records for birds coming to bait at one location in both clear weather conditions when birds can search by thermal soaring, and in heavy overcast conditions when only hill lift soaring

Figure 15

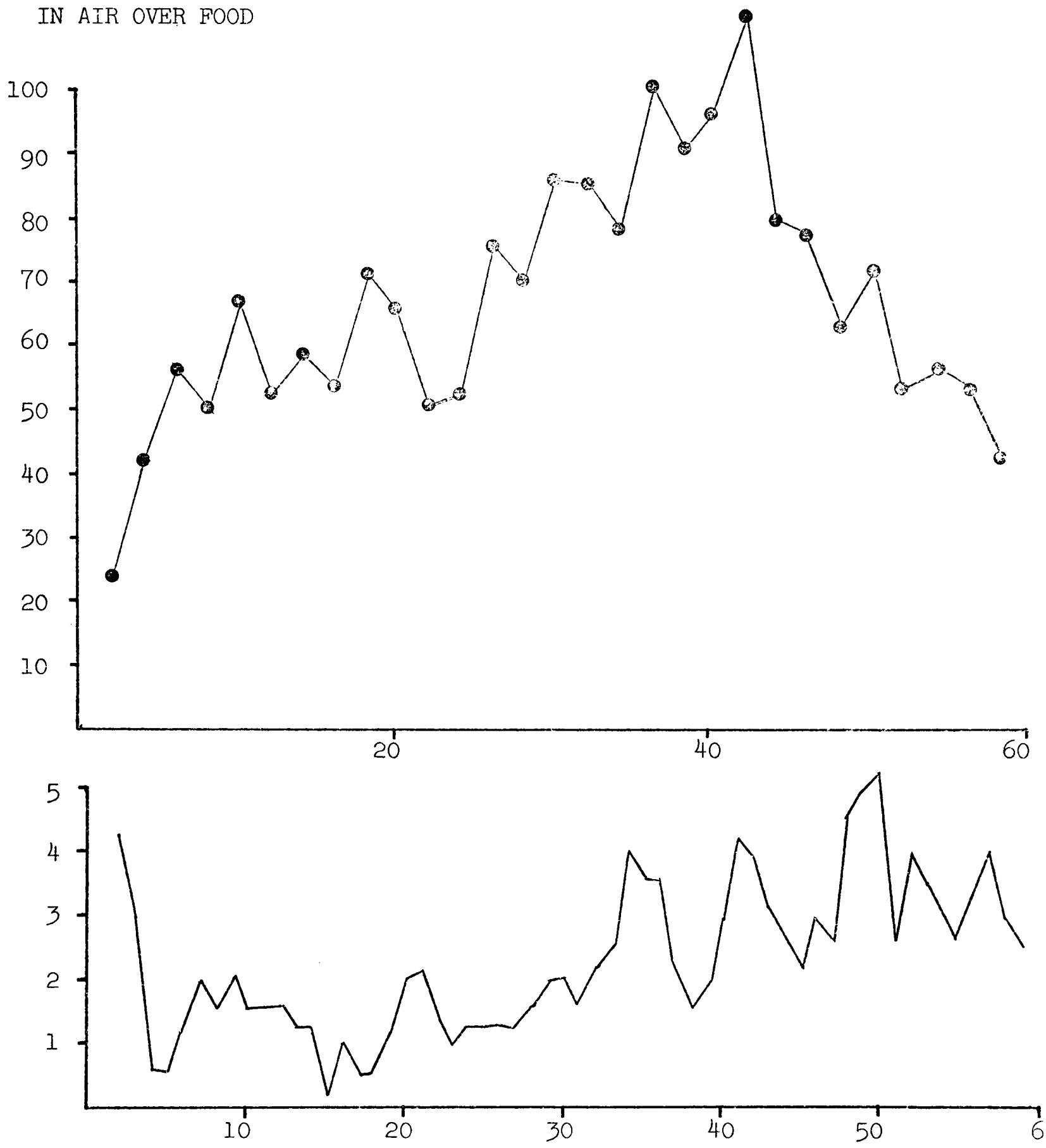
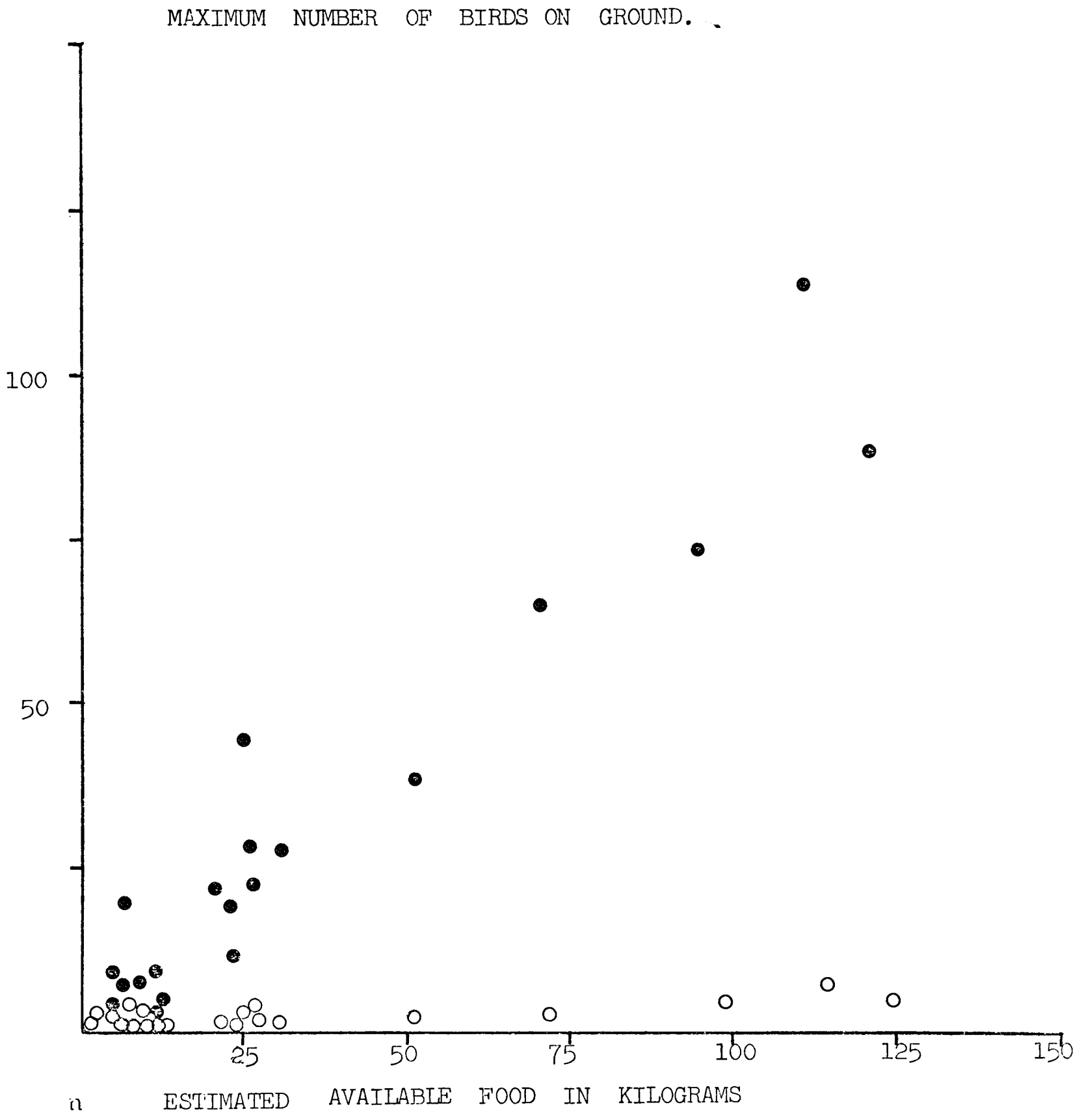

NUMBER OF BIRDS
IN AIR OVER FOOD
100
90
80
70
60
50
40
30
20
10
20
40
60
5
4
3
2
1
10
20
30
40
50
60
NUMBER OF BIRDS
LANDING ON GROUND
TIME IN MINUTES

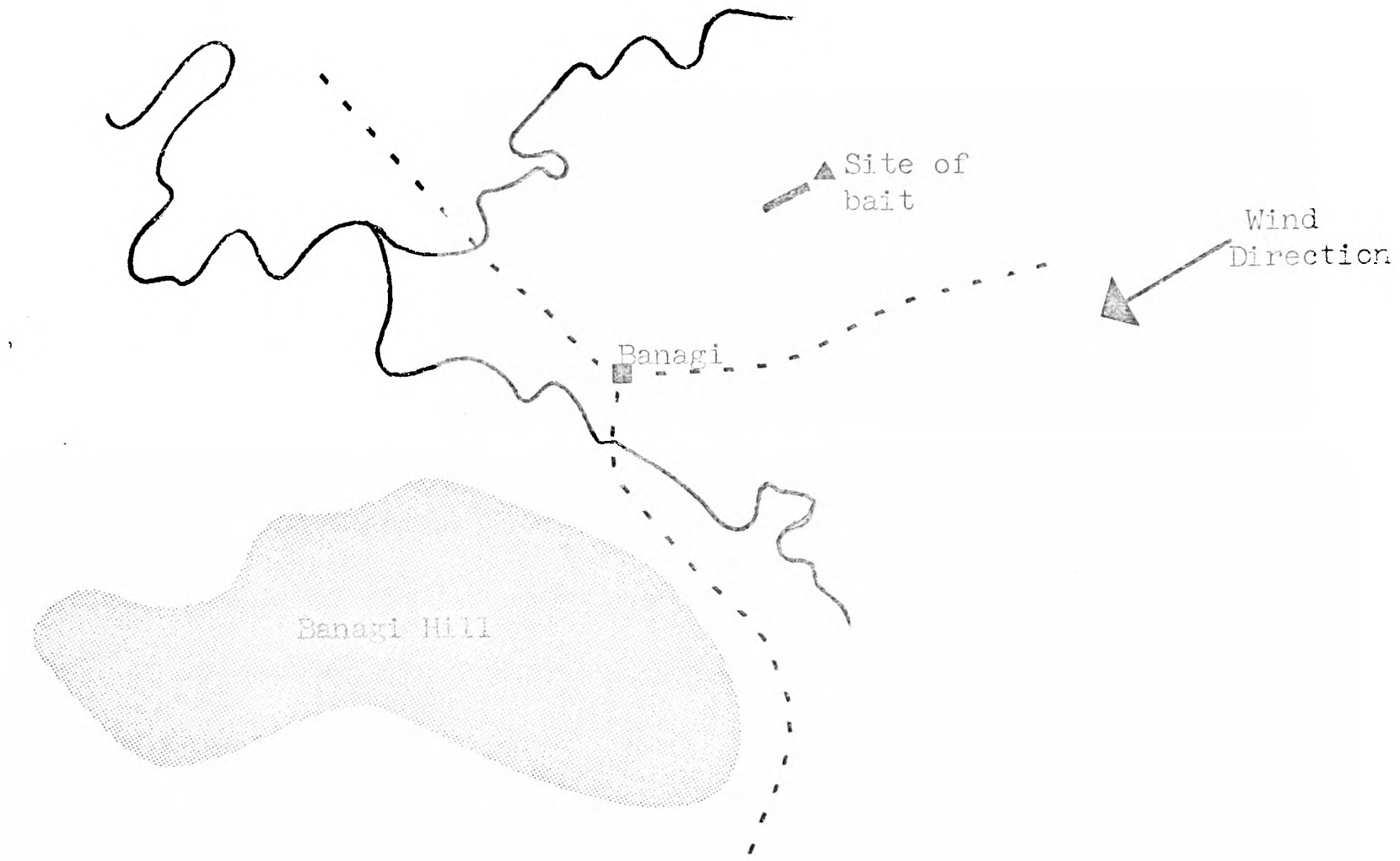
Figure 16



● Whiteback vulture Gyps africanus

○ Lappet - faced vulture Torgos tracheliotus

Figure 17



Heavy Overcast
Wind to West

Weather Conditions

Clear Sky
Wind to West

(p = less than .001 Kolmogorov Smirnov test)

soaring can be used. In clear weather conditions birds are evenly distributed throughout the area and arrive to bait from all directions. However, in overcast conditions birds cannot search so effectively and are forced to stay in the area of hill lift to the south west, and all birds arrive from this direction. During overcast conditions therefore, food may be difficult to obtain since searching is restricted to areas near hill ranges or within range of short flapping flight. This must particularly affect breeding birds which have to commute long distances between nest site and feeding areas, as well as search for carcasses. However, it is unusual for such heavy cloud conditions to persist for more than a few days at a time.

Searching Density

For both species, the density of searching birds in any area depends on the concentrations of game species in that region. This variation in density has been indicated from observations made on the number of birds entering a cone of sky of 60° diameter above the observers head during a two minute period. Counts were made by erecting a wire hoop at a known distance above the ground such that when the observer was lying below, a cone of 60° diameter was observed within the wire. All observations were made between 11.00 and 14.00 hours in clear weather conditions at regular intervals one mile apart. Except for the centre of the wildebeest concentration, observations were made on at least three separate days at each location.

Conditions	Average number of birds entering 60° cone of sky per two minute period	N
Main wildebeest concentration prior to migration - long grass plains, Moru. May 1970 500,000 + animals.	8.06	18
Short grass plains wet season, Gol kopjes Herd of 100,000 + wildebeest	1.43	45
Short grass plains wet season, Gol kopjes Large gazelle and zebra concentration.	1.13	97
Short grass plains dry season, Gol kopjes Virtually no game species in region	0.00	45
Northern woodlands, dry season. Resident game only in area.	0.11	57
Northern woodlands dry season. Wildebeest and zebra herds in area, well scattered.	0.32	45
Northern woodlands wet season. Resident species only.	0.12	52

Both griffon species are considered together here because at high

altitudes they cannot be confidently distinguished. However, it was shown earlier that away from migratory concentrations of animals, Ruppell's griffons are rare and it is only whitebacks that are normally found in these areas. These figures indicate only the comparative density of individuals in the air and take no account of birds feeding or resting on the ground. However, there is a clear preference for birds to occur in areas containing large concentrations of animals. The variations in searching density of birds may be important in utilising food. Carcasses were taken experimentally into areas and the arrival of the first bird timed, and also the mean interval between the arrival of subsequent birds.

Arrival times to carcasses

Bait either Thomson's gazelle or dressed impala carcass or dressed zebra.

	Mean time to arrival of first bird	Number arriving per minute	Number of carcasses (separate occasions)	Total Number of birds
Wildebeest concentrations, wet season, plains.	3.0	1.93	5	172
Early dry season, Soit Aye scattered zebra and gazelle groups in region	5.4	2.01	5	282
Woodlands, Banagi, wet season, resident game only in area	23.4	0.43	5	85
Dry season plains, Gol. Virtually no game in area.	76.7	0.08	3	25

In areas of moderate to high game density, the density of searching birds is high and carcasses are located relatively rapidly, and once one bird has located a carcass, subsequent birds arrive rapidly by following the movements of their neighbours. However, in areas containing almost no game animals birds are rarely seen searching and carcasses can take a long time to be located. The density of searching birds is low and few birds are led to

the area.

The height at which birds search also varies according to conditions. The height of searching birds was estimated from the percentage of the field occupied by the bird's image in a pair of 8X30 Dialyt binoculars. The glasses were initially calibrated by calculating the width of the field, and also by suspending a life size silhouette of a vulture from the top of a large rock and observing this from known distances away.

Estimates of height of searching birds

% of binocular field covered by silhouette		
	0 - 500 ft.	- 12%
	500 - 1,000	12% - 6%
	1,000 - 3,000	6% - 2%
	3,000 +	2% -

Proportion of birds observed at altidudes

	0 - 500	500-1,000	1,000-3000	3,000 +	N
Main wildebeest concentration prior to migration. Moru.	54%	46%	.6%	-	501
Plains wet season. zebra & gazelle concentration.	14%	62%	23%	-	227
Woodland in wet season. Banagi. Resident game only	-	32%	45%	23%	53

In areas of low game density birds search at higher altitudes than in areas of game concentrations. In general, therefore, birds search at highest density in areas where food is likely to be found. An estimated 76% of the food available in the Serengeti region came from migratory species and birds heavily concentrate their searching over these migratory game herds.

Utilisation of Food

It is difficult to asses to what extent the food supply is fully utilised by scavengers. During the study period it was rare to find a carcass which had not already been located by vultures. Animals which die in thick cover, which is relatively sparse in the Serengeti, cannot be seen from the air, and many woodland species retire to thick cover when sick. However, hyaena and lion locate these carcasses and vultures will sometimes enter dense bush thickets to feed, presumably having located the food from the activities of predators. The density of birds in the Serengeti is high, producing good searching efficiency. During the study period it seems probable that almost all carcasses were located and utilised. However, if any food abundance were highly peaked in occurence it may 'swamp' both the predator and scavenger populations and part of the food would go uneaten. Due to the highly synchronised birth of wildebeest, there was one brief period at the peak of calving when there was an excess of food and all predators and vultures were fully gorged and uneaten food was still available. However, this situation only lasted for about two days. Food might be similarly superabundant at the end of the dry season, but this period has not been covered by observations. This could occur if there were exceptionally heavy mortality at any one time. The nature of mortality in this season probably means that deaths are less likely to be peaked than at wildebeest calving and mortality is probably distributed over several months, perhaps making swamping of the scavenger populations less likely, although the overall food supply is probably considerably greater than at wildebeest calving.

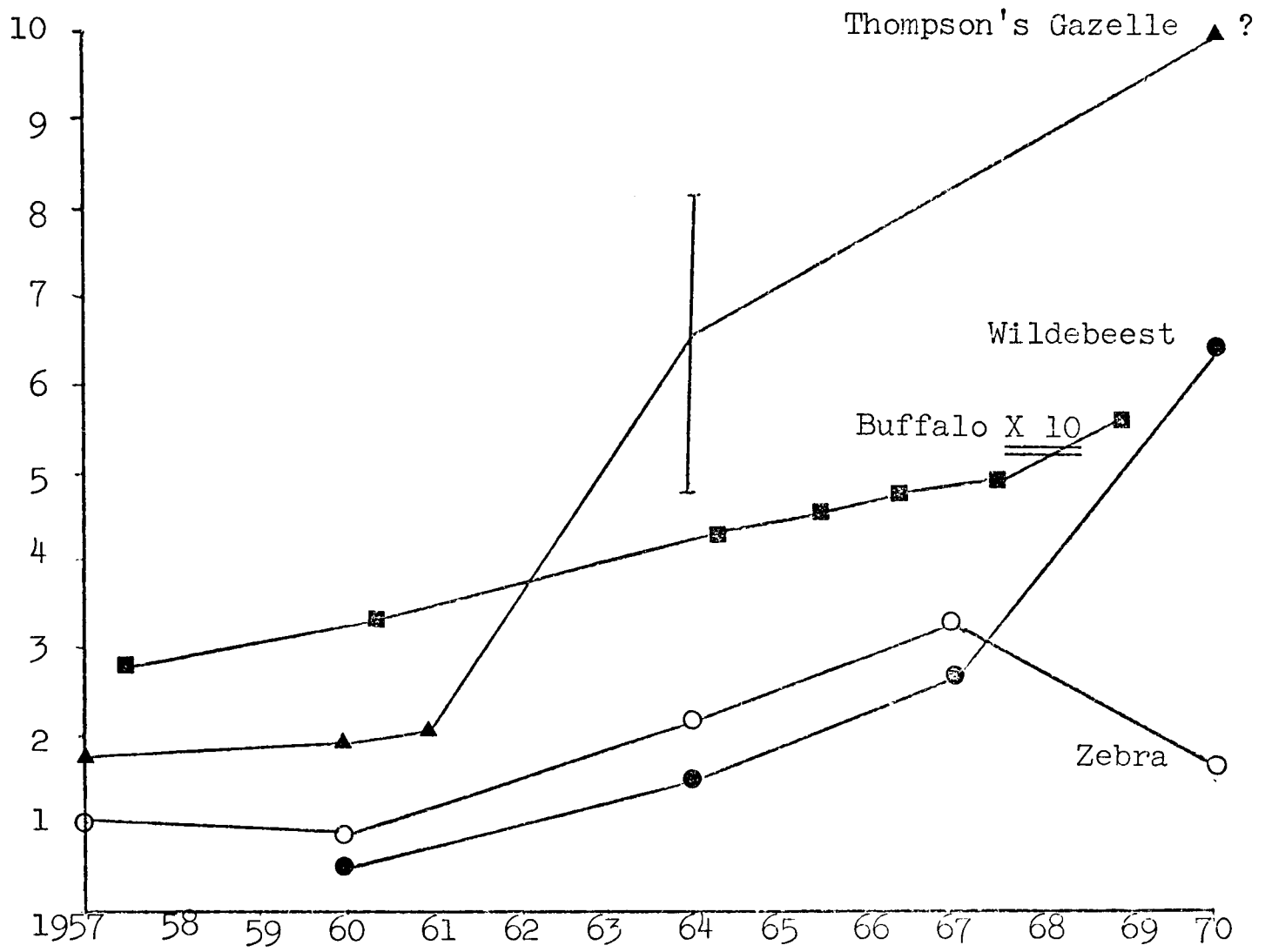
Earlier, a speculative estimate was made of the possible amount of food available per year for scavenging animals, and it is possible to consider

what population of vultures might be needed if this were to be fully utilised. Such a figure is chiefly made here for entertainment value and should not be considered as an estimate. The total amount of food that might be available to scavenging birds was considered to be of the order of 43 million kilo per year. If a griffon vulture is assumed to require about 400gms of meat per day, and if this food were uniformly spread through the year (which it is not), a maximum resident population of 290,000 birds could be supported. This figure will be considerably too large since there are known to be fluctuations in food availability. During those periods when food is abundant, the daily food intake of birds may be considerably in excess of their maintainance requirements (Fig 22) and this additional food is not necessarily used for fat storage since most birds are already carrying maximum fat stores at this time (Fig 50). Although an excess intake may be needed for building up calcium levels prior to breeding, the birds are taking in a considerably greater energy intake than is required. In addition there is probably considerable immigration and emmigration from the area during fluctuations in food availability. Bearing this in mind, the order of magnitude suggested by this exercise for the population size is not considered ridiculous, and it is reasonable to assume that the Serengeti and neighbouring regions support a population size sufficient to utilise fully the food available except during periods of exceptionaly heavy mortality.

As well as a seasonal variation in food availability, there is some evidence for changing conditions over the past decade. Fig 18 shows the results of censuses to estimate population sizes of some game species over the past twelve years. The refinements in census techniques mean that these estimates are of varying accuracy, but there seems little doubt that certain game populations in the Serengeti region have increased in size during

Estimated Population Size X 10^5

Figure 18



1957 Pearsall

1960 Grzimek & Grzimek

1961 Brooks

1964 Talbot & Stewart .

1967 Watson

Other population figures from Sinclair 1970, buffalo

1970 Norton-Griffiths pers.comm. wildebeest

Skoog pers comm. zebra

Bradley pers comm. Thomson's gazelle

the past ten years. The causes of such fluctuations in population size are still unknown, but over a time scale which exceeds the longevity of most game species, one effect must be an increase in the number of animals dying per year, although this increase will presumably not be proportional to the rate of population growth. The potential rate of increase of a griffon vulture population is slow because only one egg is laid and birds do not reach breeding age until at least six years (Appendix 1). It is therefore probable that food conditions for the vulture populations are at present relatively favourable.

From these various observations we can therefore conclude that griffon vultures obtain most of their food from carcasses of animals that die from causes of mortality other than predation. Due to the nature of these mortality factors there are considerable variations in the amount of food available through the year, and since most food comes from migratory species, there are also variations in distribution through the year. These prevent mammalian scavengers from utilising the food. However, vultures can cover large distances rapidly and concentrate their searching heavily in areas of large game concentrations. They can therefore follow the herds during their movements. The effect of fluctuations in the amount of food available through the year will now be considered by examining the food requirements of the birds.

Section 111

a) Food Requirements for Adult Birds

Energy Requirements

The basic energy requirements or standard metabolic rate of birds varies in a fixed manner according to body weight. For non passerines

$$\text{Log } M = \text{Log } 78.3 + 0.723 \text{ Log } W \pm 0.068$$ (Lasiewski & Dawson 1967)

However, studies of the food required by birds under normal cage conditions shows that the existence metabolism (energy of the food eaten minus energy lost in the faeces) is always well above the standard metabolism. Kendeigh (1970) made use of published information on the energy requirements in captivity of 18 species to correlate this existence metabolism with body weight, and found that for non passerines

$$\text{Log } M = - 0.2673 + 0.7545 \text{ Log } W \pm 0.063.$$

Therefore a whiteback vulture of average weight 5.4 kilo probably has a standard metabolic rate of about 265 kcals / day, although the existence metabolism is probably about 354 kcals / day.

Depending upon the conditions, the energy available to the bird for metabolism amounts to about 70 to 90% of the total energy intake in the food (King & Farner 1961), and a whiteback vulture might therefore be expected to require a daily energy intake of about 400 to 500 Kcals. For the Ruppell's griffon vulture of average weight 7.2 kilo, the existance metabolism would be expected to be about 440 kcals / day (standard metabolic rate 326 kcals / day), and the daily energy intake from about 490 to 630 kcals / day.

The actual energy intake of captive griffon vultures was investigated. One whiteback and three Ruppell's griffon vultures were used. These

birds were all over one year old and had been hand reared. Birds were caged together in an outdoor aviary which was not large enough to allow much exercise beyond short hop-flights between branches. Birds were fed on pure muscle tissue,which was stored in a deep freeze, with an occasional multivitamin and mineral supplement. During feeding trials each bird was hand fed each day and given a weighed amount of food. Birds were weighed when their crops were empty before and after the period of feeding. Weight changes over a period of feeding.

Species	Weight Before	Days	Total Food	Daily Intake	Final Weight	Total weight + or -	Daily gain or loss.
W-B	4.85	7	2,200	315	4.90	+ 50	+7
W-B	4.80	10	3,000	300	4.60	- 200	-20
W-B	5.10	4	1,000	250	4.90	- 200	-50
W-B	5.10	10	3,500	350	5.00	- 100	-10
W-B	4.90	4	1,400	350	5.15	+ 250	+62.5
R-G	5.8	10	3,000	300	5.43	- 370	-37
R-G	6.02	4	1,400	350	5.98	- 40	-10
R-G	5.97	7	2,800	400	6.07	+ 100	+14
R-G	5.85	5	1,750	350	5.735	- 115	-23
R-G	5.80	10	3,750	375	6.15	+ 350	+35

Fig 19 line drawn by eye

It was not possible to determine directly the calorific value of the meat used for feeding. Samples of meat were dried to constant weight in an oven at 100°C, broken into pieces and placed in a Soxhlet chloroform extractor to remove any fat, and then re-dried and weighed again. This showed that the meat used in these feeding trials had a water content of from 70 to 73% and that fat composed under 4% of the dry weight. Ledger (1968) has shown that, unlike domestic stock, in game animals there is less than 5% carcass fat usually present. The remainder of the fat free dry muscle tissue in domestic animals contains over 90% protein

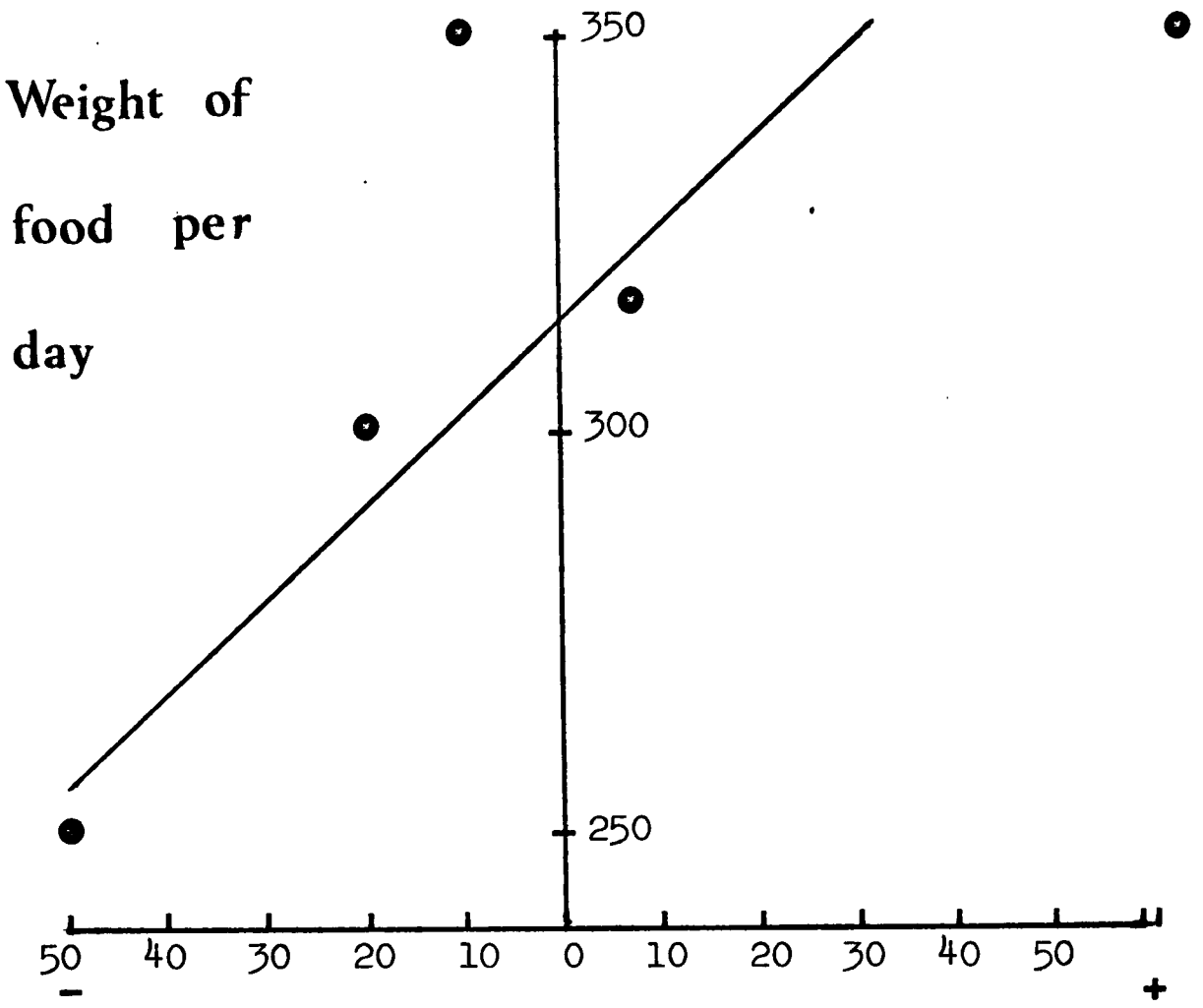
(Callow 1946), and this figure has been assumed to apply also to wildebeest muscle. The meat fed in these trials is therefore assumed to consist of 23% protein and 3% fat, and 100 gms of wet meat is assumed to have a calorific value of about 125 kcals.

Fig 19 shows that in order to maintain constant body weight a whiteback vulture probably needs about 315 gms of meat per day, representing an intake of about 400 kcals / day, and a Ruppell's griffon vultures requires about 360 gms of meat or 450 kcals / day. These figures are considerably lower than expected from the estimate made earlier from Kendeigh (1970) which assumed a required intake of from 400 to 500 kcals/day for the whiteback and 490 to 630 kcals/day for Ruppell's griffon. However, the captive birds which were used were inactive and also considerably lighter than most wild birds. If the theoretical energy intake is recalculated for birds of the same weight as those used in the feeding trials the resulting estimates of daily energy intake are 360 to 470 kcals / day for the whiteback and 416 to 534 kcals / day for Ruppell's griffon, and the observed food intake is within this range.

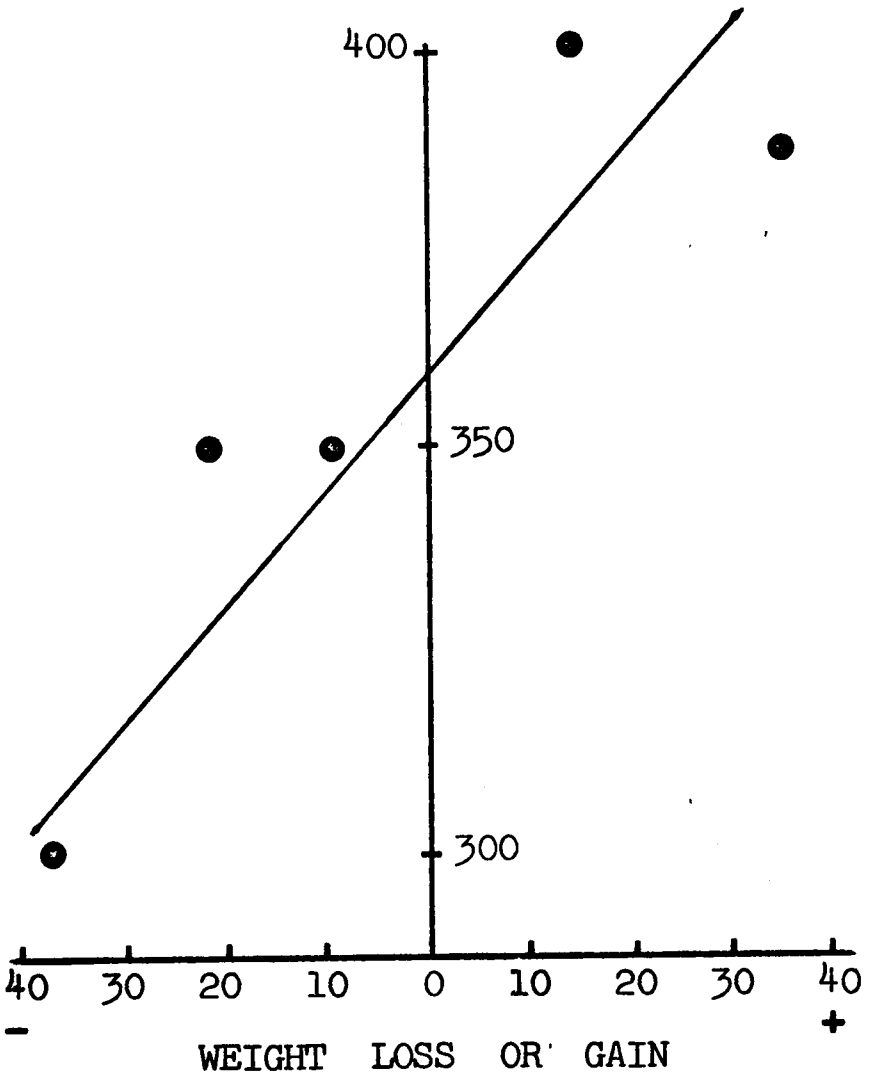
Both species would seem to be relatively efficient at absorbing energy from the food. The existance metabolism calculated from Kendeigh (1970) for the whiteback vulture was 328 kcals / day and the bird had an intake of 400 kcals/day, and absorbtive efficiency of 82%, and for the Ruppell's griffon the existance metabolism was calculated at 374 and observed to be 450 kcals/day, an efficiency of 83%.

The aim of measuring the food consumption of captive birds is to be able to estimate the food requirements of birds in the wild. However, wild birds are presumably undertaking more exercise than those in captivity and it is not known how this will influence their energy requirements.

Gyps africanus



Gyps rüppellii



Uramoto (1960) from published studies considered that wild birds required from 30% to 50% higher energy intake than captive birds. However, the extent of this discrepancy must depend on the general activity of the species considered. The snowy owl Nyctea scandiaca in the wild was estimated to take from 20% to 80% more food than in captivity (Watson 1957), and Kahl (1964) considered that a wild wood stork Mycteria americans probably had 1.5 times the intake of a captive bird. However, captive birds are sometimes fed more food than is necessary. Fitch (1946) observed that a red tailed hawk Buteo jamaicensis obtained about 100 gms of food per day in the wild, while a bird in captivity ate 140 gms of food per day. Fevolt and Craighead (1954) studied the effects of exercise on the food requirements of a golden eagle directly. An individual bird was kept for two periods in winter, one without any exercise and a second period when the bird was regularly exercised and flew about 800 yards a day. The average daily food intake to maintain body weight increased from 188 gms to 231 gms with exercise and this would suggest that exercise has some effect on food consumption. However, the flight of vultures is composed largely of gliding, and flapping flight is used only for take off and landing. Gliding is presumably relatively undemanding compared to flapping flight (Pennycuick in press) and the energy requirements of wild birds have therefore been assumed to be 10% greater than those in captivity.

Birds in the wild are therefore assumed to have food requirements 10% greater than as calculated from Kendeigh (1970), assuming an 80% absorbtive efficiency, so that an average sized whiteback vulture probably needs 480kcals per day and a Ruppell's griffon about 600 kcals / day.

However, griffon vultures cannot usually feed regularly and they rely on being able to take a large quantity of food rapidly during a temporary food abundance and then being able to withstand a period of starvation.

Thus a whiteback vulture can take about 1,100 gms of food into the crop (20% of body weight) and a Ruppell's griffon about 1,400 (19% body weight) The maximum load which the birds can carry and still be able to fly has presumably determined the weight of food that could be swallowed and the size of the crop. Both species when fully fed have considerably difficulty in leaving the ground, and if chased they can only escape by reaching a nearby tree or finding a thermal which is starting near the ground.

When fully bloated in this way, the digestion of food takes a long time. If captive Ruppell's griffon vultures are fed with meat which is injected with a heavy suspension of carmine particles, it is 6 to $7\frac{1}{2}$ hours before the first faeces appear containing carmine. A whiteback vulture requires from $5\frac{1}{2}$ to 6 hours for food to pass through the tract. Digestion is therefore slow. Captive birds would not take enough prepared food from the hand to fully extend their crops. A Ruppell's griffon fed with 1,200 gms of meat requires 24 to 27 hours before the crop has emptied, and up to 34 hours before the faeces have passed through. Wild birds which can exceed this intake presumably take proportionally longer to digest. Griffon vultures can therefore take advantage of a temporary food abundance since their maximum intake represents about 3 times their normal daily requirements, although it takes a considerable time to digest this quantity of food.

To consider the digestion of bulk quantities of food, a Ruppell's griffon vulture was regularly weighed while being fed infrequently, but given as much as it would eat at each feed. Since catching a bird and weighing it causes considerable distress, a cage was built on top of a Salter baggage balance so that both cage and bird could be weighed together. The wooden cage was too small to permit any exercise and was kept in the shade. The weight of the cage was recorded at the beginning and end

of the period of feeding and this was deducted to find the weight of the bird. The cage was fitted with a detachable floor so that faeces could be removed before weighing and only the bird's weight recorded. Water was not given since vultures do not normally drink. Two weeks of regular feeding were given for the bird to settle in the cage and it was then given as much food as it would eat, followed by a period of starvation. The bird was clearly not content with the surroundings and expressed its objection by refusing to take more than about 1 kilo of food at any one time. Fig 20 The weight falls rapidly at first while food is passing through the digestive tract. When all faecal material has left the body the bird's weight is greater than before feeding due to fat storage and water intake. This overall increase in body weight is proportional to the amount of food eaten, Fig 21, and presumably reflects a greater quantity of fat storage from a larger food intake. During subsequent days without food, weight falls steadily while energy reserves are utilised.

It is not possible to consider the efficiency of energy storage represented by this type of feeding since the effect of water untake could not be controlled in the feeding trials. However, birds are clearly able to store fat rapidly after a large food intake and utilise this over a subsequent period of food shortage. The potential value of energy storage is considered later. There is a definite limit to the weight of fat which can be carried and maximum fat stores and expendible protein are found to be sufficient to maintain a bird for about 15 days, or probably longer, without feeding. The nature of the food supply of griffon vultures has been shown to fluctuate considerably. The ability to rapidly store excess energy intake in the form of fat deposits normally enables these birds to withstand both short term daily fluctuations in feeding success and also the longer term general pattern of food availability.

FIG 20

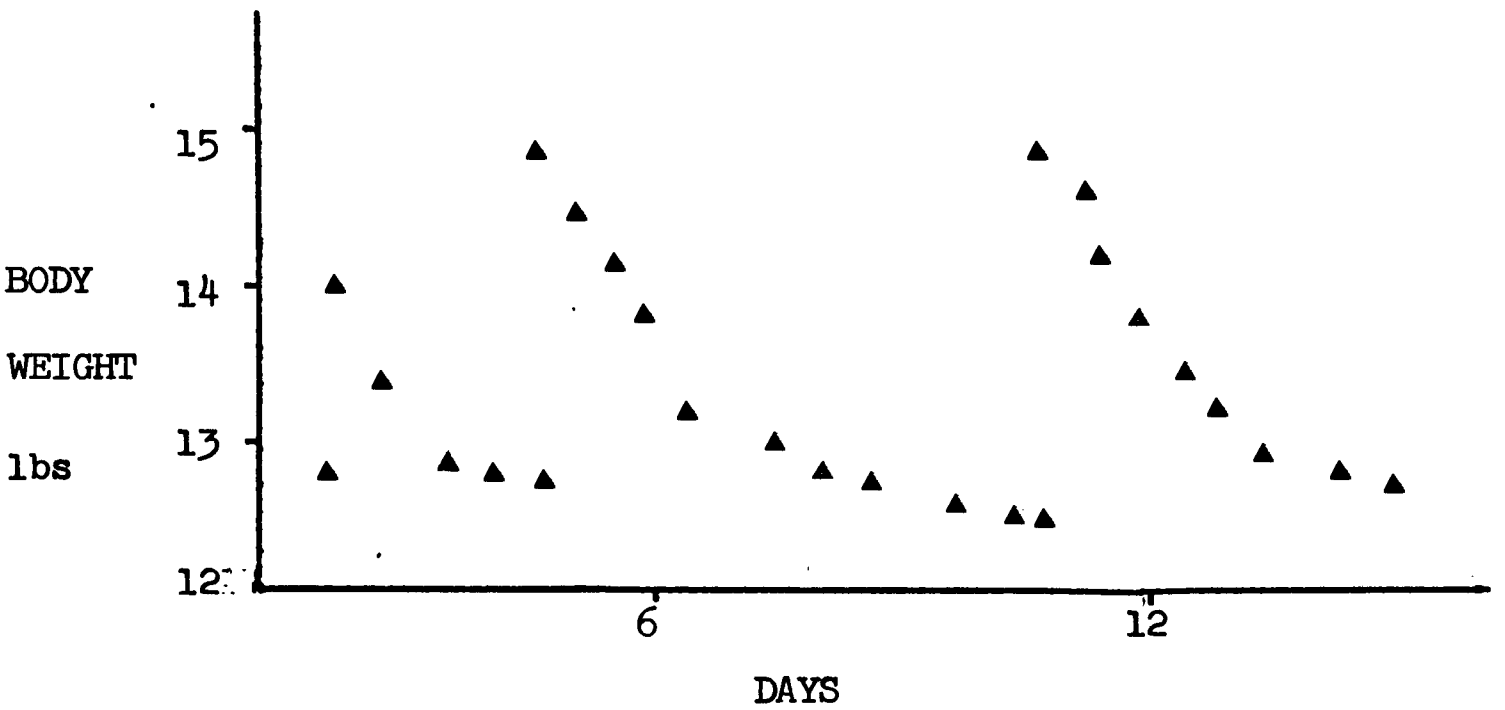
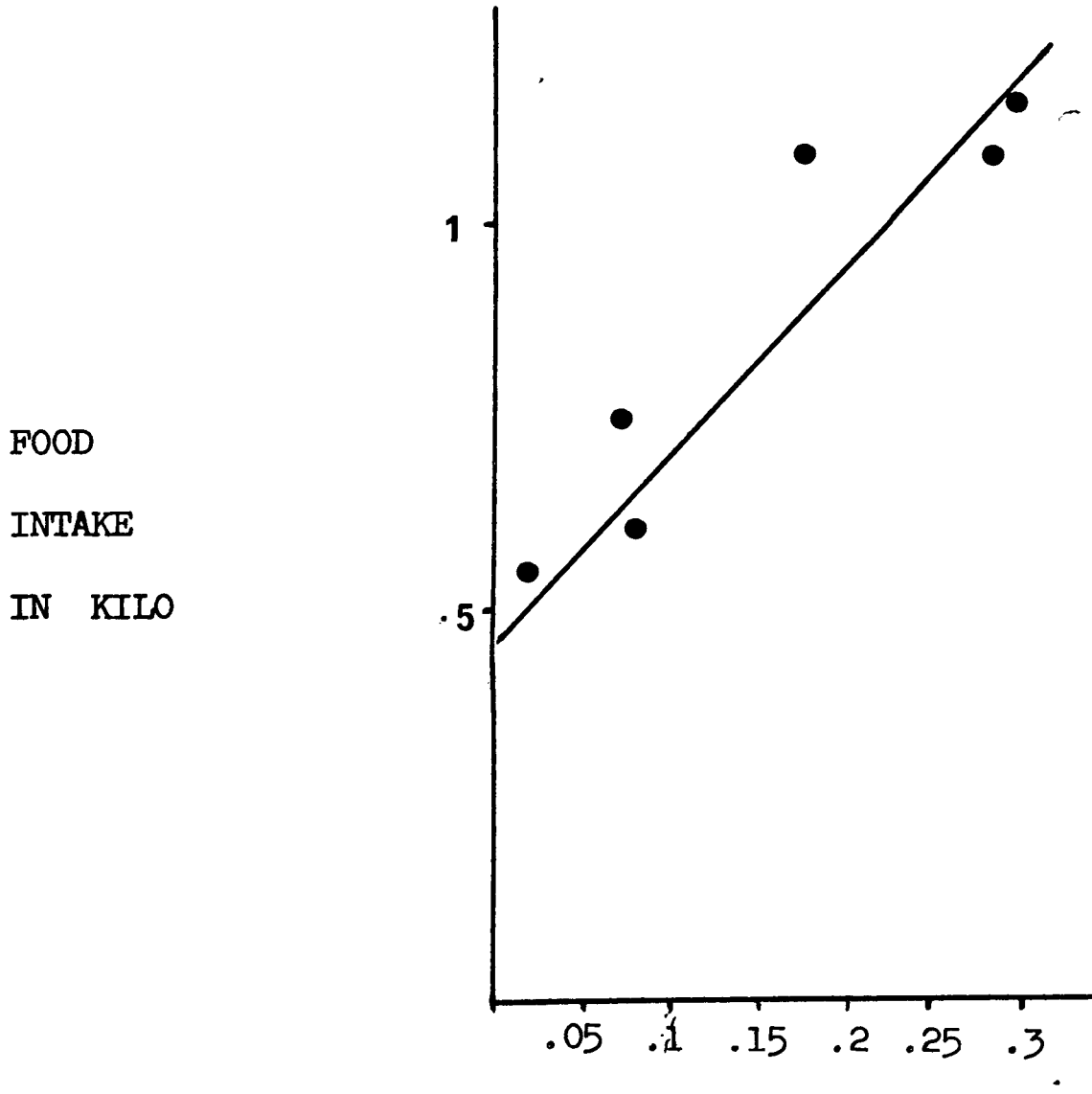


FIG 21



After food has passed through tract.

During the first half of 1970 the estimated amount of food available to the birds (Fig 10 page 29) did not fall greatly below the estimate made for the food requirements for non breeding birds. As might be expected, the fat and protein levels in non breeding birds during this period remained high and there was no indication that energy stores were being utilised to withstand a period of food shortage (Fig 22)

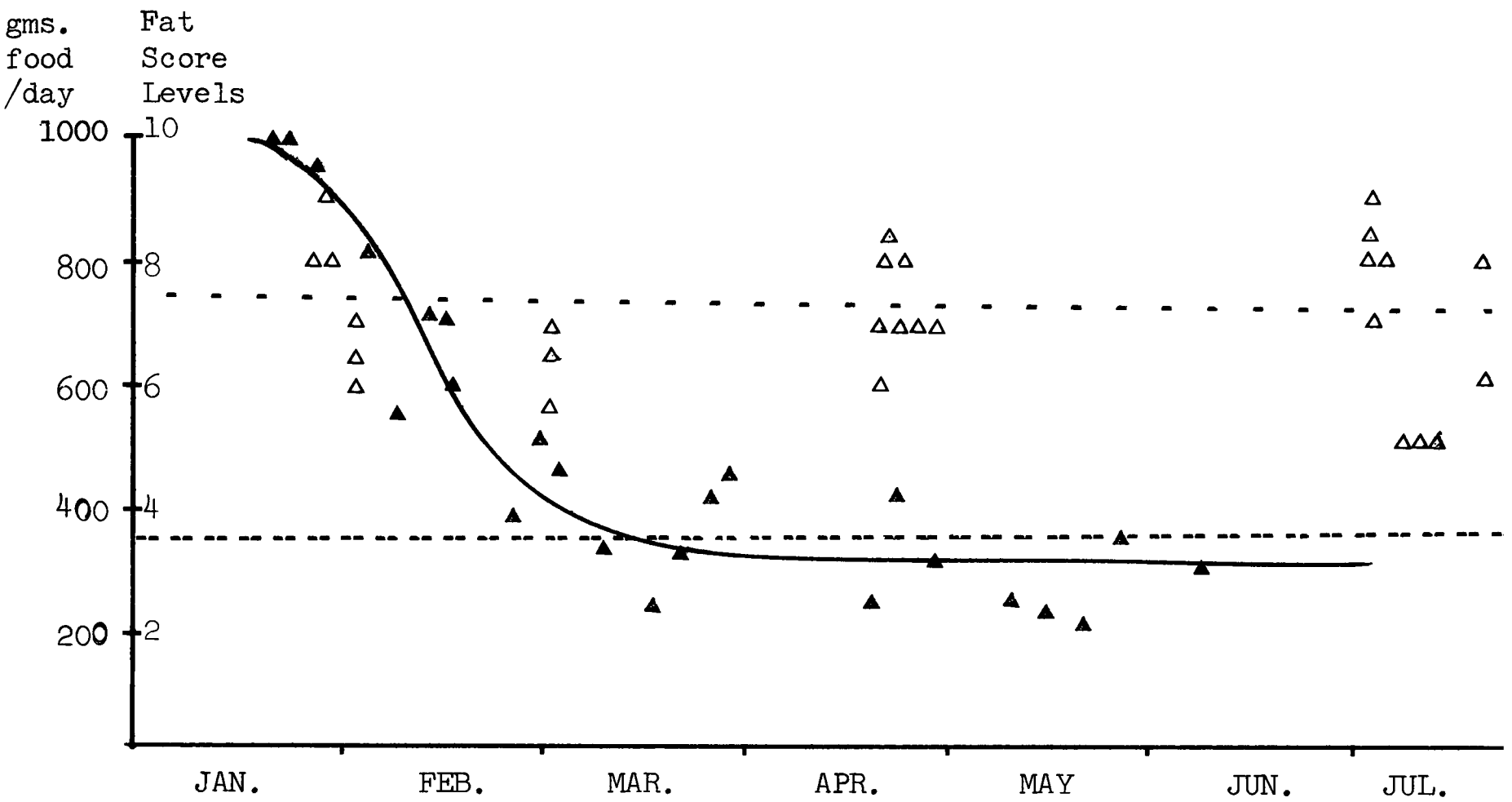
Body Temperature

The body temperature of both species of griffon vultures fluctuates up to 5 degrees Fahrenheit throughout the day, which is a normal temperature variation (King & Farner 1967) among many species of birds. Fig 23 shows the rectal temperatures taken from birds within 30 seconds of being shot. Those taken at night were shot on moonlit nights as they were sleeping in trees. There is no sign that birds become torpid at night in order to save energy, and the body temperature does not fall during the night to the same extent as has been recorded for the unrelated American turkey vulture (Heath 1962).

Food Quality

A food supply must not only be considered in terms of its quantity or basic energy value, but also for its quality. There is surprisingly little knowledge of the requirements for a nutritionally complete diet for wild birds in relation to the quality of the food available. In red grouse Lagopus l. scoticus the age of their food plant Calluna vulgaris has been found to determine density and breeding success, and both are increased following the improvement of heather quality by fertilisation (Miller, Jenkins & Watson 1966, Miller, Watson & Jenkins 1970). There is indirect evidence that the diet may be deficient in nitrogen and phosphorus (Moss 1967).

Figure 22

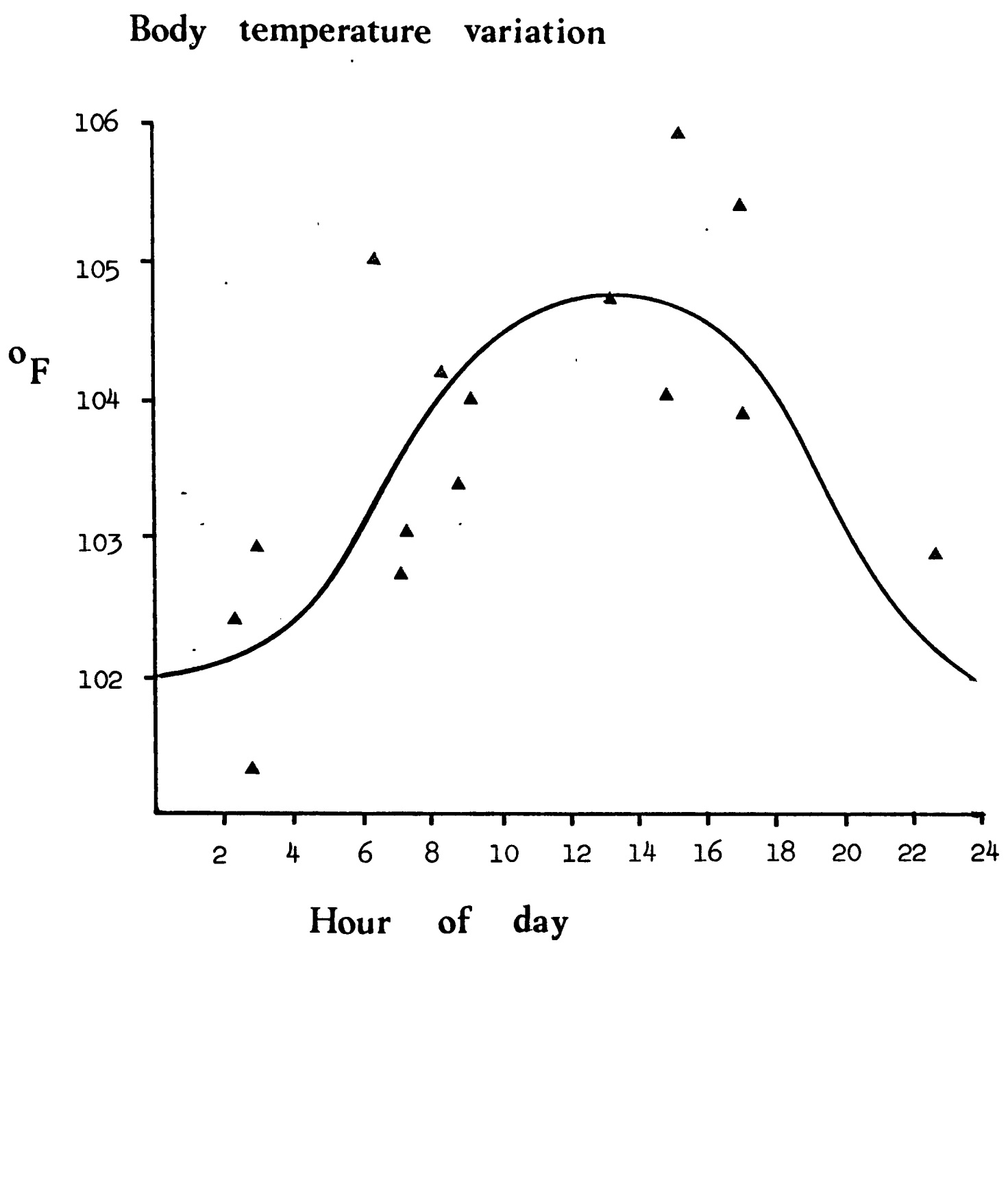


——— ▲ Estimate of food availability

- - - △ Fat score levels

-- -- -- -- -- -- Estimate of food requirements for maintemance.

Figure 23


Body temperature variation
106
105
104
103
102
°F
2
4
6
8
10
12
14
16
18
20
22
24
Hour of day

It is therefore interesting to find that grouse select parts of the plant highest in nitrogen and phosphorus (Moss 1969), and similar selection for food of particularly high quality occurs in ptarmigan Lagopus mutus, (Gardarson & Moss 1970) and capercaillie Tetrao urogallus (Pulliainen 1970).

Griffon vultures do not have a seasonal variation in the nature of their food supply, and this is always the soft tissues of large game carcasses. It is therefore important to consider to what extent this represents a nutritionally complete diet for the bird's seasonal activities. Muscle tissue in itself is not a nutritionally adequate diet since it almost completely lacks calcium and oil soluble vitamins (Wackernagel 1968). Captive birds, which were fed for convenience on muscle tissue alone, were therefore provided with a vitamin and mineral supplement. However, wild birds also take the viscera of animals, and this is important since some organs, notably the liver, contain large quantities of vitamins not generally distributed through the body. Vitamin A is virtually absent from muscle and fat tissue, although heavily concentrated in the liver (Scott 1968). Since only trace quantities are needed, vitamin deficiencies are unlikely to develop in wild birds.

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The mineral requirements of birds are only well known for domestic poultry. It is clearly unsatisfactory to use laying hens as a comparison, but domestic chickens could show the general order of importance of minerals in the avian diet. In comparing the nutrient requirements of different species of animals, Crampton (1964) found that requirements are often dissimilar if the figures for dry weight of nutrients are used. However, if they are expressed in terms of nutrients per unit of metabolisable energy, they are very similar. This is the method that was used by Moss (1967) in consideraing the nutrient requirements of red grouse, and it is used here to consider the nutrient value of the food of vultures.

Nutritional requirements of breeding poultry and nutrient content of animal soft tissues, expressed on a metabolisable energy basis.

gms per 1000 kcals.

	Ca	P	Na	K	Mg	Fe	Cu
Requirements of *							
Chicken	7.8	2.1	0.5	0.7	0.17	0.007	0.0007
Turkey	7.8	2.6	0.5				
Nutrient content **							
Muscle	0.04	1.4	0.45	2.15	0.15	0.025	0.00105
Heart	0.06	0.78	0.82	3.08	0.20	0.049	
Liver	0.057	2.14	0.59	2.23	0.14	0.09	0.039
% of chicken's requirements present in muscle tissue.	0.6%	61%	98%	328%	94%	357%	150%

* From Moss (1967) taken from Nutrient Requirements in Poultry 1962 U.S.A. Publ. nat. Res. Council, Nat. Acad. Sci. No827

** From Domestic cattle, McCance & Widdowson 1960.

Unlike vitamins, which are required in trace quantities, these major minerals are needed in relatively large amounts in the body and must be regularly present in the food. Unlike the distribution of vitamins, minerals are found in even concentrations throughout the soft tissues of animals. The percentage of major minerals available in the food of griffon vultures is found to vary considerably from the possible mineral requirements. Most minerals are present in sufficient or abundant concentrations, with the exception of calcium, and also phosphorus. An estimate of calcium requirements obtained from laying hens is unsatisfactory in comparison to the requirements of griffon vultures, but the order of magnitude of the discrepancy is exceptional and indicates that there is possibly a calcium shortage in the diet.

Approximately 99% of calcium stored in an animal's body is present in bones and teeth (Maynard 1937). The 1% found outside bone is widely spread through the soft tissues of the body, which contain about 0.01 % calcium. Griffon vultures, unlike most other birds of prey, do not have the opportunity to eat small bones, since they feed entirely off large game carcasses. The crop contents of 72 birds have been examined, and also several hundred food pellets, and no small piece of bone has been found. If small chips of bone are scattered around a carcass, birds do not try to swallow them. Their diet therefore consists exclusively of soft tissues and contains only a very small quantity of calcium.

Adult birds must be able to maintain their calcium levels on this diet. However, the calcium requirements for bone development of growing young are considerably greater than those of adult birds. A young whiteback vulture which was being hand reared was accidentally deprived of a calcium additive to the food for three weeks. It developed typical symptoms of a severe calcium deficiency (Wallach 1969) from which it later died. Kahl (1966) found that young Marabou stork could not be reared without a supply of fish and frogs in the diet, and parent birds supply this although their normal diet outside the breeding season is meat from the local abattoir. Adult and immature wedge tailed eagle Aquila audax feed mostly from carrion, but while rearing young the adult birds take almost exclusively small birds and mammals (Ridpath pers. comm.). These changes in diet are presumably necessary to supply calcium to the young chick. In cormorants Phalacrocorax carbo and herring gulls Larus argentatus young birds digest fish bones completely, although the parent birds, with lower calcium requirements, do not (Van Dobben 1952, Spaans 1970). Griffon vultures do not have the opportunity to alter their diet to supply bone to their young. It seems very probable that these birds must store calcium during the year and use this to supply a calcium rich crop secretion which

they feed to their young, and secretory cells are present in the crop. Although this is only speculation, the availability of calcium in adult birds could be an important factor in determining breeding condition.

b) MOULT

General Introduction

The growth of feathers might cause a seasonal fluctuation in energy requirements and the timing of the moult could indicate periods of food shortage. The moult sequence was therefore examined and this is described here so that the relative importance of moult as an energy demanding process can be considered.

The moult of griffon vultures is poorly known. Stresemann (1968) in his study of museum skins found that primary moult of the Aegypiinae was atypical, some species moulting descendingly (in an orderly sequence from the innermost primary to the end of the wing) when young, but irregularly (in no fixed order) when old, while others showed irregularity when young. Only the palm nut vulture Gyphohieras angolensis moulted typically descendingly. Observations have also been made in European zoos, although moult may not be typical in an abnormal climate. Fischer (1963) reported that some species of vulture in the Berlin zoo take up to seven years to complete their moult, considerably longer than is found in wild birds.

Details of moult condition were obtained from 68 whiteback vultures and 33 Ruppell's griffon, from birds caught in nets and others shot for examination. Information on the moult of flight feathers was obtained from all of these birds, but moult in other tracts was recorded from a smaller number of individuals. Three captive Ruppell's griffon and three whiteback were used to obtain additional information on the rate of growth of individual feathers. The close examination of the wing feathers normally caused considerable alarm to the birds, since they had to be forcibly restrained for several minutes. This was very undesirable in hand reared

birds because they rapidly became nervous and lost confidence in the handler. To examine and measure these birds regularly the anaesthetic 'Metomidate' was used (Appendix 111) at intervals of about three weeks.

The Moult Sequence.

The primary moult begins later than the moult of some contour feathers and possibly continues after body moult has been completed. The method used by Miller (1961), and other workers, in which the development of primary moult is used as a guide to follow through the overall stage of the moult cycle could not therefore be used. In addition, feather replacement is relatively slow and is a continuous process throughout the bird's life. Moult cannot therefore be recorded as a clear progression through the various sites of feather growth from the start to the completion over a distinct moult period.

Moult in griffon vultures is apparently complicated, and since this section concentrates on the timing of moult development, a brief summary is first given of the moult sequence.

Among the primary feathers, moult begins about ten months after the young bird leaves the nest with the replacement of the innermost (numbered 1st) primary. From this position further feather growth occurs in an orderly progression towards the tip of the wing; each feather does not start development until its neighbour has completed growth. After the first complete moult, primary replacement continues by further moult 'waves' or orderly progressions of growth outwards from the first primary position. These 'waves' may start before the previous wave has reached the end of the primary row, or alternatively a second wave may not start until all feather growth from the earlier sequence has finished. Adult birds, in breeding

plumage, particularly show variation in the timing of the start of moult waves.

Secondary feathers, however, do not show such a clear pattern. Moult does not begin in this tract until two or three primary feathers have been replaced. The innermost secondary (numbered 1st) is the first to develop. However, additional secondary sites further along the wing soon begin development and although there are no fixed positions for these 'independently' growing feathers, there is a tendency for growth to start in three areas along the wing. Further secondary development does not occur by the progression of moult waves, as was found in the primaries, but by the further growth of isolated feathers. Subsequent secondary moults continue similarly by the irregular growth of feathers, however, feathers do not usually start development near secondary positions already in growth. As in the primaries, adults show individual variation in the number of actively growing feathers. Tail moult is irregular at all ages and body moult is slow and continuous.

Nestling Development and the First Moult

At hatching, a nestling vulture is covered by short, white natal down, except for the bare abdomen area. This down covering thickens with the growth of pre-plumular down feathers, causing the colour to change to a sooty grey. At about three weeks the down is dense, and contour feathers develop in the scapular region, followed by flight feathers and a few upper wing coverts. At about five weeks the bird is protected by a layer of strongly growing back and upper covert feathers, although under feathers do not start general development until the back coverts are well grown.

At the end of the fledging period the young bird has a uniform dark brown

plumage. The skin of the head and neck is black, with a sparse cover of fine white down, and the bill is also black. The neck ruff is composed of very thin feathers up to three inches long, forming a loose tassle, unlike the dense, short ruff of older birds. The crop patch is a dark golden brown colour and all other feathers, including the ruff, back and under wing coverts are a dark brown, usually with a conspicuous streak down the feather shaft. All back and upper wing covert feathers and flight feathers have clearly pointed tips. When a juvenile feather is moulted, the replacement will develop with a rounded tip. The sequence of feather replacement in young birds can therefore be easily followed by recording the position of rounded and pointed feathers.

Primary and Secondary Moult

There are 11 primary and 25 secondary feathers in the whiteback vulture, although the outermost primary is greatly reduced and difficult to locate rapidly, and this feather has been ignored here. The first onset of moult and the subsequent sequence of feather replacement can be followed in Fig 24 . The positions of replaced flight feathers (those with rounded tips or in active growth) have here been plotted from individuals at increasingly advanced stages of wing moult. For each individual the two wings have in all cases been recorded separately, because moult is not usually symmetrical in the two wings.

The first primary is the first flight feather to be moulted. This position acts as the initiator of a moult centre and further feather replacements will proceed from this site first outwards along the primary

Birds retaining some juvenile flight feathers (with pointed tips).

Gyps africanus

Position of New or Growing Feathers (with rounded tips)

Number of New Feathers Grown	Number of Wings found in this condition	Primaries										Secondaries																				
		10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	6										N																				
2	3									n	N																				
3	1						n			n	N																				
4	0																														
5	2							n	N	N	N	n																			
6	1							N	N	N	N	n								n											
7	1							n	N	N	N	n						n			n										
7	1							n	N	N	N	n						n				n									
7	1							n	N	N	N	n					n								n						
10	1							n	N	N	N	N	N	n		N							N			N					
9	1						n	N	N	N	N	N	n				N			N											
10	1						n	N	N	N	N	N	N	n		N							N								
13	1			n	N	N	N	N	N	N	N			N			n			N		n		N							
14	1			n	N	N	N	N	N	N	N	n	N			N		n			n		N			N					
15	1			n	N	N	N	N	N	N	N			n	N		N	N						N			N			
16	1			n	N	N	N	N	N	N	N			n	N	N				N		N		N			N	N		
N = Fully grown new feather												1	3	4	4	3	4	1	1	4	2	3	0	4	3	2	1				Freqaency Observed
n = Developing new feather												25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25				Expected Random Frequency

feathers of the wing, and then later also inwards along the secondary feathers. Moult proceeds in both directions from the carpal joint, but the first three primaries are shed before secondary moult begins. The spread of this moult centre continues along the primaries and secondaries until a total of about five new feathers have been replaced. At this stage not only does the original moult centre continue to spread further along the secondary and primary rows, but also further along the secondaries additional feathers begin to fall and replacements start development.

There does not appear to be any rigidly fixed site for these new 'independently' growing feathers. However, the positions of growth are not randomly distributed and if the locations of these first independently growing secondary feathers are summed it is found that there is a tendency for growth to occur around secondaries 6, 12 and 17.

It is also probable that new sites of secondary feather growth do not necessarily either originate from, or initiate the onset of, a moult sequence which will continue along the wing. Of the new feathers developing in this region in Fig 24 where several other secondaries have already been replaced, three are growing next to a recently grown feather and might therefore have been stimulated into growth, but four are growing independently of any neighbouring growing feathers.

There is therefore a tendency for the general site of initial further secondary replacement to occur in three locations, although the feathers are not moulted in any fixed sequence or positions. The further development of secondary moult does not appear to follow from the spread of moult centres away from these three regions. . The final completion of secondary replacements results from both the slow spread of the original moult centre

and the further, apparently independent, growth of secondary feathers. Primary moult is completed by the spread of the original moult centre until this reaches the tip of the wing. One isolated primary feather was recorded growing away from the influence of the moult centre in Fig 24 and this is apparently an exception. This may, however, be caused by the accidental loss of this particular feather and its subsequent regeneration. Captive birds which had secondary and tail feathers deliberately removed would immediately start to renew the feathers, regardless of the moult condition of the neighbouring feathers. Although it is not known whether primary feathers can also regenerate in this way, this would seem to be likely.

The Rate of Feather Growth.

The time taken for the development of this moult pattern in wild birds could not be recorded because no marked birds were re-captured after moult examination. However, some indication of the time taken for this sequence of wing moult can be obtained from the rate of growth of individual feathers in captive birds. These birds were regularly examined under anaesthesia so that detailed measurements of feather size could be made. Fig 25 shows that individual flight feathers grow at a uniform rate through development, gaining about 0.44 cms. in length per day. The size of the primary feathers varies from about 31 to 45 cms in length, while the secondary feathers are of a more uniform length at about 30 to 32 cms. Fig 26 . All primary and secondary feathers which were measured grew at approximately the same rate and therefore larger feathers take proportionally longer to complete growth.

In addition to this visible growth there is also a period after the old

Figure 25

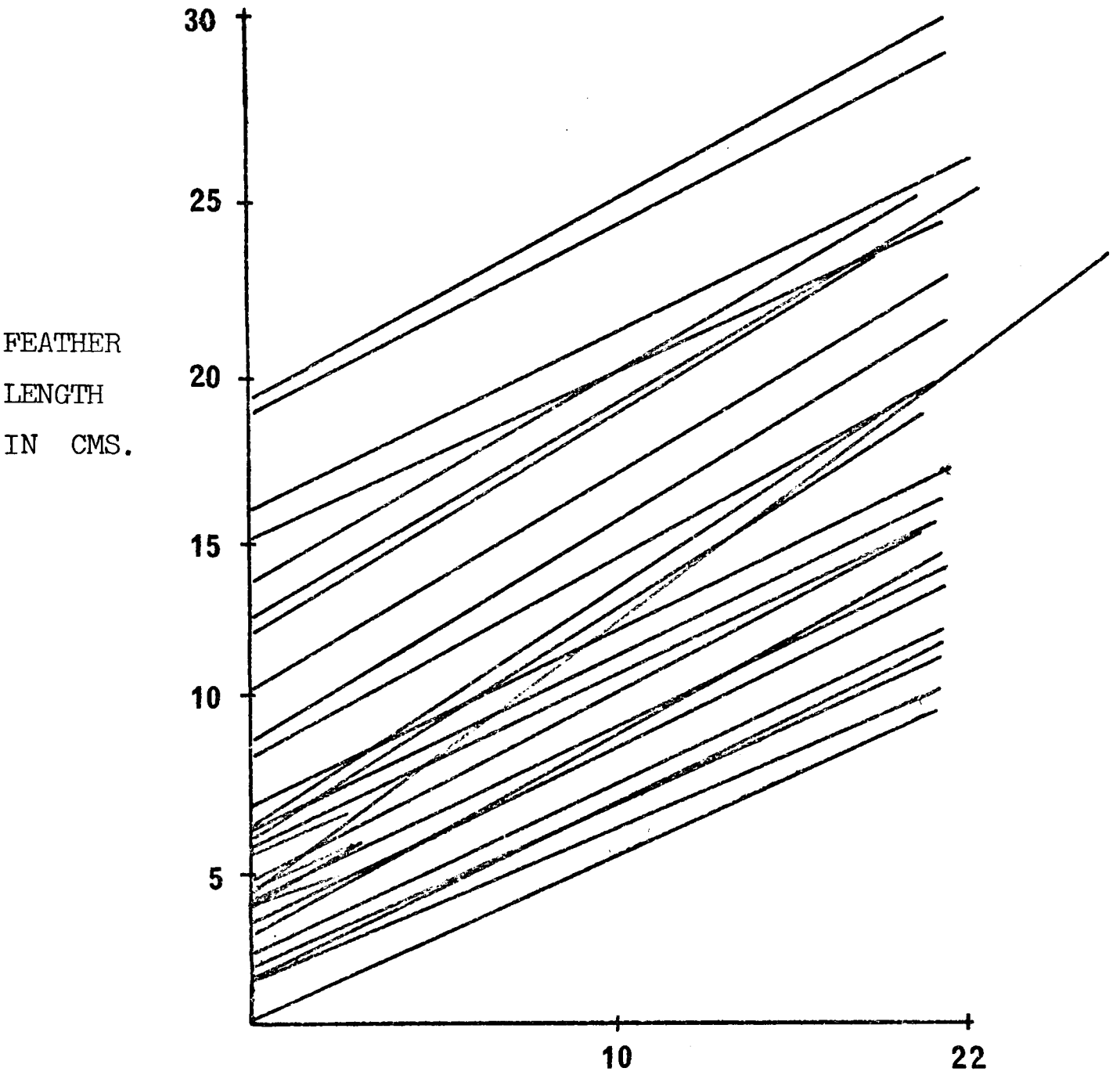

30
25
20
15
10
5
FEATHER
LENGTH
IN CMS.
10
22
TIME INTERVAL IN DAYS

Figure 26

Gyps africanus · Mean measurements of feather sizes from three birds.

Primary	10	33.3 cms.
	9	40.5
	8	42.5
	7	43.3
	6	43.6
	5	43.75
	4	40.7
	3	35.3
	2	33.2
	1	31.0
Secondaries	1	31.0
	2	32.2
	3	31.8
	4	31.7
	5	33.5
	6	32.0
	7	31.25
	8	31.0
	9	30.75
	10	30.7
	11	30.0
	12	29.7
	13	29.0
	14	29.2
	15	29.2
	16	29.5
	17.	29.0
	18	28.7
	19	28.5
	20	28.0
	21	28.0
	22	28.0
	23	28.7
	24	26.7

feather is ejected before the new growing point emerges. This seems to take between three and four weeks. A feather of 35cms. length will therefore take a total of about 100 days to develop.

Throughout moult it is essential to maintain a uniform aerofoil surface for efficient gliding flight. If one feather is missing the neighbouring feather vanes will overlap and mask the gap. However, this cannot be achieved if two or more adjacent feathers are missing. Feather replacement is not initiated until the adjoining feathers are fully grown, and such gaps do not usually develop. Out of 47 growing primary feathers recorded from immature birds, none were found to be starting development next to a feather which had not yet completed growth. Since only one feather is usually in growth at any time, the rate of spread of a moult centre would appear to be slow.

The figures derived from captive birds can be used to indicate the time taken for the progression of the moult sequence through the primaries.

Primary number	10	9	8	7	6	5	4	3	2	1
Length cms.	33	40	43	43	44	44	41	35	33	31
Estimated time for growth in days.	99	115	122	122	124	124	117	104	99	95

If we assume that it will take approximately 95 days from the initiation of growth of the innermost primary until this has completed growth and the second feather in the moult progression can be shed, then about one year from the onset of moult, this moult centre would have caused the replacements of a maximum of 3 feathers. This moult centre will therefore take at least until the end of the third year of active

moult in order to complete replacement of these ten large primary feathers.

If a single sequence of moult occured in the secondaries, it would take a minimum of 7 years to complete a cycle of moult. Wear on the feathers presumably requires that replacement must occur more frequently than this. At the end of about the first year of active moult when about five flight feathers have been replaced, individual secondary feathers start to initiate their own replacement, apparently independently and without any stimulation from an advancing moult centre. Birds in this stage of moult development have two or three such independent feathers in growth at any one time. The secondary feathers are shorter than the primaries and would take about 90 days to develop. If three feathers were moulted at a time, then about 12 new secondary feathers could be produced each year, entire replacement of the secondaries taking 2 years. However, if only two feathers are in active growth together, total replacement would take 3 years.

This would suggest that it takes a total of at least three years to complete a cycle of moult, and we can now check if this time scale is correct for wild birds. If we assume that all birds start to moult at approximately the same period after leaving the nest, then it should be possible to estimate the age of an individual bird from the stage of development of the wing moult. If at any one time in the year a collection of young birds (those with some juvenile pointed feathers present in the wing) is examined, their moult condition ought to fall into clear groups according to their respective ages. During June and July 1970 a group of 17 young birds with some juvenile feathers present were examined to see if their wing moult could be classified into age groups in this way. Young whiteback vultures leave the nest during August / September, and so

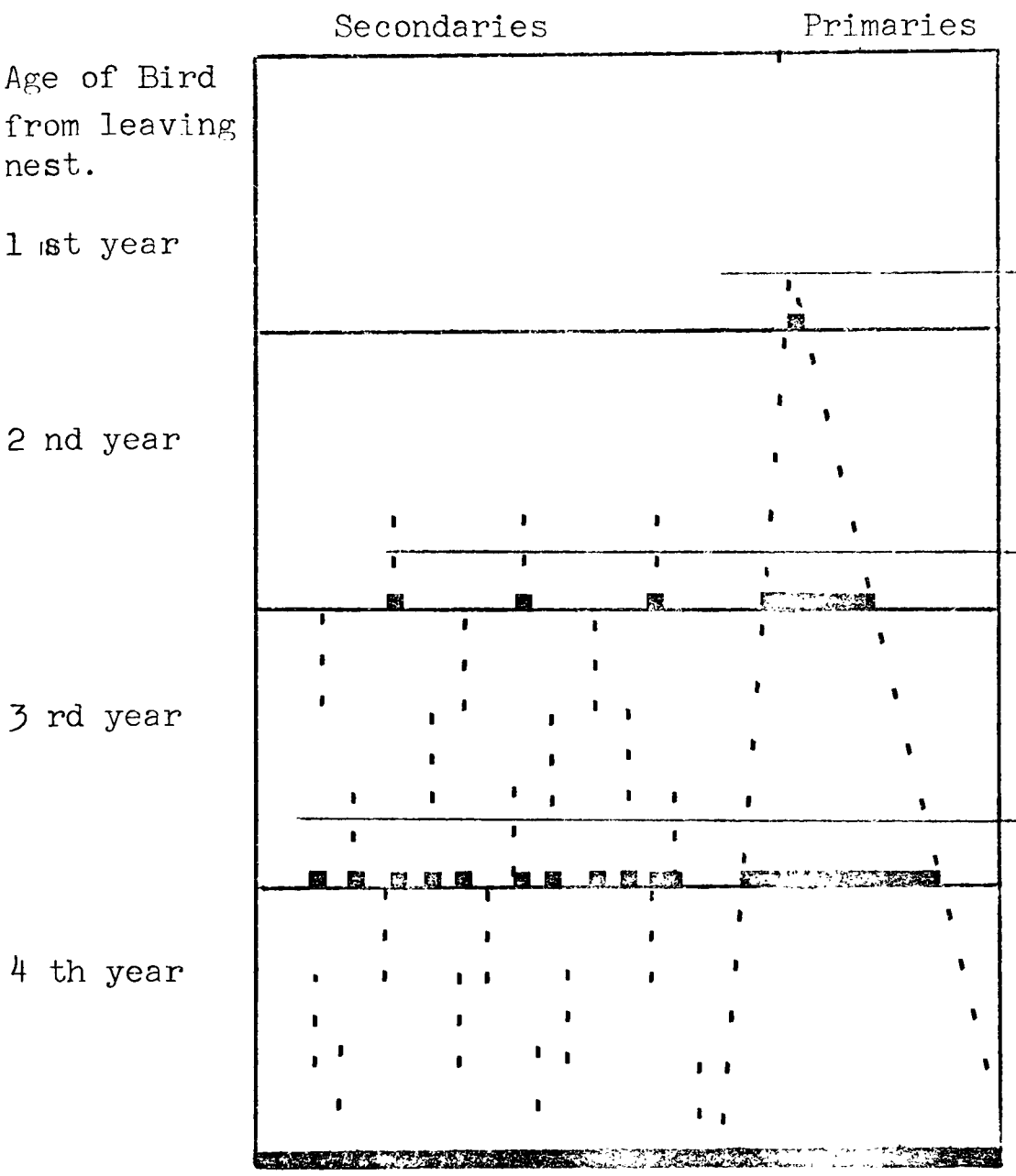
the youngest birds examined would be 10 months old.

Fig 27 shows the presumed rate of moult development based on the feather growth of captive birds. The group of wild birds show stages of moult advancements which correspond to this same pattern, and differ significantly from a uniform distribution (p = .05 Kolmogorov Smirnov test) Wild birds therefore show the estimated speed of moult development.

It would therefore appear that the moult sequence takes the following pattern. Birds retain their juvenile plumage after leaving the nest for about the first year without any feather replacement at all. Birds in captivity all started to undergo moult within one year after leaving the nest, and although it is not possible to tell from this sample of wild birds whether moult is delayed until the second or even third year, this is considered unlikely.

Towards the end of the first year of independence, birds begin moult with the shedding of the first primary feather. During the remainder of the second year the moult centre associated with the innermost primary slowly spreads along the primary row and by the end of the second year about 3 or 4 feathers have been replaced in this area. In addition, at the end of the second year, other secondary feathers start to develop independently of a moult centre. This pattern of feather growth continues until, by the end of the fourth year, the flight feathers have probably been completely replaced.

Presumed rate of moult development derived from speed of feather growth in captive birds.



Sample of young birds examined during June/July

	a	b
June	12	0
July	6	1
	3	2
	1	3
	-	4
	1	5
June	1	6
July	3	7
	1	8
	-	9
	-	10
	-	11
June	1	12
July	2	13
	1	14
	1	15
	1	16

a Number of wings found in state of moult advancement.

b Number of new feathers developed on wing.

Distribution significantly different from random.
p = .05 Kolmogorov Smirnov.

■ New Feather

Growing sites.

Tail Moult

The whiteback vulture has 12 tail feathers, the Ruppell's griffon 14. It is tempting to conclude that tail moult in griffon vultures is completely chaotic at all ages. The location of growing tail feathers has been plotted for the same group of birds in which the wing moult development was recorded.

Tail Feather Development.

Juvenile Whiteback. Birds retaining some juvenile feathers.

Position of new or growing feathers (with rounded tips).

6 5 4 3 2 1 1 2 3 4 5 6

n n

n n n n

n n n

n

There does not appear to be any spread of moult activity from a centre, any fixed sites for the onset of moult, or any symmetry between the two sets of tail feathers. Even in the first feather replacement, tail moult would appear to be completely irregular. Before abandoning the subject, it is helpful to remember that tail feather growth will be initiated following the forced removal of a feather. During the normal fighting and bickering at a carcass, tail feathers are likely to become damaged, or if the tail is stood on by another bird, it may lose some feathers. The replacement of a feather in these circumstances will have no connection with any orderly sequence.

Body Feather Replacement

The progress of body moult was only roughly estimated by recording the presence or absence of developing feathers in areas of the body. Moult is always very slow and only a few feathers are found developing in any tract.

The moult of body feathers in captive birds starts in the scapular tracts shortly before the start of primary feather moult. Feather growth proceeds slowly in the upper wing coverts and scapular region and by the end of the first year of moult activity about 1 in 30 of these feathers will have been replaced, although there is considerable individual variation in the speed of this body moult. During the following year moult proceeds also in the ventral tracts and birds at the end of the second year of moult had from 1/3rd to 1/10th of upperwing coverts replaced, 1/3rd to 1/20th of underwing coverts, 1/4 of back feathers and about 1/3rd of ventral feathers replaced. During the third year the remaining juvenile body feathers are very bady worn. Body moult may proceed more rapidly in this third year and the remainder of the old feathers be replaced by the end of the year, but if the moult continues at the same rate, then it is probable that feather replacement will not be entirely completed by the end of the fourth year and body moult will then extend beyond the period taken for wing feather replacement.

Subsequent Moulting Cycles

Immature Plumages

At the end of the fourth year a whiteback vulture has therefore lost the juvenile plumage and grown into the first immature plumage. This has uniform brown feathers, a brown ruff and back, although a few of the under wing coverts will be white. All covert feathers and flight feathers have rounded tips and the overall body colour will be considerably lighter than that of a first year bird. The ruff feathers are less elongated and more dense. The skin of the head and neck changes from the uniform black to a mottled combination of yellow and green around the head, with black spots and patches, and the covering of down on the head will be less dense than in a young bird.

This immature plumage still differs considerably from the adult plumage. Although there is great variation in the general colour of the body feathers of adults, they are usually considerably lighter than immature birds, and vary from almost white to a steel grey and brown colour. The ruff of adult birds is composed of white feathers forming a short and dense ruff patch, and the lower back area is also white forming a conspicuous white patch which is visible when the bird opens the wings. A large patch of the under wing coverts is also white in adult birds. The neck and head are also usually light in colour with occasional spots or blotches of black, and the down on the head may be very sparse.

It is not known how many complete moults the bird undergoes before it reaches this adult plumage. However, there does not appear to be any pause in moulting at the end of the first feather replacement and birds

which have completed this first total moult would appear to undergo continuous feather development. All birds recorded in immature plumage throughout the year were in active moult, and although there are four months in the year when observations have not been made, feather growth is so slow that if there were any cessation of moult this could only be for a very brief period or it would have been detected. It would seem probable that in immature birds feather replacement continues slowly throughout the year.

Subsequent Immature Primary Moult

In the 25 immature birds examined which had lost all juvenile feathers, 17% had no primaries in growth, 67% had one primary, 7% two primaries and 10% three primaries in growth. The high proportion of birds with only one feather in growth at any one time suggests that the primaries may continue to be replaced centrifugally from a single moult centre.

The organisation of this primary moult can be confirmed by estimating the age of feathers according to their degree of wear; feathers become frayed during flight and also damaged on the ground, and the colour of the feathers also fades slightly. However, it is usually only very new feathers that can be confidently recognised. In all cases where an apparently recently grown primary feather was found, it was positioned immediately inwards from a currently developing feather.

In 17% of wings where no feathers were in moult, presumably the last primary had completed growth but the next feather in the sequence had not yet been shed. In a few birds where two feathers are developing, two moult waves are found and here presumably a second moult cycle has been initiated

before the first has reached the end of the wing. These birds with two feathers in moult all had a gap of at least six feathers between the two active moult regions. The 10% of wings with three feathers in growth were considered to have at least one feather growing as a result of accidental loss.

Subsequent Secondary Moult.

The continuing moult of secondary feathers in immature birds seems very irregular. However, there is clearly some underlying organisation even if a strict sequence does not seem apparent. Growing feathers often appear to be approximately equally spaced apart although the distances vary among individuals. Some typical moult patterns are shown in Fig 28 . Feathers are clearly not shed randomly (p = less than .01 Siegel Run test).

This suggests that there may be some constant relation between areas of moult activity. To try and detect any such pattern, in Fig 29 the position of all actively growing feathers has been recorded in relation to each active secondary position. A wing with secondary 1 in moult has had the positions of all other feathers that were also actively growing at the same time recorded, and the sum of all growing sites of all wings has been plotted. This has then been repeated for secondary 2 and so throughout all secondary positions. If secondary replacement was completed by the progression of a series of evenly spaced moult waves, then this should emerge from this plot as clear parallel bands of moult activity. However, Fig 29 shows that feather distribution away from the growing site corresponds roughly to a random distribution.

Figure 28

Gyps africanus

Positions of feather growth in immature birds

Bird Number		Primaries										Secondaries																			
		10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
8	Rt.						2					5							5					3							4	
	Lt.						1					2							1								5					
94	Rt.	1					2				2			3				3			1		2			1		2			
	Lt.				1		4			2		3				2		1				2			2		3				
2	Rt.				3							4							2					2					2		
	Lt.					3							1						4							2					
10	Rt.					1								1					3			1						1			
	Lt.					2				2				1		1						4									
7	Rt.	3								2				2								3	1			3					
	Lt.	2							3							2						3									

Figure 29

Secondary Positions

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22		
X	-	1	-	2	2	-	1	2	1	-	2	4	-	2	-	2	1	-	-	-	-		
-	X	-	2	-	1	1	3	1	1	-	-	2	-	3	1	-	1	3	-	-	-		
-	-	X	-	1	3	-	-	1	1	-	1	3	1	-	-	1	-	-	-	-	-	\	0 1
-	1	-	X	-	-	1	1	2	-	3	2	2	-	2	-	2	-	-	-	-	3	\	0 1
2	-	1	-	X	1	-	-	1	-	1	1	2	-	1	1	-	-	-	-	-	-	\	3 2
2	1	3	-	1	X	-	1	-	-	1	2	4	-	2	-	2	1	2	-	-	-	\	4 3
-	1	-	1	-	-	X	-	-	1	2	-	-	-	-	-	-	-	-	-	-	1	\	3 4
1	3	-	1	-	1	-	X	-	-	1	1	2	1	2	1	1	1	1	-	-	1	\	1 5
2	1	1	2	1	-	-	-	X	-	-	1	2	-	1	-	1	1	1	-	-	1	\	5 6
1	1	1	-	-	-	1	-	-	X	-	-	1	1	-	-	2	-	-	-	-	-	\	8 6
-	-	-	3	1	1	2	1	-	-	X	-	1	-	1	2	-	1	-	-	-	1	\	5 7
2	-	1	1	1	2	-	1	1	-	1	X	-	-	1	1	1	3	1	-	-	-	\	12 8
4	2	3	2	2	4	-	2	2	1	1	-	X	-	-	1	2	2	2	-	-	1	\	7 9
-	-	1	-	-	-	-	-	-	1	-	1	-	X	-	-	1	-	-	1	-	-	\	9 10
2	3	-	2	1	2	-	2	1	-	1	2	2	-	X	-	-	1	1	-	-	-	\	10 10
-	1	-	2	1	-	-	2	-	-	2	1	1	-	-	X	-	-	-	-	-	-	\	16 11
2	-	1	2	-	2	1	1	1	2	1	3	2	1	1	-	X	-	-	1	-	1	\	13 12
1	1	-	1	-	1	-	1	1	-	1	1	3	-	1	2	-	X	-	-	-	-	\	16 12
-	3	-	1	-	2	-	1	1	-	-	-	2	-	1	-	-	1	X	-	-	-	\	16 13
-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-	1	-	-	X	-	-	\	13 14
-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	X	-	\	7 14
-	-	-	3	-	-	1	1	1	-	2	-	2	-	-	1	1	1	-	-	-	X	\	1 15
																						a	
0	0	3	4	3	2	5	7	7	13	10	10	16	13	15	15	16	14	10	3				
1	2	3	3	4	5	6	6	7	8	8	9	10	10	11	12	12	13	14	14				b

X = Secondary position in active growth.

Figures at other secondary positions (reading along the horizontal rows) indicate the number of occasions on which a wing with a feather in the X position in active growth was found to have that particular site also developing.

a' Observed frequency total along row.

b Frequency that would be expected if there were an equal probability of growth at each site.

There is therefore no evidence to suggest that feather replacement occurs by the propagation of a series of moult waves along the wing. It is difficult to age feathers confidently, but obviously recently grown feathers are usually not found next to actively growing sites.

However, it is clear from Fig 29 that the presence of a moulting feather in one site means that adjacent feathers are unlikely to be in active growth. This is demonstrated in Fig 30 which shows a breakdown of the distance between individual growing feathers. Wings have been separated here according to the number of actively growing secondary feathers on each wing. Thus for wings with five feathers in active growth, the distance from each individual growing feather to the nearest actively growing feather has been recorded. This has then been repeated for wings with 4, 3 and 2 feathers in active growth. This shows that the frequency with which a site adjacent to a growing feather had another feather in active growth was highly significantly different from the frequency expected if there were an equal probability of growth at each site. The number of wings examined is not sufficient to be able to consider further sites in this way. However, there is a very clear tendency for growing feathers to be placed a certain distance away from another growing feather.

It would therefore appear that, as in the juvenile moult, secondary replacement does not result from cycles of moult waves passing along the wing. Feathers develop apparently independently, although a site of feather growth does not develop near to other actively growing feathers.

Immature birds had an average of 2·3 feathers in active growth at any one time. If each feather requires 90 days for growth, then an average of about 13 feathers will develop each year. Each of the 25

Figure 30

Adults and Immatures Combined

Sum of wings found in the following condition

		Distance from each growing feather to nearest growing site.										
		1*	1	2	3	4	5	6	7	8	9	10 ---- 13
Number of Feathers Growing in wing	2	1.5	-	-	2	6	4	2	2	4	2	6 2
	3	5.8	-	4	11	12	6	13	6	2	2	- -
	4	10.9	2	15	21	15	8	5	-	1	1	1 -
	5	6.7	2	10	8	9	1	1	-	-	-	- -
	6	5.4	4	10	3	1	1	-	-	-	-	- -

* Frequency expected at site if there were equal probability of growth at each position

2 feathers in wing - expected frequency 30/20 = 1.5

3 feathers in wing - expected frequency 56/20 + 56/19 = 5.75

4 feathers in wing - expected frequency 69/20 + 69/19 + 69/18 = 10.91

etc.

Observed frequency of growth in site adjacent to growing site, compared to expected frequency if there were equal probability of growth at each site.

$X^2 = 18.2$, df = 4, p = 0.01.

secondary feathers might therefore be expected to be replaced about every second year.

Tail Moult in Immatures

Of the 16 immature birds examined for tail moult, 3 had no feathers in growth, 2 had one, 5 had two, 2 had three, 2 had four, 1 had five and 1 had eight. Accidental loss of feathers is probably responsible for some tail regeneration, especially in situations where large blocks of up to eight feathers are found growing together at the same stage of growth. Tail moult is probably completely irregular, as was found in juvenile moult, and 71% of developing feathers in the left tract did not have the corresponding feather of the right tract also in moult,

Contour Feather Moult

Moult was actively occuring in the upper wing covert tracts of 91% of the birds examined, in the underwing coverts in 45% of birds, in the upperparts in 91% and the underparts in 82%. Body moult appears to proceed at about the same speed as in early juvenile moult and only a few feathers are found in active growth in any tract.

Symmetry of Moult Development in the Two Wings

There is surprisingly little symmetry apparent between the growing secondary feathers of the two wings of any individual. A growing position on the right wing has been compared with the distance to the nearest

actively growing feather to the corresponding site on the left wing of the same bird, and also with the position on the left wing of another randomly selected bird. If the two wings of an individual are moulted entirely symmetrically, then both wings will have the same feather sites in growth at any one time, and distances recorded would all be 0. However, a comparison of wings from entirely unrelated birds should show a random spread of distances.

Distance to nearest actively growing feather.

	0	1	2	3	4	5	6	7	8	9
Related wings	11	7	4	5	2	1	1	0	1	0
Unrelated wings	3	6	10	4	4	0	0	1	2	2

There is clearly a tendency towards symmetry, although there is no significant difference between the relationship of growing feathers on the two wings of the same bird and those of two completely unrelated wings (Kolmogorov-Smirnov).

Primary feathers, however, which are replaced by the orderly progression of a moult wave, do show symmetry. In 62% of cases the two wings were growing in complete symmetry and in most other cases the differences between moulting positions in the two wings were only slight.

Distance to nearest actively growing feather from corresponding site on other wing.

	0	1	2	3	4	5	6
1 feather in growth	5	1	0	0	1	0	0
2 feathers in growth	3	2	0	0	0	0	0

Adult Birds

The basic pattern of moult development in adult birds does not apparently differ from that of immature birds although the timing becomes irregular. Primary moult continues by the outwards progression of moult waves. However, there is greater variation in the speed of moult in different individuals.

Percentage of birds with the following number of Primaries in Growth.

	0	1	2	3	Number of birds
Immatures	17%	67%	8%	10%	25
Adults	40%	33%	26%	2%	34

However, the higher proportion of birds with no primary feathers in growth does not simply reflect a slowing down of the rate of primary moult, but is the result of a deceleration in all flight feather growth in these individuals. Those birds with no primary feathers in growth also have significantly fewer secondary feathers growing compared to birds with two primary feathers in growth ($p = .01$ Kolmogorov-Smirnov)

		Number of Primaries in Growth		
		0	1	2
Number of Secondaries in Growth	0	9	3	0
	1	5	3	2
	2	4	4	2
	3	0	3	5
	4	2	4	1
	5	1	0	4
	6	0	0	0

This effect is not found in immature birds, where the rate of

feather growth is relatively constant. Some adult birds therefore clearly show a decline in moult activity and other individuals relatively rapid moult development compared to the normal rate of immature moult. This is not a seasonal effect and was recorded throughout the period of study.

The white tern Gygis alba (Ashmole 1968) and the white booby Sula dactylatra (Dorward 1962) also show a moult pattern which is continuous throughout the life of the bird, but in these species the moult ceases when a bird starts to breed. It is possible that in adult vultures it is only the breeding birds which show a decline or pause in moult activity and accelerated moult occurs outside the breeding season or among birds which are not breeding that year.

The middle period during rearing is the season when food is probable in shortest supply for the breeding birds (page 150) and if moult activity were to cease at any stage during breeding it might be expected to occur at this time. Five adult birds were shot from their nests towards the end of the breeding season when they were attending large chicks. However, all five birds were found to be in active moult (2 wings with three growing feathers, 2 with four, 3 with five, 2 with six and 1 with seven.) Birds apparently in breeding condition but which were collected away from the nest may have failed, or not attempted to breed that year, and cannot confidently be assumed to be actively breeding. However, three females were collected with very large ovum or greatly swollen oviducts which had clearly been on the point of, or just finished laying. Although one of these birds had no wing or tail feathers in moult, one had 5 and 2 feathers in growth in the two wings, and the third 11 and 9 (the largest number of growing feathers recorded from any bird).

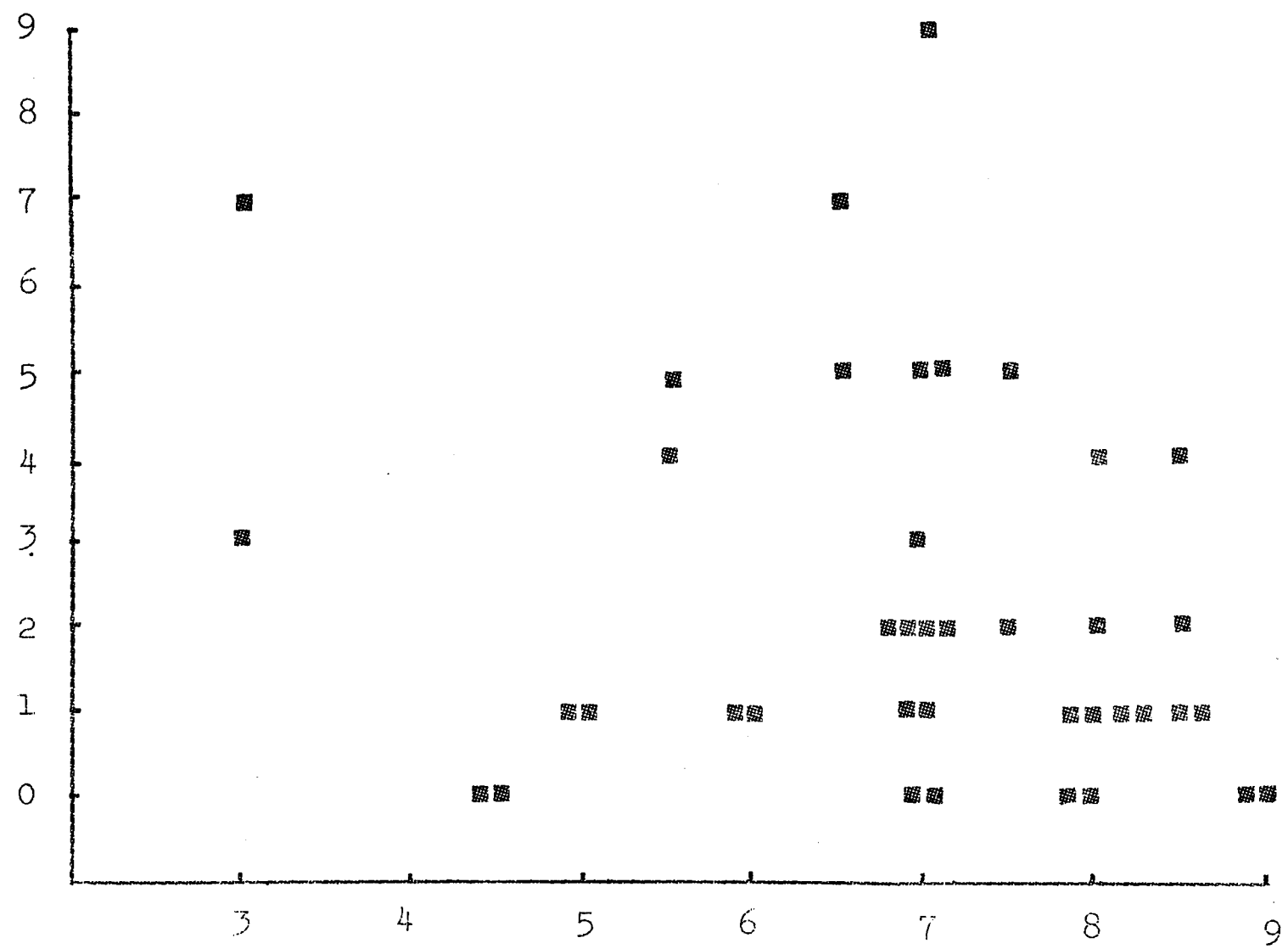
There is therefore no clear correlation of a decline in moult activity with breeding condition. Birds might be able to arrest moult at any stage in the cycle leaving feathers part grown until conditions improved. However, no adult bird is known to be able to arrest feather growth. It will be shown that nestling Ruppell's griffon cannot reduce the speed of feather growth under poor food conditions and it is unlikely that adult birds would be able to do this.

Colquhoun (1951) found that young wood pigeons Columba palumbus cease moult in cold weather, presumably due to food shortage or heat loss, and Potts (1971) found that shag Phalacrocorax aristotelis ceased moult in winter, which is the season when food is in shortest supply. The rate of moult development in vultures might be connected with food availability, and birds with few feathers in growth may be obtaining less food that those in strong moult. To examine this, in Fig 31 the number of growing feathers on the right wing of a bird has been plotted against the fat score index, a score of body condition (page 145). The degree of moult activity does not appear to be correlated with the condition of the bird.

Tail Moult in Adult Birds

Out of 28 birds examined for tail moult, 61% had no feathers in growth, 10% had one, 10% had two, 7% had three and 10% five feathers growing. There is a very high proportion of birds with no developing feathers compared to immature birds, which had 19% of individuals showing no moult. Possibly tail moult is slower, or seasonal, in adult birds. Only 28% of the feathers developing in the left tract had the corresponding feather of the right tract also in moult, which is the same proportion of symmetrical moult as was found in immature birds.

Figure 31


Number of flight feathers in growth
9
8
7
6
5
4
3
2
1
0
3
4
5
6
7
8
9
Fat score

Body Feather Moult

Most adult birds have covert feathers which are very bady worn compared to those of immature birds. Body feather moult is probably generally very greatly reduced, or possibly seasonally heavy, in adult birds and usually only a few isolated feathers could be found developing in any tract. Assuming that adult feathers wear in a similar manner to those of the immature plumage, it would appear that many covert feathers are not renewed until four or more years old. Moult was recorded in 46% of birds in the covert tracts, 27% in the underwing coverts, 27% in the ventral tracts and 42% in the dorsal tracts. There is no clear relationship between the occurence of body moult and the rate of flight feather development.

Birds in adult plumage therefore show the same basic pattern of feather replacements as immature birds, although there is a variation in the speed of moult which could not be associated with breeding or body condition.

Ruppell's Griffon vulture

The sequence of moult development for the Ruppell's griffon vulture is not known in the same detail as that for the whiteback because few juvenile birds were found during the chief study period. Observations have therefore been confined to adult birds in breeding condition and birds kept in captivity.

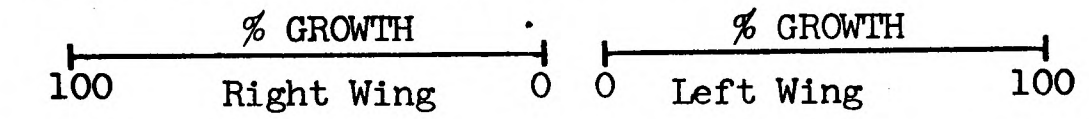
Captive birds did not start moult until about 10 months after leaving the nest. Moult then started with the innermost primary

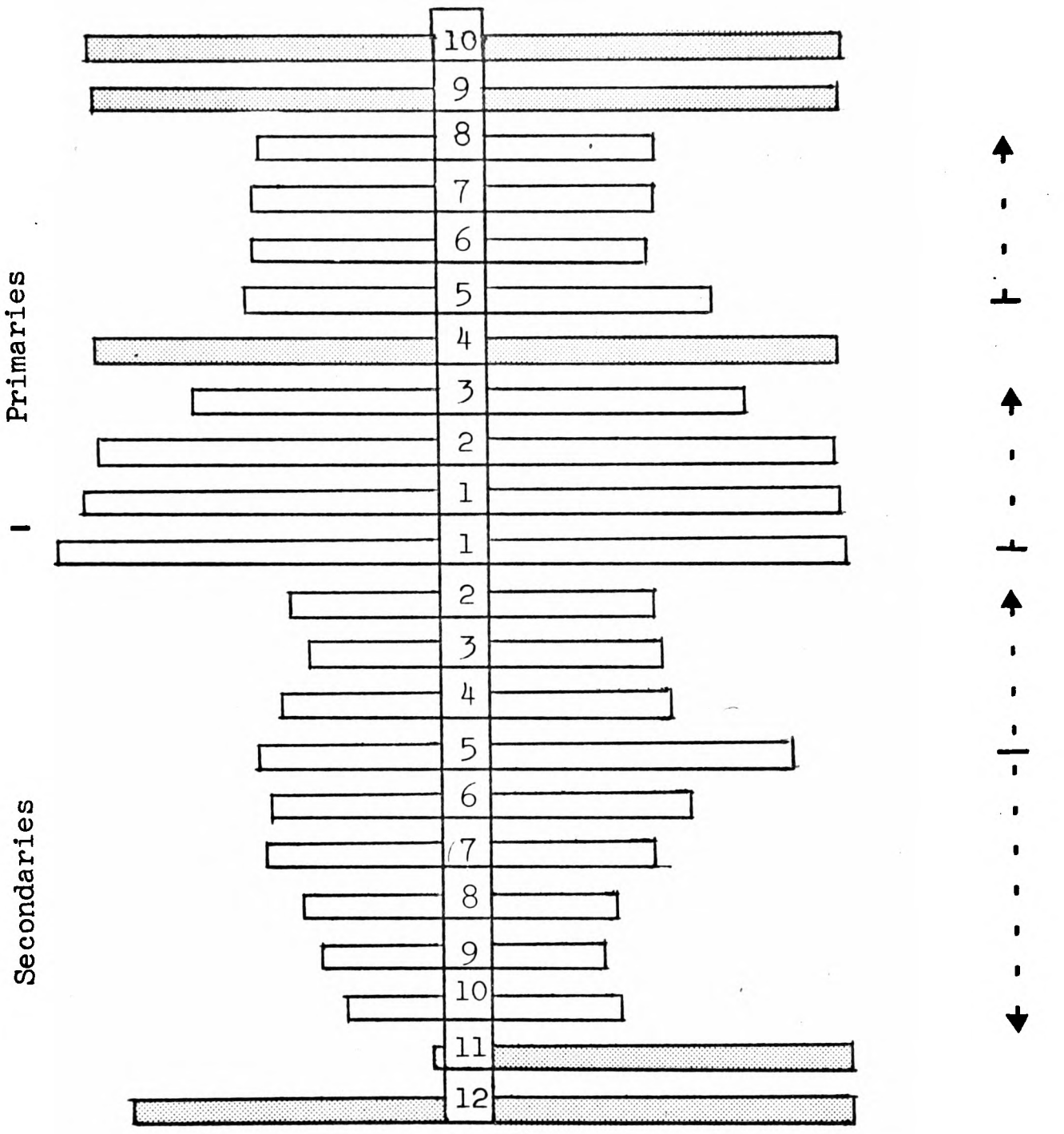
feather and from this position moult spread along the primary row causing the replacement of three primary feathers in an orderly sequence towards the tip of the wing. As in the whiteback vulture, feather growth did not begin until the adjacent feather had completed growth and about nine months were required to complete the growth of the first new primary feathers.

Captive birds did not start secondary replacement before the study finished. However, at one stage a bird was examined daily and weighed, and following this traumatic experience 29 of the flight feathers were shed within a month. This was obviously a highly aberrant reaction. However, the sequence in which these feathers were dropped was almost constant for the two wings. This suggests that this effect might have been caused by an exceptional hormonal imbalance or a uniform lowering of the threshold for growth among all follicles, resulting in a highly accelerated moult development in which the sequence of feather replacement remained normal although the intervals between feather growth were sharply telescoped. This sequence must obviously be regarded with considerable suspicion, but as shown in Fig 32 it might suggest that primary replacement is caused by two moult waves starting at primaries 7 and 11 moving towards the tip of the wing, and secondary replacement develops from a moult wave spreading in both directions from secondary 15.

However, one young bird shot in July was found to have only one primary feather moult sequence which had spread in both wings causing the replacement of five primary feathers, and secondary moult was apparently irregular with no indication of the spread of moult waves, and this suggests that normal feather replacement follows the pattern found in

Captive Gyps ruppellii 30th June 1970





Old Feather Remaining

New Feather.

the whiteback vulture.

In adult birds moult apparently proceeds very slowly.

Percentage of birds with the following number of developing tail and wing feathers.

Gyps ruppellii

	0	1	2	3	4	5	6	7	8	N
Primaries	40%	38%	20%	2%	-	-	-	-	-	25
Secondaries	29%	20%	24%	14%	4%	4%	2%	2%	-	25
Primaries + Secondaries	21%	20%	18%	10%	14%	8%	6%	-	4%	25
Tail	68%	4%	8%	8%	8%	4%	-	-	-	25

Two wings scored separately from each bird.

These figures are remarkably similar to those recorded for the whiteback vulture adult moult development, which are summarised below.

Percentage of birds with the following number of developing tail and wing feathers

Gyps africanus

	0	1	2	3	4	5	6	7	8	N
Primaries	44%	34%	20%	2%	-	-	-	-	-	25
Secondaries	30%	18%	16%	18%	12%	4%	2%	-	-	25
Primaries + Secondaries	16%	24%	16%	8%	10%	16%	4%	6%	-	25
Tail	62%	12%	8%	4%	-	12%	-	-	-	25

Two wings scored separately from each bird.

As for the whiteback vulture, Ruppell's griffon adults with no primary feathers in growth also have few secondary feathers in growth compared to birds with two primary feathers developing.

Number of Secondaries in growth	Number of Primaries in growth: 0	1	2
0	8	5	0
1	5	4	1
2	5	3	4
3	1	3	2
4	0	1	2
5	0	2	1
6	0	0	1
7	0	1	0

(p = .01 Kolmogorov Smirnov)

This species therefore also shows individual variation in the speed of feather replacement in the adults.

Body moult in this species also seems to be greatly reduced in the adults. Only a few isolated feathers are found in growth in any tract, and moult was recorded in the upper wing coverts in 36% of birds, underwing coverts in 20%, dorsal tracts in 44% and ventral tracts in 32% (25 individuals). There does not appear to be any relation between the speed of flight feather replacement and the presence of developing contour feathers.

Discussion

The general pattern of moult development in griffon vultures does not apparently differ greatly from that of other large birds of prey. The rate of moult development in the Accipitridae is generally poorly known. An incomplete annual moult seems to be characteristic of the larger eagles (Aquilid group). This is suggested by Friedman's account of Aquila rapax (1930) and supported by Jollie (1947) and also by Heinroth (1898) for Aquila clanga. However, the

bald eagle Haliaeetus leucocephalus apparently undertakes a complete moult annually (Crandall 1941) and the lammergeier Gypaetus barbatus has a complete moult of the flight feathers every year although the body plumage takes two years to renew (Serventov quoting Menzbier 1894). The golden eagle Aquila chrysaetos takes two seasons for a complete re-growth of plumage, although some tracts are renewed anually (Jollie 1947 Spofford 1946). These larger eagles therefore seem to renew their primary feathers annually, although a complete body moult may require up to two years. The griffon vulture would therefore appear to be exceptionally slow in the rate of feather replacement. However, the wings are considerably larger than those of eagles, and the unrelated Californian Condor Gymnogyps californianus which is a similar type of bird, in captivity requires two years for the completion of primary moult and individual feathers take over two months to develop, which is similar to the griffon vultures (Todd & Gale 1970).

Primary moult in the Accipitridae is always descendent, although there are often irregularities in the sequence which increase with the age of the bird (Streseman 1968). In the buzzard Buteo buteo some feathers are missed during the passage of a moult sequence and are moulted the following year out of sequence (Pierchocki 1963). Primary moult in Aquila chrysaetos may be similar to that of griffon vultures in that a second wave of moult activity may start before the first has reached the end of the wing (Jollie 1947). Primary moult can here probably be considered as a continuous activity throughout the life of the bird, with pauses during the winter period. Some other types of bird show a continuous pattern of moult activity and have pauses during the breeding seasons such as the white booby Sula dactylatra (Dorward 1962) and some tropical terns (Gygis alba Ashmole 1968). The continuous

moult activity in adult griffon vultures does fluctuate, but this could not be clearly correlated with breeding. However other birds of prey do not seem to stop feather growth during breeding and active moult has been recorded in breeding Accipiter gentilis and Accipiter nisus (Brull 1964), Buteo platypterus and Buteo lagopus (Streseman 1968) and Pernis apivorus (Dementiev 1951).

Little is known of secondary moult sequences in large birds of prey, although Streseman (1968) considered that three centres of moult activity seemed to be found from which feathers were moulted in a descendent manner, but with usually considerable irregularities. Griffon vultures do show three general regions of moult activity in the first juvenile moult, but irregularities seem the rule in further moult development.

Energy Requirements for Moult

During moult an increased energy intake will be needed both for feather growth and to compensate for the greater heat loss through the plumage while feather development is occuring. Thus in birds with short moulting periods the metabolic rate may increase during moult by up to 25% in the chaffinch Fringilla coelebs (Kock & de Bont 1944), 26% for the Ortolan bunting Emberiza hortulana (Wallgren 1954) and 45% for the domestic hen (Perek & Sulman 1945). Lustick (1970) attempted to separate these two effects and found that cowbirds Molothrus ater obscurus which moulted in the thermal neutral zone increased their oxygen consumption by only 13%, which is presumably entirely required for feather formation. Increased energy requirements above this level were found in conditions where the bird had also to compensate for additional heat loss caused by the moult. A vulture

moults so slowly that only a fraction of a percentage of the contour feathers are developing at any one time, and presumably the insulation properties of the plumage are virtually constant.

Now that the rate of moult development is approximately known, it is possible to obtain a rough estimate of the importance of moult as an energy demanding process. The dry feather weights of a whiteback vulture, which was obtained by plucking all down and contour feathers, are shown below.

Feather weights	Weight of Bird	Flight Feathers	Body Feathers	Total Feather Weight	% of body weight
Gyps africanus	4800	195	265	460	9.6%
Gyps ruppellii	7000	241	392	633	9.0%
Bald Eagle	4082	-	-	677	16.2%

(Brodkorb 1955)

If we consider a juvenile whiteback vulture which takes about three years to complete the first feather replacement, then an average of about 150gms of feathers will be produced each year. Feather tissue is composed almost entirely of keratin, which has a heat of combustion of 5.5 kcals/gm. Although the energy required for the formation of this protein by the bird will be considerably less than this, since the protein will be largely developed from amino acid precursors, we can take this figure as an approximation. This represents a production of about 825 kcals of stored energy per year. If the efficiency of this growth is taken as 10%, then an intake of about 8,250 kcals will be required for feather growth in the year. This would be provided by about 2,000 gms of protein, or about 8,000 gms of meat, or about seven 'crop fulls of food'. Actually feather growth does not develop at a constant rate during moult and some birds seem to moult considerably more slowly than this when adult. However, these figures do give a rough indication of the relative importance

of feather growth. An intake of about 8,000 gms. of food per year, or about 22 gms. per day is required for feather growth out of an estimated total of about 380 gms intake per day for total maintainance requirements (page 62). The growth of feathers therefore accounts for about 6% of the total energy intake of the bird.

King and Farner (1967) carried out this calculation for a house sparrow Passer domesticus during moult when 1.7 gms of feather tissue is produced in 60 days. Making the same assumptions as for the vulture, their figures show that the increase in energy intake for feather formation in this species is 7.6% of the total energy intake - a figure which has been confirmed by the experimental study by Blackmore (1970). The proportion of energy intake required for feather growth in a sparrow and a vulture are therefore similar, although the vulture moults continuously through 52 weeks of the year and does not complete a moult for three years, while a sparrow undertakes a total feather replacement within about 9 weeks.

c) BREEDING

Introduction

In this section the food requirements for breeding are considered, chiefly for the Ruppell's griffon. The energy requirements for egg laying and rearing the young are estimated and then compared with the availability of food through the breeding season to give an indication of how difficult it is for a bird to satisfy the energy requirements for breeding. Griffon vultures have some advantages for this type of study since they are very abundant, and breed in colonies and are therefore easier to study than most birds of prey. They also eat the same type of food throughout the year and it is possible to estimate the food availability through the breeding season. Most studies of the effect of the food supply on reproduction have been on passerine species, with important studies among the smaller birds of prey on the Kestrel (Cave 1968), Tawny Owl (Southern 1954, 1959, 1970) Arctic predators (Pitelka 1955) and Buzzard (Mebs 1964).

The breeding of large birds of prey such as vultures poses several interesting problems, especially concerning the significance of their low reproductive potential (Amadon 1964). All species take several years to reach sexual maturity and have a low reproductive rate once breeding age is reached. The two major theories on the significance of reproductive rates in birds interpret this in different ways. Wynne Edwards (1955 & 1962) considered that the reproductive rate of each species evolved through the process of group selection to equal the average yearly mortality. A group of animals which produces more offspring than are needed to balance the annual mortality will increase in size until there are more individuals

than can be supported in the area. This stock will eventually be replaced by another population whose social organisation holds the reproductive rates so as to balance the mortality, and hence can maintain an optimum population density which utilises the food resources more efficiently. A low reproductive rate, caused by both deferred maturity and small clutch size, is therefore considered to be an adjustment of the recruitment to balance a low mortality.

Lack (1954), however, considered that an animal's reproductive rate was evolved by natural selection so that each pair produced the greatest possible number of young which survive to breeding age. A small clutch size is considered to represent the greatest number of young that the parents can successfully rear to independence in the species concerned. Breeding would be deferred in such birds only if individuals which attempted to breed earlier were both unsuccessful and, by breeding, suffered a higher mortality than non breeding birds of a similar age. Birds which attempted to breed while relatively young would thus leave fewer offspring than those which deferred their breeding until later.

This latter theory implies that, for these species, during most years the rearing of the young imposes very considerable demands on the bird; demands which inexperienced or inefficient birds cannot meet. This contrasts sharply with the implications of Wynne Edward's theory, which assumes that the social organisation is holding the reproductive potential below the possible level and birds are not therefore actually breeding as fast as the food supply would allow. Theoretically the adults are capable of rearing more young than they in fact do, and immature birds are capable of obtaining sufficient food to rear young.

However, there is little evidence for either of these views, especially the effect of breeding on an individual's chance of survival. Griffon vultures have the low reproductive potential typical of large birds of prey, since only one egg is laid and sexual maturity is deferred until the 6th or 7th year (Appendix 1).

In this section the breeding season and activities are first briefly described for both whiteback and Ruppell's griffon.

Whiteback vulture

Whiteback vultures occur typically in lowland savanna country and nest on the thick mat of twigs on the edge of the crown of large Acacia trees, or on prominent tall branches projecting beyond the tree crown. The loose nest, about two to three feet in diameter, is built from small branches, as described by Brown and Amadon (1968). Nests may be isolated on a tall tree in the savanna, but tend to be concentrated on the largest trees which grow along the river courses, such as Acacia xanthophloea and Ficus sp.

An area of about 40 square miles covering part of the Seronera river and it's tributaries was used to observe whiteback breeding. About 45 nests were built, all on the crown of Acacia xanthophloea between 40 and 70 feet above the ground. This tree has very smooth and straight limbs with a powdering bark which makes it considerably more difficult to climb than most other tree species, and ground predators may be deterred from attempting to reach the nests. A pair of birds will usually defend an area of only a few feet round their nest. Very occasionally two nests may be found in the same tree, and North (1944) reported one tree containing six nests, although usually the breeding sites are well spaced along the

river. Such an aggregation of whiteback nests is sometimes referred to as a loose colony (Brown & Amadon 1968) which implies a deliberate choice of a nest site adjacent to another individual, whereas in the case of the whiteback vulture is seems probable that in any favourable area the most suitable large trees tend to grow along the rivers and nesting has to be concentrated in these areas.

A typical two and a half mile stretch of a tributary of the Seronera river supported an almost uniform xanthophlea thicket containing twelve nests. If the river is divided into 25 sections of 1/10th mile each, then none of the sections contains two nests and the distribution of nests does not differ significantly from random distribution on a run test (Siegel 1956) However, this is assuming that the tree thicket was of uniform distribution and suitability for nesting. Almost all rivers in the Serengeti which support large trees in the riverine thicket have a large number of nesting whiteback vultures.

North (1944) reported that one nest was used for breeding in nine consecutive years, although it is not known if the same pair of birds were using the nest. In the 1970 season 72% of a group of 22 nests that had successfully been used the previous year were repaired and used again, although three nests out of a group of four which had been regularly disturbed by taking measurements during the previous season were not re-occupied. This might indicate that birds usually return to their old nest site unless this has been found unsuitable, although the figures are not very conclusive ($p = .05$ Fischer exact prob. test.)

Copulation is observed from early February on, both at and away from the nest sites, lasting for about 25 to 35 seconds. There does not appear to be any display on the nest before or after copulation, which occurs

several times a day during nest building. The birds spend most of the day standing on or near the nest site, and one sex collects most of the branches and carries them in the bill. Branches were all seen to be taken from other adjacent nests, except for the green branches which line the nest and which are torn, with considerable difficulty, from the Acacia xanthophloea trees and loosely placed around the nest.

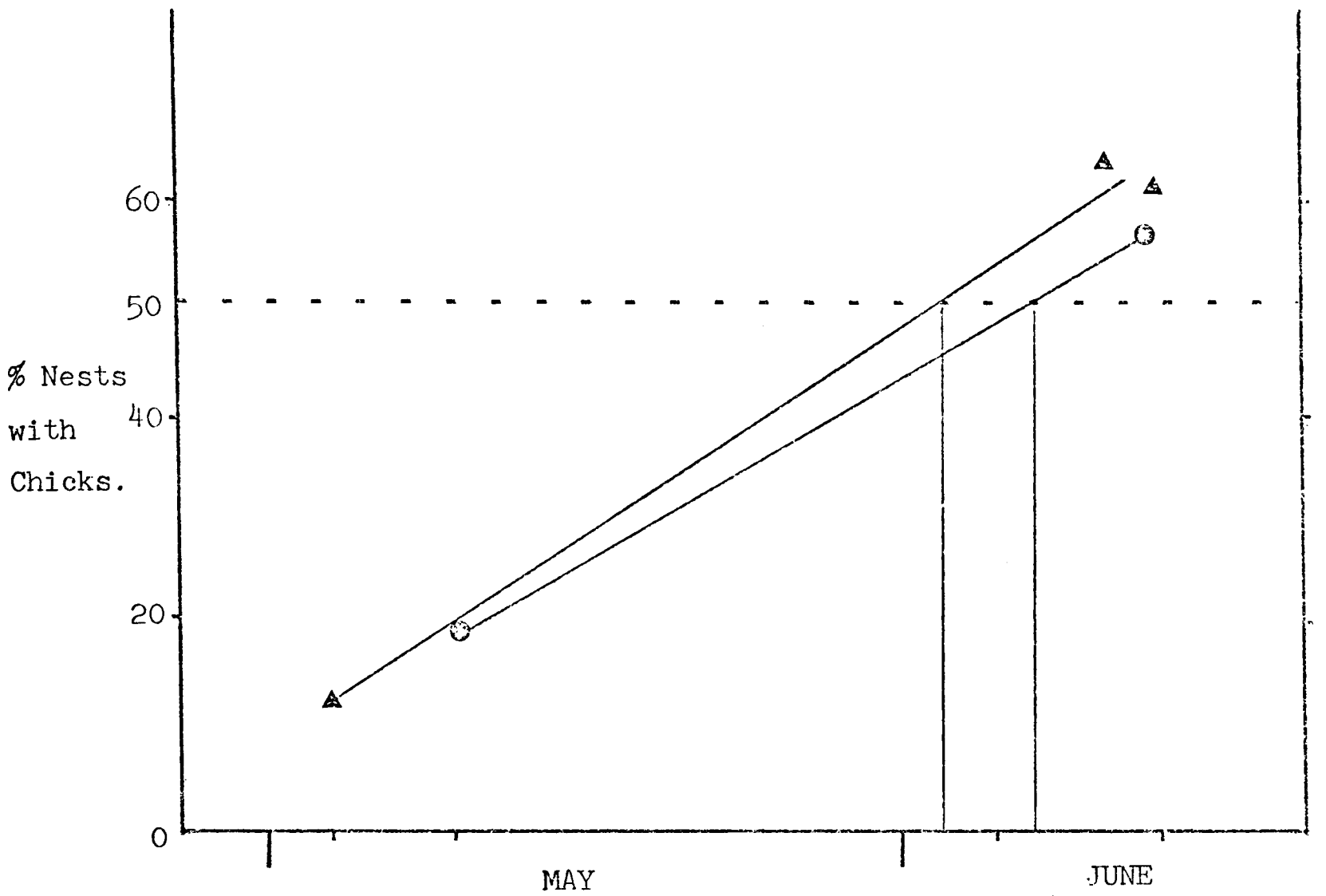
A single white egg is laid and both sexes incubate (Granvik in Jackson 1938, Van Someren 1956) for a period of about 45 days (Van Someren 1956). During incubation both birds are present at the nest for long periods.

As nests were inaccessible, the contents could be checked only by making flights in a light aircraft along the river courses and observing them from above. Incubating birds usually sit tightly on the nest and only occasionally could eggs be seen. The chick is brooded for the first few days after hatching, but after this the adult usually stands at the side of the nest shading the chick from the sun, and chicks older than a few days could be seen from the air. In Fig 33 birds which were sitting tightly on nests have been assumed to be incubating eggs. This shows that a rough approximation of the dates at which 50% of the eggs had hatched in 1969 and 1970 to be the 1st and 5th of June respectively. If these eggs are assumed to have been laid 45 days previously, this would place the date at which 50% of the successful birds had laid at approximately the 16th and 20th April for these two years.

The spread of laying was estimated in 1970 by attempting to age the chicks in the nests by comparing their size with those of hand reared young of known age, and then calculating back to the date on which the egg would have been laid. Only very brief observations could be made from a light aircraft and the dates given in Fig 34 should be considered accurate to only

Estimate of hatching date for 50% of nests. Figure 33

Gyps africanus



Assuming a constant rate of hatching

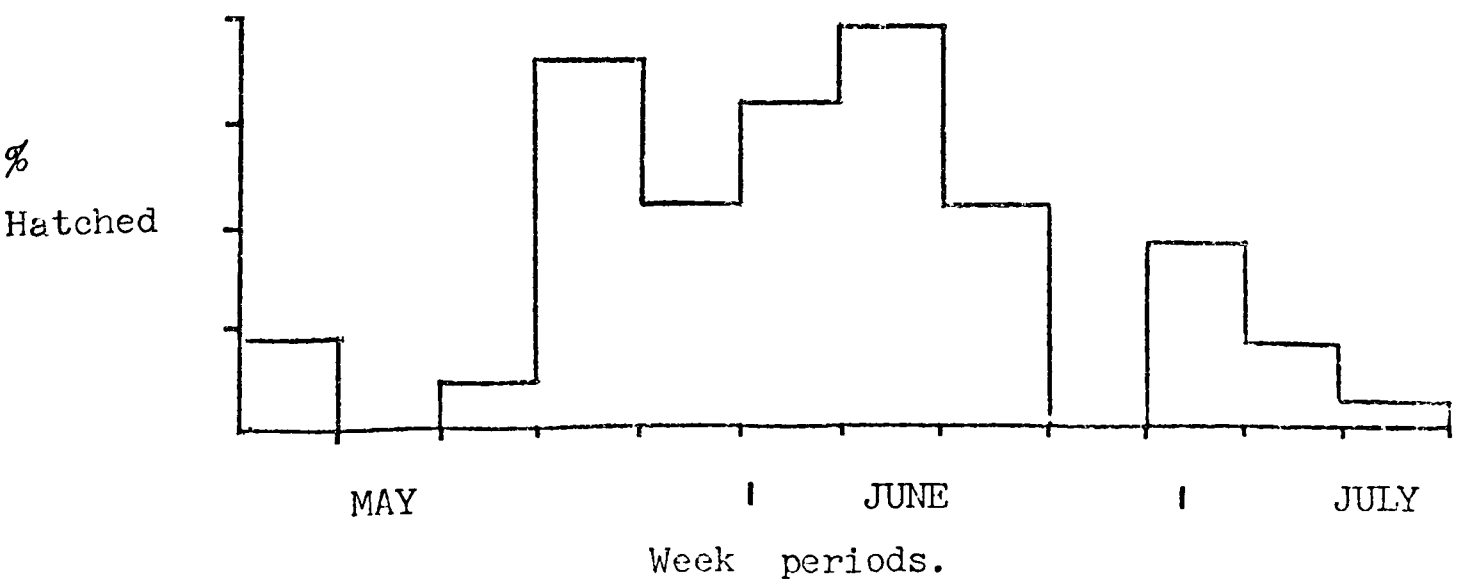
Seronera & Mbalageti rivers Figure 34

Mean number of nests 42

▲ 1969

● 1970

Gyps africanus



Sample size 44.

about ten days either way.

Both parents feed the young and there is one adult in attendance at the nest almost continuously until the young fledges. There would also seem to be some attention paid to the young by other adult birds, although the extent or importance of this is not known. At one nest the two 'parents' were shot and these birds were later found to be both males, and another nest where the two 'parents' were collected was later found to have a third adult guarding the chick.

Some indication of the carcasses on which birds were feeding could be obtained from identifying hairs which were found in the pellets produced by parent birds at the nest. The hairs of the common large ungulates have distinctive shape and pigment deposition and they can be easily identified by using a dissecting microscope and comparison with a reference collection of hair samples. Since griffon vultures specialize in taking the soft parts of carcasses, pellets are produced very infrequently and they usually consist chiefly of grass, with only a few hairs. The frequency with which hairs of different species occur in the pellets probably bears little relation to the proportion of species eaten, since in small animals, such as young gazelle, the skin is regularly torn and eaten and hairs are likely to occur frequently after feeding, while feeding off large animals such as buffalo and elephant would not be recorded because hairs would probably rarely be swallowed. However, if the hairs from a particular animal are found, it is reasonable to assume that the bird has been feeding off that animal.

Hairs identified from pellets produced by breeding birds 1969 Seronera

	May	June		July		August
	15-31	1-15	16-30	1-15	16-31	1-15
Wildebeest			*	*	*	*
Zebra			*		*	*
Gazelle	*		*	*	*	*
Total number examined	2	0	9	4	14	17

Through the breeding season the birds seem to be continuing to feed off wildebeest, zebra and gazelle, with no other species regularly represented in the pellets. During the six months of the breeding season the herds of these animals migrate from the plains into the bush country and may at some period be over sixty miles away from the nesting sites. It appears that the breeding birds continue to travel to these herds to search for food. They are not relying on the locally resident species, such as Impala and Kongoni, which are usually found only in relatively low density. Since the breeding season is extensive and the herds travel considerable distances during this period, there is no nesting area in the Serengeti which will be close to these herds throughout the season and all birds must at some period while breeding either attempt to find sufficient food from the small number of resident game, or travel considerable distances to find the larger concentrations of migrating animals.

The young are in the nest for about three to three and a half months. Breeding success was recorded from nests in the Seronera area, which were mapped and then regularly observed both from the air and the ground to check nest contents and nesting activity. Since eggs were rarely seen, the hatching success could not be determined separately. Birds were assumed to be incubating if they were recorded sitting tightly on a nest for more than 14 days. In 1969 out of 43 nests which started incubation, 40 (93%) reared chicks to within 4 to 8 weeks of fledging, when observations had to

finish. In the 1970 season, 41 nests started incubation and 34 (83%) reared chicks to fledging. Since regular observations were not possible the causes of breeding failure are not known. However, nests which failed did so early in the breeding season, and no mortality occured to any chicks beyond about four weeks of age. Breeding success was therefore high in both seasons.

Ruppell's griffon vulture

Ruppell's griffon vultures are a highland species of griffon vulture which nest colonially on cliff ledges. Observations were made, approximately every ten days, at a colony on the cliffs of the gorge of the Karian river in the Oldonyo Gol range. The Gol mountains have an eastern escarpment of vertical cliffs formed by the Eyasi rift fault, and the Karian gorge is a narrow canyon into this rift escarpment about 500 feet wide and with walls up to 900 feet high. It is possible to climb up either side of this gorge and overlook the nests built on ledges on the opposite wall, and in the 1970 season the gorge contained about 130 nests, 85 of which could be easily overlooked. The Karian river colony is only a small part of the breeding colonies on the Gol escarpment, which exceed 1,000 nests and form the largest griffon colony known in eastern Africa. However, no other part of the colony is easily accessible. The weathered quartzite cliffs provide numerous suitable nesting ledges, and the prevailing wind direction from the west produces an almost continuously rising flow of air over the cliff surfaces. Birds nesting on the ledges can therefore enter and leave the colony at all times of day and soar along in the rising air over the cliff ridge. They are not therefore dependent on waiting until the sun has generated sufficient thermals before leaving the colony. Birds are usually airborn shortly after first light and would start leaving the gorge at about 6.30 to soar along the rift escarpment.



Karian river gorge in Oldonyo Gol.



Ruppell's griffon vultures on breeding ledges.

There would not appear to be any shortage of suitable nest sites in the Karian colony. In one area of cliff watched in 1969 and 1970, of 25 nest sites in which young were successfully reared in the 1969 season, only 16 (64%) were used again in 1970, and another 11 sites were occupied which had not been used the previous year. There were also several ledges which were not used in either season, but showed the remains of nests built in previous years.

All the branches which were seen to be used for building were stolen from the nests of other birds, with the exception of the grass and green branches which the birds use to line their nests, and which were torn from the top of the cliffs and from the Euphorbia tirucalli trees at the base of the gorge. Most of the nesting material is collected by one sex, and is carried in the bill to the mate, who arranges it on the nest.

Observations on the colony could not be started before mid January in 1970, when most birds had started incubation. Copulation was frequently observed at this time, apparently from pairs which had not yet laid, lasting from 8 to 30 seconds, average 17, and accompanied by a coarse, rasping call. 24% of the mating observed occured on nest sites, 65% on rock ledges and 11% on the communal roosting ledges. Mating was observed six times in two hours on one nest site. No matings were heard after mid February.

A nest may consist of only a few branches, but nests that are renewed annually may develop into a structure about five feet across. The nest is usually lined with grass or green branches before the single white egg is laid. North (1944) has observed a single nest containing two eggs at Naivasha, but this was not observed in the 132 nests found in the Karian colony. Both sexes incubate the egg, and although the incubation period is not known, it is assumed to be about 55 days, as is found in other

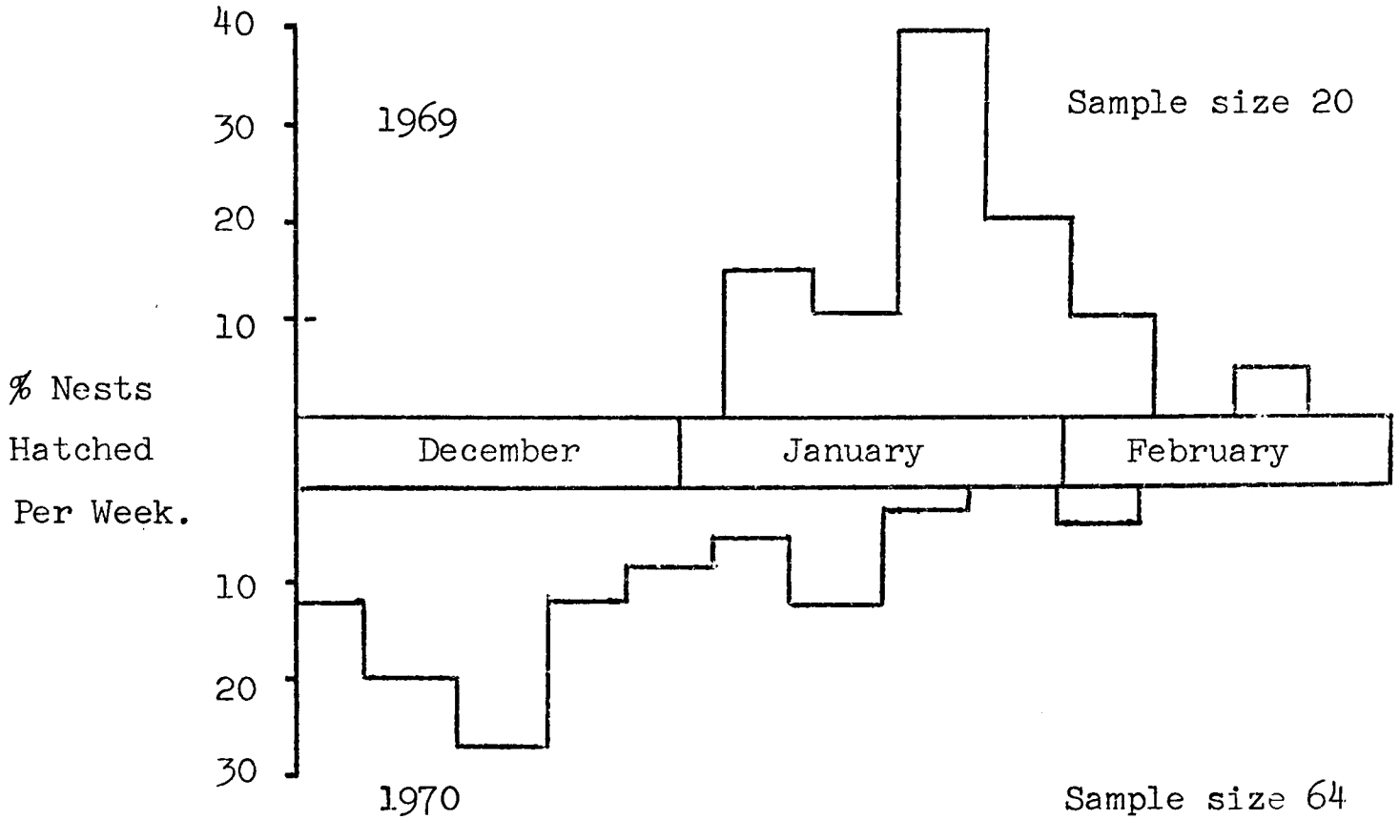
large griffon vultures.

Species	Incubation period	Source
Gyps fulvus		
7 to 8 kilo	52 days	Brown & Amadon (1968)
	58 - 65 days	Brown & Amadon (1968) captivity
	52 - 55 days	Kowalaska (1970) captivity
	53 - 59 days	Bouillault (1970) captivity
	50 - 55 days	Geilikman (1967)
	51 - 52 days	Heinroth (1922)
	50 days	Terrasse & Boudoint (1960)
	52 days	Fischer (1963)
Gyps coprotheres	52 - 53 days	Brown & Amadon (1968)
	56 - 63 days	Hurry (pers. comm.)

The approximate dates of laying in the colony were obtained by estimating the age in weeks of the chicks seen in the nests and assuming that there is a 55 day incubation. This gives an approximate median laying date as December 25th in 1970 and January 27th in 1969. The spread of laying for the two seasons is shown in Fig 35.

Not all birds in the colony lay at the same time, and in the 1970 season when two areas of the colony were studied, the area at the eastern end of the gorge was used for breeding two or three weeks earlier in the season than the western cliff ($X^2 = 17.02$, df = 9 p = 0.05). This eastern area contained the densest concentration of nesting birds and has very favourable wind conditions with overhanging rock to shade the ledges during much of the afternoon. The western cliff,however, is exposed to the full heat of the afternoon sun. The eastern area is therefore occupied first in the season and all possible ledges seem to be used. Late breeders are presumably forced to occupy the less favourable western cliff, and it is this area which showedthe excess of suitable breeding sites.

Figure 35


40
30
20
10
1969
Sample size 20
% Nests
Hatched
Per Week.
December
January
February
10
20
30
1970
Sample size 64

It is presumably advantageous to start breeding early and select a favourable breeding site, although in the 1970 season there was no significant difference in the breeding success in the two areas, or between early and late breeders ($X^2 = 0.69$, df = 1 p = 0.5).

Breeding success is high. In the 1970 season, of 85 nests in which incubation started, 73 (86%) of the eggs hatched successfully. Two nests (2.4%) were deserted after a prolonged incubation and the eggs remained in the abandoned nests for several weeks, failure presumably being due to infertility or addled eggs. Three (4.5%) were seen to have their eggs destroyed by ravens (Corvus albicollis) while they were left unguarded, and seven (8.4%) nests were found empty and unattended, presumably either due to predation, infertility or desertion followed by the egg being taken by scavengers. This failure to complete incubation is responsible for almost all of the ineffective nesting attempts, since out of 73 nests in 1970 in which an egg was known to hatch, 70 (96%) fledged, or probably did so since they reached the stage of large young.

The nests are usually situated on very isolated ledges that would be difficult for ground predators to reach. However, ravens are usually present near the cliffs during the incubation period and they attack many of the eggs which are left unattended. Since this predation is probably one of the main causes of breeding failure, it is rather surprising to find that the colony has no mutual warning or attack against these predators. A bird will attack a raven which lands on its own nest, but will pay no attention to raids on adjacent eggs. On one occasion a pair of ravens were seen breaking and eating an egg in one nest for seven minutes, while another bird sitting on a nest on the same ledge only six feet away watched the whole attack and made no attempt to drive away the predator.

Birds do not therefore seem to gain any advantage from colonial nesting as a mutual warning against predators. There are numerous, apparently suitable, isolated ledges on the Gol escarpment which are not used for breeding, and birds seem to deliberately build in areas that are adjacent to other nests. It seems very probable that the chief advantage to colonial breeding in this species is in the efficient exploitation of the food source, as has been suggested for communal roosting by Quelea quelea (Ward 1965), and wagtails (Zahavi 1971), and communal breeding by Brewer's blackbird Euphagus cyanocephalus (Horn 1968). Suitable cliff ledges for nesting may be a considerable distance from the chief food supply, and this is often irregular, transient and localised. Birds leaving the colony in the morning and which follow individuals that are flying deliberately in one direction may be led straight to a source of food which had been located the previous day.

Throughout the breeding season the base of the cliffs was examined for recent food pellets, and these were collected and examined for animal hairs.

Hairs identified from pellets produced by Breeding birds 1970

	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.
Wildebeest		*	*	*	*	*	*
Zebra			*	*			*
Gazelle				*			*

The birds would seem to be continuing to search over the migratory game concentrations of wildebeest, zebra and gazelle. At the start of the breeding season these herds are close to the breeding colonies, but later in the season birds must travel up to 100 miles to reach their feeding areas.

Food Requirements for Breeding

The breeding season is now considered, chiefly for Ruppell's griffon in terms of the food requirements of the breeding birds, firstly for egg laying, then for feeding the chick and finally the effect on the adult birds.

Food Requirements for Egg Laying.

The egg of a Ruppell's griffon vulture weighs about 200 gms (Schönwetter 1967) excluding the shell, or about 2.7% of the mean female body weight. (whiteback egg weight is 194 gms minus shell, or 3.6% of mean female weight). Lack (1968) showed that among most groups of birds the weight of the egg as a proportion of the body weight varies inversely with the body weight, so that larger species lay proportionally smaller eggs. Through the size range of most families there is a common relationahip, although between families there are often considerable differences. This type of analysis shows that the size of the eggs of vultures is of the order that one would expect when compared with the eggs of other birds of prey, and they can therefore be considered to produce an egg which is not unusually large or small for the size of the bird.

The eggs of most birds consist of about 74% water, 12% protein, 11% fat, 1% carbohydrate and 1% inorganic material (Romanoff & Romanoff 1949). An egg of approximately 200 gms. will therefore contain about 147 gms of water, 24 gms protein, 22 gms fat, 2 gms carbohydrate and 2 gms inorganic material, of about 318 kcals of stored energy (King & Farner 1961). Brody (1945) showed that in the domestic hen the net efficiency for egg production, excluding any maintainance requirements, was of the order of 70%. Thus out of 100 calories consumed above normal maintainance

requirements, 70 would be deposited in the egg. The domestic hen has been selectively bred to achieve a high efficienc, of egg production, and if we assume that a vulture would have a lower efficiency of about 50%, then in order to store 318 calories in an egg, a bird might be expected to take in about 636 kcals of food. The diet of the soft tissues of game animals contains extremely small quantities of fat (Ledger 1968) and is predominently protein. The 636 kcals required for egg formation could be provided by an intake of about 152 gms of protein, and since most muscle tissue has a water content of about 77%, this would be represented by approximately 660 gms of meat - or about 1/3rd of a crop full of food.

The actual amount of protein needed to be utilised for egg formation will be considerably greater than this figure for the energy requirements would suggest, since the amino acids needed for some egg proteins will be required in different concentrations from those represented in the food proteins. However, since the diet is almost exclusively animal protein, and this is burnt to supply maintainance energy, there is not likely to be any amino acid that is in short supply in the body. It would therefore appear that the energy required from the female to produce the egg is relatively slight compared to a small bird such as a sparrow which may produce its own weight in eggs within a week (Kendeigh 1941).

However, as well as producing the egg, the female also has to mobilize sufficient calcium for the formation of the egg shell. It has been shown that the food supply contains very little calcium, and this must presumably be supplied from the female's bone. A Ruppell's griffon eggshell weighs about 23 gms, and since 95% of the eggshell is of inorganic material, 98% of which is calcium, (Romanoff & Romanoff 1949) the female has to supply about 22gms of calcium carbonate, or about 9 gms of calcium. The adult skeleton weighs about 525 gms (mean of 4 birds), and if we assume that, as

in mammal bone, this contains about 26% mineral ash with a 36% calcium content (Maynard 1937), the total skeletol store of calcium in the female's body is only about 49 gms. The shell therefore contains about 19% of the female birds normal bone store of calcium. Taylor and Moore (1954) found that a domestic hen on a calcium deficient diet developed a 38% loss of total skeletol calcium after laying six eggs, and a loss of 19% is therefore presumably an acceptable level. Birds must be able to store this calcium prior to egg formation, but any imbalance will take a long period to replace from the food intake, although this could be done rapidly if the egg shell were eaten after the young had hatched.

In Fig 36 the weight of the empty eggshell of various large birds is plotted against their total egg weight. It can be seen that there is a clear relationship within the size range of each family, although families differ between each other. Vulture eggshells are of the order of weight that one would expect compared to other large birds of prey. Swans, pelicans and penguins all have relatively heavier shells than birds of prey, crane eggshells are a similar weight and the albatrosses have relatively light shells. A low calcium diet has not caused vultures to develop abnormally light eggshells.

Egg predation or infertility was shown to be responsible for most nesting failure. Many birds of prey have insurance against such losses, either by laying a replacement egg, or two eggs may be incubated together although only one young is reared. In the three nests where eggs were destroyed by ravens, none of the birds re-laid. However, other birds might have lost eggs and re-laid and these would not have been noticed. Mendelssohn and Marder (1969) report that the European griffon Gyps fulvus in captivity regularly relays if an egg is lost. In both whiteback and Ruppell's griffon several follicles in the ovary increase greatly in size

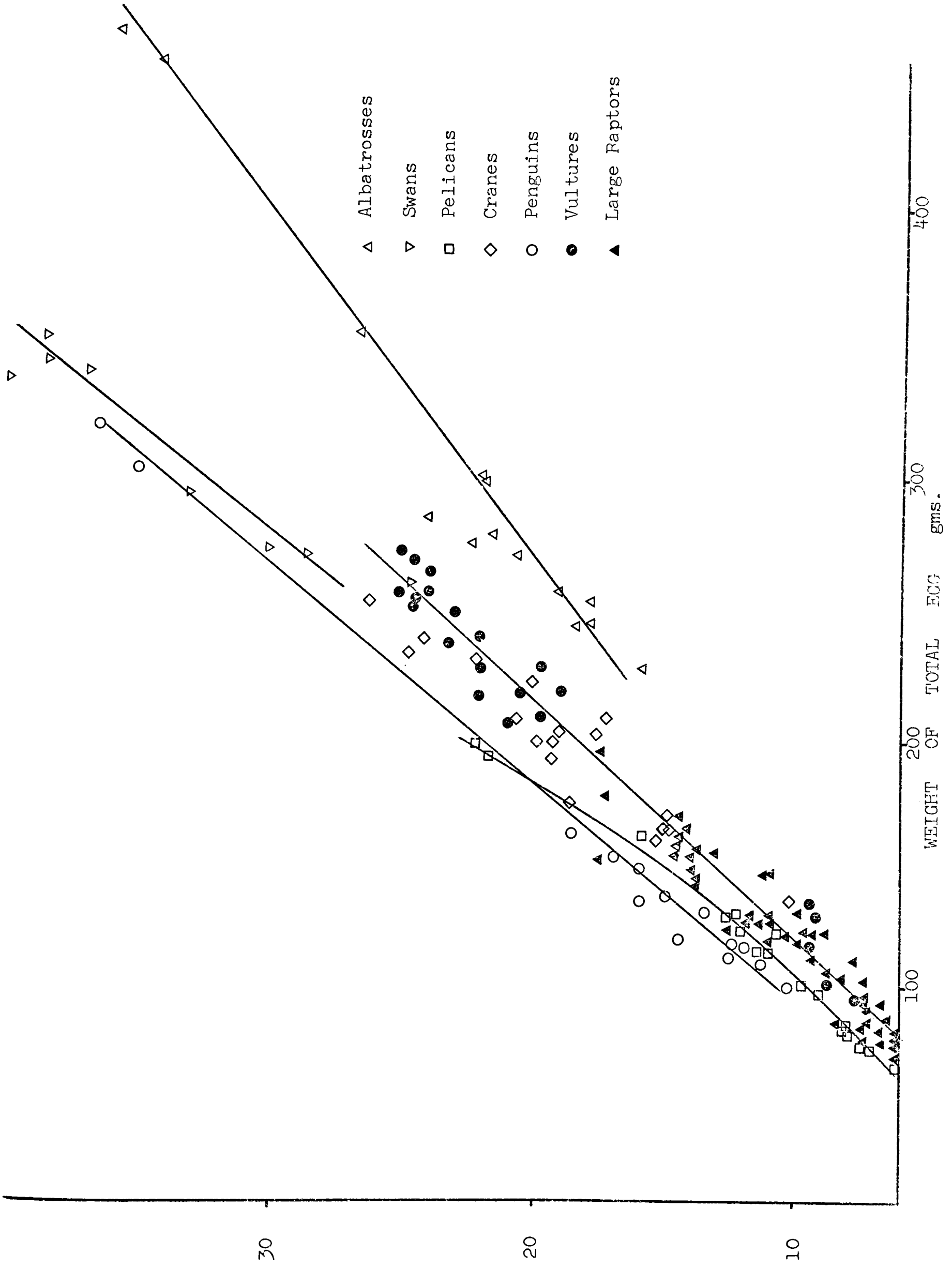

Albatrosses
Swans
Pelicans
Cranes
Penguins
Vultures
Large Raptors
WEIGHT OF SHELL ALONE gms.
10
20
30
WEIGHT OF TOTAL EGG gms.
100
200
300
400

Figure 36

before laying and these birds may also be able to lay a second egg. However, due to the prolonged incubation period, if replacements are laid for eggs lost towards the end of incubation, the delay in fledging would give the young only a poor chance of survival.

Since replacement clutches are probably of limited value, it seems curious that two eggs are not laid initially, and , if both should hatch successfully, only one young need be reared. The energy requirements for the formation of a second egg are relatively slight, but possibly the calcium requirements for the formation of the second egg shell are too great to justify the slight advantage of a reserve egg.

Food Requirements for Rearing the Chick.

A bird which is rearing young will need to find a greater amount of food than a non breeding bird, chiefly in order to be able to feed the chick. To get some idea of the food requirements for rearing young, some nestling whiteback and Ruppell's griffon vultures were hand reared to determine the food requirements during growth. Three Ruppell's griffon and three whiteback vultures were taken from the nest and fed weighed amounts of meat (muscle tissue) with the regular addition of a mulitvitamin and mineral preparation. Regular measurements were also made of the weight and body growth of a young whiteback vulture in the nest when it was being fed by its parents. These growth measurements from the wild bird were then used to check that the birds which were hand reared were gaining weight at the same rate and were not being overfed or starved. Since both the bird in the nest and the hand reared birds were growing at the same rate, they are assumed to have eaten similar amounts of food. The sexes of the birds used in these experiments were not known, but in griffon vultures there

is no sexual variation in size or weight.

Fig 37 shows the growth form recorded from a whiteback chick fed by its parents in a nest at Seronera during the 1969 breeding season. Fig 39 shows the weight of food that was fed to captive whiteback vultures during their rearing, when they were gaining weight at the same rate as the chick measured in Fig 37. Birds were kept indoors and fed twice a day for the first two weeks, and then once daily, usually being given as much food as they would take. One chick was used to obtain food requirements from the day of hatching until 35 days old. Shortly after this the bird's growth became abnormal and it eventually died from severe calcium imbalance. Two other birds were used to measure the food requirements of the larger chicks. The food taken by the growing young sometimes fluctuated considerably from day to day, and a large amount of food may be followed by a period with a loss of appetite. The results have been smoothed here by plotting a moving average of three. It is assumed that the energy requirements of these hand reared birds is the same as that of chicks in the nest. Birds were reared in the shade, and although the adult birds shade young in the nest during the middle of the day, a chick in a nest is likely to develop heat stress if it is exposed to the full sun. This causes a marked fall in the productive energy that is available for growth (Kendeigh 1969) and if this develops frequently the food requirements for growth of chicks in the nest must be greater than is represented by the food intake of captive birds.

Measures of the food supply obtained by the breeding birds could be collected only for the Ruppell's griffon, and it was therefore necessary to find the food requirements for the young of this species. Three young Ruppell's griffon chicks were collected and reared from approximately six weeks of age, and one of these birds was used to obtain estimates of

the food requirements under normal growth conditions. The nests of these birds are inaccessible and young birds could not be regularly measured in the nest. It was therefore not possible to obtain a set of figures for the growth of normal nestlings which could be used to compare with hand reared birds to ensure that they were receiving adequate food and developing normally. However, Geilikman (1967) gave figures for the growth of young Gyps fulvus, a similar sized griffon, from a colony in Soviet Armenia. In Fig 38 these figures have been plotted together with those for the whiteback as a percentage of the final weight and percentage of the fledging period. This shows that these two species of griffon vulture, of very different sizes (about 7.5 kilo and 5.3 kilo respectively), have growth curves which are similar. It has therefore been assumed that Ruppell's griffon shares the same growth form as these other griffon vultures and the captive bird gained weight at approximately the same rate as is shown by wild Gyps fulvus. Two young birds which were both collected near to the colonies as soon as the young had started to leave the nest were both below normal adult weight (6.7 and 7.1 kilo - mean adult weight 7.4 kilo), and there is no evidence to suggest that this species might have a greater food intake and continue to increase in weight, after growth had ceased, laying down fat deposits.

Since Ruppell's griffon chicks were not collected until about six weeks old, the food requirements for the first few weeks of life could not be obtained from hand reared birds. These figures have been assumed to follow the same form in relation to the rest of the food requirements as is shown by the whiteback vulture. Fig 40 is therefore a combination of the food requirements of some captive birds, with assumptions made from the whiteback food requirements.

Figure 37

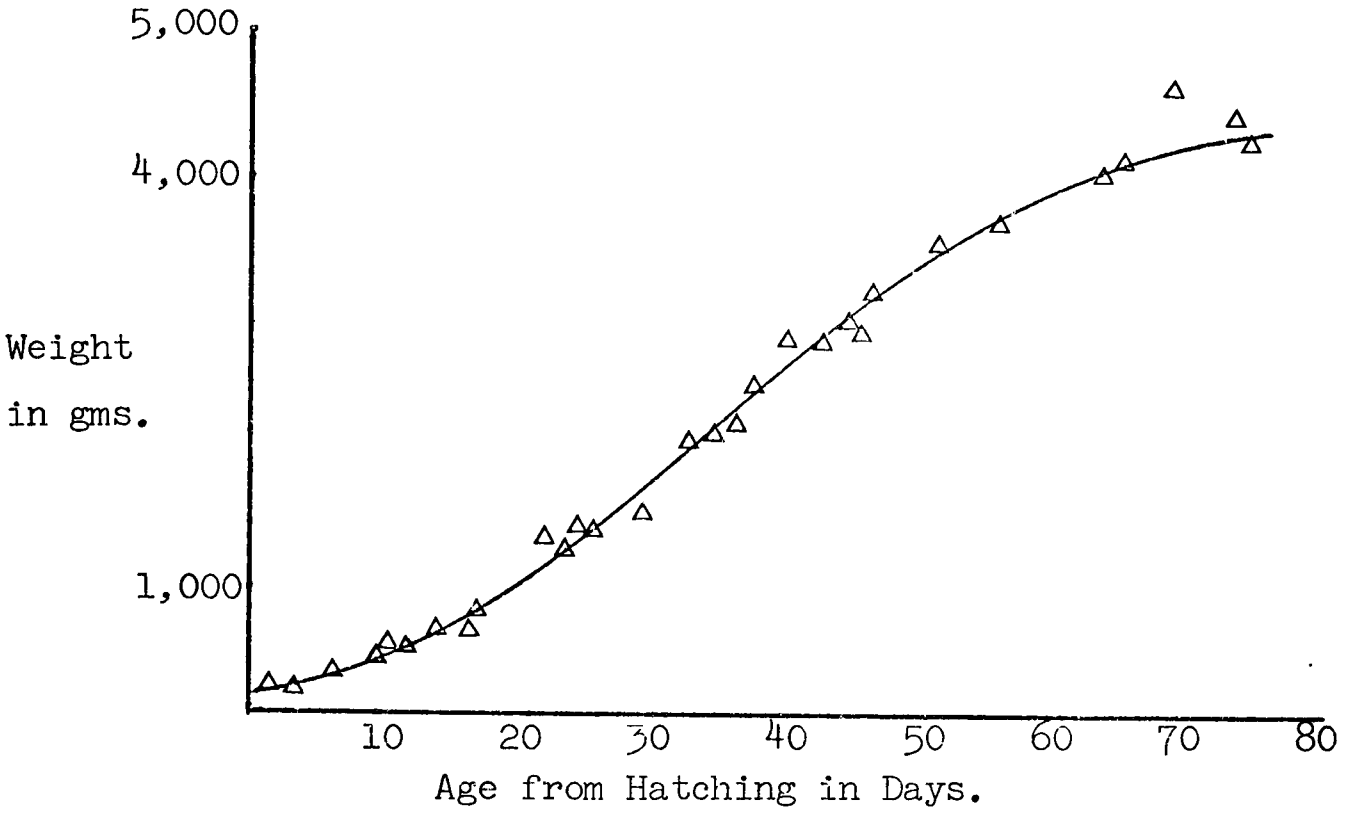
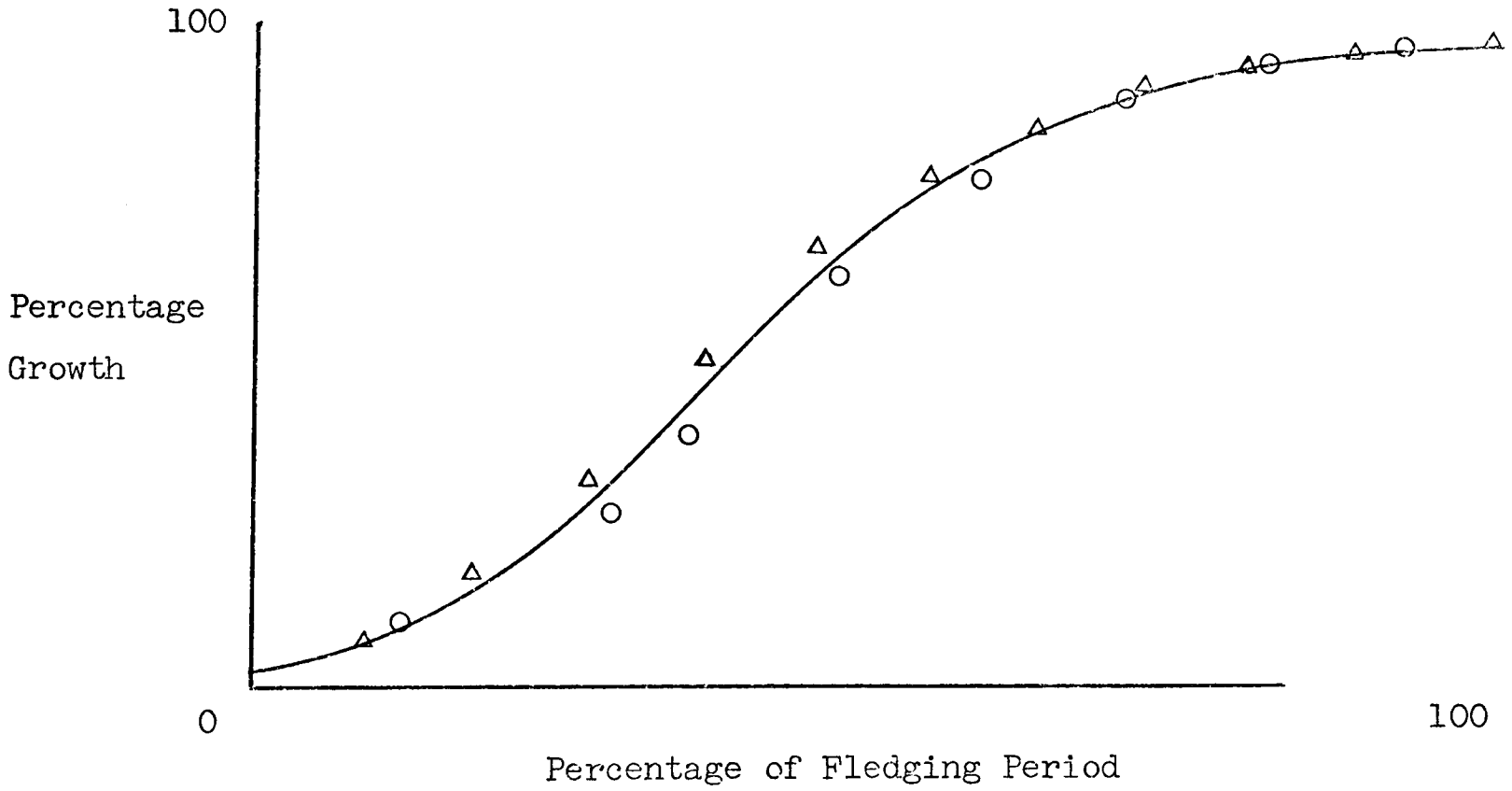


Figure 38



○ Gyps africanus

△ Gyps fulvus

Figure 39

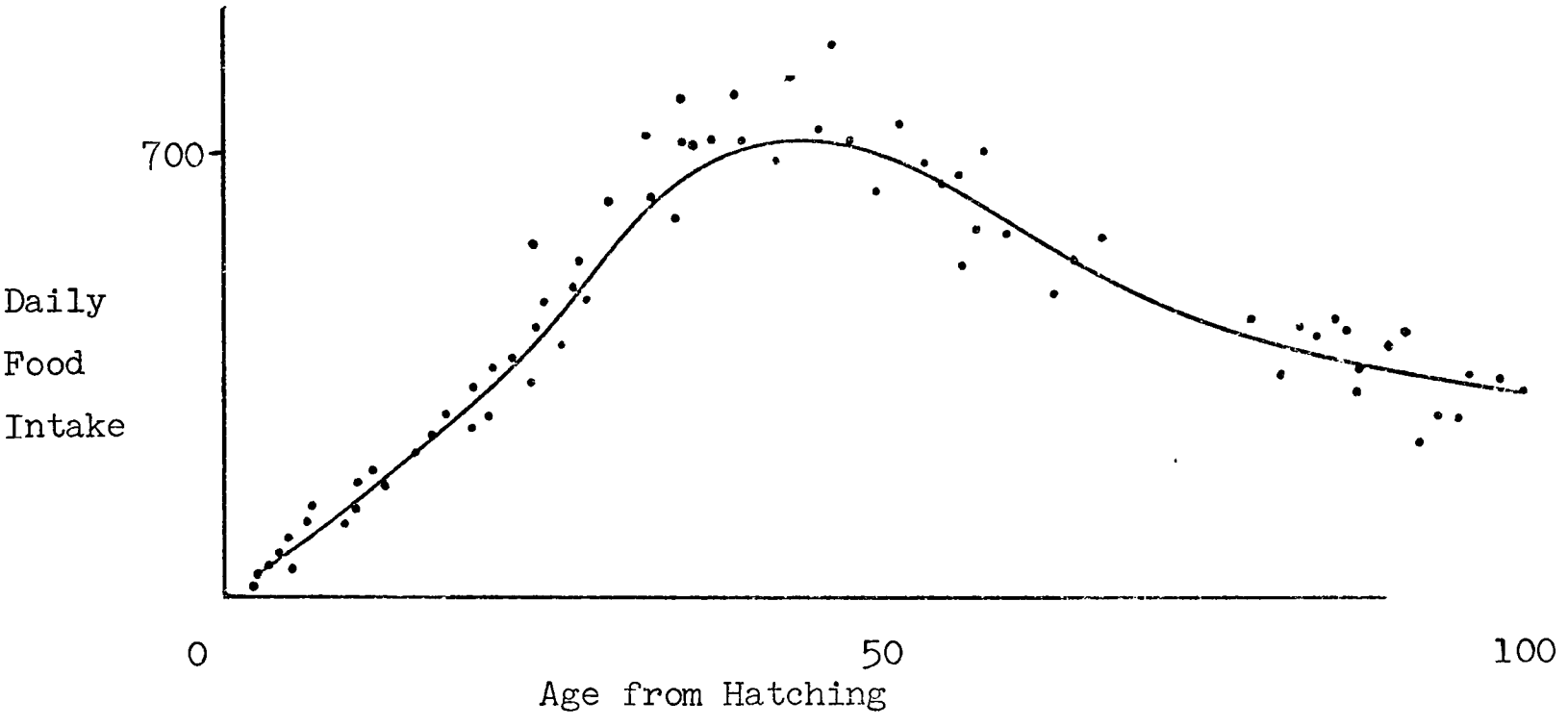
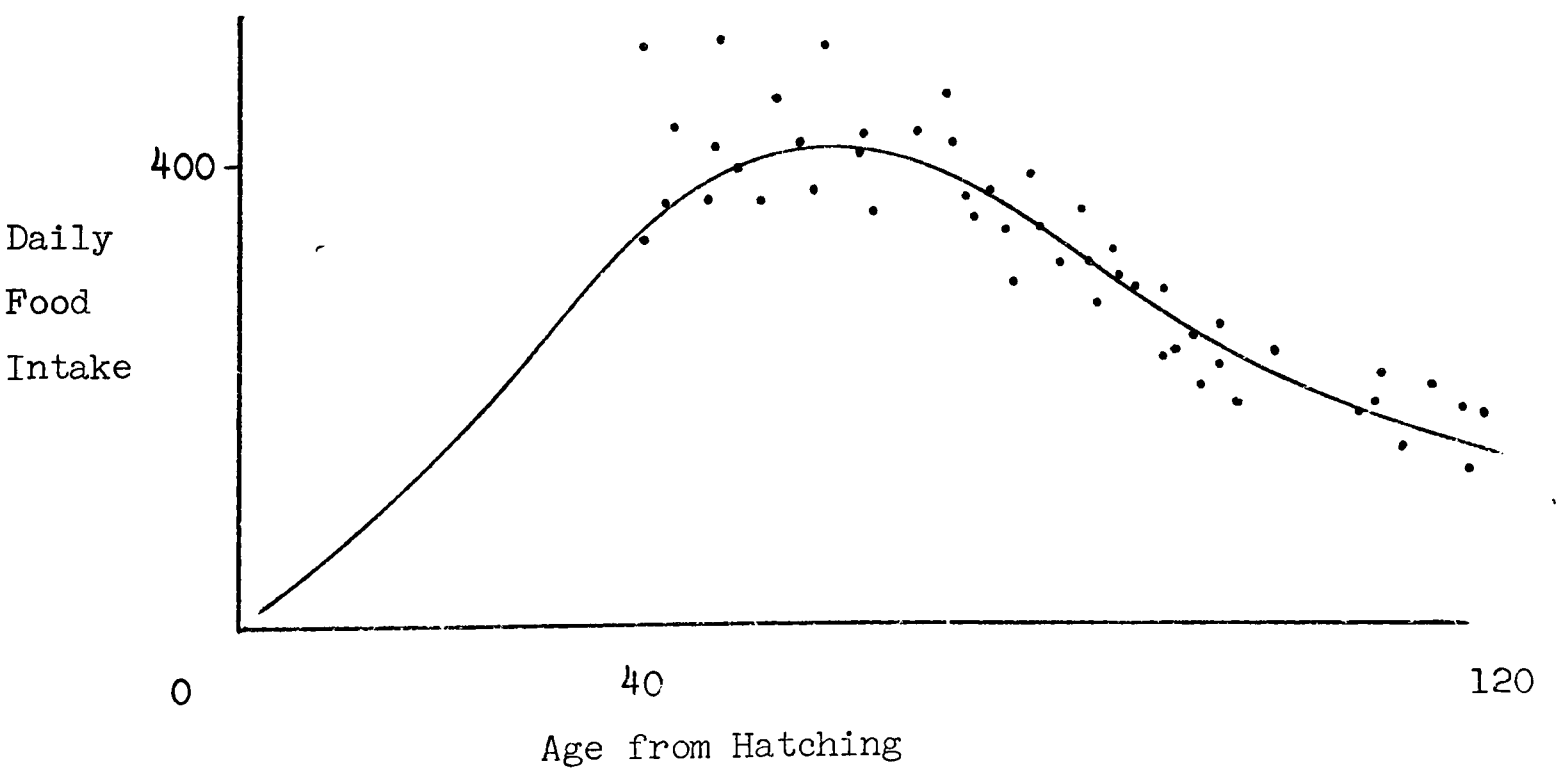


Figure 40

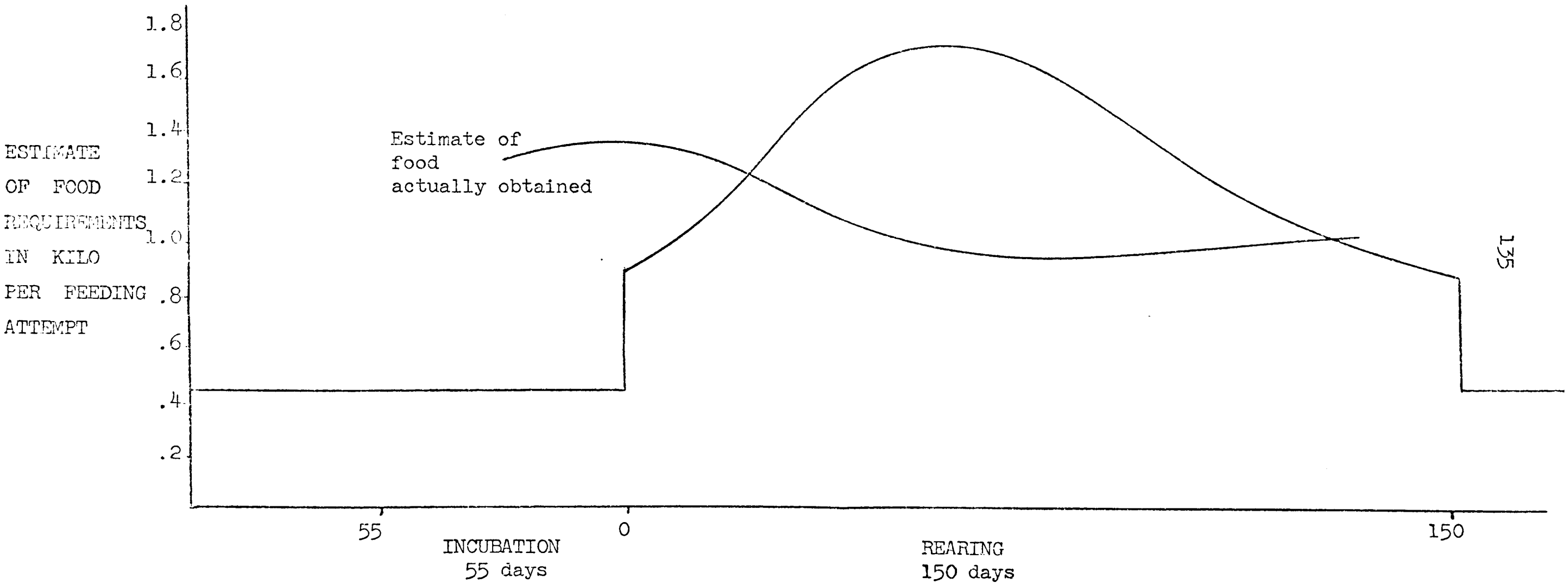


It is now possible to develop an estimate of the amount of food that an adult breeding bird would be expected to obtain through the breeding season. This has been presented in Fig 41 . This does not represent the daily food requirements of a bird through the breeding season. It shows the average amount of food that a breeding bird must obtain on each occasion that it is able to leave the colony to search for food. The food requirements have been presented in this way so that a comparison can be made later with field observations on the amount of food that is actually collected.

In doing this it has been assumed that during both incubation and the rearing of the young the two parents share nesting responsibilities and are able to spend an equal amount of time in food searching. Apart from egg production, the food requirements for both of the parents is therefore the same throughout the season. Several other simplifications and assumptions have been made in the preparation of this estimate.

During incubation it is assumed that each of the parents is able to feed every day. At each visit to a carcass at this time of the year, a breeding bird will therefore need to obtain only sufficient food to satisfy the food requirements for itself for that one day. However, by the time the chick has hatched, feeding conditions have altered so that breeding birds are now able to feed only on alternate days. At each feeding visit a bird will therefore need to obtain sufficient food to feed to the chick one day's food requirements for that particular stage in its development, as well as twice the normal daily food requirements for an adult bird - in order to satisfy its own needs for that day and the following one when it will be guarding the nest and will be unable to feed.

Figure 41


ESTIMATE OF FOOD REQUIREMENTS IN KILO PER FEEDING ATTEMPT
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
Estimate of food actually obtained
55
0
150
INCUBATION
55 days
REARING
150 days

Individual birds could not be recognised and so the exact share of the two sexes in incubating and rearing the young is not known. However, the frequency with which the two sexes leave the colony for food searching could be recorded by watching nests throughout the day and recording all changeovers that occured. Birds do not return to the nest unless they have food stored in their crops and have therefore been successful in feeding. If only one changeover occurs at a nest regularly each day, then each bird is spending one day away from the nest followed by one day guarding the chick. If, however, changeovers occur two or more times during the day, then both birds may be able to move away from the colony and feed each day. It has been shown that the breeding birds are dependent on the migratory herds for their food during the breeding season. The frequency with which birds are able to feed and return to the nest therefore presumably depends upon the distance and speed with which the birds are able to travel to the herds, as well as the food abundance and the feeding competition when they get there.

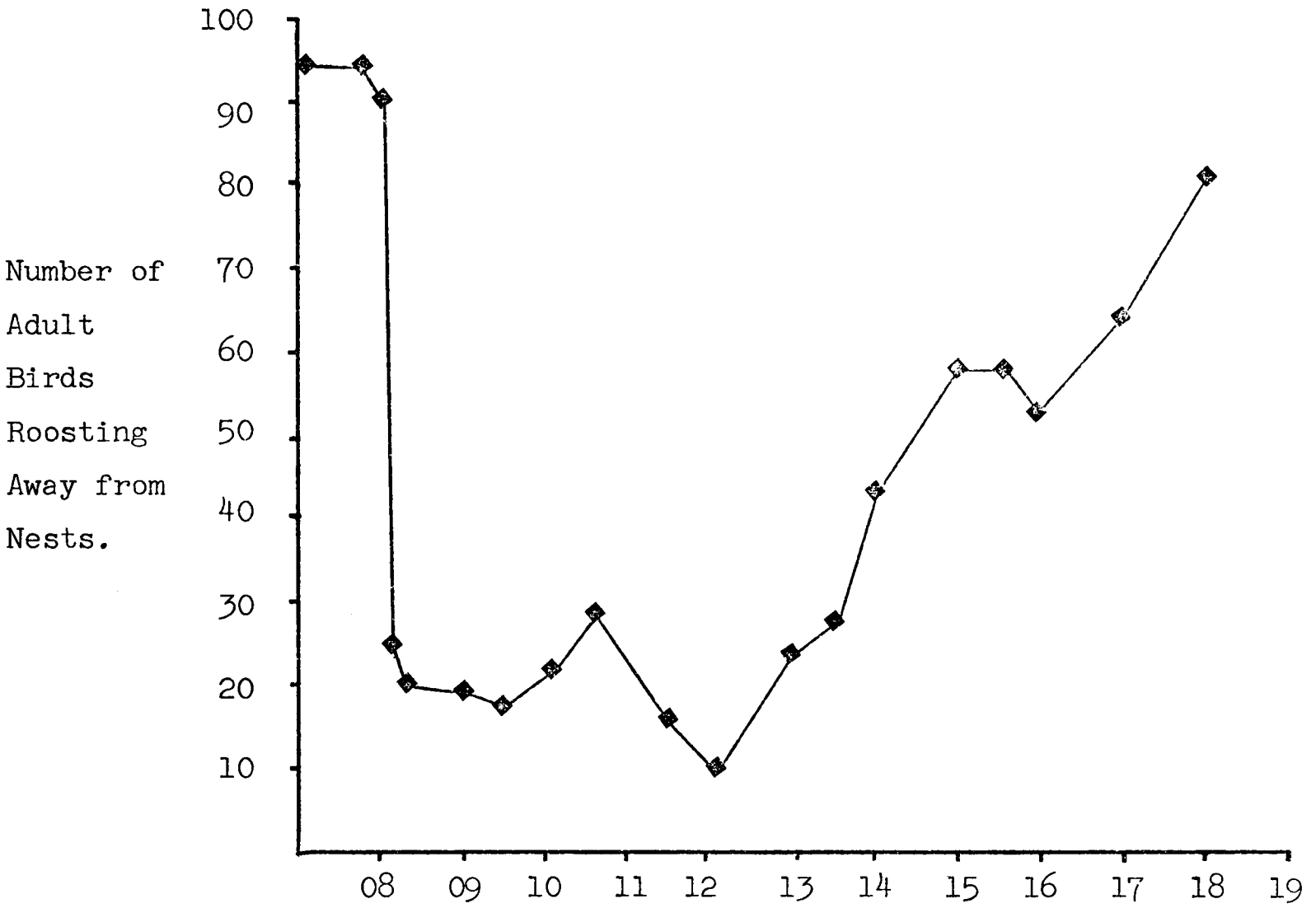
In the 1970 season a collection of 47 nests at one dense area of the colony were watched continuously for periods of two days at intervals through the breeding season.

	February		March	May	June
% nests changing	2 - 3	19 - 20	9 - 10	12 - 14	1 - 2
2 X per day or more	68%	28%	12%	0%	4%
Once per day	13%	45%	78%	53%	68%
Not seen to change	15%	34%	9%	47%	27%

Changeovers were sometimes extremely rapid and both birds might be together on the nest for only about ten seconds. It is therefore probable that some changeovers went unrecorded. During incubation in early February changeovers occured at least twice per day at most of the nests observed. At this time of the year the wildebeest herds are on the eastern plains and some groups of animals are within a few miles of the colony, and it is clear that both birds are usually able to feed each day. By late February the herds had moved about 80 miles to the south of the colonies and only about a third of the nests were changing more than once per day. By early March, most of the nests change only once per day, and this is the pattern that is maintained for the remainder of the rearing period.

Birds usually return from feeding in the early afternoon, and the changeover at the nest is usually rapid with the relieved bird leaving the nest site almost immediately. Both parents are not usually present together on the nest during rearing. However, it seems likely that relieved birds do not leave the colony on that same day, but remain in the area, either flying or occupying non-breeding ledges and communal roosts. The number of adult birds present in the colony occupying non-breeding areas increases considerably towards the late afternoon and these birds are probably those which have left their nests, but remain in the area of the colony and delay leaving to search for food until the early morning Fig 42 . There is presumably an advantage in delaying departure from the colony until the following day. The colony provides a safe roosting site for the night, but although there would be only slight chances of finding food left uneaten so late in the day the birds could travel to the game herds and roost there so that they could start searching early the next day. The chief advantage to delaying departure is probably that it enables all birds to collect together and leave in one group the following day. Birds following an individual which is flying deliberately in one direction may be led to an area with a

Figure 42



Averages from four days of observation.

good food supply.

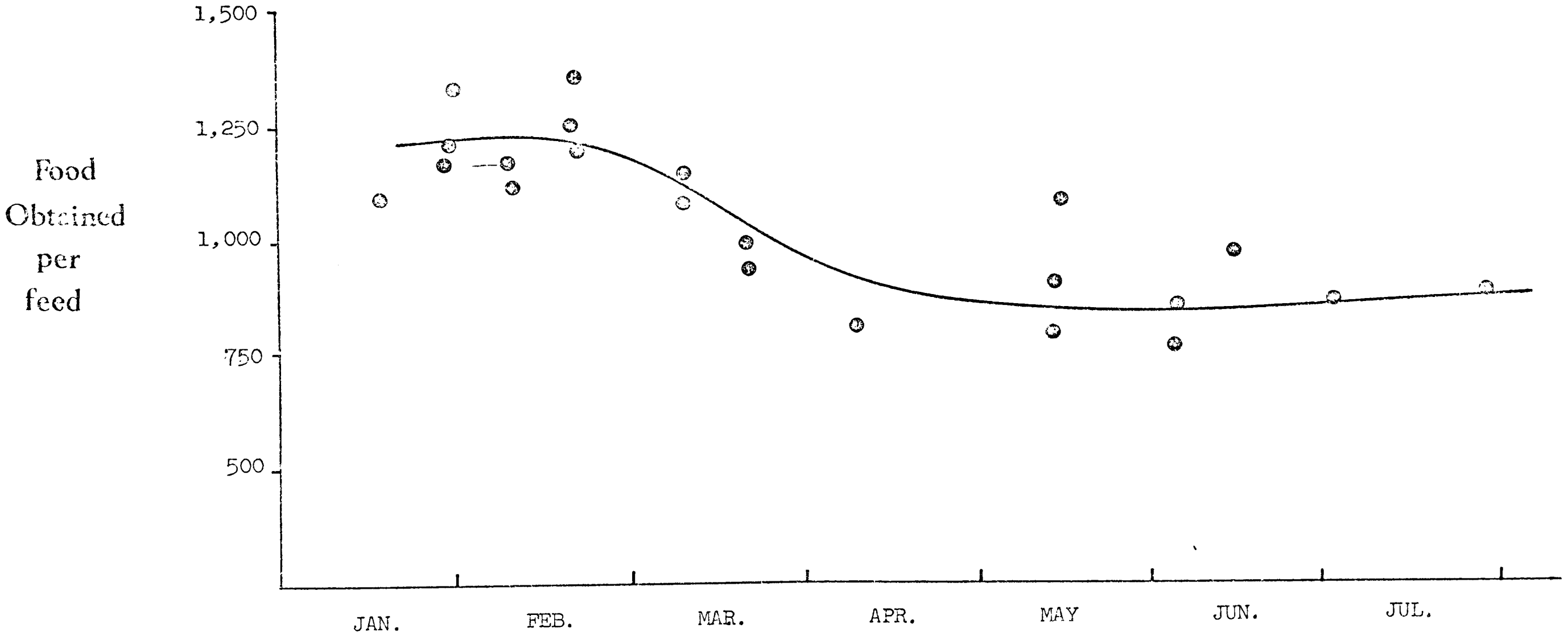
Food Supply of Breeding Birds

The amount of food that the birds were actually able to obtain through the breeding season was estimated by observing birds as they returned to their nests in the colony and recording the amount of food that they had been able to obtain. As was shown earlier, griffon vultures have an extensible crop which can be used to indicate the amount of food eaten that day. By watching an area of cliff containing 47 nests it was usually possible to obtain observations on the size of the crop of about 35 birds each day. Fig 43 shows the mean amount of food that birds nesting in the 1970 season were estimated to have been able to obtain on various days through the year. The same group of nests were used for all observations, and only successful breeding birds were recorded.

The food will have been collected several hours before the birds return to the colony and some food will probably have passed from the crop into the stomach before the birds return to their nests. However, digestion is very slow in these birds and in captivity an average of 34 hours is taken to pass a crop full of food through the digestive tract. Some of the food eaten in the morning will therefore have passed beyond the crop by the time that the birds return to the colony in the early afternoon, but this will probably be slight.

This estimate should be considered as only an approximate guide to the food that is available. The size of crop extension is considerable and estimates of the amount of food that it contains will show the general order of magnitude, but there are probably considerable differences between individuals and in the accuracy of the visual scoring. Another cause of error would be

Figure 43


Food Obtained per feed
1,500
1,250
1,000
750
500
JAN.
FEB.
MAR.
APR.
MAY
JUN.
JUL.

if some birds could feed in the afternoon of the previous day, since they would have been able to digest completely over one kilo of food by the time that they return to the colony on the following day, and this could not be detected. Also occasionally during rearing both parents may be able to feed in the same day, and this again would cause the estimate to be too low. This is likely therefore to represent less food than the birds actually obtained and must be considered only as an indication of the general trend in food conditions.

It would therefore appear that during the breeding season the amount of food that the parent birds are able to obtain is not constant, but declines as the season progresses. This decline was generally represented throughout the birds nesting in the area of the colony studied and does not result from individual pairs obtaining significantly lower quantities of food than average.

This estimate of food obtained during the season can now be directly compared with the previous estimate of food requirements (Fig 41) and this also is shown on Fig 41 . The food that the parents obtain during the second half of the breeding season might not be sufficient to supply the requirements of both adults and chick. It is important to remember that there are many assumptions and simplifications made in both of these estimates. The comparison between them is intended only to show the general trend in food conditions and requirements and should not be considered to indicate the degree of food shortage, or the duration. To see how birds are influenced by these conditions we shall first consider growing chicks, and then the effect on adult birds.

Chicks

If a fluctuation in the food supply during the breeding season is a regular event, the chicks might be adapted for this by being able to vary their rate of growth according to the amount of food that the parents were supplying. In this way they could adjust to periods when food was insufficient for their normal requirements by reducing their rate of growth in the same way as swifts (Apus apus Lack 1956) and possibly Eleonona's falcon (Falco eleonorae Walter 1968). To test if young birds could modify their growth rate according to the amount of food that the parents were supplying, three Ruppell's griffon vultures were reared for a period on different amounts of food and their growth measured. As seen in Fig 44 , the growth of feathers did not alter, although the birds were receiving different amounts of food. The feeding trials were stopped when one bird , receiving least food, became obviously weak, and this bird later developed clear hunger traces across all feathers. Presumably this bird was close to starvation, although the rate of feather growth did not decrease. Measures were also made of bone development, and this also did not alter with the food supply.

Since the young did not seem to be able to modify their rate of growth, they must presumably require roughly the amount of food estimated in Fig 40 If they were not receiving this, then the young would leave the nest in poor condition, or in extreme cases they would starve.

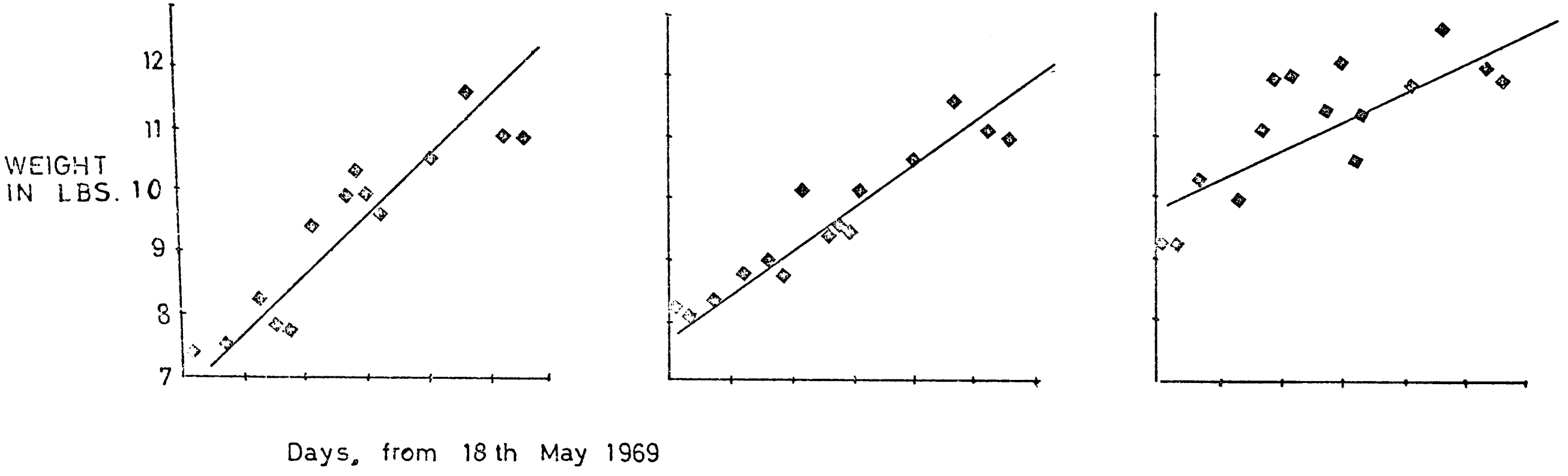
Nestling Mortality.

The survival rate for Ruppell's griffon from hatching until they leave the nest was 100% in 1969 out of 28 nests observed, and 96% for 1970 in 73 nests. Out of the three chicks which did not survive in the 1970 season, one was killed by ravens when only a few days old, and a second bird

Figure 44

GYPS RUPPELLII.

YOUNG BIRDS REARED ON DIFFERENT AMOUNTS OF FOOD



fell out of the nest when half grown. There does not therefore appear to be any evidence for chick starvation. Whiteback vultures were also shown to have an extremely high nestling survival. Only two young Ruppell's griffon were collected after fledging and these were not found to be significantly lighter than most adult birds (6.7 and 7.1 kilo). If there was a general situation in which chicks were not receiving adequate food requirements, then some parents would presumably be less efficient at food collecting and their chicks would be expected to starve. Since there is no indication of any chick starvation, it seems probable that the chick food requirements are being fully met in most, if not all, nests.

Condition of Adult Birds

If the assumptions that have been made are correct, then since the chicks would seem to be receiving sufficient food, presumably it is the adult birds which are not receiving their normal requirements. To consider the effect of the food supply on the parent birds, their body condition through the breeding season was examined by shooting a sample of adult birds at regular intervals If they are not receiving adequate food, the energy store of fat and expendible protein would be expected to fall during rearing. It was not possible to determine accurately the fat storage levels for all birds examined by making total fat extractions, and a simple method to indicate body conditions had to be devised. The weight of such a large bird is a poor indication of body condition since there is considerable variation in the size of individual birds. Even if this is taken into consideration by combining the body weight with an index of body measurements, as will be shown later, the weight will give only a rough indication of condition, and this method was not found to be sufficiently accurate.

The level of fat storage was estimated by using a visual score index of

the size of fat storage bodies in each bird. Vultures can store considerable quantities of fat in discrete areas in the body, particularly subcutaneously, in the great omentum and abdominal mesentery, and a scale of fat deposition was developed and used to score all birds after examination.

1 No fat deposits visible at all.

2 Slight deposits visible in abdomen mesentery.

3 Clear but discrete fat bodies well scattered in abdomen mesentery.

4 Continuous deposits along abdomen mesentery and some small storage in the great omentum. Other areas of body not used yet.

5 Fat storage continuous along digestive tract, concentrated over duodenum, and deposits in great omentum in a definite mass.

6 Great omentum developed into a sheet laid thinly over intestine, under 5mm thick. Skin showing few fat islands.

7 Omentum well coated, up to 1cm thick. Fat laid in clear islands under the skin.

8 Omentum over 2cm thick in some areas. Fat storage on inside of leg.

9 Deep sheets of fat in abdomen filling between intestine folds and completely covering intestine. Skin with large fat islands and fat stored conspicuously inside leg.

10 Deep sheets of fat everywhere, even under skin, and intestine almost invisible.

In practice only birds with scores 3 to 9 were found among the birds examined. Birds were collected with a .22 Hornet rifle with a X 2.5 telescopic sight. This enabled individuals to be selected from a group resting on the ground near a carcass. All birds were collected from feeding groups to ensure as great a chance of obtaining a random sample of birds as possible. Birds were shot in the head or base of the neck, and then either examined immediately or stored in a deep freeze for later study.

The visible variation in fat storage is considerable and this method probably represents a reasonably accurate way of recording the various stages of fat deposition in these birds. However, it cannot give any indication of the total quantity of fat storage represented by each of these degrees

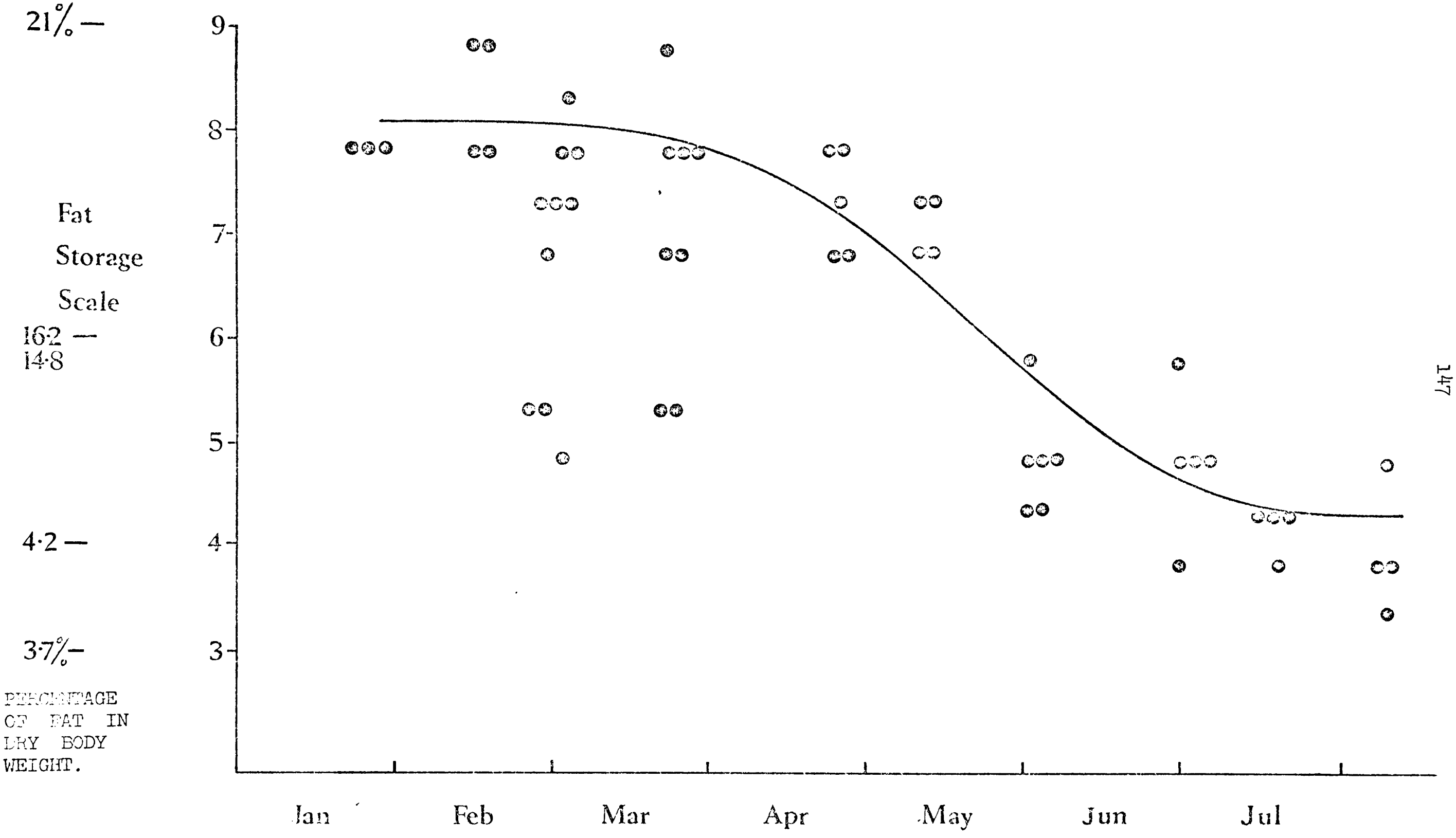
of deposition, or the relative differences in storage between the various arbitrary scores. Even accurate weighing of all the large fat bodies will not show this total quantity of fat storage because of the unknown lipid content of the various body tissues. The only way in which the amount of stored fat represented by these scores can be found is by the total extraction of fat from the body using a fat solvent, and this was carried out for five birds.

After collection these birds were stored in a deep freeze for several weeks before use. They were then examined for fat condition, dissmembered and all large muscle blocks opened by a series of knife cuts. The birds were then dried to constant weight in an oven at 105° C for about three days. They were then crushed into small pieces and placed in a cotton bag which was sealed. The bag containing the dried bird was re-heated at 100° C to drive off any absorbed moisture, weighed, and then placed in a Soxhlet chloroform extractor for about ten hours. The cotton bag was then re-heated to drive off the chloroform and weighed, the weight of extracted fat being determined by the weight difference before and after extraction.

The percentage fat dry weight for these five birds is shown against the visual score index in Fig 45 . This is clearly an insufficient number of birds to be able to judge the relative fat levels represented by the various visual scores, but they do give a valuable indication of the general level of fat storage in these birds.

It can be seen that there is a clear fall in the fat stores of breeding birds as the season progresses. During the incubation period the food requirements are relatively slight and, as would be expected, birds are able to obtain sufficient food to withstand incubation without drawing on body reserves. However, during the period when young are

Figure 45


21%
Fat
Storage
Scale
162 —
14·8
4·2 —
3·7%—
9
8
7
6
5
4
3
PERCENTAGE OF FAT IN DRY BODY WEIGHT.
Jan
Feb
Mar
Apr
May
Jun
Jul
147

in the nest the food supply for the adults is presumably not always sufficient and birds are having to depend on their stored energy reserves.

Ward (1969) found that in the yellow vented bulbul Pycnonotus goiavier, about 1.7% of the fat content of the birds came from lipids associated with living tissues and cannot therefore be considered to be available for breakdown for maintaining body metabolism. If we assume a similar figure for the vulture, then towards the end of the breeding season some birds seem to have almost exhausted their available fat deposits.

Once fat reserves have been utilised, expendible protein tissue may be used for maintaining basic metabolism, and Hanson (1962) found in Canada geese fat breakdown is sometimes accompanied by the breakdown of protein. It is therefore also necessary to consider the protein condition. The external shape of the pectoral muscle is usually considered to indicate muscle condition. Soft wire was used to record the outline form of this muscle at a fixed distance from the sternum. However, this shape was found to bear only slight relation to the actual weight of muscle tissue. The weight of the entire pectoral muscle was therefore used as a measure of protein condition, following the method of Ward (1969). Pectoralis major and minor were removed from the right side of all birds examined, and then weighed. Small samples of this muscle tissue were placed through a Soxhlet chloroform extractor. It was found that there is no appreciable fat store and the percentage dry weight does not increase with an overall rise in body fat levels Fig 46 . This tissue therefore reflects changes in protein levels only. Fig 47 shows the entire, wet weight of this muscle plotted against the visual fat score. If muscle tissue was being destroyed together with , or after, the fat reserves, then birds with low fat scores should have lighter muscles. This is not found to occur in the pectoral muscle. However, in retrospect

Figure 46

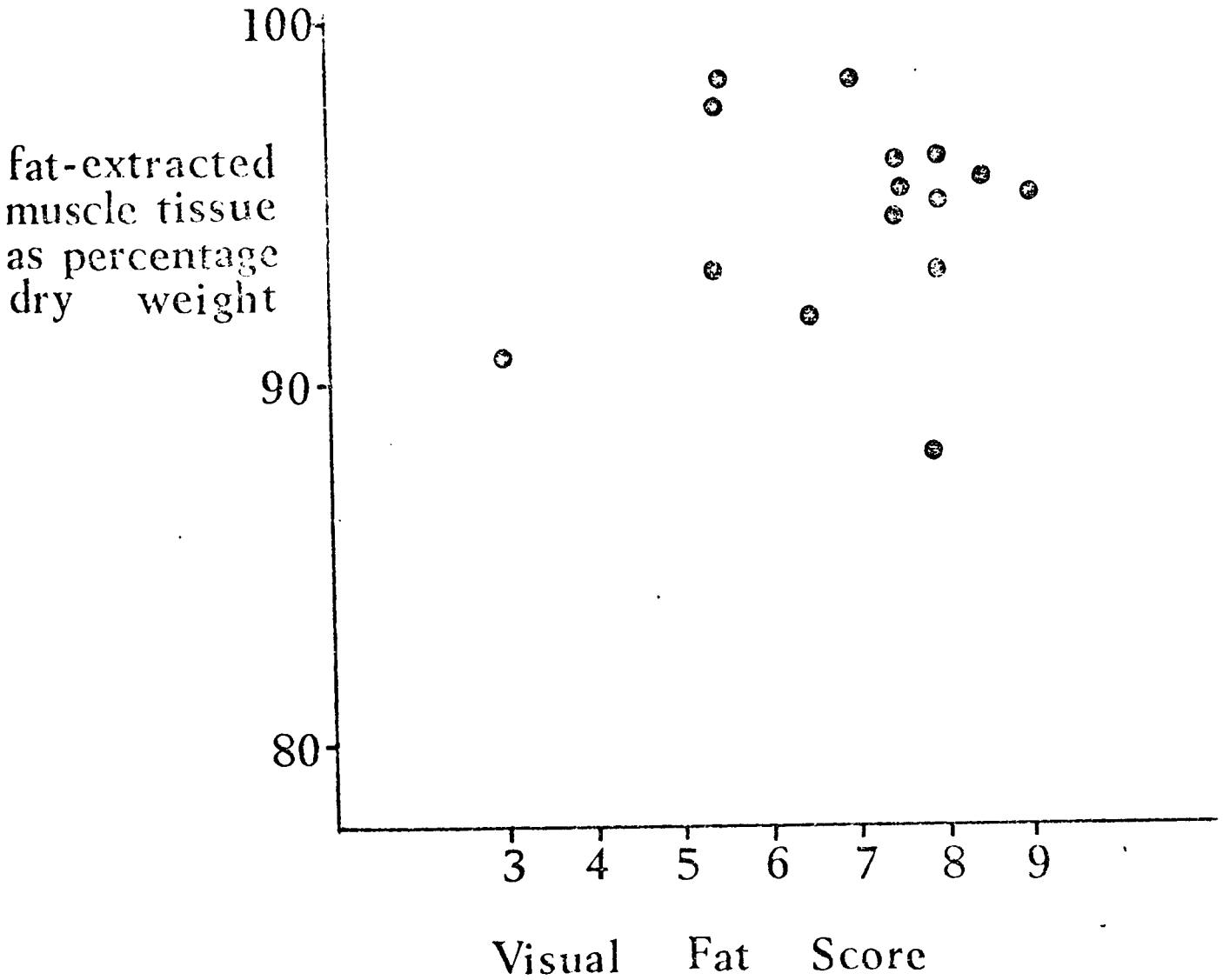
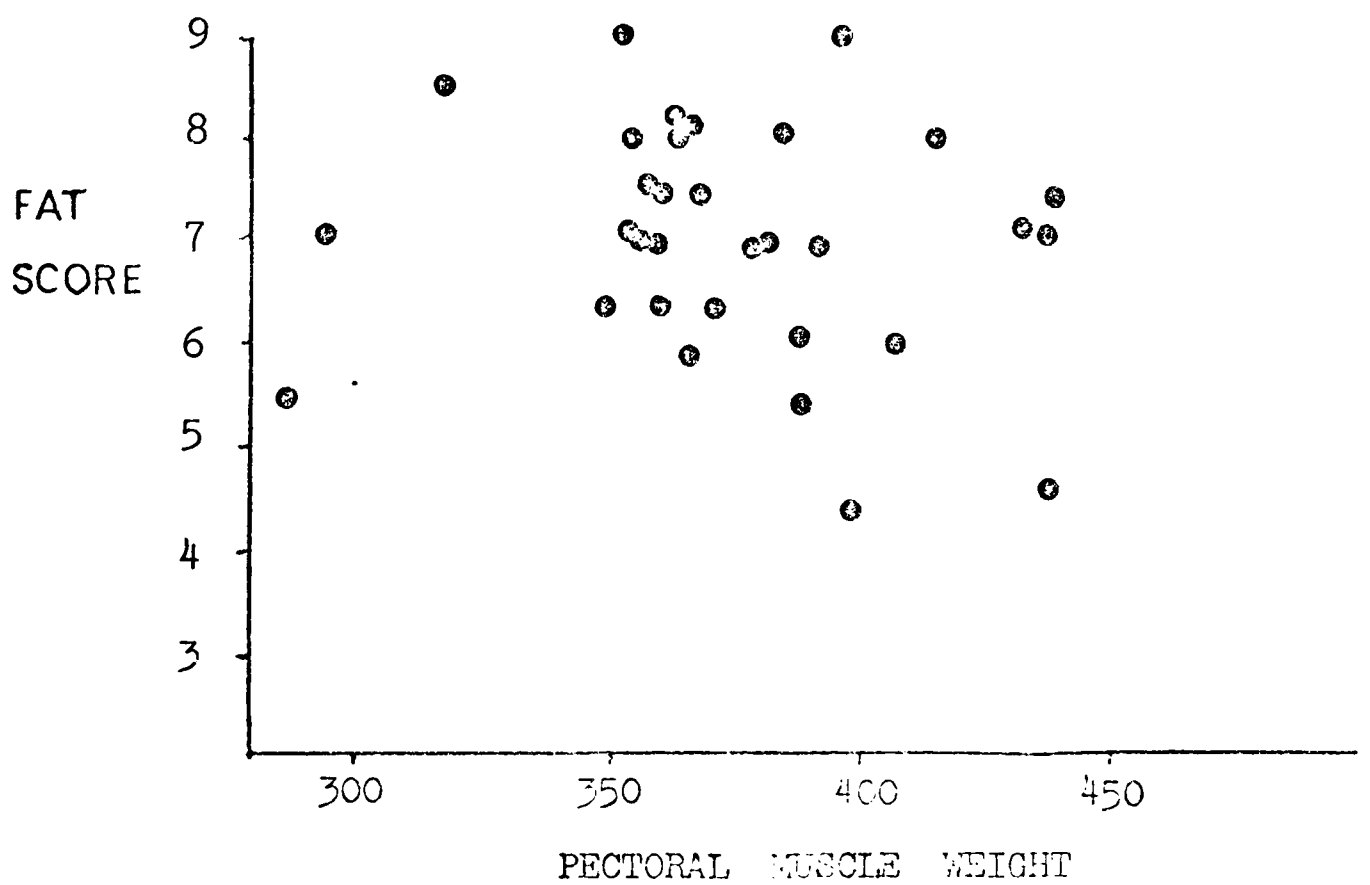


Figure 47



this particular muscle is the least likely to be sensitive to changes in protein levels. It is essential that the bird is able to take off after feeding, and even under normal conditions this is only just possible. Due to the decline in body weight following fat loss, a slight utilisation of muscle tissue is possible, but any major reduction in muscle power would prevent flight. Presumably the pectoral muscle is therefore the last reserve to be utilised.

It would therefore appear that during the breeding season in 1970 the fat deposits of breeding birds showed a decline. Protein levels of pectoral muscle were not affected and although other muscle tissue may have been utilised to some extent, this did not reach the presumably limiting stage at which pectoral tissue was reduced. It is perhaps rather surprising that there should be such a clear overall decline in fat levels, and yet no birds were found with severe protein deficiency. Presumably some birds are less efficient at feeding than others and in a situation where there is a general food shortage, these birds might be expected to show abnormally poor condition. However, this apparent uniformity of body condition estimates might only be a reflection of the small samples of birds that were examined.

Unfortunately the body condition of immature, non breeding Ruppell's griffon vultures could not be compared with that of the breeding birds because most of these young birds unexpectedly left the area at the start of the breeding season. However, the whiteback vultures were being studied at the same time and Fig 48 shows the fat scores recorded from immature whiteback vultures over this period. It has been shown that this species shares the same food supply as the Ruppell's griffon vulture. However, since these birds are not breeding, their food requirements are far less than those of breeding birds. They are also not commited to

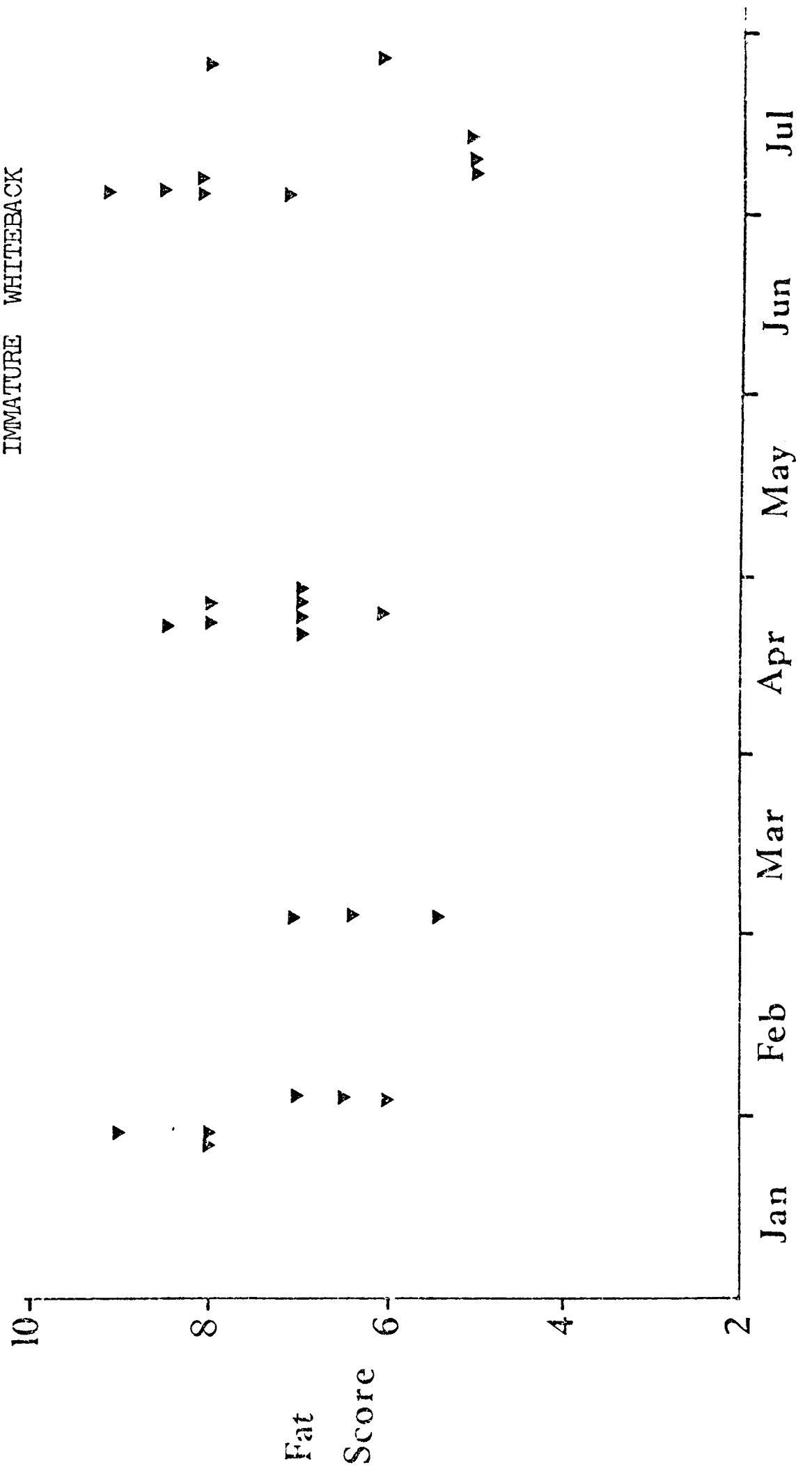

IMMATURE WHITEBACK
Fat Score
10
8
6
4
2
Jan
Feb
Mar
Apr
May
Jun
Jul

Figure 48

to returning regularly to a nest site which may be a considerable distance from the feeding areas, and can remain with the game herds through the year. Non breeding birds therefore require less food, and also presumably have better opportunities for finding it. It can be seen that, as might be expected, they are able to retain their body condition through the period in the year when the breeding birds fat deposits are falling.

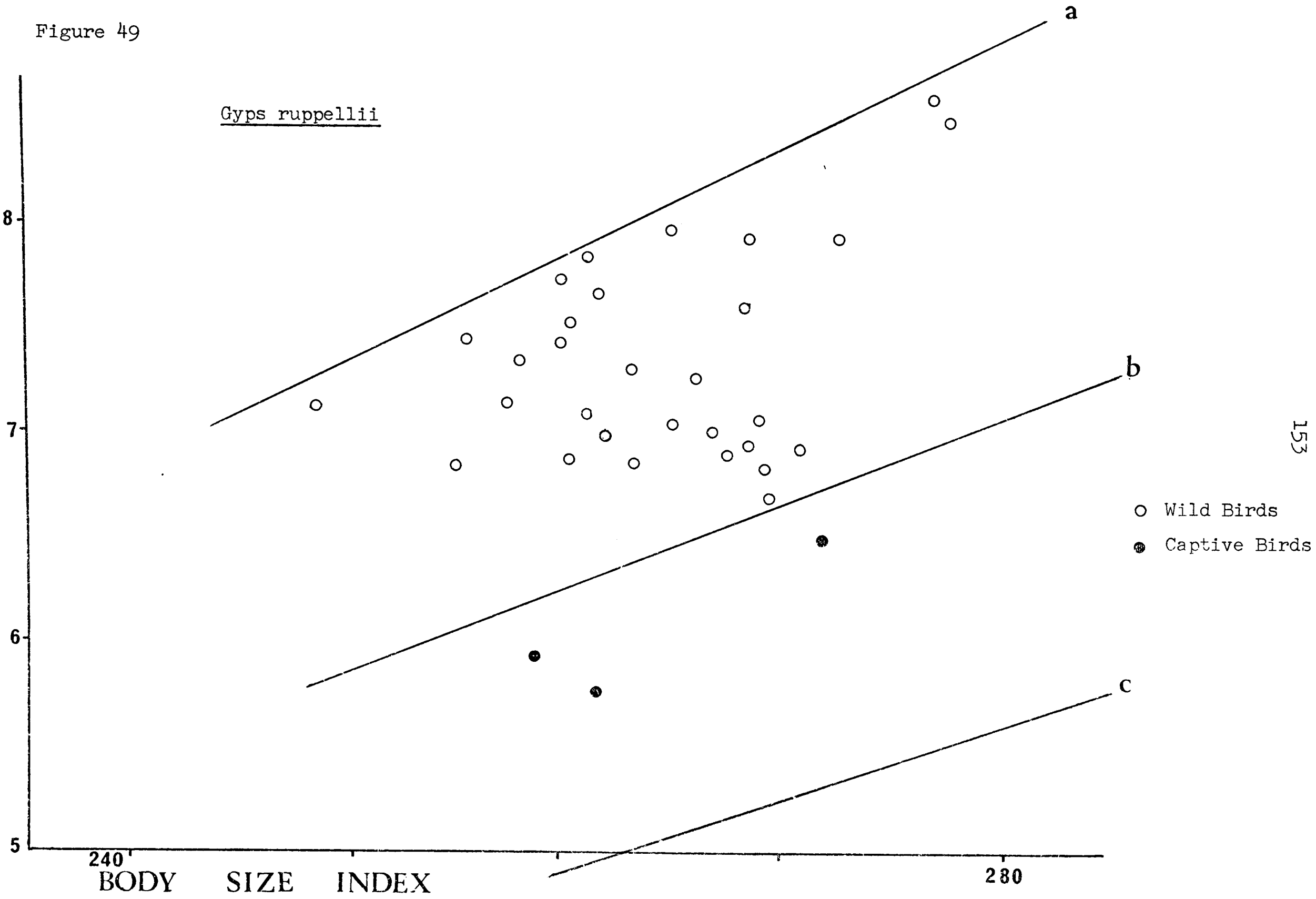
Summary of Energy Reserves

Only breeding birds therefore showed declining body condition. The range of body condition that was found is demonstrated in Fig 49 and this can be used to summarise the findings of energy storage in these birds. The body weight is here used as the indication of body condition. However, large birds such as vultures show a considerable variation in skeletol size, with a corresponding range of body weight. For this reason the body weight of the bird is, by itself, no indication of its condition.

In Fig 49 the weight of the bird is plotted against a body size index, which is made up of the measurements of bill length + bill width + tarsus length + wing span. In this way the weight of the bird can be represented together with it's size. This has been done both for birds shot and also for live birds caught in a cannon net.

The plot clearly shows that there is an upper weight limit at line 'a' which no bird is found to exceed. The shot birds near to this line were all birds which scored 8 or 9 on the visual fat score index. These birds can probably be assumed to represent individuals carrying the largest fuel reserves, including about 20% fat in dry body weight.

Figure 49


Gyps ruppellii
WEIGHT
Kilo
8
7
6
5
a
b
c
Wild Birds
Captive Birds
240
280
BODY SIZE INDEX

Since some birds seemed to almost exhaust their fat reserves during breeding, it might be advantageous to be able to carry still larger energy stores. However, a bird weighing about 8 kilo and which occasionally may take on almost 2 kilo of food in its crop is already reaching the point at which prolonged horizontal flapping flight is impossible (Pennycuick 1969). Indeed, when recently fed, these birds can only take off if there is a strong head wind and if they can enter a thermal near the ground. If larger fat deposits were stored, the increase in body weight would make opportunites for flight even more restricted and it seems likely that birds do not exceed this upper level of energy storage represented by line 'a' because this might render them totally flightless after each meal.

If an adult bird was to utilise the total maximum fat deposits of about 20% dry body weight, or about 400 gms of stored fat, assuming a metabolic rate of about 330 kcal/24 hours (Lasiewski & Dawson 1967), then this represents sufficient energy reserve to enable birds to survive for at least 12 days without feeding.

Below the line 'b', birds are presumably having to start lowering their protein levels. No wild bird was recorded in this condition. However, captive birds were sometimes fed only small quantities of food due to the difficulty of obtaining sufficient meat. The weight of these birds is found to fall within this zone and they were presumably in considerably poorer condition on occasions than any wild bird.

Finally, the line at 'c' represents the point at which both stored fat and expendible protein levels are completely exhausted and the bird dies from starvation. The only way of accurately determining this level would be to keep birds without food until the died, and then find their weight. Without undertaking this experiment, some indication of this

level can be made from Ward's study (1969) of the protein levels in starved bulbuls. These were found to have lost about 70% of the dry non fat weight of the main flight muscles compared to 'normal' healthy birds. The muscles of most birds make up about 35% (very approximately) of the normal body weight. If we assume that 70% of the muscle weight can be destroyed before death occurs, then this level will lie at about 25% of body weight lower than line 'b'. However, a vulture in good condition is only just able to develop sufficient muscle power to take off after feeding. Any large reduction in the pectoral muscle would make flapping flight impossible. The pectoral muscles of most birds make up about 17% of total body weight, regardless of the size of the bird (Greenwalt 1962), and so any bird entereing the lower part of this level would presumably have reached the stage where it was unable to take off after feeding.

The difference between lines 'b' and 'c' is caused by the utilisation of about 1,350 gms of muscle tissue, or 314 gms dry weight. If we assume this to be entirely composed of protein, this represents about 1,300 kcals of energy, or sufficient to maintain a bird for at least 5 days without feeding. Expendible protein is therefore a considerably smaller energy reserve than fat deposits, and in practice of dubious value since only a part of this protein could be utilised without making the bird flightless.

We can therefore conclude that expendible protein is of slight importance as a potential energy reserve. The breeding birds which lost much of their stored fat are therefore in considerably poorer condition than one might expect.

Considering the overall decline in body condition found through the

breeding season, it is now clear that the tentative estimates of food requirements and food availability which were compared in Fig 41 , although probably reflecting the general trends in food conditions, actually show a greater discrepancy than could be allowed for by the decline in the parent bird's condition. Of the two measures involved, the food requirements are unlikely to be lower than estimated, and are in fact probably slightly higher if the parent's requirements are larger when undertaking long flights and if the chicks are frequently under heat stress and unable to utilise food efficiently. The estimate of food availability is probably chiefly responsible for this difference. It was shown that there were several situations in which birds could have obtained more food than was recorded, and it is likely that this occured more frequently than was suspected at the time.

Whiteback vulture

This section is mostly concerned with the Ruppell's griffon, although on page 159 Fig 50 the fat levels of adult whiteback vultures through the breeding season are shown. Unfortunately these do not show such a clear pattern as has been recorded for the Ruppell's griffon, and some explanation is therefore needed. Ruppell's griffon vultures in the Serengeti area breed only in one colony in the Gol Mountains and there is no other important breeding site in this area of East Africa. All birds are therefore subject to the same conditions and have to travel the same distance to reach food. Whiteback vultures, however, breed in trees throughout the area and the ease of obtaining food will probably be partly dependent on how far an individual bird's nest is from the main migratory game herds. At some seasons of the year a bird nesting in one area may be favourably placed for feeding, and then later in the season when the herds have moved to a different region birds in this second area will find

food more readily. In a random sample of breeding birds collected at carcasses one might therefore expect a greater overall scatter in this species, reflecting the differing feeding conditions in the various nesting areas.

The Timing of the Breeding Season

The importance of the timing of the incubation, rearing and post fledging periods are considered here. The two species have been found to take the same food and they are both dependent on the migratory game animals during breeding. Although their nesting areas are different and this will affect their food searching efficiency, they are presumably both subject to the same large scale fluctuations in their food supply. However, there was a $2\frac{1}{2}$ and $3\frac{1}{2}$ month delay between the laying dates for the Ruppell's griffon and whiteback vultures in 1969 and 1970.

Egg Laying and Incubation

The variation in the laying dates for the two species indicates that food supply at the time of laying is not critical in determining the start of the breeding season for both species. Perrins showed (1970) that in some species where the weight of a single clutch is a considerable proportion of the female body weight, such as the great tit Parus major 90%, kittiwake Rissa tridactyla 24% and Oystercatcher Haematopus ostralegus 30% , nesting success is greatest in those individuals which lay earliest in the season and he has suggested that the date of laying may be determined by the availability of food for the females to form eggs. Since a griffon vulture lays an egg representing about 3% of her body weight, the energy requirements for egg formation are slight compared to the normal body reserves. In such large birds the body condition of the female to

withstand the long incubation periods will be considerably more important in determining when breeding could commence. The red footed booby Sula sula (Nelson 1969) is the only large bird with an erratic food supply in which it is thought that the start of the breeding season is controlled by the food availability, and breeding may start in any month of the year. The food supply is here most likely to influence the breeding season by its effect on the general body condition of the female and her ability to withstand the long incubation spells, which may last for six days at a time (Nelson 1968). Compared to this the small food requirements for actual egg formation must be considered to be almost negligable (5% of body weight in Sula sula). Breeding will not therefore be initiated as soon as food is available for egg formation, but must wait until the overall feeding conditions are sufficient to enable the bird to develop energy stores to withstand the initial incubation periods. They will not therefore respond rapidly to favourable food conditions, but must be dependent on a food supply in excess of their maintainance requirements for some period before egg laying.

The food supply of vultures is also erratic over any short period of time, but unlike the red footed booby, there is a predictable cycle of food availability. Since the pattern of food resources is predictable, breeding has presumably been concentrated at the period in the year which results in the greatest overall breeding success. The food supply prior to the Ruppell's griffon laying season is not known, but for the whiteback vultures it is clear that the food availability and body condition of adult birds is high for a considerable period of time before the start of laying. Fig 50 shows the body conditions of whiteback vultures in breeding plumage collected through the season, and it can be seen that almost full fat reserves are stores for several months before the onset of egg laying. This species would not therefore appear to start breeding as soon as food

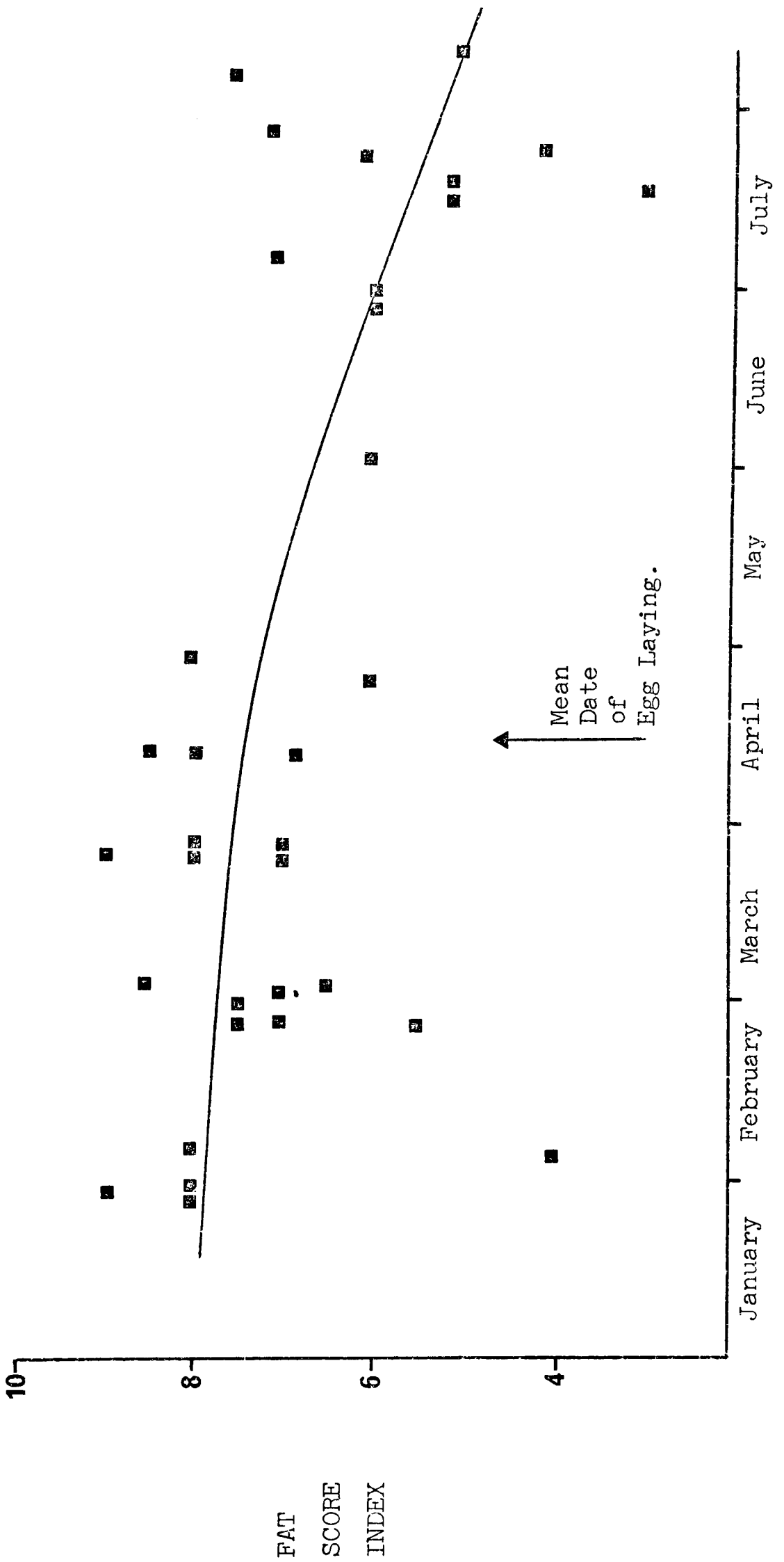

FAT
SCORE
INDEX
10
8
6
4
January
February
March
April
May
June
July
Mean
Date
of
Egg Laying.

Figure 50

conditions are adequate for egg laying and incubation, and the date of laying is probably not determined by food availability prior to incubatien.

Post Fledging

It would appear that the critical factor in determining the breeding season for both of these species is the time at which the young birds leave the nest and become independent of their parents. It seems reasonable to assume that the feeding efficiency of any bird with a complicated feeding behaviour will improve with age and experience. It has been shown that in the little blue heron Florida caerulea, young birds miss prey more frequently and capture less food per minute than adult birds (Recher & Recher 1969) and similar differences in feeding efficiency with age have also been found for the Caspian tern Hydroprogne caspia (Willard, in Recher & R. 1969) sandwich tern Sterna sandvicensis (Durn, pers.comm.), brown pelican Pelecanus occidentalis (Orians 1969) and oystercatcher Haematopus ostralegus (Norton Griffiths 1968).

Captive young griffon vultures spent a considerable time attempting to fly and soar in thermals and young birds at the breeding colonies can be seen to spend long periods practicing at gliding, and presumably efficient flight is achieved only with practice. Young birds also have to learn to find food, as well as compete at carcasses for feeding sites with adult birds. The feeding efficiency of recently fledged birds could not be observed because fledging occured at a time after the completion of both periods of field work. However, the feeding success of birds in their first year has been compared with those of birds of three years and older. First year birds can be easily recognised and distinguished from birds of three years and older by their back and covert feathers, and the aggression of these groups of birds has been compared using observations made on

April 24th and 25th at bait provided from a zebra cropping scheme in Loliondo district. The regular supply of meat had attracted a large proportion of immature whiteback vultures (over 80% of birds not in breeding plumage) and these were feeding off skinned carcasses. The conditions are therefore artificial, but it would not be possible to make these observations under normal circumstances since the proportion of first year birds in feeding groups is normally very low. The winner of each intra specific attack at a feeding site was recorded, not the initiator of the attack, although the aggressor is not usually defeated. Two year old birds were not recorded because it was difficult to age these birds rapidly. It is found that older birds attack first year old birds more frequently than expected and that first year birds are less aggressive towards experienced birds. $X^2 = 4.06$, df = 1 p = .05

Proportion of 3rd year and older birds to 1st year birds, 68;32.

Attacks	Old → Ist yr.	1st yr. → Old	Ist yr. → 1st yr.	Old → Old
Expected number of attacks	32	32	15	69
Observed number of attacks	41	25	29	56

N = 149

Presumably birds which undertake and win aggressive encounters most frequently over feeding sites will be able to obtain most food. It is reasonable to assume therefore that young birds are probably less efficient at obtaining food than experienced birds. They can compensate for this to some extent during the breeding season because immature birds have far more time to search for food than breeding birds which have to return regularly to a nest site, and they can also feed in areas too distant from the main game concentrations and from the breeding sites for breeding birds

to reach. This accounts for the high proportion of immature birds recorded at the loliondo area.

Proportion of Adult to Immature birds April & May 1970

Seronera & Western plains. Near to breeding areas	48% Adults	52% Immatures	N = 534
Soit Aye - Loliondo Away from large breeding area	20% Adults	80% Immatures	N = 137

The absence of immature Ruppell's griffon vultures during the study period may be due to these birds feeding in other areas of East Africa away from the reach of breeding birds. However, these advantages do not apply outside the breeding season. There must be a very great selective advantage in releasing the young from the nest during a period in the year when competition for food is slight and young can feed, despite their relative inefficiency in competition with adults. The degree of competition at feeding parties varies considerably according to the food supply and the amount of aggression at carcasses changes with conditions.

Inter and intra specific aggression between both griffon vultures at carcasses. All age groups

January 15th	4 attacks per minute	All Thomson gazelle carcasses. Over ten birds feeding.
March 3rd	17	
May 24th	22	
June 3rd	34	

This simple attempt to demonstrate the increase in aggression with changing food conditions covers the period from wildebeest calving in mid January when food is abundant for a short period, while later in the season the food supply becomes progressively worse and the amount of aggression increases considerably. The final figure for June is exceptionall high and from an area of very low game density. There are clearly many factors which will also contribute to overall aggression, such as number of birds present, their ages, species composition and number of feeding sites. However, aggression is obviously greatly increased when food is scarse.

It was considered that the end of the dry season is the period in the year when game mortality is probably heaviest and the food supply is therefore most abundant. Both the whiteback and the Ruppell's griffon vultures breeding seasons seem to be timed so that the young leave the nest at this period of the year. Since the whiteback nesting period is about nine weeks shorter than that of the Ruppell's griffon and they do not start breeding until later in the season, the young of both species are released together.

Rearing.

It is interesting to note that if the Ruppell's griffon vultures had started breeding about two months earlier in the 1970 season, the food supply during the rearing of the chick would have been considerably more favourable. Parent birds would apparently have been able to obtain almost all their food requirements and would not have had to depend on their body reserves. This would therefore be a favourable time for breeding if the critical factor determining the timing of the breeding season was the availability of food for the period when the young are in the nest. However, young would be released in the middle of the dry season when food is scarse. Therefore, the breeding season would not appear to be timed so as to take place when food is most abundant when the parents are feeding the young, but in order to give the fledging birds the greatest chance of survival after leaving the nest. In order to achieve this, parent birds have to rear young during a season of the year when conditions are unfavourable. Breeding is therefore a very demanding period for the adults, but presumably cannot occur at any other season of the year without heavier post fledging mortality.

In addition to the heavy food requirements of breeding, there are

other clear limitations imposed on breeding birds. A large proportion of the food of both griffon species comes from the migratory herds of wildebeest and both species apparently feed from the herds while rearing young. Presumably it is only by searching in these areas of maximum food availability that they are likely to be able to obtain sufficient food in the short time available away from the nest. However, this involves breeding birds in travelling considerable distances to reach the herds from their nesting sites, and they are limited in the time that they can spend in searching when they get there. Non breeding birds can roost in trees and stay with the game herds during their movements.

At the start of the Ruppell's griffon breeding season the herds are near to the breeding colonies, and food at this season is also abundant. From the beginning to the middle of the dry season however, the herds move into the woodlands and when in the far west or northern areas they may be over 100 miles from the colonies, and at this time the herds are widely scattered so that food is not concentrated in any one area. Pennycuick (in press) has followed with a powered glider an individual bird returning to the colonies and in dry season conditions recorded in a straight flight of $1\frac{1}{2}$ hours an average speed of 30 miles per hour. A bird might therefore take up to 3 or 4 hours to reach the feeding area after leaving the nest, and a similar time to return each day. However, at this season of the year food is not abundant and widely scattered, and these breeding birds must be at a considerable dissadvantage over resident, non breeding birds, who can start searching for food immediately after dawn, when most food is available, and continue all day. Whiteback vultures which nest in trees in the woodland areas are not at so great a dissadvantage. They have to travel further than the Ruppell's griffon to feed during the early part of the breeding season when the herds are on the eastern plains, but at this time food is relatively easy to obtain. Later in the breeding

season when it is considerably more difficult to satisfy the food requirements for breeding, the herds have moved nearer to the nesting areas and breeding birds will not have to cover such large distances as the Ruppell's griffons.

Both species show a wide scatter of laying dates, spanning about two and a half months, and presumably there is no selective advantage in any one specific brief period for egg laying. Although the proximate factor which initiates breeding is not known, it is presumably determined by a sequence in the rainfall cycle. The Ruppell's griffon appears to lay just after the start of the long rains, which occurred several weeks earlier in 1970 than in 1969 and might explain the advancement of the laying period in 1970. However, the breeding season is long, and the rainfall unpredictable. There is no assurance that the end of the dry season when the young should leave the nest will occur at a fixed interval of time after the onset of the rains. Therefore, there would not appear to be any selective advantage in one particular date for laying in all years, and the scatter of the breeding season merely reflects the unpredictability of the climatic cycle.

General Conclusions

It can be seen that during the 1970 season the rearing of a single chick was a demanding period for the breeding birds. It is clear that it would not be possible for more than one chick to be reared, and even this causes a considerable drain on the condition of the parent birds. A low reproductive rate in these birds can therefore be considered to reflect the extreme difficulty of breeding. Deferred maturity is required to enable birds to become experienced enough to be able to obtain sufficient food during the breeding season to rear a chick. Inexperienced birds which attempted to breed earlier would be unlikely to satisfy the

food requirements of the chick, and since they would have to deplete their energy reserves they would themselves be at greater risk than non breeding birds. There is certainly no evidence, or need, to suggest that the reproductive potential is being held below the possible level by the social organisation of the species, as was suggested by Wynne Edwards.

Discussion

In the Serengeti over 80% of the herbivores are migratory, and the large distances covered by these herds through the year prevents their predators from increasing sufficiently to become a major mortality factor. Other causes of mortality are therefore or far greater importance and may account for perhaps 80% of all mortality in the area. However, the nature of these mortality agents causes seasonal fluctuations in the number of deaths, together with variations in distribution caused by the movements of the herds. These conditions prevent mammalian scavengers from being able to utilise the food effectively, and these may take perhaps only 5% of the total food available to scavengers. There is therefore potentially a food supply for other scavengers, which fluctuates in quantity and distribution through the year. This is the food supply that griffon vultures utilise. They cannot obtain much food in direct competition with predators and can probably only occur commonly in an area where there is a food supply that is not effectively exploited by mammalian scavengers.

The climate enables gliding flight to be used almost exclusively and birds can therefore cover distances rapidly, and search efficiently over large areas with little expenditure of energy in a way that no mammal could ever achieve. The birds are found to be able to cover rapidly the necessary distances to reach food and to range widely while searching for food, concentrating heavily in areas of large game herds where most food is available. They can therefore exploit the food supply despite considerable variations in its distribution through the year.

However, the food supply also fluctuates in quantity and to consider; the effects of this on the bird population the food requirements and timing

of various activities have been considered in relation to the variation in the food supply. Birds can store fat very rapidly after a large food intake and use this to last over period of food shortage. This enables birds to last over short term fluctuations in feeding success and also longer term periods of low food supply. However, there is a definite limit to the amount of fat that can be carried and maximum stores of energy are perhaps sufficient to maintain a bird for a minimum of about 15 days without food. Prolonged and extensive periods of food shortage could not therefore be tolerated. It seems probable that the food supply was relatively favourable during the study period. During the first half of 1970 the food available to non breeding birds was probably sufficient to satisfy their food requirements and fat levels did not fall. No wild birds were found with fret marks on the feathers, indicating that they had not experienced conditions when body reserves had been seriously depleated.

However, the food requirements of birds could be increased seasonally by both moult and breeding. Feather replacement is continuous throughout the year and moult has been found to have a constant, but relatively slight, demand on energy supplies. However, it is rather surprising to find that this is of the same order of magnitude in relation to total food intake as for a small passerine. Since individual flight feathers take several months to develop, moult cannot be stopped rapidly when food becomes severely limited. Any feathers which develop during food shortage will show fret marks, which weaken the feather structure, and in extreme cases the additional burden of feather growth will hasten starvation. It might therefore be an advantage to cease the growth of large feathers in advance of periods which are likely to be demanding. Young, inexperienced birds after leaving the nest may face a period when they find food difficult to obtain, and in fact they do not start moult during their first ten months of independence. Adult breeding birds towards the end of the rearing period may also be unable to

obtain their food requirements, and it is rather surprising that there is not a clear pause in moult during this period. Moult can therefore be assumed to make a small, but constant demand for energy through the year.

Breeding, however, is confined to a definite season. The variation in food requirements for breeding birds through the season do not coincide with variations in the food availability, and it is considered that at some period during the rearing of the young the food requirements of the parents are probably greater than the food availability. As a result, parent birds have to be able to withstand food shortage during rearing, when they utilise their body reserves. Breeding is therefore a seasonal activity which imposes considerable additional demands on the birds. Vultures have a prolonged breeding season. In the Ruppell's griffon incubation and rearing may take eight months. Any bird which takes such a long period to breed cannot time the breeding season so that it is entirely within a period of food abundance, as most small birds do. They are therefore forced to rear their young through periods when food is sometimes plentiful and sometimes inadequate. The young must receive a fixed supply of food during this time for growth, and also become independent during a period in the year when conditions are favourable. The parent birds therefore have to withstand any food shortages. To breed successfully a griffon vulture will have to start the breeding season in very good condition, with maximum fat reserves, just to be able to survive the breeding season. Incidently, the high fledging success observed indicates that under present conditions all adult birds may be able to breed successfully, or alternatively that individuals are able to predict in advance whether they are going to be able to withstand a breeding attempt that year and birds which would not be able to rear young either do not attempt to breed, or fail to complete incubation. Carrick and Ingham (1970) have found that in the Royal penguin Eudyptes chrysolophus there is a clear correlation between breeding success and body

weight before breeding starts, and also that those birds lowest in weight do not attempt to breed. The flightless penguins are able to increase their body weight by up to 100% prior to breeding and use extensive body reserves to withstand incubation and rearing.

In order to feed the young a parent will have to be able to obtain at each feed relatively large quantities of food. At one period a breeding bird is required to obtain about four times as much food as a non breeding bird, and this is at a season when food is not abundant. Although the food required for breeding would appear to have been relatively difficult to obtain during the 1970 season, the general conditions at present are probably relatively favourable for the vultures. Over the last ten years the number of wildebeest in the Serengeti area has increased and the food supply of vultures has probably risen. Rains may occasionally fail, as in 1960, causing high mortality among game animals in some areas. This together with the subsequent increase in numbers, must have a considerable effect on the vulture population. Most studies on the food supply of birds have been made on passerine species and there are few quantitative accounts on large birds. Among the birds of prey, Southern (1970) found that in tawny owl (Strix aluco) the breeding success varied greatly with the density of small mammals, and in years when food was unusually scarse, no birds bred at all. Similarly the number of short eared owl Asio flammeus and pomerine skua Stercorarius pomarinus breeding in the arctic varied with ~~the~~ the density of their prey (Pitelka et al. 1955). It seems likely that a similar situation may occur in griffon vultures and that in some seasons it is only the most experienced, aggressive and dominent birds which are able to obtain sufficient food to breed successfully.

Appendix 1

Gyps africanus population

Since there is usually no convenient natural method of recognising the age of an individual bird, the age structure of most bird populations is calculated from the recoveries of long term ringing studies. However, in vultures the slow development of moult in young birds, and subsequent plumage changes, has enabled certain age classes to be recognised in the field. The figures for the plumage ratios present in the population cannot be used to develop an age structure because there is no evidence that the population is stable. It would seem likely that recruitment at present considerable exceeds mortality. However, in the absense of any population information some crude estimates of relative ages, which can be modified later, are useful.

As described in the Section on moult, first year old birds can be recognised by their dark, pointed covert and flight feathers. Birds in their second and third years have some of these pointed feathers remaining, but new rounded covert feathers are also present. Birds in their fourth year and older have either lost all juvenile feathers, or those remaining are so worn as to be unrecognisable. However, they have not yet aquired adult plumage. Adult birds show both a white ruff and back, and this is assumed to be the plumage attained at breeding age (no bird was found breeding with 'immature' plumage).

The proportion of these age classes present varies according to conditions Fig 1 shows figures taken during the breeding season from areas both near to the breeding sites and away from breeding areas.

FIG 1

Proportion of Adult to Immature birds
April - May 1970

	Adults	Immatures	N
Near to breeding areas Seronera	48%	52%	534
Away from large breeding areas - Soit Aye	20%	80%	137

The figures shown in Fig 2 are chosen to try and remove such bias. The ratio of adult to immature age classes is taken among herds on the Serengeti plains from January to March when breeding activity at the nest sites has not yet started. The ratio of adult to immature birds is assumed to be representative of the whole population. Figures for the proportion of the various immature age classes however are taken from observations at all times of the year, including occasions when only a small proportion of adult birds were present. There was no indication that the ratio of the various immature classes altered, and it is assumed that these are randomly represented.

FIG 2 Percentage of Plumage Classes present in population in Spring 1970

1st year plumage (Left nest previous year)	9%	
In 2nd and 3rd years	17%	(Approximately 54% 2nd years to 46% 3rd).
4th years and older immatures	26%	
Adults	48%	

Birds in their first year, which left the nest the previous September, made up about 9% of the population. Approximately the same proportion of two and three year old birds are found. If the same number of birds breed every year producing the same number of independent young, then there must have been negligible annual mortality over the last

three years. If we assume that this rate of recruitment existed in previous years, then the 26% of the population which are immature but older than 4 years probably represents about three years recruitment grouped together. However, it is unlikely that recruitment has always been as high as at present and a lower proportion of young produced per year would adjust the estimate to include a greater number of age classes. It is probable therefore that the whiteback vulture does not reach breeding age until at least 6 years of age, and probably this is an underestimate. Also, most long lived birds attain adult plumage a year or so before the first breeding attempt.

Just under 50% of the population is of breeding age. Too little is known to be able to reasonably estimate the age classes present in this part of the population. In captivity griffon vultures can live for 30 years or more (Flower. 1938, Lucas 1978).

Appendix 11

Mortality of Gyps coprotheres in southern Africa.

Gyps coprotheres replaces Gyps ruppellii ecologically in southern Africa. It is a similar sized large griffon vulture , which nests colonially on cliff ledges and whose feeding behaviour is probably close to that of the Ruppell's griffon. Over the past 20 years some breeding colonies have been regularly visited by bird ringing societies and 2088 nestlings have been marked. About 70 of these rings have been recovered at a steady rate (Fig 1) and these provide the only information known on the movements and mortality of any vulture species. I am very grateful to Dr. J.M. Winterbottom, Director of the Percy FitzPatrick Institute, for permission to examine their ringing recoveries.

Fig 2 shows the age distribution of all recovered birds. The post fledging period includes birds recovered between leaving the nest (from November to December) and the 31st December of that year. Any bird found between its first and second January 1st is classified as 1 year old, and so on. It is found that 64% of birds are recovered before the end of their first calender year of life, 79% before the end of their second year and 93% before the end of their fourth year. The oldest bird recovered was 14 years.

In captivity griffon vultures may live over 20 years (Lucas 1970) and these ringing recoveries must therefore be considered as ' incomplete ' figures since some of the birds ringed will still be alive. Haldane (1955) published a method for calculating the annual mortality rate using such incomplete data, and his method has been used to analyse the past twelve years vulture ringing recoveries. If we assume a constant mortality

Figure 1

Year Ringed	Number Recovered	Age at Recovery																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1948	1	1																				
1949	0																					
1950	2		1												1							
1951	0																					
1952	3		1			1		1														
1953	3			1	2																	
1954	4	3			1																	
1955	3	2		1																		
1956	3	2					1															
1957	8	3	3	1									1									
1958	2	1	1																			
1959	6	2		2	2																	
1960	5	5																				
1961	3	3																				
1962	5	4	1																			
1963	5	2	3																			
1964	3	2	1																			
1965	1	1																				
1966	3	3																				
1967	2	2																				
1968	2	2																				
Total	64	38	11	5	5	1	1	1	0	0	0	0	I	0	1	0	0	0	0	0	0	0

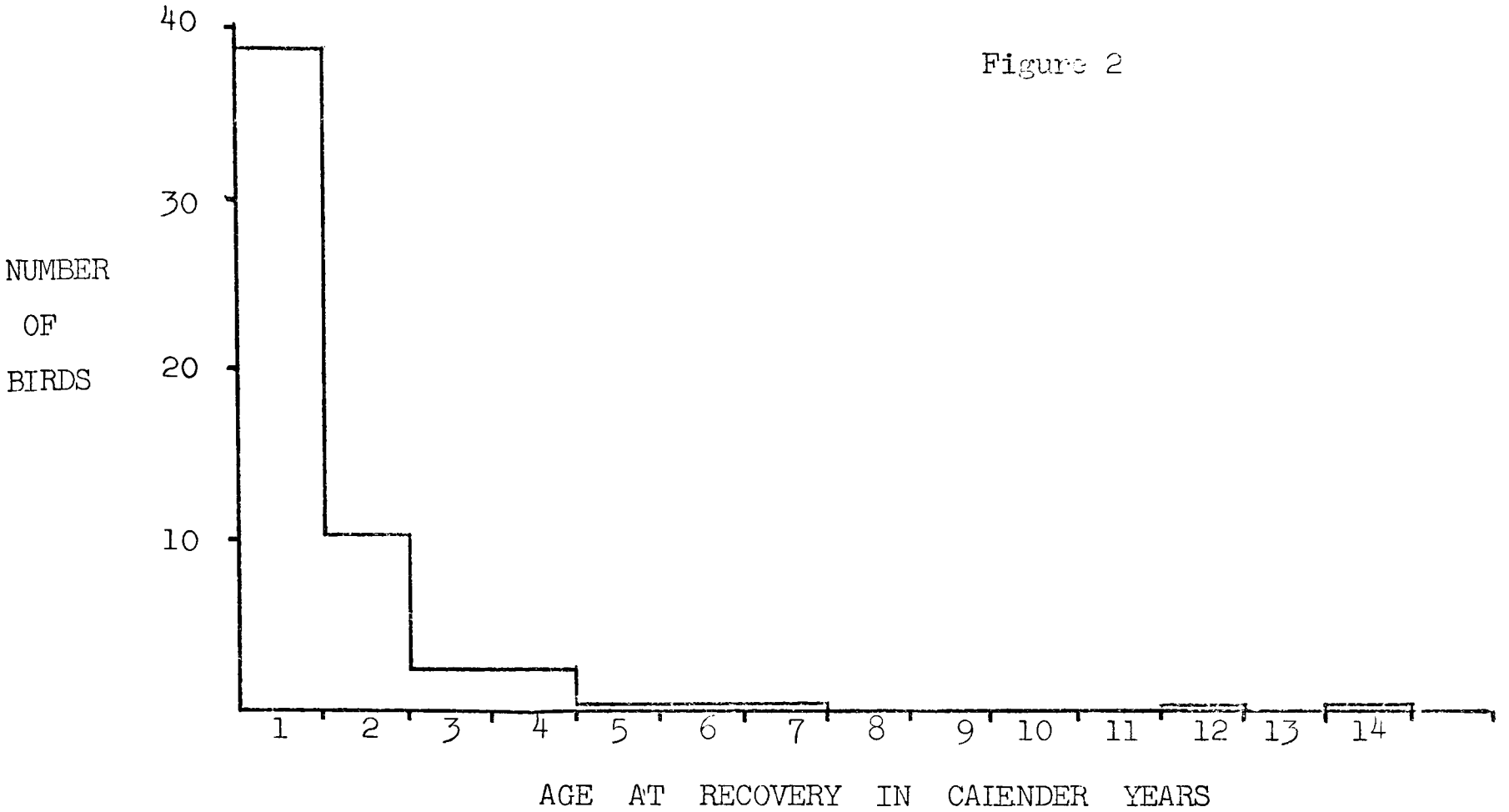
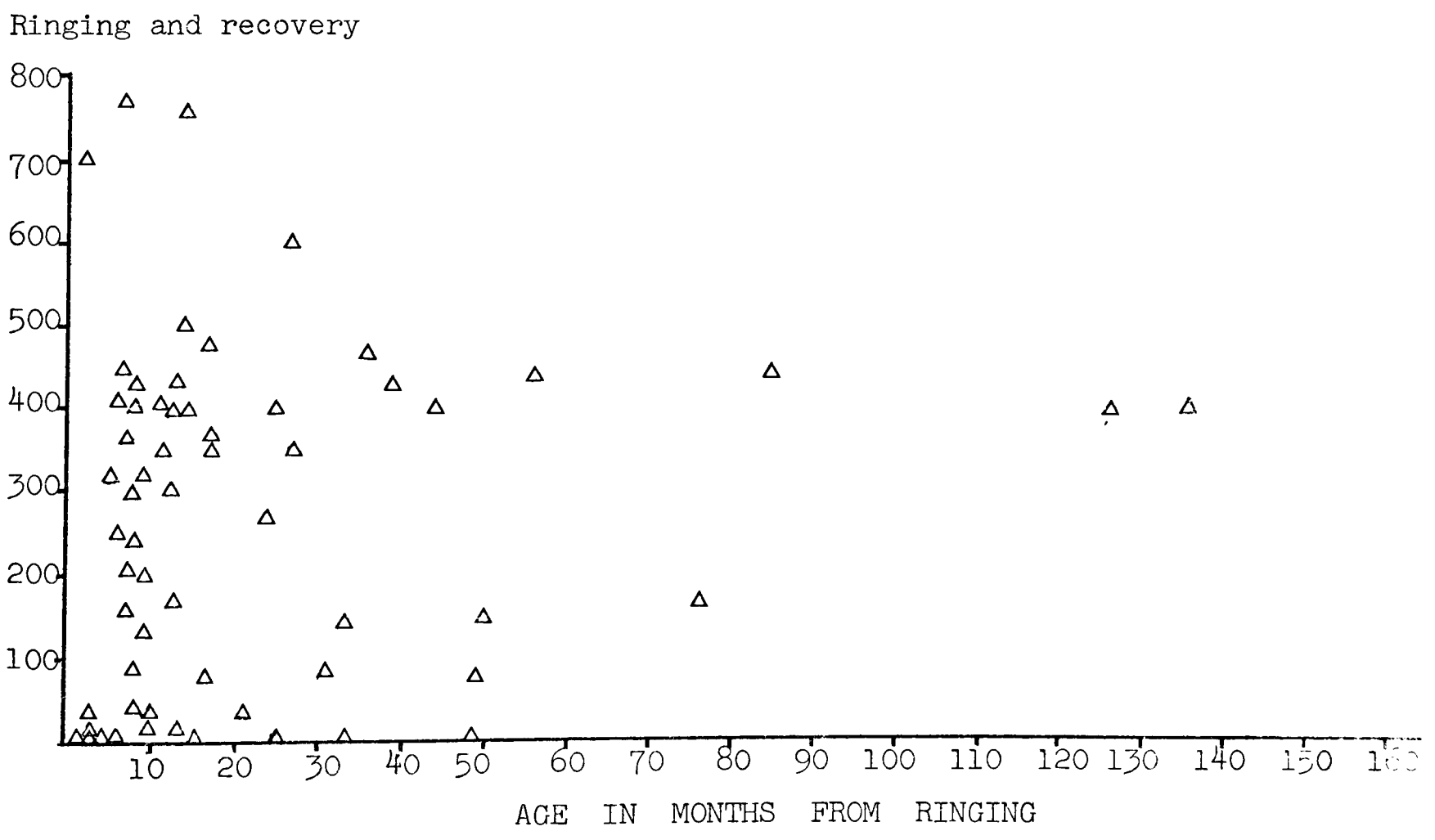


Figure 2

10 birds recovered in post fledging period.

Figure 3



rate with age, then there is an overall annual mortality rate of 55% ± 16%. However, if ringing recoveries from 12 to 20 years ago are considered to be complete (this assumes that no bird lives for longer than 12 years), the combined complete and incomplete data give a mortality rate of 44% ± 5.6%.

In order to calculate a mortality rate it is assumed that mortality is constant with age. This is very unlikely to be valid for a bird with a long period of deferred maturity. Carrick and Ingham (1970) have found that the royal penguin Eudyptes chrysolophus, which does not start to breed until from the 7th to 9th year, have minimum mortality rates in the 1st to 8th year of life of 67%, 43%, 34%, 20%, 12%, 10.4%, 8.5% and 6.8%. If the figure of 44% overall mortality is assumed, this can be used to make a theoretical age distribution where mortality is constant with age. If this is compared to the observed age distribution for complete data (recoveries from 1948 to 1955) it does not differ significantly (Kolmogorov-Smirnov D = 1.94, N = 16) and with this sample mortality does not therefore appear to differ greatly with age. However, post fledging mortality is probably considerably greater than subsequent mortality since this occurs over a period of only a few weeks.

Fig 3 shows the distance travelled from the site of the breeding colony where the bird was ringed to the point of recovery plotted against age at recovery. There is no clear pattern and birds in their first year do not show signs of a clear attachment to, or movement away from, the breeding area.

The mortality rate for the cape griffon vulture is extremely high. A figure of the order of 50% annual mortality rate is usually associated with small passerines with a high reproductive potential, such as the

Song Thrush Turdus merula 47%, Blackbird Turdus merula 42% and Robin Erithacus rubecula 62% (Lack 1954). Nothing is known of the age structure of the cape vulture population. However, in appendix 1 it is suggested that the East African whiteback vulture does not reach breeding age until at least 6 or 7 years. The cape vulture is a larger bird than the whiteback and it seems probable that this species also has several years of deferred maturity. It would therefore appear that under present conditions a high proportion of birds must die before reaching breeding age.

Only a single egg is laid (Roberts 1969) and the reproductive potential is therefore low. Lynne Hurry (pers. comm.) has examined one breeding colony of Gyps coprotheres in the Magaliesberg range in the Transvaal and he considers that there has been a marked decrease in breeding birds in recent years. There has been a decline in the number of birds ringed per year in South Africa, but this may reflect changes in intensity of ringing activity. However, Hurry visited one colony in 1962 and marked over 50 birds, while in 1963 at the same colony he could only find 24 chicks. Out of 15 nests with eggs, only 7 hatched and only 2 young were reared. In the East African Ruppell's griffon colony the hatching success was 86% and the fledging success 96% in 1970. Hurry also gives a clear description of a chick with fret marks developed on the feathers, which is a clear sign of severe food shortage, but which has never been found in wild birds in East Africa. This poor breeding success may be caused by an isolated, relatively unfavourable breeding year. However, the analysis of ringing recoveries showing a high annual mortality suggests that there may be a more extended food shortage which has been present for many years.

Compared to the estimate of age structure for the East African whiteback

population, the present cape vulture population would appear to have a mortality rate which is considerably greater than the recruitment. Southern Africa has had a steady encroachment of agriculture into regions previously occupied by game animals and this has probably resulted in a marked decline in the food available for griffon vultures. It seems probable that the cape vulture population in South Africa is at present in the process of a sharp decline in numbers. With a mortality rate of about 50% per year, most birds are dying probably before they reach breeding age, and those individuals which do start to breed could not possibly reproduce fast enough to offset this heavy mortality. The widespread abandoned breeding colonies in southern Africa and reports of poor breeding success suggest that recruitment of young birds to the population is insufficient to prevent a drastic decline in numbers. The searching methods used by griffon vultures are efficient in areas with a moderate density of birds. Once the population size declines to a low level such that each bird is searching independently of the help from other individuals, it will probably be considerably more difficult for birds to utilise any food that is available. It seems very likely that in the near future many areas of southern Africa will no longer be able to support these birds.

I am extremely grateful to D.G. Dawson who wrote the computer programme for the Haldane calculations, which made this analysis possible.

Appendix 111

Use of the drug Metomidate to facilitate the handling of vultures.

The handling of large birds of prey can cause difficulties and distress to both bird and handler. The close examination of wing feathers particularly causes disturbance and birds have to be restrained forcibly for several minutes. This is very undesirable in captive birds since they quickly become nervous and lose confidence in the handler.

In order to examine birds regularly it was therefore essential to find an effective sedative, and several drugs were tried. Most drugs developed for the restraint of large mammals, such as 'Sernylan' (phencyclidine Parke-Davis), are unsuitable for birds of prey either due to dangerously narrow ranges of tolerance for small animals or long periods of recovery. Ridpath (pers. comm.) has successfully used 'Largactil' (chlorpromazine May & Baker) for the sedation of wedge tailed eagles Aquila audax, but this drug has a slow and prolonged effect. Other phenothiazine derivatives have proved of little value in avian work (Cooper 1968). Spellerberg (1969) has successfully used pentobarbital sodium and thiopental sodium for drugging McCormick Skuas Catharacta maccormicki. The drug Metomidate (Janssen Pharmaceutica) was used by Cooper (1970) as an anaesthetic prior to minor surgery in eight species of birds of prey, and this has proved to be suitable for vultures.

Metomidate is a rapid, centrally acting anaesthetic agent causing a hypnotic effect when given in small doses. It has been used on four

species of Old World vulture, Torgos tracheliotus, Necrosyrtes monachus Gyps ruppellii and Gyps africanus on 27 occasions with no mortality. The drug was injected into the pectoral muscle and the bird immediately released. At the normal dosage used a bird would begin to react after about 2 to 5 minutes, when its eyes would start to close and the head droop. Gradually the head would be lowered, the wings begin to sag and the bird enter a light hypnotic state. There would be no sign of alarm and the bird would slowly lose awareness of its surroundings. At this stage the bird could be handled gently, but if it was severely disturbed it would suddenly 'wake up' and might fly a short distance and appear normal for a few seconds before slowly entering the hypnotic state again. The bird would then sink to the ground and slowly become lightly anaesthetised for about 30 minutes. During this period it could be freely handled. Recovery was gradual over a period of about 2 hours during which the bird would slowly come out of the hypnotic state with no sign of distress of alarm.

Initially a Ruppell's griffon vulture was injected with a dose of 8 mg/ kg. body weight, slightly less than the 10 - 15 mg / kg recomended by the manufacturers and a dose which had proved suitable with eight other species of birds of prey (Cooper 1970). The bird did not gradually enter hypnosis, but after a period of about two minutes began regular wing fluttering and rapidly entered deep hypnosis. The bird remained in this state for about 36 hours and was not fully recovered for 72 hours. Further tests showes that a suitable dose for all species was 3 to 4 mg / kg body weight, about 1/4 of the suitable dose recorded for several other birds (Mortelmans & Vercruysse 1965, Cooper 1970).

This drug appears to be ideal for short term sedation of large birds. The suitable dosage was found to be considerably lower than experience with other species would suggest. The dose can also be finely adjusted

to cause varying levels and duration of hynosis or anaesthesia as neccessary.

Species	Dose mg / kg.	Time needed to induce light hypnosis	Time needed to induce light anaesthesia	Duration of anaesthesia (mins)	Period for recovery (hours)
Gyps ruppellii	4.5	5	8	30	2
	4.0	6	10	20	1
Gyps africanus	3.0	5	10	30	3
	3.5	5	9	40	3
Torgos tracheliotus	3.2	10	25	30	2
Necrosyrtes monachus	2.5	20	35	4	1

Appendix IV

Mammal species mentioned in text.

Hunting dog	Lycaon pictus
Black backed jackal	Canis mesomelas
Golden jackal	Canis aureus
Spotted hyaena	Crocuta crocuta
Cheetah	Acinonyx jubatus
Lion	Panthera leo
Leopard	Panthera pardus
Elephant	Loxodonta africana
Black rhinoceros	Diceros bicornis
Zebra	Equus burchelli
Hippopotamus	Hippopotamus amphibius
Giraffe	Giraffa camelopardalis
Kongoni	Alcelaphus buselaphus cokii
Wildebeest	Connochaetes taurinus
Topi	Damaliscus korrigum
Waterbuck	Kobus defassa
Impala	Aepyceros melampus
Thomson's gazelle	Gazella thomsonii
Grant's gazelle	Gazella granti
Eland	Taurotragus oryx
Buffalo	Syncerus caffer

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