(Amendment to Cover)

ASPECTS OF THE ECOLOGY OF PISCIVOROUS BIRDS OF LAKE KYLE RHODESIA

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C O N T E N T S

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1. INTRODUCTION

From an early period in the lake's history research was undertaken to determine the potential of Kyle as a source of edible fish. In such a study, knowledge of the number and weight of fish consumed by piscivorous birds would seem to be an obvious consideration. Accordingly special investigation was undertaken into the food requirements of fish eating birds which live in the lake area.

The method employed, on this occasion, to obtain the required information has differed radically from that more generally used by investigators working with similar objects in view. The common practise has been to examine the stomach contents of a considerable number of birds of the same species, which have been destroyed in order to make information available. Examples of this method appear in reports by Berry (1936), Jones (1959), Olney and Mills (1963) and Mills (1965) working in Scotland, Hartley (1948) in England, Piggins (1959) in Ireland, Madsen and Sparck (1950) in Denmark, Davies (1955) in South Africa, and Bowmaker (1963) in Zambia. The number of birds destroyed when research is conducted on these lines is considerable. Madsen and Sparck, for example killed 258 White-breasted Cormorant, Davies 37 Trek Cormorant <u>Phalacrocorax capensis</u>, Bowmaker 66 Reed Cormorant and Mills 129 White-breasted Cormorant.

The bird population at Kyle was too small to consider "sampling by shooting" over a long period as this would have so drastically, affected the number of fish-eating birds as to invalidate the investigation. The method of "sampling by shooting" was, however, actually employed in a minor way over a period of eight years in order to determine whether particular species of piscivorous birds had a marked preference for particular species or size of fish. The number of birds destroyed in this way, however was negligible.

To determine the specific food requirements of different species of piscivorous birds at Kyle - both in nature and quantity - a protracted series of hand-rearing experiments was carried out during the period July 1961 to February 1968. The method is time consuming and has been adopted by few of those engaged in research with a similar object in view - by du Plessis (1957) in his work on White-breasted Cormorant, by Davison (1961 unpublished) in connection with his study of the Darter. An account of experiments on the same lines which dealt with the Fish Eagle, the Darter, the Reed Cormorant, the White-breasted Cormorant, the Grey Heron and the Night Heron was published by Junor (1965). The intention in the present instance was to repeat the former investigation but on a larger scale, in order to check the results previously obtained. Birds were again reared literally "ab ovo", and careful records were taken of the amount of food ingested, of variation in body weight (up to one week - in some cases five weeks or longer after the flying stage had been reached), of plumage development, and of the time interval between hatching and the first flight. Laborious as the method may be,it would appear to produce results which, if not of greater accuracy, are at least comparable in value with those obtained by the examination of a host of slaughtered birds. Its reliability was further ensured by comparison of the data obtained in the hand-rearing experiments, with information provided by observation of the development of chicks which had been left to the care of parent birds.

Some way of reaching a reliable estimate of the number of piscivorous birds in each species inhabiting Lake Kyle was obviously of basic importance, and fortunately the configuration of this lake made it comparatively easy to devise means by which accurate counts could be made. During my absence, after transfer, members of my former staff, trained in the methods previously used, continued to make reliable counts for May and June of 1969.

As the investigation proceeded it was realised that in addition to a reasonably accurate assessment of the amount of fish consumed by birds it was necessary to know the type and size of fish which were the main items in their diet. Further information on the seasonal abundance of both bird and fish species had to be incorporated to assess the overall impact of of bird predation on the fish. Coupled with this was the adequacy of bird roosting sites, and, still more important those factors which affected recruiting such as climatic conditions, the existence of satisfactory nesting sites and increased demand for food during breeding.

In reviewing these factors as a whole this work has a direct bearing to the theories advanced by Lack (1954) relating to density-dependency and Wynne-Edwards (1962) relating to homeostasis.

Nomenclature adopted is that used by Roberts 1957, "Birds of South Africa" revised by McLachlan and Liversidge, and Jubb 1957, "Freshwater Fishes of Southern Africa".

2. STUDY AREA

(a) Physical features.

Lake Kyle, (see Figure 1) formed in 1960 by the construction of a dam wall at the confluence of the Mtilikwe and Umshagashi rivers, is one of several lakes in Rhodesia which have been brought into being in recent years. It lies at an altitude between 1,000 and 1,040 meters above sea level, on the Central African plateau at latitude 20°15'S, longitude 31°0'E and its catchment extends over 399,000 hectares (1,540 square miles).

At its maximum it has a surface area of 9,105 hectares (22,500 acres), and its carrying capacity is 1,330 million cubic meters (293,000 million gallons). The extent of its shoreline, which has remained devoid of all aquatic vegetation, is 238 kilometers (140 miles). To the south on the lake margin there is a succession of large granite domes, while extending along each arm for about five miles there is a profusion of minor eminences (known as kopjes) and boulders. The Beza mountains and the Glenlivet range - both formations of banded ironstone - run in a general direction West South West to East North East to border the upper arms. Gorges occur where the lake penetrates one or other of these ironstone ranges and also in the domed area near the dam wall, as well as at a point six miles from the entrance of the Mtilikwe river.

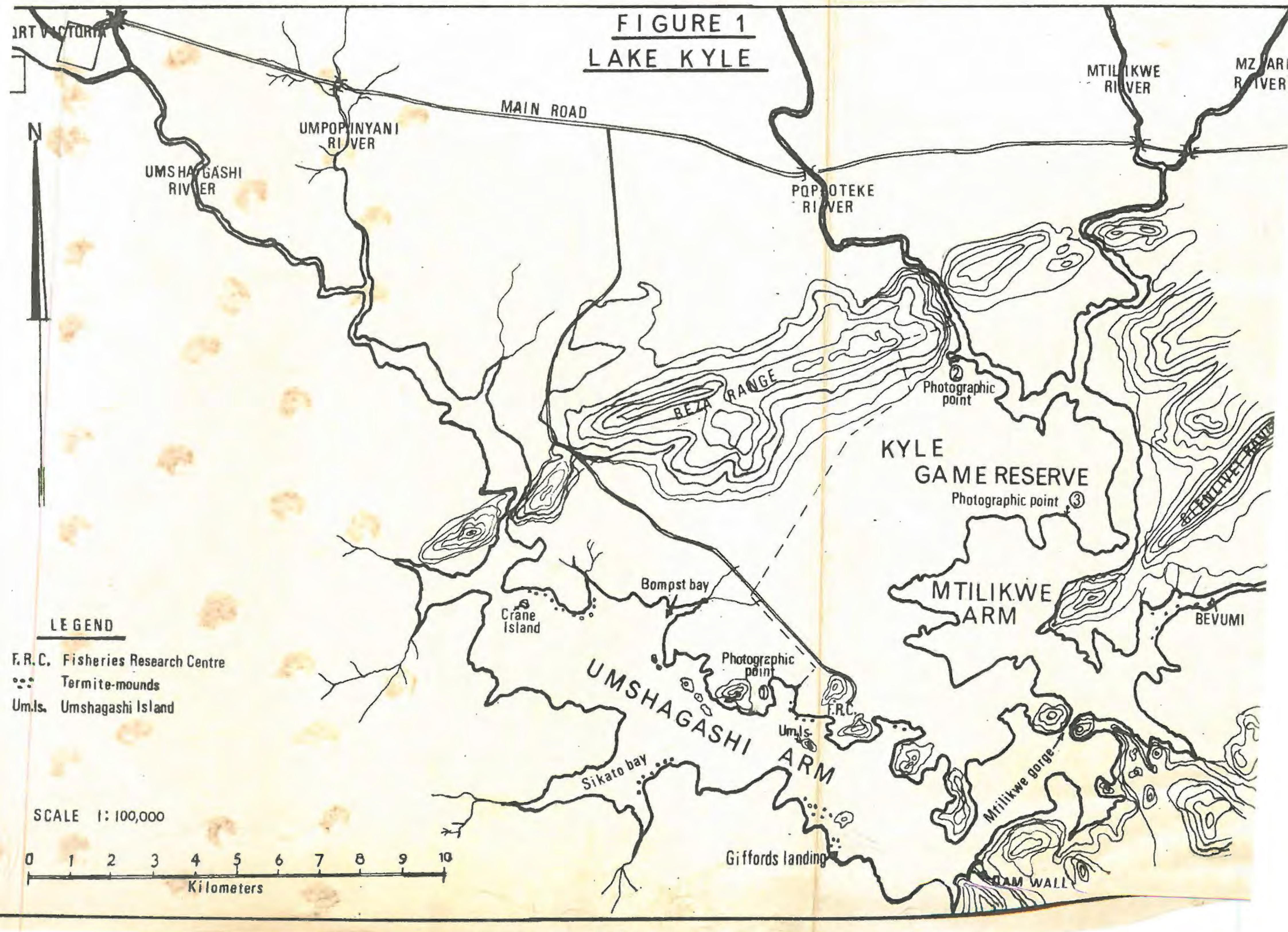


FIGURE 1
LAKE KYLE

Kyle is a V-shaped lake. The easterly arm was the course of the Mtilikwe river prior to the formation of the lake and reference will be made to this section as "the Mtilikwe arm". Its tributary rivers are the Popoteke, the Mzari and the Bevumi. The westerly arm, formed by the course of the Umshagashi, is named after this river and has two main tributaries; the Mucheke and the Umpopinyani. When reference is made to particular islands or bays, names are used, which, as yet, appear in no official nomenclature, so that some change is possible in the later designation.

The main purpose of the lake's construction was to provide water for extensive irrigation. In 1967, however, Kyle was proclaimed part of a National Park, and in addition to its main function as a reservoir, now provides facilities for boating, angling and, to a minor extent, commercial fishing by means of gill nets.

The use of its water for irrigation, naturally implies very considerable variation in water level, (see Figure 2) particularly during the "Dry Season" from mid-May to early November.

Figure 2. Water levels, from the initial stages of filling - Lake Kyle - (Information supplied by the Hydrological Branch of the Ministry of Water Development).

As already indicated, Kyle consists of two sections - an easterly and a westerly, each of which can be dealt with as a separate entity, as the connection between the two arms is very narrow. Comparative study of the bird population was therefore greatly facilitated.

It is to be noted that the lake basin was bush cleared during 1958-1959 and all trees present in inundated areas are the result of regeneration.

(b) Climate

Although Kyle is situated well within the tropics, its climate is tempered by its altitude. The degree to which temperature and rainfall vary with the season is indicated in Table I and Figure 3 below.

TABLE I

DETAILS OF WEATHER CONDITIONS AT KYLE

	Period		Maximum Temperatures Attained			Lowest temperatures Attained		Rainfall		Weather in general
				Surface Water	Atmos-pheric	Surface Water	Atmos-pheric	mm	inches	
D	Cool Season	Approximately	1965	19.5°C	27.2°C	12.2°C	2.2°C	12	0.5	Fine and Bright
R		Mid-May to	1966	18.1°C	26.7°C	11.7°C	3.9°C	53	2.1	
		Mid-August	1967	21.1°C	28.9°C	14.5°C	3.9°C	96	3.8	
			1968	20.0°C	30.0°C	11.1°C	2.2°C	35	1.4	
Y	Hot Season	Approximately	1965	25.0°C	35.0°C	15.5°C	6.7°C	37	1.5	Fine - temperatures rise during August and September
		Mid-August to	1966	26.7°C	35.5°C	15.0°C	4.4°C	81	3.2	
		Early November	1967	24.5°C	35.5°C	13.4°C	5.6°C	108	4.3	
			1968	26.1°C	36.7°C	13.4°C	6.1°C	37	1.5	
W	Wet Season	Early November	1964-65	27.2°C	35.5°C	-	-	548	21.6	Skies cloudy, rain the rule rather than the exception from November on.
E		to approximately	1965-66	27.2°C	37.2°C	15.5°C	14.5°C	528	20.8	
T		Mid-March	1966-67	27.2°C	35.5°C	18.9°C	12.8°C	700	27.6	
			1967-68	27.8°C	36.6°C	16.7°C	11.7°C	215	8.5	
			1968-69	30.0°C	32.2°C	18.9°C	11.7°C	675	26.6	
D	Autumn Season	Approximately	1965	25.5°C	31.6°C	16.6°C	6.6°C	14	0.6	Temperatures fairly constant slight fall in April. In May temperature drops further. Cool season approaching. Occasional showers.
R		Mid-March to Mid-	1966	-	32.2°C	-	5.5°C	48	1.9	
		May	1967	26.7°C	29.5°C	18.4°C	10.0°C	116	4.6	
			1968	23.9°C	29.5°C	15.6°C	8.9°C	22	0.9	
Y		to Mid-April	1969	25.6°C	27.8°C	-	-	114	4.5	

There is great variation in the rainfall at Kyle as between one area and another and also in the rainfall occurring during different rainy seasons of different years. (see Figure 4). A rain gauge at the dam wall recording station showed a total rainfall during December of 388 mm in 1964, 42 mm in 1965, 232 mm in 1966, 59 mm in 1967 and 261 mm in 1968. At the Fish

Research Centre, some 5 kilometers away from the dam wall station, the recordings for December each year were 314 mm in 1964, 82 mm in 1965, 195 mm in 1966, 49 mm in 1967 and 216 mm in 1968.

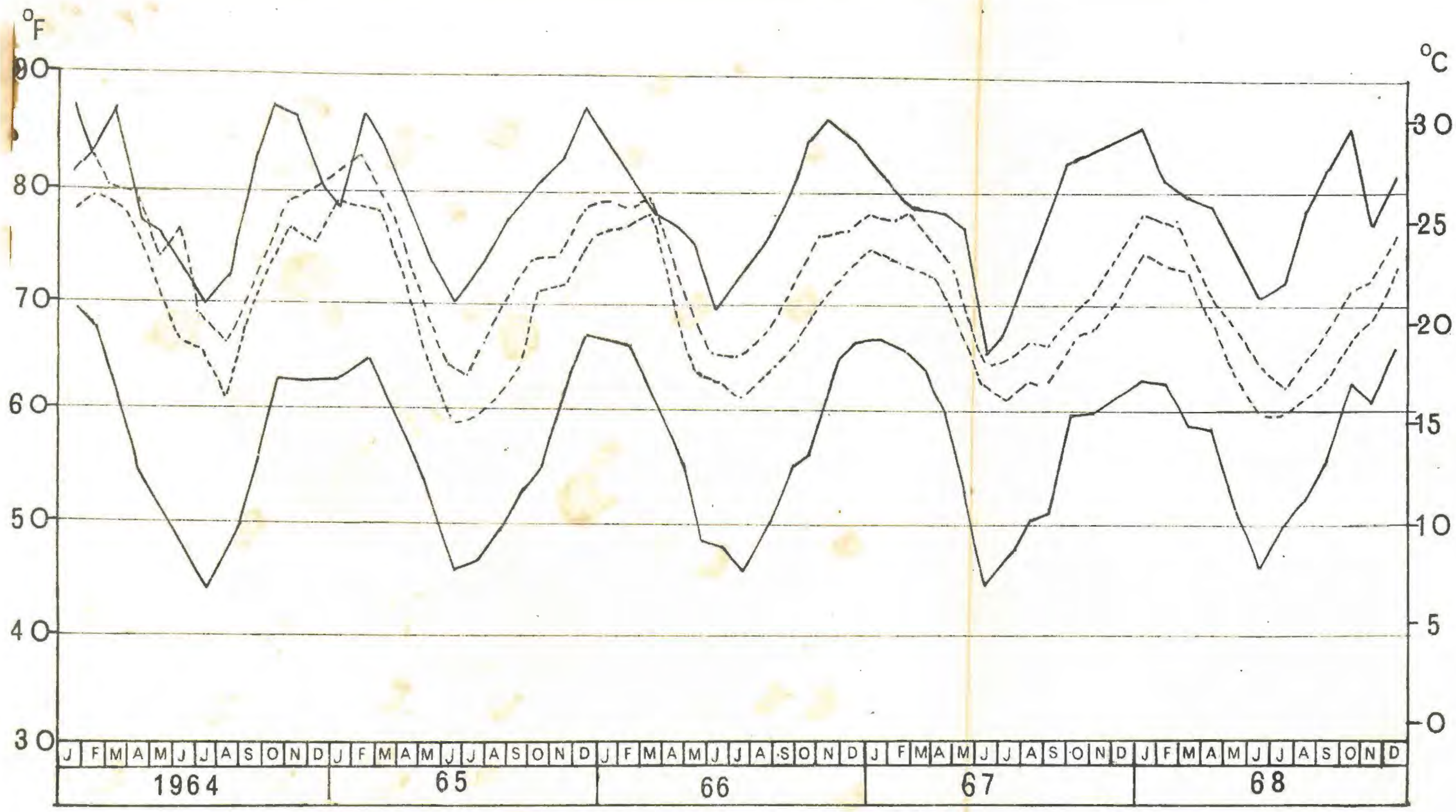


Figure 3. Mean monthly maximum and minimum water temperatures (----) at a depth of 1 meter and atmospheric temperatures (———) recorded at the Fish Research Centre, Lake Kyle, over a period of five years.

The "wet season" is usually marked by very heavy downfalls of rain while at other times of the year rain occurs as a light drizzle. The time of year when the heavy rains may be expected varies from one year to another. In the period 1964/65, they occurred in December, in 1965/66 in February, in 1966/67 in January, in 1967/68 in February, and in 1968/69 in March. Rainfall for the "wet season of 1967/68 (see Table I) in total was less than a third for the same season of the other years.

Again in 1967 there was a brief but heavy downfall of rain in October which is normally a dry, hot month.

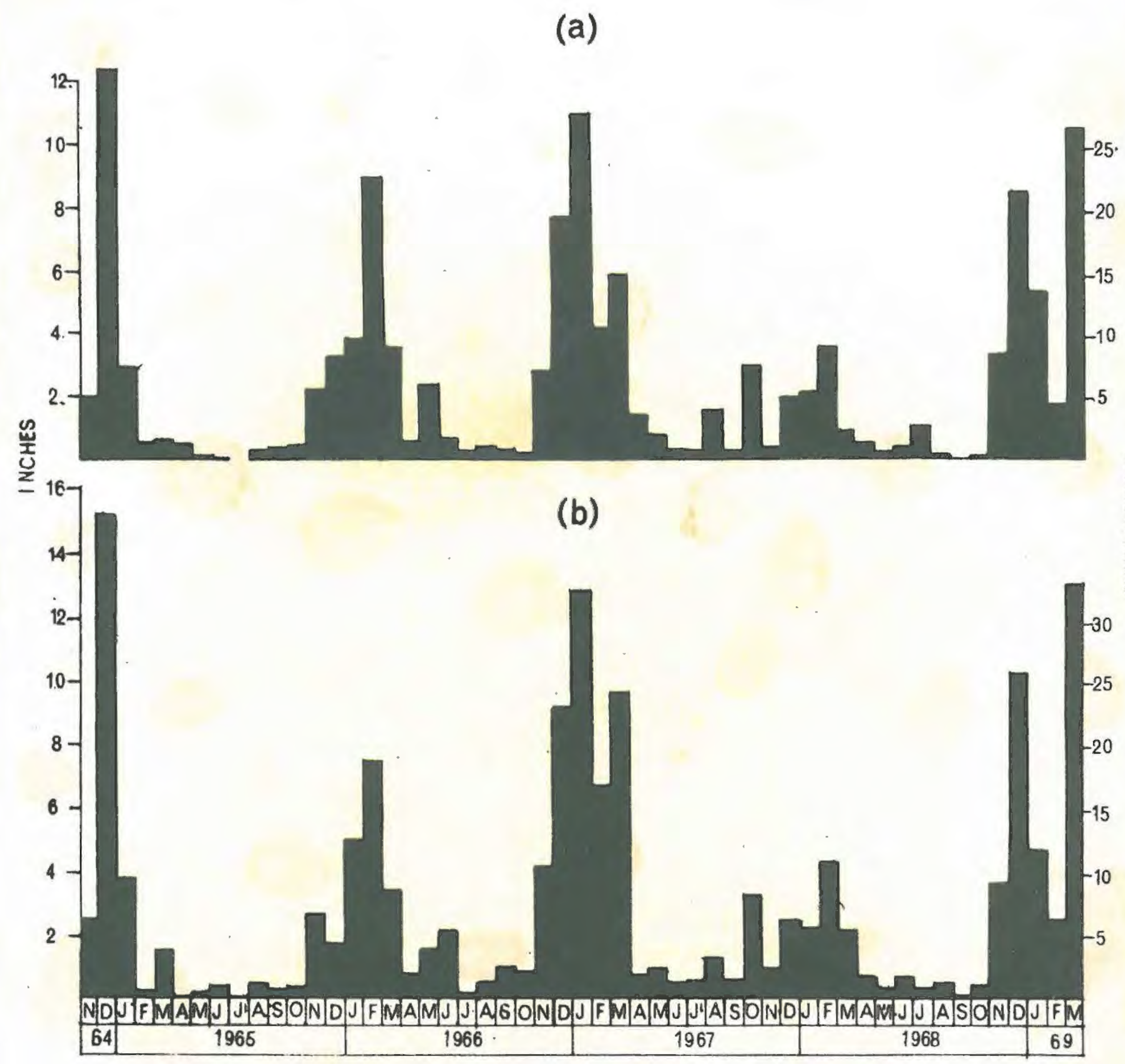


Figure 4. Showing monthly rainfall for the period November, 1964 to March 1969

(a) at the research laboratory 5 kilometers North North West of the wall, and

(b) at the wall. (Information for rainfall at the wall supplied by the Hydrological Branch, Ministry of Water Development).

3. PISCIVOROUS BIRDS OF LAKE KYLE

The fish-eating birds of the lake fall within the following categories:-

I. Purely fish eaters :

Anhingidae

i) *Anhinga rufa* (Lacépède et Daudin), 1802. Darter or Snakebird (R)

ii) *Phalacrocrax africanus* (Gmelin), 1789. Reed Cormorant(R)

iii) *P. carbo* (Linnaeus),1758. White-breasted Cormorant (R)

Alcedinidae

iv) *Ceryle rudis* (Linnaeus), 1758. Pied Kingfisher

v) *Magaceryle maxima* (Pallas),1769. Giant Kingfisher

Ardeidae

vi) *Ardea cinerea* Linnaeus , 1758. Grey Heron (R)

vii) *A. goliath* Cretzschmar , 1826. Goliath Heron (R)

viii) *A. purpurea* Linnaeus , 1766. Purple Heron

ix) *Mezophoyx intermedius* (Wagler), 1829. Yellow-billed Egret.

x) *Casmerodius albus* (Limmaeus), 1758. Great-White Heron

Podicipidae

xi) *Podiceps ruficolis* (Pallas), 1764. Cape Dabchick

((xi) not exclusively piscivorous under normal circumstances but subsist almost entirely on fish at Kyle).

Four Fish Eagles *Haliaetus vocifer* are present, living in areas where rivers enter the lake. Their fishing activity, however, is not confined to the lake area and the number of birds is insufficient to provide reliable scientific data.

II. Incidental Fish Eaters, i.e. feeding on fish only if a supply is readily available :

i) *Nycticorax leuconotus* (Wagler),1827. White-backed Night Heron.

ii) *N. nycticorax* (Linnaeus), 1758. Night Heron (R)

iii) *Ardeola ralliodes* (Scopoli), 1769. Squacco Heron (R)

iv) *Butorides striatus* (Linnaeus), 1758. Green-backed Heron (R)

v) Alopochen aegyptiacus (Linnaeus), 1766. Egyptian Goose (R)

((R) = reared in captivity)

On occasion, the stomach contents of birds listed as incidental fish eaters may not show fish remains, yet all five species have been observed at odd times to feed on fish. These birds, however, were actually of minor importance in this investigation, as they are not numerous and the prey they seize in shallow waters is inconsiderable in quantity. They have been included, however, as some study of their food requirements confirms the conclusions arrived at in the study of the purely piscivorous types.

Research has been directed mainly towards the study of birds in Category I and in particular, to those in this category which have been reared in captivity.

4. Determination of the food requirements of piscivorous birds of different types by the method of hand-rearing.

The years chosen for starting research on the lines indicated were 1965 and 1966. In this period reproductive activity among piscivorous birds was almost non-existent (a fact which will be noted later in the thesis) and it was accordingly very difficult to find specimens.

Some twenty-one chicks, however, were secured during these years and 1967 from different areas. Four Darter were obtained from Kyle during October and November, 1966, three Reed Cormorant from Lake McIlwaine in June, 1967, three White-breasted Cormorant from Lake Ngesi in July, 1967, ten Grey Heron from Kyle over a period extending from November, 1965 to March, 1967, and a Goliath Heron from Kyle in November, 1967. In all cases, unless otherwise indicated, feeding was limited to two meals a day, one in the morning, another in the evening, but where the need for more was indicated by prolonged twittering or in the case of the Grey and Goliath Herons, by a characteristic throaty appeal, the demand was met by an extra supply. Prior to the first meal at 0800 hours each day, the chicks were carefully weighed.

The food supplied during 1961 and 1962 consisted of fish fillets, but with the development of new techniques in trapping and netting, ample supplies of the small Barbus sp.and fingerlings of Tilapia sp. were obtained.

Calcium deficiency in the diet of chicks reared during 1961 and 1962 (resulting from the extraction of fish bones) was assumed to be the cause of occasional deformity in the birds and may indeed have had some effect on their development, but it is now fairly certain that over-feeding is the principal cause of leg-swelling, a condition which occurs mainly in Grey Heron and which is very similar to athritis. Apart from deformity due to unsatisfactory diet, other faults in development may appear, that of wing-twisting in Darters being most frequent. Under normal conditions, birds so affected would probably be ejected from the nest by parents or immature fellow occupants and would have little chance of reaching maturity. Nevertheless, a Darter deformed in this way survived under hand-rearing and when fully feathered, was as capable of catching fish as its normally developed relatives. Indeed, by using beak and claw, it was actually able to ascend dead tree-trunks and establish itself in a selected roosting site.

(a) Hand-rearing of Darter.

Figure 5 shows the amount of food supplied to Darter chicks designated D_1 and D_2 and to another pair named respectively J and M. It was possible to be very definite as to the age of Darter chicks D_1 and D_2 at any stage in their development, as they were actually first observed while hatching out. With them the process of hand rearing continued from 25th October, 1966, to 28th December, 1966. With J and M it lasted only from 14th November, 1966 to 12th December, 1966, as these chicks had been removed from the nest at ages estimated at 38 days for J and 39 days for M. The accuracy of this estimate was confirmed when M attempted its first flight twenty days after removal from the nest, J on the following day, that is 58 days from hatching, exactly the period required in the case of D_1 and D_2.

Darter D_2 at the flying stage.

Food was supplied twice daily (morning and evening) and no attempt was made at any time to force-feed the chicks. It is interesting to note that the amount of food consumed is initially as great as 50% of body weight. From this there is a gradual decline in food requirement (in relation to body weight) until development has reached the stage when the birds take to flight. It is then in the region of 16% of body weight and thereafter remains fairly constant.

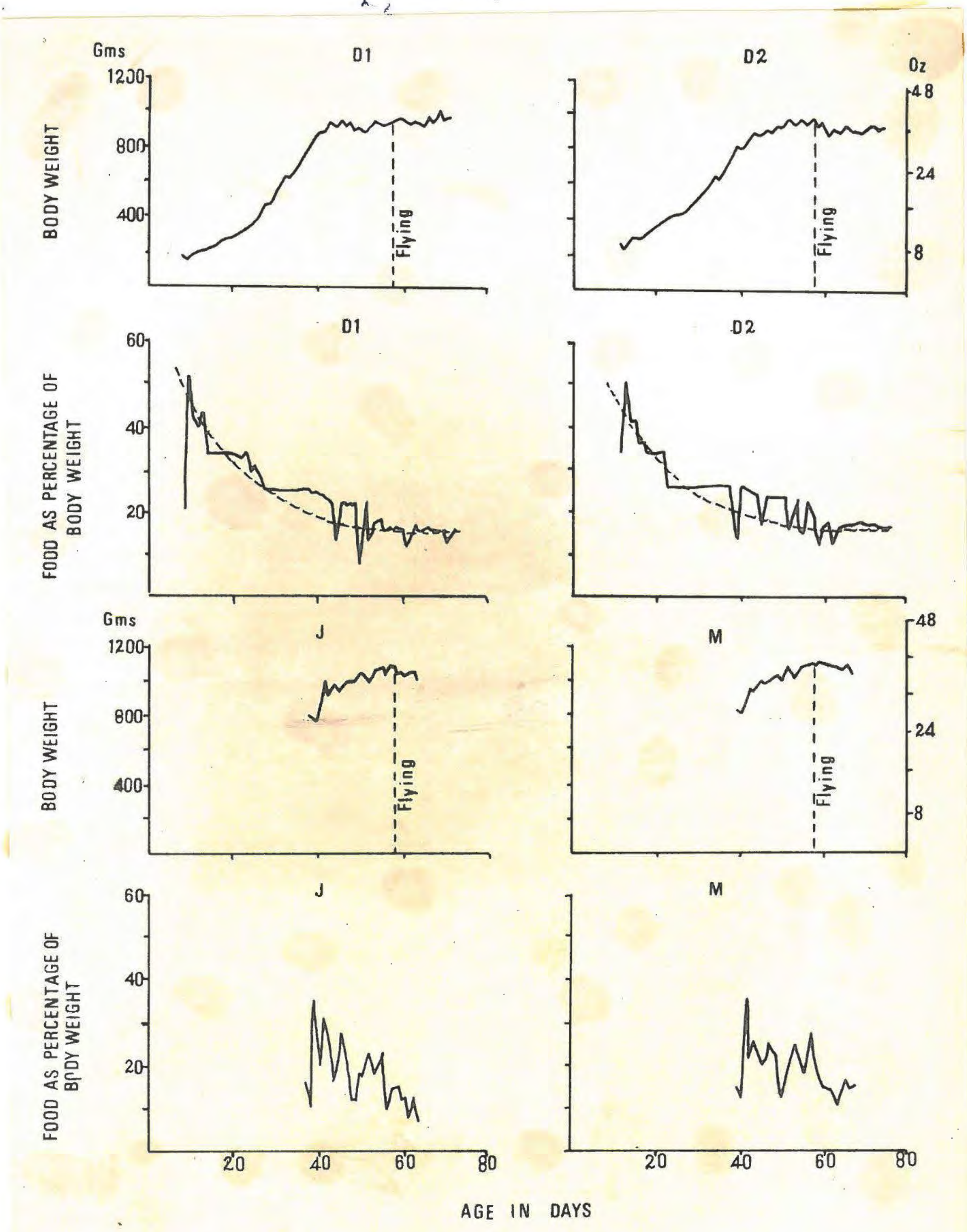


Figure 5. Daily body-weight prior to the first meal of the day and daily food intake (expressed as a percentage of body weight) of Darter chicks D_1, D_2, J and M up to 17 days past the flying stage.

(b) Hand-rearing of Reed Cormorant

Three Reed Cormorant chicks, aged approximately fifteen, fourteen and sixteen days respectively when collected, were hand-reared during the period 21st June to 14th August, 1967. (See Figure 6). The birds were ringed and bore respectively the numbers 07753, 07754 and 07755. In this experiment each bird was designated by the number it bore.

The chicks 07753 and 07755 were supplied twice daily at fixed times with as much food as they could consume, whereas 07754 was given food much more frequently throughout the day, the interval between feeding times varying from thirty minutes to an hour. The curious fact emerged that although 07754 ingested as much as thirty percent of its body weight after it had reached the flying stage (See Figure 6), a quantity far in excess of that consumed by the other two birds, yet its rate of growth and final body weight was no greater than that of 07753 and 07755. The food ingested by the latter chicks amounted in the later stage of their development to sixteen percent of their body weight, obviously the normal supply which would be received from parents when the chicks, nearing the flying stage, were being reared under ordinary wild-life conditions.

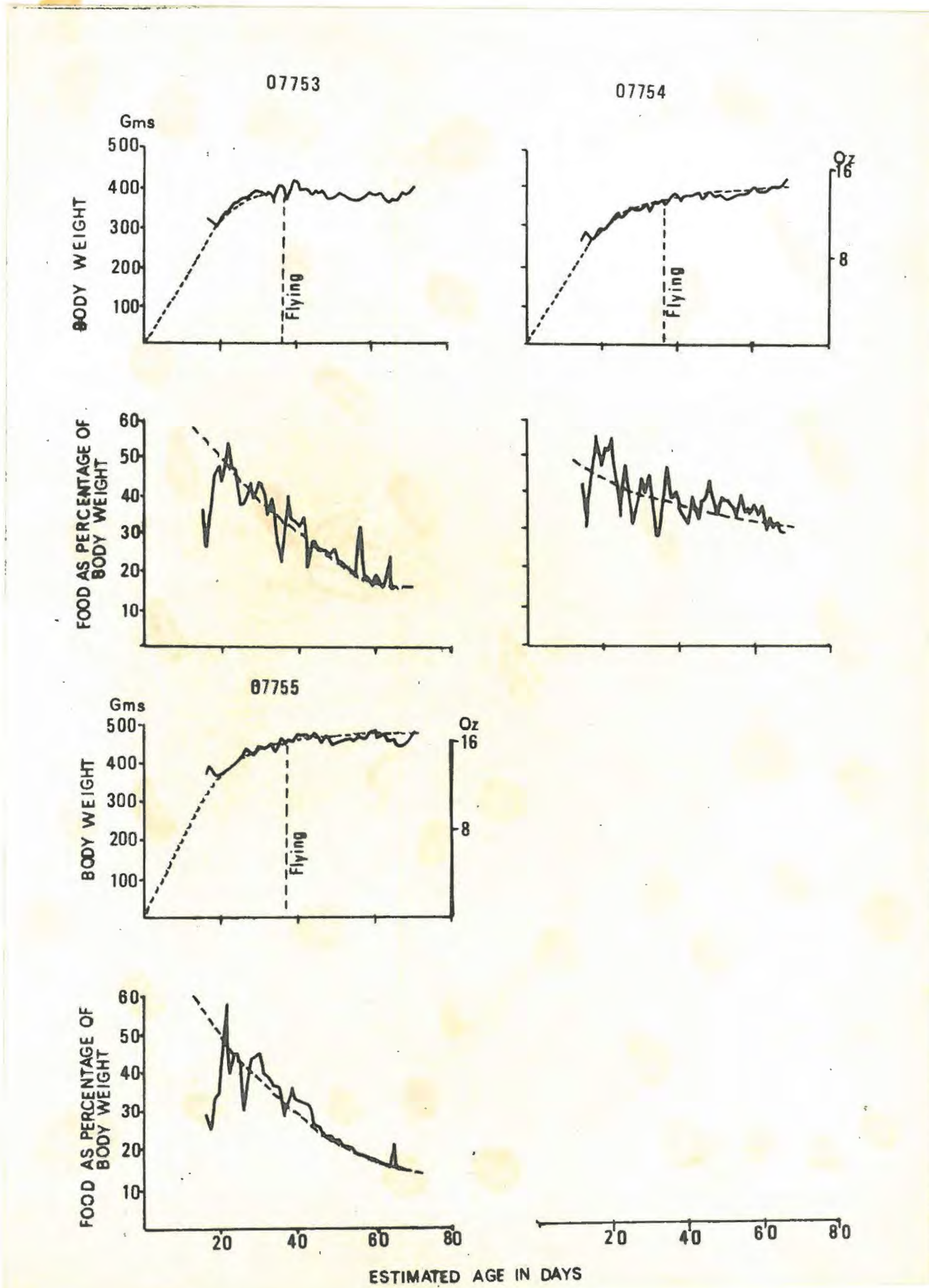


Figure 6. Daily body-weight prior to the first meal of the day and daily food intake (as a percentage of body-weight) of Reed Cormorants 07753, 07754 and 07755 up to 33 days after the flying stage had been reached.

(c) Hand-rearing of White-breasted Cormorant

Three White-breasted Cormorant chicks, which had all reache the same stage in development, were collected from different nests on Lake Ngesi on 20th July, 1967, and identification rings numbered respectively - 81, 82, and 83 were attached. Two days were allowed for nestlings to become accustomed to the presence of humans, and at the estimated age of twenty-three days a start was made with th process of recording food intake and rate of growth.

White-breasted Cormorant chicks 81, 82 and 83 at estimated age of 25 days.

Until their fortieth day these nestlings were fed twice daily with as much food as they could consume. From their forty-first day until they were 53 days old, they received daily an amount precisely 18% of their body-weight. This was supplied in equal amounts at morning and evening meals. After the birds had reached their fifty-third day there was a gradual reduction over three days in the quantity of food supplied, until the daily amount was 16% of body-weight and this percentage was maintained until the birds were fifty-eight days old and capable of flight.

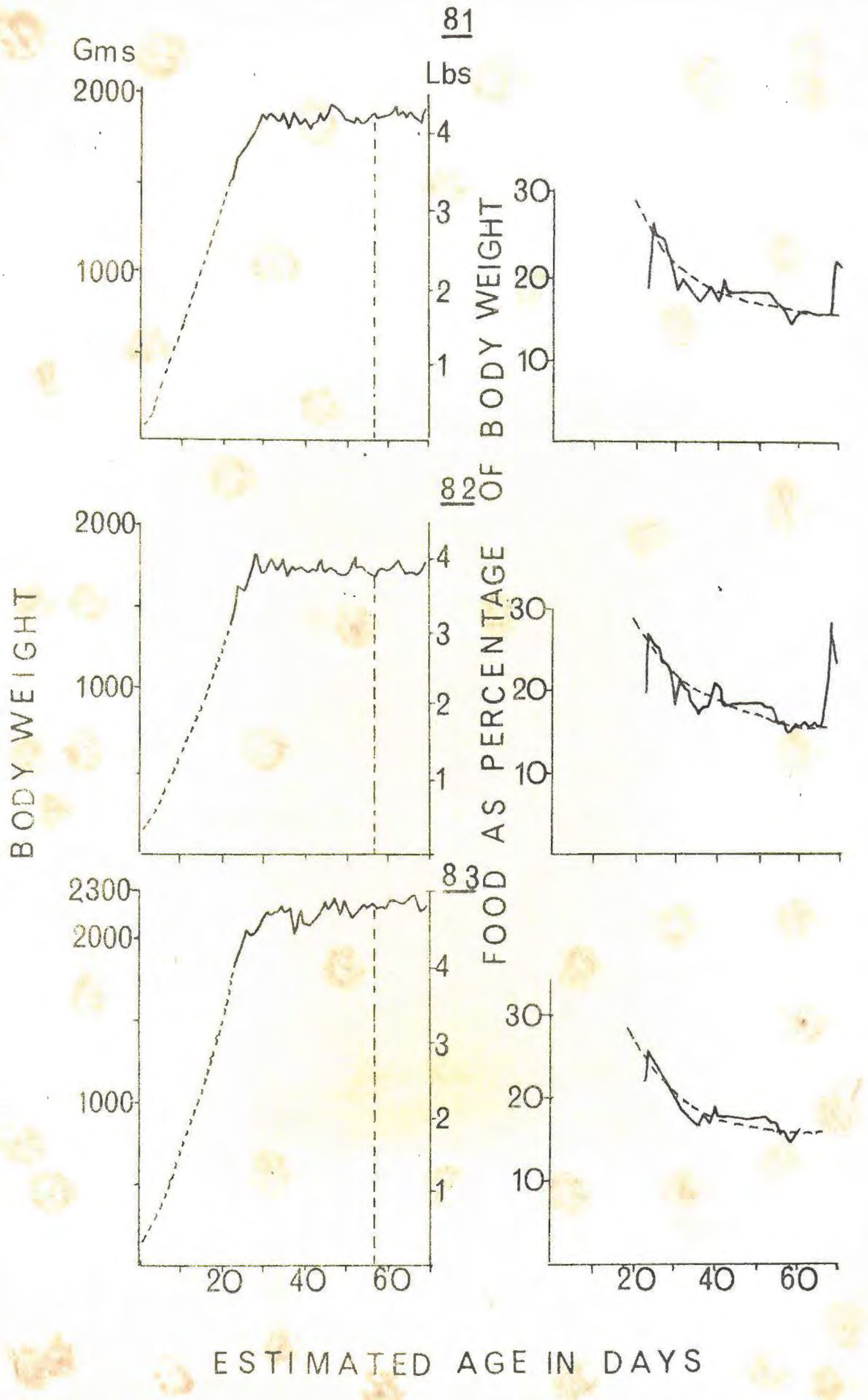


Figure 7. Daily body-weight, prior to first meal of the day and daily food intake (as percentage of body weight) of White-breasted Cormorant chicks 81, 82 and 83 up to and beyond the flying stage.

Figure 7 Shows clearly that there was neither gain nor loss in body weight in the period from when the birds were **forty** days old up to the time when they were capable of flight. The food supplied to them was therefore sufficient to maintain a constant body-weight.

Eleven days after the birds reached the flying stage further experiments were undertaken in which the subjects were supplied continuously with as much food as they could receive. The results of these experiments are given below in Table II.

TABLE II

White-breasted Cormorants when past the flying stage - continuously supplied with as much food as they could consume.

Estimated age in days	81		82		83	
	Food intake as a percentage of body weight					
69	22.0	Average 18.9%	Refused food	Average 11.8%	23.1	Average 18.9%
70	21.7		Refused food		36.0	
71	24.6		19.0		23.1	
72	21.5		18.8		Refused food	
73	Refused food		19.7		Refused food	
74	21.9		Not fed		26.5	
75	15.7		20.2		17.8	
76	24.1		17.0		24.8	

The refusal of food by chick 82 on the 69th and 70th day can be attributed to the large quantity consumed during the two days prior to the start of this experiment. See Figure 7.

A continuous and readily available food supply is not always a normal condition for birds in the wild state. When food is offered, a young bird will occasionally surfeit, but subsequently its apetite declines, even to the extent of refusing the food supplied. The White-breasted Cormorant designated 83, consumed as much as 36% of its body weight on its seventieth day, but only 23.1% on the day following and for the next two days it refused food.

White-breasted Cormorant 83, gorged to absolute capacity when 70 days old, food ingested amounted to 36% of body weight. Incapable of flying for more than 15 minutes after the meal and even after this period found difficulty in taking to the air.

The average combined consumption of all three birds, 81, 82, and 83, over the eight day period was 15.8% of the total body weight. It would appear, accordingly, that the food requirement of 16% of body weight can be accepted as valid for the White-breasted Cormorant.

Guy (1961) quotes Ward, Robinson and Collinge's estimate of 15lb (6.8 kilograms) of fish as the daily consumption of a White-breasted Cormorant. The figure is definitely too high. Meinertzhagen (1959 p.52) arrived at an estimate of 17% of body weight which is very close to the result obtained for this bird at Kyle.

(d) Hand rearing of Grey Heron

Ten birds were hand-reared. Those designated respectively Big, Small, T, K, B, 586-07747 and 586-07748, were fed until they were satiate twice daily. Birds designated 03488, No_1, and No_2 were again fed twice daily, but on a pre-determined quantity of food calculated from the amount supplied to Small.

Five chicks designated P_1, P_2, M_1, M_2, M_3 which were under parental care, were weighed in the nest at 0700 hrs, (prior to receiving their first meal) each day.

Results of these experiments are presented in summarised form in Table III(a), (b) and (c).

TABLE III

History of ten hand-reared chicks and five chicks under parental care

Grey Heron *A. cinerea*

Date of collection from the nest	Name or Number	Estimated age in days	Known age (hatching observed)	Age when flying for the first time	Reference to figures relating to growth rate and food requirements
(a) Hand reared birds - fed until satiate at 0800 hrs and 1700 hrs each day.					
15. 9.65	BIG	6	-	Not capable of flying due to swelling of joints on left leg	Figure 8a
15. 9.65	SMALL	5	-	55 days	Figure 8a
8.11.66	T	7	-	Vanished when 44 days old	Figure 8b
8.11.66	K	7	-	56 days	Figure 8b
9.12.66	B		2	60 days	Figure 8c
8. 3.67	586-07747		6	57 days	Figure 8c
8. 3.67	586-07748		6	57 days	Figure 8c
(b) Hand reared birds - food rationed and supplied in equal portions twice daily - food required to maintain a steady growth rate calculated from the amount supplied to Small					
7.12.65	03488	15	-	56 days	Figure 8a
25.10.66	No_1		6	Not recorded	Figure 8b
25,10.66	No_2		11	Not recorded	Figure 8b
No_1 and No_2 were under fed to start, growth over the first 40 days was therefore slower than that of birds reared under the conditions set out in (a) above, final weight attained was however close to that of Small					

TABLE III

(c) Birds under parental care.

Date when recordings began	Name or Number	Estimated age in days	Estimated age when flying for the first time	Reference to Figures relating to growth rate and food requirements.
10.12.65	P_1	17	Found dead in nest on 33rd day	Figure 8a
10.12.65	P_2	15	Vanished on 28th day	Figure 8a
15.11.66	M_1	2	Found dead in nest on 10th day	Figure 8c
	M_2	3	Found dead in nest on 21st day	
	M_3	3	Found dead in nest on 36th day	
	M_4	5	56 days	

It is to be noted that the normal habitat of the Grey Heron is a locality where there is ample aquatic vegetation, for example a farm dam. There its food supply will consist largely of frogs, crabs and animals of similar size. As indicated by Lowe (1954 p.65), this species in Britain often exist on such diets as water-voles *Arvicola amphibius*. At Kyle, however, which has been entirely denuded of marginal vegetation, the Grey Heron has become entirely piscivorous.

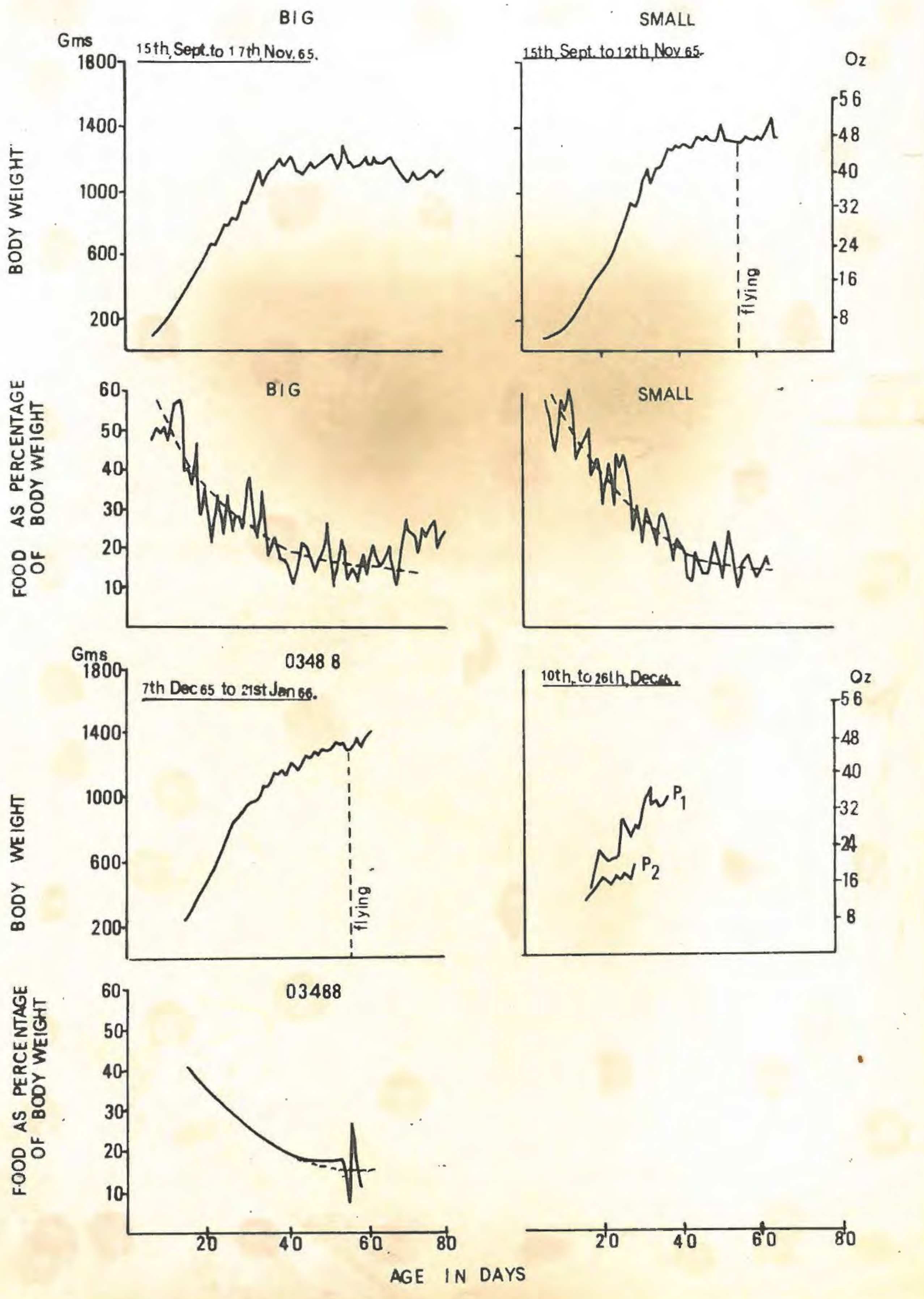


Figure 8 (a). Daily body-weights (prior to the first meal of the day) and daily food intake of hand reared Grey Heron chicks "Big", "Small" and 03488 and body weights (prior to first meal of the day) of two chicks P_1 and P_2 under parental care. (Rearing dates as indicated).

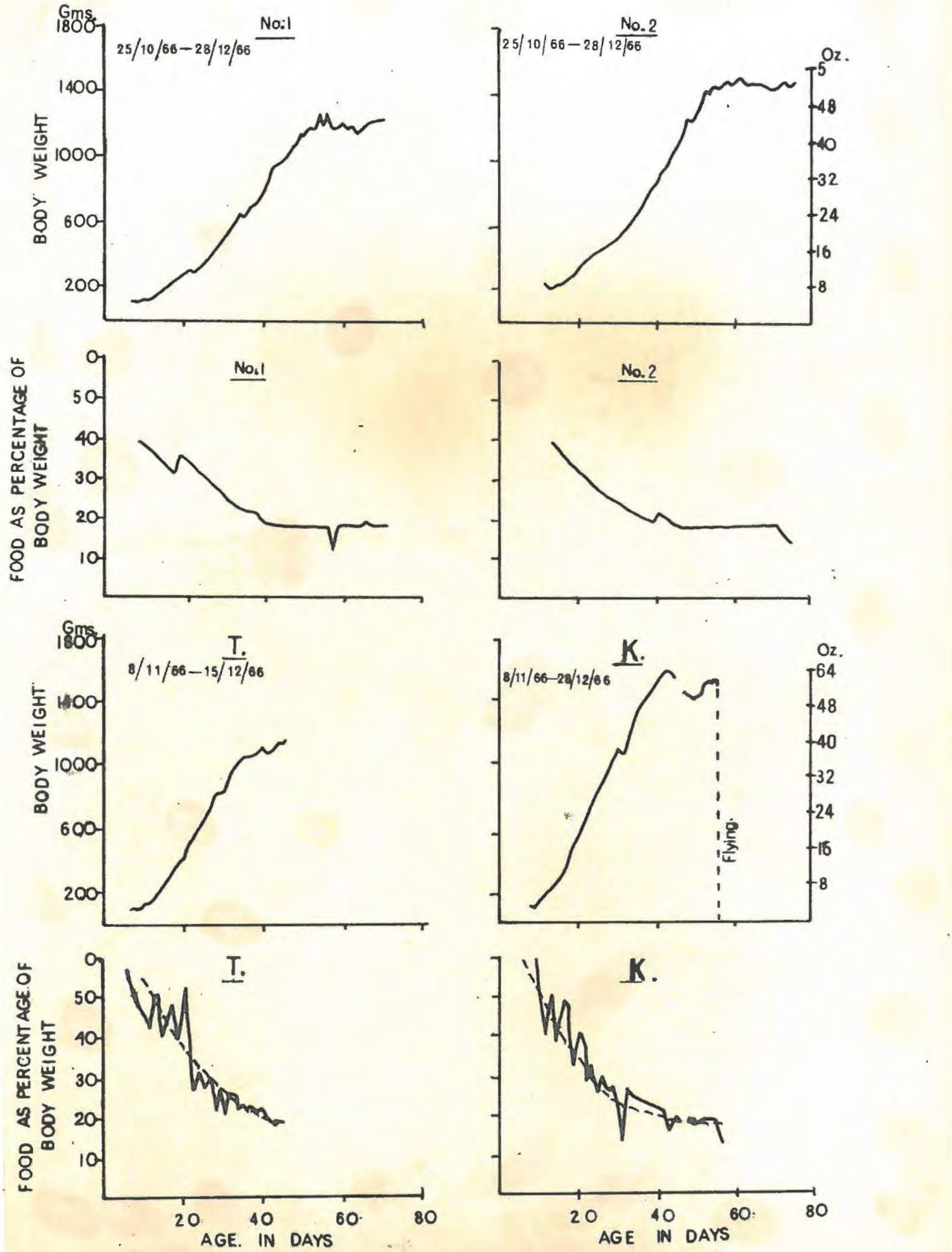


Figure 8(b). Daily body weight (Prior to the first meal of the day), and daily food intake of hand reared Grey Heron chicks No_1, No_2, T and K. (Rearing dates are indicated).

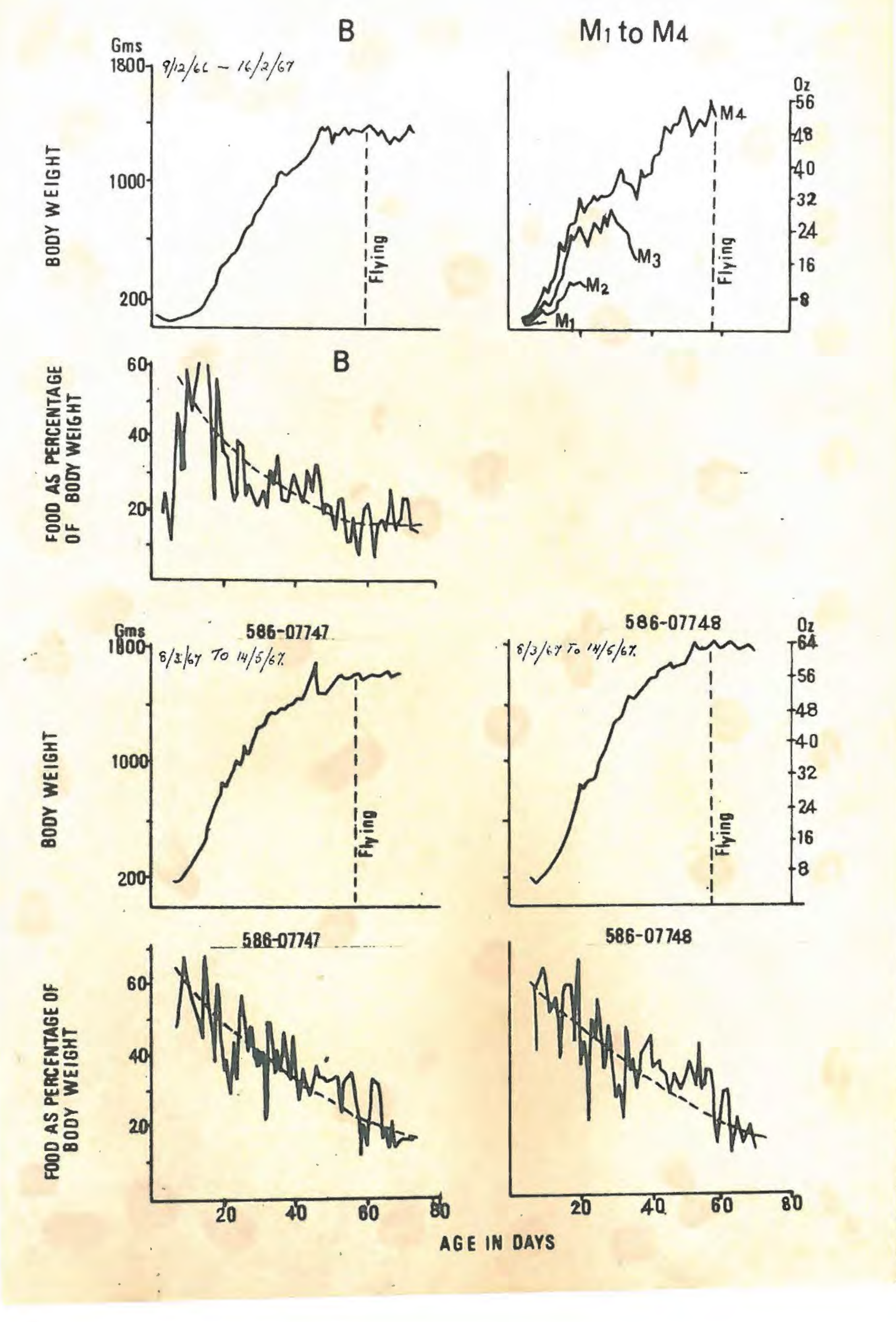


Figure 8(c). Daily body-weight (prior to first meal of the day) and daily food intake fo Grey Heron chicks B, 586-07747 and 586-07748 under hand-rearing conditions, and body weight (prior to first meal of the day) of M_1, M_2, M_3, and M_4 under parental care. (Rearing dates are indicated).

From the present experiment in hand-rearing of young birds of this species, as well as from experiments recently carried out with the Darter, Reed Cormorant and White-breasted Cormorant chicks, it may be gathered that the estimate of their food requirements appearing in an earlier publication, Junor (1965), was really on the generous side. The information gained, however, does show that the weight of fish consumed daily by adult piscivorous birds, amounts generally to 16% of their body weight. In this connection it is interesting to note that Bowmaker (1963) after examining the stomach contents of Reed Cormorants killed over a protracted period, arrived at an estimate of 15% of body weight as the normal daily food intake. This is close enough to provide confirmation of the figure arrived at in this investigation. Another noteworthy result of the experiment is the close correspondence that emerges between the development of the hand-reared chicks and that of the young birds left to the care of the parents (see Figure 8c).

(e) <u>Hand-rearing of Goliath Heron</u>

Results obtained by hand-rearing a Goliath Heron chick (see Figures 9a and b) serve to confirm those obtained in experiments with Grey Heron. Food requirements at the flying stage, and nine days thereafter, approximate 15 to 16% of body weight.

The close similarity between the development of the chick under parental care and that of hand-reared specimen indicates that daily food supply was very much the same in each case. Continuous observation of the Goliath Heron nest, from 6 a.m. to 6.30 p.m., carried out on two occasions, showed that parent birds supplied food twice during the course of of a full day. Two meals a day supplied to hand-reared birds therefore closely simulated the feeding timetable of parent birds.

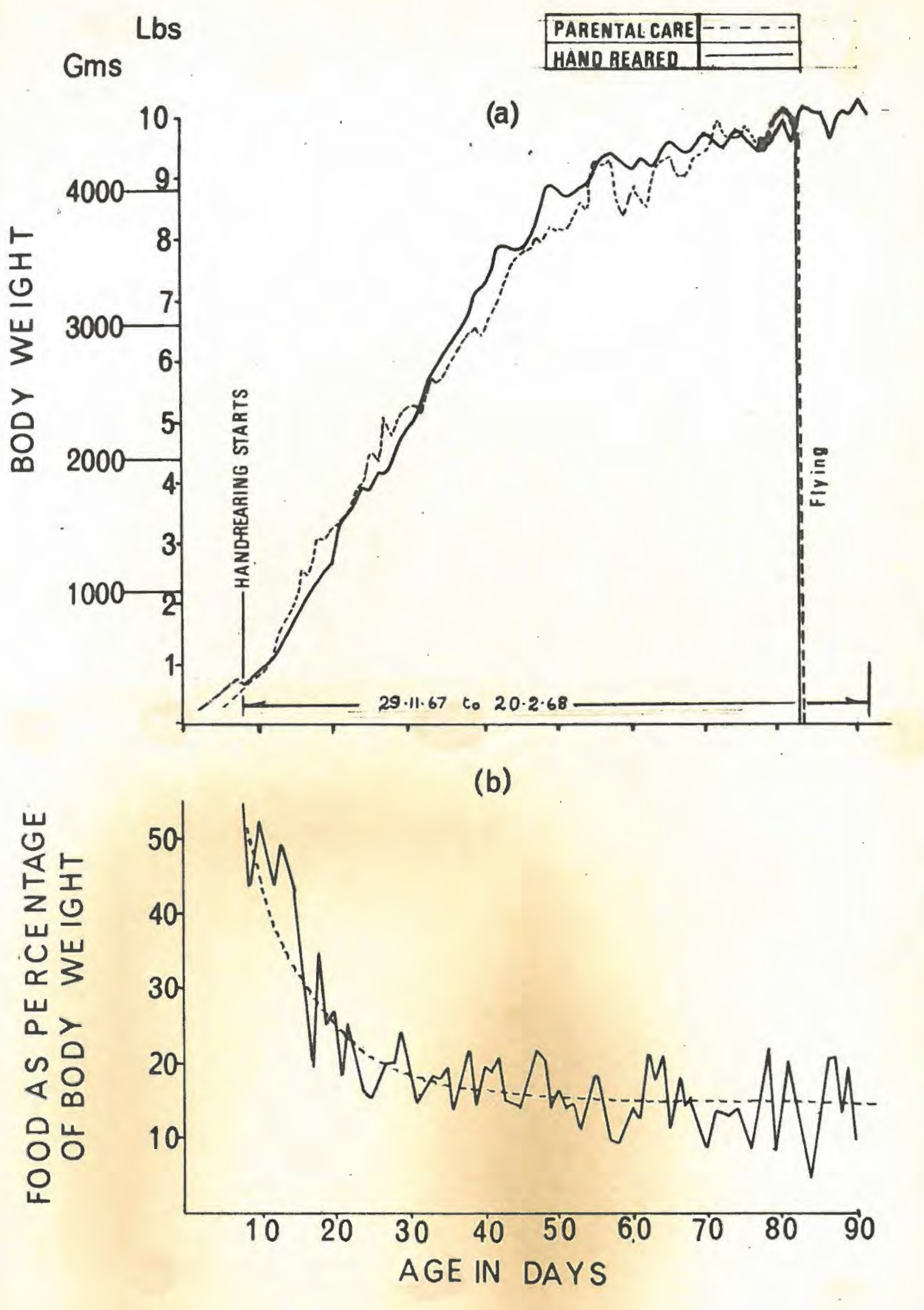


Figure 9.(a) Daily body-weight prior to the first meal of the day of two Goliath Heron chicks, one under parental care, (------), and the other under hand-rearing conditions, (———), (the latter having been removed from the nest after being fed by parent birds for 8 days) up to and beyond flying stage. (Rearing dates are indicated).

(b) Food requirements of the Goliath Heron chick under hand rearing conditions.

Hand-reared Goliath Heron at age 62 days.

Goliath Heron reared by parent birds at age 62 days.

(3 weeks before it was capable of flying)

5. Hand-rearing of chicks of partly piscivorous types

Two White-backed Night Herons and two Green-backed Herons were also hand-reared, on a diet consisting entirely of fish. Although the birds are not exclusively fish-eating, their growth and food requirements (expressed as percentage of body weight) bore a close similarity to that which had been observed in the case of purely piscivorous types.

(a) The White-backed Night Heron

Two chicks of known age, designated White and Night, were removed from the nest on 13th December, 1965, and records of food intake and body weight were made from 14th December onwards. No restriction was made on the quantity of food which was supplied twice daily - sometimes as much as 60% of body weight was consumed. In the case of White the flying stage was reached in forty-one days. Night flew on its fortieth day. The final food requirements were between 14% - 16% of body weight. (See Figure 10).

White and Night - White-backed Night Herons - reared by hand. Well past the flying stage !

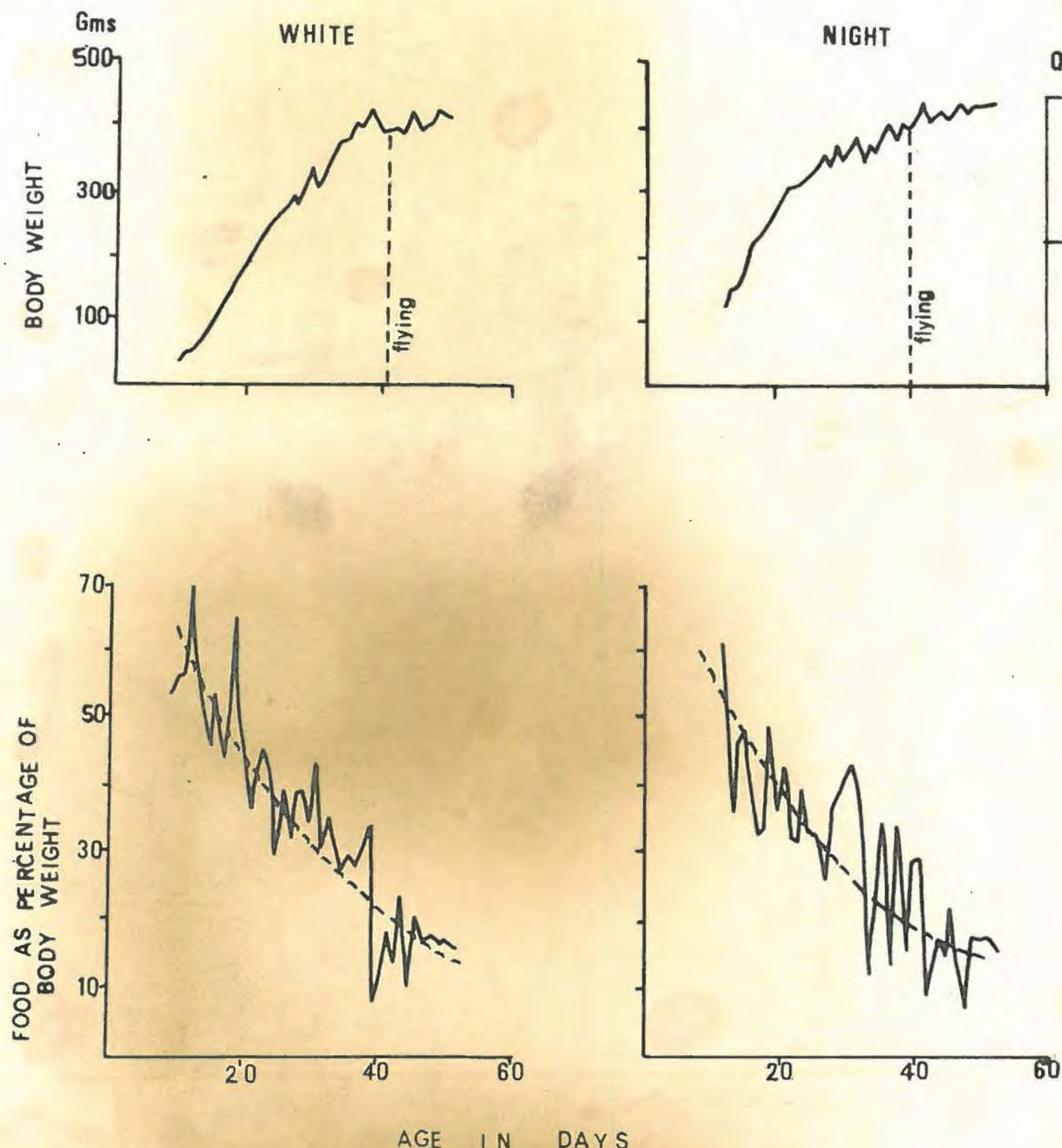


Figure 10. Daily body weight prior to the first meal of the day and food requirements (expressed as a percentage of body weight) of two White-backed Night Herons, White and Night, reared by hand during the period 14th December, 1965 to 24th January, 1966.

(b) The Green-backed Heron

Two Green-backed Heron chicks (738 and 739) of known age 12 and 13 days respectively, when removed from the nest - were reared under conditions identical with those applied to purely piscivorous types. Their hand-rearing continued from 25th November to 22nd December, 1966, and the same growth pattern was observed as in the purely fish-eating birds; but the flying stage was reached much sooner. 738 flew on its thirty-fourth day; and 739 on its thirty-fifth day.

Green-backed Heron 738 a few weeks after the flying stage had been reached.

The young birds were fed entirely on small fish and the food requirement at the flying stage was approximately 16% of body weight. (See Figure 11).

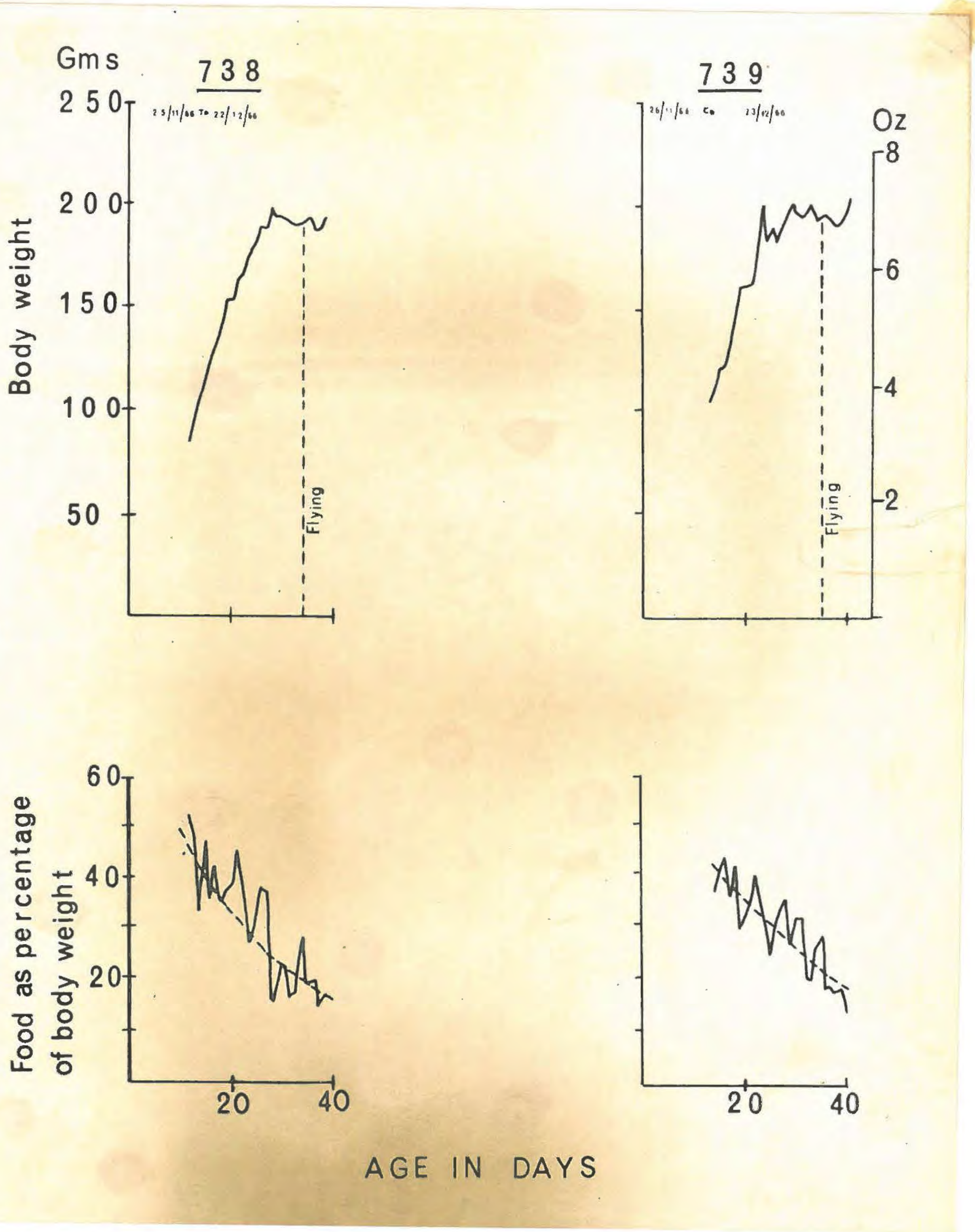


Figure 11. Daily body weight and food requirements (expressed as a percentage of body weight) of two Green-backed chicks, 738 and 739, reared by hand.

In the case of almost all the birds which have been subjects of the present type of experiment, the very frequent occurrence of 16% of body weight as the index of daily food requirements for adults, suggests that the index may have wider application. In general behaviour and in fishing method the Yellow-billed Egret and the Great-white Heron differ very little from the Grey Heron, it can therefore be assumed that the weight of fish they capture to satisfy daily needs would be a proportion of the body weight similar to that established for the Grey Heron. Again, the fishing technique of the Dabchick is very similar to that of the Reed Cormorant, as it actively pursues its prey under water, and consequently the relation between energy expended and the amount of prey seized is likely to be very much the same for both species.

The Pied and the Giant Kingfisher usually fish from a hovering position and are continuously on the move; as a result of this greater activity their food requirements should be correspondingly greater. Their average body weights are, however, extremely low and the number of these birds in relation to other purely fish-eating species is also, proportionately, very low. Any error resulting from the application of the 16% index to these birds is likely to be inconsiderable when the index is used to calculate the total weight of fish consumed by the total population of piscivorous birds.

6. Body weights of purely piscivorous species

Body weights have been determined from a representative sample of birds of each species which have come to hand in various months each year and from hand-reared specimens during the early flying stage whose weight was invariably noted before the first meal of the day. All body weights taken represent the weight of the bird after stomach contents have been deducted. A list of these body weights as well as daily food requirements (calculated as 16% of body weight) is presented in Table IV below.

TABLE IV

BODY WEIGHTS OF PISCIVOROUS BIRDS

		Source	Average weight	Daily food requirements
Darter	(3 adult males) (2 adult females)	Lake Kyle	1557gms	249gms
Reed Cormorant	(5 adult males) (7 adult females)	Lake Kyle	595gms	95gms
White-breasted Cormorant	(1 adult male) (2 adult females)	Lake Kyle	1897gms	304gms
Pied Kingfisher	(3 adult males) (3 adult females)	Lake Kyle	84gms	13gms
Giant Kingfisher	(1 adult male) (2 adult females)	Lake Kyle	345gms	55gms
Grey Heron	(1 adult male) (3 adult females)	Lake Kyle	1528gms	245gms
Goliath Heron	(2 chicks - hand-reared and under parental care + 1 adult-Verheyen Congo)	Kyle and Congo	4530gms	725gms
Purple Heron	(1 adult male)	Kyle	1217gms	195gms
Yellow-billed Egret	(1 adult female)	Kyle	906gms	145gms
Great-White Heron	(4 adult males)	Verheyen Congo	962gms	154gms
Cape Dabchick	(4 adult males) (3 adult females)	Kyle	186gms	30gms

As the Goliath Heron is comparatively rare at Kyle, the body weight of an average specimen has been assessed by consideration of the ascertained weight of two birds at the flying stage, one reared in captivity and the other by parent birds. The result has been confirmed by reference to Verheyen (1953) who gives the weight of a Goliath Heron, obtained in the Congo, as 4756 gms. As no indication is given that this includes the stomach contents it can be taken that the result obtained for the two birds, namely 4530 gms body weight is fairly reliable.

Further weights which tend to confirm those taken at Kyle are those given by Liversidge (1968) - weight of a living Reed Cormorant 655 gms, by an anonymous author in Ostrich Vol.34(4) 1967 - a Dabchick male 197.7 gms, Giant Kingfisher (average for 3 males and 7 females)

356 gms, by Britton and Dawsett (1969) Pied Kingfisher, two birds, average weight 73,25 gms, Comins (1966) average for two male and two female Giant Kingfishers 350 gms. In none of these estimates were precautions taken to ascertain the weight of the stomach contents, and it would appear that this is included with the true weight of the bird. If it is subtracted in each case from the weight supplied it will be found that the figures given differ little from those appearing in Table IV.

7. Fish species (and their size) eaten by the various types of piscivorous birds.

Excluding the Anguillidae, there are sixteen species of fish inhabiting the lake area, these are:-

Cichlidae

1.	Tilapia melanopleura	Dumeril, 1859	Introduced
2.	Tilapia mossambica	Peters, 1852	Indigenous
3.	Tilapia sparmanii	A. Smith, 1840	Indigenous
4.	Tilapia macrochir	Boulenger, 1912	Introduced
5.	Tilapia placida	Trewavas, 1941	Introduced

Cyprinidae

6.	Labeo cylindricus	Peters, 1852	Indigenous
7.	Labeo rubropunctatus	Gilchrist & Thompson, 1913	Indigenous
8.	Barbus holubi	Steindachner, 1894	Introduced
9.	Barbus trimaculatus	Peters, 1852	Indigenous
10.	Barbus paludinosus	Peters, 1852	Indigenous
11.	Barbus lineomaculatus	Boulenger, 1903	Indigenous
12.	Beirabarbus radiatus	Peters, 1853	
13.	Engraulicypris brevianalis	(Boulenger) 1908	Introduced

Clariidae

14.	Clarias gariepinus	(Burchell) 1822	Indigenous

Centrarchidae

15.	Micropterus salmoides	(Lacépède) 1802	Introduced

Mormyridae

16.	Mormyrus longirostris	Peters 1852	Introduced

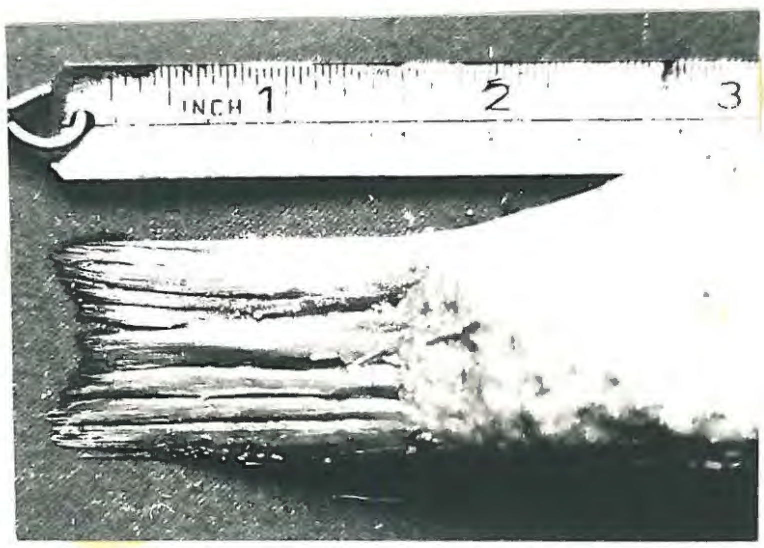
Weekly sampling, over the period March, 1967 to March, 1969, by means of a seine-net (24m in length, 2.25m in depth and of 1.27cms stretch-mesh) yielded a total of 89,690 fish of total weight 1117 kilograms. From this sampling it was concluded that the fish fauna occupying the shallow marginal zone - to be described more fully, later in the thesis (See page 72) as the "Main Fishing Zone of Piscivorous Birds" - consists of the species set out in Table V below.

TABLE V

COMPOSITION OF THE MARGINAL FISH FAUNA OF KYLE

Species	% by Numbers	% by Weight	Habits	Average weight gms
T. melanopleura	40.7	64.6)	Free swimming & widely disper-sed in all parts of marginal zone	20
T. mossambica	29.4	20.2)		8
T. sparmanii	0.2	0.2		11
T. macrochir	0.06	0.3		108
L. cylindricus	11.9	7.2	A bottom dweller tend to form large shoals	8
L. rubropunctatus	0.02	0.1)	Free swimming tend to form large shoals	54
B. trimaculatus	1.7	0.7)		5
B. paludinosus	9.7	3.6)		5.6
B. lineomaculatus	1.7	0.3)		2
Beirabarbus radiatus	3.4	0.7)		3
E. brevianalis	1.1	0.1	Tend to occupy open water	1
C. gariepinus	0.05	1.4		346
M. salmoides	0.07	0.6	Small specimens only occur - from October to December	108
	100.0	100.0		

Characteristic morphological features such as opercular bones, serrated or unserrated dorsal spines, the general body shape, the scale pattern and the shape of the caudal fin permitted easy identification of the fish consumed by different species of piscivorous birds. Moreover, a regular supply of fish of all species was available throughout each month, and fish remains from the stomachs of dead birds could be matched against fresh specimens. In this way the weight and length of the fish which had been consumed by the birds was determined.



Caudal fin of T. melanopleura. This is horizontally divided into two parts differing in colour - the difference being most apparent after death. The size of the fish can be determined from the length of this fin.

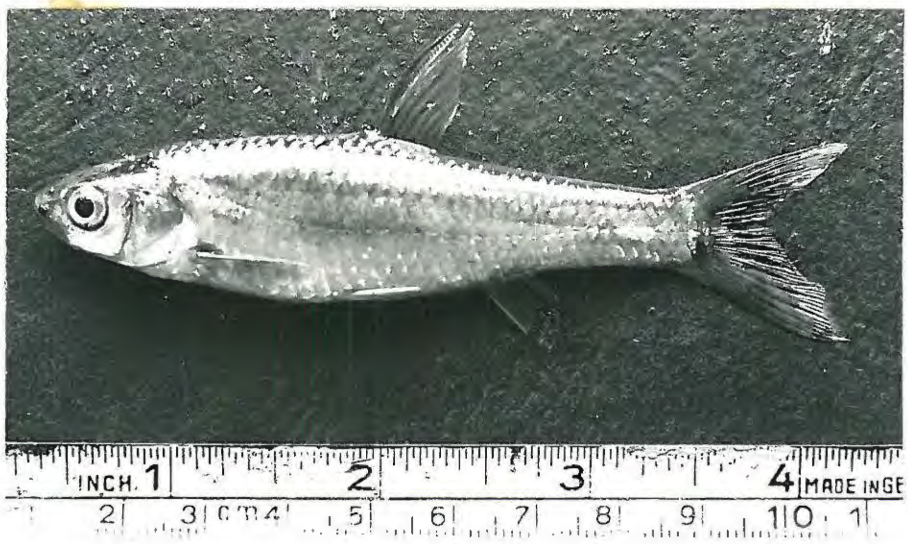
Opercular bones of T. melanopleura. The only species of Tilapia (at Kyle) with opercular bones having a concave outer edge. Again the size of the fish can be determined from these bones.

T. mossambica. Caudal fin is not divided and lateral spots persist after death (even after partial digestion has taken place).

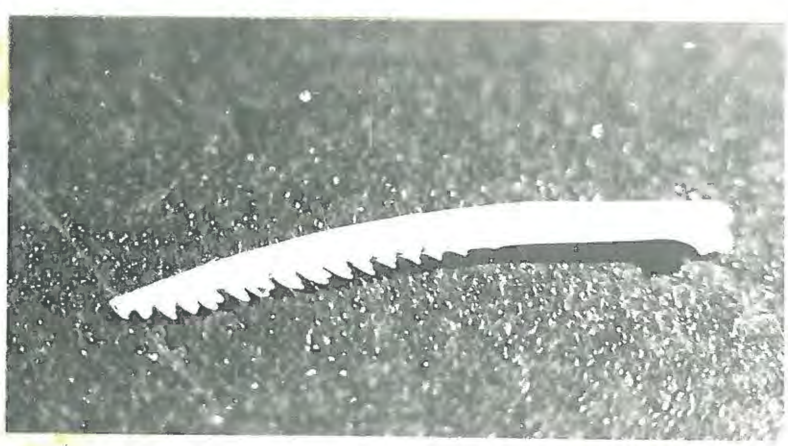
Opercular bones of T. mossambica outer edge is almost straight.

Remains of B. trimaculatus found in the stomach contents of a piscivorous bird. Caudal spot persists after death. Size of fish can be determined from the length of the caudal fin.

Unserrated dorsal spine (x 7) of B. trimaculatus. The only Barbus species with such a heavy single dorsal spine. Length of spine is related to the length and weight of the fish.



<u>B.</u> <u>paludinosus</u>. The only fish in Kyle which has a serrated dorsal spine. It also has a uniform silver colour which assists in identification.



Serrated dorsal spine of <u>B.</u> <u>paludinosus</u> (x 5). As many as eleven spines of this type have been found in the digestive tract of one Dabchick. The length of the spine bears a definite relation to the size and weight of the living fish so that it is easy to assess the weight of food more recently consumed by the bird.

The application of knowledge of this type has made possible the quantitative analysis of food remains in the stomachs of a number of birds, each of which belongs to one of six different species. These have become available for examination during one season or another over the past eight years, through a variety of circumstances. Some species have been caught in gill-nets, some have been killed by predators, a few have been shot for the purpose of this study. The result of their examination appears in Table VI below.

TABLE VI

LENGTH AND WEIGHT OF FISH SPECIES OCCURRING IN THE STOMACH CONTENTS OF SOME PISCIVOROUS BIRDS AT LAKE KYLE

(The number of the birds examined in each species is given in parenthesis)

Type of fish consumed	DARTER (5)			REED CORMORANT (12)			PIED KINGFISHER (6)			GREY HERON (4)			YELLOW-BILLED EGRET (1)			DABCHICK (8)		
	No	SIZE RANGE T.L. in mm.	Wt. in gms.	No	SIZE RANGE T.L. in mm.	Wt. in gms.	No	SIZE RANGE T.L. in MM.	Wt. in gms.	No	SIZE RANGE T.L. in mm.	Wt. in gms.	No	SIZE RANGE T.L. in mm.	Wt. in gms.	No	SIZE RANGE T.L. in mm.	Wt. in gms.
T. melanopleura	14	60 to 228	4 to 250	6	58 to 155	3.0 to 89.5	6	68 to 105	6.2 to 25.0				6	74 to 120	8 to 38			
T. mossambica				9	59 to 93	2.6 to 15.5	8	52 to 79	2.4 to 7.9				1	84	11			
B. trimaculatus	6	62 to 67.5	3.8 to 4.6	5	62 to 98	3.3 to 12.4												
B. paludinosus	33	56.5 to 90	2.3 to 11.0	6	50 to 97	1.5 to 12.1				2	52.5-82.0	1.9 to 6.6	1	64	9	25	50.5-77.5	1.55 - 5.5
B. lineomaculatus	2	44 to 45.6	Not determined															
L. cylindricus				1	79	140												
C. gariepinus	1	Only skin and parts of the head present. Unable to determine size of specimen																
M. salmoides					Found to be present among regurgitated fish remains below the nests of these birds during October													

Examination of the stomach contents of four Grey Heron destroyed for the purpose of this investigation gave no evidence that Tilapia sp. had been consumed. Close observation, however, of the birds while they were fishing indicated that the fish mentioned are actually an item in their diet and this conclusion was confirmed by examination of the food remains under their nests.

Fish of the L. cylindricus species are slightly more abundant than those belonging to the B. paludinosus species yet it appears that the latter are much more frequently encountered in the diet of piscivorous birds. There is, however, a marked difference in the appearance and general behaviour of the two species. The former is an algal-feeder, remaining close to the lake bed with which its dark colour blends perfectly, so that it is not easily seen even by creatures with as sharp eyesight as fish-eating birds. B. paludinosus are bright silver in colour, are primarily insectivorous, and they are to be found widely dispersed at various depths in the marginal zone. It is reasonable to assume therefore, that the markedly greater number of the B. paludinosus species which is found in the birds' diet can be ascribed to the fact that this fish is very easily observed under water.

In the absence of aquatic vegetation at Kyle the Cape Dabchick inhabiting the area would appear to subsist almost entirely on B. paludinosus. With this exception, however, results obtained up to the present indicate that piscivorous birds show no preference for any species of fish.

As there was no preference shown by free living birds for fish of certain species, experiments were conducted to determine the maximum size of fish that can be ingested by birds of certain types. Three of those selected for study had been hand-reared - White-breasted Cormorant, Grey Heron and Goliath Heron - the latter being the largest type of piscivorous bird inhabiting the lake. In addition, information was derived from the examination of the stomach contents of birds of the Darter, the Reed Cormorant and the Pied Kingfisher species. (See Table VI).

The maximum size of fish of certain species known to be consumed by a bird belonging to one of the six species selected is shown in Table VII.

TABLE VII

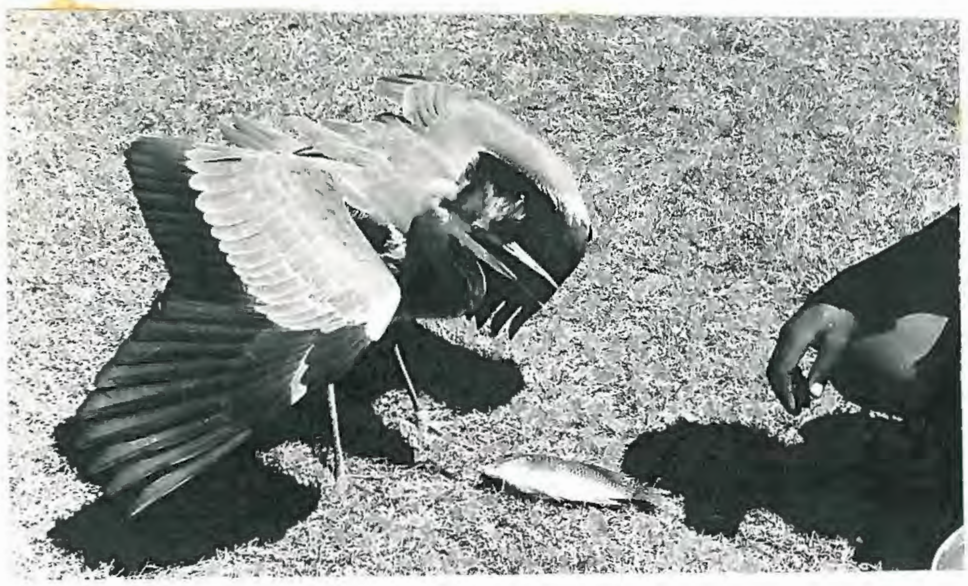
	Species	Maximum width*	Weight	Determined from
Darter	T. melanopleura	80mm	250gms	Stomach contents
Reed Cormorant	T. melanopleura	Not measured	89.5gms	Stomach contents
White-breasted Cormorant	T. mossambica	83mm	376.5gms	Feeding trials
Pied Kingfisher	T. melanopleura	Not measured	25.0gms	Stomach contents
Grey Heron	T. mossambica	66mm	154gms	Feeding trials
Goliath Heron	M. salmoides	71mm	333gms	Feeding trials

*(As the size of fish which can be swallowed is determined more by its maximum width than by its length, this measurement has been used in this case).

In all cases, the birds used in feeding trials showed signs of marked discomfort after swallowing specimens of the size indicated. The Goliath Heron, though offered larger fish, did not attempt to swallow any above 333 gms in weight. A White-breasted Cormorant, actually retained the fish it had swallowed in its buccal pouch for eighty minutes before its meal was ingested. An attempt to ingest prey of such size would seldom be made by a bird of this type under natural conditions.

FEEDING TRIALS. Grey Heron 03488 when well past the flying stage is offered a *T. melanopleura* of 269.1 gms and width 84 mm.

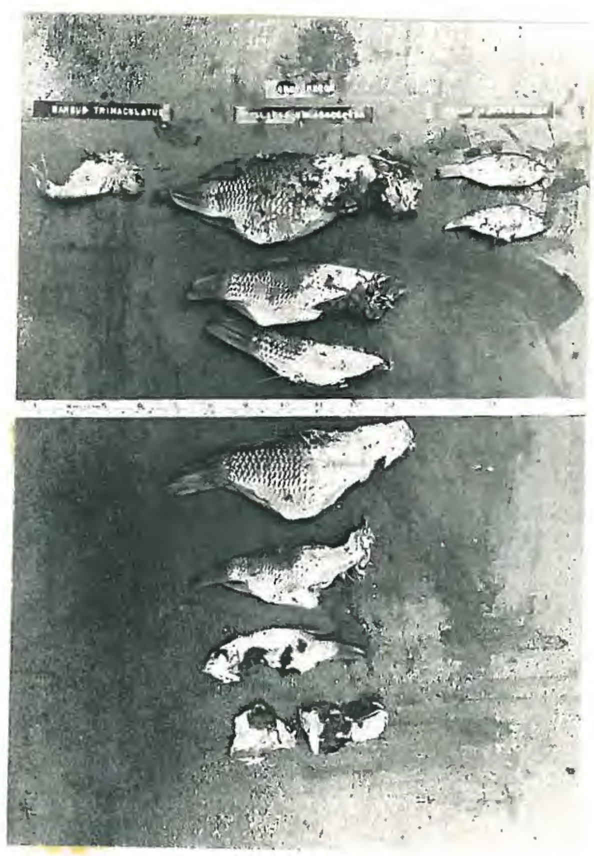
An attempt is made to swallow the fish.



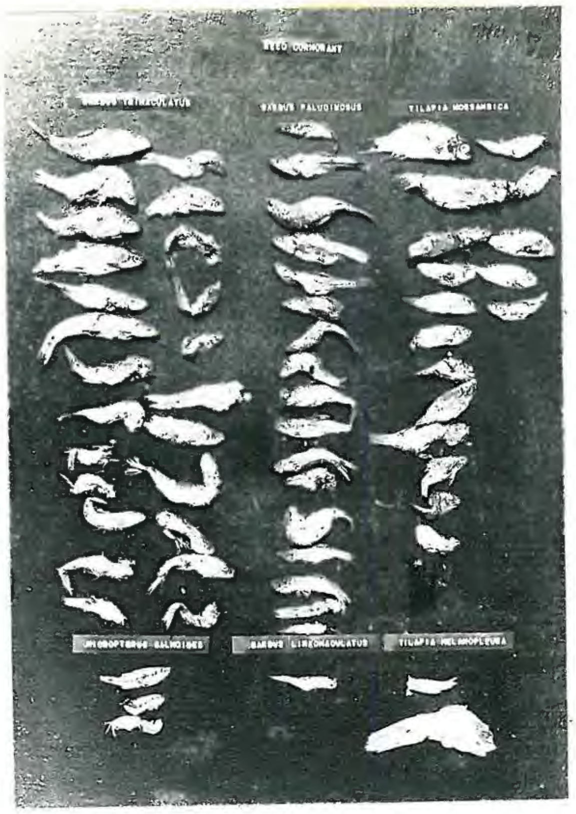
It is too large so it is rejected.

03488. After swallowing a T. melanopleura weighing 154 gms and 66 mm in width, showing marked signs of discomfort.

Chicks and adult birds occupying nests at breeding sites, when disturbed by the approach of a boat, will regurgitate their previous meal. Examination of fish collected under nests of Grey Heron and Reed Cormorants served to confirm the results obtained in the experiments just described.



Regurgitated fish found below three Grey Heron nests at a 1967 breeding site. Note Tilapia melanopleura formed the bulk of the food consumed in this instance. The largest fish, a T. melanopleura which was regurgitated by a bird in full adult plumage, measured 61 mm in maximum width - the estimated weight of the living fish 165gms (5.8 oz) was 11 gms (0.4 oz) heavier than the largest fish which could be consumed by a young bird at the flying stage.



Fish remains collected below eleven Reed Cormorant nests, holding chicks, still at the downy stage and others feathered, at the 1967 breeding colony. All fish were small and no marked preference for any particular species was evident.

It would appear that the piscivorous birds of the types which inhabit Kyle have no marked preference for fish of a definite size. There are limits however, which determine the suitability of a fish as prey for the birds. Obviously the 'gape' of a bird must be one of the limiting factors, and generally it has been established that the fish consumed by the piscivorous birds inhabiting Kyle are invariably small, ranging in length from 44 mm to 583 mm and from a bare 2.3 gms to 376.5 gms in weight. Table V (page 37) shows that the great majority of fish inhabiting the marginal zone are of dimensions which lie within these limits, so that they are suitable as prey for piscivorous birds.

8. <u>Number of piscivorous birds inhabiting Lake Kyle with brief preliminary account of method of assessment.</u>

In the case of most of the piscivorous birds already named, conditions were very favourable for obtaining a reliable estimate of the number present on lake Kyle. The rocky or stony nature of much of its border precludes the development of plant life, while the variations of water level and the presence of the herbivorous *T. melanopleura*

Part of the rocky shoreline typical of Lake Kyle, within a distance of 5 miles from the wall - taken from photograph point 1. (See Figure 1).

(Pink bellied or Sabi Bream), as described by Wager (1968) and Junor (1969), further inhibits the growth of aquatic vegetation. When the lake margin recedes, as it did after the seasonal rains (usually occurring mid-November to mid-March) of 1963/64, 1964/65, 1965/66 and 1967/68, the shore appears as a barren open expanse.

The upper part of the Mtilikwe Arm - showing the barren type of shoreline which exists at Kyle, taken from photographic point 2. (See Figure 1).

Shoreline on part of Mtilikwe Arm, June 1966 - barrenness is accentuated by water recession during the dry season. Taken from photographic point 3. (See Figure 1).

Birds are thus easily seen from a considerable distance and monthly patrols operating simultaneously in open boats, on each of the two arms of the lake, found that their task of making accurate counts of all types of fish-eating birds in the areas concerned, was easily accomplished.

Supplementary to the boat patrols, observers were stationed at fixed points on the shore (points marked O.P. on the key to figure 14, page 69) who have made note, at ten-minute intervals, of the number of Reed Cormorants (which is usually the predominant species), that have appeared in their vicinity on the way to, or from, their roosting sites. These birds do not make the journey to their resting place overland, but fly over the lake approximately three feet above its surface. This characteristic behaviour had the result that the birds flew through narrow gorges, which were used as fixed observation posts, and offered an additional advantage in making precise counts of the passing Cormorants.

Observations made as early as 1964 and repeated in the following years, indicated the Bevumi area as the roosting site favoured by the Reed Cormorant. The presence of these birds was noted during most of 1966 (with the exception of August, September and October) and on until May 1967, then again from mid-December 1967 until May 1968. Definite evidence of their special preference for the area was provided on 22nd May, 1966, when patrols remained out till well after sunset, visiting other possible roosting sites and finding all unoccupied.

On the 24th May, 1966, boat patrols assessed the total number of Reed Cormorants on Lake Kyle to be 356. On the following day, field station observers (first counting the birds on their feeding ground in the Bevumi area, prior to the evening flight) estimated the number to be 357. The fact that the two methods provided counts so close to each other makes it reasonable to assume that counts of other species made by boat patrols are equally reliable - especially those made of the number of Darters, White-breasted Cormorants and Herons.

Seasonal distribution and number of piscivorous birds at Kyle each month for the period November 1965 to June 1969 are given in the graphs (a) to (e) under Figure 12.

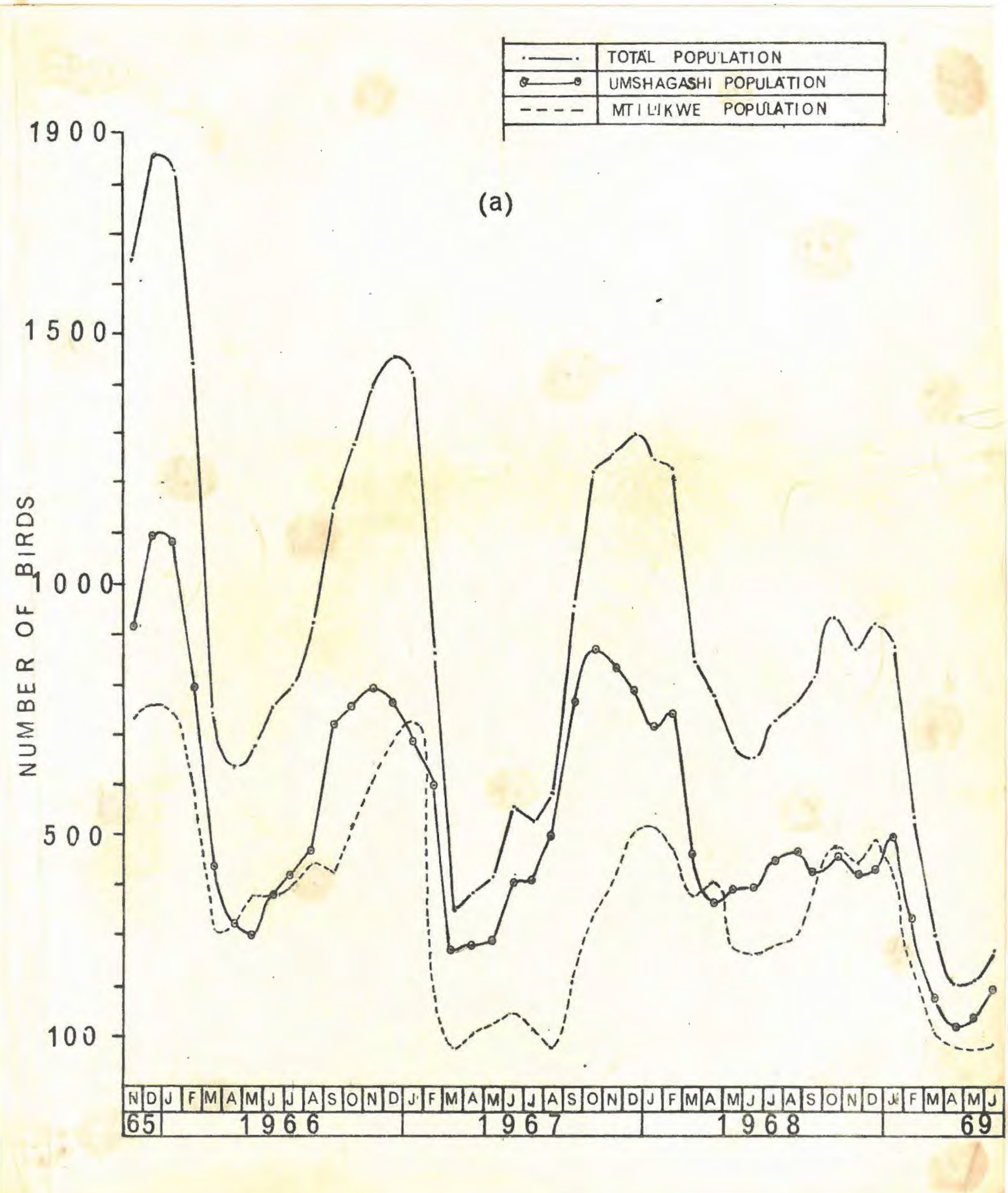


Figure 12 (a) Distribution and number of all purely fish-eating birds on Lake Kyle each month. (Counts made by patrol boats). Separate counts were made on the two arms of the lake. Umshagashi (o————o) and Mtilikwe (-------).

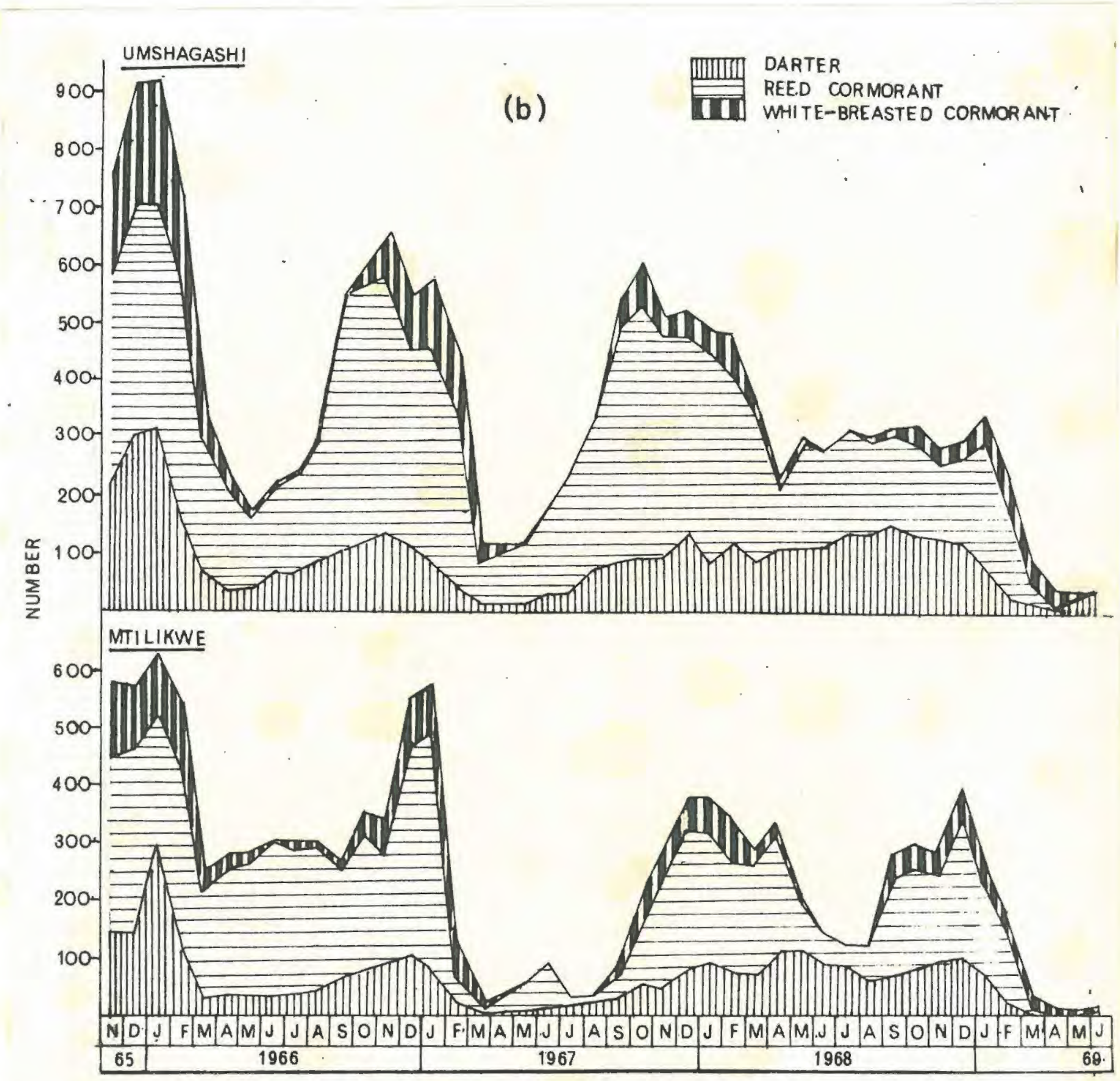


Figure 12 (b) Distribution and number of Darter, Reed Cormorant and White-breasted Cormorant.

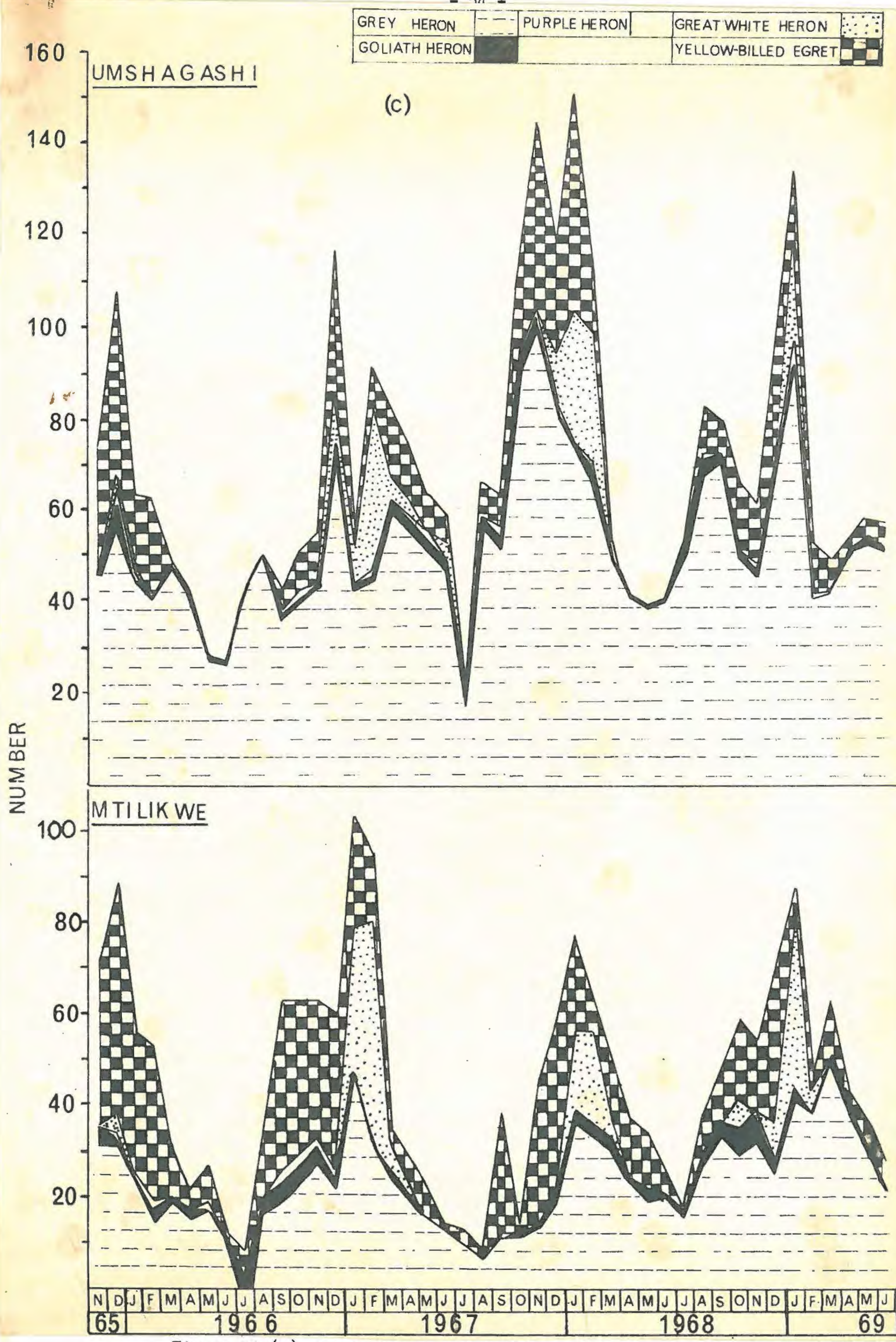


Figure 12 (c) Distribution and number of Grey Heron, Goliath Heron, Purple Heron, Great White Heron and Yellow-billed Egret. (Scale increased x 10 of that used in Figures 12(a) and (b).

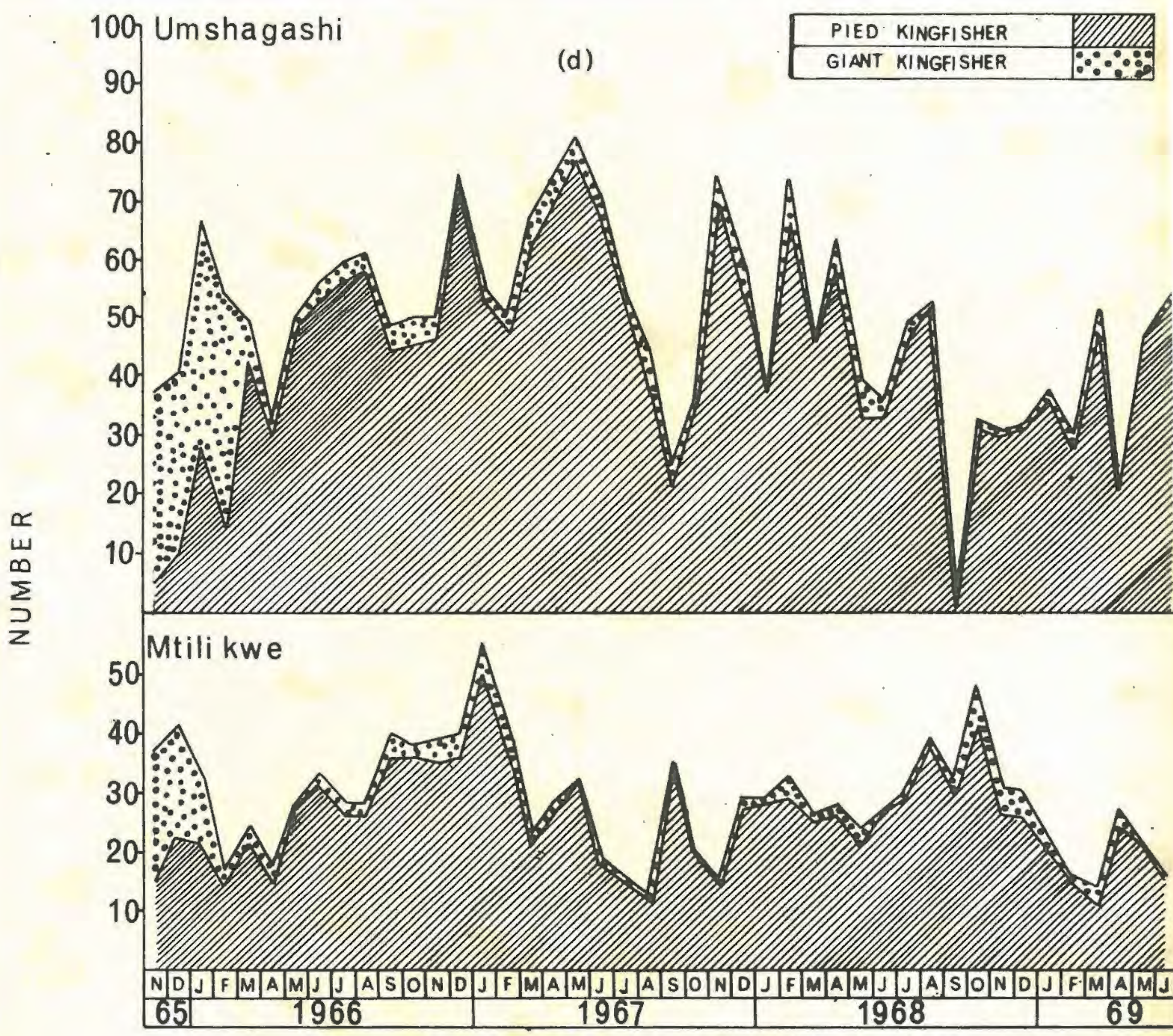


Figure 12(d) Distribution and number of Pied and Giant Kingfisher.

(Scale increased x 10 of that used in Figure 12(a) and (b)

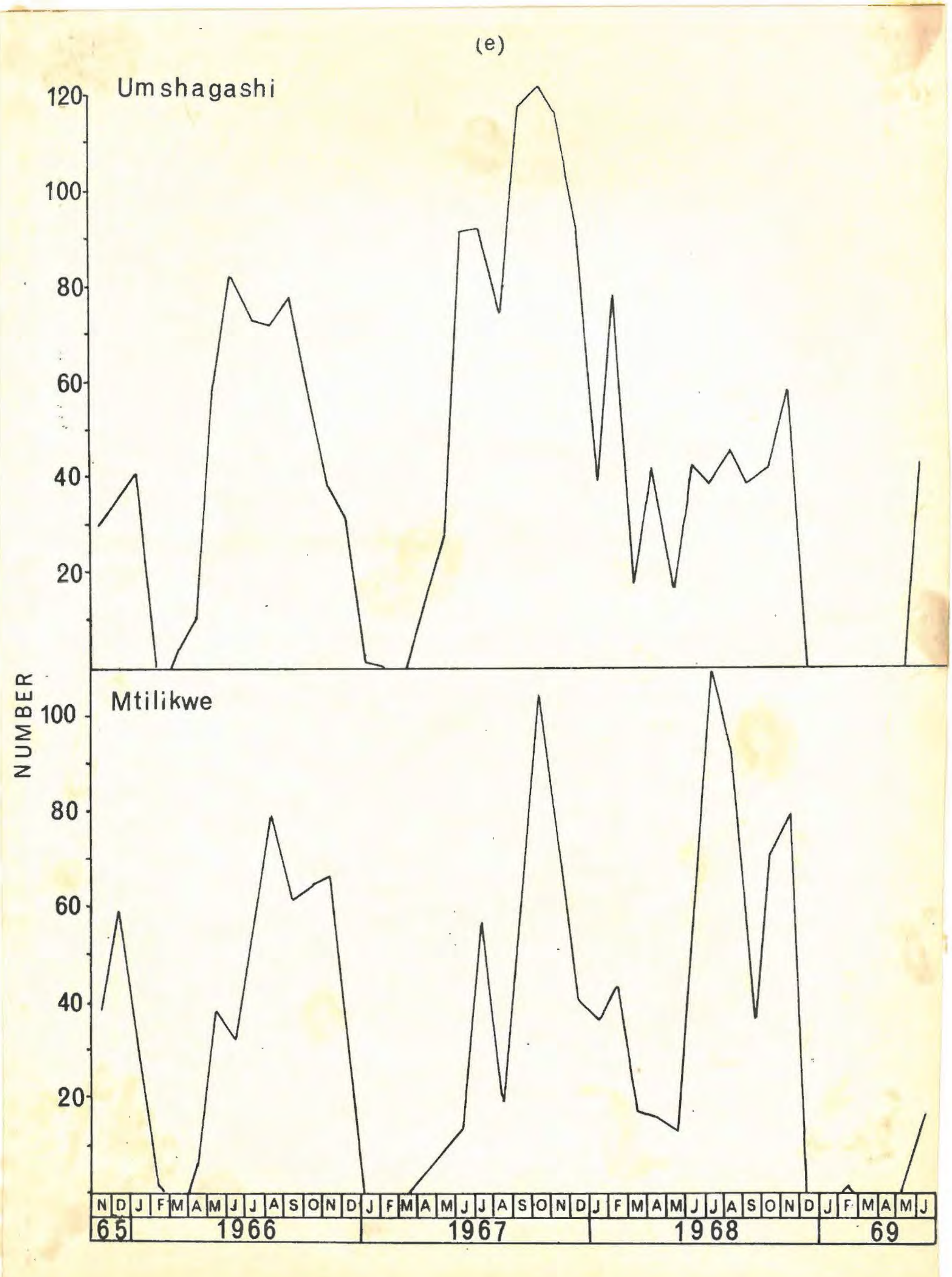


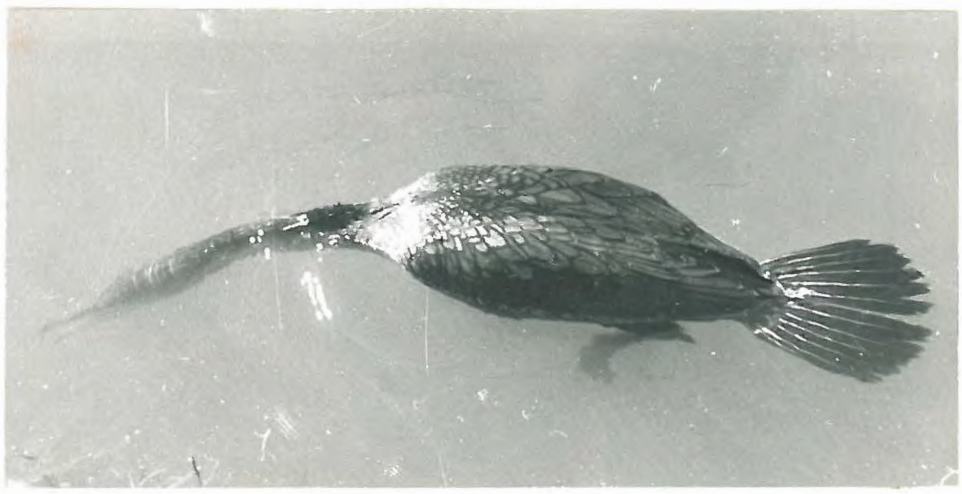
Figure 12(e) Distribution and number of Dabchick. (Scale increased x 10 of that used in Figures 12(a) and (b)).

It is obvious from the graphs 12 (a to e) that the population of piscivorous birds at Kyle is by no means static from year to year or from month to month within any one year. Yearly peak population levels attained were : 1860 in December 1965, 1455 in December 1966, 1297 in December 1967 and 932 in October 1968 (in 1968 the number declined to 873 in November and this was followed by an increase to 920 in December). Lowest ascertained totals each year were: 632 in April 1966, 348 in March 1967, 655 in June 1968 and 208 in April 1969.

9. Study of some of the (more important) factors which determine the distribution of fish-eating birds at Kyle and which also cause considerable variation in the piscivorous bird population.

(a) Fishing Methods.

Fish eating birds differ greatly in the manner in which they capture their prey, and the methods employed by certain types have at least the appearance of special efficiency, so that greater fishing pressure should result from their activity or at least the catch per unit of fishing effort should be greater. Darter, Reed Cormorant and White-breasted Cormorant, are among the more skillful, for they swim on the surface of the water but with the head immersed in search of prey. When it is sighted they dive and pursue.



A White-breasted Cormorant swimming on the surface of the water but with head immersed in search of prey.

A fish is sighted.

Diving to pursue.

Dabchick act in a manner which is very similar, but apparently they are able to see fish in the water without immersing the head. They may, however, dive to search for prey. Most of these birds prefer to search for food close inshore or in the vicinity of partly exposed dead trees, usually where the lake bed slopes gradually. The White-breasted Cormorant, however, being a stronger type of bird, exploits the deeper part of the marginal zone. The herons, on the other hand, may be described as static hunters, since, when seeking food, they stand immobile for long periods until their prey comes within striking distance. Only very occasionally has the Grey Heron been seen in water deep enough to cover any of the feathered portion of the leg. Its fishing activity therefore, is obviously confined to very shallow water.

A young Grey Heron fishing at its normal maximum depth.

The Yellow-billed Egret and Great-White Heron are approximately equal in size and neither fish in water of any depth. The Goliath Heron, however, because of its longer legs, can operate at rather greater distance from the shore and can seize prey of greater size than is available to the smaller types of bird.

Kingfishers also choose the shallows for their feeding ground, where the depth of water seldom exceeds two meters, as in water of this depth fish can be captured while swimming near the surface. The Giant type is very rare at Kyle but Pied Kingfishers are seen in creeks or on trees in the lake margin where the ground falls precipitously to the water. Their method of fishing is to dive on their prey directly from their perch perhaps from a branch as high as 4 meters above the water - or from a position maintained by hovering. Unlike most other piscivorous birds, they do not immediately swallow their catch but carry it to some suitable object against which it is forcibly struck before being ingested. They usually fish in twos or threes and apparently patrol in search of food. If a large source of fish is found they will fish in a gregarious manner. During 1966 and 1967, ponds at the Research Station, which were heavily stocked with Large-mouth Black-bass fingerlings and other small fish, attracted the attention of one or two kingfishers, which were rapidly joined by others, till as many as nine unwelcome visitors were present.

Several types of piscivorous bird seem to prefer to fish in company with other birds of their own species. A group of Dabchick will consist of two or three birds - occasionally as many as five; usually Reed Cormorant are associated in twos or threes, while as many as five or more White-breasted Cormorant will be seen fishing close to each other. In spite of this minor grouping, piscivorous birds are seen to maintain a proprietary interest in a particular fishing area, and resent intrusion by other birds. Fishing territories in the case of the Herons will often be separated by as much as four hundred yards, and the birds are often seen to return, each to its selected fishing site, day after day.

Darters which are not often seen in groups (out of the breeding season) also show a strong tendency on the part of each bird to claim its own territory. The distribution of species - particularly those with the same fishing technique, is naturally influenced by the aggressive attitude of each bird or group of birds within its own territory.

Different species of piscivorous birds on the lake very definitely exploit different zones and the zone a particular group will occupy while fishing is clearly determined by its physical make-up and general expertise in capturing prey. As a whole the fish-eating species may be divided into three categories :- (a) The waders (b) the free swimmers and (c) those that dive from above the surface of the water.

(a) The waders (which are static in their method of fishing) are limited to shallow areas, on or near the shoreline, which vary in depth according to the length of the bird's legs. In certain types of bird the length of neck permits penetration into slightly deeper water. The extent of the fishing zone exploited by "static waders" is shown below:-

Goliath Heron - from water's edge to a depth of 43cm +

Grey Heron - from the water's edge to a depth of 25cm +

Great White Heron and Yellow-billed Egret

from the water's edge to a depth of just under 25cm

Purple Heron - from the water's edge to a depth of $\pm$ 15 cm.

(b) The free swimmers on the other hand, although, at times when food is abundant they invade the zone fished by the Herons, generally fish in deeper water. The table below shows the maximum and minimum depth of water at which fishing activity was observed on the part of each of the birds named. The measurement of depth was made in the precise locality where fishing activity had taken place so that they provide the true depth of water. In the case of three of the birds the time is given for the period during which they remained immersed in pursuit of their prey. The figures supplied are the result of observation extending over three years.

	Minimum depth	Maximum depth	Average time of prolonged immersion
Darter	1.2 m	2.1 m	* Not taken(4 recordings)
White-breasted Cormorant	2.4 m	5.5 m	21.3secs. (16 recordings)
Reed Cormorant	0.6 m	4.25m	20.4 secs.(20 recordings)
Dabchick	± .15m	1.5 m	20.7 secs.(27 recordings)

*(Depth to which these birds can descend is probably greater than 2.1 m)

A sub-adult, hand-reared White-breasted Cormorant when pursuing small fish in a pond, of 0.04 hectares in surface area, was observed to swim underwater for a distance of 30 meters (91 feet) in 20.0 seconds. This indicates that these birds can descend to fair depths and can cover a wide area in a relatively short time. On the other hand, the area covered by the less powerful Reed Cormorant will be less and will be even more restricted. The zone - or area of definite depth which birds of particular species of the free swimming type find most suitable for fishing activity, would seem to be determined mainly by the distance which the bird can swim at speed underwater in pursuit of prey.

R. Jubb (1968) reported on an interesting variation in the fishing method adopted by a group of free swimmers at North End Lake in Port Elizabeth. A number of White-breasted Cormorants was seen to swim in line abreast over the small lake and to approach the shore in phalanx formation, when Gulls and Herons gorged on the mass of small fish which became stranded on the shore in an attempt to evade the Cormorants. Reforming, the Cormorants then made another purposeful advance towards another sector of the shallows. Similar higly organised method of fishing has not been observed at Kyle, but the incident shows how difficult it is to make any investigation really exhaustive.

The third category (c) Includes birds that dive on their prey from some height above the surface. These operate mostly over shallow water but occasionally are active over deeper water if fish are near the surface. Generally they are confined to the shoreline or the very shallow marginal zone.

The different zones fished by the seven species of piscivorous birds on Lake Kyle; it would appear, results in a minimum of interspecific conflict.

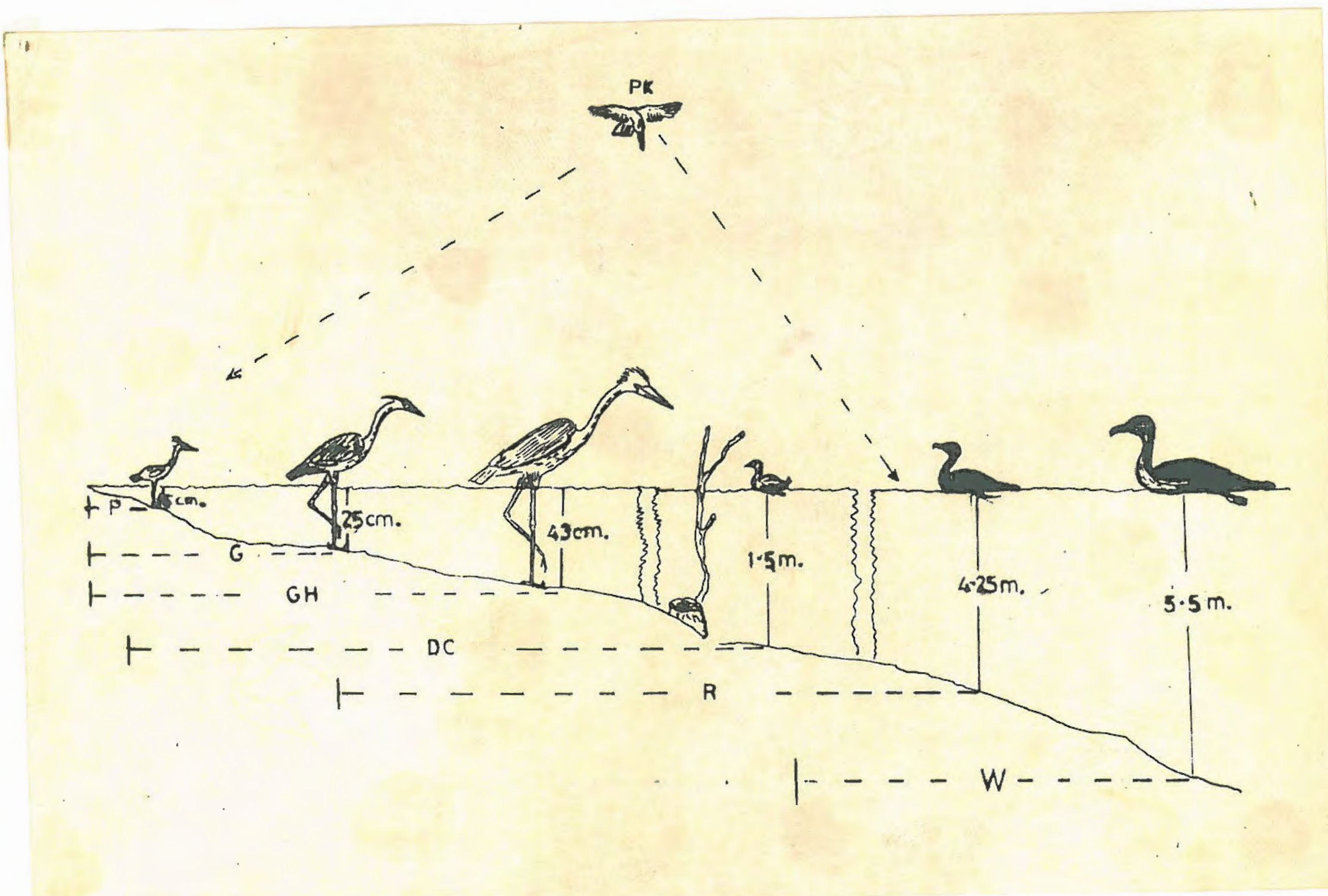


Figure 13. Schematic diagram indicating various fishing zones of piscivorous birds at Kyle. P = Purple Heron: G = Grey Heron; G H = Goliath Heron; D C = Dabchick; R = Reed Cormorant; W = White-breasted Cormorant; P K = Pied Kingfisher.

Members of the same or different species in the community of piscivorous birds utilizing the fishable area therefore settle the problem of appointment of living space. The different species are occupying different niches, as determined by their fishing methods and are therefore not competing for space or food. But for birds of the same species, which occupy the same niche, adjustment is a delicate matter and a host of compromises must be worked out through the formation of fishing territories. (evidence for this fine adjustment is given in section (f) of this thesis).

Lack (1966) in his interpretation of the principles postulated by Gause (1934), indicated that related species of birds in the same area are normally separated by habitat, feeding habits or size of prey, and such isolation has presumably been evolved because there is competition for food. In the case of the seven species of piscivorous birds for which fishing methods have been described, there is no separation by habitat or size of prey (see page 48) but by the size and general body shape of the bird which dictates depth at which fishing activity can take place. Gauses hypothesis does not appear to hold true in the case of the piscivorous birds. What they are doing is to utilize the environment or habitat in different ways. Excursions into the areas occupied by other species can happen from time to time with minimum of conflict.

b. Roosting Habits.

The White-breasted Cormorant and the Reed Cormorant are gregarious in habit and roost in colonies. The roosting area for which marked preference was shown was the Bevumi area (see Figure 1) which is protected from strong winds by high banks rising steeply from the water and by the Glenlivet range. Here, dead trees surrounded by water, one to two meters deep, were favoured as roosting sites fairly continuously until February 1967, though on occasion circumstances would force the birds to find other quarters, as in October and early November, 1966, when a marked drop in level (see Figure 2) left the previously occupied trees fully exposed. During these two months the birds made their roosting sites in trees offshore in the Gifford's Landing Stage area of the Umshagashi Arm. From 8th February to 20th March 1967, when a rapid rise in water level flooded the favourite roosting area, the Cormorants were satisfied with any trees in the vicinity surrounded by water more than one meter in depth, which offered suitable roosting accommodation. From March to May 1967 these birds roosted at the entrance to the Bevumi area and after this date nesting began on the Umshagashi Arm and roosting took place at the nest sites. Lake level dropped continuously from December 1967 to November 1968 and trees used in the Bevumi area were no longer surrounded by water by mid-November, so that these birds again sought roosting accommodation elsewhere. The area chosen in this case was the entrance to Bompst Bay. No trees were available but a granite boulder and a large termite mound on which there were many short stumps and twigs, which protruded approximately 5 meters above waterlevel provided roosting facilities - this site was in use up to mid-April (when recordings were discontinued).

In noting these particulars of behaviour in roosting, an interesting feature emerged, as it was evident that there was marked segregation of species when the same roost site was occupied by different types of birds. It was seen that the upper parts of trees and boulders were occupied by White-breasted Cormorant, the lower by Cattle Egret *Bubucus ibis* (on branches or rock faces sometimes as low as 30 cms from the water). The area in between was the preserve of the Reed Cormorant.

Part of the roost site at Bompst Bay. January 1969. White-breasted Cormorants occupy the uppermost position (Egrets had not arrived and light was fading when the photograph was taken).

The choice of roost sites by the Reed Cormorants in the Bevumi and Bompst Bay areas - is of special interest, when its distance from the most remote fishing-grounds of these birds is taken into consideration. From the Bevumi to the upper reaches of the Umshagashi arm the distance is 27 kilometers (17 miles); from Bompst Bay to the upper reaches of the Mtilikwe arm the distance is again 27 kilometers. This distance therefore between roost and fishing area would appear to be the greatest which is practicable for birds of this species and may be a factor in the selection of a roosting site.

Piscivorous birds, other than those just described, are not markedly gregarious. Provided they can find suitable trees, surrounded by water, near their feeding area, Darter will roost anywhere in its vicinity. The Grey Heron prefers dead trees above granite boulders (or large stumps) that protrude from the lake surface and not infrequently will be content to perch on the boulders themselves. The Goliath Heron will actually sleep standing in the lake margin while the habit of the Dabchick is to rest at night on the surface of the water itself. Since 1963, indeed, when the disappearance of marginal vegetation robbed them of protection against predators (such as the crocodile, leguaan and otter) these birds have tended to spend roosting time furhter and further from the shore, resting on the surface where the water is deepest and returning to marginal waters to feed during daylight. Pied Kingfishers roost on trees, showing a preference for situations where the banks of river or lake go sheer to the water. As a rule they are found in small groups of five or less. On two occasions, however, - in the first instance, between 24th and 28th May 1967, - as many as eighteen of these birds - almost the full total of Pied Kingfisher inhabiting the Mtilikwe Arm at the time, were seen to be roosting in one tree, which stood completely surrounded by water in the Mtilikwe Gorge. In the second instance during early June, 1968, sixty-four of the birds were found towards sunset to be occupying a group of trees protruding above water level, in a large bay opposite to Gifford's Landing Stage on the Unshagashi Arm. (See Figure 1). This number was almost the full total for the lake at that time.

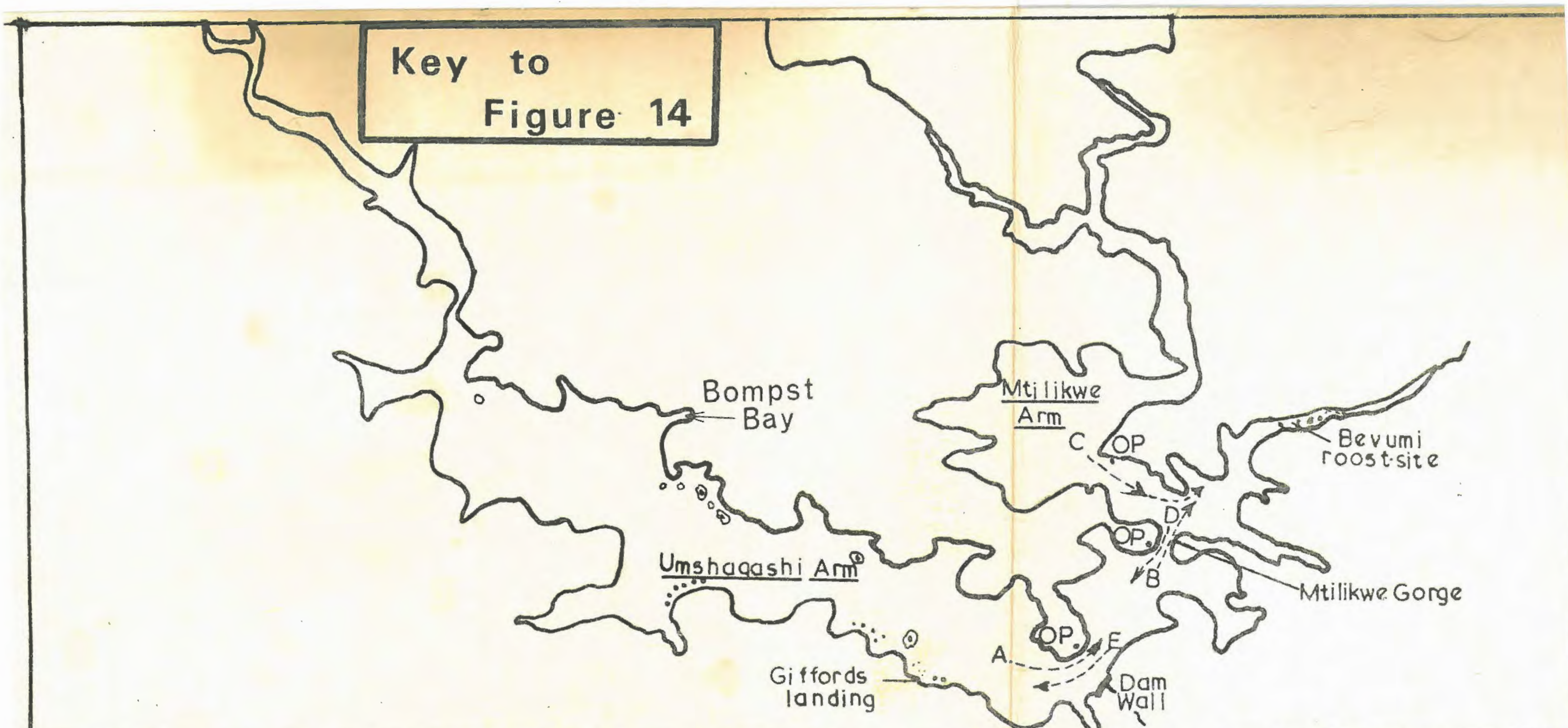
Certain birds which are night feeders seek sheltered quarters during the day and prefer situations which are screened by high banks, brushwood or dead trees. The White-backed Night Heron and Night Heron and the Green-backed Heron belong to this class.

The number of roosting sites which are acceptable to the birds appear to be adequate for the present bird population. It will be noted, however, that there is a precarious quality in these sites as their suitability may be seriously affected by a change in the surface level of the lake.

In communal roost sites there is active competition for the highest perch between individuals of the same species, such as the White-breasted Cormorant. Reed Cormorant behave in a similar manner in the restricted roosting accommodation which they occupy between the White-breasted Cormorants and the Cattle Egrets. Evidently there exists among these three species what may be described as a definite social grading or dominance of type and a dominance also within the group. White-breasted Cormorants are not challenged for possession by Reed Cormorants, which are smaller birds, and Reed Cormorants are not challenged by Cattle Egrets. There is, however, very active competition for particular sites between birds of the same species. On one occasion for instance, a White-breasted Cormorant occuppying the highest perch in the roosting site was disturbed by an approaching patrol boat and took to the air. Its perch was immediately occupied by a bird of the same species which had just arrived from the fishing area. The original occupant of the perch attempted on three occasions to dislodge the trespasser by forcibly trying to alight on the occupant and emitting threatening sounds. It finally landed on the water, went through the motions of active fishing until its competitor descended to investigate. It then immediately took to flight and regained its original position above the other roosting birds.

c) Evening flights of Reed Cormorant and time available for fishing activity.

In assessing the food potential for piscivorous birds on a stretch of water such as Kyle - the time available to the birds for fishing activity would appear to be relevant subject for consideration. Earlier in this report mention was made of the characteristic flight of the Reed Cormorant over water on what was practically a fixed route between fishing and roosting sites. Observations made by members of the staff occupying vantage points at the narrows and elsewhere have provided information which is presented in Figure 14 with an explanatory key.



A	PASSING FROM THE UMSHAGASHI ARM TO THE MTILIKWE ARM	O. P. (OBSERVATION POINT) OPPOSITE THE WALL
B	" " " " " AND THAT SECTION OF THE MTILIKWE BETWEEN THE WALL AND THE MTILIKWE GORGE TO THE BEVUMI ROOST SITE	O. P. MTILIKWE GORGE
C	PASSING FROM THE MTILIKWE ARM " " " " "	O. P. NEAR ENTRANCE TO BEVUMI
D	" " " " " INTO THAT SECTION OF THE MTILIKWE BETWEEN THE MTILIKWE GORGE AND THE WALL.	O. P. THE MTILIKWE GORGE
E	PASSING FROM THE MTILIKWE ARM TO THE UMSHAGASHI ARM	O. P. OPPOSITE THE WALL

NR = NOT RECORDED NF = NO FLIGHTS

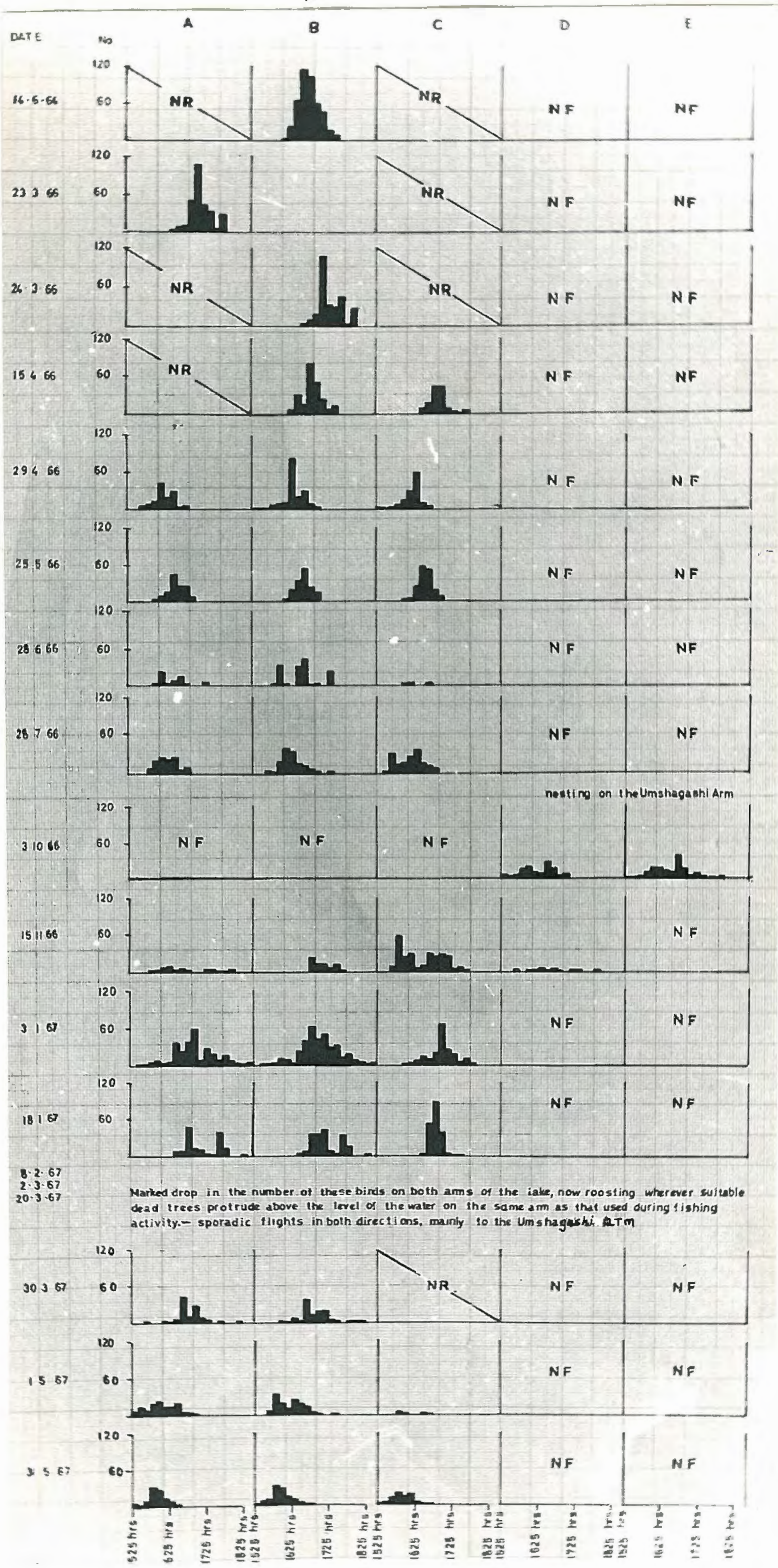


Figure14. The flight periodicity of Reed Cormorant on the way to their roosting site taken over ten minute intervals on certain dates.

The following brief table indicates the time of day when the maximum number of birds passed observation points close to the Bevumi entrance - from the Mtilikwe and from the Umshagashi and from that part of the Mtilikwe - between the Mtilikwe Gorge and the wall - during the coldest and also during one of the warm months of the year.

COLDEST MONTH

Mid-June 1964 between 1645 and 1705 hrs.

Late June 1966 between 1635 and 1655 hrs.

Early June(31/5) 1967 between 1555 and 1615 hrs.

A WARM MONTH

Late March 1966 between 1715 and 1725 hrs.

Late March 1967 between 1645 and 1725 hrs.

The time of day when the greatest number of birds is observed to be returning to their roosting-place during any one month of the year varies from year to year, but it is clear that the time of return becomes later as the weather becomes warmer. It has been noted also that practically all species of piscivorous birds suspend fishing activity at approximately the same time of the day.

It can be accepted that the earlier occurrence of evening flights during the colder months implies earlier cessation of fishing activity. It is significant that the shorter fishing period occurs during the season when fish normally occupying the shallower marginal zone are influenced by the drop in water temperature to move into deeper water.

(d) Fish density in the marginal zone taken over the period March 1967 to March 1969.

This is related to monthly assessment of the total weight of piscivorous birds present on the lake and to examination of the factors affecting fish concentrations in the main fishing zone during the period mentioned.

The main fishing zone and "fishable area"

A protracted period of sampling in which various techniques have been employed (gill netting, baited conical traps, seine netting and setting off of explosive charges) has established that the fish fauna of Kyle, occupy only the marginal zone to a depth of 6 to 7 meters (20 feet). Fish have been captured, on rare occasions, in water upto 12 to 13 meters (40 feet) but this is usually shortly after there has been a sudden rise in water level. Soon after this occurs levels again become static or start to drop and fish again confine themselves to the 7 meter zone. The greater concentration of small fish, occurs, normally in water less than 2 meters in depth. This shallower area is the main fishing zone of most piscivorous birds, although some of the larger types, which actively pursue their prey (such as the White-breasted Cormorant and the Darter) do fish in the deeper areas. The marginal fish-inhabited water extending to a depth of 7 meters has, for the purpose of this account, been termed the "fishable area".

Fish density in the main fishing zone

The principal concentration of marginal fish occurs in areas where the lake bed is one or other types - either basalt, or granite sand in association with red soil (of ironstone origin) and these areas are equally distributed through both arms of the lake. Seine netting (with a net of dimensions already mentioned on page 37) was undertaken, weekly, in fish habitats of both types and the result in each case expressed in average weight, in kilograms, of fish captured per hour of active haul each month (See Figure 15).

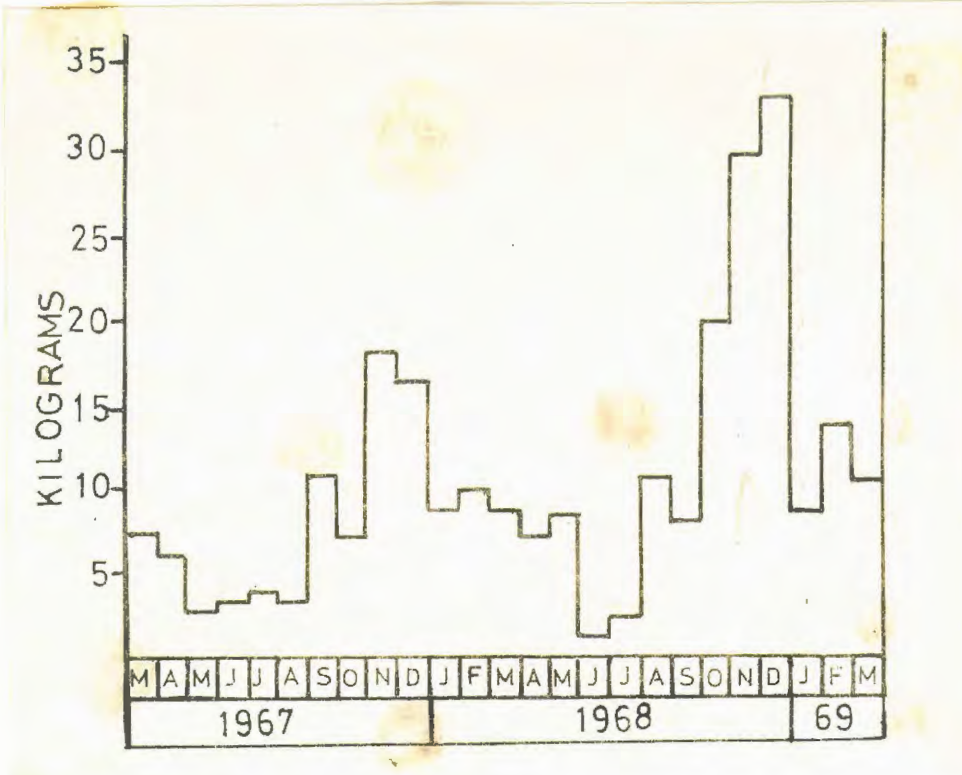


Figure 15. Average weight of fish, in kilograms, captured per hour of active haul each month.

Area of fishable water

As already indicated water over 7 meters in depth is not inhabited by fish at Kyle. The surface area of the "fishable water" as calculated for each month is presented in Figure 16.

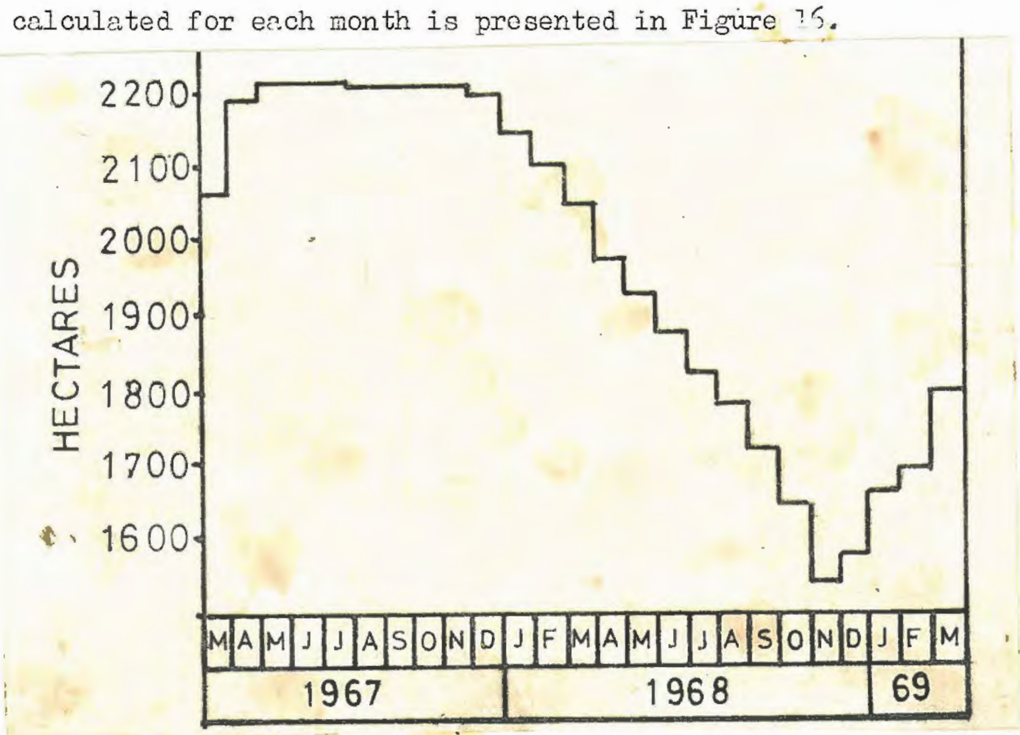


Figure 16. Average area of "Fishable water" each month in hectares

As the major part of the population of smaller fish is confined to the shallower part of the marginal zone, any rise or fall in lake level (see Figure 2, page 6) naturally caused either an increase or decrease in in the size of the "fishable area" thus causing dilution or increase in fish density. Shrinkage of the lake, due to lowering of water level, from January to November 1968, caused the fishable area to reduce from 2200 hectares to 1550 hectares. This marked reduction in the area occupied by all species of fish at Kyle resulted in a far higher density of fish occurring in November and December of 1968 than during these months in 1967.

Mean monthly marginal water temperature

Continuous recordings of maximum and minimum marginal water temperatures at a depth of 1 meter were made by means of a thermometer suspended from a bouy anchored in water of 2 meters depth. The thermometer was read daily at 0800 hrs. From results obtained in this manner mean monthly temperatures, for the middle section of the main fishing zone, were calculated (see Figure 17).

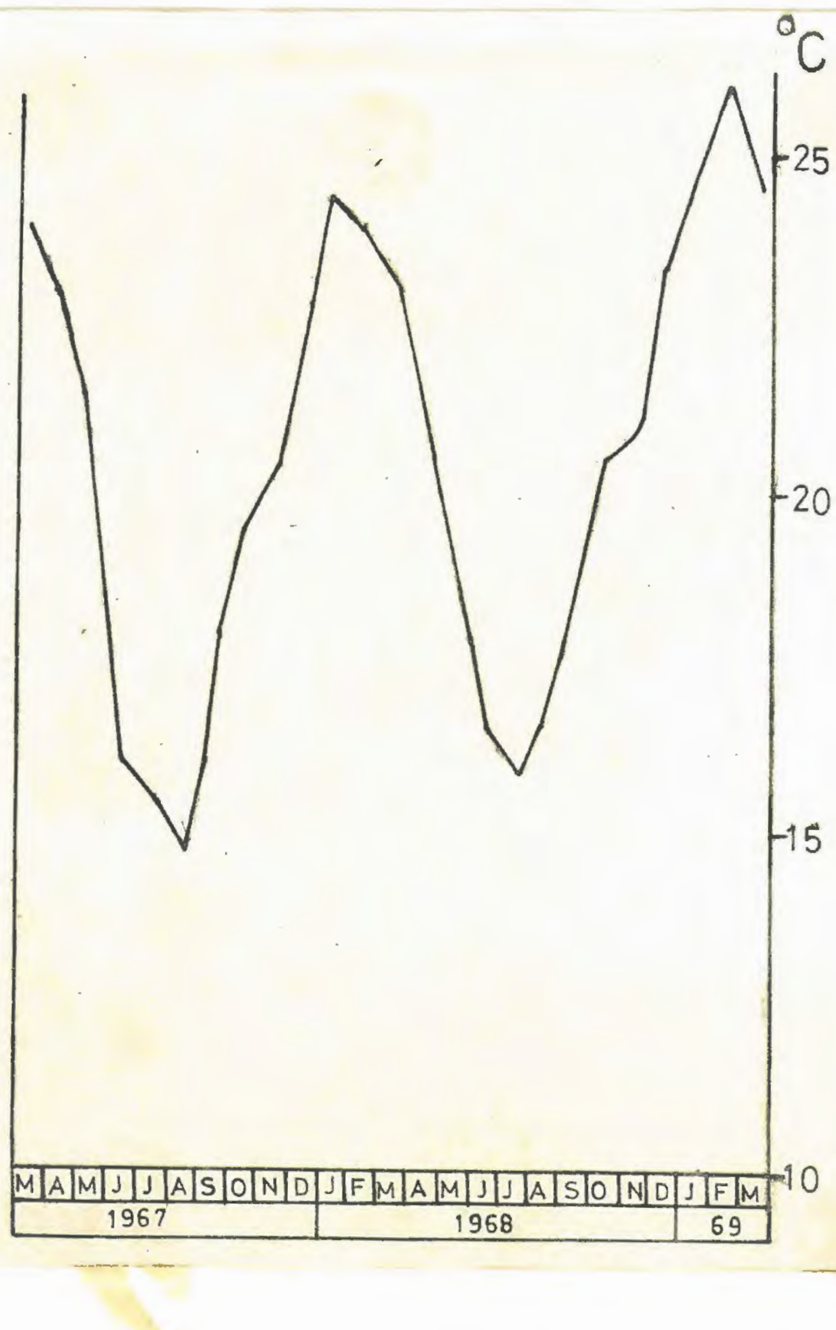


Figure 17. Mean monthly marginal water temperatures taken at a depth of 1 meter.

Water temperature has a marked effect on the fish population particularly on the number of smaller fish occupying shallow water. Seasonal lowering of temperature (see Figure 17) caused fish to move into the deeper part of the "fishable area" thus diminishing the quantity of food which was available to piscivorous birds.

Total weight of birds on the lake

From monthly counts taken of piscivorous birds present on the lake it has been possible to calculate the total weights of each species of purely fish-eating birds fishing the lake at specific times, since the normal weight of a single bird in each species has been previously determined by methods already described (See Table IV page 35) and the process is one of simple arithmetic (See Figure 18)

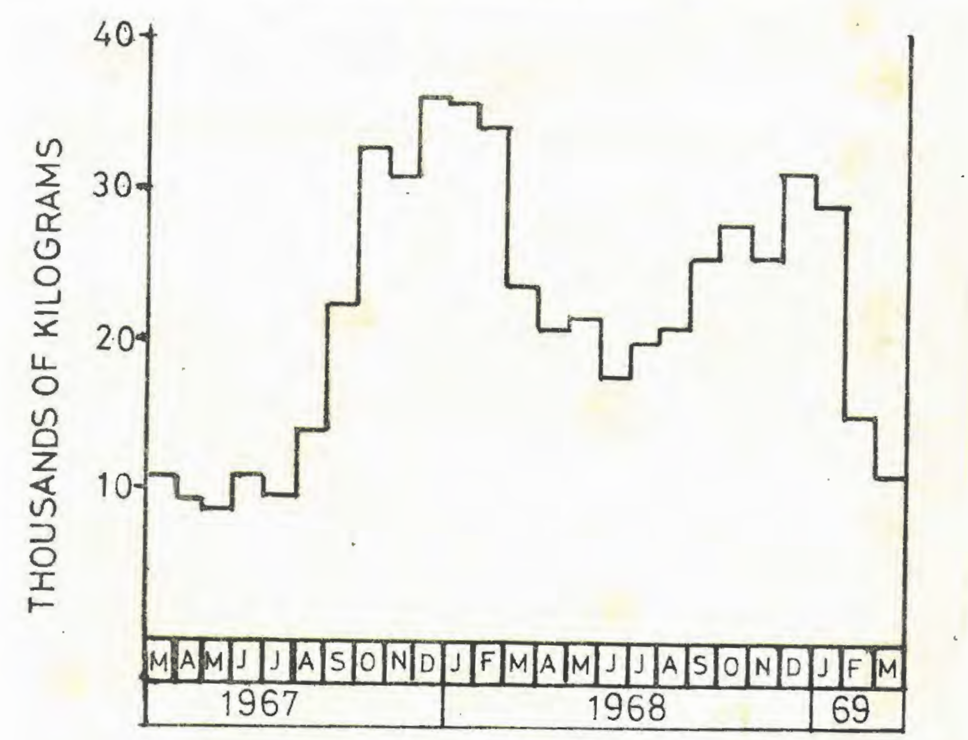


Figure 18. Average weight of birds, in thousands of kilograms, on the lake each month. (Weight of birds = mean daily weight of all birds x the number of days in each month).

As the concentration of small fish (see Table V page 37 for average weights) increased (see Figure 15) so did the weight of piscivorous birds in the area concerned (see Figure 18).

As area of fishable water has a direct bearing on the concentration of piscivorous bird prey and on the area available for occupation by the birds during fishing activity the degree of utilization of the fish resource is better expressed in weight of birds per hectare of fishable water than in total weight of birds on the lake each month (see Figure 19)

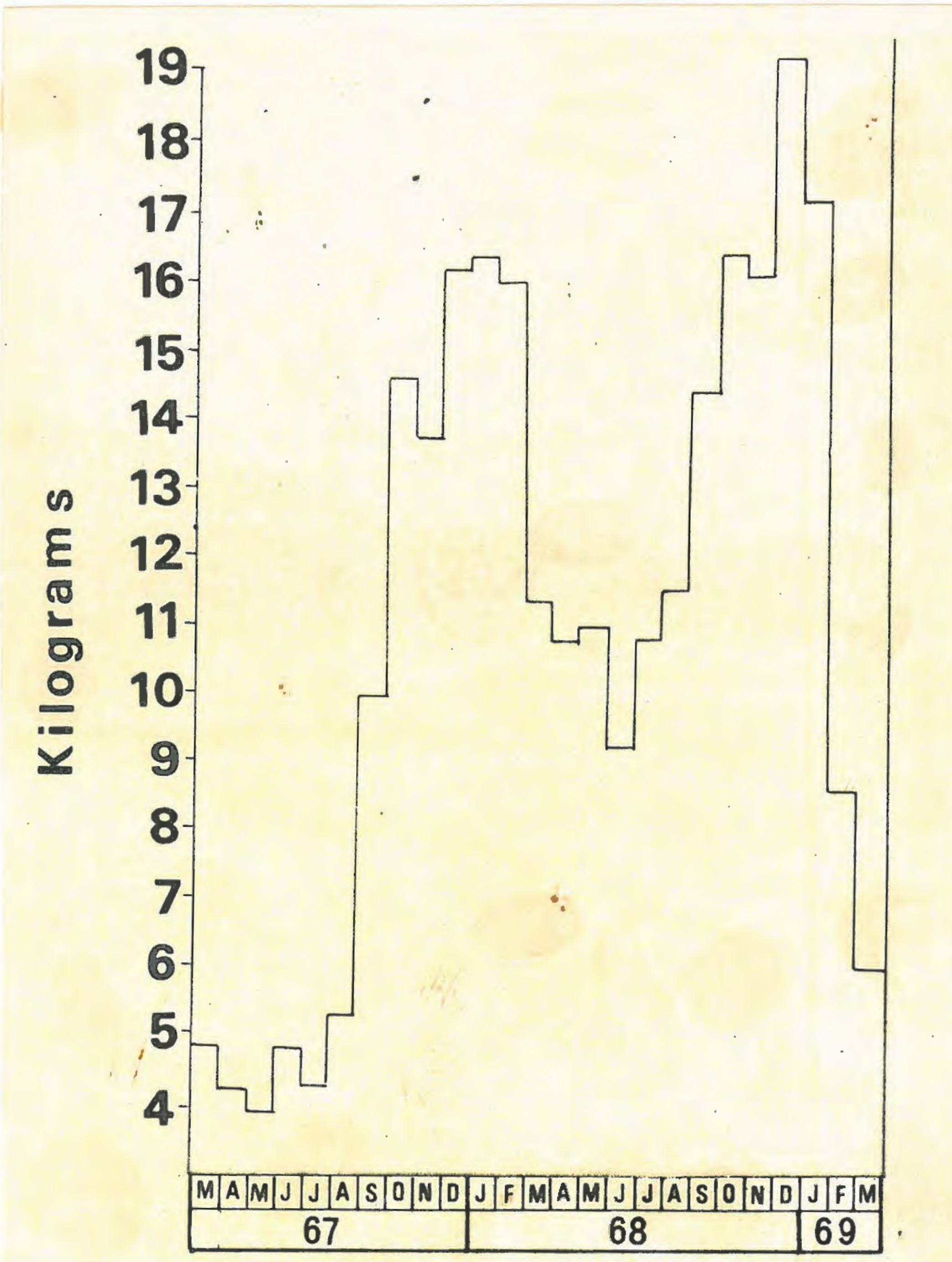


Figure 19. Weight of birds, in kilograms, per hectare of fishable water each month.

From Figure 19 it can be seen that fishing pressure was actually lower in November and December 1967 than during November and December 1968. The form of this graph closely approximates that relating to fish density (see Figure 15) indicating a close relationship between the density of prey and density of bird predators.

Predation pressure by birds was far lower in the period March to July 1967 than during March to July 1968. An explanation for the greater fishing pressure during these months in 1968 is given on page 79 of this thesis.

Migration

During monthly netting-operations to ascertain the density of fish in the marginal zone it was established that temperature has a marked effect on the fish population in the fishable zone. Fish of the type that usually occupy the shallow zone were found in deeper water when there was a marked drop in temperature. Indeed during the colder months the migration of small fish into the deeper part of the fishable area had a definite effect on the density of the fish population in those areas normally exploited by the birds. As a result the availability of their food supply was adversely affected, and these periods of scarcity coincided with the temporary annual migration of the major part of the population of certain species (see Figure 12 a, page 52) to other feeding grounds. The habit of temporary migration to which reference is now made is common in the Darter, the Cormorants and the Herons. It appears that the destination of the Darter, Reed Cormorant and White-breasted Cormorant, in particular, during their brief migration is somewhere in the lower reaches of the Mtilikwe River or in the upper reaches of other tributary rivers at a time when river flow is diminishing. They are normally least abundant on lake Kyle from March to July and there is good evidence (which in the interest of relevance is not presented here) that the habit of yearly migration is due to some innate pattern of behaviour as well as the temporary scarcity of prey.

The Mzari River during the wet season of 1966/67 (25th February, 1967)
The fast flowing and turbid water prevent piscivorous birds from fishing successfully.

The Mzari River, at the end of the 1967 Cool Season, (August, 1967).
It becomes broken up into a series of placid pools - a typical condition on most Rhodesian rivers.

Drought

The rainfall for the wet season of 1965/66 was below normal and as a result of draw-off of water from Kyle, for the purpose of irrigation, lake level dropped continuously during 1966. Rivers, however, though holding considerably less water than in years preceded by normal rain (700 mm or more) did not dry up and in addition farm dams held water throughout 1966. Shrinkage of rivers in which fishing activity is conducted during the colder months, as indicated on page 76 was probably the reason for more birds being present on Kyle during these months in 1966 than in the following year. Birds leaving the lake area found riverine fishing grounds overcrowded and thus returned to Kyle.

Many of the smaller dams and the majority of Rhodesian rivers dried up completely, for the first time in living history, during the dry-season of 1968 (see Figure 4 page 9 for rainfall for the 1967/68 rainy season). Many birds, finding it impossible to fish elsewhere, had no other alternative than to remain on Lake Kyle.

The piscivorous bird population, therefore, on the lake - as expressed in their total weight and in particular kilograms per hectare of fishable water each month - was far greater during the dry season of 1966 and 1968 than in 1967. Reduction in the area of water occupied by fish, was probably the reason for a greater density of prey available to the birds during May to September, 1966 and 1968 than during this period in 1967.

Rivers were again in full flow in November and December 1968 and by February/March 1969 all farm dams were filled with water and a rapid decline in the total weight of birds utilizing the lake was very apparent during these months in 1969. It would appear that a certain amount of overcrowding occurred during the period February to September in 1966 and 1968 (see Figure 12a page 52 relating to number of birds and Figure 19 page 76 for weight of birds per hectare of fishable water during these periods), as a large number of birds left the lake area soon after the 1966/67 rains and the departure from the lake was even more marked, when other resources became available soon after the lake began to rise in December 1968.

(e) Notes made during observation of the breeding of certain species

i) Egg production and chick survival

From periods as early as 1961 and 1962, breeding colonies of Darter, Cormorant and Grey Heron on the lake have received attention and though complete investigation of all colonies was impossible, a certain amount of information has been obtained.

From May to September, and again in November, 1961, large breeding colonies containing Darter, Reed Cormorant and Grey Heron were scattered throughout the lake area. A single colony of Reed Cormorant, which was closely observed, had an egg production of 58 and chicks which reached the flying stage numbered 35. A colony of White-breasted Cormorant containing eight nests produced 23 chicks which all reached the flying stage. Dabchick also bred on the lake, as well as a pair of Black-headed Heron A. melanocephala. The general level of chick production and survival for the year was very high.

In 1962 breeding occurred from June to November and birds confined their nesting activities mainly to the Umshagashi Arm. Again the level of chick production and survival was high. Mixed Darter and Reed Cormorant colonies containing 17 nests produced 55 chicks all of which survived. 7 scattered Grey Heron nests (situated on small regenerated trees protruding from semi-submerged termite mounds) kept under close observation, produced 19 chicks which all survived. The existence of a considerable number of nests other than those for which precise details could be taken was also observed, and from these numerous chicks emerged.

During my absence from Kyle on duty elsewhere no accurate records of nesting activity were obtained but reports received from staff on the station did, however, confirm that nesting activity amongst Darter, Reed Cormorant and Grey Heron was at a fairly high level but no White-breasted Cormorant bred on the lake during 1963.

In 1966 nests on the lake occupied by 28 Grey Heron and 8 Darter were all under close observation. Each one was numbered and its contents examined at regular intervals. It was very evident however, that reproductive activity had markedly declined from what had been noted in the period 1961-62. Information, for either period, is lacking, in respect of Kingfishers because of their habit of nesting at the end of long tunnels, but records indicate that no Darter, Reed Cormorant or indeed any piscivorous bird inhabiting the lake, with the exception of one Grey Heron and one Green-backed Heron was able to rear their young to the flying stage during 1966. (Reed Cormorant showed no signs of initiating breeding activity). It was clear that the cause of high mortality among the chicks was starvation, for when they were checked for any damage that might have been caused by predators or carelessness on the part of the parent birds, no marks giving indication of serious hurt were discernible on any of the chicks' bodies. Four Darter and six Grey Heron chicks were removed from their nests to be hand-reared and these survived.

1967 presented a very different picture. After an initial rise the lake level remained fairly constant for the rest of the year (see Figure 2, page 6). The available area of fish-inhabited water increased, but the piscivorous bird population was actually lower than during the same months of the previous year. Grey Heron began to congregate on the Umshagashi island in late June and had constructed 17 nests in July. Egg-laying continued till 26th August when their nests were deserted and the site abandoned - possibly as a result of interference by anglers fishing near the colony. In early September nesting again began but this time along the Umshagashi Arm of the lake. The same area was chosen by Darter and Reed Cormorant as offering a suitable nesting site. The following table indicates the reproductive activity of five species during 1967 and shows the high survival rate for that year.

TABLE VIII

1967 BREEDING RECORD

SPECIES	NO. OF NESTS	EGGS PRODUCED	CHICKS WHICH REACHED THE FLYING STAGE	PERIOD
Darter	15	48 av.= 3.2	36(*)	Mid-August to late November (+ one late nest in December - later abandoned).
Reed Cormorant	62	160 av. = 2.6	68(*)	Mid-August to late November
Grey Heron	17 (Umshagashi Island)	50±	Site abandoned	July to 26th August
Grey Heron	65	161 av.= 2.5	85	Mid-July to early December
Goliath Heron	1	3	1 under parental care 1 under hand-rearing	Mid-October 1967 to late February 1968

(*) : Birds reaching the flying stage could have been far more numerous but for the death of 26 "downed" and 32 feathered Reed Cormorant chicks during late October and 9 "downed" Darter chicks in the last week of November.

During 1967 no nests were constructed on the Mtilikwe Arm - perhaps because of a lack of suitable sites, resulting from considerable rise in lake level above that of the previous year (see Figure 2 page 6). There was, moreover, a very high rate of mortality among Reed Cormorant chicks between the brief period 29th October to 31st October, even when the nestlings had reached the advanced woolly-down stage of development with wing and tail feathers already present. Batches of four or five chicks were found dead in many nests. Chicks had obviously gone from their own nests into others as large groups of 4 to 5 would indicate, probably in an attempt to get food. The unseasonal rain between 25th to 30th October, did indeed cause a rapid drop in marginal temperature, but the survival of chicks still at the naked stage on Crane Island, supplies very definite indication that the cause of death was not unusually cold weather but lack of sufficient food. At a time when large clutches in the nests made greater demands, there was a serious falling off in the available supply of fish (see Figure 21) and so the nestlings starved. Rain fell again on 14th November and again during the period 19th to 25th November, causing a drop in lake surface temperature (See Figure 20). Three days later (24th November) three Darter out of a clutch of five were found dead in a nest in the Giffords Landing Stage area, and six in three nests in the Sikato Bay area.

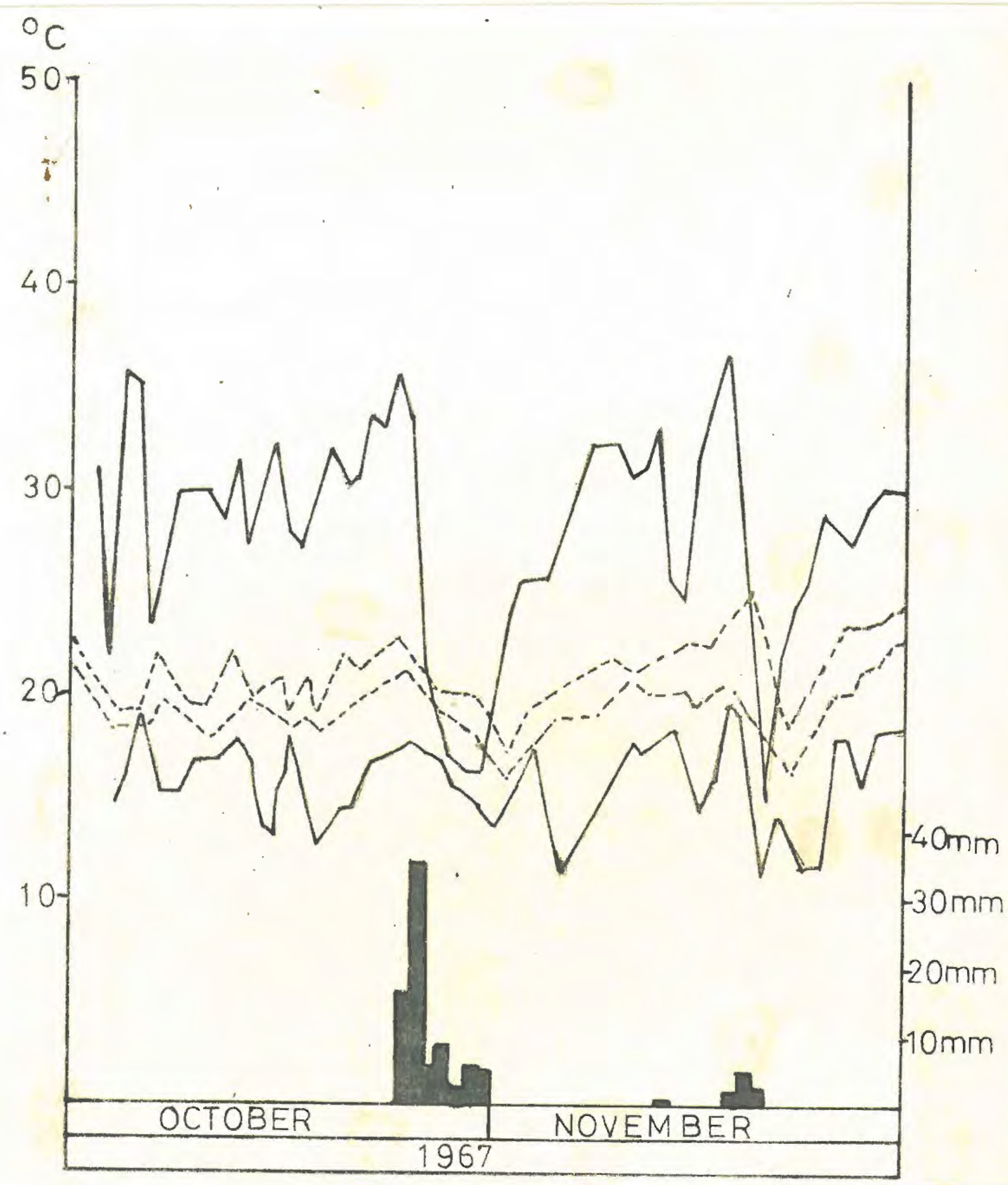


Figure 20. Daily rainfall plus marginal maximum and minimum surface water (-----) and atmospheric temperatures (———) during October and November 1967.

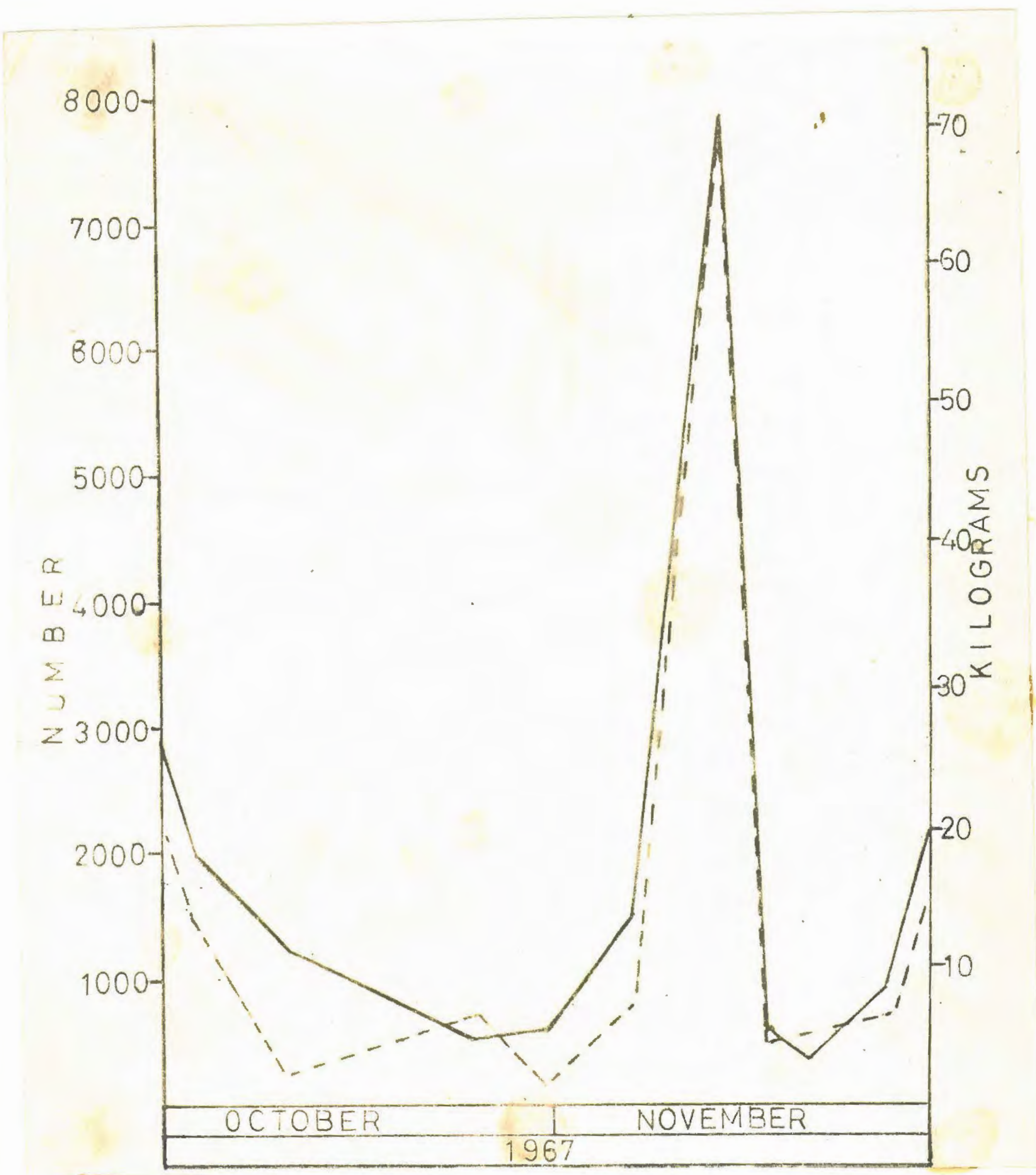


Figure 21. Catch per hour of active haul with a fine meshed seine net during October and November 1967 (taken at weekly intervals) (-- numbers, —— weight).

The obvious deduction to be made from these nesting fatalities is that fishing pressure is at a critical level during the particular period when chicks are being reared, and that a considerable drop in temperature must have very serious consequences for the young birds. The shallower part of the fishable zone is much more liable to a sudden drop in temperature than the deeper portion when unseasonal heavy rain results in an influx of colder water. The area most productive of food for the birds is the shallower zone and when a considerable part of its normal fish population is forced to move to deeper water, the effect on the availability of the birds' food supply is obvious.

It is to be noted that rainfall for the rainy season 1967/68 was very low (see Figure 4 page 9) and as a consequence all farm dams and most rivers were dry by February 1968. As a result, Dabchick moved into river courses on the Kyle catchment area but did not find suitable breeding sites and consequently returned to the lake area. The number of these birds on Kyle showed marked oscillation therefore during the period January to May 1968.

As the result of good rains, dams in the Kyle catchment filled in December 1968 and during this month all Dabchick left the lake (see Figure 12 e, page 56). It is to be noted that these birds only began to return to the lake during late May 1969, indicating that the breeding period had been prolonged, perhaps to make up for the lack of recruitment during the 1968 season.

Water level dropped continuously during 1968 (1030.2 meters A.S.L. on 1st January to 1023 meters A.S.L. on 30th November), and, as already indicated, drought conditions existing during late 1967/early 1968 prevented any rise in level during that "rainy season". The only piscivorous birds which nested successfully and produced young during 1968 were Darter and Grey Heron. Egg production and chick survival is indicated in Table IX.

TABLE IX

1968 BREEDING RECORD

SPECIES	NO. OF NESTS	EGGS PRODUCED	CHICKS WHICH REACHED THE FLYING STAGE	PERIOD
DARTER	10	20+ av = 2+	2	Mid-August to late September 1968
GREY HERON	16	51 av = 3.2	9	Mid-August to early October 1968

Investigation into the aspect of bird life now under consideration was adversely affected by the destruction of Darter nests by African children during late August. Chick production would in all probability have been slightly higher than it actually was, total egg production however was very low throughout the lake area. Again no nesting occurred on the Mtilikwe Arm.

The Yellow-billed Egrets and the Great White Heron do not nest on or near the lake. Marked decrease in the number of Yellow-billed Egrets frequenting the lake area is apparent from April to May each year. Great-White Heron were totally absent during the period March to November 1966, May to November 1967 and May to September 1968. The purpose of their temporary desertion of the lake area was not due to food shortage but to nest in their breeding grounds elsewhere.

Breeding activity of these birds was observed on the Kafue Flats, Zambia, in March and August, 1964, by Dowsett and de Vos (1965) and it is not unlikely, judging by their long period of absence from Kyle, that they travel to places as distant as Zambia for the purpose of breeding.

According to Wynne-Edwards (1962) "the actual regulation of population density is largely a matter of exercising control over recruitment and loss in population. There is usually an annual breeding season, the basic function of which is in the first case to make up losses of the preceeding year and in the second to create a new generation to succeed its progenitor. He further refers to experiments which demonstrated that recruitment is density-dependent; and it is obvious that the feed-back part of the machinery will have to be especially active just before breeding commences, in order to elicit the required response from the breeding stock and produce the quota of recruits that current economic conditions dictate". The density of birds per hectare of fishable water (expressed in Kilograms of birds) shown on page 76 of this thesis, was far lower during the period May to August 1967, the year in which recruitment was at a fairly high level, than in the same months of 1968 a year in which recruitment was extremely low. The obvious deduction to be drawn from these observations is that bird density during 1968 was above that for which current economic conditions would dictate. The complete lack of breeding amongst Reed Cormoront the most abundent species of birds on Kyle, during 1968 gives further support to these theories enunciated by Wynne-Edwards.

Nicholson (1933) stated " if an animal population continues to fluctuate in numbers over a long period between restricted limits (see figure 12(a) page 52 of this thesis) it follows that it is controlled by factors which produce an increase after low density (as in May to August 1967) and a decrease after high density" (as in May to August 1968).

Lack (1967) in his study of the Great Tit found that these birds laid larger clutches in the years when they had a greater chance than usual of raising large broods. There is no statistical evidence to show that there was any significant change in the number of eggs laid by piscivorous birds during any breeding period at Kyle. However the complete cessation of breeding by Reed Comorant and marked reduction in breeding activity of other species does indicate that density-dependent factors have a very marked influence on the reproductive activity of the piscivorous birds of Kyle. (see table VIII page 82 and table IX page 86 for the breeding records of 1967 and 1968).

ii) Relationship between water levels and breeding seasons

B. paludinosus which is the main component of the diet of Dabchicks is an anadromous type and is noted for rapid colonization of newly filled dams. Rising lake levels are preceded by full flow in the rivers and generally fairly good rain in the Kyle catchment. These fish therefore move into rain-filled dams and flooded areas at the same time as Dabchick leave the lake area to breed. Food therefore is ensured during and after the breeding season of Dabchick.

It would appear that many of the birds with which the present study is concerned, that is, the Darter, the Reed Cormornat, the White-breasted Cormorant, the Grey Heron and the Goliath Heron, start egg laying only when lake levels are static or falling (see Figure 22).

Nesting of a pair of Grey Herons took place in January 1967 when lake level was rising, two chicks hatched in early March and these were taken from the nest to be hand-reared. Again in January 1969 a pair of these birds nested on a high granite dome surrounded by water and from this nest two chicks survived. When considering the total number of nesting birds over the period 1961 to early 1969, the occurrence of two nesting incidents may be regarded as the exception rather than the rule.

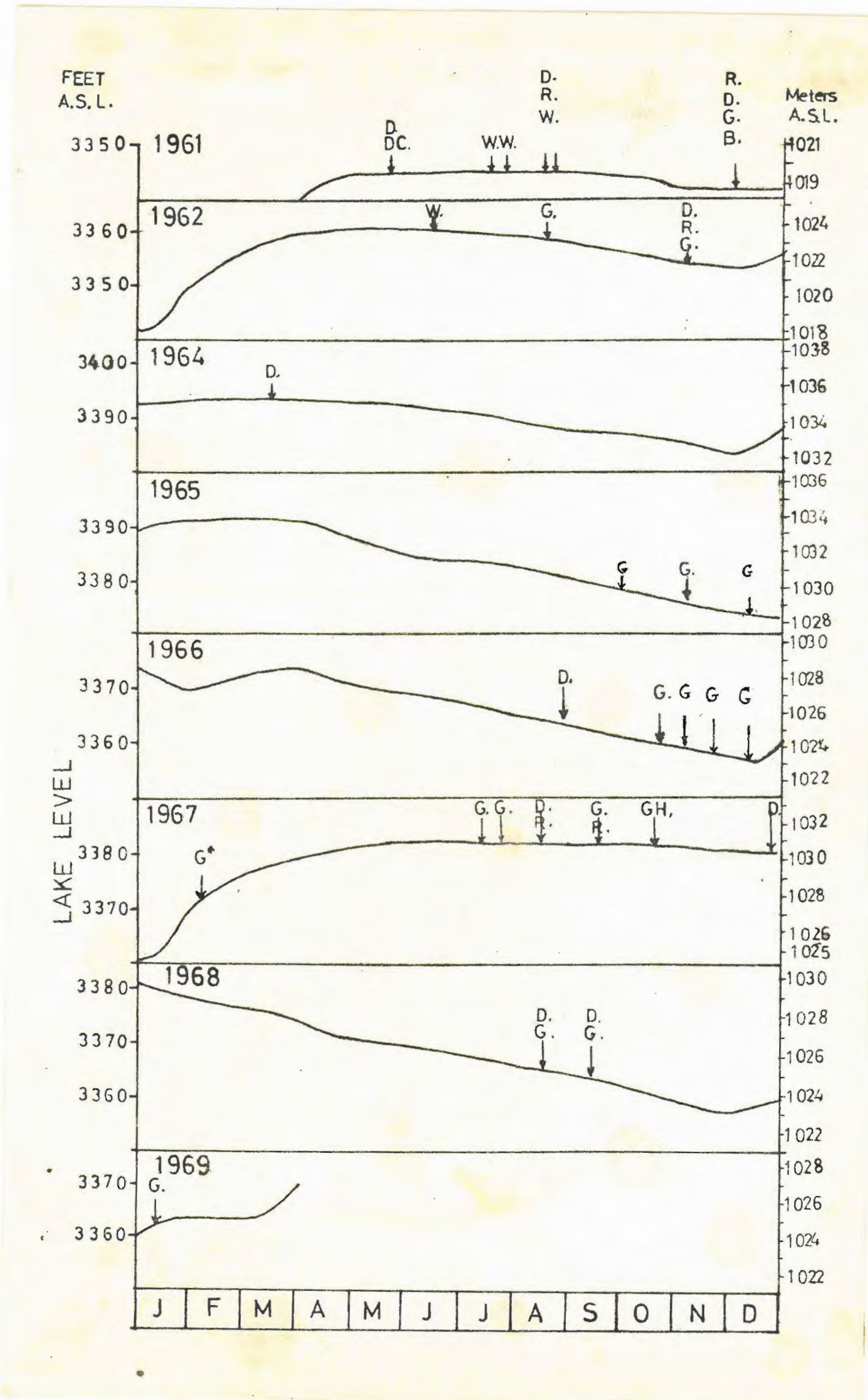


Figure 22. Egg laying activity in relation to lake level and time of year for D. Darter, R. Reed Cormorant, W. White-breasted Cormorant, G. Grey Heron, B. Black-headed Heron, G.H. Goliath Heron and D.C. Dabchick.

In the case of the Dabchick, egg laying during 1961 began in May, after vegetation ashore had been heavily flooded and provided suitable nest-sites. At this time of the year, fish of anadromous type such as B. paludinosus have already returned to the lake area. In subsequent years chick production had already been accomplished by the end of May.

A substantial rise in lake level during 1961 resulted in successful spawning of all species of indigenous fish inhabiting lake Kyle, and the virgin ground newly covered in the lake's expansion provided a wealth of food and cover for the fish fry produced. Circumstances were similar in the period January to April 1962 and also from December 1966 to June 1967. (See Figure 2, page 6). Subsequent reduction in water level during each of these years resulted in higher density of fish in the marginal zone particularly from July onwards when the marginal water became progressively warmer.

Breeding of all types of birds indicated in Figure 22 would appear to have taken place as the density of fish began to increase (see Figure 15, page 73). Simultaneously there was a shrinkage in area of fishable water and a rise in water temperature (see Figure 3 page 8). From the breeding records obtained, it would appear that the triggering influence, in breeding activity of piscivorous birds, may be the food supply rather than the level of the lake per se - whether it be static or falling. It is noticeable that 1966 and 1968 were preceded by falling lake levels. This directly affected the fish recruitment and no Reed Cormorant, the most abundant of fish-eating bird species on the lake, bred in the Kyle area during these two years.

The fishing activity of Reed Cormorants is confined to the marginal zone extending from a depth of 25 cms to 4.25 m. (See Figure 13 page 63). When weight of birds is related to area of "fishable water" (water down to 7 meters in depth), which in turn is related to the level of the lake at the time, an index of bird density is obtained. The weight of Reed Cormorants per hectare of fishable water on lake Kyle during the period March to August during 1966, 1967 and 1968 indicated that the density of these birds was higher during these months of 1966 and 1968 than during 1967, a year in which breeding activity took place. (See Figure 23).

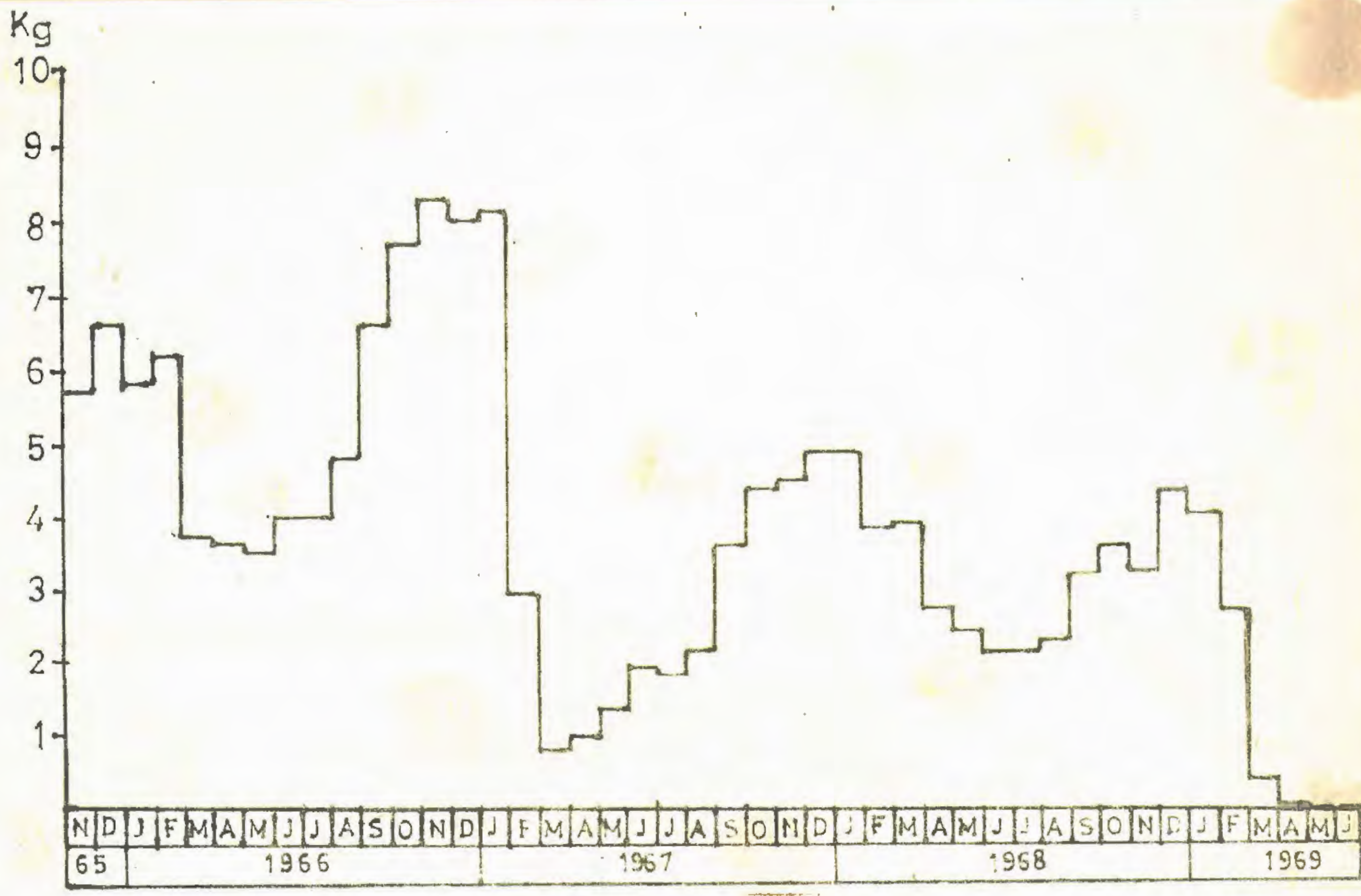


Figure 23. Weight of Reed Cormorant per hectare of fishable water during the period November 1965 to June 1969.

It would appear therefore, that food availability during the dry season of 1966 and 1968 was sufficient only to support the needs of those Reed Cormorant occupying the lake at the time. Sufficient food was not available to allow for chick production as the density of these birds, it would seem, was already at optimal level.

Breeding of all types of piscivorous birds indicated in Figure 22 would appear to take place as the density of fish begins to increase. Temperature and the state of the lake level (which determines the area of "fishable water") are the main factors which in particular combination affect fish density and in so doing influence piscivorous birds in their breeding behaviour. - This seems a valid conclusion in spite of Tienhoven's (1961) light-stimulus theory, which asserts that stronger sunlight has a definite influence on the endocrine system and especially on the hypothalmus and that this in turn affects the gonads of birds, creating an impulse to reproduce. As a result breeding takes place only in certain definite months. It is to be noted, however, that although observation over a protracted period does indicate that maximum egg laying activity occurs in these months during which the mean daily period of sunshine is sensibly on the increase, (see Figure 24) nevertheless it must also be noted that - as shown previously in this report - the Dabchick has altered its breeding time, and the Reed Cormorant during two years has shown no tendency to breed although there was no significant change from the normal either in duration or in the intensity of sunlight during the ordinary breeding period of the bird.

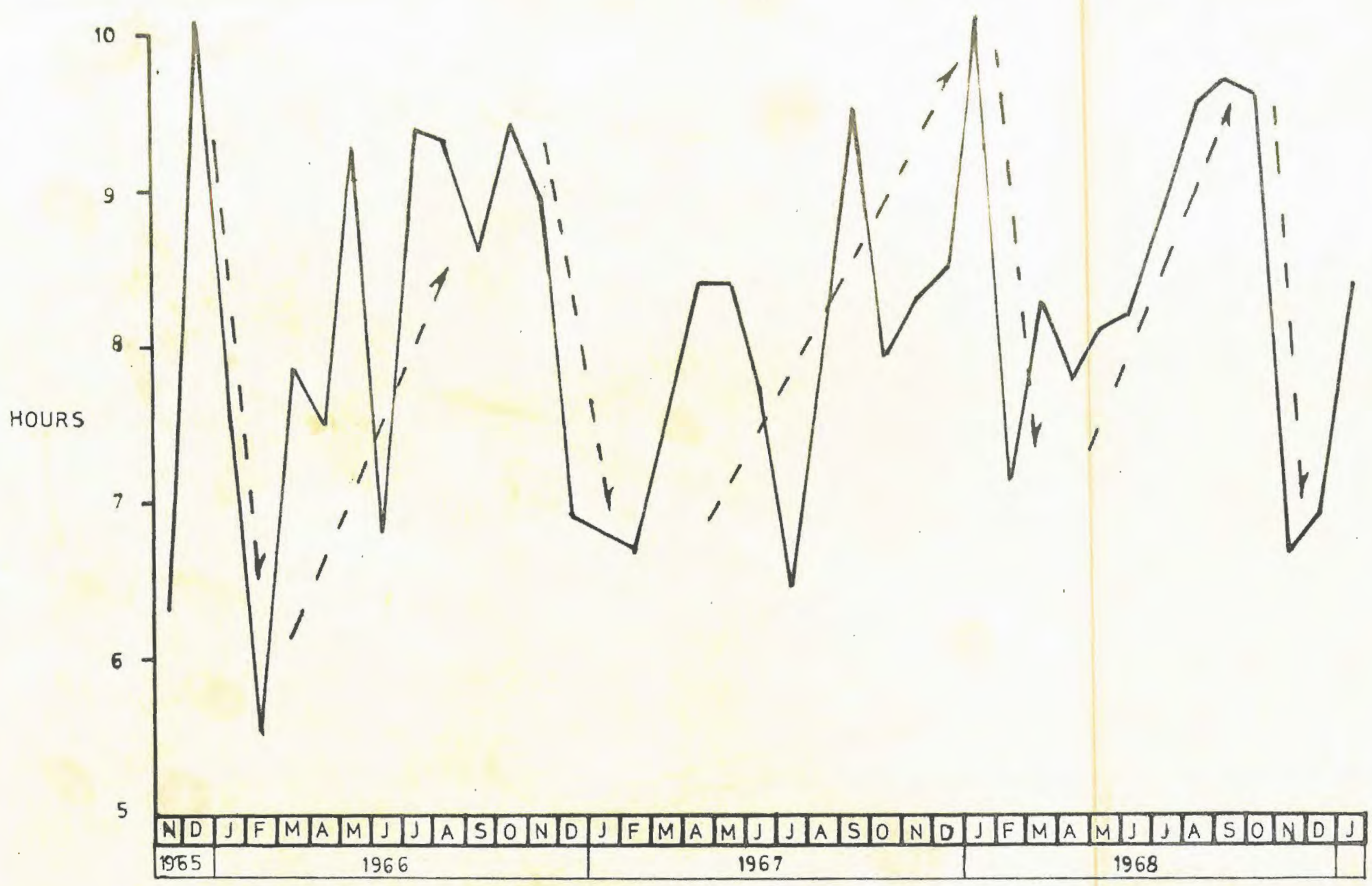


Figure 24. Mean hours of sunshine per day each month for the period November 1965 to January 1969 (Information supplied by the Meteorological Services, Ministry of Transport and Power, Rhodesia) Actual recording (— overall trend (----).

Comparable information on the effects of food supply on nesting success has been presented by Schüz (1942) for the White Stork (Ciconia ciconia), Owen (1960) for the Grey Heron and Kahl (1964) for the Wood Stork (Mycteria americana). In each case it has been indicated that change in photo-period does not seem to be a regulator of breeding activity.

(iii) Nesting Sites

The successful production of offspring by White-breasted Cormorants in the lake area was accomplished only during the early stage in the lake's history - 1961-1962. It would appear that a prerequisite for nest construction with these birds is fairly high trees, as nests constructed are usually three or four meters above water level and these must be surrounded by water. Early in the lake's history, regenerated trees sent out long supple branches, and vegetative growth was extremely rapid as a result of a constant moisture supply. These trees, when partially flooded, provided suitable nesting sites. By the time that water recession bagan in late 1962, all these trees had died and their branches were extremely brittle and weak. Lack of suitable nesting sites may thus be the reason for these birds moving elsewhere to breed.

A change in conditions from those of 1961 to late 1962 were particularly apparent when flooded grassbeds and other forms of marginal terrestrial vegetation became exposed during water recession after this period. In view of the fact that no semi-aquatic, or truly aquatic, vegetation has ever become established at Kyle, Dabchick were unable to find suitable sites on which to anchor their floating-type nests; they therefore, as in the case of the White-breasted Cormorants, sought suitable breeding sites elsewhere.

Darter, Reed Cormorant and Grey Heron would also appear to prefer breeding sites surrounded by water - a possible precaution against land predators. Supple stemmed (regenerated) trees surrounded by water were plentiful in the early stages 1961-1962, and for these a high degree of preference was evinced (see photograph overleaf).

A small Reed Cormorant breeding site typical of those chosen during 1961 and 1962.

It became apparent, however, that when the impulse to mate and produce offspring was triggered by favourable ecological conditions, any site on which nests could be constructed (even on bare ground) was chosen provided it was surrounded by water. Nests during 1967 were constructed on broken branches lying on the ground, (on flat topped rocks in the case of the Grey Heron) or even on the ground itself.

The main 1967 breeding colony of Reed Cormorant and Grey Heron. note the tremendous change in the type of nesting site available compared with those existing in 1961.

During nesting activity, it again became apparent in various mixed colonies that a very definite social grading existed. Grey Heron occupied the majority of uppermost nest sites im mixed Grey Heron/Reed Cormorant colonies, and Darter the uppermost in mixed Darter/Reed Cormorant colonies. The White-breasted Cormorant used the uppermost branches when they shared a nesting-site with other species. Darter would nest lower down and below them again the Reed Cormorants.

(f) Total weight of piscivorous birds in kilograms on each arm of Lake Kyle and weight of birds per hectare of "fishable water" in each month from November 1965 to June 1969.

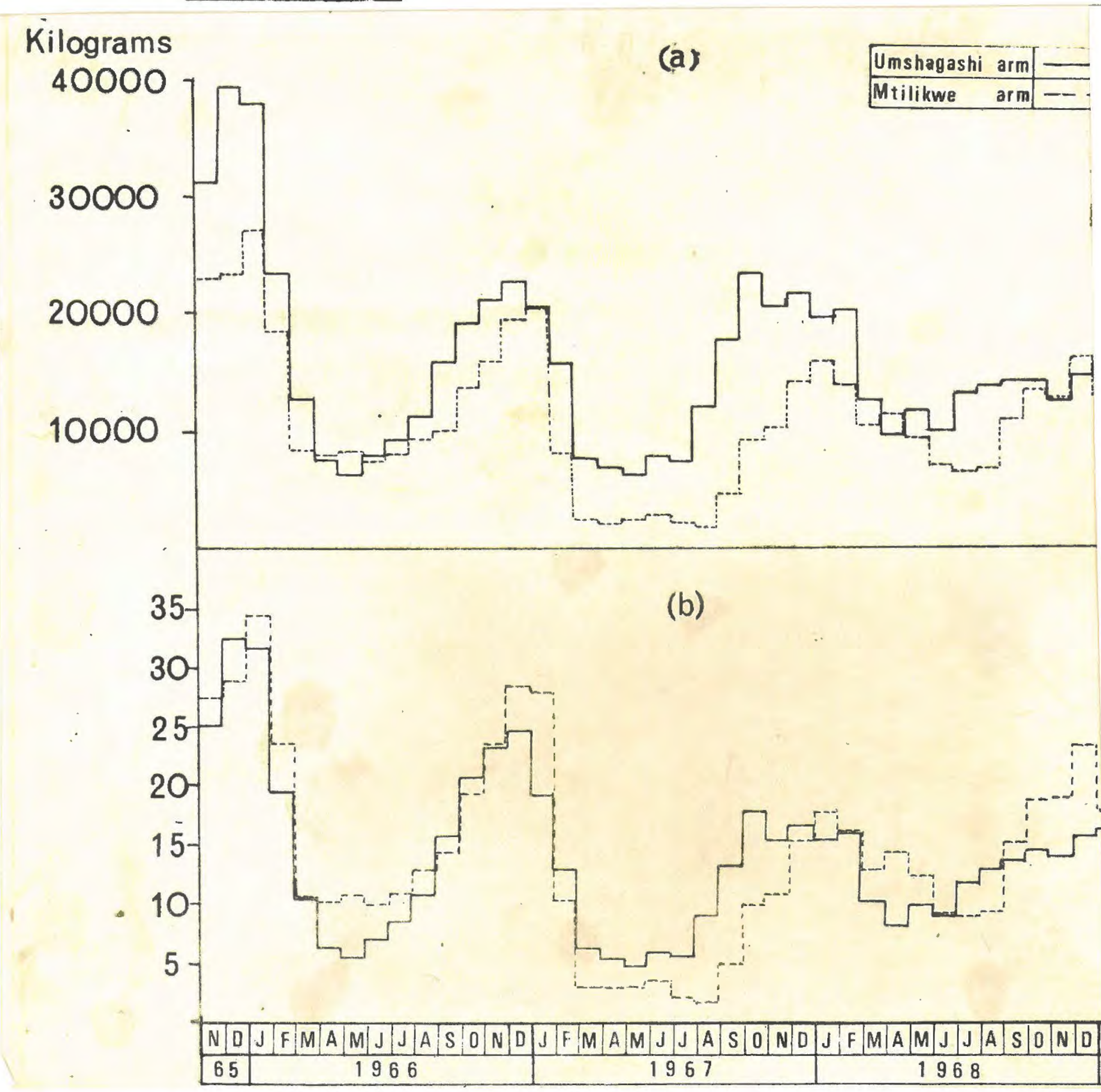


Figure 25. (a) Weight (in kilograms) of piscivorous birds on each arm of Lake Kyle each month.

(b) Weight (in kilograms) of piscivorous birds per hectare of fishable water on each arm of Lake Kyle each month.

(Period covered - November 1965 to June 1969).

The weight of birds carried, each month (see Figure 26) with the exception of April and May, 1966, April and December, 1968, is higher on the Umshagashi Arm than on the less extensive Mtilikwe section. Figure 25(b) indicates the average weight of birds per hectare of fishable water carried each month on each arm. A "bounce" or pendulum effect is noticeable. Fishing pressure was higher on the Mtilikwe in November 1965, this was followed by higher fishing pressure on the Umshagashi in December of that year. Greater pressure on the Mtilikwe occurred in January and February 1966, and equal pressure on both arms in March 1966. During April to August 1966, pressure was greater on the Mtilikwe, while in September and October 1966, it was higher on the Umshagashi. In November 1966, pressure was fairly equal on both arms.

Although fishing intensity was higher on the Mtilikwe from April to August 1966, during the corresponding period in 1967 the position was reversed. In 1968 a pattern emerged during April to June similar to that of 1966. Fishing pressure on both arms of the lake was far higher from March to August 1968, than for the same period in any other year. As has already been indicated, (page 79) severe drought conditions caused dams and most rivers to dry up completely; it would thus appear that birds were forced to remain in the lake area during the dry season of 1968. From August to December 1967, nesting activity and chick production amongst Darter, Reed Cormorant and Grey Heron was confined to the Umshagashi Arm and as a result, bird concentrations were higher on this arm. This was followed by an increase in fishing intensity on the Mtilikwe during March to June 1968.

The months of March and April saw a drop in lake level in 1966, a rise in 1967, a drop in 1968 and again a rise in 1969. Great variation in fish density occurs during these months, which precede the cold season of the year. There is also a considerable drop in the total number of fish-eating birds, and it is possible that those that continue to reside in the lake area pass frequently from one arm to the other.

Over the period of 44 months, during which close study was made of variation in piscivorous-bird population and the extent and state of the fishable area, it was found that the extent of "fishable area" on the Umshagashi section amounted on the average to 59.4% of the total, while on the Mtilikwe it was 40.6% of the total. At the same time, it was established that the total weight of piscivorous birds on the two sections was respectively 58.9% and 41.1% of the total. The significance of the close correspondence between the figures obtained for the extent of the "fishable area" in the two arms and for the piscivorous bird population on each receives attention later in this thesis

The number of birds of each species occupying the lake area shows great variation, as has been indicated in Figures 12a to e. The fact that fishing pressure per acre of "fishable water" is, in general, equal on both arms of the lake definitely implies that no type of piscivorous bird present on the lake can be excluded from the present study if sound conclusions are to be reached with respect to the area of the lake suitable for exploitation by the piscivorous birds. It seems evident that there is definite co-ordination of the fishing activity of the birds as a whole, and the number of birds of any species inhabiting either area is determined not only by the extent of the fish supply, but also by the competition provided either by birds of different type or by members of its own species. The birds studied show great variety in size and weight, yet the total weight of all birds (whose fish consumption is 16% of body weight each day) - bears a definite fixed relation to the acreage of fishable water each month.

In tables X a and b, the number of birds in each species which occupied one or other arm of the lake during the period of study is expressed as a percentage of the total number of its own kind found on the lake. Herons have been grouped together as the method of fishing is the same for all types of Herons and the area occupied during fishing activity is less extensive than that used by the free-swimming types. Kingfishers have also been grouped because the Giant Kingfisher is relatively rare.

TABLE X (a)

PERCENTAGE BY NUMBERS OF EACH SPECIES OF PISCIVOROUS BIRD ON EACH ARM OF LAKE KYLE FOR THE LAST TWO MONTHS IN 1965 AND OVER SIX MONTHLY PERIODS UNTIL JUNE 1969

U = Umshagashi Arm M = Mtilikwe Arm

SPECIES	1965		1966				1967				1968				1969		Percentage over the total period of 44 months	
	Nov-Dec		Jan-Jun		Jul-Dec		Jan-Jun		Jul-Dec		Jan-Jun		Jul-Dec		Jan-Jun			
	U	M	U	M	U	M	U	M	U	M	U	M	U	M	U	M	U	M
1. Darter	64.7	35.3	54.2	45.8	59.3	40.7	58.2	41.8	62.5	37.5	57.2	47.8	60.0	40.0	56.5	43.5	58.2	41.8
2. Reed Cormorant	55.2	44.8	51.4	48.6	56.7	43.3	63.5	36.5	78.0	22.0	58.6	41.4	53.5	46.5	59.7	40.3	59.7	40.3
3. White-breasted Cormorant	62.0	38.0	57.8	42.2	51.0	49.0	65.0	35.0	54.4	45.6	45.3	54.7	35.0	65.0	58.2	42.8	55.2	44.8
1, 2 and 3	59.4	40.5	53.0	47.0	56.8	43,2	63.1	36.9	72.6	27.4	55.6	44.4	54.5	45.5	58.6	41.4	58.7	41.3
4. Pied Kingfisher and Giant Kingfisher	46.7	53.3	67.0	33.0	63.1	36.9	66.8	33.2	69.7	30.3	64.3	35.7	48.8	51.2	67.6	32.4	63.0	37.0
5. Grey, Goliath, Purple and Great-White Herons and Yellow-billed Egret	54.2	45.8	57.5	42.5	55.0	45.0	58.8	41.2	74.9	25.1	60.5	39.5	60.7	39.3	56.9	43.1	60.3	39.7
6. Dabchick	40.1	59.9	65.1	34.9	49.1	50.9	84.1	15.9	63.9	36.1	58.8	41.2	36.1	63.9	68.9	31.1	55.2	44.8
7. All piscivorous birds	57.3	43.7	55.0	45.0	56.2	43.8	63.7	36.3	71.6	28.4	54.8	46.2	52.8	47.2	70.2	29.8	59.0	41.0
8. Available acres of fishable water	60.1	39.9	60.6	30.4	58.4	41.6	59.3	40.7	58.8	41.2	60.2	39.8	58.6	41.4	59.6	40.4	59.4	40.6
LAKE LEVELS			Drop Jan-Feb, rising slowly to end of March - drop until mid-December, followed by sudden rise.				Rising January to end of May, fairly static thereafter - very slow drop September to December				Drop from January to end of November. Slight rise in December				Rising Jan-static in Feb Rising March to April fairly static thereafter			

TABLE X (b)

PERCENTAGE BY NUMBERS OF EACH SPECIES OF PISCIVOROUS BIRD

ON EACH ARM OVER FULL-YEAR PERIODS

SPECIES	1966		1967		1968		Percentage over full three year period	
	U	M	U	M	U	M	U	M
1. Darter	56.5	43.5	61.1	38.9	56.7	43.3	57.4	42.6
2. Reed Cormorant	54.3	45.7	72.2	27.8	56.4	43.6	60.1	39.9
3. White-breasted Cormorant	55.2	44.8	60.0	40.0	40.8	59.2	53.2	46.8
1, 2 and 3	54.9	45.1	68.8	31.2	55.1	44.9	58.7	41.3
4. Pied Kingfishers & Giant Kingfishers	64.3	35.7	68.0	32.0	57.1	42.9	63.4	36.6
5. Grey, Goliath, Purple, Great White Herons and Yellow-billed Egret	56.1	43.9	66.7	33.3	57.7	42.3	61.5	38.5
6. Dabchick	53.8	46.2	66.8	33.2	45.5	54.5	55.6	44.4
7. All piscivorous birds	55.7	44.3	68.4	31.6	53.8	46.2	59.2	40.8
8. Acres of fishable water	59.6	40.4	59.0	41.0	59.4	40.6	59.3	40.7

Breeding of Reed Cormorant and Grey Heron, on the Umshagashi Arm during July-December 1967, was at a high level compared with that which occurred during the same period in 1966 and 1968, (no Reed Cormorant bred in the lake area in 1966 or 1968) and the proportion of these birds was thus far greater on the Umshagashi section than on the Mtilikwe section during this period. Dabchick leave the lake area to breed in farm dams and in reed or rush fringed pools from January to March in most years. Before setting out the birds assemble, in groups, in the formation of which there is considerable movement from one arm of the lake to the other, and of course the population incidence in either arm is considerably disturbed in the process. There was a mass exodus of Dabchick from the lake, for the purpose of breeding in 1966 and again in 1967. As the route preferred by the birds, when water is to be found in farm dams, is along the Umshagashi Arm to the area at which most of the local farm dams exist, the percentage population on the Umshagashi Arm from January to June 1967, was naturally greater than on the Mtilikwe. From January to March 1968, there was a marked coming and going on the part of Dabchick between the upper reaches of each arm and the main body of the lake. During these months, however, in 1968, dams were dry and river banks unsuitable as breeding sites so that the birds ultimately remained in the lake itself. Nevertheless throughout each period indicated in Table X (b), the number of each species of piscivorous bird on each arm would appear to remain in farily constant proportion. After any departure from the ratio of 3 to 2 the proportion would appear to be restored within a relatively short time.

It has been shown earlier in this report that there is a marked oscillation in the number of birds of each species which are active at different times on the two arms of the lake. Over a sufficiently prolonged period of time (such as that devoted to the present study) there emerges a very definite proportion, namely 3 to 2 (59.0% to 41.0%) between piscivorous bird population on the two sections. Fish-eating birds, therefore, do not crowd at random into any area. It would appear that there is actually some co-ordinated regulation of the number and weight of the species occupying definite areas.

10. Discussion.

In the course of the investigation now described it has been possible to become reliably informed of the different types of fish-eating birds which inhabit Lake Kyle, and also of the number in each species - sixteen in all, eleven of which are entirely piscivorous. A marked variation in total bird population has been noted as occurring from year to year, and also at different periods within the year - partly as the result of a temporary impulse to migrate from the Kyle area which is characteristic of certain species. Since 1965 there has been a definite decline in the total number to be found in the area. The peak pupulation of piscivorous birds at Kyle was 1860 for the year just mentioned. Diminishing totals followed in each succeeding year, until the peak was as low as 920 in October 1968. It would appear that the continued occupation of the lake area by certain birds, especially of the Cormorant species, is to some degree rendered precarious by certain factors. The chief of these is probably the inconstancy of lake-level in conjunction with vagaries in climate. The withdrawal of water for irrigation and extremes in weather conditions such as drought or un-seasonal rainfall, produce conditions which are very unfavourable to aquatic bird life, as they can have an immediate adverse effect on food supply, and can seriously interfere with nesting activity and the rearing of chicks. The years 1966 and 1968 for example, were marked by an almost complete cessation of breeding activity by the piscivorous birds at Kyle. (see Table VIII page 82 and T ble IX page 86).

Hand-rearing experiments from 1965 to the end of 1968 have permitted close study of the food requirement and development to semi maturity of young birds belonging to five species of purely piscivorous type and of two species belonging to partly piscivorous type. As a result, apart from the precise information gained with respect to their food requirements, it was possible to deduce from the overall results an index for the daily consumption of food by the average adult piscivorous bird - 16% of its body weight. Further experiments on different birds indicated that, with one exception - the Dabchick - fish-eating birds, showed no preference for any particular fish species, but that there were definite limits to the size of the fish which were acceptable as prey.

These limits as expressed in terms of length in m.m. and weight in gms. vary from something over 100mm to approximately 50 mm and from approximately 376 gms to a weight as low as 4 gm. Rare exceptions occur in which dimensions are outside this range.

Results such as those described indicate that the presence of piscivorous birds is a very advantageous circumstance for establishing satisfactory fish-production. The prey consumed is of small dimensions and the main component of their diet consists very largely of T. melanopleura which as described by Wager (1968) and Junor (1969) besides attacking fry of desirable species is mainly responsible for the disappearance of aquatic vegetation from its environment. In so far as the birds tend to limit the proliferation of Tilapia they are giving good opportunity to more desirable types of fish to reach dimensions satisfactory to the angler or the lessee of commercial fishing rights. By calculation using information obtained during the investigation (number and normal weight of birds in each species and index of daily adult food requirements) it has been possible to assess the amount of fish taken from the lake in different years. The figure for 1966 was 55,900 kilograms ($61\frac{1}{2}$ short tons) for 1967 39,600 kilograms (44 short tons) and for 1968 48,200 kilograms (53 short tons). In view of the good service the birds give in many ways this is far from excessive.

In addition to the material which has just been reviewed much information has been gained which is of interest in the study of bird ecology. There is for example, the information that has emerged with respect to the various methods employed by piscivorous birds to secure their prey - the proprietary interest of various groups in definite fishing areas - the evidence of an exclusive or dominant attitude of certain types of bird towards those of other species - of dominance also within a group during roosting or nesting. Further, comparison of the relative incidence of bird population on the two arms of the lake reveals constant proportion between the number of birds occupying each of the two areas. There is considerable evidence that continued healthy existence and the proliferation of piscivorous birds depends on the state of their food supply at certain critical periods e.g. It seems to be sufficiently established by the present investigation that a period when the lake-level is rising is very unsuitable for nesting activity, because of the dilution of the fishable area and the consequent scarcity of food for the nestlings.

The main characteristic of modern biological literature would seem to be a strong compulsion on the author to generalise. Prominent ecologists have evolved each his own theory to explain what has emerged from his research or from the investigation of others. In almost every case there has been no lack of informed criticism and of fairly successful attempts to invalidate the hypothesis presented. Milne (1957) notes "the ecological deficiencies and statistical inadequacies" in the best fields of study and "the consequent variety and contrariety of theories of natural control". Even in the minor sphere of the present study it has been found that no generalisation can be made that is not subject to exception. Frequent experiments had confirmed that the index of 16% of body-weight for daily adult food consumption was sufficiently reliable as to be used as an instrument in further research. Yet clearly it is not applicable in certain instances (e.g. when an unlimited supply of food is available - Reed Cormorant 07754 Figure 6 page 16). Again, close observation seemed to indicate very definitely that breeding activity of the piscivorous birds at Kyle was limited to periods when the level of the lake was falling or at least static - yet exceptions to the rule are noted (see page 88) in one of which healthy progeny was produced. Obviously any aspect of bird life is extremely complicated and it is necessary to be wary of dogmatic assertion. In these circumstances, when considering whether there may be any significance in the material now presented, I have thought it better to relate such facts as have emerged in the study to the work of Andrewartha and Birch (1954) Wynne-Edwards (1962), Lack (1954 & 1966), Gause (1934). Such value as the material may have, should be found in its agreement or disagreement with the conclusions enunciated by these experts.

It must be noted, however, that in publishing an account of work in the field, or in attempting to establish the validity of a hypothesis ecologists generally assume that the animals they study exist under natural conditions.

Most of them seem to be at no great pains to define the term "natural". Andrewartha and Birch name four components which demand consideration in an animal environment (i) Weather (ii) Food (iii) other animals, and organisms causing disease (iv) a place in which to live - For the present study it would be necessary to add a fifth component - the variability of the lake-level, since this is so definitely affected by the occasional withdrawal of water (which is not entirely dependent on the weather in the actual lake area) that special conditions are created for the piscivorous birds in Kyle area. A change in lake-level may lead to overcrowding of the fishable area during draw-down in the dry season or substancial decrease in the availability of food when a sudden rise in level during the rainy season results in a rapid expansion in the area occupied by those fish which are of suitable size for consumption by piscivorous birds. In addition a change in lake-level may seriously interfere with the recruitment of those fish on which the birds feed and may make the place "in which they live" (e.g. roosting or nesting sites) temporarily untenable.

Andrewartha and Birch in conducting investigations on Thysenoptera insects <u>Thrips imaginis</u> found that over a 14 year census, in all, 78 per cent of the observed fluctuations were attributed to weather factors - a situation analogous in many ways to that of the piscivorous birds, if lake-level is accepted as being weather induced. However in defence of density dependancy, Lack (1966) quotes Solomon (1967) as quoted by Nicholson (1968) followed by Smith (1961) Klomp (1962) and Varley (1963) who argued the annual fluctuations in numbers observed by Andrewartha and Birch, would not have been so closely correlated with weather factors unless, in addition, there had been a density-dependent controlling factor in operation, with this I agree.

The theory that animal population is density-dependent has many adherents today among ecologists of established reputation. Andrewartha and Birch, however, reject the theory "in toto" as dogma "a hypothesis not to be tested by empirical facts. They advance the view that in a "natural" population numbers may be limited by shortage or inaccessibility of food or other material resources such as nesting facilities. Of even greater influence than these conditions, however are periods when recruitment to a species fails to equal its loss in numbers. Nesting facilities may be rejected on the grounds that piscivorous birds at Kyle utilized any site available, when the impulse to mate was triggered by suitable ecological conditions. (see page 94).

It would initially appear that information supplied on page 52 of my thesis would add emphasis to the importance of the last factor mentioned by Andrewartha and Birch. During the forty-four months ending in June 1969 there was a marked decrease in the seasonal abundance of piscivorous birds inhabiting lake Kyle and part reason for this decline was definitely the lack of successful nesting activity. This in turn could be attributed to a shortage of food consequent on alteration of the lake-level. Lowering of lake-level however and consequent overcrowding of the "fishable area" (see page 79) during dry-seasons preceeded by below normal rainfall in years when migration to other fishing grounds (see page 77) was impossible, was the main reason for reduction or complete lack of breeding activity amongst the piscivorous birds. It can be accepted that during periods of "overcrowding", such as those just mentioned, food supply was only sufficient to meet the needs of adult birds within the Lake area. Additional demands made by chicks in the nest would have jeopardised the very existence of the adult birds. Piscivorous birds therefore react to overcrowding by curtailment or marked reduction in breeding activity and this I interpret as most certainly being density-dependent.

The conclusion reached by Wynne-Edwards (1962) is somewhat startling on first acquaintance. In his own words "it is part of our Darwinian heritage to accept the view that natural selection operates at two levels, discriminating on the one hand in favour of individuals that are better adapted, and consequently leave more surviving progeny than their fellows, and on the other hand between one species and another where their interests overlap and conflict" and later he affirms that when the two conflict, group selection is bound to win. As a prerequisite for group selection he postulates the need for " a control system in many respects analogous to the physiological systems that regulate the internal environment of the body" and " population homeostasis " tends to reach its greatest efficiency and perfection in the highest groups ". Availability of food he accepts as the ultimate determining factor. The regulating mechanism, however, ensures that animal population remains much lower than that for which the available food would be adequate. This restriction of numbers to a safe limit is secured by dispersion - behaviour as well as by the capacity to limit reproduction - both factors evolved by group selection.

As noted earlier (see page 77) certain species of piscivorous birds inhabiting the lake area were known to have a habit of migrating for brief periods each year. This as well as the almost complete cessation of breeding activity in 1966 and in 1968 were phenomena which were not inconsistent with Wynne-Edwards observation, as they certainly tended to prevent an overdrain on the food supply of the species as a whole.

It is not irrelevant at this stage to note, Wynne-Edwards rejection of the theory originated by Gause (1934) that animals of similar ecology cannot survive together in the same habitat. Examination of the feeding and nesting behaviour (see page 64) of the piscivorous bird fauna at Kyle would seem to provide strong evidence in favour of his point of view. There is another area in which I agree with Wynne-Edwards interpretation, and that is in the significance which he attaches to dominant behaviour (peck-order to use his own term) on the part of piscivorous birds - both towards members of other species and also towards members of their own kind. Observation of the manner in which groups of different bird species arrange themselves in the fishable area, in common roosting or nesting sites (see pages 65 to 68) lends strong support to his theory that peck-order may operate under group control to eliminate less desirable members of the population.

Those who accept Wynne-Edwards hypothesis of homeostasis as affected by group control are very much a minority as compared in number with those that will proceed no further in the interpretation of animal behaviour than density-dependent regulation. (Wynne-Edwards accepts the concept of density-dependency). The point of view of this group is clearly expressed by Lack (1966). "All pupulations except those about to become extinct are regulated, and this can only come about through density-dependent factors". With few exceptions biologists who agree with Lack regard the availability of food as the ultimate determining factor in the maintenance of animal population, and indications are given of many means by which the adverse effect of food shortage may be countered by a species. Migration, dispersion, reduction in the rate of reproduction, increased mortality amoung newly fledged offspring have all been mentioned as means to prevent the over utilization of natural resources. The situation at Kyle was very different however, from one in which there was always ample food resources. Migration of certain types of bird to other feeding grounds took place annually, with marked reduction in the number of migrants during the dry seasons of 1966 and 1968, when, as a result of long spells of very dry weather, the normal impulse, particularly of the Reed Cormorant, to migrate was almost completely checked. In February and March of 1969, however, Reed Cormorant deserted the lake en bloc, permitting at least some measure of recovery in the food resources.

The project now completed was originally somwhat limited in its scope. In its formal implementation however it has required careful investigation of many aspects of piscivorous bird ecology. In general, the subject selected for study would make Andrewartha and Bird's requirement of close attention to four components in an animals environment necessary - but there is an exception, as neither predators or desease caused high mortality in the adult piscivorous bird population at Kyle. In view of the special condition under which fish-eating birds exist at Kyle, it would be futile to seek for any generalization which would apply to birds of the same species living under "natural" conditions. It has been possible however to have obtained a fairly complete record of their life as it is and to note their surprising ability to accommodate themselves to their conditions. In a few instances however explanation of bird behaviour is difficult if Wynne-Edwards concept of group control must be entirely rejected. The unusually complete desertion of Kyle area by Reed Cormorant in 1969 could very easily be attributed to a special impulse affecting the species as a whole and arising from the need to prevent over utilization of food resources. In the second instant, when calculating independently the total biomass of piscivorous birds, in terms of weight and numbers, in relation to fishable area (see figure 25(b) page 95 and tables X(a) and X(b) pages 98 and 99) there is a strong suggestion of self imposed discipline in the close relation between the total weight of birds on the one hand and the total number on the other hand, found in one or other arm of the lake and the extent of the fishable area in each.

The explanation for such even utilization of the fisheries resource can only be explained in terms of density-dependency. But density-dependency would not have been accomplished in such a controlled manner unless some feed-back or homeostatic mechanism was operating at a level whereby piscivorous birds, within each species and amongst all species, could respond.

As mentioned at the beginning of this discussion the validity of many theories formulated by experts in biological study still require confirmation, but there always remains in greater or less degree the possibility that each hypothesis may be sound. Wynne-Edwards may wait long before his concept of homeostasis demands full acceptance.

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