Plate 3. A pair of African Fish Eagles call at an intruder conspecific overflying their territory. See text, pp. 81–107, especially p. 92.

Plate 4. An African Fish Eagle takes off. Note the contrasting colours of the plumage.

Plate 1. A pair of African Fish Eagles in the shade of an *Acacia* tree. The female, the larger of the two, is on the right. See text p.73.

Plate 2: An African Fish Eagle rests on a *Euphorbia* tree just after capturing a *Tilapia*, its main food in Queen Elizabeth National Park, Uganda. See text, Chapter 4.

Plate 3. A pair of African Fish Eagles call at an intruder conspecific overflying their territory. See text, pp. 81-107, especially p. 92.

Plate 4. An African Fish Eagle takes off. Note the contrasting colours of the plumage.

THE BIOLOGY OF THE AFRICAN FISH EAGLE WITH SPECIAL REFERENCE TO BREEDING IN QUEEN ELIZABETH NATIONAL PARK, UGANDA

by

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A thesis submitted in fulfillment for the degree of
Doctor of Philosophy in the University of Nairobi

December 1983

I, S.J.A. SUMBA, declare that this thesis is my original work, except where expressly stated to the contrary; and that no part has been presented for a degree in any other University.

Sumba

S. J. A. Sumba.

I, DR. JAMES J. HEBRARD, declare that this thesis has been submitted for examination with my approval as University supervisor.

James J. Hebrard

Dr. James J. Hebrard.

To

My parents, who kindled the fire in search of knowledge and truth; and the patient majority who faithfully kept that fire going.

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SUMMARY

This thesis presents the findings of a 3-year field study of the African Fish Eagle *Haliaeetus vocifer* Daudin 1858 in Queen Elizabeth National Park, Uganda. The primary objective of this study was to investigate the breeding biology of the bird with emphasis on its seasonality and nest productivity. The study also assessed the population distribution and its structure, the territorial habits and diurnal activity patterns, and the food supply of the Eagle.

Habitat variables, especially the vegetation cover and topography, along the banks of the water bodies influenced the Eagle's distribution patterns. Young birds were attracted to human settlements whereas the distribution of territorial adults bore no significant relationship to this habitat factor.

A pair of adults maintained a territory of about 29 ha. from which they excluded conspecifics and other large birds. Although the Eagle sat for about 90% of its daytime, it continuously scanned the sky for other Fish Eagles and other birds intruding into their territory. The other activities, although taking small percentages of the Eagle's daytime, were all keyed to its territorial way of life.

Fish comprised 99.7% of the bird's diet in this Park. Although most of the fish was caught by the Fish Eagle, it also pirated from neighbouring pairs and also from wandering conspecifics. Piracy attempts on other fish-eating birds were common. An adult bird ate about 275 g of fish daily, the equivalent of 10.5% of its body weight. The Eagle took fish comparable in size to that harvested by man. In removing only 1.04% of the amount of fish harvested annually by man from the Lakes Edward/George water system, the bird is not seriously competing with man for the fisheries resource and nor is it playing a significant role in the nutrient cycles of the area.

In the main study area along the Kazinga Channel, a pair had from 0-4 nests. Both mates participated in nest building and repairing. Alternate and frustration nests were built and maintained. About 15,000 kg of dry vegetative matter was locked up in their nests in the whole Park at any one time.

The breeding seasonality was correlated with a number of environmental variables of which only temperature and water levels significantly influenced the observed seasonality. Despite the lack of strong correlation between rainfall and breeding seasonality, birds preferentially laid during the rains. The breeding interval averaged about 10.7 months for all successive clutches and 12.6 months for 94 normal ones.

The Eagle laid 1-3 eggs with the 2-egg clutch being the commonest and the 3-egg one the rarest. The fresh egg averaged 133.3 g and it declined in weight with progressing incubation. The conversion efficiency of the egg materials into the body materials of the chick averaged about 70%. Both adults participated in incubation but the female did so significantly more than her mate. Eggs were incubated for 95.5% of the daytime and at 34.8 °C, well above the 25.7 °C ambient temperature. The incubation period is about 41 days. Because incubation started with the first egg, chicks were also hatched asynchronously. This resulted in sibling aggression in which the first chick dominated its siblings, especially during feedings, for the first half of the approximately 76-day nestling period. Chick losses were probably largely due to vertebrate predation and mortality decreased with age.

The nestling grew and exceeded the weight of the adult of its respective sex. The growth curve conformed with the sigmoid form of animal and other bird species and was best fitted by the Gompertz equation (Ricklefs 1967a & 1968a).

The influences of brood size, hatching order and the sex of the young on its growth rate are discussed. The growth rates of the femur, tarsus, humerus and the standard wing and the plumage changes during the nestling period are described. Nestling mortality decreased with age and was largely due to chick disappearance, most probably due to vertebrate predation.

The behaviour of the chick is described. They included sleeping, panting, defaecation, reactions to other animals and birds, and interactions between the chicks, especially sibling aggression.

The nestling was brooded intensely and for about 93% of the observation time during the first week of its life, and for a decreasing amount of time thereafter. Brooding stopped by the sixth week of the nestling period. It was almost solely undertaken by the female, the male being released from this duty in order to hunt and provide for his expanded family. Although he caught most of the prey at this time, the female delivered most of them and did most of the feeding of the brood.

The nestling period averaged 76 days and was not significantly influenced by brood size or the nest site. The maiden flight was preceded by pre-flight exercises and was made without parental coaxing. The post-fledging young fed largely on prey remains which, during the early post-fledging

period, were usually delivered on the nest, and which, during the late post-fledging period, it grabbed from the parents. The eaglet dispersed at about 112 days after its first flight or 188 days after hatching. Parents apparently did not drive away their young.

Increasing clutch size significantly decreased hatching success with the 1-egg clutch achieving 100%, the 2-egg clutch 82.3%, and the 3-egg clutch 67.2% hatching successes. Egg disappearance was the most important cause of hatching failure, infertility/addling intermediate and egg breakage the least important. Larger clutch sizes favoured the production of young. Although nestling survival was highest (75.8%) in the 1-young brood, intermediate (69.7%) in the 2-chick brood, and least (66.7%) in the 3-young brood, brood size did not significantly affect the annual survival of young. Food shortage was apparently not important in the survival of broods but chick disappearance, probably due to predation, was. Annual nest success was low, averaging 31.2% for pair-years present and 44% for active nests. The annual production averaged 0.46 young/pair, 0.65 young/active nest, and 1.49 young/successful pair. Increasing territory size and numbers of mature trees in the territories increased, although not significantly, the production of young. Additionally, increasing human disturbance about the territory affected the breeding success of the bird by reducing the numbers of nesting attempts made. Annually, 56.1% of the breeding attempts failed to fledge young, 23.4% fledged 1-young broods, 19.5% fledged 2-young broods, and only 1.0% raised 3-young broods. Eaglets reared in 1-young broods accounted for 36.3%, those raised in 2-young broods for 59.5%, and those in 3-young broods made up 4.2% of the total number of young fledged during this study. Overall, 68% of all the pairs present during the study bred, 32% did not. Of 202 breeding attempts made, 26 (13%) of them were replacement clutches.

CHAPTER 1

INTRODUCTION AND OBJECTIVES OF THE STUDY

1.1 GENERAL INTRODUCTION

For thousands of years, eagles have both fascinated and impressed mankind. It is not hard to see why for an eagle's flight is both skillful and graceful, and can hardly be surpassed by any other bird. At rest, the majestic pose, the piercing stare, and the strong foot and talons are eloquent evidences of an eagle's power over the other lesser creatures - birds and all else. An eagle is definitely at the top of the avian tree. Because of their power, eagles have for long featured prominently in fables and legends, have become national emblems, and, usually in heraldic attitudes, appear on many coats-of-arms, gateposts, and both company and public letter heads, magazines and advertisement charts.

Notwithstanding the admirable way in which the eagle enriched mankind's everyday life, man, as always, turned round and persecuted the eagle largely for allegedly preying upon his domestic animals. He also persecuted it for stealing fish and game birds from protected grounds. He robbed large numbers of the eagle's eggs just to stow away in personal and museum collections. Because of man's high rate of population increase and development efforts, he unwillingly destroyed most of the eagle's habitat through bush and forest clearing and also chemically contaminated its food chain. Through man's activities, deliberate or otherwise, many species of eagles have suffered unprecedented population declines in modern times.

1.2 THE AFRICAN FISH EAGLE

1.2.1 Classification and distribution

The African Fish Eagle is classified by Brown (1976a & b) as follows:

Order: Falconiformes
Family: Accipitridae
Sub-family: Haliaeetinae
Genus: Haliaeetus.

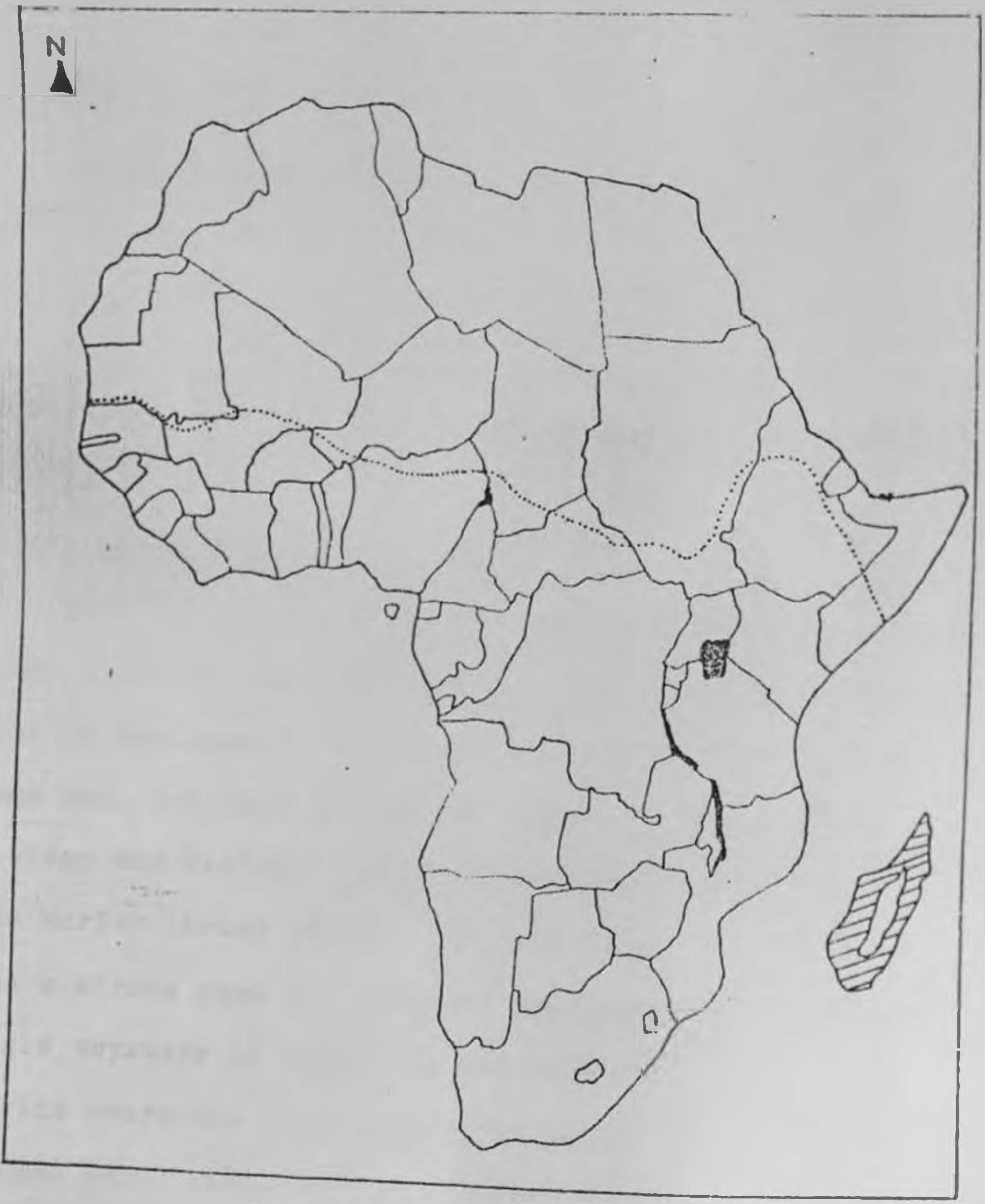
All birds of prey are classified into two orders: Falconiformes and Strigiformes. The order Falconiformes, to which the Fish Eagle belongs, comprises all diurnal birds of prey while the order Strigiformes includes the nocturnal ones. To the latter belong all owls. The family Accipitridae encompasses such birds as snake eagles, harriers and hawks, buteos, old world vultures, kites, and sea and fish eagles. The sea and fish eagles are, however,more closely related to the vultures and kites than to the other eagles in the family. The sea and fish eagles and the fishing eagles are grouped in the sub-family Haliaeetinae, a collection of raptors whose diet consists substantially of fish (Brown, op. cit.).

The genus Haliaeetus, to which the African Fish Eagle belongs, has 8 species comprising all the sea and fish eagles. They are: the American Bald Eagle Haliaeetus leucocephalus, the European or White-tailed Sea Eagle H. albicilla, White-bellied Sea Eagle H. leucogaster, Sanford's Sea Eagle H. sanfordi, Pallas' Sea Eagle H.leucoryphus, Steller's Sea Eagle H. pelagicus, the African Fish Eagle H. vocifer, and the Madagascar Fish Eagle H. vociferoides.

Of these 8 species, only the Bald Eagle is a new world species and it inhabits only the northern continent. The White-tailed Sea Eagle inhabits Europe while the White-bellied and Steller's Eagles are found in both Europe and Asia. However, the range of the White-bellied Eagle extends into Australasia as well. Pallas' Sea Eagle lives on the lakes, swamps and rivers of Central Asia. The Ethiopian Zoogeographic Region are inhabited by two species, the African Fish Eagle which occurs on the main continent and the Madagascar Fish Eagle which lives on the island of Madagascar (Fig.1.1).

The distribution of the Fish Eagle, in Africa, does not cover the whole of the continent. Brown & Amadon (1968) described it as being south of a line from Senegal through southern Sudan to Mogadishu, Somalia (Fig.1.1). In this area, its widespread distribution is, however, restricted by the presence

Fig. 1.1 Map of Africa showing distribution of the African Fish Eagle *Haliaeetus vocifer* Daudin 1800. The species occurs south of the dotted line. The distribution of the congeneric Madagascar Fish Eagle *H. vociferoides* is also shown.



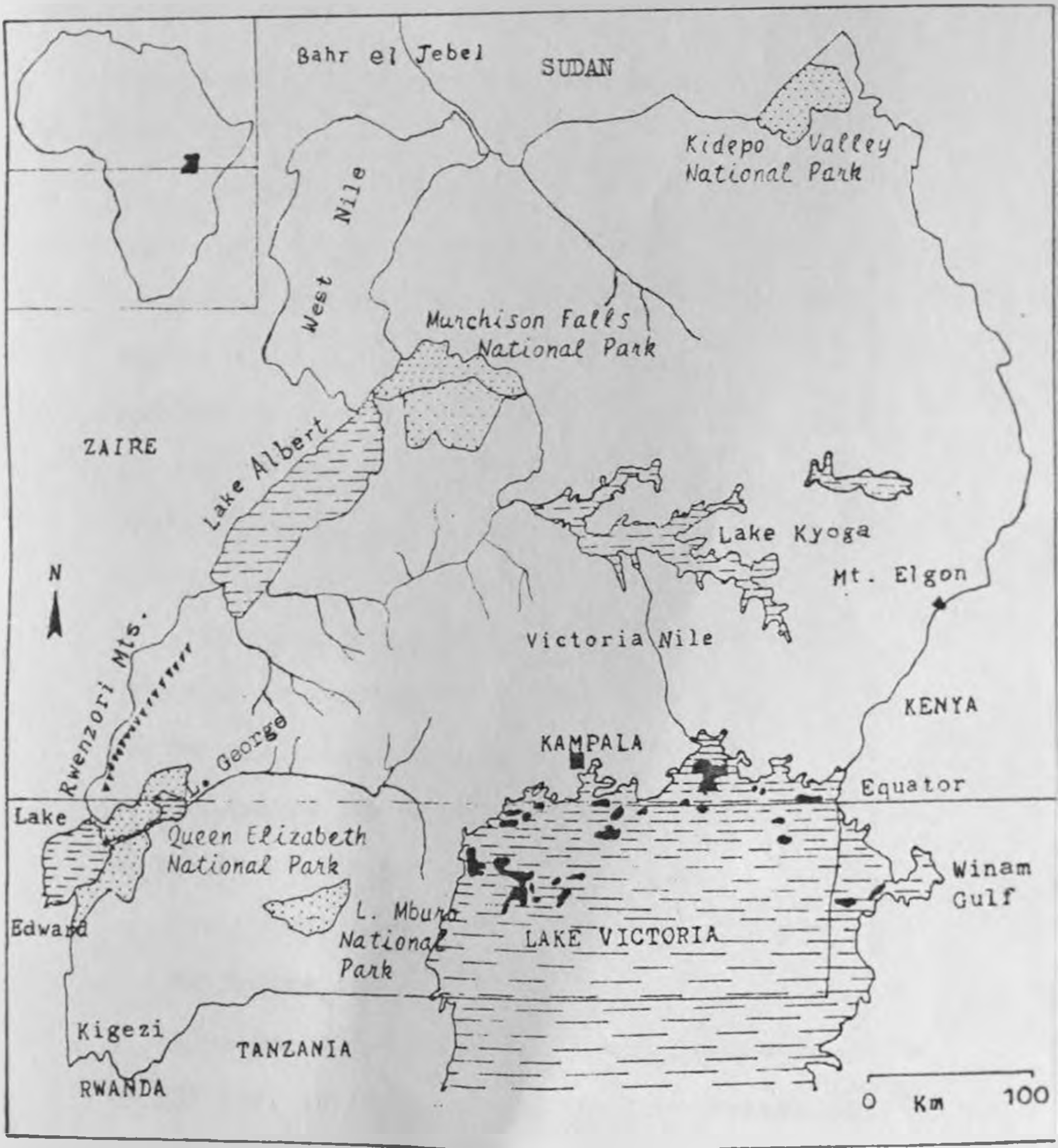
of water. Thus, in the Ogaden Province of Ethiopia and in northern and northeastern Somalia, and in the Kalahari Desert it is absent. Where water is available, the Eagle can be found along rivers in the thick tropical forests, and on inland lakes and swamps and along the shorelines of the oceans. It can also be encountered up mountains at altitudes as high as 2100 m although it is unlikely to breed above 1200 m (Mackworth-Praed & Grant 1952).

In Uganda the Fish Eagle occurs along all the major rivers and on all swamps and lakes except those high up on Mts. Rwenzori and Elgon, and in the Kigezi and West Nile Highlands. For lack of water, it is also absent from the northeastern part of the country (Fig.1.2).

1.2.2 Objectives of the study

By 1975 when this project started, Brown's (1980) book: "The African Fish Eagle", which brings to light most of the aspects of the bird's way of life had not come out, nor were his books: "Birds of Prey, their biology and ecology" (Brown 1976a) and "Eagles of the World" (Brown 1976b). At that time, too, there was a strong need for detailed studies of the Fish Eagle anywhere in its range but more so in East Africa where the bird occurs "at capacity populations" (Brown pers. comm.1975; S.K. Eltringham pers. comm. 1975). This is at least true of populations at Lakes Naivasha and Baringo in Kenya and in Queen Elizabeth

Fig. 1.2 Map of Uganda showing the location of the four National Parks (stippled) and the other main geographical features.



National Park, Uganda. Despite Brown's book on the species, the need for the study of the Fish Eagle still remains high, especially so of populations in different habitats. The need for these studies are clearly stated by Brown (1980) himself. However, the findings brought forward in Brown's (1980) book, including those of other authors, are appraised in the relevant chapters of this thesis.

Thus, this study was conceived with the main objectives of:

1. estimating the population of the African Fish Eagle in the Queen Elizabeth Park and assessing the population structure and its distribution in relation to various habitat variables,
2. describing territoriality in the bird and appraising its role in population regulation in the species,
3. examining the feeding habits and evaluating the role of the Eagle in the nutrient cycles in the ecosystem of the Park,
4. assessing the breeding biology of the bird in the Park with the view of:
    4.1 describing the nesting habits and measuring the breeding seasonality and finding out which environmental factors, if any, influence the observed seasonality,

4.2 describing the egg of the Eagle, measuring its incubation period, and ascertaining the role of each adult in incubation,

4.3 measuring the growth rates of nestlings, determining the mortality factors influencing chick survival and measuring the nestling period,

4.4 observing the behaviour of nestlings and those of their parents in relation to their influences on brood survival,

4.5 measuring the post-fledging period of the eaglet, describing its behaviour and determining how it leaves the parental territory, and

4.6 measuring the nest productivity and assessing the influences of population density of the birds and of other habitat factors on the observed productivity,

5. availing the findings of the study, through recommendations and publications, for the improved management and conservation of the African Fish Eagle in Queen Elizabeth National Park in particular and in Uganda and Africa in general, and

6. availing the findings, through publications, to science for consumption and debate.

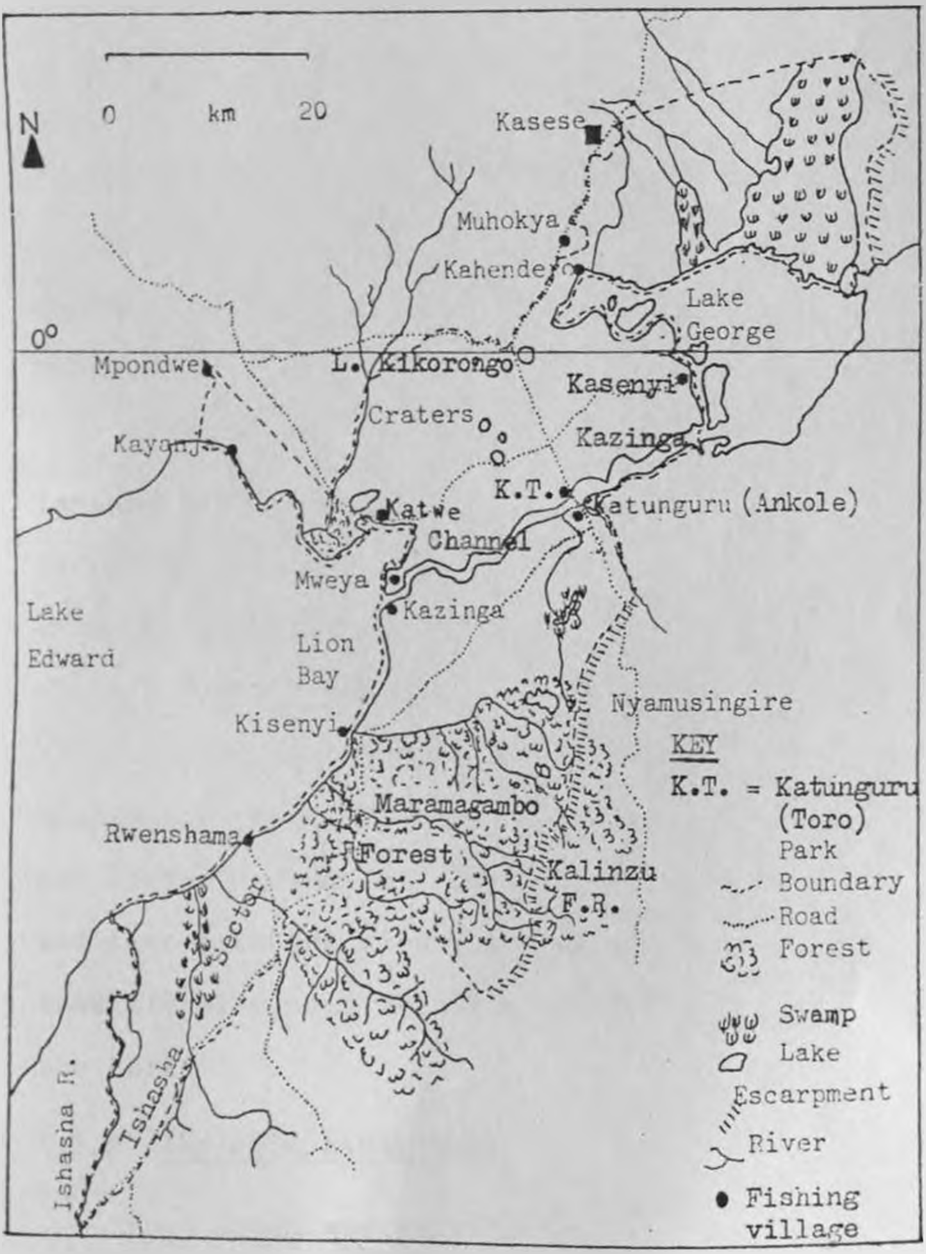
1.3 THE STUDY AREA

1.3.1 General

This study was carried out in Queen Elizabeth National Park, whose location, as well as those of major geographical features of Uganda are shown in Fig.1.2. The area now constituting the park was first gazetted a Game Reserve in 1934 and uplifted to National Park status in April, 1952. The Park covers 1978 km^2 and lies between latitudes 0^o 15'N and 0^o 35'S and longitudes 29^o 35' and 30^o 20'E. The Rwenzori Mountains (Mountains of the Moon), with its 5100 m peak, lies to the northwest of the Park, just outside its boundaries. The Park varies in elevation from 913 m on Lake Edward to 1364 m a.s.l. in the Crater Area (Fig.1.3). It borders on two large lakes: Lake George, with a surface area of approximately 260 km^2, to the northeast and Lake Edward, with an area of about 2160 km^2, to the west and southwest respectively. The Headquarters of the Park and Uganda Institute of Ecology, and Mweya Safari Lodge are situated on a 4.5 km^2 piece of land, the Mweya Peninsula, which juts out into Lake Edward.

Bordering onto Lake George, to the northeast of the Park, are large swamps which cover about 160 km^2. The swamps and the adjacent grassland are connected southwards to the remainder of the Park by a narrow strip of land between Muhokya and Kahendero Villages (Fig.1.3). To the southwest is the Crater Area of

Fig. 1.3 Map of Queen Elizabeth National Park showing the important geographical features.



the Park, a region which underwent intensive volcanic activity only about 10,000 years ago (Beadle 1974, Bishop 1970). Several volcanic craters were formed during this period, a few of which now have salty lakes in them.

The Kazinga Channel, which connects Lake George to Lake Edward, almost bisects the Park. The bushed grassland on its southern shore gives way to the Maramagambo Forest, a semi-deciduous forest of about 450 km^2. This forest partially precludes the movement of many species of animals between the northern and southern sections of the Park.

To the south of Maramagambo Forest lies the Ishasha Sector of the Park. Along the eastern border of Ishasha Sector is the Kigezi Game Reserve, a buffer zone separating the Park from the heavily settled area further east. The Ishasha River, which also acts as the international boundary between Uganda and Zaire, forms the southwestern border of the Park. Because of its large herds of antelopes and tree-climbing lions, Ishasha Sector has traditionally been the life blood of tourism in the Park.

1.3.2 The main study area

This study was largely conducted along the Kazinga Channel, between its confluence with Lake Edward and Katunguru Bridge at Katunguru Fishing Village (Fig.1.3). The Channel, whose direction and rate of flow are hardly detectable to a casual observer because of its insignificant drop in gradient (1:33,600 m) from Lake George to Lake Edward, has been likened to a narrow lake (Eltringham 1975). It is 40 km long, 0.8 km wide and about 5 m deep.

Because the Channel almost purely drains the waters of Lake George into Lake Edward, without major additions along its course, its waters are limnologically similar to those of Lake George (Beadle 1932). There have been no other limnological studies of the Channel and Lake Edward whose findings could be compared with those of the well-studied Lake George (Dunn 1972, Dunn et al. 1969, Burgis 1969, Ganf 1969 & 1972, Gwahaba 1973).

1.3.3 Climate

The importance of climate in determining the ecology of the Park was realised by the Nuffield Unit of Tropical Animal Ecology (NUTAE), the predecessor of the Uganda Institute of Ecology (UIE). Consequently, routine records of climatic factors were started in 1963. A meteorological station was established at Mweya and 21 storage rain gauges were installed throughout the Park. Lock (1967) and Field (1968) report on the earlier records, and indicate that fluctuations in daylength are negligible due to the equatorial position of the Park (Figs.1.2 & 1.3). Sunrise varies from 0644 hours at the end of October to 07:15 in mid February. Sunset is between

1846 and 1915 hours respectively.

1.3.3.1 Temperature: The ranges for both the daily minimum and maximum temperatures are very low, from 17.7°C in October to 18.8°C in May for minimum (Table 1.1a) and 27.9°C in October to 29.6°C in February for maximum temperatures (Table 1.1b). The differences between the monthly means of daily minima and maxima for any month are small; for 1964-72 they were lowest, i.e. 9.2°C, in April and May, and highest, i.e. 10.6°C, in January and February. Such small temperature variations clearly reflect the equatorial position of the Park.

1.3.3.2 Sunshine and solar radiation: Even under equatorial conditions where the sun is directly overhead at mid-day twice a year, the amounts of sunshine and solar energy available for primary production by plants can become deciding ecological factors. Thus, in this Park, Edroma (1974a) demonstrated that solar energy was the primary factor which caused competition and, therefore, resulted in the ousting of some short grasses and annuals shaded by tall ones from an area protected from grazing and burning. On the other hand, sunshine can cause serious stress to both plants and animals, especially during the dry season (sections 3.3.2.5 & 9.3.2).

Data collected during 1965-72 indicate that the amount of sunshine received in this Park varies little from one month to another, i.e. 5.0 hours in

Table 1.1 (a) Mean monthly minimum temperatures (°C) for Mweya, Queen Elizabeth National Park.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept	Oct.	Nov.	Dec.
1964	18.3	18.5	19.1	18.7	18.8	17.9	16.9	18.0	18.2	17.9	17.5	17.0
1965	17.6	18.3	18.9	18.6	18.3	17.7	17.8	18.2	17.7	18.4	18.2	17.8
1966	18.5	18.8	18.5	18.8	18.5	17.7	17.6	18.0	17.5	17.4	18.0	17.9
1967	18.1	18.4	18.9	19.0	18.9	18.2	17.6	17.9	17.4	17.6	17.8	17.9
1968	18.8	18.3	17.7	18.7	19.1	17.9	17.6	18.3	18.0	16.6	17.8	17.2
1969	17.6	18.3	19.2	17.0	16.9	18.2	19.1	18.6	17.7	17.0	18.8	19.0
1970	16.5	17.3	18.0	18.3	18.1	17.4	18.0	18.9	17.9	17.6	18.3	18.1
1971	17.4	19.0	19.0	18.5	21.4	20.3	20.5	18.5	18.1	18.4	19.6	18.3
1972	18.7	18.5	18.5	18.4	18.8	18.4	18.8	18.4	18.3	18.7	18.9	18.1
Mean	17.9	18.4	18.6	18.4	18.8	18.2	18.2	18.3	17.9	17.7	18.3	17.9

Table 1.1 (b) Mean monthly maximum temperatures (°C) for Mweya, Queen Elizabeth National Park. Dash indicates no record available.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept	Oct.	Nov.	Dec.
1964	29.4	28.4	29.6	27.3	28.5	28.9	27.8	28.3	27.9	27.7	28.2	28.2
1965	28.9	29.3	29.1	27.6	28.7	28.9	28.8	29.4	29.3	27.9	27.9	28.1
1966	29.4	29.1	28.6	28.0	29.2	25.9	28.4	29.1	27.2	25.5	27.9	29.4
1967	30.3	31.6	29.3	29.8	27.8	28.3	27.9	29.5	29.5	27.8	27.6	30.5
1968	30.3	30.0	27.1	30.3	30.0	28.3	29.5	28.3	30.6	28.3	27.9	27.7
1969	28.5	28.8	25.8	25.6	28.7	-	29.1	29.7	28.8	30.0	30.3	27.0
1970	29.4	31.0	27.6	28.8	28.2	30.3	28.6	31.2	26.9	29.0	29.5	28.2
1971	28.0	29.6	29.1	26.8	28.4	28.6	26.9	26.6	27.9	28.0	27.6	28.5
1972	27.3	28.7	28.8	27.5	26.5	27.6	30.1	26.5	27.3	26.6	26.2	27.1
Mean	29.1	29.6	28.3	28.0	28.4	28.3	28.6	28.7	28.4	27.9	28.1	28.3

April and October and 6.5 hours in July (Table 1.2), and probably from day to day. However, it is low during the wet season (April and October) and high during the dry season (July), the correlation between sunshine and rainfall being negative but significant ($r = -0.656$, $df = 10$, $P < 0.05$).

The monthly totals of the incoming solar radiation varied from 332.4 cal/cm^2/month in August to 382.0 cal/cm^2/month in September (Table 1.3). Although not strongly correlated with rainfall ($r = 0.061$, $df = 10$, $P > 0.1$), it was maximum during the rainy season. This clearly suggests that incoming solar energy is reduced by haze which is characteristic of the dry seasons when dust and smoke from grassland fires are pronounced.

1.3.3.3 Wind: The prevailing wind is largely northwesterly and westerly. During 1965-70 inclusive, wind speeds varied from 353884 wind runs per month in July to 554900 wind runs per month in December (Table 1.4).

In plants high wind speeds result in high losses of water through evapotranspiration. However, the effects of this water loss would be ameliorated by the water received during the rainy season. The repercussions of high winds on the Fish Eagle remains to be studied but they probably had some negative effects on the water budgets of the birds, especially on nestlings during panting (sections 9.3.2 & 9.4). Furthermore, high winds probably could have destroyed more of the weak *Euphorbia*

Table 1.2 The mean monthly sunshine hours at Mwoya, Queen Elizabeth National Park.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept	Oct.	Nov.	Dec.
1965	7.5	6.8	5.9	6.2	7.1	7.9	6.7	6.8	7.3	5.3	5.6	7.5
1966	6.5	5.0	5.0	5.2	4.0	5.1	7.2	6.4	5.0	6.0	5.0	6.6
1967	6.7	6.3	4.4	5.1	7.1	5.7	5.9	7.3	6.6	4.9	4.3	7.9
1968	6.1	4.4	4.2	3.1	4.8	5.4	6.7	4.8	6.8	4.5	4.0	6.0
1969	4.9	4.2	4.2	4.8	4.0	5.3	5.9	6.4	4.0	4.2	5.4	5.7
1970	3.8	6.6	4.6	4.3	5.3	6.4	6.4	3.3	5.7	4.6	7.8	5.6
1971	5.2	6.7	5.9	5.4	5.8	6.2	5.3	5.2	6.1	6.7	4.8	3.3
1972	6.2	5.6	7.0	5.5	5.2	6.0	7.9	5.8	7.1	4.0	5.6	5.8
Mean	5.9	5.7	5.2	5.0	5.4	6.0	6.5	5.8	6.1	5.0	5.3	6.1
±S.d.	1.2	1.1	1.0	0.9	1.2	0.9	0.8	1.3	1.1	0.9	1.2	1.4

Table 1.3 The total monthly solar radiation (cal/cm^2/day) for Mweya, Queen Elizabeth National Park.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept	Oct.	Nov.	Dec.
1968	412	333	348	348	344	318	318	288	374	396	347	331
1969	363	340	375	391	337	353	318	390	331	343	335	322
1970	304	371	358	316	309	360	346	301	397	384	367	357
1971	396	435	344	365	386	379	358	344	426	431	438	339
1972	337	327	406	351	345	369	426	339	382	352	321	350
Mean	362.4	361.2	366.2	354.2	344.2	355.8	353.2	332.4	382.0	381.2	361.6	339.8
±S.d.	43.7	44.6	25.3	27.3	27.6	23.3	44.3	40.2	34.7	35.4	45.9	14.1

Table 1.4 The monthly wind runs for Mweya, Queen Elizabeth National Park.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept	Oct.	Nov.	Dec.
1965	. 23530	. 76215	27463	754647	204229	638429	509828	484293	391151	500569	507898	401848
1966	651446	358061	575623	390703	697771	281641	72892	213031	992106	29983	607059	465503
1967	566751	446242	660418	337877	844457	437673	492737	555787	517336	501614	442864	959044
1968	378032	581383	378011	668132	275106	691029	350195	561820	456018	556186	455815	437006
1969	428161	506237	666300	721869	557831	397036	346734	70200	292022	714241	288611	291963
1970	567193	297441	763094	347931	357974	342140	350919	556293	420713	671171	235017	774036
Mean	435852.2	377596.5	511818.2	536859.8	489561.3	464658.0	353884.2	406904.0	511557.7	495627.3	422877.3	554900.0
±S.d.	225511.6	179123.9	270429.8	197758.5	252461.4	164467.0	156607.0	212333.5	246978.2	244605.7	138531.4	255266.4

trees used for nesting (section 5.3.1) were they not to have been protected by the tangling Capparis tomentosa and Azima tetracantha thickets.

1.3.3.4 Rainfall: According to the Thornthwaite System (Thornthwaite 1948), Queen Elizabeth Park is semi-arid with potential evaporation exceeding the mean monthly rainfall throughout the year (Spinage 1967a). This is attributed to its position in the Western Rift Valley, the rainfall pattern changing abruptly at the escarpment to one of lower intensity (Fig.1.4). Annual precipitation is highest near the eastern rift wall and lowest over Lakes George and Edward and along a belt almost directly over the Kazinga Channel (Fig.1.4). The annual means of monthly rainfall during 1964-1974 range from 667 mm at Nyamugasani to 1167 mm at Nyamusingire (Table 1.5). Typically there are two dry seasons, December to February and June to mid-August, and two wet seasons, March to May and September to November. The bimodal pattern is associated with the Intertropical Convergence System (Griffiths 1972).

Because potential evaporation exceeds monthly rainfall throughout the year (Spinage op. cit.), this results in higher evapotranspiration rates. Thus, in the dry season, the rainwaters dry up too quickly. Even during the wet season, since the rains occur in violent thunderstorms, a substantial proportion of it is lost as run-off water, especially in the over-grazed areas where the soil is compacted by animals and there

Fig. 1.4 Isohyets showing the average monthly rainfall (mm) in Queen Elizabeth National Park.

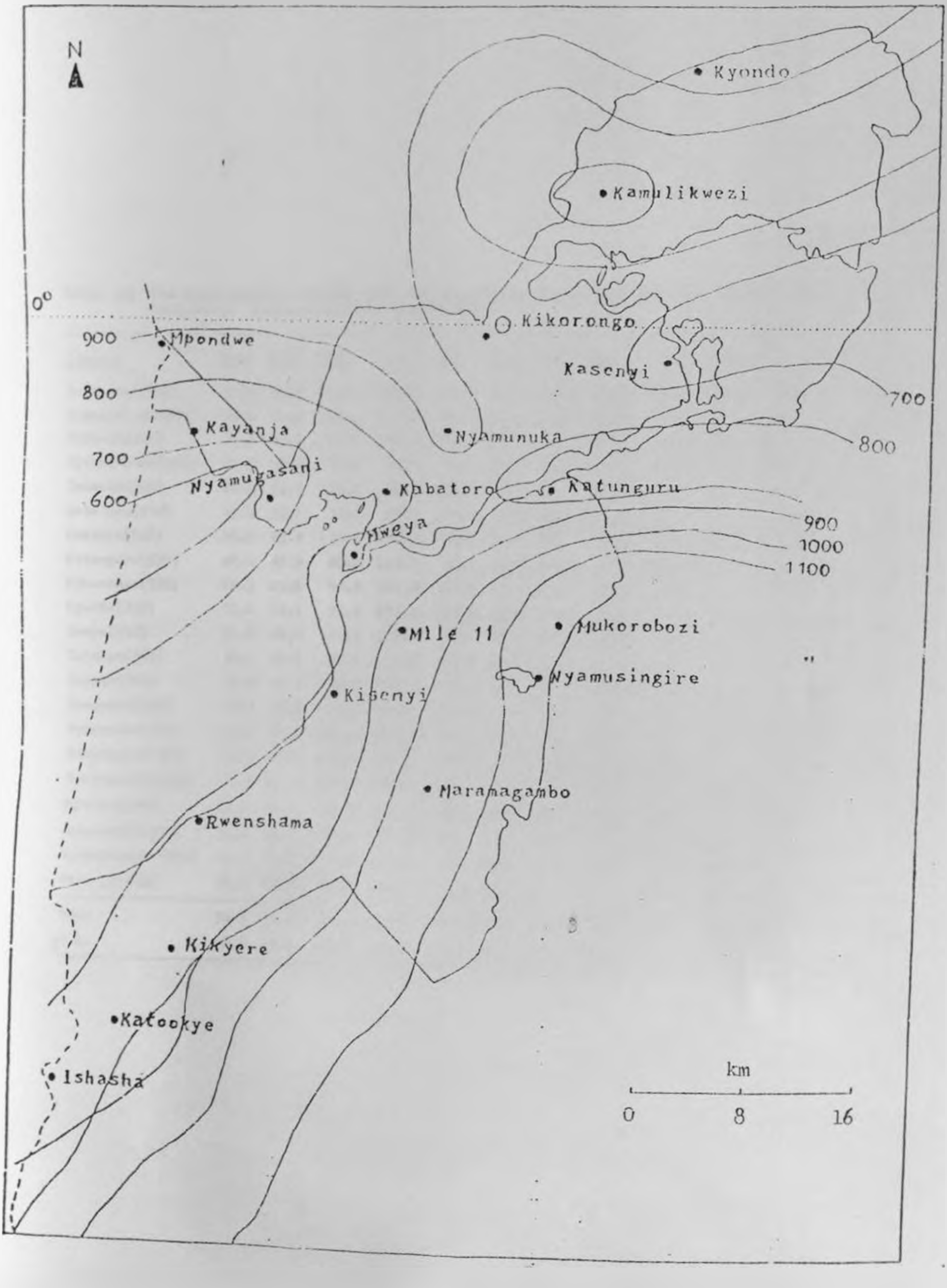


Table 1.5 The mean monthly rainfall (mm) for stations in Queen Elizabeth Park. Data for 1964 - 1974 inclusive. Altitude in m in parentheses.

Station	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept	Oct.	Nov.	Dec.	Total
Rwenshama(900)	32.4	45.6	84.6	99.6	78.4	37.3	40.1	67.7	57.8	115.1	123.7	42.4	824.7
Kamulikwezi(920)	32.6	21.1	88.3	118.8	89.7	36.7	27.3	47.1	57.6	92.1	87.7	51.9	750.9
Kayanja(920)	16.3	35.1	95.0	109.9	87.6	51.0	28.7	43.9	81.9	104.6	86.0	44.1	784.1
Nyamugasani(920)	25.2	38.6	74.9	90.2	57.6	35.1	31.4	51.0	79.1	67.0	73.2	43.6	666.9
Ishasha(930)	42.1	37.2	95.4	99.3	92.0	41.9	30.1	91.1	91.5	88.9	118.7	46.1	882.3
Kabatoro(930)	23.1	53.1	77.2	97.2	65.3	37.8	39.8	77.1	67.7	92.4	111.8	50.4	792.9
Kasenyi(930)	36.9	25.4	74.7	100.7	54.9	31.7	24.7	55.4	29.3	95.6	97.7	47.7	614.7
Katunguru(930)	48.0	48.9	88.0	124.7	72.7	54.7	26.4	72.2	65.2	111.9	113.7	57.0	883.4
Kikorongo(930)	24.3	45.6	96.7	121.8	80.2	52.1	38.7	56.8	80.2	109.6	96.6	54.4	857.0
Kyondo(930)	27.6	24.3	97.9	152.0	116.9	32.6	19.9	64.4	79.6	121.0	113.7	74.1	934.0
Mweya(930)	35.6	46.7	77.3	132.2	70.6	38.6	37.2	90.0	64.0	77.2	119.4	47.1	835.9
Katokye(960)	38.1	45.5	79.8	114.0	85.0	50.0	29.3	79.3	91.0	89.6	95.1	48.0	844.7
Kikoro(960)	24.6	46.7	88.2	109.7	100.0	30.2	21.3	59.4	67.9	120.2	135.2	53.1	866.5
Nyamweru(960)	38.2	46.8	77.7	100.8	79.4	53.6	26.4	77.0	80.7	96.9	96.2	49.2	825.9
Nyamunuka(960)	37.4	56.1	101.3	123.5	81.7	49.3	36.2	66.5	73.5	102.0	116.4	62.0	906.2
Kanyampara(990)	49.2	47.9	103.1	159.9	86.1	55.6	45.7	60.6	99.6	141.6	127.6	65.6	1042.5
Maramagambo(990)	27.9	51.4	102.8	146.1	116.1	54.8	29.7	95.6	122.6	132.9	109.3	88.0	1077.2
Mpondwe(990)	41.2	37.2	98.9	110.0	78.1	38.8	41.4	64.0	83.8	137.3	103.4	67.3	896.4
Mukorobozi(990)	37.4	64.6	123.6	153.9	145.3	57.7	29.7	88.1	129.7	137.0	112.4	75.7	1155.1
Nyamusingire(990)	44.3	65.8	106.6	135.6	117.0	67.9	31.2	104.8	133.2	146.2	142.4	72.3	1167.1
Mile 11(990)	38.6	64.2	86.6	123.8	71.4	31.4	36.7	75.0	105.2	98.3	113.7	58.0	902.9
Mean	34.3	45.1	91.4	120.2	87.0	44.7	32.0	70.8	82.9	108.4	109.2	57.0	884.3
S.d.	8.6	12.4	12.6	20.3	21.9	10.7	6.9	16.6	25.1	21.8	16.8	12.5	

is little vegetation cover to trap the water. The effects of this evaporative demand on the lives of plants and animals of the area are still to be studied.

1.3.4 Vegetation

1.3.4.1 General

The vegetation of the Park is described by Langdale-Brown (1960), Lock (1967, 1977), Field (1968) and Edroma (1975a). It consists of four main types: papyrus swamps, grassland types, wooded savannah and forests. Swampy vegetation occurs in small patches along the shorelines of the lakes and rivers. It is, however, particularly extensive along the northern and northeastern shores of Lake George (Fig.1.3). The dominant species are Cyperus papyrus, wild date or makindu palm Phoenix reclinata and the borassus palm Borassus aethiopum.

The commonest and most wide-spread plant community in the Park is the Hyparrhenia grassland (Edroma op.cit.). It is also the most important pasture community for the large mammals. In most of the grasslands H. filipendula is the dominant species with Themeda triandra as the co-dominant and the other species like Bothriochloa insculpta, Heteropogon contortus, and Chloris gayana as the major constituents (Edroma op.cit.). The majority of the grasslands are fire climax communities (Osmaston 1971, Edroma op.cit.). Closer to the banks, especially those of the Channel, due largely to heavy grazing pressure from the hippopotamus Hippopotamus amphibius, Sporobolus grassland, usually dotted with thickets or trees, begin to replace the *Hyparrhenia* grasslands. The thickets comprise largely of *Capparis tomentosa* and the trees mainly of *Euphorbia candelabrum* and *E. dawei*.

Trees were rare in the grasslands of this Park (Edroma 1975a). Stands of *Ficus* spp. and *Phoenix reclinata* swamp forest exist in the wet areas in the north; at the mouth of Nyamugasani River there is a woodland dominated by *Croton macrostachyus*; and there are almost pure stands of *Euphorbia dawei* along the northern shore of the Kazinga Channel, mid-way between Mweya and Katunguru, along the Kamulikwezi River immediately south of Kasese Town, and south of Rwenshama Fishing Village. *Acacia sieberiana*, *A. gerrardii*, *Balanites aegyptiaca*, *Ficus ficus* and *F. gnaphalocarpa* are also important components of some of the above woodlands. However, since the decline of the elephant population (section 1.3.5), there have been extensive regeneration of trees, especially *Acacia* spp., all over the Park. The formation of woodlands in areas of former grasslands, if not halted and reversed, will result in loss of habitat for strictly grassland species of mammals (e.g. topi *Damaliscus lunatus jimela* Matchie, Yoaciel & Van Orsdol 1981), the reduction of the touristic potential of the Park due to impaired visibility, and loss of diversity of habitats.

Maramagambo Forest is the largest wooded area in the Park and is contiguous with the Kalinzu Forest.

Reserve in the east (Fig.1.3). The dominant tree species is the Uganda Ironwood Cynometra alexandri. with Maesopsis eminii, Pycnanthus angolensis, Warburgia ugandensis, Diospyros abyssinica, Celtis sp. being the other component species. Along the rivers Pterygota, Pseudospondias and Treculia spp. are also common . (Osmaston 1960).

1.3.4.2 The vegetation of the main study area

Up to about 5 km from the shorelines of Lakes George and Edward, and of the Kazinga Channel, Hyparrhenia grasslands become increasingly replaced by an overgrazed mosaic Sporobolus grassland (Lock 1967, Edroma 1975a). These are due to heavy grazing pressure from the hippopotamus. Sections of shorelines are fringed by papyrus swamps and forests; in such places, e.g. north of Lake George, the grazing pressure is low.

The vegetation on both sides of the Kazinga Channel,in the main study area, consists of the overgrazed grassland type (Edroma op.cit., Lock 1967). Along the shoreline the heavy grazing pressure maintains a short grass sward of no more than 5 cm in height. This grazing prohibits the accumulation of dry grass and, consequently, fire is rare. The dominant grass species are Sporobolus pyramidalis, S. stapfianus and Microchloa kunthii which in some places occur in pure stands (Edroma op. cit.).

Close to the shores, depending on the topography, a mosaic composed of several grassland types are distinguishable. On the steep eroded slopes scattered

Cenchrus ciliaris and *Heteropogon contortus* occur as the main species. In deep gullies the vegetation becomes dense and dominated by *Cynodon dactylon*, *Panicum maximum*, *Capparis tomentosa*, *Euphorbia candelabrum* and other shrubs. In such gullies, the steep topography excludes grazing by hippopotamus, elephant *Loxodonta africana*, buffalo *Syncerus caffer* and other large herbivores. On the ridges, *Sporobolus stapfianus*, *Alternanthera pungens* and *S. pyramidalis* grasslands occur and are separated by large patches of bare ground.

In all the above grassland communities, thickets occur. They are large and numerous, and in some places, especially on steep slopes where grazing is excluded, they coalesce to form continuous stands of woody vegetation. These thickets are dominated by *Capparis tomentosa* but shrubs like *Securinega virosa*, *Terenna graveolens*, *Erythrococcus bongensis*, *Hoslundia opposita* and *Pavetta albertina* are common (Langdale-Brown *et al.* 1964, Lock 1967, Edroma 1975a).

From among the thickets, all along the shoreline, *Euphorbia candelabrum* and *E. dawei* trees are found. On the northern bank of the Channel, a relict of almost pure stand of *E. dawei* woodland occurs between Territories 20 and 40a (Fig.3.1)? The other main woody components of this woodland are *Cordia ovalis* and *Terenna graveolens*. Almost opposite the *E. dawei* woodland, on the southern shore, occurs a fringing swamp of makindu palm between Territories 49 and 54 (Fig.3.1). In gullies and other low-lying areas along both shorelines are found isolated Acacia sieberiana and Albizia sp.trees. In the main study area, the above trees, apart from the makindu palm, provide the main nesting sites for the Fish Eagle and the thickets form the main source of nest materials.

The vegetation of the region may have been considerably altered by the regular bush clearings earlier in this century in an effort to control the tsetse fly Glossina palpalis (Hale-Carpenter 1921). The shore of the Peninsula opposite Kazinga was cleared, as was that from Kazinga southward towards Lion Bay. Spinage (1970) suggested that such intensive bush clearing, rather than hippo grazing, started the sheet and gully erosion which is common along the shorelines of the region.

1.3.5 Animals in the Park

The diversity of habitats in Queen Elizabeth Park explains the diversity of animals in the area. Many species of mammals, birds, reptiles, amphibians, fishes, insects and microfauna are found. There are, for example, at least 66 species of mammals, 545 of birds (UNP 1971) and between 30 to 40 species of fishes in Lake George alone (Gwahaba 1973, Beadle 1974).

Until the mid-1970s, the Park supported one of the highest large mammal biomass in the world

(Petrides & Swank 1965, Talbot & Talbot 1963, Field 1968, Field & Laws 1970). This high biomass was largely attributable to the originally high densities of three species of mammals: the elephant Loxodonta africana africana, the hippopotamus Hippopotamus amphibius, and the buffalo Syncerus caffer. With the population declines of these and other species (Table 1.6, section 1.3.6), the biomass of the Park has been significantly reduced (G. Laker-Ojok pers. comm.). Although the Park supported a high biomass, there is a paucity of the large mammal species compared to what occur in the other parks, especially in Kidepo Valley and Murchison Falls Parks. Thus, for example, species like zebra Equus burchelli, giraffe Giraffa camelopardus, and black rhinoceros Diceros bicornis are absent. Spinage (1967a) suggested that the low species diversity may be due to the heavy human settlement in the region until recent times. When human population declined at the turn of the century (section 1.3.6), animals moved into and recolonized the vacated area. Others, such as those mentioned above, may have been excluded from the area by physical barriers like forests, large rivers or mountains. Laws et al.(1975) have argued that the paucity of grassland species of large mammals in both Murchison Falls and Queen Elizabeth Parks are largely due to the fact that much of western Uganda was once heavily wooded. After man had cleared the woodlands, grassland species of large mammals were still prevented

Table 1.6 Estimates of numbers of large mammals in Queen Elizabeth National Park.

Species	Total number Before 1980	 March 1980[7]
Buffalo	18040[1]	2037
Elephant	704[2]	150
Hippopotamus	10000[3]	4569
Kob	12500[4]	19802[8]
Topi	3100[5]	1513
Warthog	4000[4]	1135
Waterbuck	3560[6]	2095

Sources:

1. Eltringham and Woodford (1973).
2. Eltringham and Malpas (1980).
3. Eltringham (personal communication).
4. Modha and Eltringham (1976).
5. S. M. Yoaciel (personal communication).
6. Eltringham and Din (1977).
7. Douglas-Hamilton *et al*. (1980), sample count for all species except the elephant.
8. Edroma (unpubl. data) later in 1980 recorded 12840 by the total count method.

from colonizing the area because of the dense human populatior

The major species of large mammals in the Park are the elephant, the hippopotamus and the buffalo. Currently the hippopotamus Hippopotamus amphibius is the most numerous of the very large mammals. At 4,569 animals (Table 1.6), the population is only about one-third of the 14,000 animals the Park contained in the late 1950s (Bere 1959). During the 1970s the population was about 10,000 and probably fluctuated minimally. However, the number was reduced by about one-half between 1979 and 1980 (Van Orsdol 1979). Because of their restriction to the shorelines, the 14,000 hippos of the late 1950s were responsible for overgrazing which resulted in severe sheet and gully erosion along the banks. Between 1958 and 1967 about 7000 of them were culled. This considerably aided the recovery of the vegetation. During the scheme, hippos were completely eliminated from Mweya Peninsula but they have since recolonized it.

The numbers of elephants in the Park have fluctuated widely. The mean of 22 censuses between 1963 and 1971 is 2375 ± 870 animals (Malpas 1977). Numbers have substantially declined in recent years due to commercialized poaching. By March 1980, the population was as low as 150 animals (Malpas 1980, Douglas-Hamilton et al. 1980). However, because of the reduced poaching pressure since mid-1980, the population is building up again. Presently, there are at least about 900 animals in the Park, the majority of which immigrated from the neighbouring

Virunga Park, Zaire (Edroma pers.comm., P. Ssali-Naluma pers. comm.).

The buffalo Syncerus caffer is another large mammal which suffered from poaching during 1979-1980 (Van Orsdol 1979). Malpas (1980) and Douglas-Hamilton, et al. (1980) estimated the Park population at 2037 animals. During the early 1970s, Eltringham & Woodford (1973) estimated the population at about 18,000 animals and this figure apparently prevailed during the rest of the 1970s. This would indicate that between mid-1979 and mid-1980, about 90% of the buffalo population was poached. The trauma of this massacre has lingered on these animals up to the present moment.

The other large herbivores in the Park include Uganda kob Adenota kob thomasi, Defassa waterbuck Kobus defassa, bushbuck Tragelaphus scriptus, reedbuck Redunca redunca, and topi Damaliscus lunatus jimela. Topi are restricted to the part of the Park south of Maramagambo Forest. Three species of pigs are present: warthog Phacochoerus aethiopicus, the giant forest hog Hylochoerus meinertzhageni, and the African bushpig Potamochoerus porcus. The bushpig is found only in the Maramagambo Forest while the giant forest hog can be seen in the Maramagambo, the riverine forests as well as the forests on the steep walls of the craters. Sitatunga Tragelaphus spekei was seen, in the swamps of Lake George in recent years but their present status remains unknown. Four species of duikers inhabit the Park: one, the yellow-backed duiker

Sylvicarpa grimmia, lives in the grassland; and the other three, Blue duiker *Cephalophus monticola*, the red forest duiker *C. harveyi*, and *C. silvicultor*, are forest dwellers.

Several species of primates occur. Olive baboon *Papio anubis* and vervet monkey *Cercopithecus aethiops* are the most conspicuous; the former inhabits the southern bank of the Kazinga Channel but is absent on the northern side, except in the Crater Area. They are regularly found in *Euphorbia* trees, browsing the young shoots (Lock 1972a), and thereby causing a rugged appearance to trees on the south as compared with those on the northern banks of the Channel. Because of this habit, they have been suspected to prey upon the nest contents of the Fish Eagle (sections 7.4 & 8.4). Other species of primates which are restricted to the Maramagambo and riparian forests include the Chimpanzee *Pan troglodytes*, the black and white colobus monkey *Colobus guereza*, the red colobus *C. badius*, the blue monkey *Cercopithecus mitis* and the red-tailed monkey *C. ascanius*.

The lion *Panthera leo* population in the Park was estimated at 150 (Grimsdell 1969). A recent study by Van Orsdol (1981) does not give a population estimate but showed that the biomass of lions in Ishasha, at 15.45 female equivalents/pride, was about three times that of Mweya (6.2 female equivalents/pride). Leopard *Panthera pardus* is estimated to occur at a density of

0.13 animals/km^2, thus giving a total of about 250 animals for the whole Park (Myers 1976). The spotted hyaena *Crocuta crocuta* is very common but its population is largely unknown. The hunting dog *Lycaon pictus*, which was common earlier in the century, was eliminated from this Park and the last of them to be seen were shot in 1955 (Annual Reports of Uganda National Parks, 1952-1955). Other predators include the side-striped jackal *Canis adustus*, the African wild cat *Felis lybica*, and the serval *F. serval*. Viverrids include the African Civet *Civettictus civetta*, the African Palm Civet *Nandinia binotata*, the large spotted genet *Genetta tigrina*. Several species of mongooses are present: the grey mongoose *Herpestes ichneumon*, the black-tipped mongoose *H. sanguineus*, the White-tailed mongoose *Ichneumia albicauda*, the banded mongoose *Mungos mungo*, and the marsh mongoose *Atilax paludinosus*. Three species of insectivores, *Crocidula* spp. (Delany 1964), the pangolin *Manis temmiuckii*, and the ant bear *Orycteropus afer* also occur but in small numbers.

Small mammals, especially rodents are abundant. The role of these small members of the mammal community in the Park ecosystem has largely been ignored. However, Neal (1967) and Cheeseman (1975) have both demonstrated that their grazing impacts on grasslands can be as great as those of large mammals. Another common small mammal of the short and overgrazed grassland is the African Savannah Hare *Lepus crawshayi*. Its role in the ecosystem of the Park is currently under investigation.

In an area dominated by large mammals, the importance of other smaller animals tends to be overlooked. Because birds appear to be insignificant individually, the effects of their presence are not spectacularly apparent, for example, in the form of destruction to trees and over-grazing of grasslands. Nevertheless, Eltringham (1968) found that the increased population of Marabou Storks Leptoptilos crumcniferus in the 1960s led to destruction of Euphorbia dawei in and around Mweya Peninsula. Edroma (1976) reported that birds, largely weavers (Ploceidae), plucked substantial quantities of leaves of grasses, especially Cymbopogon afronardus, for the construction of their nests, and thereby significantly reduced the productivities of the affected grass species.

Birds are part of a much greater pathway for the flow of energy than are the large mammals (NUTAE, 1971). A few assessments of the role of birds in the energy flow of the Park have been made. Thus, Din (1970) found that the amount of fish consumed by White Pelicans Pelecanus onocrotalus formed 0.06% of the productivity of Lake George or approximately 7.8% of the 5 million kg of fish harvested by man in the Lake Edward/George water system in 1969. The role of the African Fish Eagle was appraised by Eltringham (1975) and has been one of the main objectives of this study (section 1.2.2 and Chapter 4). In the bushed grasslands, for every km^2, there are ca. 16,000 individuals/species of insectivorous birds. These birds, in preying largely on 'lake flies' (Chironomidae), return to the land substantial amounts of nutrients 'lost' from it to the aquatic part of the ecosystem through grazing by hippos and through sheet and gully erosion (NUTAE, 1971). Considering the high metabolic rates of such small birds relative to those of the large mammals, their consuming biomass is probably the equivalent of at least 5 to 8 buffaloes/km^2.

The appearance of much of Queen Elizabeth Park owes a lot to birds. The seeds of most of the trees and shrubs in the thickets, woodlands and forests, which are important and distinctive components of the ecosystem, are dispersed by fruit-eating birds such as barbets (Capitonidae), bulbuls (Pycnonotidae), mousebirds (Coliidae), turacos (Musophagidae), parrots (Psittacidae), and hornbills (Buccerotidae). Additionally birds, especially those feeding on nectar, are important agents of pollination.

The diversity of habitats in and around the Park is greater than that of any other Park in Africa. The habitats range from water, papyrus swamp, savannah and lowland forest in the Park itself to intermediate forest on the eastern escarpment overlooking the Park, and montane forest, heath forest and alpine moorland on the Rwenzoris. As a result of this diversity of habitats, and because the area is a transition zone between the humid lowland forest of Zaire and the dry savannahs of East Africa, the avifauna is extremely rich. Of the 744 species of birds occurring in the three oldest National Parks (Murchison Falls, Queen Elizabeth and Kidepo Valley), Queen Elizabeth Park registers 545 (73%) species, which are distributed in 65 families.

Queen Elizabeth Park is also rich in species and numbers of reptiles and amphibians, accounts of which are given by Pitman (1971). The reptiles include chamelions, lizards, snakes (both poisonous and non-poisonous), and tortoises and terrapins, while the amphibians are represented by frogs and toads. Conspicuously absent from the list of reptiles is the crocodile *Crocodilus niloticus*, which existed in the region but became extinct following volcanic erruptions some 10,000 years ago (Beadle 1974, Bishop 1970).

The fish fauna of the region is a remnant of a previously richer stock whose chequered history involved two part but catastrophic destructions (Beadle 1974). Nonetheless, there are between 32 and 40 species representing at least 11 genera and 8 families (Gwahaba 1973; Beadle, op. cit.). These are, however, predominated by the 21 species of cichlids of which only 2 species of *Tilapia* are exploited by man and none of the 17 of *Haplochromis* ever utilized. Some of the other important and harvestable fishes include the African Lungfish *Protopterus aethiopicus*, two catfishes

Clarias lazera and Bagrus docmac, the barbel Barbus altianalis, and the snoutfishes Mormyrus spp. Nile Perch Lates niloticus became locally extinct from the area during the volcanic eruptions. Although present along the Semliki River, it is being prevented from recolonizing the waters because of the presence of rapids at the exit of the above river from Lake Edward on its course to Lake Albert.

There is an abundance of both diurnal and nocturnal species of insects, each of which has an ecological role to play in the ecosystem of the Park. The termite and dung beetle are important in the mineral cycles because of their feeding on and breaking down dry vegetative matter and dung. Swarms of lake flies, large Chironomidae, which blow from the lakes in thick clouds onto the land, form important sources of food for insectivorous birds. Biting flies, especially the tsetse fly and the mosquito, are very common and are economically important because of the diseases they transmit. Of direct and great ecological significance to the plants of the Park are the butterflies and moths. Occurring in great numbers which reach outbreak proportions in some years, they are important agents of pollination. Whilst some research has been undertaken on the insect fauna of this Park, a lot still remains to be done. For example, recently Einyu (1978) described 22 new species from only two families of typhlocybine leafhoppers.

1.3.6 Human and wildlife history

The history of the area now incorporated into Queen Elizabeth Park is relatively well known (Beadle 1971, Posnansky 1971). The abundant archaeological remains indicate that the area has long been the site of human settlement. Discoveries of Middle Pleistocene hunting tools at Mweya and Katwe show that the shores of Lake Edward have been inhabited for over 50,000 years (Posnansky, op.cit.). Since about 1000 years ago, the predominantly hunting way of life had largely been replaced by a pastoral system supplemented by fishing and trading salt from Lakes Katwe and Kasenyi.

Several explorers traversed what is now the Park in the late 19th century. Stanley (1890), the first European to visit the region in 1879, noticed about 2000 huts in Katwe, and he found Mweya Peninsula had 81 huts which he described as "rich in goats and sheep." Scott Elliot (1896) passed through the area in 1889, the year Stanley returned. Both explorers testified to the material wealth of the people, particularly their large numbers of cattle.

Travelling from Kichwamba to the Kazinga Channel in 1891, Lugard (1893) noticed that the "great lake plain" was empty. Both Lugard and Scott Elliot (op.cit.) described the catastrophy which befell the region; and Lugard wrote "The great lake plain spread out before us must have swarmed at one time with elephants and buffaloes for their tracks were everywhere;but the former had left and the latter were dead." He described the plain as "good pasture, no fuel or timber, no villages." The good pasture must have resulted from the reduced grazing pressure for he remarked "animals had left and ---- dead; ---- few waterbucks ------" and "------ deserted villages surrounded by hedges of cactus ------." Perhaps the present abundance and distribution of Euphorbia candelabrum in the Park is evidence for human occupation of the area (Aerni 1970) and that the trees probably originated and spread from these settlements.

The depopulation of man in this region between 1889 and 1891 is attributed to an epidemic of smallpox (Posnansky 1971) and to rinderpest killing off their cattle. Lugard (op.cit.) suspected rinderpest originated from Italy, a theory which is still accepted (Ford 1971).

The high cattle mortality precipitated a famine among the pastoralists. Weakened by famine, the population easily succumbed to the continuing scourge of smallpox and to a newly detected disease, trypanosomiasis (sleeping sickness). Although sleeping sickness was first thought to have entered Uganda from the Semliki Valley in Zaire with the Stanley expedition of 1879, it probably was present around the Lake Edward shores earlier because of the salt trade which had been going on with Zaire (Morris 1960). Because of the movements of fishermen and salt traders, control of the disease was difficult. During 1910-12 a severe outbreak occurred, reaching as far as the western and eastern shorelines of Lake George. Extensive bush clearing was undertaken around Katwe, Kazinga, Mweya, Katunguru, Kayanja and Mpondwe in an effort to prevent a recurrence of the disease (Hale-Carpenter 1921). In addition, between 1913-14, the authorities partially evacuated Lake Katwe, leaving only a few people to maintain the salt and fishing industries.

In 1919, a second and virulent rinderpest epidemic struck the area, resulting in heavy losses of both cattle and wildlife. And despite concerted efforts to control sleeping sickness, the disease was on the increase.

These precipitated a second evacuation, in 1924, during which all but a few people remained only in Katwe and Katunguru villages.

By 1931 wildlife had repopulated the region and were once again roaming in large numbers (Worthington & Worthington 1933, Temple-Perkins 1965). The area was gazetted a game reserve in 1934. In 1952, when the area became a park, the wildlife populations were high; and under the new conservation status which stopped hunting, the populations increased rapidly. Under the new set-up, cultivation and cattle ranching were prohibited but the few people permitted to remain in the numerous villages to carry on with salt-mining and fishing were allowed to keep goats and sheep.

Since the late 1920s, only one epidemic, of blue-tongue (malarial catarrhal fever), occurred in the park in 1961. It only affected the topi population in

Ishasha, but little was known about its effects on their numbers. Of the other wildlife diseases which occur in the Park, bovine tuberculosis deserves mention. It is endemic north of Maramagambo Forest where associations between wild and domestic bovids were frequent in the past.

In the last decade, the large mammal populations of the Park suffered two human-induced declines (Edroma 1975b), The first, involving the elephant, was reported by Eltringham & Malpas (1980). The second affected the hippo, buffalo and topi populations during and immediately after the 1979 war of liberation of Uganda, and has been reported fully by Van Orsdol (1979), Malpas (1980) and Douglas-Hamilton _et al_. (1980).

Human interests have been and still remain high in this region and, consequently, pose significant threats to the continued survival of the Park. There are currently 11 fishing villages within the Park. Most of them were present when the Park was established and were permitted to remain. All of them have increased in size, well beyond their stipulated limits. This undue expansion increases the demand for land and firewood. Their livestock, presently including cattle as well, which enter the Park to graze accelerate habitat destruction (Field 1968,Musoke 1980). The domestic stock may also act as reservoirs for diseases (Woodford 1972). The villages are sources of poachers and markets for their illegally acquired meat and trophies' (Eltringham & Malpas, op.cit.). Two of these villages, Muhokya and Kahendero (Fig. 1.3), at their current rates of expansion, threaten to cut the Park into two in the very near future.

Industrialisation is another significant threat to the survival of the Park. The threat of chemical pollution, especially from Kilembe Mines, to the Park and the surrounding area is real and potentially dangerous (Edroma 1974b , c & In press). Yet, now a giant salt factory stands right inside the Park. The factory will substantially increase the population of Lake Katwe as well as the effects of illegal human activities in the surrounding. The pollution effects of this factory are potentially great and remain to be seen once it becomes operational.

Whilst some form of human habitation and industrialisation are essential for the continued exploitation of the fisheries and mineral wealth of the area, the present situation seriously undermines the survival of Queen Elizabeth National Park and, therefore, ought to be a matter of concern for the conservation ethics that the country presently upholds.

CHAPTER 2

POPULATION DISTRIBUTION AND STRUCTURE

2.1 INTRODUCTION

This Chapter presents data on population distribution and structure of the Fish Eagle in Queen Elizabeth Park. The effects of the differences in vegetation cover, gradient and human disturbance along the shorelines of water bodies on the distribution and density patterns of the adult birds are examined. From data on population structures, the adult and total life expectations in the species are estimated.

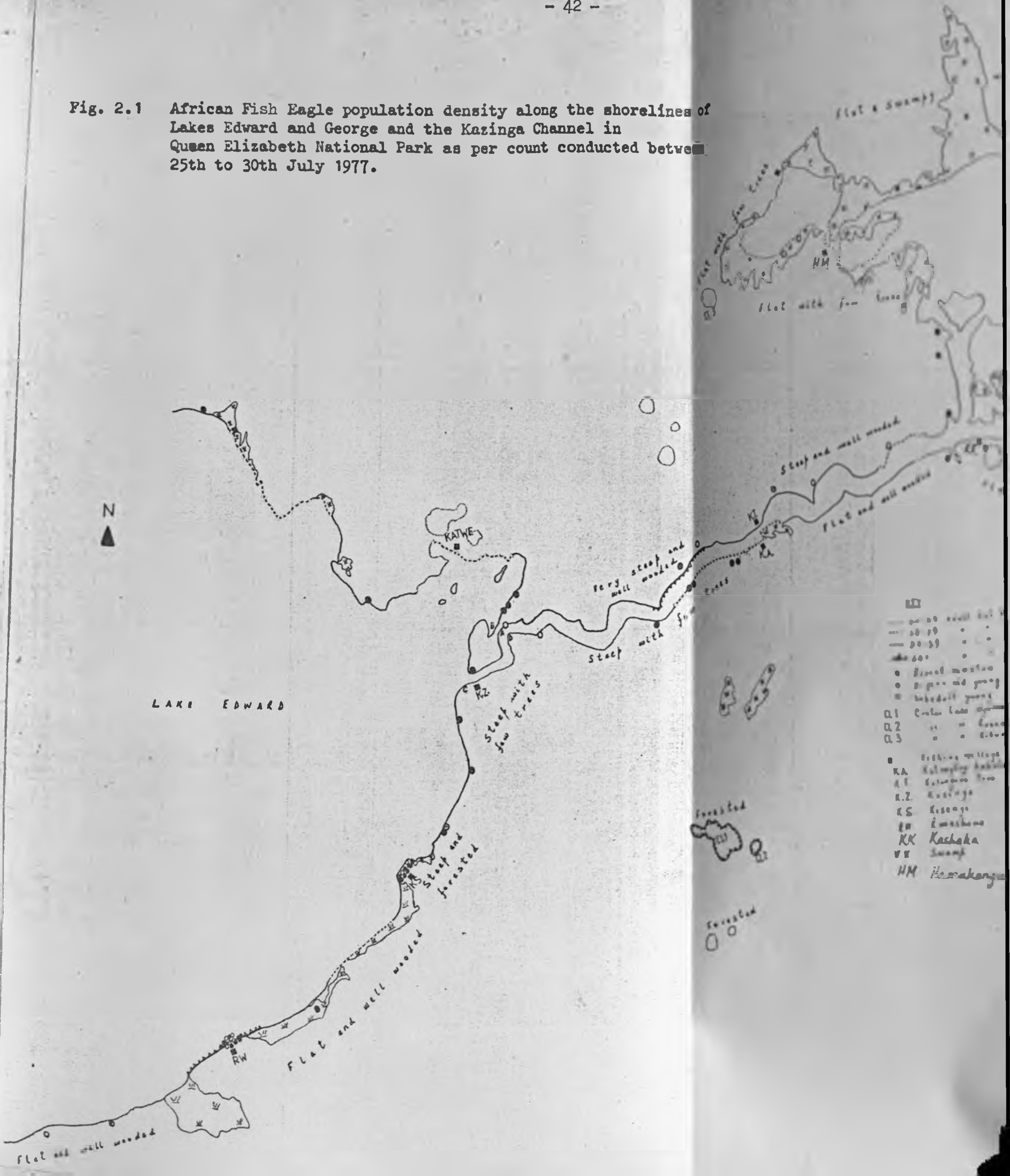
2.2 MATERIALS AND METHODS

2.2.1 Measurement of population parameters

To find out the total number of Fish Eagles present along the shorelines of all the major water systems in the Park (Fig.2.1), a survey of Lakes Edward and George, Kazinga Channel and Crater Lakes Nyamusingire, Kasanduka and Kikorongo was conducted. Lakes Edward and George, the Channel and Crater Lake Kikorongo were surveyed between 25-30 July 1977. Birds on Lakes Nyamusingire and Kasanduka were counted on 12 August 1977.

Fish Eagles were counted from a canoe powered by a 25 hp outboard motor. The boat, steered by an assistant, cruised at about 10 kmph and at between 20-30 m from the shoreline. If, for any reason, prolonged viewing was needed the boat was stopped. In the study area counts were made between the entry of the Kazinga Channel into Lake Edward and Katunguru Fishing Village, 25 km upstream (Fig.2.1). Eagles were also counted along the shoreline of Lake Edward bordering Mweya Peninsula to a point at the neck of the Peninsula. This area was occupied by Fish Eagle Pairs No.82-86 commonly referred to in various Chapters. Pair No.7 also had part of its territory stretching along this shoreline (Fig.3.1). Each shore was counted separately, the northern bank being covered first.

Fig. 2.1 African Fish Eagle population density along the shorelines of Lakes Edward and George and the Kazinga Channel in Queen Elizabeth National Park as per count conducted betwe 25th to 30th July 1977.



Counts in and around Mweya Peninsula were carried out along the 9 km shoreline of the Peninsula between points A and B, and 5 km shoreline on the southern bank of the Channel between points C and D (see Fig. 2.1). Being an area with high human influence, data on population density and structure from this area were collected with the aim of comparing them with those of birds in the main study area.

All Fish Eagles, including young of the various age classes, were recorded and their positions entered on maps. Sketch maps were used during counts in the main study area. During the park-wide count, however, a map with a scale of 1:50,000 was used. During the latter count the shorelines were divided into 5 km sections in order to ease counting and correct entry of birds seen. Details of whether adults and young were present in pairs, singly or in bands were also included. From these counts, the densities of both adults and young were calculated. The population structure of birds was determined using the ageing method divised by Brown & Cade (1972). I had been thoroughly briefed by Brown on the applicability of this method to Fish Eagle population studies before the commencement of this research programme. Greenspan & Torre-Bueno (2971), without the aid of the above method, successfully aged adult, subadult and juvenile birds in this Park. Eltringham (1975) used this method but, apparently, lumped all young into the juvenile age class. Brown & Hopcraft (1973) expanded the method by separating the subadult class into 2 sub-classes of early and late subadults. In this study, for ease of identification of the birds, the 2 classes were treated as one --- the subadult class. The percentages of subadults were used to calculate the bird's adult lifespan according to the following formula suggested by A.W. Diamond (pers. comm.):

$s = \frac{2 - m}{2m}$, where s = adult lifespan in years,

m = mortality out of 100 adults.

2.2.2 Habitat preference by adults

As population and breeding surveys progressed it was realised that adult birds were more common along certain sections of shorelines of the Channel than in others. To find out the causes of these uneven population distributions, both the northern and southern banks of the Channel were divided into a) 3 classes according to gradient: very steep, steep, and flat; b) 4 classes according to vegetation cover: forested, well-wooded, few trees, and treeless zones; and c) 5 classes of combinations of gradient and their vegetation cover: very steep and forested, very steep and well-wooded, flat and well-wooded, steep and almost treeless, and flat and almost treeless. All territories occurring within each of the above classes of shoreline features were recorded. The distances covered by the respective classes were measured. From these data the percentages of total shoreline length covered by territories occurring in each class were calculated. From the percentages obtained, the preference shown by Fish Eagles for each shoreline feature was calculated according to the method suggested by A.W. Diamond (pers. comm.):

$$\text{Preference Index} = \frac{\%\text{ of territories occurring in a habitat feature}}{\%\text{ of shoreline covered by that habitat feature}}$$

Preference index of 1.0 indicates no choice by Fish Eagles, an index of less than 1.0 shows avoidance, and that of more than 1.0 demonstrates that the birds preferred that habitat feature or combination of features.

During the park-wide count, however, the Eagle's choice for shoreline type was not determined by use of preference index. Rather it was determined by the differences in the densities of birds along the 5 km sections of the shorelines (section 2.2.1).

2.3 RESULTS

2.3.1 Habitat preference by adults

The Fish Eagle population distribution patterns in the Park (Fig.2.1) show that the birds were more abundant along shorelines backed by high and well-wooded ground than along those that were low-lying, had few trees and were fringed by swamps. In the study area, the birds showed no clear preferences for gradient although flat ground was clearly avoided (Table 2.1). Adults strongly favoured forested shorelines, well-wooded ones were slightly preferred, and those that had few trees and were treeless were avoided (Table 2.2). Very steep and forested shorelines were very highly favoured while flat and treeless ones were clearly avoided (Table 2.3). Steep and well-wooded, flat and well-wooded, and steep and almost treeless banks had no clear preferences shown for them. Other habitat factors like water depth, turbulence and turbidity, and the distribution of fish in the Channel were not measured. The influences of these factors on the distribution patterns of the birds in the study area, and indeed in the whole Park, therefore, remain to be studied.

2.3.2 Distribution and density patterns in the Park

Only one park-wide Fish Eagle survey was conducted during this study. The results indicate that the birds occur along the shorelines of all the fresh water bodies in the Park but were distributed at different population densities (Fig.2.1 & Table 2.4). The crater lakes had the highest densities, L. Edward and the Channel intermediate densities, while L. George and islands had the least densities of adult birds. Overall, there were 2.5 adults/km and 0.4 young/km of shoreline. The coefficients of variations indicate how widely the densities of both adult and young birds varied along the shorelines.

Table 2.5 clearly shows that Crater Lakes Nyamusingire and Kasanduka, in Maramagambo Forest (Fig.2.1), attracted far higher numbers of adult Fish Eagles than Crater Lake Kikorongo. Although slightly smaller than L. Kikorongo, L. Kasanduka had 9 times the number of adults/km than the former. This was most probably because the banks of L. Kasanduka is thickly forested while that of L. Kikorongo is poorly-wooded. Thus almost solely because their shorelines are forested, Lakes Nyamusingire and Kasanduka attracted the highest numbers of adult birds in the whole Park.

Table 2.1 The preference indices of territorial Fish Eagles for terrain in the study area along the shorelines of the Kazinga Channel, Queen Elizabeth Park. Preference index defined in text. Note that gradients along the shoreline were subjectively measured and, therefore, do not provide rigorous assessment of the preference indices.

Gradient along shoreline	Shoreline length (km)	Shoreline %	Territories No.	Territories %	Preference index
Very steep	24.60	44.8	42	48.8	1.09
Steep	17.05	31.1	28	32.6	1.05
Flat	13.20	24.1	16	18.6	0.77
Total	54.85	100.0	86	100.0	

Table 2.2 The preference indices of territorial Fish Eagles in relation to the abundance of trees in the study area, Kazinga Channel, Queen Elizabeth Park. Note that tree abundance was estimated subjectively and, therefore, does not provide a rigorous assessment of a preference index.

Nature of Shoreline	Shoreline length (km)	Shoreline %	Territories No.	Territories %	Preference index
Forest	11.40	20.8	23	26.7	1.28
Well-wooded	14.75	26.9	25	29.1	1.08
Few trees	21.70	39.6	29	33.7	0.85
Treeless	7.00	12.8	9	10.5	0.82
Total	54.85	100.1	86	100.0	

Table 2.3 The preference indices of territorial African Fish Eagles in Queen Elizabeth National Park for combinations of terrain and vegetation cover in the study area along the shores of Kazinga Channel. Note that both gradient and vegetation cover were subjectively estimated and, therefore, do not provide rigorous assessment of the preference indices.

Nature of shoreline	Shoreline length (km)	Shoreline %	Territories No.	Territories %	Preference index
Very steep & forested	9.50	17.3	20	23.3	1.35
Steep & well-wooded	12.75	23.2	19	22.1	0.95
Flat & well-wooded	6.90	12.6	11	12.8	1.02
Steep & almost treeless	16.50	30.1	25	29.1	0.97
Flat & almost treeless	9.20	16.8	11	12.8	0.76
Total	54.85	100.0	86	100.1	

Table 2.4 Population densities of the Fish Eagle in Queen Elizabeth Park. Ind. young = Independent young, N = number of 5km sections of shorelines.

			No. of Fish Eagles			No. of birds/km		
Water body	Length (km)	N	Adult	Ind. young	All young	Adults	Ind. young	All young
Kazinga Ch.	83.6	18	204	6	15	2.35±1.05	0.07±0.10	0.17±0.16
L. Edward	86.3	18	225	25	36	2.64±1.04	0.28±0.72	0.40±0.76
L. George	112.7	24	109	8	10	0.99±0.80	0.07±0.13	0.88±0.13
Islands	42.0		53	2	2	1.26	0.05	0.05
Craters	17.2		92	1	6	5.35	0.06	0.35
Total	341.8		683	42	69			
Mean ± S.d.						2.52±1.73	0.11±0.10	0.21±0.16

Table 2.5 Population densities of adult and young Fish Eagles along the shorelines of crater lakes in Queen Elizabeth Park.

		Number of birds			Birds/km		
Crater lake	length (km)	adults	young	total	adult	young	all
Nyamusingire	11.0	77	6	83	7.00	0.55	7.55
Kasanduka	2.6	13	0	13	5.00	0.00	5.00
Kikorongo	3.6	2	0	2	0.56	0.00	0.56
Total	17.2	92	6	98			
Mean					5.35	0.35	5.70

Of the main water bodies, L. Edward had the highest density of adults, Kazinga Channel was intermediate, and L. George the least (Table 2.4). L. Edward had a significantly higher density than that of the Channel ($t = 78.378$, $df = 34$, $P < 0.001$, Table 2.4), and than that of L. George ($t = 51.887$, $df = 40$, $P < 0.001$, Table 2.4). The Channel had a density significantly higher than that of L. George ($t = 39.193$, $df = 40$, $P < 0.001$, Table 2.4). The differences in the densities along the shorelines of these water bodies were due largely to differences in the vegetation covers along their banks. Of them all, L. Edward has the best wooded shorelines and L. George the least wooded banks.

Probably due to habitat preferences (section 2.3.1), the flat, poorly-wooded, and extensively swampy northern and western shorelines of L. George had significantly fewer adult Eagles than did the steep, well-wooded, and non-swampy southern and eastern bank (Table 2.6). Similarly, the better wooded southern bank of L. Edward had a higher density of birds than the poorly wooded north (Table 2.6). The negative effect the swamp fringes along the southern shoreline would have had on the density of birds was probably offset by the presence of a forested and well-wooded hinterland (Fig.2.1)

The distribution and density patterns of adult birds were not affected by the presence of fishing villages (Table 2.7). Water turbidity, waviness and depth, and the distributions and densities of fishes in the water bodies were not measured. Their influences on the distribution and density patterns of the Eagle in the Park could not, therefore, be assessed.

The densities of both the independent and all age classes of young along the shorelines of the water bodies were extremely low and highly variable (Table 2.4). Lake Edward had a higher density of independent young than L. George ($t = 3.043$, $df = 40$, $P < 0.01$, Table 2.4) and than the Channel ($t = 2.341$, $df = 34$, $P < 0.05$, Table 2.4). The Channel and L. George, however, had similar overall densities of independent young. Data from the 5 km sections

Table 2.6 Population densities of adult Fish Eagles along the shorelines of Lakes George and Edward (islands excluded) and the Kazinga Channel, Queen Elizabeth Park. N = Number of 5km sections of shorelines.

Shorelines compared	Shoreline length (km)	N	Total adults	Adult bird/km range	Adult bird/km Mean ± S.d.	t-value
L. George						
North & West	78	16	58	0.0-2.7	0.79±0.66	57.143***
South & East	35	7	51	0.2-3.2	1.43±0.96	
L. Edward						
North	44	9	95	0.4-3.4	2.16±1.08	6.482***
South	42	9	130	1.8-4.0	3.12±0.78	
The Channel						
North	42	9	122	0.0-4.6	2.67±1.30	1.952NS
South	42	9	84	0.8-2.6	2.02±0.66	

Table 2.7 Population densities of adult Fish Eagles in relation to the presence or absence of fishing villages along the shorelines of the main water bodies in Queen Elizabeth Park. N = Number of 5km sections of shorelines.

Nature of shoreline	Length (km)	N	Total adults	Number of birds/km range	Number of birds/km Mean ± S.d.	t-value
Inhabited	67	14	124	0.0-3.8	1.87 ± 1.22	0.207NS
Uninhabited	215	45	416	0.0-4.8	1.92 ± 1.21	

of shorelines (Table 2.4) indicate that the densities of adults and independent young are significantly correlated ($r = 0.291$, df = 58, $P < 0.05$). This result, therefore, shows that independent young did not necessarily avoid shorelines with high densities of adult birds. Their distribution was, however, not even; on L. Edward they notably clumped on the southern shoreline at Rwenshama and Kisenyi Fishing Villages, and on L. George they were attracted to Kashaka and Hamukungu Fishing Villages (Fig.2.1).

2.3.3 Density in the study area

There were 35 surveys in the main study area and 21 additional ones in the Mweya Peninsula area. The results of counts in the main study area are presented in Table 2.8 a–c. The percent covariations (C.V.s) indicate how little adult Fish Eagle numbers and their densities fluctuated around the mean values. However, during all years of study the northern shoreline had significantly more birds/km than the southern bank ($t = 16.48$, df = 14; $t = 571.43$, df = 28; and $t = 52.00$, df = 22; $P < 0.001$ for the years 1975/6, 1976/7 & 1977/8 respectively). The apparent increase in densities along both shorelines with the progress of the study was not an actual increase in the population of the territorial birds (section 12.3.6); rather it was largely due to an improvement in detecting birds resting in shades of trees with thick foliage during hot periods of the day. A further evidence that the increase in the population was not real is the fact that during none of the surveys was the full compliment of territorial birds ever realised along any of the shorelines (see Table 2.8). The probable reason for the northern bank having a higher density than the southern one is because it is better wooded than the southern bank.

Table 2.9a–c demonstrate how low and highly variable the densities of young were in the study area. Furthermore, the results indicate that, throughout the study period, the northern shoreline had significantly higher densities of young than the southern shoreline ($t = 9.756$, df = 14 for 1975/6; $t = 20.00$, df = 28 for 1976/7; and $t = 62.50$, df = 22 for 1977/8; $P < 0.001$ in each case).

Table 2.8 (a) Population density of adult Fish Eagles in the main study area in Queen Elizabeth Park, April 1975 - March 1976. NS = northern shoreline of Kazinga Channel including 5.0 km shoreline of L. Edward surrounding Mweya Peninsula, total distance = 30km; SS = 25km southern shoreline of the Channel. During 1975/6, NS had a maximum of 100 territorial birds while SS had 72 of them.

Date of count	Number of adults			Adults/km		
	NS	SS	Total	NS	SS	Mean
5.6.75	75	53	128	2.5	2.1	2.3
19.6.75	84	58	142	2.8	2.3	2.6
18.7.75	88	67	155	2.9	2.7	2.8
4.8.75	92	63	155	3.1	2.5	2.8
18.8.75	86	59	145	2.9	2.4	2.6
5.9.75	63	62	125	2.1	2.5	2.3
16.9.75	80	64	144	2.7	2.6	2.6
3.10.75	88	59	147	2.9	2.4	2.8
Total	656	485	1141			
Mean	82.0	60.6	142.6	2.74	2.44	2.6
±S.d.	9.3	4.3	11.1	0.31	0.18	0.21
% C.V.	11.3	7.1	7.7	11.3	7.4	8.1

Table 2.8 (b) Population density of adult Fish Eagles in the main study area in Queen Elizabeth Park, April 1976 - March 1977. Abbreviations and distances as in Table 2.8a. During 1976/7 NS had a maximum of 102 territorial birds while SS had 74 of them.

Date of count	Number of adults			Adults/km		
	NS	SS	Total	NS	SS	Mean
26.4.76	92	64	156	3.1	2.6	2.8
14.6.76	93	63	156	3.1	2.5	2.8
26.8.76	98	59	157	3.3	2.4	2.9
5.9.76	89	62	151	3.0	2.5	2.7
24.9.76	78	62	140	2.6	2.5	2.5
30.9.76	95	70	165	3.2	2.8	3.0
5.10.76	86	72	158	2.9	2.9	2.9
28.10.76	90	70	160	3.0	2.8	2.9
15.11.76	93	67	160	3.1	2.7	2.9
14.12.76	88	67	155	2.9	2.7	2.8
28.12.76	90	66	156	3.0	2.6	2.8
24.1.77	97	68	165	3.2	2.7	3.0
8.2.77	95	72	167	3.2	2.9	3.0
25.2.77	87	63	150	2.9	2.5	2.7
15.3.77	88	61	149	2.9	2.4	2.7
Total	1359	986	2345			
Mean	90.6	65.7	156.3	3.03	2.63	2.83
±S.d.	5.1	4.1	7.0	0.18	0.17	0.14
% C.V.	5.6	6.2	4.5	5.9	6.5	4.9

Table 2.8 (c) Population density of adult Fish Eagles in the main study area in Queen Elizabeth Park, April 1977 - March 1978. Abbreviations and distances as in Table 2.8a. During 1977/8, NS had a maximum of 102 territorial birds while SS had 70 of them.

Date of count	Number of adults			Adults/km		
	NS	SS	Total	NS	SS	Mean
7.4.77	91	62	153	3.0	2.5	2.8
29.4.77	92	71	163	3.1	2.8	3.0
10.5.77	89	66	155	3.0	2.6	2.8
13.6.77	95	64	159	3.2	2.6	2.9
30.6.77	93	56	149	3.1	2.2	2.7
16.8.77	92	67	159	3.1	2.7	2.9
30.8.77	91	69	160	3.0	2.8	2.9
7.10.77	94	68	162	3.1	2.7	2.9
19.10.77	95	69	164	3.2	2.8	3.0
27.10.77	91	70	161	3.0	2.8	2.9
8.11.77	91	74	165	3.0	3.0	3.0
29.12.77	97	69	166	3.2	2.8	3.0
Total	1111	805	1916			
Mean	92.6	67.1	159.7	3.08	2.69	2.9
±S.d.	2.3	4.7	5.1	0.08	0.20	0.1
% C.V.	2.5	7.0	3.2	2.6	7.4	3.4

Table 2.9 (a) Population density of young Fish Eagles in the main study area in Queen Elizabeth Park, April 1975 - March 1976. Abbreviations and distances as in Table 2.8a.

Date of count	Number of young			Birds/km		
	NS	SS	Total	NS	SS	Mean
5.6.75	5	1	6	0.17	0.04	0.11
19.6.75	9	2	11	0.30	0.08	0.20
18.7.75	6	5	11	0.20	0.20	0.20
4.8.75	3	1	4	0.10	0.04	0.07
18.8.75	0	1	1	0.00	0.04	0.02
5.9.75	0	0	0	0.00	0.00	0.00
16.9.75	0	2	2	0.00	0.08	0.04
3.10.75	1	4	5	0.03	0.16	0.09
Total	24	16	40			
Mean	3.00	2.00	5.00	0.10	0.08	0.11
±S.d.	3.38	1.69	4.21	0.11	0.07	0.08
% C.V.	112.7	84.5	84.2	110.0	87.5	72.7

Table 2.9 (b) Population density of young Fish Eagles in the main area in Queen Elizabeth Park, April 1976 - March 1977. Abbreviations and distances as in Table 2.8a.

Date of count	Number of young			Birds/km		
	NS	SS	Total	NS	SS	Mean
26.4.76	17	2	19	0.57	0.08	0.35
14.6.76	2	3	5	0.07	0.12	0.09
26.8.76	2	0	2	0.07	0.00	0.4
5.9.76	0	0	0	0.00	0.00	0.00
24.9.76	0	2	2	0.00	0.08	0.04
30.9.76	0	0	0	0.00	0.00	0.00
5.10.76	0	0	0	0.00	0.00	0.00
28.10.76	3	0	3	0.10	0.00	0.05
15.11.76	3	6	9	0.10	0.24	0.16
14.12.76	6	1	7	0.20	0.04	0.13
28.12.76	11	0	11	0.37	0.00	0.20
24.1.77	19	0	19	0.63	0.00	0.35
8.2.77	14	0	14	0.47	0.00	0.25
25.2.77	11	2	13	0.37	0.08	0.24
15.3.77	5	0	5	0.17	0.00	0.09
Total	93	16	109			
Mean	6.2	1.07	7.27	0.21	0.04	0.13
±S.d.	6.54	1.71	6.62	0.22	0.07	0.12
%C.V.	105.5	159.8	91.1	104.8	175.0	92.3

Table 2.9 (c) Population density of young Fish Eagles in the main study area in Queen Elizabeth Park, April 1977 - March 1978. Abbreviations and distances as in Table 2.8a.

Date of count	Number of young			Birds/km		
	NS	SS	Total	NS	SS	Mean
7.4.77	9	3	12	0.30	0.12	0.22
29.4.77	9	5	14	0.30	0.20	0.25
10.5.77	4	0	4	0.13	0.00	0.07
13.6.77	4	3	7	0.13	0.12	0.13
30.6.77	4	6	10	0.13	0.24	0.18
16.8.77	4	4	8	0.13	0.16	0.15
30.8.77	3	5	8	0.10	0.20	0.15
7.10.77	3	2	5	0.10	0.08	0.09
19.10.77	6	1	7	0.20	0.04	0.13
27.10.77	4	7	11	0.13	0.28	0.20
8.11.77	3	0	3	0.10	0.00	0.05
29.12.77	8	0	8	0.27	0.00	0.15
Total	61	36	97			
Mean	5.08	3.0	8.08	0.17	0.12	0.15
±S.d.	2.31	2.45	3.26	0.08	0.10	0.06
% C.V.	45.5	81.7	40.3	47.1	83.3	40.0

A comparison of the density of independent young in the main study area with that of Mweya Peninsula indicates that the study area had significantly fewer birds than the Mweya area (Table 2,10). The scavenging opportunities at Kazinga Fishing Village and in Mweya probably resulted in more of these birds being encountered in the Mweya area refer (section 2.3.2 above).

2.3.4 Population structure and longevity

During the whole Park survey, adult Fish Eagles made up 90.8% of the 752 birds encountered, subadults 2.5%, 2-year olds 3.1% and recent immatures 3.6% (Table 2.11). The numbers of adults and young differed significantly from shore to shore (Table 2.12) indicating that both were not evenly distributed along the various banks (Fig.2.1). Table 2.12 (also Fig.2.1) clearly indicates that the southern bank of L. Edward had all age classes of young while the northern had only the young of the year; northern Kazinga Channel had all age classes of young while the southern bank had largely recent immatures. It is interesting to note that the tiny L. Edward Islands and the small Crater Lakes Kasanduka and Kikorongo had no young at all. Perhaps because of their small sizes any young that visited them were probably quickly detected and evicted by the resident adults. Crater L. Nyamusingire, on the other hand, had largely the young of the year. The distribution and density patterns of the birds have, however, already been discussed (section 2.3.2). This section discusses the population structure of the birds.

Since bereaved adult Fish Eagles recruit replacements from the subadult segment of the population, this portion effectively represents the adult mortality experienced by the population. According to the 2.5% subadults in the Park population (Tables 2.11 & 2.12), the Eagle would have to live for 39.5 years as an adult in order to replace itself. Since it takes 4 years for a young to become adult (Brown & Cade 1972), the bird would therefore, have a total lifespan of 43.5 years. A reasonably good adult longevity estimate

Table 2.10 Population densities of independent young Fish Eagles in the main study area and Mweya Peninsula.

Area	Shoreline length(km)	No. of counts	Total young resighted	Numbers of young/km	t-value
Mweya	14	21	21	0.07±0.12	16.67***
Study area	55	35	73	0.04±0.04	

Table 2.11 African Fish Eagle population structure in Queen Elizabeth Park during the park-wide survey, July - August 1977.

Area	Length (km)	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
						Eagles	Young	Adults	Young
Kazinga Ch.	83.6	204	5	1	9	219	15	93.2	6.8
L. Edward	86.3	225	9	16	11	261	36	86.2	13.8
L. George	112.7	109	3	5	2	119	10	91.6	8.4
Islands	42.0	53	1	1	0	55	2	96.4	3.6
Craters	17.2	92	1	0	5	98	6	93.9	6.1
Total	341.8	683	19	23	27	752	69		
% age classes		90.8	2.5	3.1	3.6			90.8	9.2

Table 2.12 African Fish Eagle population structures along various shorelines in Queen Elizabeth Park during the park-wide survey, July - August 1977.

Area	Shoreline (length,km)	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
						Adults	young	Adults	young
Kazinga Channel	North (41.8)	120	4	1	3	120	8	93.7	6.3
	South (41.8)	84	1	0	6	84	7	92.3	7.7
Lake Edward	North (44.0)	95	0	0	5	95	5	95.0	5.0
	South (42.3)	130	9	16	6	130	31	80.7	19.3
	Islands (4.0)	8	0	0	0	8	0	100.0	0.0
Lake George	North (78.0)	58	2	2	2	58	6	90.9	9.1
	South (34.7)	51	1	3	0	51	4	92.7	7.3
	Islands (38.0)	45	1	1	0	45	2	95.6	4.4
Crater Lakes	Nyamusigire (11.0)	77	1	0	5	77	6	92.8	7.2
	Kasanduka (2.6)	13	0	0	0	13	0	100.0	0.0
	Kikorongo (3.6)	2	0	0	0	2	0	100.0	0.0
Total	(341.8)	683	19	23	27	683	69		
% age classes		90.8	2.5	3.1	3.6	X^2=27.409*		90.8	9.2

of 17.4 years, 21.4 years total lifespan, is obtained when the population structure along the southern shoreline of L. Edward is used (Table 2.12).

In the main study area, the results of the population structures revealed very low numbers of young with extremely high covariations around the means (Tables 2.13a-c). During the 1975/76 period subadults averaged only 1.1% of the total birds resighted. This figure gives a very low mortality rate in the Eagle and, consequently, an unlikely adult lifespan of 90.4 years and a total longevity of 94.4 years. In 1976/7 the subadults averaged only 0.5% and this figure gives the improbable adult lifespan of 199.5 years and total life of 203.5 years. The 0.6% subadult proportion in the population of 1977/8 gives the bird the unlikely adult lifespan of 166 years and a total longevity of 170 years.

In the Mweya Peninsula area the percentages of subadults were still low (Table 2.14a-c). Only the 3.8% (1975/6) and 2.9% (1977/8) subadult proportions give the Fish Eagle the reasonable adult lives of 26 and 34 years respectively. These figures would result in longevities of 30 and 38 years respectively.

The whole park survey, the 35 counts in the main study area and the 21 counts in the Peninsula area gave a total of 6927 bird encounters. Of these, 6547 (94.5%) were adults, 69(1.0%) were subadults, 67(1.0%) were 2-year olds, and 244 (3.5%) were recent immatures. The 1.0% subadult proportion in this population would give the Fish Eagle the improbable adult lifespan of 99.5 years and a longevity of 103.5 years. Using the best estimates of population structures obtained during this study, the African Fish Eagle in this Park probably has to live for about 30 years as an adult, 34 years in total, in order to replace itself (Table 2.15).

2.4 DISCUSSION

In all areas where it has been studied, the African Fish Eagle shows distribution patterns which are closely related to the habitat features along the banks of the water bodies. It prefers well-wooded and steep banks to

Table 2.13 (a) African Fish Eagle population structure in the main study area in Queen Elizabeth Park, April 1975 - March 1976.

Date of count	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
					Eagles	Young	Adults	Young
5.6.75	128	5	1	0	134	6	95.5	4.5
19.6.75	141	4	2	5	152	11	92.8	7.2
18.7.75	154	2	4	5	165	11	93.3	6.7
4.8.75	155	0	1	3	159	4	97.5	2.5
18.8.75	144	1	0	0	145	1	99.3	0.7
5.9.75	125	0	0	0	125	0	100.0	0.0
16.9.75	144	0	0	2	146	2	98.6	1.4
3.10.75	143	1	0	4	148	5	96.6	3.4
Total	1134	13	8	19	1174	40		
Mean	141.8	1.6	1.0	2.4	146.8	5.0		
±S.d.	10.7	1.9	1.4	2.2	12.8	4.2		
%C.V.	7.5	118.8	140.0	91.7	8.7	84.0		
% age classes	96.6	1.1	0.7	1.6			96.6	3.4

Table 2.13 (b) African Fish Eagle population structure in the main study area in Queen Elizabeth Park, April 1976 - March 1977.

Date of count	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
					Eagles	Young	Eagles	Young
26.4.76	154	0	0	19	173	19	89.0	11.0
14.6.76	156	2	0	3	161	5	96.9	3.1
26.8.76	157	1	0	1	159	2	98.7	1.3
5.9.76	151	0	0	0	151	0	100.0	0.0
24.9.76	140	2	0	0	142	2	98.6	1.4
30.9.76	165	0	0	0	165	0	100.0	0.0
5.10.76	158	0	0	0	158	0	100.0	0.0
28.10.76	160	0	0	3	163	3	98.2	1.8
15.11.76	160	2	3	4	169	9	94.7	5.3
14.12.76	155	0	1	6	162	7	95.7	4.3
28.12.76	156	2	0	9	167	11	93.4	6.6
24.1.77	165	2	0	17	184	19	89.7	10.3
8.2.77	167	0	0	14	181	14	92.3	7.7
25.2.77	150	1	2	10	163	13	92.0	8.0
15.3.77	149	0	0	5	154	5	96.8	3.2
Total	2343	12	6	91	2452	109		
Mean ±S.d.	156.2 7.0	0.8 0.9	0.4 0.9	6.1 6.4	163.5 10.8	7.3 6.6		
%C.V.	4.5	112.5	225.0	104.9	6.6	90.4		
% age classes	95.6	0.5	0.2	3.7			95.6.	4.4

Table 2.13 (c) African Fish Eagle population structure in the main study area in Queen Elizabeth Park, April 1977 - March 1978.

Date of count	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
					Eagles	Young	Adults	Young
7.4.77	153	2	3	7	165	12	92.7	7.3
29.4.77	163	2	5	7	177	14	92.1	7.9
10.5.77	155	0	0	4	159	4	97.5	2.5
13.6.77	159	2	1	4	166	7	95.8	4.2
30.6.77	149	1	4	5	159	10	93.7	6.3
16.8.77	159	0	3	5	167	8	95.2	4.8
30.8.77	160	1	3	4	168	8	95.2	4.8
7.10.77	162	1	0	4	167	5	97.0	3.0
19.10.77	164	1	0	6	171	7	95.9	4.1
27.10.77	161	2	2	7	172	11	93.6	6.4
8.11.77	165	0	0	3	168	3	98.2	1.8
29.12.77	166	0	1	7	174	8	95.4	4.6
Total	1916	12	22	63	2013	97		
Mean	159.7	1.0	1.8	5.3	167.8	8.1		
±S.d.	5.1	0.9	1.7	1.5	5.4	3.3		
%C.V.	3.2	90.0	94.4	28.3	3.2	40.7		
% age classes	95.2	0.6	1.1	3.1			95.2	4.8

Table 2.14 (a) African Fish Eagle population structure in Mweya Peninsula, Queen Elizabeth National Park, April 1975 - March 1976.

Date of count	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
					Eagles	Young	Adults	Young
4/75	20	1	0	2	23	3	86.9	13.1
5/75	22	1	1	3	27	5	81.5	18.5
6/75	23	4	3	3	33	10	69.7	30.3
7/75	23	1	3	2	29	6	79.3	20.7
8/75	20	1	0	1	22	2	90.9	9.1
9/75	23	0	0	0	23	0	100.0	0.0
10/75	24	0	0	2	26	2	92.3	7.7
3/76	24	0	0	4	28	4	85.7	14.3
Total	179	8	7	17	211	32		
Mean	22.4	1.0	0.9	2.1	26.4	4.0		
±S.d.	1.6	1.3	1.4	1.2	3.7	3.1		
%C.V.	7.1	130.0	155.6	57.1	14.0	77.5		
% age classes	84.8	3.8	3.4	8.0			84.8	15.2

Table 2.14 (b) African Fish Eagle population structure in Mweya Peninsula, Queen Elizabeth National Park, April 1976 - 1977.

Date of count	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
					Eagles	Young	Adults	Young
4/76	23	0	0	5	28	5	82.1	17.9
6/76	23	0	0	5	28	5	82.1	17.9
7/76	23	1	1	2	27	4	85.2	14.8
8/76	23	0	0	1	24	1	95.8	4.2
9/76	24	0	0	0	24	0	100.0	0.0
12/76	22	0	0	5	27	5	81.5	18.5
3/77	23	0	0	1	24	1	95.8	4.2
Total	161	1	1	19	182	21		
Mean	23.0	0.14	0.14	2.7	26.0	3.0		
±S.d.	0.6	0.4	0.4	2.2	1.9	2.2		
%C.V.	2.6	285.7	285.7	81.5	7.3	73.3		
% age classes	88.5	0.5	0.5	10.4			88.5	11.5

Table 2.14 (c) African Fish Eagle population structure in Mweya Peninsula, Queen Elizabeth National Park, April 1977 - March 1978.

Date of count	Full adults	Sub-adults	2-year olds	Recent young	Total		Percent	
					Eagles	Young	Adults	Young
5/77	22	0	0	0	22	0	100.0	0.0
6/77	22	0	0	0	22	0	100.0	0.0
8/77	24	0	0	4	28	4	85.7	14.3
9/77	24	0	0	2	26	2	92.3	7.7
12/77	17	1	0	0	18	1	94.4	5.6
1/78	22	3	0	2	27	5	81.5	18.5
Total	131	4	0	8	143	12		
Mean	21.8	0.7	0	1.3	23.8	2.0		
±S.d.	2.6	1.2		1.6	3.8	2.1		
%C.V.	11.9	171.4		123.1	16.0	105.0		
%age classes	91.6	2.9	0.0	5.5			91.6	8.4

Table 2.15 Adult and total Fish Eagle lifespans from the best estimates of population structures in Queen Elizabeth Park, Uganda. Best estimate of population structure is one whose subadult segment gives an adult lifespan of not more than 40 years. Figures in parentheses are numbers of counts.

Survey area	Length (km)	Distance (km)	Total birds	Subadults		Lifespan (yrs)	
				No.	%	Adult	Total
Whole park	342(1)	342	752	19	2.5	39.5	43.5
L. George (north)	78(1)	78	64	2	3.1	31.8	35.8
Kazinga (north)	42(1)	42	128	4	3.1	31.8	35.8
L. Edward (south)	42(1)	42	161	9	5.6	17.4	21.4
Mweya (1975/6)	9(8)	72	221	8	3.8	25.8	29.8
Mweya (1977/8)	9(6)	54	143	4	2.8	35.2	39.2
Total	522(18)	630	1469	46			
Mean					3.5*	30.3	34.3
±S.d.					1.1	7.7	7.7

* This figure, used on its own, gives an adult lifespan of 28.1 years and, therefore, a longevity of 32.1 years.

those which have few or no trees and are flat (Eltringham 1975; Thiollay & Meyer 1978). Although there has been no practical demonstration of any correlation between the distribution patterns of the bird and those of fish, the distribution of fish has been suggested as a habitat factor that influences its distribution patterns along the shorelines of water bodies on which the Eagle is sedentary (Brown & Hopcraft 1973, Eltringham op.cit., Green 1964). The depth, turbidity and waviness of the water body contribute towards the hunting and breeding success of the Eagle and clear, still and shallow waters are optimal in these respects (Brown & Hopcraft, op.cit.; Thiollay & Meyer, op.cit.). Such water bodies would therefore be preferred to deep, opaque and turbulent ones. Thus, Green (op.cit.) found that Fish Eagles were rare along the steep banks of L. Albert, a fact which he relates to the deep offshore water carrying few fish.

During this study, Fish Eagles were markedly more common along steep, well-wooded and non-swampy shorelines than along flat, treeless and swampy ones. The productivity and distribution of fish in L. Edward and the Kazinga Channel have not been measured but in L. George fish distribution has been shown to decrease from inshore to offshore sites and from the southwestern towards the northeastern parts of the lake (Gwahaba 1973). The low density of fish in the north-eastern section of the lake, per se, cannot explain the low density of Fish Eagles in that area. There are enough fish in the area (13,000 fish/ha; Gwahaba, op.cit.) to support a higher density of Eagles than was recorded. What seem critical in explaining the low density of birds along this section of L. George are the extensive Cyperus papyrus and C. latifolius swamps bordering its shoreline and the consequent lack of robust trees within reasonable distance from the shoreline for the Eagles to perch and nest upon. This observation is supported by the fact that where Ficus sp. trees are available, the Eagles are locally more numerous.

Along the southern shoreline of L. Edward, papyrus swamps also fringe sections of the bank but the swamps are not as extensive as those in north-eastern L. George and they are backed by forested and well-wooded hinterlands (Fig. 2.1). Thus, the southern bank of L. Edward had the highest density of Eagles in the whole Park. Along the Channel, the northern bank is better wooded than the southern one. Probably because of this rather than any other habitat factor, the northern bank had a higher population density of adults than the southern one.

The findings that Fish Eagles are fewer along swampy and treeless shorelines than along swampy but well-wooded banks, and less common along treeless shorelines as compared to well-wooded ones clearly demonstrate the importance of trees in the distribution of the bird. These results further indicate that the presence of trees within reasonable distances of the shorelines probably overrides food availability in influencing the distribution patterns of the birds in this Park. The extremely high densities of Eagles along the banks of Crater Lakes Nyamusingire and Kasanduka, in Maramagambo Forest (Fig.2.1), further emphasize the importance of trees to the Eagle.

Trees are not necessary as perching sites. Along treeless shorelines Fish Eagles will perch on low bushes or even sit on dense mats of floating Pistia stratiotes or directly on the ground. Eltringham (1975) and Greenspan & Torre-Bueno (1971) made similar observations on this population earlier on. These observations do indicate that trees are an important resource to the Fish Eagle, and are probably more so as nesting rather than perching sites.

Along a 209 km shoreline of L. Albert, Green (1964) reported that the overall Fish Eagle density was 0.8 birds/km, but in one 2 km stretch where there was a fishing village the density rose to 11 birds/km. Although Brown & Hopcraft (1973) did not give densities for the L. Naivasha Fish Eagle population, they reported that the birds were not resented by the riparian land owners or fishermen. They also found that the young favoured and congregated in the lagoons where there were few or no pairs of territorially aggressive adults (Brown 1980). During this study, adult birds showed no significant differences in their densities between inhabited and uninhabited banks. Furthermore, the densities of adults and independent young were significantly correlated, thus indicating that such young did not necessarily avoid shorelines with high densities of adult birds. Subadults were, however, regularly encountered on the rubbish dumps in Mweya Peninsula while along other shorelines they tended to congregate at the fishing villages (Fig.2.1 & Table 4.9). In this Park young Eagles are attracted to fishing villages because of the improved scavenging opportunities they offer. At all of them, large quantities of partly rotten fish and fish offals are discarded daily. Both young and non-territorial adults made use of this regular carrion. In these villages, especially at Rwenshama (Fig.2.1), large numbers of other birds, namely Marabou Storks *Leptoptilos crumeniferous*, vultures (Aegypiinae), Pied Crows *Corvus alba*, Black Kites *Milvus migrans*, Hammerkops *Scopus umbretta*, herons (Ardeadae), Yellow-billed Storks *Ibis ibis*, Saddle-billed Storks *Ephippiorhynchus senegalensis*, Sacred Ibises *Threskiornis aethiopicus*, Hadada Ibises *Hagedashia hagedash*, and African Spoonbills *Platalea alba* also scavenged alongside the Fish Eagles (Table 4.9).

At L. Naivasha, the Fish Eagle was not persecuted by man and, therefore, human interference was not an important reason for the variations in its breeding success (Brown & Hopcraft 1973). The similarities in the densities of adults along inhabited and uninhabited shorelines, and the clumping of young around human habitations clearly demonstrate the impartiality of man towards the bird in this park. Despite this, however, pairs at the foci of human activities suffered reduced breeding success through, probably, inadvertent rather than deliberate human interferences with their nesting activities (section 12.3.4).

The usefulness of studying the population structure of any species is to know more about its life history. For any bird species, the presence of too many subadults in its breeding population is indicative of the instability of the population and for a raptor the population concerned is not healthy (Brown 1976 a & b). At L. Naivasha, Brown & Hopcraft (1973) recorded 80.3% adults, 9.2% subadults, 3.9% 2-year olds, and 6.6% recent immatures in the 1968-69 Fish Eagle population. During 1970-71 study, these authors recorded 85.6% adults, 6.1% subadults, 2.6% 2-year olds, and 5.7% recent immatures. Using the 1970-71 data they found that the subadults comprised 4.2% of the population on the lake. This figure agreed with Brown & Cade's (1972) finding that the normal replacement rate of bereaved adults lies between 4-6%. At the above replacement rate the Fish Eagle would have an adult lifespan of between 16 and 24 years and a total life expectancy of 20-28 years.

For 5 counts of Mweya Peninsula Fish Eagles (7-29 July 1971), Greenspan & Torre-Bueno (1971) reported 168 bird resightings. Of these, 106 (63.5%) were adults, 12 (7.7%)were subadults, and 50 (28.8%) were juveniles. The 7.7% subadults would give the Fish Eagle an adult life of 12.5 years and a total longevity of 16.5 years. In another 2-month study of the same population, Thiollay & Meyer (1978) reported 70.2% adults, 5.7% subadults, 6.9% 2-year olds, and 17.2% recent immatures. The percentage of subadults gives the Eagle an adult life of 17 years and a life expectancy of 21 years. Thiollay & Meyer (op.cit.), however, reported an adult lifespan of 25 years and a longevity of 29 years.

Because of the extremely low overall percentages of subadults in counts during my study, some improbable estimates of the adult and total lifespans of the Fish Eagle have been made. However, using the best estimates of the population structure, the Eagle would have to live ca.30 years ~~as an~~ adult, and therefore 34 years total life, in order to replace itself (Table 2.15). In the course of this work only the population structure along the southern shoreline of L. Edward gave adult and total life expectancies which fell within the ranges of life expectancies given by Brown & Cade (1972). Counts in the Mweya area in the 1975/6 study period gave adult and total life expectancies which agreed with those obtained by Thiollay & Meyer (1978).

The following factors probably contributed to the very low numbers of independent young during the present surveys. Independent young are not as vociferous as recently fledged ones are (section 11.3.3). Secondly, independent young adopt cryptic and retiring habits (Brown 1980, Greenspan & Torre-Bueno 1971). These habits, therefore, make them difficult to spot, especially in wooded habitats. Thirdly, both adult and young scavenge (Brown 1980). Probably because of this behaviour, many independent young could have been scavenging in the hinterlands and were, therefore, missed during surveys. Due to these considerations the numbers of independent young in all the surveys should have been higher than what were recorded, thus giving the Eagle a lower expectation of life than has been estimated. The 17-year adult lifespan calculated from the population structure along the southern bank of L. Edward probably represents the minimum age requirement for the Park Fish Eagle to replace itself. The maximum adult lifespan, on the other hand, may be close to the 24 years calculated by Brown & Cade (op.cit.) and the 25 years obtained by Thiollay & Meyer (op.cit.). It is, however, unlikely that the adult lifespan can exceed the 30-year mean estimated during this study. Perhaps their generally idle way of life (section 3.3.2) permits them to reach a great age (Brown, op.cit.).

More carefully planned population structure studies are still required to establish how long the wild African Fish Eagle lives in order to perpetuate its kind. Such studies should, however, be supplemented by both ringing and telemetry records which will help to unravel the patterns of movements and dispersal of the independent immature bird.

CHAPTER 3

TERRITORIALITY AND ACTIVITY PATTERNS

3.1 INTRODUCTION

The concept of territoriality in birds of prey is as old as Aristotle (Brown, 1970a). Although age-old, serious study of the subject started only recently with Howard's (1920) treatise on "Territory in bird life." Since Howard's work, the study of territoriality has grown to cover virtually all forms of animal life.

Territoriality is a widespread phenomenon in birds e.g. Schoener 1968; J, Brown 2969 for reviews), and especially so among birds of prey (Brown 1970a, 1976a, b & c, 1980). Despite serving to apportion, in an orderly manner, resources like food, mates, nest site, activity space, etc. whose efficient utilization has not been favoured by gregariousness (Schoener op.cit.), the evolutionary importance of territorial behaviour in birds, especially in regards to regulation of populations, has become a matter of controversy (e.g. Wynne-Edwards 1959, 1962, 1963; Lack 1966; J. Brown 1969).

In the African Fish Eagle, the early studies of Brown (1955, 1970a) tended to play down the fiercely territorial nature of the bird, probably because the population studied was small, insular and isolated, and apparently migratory. However, recent studies by both Brown and other authors, especially ~~Greenspan &~~ Torre-Bueno (1971), have shown that the Fish Eagle is intensely territorial. This study, therefore, sought to:

a) confirm the existence of territoriality in the Fish Eagle in Queen Elizabeth Park,

b) describe the diurnal activities of the Eagle and evaluate their relationship with the territorial habit of the bird, and

c) assess the importance of territoriality in the Fish Eagle, especially in relation to population regulation in the species.

3.2 METHODS

3.2.1 Terminology

3.2.1.1 Territory

There are two principal definitions of territory. The first by Noble (1939), simply labels a territory as "any defended area." However, Pitelka (1959) has suggested that a territory be defined as "an exclusive area" because "the fundamental importance of territory lies not in the mechanism (overt defense or any other action) by which the territory becomes identified with its occupant, but the degree to which it is in fact used exclusively by its occupant." Much as the territory of the Fish Eagle during this study was a defended area, it was exclusively used by the pair of birds which occupied it, and by their young during the post-fledging period when the young were still dependent on the adults (Chapters 11 & 12).

3.2.1.2 Eagle-day

An eagle-day describes the period of time from dawn, when the Fish Eagle makes its first call, to dusk, when the bird retires to its roost and makes the last call. Its length varies with habitats, probably depending on the latitude and the seasons of the area. At L. Naivasha, Brown (1980) used an eagle-day spanning about 13 hours, starting at 0530 and ending at 18:30. In Queen Elizabeth Park, the Fish Eagle was also active for 13 hours, the day starting around 06:30 and ending at 19:30.

3.2.1.3 Distinction of sexes

In relating a particular behaviour to a specific Fish Eagle, it was important to differentiate between the sexes of a pair under observation. An adult female is bigger than her mate by 10-15% in all dimensions (Brown 1976a, b & 1980; Brown & Amadon 1968; Mackworth-Praed & Grant 1952; Frontispiece Plate 1). She weighs from 3000 to 3600 g while the male weighs between 2000 and 2500 g, and she has a mean standard wing length of about 58 cm as compared to 53 cm for the male (Brown 1980). In flight the female, because of her large size, has slower wing beats (4-5 times/second) than the male (5-6 times/second) (Brown op.cit.).

The calls are characteristically different, the male's being higher-pitched than the female's. Although the calls can vary, the variation between individuals is greater than it is for an individual (Greenspan & Torre-Bueno 1971). This point is significant in identifying a Fish Eagle, by calls, from several others that might be soaring high up in the sky. Thus, using the above characteristics it was possible to distinguish between the male and female of a particular pair and to identify a specific male or female from a group of soaring birds.

3.2.2 Sampling methods

To determine the distribution of the territories in the main study area along the Kazinga Channel, their approximate boundaries had to be known. For each territory, this was achieved by noting on sketch maps the positions of the birds, during surveys, in relation to the principal features of the territory, i.e. the large trees upon which the birds perched, ridges and gullies along the slopes of the territory, and sand spits and bays along the shorelines. The positions of nests, when present (section 5.3.1), and of favourite perch trees, and the regular territorial disputes between neighbouring pairs helped to fix the boundaries of a territory relative to those of the neighbouring pairs. Having estimated the approximate limits of territories, the shoreline lengths of 20 territories, selected from a table of random numbers, were measured. During the whole study period, for the 20 territories, the farthest positions birds perched inland in their territories were noted by marking the trees upon which they sat and later measuring the distances from the land-water interfaces. This measurement gave part of the width of the territory on the land section of it.

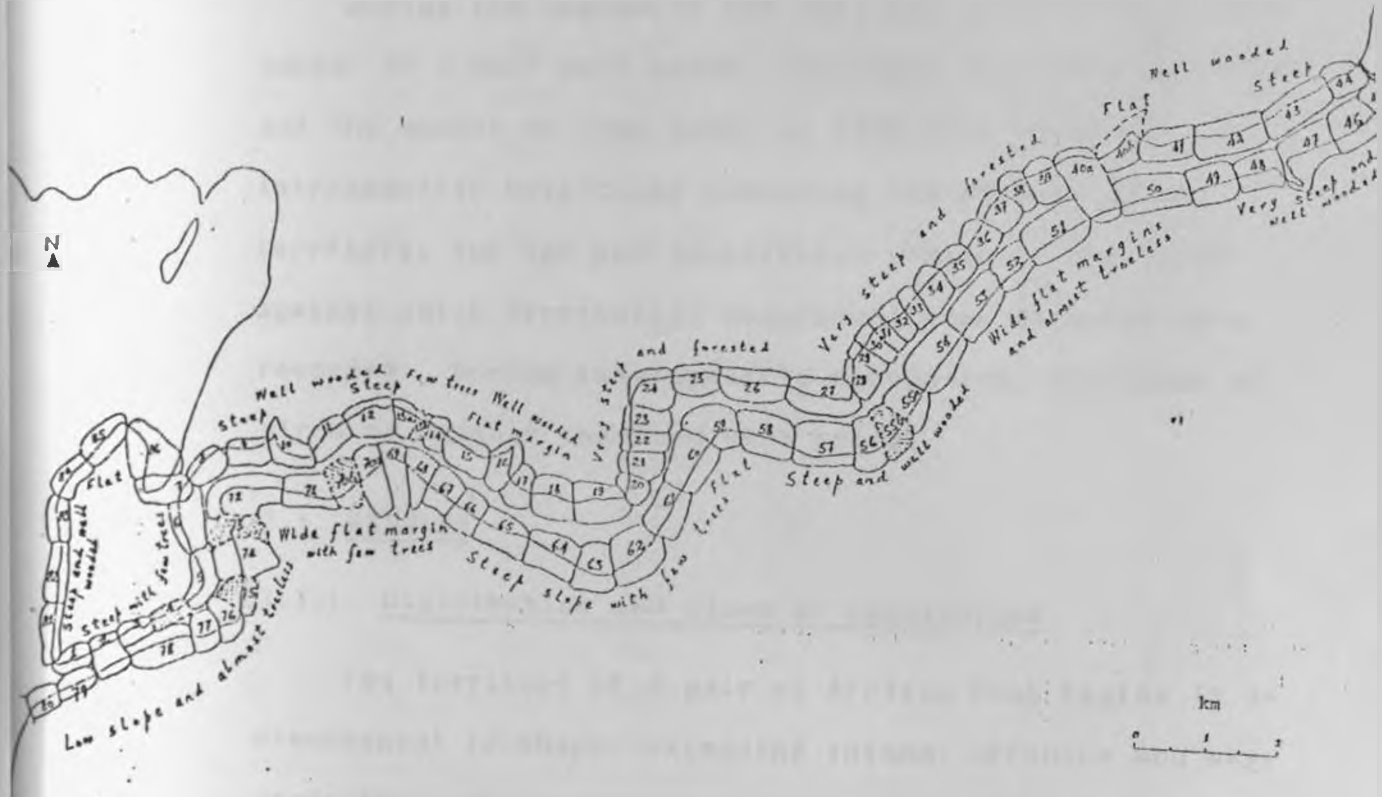
On the Channel, I noted that any 2 pairs, on the opposite banks divided it virtually in the middle, between themselves. Where the Channel was too narrow, 500 m or less, the boundaries of territories on the water coincided. However, where it was wider than 500 m there existed a narrow band of water, running almost mid way along the Channel, which could appropriately be termed no-man's-land (Fig.3.1). Thus the width of the territory in the water was dependent on the width of the Channel. Nowhere was this distance more than 400 m, and was estimated by dividing the width of the Channel. Thus, the total width of a territory was obtained by adding the two measurements of the widths of the land and water sections of it.

The method used in determining the relationships between territory size and the vegetation cover along the banks, and between territory size and the combinations of gradient and vegetation cover along the banks of the Channel has already been described in reference-to habitat preference by the bird (section 2.2.2).

All diurnal activities of Fish Eagles were identified, and they fitted into 4 main classes: sitting, flying, eating and 'others'. Flights were further subdivided into territorial flights (in defence of the territory)

D

Fig. 3.1 Territories of African Fish Eagles in the main study area along the Kazinga Channel, Queen Elizabeth National Park. Stippled territories were those abandoned during the study period and cross-hatched ones were those taken up after the commencement of the study.



soaring (also subdivided into low and high soaring) flights, ordinary or perch to perch flights, and fishing (subdivided into perch to water and circling) flights. Included under 'others' were such activities like drinking and bathing, preening, mating, and chasing other birds. Since all these activities, apart from high soaring flights, took place within the territory, I decided to treat them in the context of the territorial way of life of the species.

During the course of the day, all activities of each member of a pair were noted, the times they were performed and the amount of time spent on them were recorded. In intraspecific activities involving the defence of the territory, the age and territorial status of the birds against which territorial behaviours were directed were recorded. During interspecific encounters, the names of birds or animals involved were noted.

3.3 RESULTS

3.3.1 Distribution and sizes of territories

The territory of a pair of African Fish Eagles is 3-dimensional in shape, extending inland, offshore and skywards from any stretch of shoreline that the pair controls. Territories were regularly spaced (Fig.3.1). Twenty territories averaged 525 m of shoreline length (Table 3.1). Because the territory extended both inland and offshore, the area under it included both land and water. However, the area on land depended on how far inland the nest or favourite perches and roost trees were, and that under water on the width of the Channel (Table 3.1). Because nests

Table 3.1 Territory size in the African Fish Eagle in Queen Elizabeth Park. Twenty territories, selected from a table of random numbers, were measured.

	Width (m)			Length(m)	Area (ha)		
Pair No.	Land	Water	Whole	Shoreline	Land	Water	Whole
8	200	300	500	650	13.0	19.5	32.5
15	200	300	500	650	13.0	19.5	32.5
17	300	300	600	400	12.0	12.0	24.0
23	100	400	500	350	3.5	14.0	17.5
25	150	300	450	600	9.0	18.0	27.0
29	150	400	550	200	3.0	8.0	11.0
31	150	300	450	150	2.3	4.5	6.8
34	200	400	600	400	8.0	16.0	24.0
38	300	400	700	350	10.5	14.0	24.5
43	200	300	500	900	18.0	27.0	45.0
46	200	400	600	650	13.0	26.0	39.0
48	200	300	500	250	5.0	7.5	12.5
59	250	400	650	600	15.0	24.0	39.0
62	300	400	700	700	21.0	28.0	49.0
64	300	300	600	750	22.5	22.5	45.0
69	900	200	1100	300	27.0	6.0	33.0
73	500	200	700	300	15.0	6.0	21.0
78	300	200	500	900	27.0	18.0	45.0
83	200	200	400	600	12.0	12.0	24.0
85	200	200	400	800	16.0	16.0	32.0
Total	5300	6200	11500	10500	265.8	318.5	584.3
Mean	265.0	310.0	575.0	525.0	13.3	15.9	29.2
±S.d.	172.5	78.8	155.2	231.4	7.3	7.3	12.1
% C.V.	65.1	25.4	27.0	44.1	54.9	45.9	41.4

averaged only 110 m from the nearest shoreline (section 5.3.1), the width of the land section of the territory, averaged only 265 m (Table 3.1), thus clearly indicating that it did not extend far inland and also not far beyond the nest. For the area under water, the width averaged only 310 m (Table 3.1). The percent coefficient of variations (C.V.s) of these two widths demonstrate how little a pair can do in extending its territory offshore compared to doing so inland.

The territories averaged 29 ha, with an average 15.9 ha in water and 13.3 ha on land (Table 3.1). Variations from the above mean acreages were great (Table 3.1 & Fig.3.1) and probably depended on factors like the aggressiveness of a pair of Eagles, the fish productivity of the water under the pair's control, the topography of the banks, and on the number of trees in the territory. How most of these factors influenced territory size was not studied. However, territory size increased significantly from forested to almost treeless banks (Fig.3.2) and also it increased, although not significantly, as the banks became flatter and more devoid of trees (Fig.3.3, see also section 2.3.1).

3.3.2 Diurnal activities and their relationships with the territorial behaviour of the species

The time spent by birds on various activities are given in Table 3.2. Overall, the male was more active than his mate in all activities they undertook. The Eagle spent most, 89.6%, of its time perched. During this period, however, it regularly scanned the sky for

Fig. 3.2 The influence of vegetation on territory size in the Fish Eagle in Queen Elizabeth Park. On the X-axis, 1 represents forested bank, 2 well-wooded shoreline, 3 shoreline with few trees, and 4 an almost treeless bank. Because trees were not physically counted, the classes of tree abundance are, therefore, not rigorous.

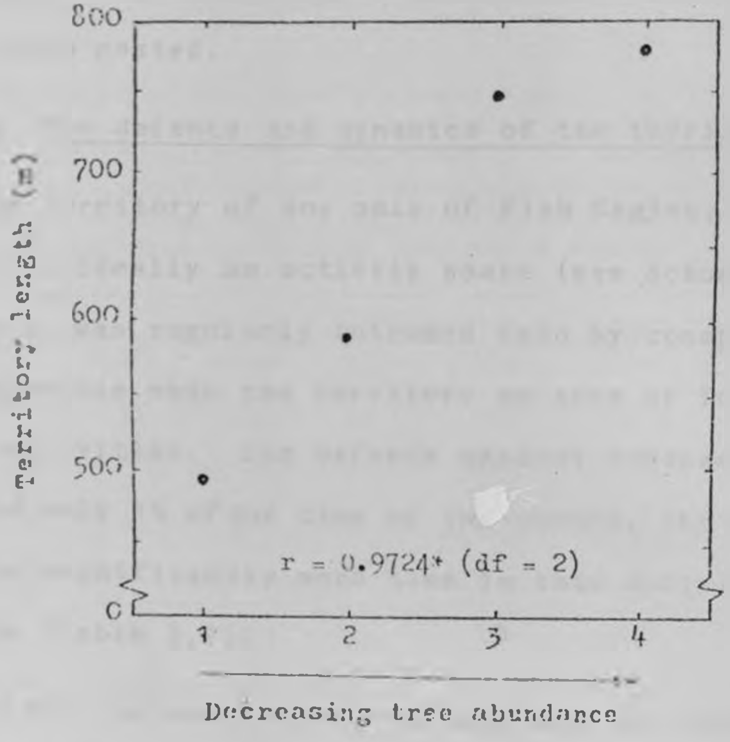
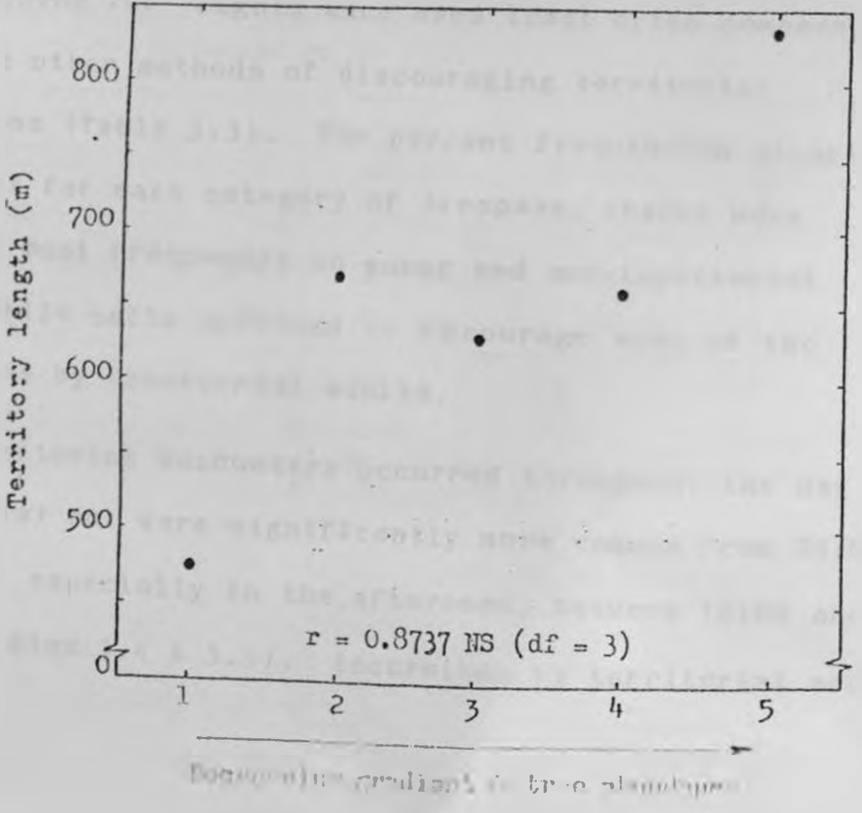


Fig. 3.3 The influence of the nature of the shoreline on the size of the territory of the Fish Eagle in Queen Elizabeth Park. On the X-axis, 1 represents very steep and forested shoreline, 2 steep and well-wooded, 3 flat and well-wooded, 4 steep and almost treeless, and 5 represents flat and almost treeless banks. Because both gradient and tree abundance were not physically measured, the classification of the shoreline is, therefore, not rigorous.



intruders and the water for opportunities to catch fish and it also rested.

3.3.2.1 The defence and dynamics of the territory

The territory of any pair of Fish Eagles, during this study, was ideally an activity space (see Schoener 1968). Because it was regularly intruded into by conspecifics, the incursions made the territory an area of intense territorial activities. Its defence against trespass, however, occupied only 1% of the time of the owners, the male spending significantly more time in this activity than his mate (Table 3.2).

In all the trespasses, the age and the territorial status of the intruder featured significantly. Of 282 intrusions, young Fish Eagles trespassed most frequently and non-territorial or wandering adults trespassed least so (Table 3.3). A pair defended its territory by calling at the intruder, chasing it and, if overrun, by buzzing and taloning it. Fights were used least often compared with the other methods of discouraging territorial incursions (Table 3.3). The percent frequencies clearly show that for each category of trespass, chases were employed most frequently on young and non-territorial adults while calls sufficed to discourage most of the incursions by territorial adults.

Territorial encounters occurred throughout the day (Fig. 3.4a) but were significantly more common from 09:00 to 17:00, especially in the afternoon, between 12:00 and 17:00 (Tables 3.4 & 3.5). Incursions by territorial adults

Table 3.2 The amount of time the Fish Eagle spent on various activities. Observations made on 10 non-breeding pairs for varying periods of time totalling 26.8 eagle-days. See text for activities included under "others". Chi-square was performed on raw data. Sit. = sitting, terr. = territorial, soar. = soaring, ord. = ordinary, fish. = fishing, and eat. = eating.

	Time (min) spent on activity							
Sex	Sit.	Terr.	Soar.	Ord.	Fish.	Eat.	Other	Total
Male	9136	121	565	96	209	271	42	10440
(%)	(87.5)	(1.2)	(5.4)	(0.9)	(2.0)	(2.6)	(0.4)	(100.0)
Female	9563	81	283	62	76	351	24	10440
(%)	(91.6)	(0.8)	(2.7)	(0.6)	(0.7)	(3.4)	(0.2)	(100.0)
Total	18699	202	848	158	285	622	66	20880
(%)	(89.6)	(1.0)	(4.1)	(0.8)	(1.4)	(3.0)	(0.3)	(100.2)

$X^2 = 196.031^{***}$ (df = 6)

Table 3.3 Intraspecific encounters in the Fish Eagle in Queen Elizabeth Park. Figures in parenthesis are percent frequencies. Chi-square was performed on raw data.

	Frequency of use of method			
Status of intruder	Calls	Chases	Fights	Total
Territorial adult	51 (73.9)	9 (13.0)	9 (13.0)	69 (99.9)
Non-territorial adult	11 (39.3)	13 (46.3)	4 (14.3)	28 (99.9)
Non-territorial young	56 (30.3)	98 (53.0)	31 (16.8)	185 (100.1)
Total	118	120	44	282
% frequency	41.8	42.6	15.6	100.0

$X^2 = 42.337^{***}$ (df = 4)

Fig. 3.4

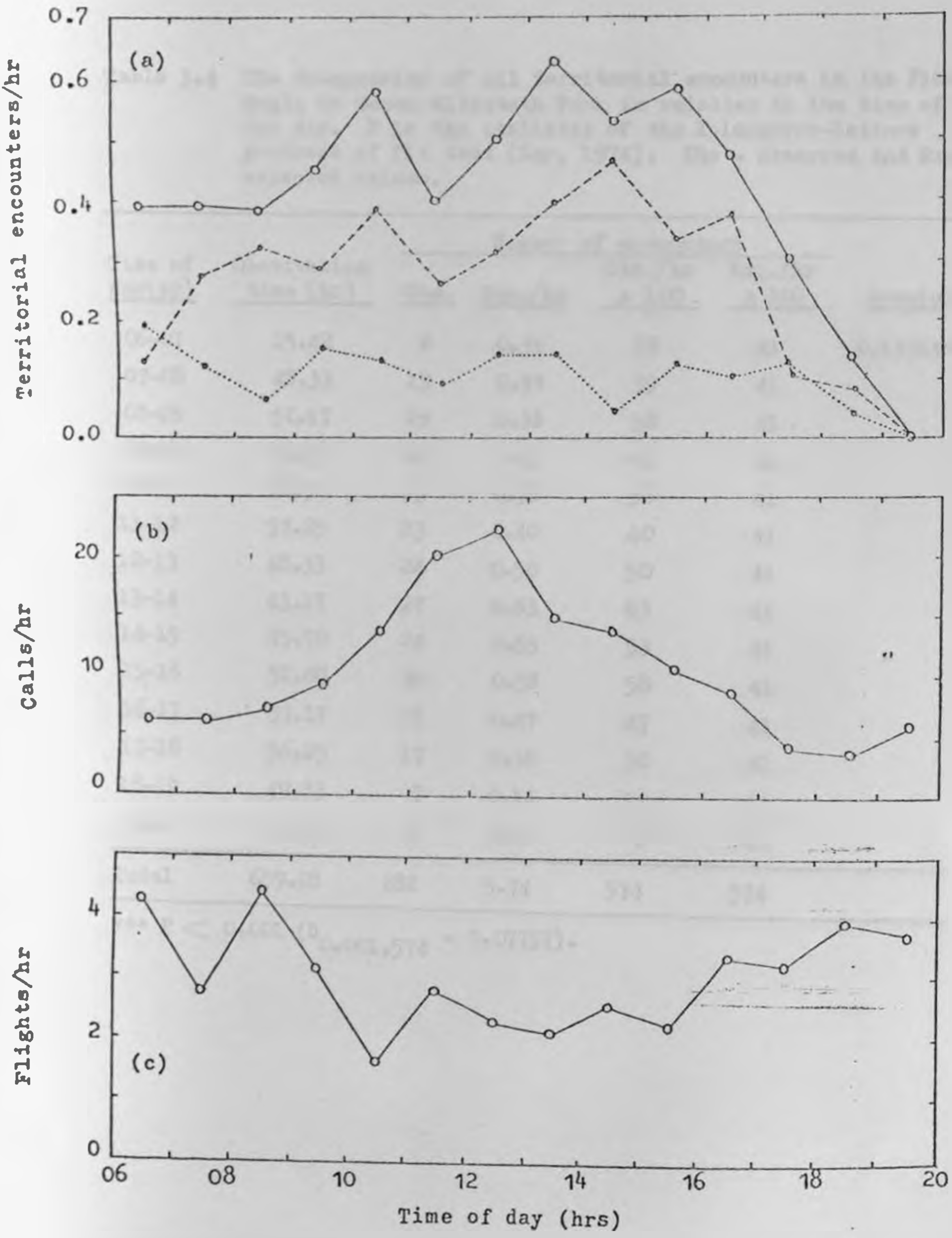

(a)
Territorial encounters/hr
0.7
0.6
0.4
0.2
0.0
(b)
Calls/hr
20
10
0
(c)
Flights/hr
4
2
0
06
08
10
12
14
16
18
20
Time of day (hrs)

Table 3.4 The frequencies of all territorial encounters in the Fish Eagle in Queen Elizabeth Park in relation to the time of the day. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974). Obs = observed and Exp = expected values.

		Number of encounters				
Time of day(hr)	Observation time (hr)	Obs.	Obs./hr	Obs./hr x 100	Exp./hr x 100	D-value
06-07	15.42	6	0.39	39	41	0.13763***
07-08	48.33	19	0.39	39	41	
08-09	50.17	19	0.38	38	41	
09-10	53.33	24	0.45	45	41	
10-11	60.58	35	0.58	58	41	
11-12	57.25	23	0.40	40	41	
12-13	48.33	24	0.50	50	41	
13-14	43.17	27	0.63	63	41	
14-15	45.50	24	0.53	53	41	
15-16	52.08	30	0.58	58	41	
16-17	57.17	27	0.47	47	41	
17-18	56.25	17	0.30	30	41	
18-19	49.83	7	0.14	14	41	
19-20	21.67	0	0.00	0	41	
Total	659.08	282	5.74	574	574	

*** $P < 0.001$ ($D_{0.001,574} = 0.07757$).

Table 3.5 The frequencies of territorial incursions by young Fish Eagles in Queen Elizabeth Park in relation to the time of the day. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974). Obs. = observed and Exp. = expected values.

		Number of incursions				
Time of day(hr)	Observation time (hr)	Obs.	Obs./hr	Obs./hr x 100	Exp./hr x 100	D-value
06-07	15.42	2	0.13	13	26.4	0.16280***
07-08	48.33	13	0.27	27	26.4	
08-09	50.17	16	0.32	32	26.4	
09-10	53.33	15	0.28	28	26.4	
10-11	60.58	23	0.38	38	26.4	
11-12	57.25	15	0.26	26	26.4	
12-13	48.33	15	0.31	31	26.4	
13-14	43.17	17	0.39	39	26.4	
14-15	45.50	21	0.46	46	26.4	
15-16	52.08	17	0.33	33	26.4	
16-17	57.17	21	0.37	37	26.4	
17-18	56.25	6	0.11	11	26.4	
18-19	49.83	4	0.08	8	26.4	
19-20	21.67	0	0.00	0	26.4	
Total	659.08	185	3.69	369	369.6	

*** $P < 0.001$ ($D_{0.001,369} = 0.09675$).

also differed significantly with the time of the day (Table 3.6), but there were no marked peaks and troughs as for those of all birds and of young (Fig. 3.4a).

The facts that the Fish Eagle called at, chased and physically fought with intruding conspecific demonstrate that it is strongly territorial. The strength of attachment of a pair to the territory is shown in Table 3.7. During 35 counts in the study area, the rate of occupancy (residence) for 86 pairs averaged 76.2%. If 3 pairs which later abandoned their territories were excluded from this analysis, the rate would go up to about 81%. These were high residence rates and indicate that the Fish Eagle has a strong attachment to its territory. Since the male soared more than his mate (Tables 3.2 & 3.11), most birds which resided in their territories at the times of the counts were probably females.

Although Fig. 3.5 indicates that small territories along densely populated shorelines had higher residence rates than large ones along sparsely populated banks, territory size was not significantly correlated with territorial occupancy (Fig.3.6). This finding, therefore, suggests that a pair occupying a small territory resided in it and, consequently, defended it just as much as a pair holding a large one. This finding was expected since the very high density of birds in the area would indicate that both small and large territories were probably similarly covetted by non-territorial birds and those in marginal territories.

Table 3.6 The frequencies of territorial incursions by territorial adult Fish Eagles in Queen Elizabeth Park in relation to the time of the day. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974). Obs. = observed and Exp. = expected values.

Time of day(hr)	Observation time (hrs)	Number of incursions Obs.	Obs./hr	Obs./hr x 100	Exp./hr x 100	D-value
06-07	15.42	3	0.19	19	10.3	0.13690**
07-08	48.33	6	0.12	12	10.3	
08-09	50.17	3	0.06	6	10.3	
09-10	53.33	8	0.15	15	10.3	
10-11	60.58	8	0.13	13	10.3	
11-12	57.25	5	0.09	9	10.3	
12-13	48.33	7	0.14	14	10.3	
13-14	43.17	6	0.14	14	10.3	
14-15	45.50	2	0.04	4	10.3	
15-16	52.08	6	0.12	12	10.3	
16-17	57.17	6	0.10	10	10.3	
17-18	56.25	7	0.12	12	10.3	
18-19	49.83	2	0.04	4	10.3	
19-20	21.67	0	0.00	0	10.3	
Total	659.08	69	1.44	144	144.2	

** $P < 0.01$ ($D_{0.01,144} = 0.13431$).

Table 3.7 Territory occupancy by the Fish Eagle during 35 counts in the study area along the Kazinga Channel, Queen Elizabeth Park. Number of times present indicates at least one member of a pair was resident on their territory. Four pairs which took up territories after commencement of the study were excluded from this analysis. Occupancies marked with asterisks are of 3 pairs which abandoned their territories during the study. Occupancy rate = Number of pair visits bird(s) was(were) present in territory divided by total number of pair visits made to the territory.

No. of times present	No. of pairs	Number of pair visits			Occupancy rate(%)
		Present	Absent	Total	
35	26	910	0	910	100.0
34	18	612	18	630	97.1
33	19	627	38	665	94.3
32	5	160	15	175	91.4
31	4	124	16	140	88.6
30	4	120	20	140	85.7
29	1	29	6	35	82.9
28	1	28	7	35	80.0
27	1	27	8	35	77.1
26	2	52	18	70	74.3*
25	1	25	10	35	71.4
22	1	22	13	35	62.9
21	1	21	14	35	60.0*
15	1	15	20	35	42.9
12	1	12	23	35	34.3*
Total	86	2784	226	3010	
Mean ± S.d.					76.2 ± 19.3

Fig. 3.5 Territorial occupancy by the African Fish Eagle in the main study area along the Kazinga Channel, Queen Elizabeth National Park, during 35 counts (April 1975 - March 1978). Pairs which took up territories after the commencement of the study are omitted from this analysis. (●) indicated territory was occupied by at least one member of the pair on all 35 occasions when counts were made, (o) territory occupied from 33-34 times, (◆) territory occupied from 30-32 times, (▲) territory occupied 29 times or less.

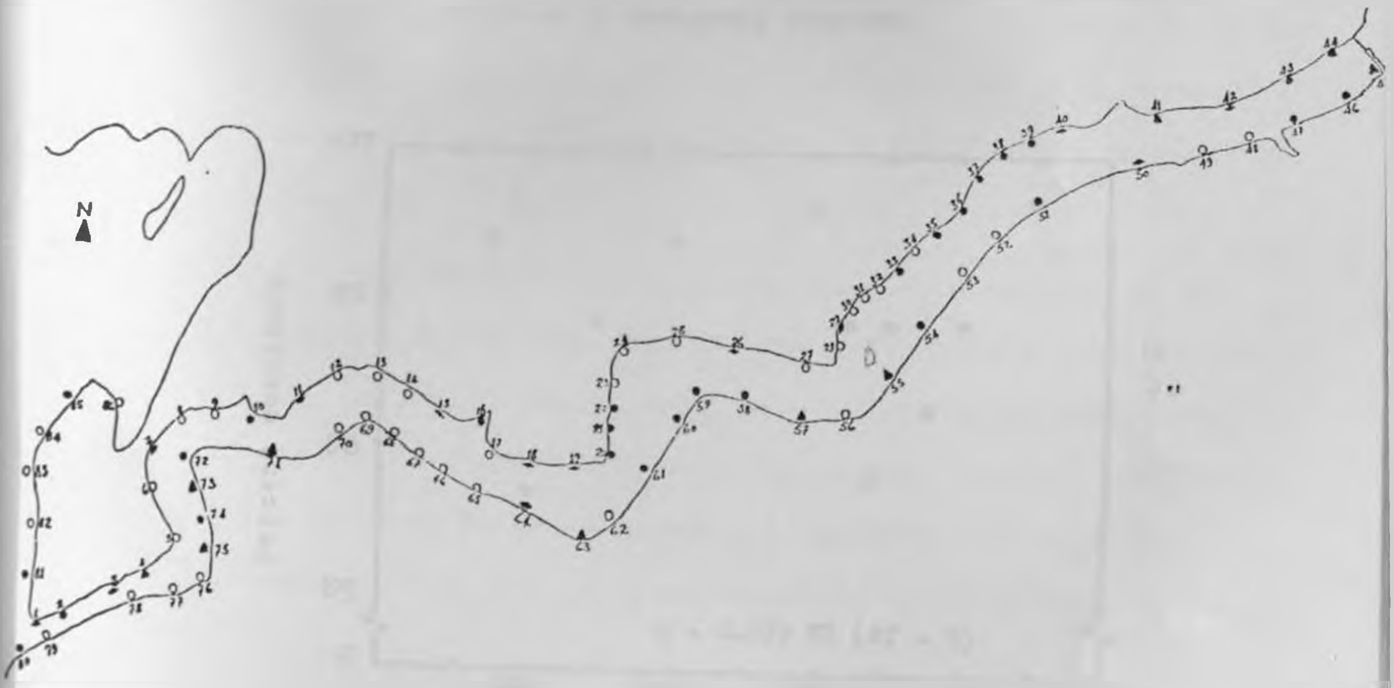
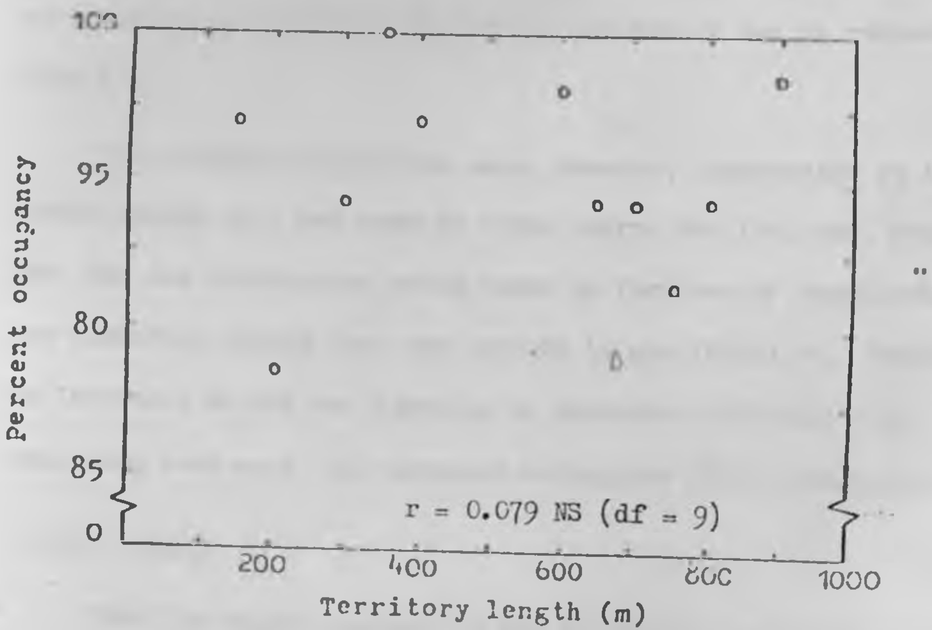


Fig. 3.6 The relationship between territory size and its occupancy by African Fish Eagles in Queen Elizabeth National Park. Twenty territories were used in this analysis. The graph shows only 11 points because the lengths used were in multiples of 50 and some lengths accounted for 2 or 3 occupancy records.



Just as the population of Fish Eagles remained stable throughout the study period (section 2.3.3), so did the numbers of territories. However, minor changes occurred. Thus, during 1975/6, Territory No.4 was abandoned while Nos.73 and 75 were vacated during the 1976/7 study period. The birds which owned these territories abandoned them because they were so marginal that they all lacked trees which the occupants could have used as nest sites (Fig.3.1).

The abandoned territories were not occupied by other new Fish Eagles, rather they were annexed, shortly after being vacated, by the owners of neighbouring territories. Thus Territory No.75 was completely annexed by Pair No.76. Territories 4 and 73, however, were partitioned by Pairs No.3 and 5 and Nos.72 and 74 respectively (Fig.3.1).

The vacated territories were, however, compensated by the establishment of 4 new ones by 4 new pairs: Nos.13b, 40b, 55b, and 70b; the new territories being named so for fear of complicating the numbering system that was already in use (Fig.3.1). Residence in Territory No.40b was taken up in September 1975 while the remaining ones were all occupied during the 1976/7 study period.

3.3.2.2 Calls

The Fish Eagle started its day by calling and continued to call throughout the day (Fig.3.4b). The first calls were made at the roost tree, and 20 such calls made between 06:25 and 06:46 had their mean time at 06:38.

During 17 dawn-dusk observations, the 34 Fish Eagles made 2341 calls, averaging ca. 69 calls/bird/day. Fish Eagles called significantly more between 10:00 and 15:00 than at other times of the day (Table 3.8 & Fig.3.4b).The notion that the Fish Eagle's call is an integral component of its territoriality is supported by the fact that calls were significantly correlated with territorial incursions ($r = 0.579$, $df = 12$, $P < 0.05$).

3.3.2.3 Flights

The Fish Eagle made 4 types of flights: the territorial, the soaring, the ordinary or perch to perch, and the fishing flights. Territorial flights, like perch to perch ones, were short and were for attacking intruders, especially conspecifics. Of 1493 minutes the Eagle spent in flight, 13.5% of the time was for territorial defence, 56.8% for soaring, 10.6% for perch to perch, and 19.1% for fishing flights. Three hundred eighty seven territorial flights were recorded in 50.7 eagle-days, giving a mean of 7.6 flights/day. Territorial flights occurred throughout the day, but were significantly more common between 08:00 and 17:00 than during other periods of the day (Table 3.9) and their temporal frequencies were significantly correlated with those of territorial encounters ($r = 0.916$, $df = 12$, $P < 0.001$). However, their frequencies were highly significantly correlated with those of intrusions by

Table 3.8 The frequencies of calls made by the Fish Eagle during 17 pair-days in Queen Elizabeth Park in relation to the time of the day. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974). Obs. = observed and Exp. = expected values.

Time of day(hr)	Observation time (hrs)	Number of calls				D-value
		Total	Calls/hr	Obs./hr	Exp./hr	
06-07	4.17	26	6.24	6	10.4	0.13112*
07-08	17.00	103	6.06	6	10.4	
08-09	17.00	120	7.06	7	10.4	
09-10	17.00	155	9.12	9	10.4	
10-11	17.00	237	13.94	14	10.4	
11-12	17.00	342	20.12	20	10.4	
12-13	17.00	379	22.29	22	10.4	
13-14	17.00	257	15.12	15	10.4	
14-15	17.00	230	13.53	14	10.4	
15-16	17.00	177	10.41	10	10.4	
16-17	17.00	145	8.53	9	10.4	"
17-18	17.00	70	4.12	4	10.4	
18-19	17.00	61	3.59	4	10.4	
19-20	6.83	39	5.71	6	10.4	
Total	215.00	2341	145.84	146	145.6	

* $P < 0.05$ ($D_{0.05,146} = 0.11119$).

Table 3.9 The frequencies of territorial flights made by the Fish Eagle in Queen Elizabeth Park in relation to the time of the day. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974). Obs. = observed and Exp. = expected values.

Time of day(hr)	Observation time (hrs)	Number of flights				D-value
		Obs.	Obs./hr	Obs./hr x 100	Exp./hr x 100	
06–07	15.42	4	0.26	26	54.9	0.15447***
07–08	48.33	23	0.48	48	54.9	
08–09	50.17	33	0.66	66	54.9	
09–10	53.33	37	0.69	69	54.9	
10–11	60.58	44	0.73	73	54.9	
11–12	57.25	36	0.63	63	54.9	
12–13	48.33	35	0.72	72	54.9	
13–14	43.17	37	0.86	86	54.9	
14–15	45.50	35	0.77	77	54.9	
15–16	52.08	37	0.71	71	54.9	
16–17	57.17	41	0.72	72	54.9	
17–18	56.25	16	0.28	28	54.9	
18–19	49.83	9	0.18	18	54.9	
19–20	21.67	0	0.00	00	54.9	
Total	659.08	387	7.69	769	768.6	

*** $P < 0.001$ ($D_{0.001;769} = 0.06702$).

young Eagles ($r = 0.960$, df = 12, $P < 0.001$) but not significantly correlated with those of intrusions by territorial adults ($r = 0.344$, df = 12, $P > 0.1$). These findings are consistent with the results that, as a method of discouraging territorial trespass, chases were most frequently employed against young than against territorial adults whose incursions were mostly repulsed by calls (section 3.3.2.1).

Depending on weather, the Fish Eagle performed soaring flights almost daily. These flights accounted for 4.1% of the Eagle's time (Table 3.2). Soaring began from 10:00 and continued until evening. They were significantly more common between 10:00 and 15:00 than during other periods of the day (Table 3.10). The Eagle made 2 types of soaring flights. The low soaring flight which was undertaken from 10:00 to 19:00, but was significantly more common between 10:00 and 17:00 and the high soaring flight which was performed almost exclusively between 10:00 and 15:00 (Table 3.10). The low soaring flights were significantly shorter than the high ones ($t = 2.356$, df = 93, $P < 0.05$; data in Table 3.11). Additionally, the low flight was more frequently performed than the high one and more frequently by the males (Table 3.11).

During the low soaring flight the Eagle remained largely within their territorial airspace and never went higher than about 100 m up in the sky. This type of soaring flight was performed repeatedly, even up to 8-10 per day, and they usually occurred within a few

Table 3.10 The frequencies of soaring flights made by the Fish Eagle in Queen Elizabeth Park in relation to the time of the day. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974). Obs. = observed and Exp. = expected values.

Time of day(hr)	No. of all flights			No. of low flights			No. of high flights		
	Obs.	Exp.	D-value	Obs.	Exp.	D-value	Obs.	Exp.	D-value
06-07	0	7.93	0.28571***	0	4.86	0.28571***	0	1.93	0.28571*
07-08	0	7.93		0	4.86		0	1.93	
08-09	0	7.93		0	4.86		0	1.93	
09-10	0	7.93		0	4.86		0	1.93	
10-11	14	7.93		8	4.86		6	1.93	
11-12	15	7.93		6	4.86		8	1.93	
12-13	22	7.93		10	4.86		4	1.93	
13-14	17	7.93		10	4.86		3	1.93	
14-15	18	7.93		12	4.86		4	1.93	
15-16	8	7.93		8	4.86		0	1.93	
16-17	10	7.93		9	4.86		1	1.93	
17-18	4	7.93		2	4.86		1	1.93	
18-19	3	7.93		3	4.86		0	1.93	
19-20	0	7.93		0	4.86		0	1.93	
Total	111	111.02		68	68.04		27	27.02	

* $P < 0.05$ ($D_{0.05,27} = 0.25438$),

*** $P < 0.001$ ($D_{0.001,68} = 0.23289$),

*** $P < 0.001$ ($D_{0.001,111} = 0.18384$).

Table 3.11 The types, frequencies and durations (in minutes) of soaring flights performed by the Fish Eagle in Queen Elizabeth Park. Chi-square test was performed on frequency data.

	Low soaring flight			High soaring flight				Overall
Bird	n	Mean ± S.d.	Range	n	Mean ± S.d.	Range	Total	Mean ± S.d.
Male	55	9.1 ± 5.5	2-24	14	33.9 ± 11.2	21-54	69	14.1 ± 12.2
Female	5	7.2 ± 4.9	3-13	3	39.7 ± 24.7	17-66	8	19.4 ± 21.7
Both birds	8	12.0 ± 5.6	4-18	10	30.8 ± 18.0	22-65	18	22.4 ± 17.2
Total	68			27			95	
Overall Mean ± S.d.		9.3 ± 5.5			33.4 ± 15.2			16.0 ± 14.2

$X^2 = 9.103^*$ (df = 2)

Table 3.12 The frequencies of ordinary and fishing flights made by the Fish Eagle during 18 pair-days (dawn-dusk) of observations. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974).

Time of day(hr)	Observation time (hrs)	Number of flights		D-value
		Observed	Expected	
06-07	4.17	18		
07-08	18.00	51	53.3	0.05312*
08-09	18.00	81	53.3	
09-10	18.00	58	53.3	
10-11	18.00	31	53.3	
11-12	18.00	52	53.3	
12-13	18.00	43	53.3	
13-14	18.00	40	53.3	
14-15	18.00	48	53.3	
15-16	18.00	42	53.3	
16-17	18.00	62	53.3	
17-18	18.00	60	53.3	
18-19	18.00	72	53.3	
19-20	6.83	26		

* $P < 0.05$ ($D_{0.05,640} = 0.04838$).

Two types of fishing flights were undertaken by the Fish Eagle: the perch to water flight or fishing sortie (Brown1980) and the low circling flight which was made directly above and close to the water surface. The importance of these methods in the fishing efforts and success of the Eagle are discussed in section 4.3.2.1. Like perch to perch flights, fishing sorties were very short, lasting no more than a few seconds. However, 14 circling flights averaged 4.3 minutes (range: 1.6-9.8 minutes). The male spent 2% of his and the female 0.7% of her daytime on fishing flights; for both members of a pair, this activity occupied only 1.4% of their combined daylight time (Table 3.2).

3.3.2.4 Feeding

The Fish Eagle started to eat soon after prey was caught. Most prey were eaten while still alive and twitching. The time taken to finish a meal did not differ significantly between the sexes of a pair (Table 3.13). For both birds 46 meals took an average of 25.7 minutes to complete. This time would represent only 3.3% of the 13-hour eagle-day (cf Table 3.2).

3.3.2.5 Other diurnal activities

In addition to those already described, the Fish Eagle exhibited other behaviours. These included drinking, bathing, mating, preening, and chasing other birds. These activities were either irregular or of very short durations, thus I combined them into one sub-heading.

Table 3.13 The durations (minutes) of feeding, drinking and bathing in the Fish Eagle in Queen Elizabeth Park.

Activity	Sex	n	Time (minutes) Mean ± S.d.	Time (minutes) Range	t-value	df
Feeding	Male	23	26.7 ± 12.4	7-53	0.450 NS	44
	Female	23	24.7 ± 13.9	7-50		
	Both birds	46	25.7 ± 13.1	7-53		
Drinking	Unknown	6	3.5 ± 1.4	2-5		
Bathing	Unknown	7	18.4 ± 9.0	11-35		

Occasionally, a Fish Eagle drank water and took a bath. On 6 occasions drinking lasted between 2-5 minutes, averaging 3.5 minutes (Table 3.13). While drinking the bird stood by the shoreline and dipped its beak into the water a few times and then left. On the other hand, baths took longer than drinking. Seven timed baths averaged 18.4 minutes (Table 3.13). When bathing, the Eagle waded knee or belly-deep into the water and then dipped its head and tail regions successively into the water and splashed it all over itself by beating its wings and dipping its tail into it. The bird then waded ashore or flew to a perch where, normally facing into the sun, it opened both wings and dried itself. Since most drinking and bathing took place during the afternoons and evenings, they could have been induced by excessive heat loads experienced during the day (see panting, sections 9.3.2 & 9.4).

Mating and preening were so brief or so irregular that records were not kept of the time the Fish Eagle spent on them. Copulations occurred throughout the year, during both the breeding and non-breeding cycles of the birds, and it will be described in detail in section 5.3.8. Preening occurred any time of the day. It was especially common after an incubation or brooding stint, a bath and after copulation (section 5.3.8). No social preening was ever observed during this study.

Apart from interactions with conspecifics (section 3.3.2.1 above), the Eagle also spent some of its daytime interacting with other birds and animals, usually chasing them. Of 298 incidences, 293 (98.3%) of them involved other birds and the remaining 5 (1.7%)

involved mammals (Table 3.14). Interactions initiated by the Eagle predominated (82.9%) over those initiated by the other birds and mammals (17.1%).

Breeding Fish Eagles, especially those with nestlings, chased all large birds which overflew or alighted in their territories (section 10.3.2). Additionally, large birds, especially Marabou Storks Leptoptilos crumeniferus, were displaced from roost trees. Egyptian Geese Alopochen aegyptiacus were chased from eyries which they frequently investigated (see section 5.3.7) and while they were in the territorial waters or overflying the airspace of any pair of Fish Eagles. Vultures, especially Hooded Vultures Necrosyrtes monachus, were driven away as they were mounting thermals in order to soar. However, attempts failed to chase away the White-headed Vulture Trigonoceps occipitalis while they were appropriating the prey of bands of young Fish Eagles (section 4.3.2.2). Vultures were also displaced from roost trees, especially on days when they fed on carcasses in the territories of the Fish Eagles.

The Fish Eagle also chased and grounded several species of birds in piracy attempts (Table 3.14). On the other hand, some of the birds on which piracies were attempted also tried to rob the Eagle of its prey. Both types of piracy are discussed elsewhere (section 4.3.2.2).

The Peregrine Falcon Falco peregrinus, the Spurwing Plover Hoplopterus spinosus and the Pied Crow Corvus alba molested the Fish Eagle (Table 3.14). They normally did so by repeatedly buzzing the Eagle wherever they found it. The Plover, however, carried this molestation further than the others. On 3 of the 12 occasions it was seen buzzing the Fish Eagle, it forced the Eagle to temporarily

Table 3.14 Interspecific interactions between the Fish Eagle and other birds and animals in Queen Elizabeth Park. All first or single entries are of incidences initiated by the Fish Eagle, those in parentheses were started by the species of bird or animal involved in the interaction.

Affected bird or animal species	Nature and frequency of interaction				
	Territorial	Piracy	Molestation	Not clear	Total
Vulture	24	0(5)	0	0	24(5)
Osprey?	0	3	0	0	3
Tawny Eagle	3	0	0	0	3
Bateleur	1	0	0	0	1
Kite	1	0	0(2)	0	1(2)
Peregrine	0	0	0(4)	0	0(4)
Egyptian Goose	15	0	0	16	31
Marabou Stork	74	0	0	4	78
Pelican	0	21(1)	0	0	21(1)
Pied Kingfisher	0	4	0	6	10
Saddle-billed Stork	1	2(2)	0	3(3)	6(5)
Goliath Heron	0	5(2)	0	1	6(2)
Long-tailed Cormorant	0	1	0	0	1
Yellow-billed Stork	0	2(4)	0	1	3(4)
Hammerkop	0	0(8)	0	3	3(8)
Sacred Ibis	0	0	0	3	3
Hadada Ibis	0	0	0	7	7
White-winged Black Tern	0	0	0	8	8
Little Egret	0	0	0	1	1
Water birds (various)	0	0	0	23	23
Spurwing Plover	0	0	0(12)	2	2(12)
Pied Crow	0	0	8(5)	0	8(5)
Hippopotamus	0	0	0	2(1)	2(1)
Long-tailed Mongoose	0	0	0	1	1
Leopard	0	0	0	1	1
Total	119	38(22)	8(25)	82(4)	247(51)

discontinue feeding. However, on none of these incidences did the Eagle leave behind its prey as it flew away.

For no obvious reasons, the Fish Eagle also chased or dived at several species of birds. The majority of these birds were small ones which the Eagle could easily have killed were it to have caught them. For this reason I suspected that such interactions probably had predatory intentions (section 4.3.1).

On 23 November, 1975, one of the post-fledging young of Pair No.6 made a dive at the head of a lone hippopotamus. The hippo ducked, only to emerge about 3 minutes later. On the same day, while returning from an intense border clash with Pair No.5, the male of Pair No.6 dived at the head of another hippo which also ducked. In both cases there were no follow up dives at the hippos.

As I watched Pair No.6 on 4 September 1976, for the role of each adult during brooding, the two birds suddenly started to make the "ook-ook" alarm call and repeatedly swooped at something hidden from me by a bush. A few seconds later a subadult leopard lept into an open area and the birds continued to dive at it until it disappeared into dense thickets some 50 m away from where it emerged. Soon after the leopard disappeared, the birds settled down.

On 20 November 1975, as members of Pair No.7 sat on the ground by the shoreline, a Long-tailed Mongoose Herpestes ichneumon emerged from a nearby bush. The birds watched the animal as it advanced towards them. About 10 m from the birds it diverted its course, apparently to avoid walking straight onto them. Nevertheless, both birds attacked it, swooping on it in turns. Each time an Eagle approached, the Mongoose lept high up in the air as if to bite it.

About 2 minutes later the Eagles abandoned the attack and flew away. Standing at the edge, the Mongoose repeatedly reached into the water with its muzzle. Eventually it dragged out a large fish, probably a dead one because there was no flapping by the prey. As it retreated into the bush, no Fish Eagle ever attacked it again.

3.4 DISCUSSION

Territoriality is a widespread phenomenon in birds (e.g. Schoener 1968; J. Brown 1969) and is especially common among birds of prey (Brown 1970a, 1976a, b & c, 1980). Despite early and protracted studies of the African Fish Eagle (e.g. Brown 1955, 1970a), territoriality in the species has only recently been definitively demonstrated (Greenspan & Torre-Bueno 1971) and has since been accepted as being a habit of this bird (Brown & Hopcraft 1973, Eltringham 1975, Thiollay & Meyer 1978). And Brown (1980) states that the Fish Eagle "is the most intensely territorial bird of prey" he ever knew.

J. Brown (1969) postulated that territorial species tend to occur in regular dispersion patterns rather than in random or clumped ones, and that their territories abut extensively instead of overlapping. Apart from the 7 pairs of Fish Eagles Brown (1970a & 1980) studied on the Raboor Islands, Winam Gulf, L. Victoria, whose territories overlapped extensively, the dispersion patterns of Fish Eagles in other habitats have conformed with the general pattern proposed for territorial species. Thus at Lakes Naivasha and Baringo (Brown 1980) and along the Kazinga Channel in this Park (Eltringham 1975, Thiollay & Meyer 1978), the Fish Eagle is regularly dispersed. During this study, too, Fish Eagles were regularly distributed and their territories abutted rather than overlapped.

The regular distribution pattern and the vigorous defence of the Fish Eagle's territory facilitate the mapping out of the defended area (Noble 1939) and, therefore, the determination of its size. Thus the single pair that Greenspan & Torre-Bueno (1971) intensively studied in this Park had a territory measuring 800 m long and 325 m wide. It covered an area of 26 ha, 30% of which was under water. Thiollay & Meyer (1978) found that the diameters of territories along the Channel varied from 200-900 m and they covered 20-50 ha. At L. Naivasha the territory length averaged 300 m but varied from 180-400 m, and it covered 3-4 ha of water (Brown 1980).

During this study, 20 territories averaged 525 m of shoreline length and 575 m in width. They ranged from 6.8-49.0 ha, averaging 29 ha. The portion under water averaged 15.9 ha, or 54.5%, and that on land 13.3 ha, or 45.5%, of the area (Table 3.1). Thus Fish Eagle territories in this Park are considerably larger than those of birds at L. Naivasha, Kenya.

Brown (1980) states that the amount of time spent by the Fish Eagle on various activities differ from one habitat to another. Thus, at L. Naivasha, pairs inhabiting lagoons were more active than those living on the open lake. Although Brown found that the male was more active than the female, the Eagle spent 90-95% of its time sitting, "most of it certainly just loafing". During this study, too, the male was more active than the female. Much as the Eagle sat, apparently doing nothing, for a very highly disproportionate amount of its daytime, this time was not necessarily spent idle. As it sat, the bird continuously scanned the sky, clearly in anticipation of intrusions by conspecifics into their territory. This almost day-long watchfulness, the conspicuous perching, accentuated colouration

(Frontispiece Plate 4), the all-day calling and the frequent perch to perch flights definitely advertised and, therefore, greatly enhanced the chances of a pair of Fish Eagles to defend their territory against intruders.

Greenspan & Torre-Bueno (1971) found that Fish Eagle calls were significantly associated with certain activities like flying and mating but not so with others. Because the calls by one member of a pair strongly evoked responses in the partner, these authors hypothesized that a main function of calls is a social one related to the maintenance of the pair-bond (section 5.3.8) and the coordination of mutual activities. They also noted that calling was particularly associated with the presence of flying intruders, and that the calls of a pair were stimulated, although not so strongly as those of a pair, by calls of other pairs. These findings suggest that calls served a territorial function as well.

During this study, the Eagle started its day by calling, and did so throughout the day. The temporal frequencies of calls were significantly correlated with those of territorial incursions (Fig.3.4), thus indicating that, apart from serving a social function, calls were also used during territorial interactions. The advantages of using calls to deter intrusions by conspecifics are discussed below.

At L. Naivasha, Brown (1980) found that Fish Eagles spent 2.7% of their 750-minute eagle-day soaring and that these flights were not connected with feeding or territorial defence. During this study, the birds soared for 4.1% of the 780-minute day and they made two kinds of soaring flights: the low and short, and the high and prolonged soaring flights. When performing the low soaring flight, which was limited to the territorial airspace of the pair, no other birds, apart from the young of the pair, were tolerated nearby. In fact, the Eagle frequently used the low soaring flight to catch up with and drive away conspecifics and other large birds that trespassed their airspace. Probably because of using low soaring flights in territorial defence, the frequencies of these flights showed a higher correlation with those of intrusions by young ($r = 0.661$, $df = 12$, $P < 0.01$) than with those of territorial adults ($r = -0.035$, $df = 12$, $P > 0.1$). This is in agreement with Greenspan & Torre-Bueno's (1971) results that Eaglets intruded for longer periods and they entered the core area of the territory more than adults. Furthermore, the above correlation coefficients are consistent with the findings that chases and fights (Table 3.3) were more frequently employed against young birds (69.8% of cases) than against territorial adults (26% of cases). The coefficients also conform with the results that calling alone deterred 73.9% of the intrusions by adults whereas it discouraged only 30.3% of the incursions by young birds. The fact that the male performed significantly more of the low soaring flights than the female (Table 3.11) suggests that he was more active in the defence of the territory than his mate.

Fish Eagles, during this study, also caught fish from soaring flights but they did not use this method of hunting regularly. That the temporal frequencies of soaring flights were not significantly correlated with those of fishing attempts ($r = -0.091$, $df = 12$, $P > 0.1$ for both low and high soaring flights) supports the above view. Soaring flights in the Fish Eagle probably served functions other than those connected with fishing.

The high soaring flights, however, were performed well above the airspace of any pair and were highly social. The participating Fish Eagle joined or was joined by other conspecifics and other large birds. These flights probably served both as a social display and as an exercise (Brown 1980).

The Fish Eagle spent about 3% of its daytime feeding, a very large percentage of its time compared to other activities. Considering the highly piratical habit of the bird (Brown 1970a, b & c & 1980;), it would have been more adaptive for it to bolt its prey rather than eating it piece-meal (section 4.3.3). It was not surprising that the comparatively long time spent feeding resulted in many conspecifics and other birds being attracted to and, therefore, attempting to pirate from the feeding bird (section 4.3.2.2). However, the Eagle greatly reduced the chances of losing its prey through piracy by its vigilance and the strong territorial disposition.

The evolutionary significance of territoriality in birds is a controversial one (e.g. Wynne-Edwards 1959, 1962, 1963; Lack 1966; J. Brown 1969). However, Hinde (1956) argued that territories in birds conferred several advantages to the owners: a) familiarisation of the owners with the environment in the area under their control; b) the advantage of prior ownership during aggressive encounters; c) protection of nest and nest site; d) prevention of epidemics; e) reduction of loss to predation for cryptic species; f) prevention of inbreeding; g) facilitation of pair formation and the maintenance of the pair-bond; h) prevention of interference with breeding activities; and i) all advantages accruing from the restriction which territorial behaviour imposes on the number of individuals using a limited food resource, including both short term advantages to the individual, e.g., in ensuring enough food for the young during critical periods, and long term advantages to the population, e.g. in density control.

Kalela (1954 in J. Brown 1969) and Wynne-Edwards (1959, 1962, 1963) proposed that territorial behaviour has evolved because of its limiting effects on population densities by preventing overpopulation and the resulting depletion of prey populations. Howard (1920) also considered regulation of populations an important function of territoriality. This hypothesis has, however, been criticised by several authors (e.g. Lack 1966; J. Brown 1969) for the reason that the proponents argued that it evolved through intergroup selection (Wynne-Edwards 1963) rather than via individual selection (J.Brown 1964).

According to J. Brown (1969), the most important function of territoriality in population regulation is its effect of excluding some individuals from breeding at all, and thereby resulting in non-breeding floaters. To conclusively demonstrate that territorial behaviour regulates a population, he argued that it is necessary to prove that a) the breeding population is stable, b) non-breeding floating adults or surpluses are present and make up a significant proportion of the population, and c) individuals are being prevented from taking up new territories, and therefore from breeding, in the defended area by the aggressive behaviour of the territory owners.

Like the L. Naivasha population (Brown & Hopcraft 1973, Brown 1980), the breeding Fish Eagle population on the Kazinga Channel was stable (sections 2.3.3 & 12.3.6), thus conforming with J. Brown's (1969) condition for territorial behaviour to regulate the population of a species. Although a much lower proportion than was found in other studies, 32% of all pairs, during this study did not breed (sections 12.3.6 & 12.4). Much as this high proportion of non-breeding birds might have greatly reduced reproductive success, and therefore contributed significantly to population regulation in the species, the non-breeders were not the ecological equivalents of the floaters of J. Brown (1969). Nevertheless, floaters were present in the population but their number was not determined. Although pairs which acquired new territories accounted for only a small fraction of the total number of pairs studied (4 out of 259 pairs), the fact that paired birds forced their way into and took up new territories in an already tightly packed shoreline is eloquent evidence that floaters probably constituted a substantial proportion of the Fish Eagle population in this Park. Consequently, they were probably excluded from taking up new territories, and therefore from breeding, along the shorelines by the aggression of territory holders. Furthermore, it is inconceivable to think that, during the 3-year study period, no birds were bereaved. The fact that no bird, except the female of Pair No.75 (Fig.3.1), was resident alone in their territory for any detectable period of time is another evidence for probably a large number of floaters to have existed in the Fish Eagle population of this study.

Brown (1980) has suggested that the high rate of non-breeding among established pairs of Fish Eagles, constituting from one-third to one-half of the populations (section 12.4) is the main mechanism by which the birds regulate their populations, and that it operates through social behaviour. He argued that if Fish Eagles, in being spaced regularly along shorelines, are at capacity population and if every pair spent at least 80% of its time defending its territory against conspecifics by vocal challenge or actual combat would have such distracting activities interfere with its breeding drive or make it less successful. Because of having larger territories, and therefore experiencing fewer territorial encounters, than Fish Eagles in other habitats, Brown (op. cit.) reported that the 7 pairs at Winam Gulf, L. Victoria, fledged more young (0.57 young/pair/year) than those at L. Naivasha (0.47 young/pair/year, Brown & Hopcraft 1973, Brown 1980) and than those on the Kazinga Channel (0.42 young/pair/year, Thiollay & Meyer 1978). The above argument (Brown 1980) is consistent with J. Brown's (1969) view that territoriality, apart from excluding some individuals from breeding, can also depress reproduction through other density-dependent behaviours. Thus, at high population densities the increased frequencies of agonistic encounters resulting from the compression of territories and the presence of floaters continually attempting to establish territories in already occupied areas depress reproductive success. Depression of reproduction at high population densities in mammals is well known (Christian 1963). In birds, too, it has been reported for many species other than the Fish Eagle (e.g. Kluijver 1951 & 1963, Lack 1958 & 1966, Perrins 1965, Carrick 1963, Jenkins 1961a & b).

During this study, the Fish Eagle had an annual productivity of 0.46 young/pair, and it increased, although not significantly, with increasing territory size (section 12.3.4 & 12.4). Although a correlation between territory size and the frequencies of territorial encounters is not available, the above finding is consistent with Brown's (1970a, 1980) suggestion that pairs which are close together tend to have more territorial encounters which, consequently, result in their breeding less successfully than those which are farther apart. The positive correlation between reproductive success and territory size during this study conforms with J. Brown's (1969) view that, at high population densities, other density-dependent territorial behaviours can depress reproduction.

Thus, the stability of the breeding population and the presence of floaters in the whole population during this study were suggestive of the view that territoriality in the species probably evolved to regulate the population (J. Brown 1969). It probably did so through the aggressive exclusion of some individuals from taking up new territories in the defended area, and therefore from all other benefits, including breeding, that individuals enjoyed after having acquired territories (Hinde 1956). The high proportion (32%) of non-breeders among the established pairs and the positive correlation between reproductive success and territory size were manifestations of the other effects of territorial behaviour, at high densities, in depressing reproduction (J. Brown op. cit.). Notwithstanding Lack's (1966) view that the above density-dependent effects of territorial behaviour have not been shown to be the primary factors responsible for reducing populations from high levels, the high proportion of non-breeding birds in an established population of Fish Eagles probably plays a significant role in the regulation of population in the species. Brown (1980) considered it the most important population regulation mechanism in the Fish Eagle. However, the extent non-breeding plays in population regulation in the species in this Park still remains to be quantified.

Apart from territoriality probably contributing significantly to regulate the population of the Fish Eagle in this Park and elsewhere, the roles of other environmental factors like nest site and food supply in this population control process need not be overlooked. Lack of nest sites and the collapse of badly built nests and of those built in insecure limbs of trees can stop eagles from breeding or from realizing high reproductive successes (Brown 1970b, 1974a & b, 1980). Thus, in Ayres' Hawk Eagle *Hieraaetus dubius*, Brown (2974b) concluded that the rarity of the species was probably attributable to its poor reproductive success which, in turn, was due to the persistent collapse of the nests. However, the lack of nest sites for some pairs of Fish Eagles and the collapse of a few of their nests during this study (sections 2.3.1, 8.3.4 & 12.3.4) could not have been major regulatory factors on their population.

In temperate regions, food supply has been known to control the population densities of predators like the Short-eared Owl *Asio flammeus* in Britain (Lockie 1955) and in Alaska (Pitelka *et al*. 1955a & b); the Pomarine Jaeger *Stercorarius pomarinus* in Alaska (Lack 1966); the Spanish Imperial Eagle *Aquila heliaca* (Lack op. cit.); the Sea Eagle *Haliaeetus albicilla* in Sweden (Halander 1983); Cooper's Hawk *Accipiter cooperii*, the Marsh Hawk *Circus cyaneus*, the Sparrowhawk *Accipiter collaris* and several owls (Strigidae) in Michigan and Wyoming (Craighead & Craighead 1956). Unlike the above temperate predators, the African Fish Eagle, in all habitats where it has been studied, especially at L. Naivasha (Brown 1980) and in this Park (section 3.3.2.3), hunts for such a very small proportion of the day that food supply cannot be considered as a factor that plays a significant role in the regulation of the population of the species.

CHAPTER 4

THE FOOD SUPPLY OF THE FISH EAGLE

4.1 INTRODUCTION

The Fish Eagle is largely a fish-eating bird of prey (Brown 1980). However, it is known to take eggs and young and even adults of waterbirds, and occasional carrion (Brown, op.cit., Porter 1903, Roberts 1958, Clancy 1964). It is also reported to eat such unusual prey as rats (Roberts, op.cit.) and frogs (Bannerman 1953).

Although it will readily pirate from conspecifics and other piscivorous birds, the Eagle largely eats prey it has caught (Brown, op.cit.). Despite hunting throughout the day, the fishing effort is more concentrated at certain times of the day than during others (Brown, op.cit.; Greenspan & Torre-Bueno 1971). Turbulent and murky water (Brown, op.cit.) and the position of the bird's shadow (Favaloro 1944, Greenspan & Torre-Bueno, op.cit.) are all thought to influence the fishing success.

Whitfield & Blaber (1978), working at Lake St. Lucia, South Africa, gave the first account of the numbers of fishes the Fish Eagle ate and they showed that fishes shoaling at the surface were caught most. However, they did not relate the numbers of the fishes taken to their abundance in the lake. Apart from the above study, quantitative examinations of the food of the Fish Eagle in relation to types, abundance and sizes of prey exploited, and in relation to seasonal fluctuations of prey are still lacking.

Using a captive bird, Stowell (1958) estimated that the daily food requirement of the adult is about 1 lb (454 g) of fish. Brown (1980) estimated it at only 225 g or about 8% of the bird's body weight. Green (1964), using Stowell's figure, found that the Fish Eagle population on L. Albert would take only 0.5% of the annual catch made by fishermen. Eltringham (1975), also using Stowell's figure, calculated that the Fish Eagle population of L. George would catch only 0.2-0.3% of the total annual fish production of the lake or only 0.8-1.1% of the amount harvested by man.

This study, therefore, aimed to:

(a) identify and quantify the food of the Fish Eagle in this Park,

(b) describe the hunting methods used and assess their successes,

(c) examine the effects of the feeding habits of the bird on the fisheries resource of the area and to appraise the extents of competition for this resource between man and the Fish Eagle, and,

(d) evaluate the role of the Eagle in nutrient transfer from water to land.

4.2 METHODS

4.2.1 The food and hunting methods

The types of food the Fish Eagle ate were assessed by observing live prey caught and by collecting prey remains dropped under feeding perches. Territorial birds obtained prey largely by hunting. However, both intraspecific and interspecific piracies were practiced. Birds, especially non-territorial adults and young, also scavenged.

It was not possible to separate the hunting activity of the Fish Eagle from that of a resting one, especially in birds whose nests (section 5.3.1) or hunting/resting perches were close to the shoreline (Brown 1980). Thus it was not possible to measure, in terms of time, the amount of hunting the Eagle did in the course of the day (section 3.3.2). The hunting efforts of the birds were therefore measured in terms of the hunting attempts (dives) they made.

The Eagle mounted its fishing attempts from perches, soaring flights and from low searching or circling flights made close above the water surface. During 7 dawn-dusk observations the numbers of all fishing attempts that 5 pairs made were recorded and whether a dive was initiated from a perch, a soaring or circling flight was noted. From these records the importance of each of the above fishing methods was assessed.

All dives and catches the Eagle made were recorded. Where possible, birds making dives and catches were sexed. From these data, the hunting efforts and successes of the sexes and of the pair were calculated. Hunting success was calculated as follows:

$$\text{Hunting success} = \frac{\text{No. of catches made}}{\text{No. of dives made}},$$

and was expressed as a percentage.

The time of the day when dives and catches were made were noted. From the numbers of dives and catches recorded for each hourly interval, I could assess, by the Kolmogorov-Smirnov or the D-test (Zar 1974), if the Fish Eagle made greater hunting efforts and successes during certain hours of the day than during others.

Incidences of intraspecific piracies and their successes were noted. The status (territorial, non-territorial adult or young) of the pirating or victimised bird was recorded. These data allowed for the determination of the status of birds using piracy more frequently than the others. All observed interspecific piracies and their successes and the species of the victimised birds were recorded. Piracies by other species of birds on the Fish Eagle were also noted.

4.2.2 Predation pressure on fish

Since fish constituted the staple diet of the Fish Eagle in the Park, it was necessary to assess the predation (exploitation) pressure the Eagle exerted on this resource. Live prey was generally identified as Tilapia sp. or catfish (Clariidae or Bagridae). From prey remains, however, I was able to distinguish between Clarias and Bagrus specimens. The numbers of each of the 3 types of fish were determined from these remains. Using these numbers and the densities of fish per hectare of L. George (Gwahaba 1973), an evaluation of the predation pressure the Fish Eagle exerted on the types of fish was made. Gwahaba's data were used because of the lack of similar information on the Kazinga Channel despite the fact that the two water bodies may have contained different densities of fishes. Perhaps Beadle's (1932, 1974) findings that L. George and the Kazinga Channel are limnologically similar further justify, although not wholly, the use of the L. George data.

The practice of using body organs in determining the ages, weights and growth rates of animals is widespread (e.g. Dasmann 1966, Taber 1963, Larson & Taber 1980). Both skeletal features and specific body organs can be used. Thus, for example, Laws et. al. (1967, 1975) successfully predicted the weights, ages and conditions of elephants Loxodonta africana in Uganda by use of hind leg weights, shoulder heights and jaw lengths. Malpas (1977) in addition to the above methods, used the eye lens weights to predict ages of elephants in Murchison Falls and Queen Elizabeth National Parks.

Eruption sequences, wear patterns and cementum lines of teeth have been widely employed to age ungulates in this Park (Spinage 1967a & b, Grimsdell 1969, Kodha 1971). In fishes, the techniques of examining scales, operculi, vertebrae, otoliths and other structures for age and weight determinations are also common (e.g. Balon 1971, Garrod 1959). Similarly, during this study, the operculi of Tilapia spp. and the heads of Clarias and Bagrus spp. recovered from the territories were used to predict the sizes of fish the Fish Eagle ate.

The fresh weights and head-tail lengths of 335 Tilapia spp. landed at Mweya Pier on 18 August 1976 were recorded. Their operculi were removed, cleaned, sun-dried and measured (Fig. 4.1). Similarly, the fresh weights and head-tail lengths of 161 Clarias and 234 Bagrus spp. were noted. Their head lengths were measured (Figs. 4.2 & 4.3). These data permitted the categorisation of the prey fishes, represented by the operculi and heads recovered from prey remains, into size classes. From the numbers of collected operculi and heads, I could evaluate predation pressures the Fish Eagle exerted on fishes in the various size classes.

To find out whether predation pressure shifted from wet to dry seasons the respective types of fish remains were placed into seasonal collections which covered 3 wet and 5 dry seasons. For each fish type the Spearman's Rank Correlation Test (Zar 1974) was used to ascertain if there were seasonal shifts in the frequencies of fish taken by the Eagle in relation to their sizes.

That overlaps existed between man and the Fish Eagle in the exploitation of the fisheries resource of the area was realized at the beginning of the study. There were overlaps in the types of fish exploited, and for each fish type, in the sizes taken. The degree of overlap for the sizes of each fish type exploited was once more examined by the above Correlation Test.

The daily and annual amounts of fish the Fish Eagle removed from the waters of the Park were estimated from the numbers of fish an Eagle captured during dawn-dusk observations. The daily food requirement of the bird was estimated from the fishes it landed and which were subsequently recovered after it had finished eating.

Fig. 4.1 Line drawings of *Tilapia* sp. (top) and its operculum (bottom) to show the measurements used in deriving the weights (Wt) and head-tail lengths (HTL) of the species from the lengths of the opeculi (OPL) which were recovered from Fish Eagle territories in the study area.

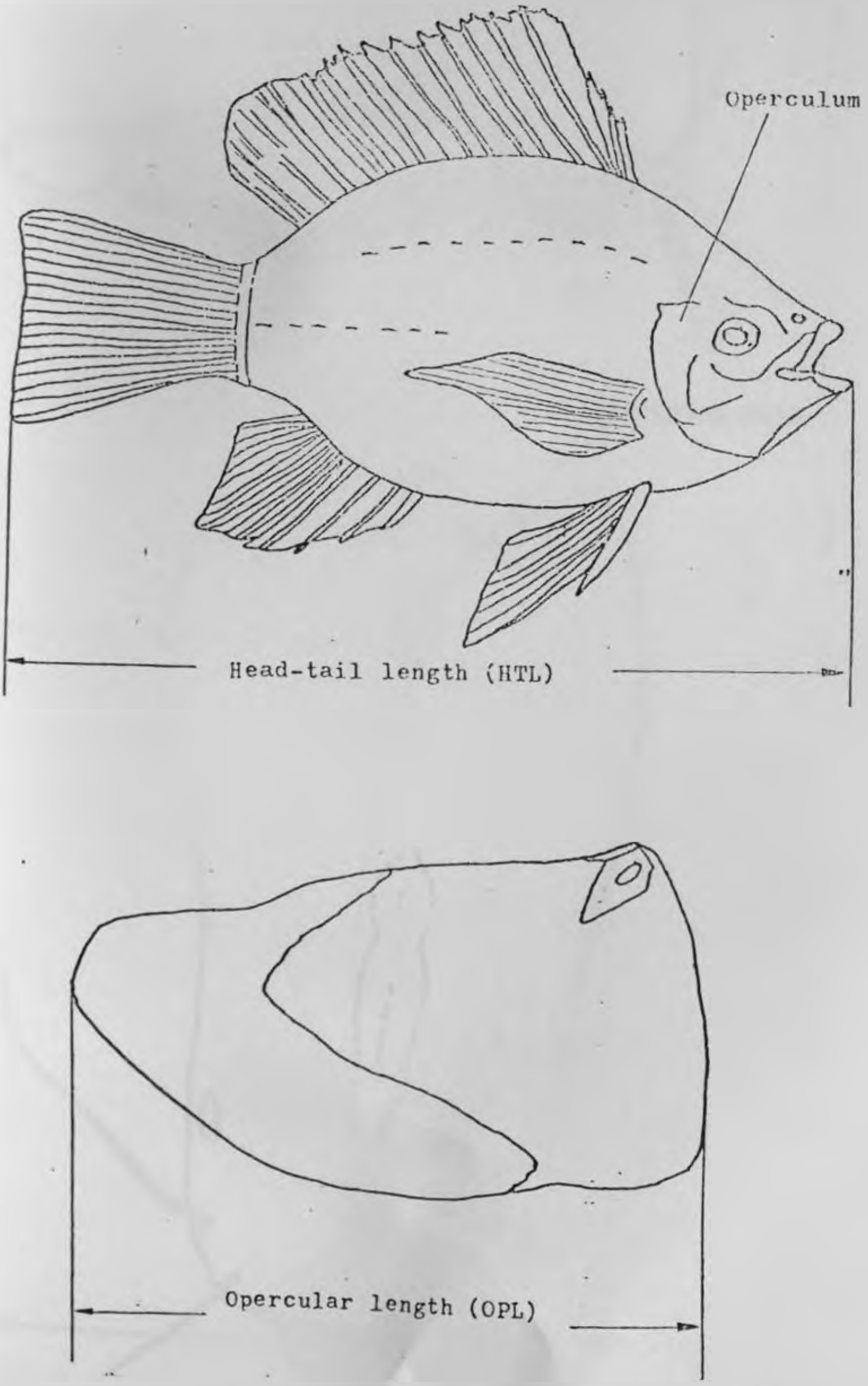


Fig. 4.2 Line drawing of *Clarias* sp. (top) and the head (bottom) to show the measurements used in deriving the weights (Wt) and head-tail lengths (HTL) of the species from the lengths of heads (HL) recovered from Fish Eagle territories in the study area. Head lengths were measured so because most collected heads had the bony crests beyond the elongated hole damaged.

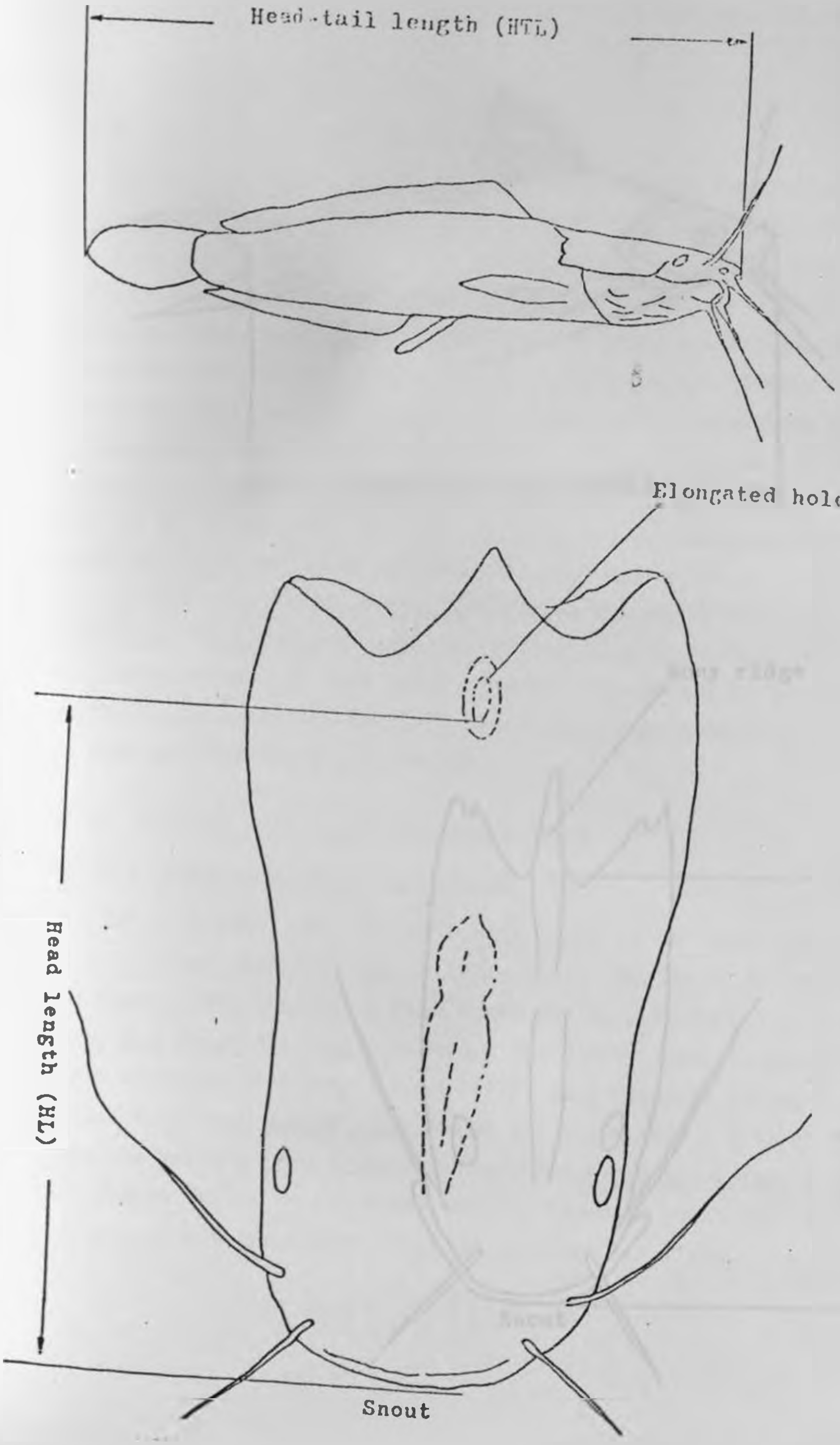
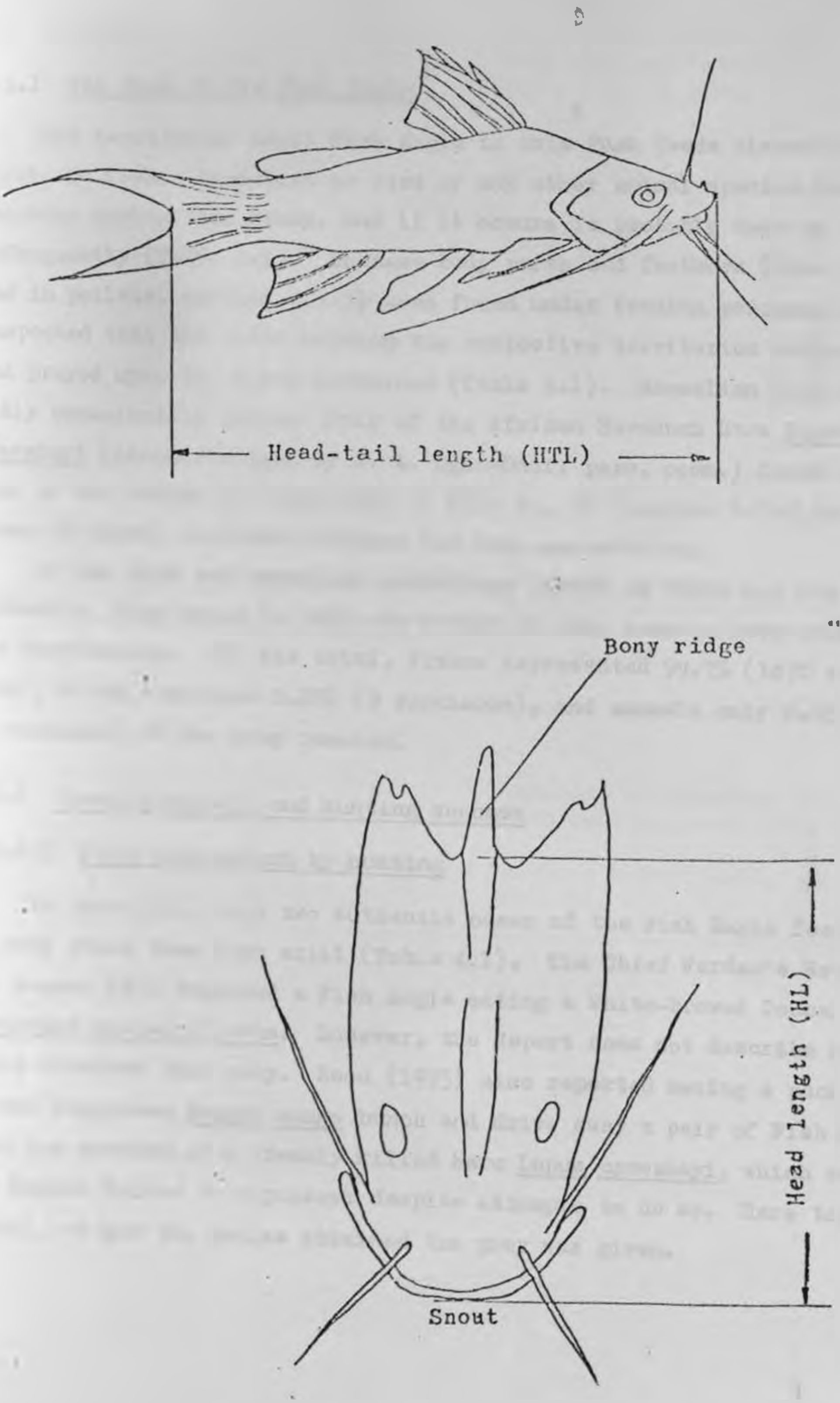


Fig. 4.3 Line drawing of *Bagrus* sp. (top) and the head (bottom) to show the measurements used in deriving the weights (Wt) and head-tail lengths (HTL) of the species from lengths of heads (HL) recovered from the Fish Eagle territories in the study area. Head-tail length was measured only upto the fork of the tail because in most freshly landed fishes one or both lobes of the tail were frequently damaged.



Using the above data, the fish productivity data for L. George (Din & Eltringham 1974, Gwahaba 1973), and the known numbers of Fish Eagles on that lake, estimates of the annual fish harvests were made. These were then compared with the annual human harvests from the same lake.

4.3 RESULTS

4.3.1 The food of the Fish Eagle

The territorial adult Fish Eagle in this Park feeds almost exclusively on fish. Predation on bird or any other animal species was not observed during this study, and if it occurs it probably does so very infrequently (Table 4.1). Because body parts and feathers (also contained in pellets, section 4.3.3) were found under feeding perches, it was suspected that the birds holding the respective territories captured and preyed upon the birds concerned (Table 4.1). Mammalian prey is probably occasionally taken. Hair of the African Savannah Hare Lepus crawshayi (identification by A. A. Ogen-Odoi, pers. comm.) found in the guts of two 8-week old nestlings of Pair No. 86 (section 8.3.4 for cause of death) provided evidence for this speculation.

If the bird and mammalian predations listed in Table 4.1 are authentic, they bring to 3480 the number of prey remains recovered from the territories. Of this total, fishes represented 99.7% (3470 specimens), birds comprised 0.26% (9 specimens), and mammals only 0.03% (1 specimen) of the prey remains.

4.3.2 Hunting methods and hunting success

4.3.2.1 Food procurement by hunting

In this Park, only two authentic cases of the Fish Eagle feeding on prey other than fish exist (Table 4.1). The Chief Warden's Report for August 1973 reported a Fish Eagle eating a White-browed Coucal Centropus superciliosus. However, the Report does not describe how the Eagle obtained this prey. Rood (1975) also reported seeing a pack of Banded Mongooses Mungos mungo bunch and drive away a pair of Fish Eagles from the carcass of a freshly killed hare Lepus crawshayi, which carcass the Eagles failed to repossess despite attempts to do so. Here too no details of how the Eagles obtained the prey was given.

Table 4.1 A record of prey items other than fish suspected taken by the Fish Eagle in Queen Elizabeth Park.

Date	Name of prey	Comment and source
18.3.75	White-winged Black Tern (*Chlidonias leucoptera*)	Left wing and feathers recovered under feeding perch (Pair No. 7).
23.11.75	Unidentified bird	Feathers in pellets under feeding perch (Pair No. 6).
18.1.76	Unidentified bird	Feathers in pellets under feeding perch of (Pair No. 3).
28.4.76	White-winged Black Tern (*Chlidonias leucoptera*)	Feathers under feeding perch of Pair No. 6 (N. Okurut L'Otai, pers. comm.)
16.12.76	White-winged Black Tern (*Chlidonias leucoptera*)	Feathers under feeding perch (Pair No. 6).
19.12.76	Savannah Hare (*Lepus crawshayi*)	Hair found in gut contents of two 8-week old chicks (Pair No. 87) which were probably eaten by a leopard.
12.1.77	Crowned Plover (*Stephanibyx coronatus*)	Fresh and pinkish left leg and feathers under feeding perch (Pair No. 8).
18.1.77	Pied Kingfisher (*Ceryle rudis*)	Feathers under perch (Pair No. 82).
21.1.77	Pied Kingfisher (*Ceryle rudis*)	Mandibles and feathers in pellets under feeding perch (Pair No. 6).
27.2.77	White-winged Black Tern (*Chlidonias leucoptera*)	Feathers under feeding perch (Pair No. 6).

During this study the territorial bird normally ate fish which it caught. Such prey was usually hunted by sitting on favourite perches and watching the water. From such perches fishing sorties of brief flight durations, usually lasting no more than a minute, were made (section 3.3.2.3). However, prey were also captured from soaring and searching or circling flights. Hunting by circling was usually employed during windy conditions, at a time when hunting by sitting on perches had apparently become difficult because then the wind shook both the Eagle and its perch. During such weather, Fish Eagles from adjacent territories could be seen flying to and fro over their respective territorial waters and turning round just at the borders. Dives were most frequently launched from perches and least so from soaring flights (Table 4.2a). Although the hunting successes of the 3 methods did not differ significantly (Table 4.2b), fishing attempts from perches succeeded more often than those from soaring and circling flights.

During this study, 436 dives were observed (inclusive of those by young), of which 288 succeeded, hence giving the Eagle a hunting success of ca. 66%. For 353 sorties where the sexes of the birds making the dives and catches were known, the male made significantly more dives than the female (Table 4.3a). He succeeded in 65% of his fishing attempts while the female did so in about 78% of hers (Table 4.3b). However, these successes did not differ significantly between the sexes (Table 4.3b). Overall, about 69% of all the sorties of the pair succeded (Table 4.3b), a success rate which compares well with the 66% registered for all observed dives.

Records for 7 dawn-dusk watches on 5 pairs of birds showed that dives are made at any time of the day and with fairly equal frequencies (Tables 4.4 & 4.5). For west bank pairs, however, significantly more fishes were caught between 07:00-12:00 and 18:00-19:00 than at other times of the day (Table 4.4). For east bank pairs, however, catches occurred equally well during all hours of the day (Table 4.5).

4.3.2.2 Food procurement by piracy

Piracy is another method by which the Fish Eagle obtained prey. Both intraspecific and interspecific piracies were practised (Tables 4.6 & 4.7). In the former case, any pair of Eagles deprived their neighbouring pairs and both non-territorial adults and young of prey that these birds obtained.

Table 4.2 (a) The frequencies of fishing attempts (dives) of the Fish Eagle in Queen Elizabeth Park in relation to the hunting methods used. Five pairs were observed for 7 dawn-dusk days.

Number of	Dives initiated from Perch	Soaring	Circling	Total
Observed dives	56	1	14	71
Expected dives	23.7	23.7	23.7	71.1
	X^2 = 69.733***, df = 2			

Table 4.2 (b) The hunting successes of the Fish Eagle in relation to the hunting methods used. Five pairs were observed for 7 dawn-dusk days.

Number of	Dives initiated from Perch	Soaring	Circling	Total
Observed dives	56	1	14	71
Observed catches	35	0	6	41
	X^2 = 1.168 NS, df = 2			
Hunting success (%)	62.5	0	42.9	57.7

Table 4.3 (a) The hunting effort, as measured in terms of fishing attempts, of the Fish Eagle in Queen Elizabeth Park in relation to the sex of the bird. Birds were observed for 659.8 hours.

Number of	Sex of bird		
	Male	Female	Total
Observed dives	254	99	353
Expected dives	176.5	176.5	353
	X^2 = 68.059***, df = 1		

Table 4.3 (b) The hunting success of the Fish Eagle in Queen Elizabeth Park in relation to the sex of the bird.

Number of	Sex of bird		
	Male	Female	Total
Observed dives	254	99	353
Observed catches	165	77	242
	X^2 = 0.975 NS, df = 1		
Hunting success (%)	65.0	77.8	68.6

Table 4.4 The numbers of fishing attempts and catches west bank Fish Eagle Pairs No. 5 and 6 made during 7 dawn-dusk observations. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar 1974). In calculating D, the data for 06-07 and 19-20 hours were excluded because observations during them were shorter than during the other time intervals. Obs. = observed, Exp. = expected values.

Time	Obs. time	No. of dives			No. of Catches		
(hr)	(hrs)	Obs.	Exp.	D-value	Obs.	Exp.	D-value
06-07	4.6	4			3		
07-08	14.0	10	9.3	0.09643 NS	8	6.0	0.18056*
08-09	14.0	15	9.3		11	6.0	
09-10	14.0	11	9.3		9	6.0	
10-11	14.0	12	9.3		8	6.0	
11-12	14.0	9	9.3		7	6.0	
12-13	14.0	4	9.3		1	6.0	
13-14	14.0	9	9.3		3	6.0	
14-15	14.0	6	9.3		4	6.0	
15-16	14.0	8	9.3		3	6.0	
16-17	14.0	9	9.3		5	6.0	
17-18	14.0	10	9.3		5	6.0	
18-19	14.0	9	9.3		8	6.0	
19-20	5.4	0			0		

NS = not significant ($D_{0.1,112} = 0.11411$),

* $P < 0.05$ ($D_{0.05,72} = 0.15755$).

Table 4.5 The numbers of fishing attempts and catches east bank Fish Eagle Pairs No. 72, 73 and 74 made during 7 dawn-dusk observations. D is the statistic of the Kolmogorov-Smirnov goodness of fit test (Zar, 1974). In calculating D, the data for 06-07 and 19-20 hours were excluded because observations during them were shorter than during other time intervals. Obs. = observed, Exp. = expected values.

Time (hr)	Obs. time (hrs)	No of dives Obs.	No of dives Exp.	D-value	No. of catches Obs.	No. of catches Exp.	D-value
06-07	6.9	2			2		
07-08	21.0	10	10.3	0.05484 NS	5	6.9	0.06506 NS
08-09	21.0	11	10.3		9	6.9	
09-10	21.0	15	10.3		11	6.9	
10-11	21.0	12	10.3		8	6.9	
11-12	21.0	8	10.3		6	6.9	
12-13	21.0	4	10.3		4	6.9	
13-14	21.0	12	10.3		6	6.9	
14-15	21.0	10	10.3		6	6.9	
15-16	21.0	14	10.3		11	6.9	
16-17	21.0	7	10.3		3	6.9	
17-18	21.0	17	10.3		12	6.9	
18-19	21.0	4	10.3		2	6.9	
19-20	8.1	0			0		

NS = not significant for dives ($D_{0.1,124} = 0.10852$),

NS = not significant for catches ($D_{0.1,83} = 0.13226$).

Table 4.6 (a) Intraspecific piracy in the Fish Eagle in Queen Elizabeth Park. For each entry the first represents frequencies of piracy attempts, and the second, in parentheses, frequencies of successes. Chi-square test was performed on frequencies of attempts.

	Pirate and frequencies of piracy		
Victim	Adult	Young	Total
Adult	17(2)	72(12)	89(14)
Young	16(6)	10(6)	26(12)
Total	33(8)	82(18)	115(26)
	χ^2 = 17.510***, df = 1		
Pirating success (%)	24.2	22.0	22.6

Table 4.6 (b) The frequencies of successful intraspecific piracies in the Fish Eagle in Queen Elizabeth Park. For each entry the first represents frequency of success, and the second, in parentheses, percent success of respective piracy attempts in Table 4.6a above. Chi-square test was performed on raw data.

	Pirate and frequencies of success		
Victim	Adult	Young	Total
Adult	2(11.8)	12(16.7)	14(15.7)
Young	6(37.5)	6(60.0)	12(46.2)
	χ^2 = 3.843*, df = 1		

Table 4.7 Interspecific piracies between the Fish Eagle and other bird species in Queen Elizabeth Park. Numbers in parentheses represent frequencies of successful piracy attempts on the Fish Eagle by the respective species of bird. Asterisk indicates bird managed to pick morsels, but not whole prey, after Eagle had jumped off.

Victim or pirate	No. of piracy attempts	
	By the Eagle	On the Eagle
Pelecanus spp.	21	1(0)
Ardea goliath	5	2(1)
Ephippiorynchus senegalensis	2	2(0)
Ibis ibis	2	4(0)
Phalacrocorax africanus	1	0
Ceryle rudis	4	0
Leptoptilos crumeniferus	0	14(4)
Trigonoceps occipitalis	0	5(5)
Scopus umbretta	0	8(0*)
Total	35	36(10)

Neighbours were robbed when they killed prey at the boundaries of their contiguous territories (Fig. 3.1, section 3.3.1). However, wandering adults and young were robbed when they caught prey in the territorial waters of adults whose areas they trespassed in order to subsist.

Although seemingly a compulsive pirate (Brown 1976a & b, 1980), the adult Fish Eagle pirated only when good opportunities prevailed. Thus, piracy was more commonly employed by young than adults and that attempts were significantly higher on adult than on young birds (Table 4.6a). Attempts on young were few compared to those on adults probably because of their cryptic habits (section 2.4) which perhaps resulted in few of their catches being detected. The 10 piracy attempts on young by other young (Table 4.6a) were made on recently fledged birds that were still dependent on their parents for both food and protection. All the 16 piracies on young by adults were on independent birds which caught prey in the territorial waters of the adults who consequently tried to deprive them of the prey. Both the adult and young had similar pirating successes (Table 4.6a). Only 26 of 115 attempts succeeded; thus giving an overall success of only 22.6%. Compared with the hunting success rate 66%, hunting, therefore, is a more successful method of prey procurement than pirating from conspecifics.

The ages of the pirate and the victim significantly influenced pirating success (Table 4.6b). Thus both young and adult birds succeeded less often in depriving adults of prey than when they robbed young. The experience of the victim in defending its prey probably explains why piracy was more successful against young than against adults. Thus, adult and paired Fish Eagles defended each other well when attacked by pirates, whether by the members of a neighbouring pair or wandering birds. No successful piracy on a pair by a neighbouring pair was observed throughout the study. The 2 successful piracies by adults on other adults (Table 4.6a) were from wandering adults that caught prey in the territories of established birds. Of the 12 successful piracies young made on adult birds, 7 (58%) of them succeeded because the young were moving in bands of 2 or more birds. During such a robbery, the first young attacked the adult with the prey, and if it did not remove the prey then the second or third young usually succeeded. The mate of the victim normally did little to recover the prey because its defence efforts were usually overwhelmed by having to chase the young birds out of their territory.

By the time the victim had sufficiently recollected itself, the pirate was already out of their territory or had dropped down and had retreated into the recess of a thick bush, and probably had already begun to consume the loot. When there were only 2 young, the advances of the second young to pirate after the first had failed were at times successfully blocked by the mate of the prey owner.

Prey obtained by a band of wandering young Eagles changed hands a lot among the members. However, beacuse none of them successfully appropriated the prey, all members of the group participated in the meal. This mode of existence probably conferred upon each member of the group advantages which enhanced its chances of survival relative to living solitarily (section 4.4).

The Fish Eagle also robbed other species of birds of their prey (interspecific piracy, Table 4.7). No success rates are given because no bird that the Eagle tried to victimise ever dropped or disgorged prey which the pirate subsequently recovered (Brown 1980).

The Goliath Heron *Ardea goliath* and the Saddle-billed Stork *Ephicpiorynchus senegalensis* did not take to flight nor did they drop or disgorge their prey when attacked by the Fish Eagle. Instead they quickly swallowed their prey and then directed their dagger-like bills towards the pirate in self-defence. However, no bodily contacts were witnessed between the Fish Eagle and any of these birds because the Eagle never came so close as to talon them.

The White Pelican *Pelecanus onocrotalus* and Pink-backed Pelican *P. rufescens*, and the Yellow-billed Stork *Ibis ibis* normally took off well before a Fish Eagle reached them, although at times they were surprised such that they could not take to the wing. There were also instances when the Eagle overtook the pelicans and forced them to the ground or on water. However, in all attacks observed, no Fish Eagle ever alighted beside the victim nor did it catch in mid-air prey that an affected bird dropped or disgorged.

It is interesting to watch to what limits the Fish Eagle can go on with its piratical trait and, therefore, to note how compulsive the habit is in the species. During the study, on many occasions the Fish Eagle chased the tiny Pied Kingfisher *Ceryle rudis* when these birds had no fish in their bills.

Such chases were interpreted as having had predatory motives (section 3.3.2.5). However, should a Kingfisher that had originally been ignored by an Eagle catch prey, it was attacked immediately. During the chase, the two birds turned weird corners but the light and agile Kingfisher outran the Eagle in all attempts witnessed (Table 4.7). And none of the Kingfishers ever dropped the prey it had caught.

The single piracy attempt on the Long-tailed Cormorant *Phalacrocorax africanus* happened as the male of Pair No. 6 was circling above the water where the cormorant was hunting. Just as the cormorant emerged to swallow a fish it had caught, the Eagle made a strike which the cormorant successfully evaded by submerging. It re-surfaced by the shoreline about 80m away from the place of attack. The Eagle apparently ignored it for it did not attack it again after it resurfaced.

Piracy is normally not a one way affair. Much as the Fish Eagle attempted to pirate from other species of birds so did some of the affected birds try to deprive the Eagle of its prey (Table 4.7). Whenever, the Fish Eagle alighted to feed on the ground by the shoreline, the Hammerkop *Scopus umbretta*, Marabou Stork *Leptoptilos crumeniferus*, Saddle-billed Stork, Yellow-billed Stork, Goliath Heron, Sacred Ibis *Threskiornis aethiopicus* and the Hadada Ibis *Hagedashia hagedash* were attracted to the scene and could be seen waiting on or moving around the Eagle. The Marabou Stork, Saddle-billed Stork and the Goliath Heron sometimes came so close that the Eagle was forced to fly away with its prey. During such hurried take-offs prey at times dropped and both the Eagle and the pirate-to-be scuffled over it. The Eagle retrieved most of its booties but twice the Marabou Stork and once the Goliath Heron successfully grabbed the prey and swallowed them (Table 4.7). At Rwenshama (Fig. 2.1), twice again the Marabou Stork pirated successfully from post-fledging young whose parents failed to retrieve the prey.

As they approached the feeding Fish Eagle, the Yellow-billed Stork and the Hammerkop were usually easily scared off. However, they at times made quick dashes at unsuspecting Eagles which, in surprise, lept high in the air leaving the prey on the ground. In all such incidences (Table 4.7), the Eagles recovered their prey. As the Storks fumbled to swallow the large fishes, the Eagles attacked and forced them to drop the prey.

Normally, both birds waited until the Eagle had finished its meal and had moved away before scampering to the site to pick up discarded parts of the prey.

On 22 July 1976, the male of Pair No. 72 (Fig. 3.1) caught a very big fish close by the shoreline but it was too heavy to carry away. The Eagle dragged the prey ashore but before reaching dry land, 5 pelicans rushed, en masse, towards the Eagle apparently ready to pirate. The Eagle surrendered the fish which apparently escaped.

On 5 occasions when bands of young Fish Eagles successfully robbed prey from territorial adults and the members were scuffling over the spoils, the White-headed Vulture Trigonoceps occipitalis dropped onto the bands (Table 4.7). After brief struggles with the young Eagles, these Vultures usually assumed control of the prey. However, no prey was wholly appropriated by the Vultures because, as the food item changed hands among the Vultures, the Fish Eagles also assumed brief controls over the disputed prey and, therefore, fed too.

4.3.2.3 Food procurement by scavenging

The Park provides regular game animal carcasses for all scavenging animals. The fishing industry, which is permitted in this Park, also offers regular additional carrion. The Fish Eagle and many other scavenging birds make use of this daily and readily available carrion (Table 4.8). It is, however, evident that the young are given to scavenging both in the fishing villages and other areas of the Park. Because territorial birds hardly leave their areas (section 3.3.2.1), any adults found scavenging were probably non-territorial birds.

4.3.2.4 The capturing of prey

Fish is caught by a fast dive with the Eagle momentarily checking just before the kill is made or water is touched. Prey is caught in the first 5-10 or so cm of water. The fish is grasped by the powerful but opposing grips of 4 long, curved and sharp talons at the end of each tarsus and is normally carried by both feet.

Table 4.8 Incidences of scavenging by the Fish Eagle in Queen Elizabeth Park. For each visit to Rwenshama Fishing Village, the single + sign indicates presence of adults while young birds were always present in great numbers.

Date	Area of the Park	No. of Fish Eagles		Carcass	Comment
		Adults	Young		
16.4.75	Mweya	1	0	Animal matter	On rubbish dump
10.6.75	"	0	3	" "	" " "
18.6.75	"	0	2	" "	" " "
18.2.76	Rwenshama	+	+++	Scraps of Fish	Plenty of other scavenging birds
11.3.76	Rwenshama	+	+++	Scraps of fish	Plenty of other scavenging birds
19.3.76	Rwenshama	+	+++	Scraps of fish	Plenty of other scavenging birds
15.11.76	Kazinga	0	5	Scraps of fish	Plenty of other scavenging birds
28.12.76	Mweya	0	2	Animal matter	On rubbish dump
25.2.77	Kazinga	0	2	Scraps of fish	Plenty of other scavenging birds
29.4.77	Kazinga	0	4	Scraps of fish	Plenty of other scavenging birds
13.6.77	Kazinga	0	3	Scraps of fish	Plenty of other scavenging birds
30.6.77	Kazinga	0	4	Scraps of fish	Plenty of other scavenging birds
30.8.77	Kazinga	0	3	Scraps of fish	Plenty of other scavenging birds
27.10.77	Kazinga	0	3	Scraps of fish	Plenty of other scavenging birds
18.7.75	Area of Pair No. 8	2	2	Lung fish	1 Marabou Stork, 2 Sacred Ibises & Hammerkop around.
5.7.76	Area of Pair No. 72	0	8	Unidentified but probably pirated fish	4 White-headed and 1 Hooded Vultures, & Marabou Storks around.

Cont'd

Table 4.8 cont'd.

Date	Area of the Park	No. of Fish Eagles Adults	No. of Fish Eagles Young	Carcass	Comment
20.7.76	Area of Pair No. 73	2	9	Unidentified but probably pirated fish	No other birds
22.7.76	Area of Pair No. 73	0	2	Unidentified but probably pirated fish	1 White-headed Vulture present.
22.6.77	Area of Pair No. 82	0	11	Hippopotamus calf	2 White-headed, several Hooded & White-backed Vultures & Marabou Storks present.

4.3.3 Feeding methods and food sharing

Once prey was captured a Fish Eagle normally returned to a favourite feeding perch. Heavy prey, however, forced the Eagle to alight anywhere along the shoreline where the prey was partly eaten before being taken to a feeding perch.

When eating on a perch, the Eagle held down its prey with the talons of one foot, those of the other foot served to grip the branch and to maintain balance. Horizontal branches were preferred. On the ground, however, both feet could be used to hold down the prey. Small pieces of flesh were torn off the prey with the aid of the powerful and hooked beak. During feeding balance was maintained by regular spreading and half opening of wings and the tail.

Field and laboratory observations on a captive juvenile showed that a Fish Eagle feeding on a cichlid usually started to dismember the prey from the base of the neck first, the opercular or pectoral fin joints serving as the initial points of attack. From either of these places the Eagle devoured the head of the prey before proceeding to the trunk and tail regions. When feeding on a catfish, however, it usually attacked the anal or pelvic regions of the prey first, the joints of the anal or pelvic fins serving as the initial points of dismemberment. The Eagle discarded the gill apparatus and gut of all types of fish. Bones, scales and whole or fragments of fins and operculi were also swallowed; the bones and bony fragments being aligned base first to facilitate swallowing.

When feeding on the ground, grasses and other vegetative materials were also swallowed with pieces of flesh. However, these materials and undigested bones and scales were regurgitated in pellets. Once the captive Eagle was offered a dead stripped grass mouse Lemniscomys sp. (A. A. Ogen-Odoi, pers. comm.), and the next day two pellets of undigested hair, teeth and claws were found in the cage. On another occasion the bird was given a dead Black-headed Weaver Ploceus cuculatus bohndorffi and the following day pellets containing undigested feathers, claws and mandibles of the bill were again found in the cage. Pellets containing fish scales and feathers were also found under feeding perches of Fish Eagles (Table 4.1). Since the regurgitation of pellets by adults was not observed, their production by the adults was inferred from the fact that the captive juvenile produced them.

Food sharing between the sexes of a pair occurred during both the breeding and non-breeding periods. Of 76 observed feeding bouts, 54 (71.1%) of the prey were shared. For the 54 cases of sharing, 31 (57.4%) of them occurred during the breeding and 23 (42.6%) during the non-breeding phases of the pair. For the 22 cases of non-sharing, 15 (68.2%) of them happened during the breeding and 7 (31.8%) during the non-breeding cycles. However, the frequencies of sharing and non-sharing of prey did not differ significantly with the breeding status of the pair ($\chi^2 = 0.744$, df = 1, $P > 0.1$: n = 76).

There were times when a pair of Eagles captured a fish that was too big to satiate their appetites. After failing to finish a prey, an Eagle took the remains to the nest or left it on the feeding perch. From either places the mate of the bird that had already fed retrieved the left-over and fed on it. If it also failed to finish the food, the remaining piece was still left on the nest or the feeding perch. In turns, both birds returned to feed on the left-over until it was exhausted. Occasionally several drying pieces of partly eaten prey could be found on the feeding perches or nests. In breeding birds, such pieces of fish can be seen strewn about the nest edge, especially during the early part of the fledging period when the young were not yet voracious enough to consume such larders of prey (section 10.3.3 & Plate 5).

4.3.4 Predation pressure on fish

4.3.4.1 Predation pressure relative to fish types and their abundance

During this study, no assessment was made of the relative abundance of the fish types occurring in the Kazinga Channel. The fish catch statistics in the Fisheries Office, Kichwamba, are biased towards the commercially exploitable species only and were, therefore, of little use for this work. Beadle (1932 & 1974) reports that limnologically the Channel is more similar to L. George than to L. Edward. For these reasons Gwahaba's (1973) data on fish species in L. George were used to assess the predation pressure Fish Eagles in the Park exerted on each species of fish they preyed upon relative to its abundance.

Gwahaba (1973) lists 32 species of fish occurring in L. George and that these species represented 12 genera and 8 families (Table 4.9). However, Dunn (1972) reports that there are about 20 other species of fish in addition to the 21 cichlid species occurring in the lake. This study found that the Fish Eagle regularly exploits only 4 of the 32 species present in L. George and, therefore, in the Kazinga Channel as well (Table 4.9). The Table also shows that both the Eagle and man are basically exploiting the same species of fish.

Gwahaba (op cit.) reported that ca. 55222 fishes/ha occur in L. George. Of these there are 49730 Haplochromis spp., 171 Tilapia spp., 11 Clarias lazera, 11 Bagrus docmac, 6 Protopterus aethiopicus, and 5293 Aplocheilichthys spp. Only 3 of the above 6 genera were represented in the 3470 fish remains collected from the Fish Eagle territories during this study. These included 2872 (82.8%) Tilapia spp., 327 (9.4%) Clarias lazera, and 271 (7.8%) Bagrus docmac. A Chi-square test on the numbers of fish taken by the Eagle and those of fish present in each hectare of water suggests that Fish Eagle predation pressure was proportional to the densities of the respective fishes which the Eagle was catching (Table 4.10).

4.3.4.2 Predation pressure in relation to sizes of fish

Figs. 4.4, 4.5 and 4.6 attest to the reliabilities of using the bony remains of fishes for estimating the total lengths and live weights of fish caught by the Fish Eagle in this Park. The results show that there were direct and significant relationships between the opercular length and total length (Fig. 4.4a), opercular length and live weight (Fig. 4.4b), and live weight and total length (Fig. 4.4c) of Tilapia sp. There were also significant linear relationships between the head lengths and head-tail lengths, head lengths and live weights, and live weights and head-tail lengths of both Clarias and Bagrus spp. (Fig. 4.5 & 4.6 respectively).

The sizes of fish taken by the Eagle and the predation pressure exerted on the respective size classes are shown in Figs. 4.7-4.9. In the genus Tilapia the smallest fish represented in the prey remains weighed 240 g and measured 24 cm (Fig. 4.7).

Table 4.9 The types of fish occurring in Lake George and probably in the Kazinga Channel as well. This list is adopted from Gwahaba (1973) with slight modifications. The asterisk (s) outside parentheses indicates exploitation by the Fish Eagle. One asterisk shows infrequent exploitation and two asterisks regular exploitation. The asterisk inside parentheses shows that the fish is commercially exploited by man as well.

Family	Genus	No. and name(s) of species
1. Lepidosirenidae	*Protopterus*	1 sp. *aethiopicus* *(*)
2. Mormyridae	*Marcusenius*	1 sp. *nigricans*
	Mormyrus	1 sp. *kannume*
3. Cyprinidae	*Barbus*	3 spp. *(*) *altianalis*, *kerstenii* and *neglectus*
4. Bagridae	*Bagrus*	1.sp. *docmac***(*)
5. Clariidae	*Clarias*	1 sp. *lazera* **(*)
6. Cyprinodontidae	*Aplocheilichthys*	2 spp. *eduardensis* and *pumilus*
7. Anabantidae	*Ctenopoma*	1 sp. *muriei*
8. Cichlidae	*Astatoreochromis*	1 sp. *allaudi*
	Haplochromis	17 spp. (various names).
	Hemihaplochromis	1 sp. *multicolor*
	Tilapia	2 spp.**(*) *nilotica* and *leucosticta*.

Table 4.10 The predation pressure exerted by the Fish Eagle on fish types relative to the abundance of the respective fishes. Density data for fish were obtained from Gwahaba (1973).

	Type of fish			
	Tilapia	*Clarias*	*Bagrus*	Total
Number/ha	171	11	11	193
Number predated	2872	327	271	3470

X^2 = 4.574 NS, df = 2

Fig. 4.4a The relationship between opercular length a head-tail length of *Tilapia* spp. in Queen Elizabeth National Park.

Fig. 4.4b The relationship between opercular length fresh weight of *Tilapia* spp. in Queen Elizabeth National Park.

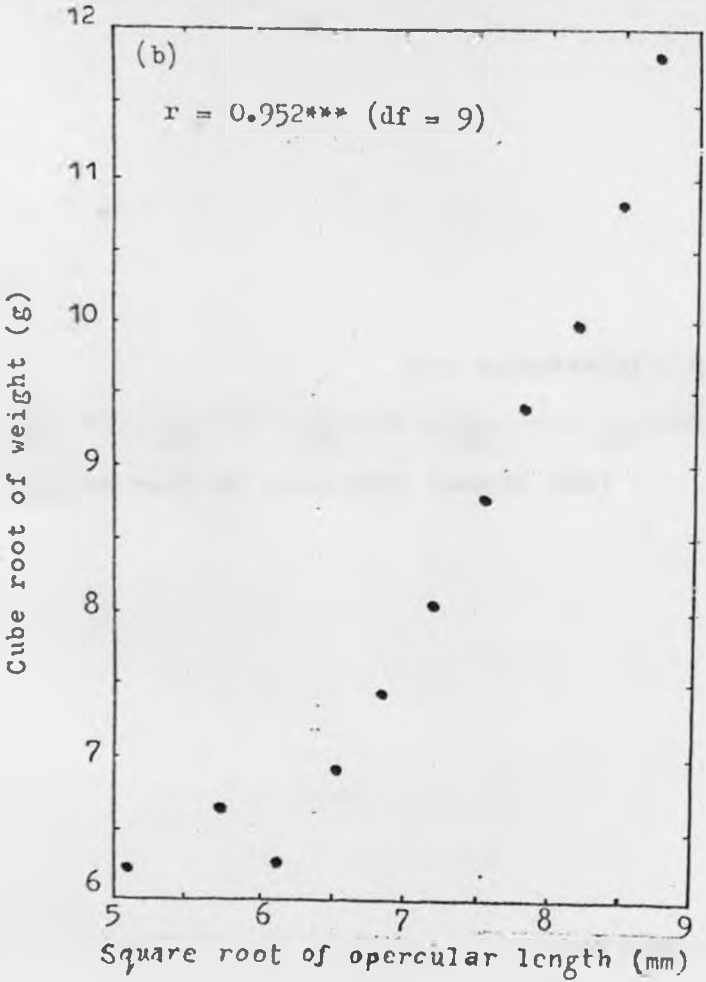

(b)
r = 0.952*** (df = 9)
Cube root of weight (g)
12
11
10
9
8
7
6
5
6
7
8
9
Square root of opercular length (mm)

Fig. 4.4

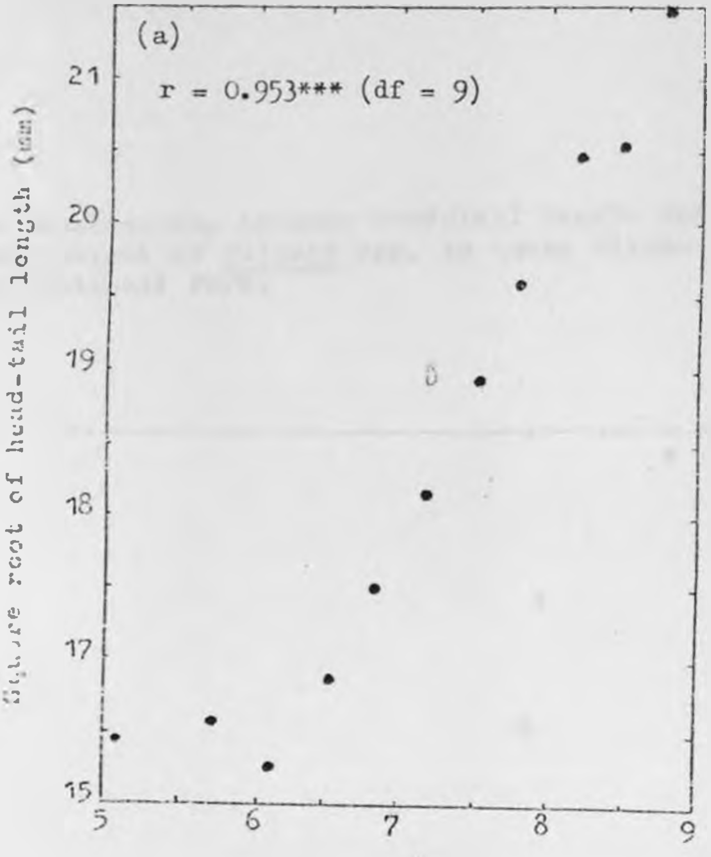
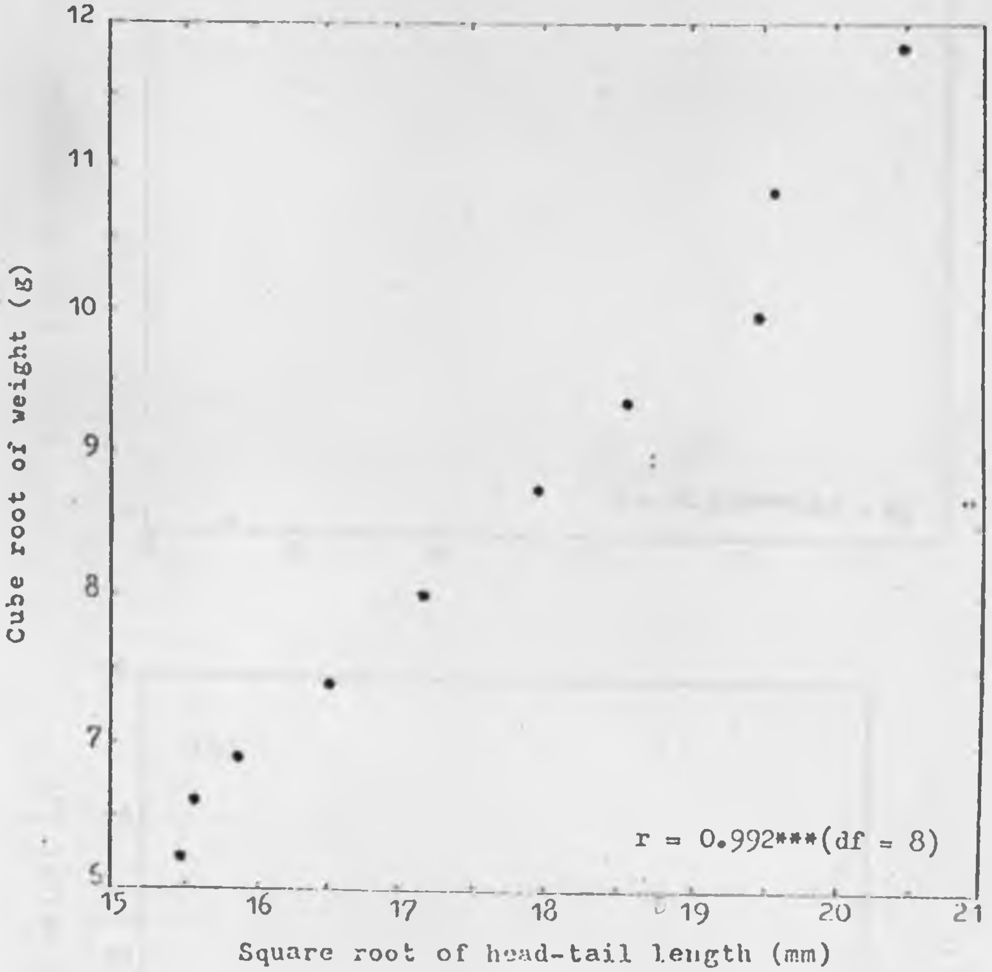

(a)
r = 0.953*** (df = 9)
Square root of head-tail length (mm)
21
20
19
18
17
15
5
6
7
8
9

Fig. 4.4c The relationship between head-tail length and fresh weight of Tilapia spp. in Queen Elizabeth National Park.



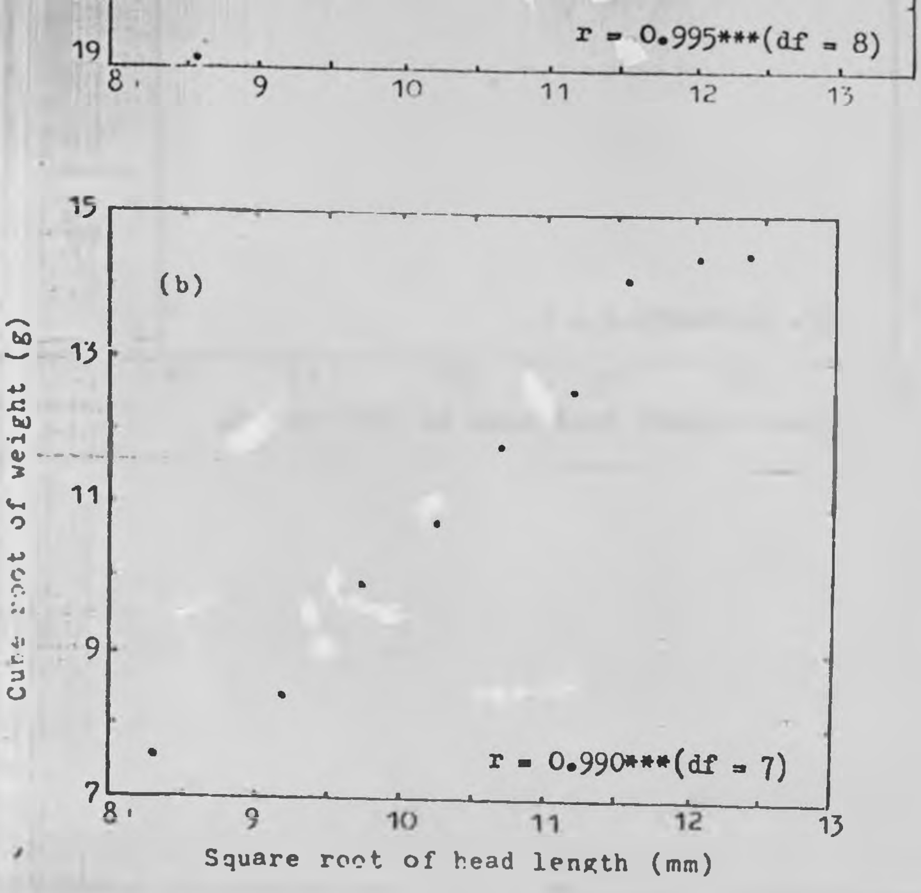

r = 0.995***(df = 8)
19
8
9
10
11
12
13
(b)
15
13
11
9
7
Cube root of weight (g)
r = 0.990***(df = 7)
8
9
10
11
12
13
Square root of head length (mm)

Fig. 4.5 a) The relationship between head length and head-tail length of *Clarias lazera* in Queen Elizabeth National Park.

b) The relationship between head length and fresh weight of *Clarias lazera* in Queen Elizabeth National Park.

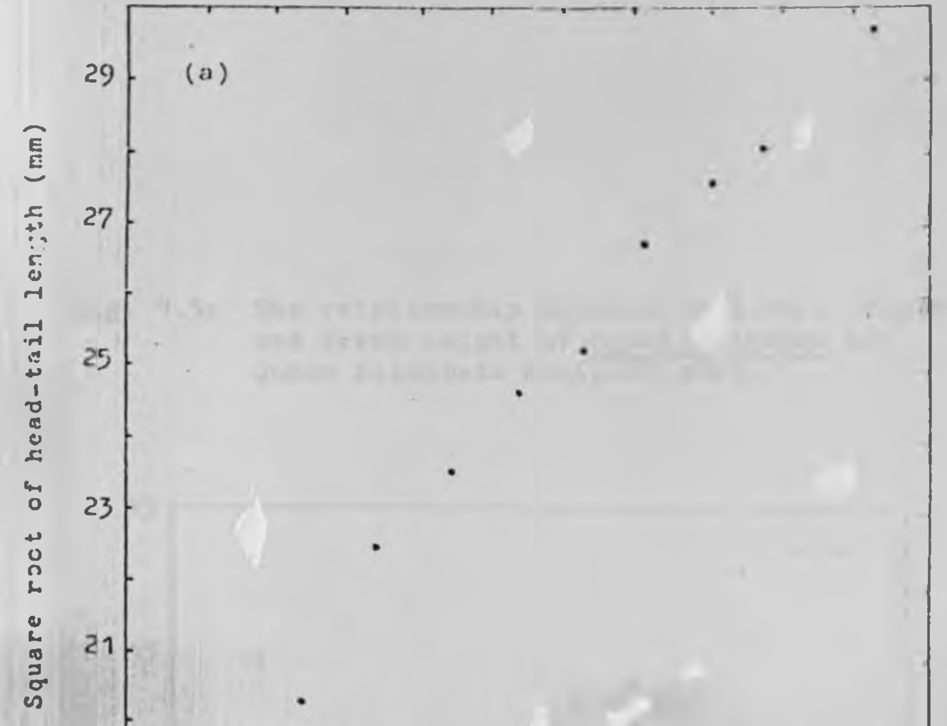


Fig. 4.5c The relationship between head-tail length and fresh weight of <u>Clarias lazera</u> in Queen Elizabeth National Park.

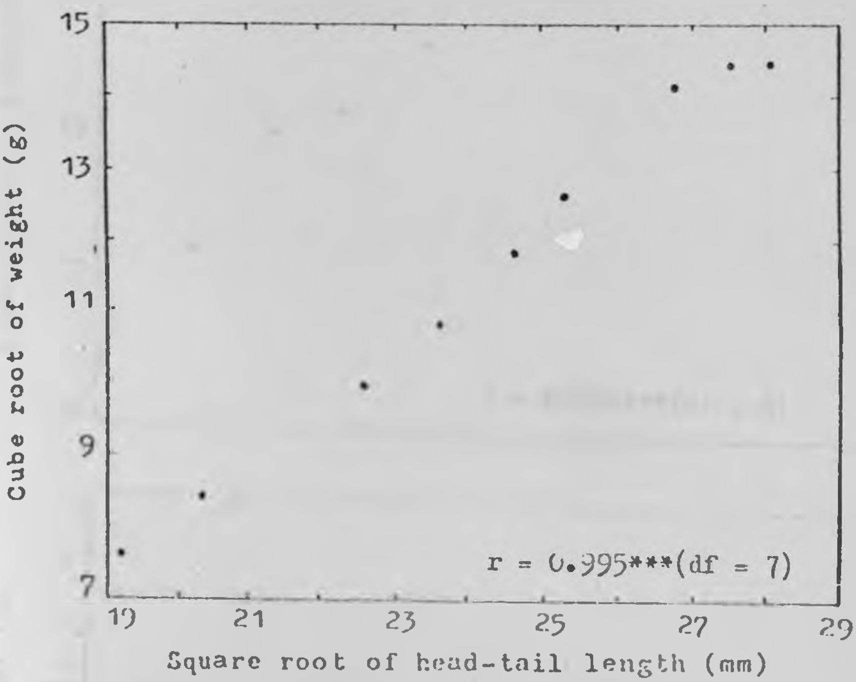
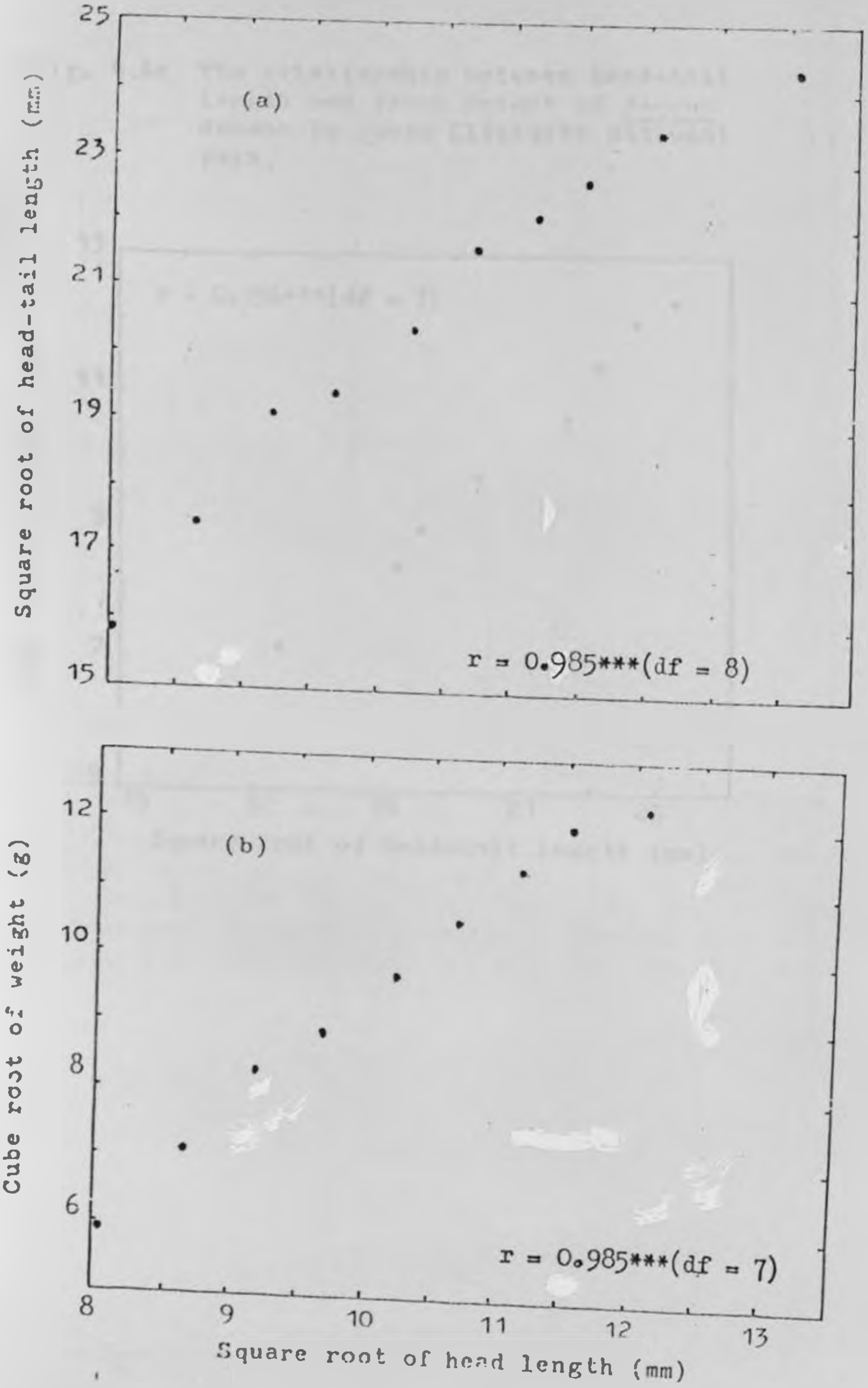


Fig. 4.6 a) The relationship between head length and head-tail length of *Bagrus docmac* in Queen Elizabeth National Park.

b) The relationship between head length and fresh weight of *Bagrus docmac* in Queen Elizabeth National Park.



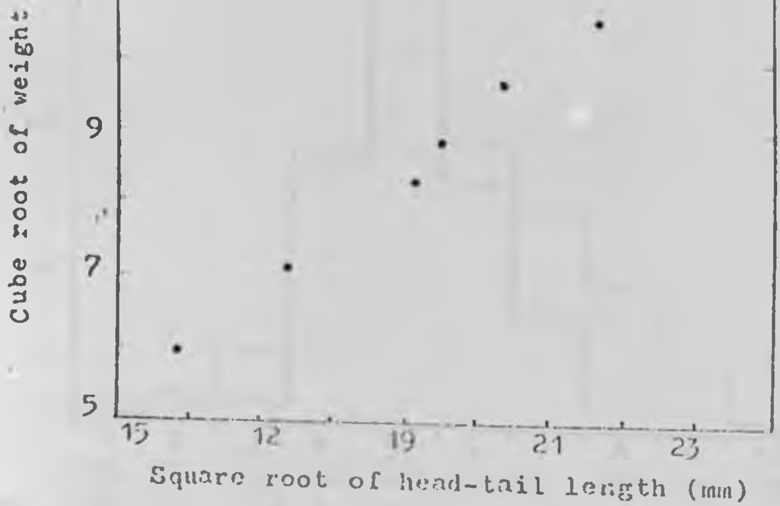

Cube root of weight
5
7
9
15
17
19
21
23
Square root of head-tail length (mm)

Fig. 4.6c The relationship between head-tail length and fresh weight of *Bagrus* docmac in Queen Elizabeth National Park.

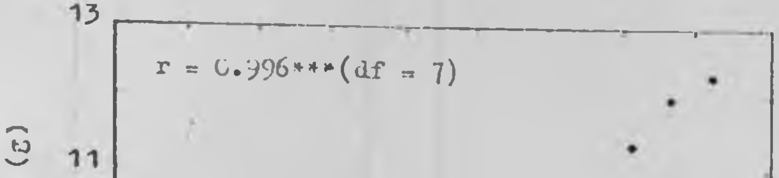
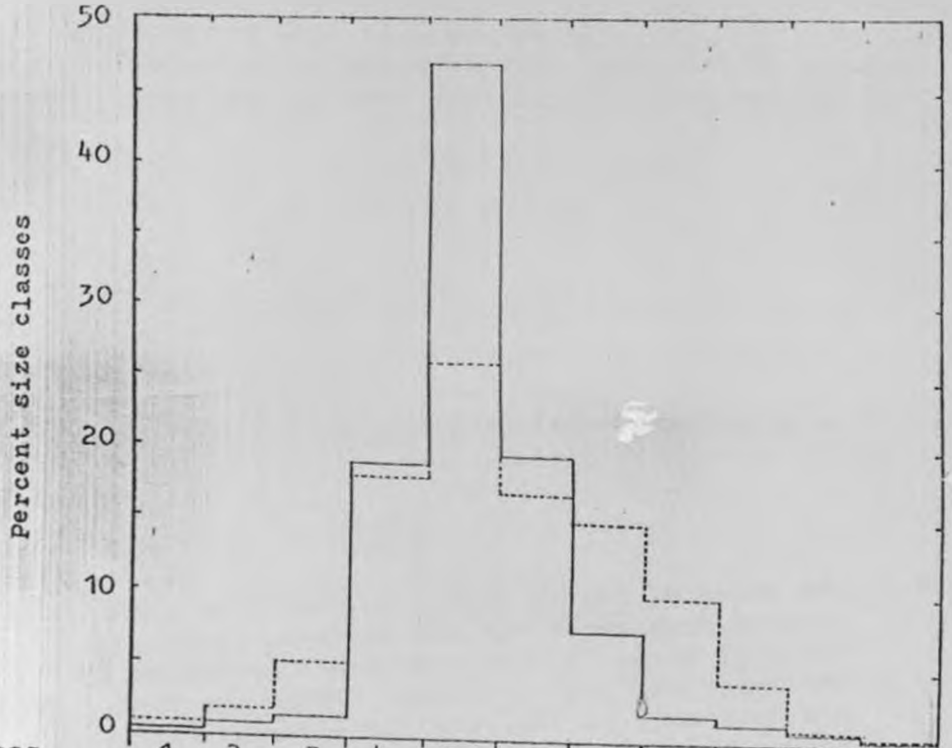


Fig. 4.7 The sizes of *Tilapia* spp. harvested by the African Fish Eagle and man in Queen Elizabeth National Park. (---) represents Fish Eagle predation and (___) represents predation by man. Below the Fig. are data used in deriving the sizes of fish preyed upon by the Fish Eagle. Thus n_1 = number of prey remains (operculi) recovered from the territories; and n_2 = number of freshly landed *Tilapia* whose weights (Wt), and operculi (OPL) and head-tail (HTL) lengths were taken.

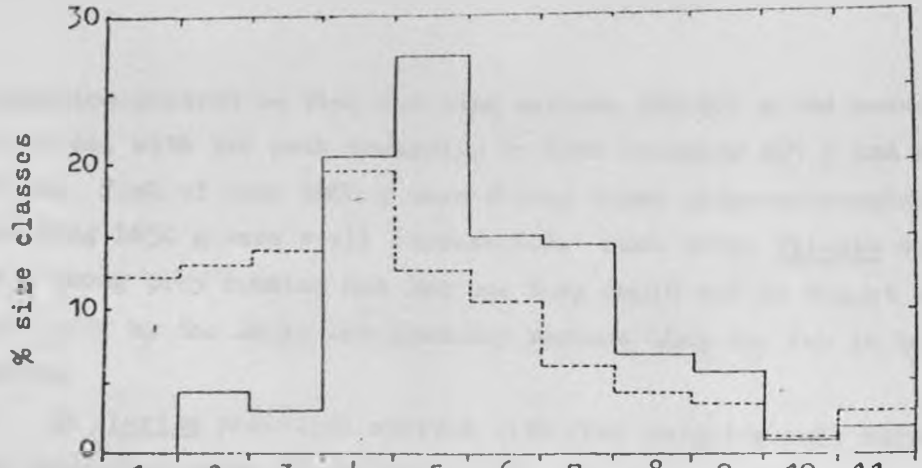


Size class	1	2	3	4	5	6	7	8	9	10	11
N_1	34	55	152	514	743	492	437	282	112	37	14(N_1=2872)
Mean OPL (mm)	26	33	38	43	47	52	57	61	67	72	77
N_2	2	3	5	63	157	65	25	6	5	3	1(N_2=335)
Mean Wt (g)	240	290	245	327	405	513	665	821	981	1270	1650
Mean HTL (mm)	240	243	234	253	273	295	323	346	279	383	420

Fig. 4.8 The sizes of *Clarias lazera* harvested by the African Fish Eagle and man in Queen Elizabeth National Park. (----) represents predation by the Eagle and (——) by man. Below the Fig. are data used in deriving the sizes of fish preyed upon by the Eagle. Thus n_1 = number of prey remains (heads) recovered from the territories; and n_2 = number of freshly landed fishes whose weights (Wt), and head (HL) and head-tail (HTL) lengths were taken.

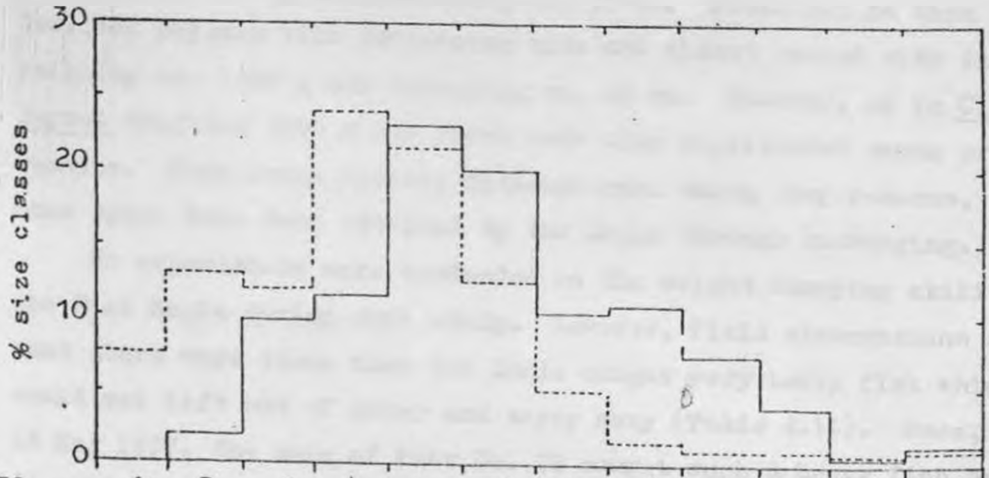
Fig. 4.9 The sizes of *Bagrus docmac* harvested by the African Fish Eagle and man in Queen Elizabeth National Park. (----) represents predation by the Eagle and (——) by man. Below the Fig. are data used in deriving the sizes of fish preyed upon by the Eagle. Thus n_1 = number of prey remains (heads) recovered from the territories; and n_2 = number of freshly landed fishes whose weights (Wt), and head (HL) and head-tail (HTL) lengths were taken.

Fig. 4.8



Size class	1	2	3	4	5	6	7	8	9	10	11
n_1	40	43	45	64	42	34	20	14	11	4	10 (N_1= 327)
Mean HL (mm)	60	74	85	95	105	115	125	134	145	154	173
n_2	0	7	5	33	44	24	23	11	9	2	3 (N_2= 161)
Mean Wt (g)	<434	434	594	977	1249	1656	2000	2818	2983	3000	4768
Mean HTL (mm)	369	369	414	509	557	608	641	715	759	788	881

Fig. 4.9



Size class	1	2	3	4	5	6	7	8	9	10	11	12
n_1	21	35	32	65	58	34	15	4	2	2	1	2 (N_1 = 271)
Mean HL (mm)	51	65	75	85	94	105	115	125	133	146	153	180
n_2	0	4	23	27	54	47	24	25	17	9	1	3 (N_2 = 234)
Mean Wt (g)	<213	213	363	573	708	914	1171	1441	1715	1848	3050	6033
Mean HTL (mm)	<252	252	305	366	379	414	468	488	511	538	590	843

Predation centred on fish weighing between 327-821 g and measuring 25-35 cm, with the peak occurring on fish weighing 405 g and measuring 27 cm. Fish of over 1000 g were rarely taken although specimens weighing 1650 g were still represented. Such large *Tilapia* spp. were rare among prey remains not because they could not be caught and carried away by the Eagle but probably because they are few in the water system.

In *Clarias* predation started with fish weighing well below 400 g and measuring under 37 cm (Fig. 4.8). Predation on *Clarias* rose and declined gradually with the peak occurring on fish weighing ca. 980 g and measuring ca. 51 cm. Recovered prey remains also represented fish weighing 3000 g and above (Fig. 4.8). Such very large prey were probably not caught by the Eagle but could have been scavenged from rotten fishes discarded by fishermen or those that died. Once washed ashore, such prey were probably partly consumed before being carried to the feeding perches or nests.

Predation on *Bagrus* commenced with fish weighing well below 200 g and measuring under 25 cm (Fig. 4.9). Peak predation centred on fish weighing ca. 570 g and measuring ca. 37 cm. Predation on this fish declined rapidly with increasing size and almost ceased with fish weighing ca. 1440 g and measuring ca. 49 cm. However, as in *Clarias*, *Bagrus* weighing 3000 g and above were also represented among prey remains. Such large fishes, although rare among prey remains, could once again have been obtained by the Eagle through scavenging.

No experiments were conducted on the weight carrying ability of the Fish Eagle during this study. However, field observations showed that there were times when the Eagle caught very heavy fish which it could not lift out of water and carry away (Table 4.11). Once, on 18 May 1977, the male of Pair No. 72 caught such a heavy fish and lifted it well above the water but dropped it back. On 19 August 1975, however, the incautious female of Pair No. 6 was pulled right below the water surface and the bird swam ashore, without the prey, probably because her feathers were too wet. On six occasions, various Fish Eagles managed to bring heavy prey ashore by swimming while once an attempt was made to drag out such prey after having caught it in shallow water (Table 4.11). Estimates of the weights of some of these fishes were made using the relationships between their body parts as described earlier on. The weights suggest that prey weighing more than 2 kg can hardly be lifted and carried away by the Eagle.

Table 4.11 Estimates of the weight carrying ability of the Fish Eagle in Queen Elizabeth Park. HL = head length, HTL = head-tail length, Wt = weight. Where appropriate, the first entry represents derived weight or head-tail length (see text) and that in parentheses represents actual weight or head-tail length.

	Pair		Name and size of prey taken				
Date	No.	Sex	Name	HL(cm)	Wt(g)	HTL(cm)	Comment
18.5.75	5	Male	Clarias	12.6	2055 (1750)	65.3 (65.0)	Brought prey ashore by swimming ca.50m.
5.9.75	65	Male	Bagrus	15.3	2150 (2160)	56.2 (56.5)	Swam ca.20m. Recovered whole prey. Weight and head-tail length are from actual measurements.
22.7.76	72	Male	?	-	-	-	Could not lift prey it caught in shallow water, dragged it ashore but lost it due to piracy attempt by pelicans (see section 4.3.2.2).
5.8.76	74	Male	?	-	-	-	Brought prey ashore by swimming. Prey remains not recovered.
16.9.75	60	Female	Clarias	13.4	2409 (2120)	69.5 (70.0)	Lifted prey with great difficulty and landed alon shoreline ca.30m away from site of capture. Prey virtually touching water surface as the bird flew.
18.3.76	6	Female	Bagrus	16.4	2628 (2400)	60.1 (60.5)	Prey brought ashore by swimming ca.50m, Remains recovered after it was partly eaten.
15.8.76	72	Female	Clarias	13.0	2228 (1900)	67.4 (67.8)	Brought prey ashore by swimming ca.80m, rested 3 times with wings spread over water surface. Remains recovered after being partly eaten.
17.5.77	8	Female	Clarias	13.6	2501 (1750)	70.6 (70.8)	Swam ca.50m to bring prey ashore. Rested twice en-route with wings spread over water surface. Prey remains recovered after being partly eaten.
19.8.75	6	Female	?	-	-	-	Bird swam ca.30m ashore without prey.
18.5.77	72	Male	?	-	-	-	Prey lifted out of water but dropped back.

4.3.4.3 Predation pressure in relation to seasons

During 5 dry and 3 wet seasons, 3186 prey remains were recovered from Fish Eagle territories. They consisted of 2872 (90.1%) Tilapia, 185 (5.8%) Clarias, and 129 (4.0%) Bagrus spp. A Chi-square test showed that the numbers of each fish type taken by the Eagle did not differ significantly between the seasons (Table 4.12).

For each of the 3 fish types taken during the seasons, there was no seasonal shift in predation pressure on the various size classes. The agreement between dry and wet season size classes predated was highly significant for Tilapia spp. (Table 4.13), for Clarias lazera (Table 4.14) and for Bagrus docmac (Table 4.15).

4.3.5 Comparisons of human and Fish Eagle fish predations

4.3.5.1 Overlaps in the sizes of fish exploited

It was shown in Table 4.9 that there was an overlap between man and the Fish Eagle for the types of fish they exploited. However, there was yet another overlap in the sizes of fish the two predators harvested from the waters. In Tilapia the overlap in the sizes of fish taken was highly significant (Table 4.16 & Fig. 4.7). The overlap was slight and not significant for Clarias lazera (Table 4.17 & Fig. 4.8). Although slight, the overlap was significant for Bagrus docmac (Table 4.18 & Fig. 4.9).

For Tilapia the peaks for both human and Fish Eagle predations coincided in size class 5 (Fig. 4.7). However, human predation on Tilapia had a more restricted spread than that of the Eagle probably because of regulations imposed on the sizes of gill-nets used by man. Whereas in the Fish Eagle no similar regulations are operative, the spread in the predation pressure on the sizes of Tilapia reflected the ability of the Eagle to exploit the available sizes of fish. Very small fishes were apparently more difficult to catch than medium and large-sized ones while the very large specimens were probably too scarce to be taken frequently.

For Clarias, peak human and Fish Eagle predations were one size class apart (Fig. 4.8). Because of the restrictions on the sizes of gill-nets used by man, comparatively the Eagle took small-sized Clarias more often than man did.

Table 4.12 Seasonal Fish Eagle predation on the most frequently taken types of fish in Queen Elizabeth Park.

	Type and number of fish taken			
Season	Tilapia	Clarias	Bagrus	Total
Dry	1606	114	75	1795
Wet	1266	71	54	1391
Total	2872	185	129	3186

$X^2 = 2.484$ NS, df = 2

Table 4.13 Seasonal Fish Eagle predation on Tilapia spp. in Queen Elizabeth Park in relation to the sizes of the fish. For the live weights, and total and opercular lengths of fishes in the different size classes see Fig. 4.7.

	Numbers of fish taken in respective size classes											
Season	1	2	3	4	5	6	7	8	9	10	11	Total
Dry	24	34	94	275	414	266	260	151	54	28	6	1606
Wet	10	21	58	239	329	226	177	131	58	9	8	1266

Spearman's r = 0.998,

Student's t = 48.574***, df = 9.

Table 4.14 Seasonal Fish Eagle predation on *Clarias lazera* in Queen Elizabeth Park in relation to the sizes of the fish. For live weights, and total and head lengths of fishes in the different size classes see Fig. 4.8.

Season	Numbers of fish taken in respective classes											
	1	2	3	4	5	6	7	8	9	10	11	Total
Dry	17	16	17	17	18	14	7	4	3	1	0	114
Wet	4	12	11	17	7	9	6	3	1	1	0	71

Spearman's r = 0.770,

Student's t = 3.626**, df = 9.

Table 4.15 Seasonal Fish Eagle predation on *Bagrus docmac* in Queen Elizabeth Park in relation to the sizes of fish. For live weights, and head and head-tail lengths in the different size classes see Fig. 4.9.

Season	Numbers of fish taken in respective classes												
	1	2	3	4	5	6	7	8	9	10	11	12	Total
Dry	5	13	7	20	11	12	3	1	1	2	0	0	75
Wet.	6	7	8	13	9	5	5	1	0	0	0	0	54

Spearman's r = 0.888,

Student's t = 6.110***, df = 10.

Table 4.16 Overlaps in human and Fish Eagle predations on Tilapia spp. in Queen Elizabeth Park in relation to the sizes of the fish. For live weights, and total and opercular lengths of fishes in the different size classes see Fig. 4.7.

Predator	Numbers of fish taken in respective classes											
	1	2	3	4	5	6	7	8	9	10	11	Total
Human	2	3	5	63	157	65	25	6	5	3	1	335
Fish Eagle	34	55	152	514	743	492	437	282	112	37	14	2872

Spearman's r = 0.986,

Student's t = 18.002***, df = 9.

Table 4.17 Overlaps in human and Fish Eagle predations on Clarias lazera in Queen Elizaboth Park in relation to the sizes of the fish. For live weights, and total and head lengths of fishes in the different size classes see Fig. 4.8.

Predator	Numbers of fish taken in respective classes											
	1	2	3	4	5	6	7	8	9	10	11	Total
Human	0	7	5	33	44	24	23	11	9	2	3	161
Fish Eagle	40	43	45	64	42	34	20	14	11	4	10	327

Spearman's r = 0.382,

Student's t = 1.239 NS, df = 9.

Table 4.18 Overlaps in human and Fish Eagle predation on Bagrus docmac in Queen Elizabeth Park in relation to the sizes of the fish. For live weights, and head and head-tail lengths of fishes in the different size classes see Fig. 4.9.

Predator	Numbers of fish taken in respective classes 1	2	3	4	5	6	7	8	9	10	11	12	Total
Human	0	4	23	27	54	47	24	25	17	9	1	3	234
Fish Eagle	21	35	32	65	58	34	15	4	2	2	1	2	271

Spearman's r = 0.594,

Student's t = 2.337*, df = 10.

Table 4.19 The food requirement of the Fish Eagle. Data from fish which the Eagle landed by swimming and prey remains recovered after the bird had eaten. Actual = weight of prey remains and derived = weight calculated from head-tail length measurement (see section 4.3.4.2). Calculated amount of food consumed = derived weight less actual weight of prey, and actual weight of food consumed = calculated weight less 10% waste factor. Three adult Entebbe Zoo male Fish Eagles averaged 2250g, and 2 adult females averaged 2835g. Entries marked with asterisks are weights of food as % of 2542.5g, the average of male and female weights.

Sex of bird	Fish taken	Weight of prey(g) Actual	Derived	Food consumed(g) Calculated	Actual	Food as % body weight Calculated	Actual
Male	Clarias	1750	2055	305	274.5	13.6	12.2
Female	Clarias	2120	2409	289	260.1	10.2	9.2
Female	Bagrus	2400	2628	228	205.2	8.0	7.2
Female	Clarias	1900	2228	328	295.2	11.6	10.4
Female	Clarias	1750	2501	375.5	337.9	14.8*	13.3*
Mean ±s.d.				305.1 54.0	274.5 48.6	11.6 2.7	10.5 2.4

Human and Fish Eagle predation peaks in Bagrus were also one size class apart (Fig. 4.9) and, once again, the Eagle took small-sized Bagrus more frequently than man.

4.3.5.2 Consumptions of fish

An estimate of the daily food requirement of the wild adult Fish Eagle is given in Table 4.19. Although few, the data show that the adult bird ate about 275 g of fish daily, an equivalent of ca. 10.5% of its body weight.

A recently fledged young, probably a female, which was kept in captivity between 10 February, 1978 and 30 September, 1980, was weighed on 15 occasions prior to being given food (fish) during a feeding experiment which ran for the whole of 1978. During the period, the growing bird averaged 2873.7 g although its weight fluctuated between 2475 g at time of capture and 3050 g by the end of September 1978. It was fed on alternate days, and its food consumption averaged 415 g (320-580 g) of fish, an equivalent of ca. 14.5% (10.7-19.3%) of its body weight. The lowest amount of food it ever ate was 150 g and the highest was 690 g, which amounts respectively corresponded to 5.2% and 24.0% of its average weight. Since it ate every other day and still gained weight, its daily food requirement probably must have been around 7% of its weight or ca. 210 g of fish.

In 78 eagle-days of dawn-dusk observations, the 78 Fish Eagles captured 58 fishes (Table 4.20). They lost 3 of the 58 fishes through piracy. The 55 fishes which they retained represented 0.71 fish/Eagle/day or 259 fishes/Eagle/year. From the recovered prey remains it was found that the Eagle mostly preyed upon Tilapia weighing 405 g (Fig. 4.7), Clarias weighing 977 g (Fig. 4.8), and Bagrus weighing 573 g (Fig. 4.9). The data, therefore, suggest that the Eagle took prey weighing, on average, 651.7 g (357.7 - 945.7g) most frequently. From the rate of predation (0.71 fish/Eagle/day) and the average weight of prey (651.7 g) taken most frequently, each adult bird, consequently, harvested from the waters ca.462.7 g (254-671.4 g) of fish daily or 168.9 kg (92.7 - 245.1 kg) annually. For convenience, it was assumed a juvenile bird consumed as much food as an adult.

Table 4.20 Daily fish catches by the Fish Eagle in Queen Elizabeth Park.

Date	Pair No.	Sex	Catch made	Ca.wt(g)	Birds feeding on it
13.7.76	6	Male	2 Tilapias	800,500	Both male & female
	73	Male	Unidentified	–	–
		Female	"	–	–
	8	Male	"	Large	Both male & female
	72	Male	"	Large	Both male & female
	74	?	"	–	–
14.7.76	6	Male	2 Unidentified	Both small	Male alone
	73	Female	Unidentified	Small	Female alone
	8	?	"	–	–
	72	?	"	–	–
16.7.76	6	Male	Clarias	700	Both male & female
	8	Male	Unidentified	–	–
	72	Male	"	–	–
		Female	"	–	–
	5	Male	"	–	–
		Female	"	–	–
22.7.76	6	Male	2 Tilapia	400,900	Both male & female
		Female	Bagrus	–	Female alone
	72	Male	Catfish?	Large	Lost due to piracy
	5	?	Unidentified	–	–
	73	Male	"	–	–
		Female	2 Unidentified	–	–
29.7.76	6	–	–	–	Neither fed all day
	73	Male	Unidentified	–	–
		Female	2 Unidentified	–	1 lost due to piracy
	5	Female	Unidentified	–	–
	74	Male	"	–	Male & female
	8	?	"	–	–
	72	Male	"	–	Male & female

Cont'd.

Table 4.20 cont'd.

Date	Pair No.	Sex	Catch made	Ca.wt(g)	Birds feeding on it
31.7.76	6	Male	Unidentified	–	Ate alone
		Female	Tilapia	400	Ate alone
	73	Male	Unidentified	–	Both male & female
	8	Male	"	–	Ate alone
		Female	"	–	Ate alone
	74	Male	"	–	–
6.8.76	6	Male	1 catfish 1 Tilapia	500 300	1 taken to nest with 2 one-week old chicks 1 lost (piracy)
	8	Female	Unidentified	–	–
	72	Male	"	–	–
	73	Male	"	–	–
	5	Male	"	–	–
		Female	"	–	–
	74	?	Unidentified	–	–
16.8.76	6	Male	2 Tilapias	200,300	1 to nest with 2 two-week old chicks.
		Female	Tilapia	500	Taken to nest
	72	Male	Unidentified	–	Both male & female
	74	Male	2 Unidentified	–	Both male & female
	5	Male	"	–	–
		Female	Unidentified	–	–
	73	Male	"	–	–
	8	Male	Unidentified	–	–
Total	39 pair-days 78 eagle-days		58 kills, 3 lost =55 kills retained		

Kills/Eagle/day = 0.71 fish = 259 fish/Eagle/year.

Thus the 752 Fish Eagles counted in the whole Park (section 2.3.2), therefore, removed from the waters 127,012.8 kg (69,710.4 - 184,315.2 kg) of fish annually.

Data in the Fisheries Office, Kichwamba, indicate that between 1975 and 1978, man harvested, on average, 12,240,000 kg of fish annually from Lakes Edward and George and the Kazinga Channel (S. Katuramu, pers. comm.). Thus the amount of fish taken annually by the 752 Fish Eagles in the Park represents only 1.04% (0.57 - 1.51%) of the quantity harvested by man.

Din & Eltringham (1974) estimated that the fish productivity of L. George is ca. 18,500,000 kg/year. Gwahaba (1973) found that the lake had a mean productivity of 23.3 g/m^2, thus giving a productivity of 14,706,960 kg of fish/year (lake area = 263 km^2). The 119 Fish Eagles found on that lake (section 2.3.2), therefore, harvested from it ca. 20,099.1 kg (11,031 - 29,166.9 kg) of fish annually. This amount represents only 0.11% (0.06-0.16%) of the total annual fish production estimated by Din & Eltringham (op cit.) or only 0.14% (0.075-0.20%) of that given by Gwahaba (op cit.).

Between 1974 and 1978, man harvested from L. George an average of 3,757,720 kg fish/year (S. Katuramu, pers. comm.). Thus the amount of fish harvested annually from the lake by the Fish Eagle is only 0.53% (0.29-0.78%) of the amount exploited by man.

4.4 DISCUSSION

The main food of the African Fish Eagle is fish (Brown 1970a & 1980). However, eggs and young and even adults of waterbirds, and carrion are also eaten (Brown, op cit.). In South Africa, the Fish Eagle is reported to take fish, rats, young of other birds and occasional carrion (Porter 1903, Roberts 1958, Clancey 1964). In West Africa it is reported to take frogs as well (Bannerman 1953).

In exceptional habitats like alkaline lakes and seasonal swamps where there are no fish or are present in inadequate quantities, the Fish Eagle can make a staple diet out of the adults and also of the eggs and young of waterbirds that might inhabit or breed in them (Brown 1970a, b & 1980; Urban 1975; Cunningham-van Someren & Richards 1977).

Nevertheless, even in areas where there are apparently adequate fish prey to meet its food requirements, the Eagle can still raid nests of other birds of their eggs and young. It plundered the heronries of the Great White Egret Casmerodius albus and Sacred Ibis Threskiornis aethiopicus in the Kano Plains, near L. Victoria, Kenya (Parsons, pers. comm.). In Akagera National Park, Rwanda, it would wait for long periods around the colonies of African Darters Anhinga rufa and cormorants Phalacrocorax spp. whose nests it eventually robbed of eggs and young (Thilollay, pers. comm.).

Brown (1970a) reported Fish Eagles as subsisting on the adults of waterbirds, especially flamingos Phoenicopterus ruber and Phoeniconaias minor, on alkaline Lakes Bogoria (Hannington) and Elmenteita, Kenya. Evans & Campbell (1977) saw a Fish Eagle knock down and eat a Ringed Plover Charadius hiaticula which they had just released after having mist-netted it during their Tana River Expedition in 1976. In this Park, Eltringham (1975) and N. Ckurut L'Ctai (pers. comm.) reported seeing Fish Eagles eat a White-browed Coucal Centropus superciliosus and a White-winged Black Tern Chlidonias leucoptera respectively. In both cases, however, how the birds were obtained were apparently not witnessed.

At L. Naivasha, Clapp (1976) found a pair feeding on a carcass of an African Hare Lepus capensis which he suspected the birds killed. He also quoted his friend witnessing two birds fight over a dead Kirk's Dik-dik Rhynchotragus kirkii, which probably one of the combatants killed. In this Park, Rood (1975) saw a pack of Banded Mongooses Mungos Mungo appropriate, from a pair, most of the meat of a freshly killed African Savannah Hare L. crawshayi.

. During this study, territorial birds almost exclusively preyed upon fish. No live prey other than fish was seen taken by them. Nevertheless, feathers and other body parts of birds found under feeding perches suggest that birds are probably eaten occasionally. Additionally, the motives for which the Eagle chased small birds in this Park (section 3.3.2.5) remains unresolved unless explained in terms of predation.

The territorial Fish Eagle largely caught its own prey although piracy was also practiced. Fishing dives were attempted from perches, from soaring flights and from low circling flights made close above the water surface.

Fishing attempts made from perches were the most common while those from soaring flights the least so. Brown (1980) also states that most fish are caught by short flights made from perches. Much as fishing attempts are made while birds are soaring, this is a most unusual way of hunting. Such soaring flights are probably connected with social and territorial displays (section 3.3.2.3) rather than with hunting. Brown (op cit.) believes that they are purely territorial.

In the related Bald Eagle Haliaeetus leucocephalus, Southern (1963) distinguished 4 methods of hunting. Firstly, dives are made from perches and, as in the Fish Eagle, this is the most commonly used fishing method. A second method is by making dives after a short circling flight over the water. A third hunting method, which very few Bald Eagles use, is to stand by the water edge and to reach into water for prey by their beaks or talons. This probably is a method that is used to pick up dead or live but trapped prey. Such method of fishing was not recorded for the Fish Eagle although it could have been employed on dead or small live prey when fishing in shallow water. Fourthly, both adult and young Bald Eagles waded in shallow water and caught fish with the beaks. Southern (op cit.) found this method to be the most successful technique of fishing. No such method of fishing was practised by the Fish Eagle during this study. All prey captures witnessed involved the use of talons. On San Juan Island, Retfalvi (1965) also found that the Bald Eagle used all the above hunting methods but the most commonly employed was the steep dive from the perch.

Brown (1980) reported that Fish Eagle spend from 90-95% of their time perched on trees, surveying the water or merely resting. He also concluded that males are always more active than the larger females. During this study, the hunting efforts of the birds, as numbers of dives made, indicate that the male is more active than the female (sections 3.3.2.3 & 10.3.3)

Fish Eagles in this Park succeeded in about two-thirds of all their fishing attempts, with both sexes scoring similar successes. Probably using records largely from L. Naivasha, Brown (1976b) reported that the birds made from 2-10 dives per kill.

At L. Naivasha and at Mida Creek, Kenya Coast, Brown (1980) found that Fish Eagles made greater hunting efforts and succeeded better when the water was wavy and murky.

In calm and clear water, Brown argues that Fish Eagles seem to know that prey would detect their approaches more easily and, therefore, evade them. Birds in this Park also hunted during windy conditions and most of the dives made from circling flights were undertaken during such conditions. The small sample size, however, precludes a firm conclusion on whether or not sorties made during windy conditions are as successful as Brown (op cit.) suggests.

Favaloro (1944) observed the White-bellied Sea Eagle Haliaeetus leucogaster fishing against the sun. This, he argued, is explained by the fact that a fish at the surface of water or just rising to the surface would dive back into the depths on seeing an Eagle's shadow pass over it. It would, therefore, be an advantage for any fishing eagle to hunt while flying into the sun so that its shadow is behind it and would not scare away potential prey. In assessing this suggestion, Greenspan & Torre-Bueno (1971) found that the pair of Fish Eagles that they extensively observed in this Park made more dives in the afternoon, a period when the birds were flying into the sun, than at other times of the day. However, the hunting success of the birds during this period was not significantly different from those recorded at other times of the day.

During this study Fish Eagles made dives during all hours of the day and with fairly equal frequencies. Although more work is needed on this aspect of the Eagle's biology, available data suggest that some birds were more successful in the morning (07:00-12:00) when their shadows were behind them and in the evening (18:00-19:00) when their shadows had disappeared, than at other times of the day. Thus, whilst the positions of the shadows of the birds may be important in their hunting successes (Favaloro, op cit.), other factors like the waviness of the water and its clarity (Brown 1980) need to be considered as well.

Brown (1980) suggests that adults are more piratical than young birds. Because young birds become particularly affected by this habit, they tend to move away from areas where adults are more plentiful to congregate in those where they are fewer (Brown 1980, Brown & Hopcraft 1973). Contrary to Brown's suggestion, young Fish Eagles in this Park used piracy more often than adults.

The facts that the densities of young were significantly and positively correlated with those of adults indicate that young birds do not necessarily avoid shorelines with high densities of the adults (section 2.3.2). Congregations of young birds were witnessed in this Park, and these were apparently in response to better scavenging opportunities at the fishing villages rather than in avoidance of adult birds which persecute them (sections 2.3.2, 2.3.3 & 2.4).

Although similar, the pirating successes of both adult and young birds were low (24% and 22% respectively), averaging 22.6%. At such a low rate of success, piracy from conspecifics is, therefore, a more inferior method of food procurement than hunting whose rate of success was ca. 66%. Since piracy is also a great risk to the pirate, it should not have been evolved at all!

Both adult and young Fish Eagles succeeded less often when pirating from adults than when they did so from young birds. These findings suggest that the experience of the victim-to-be is important in defending the coveted prey. Young birds succeeded more often when robbing adults when they are in bands of 2 or more individuals than when they tried so singly. Thus, by associating itself with a wandering group of other young, the young bird greatly enhanced its chances of survival than by living solitarily. As a team the band more easily acquires prey, both by piracy and hunting, than would single birds. Secondly, whatever prey the band obtains would be better defended by the members for the sole use of the group. If the prey has been pirated from adults, the owners usually failed to re-possess it just as other adults failed to take it away from the group of young. Prey obtained by hunting by a member of the band would hardly be removed from the group through intraspecific piracy. Thirdly, this mode of existence stops the White-headed Vulture Trigonoceps occipitalis which usually drops onto any band of young Fish Eagles that has just acquired prey from appropriating the food. Fourthly, membership of any young into the band spreads the risks of attacks by adults during both piracy and territorial (section 3.3.2.1) encouters to all members of the group.

Brown (1980) lists several species of other birds that are deprived of their prey by the Fish Eagle, and asserts that such large birds as the Goliath Heron Ardea goliath and pelicans Pelecanus spp. are forced to abandon their prey or disgorge them.

A Hammerkop *Scopus umbretta* was several times successively robbed of its prey by a Fish Eagle. It only managed to feed after having first satisfied the appetite of the voracious Eagle (Brown, op.cit.). Although the Fish Eagle tried to deprive several other species of birds of their prey, none of them dropped or disgorged prey that the Eagle subsequently picked. Birds like the Saddle-billed Stork *Ephippiorynchus senegalensis* and the Goliath Heron defended their prey successfully against the Eagle. They, in addition to the Marabou Stork *Leptoptilos crumeniferus*, also turned on the Fish Eagle and successfully deprived it of its prey.

At Lake St. Lucia, South Africa, Whitfield and Blaber (1978) identified 88 of 101 fishes caught by the Fish Eagle. The specimens included 58 mullet (*Mullus* spp.), 13 catfish (Clariidae and Bagridae), 8 spotted grunters (Theraponidae), 5 garfish (Belonidae), and 4 river bream (Cyprinidae). They also demonstrated that the Eagle largely took surface-feeding fish or fish that shoaled on the surface. They, however, did not show whether or not the numbers of fishes taken by the Eagle were proportional to the densities of the fishes in the lake.

During this study the predation pressure exerted by the Fish Eagle on its prey was proportional to the densities of the fish types. Thus *Tilapia* spp., the most abundant of the prey fishes, was caught most and *Bagrus* spp. least so. Both *Tilapia nilotica* and *T. leucosticta* feed on phytoplankton (Worthington 1929a, Fish 1955) and are, therefore, frequently at or near the surface. *T. nilotica* also shoals near the surface of water (Worthington, op cit.). Apart from being common in shallow waters (Worthington, op cit.), all *Clarias* spp. habitually come to the water surface for additional supplies of atmospheric oxygen (Greenwood 1966). Additionally, *Clarias* are largely carnivorous fishes (Worthington 1932, Poll 1939). Apart from preying on other fishes (Worthington, op cit. & 1929a, Graham 1929, Hulot 1956, Corbet 1961), *Bagrus docmac* is common in the shallow waters of the L. Edward/L. George water systems (Worthington 1932). Thus, the life habits of the above fish types render them highly vulnerable to predation by the Fish Eagle.

In this Park, the Fish Eagle preys upon fishes similar in sizes to those taken by man. In *Tilapia* spp. the agreement in the sizes taken by the two predators is highly significant (Table 4.13 & Fig. 4.7).

According to Gwahaba (1973), the smallest maturing T. nilotica measures ca. 18 cm total length, and at 24 cm virtually all fish are mature. When fish mature, their growth rates are considerably slowed down (Lowe-McConnell 1958). This can cause an accumulation in numbers of fish varying minimally in size and yet varying greatly in age. Thus, just as man, the Fish Eagle in this Park is almost exclusively preying on Tilapia which are sexually mature and have perhaps many times reproduced themselves.

The agreement between the sizes of Clarias spp. taken by the Eagle and man is not significant (Table 4.14 & Fig. 4.8) but that for the predation of Bagrus docmac is significant (Table 4.15 & Fig. 4.9). For both types of fish, the sizes at sexual maturity are not known. Thus, in case of feeding on sexually immature fishes, both man and the Eagle are to blame because the small-sized fishes which the Eagle is taking are within the range of sizes exploited by man. However, in the event of damage to the stock of each fish type, the degree of blame would depend on the amount of such prey that are taken by each predator. By preying upon Clarias and Bagrus, large and small, the Fish Eagle is still being beneficial to man in that it is helping to reduce the populations of fishes which are carnivorous upon other fishes (Brown 1970a & 1980).

In South Africa, Jubb (1968) and Junor (1968), by use of skulls of catfishes, estimated that the Fish Eagle can carry fishes weighing from 400 g to 1140 g. Tomkinson (1975), using freshly caught fish, found that the heaviest fish, a catfish, that the Eagle carried weighed 2340 g. This fish was, however, landed with difficulty although it was caught near the shore. In tests with 55 stunned bait fishes, the Eagle lifted and carried away fish weighing 2000 g and less without difficulty, but fish of over 2000 g was not moved more than 50 m.

Six times during this study the Fish Eagle brought prey, all catfishes, ashore by swimming. Once, on 19 August 1975, the female of Pair No. 6 was pulled right below the water surface by an apparently too heavy a fish. It had to swim ashore ca. 30 m, without the prey, probably because her feathers had become too wet.

On yet another occasion on 18 May 1977, the male of Pair No. 72 caught a fish which he lifted well above the water surface but dropped it back probably because the prey was too heavy or struggled too strongly or both.

Five out of the six prey landed by the Fish Eagle by swimming weighed from 2055-2628 g (Table 4.11). Probably because of his smaller size, the male landed comparatively smaller prey than his mate. Although few, these results indicate that the Fish Eagle can hardly carry prey of 2000 g and above but can still catch and land prey as heavy as 2628 g, probably heavier, by swimming.

Helander (1983) found that the Sea Eagle Haliaeetus albicilla in Sweden has a wide food spectrum. Although primarily associated with aquatic prey, the Eagle took all sorts of food and was opportunistic. It shifted between different prey in accordance with their availability in space and time. A similar conclusion is apt for the Bald Eagle H. leucocephalus (Snow 1973a). Although the types of food taken by the Fish Eagle have been well documented, quantitative assessments of them have generally been lacking. The numbers of prey items taken by the Fish Eagle during this study indicate that its food did not vary with time. The lack of seasonal shift in the Eagle's predation pressure on its prey would demonstrate that its food base, in this Park, is relatively stable throughout the year.

Because the Fish Eagle is generally inactive for 85-95% of the daytime and all night, and is a tropical bird, Brown (1980) estimated its daily food needs at only 4.85% of its body weight or ca. 135 g of fish. On the basis of food requirements of temperate birds of prey, Brown (op cit.) calculated a revised daily food consumption of 255 g of fish or 8% of the Eagle's body weight. Stowell (1958), using a captive adult, estimated that the Fish Eagle eats about 1 lb (454 g) of fish daily, with another 1 lb being allowed as wastage. Brown (op cit.) considers Stowell's finding a gross over-estimate. During this study, I found that the adult bird comsumed ca. 275 g of fish/day, which amount represented ca. 10.5% of its body weight. Greenspan & Torre-Bueno (1971) once saw an adult bird consume almost completely a 27 cm Tilapia sp. This fish probably weighed about 400 g (Fig. 4.7 & section 4.3.4.2). Allowing for considerable wastage of about one-fourth the prey, the Fish Eagle in question must have eaten no less than 300 g of the fish.

A captive juvenile which was fed on alternate days during this study, ate an average of 210 g of fish daily. This food consumption represented about 7% of its body weight. Since it gained weight, this amount of food sufficed for its daily energy requirements probably because of its idle life. Until more data are presented to the contrary, it is, therefore, safe to assume that the daily food requirement of the wild adult Fish Eagle ranges between 5-10% of its body weight or ca. 150-300g of fish.

On L. Albert, Green (1964) estimated that the 167 adult Eagles he counted along the 209 km shoreline consumed only 0.5% of the annual catch made by fishermen. Eltringham (1975) calculated that the 123 Eagles he found on L. George harvested only 0.2-0.3% of the total annual fish production of the lake or only 0.8-1.1% of the amount caught by man. Both authors used Stowell's (1958) figure of 1 lb for the daily food consumption of the Eagle for calculating the amounts of fish taken by the Eagle from the above lakes. Accordingly, Brown (op cit.) revised the above findings and suggested that for L. Albert the Fish Eagle removes only 0.13% of the annual catch while for L. George the bird takes only 0.05-0.075% of the annual fish production and only 0.2-0.3% of the fisherman's annual harvest.

Comparing the weight of prey captured by the Fish Eagle per day (462.7 g) with the daily food consumption (274.5 g), one realizes that there is a considerable wastage of about 40%, which amount is far in excess of the 10% wastage assumed by Brown (1980). For this reason the amounts of fish harvested by the Fish Eagle during this study were calculated using the weight of prey captured (462.7 g) rather than the amount consumed (274.5 g) per day. Thus the 752 Fish Eagles counted in the whole Park (section 2.3.2) removed 127,012.8 kg of fish annually. This is only 1.04% of the amount harvested by man. For L. George whose annual fish production was estimated at 14,706,960 kg (Gwahaba 1973) and 18,500,000 kg (Din & Eltringham 1975), the 119 Eagles I found on it would harvest only 20,099 kg of fish annually. This amount represents only 0.14% of the annual production estimated by Gwahaba (op cit.) or only 0.11% of that determined by Din & Eltringham (op cit.). Data in the Fisheries Office, Kichwamba, indicate that between 1974 and 1978, man harvested from L. George an average of 3,757,720 kg of fish annually (S. Katuramu, pers. comm.). The amount of fish taken annually from this lake by the Eagle would, therefore, represent only 0.53% of that exploited by man. At such low rates of removal of fish from the water systems, the African Fish Eagle cannot, therefore, be in serious competition with man nor can it be playing a significant role in the transfers of nutrients from water to land.

CHAPTER 5

THE NEST AND MAINTENANCE OF PAIR-BOND

5.1 INTRODUCTION

Eagle nests are platforms of sticks and grasses which are used year after year(e.g. Brown 1970, 1976 & 1980; Brown & Amadon 1968; McGahan 1968; Sprunt et. al, 1973). Alternate and frustration nests are common (Postupalsky 1972; McGahan, op.cit.; Snow 1973) Although most eagles build their own nests, they frequently appropriate other birds' nests and their own nests are often appropriated by other species (Brown 1974b, 1976a & b; Postupalsky, op.cit.). Many smaller birds, especially weavers (Plocineae), associate their nests with those of raptors (Brown 1976a & b & 1980).

In most temperate zone raptors, the pair-bond is probably dissolved as the birds migrate to wintering grounds (Brown 1976a, b & c; Brown & Amadon, op.cit.; Retfalvi 1965; Snow, op.cit.). Various behaviours like courtship displays, feeding, copulation, nest building and repairing, territoriality and mutual preening have been associated with the maintenance of the pair-bond(Hinde 1964, Brown, op.cit.; Brown & Amadon, op.cit.; Retfalvi, op.cit.; Greenspan & Torre-Bueno 1971).

This Chapter describes the nest of the Fish Eagle and assesses its uses in the life of the bird. An estimate of dry vegetative materials locked up in the nests is given. Nesting associations and appropriations between the Fish Eagle and other birds are examined. The maintenance of pair-bond in the species is described.

5.2 METHODS

In the study area I counted all nests in each territory of a pair, recorded the nest trees used, and noted the positions of nests in the trees. The distance between a nest tree and the nearest shoreline was measured. In 20 randomly selected territories, nest trees and other mature trees within 1 km of the shoreline were counted. Trees were identified at least to generic level, to determine whether or not the Eagles selected certain types of trees as their nest sites.

Nest structure and dimensions were observed and measured from 4 nests whose trees blew down and from those whose trees could be climbed. Only 4 species of woody plants were common in the destroyed nests. It was difficult to indentify the other species because they had decayed extensively. The species compositions, by weight, of the identifiable plants and of those which could not be indentified (referred to as others) were calculated. These were then expressed as percentages of the total weight of undecayed materials. This mode of expression permitted comparisons of the species compositions of the nest materials with those from 40 bushes chosen from the vicinities of the destroyed nests. Bushes were Sampled ~~smapled~~ by laying two 100m line transects in each territory containing a destroyed nest. The transects orginated at the nest tree and ran at right angles to each other. Along each transect 5 bushes were examined, 1 at the source and the other 4 at 20m intervals. The nearest bush at each of the intervals was examined. The total number of times a plant species occurred in the 40 bushes divided by the total number of species recorded gave the frequency of each plant type. This frequency was then expressed as a percentage of the total number of species counted.

The types of materials used for nest lining were also identified but were not weighed individually. Any other odd items found in the nest were also recorded.

Nest building and repairing activities were observed with the aims of establishing:

a) the role of each sex in nest building/repairing,

b) the rate of nest building/repairing in relation to the abundance of building materials, and

c) the rate of nest building in relation to proximity to egg-laying.

Birds of prey have alternate and frustration nests which they use yearly or between breeding attempts (Postupalsky 1974). In pairs with multiple nests, I tried to establish the patterns of their use because nestling mortalities among birds are sometimes attributed to nest infestations by arthropods (Ricklefs 1969, section 8.3.4). With repeated repair and use raptor nests acquire distinct layers (Brown 1976a, b & c & 1980). The number of layers a Fish Eagle eyrie contained could not be easily counted from intact nests but were determined from the fallen ones.

The amount of dry woody materials locked up in eyries in the whole park was estimated from the mean weight of the destroyed nests. This was only possible after having determined the numbers of pairs of Fish Eagles (section 2.3.2), and therefore territories (section 3.3.1), in the whole Park and having calculated the average number of nests per pair.

Nesting associations between Fish Eagles and any other birds were noted. Investigations and appropriations of eyries by other large birds were also recorded.

Various behaviours of raptors like those mentioned in section 5.1 have been associated with the maintenance of pair-bonds. During this study any behaviour which was displayed by the Fish Eagle and was thought to function in maintaining the pair-bond was recorded.

5.3 RESULTS

5.3.1 The number of nests per pair

During a survey between 16-19 September 1975, 98 nests were counted in 79 of the 86 terrotories in the study area. The birds had from 0-4 nests/pair, averaging 1.14 nests/pair overall and 1.24 nests/pair with with a nest (Table 5.1). Pairs No. 4, 44, 45 and 75 (Fig. 3.1) had no nests probably because they had no mature and tall enough trees on which to site them.

Nests were built on trees situated right from the shoreline up to a distance of ca. 1 km inland. The number of nests declined significantly with increasing distance from the shoreline (Fig. 5.1). Eighty-one nests averaged 0.11 ± 0.14 km from the bank with 75 (92.6%) of them being located within 0.25 km of the shoreline. Counts of all mature trees in 20 territories selected from a table of random numbers indicated that the Eagles used any mature tree as a nest site (Table 5.2). Nevertheless, selection indices showed that <u>Acacia sieberiana</u> and <u>Euphorbia dawei</u> were more strongly selected for than the other species of trees (Table 5.2). Crown nests predominated over those in the forks of trees (Table 5.3). The majority of nest trees could not be climed and their heights could not, therefore, be measured. Twenty four nest trees, however, averaged 5.96 ± 1.36 m (3.6 - 9.8 m).

5.3.2 Nest structure, dimensions and shape

The nest is a platform of dry sticks and grasses.

Table 5.1 The numbers of nests per pair of Fish Eagles in Queen Elizabeth Park during a survey from 16-19 September 1975

Pairs with following numbers of nests					Total		Mean (±SE) nest/pair	
0	1	2	3	4	pairs	nests	with nest	overall
7	64	12	2	1	86	98	1.24 ± 0.06	1.14 ± 0.07

Fig. 5.1 The relationship between African Fish Eagle nests and their distances from the nearest shoreline. A total of 81 nests was used in this analysis.

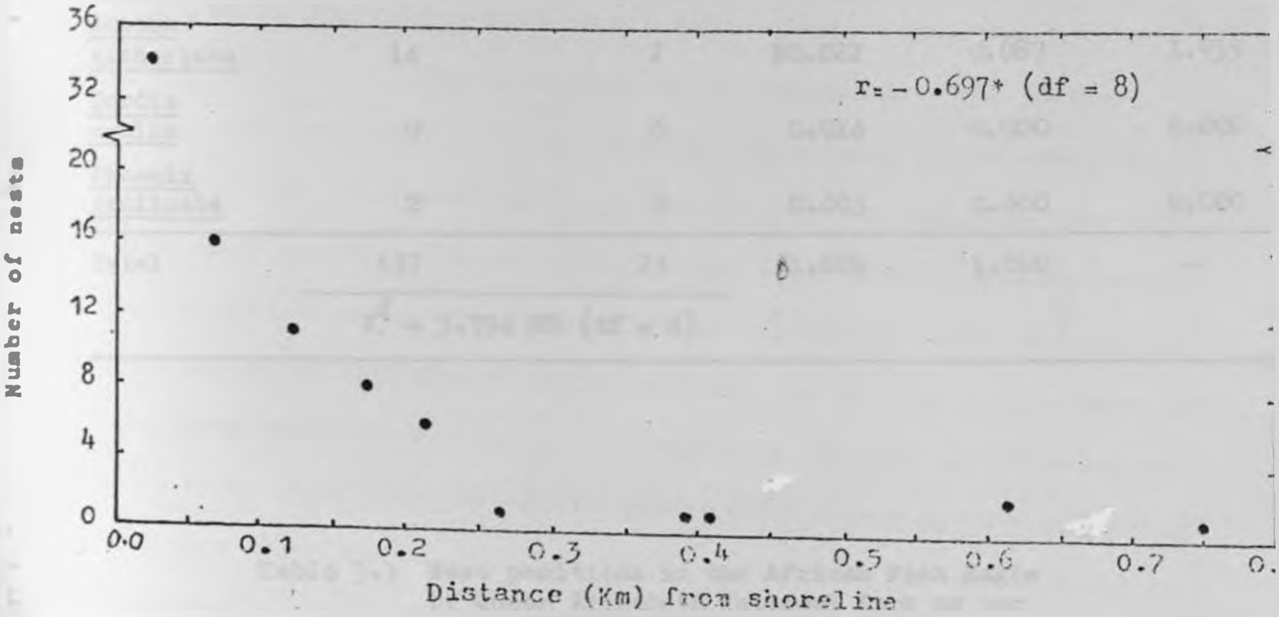


Table 5.2 The distribution and the selection indices of nest trees in relation to the abundance of the respective tree species in 20 randomly selected territories of Fish Eagles in Queen Elizabeth Park. Selection index = proportional (Prop.) use of a tree species as nest tree divided by the proportional abundance of the species.

Tree species	Numbers in 20 territories	Numbers used as nest tree	Prop. abundance	Prop. use as nest tree	Selection index
Euphorbia candelabrum	486	14	0.763	0.609	0.798
Euphorbia dawei	126	7	0.198	0.304	1.535
Acacia sieberiana	14	2	0.022	0.087	3.955
Cordia ovalis	9	0	0.014	0.000	0.000
Phoenix reolinate	2	0	0.003	0.000	0.000
Total	637	23	1.000	1.000	-

$X^2 = 5.794$ NS (df = 4)

Table 5.3 Nest positions in the African Fish Eagle of Queen Elizabeth National Park as per survey conducted between 16-19 September 1975.

Nest tree	Nest position		Total	
	Crown	Fork	No.	%
Euphorbia candelabrum	43	6	49	50.0
Euphorbia dawoi	28	3	31	31.6
Acacia spp.	7	4	11	11.2
Albizzia spp.	0	3	3	3.1
Cordia ovalis	1	0	1	1.0
Bush and tree-stumps	3	0	3	3.1
Total	82	16	98	100.0

$X^2 = 20.958$***(df = 5)

The base and sides consist of stronger and larger dry branches with lighter materials towards the centre. During nest building, the branches are simply placed and pressed down on top of one another. Some criss-crossing occurs, especially at the periphery, and it is this interlacing of materials which gives the nest a firm structure.

Nests built on *Euphorbia* trees were similar in width but those sited on *E. candelabrum* were significantly deeper than those on *E. dawei* (Table 5.4). The nest floor depths and widths were, however, comparable (Table 5.4). Nests on other trees could not be measured although nest dimensions and shape varied with the nest tree type and with their positions on the trees. Crown nests were invariably saucer-shaped while those in the forks of trees cup-shaped. With repeated use the cup-shaped nest slowly transformed into an inverted cone. Nests in the forks of trees were normally cone-shaped and they probably assumed this shape right from the start since the "V" formed by the branches of the nest trees had to be filled in before the nest was large enough to comfortably accommodate the breeding birds.

5.3.3 Nest materials

Fish Eagles selected branches of particular species of plants for nest construction (Table 5.5). *Capparis tomentosa*, a bush with the highest frequency in the study area, formed the major source of nesting material. *Azima tetracantha*, *Erythrococus bongensis* and *Terena graveolens* were used in similar proportions. Other species of plants were also used (Table 5.5) and the Eagle used both thorny and non-thorny branches. Both *C. tomentosa* and *A. tetracantha* bear thorns. Despite their fairly equal frequencies in the study area, *C. tomentosa* was more used as nest material than *A. tetracantha* probably because the latter bears much

Table 5.4 The dimensions of 13 Fish Eagle nests in relation to the types of *Euphorbia* species on which they were built. In each case student's t was calculated using the formula for small sample sizes; df = 11 for each test.

Nest tree	No. of nests	Nest dimensions (cm)		Nest floor dimensions (cm	
		width	depth	width	depth
E. candelabrum	7	89.4±7.8 (66.3-128.9)	127.3±15.0 (71.8-196.4)	25.4±1.9 (18.6-35.7)	4.8±0.5 (2.2-7.1)
E. dawei	6	107.0±5.3 (89.4-122.6)	23.5±3.4 (11.5-36.4)	27.7±2.8 (17.8-38.9)	5.3±0.6 (2.9-7.3)
	t-value	-1.654 NS	5.786***	-0.645 NS	-0.467 NS

Table 5.5 The percent frequencies of nest materials and their composition by weight in 4 nests of Fish Eagles in Mweya Peninsula. The 0.3% shortage in the % composition is made up for by the lining materials which were largely grass spp.

Nest material	% frequency in study area	% composition in 4 nests
Capparis tomentosa	19.5	88.3
Azima tetracantha	16.4	2.4
Erythroccocus bongensis	10.7	2.2
Terena graveolens	6.9	2.0
Other species	46.4	4.8
Total	99.9	99.7
	X^2 = 96.408***, (df = 4)	

Table 5.6 The role of each sex of the Fish Eagle in the building or repairing of the nest.

Pair No.	Date	Nest material/min/sex Male	Female
86	3.1.77	0.27	0.22
	4.1.77	0.23	0.54
	7.1.77	0.24	0.33
	8.1.77	0.17	0.12
		X^2 = 0.119 NS (df = 3)	
82	18.10.76	0.29	0.31
	19.10.76	0.22	0.34
	20.10.76	0.24	0.29
		X^2 = 0.009 NS (df = 2)	

longer and more formidable thorns than the former species. *Erythrococus bongensis*, *T. graveolens* and the other bushes however, bear no thorns.

Occasionally *Phragmites* sp. (Arundineae) and *Cyperus* spp. (Cyperaceae) were incorporated in the nests. Odd items like broken pieces of fishnet, polythene sheets and pieces of barbed fencing wire were also found in eyries. These were embedded in the nest floor as lining materials or simply strapped around the nest edge.

Grasses and forbs of various species were used as lining materials, but tufts of *Sporobolus* spp. were the major item. Nile cabbage *Pistia stratiotes* was another plant commonly used for lining nests. Dung boluses, especially those of elephants *Loxodonta africana* were also found in the nest floor. Nests of other bird species, especially those of weavers (Plocineae), were regularly encountered as lining materials.

Fish Eagles added green branches or leaves, particularly those of *T. graveolens*, to their nest floors; and these materials were incorporated and leaves of *C. tomentosa*, *A. tetracantha*, *Securinega virosa* and other plants were also used. The Eagle simply broke off branches and leaves with its talons as it flew past a bush and immediately brought the spray to the nest. Both sexes brought the green materials to the nest, usually when relieving each other from incubation or brooding.

5.3.4 Nest building and repairing

Observations on 2 pairs showed that both sexes brought similar amounts of building materials to the nest (Table 5.6). Usually leafless branches were used, and such twigs were normally carried to the nest in the talons.

The birds also picked up twigs in their bills but these were immediately transferred to the feet on take-off. They normally flew directly to the nest after picking up the materials, and flapping flight and landing were encumbered by the materials.

The rates of nest-building measured in terms of building materials brought to the nests by Pairs No. 82 & 86, did not differ significantly between the pairs in relation to their times of egg-laying ($t = 0.027$, $df = 5$, $P > 0.1$; data in Table 5.6). Thus Pair No. 82 which had only 3.5 weeks to laying its clutch brought materials to its nest at about the same rate as Pair No. 86 which had a much longer time (9 weeks) to egg-laying.

Any pair that had a nest visited it regularly, even during the non-breeding period. Since it was visited so often the nest occasionally had a stick added to it or the existing materials re-arranged. Serious and protracted repairs were, however, made on nests only once a year. Pairs with multiple nests tried to repair all their nests, but usually only one was fully repaired.

Prior to and during nest repair both partners of a pair spent varying amounts of time standing on the nest or nest-tree (Fig. 5.2). The time spent on the nest was significantly but unexpectedly inversely related with the proximity to egg-laying although it would have been expected that pairs which were about to lay should have stayed longer on the nest than those whose laying times were further away. The female, however, spent significantly more time on the nest than her mate (Table 5.7).

Fig. 5.2 The time spent on the nest by male and female Fish Eagles in relation to proximity to egg-laying. Solid circles represent male and open ones female.

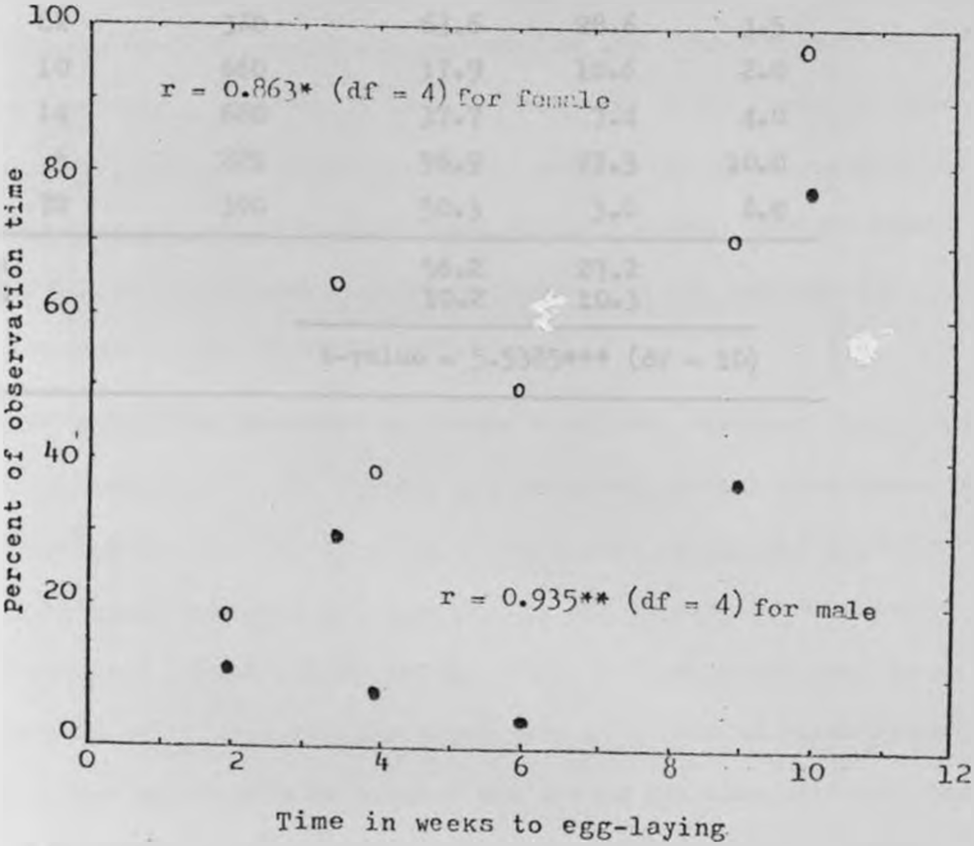


Table 5.7 The time spent by each sex of Fish Eagles on the nest prior to commencement of breeding in the species. * indicates time pair laid after completion of nest.

Pair No.	Observation time (min)	% time on nest		Time* (weeks)
		Female	Male	
87	750	70.6	36.5	9.0
82	360	63.6	28.6	3.5
10	660	17.9	10.6	2.0
14	660	37.7	7.4	4.0
5	225	96.9	77.3	10.0
72	390	50.3	3.0	6.0
Mean		56.2	27.2	
± SE		10.2	10.3	

t-value = 5.5385*** (df = 10)

Materials in the Fish Eagle nests became layered with each repair or breeding attempt. Of 4 nests examined, two on *Euphorbia candelabrum* had 9 and 13 layers each and another 2 on *E. dawei* contained 6 and 8 layers respectively. Since the repairs preceed egg-laying which is usually annual (section 6.3.3), the layers are good indices of the approximate ages of the nests.

5.3.5 Alternate and frustration nests

Fish Eagles in this Park had both alternate and frustration nests. Eighty six pairs had on average 1.14 nests/pair overall (Table 5.1). The origin of these multiple nests was realised as the study progressed. Pairs whose breeding attempts failed sometimes built new nests or repaired old ones (alternate nests) for their next breeding attempts while those which bred successfully still used the old nests. Use of alternate nests during subsequent breeding attempts did not enhance the breeding success of the bird (Table 5.8).

Pairs which lost clutches or broods sometimes replaced them almost immediately (section 6.3.3). Twenty six such replacement clutches were recorded during this study, of which 11 were laid in the old nests in which the original breeding attempts failed and 15 were laid in newly built or repaired (frustration) nests. Thus, a frustration nest is an alternate nest built, repaired or frequented by a pair of birds subsequent to a nesting failure at another one during the same breeding cycle (Postupalsky 1974). Using frustration nests did not significantly improve the breeding success of the Fish Eagle relative to laying in the old ones (Table 5.9).

Table 5.8 An assessment of whether subsequent breeding attempts of the Fish Eagle were more successful in old than in alternate nests.

	Number of breeding attempts			Young	Mean no. young/nest	
Nests	Total	Succeeded	Failed	fledged	Active	Successful
Old	62	32	30	49	0.79	1.53
Alternate	47	24	23	36	0.77	1.50
Total	109	56	53	85	–	–
	$X^2 = 0.018$ NS (df = 3)					

Table 5.9 An assessment of whether re-nesting in the Fish Eagle was more successful in old than in frustration nests.

	No. of breeding attempts which		
Nests	succeeded	failed	Total
Old	6	5	11
Frustration	10	5	15
Total	16	10	26
	$X^2 = 0.395$ NS (df = 1)		

Because frustration nests and re-nesting attempts were common, one would have expected that pairs that failed in all their breeding attempts would have more nests and breeding attempts than those that succeeded in all their nesting attempts. However, the numbers of nests built and breeding attempts made by these two categories of pairs did not differ significantly (Table 5.10).

5.3.6 Vegetative materials locked up in nests

Four nests were weighed to estimate the amount of woody materials locked up in Fish Eagle eyries in the whole Park. The 4 nests averaged 36.58 ± 14.50 kg (17.4 – 58.2 kg.). The nest survey of 16–19 September 1975 gave on average 1.14 nests/pair overall (Table 5.1). During the July-August 1977 park-wide survey, 683 adult Fish Eagles were counted along the shorelines of Lakes Edward and George and the Kazinga Channel, and Crater Lakes Nyamusingire, Kasenduka and Kikorongo, a total distance of 342 km. During the survey, a total of 354 territories were estimated for both paired and unpaired birds. The 354 territories would give a total of 404 nests. Using the average nest weight of 36.58 ± 14.50 kg the estimated 404 nests would account for ca. 14,778 ± 5,858 kg of dry vegetative materials locked up in eyries at any one time in the whole Park. This is a conservative estimate because only undecayed materials were used to calculate the average nest weight and Fish Eagles along the many rivers that traverse the Park were not counted. Including birds that inhabit all the rivers in the Park would probably increase the above weight by about 10–15%.

Table 5.10 An assessment of whether Fish Eagle pairs which failed in all their breeding attempts built more nests than those which succeeded in all their breeding attempts.

Pairs	Number of Pairs	Number of Nests	Number of Attempts	Total
Succeeded	13	18	26	57
Failed	18	37	30	85
Total	31	55	56	142

X^2 = 2.2225 NS (df = 2)

Table 5.11 The association between Fish Eagle nests and weaver colonies in Queen Elizabeth Park.

	Number of Eagle nests	Number of Weaver colonies
Associated	5	5
Not associated	93	19
Total	98	24

X^2 = 6.322* (df = 1)

5.3.7 Nesting association and nest appropriation

The most common type of nesting association between the Fish Eagle and other birds involved the social weaverbirds. Nests of single and mixed colonies of Ploceus melanocephalus fisheri, P. intermedius intermedius, and P. cuculatus bohndorffi were built on Fish Eagle nest trees. The association between the weaver colonies and Fish Eagle nests was significant (Table 5.11).

Observed nest appropriations involved the Martial Eagle Polemaetus bellicosus, the Egyption Goose Alopochen aegyptiacus and the Fish Eagle. In April 1975 a pair of Martial Eagles was found incubating in a small nest in an Euphorbia candelabrum tree. By mid-May the breeding attempt was presumed a failure because the nest was abandoned. On 29 November 1977 Fish Eagle Pair No. 2 was incubating a 2-egg clutch in the same nest. The nesting attempt of these birds also failed because between late December 1977 and 6 January 1978 both birds were regularly encountered on the opposite shore and the nest was empty. Which pair of birds built the nest was, however, difficult to determine.

On 24 January 1977 an Egyptian Goose was seen incubating in the nest of Fish Eagle Pair No. 14 (Fig. 3.1). The nest was sited on a 10-12 m tall E. dawei tree. From a vantage point, some of the dirty-white eggs and feather lining could be clearly seen. On 14 February 1977 no Geese were seen on the nest nor in the vicinity, and there were no eggshells in the nest or under the nest tree. I, however, assumed that the eggs had hatched, and that the adult Geese and their brood had gone. This record confirmed why Egyptian Geese regularly alighted on Fish Eagle nests and why they also investigated them.

On 24th April 1977 an interesting observation was made of a lone Goose that was actively scooping, with its bill, a hole in the eyrie of Fish Eagle Pair No. 82. On 30 July 1977 two cases of Fish Eagle nest investigations by Egyption Geese were recorded. However, none of these incidents resulted in the Geese breeding in the investigated nests.

5.3.8 The pair-bond

There was year-round contact between the sexes of a Fish Eagle pair. This contact may have reduced the frequencies of such courtship displays as cartwheeling which were regularly observed in the Bald Eagle (Retfalvi 1965) and the Sea Eagle (Brown 1976 a). Regular courtship displays are associated with the maintenance of pair-bond in raptors generally (Hinde 1964; Retfalvi, op.cit.; Brown 1976a & c & 1980; Brown & Amadon 1968).

Year-round territoriality, vocalization, sharing of food, copulation, visits to the nest and the occasional adding of building materials to it probably function to maintain pair-bond in the Fish Eagle. Territoriality and vocalization are described in section 3.3.1 and visits to and the adding of materials to the nest in section 5.3.4. This section, therefore, only concerns itself with the description of copulation and the vocalizations associated with it, and courtship feeding. Copulation and courtship feeding have been observed in the context of each other and are, therefore, treated as a unit.

5.3.8.1 Permissive courtship feeding and copulation

Copulation in the Fish Eagle occurred at any time. Coition took place on the ground, the nest, the nest tree, and on other perch trees.

The male was observed to bring remains of or whole prey to the female. After feeding on the prey, he flew straight to where the female was perched. At times he took the prey to one of the feeding perches or the nest when the female was on the far end of their territory and sometimes out of view. In such a case he called until she arrived or flew and delivered the prey to her. The female then approached and took the prey without any resistance from him. The birds normally called (soft duets) immediately before or after the food-pass. Invariably the male left to hunt or soar while the female fed. Occasionally such a food-pass was accompanied by mating. The coition was normally preceded and followed by soft duetting. The female frequently allowed her mate to partake of her prey but she did not take it to him. She normally left it on a feeding perch where he came for it. The male sometimes begged for a share in the female's prey, but he never forcefully staked a claim to it as the female did with his prey. "

5.3.8.2 Forced courtship feeding and copulation

In this type of feeding the female flew to the male that had caught prey and was quietly eating it. She sat beside him in a soliciting posture: head forward and low and tail raised. As she begged for food, she also emitted a series of soft but high-pitched infantile calls similar to a dove-like coo (Greenspan & Torre-Bueno 1971) and similar to those uttered by dependent young begging for food. She carefully and submissively moved nearer and nearer the male. He, in turn, often moved further away or flew away. At times he soared for some moments before alighting and she invariably followed.

Persistent begging and attempts to forcefully grab the prey resulted in the male relinquishing the prey to her. Less often she succeeded in grabbing the quarry from the incautious male. Once she grabbed the prey the male usually left it to her but occasionally a tug-of-war ensued resulting in the prey being torn between the contestants. During such food-passes the birds occasionally mated. The copulation was immediately after the food-pass or a little while later. In the former case the male simply alighted on the female's back and they mated as if the solicitation for food was enough stimulus for coition. When some moments elapsed between the food-pass and copulation both birds assumed cowered postures, made infantile begging calls (the soft dove-like coo or the 1- or 2-syllable duet ending in a coo), almost in unison, and mated. In this case solicitation for mating could again have been initiated by the female probably to forestall an attempt by the male to regain his prey.

5.3.8.3 Pre- and post-copulatory behaviour

Three types of vocalizations were associated with copulation. They were given from a few seconds to about one minute prior to and after a mount and during copulation itself. The first type was a dove-like coo which was normally given less than 10 seconds before mating. Once this soft coo was given by a pair copulation was inevitable. It was difficult to discern which of the sexes gave it. The second type of vocalization was a soft cry; a moaning or cawing type of sound. This call was given when the male had mounted and it was not possible to identify the sex giving it. From about 20 seconds before or after a mount there was a third type of call.

This was the duet but it was more muted than the normal one. It invariably ended in the soft dove-like coo after the first or second syllable.

Mounts lasted from 5-30 seconds. Only when the female deflected her tail to facilitate cloacal contact was copulation considered successful. There were times when the female did not do so and the male dismounted shortly after mounting.

Greenspan & Torre-Bueno (1971) observed mutual preening between the members of a pair some half hour or so before or after a mount. No such social preening was witnessed during this study. Bill-touching of a partner's forehead occurred only twice in the adults of pair No. 6 and in both cases the birds duetted instead of preening. In neither case did they mate.

Immediately after coition both birds vigorously shook themselves and each preened itself for varying lengths of time. The birds, especially the male, usually flew to another perch or soared within 5 minutes or so after coition.

5.4 DISCUSSION

Along the Kazinga Channel Euphorbia spp. abound and, therefore, provide secure nesting sites for any large birds. Fish Eagles nesting within 1 km of the shores took advantage of these trees but should Acacia spp. be available they were preferred to other trees. Normally the tallest trees were used. With the exception of 2 dry Albizia spp. and 8 E. dawei trees with drying tops, all other nest trees were live.

In Michigan Ospreys Pandion haliaectus built nest 3-4 miles away from the nearest water body and preferred dead trees as their nest sites (Postupalsky 1972).

The colonial nesting habits of Pink-backed Pelicans Pelecanus rufescens (Din 1970) in this Park and of Marabou Storks Leptoptilos crumeniferus elsewhere (Kahl 1966, Pomeroy 1977) considerably damaged nest trees. Although the extent of damage to nest trees was not measured, terminal shoots growing through dis-used Fish Eagle nests, however, proved that tree growth was hampered, probably by the weight of the accumulated nest materials and the actual activities of the birds during breeding. The amount of damage done was probably too little to warrant concern.

The biggest raptor nests are found in temperate regions probably because the nest materials rot more slowly than those in the tropics (Brown 1976a & b). The size of any Fish Eagle nest in this Park depended to a great extent on the nest tree and how long it had been in use. Some of the largest and probably the oldest nests in the Park were on E. candelabrum. Those in the crowns of E. dawei could not last long because the supple branches would not stand extended accumulations of materials; they broke or simply tipped over the nests or portions of them.

Many raptors species are known to add green branches or leaves to their nest floors (Brown 1955, 1970a, 1976a, b & c; Brown & Amadon 1968, Postupalsky 1972). This normally happens at the end of nest building or repairing. Brown (1976a, b & c) suggested that these materials are used to receive the eggs. Fish Eagles also incorporated green materials into their nests and this occurred throughout the breeding cycle.

In so doing they could have been covering the messy remains of prey and the faeces of few-week-old chicks (section 9.3.3).

Apart from snake eagles, most raptors occupy their nests for several years, and many species also have one or more alternate nests which they repair and sometimes use (Brown 1976a). In temperate regions eagles seem to build many more nests per pair than related tropical species. The Sea Eagle in Norway built 1-11 nests, averaging 2.4 nests per pair (Brown, op.cit.). The Bald Eagle is known to move to alternate nest sites between breeding seasons (Sprunt _et al_., 1973), and McGahan (1968) described them as having supernumerary nests. Verreaux's Eagle _Aquila verreauxi_ in the Matopos Hills, Zimbabwe, built 1.4 nests per pair while in Scotland the related Golden Eagle _A. chrysaetos_ built on average 2.3 nests per pair (Brown, op.cit.). In America the Golden Eagle is reported to build 1-14 nests although 2-3 is usual (Snow 1973a). In this Park, the Fish Eagle had 1-4 alternate nests, averaging 1.1 nests per pair overall.

Building of new nests by any pair of eagles may coincide with changes of mates or may be related to hazards to clutches or broods in old nests (Brown 1955). During this study, building of new nests was more common among Fish Eagle pairs that had more breeding failures than those which succeeded. Building of new nests as a result of mate change was not observed nor was mate change ever witnessed.

Many birds, notably raptors, appropriate nests of other species for their own use. All falconets and pygmy falcons _Poliohierax_ and _Microhierax_ spp. breed in other birds' nests (Brown 1970a, 1976a & b).

Ayre's Hawk Eagle Hieraaetus dubius appropriated the old nest of Harrier Hawk Polyboroides typus in Embu District, Kenya (Brown 1974b). In Michigan Postupalsky (1972) and in Ontario Grier (1974) found Ospreys taking over old Bald Eagle nests. During this study breeding Fish Eagles were not tolerant of any large birds investigating their nests or intruding in their territories (section 10.3.2). Despite this defence, a pair of Egyptian Geese bred, probably successfully, in the nest of a pair of Fish Eagles. This, however, happened during the non-breeding period of the pair concerned. J. Jumbe (Unpubl. MS) reported that a pair of Fish Eagles appropriated the nest of a pair of Egyptian Geese in the Park. Because Egyptian Geese normally nest on the ground but can do so in trees by acquiring the abandoned nests of other large birds (Mackworth-Praed & Grant 1952), the reverse of Jumbe's claim is probably true.

CHAPTER 6

THE BREEDING SEASONALITY

6.1 INTRODUCTION

Animal breeding cycles are determined by proximate and ultimate control mechanisms (Lofts & Murton 1968). A proximate control mechanism is a causative factor that immediately precedes the effect whereas an ultimate one is remotely causative but does not lead immediately to the effect (Thomson 1964).

Thus in temperate regions seasonal changes in photoperiod act as reliable environmental cues, proximate factors, to which many species of birds immediately respond by breeding. In many north temperate species photostimulation triggers full gametogenesis in the male but only partial ovarian development in the female (Immelmann 1971, Lofts & Murton, op.cit.). In the tropics, equatorial regions particularly, changes in photoperiod are not sufficiently large to be used as proximate factors and many birds have evolved to respond in their breeding cycles to other environmental cues such as rainfall and the conditions of the vegetation (Voous 1950, Moreau 1950, Marshall & Disney 1957). Apart from immediate environmental control, mutual stimulation between the members of a pair or group (Immelmann, op.cit.) has been found to exert some additional influences on the timing of avian reproduction. In some species only the presence of the male, through courtship displays and other behavioural activities, leads the female to full ovarian development, which consequently results in the synchronization of breeding activities of the members of a pair (Marshall 1936, Burger 1949, Lehrman 1959, 1964a & b & 1965, Hinde 1967).

Female courtship has been observed to influence gametogenesis in the male too, but only to lesser extent than male courtship influencing avarian development (Burger 1953, Lehrman 1959).

In this study an attempt has been made to link the breeding seasonality of the African Fish Eagle with a variety of factors, both environmental and social.

6.2 METHODS

6.2.1 The environment and breeding seasonality

Seasonality in egg-laying by the Fish Eagle was assessed by recording all breeding attempts which had clutches. In inaccessible nests the presence of a clutch was assumed when the pair commenced incubation. Fortnightly breeding surveys revealed which month a pair started incubation. These records permitted the determination of the breeding seasonality of the birds during the 1975-1978 study period.

In order to determine the causes of breeding seasonality the seasonality in egg-laying was correlated with a variety of environmental factors: i.e. rainfall, temperature, wind velocity, sunshine hours, solar radiation, changes in water level and mean monthly fish catches by local fishermen as indices of monthly fluctuations in food supply in the study area.

Climatic data were obtained from the Meteorological Station in Mweya (Fig. 1.3). Breakdowns of equipments, however, necessitated the use of climatic data collected well before this research programme commenced. Water level records from 1975-1978 inclusive were obtained for Kisenyi Fishing Village (Fig. 1.3) from Entebbe Hydrometeorological Office, Ministry of Lands, Mineral and Water Resources.

During the study no determinations of monthly fish productivities were carried out in Kazinga Channel or in Lakes Edward and George. For this reason the monthly fluctuations in fish catches at Katunguru Village (Fig. 1.3), which harvests its fish solely from the Channel, were used as indirect measures of fluctuations in the food supply of the Fish Eagles in the study area. Fish catch statistics for 1974-1980 inclusive were obtained from the Regional Fisheries Office, Kichwamba.

6.2.2 The social aspect of breeding

The role of intrapair stimulation in the timing of breeding in the Fish Eagle was not measured because the birds maintained year-round pair-bonds and territories. However, an attempt was made to measure the effects of interpair or group stimulation on the timing and synchronization of breeding. As breeding surveys progressed it was realised that some pairs of birds, from 2 up to a maximum of 6 pairs per breeding group, were nesting at about the same time in particular sections of the shoreline. They were within both sight and vocal contact with one another. Such a group of pairs, all breeding synchronously, formed a discrete breeding group. The possible influence of interpair stimulation on the breeding of the birds was measured by calculating the mean laying interval (in days) for each group and correlating the intervals with the breeding group sizes.

6.2.3 The breeding interval

For pairs which laid successive clutches, including re-laid ones (defined below), the dates when incubation commenced were determined from the fortnightly surveys.

From these records the interval between any 2 clutches of a pair was calculated. Re-laying in the Fish Eagle was a frequent phenomenon and a re-laid clutch was one resulting from a nesting attempt made in 6 months or less of an original clutch or brood being lost.

6.3 RESULTS

6.3.1 The environment and breeding seasonality

Fish Eagles in the Park laid year-round (Fig.6.1). Excluding re-laying attempts the breeding seasonality shows that the 7 months from November to May, each year, were less favourable for commencement of breeding. This resulted in a pronounced peak in egg-laying occurring every year and the peak centering on the period from June to October.

Data on environmental factors with which breeding seasonality of the Fish Eagles were correlated are given in Tables 6.1-6.3. The results of correlation analyses relating the time of egg-laying to environmental variables in Table 6.4, show that only temperature and changes in water level were significantly correlated with breeding seasonality. The coefficients were negative indicating that more pairs of birds laid when temperatures and water levels were low.

It is interesting to note that egg-laying was not significantly correlated with the rainfall seasonality (Table 6.4) despite the distribution of pairs laying during the wet and dry seasons of the area being significantly different from one another with more pairs laying during the long wet and short dry seasons than during the other two seasons (Table 6.5). The distribution of pairs laying during each year (Table 6.5) show that the birds exhibited a clear preference for breeding during the long wet season (Fig. 6.2a & b).

Fig. 6.1 The egg-laying seasonality of the African Fish Eagle in Queen Elizabeth Park, April 1975 - March 1978. Dashed line represents the total of normal and re-laid clutches.

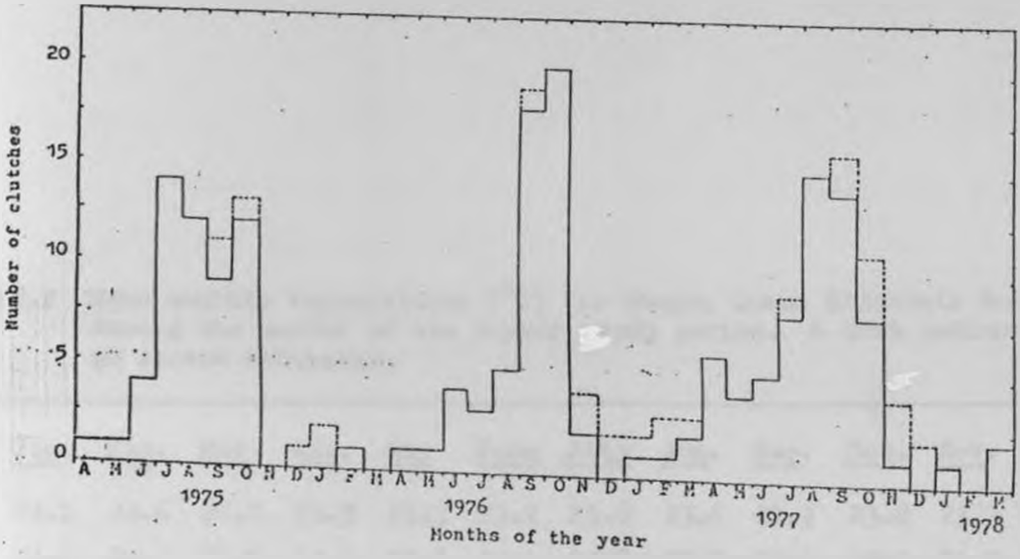


Table 6.1 Monthly rainfall (mm) for Mweya, Queen Elizabeth Park, during the months of the 3-year study period on the Fish Eagle.

Year	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1975	31.4	14.1	51.4	163.2	83.9	17.2	25.0	117.9	96.5	131.1	54.8	27.8	814.3
1976	2.8	54.6	14.7	45.1	160.2	14.0	6.7	63.0	104.3	108.2	100.5	53.8	727.9
1977	46.2	46.7	85.1	132.2	65.3	72.9	99.5	111.3	63.4	43.4	157.8	70.4	994.2
1978	3.0	28.8	97.5	93.6	128.1	15.0	23.3	71.3	24.3	132.5	90.4	17.0	724.8

Table 6.2 Mean monthly temperatures (°C) for Mweya, Queen Elizabeth Park, during the months of the 3-year study period. A dash indicates no record available.

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1975	24.1	24.6	22.7	23.9	23.7	23.2	23.6	23.6	21.7	23.8	23.3	23.7
1976	24.6	24.3	24.8	24.1	24.6	24.1	23.8	23.7	23.5	24.3	23.3	24.0
1977	24.2	24.2	24.3	24.1	24.6	22.9	22.5	23.2	22.9	-	-	-
1978	-	-	-	-	-	-	23.9	25.1	27.6	25.5	23.4	23.3

Table 6.3 Data on environmental factors with which the breeding seasonality of the Fish Eagle in Queen Elizabeth Park were correlated.

Environmental factor	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec
Mean monthly rainfall (mm, 1965-78)	26.7	49.0	74.4	123.2	87.1	42.9	60.6	73.3	76.4	78.8	109.2	39.
Mean of mean monthly temperature (°C, 1964-74)	23.5	24.0	23.5	23.2	23.6	23.0	23.4	23.5	23.1	22.8	23.2	23.
Mean of monthly wind runs (in millions, 1965-70)	0.436	0.378	0.553	0.540	0.511	0.472	0.333	0.411	0.527	0.496	0.425	0.5
Mean of mean monthly sunshine hours (1965-72)	6.0	5.8	5.4	5.2	5.6	6.1	6.5	5.7	6.1	5.1	5.5	6.
Mean of mean monthly radiation (cal/cm²/day, 1968-72)	362.4	361.2	366.2	354.2	344.2	355.6	353.2	332.4	382.0	361.2	361.6	339.
Mean of mean monthly water level (m., 1975-78)	4.705	4.578	4.553	4.565	4.583	4.567	4.375	4.440	4.550	4.617	4.750	4.81
Mean monthly fish catch (tons, 1974-80)	35.2	38.6	29.0	42.6	26.1	26.0	25.5	38.2	38.1	45.1	33.6	39.

Table 6.4 Results of correlation analysis relating the time of egg-laying in the Fish Eagle to environmental variables. r = correlation coefficient; r^2 = coefficient of determination; 100 r^2 = % variation explained by the association between breeding seasonality and an environmental factor; df = 34 for each factor.

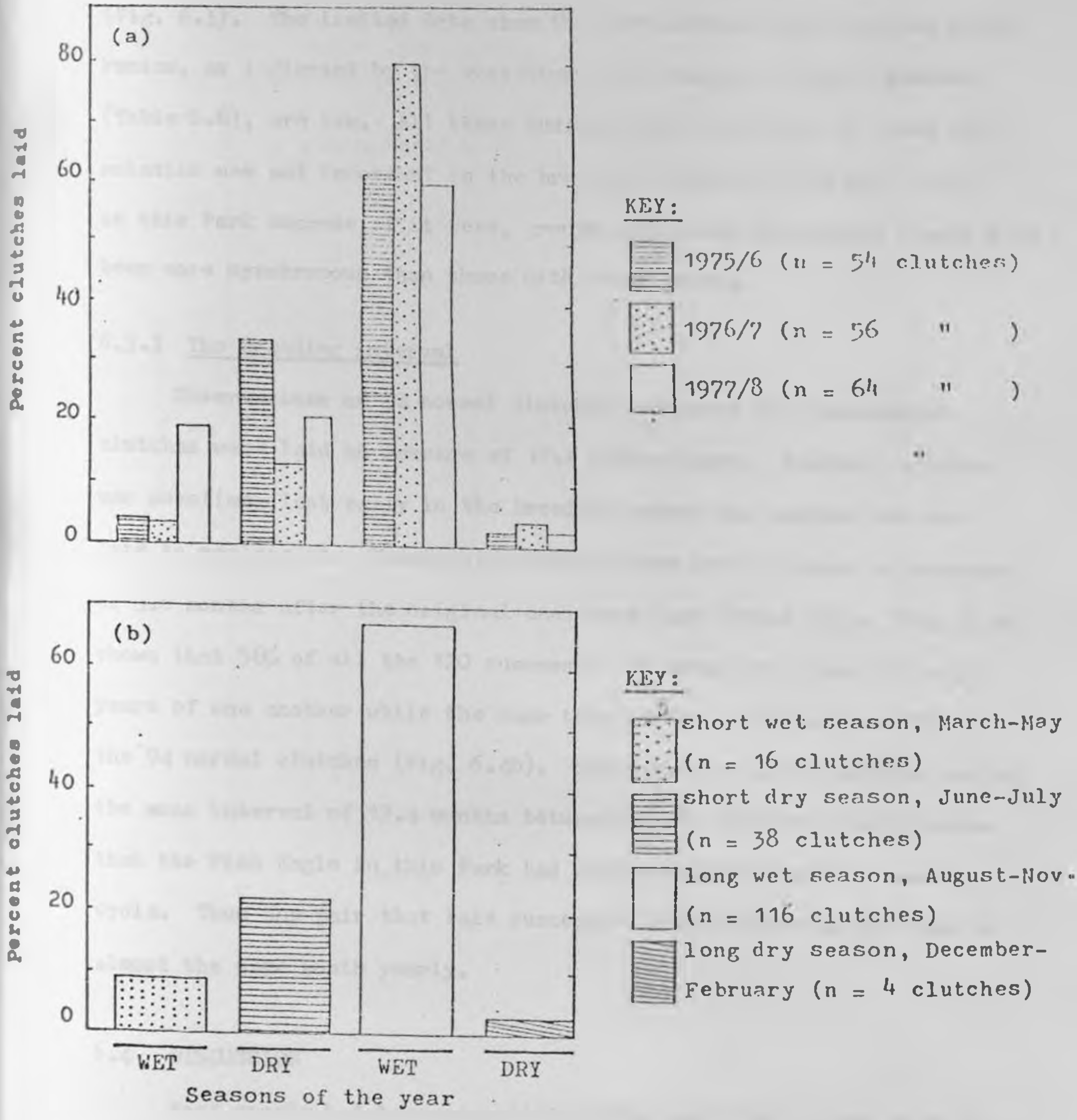
Environmental factor	r	r^2	100 r^2 (%)
Mean monthly rainfall (1975-78)	0.273 NS	0.075	7.5
Mean of mean monthly rainfall (1965-78)	0.160 NS	0.026	2.6
Mean of mean monthly temperature (1964-74)	-0.404*	0.163	16.3
Mean monthly temperature (1975-78)	-0.382*	0.146	14.6
Mean of mean monthly windspeed (1965-70)	-0.171 NS	0.029	2.9
Mean of mean monthly sunshine (1965-72)	0.0054 NS	0.00005	0.003
Mean of mean monthly radiation (1968-72)	0.176 NS	0.031	3.1
Mean of mean monthly water level (1975-78)	0.448**	0.201	20.1
Mean monthly fish-catch (1974-80)	0.223 NS	0.050	5.0

Table 6.5 Seasonal frequencies of Fish Eagle pairs commencing incubation of normal clutches in Queen Elizabeth Park. For each entry, the first number represents raw count, and the number in parentheses the percent frequency of clutches. Chi-square test was performed on raw data.

	Numbers of pairs laying during			
Season	1975/6	1976/7	1977/8	Total
Short wet	2 (3.7)	2 (3.6)	12 (18.7)	16 (9.2)
Long wet	33 (61.1)	45 (80.4)	38 (59.4)	116 (66.7)
Short dry	18 (33.3)	7 (12.5)	13 (20.3)	38 (21.8)
Long dry	1 (1.9)	2 (3.6)	1 (1.6)	4 (2.3)
Total	54 (100.0)	56 (100.0)	64 (100.0)	174 (100.0)

X^2 = 96.094***(df = 6)

Fig. 6.2 Frequencies of clutches in the African Fish Eagle in Queen Elizabeth National Park: a) the percent frequencies of 174 normal clutches in relation to the seasons of each year of the study; b) the percent distribution of the above clutches in relation to seasons for the whole study period April 1975 - March 1978.



6.3.2 The breeding seasonality and social factors

Some pairs of Fish Eagles bred in discrete groups. A correlation of the mean laying intervals (in days) of the groups with the group sizes demonstrates that the laying intervals increased with increasing group sizes and, therefore, with the distances between breeding pairs (Fig. 6.3). The limited data show that the within-group breeding synchronies, as indicated by the variations from the mean laying intervals (Table 6.6), are low. All these indicate that interpair or group stimulation was not important in the breeding biology of the Fish Eagle in this Park because if it were, groups containing more pairs should have been more synchronous than those with fewer pairs.

6.3.3 The breeding interval

Observations on 94 normal clutches indicated that successive clutches were laid an average of 12.4 months apart. However, a clutch was sometimes lost early in the breeding season and another one was laid to replace it. Twenty six such clutches were replaced an average of 3.6 months after the original ones were lost (Table 6.7). Fig. 6.4a shows that 58% of all the 120 successive clutches were laid 0.75–1.25 years of one another while the same time period accounted for 73% of the 94 normal clutches (Fig. 6.4b). Although the laying interval varied the mean interval of 12.4 months between normal clutches clearly shows that the Fish Eagle in this Park had an approximately annual breeding cycle. Thus any pair that laid successive normal clutches had them in almost the same month yearly.

6.4 DISCUSSION

Food supply had been suggested as the most likely agent that initiates the breeding seasons of African birds of prey (Brown 1955,

Fig. 6.3 The relationship between breeding group size and laying interval in the African Fish Eagle in Queen Elizabeth National Park. N = 38 breeding groups with 106 breeding attempts.

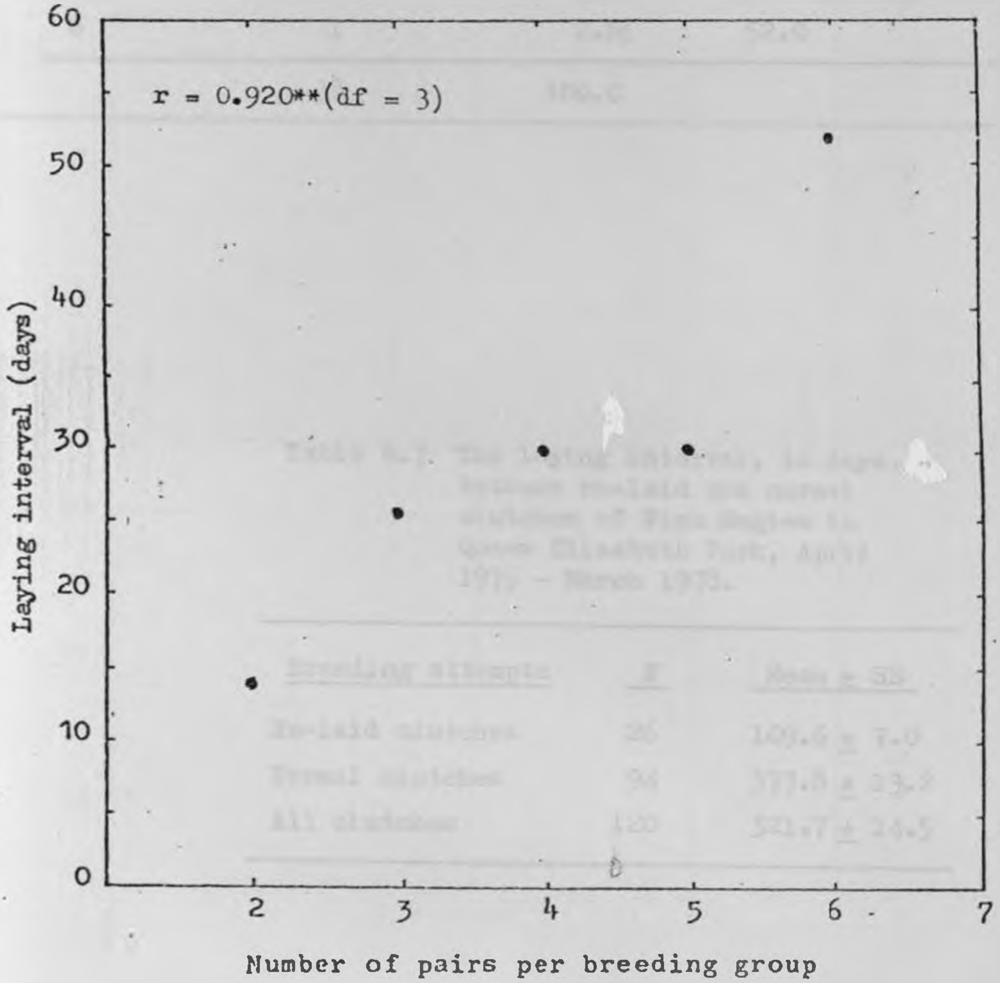


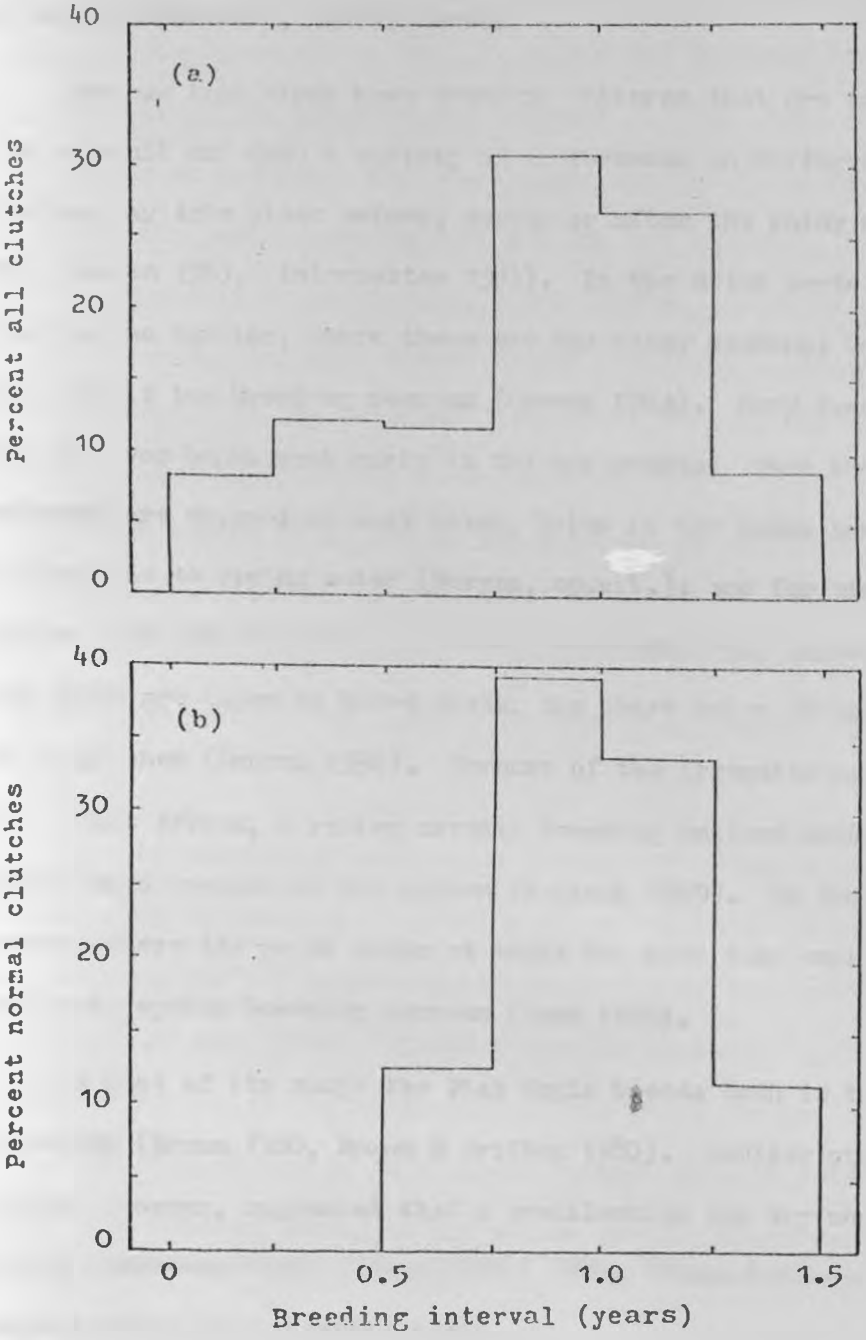
Table 6.6 The intervals between clutches in breeding groups of Fish Eagles in Queen Elizabeth Park, April 1975 - March 1978. N = 38 breeding groups with 106 breeding attempts.

Group size			Laying interval (days)	
Pairs/group	No. of groups	% of total	Mean ± SE	Range
2	19	50.0	14.7 ± 4.7	0-44
3	12	31.6	25.7 ± 10.1	2-62
4	4	10.5	30.2 ± 17.5	8-54
5	2	5.3	30.0 ± 23.1	16-44
6	1	2.6	52.0	
	38	100.0		

Table 6.7 The laying interval, in days, between re-laid and normal clutches of Fish Eagles in Queen Elizabeth Park, April 1975 - March 1978.

Breeding attempts	N	Mean ± SE
Re-laid clutches	26	109.6 ± 7.0
Normal clutches	94	377.8 ± 13.2
All clutches	120	321.7 ± 14.5

Fig. 6.4 The percent frequencies of successive African Fish Eagle clutches in Queen Elizabeth National Park in relation to the breeding interval. For (a), n = 120 successive normal and re-laid clutches; for (b) n = 94 normal successive clutches.



1970a, Brown & Amadon 1968, Brown & Britton 1980, Moreau 1966), but it would be most useful as a timer in places where prey populations experience wide seasonal fluctuations. The most favourable breeding season and what factors initiate breeding in tropical African raptors are still, therefore, poorly known.

African land birds have breeding patterns that are associated with rainfall and show a variety of preferences in different areas; breeding may take place before, during or after the rainy season (Moreau 1950, Benson 1963, Winterbottom 1963). In the drier parts of Africa, close to the equator, where there are two rainy seasons, most bird species exhibit two breeding seasons (Moreau 1964). Many species that nest in river banks nest early in the dry season. When the water is low, sandbanks are exposed as nest sites, holes in the banks are unlikely to flood due to rising water (Moreau, op.cit.); and for piscivorous species fish may be easier to catch (Bannerman 1953, Moreau, op.cit.). Many birds are known to breed during the short rains whilst avoiding the long ones (Moreau 1950). Because of the irregular rainfall pattern in East Africa, a rather erratic breeding pattern occurs among several bird species of the region (Haylock 1959). In West Africa, however, where the rains occur at about the same time every year, birds have more regular breeding seasons (Ward 1965).

In most of its range the Fish Eagle breeds both in the wet and dry months (Brown 1980, Brown & Britton 1980). Earlier studies of the species, however, suggested that a predilection for dry season breeding existed (Bannerman 1953, Brown 1960 & 1970a, Brown & Hopcraft 1973, Benson & White 1957, Stowell 1958).

This preference for dry season breeding has been confirmed by Brown (1980) for the northern and southern tropical regions of Africa in which there are distinctly two long seasons, one dry and one wet. Thus, according to Brown (op.cit.), in Senegal, northern Nigeria, Chad and the Sudan, the scanty breeding records suggest that the Fish Eagle starts egg-laying early in the dry season and probably breeds solely in the dry months. In the southern tropical region, where the breeding seasonality of the Eagle has been better studied in Zambia, Malawi and Zimbabwe, the bird breeds in both dry and wet seasons. However, peak egg-laying occurs in April–July, a dry season. In Botswana and S.W. Africa/Namibia, the Eagle breeds during April–July, in the cold but dry winter months. In the Transvaal area of S. Africa, the bird breeds during April-August, solely in the cool but dry winter months. However, in the Cape region in S. Africa breeding occurs during May–October, in the cold but wet winter period. The wet winter breeding along the Cape region and the eastern coastal areas of S. Africa has been reported as early as the turn of the century (Porter 1903, Roberts 1958, Clancey 1964).

In the equatorial regions of Africa, the Fish Eagle breeds during both dry and wet seasons. In the rift valley lakes of southern Ethiopia, just outside the 5°N latitude, it breeds during August–January, mainly in the dry season (Brown, op.cit.; Brown & Britton, op.cit.; Brown & Hopcraft, op.cit.). In northern Tanzania along the Mwanza to Musoma shoreline of L. Victoria, the scanty records show that the Eagle breeds during May–October, wholly a dry season period (Brown op.cit.; Brown & Britton, op.cit.; Stowell 1958).

In the Winam Gulf, L. Victoria, in western Kenya breeding occurs in most months, with the main peaks in May and August and a minor one in December (Brown, op.cit.; Brown & Britton, op.cit.). At L. Naivasha, Kenya, breeding takes place throughout the year with peak laying occurring during the wettest months, April-June (Brown, op.cit.; Brown & Britton, op. cit.; Brown & Hopcraft, op.cit.). At the Kenyan coast, breeding occurs in most months with peak egg-laying during May-July, a dry season (Brown, op. cit.; Brown & Britton, op.cit.). In Uganda, along the R. Nile in Murchison Falls Park, breeding is apparently year-round; a peak probably occurs during October-November, at the beginning of the dry season (Brown, op.cit.; Brown & Britton, op.cit.).

The African Fish Eagle in Queen Elizabeth Park lays eggs almost year-round (Fig. 6.1). During each of the 3 years of study, however, peak egg-laying centered on the longer rainy season, August-November (Fig. 6.1 & 6.2). Despite the preference for wet season breeding (Fig. 6.2 & Table 6.5), rainfall was not significantly correlated with the breeding seasonality (Table 6.4). This suggests that rainfall is not a proximate cause of breeding in the species in the area.

In Africa the breeding seasons of birds-of-prey are particularly complicated and it is not clear yet what environmental releasers, if any, trigger breeding. The bigger species tend to have young in the nests during the dry seasons when, at least in some cases, vertebrate prey and carrion are probably more numerous and accessible when cover is reduced (UNP 1971; Moreau 1974, 1966; Lack 1968). At his time hunting is not regularly interrupted by bad weather (Brown 1976a & b; Moreau, op.cit.).

Brown & Britton (1980) stated that the breeding seasons of the Fish Eagle were difficult to correlate with the food supply. They suggested that the preference shown for dry season breeding indicated that climatic factors probably overrode food supply in influencing the breeding of the Eagle. Bannerman (1953) and Moreau (op cit.) suggested that piscivorous birds should breed when water levels are low and prey more easily caught. This would enable the female to have enough food while laying eggs and the adults to catch enough prey to raise the young. The fact that more pairs of Fish Eagles in this Park laid when water levels were low (Table 6.4) would tend to agree with the above theory and would suggest that food supply is probably one of the most important factors that influence the timing of breeding in the species. However, the facts that the adult Fish Eagle is inactive for ca. 90% of the day (section 3.3.2) and has a high hunting success rate (section 4.3.2) would negate the above contention and, therefore, indicate that it has no problems catching prey in this area. According to the above theory, the breeding seasonality perhaps favours the recently independent young more than it favours the adult in that the majority of such young appear in the study area during the long dry season, December - February, and the short wet one, March - May (section 2.3.3, especially Table 2.9b & c). During these dry months the receding water level probably enables the inexperienced young to obtain prey more easily than they would have during the wet months.

More pairs of birds laid when temperatures were low. Because the fluctuations in both the mean monthly and mean of mean monthly temperatures in Mweya do not normally exceed 5°C (Tables 6.2 & 6.3 respectively), there are no obvious advantages the Fish Eagle would derive by breeding when temperatures are low.

In many seabirds and other colonial nesting species, courtship and other social activities have been shown to have stimulating and synchronizing effects within the breeding colony. In these species, the onset of egg-laying is highly synchronized within the colonies or different parts of the colonies (Lack & Emlen 1939, Lees 1946, Disney & Marshall 1956, Medway 1962, Ward 1965, Snow & Snow 1967, Nelson 1968, Brown & Urban 1969). When nesting communally pairs of these birds do so earlier than those nesting outside the colonies. The performance of courtship or nesting behaviour by one pair or group of pairs immediately stimulates other pairs to do the same and, therefore, leads to closely synchronized breeding activities. This group stimulation (the Fraser Darling Effect: Darling 1938) has been demonstrated experimentally for the Ring Dove *Streptopelia risoria* (Lehrman 1964a & b, 1965) and the Budgerigar *Melopsittacus undulatus* (Brockway 1964).

Social stimulation of adjacent pairs to display exists in the Fish Eagle (Brown 1980). In the birds that nested semi-colonially in the Winam Gulf, L. Victoria, and accomplished breeding within a short time (Brown 1960), social stimulation for synchronizing breeding activities probably existed. This was, however, not acknowledged by Brown (1980). Despite some pairs of birds laying in discrete groups, synchronization of breeding activities was not demonstrated during this study. This suggests that interpair or group stimulation for breeding does not exist in the population studied.

Although several environmental variables have been examined in relation to the breeding seasonality of the Fish Eagle during this study, none of them has sufficiently explained the observed seasonality. However, in future studies of the species the influences of such factors as social stimulation, age and experience of the breeding birds

(Lack 1968), condition of the vegetation (Voous 1950, Moreau 1950, Marshall & Disney 1957) and, probably, limitations in nest sites (Brown 1970b & 1974, Postupalsky 1974; see also section 5.3.1) need closer investigations.

During this study, the Fish Eagle exhibited an approximately annual breeding cycle which is reasonable for a bird of its size. Two successful breeding cycles cannot occur in any temperate cycle because of restrictions imposed by the climate, and even in the tropics it is unlikely where there are 6-month marked dry and wet seasons (Brown 1976b). At L. Naivasha the bird reared 2 broods per year and in one pair 3 broods in 18 months (Brown & Hopcraft 1973). However, this was not witnessed during this study.

Re-laying in the Fish Eagle was common during the present study with 26(13%) of all breeding attempts being replacement clutches. These clutches were laid an average of 3.6 months after the original ones were lost (Table 6.7). In the Kafue Flats, Zambia, a pair from whose nest Colebrook-Robjent (1974) collected 3 eggs laid another clutch of 3 eggs 30–40 days after the loss of the original clutch. Fentzloff's (1977) captive European Sea Eagle female re-laid after a 19-day interval in 1973 and a 29-day one in 1974 when her original clutches were either removed for artificial incubation or accidentally broken. Such short re-laying intervals are probably only possible under the ideal conditions of captivity. Bent (1937) reported that when a clutch of the American Bald Eagle is taken early enough in the breeding season it can be replaced in a bout 4 weeks. The Crowned Eagle Stephanoaetus coronatus, Verreaux's Eagle Aquila verreauxi and Ayre's Hawk Eagle Hieraaetus dubius all replace lost clutches and broods but they also do so in weeks or months (Brown 1976a & b).

Breeding eagles re-lay for a number of reasons. Their clutches could have been removed by egg-collectors and almost all temperate birds of prey are affected in this regard (Snow 1973a & b). The Fish Eagle, like most African raptors, is still safe as far as egg-collection is concerned. Eagles may also re-lay when they lose their clutches or broods to natural disasters like predation, inclement weather and diseases.

CHAPTER 7

THE EGG

7.1 INTRODUCTION

Raptor eggs are laid at intervals and, consequently, hatch asynchronously, if incubation started with the first egg (Bent 1937; Brown 1970, 1976a, b & c, 1980; Brown & Amadon 1968; Meyburg 1974; Moll 1970). Both day and night laying have been reported by Brown (1955). Eagle eggs are generally dull white, either marked with brown or unmarked (Brown 1976a). In the genus *Haliaeetus* the eggs are usually chalky-white with rough, unstreaked shells (Mackworth-Praed & Grant 1952; Brown 1955, 1970a, 1976a, b & c & 1980; Brown & Amadon, op.cit; Mebs 1972). Eggs vary in size depending on the species, but normal clutches are from 2-7% of the female's weight (Brown 1976b). Successive clutches with a constant number of eggs in a particular pair may indicate that mate change involving the female has not occurred (Brown 1955).

In eagles laying 1-egg clutches the female invariably incubates alone and in those with larger clutches the male takes a small share in incubation (Brown 1976a). Nest relief ceremonies during breeding have not been recorded in eagles although reliefs of and visits to an incubating/brooding mate are common. The efficiency of conversion of the nutrient materials of the egg into the body materials of the chick varies with the species of eagle. The incubation period also depends on the species of raptor but for related ones it is slightly longer in the tropics than in temperate regions (Brown 1976a & b; Brown & Amadon, op.cit.).

This study of the Fish Eagle, therefore, aimed to:

a) ascertain the role of the sexes during incubation,

b) establish the length of the incubation period,

c) find out whether or not eggs were laid and hatched at invtervals and to observe the hatching procedure,

d) assess whether or not adults assisted chicks during hatching,

e) establish whether or not successive clutches of particular pairs had constant numbers of eggs,

f) determine the efficiency of conversion of nutrient materials of the egg into the body materials of the chick, and

g) assess mortality rate of eggs during the incubation period and identify the possible causes of the observed mortality.

7.2 MATERIALS AND METHODS

7.2.1 The roles of the sexes during incubation

The role of each sex during incubation was investigated by observing 6 breeding pairs for varying lengths of time. Adults were distinguished by their relative sizes and calls (see section 3.2.1.3). Night observations were carried out on only one pair (No.6, Fig. 3.1). Since an adult incubated throughout the night, the sex of the bird that incubated during a particular night was determined by the calls it made at dusk before it settled for night incubation. Prior to leaving the nest the following morning the birds duetted and these calls were once again used to confirm the identity of the sex of the bird that had been made the previous evening.

7.2.2 Incubation period and laying and hatching intervals

The incubation period was determined from eggs for which laying and hatching dates were known to within 24 hours. In nests with 2 or 3 eggs all the eggs were marked by scratching Roman numerals on them in the order in which they were laid. The laying and hatching intervals were determined from the marked eggs while the hatching procedure and duration were observed from the eggs of Pairs No. 1 and 3 whose eggs were checked at 3-hour intervals during the day.

7.2.3 Egg measurements

Egg length and breadth were measured with Vernier Callipers. The length was measured as the maximum distance between the two poles and the breadth as the maximum width at the broadest portion of it. Din (1970) used the same method for measuring the dimensions of Pink-backed Pelican Pelecanus refescens eggs in this Park. Fresh egg weights and weights of newly hatched chicks were taken using a 300 g capacity spring balance. Eggs and chicks were placed in a pre-weighed perforated polythene bag for weighing.

7.2.4 Behaviours associated with incubation

Various behaviours are associated with incubation in birds of prey. These include bringing food to the nest or feeding perch for the incubating partner, bringing of nest materials, visits to the incubating bird and the relief of the incubating bird by the other (Brown 1970a & 1976). All such behaviours that were seen in connection with incubation were recorded.

7.2.5 Incubation temperature

Temperatures of the egg, air and nest-edge were recorded from the nest of Pair No. 1 (Fig. 3.1). Records were made at hourly intervals and for all the hours of the day. Temperatures were recorded using a six-way electronic thermistor which allowed the recording of the three temperatures in one operation without undue disturbance to the incubating bird. Incubation temperature was taken with the black body of the thermistor touching one of the eggs and its position was adjusted from time to time during periods when the birds were relieving each other. Air temperatures were taken in the shade of the nest tree at about 1 m above ground. Nest-edge temperatures were recorded with the black body placed at the rim of the nest and so positioned as to avoid direct solar radiation.

7.2.6 Egg mortality

Egg mortality was studied by noting all egg disappearances as incubation progressed. The probable causes of the losses were recorded. Calculations of mortality rates, as percent losses day^{-1}, followed Ricklefs' (1969a) method:

$$m = \frac{(\log_e P)}{t}$$, where m = instantaneous mortality rate,

p = proportion of eggs surviving,

t = time in days,

e = base of the natural logarithm.

7.3 RESULTS

7.3.1 Egg-laying interval and egg colour

In Pair No. 1 the first egg was laid on 23 February 1977.

Subsequent daily checks revealed a second egg at 1830 hours on 27 February 1977. This clutch gave an egg-laying interval of 4 days. In another nest (Pair No. 40b) the eggs had a laying interval of 3 days. The first egg was laid on 3 October 1977 and not until 6 October was the second egg present in the nest. With additional data from other nests, a mean egg-laying interval of 2.8 days was calculated (Table 7.1).

A freshly laid egg was chalky-white with a rough, unstreaked shell, and as incubation progressed the shell became dirty-white. The first egg of Pair No. 1 had irregular pale bluish dots on its broader end while the second egg was pure white. No other case of marking on eggshells was observed. Upon hatching, the insides of the shells were pale blue.

7.3.2 The clutch size

The clutch size ranged from 1-3 eggs, averaging 1.94 eggs/nest for the study period. There was no significant year-to-year variation of the frequencies of the respective clutch sizes (Table 7.2). Overall, the 2-egg clutch was commonest and the 3-egg one rarest. No 4-egg clutch was recorded.

The successive clutch sizes of individual pairs varied considerably (Table 7.3). In only 1 (No. 6) out of 8 pairs with 3 and 4 successive clutches did the clutch size remain constant at 2 eggs/clutch.

7.3.3 Egg measurements

Length and breadth measurements of 16 eggs averaged 76.74 x 59.75 mm respectively and 7 fresh eggs weighed an average of 133.3 g (Table 7.8). Brown & Amadon (1968) give a mean weight of 3400 g for 2 adult female

Table 7.1 The incubation period and laying and hatching intervals (in days) in the African Fish Eagle (* chick died at hatching; total eggs checked = 17, in parentheses)

Pair No.	Egg No.	Date laid	Laying interval	Date hatched	Hatching interval	Incubation period
6	1	6.6.75		15.7.75		40
	2	8.6.75	2	17.7.75	2	40
	1	26.6.76		4.8.76		40
	2	29.6.76	3	7.8.76	3	40
	1	7.10.77		16.11.77		40
	2	9.10.77	2	18.11.77	2	40
1	1	23.2.77		4.4.77		41
	2	27.2.77	4	Lost	-	-
82	1	13.11.76		24.12.76		42
	2	15.11.76	2	26.12.76	2	42
	3	18.11.76	3	Chick died*	-	-
87	1	16.9.76		25.10.76		40
	2	19.9.76	3	28.10.76	3	40
	1	22.4.77		1.6.77		41
	2	25.4.77	3	4.6.77	3	41
40b	1	3.10.77		Clutch lost	-	-
	2	6.10.77	3		-	-
3	1	17.10.75	-	27.11.75	-	41
Total	(17)		25		15	
Mean ± SE			2.8±0.2		2.5±0.2	40.6±0.2

Table 7.2 Clutch size frequencies for 68 Fish Eagle breeding attempts in Queen Elizabeth National Park.

Year	Number of nests	Frequency of clutches			Total eggs laid	Mean clutch size
		1	2	3		
1975/76	22	8	7	7	43	1.95
1976/77	22	6	13	3	41	1.86
1977/78	24	3	18	3	48	2.00
Total	68	17	38	13	132	
Overall Mean ± SE		5.7±1.5	12.7±3.2	4.3±1.3		1.94±0.04
		χ^2 = 9.351 NS (df = 4)				

Table 7.3 Successive clutch sizes of the Fish Eagle in Queen Elizabeth Park. Forty-three clutches from 19 pairs considered in this analysis.

Successive clutch sizes	No. of pairs	Successive clutch sizes	No. of pairs
1-1	1	2-1-2	1
1-1-2	2	2-2	2
1-2	1	2-2-2-2	1
1-2-2-2	1	2-3	1
1-3-2-2	1	3-2	1
1-3-2-3	1	3-2-2	1
2-1	2	3-2-3-2	1
		3-3	2

Fish Eagles but 2 adults in Entebbe Zoo averaged 2875 g. During this study, clutch size was significantly correlated with the Zoo female weight (Fig. 7.1). The mean weight of 2-egg clutches was significantly less than that of the 3-egg ones ($t = 11.861$, $df = 6$, $P < 0.001$; data in Table 7.4) and therefore accounted for far less of the female weight than the 3-egg clutches.

In both the 2- and 3-egg clutches, laying order did not significantly influence the weights of the eggs (Table 7.4). Only the first eggs of 2-egg clutches were significantly heavier than the the third ones of 3-egg clutches ($t = 3.290$, $df = 6$, $P < 0.05$).

7.3.4 The roles of the sexes during incubation

In 559.7 hours (43 eagle-days) of day and night observation on 6 pairs in 8 breeding attempts, total male and female incubation averaged 95.5% of the observation time (Table 7.5). The male took part in only 31% of the total incubation load and the female about 64% of it. Eggs were exposed for 4.5% of the total observation time.

During the night the female apparently incubated alone (Table 7.5). Eggs were incubated all night, the bird occasionally getting up briefly. Daytime incubation involved both sexes. In 474.2 hours of observation the male incubated for about 37% and the female for 58% of the period. Eggs were exposed for about 5% of the time (Table 7.5). The results in Table 7.6 further show that during the day total incubation varied insignificantly from pair to pair. However, the female took a significantly larger proportion of the incubation burden than the male (Table 7.6, see also Fig. 7.2). Occasionally, however, his share exceeded that of the female (e.g. Pairs No. 74 & 10, Table 7.6). Throughout this period, incubation exceeded 90% of the observation

Fig. 7.1 The relationship between clutch size and the female weight in the African Fish Eagle in Queen Elizabeth National Park. Mean weight of 2 Entebbe Zoo females = 2835 g; n = 1 clutch for C/1, n = 3 clutches for C/2, and n = 5 clutches for C/3, ranges are shown. Note that clutches are from wild birds while mean female weight is from captive birds.

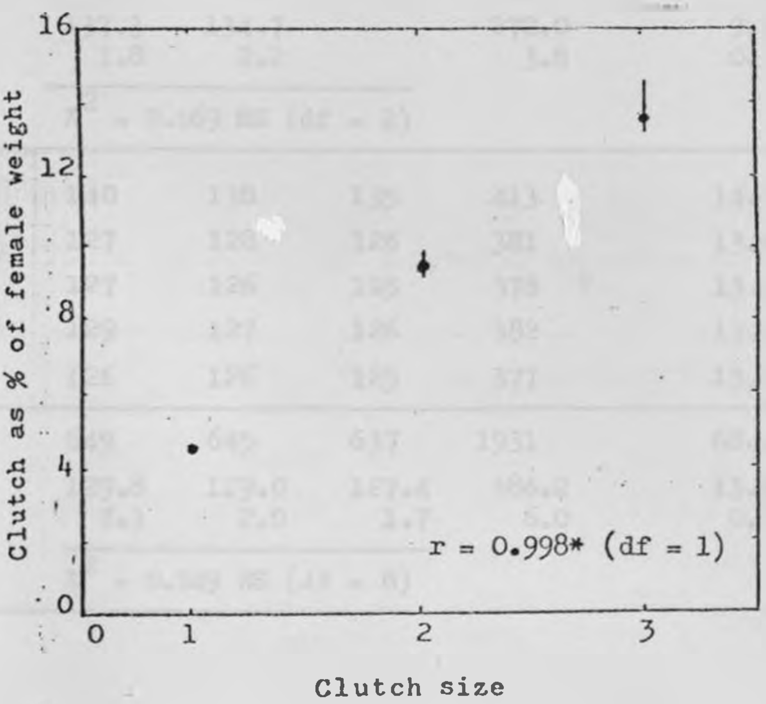


Table 7.4 The relationship between clutch size and female weight in the Fish Eagle. Note that clutches are from wild birds whereas female weights are from captive birds. Mean weight of 2 Entebbe Zoo females = 2835g.

Clutch size	Fresh wt. (g) of			Clutch wt. (g)	Clutch wt. as % female wt.
	Egg 1	Egg 2	Egg 3		
1-egg	127	-	-	127	4.5
2-egg	140	140	-	280	9.9
	133	131	-	264	9.3
	139	133	-	272	9.6
Total	412	404		816	28.8
Mean ±S.E.	137.3 1.8	134.7 2.2		272.0 3.8	9.6 0.1
	X^2 = 0.069 NS (df = 2)				
3-egg	140	138	135	413	14.6
	127	128	126	381	13.4
	127	126	125	378	13.3
	129	127	126	382	13.5
	126	126	125	377	13.3
Total	649	645	637	1931	68.1
Mean ±S.E.	129.8 2.3	129.0 2.0	127.4 1.7	386.2 6.0	13.6 0.2
	X^2 = 0.049 NS (df = 8)				

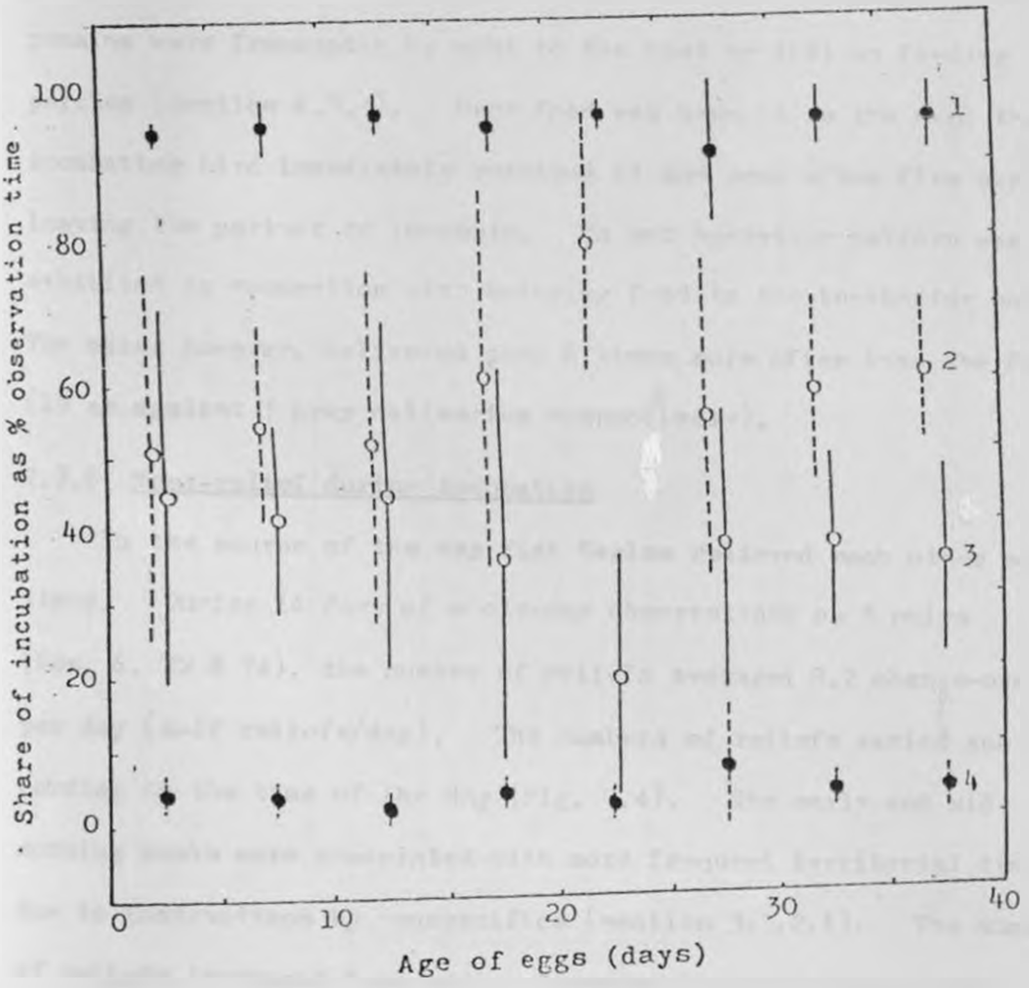
Table 7.5 The roles of the sexes of the Fish Eagles in Queen Elizabeth Park in day and night incubation. Observations on 6 pairs during 8 breeding attempts. Obs. = observation; figures in parentheses are observation times in hours.

Incubation period	Share in incubation				
	Obs. time	% Male	% Female	% total	% Nil
Daytime	474.2	36.9 (174.8)	57.9 (274.5)	94.8	5.3 (24.95)
Night	85.5	0.0 (0.0)	100.0 (85.5)	100.0	Trace
Total	559.7	31.2 (174.8)	64.3 (360.0)	95.5	4.5 (24.95)

Table 7.6 The share of daytime incubation according to sex by various Fish Eagle pairs.

Pair No.	Year of breeding	Obs. time (min)	Percent share of incubation			
			Female	Male	Total	NIL
74	1975	4616	39.2	54.5	93.7	6.3
74	1976	6070	51.7	43.5	95.2	4.8
72	1976	5155	54.2	42.3	96.5	3.5
6	1976	9713	72.4	20.9	93.3	6.7
6	1977	460	81.3	16.3	97.6	2.4
8	1976	625	56.4	42.5	98.9	1.1
10	1976	1285	45.8	52.1	97.9	2.1
87	1977	530	75.5	21.7	97.2	2.8
Total		28454				
Mean			59.6	36.7	96.3	3.7
±S.E.			5.0	4.9	0.7	0.7
			t = 14.313***(df = 14)			

Fig. 7.2 The sharing of daytime incubation in the African Fish Eagle in relation to the age of the clutch. Data from 4 pairs observed for a minimum of 75 hours each; 1 represents total incubation by both male and female, 2 female, 3 male, and 4 nil incubation loads; circles represent means and bars standard deviations.



time (Fig. 7.2). In relation to the time of the day, the male's share of the incubation load decreased by about 18% from morning towards the evening while that of the female compensatingly increased by about 15% (Fig. 7.3).

7.3.5 Food-sharing during breeding

A Fish Eagle brought food to the incubating partner. Food remains were frequently brought to the nest or left on feeding perches (section 4.3.3). Once food was brought to the nest the incubating bird immediately received it and soon after flew away leaving the partner to incubate. No set behaviour pattern was exhibited in connection with bringing food to the incubating partner. The male, however, delivered prey 6 times more often than the female (19 as against 3 prey deliveries respectively).

7.3.6 Nest-relief during incubation

In the course of the day Fish Eagles relieved each other several times. During 14 days of whole-day observations on 3 pairs (Nos. 6, 72 & 74), the number of reliefs averaged 8.2 change-over per day (4-12 reliefs/day). The numbers of reliefs varied according to the time of the day (Fig. 7.4). The early and mid morning peaks were associated with more frequent territorial disputes due to instructions by conspecifics (section 3.3.2.1). The numbers of reliefs increased from early afternoon towards evening again because of an increase in territorial encounters. The bird that incubated through the night, normally the female, flew off the nest just before or soon after sunrise. Occasionally it stayed up to almost 09:00, especially on cold mornings. Once an incubating bird got off the nest it was almost immediately replaced, although at times

Fig. 7.3 The roles of the sexes of African Fish Eagles in daytime incubation in relation to the time of the day. Data from 4 pairs observed for a minimum of 75 hours each; 1 represents total incubation by both male and female, 2 female, 3 male and 4 nil incubation loads; circles represent means and bars standard deviations.

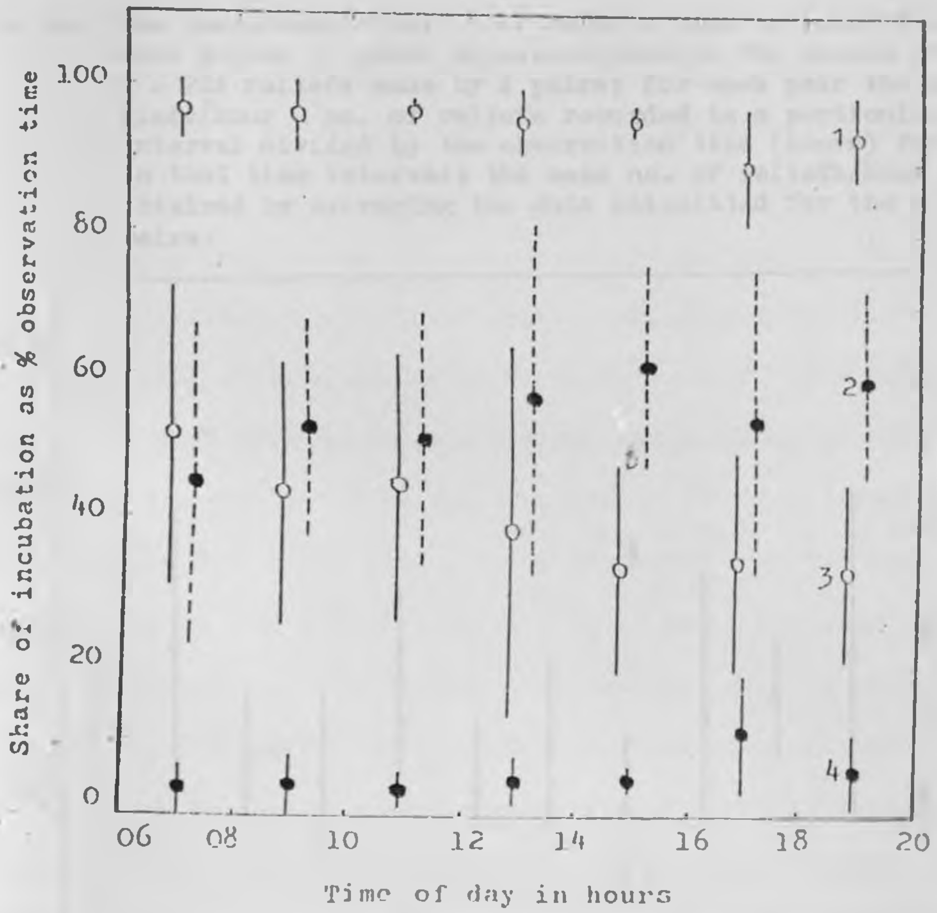
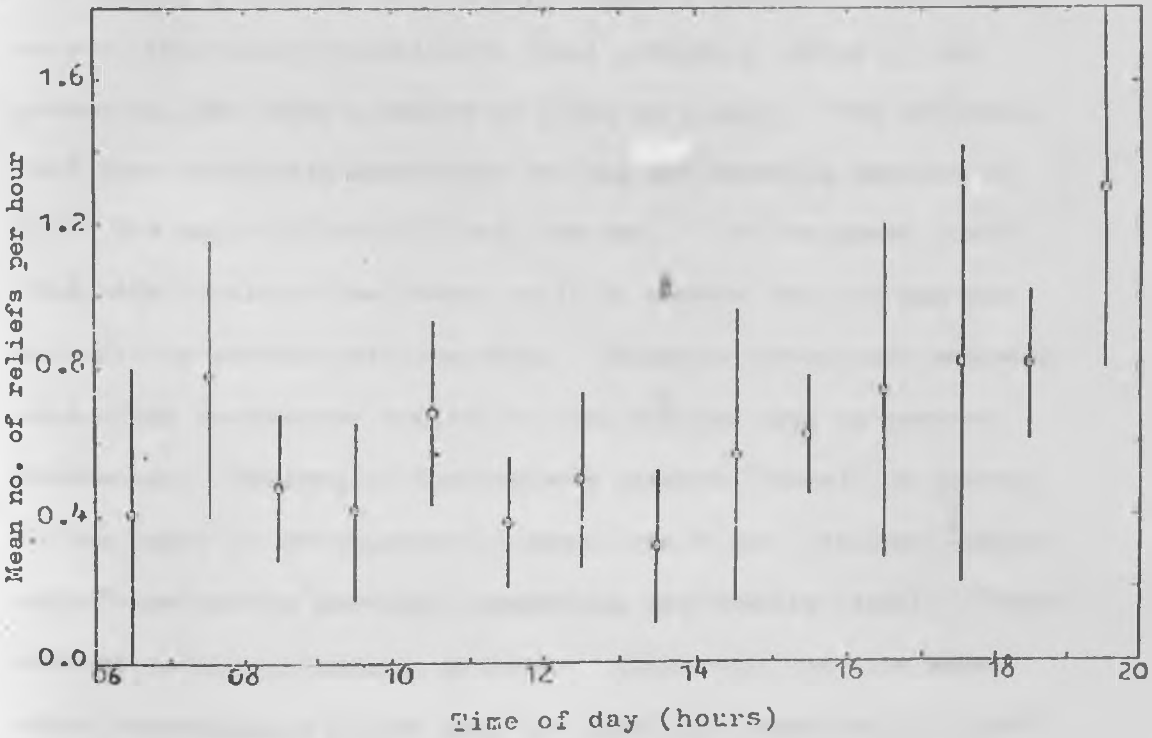


Fig. 7.4 The mean number (+s.d.) of reliefs made by incubating pairs of Fish Eagles in Queen Elizabeth Park in the course of the day. N = 224 reliefs made by 4 pairs; for each pair the no. of reliefs/hour = no. of reliefs recorded in a particular time interval divided by the observation time (hours) for the pair in that time interval; the mean no. of reliefs/hour was obtained by averaging the data calculated for the 4 breeding pairs.



the relieving bird took longer than usual to come.

With or without food, the relieving bird, especially the male, approached the incubating bird in a typical submissive posture (head forward and lowered, wings half-opened and drooped and the body slightly raised). This was so especially when the incubating bird did not readily respond by getting up and stepping aside. If the incubating female was reluctant to get off, the male often flew away. On the other hand if the female came to relieve, the male was prompt in getting off and did not spend much time by the nest edge. When the female took long to relieve him the male sometimes flew off and joined her.

During a change-over the pair normally duetted. This could be with the bird-to-be-relieved still sitting or after it had gotten up, and often a series of duets were made. The relieving bird then cautiously approached the egg and standing astride it, moved the egg with its bill and then sat. It then moved itself from side to side a few times, as if to ensure that the egg was actually in contact with its skin. Twigs and other nest materials were often re-arranged before the bird settled down to serious incubation. Meanwhile, the relieved partner flew off to a perch. On the perch it very vigorously shook itself and initiated comfort activities such as preening, scratching and shaking itself. These activities spanned several minutes. Frequently the bird made a short reconnaisance flight over the territory immediately it left the nest but more often it alighted nearby to preen before undertaking the flight. Then it settled to rest or began hunting.

7.3.7 Visits to an incubating bird

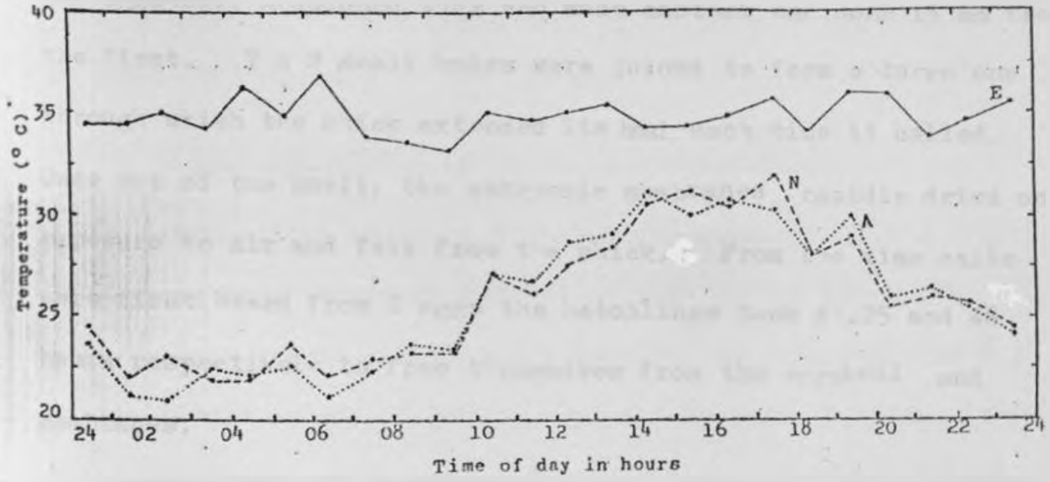
An incubating bird was frequently visited without actually being relieved. A bird that had been recently relieved would fly back to the nest, initiate a duet and fly away again after a very brief stay at the nest. It might alight on the nest itself or on some convenient branch of the nest tree or a nearby perch. It usually brought no food or nest material along. In some cases the incubating bird got up and flew away too, as the visiting bird flew off. This was more common when the male was visited by the female. This abrupt flying off by the male, after a very brief incubation stint, led to the female taking on an added incubation burden.

Visiting birds at times came to the nest with some kind of nest material: green leafy branches, dry branches or water weeds. This was usually deposited by the nest-edge after which the visitor flew off. No particular patterns of behaviour, like receiving the nest material, were shown by them. The material so brought was added to the nest structure, normally some time after being brought, and usually by the sitting bird.

7.3.8 Incubation temperature

Eggs were incubated at a mean temperature of 34.8° C which was about 9.0° C above the mean air temperature of 25.7° C. The incubation temperature was less variable than air and nest-edge temperatures (Fig. 7.5). The latter temperatures were similar and both were constantly below the incubation temperature.

Fig. 7.5 Egg, nest-edge and air temperatures in relation to time of the day as measured from the nest of Fish Eagle Pair No. 1 between 5-25/3/77. E = egg, N = nest-edge and A = air temperatures.



7.3.9 Incubation period and the hatching process

The incubation period for 14 eggs varied from 40-42 days, averaging 40.6 days (Table 7.1). Hatching began with the young calling and pecking the eggshell. The hatchling then cracked a tiny hole in the broader end of the shell with the aid of the egg-tooth and widened it. Complete rapture of the shell was probably achieved through body movements. Eventually the chick detached itself from the shell and embryonic membranes. During the process the chick in Egg 1 of Pair No. 1 made an initial crack in the eggshell, abandoned this and made another one some 15 mm from the first. The 2 small holes were joined to form a large one through which the chick extended its head each time it called. Once out of the shell, the ambryonic membranes rapidly dried on exposure to air and fell from the chick. From the time calls were first heard from 2 eggs the hatchlings took 4[illegible].25 and 46 hours respectively to free themselves from the eggsheil and membranes.

Large pieces of eggshell were frequently found under nest trees where they had probably been so disposed by the adults. Smaller pieces often remained in the nest and were eventually buried intact in the nest.

There is apparently no parental assistance to chicks during hatching. Egg 3 of Pair No. 82 had a tiny hole on it at 15:00 on 30 December 1976 while the 2 older siblings were about 6 and 4 days old respectively. At 17:00 on 1 January 1977 the chick had died with the head well out of a fairly large hole in the eggshell.

7.3.10 The laying and hatching intervals

The hatching intervals were the same as the laying intervals for respective eggs (Table 7.1). This would indicate that incubation in the Fish Eagle starts with the first egg laid.

7.3.11 The conversion efficiency

Eggs declined in weight with incubation and towards the end of the incubation period they were 81.4% of their fresh weights (Fig. 7.6). Using the mean weight of 1-day old chicks, however, the hatchling was 70.5% of the mean weight of the fresh eggs (i.e. a mean conversion efficiency of 70.5% from egg materials to the body materials of the chick).

7.3.12 Hatchling weight relative to adult weight

Eleven chicks, weighed at hatching, averaged 91.8 g (72–106 g). The chicks were therefore hatched at 3.2% of the Entebbe Zoo female weight (mean weight = 2835 g for 2 adults) as compared with 2.7% of the female weight of 3400 g reported by Brown & Amadon (1968). Since the weight of the male (2241.5 g) given by Brown & Amadon (op.cit.) is similar to that of the Zoo male (mean of 2250 g for 3 adults), the chicks averaged 4.1% of the male weight.

7.3.13 Egg mortality

The mortality rate of the Fish Eagle egg during this study was low, averaging 0.74% day^{-1}. The mortality rate was fairly uniform during the first 5 weeks of the 6-week incubation period (Fig. 7.7). Because of disappearance, probably due largely to predation, it greatly increased during the last week. In accounting for 21 (70.0%) of the 30 eggs which failed to produce

Fig. 7.6 The decline in egg weight in the African Fish Eagle in relation to the age of the clutch. N = 95 weight records with a minimum of 6 records for each age group (i.e. 0-5, 6-10, ---, 41-45 days). The figure 1 represents the mean (± s.d.) weight of 7 fresh eggs, and 2 the mean (± s.d.) weight of 7 hatchlings.

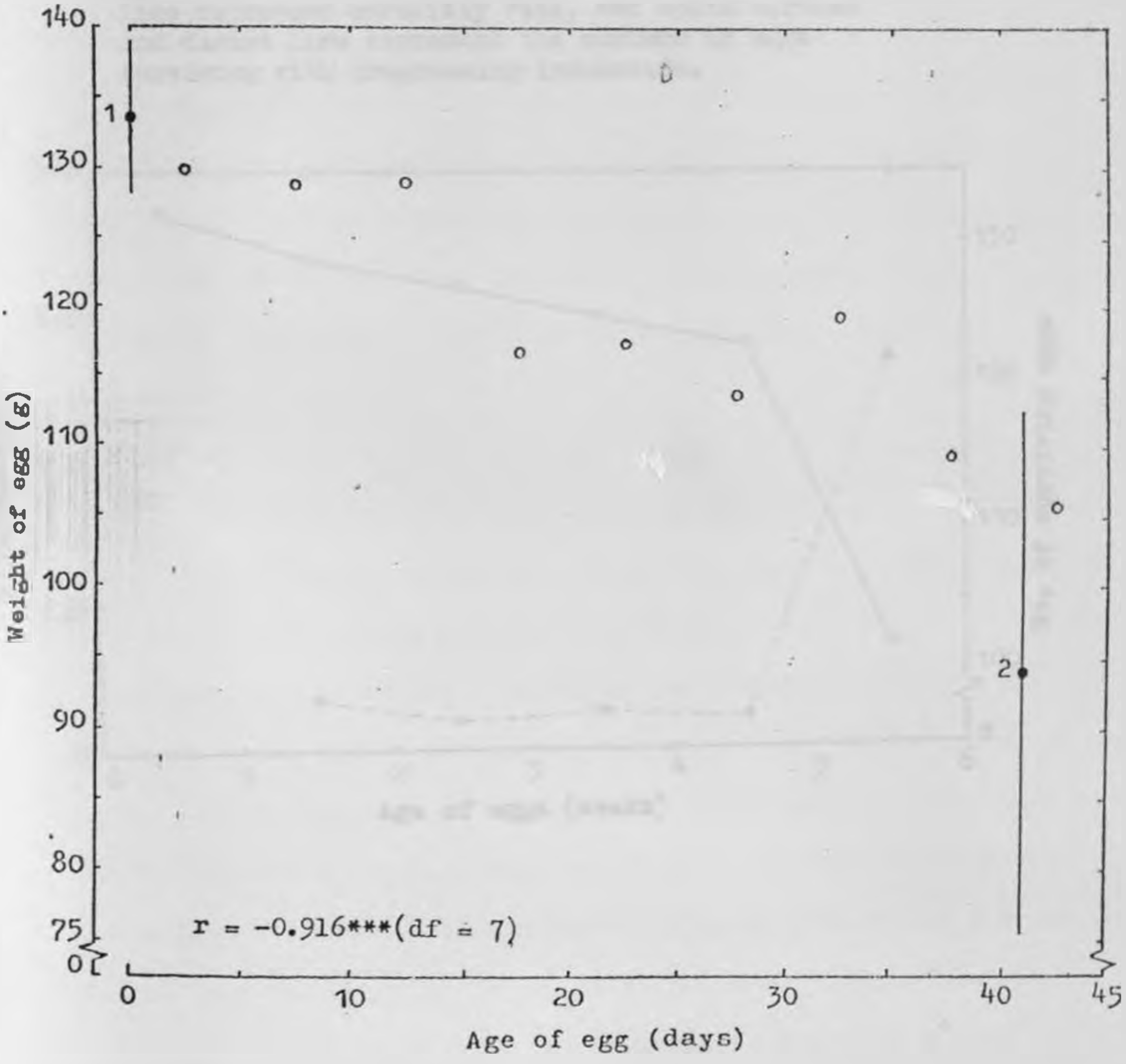
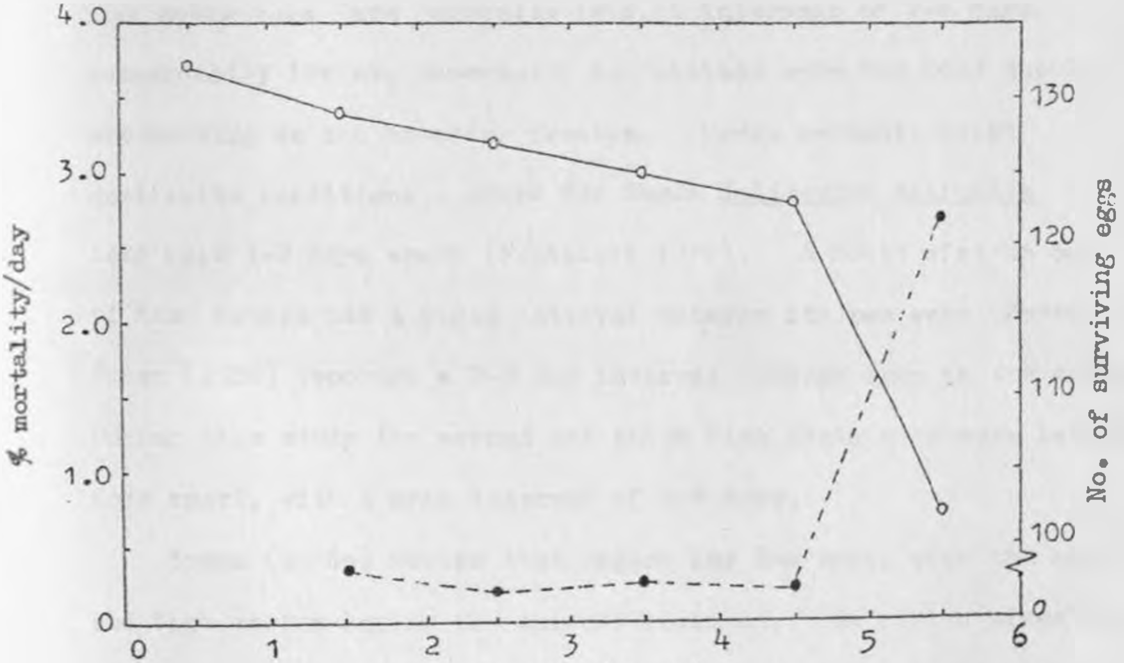


Fig. 7.7 The mortality of African Fish Eagle eggs in Queen Elizabeth National Park. Open circles and solid line represent mortality rate, and solid circles and dashed line represent the numbers of eggs surviving with progressing incubation.



young, egg disappearance was the most significant cause of egg mortality and chick death during pipping the least so (Table 7.7).

Egg mortality differed significantly in relation to clutch size (Table 7.7) with the 1-egg clutches incurring no losses, while the 2- and 3-egg clutches respectively lost 21.1% and 35.9% of their eggs.

7.4 DISCUSSION

Brown (1955, 1970a, 1976a & b) and Brown & Amadon (1968) state that eagle eggs are generally laid at intervals of 2-4 days, occasionally longer, especially in habitats were the food supply are limiting to the breeding females. Under probably ideal capitivity conditions a caged Sea Eagle *Haliaeetus albicilla* laid eggs 1-2 days apart (Fentzloff 1977). A South African pair of Fish Eagles had a 6-day interval between its two eggs (Porter 1903). Brown (1980) reported a 2-3 day interval between eggs in the species. During this study the second and third Fish Eagle eggs were laid 2-4 days apart, with a mean interval of 2.8 days.

Brown (1976a) states that eagles lay 1-4 eggs, with the sea and fish eagles laying the largest clutches. No clutch sizes are given for the Fish Eagle populations of Winam Gulf, L. Victoria, and L. Naivasha by Brown (1960) and Brown & Hopcraft (1973) respectively A mean clutch size of 2.33 eggs for 9 breeding attempts in a South African pair was reported (Steyn 1972). Brown (1980) also gave a mean clutch size of 1.93 eggs for 68 clutches from Eastern and Southern Africa. With a mean clutch size of 1.94 eggs, the Fish Eagle in this Park conformed with the clutch size of the genus and the 2-egg clutch is normal for the species (Table 7.8). No 4-egg

Table 7.7 Egg mortality in the Fish Eagle by clutch size for known clutches during the study period 1975-78.

	Clutch size			
	C/1	C/2	C/3	Total
N(eggs laid)	17	76	39	132
Mortality factor				
Egg breakage	0	0	2	2
Chick death	0	0	1	1
Infertility/addling	0	1	5	6
Disappearance	0	15	6	21
Total eggs lost	0	16	14	30
% of individuals	0.0	21.1	35.9	22.7
% of losses	0.0	53.3	46.7	100.0

Table 7.8 Comparisons of the clutch size, egg dimensions and fresh egg weights in the African Fish Eagle related sea and fish eagles, the fishing eagle and the Vulturine Fish Eagle. For this study n n = 7 for fresh egg weights.

Bird Name	Country	Clutch size range	Clutch size normal	Length (mm) range	Length (mm) mean	Breadth (mm) range	Breadth (mm) mean	Fresh weight(g) range	Fresh weight(g) mean	
Haliaeetus vocifer	Uganda	1-3	2	71-85.0	76.74	56.0-[illegible].5	59.75	125-140	133.3	Thi
" "	West & Equatorial Africa	1-2	2	70-76	-	53-57	-	-	-	Ban
" "	S. Africa	1-2	?	-	76.2	-	57.15	-	-	Por
" "	" "	1-3	2	-	-	-	-	-	-	Ste
" "	" "	-	2	67-77.5	70.7	50.8-[illegible].3	54.5	-	-	Rob
" "	Zambia	1-3	?	-	-	-	-	-	-	Col
" "	Africa	1-4	2	63.5-80.0	72.2	48.2-[illegible].0	54.5	-	120	Bro
" "	"	-	2	-	73.0	-	55.0	-	-	Ma
H. vociferoides	Madagascar	1-3	2	-	-	-	-	-	-	Br
H. albicilla	Eurasia	1-4	2	-	73	-	58	-	-	Br
" "	Germany	1-3	-	73-78	75.4	52-6[illegible]	55.6	112-130	123	Fe
H. leucocephalus	N. America	1-4	2	-	-	-	-	-	-	Br
H. pelagicus	N.E. Asia	1-3	2	-	80	-	60	-	-	Br
H. leucogaster	S.E. Asia & Australia	1-3	2	-	-	-	-	-	-	B
H. leucoryphus	Eurasia	1-4	2+	-	-	-	-	-	-	B
Ichthyophaga ichthyaetus	S.E. Asia	2-4	(2.5?)	-	-	-	-	-	-	B
Gypohierax angolensis	Africa	1	1	-	69	-	52	-	-	

clutch was found, which probably supports the view that tropical eagles lay smaller clutches than their temperate relatives (Brown 1955, 1970a, 1976a & b; Brown & Amadon 1968).

Fish Eagle clutches in this Park averaged [illegible]% of the female's body weight, and each clutch size took significantly different proportions of her weight (Fig. 7.1). The 2-egg clutch weighed 9.6% while the 3-egg one 13.6% of the female's weight. These weights are much higher than those suggested by Brown (1976b), i.e. that normal clutches of various eagles weigh from 2-7% while the exceptionally large 4-egg clutches of the Golden Eagle <u>Aquila chrysaetos</u> only weigh up to 9% of the female weight.

Fish Eagle egg dimensions given by Porter (190[illegible]), Mackworth-Praed & Grant (1952), Bannerman (195[illegible]), Roberts (1958), and Brown (1976b & 1980) were not significantly different from the ones of this study ($X^2 = 0.047$, df = 5, P [illegible] 0.1; data in Table 7.8). Fresh egg weights were not given by these authors. An egg of a wild Sea Eagle measured 74 x 60 mm and 3 eggs of a captive female averaged 76.7 x 55.3 mm and 123 g (Fentzloff 1977). Although the Sea Eagle female is about 47% heavier than the Fish Eagle female (Brown 1970a & 1976a, b & c), they laid eggs of similar dimensions and weights. This is in agreement with Brown's (1976a) and Brown & Amadon's (1968) suggestions that smaller raptors generally lay heavier eggs than their larger relatives.

Brown (1955) suggested that in most eagles a constant clutch size in a pair was indicative of the same female laying the successive clutches. During this study, in 42% of all breeding attempts with successive clutches the clutch sizes changed. Because of the strong pairbond exhibited by Fish Eagles (section 5.3.8), it is inconceivable to expect such a high rate of mate change involving only the female. It would, therefore, be difficult to use clutch sizes as an indication of wether or nota female laid particular clutches. The maintenance of a constant clutch size by the female of any pair of wild Fish Eagles or other raptors during successive breeding attempts may be rendered unlikely by factors such as variations in food supply, diseases and other environmental conditions. The Sea Eagle female in Fentzloff's (1977) study laid 2-egg clutches 6 times successively probably because of the ideal feeding and veterinary conditions availed to it during captivity.

As in the related Sea Eagle and the Bald Eagle Haliaeetus leucocephalus, incubation in the Fish Eagle started with the first egg. This phenomenon resulted in asynchronous hatching of the young, the effects of which are discussed in section 9.3.5. The female incubates for from 75-85% of the total incubation in most species of eagles and often alone in snake eagles which normally lay 1-egg clutches (Brown 1976a & b). In the Fish Eagle, too, the male takes only a small share in incubation (Brown 1976b) & 1980). Roberts (1958) reported that the female incubated alone. This study, however, showed that both sexes incubated although the female did so singificantly more than her mate. His share of the incubation load was, nevertheless, large by eagle standards, i.e. 37% of daytime incubation. Only in the Sea Eagle does the male's share of 25-30% of daytime incubation (Brown 1976a & c) approach that of the Fish Eagle. The constantly high total incubation time exhibited by the Fish Eagle and the small variations in it are important in ensuring the fairly uniform temperature (Fig. 7.5) that is required by the developing embryos. It is also important in ensuring that eggs are not lost to predators.

Total incubation declined throughout the day for the male while it increased for the female (Fig. 7.3). This decline corresponded to periods of increased territorial activities of the birds (section 3.3.2.1). These changes in the shares of the respective sexes are only explicable by their roles in territorial defence in which the male is more active than his mate. The fact that the female incubated significantly more than him also clearly points to his role in activities other than incubation.

Special nest relief ceremonies occur in birds that follow set incubation patterns, e.g. Marabou Storks Leptoptilos crumeniferus (Kahl 1968), Pink-backed Pelican Pelecanus rufescens (Din 1970), shags Phalacrocorax sp. (Snow 1960), and gannets Sula spp. (Nelson 1967). In eagles this behaviour is lacking and it is not mentioned in Brown (1955, 1970, & 1980) or Brown & Amadon (1968). No elaborate nest relief ceremonies have been described for the Fish Eagle nor has it been observed during this study. Visits with or without nest material or food to the incubating bird probably helps to maintain the pair-bond and to enhance the synchronisation of breeding activities. Brown (1955) interpreted such visits as being merely habitual.

In the Verreaux's Eagle Aquila verreauxi the conversion efficiency of nutrient materials of the egg into the body materials of the chick is about 82%, it ranges from 82.6-87% in the Golden Eagle A. chrysaetos (Brown 1976b). Brown considered these to be very efficient conversion ratios. With a ratio of only 70.5% the Fish Eagle has a much lower conversion efficiency than those of the above raptors.

The mortality rate of the Fish Eagle egg during this study was low, averaging 0.74% day^{-1}. This is in agreement with Ricklefs' (1969a) conclusion that the mortality rates of eggs and nestlings of raptors are generally less than 1.0% day^{-1}. This mortality rate is not too dissimilar to the rate, 1.2% day^{-1}, calculated for the egg of the Bald Eagle in Alaska (Hensel & Troyer 1964). In Montana, McGahan (1968) found that the Golden Eagle suffered an egg mortality rate of only 0.58% day^{-1}.

Inability of eggs to hatch due to causes like egg breakage by sitting birds, addling and chick death during pipping can be a major tell-tale for an environment highly contaminated with toxic substances such as organochlorine compounds (Gilbertson 1975, Anderson & Hickey 1974, Helander 1983). Because of thin eggshell syndrome largely due to contamination by DDT, egg breakage became a significant cause of population crashes in most raptors and many other birds in North America and Europe (e.g. Gilbertson, op.cit.; Anderson & Hickey, op.cit.). During this study, however, egg breakage accounted for only 2(6.7%) of the 30 eggs that did not produce young.

The fact that the 1-egg clutch was not affected by any of the mortality factors is important in that it shows that either all these eggs were fertile or that during incubation they were all properly covered by the sitting birds so that embryo death could not occur. Secondly, the finding that egg breakage was one of the least important factors and that it never affected the 1- and 2-egg clutches precludes it as a significant cause of hatching failure. The two eggs which broke during the study were apparently cracked by the departing birds as I approached their nests for clutch size determination and other egg records. Both eggs subsequently disappeared without trace and were probably predated by the incubating birds. Although not witnessed during this study, canibalistic tendencies in raptors have been reported (Meyburg 1974). It was not established whether the infertile/addled eggs did not hatch due to actual infertility or embryo death during incubation. The 21 ([illegible]) remaining eggs disappeared without trace and were probably lost to predation.

These results should not imply that the waters and the environs of the Park are not chemically polluted, but simply that chemical contamination is not high enough to cause egg mortality. Edroma (1974a & b & In press) demonstrated that some areas of the Park and its waters, especially L. George, and its wildlife suffer from copper and other environmental pollutents. Some organochlorines and organophosphates have been and are still being used in intensive agricultural and livestock farms which surround the Park. The effect of these chemicals on the reproductive potential of the Fish Eagle and those of other fish-eating birds in the Park remain to be studied.

Predation of both eggs and nestlings is thought to be a negligible mortality factor in raptorial birds because of the abilities of the adults to defend their nests (Ricklefs 1969a). I recorded no predation on eggs during this study but it was suspected for most of the egg disappearances. Olive Baboons Papio anubis, Vervet Monkeys Cercopithecus aethiops, Monitor Lizards Varanus nilotica and unidentified snakes were probably responsible for most of the egg losses (see section 8.4 for a discussion of mortality factors among nestlings).

CHAPTER 8

GROWTH AND MORTALITY PATTERNS OF NESTLINGS

8.1 INTRODUCTION

The increase in the weight of an organism is the sum of many simultaneous processes (Ricklefs 1968a). There are marked changes in the proportions of basic body constituents like protein, water, ash and lipid (Bailey, et al. 1960, Ricklefs 1967a) and in the relative sizes of the body organs (Brody 1945, Ricklefs 1967a) during the course of growth. Patterns of weight increase vary considerably among species of birds due to the selective forces producing the adaptation for breeding (Ricklefs 1968a). For instance the young of large speceis usually need more time to reach adult sizes than those of small ones, and young which are fed by their parents grow more rapidly than those which feed themselves (Ricklefs 1968a). Growth rates can also be influenced by clutch size (Lack 1948 & 1954); fluctuations in the availability of food supply for Emus (Thomas 1964), the Procellariiformes (Lack 1948), Common Swift (Lack & Lack 1951) and for passerines (Willson 1966); sexual dimorphism (Ricklefts 1968a); and probably the lack of predation pressure for birds nesting on oceanic islands (Dorward 1962).

According to Ricklefs (1967b) there are 3 equations by which the growth rates of birds can be mimicked, namely logistic (Robertson 1923), Gompertz (Laird, et al. 1956), and von Bertalanffy (von Bertalanffy 1960) growth curves. These growth curves tend to be species-specific (Ricklefs 1968a).

The causes of nestling mortality in the population of Fish Eagles were identified. The observed mortality rate was low and is discussed in relation to the advancing age of the young and its increasing capability to defend itself and that of adults to defend their nest (Ricklefs 1969a).

8.2. MATERIALS AND METHODS

8.2.1 Patterns of growth by weight

Chicks from 10 accessible nests were weighed at various stages during the nestling periods. Three types of "Pesolas" with capacities of 300 g, 1000 g, and 5000 g were used. Chicks of 1000 g or less were weighed while tucked into a pre-weighed and punctured polythene bag. Nestlings of over 1000 g were carefully tied up with a strap before weighing. Such large chicks were hooded using a bag made from black clothing. Weights were taken when the chicks stopped struggling. From these weights the proportions of adult weight attained by the young and the forms and rates of their growth curves were determined.

8.2.1.1 The growth curve

The net increase in the body weight of the young during growth must equal the body weight of the adult (Ricklefs 1968a). Because the female chick attained a higher asymptotic weight than the male, their sexes were distinguishable. Thus the proportion of adult weight attained by each chick was calculated by expressing the chick's weight at a given age as a percentage of the adult weight of its own sex. The ratio of the asymptote of the growth curve to adult body weight was calculated for each nestling by dividing its asymptotic weight by the weight of the adult of its own sex (Ricklefs, op cit.).

In determining the growth rates of nestlings, weights of adults and measurements of their body parts were used as standards. These measurements were obtained from 5 birds (3 males and 2 females) at Entebbe Zoo. Data from such sources as Brown (1970a, 1976a, b & c), Brown & Amadon (1968), Grzimek (1972), Mackworth-Praed & Grant (1952), Ricklefs (1967b, 1968a & 1969a) were also used.

8.2.1.2 The growth rate

(i) The overall growth rate, K

The overall growth rate, K (g/day), is the mean growth rate over the whole nestling period (Ricklefs 1967b). For each chick it was calculated using the Gompertz equation (Ricklefs, op cit.).

Thus: $K = e\frac{dWi}{dt}$, where e = base of the natural logarithm,

$\frac{dWi}{dt}$ = slope of growth curve at inflection point (i),

and Wi = weight and t = time (days) at inflection point.

From the values of K the rates of growth of various chicks are directly comparable. However, only chicks whose K were calculated by the same equation can have their K values compared.

(ii) The t_{10-90}

The t_{10-90} is the time interval required to complete growth from 10-90% of the asymptotic weight (Ricklefs, op cit.).

Thus:

$$t_{10-90} = \frac{C90 - C10}{dW/dt},$$ where

C_{10} = the conversion factor of 0.1 of the asymptotic weight,

C_{90} = the conversion factor of 0.9 of the asymptotic weight, and

$\frac{dW}{dt}$ = slope of the growth curve.

According to Ricklefs (1968a), t_{10-90} can also be calculated from the fledging period of the brood. Thus t_{10-90} = 0.57 x fledging period. Using t_{10-90} the growth rates of chicks, even if fitted by different growth equations, can be compared.

(iii) The absolute growth rate

The absolute growth rate is an index of the daily weight increases of the growing organism over the whole growth period and is expressed in g/day. Using this index, chicks of similar ages or the growth rates at the points of inflection could be compared. Absolute growth rate was calculated as follows:

Absolute growth rate (dw/dt) = KW ($\log_e W$), where

K = overall growth rate in g/day,

W = asymptotic weight in g.

8.2.2 Growth of other body parts

While weighing chicks, their tarsi, femur, humeri and standard wings were also measured using a 5 m flexible metalic tape measure. The standard wing was the distance from the end of the folded wing at the carpal joint to the tip of the longest primary feather (when feathers present). Lengths of the tarsus, femur and humerus were taken as the lengths of the respective bones, from one joint to the other. From these measurements the proportions of adult sizes attained by and the forms of the growth curves of the respective body parts were determined.

8.2.3 The plumage and age of the nestling

The nestling was classiflied into plumage types and age classes from hatching till leaving the nest. This was achieved by recording the age of appearance or disappearance of a particular feather type, viz. the first and second downs and feathers of the main tracts. The colours of the skin, bill, caruncle, cere, eye, tarsus, foot and talon were recorded. Additionally, the roughening of the foot due to the development of spicules and the locomotory behaviour of the young were also noted.

8.2.4 Nestling mortality

Nestling mortality was studied by noting all chick losses as the fledging period progressed. The probable causes of the losses were recorded. Calculations of mortality rates, as percent losses day^{-1}, followed Ricklefs' (1969a) method:

$$m = -\frac{(\log_e p)}{t}$$

where m = instantaneous mortality rate (% day^{-1}),

p = proportion of chicks surviving and

t = time in days during the fledging period.

8.3 RESULTS

8.3.1 Weight gain and the growth curve

Fig. 8.1 shows weight gains by nestling Fish Eagles with increasing age. Both male and female chicks exceeded the weight of Entebbe Zoo adults. The female nestlings, however, did not reach the adult female weight of 3400 g reported by Brown & Amadon (1968). The ratios of the asymptotes of the growth curves of nestlings to adult body weights (Ricklefs 1968a) clearly indicate that male chicks fledged at adult male weights while female nestlings did so at weights above those of adult females (Table 8.1). The growth curves conformed with the sigmoid form of animal and bird species (Needham 1964, Ricklefs 1969b).

Fig. 8.1 (a) Weight gain in 3 male nestling Fish Eagles in Queen Elizabeth Park. Sample size, n = 29 weight records, ranges are shown where appropriate; ZM represents mean weight (= 2250 g) of 3 adult Entebbe Zoo males.

Fig. 8.1 (b) Weight gain in 6 female nestling Fish Eagles in Queen Elizabeth Park. Sample size, n = 47 weight records, ranges are shown where appropriate; ZF represents mean weight (= 2835 g) of 2 adult Entebbe Zoo female; represents the 3400 g female weight given by Brown & Amadon (1968).

Fig. 8.1

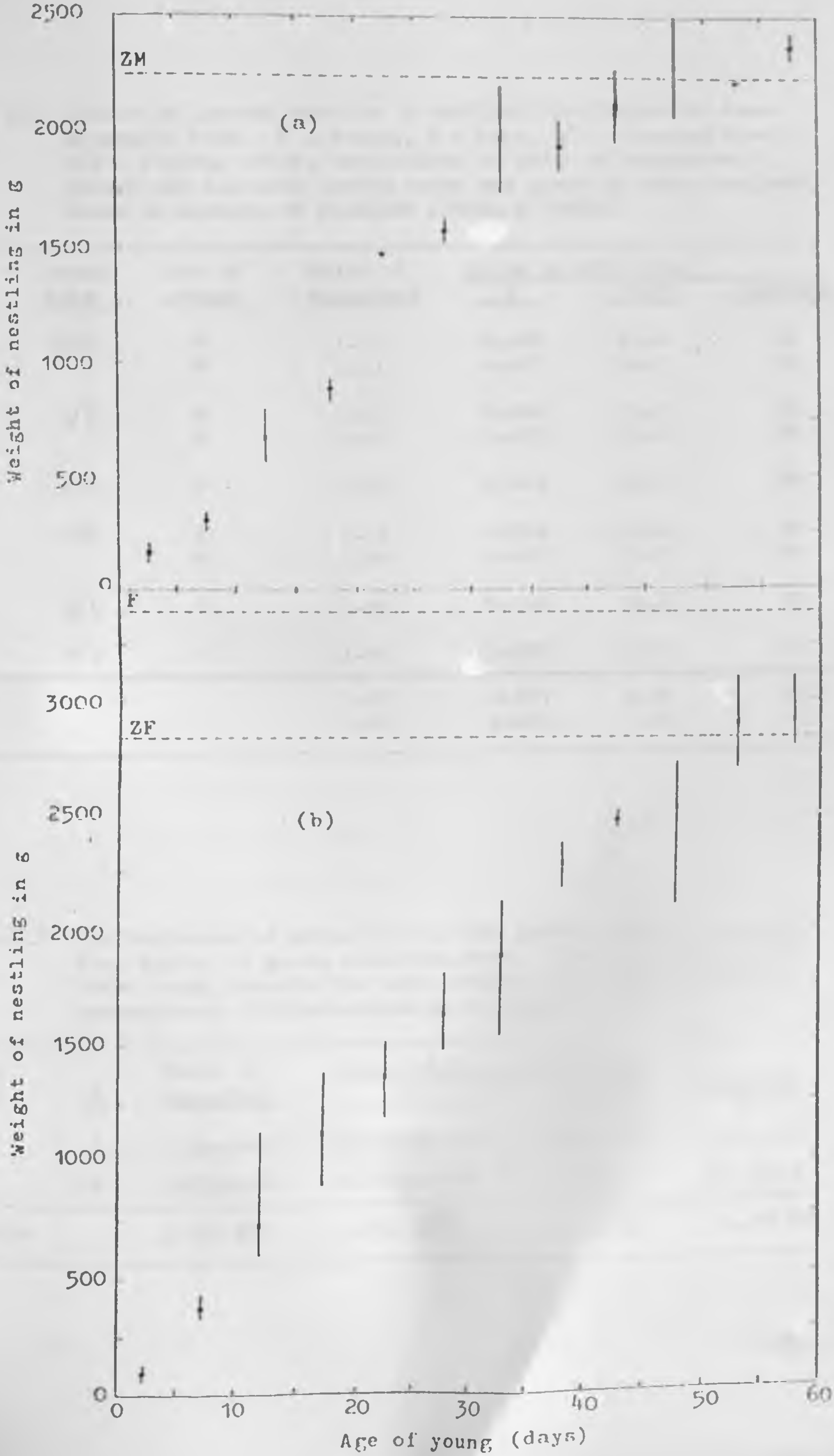

2500
ZM
(a)
2000
1500
1000
500
0
F
Weight of nestling in g
3000
ZF
2500
(b)
2000
1500
1000
500
0
Weight of nestling in g
0
10
20
30
40
50
60
Age of young (days)

Table 8.1 Indices of growth rate for 9 nestling Fish Eagles in Queen Elizabeth Park. F = Female, M = Male, B/1 = 1-young brood, B/2 = 2-young brood; definitions of ratio of asymptote, K, t10-90 and absolute growth rates are given in text; analyses based on methods of Ricklefs (1967a & 1968b).

Pair No.	Brood size	Sex of young	Ratio of asymptote	Chick growth rates		
				K	t10-90	Absolute
82	B/2	F	1.13	0.068	45.4	81
		F	1.13	0.067	46.3	72
86	B/2	F	1.13	0.082	37.7	82
		F	1.02	0.077	39.8	78
87	B/1	F	1.09	0.063	49.1	86
87	B/2	F	1.13	0.054	57.6	69
		M	1.00	0.078	39.7	70
23	B/1	M	1.00	0.106	29.2	72
82	B/1	M	1.04	0.098	31.5	72
Mean			1.07	0.077	41.8	75.8
±SE			0.02	0.005	2.8	1.9

Table 8.2 The influence of brood size on the growth rates of nestling Fish Eagles in Queen Elizabeth Park. Student's t was calculated using formula for small sample sizes, df - 7 for all comparisons. Abbreviations as in Table 8.1

Brood size	N	Ratio of asymptote	Mean (±S.d.) growth rates		
			K	t10-90	Absolute
B/1	3	1.04±0.04	0.089±0.019	36.6±8.9	67.7±6.6
B/2	6	1.09±0.06	0.071±0.009	44.4±6.7	75.3±5.2
t-value		1.222 NS	1.701 NS	1.300 NS	0.306 NS

Growth rate data for K and t_{10-90} (Table 8.1) indicate that chicks grew and attained adult weights at different rates. Brood size (Table 8.2) and hatching order (Table 8.3) did not significantly affect growth rates but the sex of the young did. Male chicks grew significantly faster than the females (Table 8.4). Sexual dimorphism resulted in differential growth rates between male and female nestling African Fish Eagles as well as the nestlings of other raptors (Table 8.5). A comparison of t_{10-90}, as calculated from the fledging periods of the broods, for the Fish Eagle and other members of the genus Haliaeetus is also given (Table 8.6).

At the inflection point of its growth curve each chick gained weight fastest (Fig. 8.2). A comparison of the absolute growth rates at these points shows that brood size (Table 8.2), hatching order (Table 8.3) and the sex of the young (Table 8.4) respectively had no significant influence on daily weight gain.

8.3.2 The growth of body parts

The tarsus, femur and humerus reached adult sizes by fledging time (Fig. 8.3) while the standard wing had not. It was only about 75% of the adult magnitude by the time the chick left the nest (Fig. 8.3). The growth curves of these body parts were also sigmoid in form.

8.3.3 The plumage and age of the nestling

The changes in plumage, colours of the various body parts and the locomotion of the young are summarised in Table 8.7 and illustrated in Plates 5-7. Age classes, largely based on plumage, and their approximate durations are also shown in the Table. The ages are approximations because the criteria involved in the

Table 8.3 The influence of hatching order on the growth rates of nestling Fish Eagles in Queen Elizabeth Park. Student's t was calculated using formula for small sample sizes, df = 4 for all comparisons; C_1 = first and C_2 = second chicks of 2-young brood. Other abbreviations as in Table 8.1.

Hatching order	N	Ratio of asymptote	Mean (±S.d.) growth rates		
			K	t10-90	Absolute
C_1	3	1.13±0.00	0.068±0.011	46.9±8.2	77.3±5.9
C_2	3	1.05±0.06	0.074±0.005	41.9±3.1	73.3±3.4
t-value		1.980 NS	0.674 NS	0.808 NS	0.830 NS

Table 8.4 The influence of sex on the growth rates of nestling Fish Eagles in Queen Elizabeth Park. Student's t was calculated using the formula for small sample sizes and df = 7 for all comparisons. Other abbreviations as in Table 8.1.

Sex of young	N	Ratio of asymptote	Mean (±S.d.) growth rates		
			K	t10-90	Absolute
Male	3	1.01±0.02	0.094±0.012	33.5±4.5	71.3±0.9
Female	6	1.11±0.04	0.069±0.009	46.0±6.5	78.0±5.9
t-value		3.381*	3.088*	2.644*	1.735 NS

Table 8.5 Influence of sexual dimorphism on the growth rates of 4 species of raptors. See text for definitions of K and t10-90; M = male and F = female.

Species	N	Sex	Adult weight(g)	Growth rate K	Growth rate t10-90	Source
Fish Eagle	3	M	2250	0.094	33.5	This study
(*Haliaeetus vocifer*)	6	F	2835	0.069	46.0	"
Golden Eagle	1	M	4136	0.078	39.1	Ricklefs (1968b)
(*Aquila chrysaetos*)	2	F	5050	0.078	39.1	"
Cooper's Hawk	4	M	-	0.257	17.1	"
(*Accipiter cooperii*)	1	F	471	0.187	23.5	"
Red-tailed Hawk	4	M	882	0.208	22.2	"
(*Buteo jamaicensis*)	4	F	1275	0.168	26.3	"

Table 8.6 The time interval required to complete growth from 10-90% of the asymptotic weight (t10-90) in the African Fish Eagle and its temperate allies. According to Ricklefs (1968b) t10-90 = 57% of the fledging period; weight records are from Brown (1976a, b & c) Brown & Amadon (1968), and Grzimek (1968); and fledging periods (days) from Brown (op.cit.).

Name of bird	Distribution	Adult wt.(g)	Fledging period	t10-90 (days)	Source
Haleaeetus vocifer	Tropical	2542.5	76	43.3	This study
Haliaeetus vocifer	"	2820.8	70	39.9	Ricklefs (1968b)
H. leucocephalus	Temperate	5000.0	75	42.8	" "
H. albicilla	"	4650.0	70	39.9	Estimated as above
H. pelagicus	"	7500.0	70	39.9	" " "
H. leucogaster	"	?	70	39.9	" " "
H. leucoryphus	"	?	90	51.3	" " "

Fig. 8.2 The absolute growth rate (g/day) of the single chick of Pair No. 82 (1977). The graph is representative of all chick growth patterns.

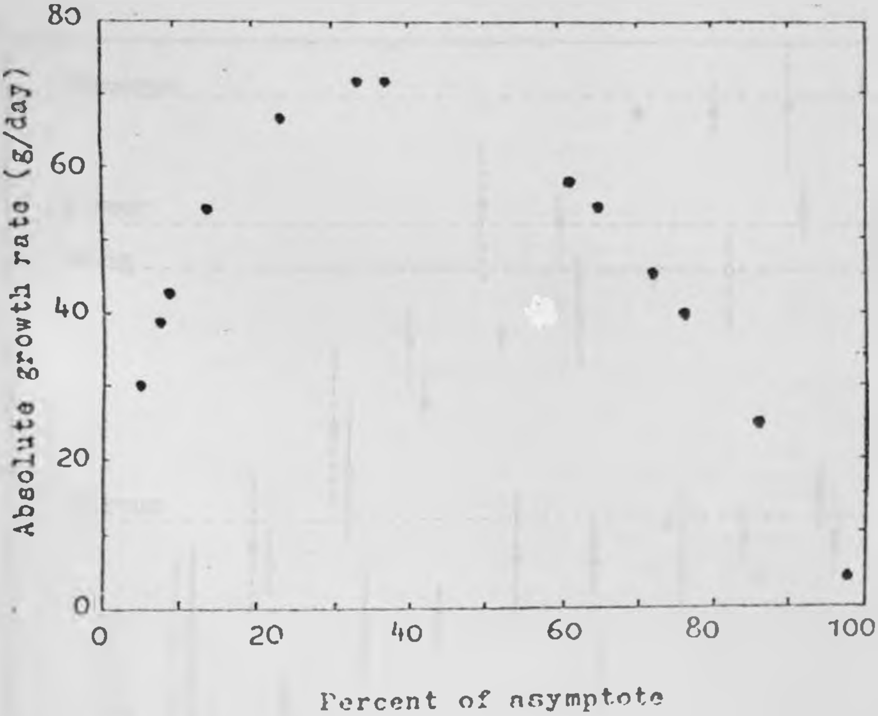


Fig. 8.3 The growth curves of body parts of nestling Fish Eagles in Queen Elizabeth National Park. Solid circles and dashed lines represent growth curve of humerus, adult size = 225 mm; open circles and solid lines represent growth curve of femur, adult size = 190 mm; solid circles and solid lines represent growth curve of tarsus, adult size = 110 mm; open circles and dashed lines represent growth curve of standard wing, adult size = 545 mm; circles represent means, and ranges are indicated.

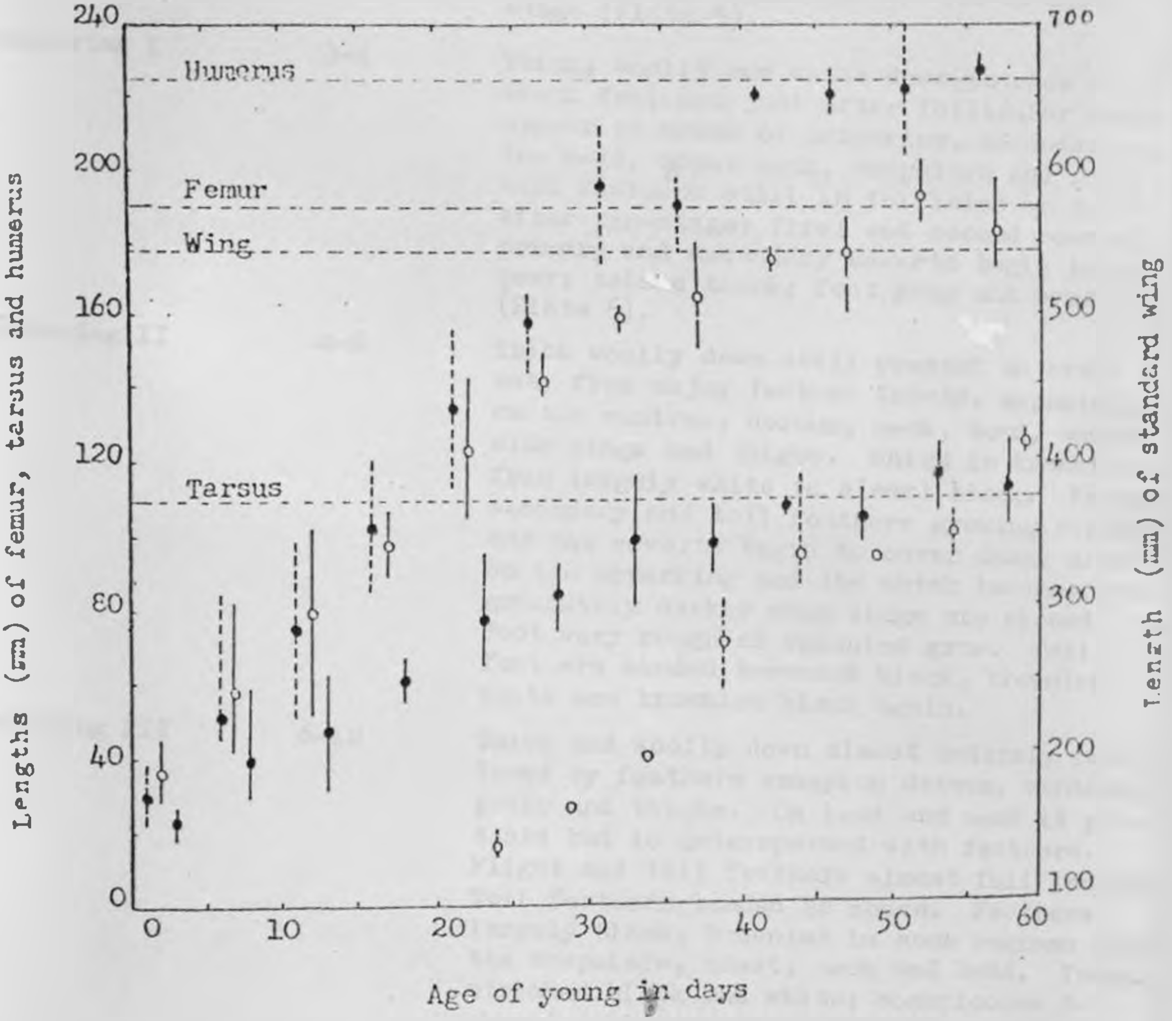


Table 8.7 Age criteria and plumage description of the nestling African Fish Eagle.

Age class	Age(weeks)	Plumage and other body part descriptions
Downy I	0–1	Sparse, light and white down; skin fleshy pink; bill dark grey; caruncle creamy white; cere light grey; eyes olive-brown; tarsus and talons pale fleshy pink; foot fleshy pink and smooth; chick propels itself by tarsi and wing tips.
Downy II	1–3	Thick, woolly and white down; bill dark grey; talons greyblack; foot grey and begi ning to roughen. Chick moves on tarsi at first then on the feet proper. Dark feather plugs of primaries, scapulars and forehead begin to appear by the end of this stage (Plate 5).
Feathering I	3–4	Thick, woolly and white down; patches of black feathers just after follicular stage appear in areas of primaries, secondaries, the head, upper neck, scapulars and rump; tail feathers still in follicles or just after pin-stage; first and second rows of primary and secondary coverts begin to appear; talons black; foot grey and rough (Plate 6).
Feathering II	4–6	Thick woolly down still present on areas away from major feather tracts, especially on the ventrum, dorsum, neck, head, underside wings and thighs. Chick in transitio from largely white to almost black. Primar secondary and tail feathers growing rapidly and the coverts begin to cover downy areas on the upperwing and the chick becomes progressively darker when wings are closed. Foot very rough as spicules grow. Tail feathers banded brownish black, brownish white and brownish black again.
Feathering III	6–10	Thick and woolly down almost entirely replaced by feathers exaepton dorsum, ventrum, groin and thighs. On head and neck it persists but is interspersed with feathers. Flight and tail feathers almost full length. Tail feathers banded as above. Feathers largely black, brownish in some regions like the scapulars, chest, neck and head. Young streaked black and white; conspicuous V-shaped collar of white area on chest and back just below the neck. Bill grey black; cere grey; eyes olive brown; tarsus pale flesy pink; talons grey black; foot with wel developed spicules (Plate 7). Young flies at end of this stage.

Plate 5. Downy young, age class II. Note the gaping bill of the chick due to panting and the remains of fish in the nest.

Plate 6. Feathering young, age class I.

Plate 7. The young of Fish Eagle Pair No. 6 (1975), one week after coming out of the nest, in its first year mottled black and white plumage.

Plate 8. A subadult Fish Eagle in its 3rd year plumage. Note the increasing whitening of the neck and chest. This is true also of the shoulders and back.

Plate 9. A late subadult African Fish Eagle in its 4th year plumage. Note the almost pure white head and chest.

ageing of the young are continuous processes which are difficult to divide into distinct stages.

8.3.4 Nestling mortality

At various stages during the fledging period some nestlings disappeared (Fig. 8.4). Chick losses were highest during the 1st and 2nd weeks after hatching, fluctuating minimally thereafter. During these two weeks alone, chick death accounted for 46% of all losses or for 17% of the total number of young (Table 8.8). Mortality was lowest among B/3 young, probably due to the small sample size, and highest but similar in the B/1 and B/2 broods (Table 8.8). Mean mortality, for the whole period, averaged only 0.53% per day (Table 8.8). Chick mortality, however, did not differ significantly with respect to brood size (Table 8.9).

Brood losses were due to disease/starvation and disappearance/predation (Table 8.10). From scratches on the nest tree a leopard was once suspected to have killed and eaten the 2 eight-week old chicks of Pair No. 86. In the remainder of the chick losses it was not possible to ascertain whether disease, starvation or predation were the causes of mortality. Olive Baboons <u>Papio anubis</u> which live on the southern bank of the study area and Vervet Monkeys <u>Cercopithecus</u> <u>aethiops</u> often climbed <u>Euphorbia</u> and other trees upon which Fish Eagles nest. Unidentified snakes and Monitor Lizards <u>Varanus</u> <u>niloticus</u> were found in nests and nest trees on several occasions.

Six nest trees blew down during rainstorms during this study but the nest mortality due to this cause could not be determined because the nest contents were not known. Badly built nest and

Fig. 8.4 Nestling mortality in the African Fish Eagle in relation to the age of the brood (open circles represent number of surviving young and solid circles the % mortality).

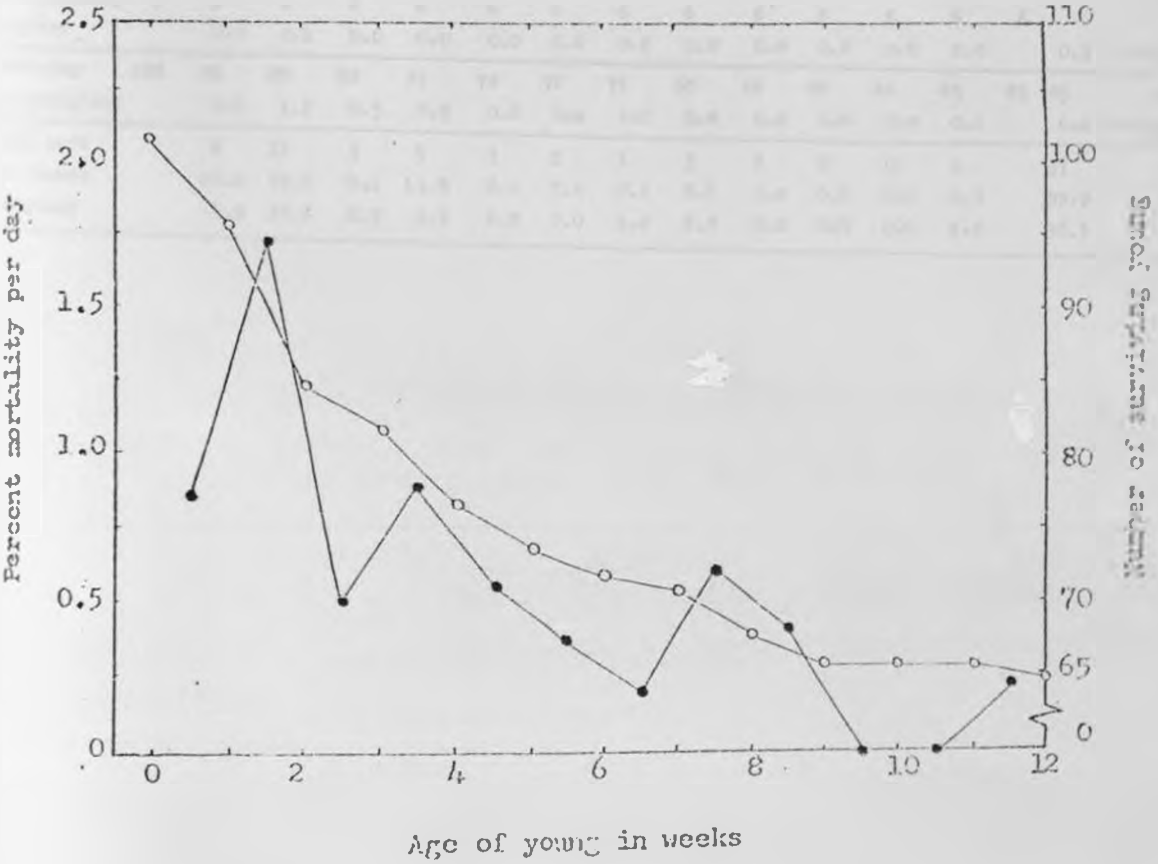


Table 6.8 Nestling mortality in the Fish Eagle in Queen Elizabeth Park by brood size in relation to the age of nestlin
Data from nests with known clutches. Calculations followed Ricklefs (1969a).

Age in weeks	0	1	2	3	4	5	6	7	8	9	10	11	12	13	Total	Mean ± SE
B/1 chicks surviving	23	22	21	20	17	16	16	15	14	14	14	14	14	14		
% mortality/day		0.6	0.7	0.7	2.3	0.9	0.0	0.9	1.0	0.0	0.0	0.0	0.0		7.1	0.59±0.24
B/2 chicks surviving	70	65	58	56	54	52	50	50	48	46	46	46	45	45		
% mortality/day		1.1	1.6	0.5	0.5	0.5	0.6	0.0	0.6	0.6	0.0	0.0	0.3		6.3	0.53±0.20
B/3 chicks surviving	9	9	6	6	6	6	6	6	6	6	6	6	6	6		
% mortality/day		0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0		0.3	0.025±0.08
Chicks surviving	102	96	85	82	77	74	72	71	68	66	66	66	65	65	65	
% mean mortality/day		0.9	1.7	0.5	0.9	0.6	0.4	0.2	0.6	0.4	0.0	0.0	0.2		6.4	0.53±0.20
Total chicks lost		6	11	3	5	3	2	1	3	2	0	0	1		37	
% of total losses		16.2	29.7	8.1	13.5	8.1	5.4	2.7	8.1	5.4	0.0	0.0	2.7		99.9	
% of total young		5.9	10.8	2.9	4.9	2.9	2.0	1.0	2.9	2.0	0.0	0.0	1.0		36.3	

Table 8.9 The numbers of nestling Fish Eagles lost by brood size in relation to the numbers hatched. Data from known clutches only, April 1975 - March 1978.

	Brood size			
	B/1	B/2	B/3	Total
No. of young hatched	23	70	9	102
No. of young lost	9	25	3	37
Total	32	95	12	139

$X^2 = 0.057$ NS (df = 2)

Table 8.10 The probable causes of Fish Eagle nestling mortality by brood size for known clutches, April 1975 - March 1978.

	Brood size				Percent of	
	B/1	B/2	B/3	Total	Chicks	losses
N(eggs hatched)	23	70	9	102	-	-
Mortality factor						
Starvation/disease	1	7	0	8	7.8	21.6
Disappearance/predation	8	18	3	29	28.4	78.4
Total losses	9	25	3	37	36.3	100.0
% of hatchlings	39.1	35.7	33.3	36.3	-	-
% of all losses	24.3	67.6	8.1	100.0		

those built on insecure trees caused 5 out of the 202 breeding attempts to fail; and again nest contents were not known. One type of fly Stomoxys sp. sucked the blood of feathering young but was not observed feeding on the downy chick. The effects of its blood-sucking habit on the nestling mortality of the Fish Eagle was not studied.

8.4. DISCUSSION

The increase in weight of an organism results in a growth curve which can be described by its magnitude (i.e. the proportion of adult weight attained with the age of the young), the form of the curve, and its average rate of increase (Ricklefs 1968a). The average rate of increase of the curve for all species of birds can be calculated by one of the following equations: logistic (Robertson 1923), Gompertz (Laird, et al 1965) and von Bertalanffy (von Bertalanffy 1960). Ricklefs (1968a) further found that large and more slowly growing species of birds show a preponderance of Gomperts- and von Bertalanffy-type growth curves. In this study the growth curve of the African Fish Eagle was best fitted by the Gompertz equation probably because it is a large and slow growing bird.

Nestling Fish Eagles fledged at weights higher than those of adults. The ratio of the asysmptote of the growth curve to the adult body weight (Ricklefs, op cit.) averaged 1.07. In some raptors like the Golden Eagle Aquila chrysaetos, Screech Owl Otus asio and Snowy Owl Nyctea scandiaca this ratio is below 0.9 (Ricklefs, op cit.). In small land birds this ratio is important in demonstrating whether or not a bird feeds on the ground, aerially, from among foliage or from a perch. A ratio of 1.0 or higher indicates that the bird's flight locomotory apparatus is well developed and that hunting by flight is an important means of obtaining prey (Ricklefs, op cit.). The rather high ratio, although based on few adult weight records, would similarly indicate that hunting by flight is an important method of securing prey in the Fish Eagle. However, the Fish Eagle hunts mostly by sitting on perches and watching the water for prey (section 4.3.2.1). Fish Eagle young should, therefore, have exhibited a ratio similar to those of the Golden Eagle and Screech and Snowy Owls. Perhaps the rather high ratio is a result of high amounts of reserved fat.

The growth curve of the Fish Eagle was best fitted by the Gompertz equation (Laird, et al. 1965). This is in agreement with Ricklefs' (op cit.) finding that large and more slowly growing species of birds show a preponderance of Gompertz- and von Bertalanffy- type growth curves.

The overall growth rate, K, of the nestling was quite low, averaging 0.077 g/day. It is similar to the growth rate of the Golden Eagle (Table 8.5), yet the Golden Eagle is 1.8 times heavier than the Fish Eagle. Temperate passerines and raptors generally grow more rapidly than tropical species, and they raise more than two young per brood (Ricklefs 1968a & 1976). The Golden Eagle (Brown 1976b & c, Snow 1973b) and the Fish Eagle (Brown 1970a, 1976b & c) lay similar clutches and raise less than 1 young per pair. Despite their generic differences the similarities in their growth rates could have arisen because the smaller tropical Fish Eagle grew more slowly than the much larger temperate Golden Eagle. However, similar data from the genus Haliaeetus are not available for comparison.

The time needed to complete growth from 10-90% of the asymptote in most raptors ranges from 16.7-32.9 days (Ricklefs, op cit.). From clutch size and fledging period given by Brown (1960), Ricklefs estimated that the t_{10-90} for the Fish Eagle was 40 days and that for the Bald Eagle 43 days.

The t_{10-90} of the Fish Eagle during this study ranged from 29.2-57.6 days, averaging 41.8 days (Table 8.1). Using the mean fledging period of 76 days (section 11.3.1) the t_{10-90} is 43 days. There is, therefore, agreement in this growth rate of the Fish Eagle of this study and that of the Winan Gulf, L. Victoria. This growth rate of the Queen Elizabeth Park Fish Eagle is also similar to those of the other members of the genus *Haliaeetus*, particularly to that of *H. leucocephalus* (Table 8.6).

Several families of birds show sexual dimorphism in adult body weights, and in the families *Accipitridae* and *Icteridae* some members exhibit sexual dimorphism in their growth patterns (Ricklefs, op cit.). In Cooper's Hawk *Accipiter cooperii* and the Red-tailed Hawk *Buteo jamaicensis* the smaller males grow faster than the females (Ricklefs 1968a & 1976). During this study the Fish Eagle also showed dimorphism in the growth rates of the sexes with the smaller male growing significantly faster than the female (Table 8.4). Only in the sexually dimorphic Golden Eagle did the sexes grow at the same rates (Table 8.5). Using weights gained by chicks without calculating the actual growth rates Brown (1976c) wrongly concluded for raptors generally that female chicks, which when adult might be twice heavier than males, grew faster.

The absolute growth rate (g/day) of the chick (Fig. 8.3) was rapid during the early part of the fledging period, reached a maximum at the inflection point and then decreased until it was almost zero at the time the eaglet left the nest. The inflection point was reached at about a third of final weight and this agrees with Ricklefs' (1968a) finding that growth rates fitted by the Gompertz equation have their inflection points at about 37% of the asymptote.

The tarsus, femur and humerus were fully grown between 55 and 60 days of age (Fig.8.3), 2-3 weeks before the mean fledging period of 76 days. It is important that these parts, especially the tarsus and femur, reach adult sizes before fledging because of the bird's method of feeding. From about 50 days of age till independence, the young feeds itself by tearing pieces of flesh from prey delivered by one of the parents (section 9.3.5.2). It is, therefore, imperative that the young developed the bones and, probably, muscles which help it during feeding prior to leaving the nest.

The standard wing was only 75% of the adult size when the young fledged (Fig. 8.3) and its slower rate of development probably explains why there is minimal and clumsy flying by the bird immediately after fledging. However, it must have reached adult dimensions during the post-fledging period, a time during which the eaglet was still fed and protected by the parents. By the time the nestling fledged, its standard wing was only 69-87% of the adult measurements (469-595 mm) given by Mackworth-Praed & Grant (1952). Since one of the most important wing bones, the humerus, had already achieved full growth by fledging time, the standard wing probably did not because of the flight feathers not attaining adult dimensions by this time.

As an adaptation to life in open nests, chicks of snake eagles (Circaetinae) and the Bateleur <u>Terathopius</u> <u>ecaudatus</u> grow feathers first on the dorsum, and the heads and wings become feathered before the under-sides. This mode of feather development has been shown to protect the nestlings against heat stress (Brown 1976b). Fish Eagles were also reared in open nests and their feathering sequence conformed to the same trend. However, the role played by this mode of feather development in the protection of young against heat remains to be studied. Nestlings were shielded from heat and rain by their parents and otherwise avoided heat stress through thermoregulatory behaviour (section 9.3.1).

Ricklefs (1969a) quoted the following factors as causes of mortalities among birds: hatching failutre due to infertility, death of embryo and death during hatching, brood parasitism, nest infestation by arthropods, competition for nest sites in adults, adult mortality, desertion, starvation, predation and inclement weather. Brood losses during this study were due to disease or starvation and disappearance or predation. Predation is thought to be a negligible mortality factor in raptorial birds becuase of the capabilities of both young and adults to defend themselves and their nests (Ricklefs, op cit.). Although predation on nestling Fish Eagles was not observed, it was still suspected as the cause of most chick losses. From scratches on the nest tree a leopard *Panthera pardus* was once suspected to have killed and eaten the 2 eight-week old chicks of Pair No. 86. In the remainder of the losses, it was not possible to ascertain whether disease, starvation or predation were the causes of mortality. Primates have been increasingly shown to be partial carnivores despite their being largely vegetarian (Van Lawick-Goodall 1971, T. Butynski, pers. comm.). Olive Baboons *Papio anubis* (Rowell 1966 & pers. domm.) and Vervet Monkeys *Cercopithecus aethiops* (Struhsaker 1967 & pers. comm.) have all been known to supplement their vegetatian diets with animal matter. These species, all of which have been observed climbing nest and other trees in the study area, could have been responsible for some of the Fish Eagle egg and chick disappearances. The Monitor Lizard <u>Varamus</u> <u>niloticus</u>, a scavenger with predatory tendencies (Edroma & Ssali 1983, G. Laker-Ojok, pers. comm.) and unidentified snakes, both found in nest trees, probably contributed towards some of the egg and nestling martalities.

Predation and inclement weather are alike in their effects on nesting mortalities in that they usually result in destructions of whole clutches and broods and they can occur at any point in the nesting period (Ricklefs 1969). During this study six nest trees blew down during rainstorms, but the mortality due to this cause could not be determined because the nest contents were not known.

Badly built nests and those sited in insecure trees are significant causes of poor nesting success among eagles in general (Brown 1970b). In Embu District, Kenya, badly built nests was the major cause of breeding failure in the Ayre's Hawk Eagle <u>Hieraaetus</u> <u>dubius</u>. These two mortality factors caused 5 out of 202 Fish Eagle breeding attempts in this study to fail. Because the nest contents were not known, their effects on egg and chick losses could not be ascertained.

Blood-sucking flies were responsible for the deaths of seven out of 15 Red-tailed Hawk <u>Buteo</u> <u>jamaicensis</u> chicks in California in a year (Fitch <u>et</u> <u>al</u>. 1946). One type of biting fly <u>Stomoxys</u> sp. sucked the blood of feathering young Fish Eagles but was not observed feeding on downy chicks. The effects of the blood-sucking habit of the fly on nestling mortality in the Fish Eagle was, however, not studied.

Lack (1954) emphasized asynchronous hatching and selective starvation as being common features of raptorial nesting behaviour. Starvation can be suspected as a cause of mortality when mortality rates are greater during the nestling than the egg periods and when within-brood losses are high (Ricklefs, op cit.). From Brown's (1960) data Ricklefs (1969a) calculated that the Fish Eagles of Winam Gulf, L. Victoria, lost young 8 times more rapidly than eggs, thus suggesting that starvation was a significant factor in the losses of the young. In Alaska the Bald Eagle had a lower nestling mortality rate of 0.65% per day than the egg mortality rate, 1.27% per day (Hensel & Trover 1964). In Montana the Golden Eagle also had a lower chick mortality rate than that experienced by the egg, i.e. 0.28% and 0.58% per day respectively (McGahan 1960). During this study asynchronous hatching and selective starvation were observed (Sumba & Pomeroy, In press & section 9.3.5) but the chick mortality rate of 0.53% per day was lower than that of the egg, 0.74% per day. Furthermore, when starvation plays a prominent role in nestling survival mortality rates increase continuously during the nestling periods as the young grow in size and require energy at more rapid rates as for many species of marsh-nesting icterids (Petersen & Young 1950, Young 1963). In this Park, the findings that Fish Eagle nestling mortality was lower than egg mortality and that nestling mortality decreased with the age of the young clearly suggest that starvation was probably unimportant in the observed nestling mortalities.

CHAPTER 9

BEHAVIOUR OF THE NESTLING

9.1 INTRODUCTION

The behaviours exhibited by the nestling Fish Eagle depended on the situations to which it was exposed. Thus, the day to day weather conditions, and disturbances by man and other animals and competition for parental care, especially feeding, elicited different reactions which seemed of survial value to the growing chick.

9.2 METHODS

9.2.1 Nest behaviour

The sleeping and resting times of the young were not measured. However, the time spent by the young of Pair No. 6 (1975) at the nest edge as they matured was recorded. This was done by noting, to the nearest minute, the time the chicks moved to and from the nest edge and expressing it as a percentage of the observation time. The prevailing weather conditions during observations were recorded.

9.2.2 Panting

Panting in the Fish Eagle occurs in both young and adults. It consists of the bird rapidly inflating its lungs with its bill agape. The tongue is usually lifted clear of the floor of the lower mandible and pushed forward (Plate 5).

Panting was observed in the 11-week old chick of Pair No. 6 from 07:30-19:30 on 26 September 1975. Only the larger chick (C_1) of the 2-young brood was observed. The duration of panting was recorded as the time when the chick opened its bill, in the typical panting manner, and when it closed it. For each hourly interval the time the bird panted was recorded and panting duration expressed as a percentage of the respective hourly intervals.

9.2.3 Defaecation

The method the chick used in defaecating and the distance from the nest floor, the watery faeces were discharged were noted as the young matured. The distance the stream of faeces was discharged was noted in qualitative terms as a) in the nest floor, b) on the nest rim and c) outside the nest.

9.2.4 Interspecific behaviour

Any reactions of attraction, indifference, fear and aggression on the part of the nestling towards human being on the nest were recorded whenever weight and other body measurements were being taken. Similar observations were made of their reactions to other birds on the nest or flying past and to animals walking or grazing below.

9.2.5 Intraspecific behaviour

In 2- or 3-young broods intraspecific interactions were largely sibling aggression in which the older chick showed overt aggression towards the younger chick (s). For this reason sibling aggression was studied in detail, especially with respect to its effects on the feeding behaviour, growth patterns, and survival of the young.

The effects of sibling aggression on the physical and behavioural development of the young were observed in all accessible nests, but most closely in those of Pairs No.6 and 82. The feeding pattern was assessed by recording the number of morsels each chick received and observing the feeding behaviour and the food proffering sequence during each meal. Fledging successes for C_1, C_2 and C_3 were calculated from 52 nests whose contents were known at hatching. Ten of these nests were accessible for measurements and closer observations of the young for signs of sibling strife.

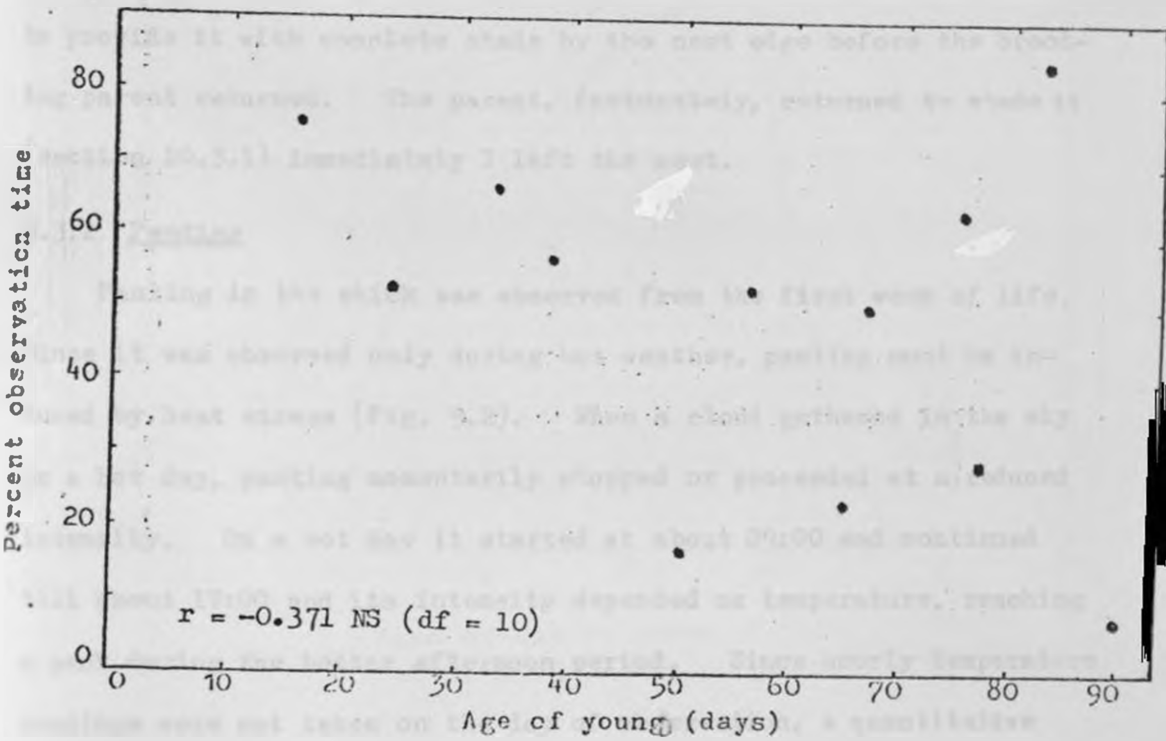
9.3 RESULTS

9.3.1 Nest behaviour

During the downy stage, when a nestling was uncovered it slept and rested for considerable periods of time. The resting posture consisted of lying on the tarsi and belly with the head laid down to one side or propped up and directed straight forward and the stumpy wings half opened. Nestlings also lay on their sides with the upper legs. The talons of such legs were normally fully opened. Gradually the nestling became more and more active; it crawled about the nest floor largely on its tarsi while occasionally being supported by the wing tips as it moved.

Chicks lay in one of two positions in the nest; on the nest floor or at the edge. Nestlings of all ages moved to the nest edge to rest although the time spent at the nest edge was not significantly correlated with age (Fig. 9.1). Whenever a downy young was left exposed by the brooding parent, and there was strong sunshine, it crawled away from the centre of the nest. Older young, in the feathering and feathered stages, also moved to the nest edge during the hot periods of the day. Although there was no significant correlation between movement to the nest edge and the age of the young, the gradual reduction in the amount of time spent at the nest edge with maturity might be due to the increasing capability of the young to thermoregulate its body heat. Exposed as nests normally are (section 5.3.1),

Fig. 9.1 Percent of observation time the older young (C_1) of Fish Eagle Pair No. 6 (1975) spent at the nest edge as a function of its age. Total observation time = 53.08 hours.



it was not unusual to record nest floor temperatures of 40° to 45° C while the corresponding values for the nest edge were 32° to 37° C. The following observation illustrates what probably happened often in nests in this Park:

> 28 November 1975, a very hot day, at about 11:30 an unusaually high nest floor temperature of 51.0° C was recorded in nest of Pair No.3, the corresponding nest edge temperature was only 32.5° C. The only chick in the nest, about two days old, called incessantly when momentarily placed in the nest floor and struggled to the nest edge in the shade of a leafy branch where it immediately stopped calling. It panted heavily both at the nest edge and in the nest floor.

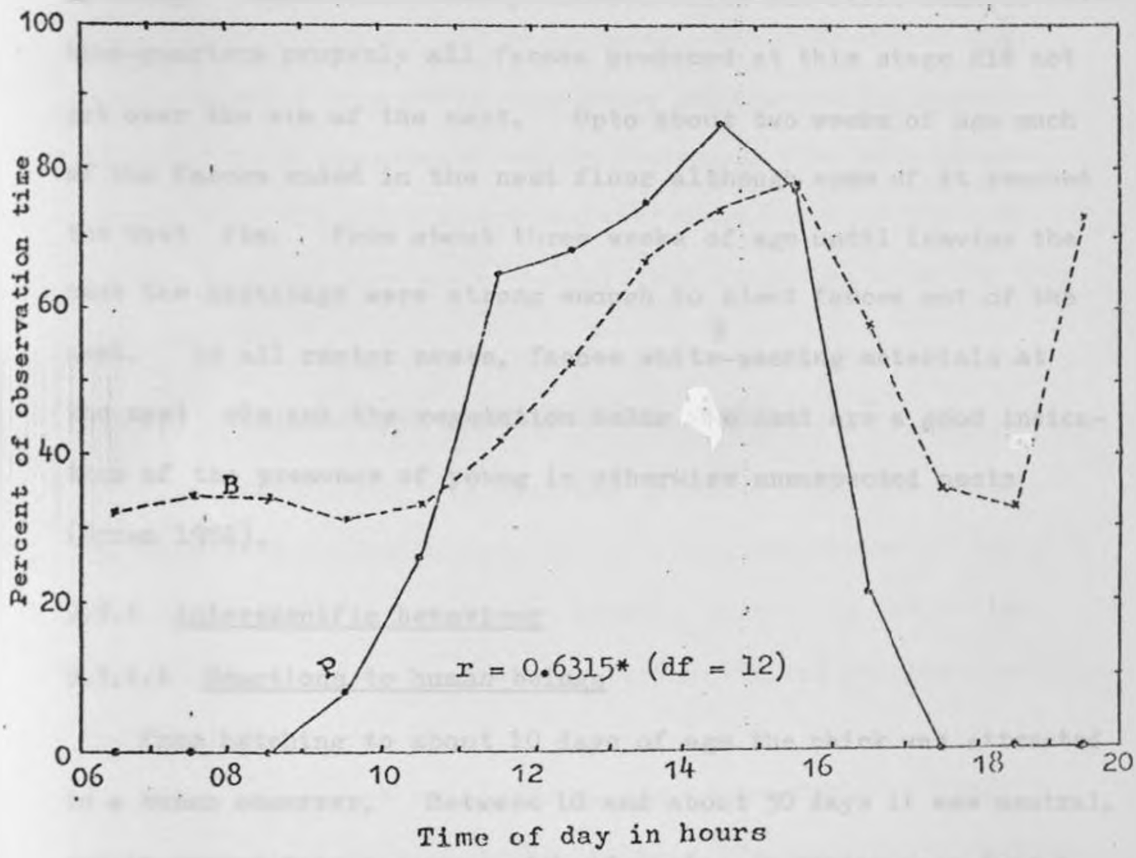
During measurements, care was taken not to expose it to the excessive heat of the floor. Additional leafy branches were used to provide it with complete shade by the nest edge before the brooding parent returned. The parent, fortunately, returned to shade it (section 10.3.1) immediately I left the nest.

9.3.2 Panting

Panting in the chick was observed from the first week of life. Since it was observed only during hot weather, panting must be induced by heat stress (Fig. 9.2). When a cloud gathered in the sky on a hot day, panting momentarily stopped or proceeded at a reduced intensity. On a hot day it started at about 09:00 and continued till about 17:00 and its intensity depended on temperature, reaching a peak during the hotter afternoon period. Since hourly temperature readings were not taken on the day of observation, a quantitative relationship between panting and temperature could not be established. However, the panting behaviour of the nestling and the brooding behaviour of adults were significantly correlated (Fig. 9.2).

During panting the chick lost a clear salty fluid from its beak. This liquid probably originated from a pair of nasal

Fig. 9.2 The panting behaviour of an eleven week old nestling Fish Eagle as observed on 26.9.75. P = Panting behaviour of young; B = mean brooding behaviour of parents as in Fig. 10.1.



salt glands which the Eagle possesses (Cunningham van Someren, pers. comm.).

9.3.3 Defaecation

The chick defaecated in a characteristic posture, with the hind-quarters elevated and the fore-quarters depressed. With the cloaca raised, a stream of whitish fluid was squirted, usually well out of the nest. This mode of defaecation was exhibited right from hatching. Because the newly hatched chick was still weak to raise its hind-quarters properly all faeces produced at this stage did not get over the rim of the nest. Upto about two weeks of age much of the faeces ended in the nest floor although some of it reached the nest rim. From about three weeks of age until leaving the nest the nestlings were strong enough to eject faeces out of the nest. In all raptor nests, faeces white-washing materials at the nest rim and the vegetation below the nest are a good indication of the presence of young in otherwise unsuspected nests (Brown 1976).

9.3.4 Interspecific behaviour

9.3.4.1 Reactions to human beings

From hatching to about 10 days of age the chick was attracted to a human observer. Between 10 and about 30 days it was neutral, and it showed fear responses like freezing or moving away from a human being between 30 days of age and leaving the nest. A few days prior to flight, however, it became aggressive and threatened any human observer in the nest as evidenced below:

> At 59 days of age, on 21/2/77, the only chick of Pair No. 82, lying by the nest edge, was approached for measurements. As soon as it saw me it jumped from the far end of the nest in a typical spreadengled threatening attitude. It stopped

> right in front of me, the eyes glaring, the feet outstretched with the talons spread out, the wings half-opened, the mouth gaping as if ready to bite, and the bird reared as if it was going to fall on its back. I retreated down the ladder and it went back to the very place it had been lying. A second climb up the nest did not elicit any further aggression but it was difficult to dislodge for it held strongly onto nest materials with its talons and bill. Clear signs of fear were then displayed. Three days later, when I came to ring it and take additional measurements, the eaglet flew away, probably prematurely.

Several eaglets were handled during the last stages of their fledging periods and no problems were encountered with them. Most of them froze when being approached for measurements but a few threatened before freezing. In such circumstances they bit and taloned whatever came close to the head and the feet and they made high-pitched squeaking cries as they were handled.

9.3.4.2 Reactions to other birds and animals

The reactions of the nestling to other birds and animals can only be described generally and non-quantitatively, and only for young not being brooded or closely guarded by the adults. When adults were on the nest few birds alighted or flew close (section 10.3.2).

Many species of small birds, e.g. House Sparrows Passer domesticus. weavers (Ploceidae), bulbuls (Pycnonotidae), sunbirds (Nectariniidae), kingfishers (Alcedinidae) and canaries (Fringillidae) alighted on Fish Eagle nests, with or without young, when the adults were not around. They picked up pieces of prey and nesting materials like grass and feathers from the eyries. Downy chicks were indifferent to all these birds, none of which molested them. Feathering and feathered young watched them with interest as they jumped about but did not drive them away. When large birds like kites *Milvus* spp., crows *Corvus* spp., vultures (Accipitridae), Marabou Storks *Leptoptilos crumeniferus*, pelicans *Pelecanus* spp., and Egyptian geese *Alopochen aegyptiacus* flew past or circled above the nest downy young remained unperturbed, but large chicks froze. Normally large chicks appeared attracted by their parents soaring above them.

Only large young exhibited interest in large animals grazing below or walking past the nest trees, and they showed no signs of fright. Encounters between tree-climbing animals and young were not witnessed.

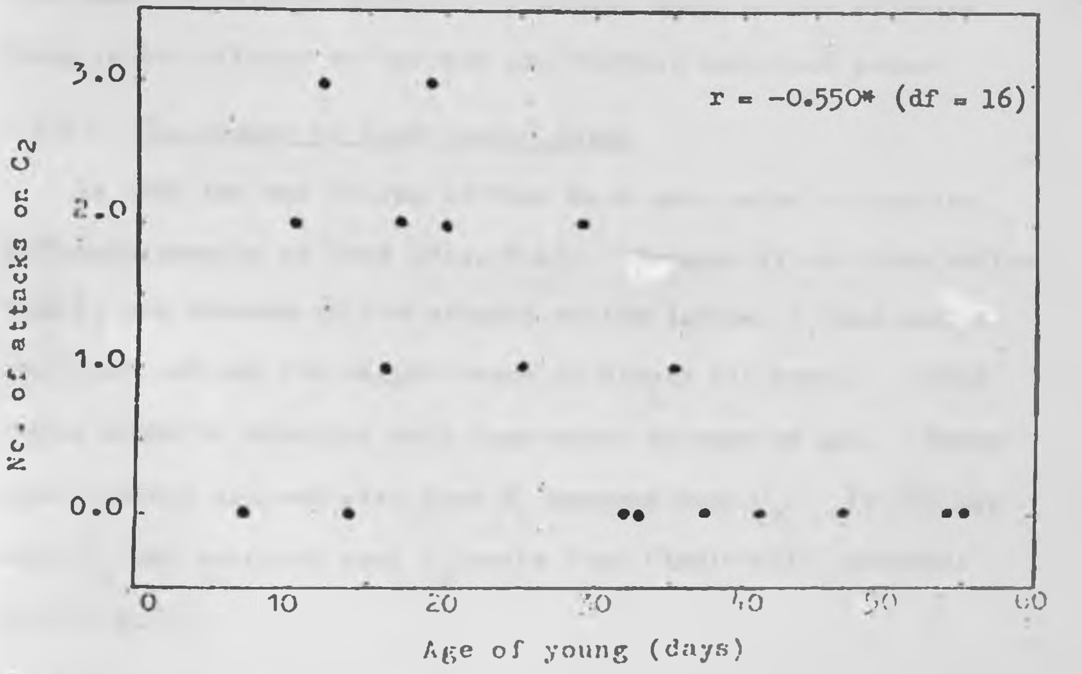
9.3.5 Intraspecific behaviour (sibling aggression)

In the Fish Eagle one of the most fascinating behaviours of nestlings was sibling aggression. It was suspected to be one of the most important nestling mortality factors because it occurred in all broods with more than one young.

Because of the asynchronous hatching of eggs (section 7.3.10) by the time the second (C_2) and third (C_3) chicks hatched the oldest young (C_1) was already strong and aggressive towards them. Overt aggression only occurred during the first 30 days or so of the brood's life, the correlation between numbers of attacks and the age of the brood being significant (Fig. 9.3). From then on the younger chick successfully resisted further attacks of the older brood-mate.

During the early part of the fledging period C_1 attacked and tore the head and/or back of its sibling. Siblings with wounded heads and/or backs were recorded in 6 out of the 10 accessible nests, and the effects of this aggression on the physical and behavioural

Fig. 9.3 The relationship between the numbers of attacks the younger sibling (C_2) of Fish Eagle Pair No. 6 (1975) received from the elder young (C_1) during sibling aggression and the age of the brood.



development of siblings are described in Tables 9.1 & 9.2. The elder young showed aggression towards the younger chick both in the presence and absence of the parents, and when the adults were present they were unconcerned as the young fought. The nestlings also fought during both feeding and non-feeding periods. The repeated attacks resulted in the younger nestling withdrawing on C_1's approach, and in the chicks eating different amounts of food.

The effects of sibling aggression on the survival of the brood and the related adaptive behaviour shown by the affected young in its efforts to survive are further described below:

9.3.5.1 The number of food pieces eaten

In 1975 the two chicks of Pair No.6 were noted to receive different amounts of food (Fig. 9.4). Because it was more active than C_2 and because of its attacks on the latter, C_1 was usually fed first and had the bigger share in almost all meals. Their shares began to equalize only from about 40 days of age. Every time a parent arrived with food C_1 knocked down C_2. It was not until C_1 was satiated that C_2 could feed (Table 9.1; records: 22.7-13.8.75).

9.3.5.2 Feeding strategies

Having survived up to about 30 days of age, C_2 effectively resisted the attacks of C_1 and henceforth, was rarely attacked. Both chicks then employed different strategies in securing the larger share at each meal. They took advantageous positions during feeding times, usually by being very near to the feeding parent. Thus, pieces of food destined, say, for C_1 could be grabbed by C_2, and vice versa, before the farther chick had got it.

Table 9.1 The effects of sibling aggression in a 2-chick brood (Pair No. 6) on the feeding behaviour of the nestlings. Age refers to that of C1.

Date	Age (days)	Attacks on C$_2$	Comments
22.7.75	7	0	Female feeding; chicks slow at eating; 34 morse to C$_1$ and only 3 to C$_2$.
25.7.75	10	2	Female feeding; chicks slow; C$_1$ ate 52 morsels and C$_2$ 6 morsels; C$_2$ withdrew after second attack.
27.7.75	12	3	Female feeding; C$_1$ ate 32 morsels and C$_2$ 11 morsels; C$_2$ withdrew after third attack.
29.7.75	14	0	Female feeding; chicks on either side of parent C$_1$ swallowing morsels faster than C$_2$; C$_1$ ate 73 morsels and C2 45 morsels.
31.7.75	16	1	Female feeding; C$_2$ withdrew to side of parent. Order in which morsels were offered C$_1$: 42.1.1.1.22.25 (92 morsels) and C$_2$: 4.7.8.6.0 (25 morsels).
1.8.75	17	2	Female feeding; C$_2$ withdrew when assaulted twice before start of feeding; tiny remains of fish; C$_1$ ate 43 morsels and C$_2$ none.
3.8.75	19	3	Female feeding; C$_1$'s crop full; C$_2$'s crop not showing and withdrew after third attack. C$_1$ at 86 morsels and C$_2$ 11 morsels.
4.8.75	20	2	C$_1$ full crop; C$_2$ crop not showing; C$_2$ resisted attacks and tore morsels from prey as parent held it. C$_1$ ate 97 morsels and C$_2$ ate 6 self-fed morsels.
9.8.75	25	1	Female feeding; C$_2$ withdrew after attack at start of feeding but fed after C$_1$ was satiated and wandering about; C$_1$ ate 86 morsels and C$_2$ 29 morsels.
13.8.75	29	2	Female feeding; C$_2$ withdrew after second attack, fed when C$_1$ was satiated and wandering about; C$_1$ ate 76 morsels and C$_2$ ate 21 morsels.
16.8.75	32	0	Female feeding; alternate feeding sequence C$_1$: 47.6 (53) & C$_2$: 7.13 (20); adult between young but C$_1$ nearer adult; C$_2$ tore some morsels from prey as parent held it.

Cont'd

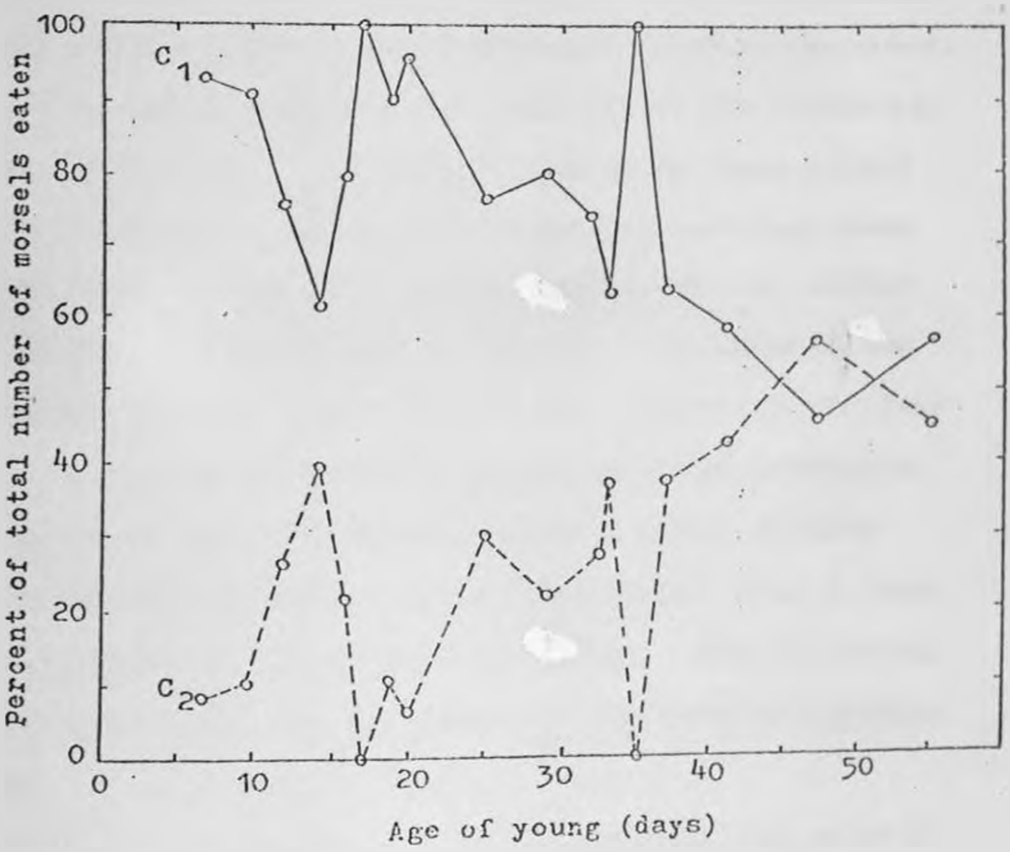
Table 9.1 Cont'd

Date	Age (days)	Attacks on C_2	Comments
17.8.75	33	0	Female feeding; alternate feeding sequence C_1: 18.14.17.2.18.0 (69 morsels) and C_2: 4.10.8.9.10 (41 morsels); competitive feeding but C_1 nearer adult; C_2 tore morsels as parent held down prey.
19.8.75	35	0	C_2 self-feeding on remains of prey; C_1 unconcerned.
		1	Female feeding; C_2 withdrew after attack; remains of bony head part of Clarias sp. C_1 ate 22 morsels while C_2 ate none.
21.8.75	37	0	Female feeding; C_1: 8.13.5.9.16.12.10 (73 morsels) and C_2: 10.11.6.4.5.3.5 (44 morsels); competition between young.
			C_2 self-fed on 25 morsels torn from prey as parent held it down.
25.8.75	41	0	Female feeding; chicks competitive; C_1: 8.10.9.16.13 (56 morsels) and C_2: 6.12.9.12.2 (41 morsels).
			C_2 self-fed on 30 morsels which it tore for itself from prey which it struggled to hold down; feeding done in presence of parent.
31.8.75	47	0	Female feeding; chicks highly competitive (twice pulled at same morsels); C_1: 3.12.4.6.3 (24 morsels) and C_2: 5.17.4.2.3 (31 morsels).
7.9.75	54	0	C_2 self-feeding in absence of parent; ate 11 morsels from dry remains of prey which it struggled to hold down.
8.9.75	55	0	Female feeding; stiff competition between young; C_1: 3.5.11.15.12.2 (48 morsels) and C_2: 4.6.11.10.3.2 (36 morsels).
			Self-feeding during presence of adult; tiny remains of prey, each chick tore morsels for itself; C_1 ate 7 morsels and C_2 ate 13 morsels.
			C_2 self-fed on 30 morsels before offering 3 morsels to C_1 after prolonged begging by C_1; feeding done in absence of adult.
			Female feeding; stiff competition between young; C_1: 2.7.11.14.7.8.9 (59 morsels) and C_2: 3.4.6.11.10.8.7 (49 morsels).
17.9.75	64		Parent brought prey and the young fed themselves; first young to grab prey fed until satiated.

Table 9.2 The physical and behavioural developments of C_1 and C_2 (Pair No. 82) in the early part of brood life in relation to sibling aggression.

Date	Age(days)		Weight (g)		Food remains	Comments
	C1	C2	C1	C_2		
28.12.76	3	1	120	84	Tilapia sp. (200g)	Crop of C_1 fuller than of C_2; both chicks active.
30.12.76	5	3	182	128	Tilapia sp. (142g)	Head of C_2 wounded; bill marks and blood clots indicative of sibling aggression.
31.12.76	6	4	212	126	Bagrus sp. (110g)	C_1 active and healthy, crop very full; C_2 aggressed and head still with fresh wounds.
					Tilapia sp. (410g)	Area of wound on C_2's head increasing, withdrawal behaviour intense, crop empty (hand-fed 18g morsels of fish), C_2 emaciated compared with healthy C_1.
3.1.77	9	7	334	138	Haplochromis sp. (50g & 20g)	C_1 strong and healthy, crop full; C_2 weak and thin, crop empty (hand-fed 20g morsels), bare head still extending; intense withdrawal behaviour on C_1's approach.
6.1.77	12	10	560	150	Tilapia sp. (40g)	C_1 active and healthy, crop full; C2 very weak, crop empty (hand-fed 26g morsels), head badly wounded, withdrawal behaviour more intense.
9.1.77	15	13	790	320	-	C_1 active and healthy, crop full; C_2 regaining strength, wounded head healing, crop full.
11.1.77	18	-	865	-	Tilapia sp. (120g)	C_1 active and healthy, crop full; C_2 disappeared without trace.

Fig. 9.4 The percent of total morsels eaten by each nestling in a 2-young brood of African Fish Eagle Pair No. 6 (1975). The disparities in amounts of food eaten were due to sibling aggression in the species (see text). C_1= older young, and C_2 = younger sibling.



The young nearer the feeding parent, therefore, ate many more morsels than the other (Table 9.1; records: 16-31.8.75).

The second strategy the competing chicks employed was to supplement their number of morsels by self-feeding (Table 9.1; records: 4-25.8.75). Here, as the feeding parent held down the prey the chick getting fewer morsels tore for itself pieces from the prey. This behaviour was first noted when the young of Pair No.6 were about 3 weeks old and C_2 regularly did so.

A third method was for the young to feed themselves when food was available, usually in the absence of any of the parents. The chick simply held the prey and tore pieces from it for itself. This type of feeding appeared by the 35th day of life (Table 9.1; records: 19.8-7.9.75). During such feeding the young without prey begged and chased the one with it and both nestlings moved round and round the nest, with the one holding the prey walking as if wearing an oversized boot on one foot. Occasionally the chick without the food item grabbed it and a tug-of-war with legs ensued. Fragile prey once broke and separated the contestants. Such tugs-of-war were rare because the chick holding the prey often successfully defended it by half-opening the wings to cover it and by threatening the approaching sibling. When threatened, the brood-made resorted to begging rather than forcefully staking a claim.

Competitive feeding appeared between nestlings from about 30 days of their life, the time when C_2 successfully resisted the assaults of C_1. During such feeding fast swallowing of the pieces of flesh profferred by the parent was important; the average time taken per morsel by two nestlings being significant in relation to their age (Fig. 9.5). Any chick that took morsels from the parent's bill and swallowed them fast drew the feeding

Fig. 9.5 The time taken by a 2-young brood of Fish Eagle Pair No. 6 (1975) to swallow pieces of food proffered to them by one of the parents.

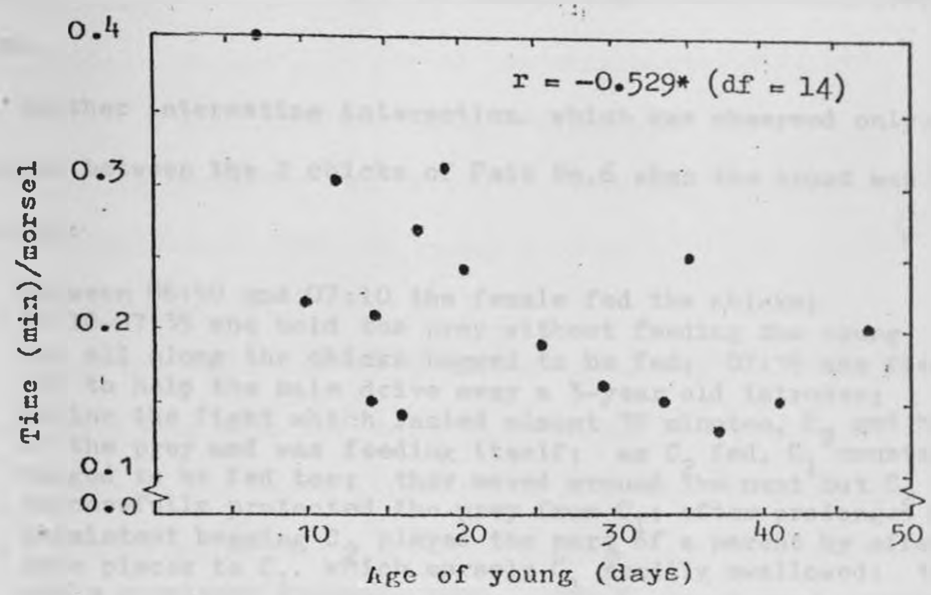
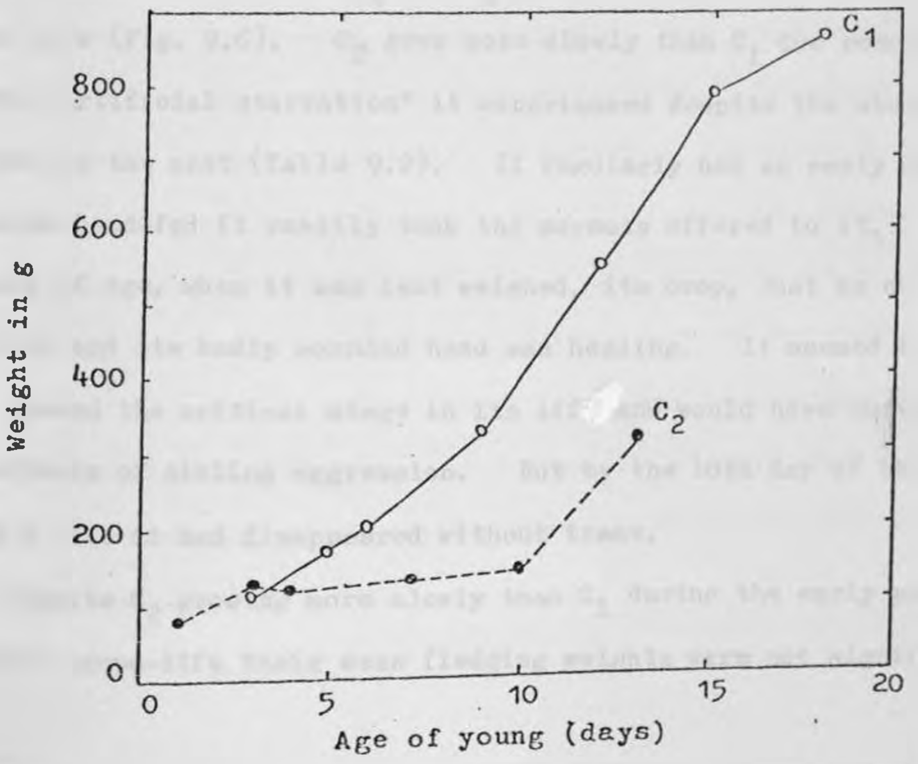


Fig. 9.6 The growth curves of 2 young of Fish Eagle Pair No. 82 in the early part of the nestling period. C2 disappeared on the 18th day of the brood's life.



attention of the parent which offered many more morsels to it before giving to the other chick (see alternate feeding sequences, Table 9.1). However, the significant relationship between the time per morsel and the age of the brood might not be due to sibling competition alone; normal maturation of the chicks might have contributed to it too.

Another interesting interaction, which was observed only once, occurred between the 2 chicks of Pair No.6 when the brood was 53 days old:

> Between 06:50 and 07:10 the female fed the chicks; 07:10-07:35 she held the prey without feeding the young and all along the chicks begged to be fed; 07:35 she flew off to help the male drive away a 3-year old intruder; during the fight which lasted almost 30 minutes, C_2 got hold of the prey and was feeding itself; as C_2 fed, C_1 constantly begged to be fed too; they moved around the nest but C_2 successfully protected the prey from C_1; after prolonged and persistent begging C_2 played the part of a parent by offering some pieces to C_1, which morsels C_1 readily swallowed; the whole scene was, however, interrupted by the female returning at about 08:07 and resuming the feeding herself.

9.3.5.3 The growth and fledging success of siblings

Sibling aggression, acting through "acceptance of intimidation" and causing artificial food shortage and starvation in the younger sibling (Meyburg 1974), was thought to have been the cause of the different growth patterns of C_1 and C_2 in the early part of their brood life (Fig. 9.6). C_2 grew more slowly than C_1 due possibly to the "artificial starvation" it experienced despite the abundance of food in the nest (Table 9.2). It regularly had an empty crop and when hand-fed it readily took the morsels offered to it. At 13 days of age, when it was last weighed, its crop, just as of C_1, was full and its badly wounded head was healing. It seemed to have passed the critical stage in its life and would have survived the effects of sibling aggression. But by the 18th day of the brood's life it had disappeared without trace.

Despite C_2 growing more slowly than C_1 during the early part of their brood-life their mean fledging weights were not significantly different (Table 9.3). This would indicate that the effects of sibling agression were probably limited to the earlier part of brood-life. During this period its most significant effect is apparently to eliminate the younger siblings. After this period, once sibling agression has failed to eliminate the younger chicks, fledging weights. Even in 1- and 2-young broods the mean fledging weights were similar (Table 9.3).

Data are presented in Table 9.4 on sibling survival in 52 nests with more than one young in relation to the hatching sequences of the chicks and brood sizes. The fledging successes of nestlings did not differ significantly with respect to both hatching order and brood size (Table 9.4). These results indicate that sibling agression was not an important brood mortality factor, because if it were far fewer C_2 and C_3 and B/2 chicks than recorded would have survived.

9.4 DISCUSSION

Din (1970) recorded a temperature of 111° F (43.9° C) in the open nests of Pink-backed Pelicans in this Park and commented on the dangers of disturbing the brooding adults. The naked (psilopaedic) young could easily be killed by prolonged exposure to such high nest temperatures. King & Farner (1961) observed that behavioural thermoregulation by which the bird seeks a cooler place and reduces activity during the hot part of the day is important in reducing heat stress. Nestling Fish Eagles probably avoided excessive heat stress by moving to the nest edge which was cooler and perhaps better aerated than the hotter and structurally less ventilated nest floor.

Table 9.3 The mean fledging weights (g) of nestling Fish Eagles in relation to their hatching orders and brood sizes. Student's t was calculated using formula for small sample sizes.

Hatching order or brood size	Fledging weight (g) Mean + S.d.	Range	n	t-value	df
C_1	2775.0±188.7	2500–2950	4	0.574 NS	6
C_2	2558.8±624.5	1900–3410	4		
B/1	2282.5±92.5	2190–2375	2	1.021 NS	8
B/2	2666.9±473.8	1900–3410	8		

Table 9.4 The fledging successes of nestling Fish Eagles in relation to their hatching orders and brood sizes.

Hatching order or brood size	Number of young Hatched	fledged	% fledging success
C_1	52	39	75.0
C_2	52	37	71.2
C_3	3	2	66.7
	X^2 = 0.040 NS, df = 2		
B/1	23	12	52.2
B/2	70	47	67.1
	X^2 = 0.395 NS, df = 1		

The role of panting in temperature regulation has been highlighted for young White Pelicans (Bartholomew *et al.* 1953); for young pelicans, herons and gulls (Bartholomew & Dawson 1954); and for the Sooty Tern (Howell & Bartholomew 1962). In discussions on thermoregulation the importance of the respiratory tract as one of the means of heat loss for birds is stressed (Salt & Zeuthen 1961, King & Farner, op cit. and Hutchinson 1954 & 1964). That the importance of heat loss through the evaporation of water from respiratory tract increases with temperature was demonstrated in the pigeon (Kaiser 1929), the English Sparrow (Kendeigh 1944) and in the domestic hen (Hutchinson 1954).

King & Farner (op cit.) state that "As the environmental temperature approaches and exceeds the upper critical temperature heat loss by evaporation from respiratory surfaces becomes relatively more important and is finally the sole method of heat loss. In this range, panting and also gular fluttering begin and provide a marked increase in exchange of air over moist surface, primarly over the non-respiratory surface of the respiratory system, i.e. the mouth cavity, pharynx and bronchi (and possibly air sacs)." In the open nest of the Fish Eagle the environmental temperature probably regularly exceeded the upper critical temperatures of the breeding adults and the young. By panting, both adults and chicks undoubtedly rid themselves of considerable heat. During panting a nestling lost a clear salty liquid from its beak, and this liquid probably originated from a pair of nasal (supraorbital) salt glands which the bird possesses (G. R. Cunningham-van Someren, pers. comm.). This hypertonic salt solution ran along the inner surface of the upper mandible and appeared as a bead on the curved tip of the mandible.

The sinuses in the nasal cavities of birds are generally good heat exchangers (. F. I. B. Kayanja, pers. comm.). Probably through the evaporation of some of this fluid in the nasal cavities both adult and young Fish Eagles lost some of their heat loads. Through the excretion of this solution birds also rid themselves of excess salts and the extent to which this liquid loss served to excrete the salts is still to be investigated. Oceanic birds have been known to rid themselves of excess salts by a similar process (Schmidt-Nielsen et al., 1958, Fange et al., 1958a & b).

Early in the fledging period young Fish Eagles were attracted to human observers probably because they had not learnt to distinguish between their parents and other animals. During mid-fledging, however, the indifference shown could be because they were already able to differentiate between the parents and other animals but had not probably experienced frightening stimuli. This is a stage when the young could be highly vulnerable to predation since they were physically incapable of defending themselves (Ricklefs 1969a). However, one of the parents was usually on guard although not necessarily on the nest (section 10.3.2). During the last part of the nestling period, the exhibition of both fright and threat could deter a potential predator from attacking them. Additionally, the physical capabilities of the nestlings at these later stages made them better able to defend themselves against predation (Ricklefs, op cit.).

Because raptor eggs are laid at intervals they consequently hatch at intervals too. This is because incubation invariably starts with the first egg before the full complement of the clutch has been laid. Meyburg (1974), however, recorded synchronous in some pairs of the Spanish Imperial Eagle Aquila haliaca which indicated that incubation started after the last egg had been laid. Asynchronous hatching has also been recorded in the Lesser Spotted Eagle A. pomerina, African Hawk Eagle Hieraaetus spilogaster, Spanish Imperial Eagle and White-tailed Sea Eagle Haliaeetus albicilla (Meyburg, op cit.); in the Golden Eagle A. chrysaetos (Ingram 1959); in the Bald Eagle (Bent 1937); and in the African Fish Eagle (Steyn 1972).

Asynchronous hatching has been thought to ensure the survival of the older chick during times of food shortage (Lack 1966). It operates through aggressive subordination of the younger sibling and/or denial of adequate feeding. Meyburg (1974), however, concluded that food shortage was not involved in the death of the younger sibling. In fact, in most cases, there was enough food to sustain the chicks. In the Queen Elizabeth Park Fish Eagle population food shortage could not have been involved in the deaths or disappearance of the second or third chicks. Food was always abundant, at least in the early part of the nestling period (Table 9.2). An important cause of death or disappearance among second or third siblings could also have been the denial of adequate feeding resulting from excessive attacks by the older siblings as was the case in Meyburg's study.

In some species of raptors sibling aggression has been known to result in the fledging of only one chick, usually the oldest, at the expense of others. In the Golden Eagle it is believed the second chick was usually killed by the first (Ingram, op cit.). Meyburg's observations on the Spanish Imperial, Lesser Spotted, African Hawk and the White-tailed Sea Eagles, however, showed that actual killing of one chick by another happens very rarely, if at all. He suggested that the critical factor in the elimination of the younger chick was the hatching interval which operated through "acceptance of intimidation" to cause artificial food shortage and starvation in the younger sibling. In the Lesser Spotted Eagle he witnessed the remains of a C_2 which died as a result of sibling strife being fed to C_1 and the remainder devoured by the feeding parent. Second and third siblings which disappeared from broods of Fish Eagles in this Park may have died or been killed by their older young; their bodies could have, subsequently, been eaten by the surviving chicks and the feeding parents, because any other causes of death, like predation, should have involved both the oldest chicks and their young siblings too.

In the Spanish Imperial and the Golden Eagles the elder young attacked and tore the backs of the younger one (Meyburg op cit.). A South African Fish Eagle chick delivered twisting pecks to various parts of the body of its younger sibling (Steyn 1972). In this study, the older nestlings largely attacked the heads of the younger chicks although the backs were also wounded.

The reasons for this aggression are not clear but Lack (1966) interprets asynchronous hatching as being of value in ensuring the survival of the older chick during periods of food shortage. It would therefore be of no advantage to the older chick in food-rich areas or during periods of food abundance. Furthermore, according to the theory of sociobiology (Hamilton 1964) relatedness should reduce competition or fights among full-sibs. It is therefore paradoxical that Fish Eagle or any other raptor siblings should fight, even to the points of killing each other, when the territorial behaviour of the breeding pairs should have ensured their full-sibship or relatedness through monandrous insemination of their mothers. Nonetheless the sibling aggression shown by nestling Fish Eagles may be an inherited trait of the genus that has persisted with time in the species. But its advantages in ensuring food supply for and the survival of the first chicks as postulated by Lack (op cit.) has not come out clearly during this study.

Sibling strife in birds is not confined to birds of prey alone. It has been reported, for example, in the Blue-faced Booby Sula dactvlatra personata (Kepler 1969). In this Park it has also been observed in the Pink-backed Pelican (Din 1970).

CHAPTER 10

PARENTAL CARE OF NESTLINGS

10.1 INTRODUCTION

In eagles parental behaviour varies according to species and among individuals within species. Brown (1976b) generalised that if the female icubated alone she will normally brood alone. In some species like the Golden Eagle *Aquila chrysaetos* the male took a greater share in brooding than in incubation, and in others such as the Crowned Eagle *Stephanoaetus coronatus* the male shared in incubation but seldom or never brooded young. In yet other species, e.g. the Martial Eagle *Polemaetus bellicosus*, Ayre's Hawk Eagle *Hieraaetus dubius*, all snake eagles (Circaetinae) and the Bateleur *Terathopius ecaudatus* the males do not brood at all (Brown, op.cit.).

Both sexes in the African Fish Eagle *Haliaeetus vocifer* incubate and brood. As in the related Bald Eagle *H. leucocephalus* (Herrick 1933) however, much of the brooding was done by the female. Because she did much of the brooding the female also guarded the young.

The amount of food brought to the nests of most raptors always sharply increased immediately after hatching and the killing rates of the males normally doubled or trebled at this time (Brown 1976a & b). Usually the female fed the chicks and normally on prey collected from or brought into the nest by the male.

10.2 METHODS

10.2.1 Brooding of young

The role of the sexes in brooding young was assessed largely by watching Pair No.6 (1975 & 1976) and, to varying extents, other pairs. The times each sex started and stopped brooding were noted. From these records the amounts of brooding done by each sex and the amount of time the young were left exposed were determined.

During the first 8 weeks of the nestling period, the total time parents brooded young was obtained for each hourly interval during the day. These were then divided by the total observation time for the respective hourly intervals and expressed as percentages. These data gave the temporal pattern of daytime brooding in relation to the age of the brood. Mean daytime brooding pattern was calculated by averaging the data for the 8 weeks.

10.2.2 Guarding of young

During both incubation and fledging periods all observed interspecific encounters between breeding pairs of Fish Eagles and other animals (birds, mammals and reptiles) were recorded. Notes were made as to whether an interaction was in probable defence of the nest and/or young, or mere molestation of the pair of Eagles by the intruder. Whether an adult of the brooding pair was guarding the young or not was assessed by estimating its position and entering as: on the nest or nest tree, near the nest (50-100 m away), and far from the nest (100+ m away).

10.2.3 <u>The feeding of young</u>

The hunting activities of breeding pairs were investigated by documenting:

10.2.3.1 <u>Food procurement</u>

During both incubation and brooding periods the durations of flight hunting were continuously recorded for each adult. Hunting duration, in this sense, is the amount of time spent by a member of a pair hunting by low flights and low and short soars over the water surface; otherwise Fish Eagles normally hunted by watching the water while perched by the shoreline (section 4.3.2.1). Perch hunting was impossible to separate from rest and was therefore not measured. The duration of all bouts of flight hunting during an observation period was expressed as a percentage of that observation time. Stinson (1978) used the length of the hunting trip to measure the hunting efforts of Ospreys <u>Pandion haliaetus</u> but this method could not be employed here because Fish Eagles hunted virtually all the time because of their nests being almost at the water fronts (section 5.3.1).

A stoop is a dive or sortie (Brown 1970a, 1976 & 1980; Brown & Hopcraft 1973) made by a bird, usually raptor, at an object at a lower level. During hunting, Fish Eagles made stoops and killed prey, usually fish, at the water surface. The number of stoops/adult/ day was the number of dives made by each adult divided by the observation time (in days) while the number of prey captured/adult/ day was the number of successful stoops divided by the observation time (in days) during which that number of dives was made.

10.2.3.2 The frequency of feeding young

The number of prey delivered to the brood/adult/day was the number of food items brought to the nest by each adult divided by the observation period (days). The number of times each sex fed young was also recorded. Prey availability to the brood was assessed by noting the types, numbers, and weights of all food items found in the nest of Pair No.82 as the breeding cycle progressed.

The daily frequency of meals offered to the brood as a function of its age was calculated by dividing the number of observed feedings by the amount of time the Eagles were watched. The number of pieces of flesh proffered by the feeding parent to the brood at each meal was also recorded. The times when young were fed were noted. These records permitted the analysis of the distribution of the meals, on hourly basis, for the whole eagle-day.

10.3 RESULTS

10.3.1 Brooding of young

Table 10.1 shows that as a nesting Fish Eagle advanced in age the time the parents spent brooding it

Table 10.1 The proportion of daytime brooding according to sex in the Fish Eagle Pair No. 6 in relation to the age of the brood. Student's t was calculated using formula for small sample sizes and tested the means of male and female shares of brooding. Note that the results for only one pair of birds may not have necessarily reflected a true picture of the Fish Eagle's behaviour.

Age (weeks)	Obs. time (min)	% share of brooding by sex			% nil brooding
		Male	Female	Total	
1	1700	2.5	90.8	93.3	6.7
2	3486	0.4	74.4	74.8	25.2
3	2455	4.5	57.4	61.9	38.1
4	515	0.0	43.9	43.9	56.1
5	680	0.0	22.7	22.7	77.3
6	1280	0.1	6.4	6.5	93.5
7	430	0.0	0.0	0.0	100.0
8	850	0.0	0.0	0.0	100.0
9	345	0.0	0.6	0.6	99.4
10	525	0.0	0.0	0.0	100.0
11	705	0.0	0.0	0.0	100.0
Total	12971				
Mean±SE		0.7±0.4	26.9±9.8		
		t = 2.551*, df = 20			

during the day was gradually reduced until brooding ceased altogether by the 7th week of brood life. The temporal patterns of daytime brooding in relation to the age of the brood show that during the first week the chick was brooded for almost all the daytime period (Table 10.2 & Fig.10.1).

From the 2nd to the 6th week the young was brooded largely during the colder and hotter parts of the day, the amount of parental care in this respect being slowly scaled down as the young matured (compare weeks 3 and 6, Fig. 10.1). The mean temporal brooding pattern shows that brooding reached a peak during the hotter afternoon period, between 13:00 and 16:00. This behaviour probably underlines the importance of heat stress in the survival of the nestling (section 9.3.2).

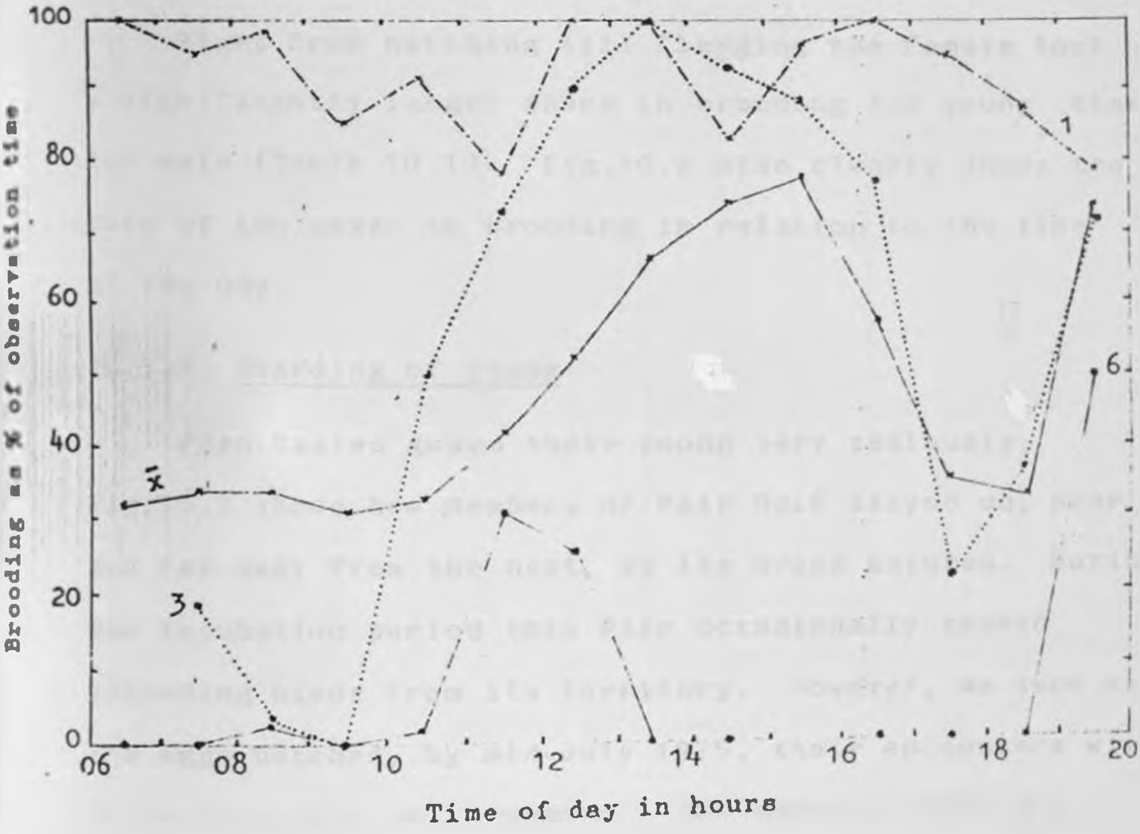
During brooding adults provided warmth by sitting on the tiny young, while shading was done by the parent standing between the chick and the sun such that its shadow was cast onto the eaglet. During early fledging, warmth- or shade-seeking young went beneath the partly fluffed feathers of the crouching adult. By mid-fledging onwards the chick had become too large to comfortably fit under the crouching or standing parent. It probably had to rely largely on its down and feathers, and behavioural and physiological thermoregulation to keep warm or avoid excessive heat loads.

Fish Eagles brooded young by night for much longer than during daytime. At dusk one parent, usually the

Table 10.2 Temporal patterns of daytime brooding in Fish Eagle pair no. 6 in Queen Elizabeth Park in relation to the age of the brood. Data from 1975 and 1976 breeding seasons combined; Observation time is in hours and total observation time = 189.93 hours. However, observation of only one pair of birds could have biased overall Fish Eagle behaviour.

Time of day (hours)	Age of young (weeks) 1	2	3	4&5	6	7&8	Mean ± SE
0600-0700	100.0	60.0	-	0.0	0.0	0.0	32.0±18.4
0700-0800	95.0	91.7	18.9	0.0	0.0	0.0	34.2±17.3
0800-0900	98.3	100.0	3.9	0.0	2.5	0.0	34.1±18.8
0900-1000	85.0	100.0	0.0	0.0	0.0	0.0	30.8±17.9
1000-1100	91.7	50.0	49.6	5.6	1.7	0.0	33.1±13.8
1100-1200	78.3	50.0	72.9	20.6	31.1	0.0	42.2±11.4
1200-1300	100.0	50.0	89.6	50.0	25.6	0.0	52.5±14.1
1300-1400	100.0	98.8	100.0	100.0	0.0	0.0	66.5±19.2
1400-1500	83.3	92.9	93.3	100.0	0.0	-	73.9±16.7
1500-1600	95.8	98.5	88.3	100.0	-	0.0	76.5±17.2
1600-1700	100.0	68.7	77.2	100.0	0.0	0.0	57.7±17.3
1700-1800	95.0	42.4	22.2	53.3	0.0	0.0	35.5±13.5
1800-1900	87.5	40.2	36.7	-	0.0	0.0	32.9±14.4
1900-2000	78.4	91.4	71.7	-	50.0	-	72.9± 7.5
Mean	92.0	73.9	55.7	44.1	8.5	0.0	-
±SE	2.1	6.2	9.5	12.5	4.3	0.0	
Obs. time	28.33	58.10	40.92	19.92	21.33	21.33	

Fig. 10.1 The temporal patterns of daytime brooding in the Fish Eagle in Queen Elizabeth National Park in relation to the age of the brood. 1, 3 and 6 respectively represent the 1st, 3rd and 6th weeks of the nestling period; and $\bar{X}$ represents the mean brooding pattern of the adults for the first 6 weeks of the 11-week fledging period.



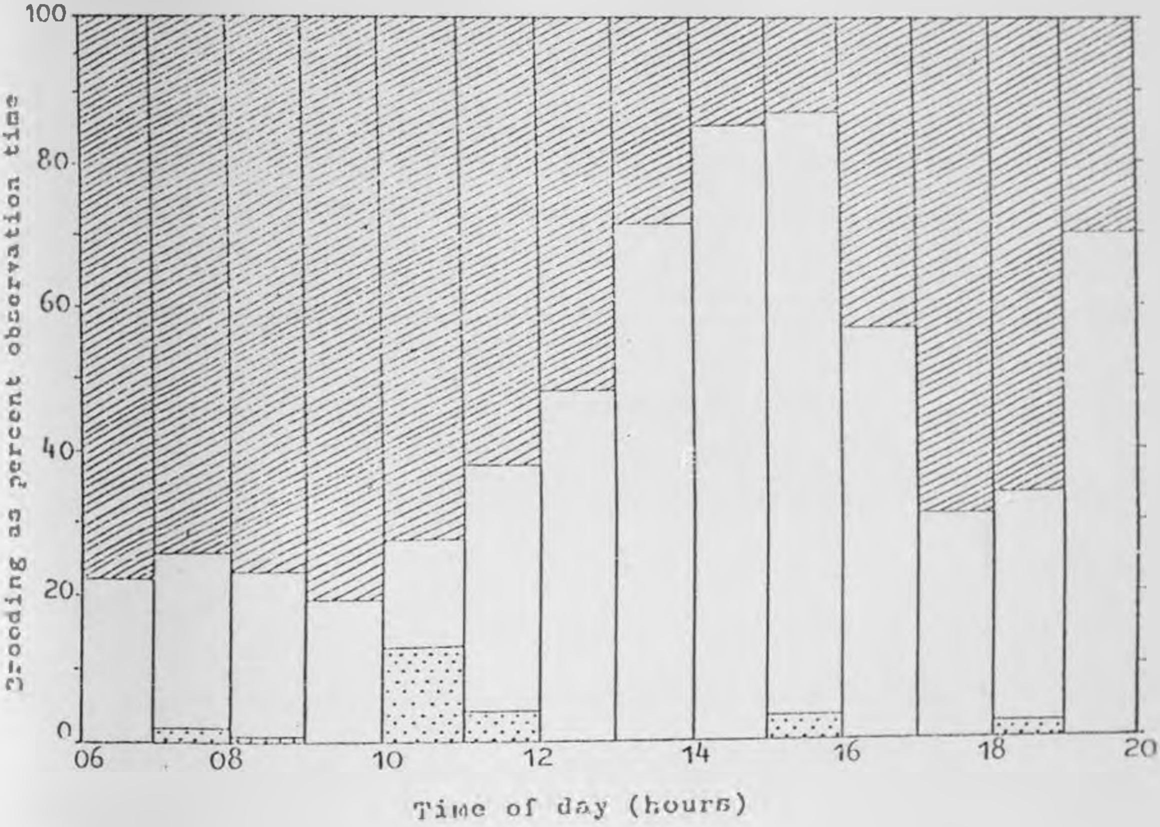
female, returned to the nest and stayed with the young till day-break. Night brooding continued up to about 30-40 days of life, by which time the eaglets were almost fully feathered. From this stage onwards the young were not brooded, although one of the parents slept on the nest beside them. Once fully feathered the eaglets slept on the nest alone, the parents sleeping on nearby roosting perches or on the nest tree itself.

Right from hatching till fledging the female took a significantly larger share in brooding the young than the male (Table 10.1). Fig.10.2 also clearly shows the role of the sexes in brooding in relation to the time of the day.

10.3.2 Guarding of young

Fish Eagles guard their young very zealously. Fig.10.3 shows how members of Pair No.6 stayed on, near and far away from the nest, as its brood matured. During the incubation period this Pair occasionally chased intruding birds from its territory. However, as soon as the eggs hatched, by mid-July 1975, their encounters with birds increased in frequency. The adults chased all large birds, e.g. Marabou Stork Leptoptilos crumeniferus, Egyptian Goose Alopochen aegyptiacus, all vultures (Accipitridae) and Pied Crow Corvus alba, which approached to within about 30 metres of the nest. Chasing reached a peak at about mid-fledging and then dropped off during the post-fledging period (Fig.10.4). Marabou Storks

Fig. 10.2 The proportion of daytime brooding according to sex in the Fish Eagle Pair No. 6 in relation to the time of the day. Total observation time = 216.18 hours. The least observation time was 2.5 hrs for 0600-0700 and the highest 24.1 hrs for 1700-1800 hrs. The results for only one pair of birds may not necessarily reflect a true picture of the Fish Eagle's behaviour.



KEY:

▨ Nil brooding as % of total observation for the hourly interval.

□ Female brooding as % of total observation for the hourly interval.

░ Male brooding as % of total observation for the hourly interval.

Fig. 10.3 Parental guarding of young in Fish Eagle Pair No. 6 (1975) in relation to the age of the brood. Solid circles and solid line represent parent on nest or nest tree, solid circles and dashed line parent 50-100 m from nest, open circles and dotted line parent 100+ m away. Distances were subjectively estimated and observation of one pair of birds could have biased overall Fish Eagle behaviour.

Fig. 10.4 The number of birds, other than African Fish Eagles, chased by Pair No. 6 during the 1975 breeding season in relation to the age of the 2-young brood. Dotted line represents Marabou Storks chased, and solid line represents all birds chased. Monthly totals were used to plot graph. Observation of only one pair of birds could have biased overall Fish Eagle behaviour.

Fig. 10.4

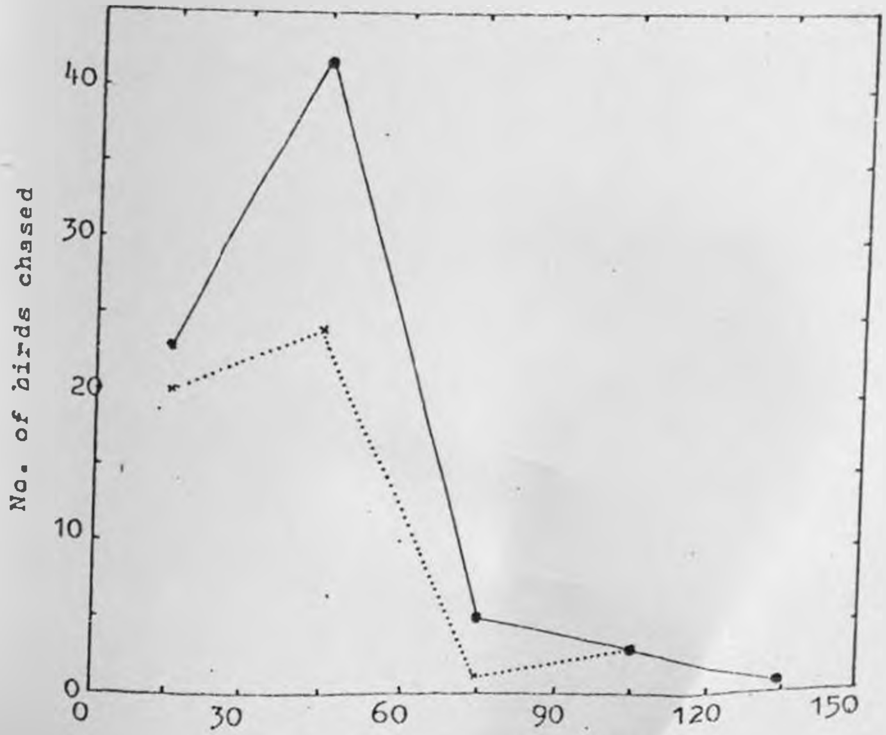
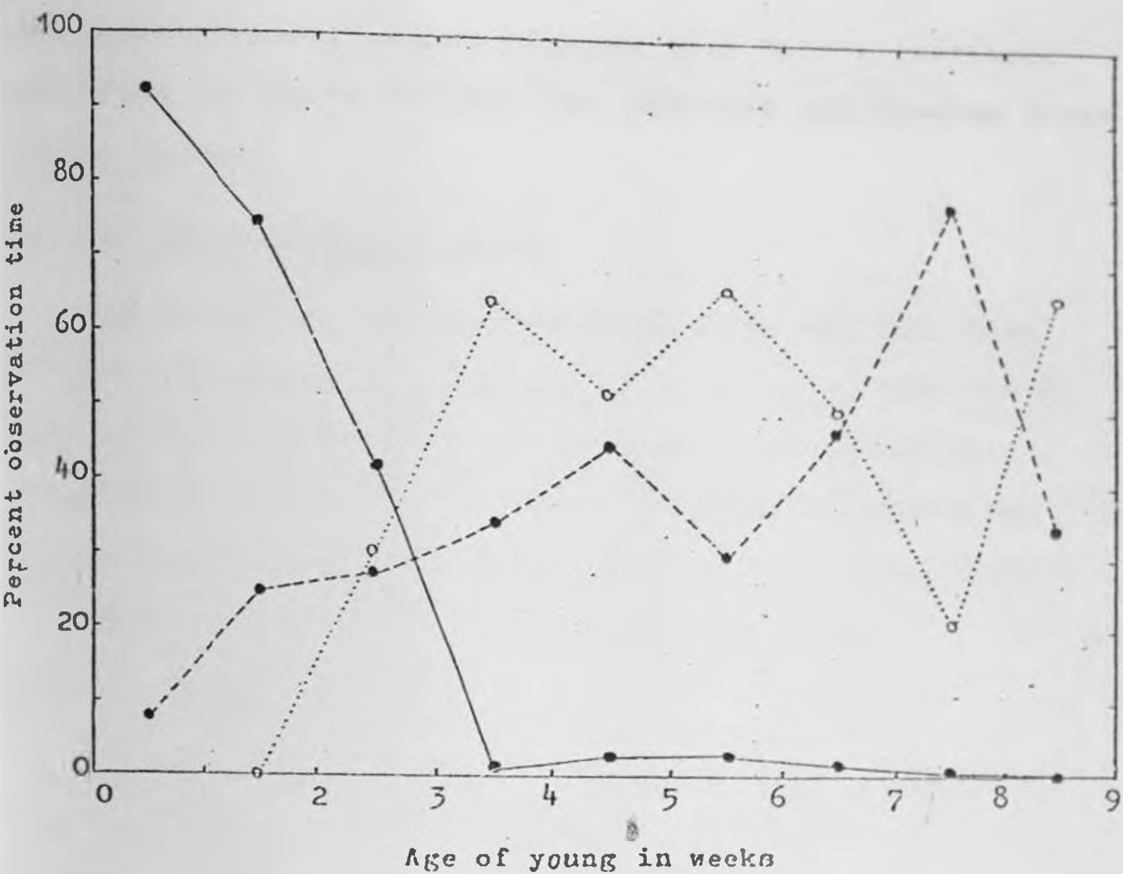

No. of birds chased
40
30
20
10
0
0
30
60
90
120
150
Age of young in days

Fig. 10.3


100
80
60
40
20
0
Percent observation time
0
2
3
4
5
6
7
8
9
Age of young in weeks

were more commonly chased because this Pair's territory straddled the route between the roosting and feeding areas of the storks.

10.3.3 The feeding of young

In assessing the hunting activities and the roles of breeding adults in feeding their young all day-to-day data on hunting activities were summarized on weekly bases (Tables 10.3,10.4 & 10.5) in order to reduce any biases which could have arisen due to brief observations on some of the days during a particular week.

10.3.3.1 Food procurement

The male increased his flight hunting, although not significantly, by 1.4 times from incubation to brooding (Table 10.3). Over the same periods the female's flight hunting increased two-fold but the mean durations were also not significantly different (Table 10.3). Only during the incubation period did the male hunt significantly more than his mate (Table 10.3). During the nestling period flight hunting decreased, although not significantly, in the male as the young matured while it significantly increased in the female (Fig.10.5). There were no significant changes in the numbers of dives that the male and female made per day from incubation to brooding (Table 10.4). During the nestling period the male made significantly more stoops/day than the female but the numbers were not significantly higher than hers during the incubation period (Table 10.4).

Table 10.3 The durations of flight hunting by the sexes of breeding pairs of Fish Eagles in Queen Elizabeth Park during incubation and nestling periods. Age with - sign is during the incubation period; Student's t was calculated using formula for small sample sizes.

Age (weeks)	Obs. time (eagle-days)	Percent hunting duration		t-value
		Male	Female	
-4	1.00	1.9	1.1	
-3	1.97	2.0	1.2	
-2	1.67	1.6	0.4	
-1	2.79	1.8	0.6	
Total	7.43			
Mean±SE		1.8±0.1	0.8±0.2	4.715**(df = 6)
1	1.94	4.0	0.0	
2	1.50	3.1	1.6	
3	2.30	2.3	1.4	
4	0.29	1.3	2.0	
5	0.58	3.5	2.6	
6	0.80	1.5	2.6	
Total	7.41			
Mean±SE		2.6±0.4	1.7±0.4	1.506 NS (df = 10)
t-value (df = 8)		1.419 NS	1.738 NS	

Fig. 10.5 The duration of flight hunting in male and female African Fish Eagles in Queen Elizabeth National Park as functions of the age of their brood. Open circles represent male hunting and solid ones female hunting.

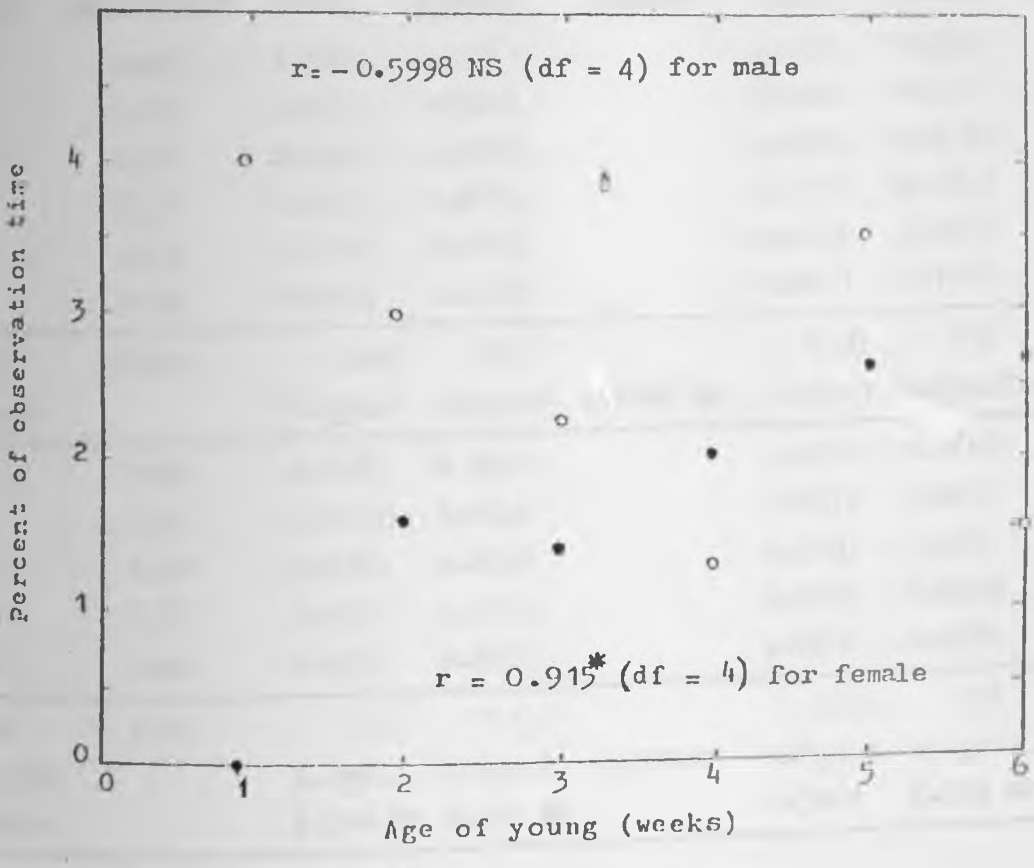


Table 10.4 The numbers of stoops and prey captured by the sexes of Fish Eagle Pair No. 6 (1976) in Queen Elizabeth Park. For each entry, the first figures are numbers of stoops or prey per day; the second, in parentheses, are the numbers of stoops or preys captured during the respective observation periods; Student's t was calculated using the formula for small sample sizes. Observation of only one pair of birds could have biased the overall Fish Eagle behaviour.

Age (weeks)	Obs. time (eagle-days)	Numbers of stoops/day			Numbers of prey killed/		
		Male	Female	t-value	Male	Female	t-value
-6	0.68	5.9(4)	1.5(1)		1.5(1)	1.5(1)	
-5	1.97	3.6(7)	0.5(1)		2.0(4)	0.5(1)	
-4	2.96	2.0(6)	0.0(0)		1.7(5)	0.0(0)	
-3	2.41	2.1(5)	0.4(1)		1.2(3)	0.4(1)	
-2	1.67	0.0(0)	0.0(0)		0.0(0)	0.0(0)	
-1	2.79	0.7(2)	1.1(3)		0.4(1)	0.7(2)	
Total	12.48	(24)	(6)		(14)	(5)	
Mean±SE		2.4±0.8	0.6±0.2	1.9996 NS	1.1±0.3	0.5±0.2	1.308 NS
1	1.94	4.1(8)	0.0(0)		1.0(2)	0.0(0)	
2	2.65	4.5(12)	0.4(1)		2.6(7)	0.4(1)	
3	2.30	2.6(6)	0.4(1)		1.7(4)	0.4(1)	
4	0.58	5.2(3)	1.7(1)		3.5(2)	0.0(0)	
6	0.80	3.8(3)	0.0(0)		3.8(3)	0.0(0)	
Total	8.27	(32)	(3)		(18)	(2)	
Mean±SE		4.0±0.3	0.5±0.3	6.579***	2.5±0.4	0.2±0.1	4.275**
t-value		1.546 NS	0.255 NS		2.361*	1.124 NS	

* df = 9, ** df = 8, *** df = 8.

Table 10.5 The numbers of prey captured and delivered to the brood by the sexes of Fish Eagle Pair No. 6 (1976) in Queen Elizabeth Park. Figures in parentheses are numbers of prey items captured and delivered during the respective observation periods; Student's t was calculated using the formula for small sample sizes. Observation of only one pair of birds could have biased overall Fish Eagle behaviour.

Age of brood (weeks)	Obs. time (eagle-days)	Numbers of prey items captured/day Male	captured/day Female	delivered/day Male	delivered/day Female
1	1.94	1.0(2)	0.0(0)	1.0(2)	0.0(0)
2	2.65	2.6(7)	0.4(1)	2.3(6)	0.8(2)
3	2.30	1.7(4)	0.4(1)	1.3(3)	0.9(2)
4	0.58	3.5(2)	0.0(0)	1.7(1)	1.7(1)
6	0.80	3.8(3)	0.0(0)	1.3(1)	1.3(1)
Total	8.27	(18)	(2)	(13)	(6)
Mean±SE		2.5±0.4	0.2±0.1	1.5±0.2	0.9±0.3
t-value		4.275* (df = 8)		1.654 NS	

The male captured significantly more prey/day during the fledging than during the incubation period (Table 10.4), the killing rate rising by more than two-fold. The killing rate of the female, however, dropped, although not significantly, to only 40% over the same periods (Table 10.4). The male captured significantly more prey/day than the female only during the nestling period; their kills were similar during the incubation period (Table 10.4).

10.3.3.2 The frequency of feeding young

Prey delivery to the nest occurred with consistency only after the eggs had hatched. During the period the male delivered to the brood only about one-half the prey he captured (Table 10.5). The female, on the other hand, brought to the nest significantly more prey/day than she actually killed ($t = 2.320$, $df = 8$, $P < 0.05$; data in Table 10.5).

During this period 19 (95%) of the 20 fish caught by the Eagles were delivered to the brood. Although 4 of the 19 fish were collected by the female from the male, both sexes delivered to the nest similar numbers of prey/day (Table 10.5). The Table further shows that the male brought to the nest more prey items than his mate in the early part of the fledging period. During mid-fledging, however,their prey deliveries were similar.

Table 10.6 shows the availability of food to a brood in the course of its development. As the young matured, less and less food in the form of prey remains was encountered in the nest and often none at all, especially

Table 10.6 Remains of prey in the nest of Pair No. 82 with the age of the brood between 21.12.76 and 21.2.77. Age shown with - sign is prior to hatching; C_2 lost without trace after its 13th day of age.

C1's age (days)	No. of young	Remains of Prey No.	Remains of Prey Wt. (g)	Prey type and portion	Crop of young C1	Crop of young C2
-3	0	0	Nil	–	[illegible]	–
3	2	1	200.0	*Tilapia* sp., tail	full	full
5	2	2	442.0	*Tilapia* sp., tail	full	½ full
6	2	2	520.0	*Tilapia* & *Bagrus* spp.	full	empty
9	2	2	68.5	*Haplochromis*? sp.	full	empty
12	2	1	40.0	Tilapia sp., tail	full	empty
15	2	0	Nil	–	full	½ full
17	1	1	120.0	*Tilapia* sp., head	full	lost
25	1	0	Nil	–	full	–
28	1	0	Nil	–	½ full	–
31	1	0	Nil	–	empty	–
36	1	0	Nil	–	full	–
39	1	0	Nil	–	empty	–
49	1	0	Nil	–	empty	–
56	1	0	Nil	–	full	–
59	1	1	20.0	*Haplochromis*? sp., tail	½ full	–

in the latter part of the nestling period. The state of the crop of each young, however, indicated that the young were not necessarily being starved.

Nestlings were fed almost solely by the female. In 39 cases of brood feeding by Pair No.6 (1975 & 1976), the female fed chicks in 38 (97.4%) of them (Table 10.7). The only time the male fed the brood was a rather special one and is described below:

> 21.8.76; sunny bright day; 10:00-14:58 female brooding two 15- and 17-day old chicks; at 14:58 she left; 15:02 male arrived with a ca. 300 g Tilapia sp. caught at 14:43; 15:02-15:19 male restless on the nest while chicks incessantly begging and moving about; 15:19-15:34 he fed the young, standing for long moments craning his head in the direction of the female hunting by the shore; he fed only 14 morsels to C_1 and 38 to C_2; C_1 retired to far end of nest at 15:26 after long waits for morsels; 15:35 he flew off to a nearby perch leaving the prey on the nest; 15:59 female returned to nest; both chicks begged for feeding; between 16:00 and 16:39 she fed them until their crops started to bulge; 16:39 the female flew off and ate the remains of prey on nearby perch; 18:13 the female caught another Tilapia sp.; between 18:15 and 18:46 she fed 82 and 43 pieces to C_1 and C_2 respectively.

The two feedings by the female after the male's suggest that the male fed the chicks inadequately. The long intervals between morsels and the craning of his head in the direction of the female indicated that he probably was uneasy at feeding the chicks in the absence of his mate.

On 24.8.76, at 10:03, the male brought another ca.300 g Tilapia sp. and was prepared to feed the brood when the female arrived, took the fish and fed the chicks herself. Several times he was seen to rise from brooding and grasp the remains of prey by the nest rim and prepare

Table 10.7 The role of the sexes of Fish Eagle Pair No. 6 in Queen Elizabeth Park in feeding their young. Data for age 9+ weeks were not used in the calculation of the Total and Mean because by this age the young were feeding themselves on prey delivered by either of the parents. Observation of only one pair of birds could have biased overall Fish Eagle behaviour.

Age (weeks)	Obs. time (eagle-days)	No. of meals	No. of meals/ eagle-day	Times fed young	
				Male	Female
1	2.18	6	2.75	0	6
2	4.47	11	2.46	0	11
3-4	4.69	12	2.56	1	11
5-6	2.67	5	1.87	0	5
7-8	1.64	5	3.05	0	5
Total	15.65	39	-	1	38
Mean±SE	-	-	2.54±0.17	-	-
9+	0.98	6	6.12	0	0

as if to feed the young. Suddenly he would turn round and fly off with the prey, leaving the chicks crouched in feeding postures. Shortly afterwards he returned leading or accompanying the female who now carried the same prey remains which she proceeded to feed to the brood.

In 216.18 hours (16.63 eagle-days) of observation in 1975 and 1976, Pair No.6 offered food 39 times to their 2 broods of 2 nestlings each. This gave an average of 0.18 meals/hour or 2.35 meals/day. In 3 days of dawn-dusk observations during the 1st, 2nd and 3rd weeks of the fledging period, the same Pair fed its brood 2,3 and 2 meals per day respectively. As the brood matured, it was offered a fairly constant number of meals per day ($r = 0.06$, $df = 3$, $P > 0.1$; data in Table 10.7). From the 9th week until fledging chicks fed themselves on prey deposited in the eyrie by either of the parents. During this self-feeding period the young ate more than twice the number of meals as when fed by the parents (Table 10.7).

The amount of flesh that satiated a growing chick at a meal increased, although not significantly, as it advanced in age (Fig.10.6). The number of morsels ranged between 40 pieces of flesh when the chick was about 1 week old and ca.110 pieces when it was from 2-6 weeks old. The amount of food eaten at a given time, however, probably depended on the amount taken during the previous meal and how long ago the meal was. The drop in the number of morsels during the 7th week, in the above Figure, coincided with the onset of self-feeding by the nestlings

Fig. 10.6 The number of food pieces fed to a brood of 2 nestling Fish Eagles (Pair No. 6, 1975) in Queen Elizabeth National Park in relation to age.

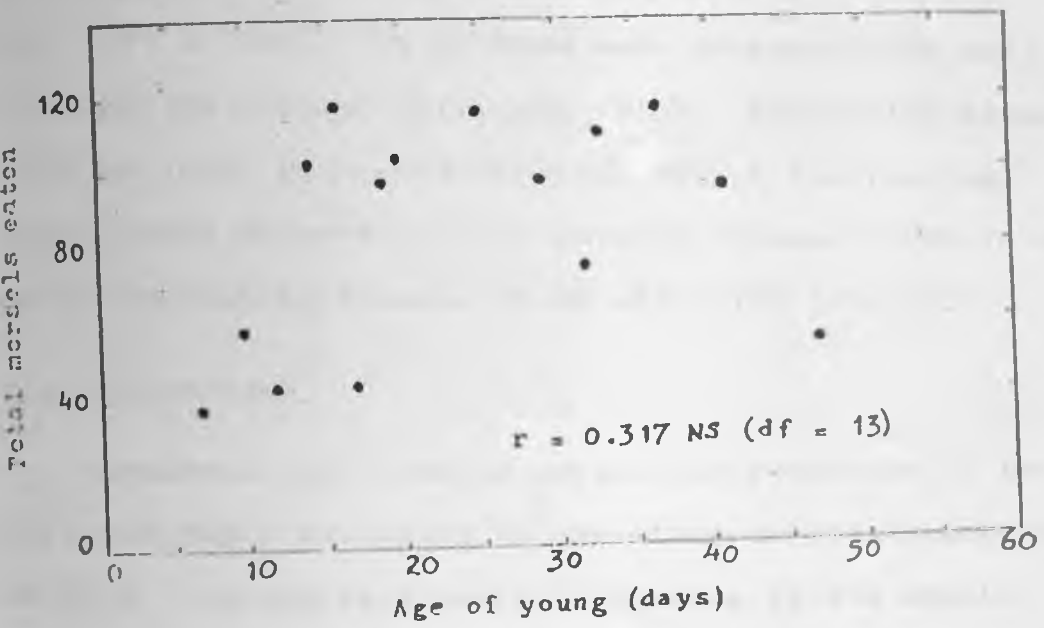
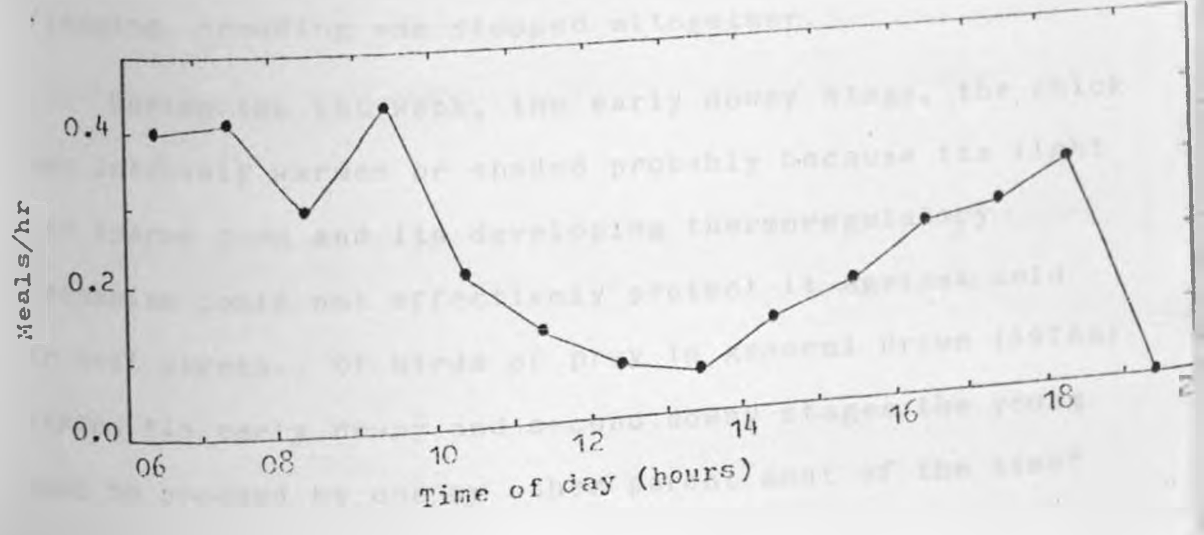


Fig. 10.7 The feeding rates of nestling Fish Eagles in Queen Elizabeth National Park. N = 45 feedings to 2 broods of Pair No. 6 during 1975 and 1976 breeding cycles. See text for how no. of meals/hr was calculated.



during parental feeding sessions.

Adults fed their broods beginning a few minutes after daybreak almost up to nightfall (Fig.10.7). Of 45 meals given to 2 broods of 2 nestlings each by Pair No.6 (1975 & 1976), 42% of them were between 06:00 and 11:00 and 38% between 16:00 and 19:00. The period between 11:00 and 16:00 accounted for only 20% of the feedings. Feeding peaks occurred in the morning between 07:00-10:00 and in the evening between 18:00 and 19:00 (Fig.10.7).

10.4 DISCUSSION

Throughout the fledging period the behaviour of the adult Fish Eagle was keyed to the stage of development of the chick. During this period, brooding by the adults decreased with the age of the young. Brooding provided the growing chick with both warmth and shade. Temporal patterns of brooding showed that a nestling was brooded throughout the day during the first and second weeks of the fledging period and only during the hot afternoon periods from the 3rd - 6th weeks. From the 7th week until fledging, brooding was stopped altogether.

During the 1st week, the early downy stage, the chick was intensely warmed or shaded probably because its light and sparse down and its developing thermoregulatory mechanism could not effectively protect it against cold or heat stress. Of birds of prey in general Brown (1976a) stated "In early downy and second downy stages the young must be brooded by one or other parent most of the time" and "The female seldom goes far, however, and will return almost at once if rain falls or the sun becomes very hot; either of these, especially hot sun can kill small chicks quickly------ which photographers should remember."

From the second downy stage until the second feathering stage, weeks 2-6 of the nestling period, brooding was limited to the hotter periods of the day, especially the afternoons. This temporal pattern of brooding demonstrated two things: 1) that the second coat of thicker and woollier down probably adequately protected young against cold; and 2) that the timing of the brooding signified shading whose importance in the life of the brood was clearly demonstrated by the high frequencies of brooding during the hotter afternoons. The high frequencies of brooding during hot periods would also indicate that loss of body heat by the chick through the evaporation of water, especially from the respiratory surface, was probably not fully developed. The importance of shading in the life of a chick was also pointed out by Brown (op.cit.) when he reported that the amount of time spent brooding could be reduced almost at hatching, and 2- or 3-day old young could be left for hours, especially in well-shaded nests in warm countries.

In the population studied both sexes brooded young, although the male took a significantly smaller share in this role than the female. This could have released him for other activities, especially that of providing food for his expanded family. In the related Bald Eagle

Haliaeetus leucocephalus both sexes incubated and brooded, but again much of the brooding was done by the female (Herrick 1933). Brown (1970a, 1976a & b), Brown & Amadon (1968) and Brown & Hopcraft (1973) do not give data on the extents to which the Fish Eagle populations they studied brooded, but they generally agree that both sexes did so with the female taking a larger share than her mate.

During the downy stage most eagles guard their small young, and some like the Crowned Eagle *Staphanoaetus coronatus*, African Hawk Eagle *Hieraaetus fasciatus* and Ayre's Hawk Eagle *H. dubius* become aggressive to human beings (Brown 1976b). In the Bald Eagle, one or both parents remained at the nest constantly for the first 3-4 weeks of the chick's life (Snow 1973a) and in the Sea Eagle *H. albicilla* the female stayed near the nest for most of the time during this period (Brown 1976c). Female Ospreys *Pandion haliaetus* with unfledged young spent over 95% of the daylight hours at the nest (Stinson 1978). As a nestling Fish Eagle aged, parental brooding was gradually reduced but it was still guarded against would-be predators. One of the parents, usually the female, perched on the nest or within view of it while the other hunted or rested at the far end of the territory. Close guarding of young continued until they were about 7 weeks old but the adults continued to chase other birds out of the territory well into the post-fledging period.

Overall, the male Fish Eagle was more active than the female in all aspects of food-procuring activities during both the incubation and nestling periods. The durations of flight hunting went up by 1.4 and 2.0 times in the male and female respectively from incubation to brooding. Despite the increase in the male's flight hunting from incubation to brooding, it decreased as the brood matured. Similar data on the duration of flight hunting are not available in other raptors but Stinson (op.cit.) found that the length of the hunting trip increased from the fledging to the post-fledging periods in the male Osprey. He suggested that this could have been so because of the male's declining attentiveness to the brood rather than due to the increasing difficulty of capturing prey. Although flight hunting declined in the male Fish Eagle with the maturity of the brood, he still captured more prey/day than the female whose flight hunting actually increased. Thus whether the male's flight hunting decreased because of his declining attentiveness and that of the female compensatingly increased due to her increasing attentiveness to the brood merit further investigations.

Brown (1976b) found that in 7 species of eagles in Kenya the killing rates of the males almost trebled from 0.3 prey/day during incubation to 0.8 prey/day during the brooding periods; in 3 species, Ayre's Hawk Eagle, Martial Eagle <u>Polemaetus bellicosus</u>, and the Brown Snake Eagle <u>Circaetus cinereus</u> the figures actually went up from 0.3 to 0.87 prey/day. He further pointed out that it was clear that male eagles doubled or trebled their rate of killing just after the hatch. This was to enable them meet the food demands of their enlarged families. The killing rate in the male Fish Eagle actually doubled from 1.13 prey/day during the incubation period to 2.52 prey/day during brooding. In the female, however, it decreased from 0.52 prey/day during incubation to 0.16 prey/day during brooding. This could have been so only because the male brooded and guarded young less often than his mate.

Of great interest is the fact that the Fish Eagle killed many more prey than the eagles Brown (1976b) studied. Similar data on killing rates are not available for the Bald Eagle and the Sea Eagle, but male Osprey brought prey to the nest at the rate of 8 fish/day during the fledging period (Stinson, op.cit.). These were, however, much smaller fish (mean weight = 2$\underset{0}{3}$7.1 g) than those caught by the Fish Eagle (mean weight = 651.7 g, section 4.3.5.2) during this study.

Up to the end of the feathering stage male raptors normally bring most prey to the nest, but thereafter the females deliver prey at least as much or more than the males (Brown, op.cit.). In the Fish Eagle, as in the Sea Eagle (Brown 1976c), most of the prey were brought to the nest by the male in the early part of the fledging period. During the latter part of it, however, both adults delivered prey equally. During the whole nestling period both sexes of the Bald Eagle delivered prey equally to the nest (Retfalvi 1965). Male Ospreys caught 98 percent of the fish which were brought to the nest during the whole nestling period (Stinson, op. cit.). In other non fish-eating eagles like Ayre's Hawk Eagle and Wahlberg's Eagle Aquila wahlbergi the males delivered more prey to the nest than their mates throughout the fledging period. The male Crowned Eagle delivered more prey than his mate only during the early part of the nestling period but much less than her in the latter part of it (Brown 1976b).

Crowned Eagles gorged themselves before taking prey to the nest (Brown 1976b). Out of 117 prey delivered to the nest by male Ospreys, 108 (88%) of them were intact (Stinson 1978). During this period, unlike in the post-fledging one (section 11.3.3), both adult Fish Eagles delivered whole prey to their nestlings.

The males of some eagles feed young. In the Bald Eagle both sexes fed chicks (Herrick 1933) but the female did so more often than the male (Retfalvi op.cit.). The male Sea Eagle fed young almost as often as the female (Willgohs 1961) while the Golden Eagle Aquila chrysaetos male did so occasionally (Brown 1976c). The male Fish Eagle was also prepared to feed nestlings but rarely did so possibly because the female did not allow him to. Similarly, female Verreaux's Eagle A. verreauxi grabbed prey from the male and delivered or fed it to the young herself (Brown 1976b). The males of some species like the Ayre's Hawk and Wahlberg's Eagles never feed chicks at all (Brown, op. cit.). Just as all eagles are gentle and solicitous while feeding chicks (Brown 1970a, 1976a, b & c), so were African Fish Eagles.

CHAPTER 11

THE FLEDGED YOUNG

11.1 INTRODUCTION

The Fish and Sea Eagles fledge their young in 65-105 days (Brown 1976a, b & c). A larger brood may take longer to fledge than a smaller one (Brown 1976b). The maiden flight is made independent of parental coaxing and usually after extensive preflight exercises (Brown 1976a, b & c; Retfalvi 1965; Kussman and Frenzel 1972).

Fledged young remain in their parental territories for varying periods of time depending on the species of raptor concerned, the type of food eaten and habitat occupied. During this period the young are fed largely on food remains brought by either of the parents while the eaglets learn to kill prey for themselves. Depending on the size of preferred prey and the difficulty of killing it, the eaglets learn to kill for themselves early or late in the post-fledging periods (Brown, op cit.).

Various behaviours are shown by adults during food deliveries to their young and by the eaglets during food procurement from the parents (Brown, op cit.; Retfalvi, op cit.). Young hobbies Falco spp. and sparrowhawks Accipiter spp. often meet adults and receive prey a little distance away from the nest, whereas young harriers Circus spp. soon learn the aerial food-pass technique practiced with such skill by their parents (Brown 1976c). Food calls by the adults to the young and hunger calls by the eaglets are common and have been described for the Crowned Eagle Stephanoaetus *coronatus*, Verreaux's Eagle *Aquila verreauxi* (Brown 1976b), and the Bald Eagle *Haliaeetus leucocephalus* (Retfalvi, op cit.).

The young of most species leave the parental territories of their own accord (Brown 1970, 1976a, b & c). Buzzards *Buteo* spp. and African Fish Eagles *H. vocifer*, however, regularly attack their young yet such attacks have been regarded as being regular territorial behaviour (Brown 1976b).

Observations on post-fledging Fish Eagles during this study were made with the view to:

a) determing fledging and post-fledging periods and comparing them with those of other raptors, especially those of the genus *Heliaeetus*;

b) establishing whether or not the fledging period was affected by brood size and nest site;

c) finding out whether or not the maiden flight was coaxed by the adult birds;

d) assessing the post-fledging feeding of the eaglets and describing behaviours of adults and young associated with it; and

e) establishing whether or not the eaglet left the parental territory of its own accord.

11.2 METHODS

11.2.1 The fledging and post-fledging periods

The fledging period, i.e. from hatching to first flight, of an eaglet was determined by recording the date the young hatched and the date it left the nest. These events were recorded within 1-2 days of their occurrences. The intervals between them gave the fledging periods of 28 eaglets. For 19 young the post-fledging periods were similarly determined, viz. by knowing the dates the maiden flights were made and those on which the young disappeared from their parental territories.

How long a particular young took to fledge was also assessed in relation to whether it was reared in an open or "closed" nest site. A "closed" nest was one situated among branches of trees such that the nest was overhung by branches. To find out if maiden flights were coaxed by adults, 3 young were observed to determine whether their flights were made in the presence or absence of their parents or if the adults in any way induced the young to make the flights.

The dates fledged young started to roost on perches were noted. From these records the ages of young at perch-roosting were calculated. Whether young from larger broods roosted on perches earlier than those from smaller sizes was determined from the above age data.

11.2.2 Post-fledging feeding of young

The feeding of eaglets was assessed by observing pairs with fledged young for prey items they caught and delivered to the young. The observation periods were recorded and the amounts of food available to an adult and to an eaglet per day were calculated. Behaviours of adults during food deliveries to young and of young during food procurement from adults were recorded.

11.2.3 The departure of the eaglet

This was assessed by observing eaglets nearing the ends of their post-fledging periods for signs of harassment from their parents. Young of Pairs No.6 (1975 , 1976 & 1977), 8 (1976), 83 (1977) and 86 (1976) were accordingly observed.

11.3 RESULTS

11.3.1 The fledging period

The fledging periods of 28 young from the 3 brood sizes averaged 76 days. Although the fledging periods were significantly correlated to brood sizes (Fig. 11.1), brood sizes did not significantly influence the fledging periods (Table 11.1). The shortest fledging period (62 days) was recorded for a 1-young brood (Pair No. 82) from which measurements were regularly taken. Three days before it left the nest this young was ringed and other measurements taken. The day it first flew it did so because I was approaching it for more records. Thus its flight could have been premature.

Another factor that seemed to affect the duration of the fledging period was the nest site. Nests sited among branches of trees were not ideal for pre-flight exercises and eaglets reared in such nests seemed hampered in their practices by branches overhanging the nests. However, the mean fledging periods of young reared in open and "closed" nest sites were not significantly different from each other (Table 11.2).

11.3.2 The first flight

Before making its first flight an eaglet did a lot of wing-flapping and jumping exercises on the nest or nearby branches of the nest tree. On 25 September 1975 the following record was taken on an eaglet's practice for its maiden flight:

> 16:00; overcast, cool but strong wind and then drizzle; between 16:00 and 16:15 both young of Pair No. 6 were lying flat on the nest floor; adult male brought elephant Loxodonta africana dung bollus, placed it on the nest floor and left immediately; none of the young stirred; about 16:15 both eaglets got up, flapped their wings vigorously; at 16:30 one of them was lifted clear off the nest, about 0.5 m above the nest floor, with the wings

Fig. 11.1 The relationship between fledging period and brood size in the African Fish Eagle. N = 4 young for B/1, n = 18 young for B/2 and n = 6 young for B/3; means and standard deviations shown.

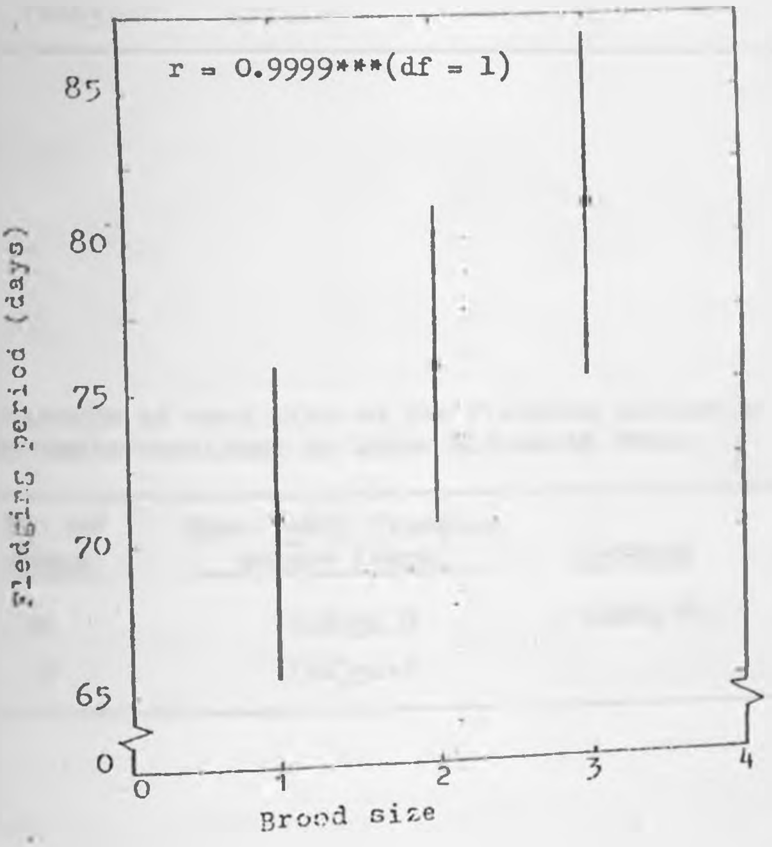


Table 11.1 The fledging periods of 28 young Fish Eagles in Queen Elizabeth Park in relation to brood size. For comparing the means of B/1 and B/3, Student's t was calculated using the formula for small sample sizes.

Brood size	No. of young	Fledging period (days)		t-value	df
		Mean ± SE	Range		
B/1	4	70.5±2.5	62-75	B/1 vs B/2 0.473 NS	20
B/2	18	75.7±1.2	66-83	B/2 vs B/3 0.868 NS	22
B/3	6	81.0±2.4	73-90	B/1 vs B/3 0.422 NS	8
Overall mean ± SE		76.1±1.2			

Table 11.2 The influence of nest site on the fledging periods of 28 Fish Eagle nestlings in Queen Elizabeth Park.

Nest site	No. of young	Mean (±SE) fledging period (days)	t-value	df
Crown (open)	24	75.92±1.3	0.067 NS	26
Fork (closed)	4	77.25±1.9		

> out-spread; the tail feathers too were spread out and slightly depressed; both legs were extended and their talons outspread; the uplift lasted only a few seconds and was performed against the wind; coming down onto the nest was very gentle so that the eaglet looked as if it was hovering; both chicks tried, almost alternately, and a total of 7 such hoverings were witnessed in about 20 minutes; several attempts, however, did not result in uplifts; the latter type of attempts were performed with the talons firmly gripping the nest materials so that, with the wings and tail out-spread and the legs fully extended, the eaglet looked like resisting forceful detachment from the nest.

Such exercises were witnessed after the feathering stage, and they were not limited to windy days. From about 50 days of age these exercises became more frequent. These hoverings foreshadowed the eaglet's leaving the nest.

The maiden flights were made when the adults were away from the nests and apparently out of view of the young. Two young reared in the nest of Pair No. 6 in 1976 made their first flights on 23 and 29 October (80th & 83rd days of ages respectively). Chick No. 1 (C_1) made a short and clumsy downslope glide from the nest, sited on a ca. 12 m high *Euphorbia dawei* tree, and alighted some 70-80 m away on a bare patch of ground at 15:43. Before returning to the nest at about 18:15, it made several short hops and flapping flights up the slope. At about 17:25 it made a franctic effort and flew up to the lower branches of another *E. dawei*, 20-25 m away from the nest tree. From 17:25 to 18:15 the eaglet did not attempt any more flying, it simply preened its fluffed feathers. The parents did not seem concerned; they hunted, rested, and flew around. Each time a parent passed overhead the eaglet looked at it but only briefly.

The second eaglet of this pair made its flight at 15:45 on 29th October 1976. The flight was again downslope, a short glide of about 50 m. It landed very clumsily on the crown of a short

E. dawei tree. C_2 went back to the nest at about 18:00, again through a series of short flights and hops up the slope. It ascended to the nest by making a more-or-less down-slope flight from the crown of another *E. dawei*. the same tree used by C_1 on its maiden flight.

The single eaglet of Pair No. 82 made its first flight on its 62nd day of life and this flight was thought to have been premature. Its flight was fairly long, a clumsy flapping flight of about 250-300 m. It consisted of many turns, apparently in search of the parents as it eventually alighted by one of them. The initial course of the flight was down-slope but this could have been by chance since the eaglet re-oriented its flight path towards the parents, a near right angle turn from the initial direction.

Alighting on a bush did not present as great problems to an eaglet doing so for the first time as landing on a tree like *E. candelabrum*. Eaglets landing on the straight and upward pointing branches of these trees regularly missed the tips of the branches and a struggle ensued to regain station. It looked as if the eaglet alighted on the chest; frantically beating its wings, it tried to climb the branch and get to the tip. These frantic efforts to regain station on *E. candelabrum* branches were not limited to eaglets only; adults also often failed to make proper landings on such branches.

11.3.3 The feeding of the eaglet

In 9.03 eagle-days of observations on 6 pairs with post-fledging young, the 12 adults caught a total of 24 fishes (about 15,640 g, Table 11.3). The data would give an average of 2.22 prey items (1,447 g) per pair per eagle-day or 1.11 prey units

Table 11.3 The amount of prey captured and delivered by 6 pairs of Fish Eagles to their post-fledging young. One eagle-day = 13 hours, i.e. 0630–1930 hours; figures in parentheses are actual numbers of prey items captured or delivered by the respective sexes during the respective periods (eagle-days) of observations; figures outside parentheses are prey units captured or delivered by respective adult per eagle-day; to change prey units into actual weights multiply by 651.7g, the mean weight of each prey item (see section 4.3.5.2).

No. of young	Obs. time	Prey captured/day			Prey delivered/day		
		Male	Female	Total	Male	Female	Total
1	1.86	0.54 (1)	1.08 (2)	1.61 (3)	0.00 (0)	1.08 (2)	1.08 (2)
1	0.71	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
2	4.67	2.14 (10)	1.28 (6)	3.43 (16)	0.86 (4)	1.28 (6)	2.14 (10)
2	0.64	0.00 (0)	3.13 (2)	3.13 (2)	0.00 (0)	3.13 (2)	3.13 (2)
2	0.42	2.38 (1)	0.00 (0)	2.38 (1)	0.00 (0)	0.00 (0)	0.00 (0)
2	0.73	1.37 (1)	1.37 (1)	2.74 (2)	0.00 (0)	1.37 (1)	1.37 (1)
Total 10	9.03	(13)	(11)	(24)	(4)	(11)	(15)
Mean		1.07	1.14	2.22	0.14	1.14	1.29
±SE		0.42	0.44	0.46	0.24	0.44	0.45

Table 11.4 An estimate of the amount of food availed to post-fledging young Fish Eagles in Queen Elizabeth Park in relation to brood size. Mean prey items delivered/pair/day obtained from raw data in Table 11.3; Available prey/adult/day = Mean prey delivered/pair/day multiplied by 651.7g, the mean weight of 1 prey item; Available prey/young/day = Mean prey delivered/pair/day multipled by the mean prey weight then divided by 2, this being so because the adult who caught the prey normally consumed about one-half the prey before delivering it to the young; and in a 2-young brood this quantity has to be halved again to obtain the food available to each eaglet. Figures in parentheses are the numbers of broods as in Table 11.3.

Brood size	Obs. time	Mean (±SE) prey items delivered/day	Available prey (g/day)	
			adult	young
B/1	2.57	0.54 ± 0.62	351.9	176.0
B/2	6.46	1.66 ± 0.57	1081.8	270.5
Total	9.03			
Overall mean±SE		1.29 ± 0.45	840.7	

(723 g) per adult per day. Of the 24 fishes, they delivered 15 of them to their young, an average of 1.29 prey items (841 g) per brood per day. If, however, as usually happened, only one of the parents ate a maximum of one-half the prey, a brood of 2 young would have available 0.65 prey (i.e. 420 g). Each young would, therefore, have available 0.32 prey unit (210 g) to itself, if they shared the prey equally. A brood of 1 young would, under the above conditions, have all the 0.65 prey (420 g) to itself. The derivation of the above estimates are shown in Table 11.4. Depending on the brood size it probably ranged from 0-300 g per young/day.

During this period both adults captured similar amounts of prey/day (Table 11.5). However, the female delivered significantly more prey to the young than the male (Table 11.5). Considering the sexes individually, the result further shows that the male delivered significantly far less prey than he caught (Table 11.5), while his mate delivered all those she captured. Pairs caring for 2-young broods captured significantly more prey than those supporting 1-young broods (Table 11.6). Although the 2-young brood was availed slightly more prey items than the 1-young brood, the amounts did not differ significantly (Table 11.6). Parents did not deliver to their young all the prey captured; the amounts each brood size received did not differ significantly from what the adults had obtained (Table 11.6).

Food deliveries to young were effected on the nest, ground, feeding perches, and aerially(Table 11.7). At the start of the post-fledging period young begged for prey from the nest and food was delivered to them on the nest. As they approached independence, feeding on the ground or perches became more regular. This shift

Table 11.5 Comparisons of amounts of prey captured and delivered (per eagle-day) to post-fledging young Fish Eagles in order to evaluate the roles of the sexes in feeding their young. Raw data from which mean data were calculated are in Table 11.3.

	Mean (±SD) prey captured/day	Mean (±SD) prey delivered/day	t-value	df
Male	1.07 ± 0.96	0.14 ± 0.32	3.277**	10
Female	1.14 ± 1.05	1.14 ± 1.05	0.000 NS	10
t-value	1.116 NS	2.886*		
df	10	10		

Table 11.6 Comparisons of the amounts of prey captured and delivered (per eagle-day) to post-fledging young Fish Eagles in relation to brood size. Raw data in Table 11.3; for within-brood comparisons proceed across the page and down the page for between-brood ones; Student's t was calculated using the formula for small sample size.

Brood size	Mean (±SD) prey captured/day	No. of pairs	Mean (±SD) prey delivered/day	No. of pairs	t-value	df
B/1	0.81 ± 0.81	2	0.54 ± 0.54	2	0.277 NS	2
B/2	2.92 ± 0.39	4	1.66 ± 1.14	4	1.805 NS	6
t-value	3.507*		1.073 NS			
df	4		4			

Table 11.7 A record of where prey were delivered by adult Fish Eagles to their post-fledging young in Queen Elizabeth Park (N = 15 prey items).

Pair No.	No. of young	Number of times prey delivered on: Nest	Ground	Perch	Aerially
8	1	0	2	0	0
87	1	0	0	0	0
6	2	3	3	1	2
1	2	0	2	0	0
88	2	0	0	0	0
82	2	0	2	0	0
Total	10	3	9	1	2

Table 11.8 A record of whether or not prey were delivered whole and with or without struggle by adult Fish Eagles to their post-fledging young in Queen Elizabeth Park (N = 15 prey items).

Pair No.	No. of young	Number of times prey delivered Whole	Remains	With struggle
8	1	1	1	1
87	1	0	0	0
6	2	0	10	7
1	2	0	2	2
88	2	0	0	0
82	2	0	1	1
Total	10	1	14	11

in feeding station was largely an outcome of the young following and incessantly begging from adults immediately they made kills.

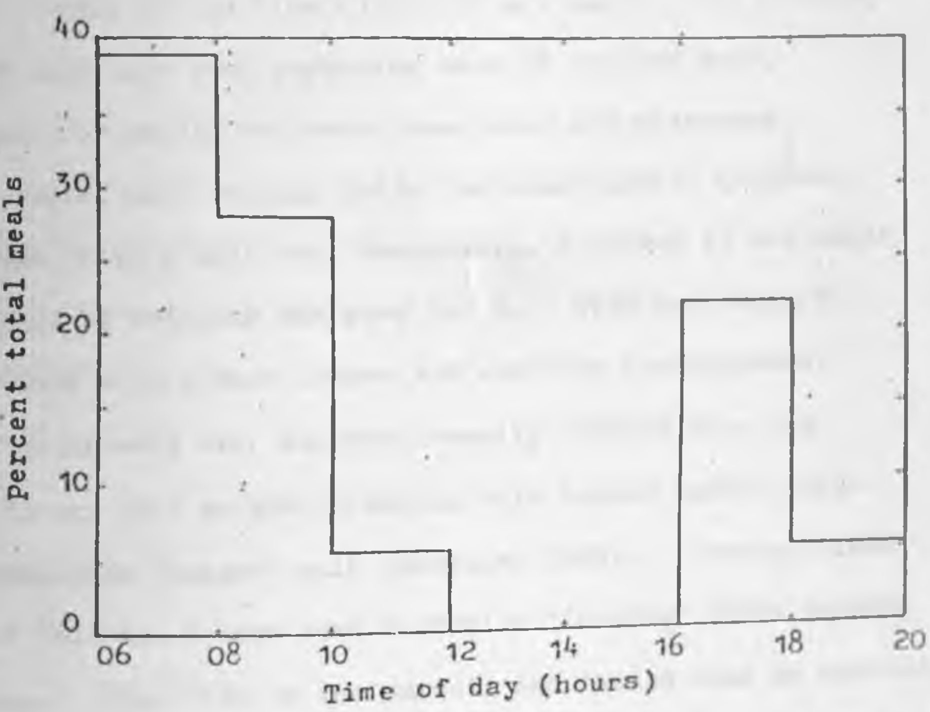
Eaglets fed largely on remains of prey already eaten by either of the parents, and they got them after prolonged begging and chasing of the adults (Table 11.8). An observation on 16 April 1976 on Pair No. 1 and their 2 young illustrates this point:

> 06:30-06:44, adults perched together; both young on a perch about 80 m away; 07:45 female killed a ca. 500 g Tilapia sp; between 07:45-08:15 she fed on the ground but changed places 4 times because both young were incessantly begging and attempting to grab prey from her; 08:15 one of the young successfully grabbed the prey after a short struggle with the adult and fed till about 09:05, and all along the second young made vain attempts to secure the prey from the first (cf with behaviour of nestlings, section 9.3.5); it apparently got satisfied and left the remains of the prey to the sibling which fed until 09:45.

Fig. 11.2 shows the distribution of meals of post-fledging young in relation to the time of the day. Although the sample size is small, the figure shows that two-thirds of the meals occurred early in the morning between 06:00-10:00 and one-fifth of them in the evening between 16:00-18:00. Much as nestlings received food throughout the day (Fig. 10.7 & section 10.4.3), the timing of their peak feedings were similar to those of post-fledging young.

There was no sustained observation to ascertain how regularly adults supplied their post-fledging young with prey. Available data, however, would suggest that eaglets obtained remains of prey as the parents had them, at least once every two days. In 9.03 eagle-days of observation on 6 pairs (Table 11.3), the adults caught a total of 24 prey items of which the young partook in 15 (62.5%) of them. Although these observations were not continuous, they give a measure of the proportion of prey in which young took part.

Fig. 11.2 The feeding time of post-fledging African Fish Eagle in Queen Elizabeth National Park (n = 18 prey).



Since paired adults caught prey almost daily, the young must have eaten a minimum of 50% of them.

Eaglets supplemented the food they obtained from their parents by making their own kills, especially towards the end of the post-fledging periods. By 52 days after first flight (131 days of age), both young of Pair No. 6 were spending considerable proportions of their time hunting by perching close to the shoreline where they made stoops at both living and non-living objects in the water. At 66 days after the maiden flight (145 days of age), C_1 killed a tiny fish. Thus by the time an eaglet was leaving the parental territory it must have been capturing most of its own prey.

Food calls by adults to their young were not witnessed. Instead, an eaglet made begging calls (swii-swii-swii) whenever, it saw a parent with a kill and, invariably, followed if the adult did not respond by bringing the prey to it. This call was at times alternated with a much louder and shriller (ook-ook-ook) one. The latter call was, however, usually uttered when the eaglet was hungry just as post-fledging Bald Eagles made a gull-like yaap-yaap-yaap "hunger" call (Retfalvi 1965). Several times the young of Pair No. 6 were seen virtually "forcing" their parents to go hunting. They flew to the parents and landed near or circled over them while making this call as if alarmed. Both types of calls were very common in the late afternoons and evenings although they could be heard any time of the day. Once a young has had a satisfying meal the calls ceased even if it had been very noisy prior to the meal.

Begging for food in the Fish Eagle begun when a young saw one of its parents, its sibling, or even an intruder Fish Eagle with prey.

Begging consisted of the young standing in a submissive posture with the head almost levelled, the neck extended and the wings slightly spread out and drooped. This posture was accompanied by the begging call. If no response was shown by the feeding bird, then a normal attitude was assumed although the calls often continued. Begging continued until food was delivered or finished. If the feeding bird tried to fly away the eaglet normally followed. Begging was effected from the nest, ground or a perch. On several occasions, however, the young flew to the nest to beg although it might have started doing so elsewhere when a parent first appeared with prey. This indicated that an eaglet still regarded the nest as a normal feeding place.

Adults often soared with prey (and also with non-food items) in their talons when an eaglet was begging for food. Frequently, the young followed the soaring adult and occasionally succeeded in wresting prey off its talons. The 2 aerial food-passes listed in Table 11.7 occurred in this context. Although adult mates delivered prey to each other, no aerial food-passing between them was ever witnessed.

At times both adults and young soared with twigs or pieces of fish-nets. Elements of piracy began to appear in the post-fledging young during these soars. It approached the adult, and when directly below it the eaglet rolled over on its back and extended its legs and contact was invariably made. The young bird often successfully grabbed away from the talons of the adult whatever it was carrying. This involved not only grabbing items from its parents but also objects from its own siblings. This is how independent young, usually travelling in bands, pirated and lived off the food of territorial adults (see section 4.3.2). As if to perfect the pirating technique several such soars, usually of short durations, were made almost daily. The fact that I did not observe paired adults passing food to each other in this manner, but regularly saw them robbing from adjacent pairs would suggest that this was apparently the appearance of the piracy trait in the young Eagle.

11.3.4 Roosting of eaglets

Eight eaglets from 5 broods started roosting on perches when 99 days old (Table 11.9). The mean ages at perch-roosting for the 2 brood sizes were not significantly different from each other. The intervals between first flight and perch-roosting averaged 22 days and brood size did not significantly influence it. In both cases, however, larger samples are needed on all brood sizes, especially B/1 and B/3, in order to meaningfully interpret whether or not social stimulation of siblings in 2- and 3-young broods caused eaglets to become more exploratory and prying, which could have encouraged them to roost earlier than those from 1-young broods.

When it stopped sleeping on the nest, the eaglet usually roosted on the same tree as its parents. In late 1976 and early 1977, however, the 2 young of Pair No. 6 roosted on the lower branches of the nest tree some 100 m away from the roost tree of the adults.

11.3.5 The post-fledging period

The post-fledging periods of 19 young from the 3 brood sizes averaged 112 days (Table 11.10). There was no significant correlation between post-fledging period and brood size ($r = 0.0997$, $df = 1$, $P > 0.1$). Larger sample sizes are needed, especially for B/1 and B/3,

Table 11.9 The age of Fish Eagles in Queen Elizabeth Park at the time of perch-roosting and the interval between maiden flight and perch-roosting in relation to brood size. Student's t was calculated using the formula for small sample sizes, df = 6 in both cases; ages of young and intervals between flight and roosting are in days.

Brood size	No. of young	Mean age ±SE	t-value	Mean interval ±SE	t-value
B/1	2	101.0 ± 2.1	0.782 NS	25.0 ± 0.7	0.771 NS
B/2	6	97,8 ± 1.9		21.5 ± 2.2	
Overall mean±SE		98.6 ± 1.6		22.4 ± 1.8	
Range		93 - 105		13 - 27	

Table 11.10 The post-fledging periods (days) of 19 young Fish Eagles in Queen Elizabeth Park in relation to brood size.

Brood size	No. of young	Post-fledging period Mean ± SE	Post-fledging period Range	t-value		df
B/1	3	115.0 ± 3.3	110 - 123	B/1 vs B/2	0.095 NS	11
B/2	10	109.3 ± 3.3	99 - 135	B/2 vs B/3	0.146 NS	14
B/3	6	115.7 ± 1.1	112 - 120	B/1 vs B/3	0.129 NS	7
Overall mean±SE		112.2 ± 2.0				

in order to establish the nature of the relationship. However, the mean periods of young from the 3 brood sizes did not differ significantly.

11.3.6 Departure of the eaglet

On 17 August 1976 Pair No. 83 had 3 newly hatched chicks in the nest. By late October-early November all 3 young were flying around in the territory. On 7 February 1977 one of the adults was seen chasing and buzzing the eaglets. On 11 February another bout of chasing and buzzing occurred, and this time both adults participated. In the afternoon of 15 February yet another attack on the young was recorded. By 18 February one of the eaglets had disappeared and was presumed to have left the territory. On 27 February and 2 March the remaining 2 eaglets were still being harassed by the adults. On 5 March only 1 eaglet had remained in the territory but by mid-March it too had departed.

On the evening of 19 January 1977 the female of Pair No. 6 attacked and chased 1 of their 2 young hatched in early August 1976. The adults were hunting separately at the borders of their territory when this incident occurred. As the young flew towards the female she attacked it, and it retreated to their roosting branch on the nest tree, hotly pursued by the adult. The other young also took off from their original perch and joined its sibling. The female returned, without any further attack on the eaglet, to the same perch from which it had been hunting prior to the encounter and continued hunting. The male however, remained unconcerned during the incident. By the end of February 1977 both eaglets had left the territory. This was the only such incident for Pair No. 6 during the 3-year study period during which it fledged three 2-young broods.

Several other pairs were observed during the post-fledging periods but no attacks on young were ever witnessed. During attacks by the parents the eaglets made the ook-ook-ook alarm calls and either dodged or turned on their backs, with the legs and talons extended, to parry the attacks.

The adults, on the other hand, gave the normal duets or individual calls uttered when pursuing intruders. When being chased, eaglets tended to keep together just as bands of independent young did when passing through territories (section 4.3.2.2). Once the adults were too close to them the eaglets alighted, usually on the ground, and retreated into the nearest bushes. They also alighted on the lower branches of trees with dense canopies from which they were difficult to dislodge.

11.4 DISCUSSION

Brown (1976a, b & c) reported that the fledging periods of the Fish Eagle <u>Haliaeetus</u> <u>vocifer</u> and the White-bellied Sea Eagle H. <u>leucogaster</u> are between 65-80 days, the Sea Eagle <u>H</u>. <u>albicilla</u> 70-90 days, and that of the much larger Pallas' Sea Eagle <u>H</u>. <u>leucoryphus</u> 70-105 days. Roberts (1958) estimated that a South African pair of Fish Eagles fledged its 2-young brood in a period of about 60 days. Nestling Fish Eagles in this Park left the nest between 62 and 90 days of age.

In eagles in general, a larger brood takes longer to fledge than a smaller one (Brown 1976b). During this study the fledging period of the Fish Eagle was directly related to brood size and young from the 3 brood sizes fledged at similar ages.

At Lakes Victoria and Naivasha eaglets dispersed 2-3 months after their first flights or 4-5 months after hatching (Brown, op cit.; Brown & Hopcraft 1973). The Sea eaglet leaves the parental territory about 2 months after its first flight or when 4-5 months old (Brown 1975c) and the young Bald Eagle departs when 5-6 months old (Snow 1973a). The Fish Eaglet in this Park left its parental territory 3-4.5 months after first flight or 5.5-7 months after hatching. Thus the eaglet became independent of its parents 1.5-2 months later than that of L. Naivasha. It also dispersed about 2 months later than the related Sea Eaglet but at about the same age as the Bald Eagle young (Brown, op.cit.; Snow, op.cit.).

Young Snake Eagles (Circaetinae), Crowned Eagles Stephanoetus coronatus and Harpy Eagles Harpia harpyja are believed to have protracted post-fledging periods in order to better prepare them to survive the dangerous periods between independence and sexual maturity (Brown 1976a). Since the Fish Eagle is strongly territoral and highly piratical (Brown 1976b; sections 3.3.2.1 & 4.3.2.2), the late dispersal of its young as compared with those of the related temperate Sea Eagle may be necessary to give the young more time to better prepare to fend for itself at independence. It must be able to kill prey for itself and to defend the prey from conspecifics and other large piscivorous birds (Chapter 4). It must also be able to defend itself against the attacks of other adult Fish Eagles through whose territories it has to pass in order to survive. The late dispersal of young may also reflect the apparent ease with which parents actually obtain prey.

The maiden flight of the young Fish Eagle occurred without apparent parental coaxing and usually in the absence of the adults just as in the young Bald Eagle (Retfalvi 1965; Kassman & Frenzel 1972) and the Sea and Golden Eagles (Brown 1976b & c). Extensive pre-flight exercises were necessary precursors to the flight. Despite these practices the maiden flight was short and awkward compared with those of adults. It looked uncoordinated and apparently aimless as those of the young Bald Eagle (Kussman & Frenzel, op.cit.). The landing too was awkward and uncoordinated, with the bird clumsily falling, as it were, on the ground, bush or tree; again similar to the landing of the young Bald Eagle (Retfalvi, op.cit.)

Throughout the post-fledging life of the young Verreaux's Eagle Aquila verreauxi the adults bring prey to the nest. Both the Crowned and Verreaux's Eagles make food calls to the young, and in the former food is delivered onto the nest only when the young solicits for it (Brown 1976b).

Adult Fish Eagles did not give food calls to their young during this study. This could be so because nearly all prey killed by the adults were in full view of the young. Earlier in the post-fledging period, food for the young was brought and delivered to it on the nest and the eaglet solicited for feeding from the eyrie. As the young approached independence, however, it did not allow adults to bring prey to the nest; it followed them and received or grabbed prey wherever the parents had alighted to feed.

As in the Crowned Eagle (Brown, op cit.) and the Osprey Pandion haliaeetus (Stinson 1978), both adult Fish Eagles brought prey to their young. In all three species, however, the female delivered significantly more prey items than the male. Working on the time budget of breeding Osprey Stinson (op.cit.) suggested that the increasing length of hunting trips by the foraging male with unfledged young appeared to be due to his declining attentiveness to hunt and not to the increasing difficulty of capturing prey. The male Fish Eagle could similarly have provided far less prey to their post-fledging young than he captured because of his declining attentiveness to the young. He caught similar amounts of prey as the female and she did not collect prey from him as she did during the nestling period (section 10.3.3). In the Verreaux's Eagle the female claims all prey items from the male and delivers them herself to the young (Brown, op.cit.).

In Crowned Eagle and Verreaux's Eagle only prey remains are brought to post-fledging young (Brown, op.cit.). The African Fish Eagle behaved similarly. Stinson (op.cit.) does not mention whether or not Ospreys gorged themselves before delivering prey to their post-fledging young.

Post-fledging young of most species of eagles supplement the food supplied to them by their parents by making their own kills (Brown 1976b), and this was also true of Fish Eagles. The earliest observed kill was 66 days after flight, a comparable age with a young Crowned Eagle whose earliest kill was 61 days after the maiden flight (Brown, op.cit.).

An Osprey young reportedly killed its first prey within a week of leaving the nest (Brown 1976c).

According to Brown (1976b & c) piracy is thought to have evolved from the carrion-eating habit and is a common feeding strategy in groups of birds such as kites (Elaninae and Milvinae), Sea and Fish Eagles (Haliaeetinae), the Bateleur Terathopius ecaudatus, vultures (Aegypiinae), and caracaras (Polyborinae). It is almost a compulsive trait of the Fish Eagle who will rob prey from all large fish-eating birds. It will also pirate from other Fish Eagles including its own young and mate. An incubating bird will leave the nest to pursue another Fish Eagle with prey (Brown 1976b & 1980). Piracy is one of the methods immature Fish Eagles use to obtain prey from large piscivorous birds and from paired adult Fish Eagles as the young wander through their territories (section 4.3.2.2). Since almost all kills by adults were made within sight of the young, a hungry eaglet could not permit adults to feed first. This could have led to the development of the prolonged begging behaviour and perhaps piracy in the young because adults were not prepared to relinquish prey before they themselves have fed. The regular soaring flights performed by adults with prey in their talons and the subsequent following and grabbing of the prey from the talons of the adults by young probably assisted the young in perfecting the pirating habit.

How young raptors leave their parental territories still remains to be resolved. It is often supposed that at the end of the post-fledging period the young were driven away by the adults but evidence for this is in most species slight or non-existent (Brown 1976c). In all probability they simply leave the parental areas of their own accord although a young Verreaux's Eagle was seen to be driven away by the parents (Brown 1976a). The repeated attacks on young buzzards Buteo spp. and Fish Eagles by their parents were interpreted by Brown as being regular territorial behaviour rather than deliberate expulsion of the young. Additional observations are required in order to establish whether or not adult Fish Eagles expelled their eaglets from their territories or the young left of their own accords. The reason for an Eaglet to leave its parents' territory remains unclear, but some or all of the following aspects of the biology of the African Fish Eagle merit attention in future investigations:

(i) parental attacks and their possible effects on the dipersal of the eaglet;

(ii) the regularity of parental feeding of the post-fledging young, especially as it approaches independence;

(iii) the capability of the young to:- (a) defend itself, (b) catch its own prey, (c) defend its prey and (d) pirate; and

(iv) the possible influences of other independent young passing through the parental territory.

CHAPTER 12

NEST PRODUCTIVITY

12.1 INTRODUCTION

This Chapter presents data on the breeding success of the Fish Eagle in Queen Elizabeth National Park and appraises it in relation to some environmental factors. The relationships between clutch size and hatching success, clutch size and productivity, and brood size and nestling survival are examined. The influences of territory size, density of mature trees in the territories, and of human disturbance about the territory on the breeding success of the bird are discussed.

12.2 METHODS

12.2.1 Terminology

The terminology used in this Chapter follows Postupalsky (1974) and is thoroughly defined there. The terms used here are briefly defined as:-

Territory: an area containing one or more nests, used by a mated pair of birds, usually for many years in succession. Occupied: a nest or territory used by a mated pair of birds, regardless of whether breeding or not. Active: a nest or territory in which eggs were laid. Successful: a nest or territory or pair producing fledged young. Unsuccessful: a nest or territory or pair not producing fledged young (includes non-breeding, hatching-failure and losses of whole broods). Nest success: the proportion of occupied nests or territories producing fledged young. Productivity: the average number of fledgling per occupied nest.

12.2.2 Sampling methods

In seasonally breeding raptors, especially those of temperate regions, a minimum of two visits to each occupied nest is enough to determine which nests are occupied, and to calculate nest success and productivity (Postupalsky, 1974). Because the birds of this Park breed throughout the year (section 6.3.1), breeding surveys on them were carried out fortnightly. Additional checks were made on some occupied nests as and when necessary.

In the study area, all occupied nests were checked for the numbers of eggs laid, and young hatched and fledged. In all nests where hatching occurred, minimum clutch size (section 12.3.3) was determined from the numbers of hatchlings and unhatched eggs.

Fish Eagles showed different population densities along the shorelines of water bodies in the Park (see Fig. 2.1 & section 2.3.2). The influence of varying densities on the breeding success of the birds was assessed by correlating productivity data with territory sizes. The birds also exhibited different densities along shorelines in relation to their woodedness, and mature trees were considered one of the vital resources in their nesting requirements (section 2.3.1). Thus nest productivity was correlated with the numbers of mature trees in the territories. In assessing breeding success in relation to the numbers of trees all territories were categorised into those having 0-4, 5-9, 10-19, 20-29, 30-49, and 50 + trees in them. For each territory all mature trees were counted.

In the main study area there are 3 human settlements: namely Mweya Peninsula which harbours the headquarters of the Park, Mweya Safari Lodge, and the Uganda Institute of Ecology; and Kazinga and Katunguru Fishing Villages (see Fig. 1.3). In increasing distances from each of the fish-landing piers of Katunguru Toro, Katunguru Ankole and Kazinga, breeding records were kept for 6 pairs of Eagles. The pairs observed were Nos. 79–84 for Kazinga, 40a–44 for Katunguru Toro, and 45–50 for Katunguru Ankole (see Fig. 3.1). Productivity data for these pairs were correlated with their increasing distances from the piers. In assessing the effects of human disturbance on the breeding success of the birds, I assumed that pairs with territories nearest human centres received the highest levels of interference with their breeding activities.

12.3 RESULTS

12.3.1 Clutch size and hatching success

The clutch size of the Fish Eagle, during this study is discussed in section 7.3.2. This section, therefore, discusses the influence of clutch size on the hatching success of the birds.

In the sample Fish Eagle population with known clutch sizes hatching success did not differ significantly between clutch sizes and between years (Table 12.1). The 1-egg clutches, however, hatched all their eggs, and hatching success decreased significantly with increasing clutch size ($r = -0.9990$, $df = 1$, $P < 0.05$). The mean hatching successes also did not differ significantly from year to year ($t = 0.397$ for 1975/6 vs 1976/7, $t = 0.031$ for 1976/7 vs 1977/8, and $t = 0.507$ for 1975/6 vs 1977/8; $df = 4$ and $P > 0.1$ for each test).

Of 132 eggs laid in the known clutches, 30 (23%) of them did not hatch. Egg mortality did not differ significantly with clutch sizes and the causes of hatching failure (Table 12.2). However,

Table 12.1 The hatching success of the Fish Eagle in Queen Elizabeth Park in relation to clutch size. N = number of known clutches; for each entry the first figure represents percent hatching success and the second, in parentheses, the frequency of clutches; Chi-square test was performed on percent hatching success.

Period	N	Total eggs	Clutch size 1	Clutch size 2	Clutch size 3	Mean
1975/6	22	43	100.0 (8)	100.0 (7)	57.1 (7)	85.7
1976/7	22	41	100.0 (6)	69.2 (13)	66.7 (3)	78.6
1977/8	24	48	100.0 (3)	77.8 (18)	77.8 (3)	85.2
Total	68	132	(17)	(38)	(13)	
Mean			100.0	82.3	67.2	83.2
			$X^2 = 8.549$ NS, df = 4			

Table 12.2 The frequencies of unhatched Fish Eagle eggs in Queen Elizabeth Park in relation to clutch size and the causes of hatching failure. For each entry the first figure represents the number of eggs and the second, in parentheses, the percent frequency. Chi-square test was carried on percent frequency.

Cause of hatching failure	Clutch size 1	Clutch size 2	Clutch size 3	Total
Breakage	0	0	2 (14.3)	2 (6.7)
Chick death	0	0	1 (7.1)	1 (3.3)
Infertility/addling	0	1 (6.2)	5 (35.7)	6 (20.0)
Disappearance	0	15 (93.8)	6 (42.9)	21 (70.0)
Total eggs lost % of eggs laid	0	16 (100.0)	14 (100.0)	30 (100.0)
	$X^2 = 7.495$ NS, df = 4			

the 1-egg clutches incurred no losses while the 2-egg and 3-egg clutches lost 21.1% and 35.9% of their eggs respectively. The fact that the 1-egg clutches were not affected by any of the mortality factors is important in that it shows that either that all C/1 eggs were all fertile or that during incubation they were all properly covered by the sitting birds so that embryo death could not occur. The finding that egg breakage was the least important mortality factor and that it never affected the 1-egg and 2-egg clutches precludes it as a significant cause of hatching failure. The 2 eggs which broke were apparently cracked by the departing birds as I approached their nests for clutch size determination and other egg measurements. Both eggs subsequently disappeared without trace and were probably predated by the incubating birds. In one nest only the cracked egg disappeared while in the second nest an intact egg also disappeared leaving the third egg to hatch. It was not established whether the infertile/addled eggs did not hatch due to actual infertility or due to embryo death during incubation. The 21 remaining eggs disappeared without trace and were probably lost to predators.

12.3.2 Clutch size and productivity

In Fish Eagles whose clutches were known, the numbers of young/successful nest did not differ significantly between years and between the clutch sizes (Table 12.3). In the population of the whole study area, the numbers of young/successful nest were also similar between years and clutch sizes (Table 12.3). Comparing the 1975–78 frequencies, this productivity was similar in birds with known clutches and those of the whole study population ($X^2 = 0.0001$, df = 2, $P > 0.1$). Nonetheless, for both

Table 12.3 The productivity of the African Fish Eagle in Queen Elizabeth Park in relation to clutch size. N = number of successful nests; for each entry the first number represents the number of young/successful nest and the second, in parentheses, the number of successful nests; Chi-square test carried out on the number of young/successful nest.

Source of data	Period	N	No. young fledged	Clutch size 1	Clutch size 2	Clutch size 3
Known clutches	1975/6	11	17	1.0 (3)	2.0 (3)	1.6 (5)
	1976/7	12	19	1.0 (4)	1.71 (7)	3.0 (1)
	1977/8	14	27	1.0 (2)	2.0 (10)	2.5 (2)
	1975-78	37	63	1.0 (9)	1.90 (20)	2.0 (8)
				X^2 = 0.340 NS, df = 4		
Whole population	1975/6	26	36	1.0 (14)	2.0 (7)	1.6 (5)
	1976/7	27	41	1.0 (12)	1.86 (14)	3.0 (1)
	1977/8	36	56	1.0 (16)	1.94 (18)	2.5 (2)
	1975-78	89	133	1.0 (42)	1.92 (39)	2.0 (8)
				X^2 = 0.290 NS, df = 4		

Table 12.4 The frequencies of brood sizes of the Fish Eagle in Queen Elizabeth Park. N = number of broods.

Source of data	Period	N	No. of chicks	Brood size 1	Brood size 2	Brood size 3	Mean brood size
Known clutches	1975/6	21	34	9	11	1	1.62
	1976/7	20	30	11	8	1	1.50
	1977/8	20	38	3	16	1	1.90
	Total	61	102	23	35	3	
	Mean±SE						1.67±0.12
				X^2 = 7.396 NS, df = 4			
Whole population	1975/6	36	53	20	15	1	1.47
	1976/7	40	59	22	17	1	1.48
	1977/8	46	75	18	27	1	1.63
	Total	122	187	60	59	3	
	Mean±SE						1.53±0.05
				X^2 = 3.178 NS, df = 4			

populations the 2-egg and 3-egg clutches fledged twice as many young as the 1-egg clutches. These results, therefore, clearly demonstrate that in the Fish Eagle of this Park, laying 2- and 3-egg clutches was more advantageous in producing young than laying 1-egg clutches.

12.3.3 Brood size and nestling survival

For birds with known clutches, brood size averaged 1.67 chicks/nest and the frequencies did not differ significantly between the years of study (Table 12.4). Using minimum clutch data from the whole Fish Eagle population, brood size averaged 1.53 chicks/nest and the frequencies did not differ significantly between the years (Table 12.4). The average brood size obtained from known clutches and that calculated from minimum clutches were not significantly different ($t = 1.083$, $df = 4$, $P > 0.1$).

Nestling survival was highest in the 1-chick brood, intermediate in the 2-chick brood, and least in the 3-chick one (Table 12.5). Overall, nestling survival averaged 70.7%.

Brood size did not significantly influence the annual survival of young ($t = 1.308$ for B/1 vs B/2 chicks, $t = 0.369$ for B/1 vs B/3 chicks, and $t = 0.09$ for B/2 vs B/3 chicks; $df = 4$ and $P > 0.1$ for each comparison; data in Table 12.5). About 68% of 127 chicks hatched in the 2- and 3-young broods survived as whole broods, 29% of them disappeared as whole broods, and only 1.6% of them respectively survived and disappeared as parts of broods (Table 12.6). None of these chicks was found dead in the nest. These findings clearly demonstrate that sibling aggression and food shortage were not important factors in the survival of 2- and 3-young broods (see section 8.3.4). Although predation was not observed, these results

Table 12.5 Nestling survival in the Queen Elizabeth Park Fish Eagle in relation to brood size. Analysis based on whole Fish Eagle population in the study area.

	Brood size														
	1			2				3					Total		
Period	fledged	died	% survival	2 fledged	1 fledged	died	% survival	3 fledged	2 fledged	1 fledged	died	% survival	fledged	died	% survival
1975/6	15	5	75.0	20	1	9	70.0	0	0	0	3	0.0	36	17	67.9
1976/7	14	8	63.6	24	0	10	70.6	3	0	0	0	100.0	41	18	69.5
1977/8	16	2	88.9	36	1	17	68.5	3	0	0	0	100.0	56	19	74.7
Total	45	15		80	2	36		6	0	0	3		133	54	
Mean			75.8				69.7					66.7			70.7

Table 12.6 The frequencies of surviving and disappearing nestling Fish Eagles in Queen Elizabeth Park. N - number of chicks.

Brood size	N	Whole brood		Part brood	
		fledged	not fledged	fledged	not fledged
2/2	118	80	34	2	2
2/3	9	6	3	0	0
Total	127	86	37	2	2
%	100.0	67.7	29.1	1.6	1.6

would implicate it as a more important environmental factor in the survival of nestlings in this Park than were sibling aggression and food shortage (see sections 8.3.4 & 8.4).

12.3.4 Nest success and productivity

African Fish Eagles in this Park normally bred once a year (see section 6.3.3). However, because of losing clutches or broods early in their nesting cycles some pairs made replacement breeding attempts. For this reason, a pair of Fish Eagles or any raptor species occupying a territory for a year can be rightly described as a pair-year (Brown 1976a & 1980).

During this study annual Fish Eagle nest success was low averaging 44% for all active nests and 31% for pair-years present (Table 12.7). Productivities did not differ significantly between years although the success/pair-year was more varied, as indicated by percent C. Vs., than success/active pair.

Nest productivities averaged 0.46 young/pair, 0.65 young/active pair, and 1.49 young/successful pair (Table 12.7). Productivities did not differ significantly between the years of study although the percent C. Vs. show that young/pair overall was most varied while young/successful pair was least so.

The number of young fledged per pair of Fish Eagles increased with increasing territory size (Fig. 12.1). Although not statistically significant, the increased breeding success with increasing territory size nonetheless suggests that decreasing population densities of the Eagles improved their breeding success.

Breeding success also increased, although not significantly, with increasing numbers of mature trees in the Fish Eagle territories (Fig. 12.2). Since the Eagles in the Park nested on bushes as well

Table 12.7 Nest success and productivity of the Fish Eagle in Queen Elizabeth Park. Figure inside parentheses are the actual pairs of Fish Eagles present in the study area; those outside parentheses are pair-years present during the respective years of study; see text for definition of pair-year.

	Number of pairs			Total young	% nest success (pairs)		Productivity/pair		
Period	Studied	Active	Successful	fledged	All	Active	All	Active	Successful
1975/6	92 (86)	60	26	36	28.3	43.3	0.39	0.60	1.38
1976/7	97 (88)	67	27	41	27.8	40.3	0.42	0.61	1.52
1977/8	96 (85)	75	36	56	37.5	48.0	0.58	0.75	1.56
Total	285 (259)	202	89	133					
Mean	95.0 (86.3)	67.3	29.7		31.2	43.9	0.46	0.65	1.49
±S.d.	2.6 (1.5)	7.5	5.5		5.5	3.9	0.10	0.08	0.09
% C.V.	2.7 (1.7)	11.1	18.5		17.6	8.9	21.7	12.3	6.0
					X^2=0.323 NS, df=2		X^2 = 0.024 NS, df = 4		

Fig. 12.1 The influence of territory size on the breeding success of the Fish Eagle in Queen Elizabeth Park. In this analysis, 285 pair-years had 202 active nests with 133 fledged young. The graph shows only 8 points because all the active nests fitted in the following 8 territory size classes: 300-400, 400-500, 500-600, 600-700, 700-800, 800-900, 900-1000 and 1000+ m.

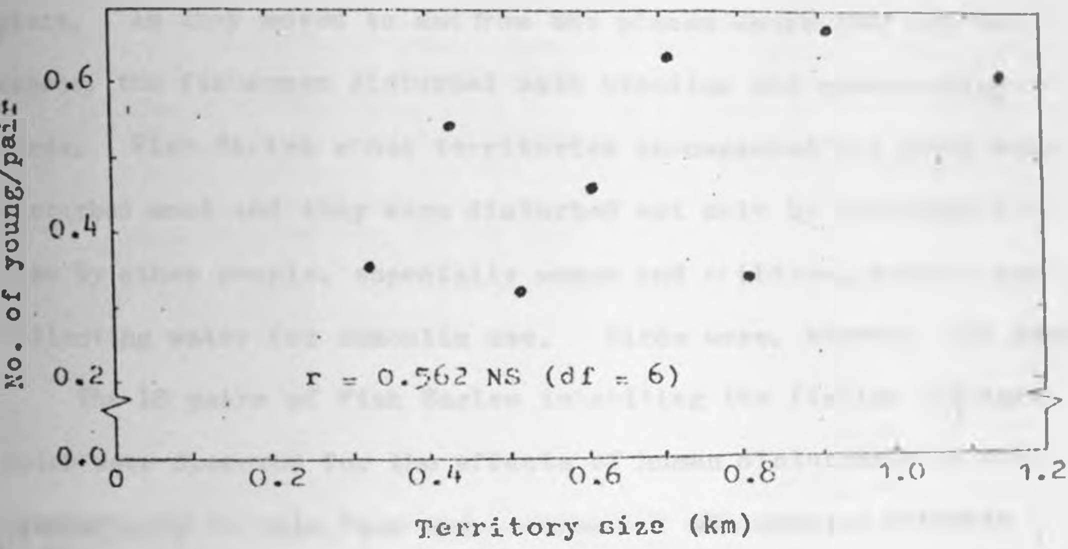
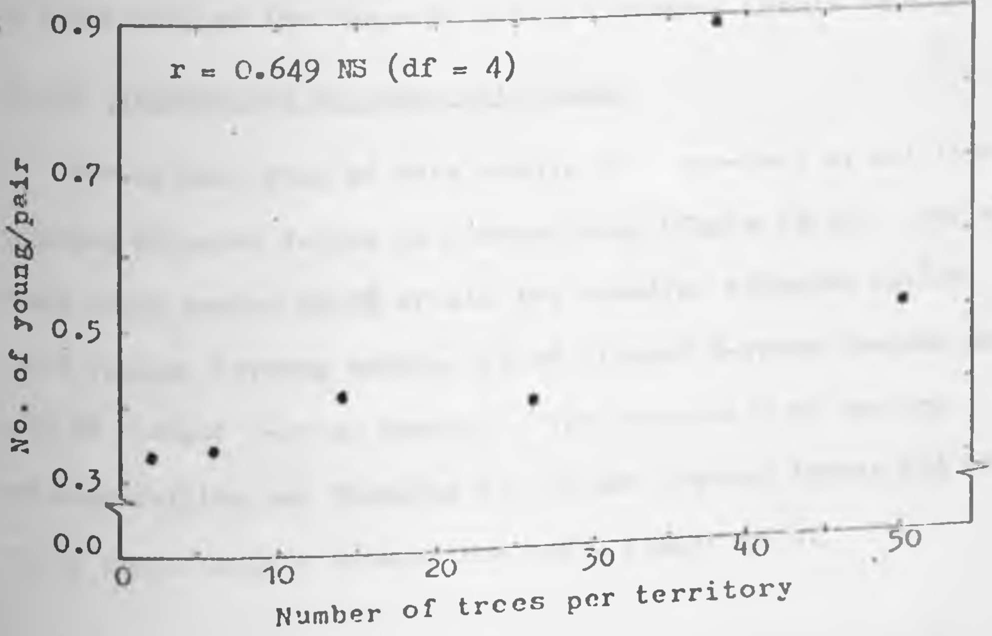


Fig. 12.2 The influence of the numbers of trees in the territories of Fish Eagles in Queen Elizabeth Park on their breeding success. Twenty randomly selected territories were used in this analysis. However, the graph shows only 6 points because of the grouping of territories according to the numbers of trees they had (see section 12.2.2). Thus each class absorbed more than 1 of the 20 sampled territories.



as stumps of trees (see Table 5.3), increasing numbers of mature trees provided them with more secure nest sites which probably increased the numbers of their successful breeding attempts.

After the day's poaching of fish, unlicenced fishermen hid their canoes upto about 1 km away from the gazetted fish-landing piers. As they moved to and from the places where they hid the canoes, the fishermen disturbed both breeding and non-breeding birds. Fish Eagles whose territories encompassed the piers were disturbed most and they were disturbed not only by fishermen but also by other people, especially women and children, washing and collecting water for domestic use. Birds were, however, not pelted.

The 18 pairs of Fish Eagles inhabiting the fishing villages which were observed for the effects of human disturbance on nest productivity in this Park made a total of 43 breeding attempts and fledged 34 young. Breeding data for them indicate that nest productivity increased, although not significantly, with decreasing human disturbance about the territory (Fig. 12.3). Since the numbers of breeding attempts and of young fledged by these pairs were significantly correlated ($r = 0.668$, $df = 16$, $P < 0.01$), human disturbance, therefore, significantly reduced the production of young only at the focus of the disturbance (Table 12.8).

12.3.5 Proportions of nests with young

During each year of this study, over one-half of all Fish Eagle breeding attempts failed to fledge young (Table 12.9). For the whole study period 56.1% of all the breeding attempts failed, 23.4% fledged 1-young broods, 19.5% fledged 2-young broods, and only 1% fledged 3-young broods. The frequencies of nesting attempts failing and fledging 1-, 2- and 3-young broods did not differ significantly between the years (Table 12.9).

Fig. 12.3 The influence of human disturbance on the breeding success of the Fish Eagle in Queen Elizabeth Park. The graph shows only 6 points although 54 pairs which made 43 breeding attempts and raised 34 young were used in this analysis because from each of the 3 fish landing piers (see last paragraph, section 12.2.2), each year, 6 pairs were observed for the effects of human disturbance on the breeding success of the Eagles. The pair at the pier corresponded to distance unit (territory) zero, the next to it corresponded to distance unit 1, ———, and the 6th pair away from the pier corresponded to distance unit 5. The numbers of active nests and young raised for each distance unit from all the 3 piers were pooled and permitted the calculation of the number of young/ active nest for the respective distance units, and were then used in plotting the graph.

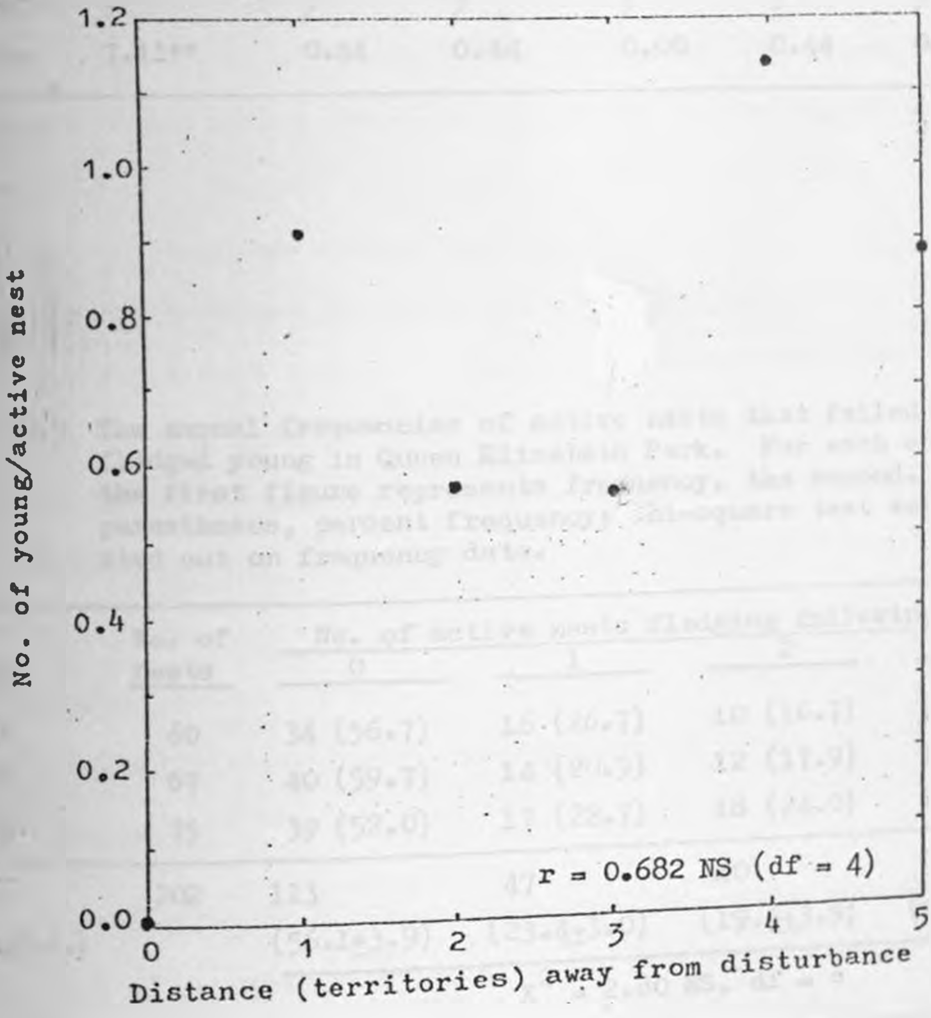


Table 12.8 The observed and the expected numbers of breeding attempts of Fish Eagles of Queen Elizabeth Park that held territories in the vicinities of fishing villages. For each Chi-square test, degrees of freedom = 1, and for each territory the number of pairs under observation = 3.

Breeding attempts	Distance (territories) away from disturbance					
	0	1	2	3	4	5
Observed	1	11	7	9	7	8
Expected	9	9	9	9	9	9
X^2 value	7.11**	0.44	0.44	0.00	0.44	0.11

Table 12.9 The annual frequencies of active nests that failed and fledged young in Queen Elizabeth Park. For each entry the first figure represents frequency, the second, in parentheses, percent frequency; Chi-square test was carried out on frequency data.

Period	No. of nests	No. of active nests fledging following broods			
		0	1	2	3
1975/6	60	34 (56.7)	16 (26.7)	10 (16.7)	0 (0.0)
1976/7	67	40 (59.7)	14 (20.9)	12 (17.9)	1 (1.5)
1977/8	75	39 (52.0)	17 (22.7)	18 (24.0)	1 (1.3)
Total (Mean±S.d.)	202	113 (56.1±3.9)	47 (23.4±3.0)	40 (19.5±3.9)	2 (0.9±0.8)
		$X^2 = 2.80$ NS, df = 6			

For nesting attempts which fledged young, the frequencies of young fledged were not significantly different between years and between brood sizes (Table 12.10). Eaglets fledged in 1-young broods formed 36.3%, those in 2-young broods 59.5%, and those fledged in 3-young broods 4.2% of all young raised during the study period.

12.3.6 The breeding frequency and replacement clutches

The numbers of pairs present during each of the 3 years of study ranged from 85-88; thus giving a total of 259 pairs. The population remained stable at an annual mean of ca. 86 pairs (Table 12.11). Because replacement clutches were common (section 6.3.3), there were altogether 285 pair-years (section 12.3.4) present during the study period. The frequencies of pairs and pair-years did not differ significantly from year to year as were also those of their breeding attempts (Table 12.11). Overall, 68% of the pairs and 71% of the pair-years were active.

Twenty six (13%) of the 202 Fish Eagle breeding attempts made during this study were replacement clutches while 176 (87%) of them were original ones. The numbers of these clutches did not differ significantly with the years of the study (Table 12.12).

12.4 DISCUSSION

Contamination of the environment, and therefore food sources, with chemical pollutants, especially DDE and organochlorine insecticides, has resulted in the impairments of the reproductive potentials of many raptor species in both North America and North Western Europe (e.g. Anderson & Hickey 1974). The reproductive

Table 12.10 The annual frequencies of young fledged by successful Fish Eagle nests in Queen Elizabeth Park. For each entry the first figure represents frequency, the second, in parentheses, percent frequency; Chi-square was carried out on frequency data.

Period	No. of nests	Total young	Number of young fledged by brood size 1	2	3
1975/6	26	36	16 (44.4)	20 (55.6)	0 (0.0)
1976/7	27	41	14 (34.1)	24 (58.5)	3 (7.3)
1977/8	36	56	17 (30.4)	36 (64.3)	3 (5.4)
Total	89	133	47	80	6
(Mean±S.d.)			(36.3±7.3)	(59.5±4.4)	(4.2±3.8)
				X^2 = 3.981 NS, df = 4	

Table 12.11 The frequencies of actual pairs and pair-years, and of breeding and non-breeding Fish Eagles in Queen Elizabeth Park. Degrees of freedom = 2 for each Chi-square test.

Year of study	Actual pairs	Pair-years	Number of actual pairs Bred	Not bred	Number of pair-year Bred	Not bred
1975/6	86	92	54	32	60	32
1976/7	88	97	58	30	67	30
1977/8	85	96	64	21	75	21
Total	259	285	176	83	202	83
% of total			68.0	32.0	70.9	29.1
Mean±S.d.	86.3±1.5	95.0±2.6	58.7±5.0	27.7±5.9	67.3±7.5	27.7±5.9
X^2 value	0.070 NS		3.280 NS		4.056 NS	

Table 12.12 The frequencies of original and replacement clutches of the Fish Eagle in Queen Elizabeth Park.

Year of study	Number of		Numbers of clutches		
	Actual pairs	Pair-years	Original	Re-laid	Total
1975/6	86	92	54	6	60
1976/7	88	97	58	9	67
1977/8	85	96	64	11	75
Total	259	285	176	26	202
Mean±S.d.	86.3±1.5	95.0±2.6	58.7±5.0	8.7±2.5	67.3±7.5
χ^2 value	0.070 NS			0.652 NS	

potentials of raptors are impaired by these chemicals through their interference with the metabolism of eggshell formation such that eggshells become thin and the eggs readily break during incubation. In an affected species, this thin eggshell syndrome leads to poor hatching success and an ever decreasing brood size with progressive contamination.

In the genus Haliaeetus, the most recent study of the reproduction of the White-tailed Sea Eagle Haliaeetus albicilla in Sweden has shown that the average brood size did not change in Lapland (Helander 1983). At the Baltic Coast, however, brood size was constant until 1950, and then declined rapidly until the mid-1960s. Helander attributed the rapid changes in brood size to decreases in the hatching success of the eggs due to DDE and PCB contamination.

A South African pair of Fish Eagles that Steyn (1972) studied between 1953 and 1964 had an average hatching success of 77.8%. However, he did not discuss this success rate in relation to environmental pollution. During this work, hatching success averaged 83% and it did not differ significantly between the years of study. Egg disappearance was the more important cause of hatching failure than infertility/addling and egg breakage. Although eggs were not analysed for chemical pollutants, the findings that egg breakage formed a small fraction (7%) of the eggs which failed to hatch, and brood size did not change significantly from year to year indicate that chemical pollution is probably not an important environmental factor in the reproductive biology of the Fish Eagle in this Park (see section 7.4).

This study demonstrates that chick survival decreased, although not significantly, with increasing brood size (Table 12.5).

Since chick survival was not significantly influenced by brood size and annual average brood survival was similar between years indicate that food shortage was not an important environmental factor in the survival of nestling Fish Eagles in this Park and that the prey base was stable. The fact that 97% of all the chicks in 2- and 3-young broods survived and disappeared as whole broods rather than as parts of broods (Table 12.6) further demonstrates that sibling aggression, and its attendant artificial starvation (Meyburg 1974; see section 9.7.5), was not a significant factor in the survival of nestlings. The high rate (29%) of whole brood disappearance, however, implicated predation as a habitat factor that significantly influenced brood survival (section 8.3.4).

Nest productivity obtained by Thiollay & Meyer (1978) for the Fish Eagle in this Park during 1976 and those of this study are not significantly differant ($X^2 = 0.006$, df = 2, $P > 0.1$; data in Table 12.13). Productivities in other habitats are also similar to those of this study ($X^2 = 0.305$, df = 12, $P > 0.1$; data in Table 12.13). These results, therefore, suggest that the habitats of the Fish Eagle, in areas so far studied, are still safe from pollution. However, recent studies in Zimbabwe have shown that pesticide residues are incrdasingly accummulating in both terrestrial and aquatic habitats and consequently in the eggs of birds inhabiting them (Tannock et al. 1983)

The number of young/pair gives the replacement rate of the species (Brown 1976a, b & c; Brown & Hopcraft 1973). It averaged 0.46 young/pair during this study and is similar to Thiollay & Meyer's (1978) value of 0.42 young/pair for the same population. Since the Fish Eagle populations of L. Victoria, L. Naivasha,

Table 12.13 The nest successes and productivities of the African Fish Eagle in 7 Eastern and Southern African studi
Figures marked with asterisks were given by Brown (1980) and not by the original authors.

Source	Area & Period	No. of pairs			No. young fledged	% nest success		Productivity/pair		
		All	Active	Successful		All	Active	All	Active	Success
This study	Kazinga Channel (1975 – 78)	285	202	89	133	31.2	43.9	0.46	0.65	1.49
Thiollay & Meyer (1978)	Kazinga Channel (1976)	100	47*	37	42	37.0	78.7	0.42	0.53*	1.13
Brown (1960 & 1980)	Lake Victoria (1953 – 55)	21	12	10	12	47.6	83.3	0.57	1.00	1.20
Brown & Hopcraft (1973), Brown (1980)	Lake Naivasha (1968 – 69)	56	35	21	28	37.5	60.0	0.50	0.80	1.34
Brown & Hopcraft (1973), Brown (1980)	Lake Naivasha (1970 – 71)	56	36	20	25	35.7	55.6	0.45	0.69	1.25
Steyn (1972) Brown (1980)	South Africa (1953 – 64)	9	9	9	9	100.0	100.0	1.00	1.13	1.50
Steyn (1974) Brown (1980)	Botswana (1971)	20	12	7	8	35.0	58.3	0.40	0.67	1.14

Botswana, South Africa and this Park realized similar productivities they, therefore, have similar rates of replacement of the species.

Brown & Amadon (1968) believed that close proximity of nests, probably acting through interpair interferences with breeding activities, was the likely cause of the lower breeding success they recorded for a Fish Eagle population they studied. Brown (1980) reported that in capacity populations territorial combat may be so fierce that it actually holds down the breeding rate. Along the Kazinga Channel, Fish Eagle population density is higher than those in other areas. During this study, increasing territory size increased, although not significantly, the production of young. This clearly demonstrates that increasing population density depresses the breeding success of the birds. Probably because of the higher density and presumably because of more frequent territorial disputes, only 44% of all nesting attempts in this Park fledged young as compared to 83% in L. Victoria, 58% in L. Naivasha, 58% in Botswana, and 100% in South Africa (Table 12.13). Because their study was very short, Thiollay & Meyer (1978) underestimated the number of active nests and, consequently, overestimated the nest success (79%) of the Kazinga Channel Fish Eagle population (Table 12.13).

The effects of density in reducing the Fish Eagle's breeding success in this Park was probably also complicated by other habitat factors. Thus increasing numbers of mature trees in the territories increased the production of young presumably through the provision of more secure nesting sites (Brown 1970b). Shallow and calm water also favoured the productivity of birds in this Park (Thiollay & Meyer 1978) probably because shallow water contained more fish than deep water (Green 1964, Gwahaba 1973) and its calmness eased the capture of prey (Bannerman 1953).

Juedemann (1973) found that Bald Eagles *Haliaeetus leucocephalus* nesting in areas relatively more distant from human activities had better productivity than those closer to them. Helander (1983) demonstrated that human disturbance about the territory was a major cause of nesting failure in the Sea Eagle in Swedish Lapland. Human disturbance, added to the effects of chemical pollutants in the eggs, resulted in poor productivity and declining populations of the Sea Eagle in Europe (Palokangas *et al.* 1972a & b; Anderson & Hickey 1974). Road development stopped Steyn's (1972) South African Fish Eagle pair from ever breeding but Brown & Hopcraft (1973) found that L. Naivasha birds were unaffected by human interference. During this study, human disturbance reduced Fish Eagle breeding success but its effects were highly localised to pairs whose territories were at the foci of the disturbances.

Two out of 202 Fish Eagle breeding attempts fledged 3-young broods during this study. Only one other case of Fish Eagles rearing three young occurred in the Kafue Flats, Zambia (Colerook-Robjent 1974). In the eight species of the genus only *Haliaeetus leucocephalus*, *H. albicilla* and *H. pelagicus* had been known to fledge three young (Brown 1976a, b & c; Brown & Amadon 1968). The two cases of 3-young broods fledged in this Park and that of Colerook-Robjent(1974) therefore adds *H. vocifer* to the list of species that can rear 3-young broods.

At L. Naivasha, Brown & Hopcraft (1973) found that the total number of Fish Eagle pairs remained stable during their studies in 1968-69 and 1970-71. During this study, too, a similar stability was recorded. Although the number of pairs remained stable, minor changes occurred in both the Queen Elizabeth Park and L. Naivasha populations. In this Park, as in the Naivasha study, whenever a pair abandoned a territory, the area was not taken over by a new pair, rather it was annexed by adjacent ones.

In dense populations of Fish Eagles, high proportions of pairs do not breed and non-breeding may account for one-third to one-half of a population not breeding each year (Brown 1980). In Lakes Victoria and Naivasha respectively 43% and 37% of the pairs did not breed. In Botswana 40% did not breed. On the Kazinga Channel, non-breeding accounted for 67% of the 100 pairs Thiollay & Meyer (1978) observed. Non-breeding averaged only 32% during this study. It has been suggested that such a high rate of non-breeding helps to limit the Fish Eagle population and that it operates through natural social population regulation mechanism (Brown 1980). An appraisal of this and other population regulation theories were discussed in section 3.4.

According to Brown (1976a, b & c), eagles seldom replace lost clutches, although those in the tropics will do so more readily than those in temperate regions. The Crowned Eagle <u>Stephanoaetus coronatus</u>, Verreaux's Eagle <u>Aquila verreauxi</u> and Ayre's Hawk Eagle <u>Hieraaetus dubius</u> have been reported to replace lost clutches, and the replacements may take weeks or months (Brown, op cit.). In the Bald Eagle when a clutch is removed or lost early in the breeding season it can be replaced in 4 or more weeks(Bent 1937). A captive White-tailed Sea Eagle female replaced a clutch in a 19-day interval and another in a 29-day interval (Fentzloff 1977). In a South African Fish Eagle pair, Steyn (1972) reported one case of a replacement clutch, but he did not state the interval between the original and the replacement clutches. In the Kafue Flats, Zambia, Colerook-Robjent (1974) recorded a clutch replaced in a 3-week interval from the time he removed the original clutch. Thirteen percent of all Fish Eagle breeding attempts during this study comprised of replacement clutches and the clutches were laid on average 3.6 months from the loss of the original clutches (section 6.3.3). This finding clearly demonstrates that the African Fish Eagle replaces lost clutches, and perhaps does so more commonly than had been thought.

CHAPTER 13

CONCLUDING REMARKS

13.1 Distribution

As in other areas, this study has shown that the distribution of the African Fish Eagle in Queen Elizabeth National Park, and Uganda generally, is very much dependent on the presence of water. In parts of the country where, in modern times, the rate of swamp drainage has accelerated due to high human population growth and diversification of agriculture, the habitat of the Fish Eagle is dwindling fast. The nationwide creation of fish ponds and dams, which had been encouraged by the Fisheries Department during the 1960s, is the only sure way for man to promote the wide-spread distribution of the species. However, since an Eagle would consume about 100 kg of fish annually or remove from any such pond ca. 260 good-sized fishes per year, its presence on a fish pond would probably be resented by most fish pond owners.

The study also showed that another habitat variable which significantly influences the distribution pattern of the Fish Eagle, and to an extent its nest productivity, is the presence of trees. Forested and well-wooded shorelines, during this study, attracted higher population densities of the adult birds than did treeless ones. Thus, any national land use practice which encourages woodland formation in an area will, of necessity, be promoting the colonization, probably in great numbers, of any water in that area provided the water mass concerned has some fish and is not above 2100 m a.s.l. If the conservation of the African Fish Eagle is to be assured in the three National Parks (Queen Elizabeth, Murchison Falls and Lake Mburo) where it occurs, it is imperative that the authorities discourage policies which will in the long run lead to complete woodland destruction along the banks of the water bodies in these Parks.

Human settlements along the shorelines of Lakes Edward and George and the Kazinga Channel, in this Park, did not significantly affect the distribution of the Fish Eagle. During the study, both the fishermen and the other people were impartial to the bird. There was no evidence of persecution of the bird, even of pelting by the children of the 11 fishing villages. Nevertheless, a few pairs of birds which inhabited shorelines bordering onto the villages did not breed at all probably because they became too wary of the constant presence and activities of the people. Non-breeding by such few pairs of birds around the fishing villages could not have significantly influenced the overall annual nest productivity of the species in the whole Park. Evidently, human interference with the breeding activities of the African Fish Eagle in Queen Elizabeth Park does not contribute greatly to its population regulation and, therefore, does not constitute a conservation management problem for the species.

In providing daily refuse in the form of rotting fishes and fish offals which they discard, the villages attract large numbers of young Fish Eagles. The presence of these villages probably greatly enhances the survival of the young birds and, thereby, promotes a healthy population of the species.

13.2 Tourism

Animals, especially large mammals, are the main attractions for tourists coming into the national parks. However, birds and other lesser creatures feature prominently for some visitors.

Of the 545 species of birds present in Queen Elizabeth Park, birds of the shoreline are abundant. Few of these, if any, rival the African Fish Eagle in beauty and in the variety of displays they make. The Fish Eagle's call, uttered throughout the day and with the head tossed right onto the back, is an unforgettable sound of the African bush. Its mid-air cartwheeling fight with any other intruding Fish Eagle during territorial defence, although extremely rare is an aerial acrobatic display to be marvelled at. The steep and fast dive to kill a fish from the first 10-15 cm of water, by the powerful grip of talons at the end of the feet, is yet an awe-inspiring feat. The bulky nest of twigs, usually set atop a Euphorbia tree, is an impressive mark on the landscape.

13.3 Nutrient cycle

Upto mid-1979, between 10,000-12,000 hippopotami inhabited Queen Elizabeth National Park. Presently, there are at least 5,000 of them along the shorelines and in the wallows. Daily, these animals remove large quantities of grass as their food. However, because they spend the whole day in water, over 90% of their daytime defaecation is done in the water and this results in a net drain of nutrients from land to water. The African Fish Eagle, although contributing insignificantly, in conjunction with other fish-eating birds and man, and insectivorous birds which largely feed on lake flies, help to return some of the nutrients to the land. The more luxuriant and vigorous growth of vegetation under the regular feeding perches of the Fish Eagle than of the vegetation elsewhere is clear evidence that the decay and mineralisation of fish remains and bones are responsible for this. However, this is so localised as not to have a great impact on the general nutrient cycle of the Park.

13.4 Indicator species

Although this study has shown that the African Fish Eagle is not contributing significantly to the nutrient flow in Queen Elizabeth Park, the Eagle, nonetheless, has an important role to play in the ultimate health of the Park and the surrounding area as an indicator species.

Endowed with a variety of mineral wealth, the region in which this Park occurs is likely to become an industrial nerve centre of the country. The rich agricultural and livestock potentials are clearly manifested by the growing number of both government and private farms. To boost production, these farms are increasingly using both organochlorines and organophosphates whose persistent and detrimental effects on the environment are already well known. The African Fish Eagle, as a top predator on the food chain stemming from the aquatic habitat, will have a role to play in bringing to light how much chemical pollution the Park is absorbing from the surrounding region.

Although no eggs and Fish Eagle body parts were analysed for pollutants, this study showed that egg-breakage was not an important factor in the breeding success of the birds. Furthermore, the lack of significant variation in the annual nest productivities indicate that the birds are breeding normally. The productivities are also similar to those obtained for the species in other habitats such as Lake Naivasha in Kenya and along the Chobe and Boro Rivers in Botswana. These results would, therefore, demonstrate that pollution of the Park with organochlorines and organophosphates is probably still low. However, it is imperative that a research programme be started to continually monitor the nest productivities of these birds in order to follow the rate at which the Park, especially its waters, are being polluted and to detect, in time, the threshold at which the population will begin to decline. Such a study should be corroborated by regular cropping schemes, say, at 5-year intervals, during which a few territorial birds are sacrificed to provide samples for laboratory assays of various chemical pollutants.

13.5 In retrospect

Despite the lack of supportive data from laboratory assays, the African Fish Eagle of Queen Elizabeth National Park may be said to be safe from the detrimental effects of chemical pollution which has wrecked populations of most birds of prey in Europe and North America in the 1950s and 1960s. With its high densities of African Fish Eagles, Queen Elizabeth Park probably served as a source of dispersal of the bird to the surrounding regions in the past. It will continue to do so only if organochlorines, organophosphates and any other chemicals hazardous to man and to the environment are used more carefully and wisely.

REFERENCES

AERNI, M. J. (1970). A study of poaching and attitudes of local inhabitants towards wildlife in Uganda. Unpubl. Report to Uganda National Parks.

ANDERSON, D. W. & HICKEY, J. J. (1974). Eggshell changes in raptors from the Baltic region. Oikos 25: 395-401.

BAILEY, C. B., KITTS, W. D. & WOOD, A. J. (1960). Changes in the gross chemical composition of the Mouse during growth in relation to the assessment of the physiological age. Canada J. Anim. Sci. 40: 143-155.

BAILEY, N. T. J. (1974). Statistical Methods in Biology. The English Universities Press Ltd., London.

BALON, E. K. (1971). Age and growth of Hydrocynus vittatus Castelnau, 1861, in Lake Kariba, Sinazongwe area. Fish. Res. Bull. Zambia 5: 89-118.

BANNERMAN, D. A. (1953). The Birds of West and Equatorial Africa - 1. Oliver and Boyd, Edinburgh.

BARTHOLOMEW, G. A. & DAWSON, W. R. (1954). Temperature regulation in young pelicans, herons and gulls. Ecology 35: 466-472.

BARTHOLOMEW, G. A., DAWSON, W. R., & O'NEILL, E. J. (1953). A field study of temperature regulation in young White Pelicans Pelecanus erythrorhynchos. Ecology 34: 554-560

BEADLE, L. C. (1932). The waters of some East African lakes in relation to their fauna and flora. J. Linn. Soc. Zool. 38: 157-211.

BEADLE, L. C. (1971). The Uganda National Parks in prehistoric times. 1. Landscape changes. In Uganda National Parks Handbook: pp 121-124. 5th Ed. Longman Uganda Ltd., Kampala.

BEADLE, L. C. (1974). The Inland Waters of Tropical Africa. An Introduction to Tropical Limnology. Longman, London.

BENSON, C. W. (1963). Breeding seasons in the Rhodesias and Nyasaland. Int. Orn. Congr. 13: 626-639.

BENSON, C. W. & WHITE, C. M. N. (1957). Check List of the Birds of Northern Rhodesia. Government Printer, Lusaka.

BENT, A. C. (1937). Life histories of North American birds of prey, Order Falconiformes. Part 1. U.S. Nat. Mus. Bull. 167: 321-348.

BERE, R. M. (1959). Queen Elizabeth National Park. *The Oryx 5:* 116-124.

BERTALANFFY, L., VON. (1960). Principles and Theory of Growth. p.p. 137-259. In W. W. Nowinski (ed.), Fundamental Aspects of Normal and Malignant Growth. Elsevier, Amsterdam.

BISHOP, W. W. (1970). Pleistocene strategraphy in Uganda. *Geol. Surv of Uganda. Memoir 10.*

BROCKWAY, B. F. (1964). Ethological studies of the budgerigar: reproductive behavior. *Behavior 23*: 294-325.

BRODY, S. (1945). Bionergetics and Growth. Reinhold, New York.

BROLEY, C. L. (1947). Migration and nesting of Florida Bald Eagles. *The Wilson Bull 59:* 3-20.

BROLEY, C. L. (1950). The plight of the Florida bald eagle. *Audubon Magazine 52(1):* 42-49.

BROLEY, C. L. (1958). The plight of American bald eagle. *Audubon Magazine 60 (4):* 162-163.

BROOKS, A. C. (1957). Notes on some ecological studies in Queen Elizabeth National Park with some particular references to grasses. Unpubl. Report to Game and Fisheries Dept., Uganda.

BROWN, J. L. (1964). The evolution of diversity in avian territorial systems. *The Wilson Bull. 6:* 160-169.

BROWN, J. L. (1969). Territorial behavior and population regulation in birds. A review and re-evaluation. *The Wilson Bull 81 (3):* 293-329.

BROWN, L. (1955). Eagles. Michael Joseph, London.

BROWN, L. (1960). The African Fish Eagle *Haliaeetus vocifer* especially in the Kavirondo Gulf. *Ibis 102*: 285-297.

BROWN, L. (1970a). African birds of prey. Collins, London.

BROWN, L. H. (1970b). Some factors affecting breeding in eagles. *Ostrich Sup. 8:* 157-167.

BROWN, L. H. (1974a). Data required for effective study of populations. *Raptor Research Rep. 2:* 7-20. Raptor Research Foundation. Vermilion, Ohio.

BROWN, L. (1974b). Is poor breeding success a reason for the rarity of Ayre's Hawk Eagle? *Ostrich 45:* 145.

BROWN, L. (1976a). Birds of prey, their biology and ecology. Hamlyn, London.

BROWN, L. (1976b). Eagles of the World. David & Charles. London.

BROWN, L. (1976c). British birds of prey. Collins, London.

BROWN, L. (1980). The African Fish Eagle. Bailey Bros. & Swinfen Ltd. Folkestone (SA).

BROWN, L. H. & AMADON, H. (1968). Hawks, Eagles and Falcons of the World. Country Life/Hamlyn, Feltham.

BROWN, L. H. & BRITTON, P. L. (1980). The breeding seaons of East African birds. EANHS, Nairobi.

BROWN, L. H. & CADE, T. J. (1972). Age classes and population dynamics of the Bateleur and African Fish Eagle. *Ostrich 43:* 1-15.

BROWN, L. H. & HOPCRAFT, J. B. D. (1973). Population structure and dynamics in the African Fish Eagle *Haliaeetus vocifer* (Daudin) at Lake Naivasha, Kenya. *E. Afr. Wildl. J. 11:* 255-269.

BROWN, L. H. & URBAN, E.K. (1969). The breeding biology of the Great White Pelican *Pelecanus onocrotalus* at Lake Shala, Ethiopia. *Ibis 111:* 199-237.

BRUNS, H. (1972). Pigeons: Rock doves & domestic pigeons. *In* Animal Life Encyclopedia. Van Vostrand Reinhold Co., New York.

BURGER, J. W. (1949). A review of experimental investigations on seasonal reproduction in birds. *The Wilson Bull. 61:* 211-230.

BURGER, J. W. (1953). The effect of photic and psychic stimuli on the reproductive cycle of the male Starling *Sturnus vulgaris*. *J. exp. Zool. 124:* 227-239.

BURGIS, M. J. (1969). A preliminary study of the ecology of zooplankton in Lake George, Uganda. *Verh. Internat. Verein. Limnol. 17:* 297-302.

CARRICK, R. (1963). Ecological significance of territory in the Australian Magpie *Gymnorhina tibicen*. *Proc. Int. Orn. Congr. 13:* 740-753.

CAVE, F. O. & MAcDONALD, J. D. (1955). Birds of the Sudan. Oliver and Boyd, Edinburgh.

CHEESEMAN, C. L. (1975). The population biology of small rodents in the grassland of Rwenzori National Park, Uganda. Ph.D. Thesis, University of Southampton.

CHRISTIAN, J. J. (1963). Endocrine adaptive mechanisms and the physiologic regulation of population growth. *In* Physiological mammalogy, Vol. 1. Mammalian Populations (Mayer, W. V. & R. G. van Gelder, eds.): 189-353. Academic Press, New York.

CLANCEY, P. A. (1964). The Birds of Natal and Zululand. Oliver and Boyd, Edinburgh.

CLAPP, J. A. (1976). Observations on a Fish Eagle feeding on an African hare at Lake Naivasha. EANHS Bulletin (Nov/Dec 1976): 140-142.

COLEROOK-ROBJENT, J. F. R. (1974). African Fish Eagle rearing three young. Ostrich 45: 144-145.

CORBET, P. S. (1961). The food of non-cichlid fishes in the Lake Victoria Basin, with remarks on their evolution and adaptation to lacustrine conditions. Proc. Zool. Soc. Lond. 136: 1-101.

CRAIGHEAD, J. J. & CRAIGHEAD, F. C. (1956). Hawks, owls, and wildlife. Stackpole, Harrisburgh.

CUNNINGHAM-VAN SOMEREN, G. R. & RICHARDS, D. K. (1977). A note on the Flora and Fauna of two Seasonal Swamps in the Rift Valley. EANHS Bulletin (Sept/Oct. 1977): 96-104

DARLING, F. F. (1938). Bird flocks and the breeding cycle. Cambridge.

DASMANN, R. F. (1966). Wildlife biology. John Wiley & Sons, Inc., New York.

DELANY, M. J. (1964). An ecological study of the small mammals in the Queen Elizabeth National Park, Uganda. Rev. Zool. Bot. Afr. 70: 149-229.

DIN, N. A. (1970). General biology of two species of pelicans (Pelecanus onocrotalus and P. rufescens) in Queen Elizabeth National Park, Uganda. M.Sc. Thesis, Makerere University College, University of East Africa.

DIN, N. A. & ELTRINGHAM, S. K. (1974). Ecological separation between white and pink-backed pelicans in the Rwenzori National Park, Uganda. Ibis 116: 28-43.

DISNEY, H. J. de S. & MARSHALL, A. J. (1956). A contribution to the breeding biology of the weaver-finch Quelea quelea (Linn) in East Africa. Proc. Zool. Soc. Lond. 127: 379-387.

DORWARD, D. F. (1962). Comparative biology of the White Booby and the Brown Booby Sula spp. at Ascension. Ibis 103b: 174-220.

DOUGLAS-HAMILTON, I., MALPAS, R., EDROMA, E., HOLT, P., LAKER-OJOK, G., & WEYERHAEUSE, R. (1980). Uganda elephant and wildlife survey. Unpubl. Report to IUCN.

DUNN, I. G. (1972). Ecological studies on the fish of Lake George, Uganda, with particular reference to the Cichlid genus Haplochromis. Ph.D. thesis, University of London.

DUNN, I. G., BURGIS, M. J., GANF, G. G., McGOWAN, L. M. & VINER, A. B. (1969). Lake George: A limnological survey. Verh. Internat. Verein. Limnol. 17: 284-288.

EDROMA, E. L. (1974a). Effects of clipping treatments on the productivity and plant populations in two contrasting grassland types in Rwenzori National Park, Uganda. Proc. IBP Symp. Trop. Grassland Biome. Varanasi, India. 17-22 Jan. 1974.

EDROMA, E. L. (1974b). Copper Pollution in Rwenzori National Park, Uganda. J. appl. Ecol. 11: 1043-1056.

EDROMA, E. L. (1974c). Pollution in wildlife areas of Uganda. Proceedings of Workshop on Environment and Rural Development in East Africa. KENDEV. 22: 1-13.

EDROMA, E. L. (1975a). Influences of burning and grazing on the productivity and dynamics of grasslands in Rwenzori National Park, Uganda. Sc.D. Thesis, University of Giessen.

EDROMA, E. L. (1975b). Poaching and human pressures in Rwenzori National Park, Uganda. Uganda J. 37: 9-18.

EDROMA, E. L. (1976). Effects of removing leaves by birds on the performance of Cymbopogon afronardus in Rwenzori National Park. Uganda J. 38: 109-112.

EDROMA, E. L. (In press). Chemical pollution in Queen Elizabeth National Park, Uganda. Proceeding of Third Symposium on Environmental Science in Developing Countries. 16-21 April, 1983, Cairo, Egypt.

EGGELING, W. J. (1951). The Indigenous Trees of the Uganda Protectorate. 2nd ed. The University Press, Glasgow.

EINYU, P. (1978). A study of the systematics and ecology of the Typhlocybine Leafhoppers (Cicadellidae: Typhlocybinae) of Rwenzori National Park, Uganda. M.Sc. Thesis, Makerere University.

ELTRINGHAM, S. K. (1968). An experiment in the control of marabou storks. E. Afr. Wildl. J. 6: 147-148.

ELTRINGHAM, S. K. (1975). Territory size and distribution in the African Fish Eagle. J. Zool. Lond. 175: 1-13.

ELTRINGHAM, S. K. & DIN, N. A. (1977). Estimates of population size of some ungulate species in Rwenzori National Park, Uganda. E. Afr. Wild. J. 15: 305-316.

ELTRINGHAM, S. K. & MALPAS, R. C. (1980). The decline in elephant numbers in Rwenzori and Kabalega Falls Parks, Uganda. *Afr. J. Ecol. 18:* 73-86.

ELTRINGHAM, S. K. & WOODFORD, M. H. (1973). The numbers and distribution of the buffalo in Rwenzori National Park, Uganda. *E. Afr. Wildl. J. 11:* 151-164.

EVANS, S. & CAMPBELL, K. (1977). Ringed Plover taken by Fish Eagle. *EANHS Bulletin* *(May/June 1977):* 63.

FANGE, R., SCHMIDT-NIELSEN, K. & OSAKI, H. (1958a). The salt gland of the herring gull (*Larus argentatus*). *Biol. Bull. 115:* 162-171.

FANGE, R., SCHMIDT-NIELSEN, K. & ROBINSON, M. (1958b). Control of secretion from the avian salt gland. *Am. J. Physiol. 195:* 321-326.

FAVALORO, N. (1944). The white-breasted sea eagle along the Murry Valley. *The Emu 43:* 233-242.

FENTZLOFF, C. (1977). Successful breeding and adoption of Sea Eagles (*Haliaeetus albicilla*). *In* Papers on the Veterinary Medicine and Domestic Breeding of Diurnal Birds of Prey. Cooper, J. E. and Kenward, R. E. (ed). British Falconers' Club. pp 71-94.

FIELD, C. R. (1968). The food habits of some ungulates in Uganda. Ph.D. Thesis. University of Cambridge.

FIELD, C. R. & LAWS, R. M. (1970). The distribution of the larger herbivores in Queen Elizabeth National Park, Uganda. *J. appl. Ecol. 7:* 273-294.

FISH, G. R. (1955). The food of *Tilapia* in East Africa. *Uganda J. 19:* 85-89.

FISHER, R. A. & YATES, F. (1963). Statistical Tables for Biological, Agricultural and Medical Research. 6th ed. Oliver and Boyd Ltd., Edinburgh.

FITCH, H.S., SWENSON, F. & TILLOTSON, D. F. (1964). Behavior and food habits of the Red-tailed Hawk. *Condor 48:* 205-237.

FORD, J. (1971). The Role of the Trypanosomiasis in African Ecology: A study of the Tsetse Fly Problem. Clarendon Press, Oxford.

GANF, G. G. (1969). Physiological and ecological aspects of the phytoplankton of Lake George, Uganda. Ph.D. Thesis, University of Lancaster.

GANF, G. G. (1972). The regulation of net primary production in Lake George, Uganda, East Africa. *Proc. IBP-UNESCO Symp. on Productivity Problems of Freshwaters:* 693-708.

GARROD, D. J. (1959). The growth of *Tilapia esculenta* Graham in Lake Victoria. *Hydrobiologia 12 (4):* 268-298.

GILBERTSON, M. (1975). A Great Lakes Tragedy. *Nature Canada 4 (1):* 22-25.

GRAHAM, M. (1929). *The Victoria Nyanza and its Fisheries.* Crown Agents for the Colonies: London.

GREEN, J. (1964). The numbers and distribution of the African Fish Eagle *Haliaeetus vocifer* on the eastern shore of Lake Albert. *Ibis 106:* 125-128.

GREENSPAN, B. & TORRE-BUENO, J. (1971). *Aspects of the biology of the African Fish Eagle (Haliaeetus vocifer), with special reference to vocalisation and territoriality.* Unpubl. Rep. Rockefeller University Field Course in Animal Behaviour, Uganda, 1971: 1-73.

GREENWOOD, P. H. (1966). The fishes of Uganda. The Uganda Society, Kampala.

GRIER, J. W. (1974). Reproduction, organochlorines, and mercury in Northwestern Ontario Bald Eagles. *The Canadian Field-Naturalist 88:* 469-475.

GRIFFITHS, J. F. (ed.) (1972). World Survey of Climatology, Vol. 10: Climates of Africa. Elsevier, The Hague.

GRIMSDELL, J. J. R. (1969). Ecology of the Buffalo *Syncerus caffer* in western Uganda. Ph.D. Thesis, University of Cambridge.

GRZIMEK, B. (ed.) (1972). Birds 1. *In* Grzimek's Animal Life Enchclopedia, Volume 7, pp 336-431. Van Nostrand Reinhold Company, New York.

GWAHABA, J. J. (1973). Population studies of the more abundant fish species in Lake George, Uganda. M.Sc. Thesis, Makerere University, Kampala.

HALE-CARPENTER, G. D. (1921). Unpubl. Report to S. M. O., Uganda Govt. Medical Files, Entebbe.

HAMILTON, W. D. (1964). The genetical evolution of social behaviour. *J. Theor. Biol. 7:* 1-52.

HAYLOCK, J. W. (1959). Investigations on the habits of Quelea birds and their control. Government Printer, Nairobi, Kenya.

HELANDER, B. (1983). Reproduction of the White-tailed Sea Eagle *Haliaeetus albicilla* (L.) in Sweden, in relation to food and residue levels of organochlorine and mercury compounds in the eggs. Ph.D. Thesis, University of Stockholm.

HENSEL, R. J., & TROYER, W. A. (1964). Nesting studies of the Bald Eagle in Alaska. Condor 66 (4): 282-286.

HERRICK, F. R. (1933). Daily life of the Amercian eagle: The Auk 50 (1): 35-53.

HINDE, R. (1967). Aspects of the control of avian reproductive development within the breeding season. Int. Orn. Congr. 14: 135-154.

HINDE, R. A. (1956). The biological significance of territories of birds. Ibis 98: 340-369.

HINDE, R. A. (1964). Intraspecific communication in animals. Res. Publs. Assn. Res. nerv. ment. Dis. 42: 62-68.

HINDE , R. A. (1966). Animal behaviour: A synthesis of ethology and comparative psychology. McGraw-Hill, New York.

HINDE, R. A. (1974). Biological bases of human social behaviour. McGraw-Hill Book Co., New York.

HOWARD, H. E. (1920). Territory in bird life. Dutton and Co., New York.

HOWELL, T. R. & BARTHOLOMEW, G. A. (1962). Temperature regulation in the Sooty Tern Sterna fuscata. Ibis 104: 98-105.

HULOT, A. (1956). Apercu sur la question de la peche in industrielle aux lacs Kive, Edouard et Albert. Bull. Agric. Congo Belge 47: 3-68.

HUTCHINSON, J. C. D. (1954). Heat regulation in birds. In Progress in the Physiology of Farm Animals. (J. Hammond, ed.), Vol. 1, pp 299-362. Butterwoths, London.

HUTCHINSON, J. C. D. (1964). Heat regulation. In Thomson, A. L. (ed.). A New Dictionary of Birds: 361-363. Nelson, London.

IMMELMANN, K. (1971). Ecological aspects of periodic reproduction. In Avian Biology Vol. 1, D. S. Farner & J. R. King (ed.), pp 341-376.

INGRAM, C. (1959). The importance of juvenile cannibalism in the breeding biology of certain birds of prey. Auk 76: 218-226.

JENKINS, D. (1961a). Social behaviour in the partridge Perdix perdix. Ibis 103a: 155-158.

JENKINS, D. (1961b). Population control in protected Partridges (Perdix perdix). J. Anim. Ecol. 30: 235-258.

JUBB, R. A. (1968). More about Fish Eagles. Piscator 72: 25-26.

JUENEMANN, B. G. (1973). Habitat evaluations of selected Bald Eagle nest sites on the Chippewa National Forest. M.Sc. Thesis, University of Minnesota.

JUNOR, F. J. R. (1968). The African Fish Eagle: brief observations on the weight of fish that can be carried by the Fish Eagle *Haliaeetus vocifer*. *Piscator 72:* 22-24.

KAHL, M. P. (1966). A contribution to the ecology and reproductive biology of the Marabou Stork *(Leptoptilos crumeniferus)* in East Africa. *J. Zool. 148:* 289-311.

KAHL, M. P. (1968). Recent breeding records of storks in East Africa. *J. E. Afr. Nat. Hist. Soc. Nat. Mus. 27:* 67-72.

KALELA, O. (1954). Ueber den Revierbesitz bei Voegeln und Saeugetierem als populationsoekologischer Faktor. *Ann. Zool. Soc. "Vanamo". 16:* 1-48.

KAYSER, C. (1929). Regulation thermique apres section medulliare dorsale chez le pigeon. *Compt. rend. soc. biol. 100:* 286-288.

KENDEIGH, S. C. (1944). Effect of air temperature on the rate of energy metabolism in the English Sparrow. *J. Exptl. Zool. 96:* 1-16.

KEPLER, C. B. (1969). The breeding biology of the Blue-faced Booby *(Sula dactylatra personata)* on Green Island, Kure Atoll. R. A. Paynter Jr. (ed.). Nattall Ornithological Club, Cambridge, Massachusetts.

KING, J. R. & FARNER, R. S. (1961). Energy metabolism, thermoregulation and body temperature. *In* Biology and Comparative Physiology of Birds, Vol. II; A. J. Marshall (ed.). pp 215-288. Academic Press, New York.

KLUIJVER, H. N. (1951). The population ecology of the Great Tit *parus m. major*. *Ardea 39:* 1-135.

KLUIJVER, H. N. (1963). The determination of reproductive rates in Paridae. *Proc. XIII Intern. Ornithol. Congr.:* 706-716.

KOIVUSAARI, J., NUUJA, I., PALOKANGAS, R. & VIHKO, V. (1972a). Decrease in eggshell thickness of the white-tailed eagle in Finland during 1884-1971. *Ornis Fennica 49:* 11-13.

KOIVUSAARI, J., LAAMANEN, A., NUUJA, I. POLOKANGAS, R. & VIHKO, V. (1972b). Notes on the concentrations of some environmental chemicals in the eggs of the white-tailed eagle and the Osprey in the Quarken area of the Gulf of Bothnia. *Work-Environ - Health 9:* 44-45.

KUSSMAN, J. V. & FRENZEL, L. D. (1972). Post-fledging activity of bald eagles on the Chippewa National Forest. *Unpubl. Rep. of 34th Annual Midwest Fish and Wildlife Conference, Dec. 10-13. 1972.* Des Moines, Iowa.

LACK, D. (1948). The significance of clutch size. Part 3. *Ibis 90:* 25-45.

LACK, D. (1954). The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

LACK, D. (1958). A quantitative breeding study of British tits. Ardea 46: 92-124.

LACK, D. (1966). Population studies of birds. Clarendon Press, Oxford.

LACK, D. (1968). Ecological adaptations for breeding in birds. Methuen, London.

LACK, D. & EMLEN, J. T. (1939). Observations on breeding behaviour in Tricolored Redwings. Condor 41: 225-230.

LACK, D. & LACK, E. (1951). The breeding biology of the Swift Apus apus. Ibis 93: 501-546.

LAIRD, D., TYLER, S. A. & BARTON, A. D. (1965). Dynamics of normal growth. Growth 29: 233-248.

LANGDALE-BROWN, I. (1960). The vegetation of the Western Province of Uganda. Uganda Dept. Agric. Memoirs. Ser. 2(4): 1-111.

LANGDALE-BROWN, I., OSMASTON, H. A. & WILSON, J. G. (1964). The vegetation of Uganda and its bearing on land use. Govt. Printer, Entebbe.

LARSON, J. S. & TABER, R. D. (1980). Criteria of sex and age. In Wildlife Management Techniques Manual, 4th edition, S. D. Schemnitz (ed.). The Wildlife Society, Washington, D. C. pp. 143-202.

LAWS, R. M., PARKER, I. C. S., & ARCHER, A. L. (1967). Estimating live weight of elephants from hind leg weights. E. Afr. Wildl. J. 5: 106-111.

LAWS, R. M., PARKER, I. C. S., & JOHNSTONE, R. C. B. (1975). Elephants and their habitats. The ecology of elephants in north Bunyoro, Uganda. Clarendon Press, Oxford.

LEES, J. (1946). All the year breeding of the Rock-Dove Brit. Birds 39: 136-141.

LEHRMAN, D. S. (1959). Hormonal responses to external stimuli in birds. Ibis 101: 478-496.

LEHRMAN, D. S. (1964a). The reproductive behaviour of ring doves. Scient. Amer. 211 (5): 48-54.

LEHRMAN, D. S. (1964b). Control of behaviour cycles in reproduction. In Social behaviour and organisation among vertebrates: 143-166. Etkim, W. (ed.). University of Chicago Press, Illinois.

LEHRMAN, D. S. (1965). Interactions between internal and external environment in the regulation of the reproductive cycle of the Ring Dove. In Sex and behaviour. Beach, F. A. (ed.), John Wiley & Sons, New York.

LOCK, J. M. (1967). The vegetation of Uganda in relation to grazing and soils in Queen Elizabeth National Park, Uganda. Ph.D. Thesis. University of Cambridge.

LOCK, J. M. (1972a). Baboons feeding on Euphorbia candelabrum. E. Afr. Wildl. J. 10: [illegible].

LOCK, J. M. (1972b). The effects of Hippopotamus grazing on grasslands. J. Ecol. 60: 445-467.

LOCK, J. M. (1977). The vegetation of Rwenzori National Park Uganda. Bot. Jahrb. Syst. 98: 372-448.

LOCKIE, J. D. (1955). The breeding habits and food of the Short-eared Owls after a Vole plague. Bird Study 2: 53-69.

LOFTS, B. & MURTON, R. K. (1968). Photoperiodic and physiological adaptations regulating avian breeding cycle and their ecological significance. J. Zool. 155: 327-394.

LOWE-McCONNELL, R. H. (1958). Observations on the biology of Tilapia nilotica Linne in East African waters. Rev. Zool. Bot. Afr.57: 129-170.

LUGARD, F. D. (1893): The rise of our East African Empire II. London.

MACKWORTH-PRAED, C. W. & GRANT, C. H. B. (1952). Birds of Eastern and North Eastern Africa. African Handbook of Birds, Ser. 1. Vol. 1. Longmans, Green & Co., London.

MACKWORTH-PRAED, C. W. & GRANT, C. H. B. (1952). Birds of the southern third of Africa. African Handbook of Birds, Ser. 11. Vol. 1. Longmans, London.

MALPAS, R. C. (1977). The ecology of the African elephant in Rwenzori and Kabalega Falls National Parks, Uganda. Ph.D. Thesis, University of Cambridge.

MALPAS, R. C. (ed.), (1980). Wildlife in Uganda. Unpbl. Rep. to IUCN.

MARSHALL, A. J. (1961). Breeding seasons and migration. In Biology and comparative physiology of birds, Vol. 11; A. J. Marshall (ed.). pp. 397-332. Academic Press, New York.

MARSHALL, A. J. & DISNEY, H. J. de S. (1957). Experimental induction of the breeding season in a xerophilous bird. Nature. Lond. 180: 647.

MARSHALL, F. H. A. (1936). Sexual periodicity and the causes which determine it. Phil. Trans. Roy. Soc. London B. 226: 423-456.

MATHISEN, J. E. (1968). Effects of human disturbance on nesting of bald eagles. Journ. Wild. Management 32 (1): 1-6.

McGAHAN, J. (1968). Ecology of the golden eagle. Auk 85 (1): 1-12.

NEBS, T. (1972). Falcons and their relatives. In Grzimek's Animal Life Encyclopedia 7(1): 382.

MEDWAY, L. (1962). The swiflets (Collocalia) of Niah Cave, Sarawak. Ibis 104: 45-66, 228-245.

MEYBURG, B. U. (1974). Sibling aggression and mortality among nestling eagles. Ibis 116: 224-228.

MODHA, K. L. (1971). Ecology of the Uganda Kob Adenota kob thomasi Neumann in the Queen Elizabeth National Park, Uganda. M.Sc. Thesis, University of East Africa (Makerere).

MODHA, K. L., & ELTRINGHAM, S. K. (1976). Population ecology of the Uganda kob (Adenota kob thomasi Neumann) in relation to the territorial system in the Rwenzori National Park, Uganda. J. Appl. Ecol. 13: 453-473.

MOLL, K. H. (1970). Aufgaben und Probleme der Tierfotografie. Naturschutzarb Bln. Brandenb. 6: 76-80.

MOREAU, R. E. (1950). The breeding seasons of African Birds - 1. Land birds. Ibis 92: 223-267.

MOREAU, R. E. (1964). Breeding season. In A New Dictionary of Birds. A. L. Thomson (ed.), pp. 106-108. Nelson, London.

MOREAU, R. E. (1966). The Bird Faunas of Africa and its Islands. Academic Press, New York.

MORRIS, K. R. (1960). Studies on the epidemiology of sleeping sickness in East Africa. III. The endemic areas of Lakes Edward and George in Uganda. Trans. Roy. Soc. Trop. med. hyg. 54: 212-224.

MUSOKE, M. B. (1980). Overbrowsing of Capparis tomentosa bushes by goats in Rwenzori National Park, Uganda. Afr. J. Ecol. 18: 7-10.

MYERS, N. (1976). The leopard Panthera pardus in Africa. IUCN Monograph 5, Morges.

NEAL, B. R. (1967). The ecology of small rodents in the grassland community of the Queen Elizabeth National Park, Uganda. Ph.D. Thesis, University of Southampton.

NEEDHAM, A. E. (1964). The growth process in animals. Putnam & Sons, London.

NELSON, J. B. (1967). Colonial and cliff nesting in the gannet. Ardea 55: 60-90.

NELSON, J. B. (1968). Galapagos, island of birds. Longmans, London.

NOBLE, G. K. (1939). The role of dominance in the life of birds Auk 56: 263-273.

NUTAE (1971). Ornithological studies. *In* Nuffield Unit of Tropical Animal Ecology: An account of wildlife research in the Uganda National Parks. pp. 14-16.

OSMASTON, H. A. (196[illegible]). A working plan for Maramagambo Forest. Unpubl. Report to Uganda Forest Department, Entebbe.

OSMASTON, H. A. (1971). The vegetation of Murchison Falls and Queen Elizabeth National Parks. *In* Uganda National Parks Handbook, pp. 95-118. 5th ed., Longman Uganda Ltd., Kampala.

PALOKANGAS, R., KOIVUSAARI, J. & NUUJA, I. (1970). Merenkurkun alueen merikotkakanta 1960-luvalla (English Summary: Incidence of the White-tailed Eagle in the region of the Quarken Straits in the 1960s). *Ornis Fennica 47:* 180-184.

PERRINS, C. M. (1965). Population fluctuations and clutch size in the Great Tit *Parus major* L. *J. Anim. Ecol. 34:* 601-647.

PETERSEN, A. & YOUNG, H. (1950). A nesting study of the Bronze Grackle. *Auk 67:* 466-476.

PETRIDES, G. A, & SWANK, W. G. (1965). Population densities and the range carrying capacity for large mammals in Queen Elizabeth National Park, Uganda. *Zool. Africana 1:* 209-225.

PITELKA, F. A. (1959). Numbers, breeding schedule, and territoriality in pectoral Sandpipers of Northern Alaska. *Condor 61:* 233-264.

PITELKA, F. A., TOMICH, P. Q. & TREICHEL, G. W. (1955a). Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecol. Monogr. 25:* 85-117.

PITELKA, F. A., TOMICH, P. Q. & TREICHEL, G. W. (1955b). Breeding behaviour of jaegers and owls near Barrow, Alaska. *Condor 57:* 3-18.

PITMAN, C. R. S. (1971). Reptiles and Amphibians of Murchison and Queen Elizabeth National Parks. *In* Uganda National Parks Handbook; pp. 77-83. 5th ed. Longman Uganda Ltd., Kampala.

PLAGE, G. D. (1974). A three-day watch at a Fish Eagle's nest in Botswana. *Ostrich 45:* 143-144.

POLL, M. (1939). *Poissons. Explor. Parc. Nat. Albert. Mission G. F. de Witte* (1933-1935). *Fasc. 24:* 1-81. Inst. Parcs Nat. Congo Belge. Bruxelles.

POMEROY, D. E. (1977). The biology of the Marabou Stork in Uganda: Part 1. Some characteristics of the species and the population structure. *Ardea 65:* 1-24.

PORTER, R. H. (1903). The Fauna of South Africa. Birds III. Stark and Sclater.

POSNANSKY, M. (1971). Uganda National Parks in prehistoric times. 2. Early man. *In* Uganda National Parks Handbook: pp. 125-135. 5th ed. Longman Uganda Ltd. Kampala.

POSTUPALSKY, S. (1972). Status of the Osprey in Michigan. Transactions of the North America Osprey Research Conference, 10-12 Feb., Williamsburg, Va. *In* J. C. Ogden (ed.). pp. 153-165.

POSTUPALSKY, S. (1974). Raptor reproductive success: some problems with methods, criteria and terminology. *Raptor Research Report 2:* 21-31.

RATCLIFE, D. A. (1963). The status of the Peregrine in Great Britain. *Bird Study 10:* 56-90.

RETFALVI, L. I. (1965). Breeding behaviour and feeding habits of the bald eagle (*Haliaeetus leucocephalus* L.) on San Juan Island, Washington. M. Sc.(Forestry) Thesis, University of British Columbia, Vancouver.

RICKLEFS, R. E. (1967a). Relative growth, body constituents and energy of nesting Barn Swallows and Red-Winged Blackbirds. *Auk 84:* 560-570.

RICKLEFS, R. E. (1967b). A graphic method of fitting equations to growth curves. *Ecology 48(6):* 978-983.

RICKLEFS, R. E. (1968a). Patterns of growth in Birds. *Ibis 110(4):* 419-451.

RICKLEFS, R. E. (1968b). On the limitation of brood size in passerine birds by the ability of adults to nourish their young. *Proc. Nat. Acad. Sci. 61:* 847-851.

RICKLEFS, R. E. (1969a). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology 9:* 1-48.

RICKLEFS, R. E. (1969b). Preliminary models for growth rates of altricial Birds. *Ecology 50:* 1031-1039.

RICKLEFS, R. E. (1969c). Natural selection and the development of mortality rates in young birds. *Nature 223:* 922-925.

RICKLEFS, R. E. (1976). Growth rates of birds in the humid New World tropics. *Ibis 118:* 179-207.

ROBERTS, A. (1958). The Birds of South Africa. Revised by G. R. McLachlan and R. Liversidge.

ROBERTSON, T. B. (1923). The Chemical Basis of Growth and Senescence. Lipponcott, Philadelphia.

ROOD, J. P. (1975). Population dynamics and food habits of the banded mongoose. E. Afr. Wildl. J. 13: 89-112.

ROWELL, T. E. (1966). Forest living baboons in Uganda. J. Zool. Lond. 149: 344-364.

SALT, G. W. & ZEUTHEN, E. (1961). The respiratory system. In Biology and Comparative Physiology of Birds, Vol. 1: (A. J. Marshall ed.), pp. 353-404. Academic Press, New York.

SCHMIDT-NIELSEN, K., JORGENSEN, B. & OSAKI, H. (1958). Extrarenal salt excretion in birds. Am. J. Physiol. 193: 101-107.

SCHOENER, T. W. (1968). Sizes of feeding territories among birds. Ecology 49(1): 123-141.

SCOTT ELLIOT, G. F. (1896). A Naturalist in Mid-Africa. Innes and Co. London.

SNOW, B. K. (1960). The breeding ecology of the Shag (Phalacrocorax aristotelis) on the Island of Lundy, Bristol Channel. Ibis 102: 554-575.

SNOW, C. (1973a). Southern Bald Eagle Haliaeetus leucocephalus leucocephalus and Northern Bald Eagle Haliaeetus leucocephalus alascanus. Habitat Management Series for Endangered Species Report No. 5; Technical Note of Bureau of Land Management, U. S. Department of the Interior.

SNOW, C. (1973b). Golden Eagle Aquila chrysaetos. Habitat Management Series for Unique or Endangered Species Report No. 7; Technical Note of Bureau of Land Management, U. S. Department of the Interir.

SNOW, D. W. & SNOW, B. K. (1967). The breeding cycle of the Swallow-tailed Gull Creagus furcatus. Ibis 109: 14-24.

SOUTHERN, W. E. (1963). Winter populations, behaviour and seasonal dispersal of bald eagles in Northwestern Illinois. The Willson Bulletin 75(1): 42-55.

SPIEGEL, M. R. (1961). Schaum's Outline of Theory and Problems of Statistics. MacGraw-Hill Book Co., New York.

SPINAGE, C. A. (1967a). The autoecology of the Uganda waterbuck Kobus defassa ugandae with special reference to territoriality and population controls. Ph.D. Thesis. London University.

SPINAGE, C. A. (1967b). Ageing the Uganda waterbuck Kobus defassa ugandae Neumann. E. Afr. Wild. J.5: 1-17.

SPINAGE, C. A. (1970). Population dynamics of the Uganda waterbuck (*Kobus defassa ugandae* Neumann) in Queen Elisabeth National Park, Uganda. *J. Amim Ecol. 39:* 51-78.

SPRUNT 1V, A., ROBERTSON, Jr. W. B., POSTUPALSKY, S., HENSEL, R. J., KNODER, C. E. & LIGAS, F. J. (1973). Comparative productivity of six bald eagle populations. *38th Transactions of the North American Wildlife and Natural Resources Conference:* 95-106.

STANLEY, H. M. (1890). In Darkest Africa on the Quest, Rescue and Retreat of Emir, Govern.or of Equatoria. Sampson, Law, Marston & Co., London.

STEYN, P. (1972). African Fish Eagle: a record of breeding success. *Ostrich 43:* 181-182.

STEYN, P. (1974). Eagle Days. Purnell, South Africa.

STINSON, C. H. (1978). The influence of environmental conditions on aspects of the time budgets of breeding Ospreys. *Oecologia 36:* 127-139.

STOWELL, R. F. (1958). Notes on the behaviour in captivity of the African Fish Eagle (*Cuncuma vocifer*). *Ibis 100:* 457-459.

STRUHSAKER, T. T. (1967). Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai Amboseli game reserve, Kenya. *Ecology 48:* 891-904.

SUMBA, S. J. A. & POMEROY, D. E. (In press). Sibling agression in the African Fish Eagle in Uganda. *Proc. V. Pan-Afr. orn. congr.* 23-30 August, 1980, Lilongwe, Malawi.

TABER, R. D. (1963). Criteria of sex and age. *In* Wildlife Investigational Techniques, 2nd ed., H. S. Mosby. (ed.). The Wildlife Society, Blacksburg, Va. 119-189.

TALBOT, L. M. & TALBOT, M. H. (1963). The high biomass of wild ungulates on East African Savanna. *Trans. N. Ame. Wild. Conf. 28:* 465-476.

TEMPLE-PERKINGS, E. A. (1965). The country now the Queen Elizabeth National Park as I have known it from fourty years ago. Unpubl. MS. to Uganda National Parks.

THIOLLAY, J. M. & MEYER, J. A. (1978). Densite, taille des territoires, et production dans une population d'Aigles pecheurs *Haliaeetus vocifer* (Daudin). *La Terre et la Vie, 32:* 203-219.

THOMSON, A. L. (1964). A new Dictionary of Birds. Nelson, London.

THORNTHWAITE, C. W. (1948). An Approach towards a rational Classification of climate. Geog. Rev. 38: 55-94.

TOMKINSON, D. J. (1975). Notes on the mass-carrying ability of the African Fish Eagle. Lammergeyer 22: 19-22.

UNP (1971). Birds. In Uganda National Parks Handbook. pp. 55-76. 5th ed., Longman Uganda Ltd. Kampala.

URBAN, E. K. (1975). Birds and research at Ethiopia's Lakes Shala and Abiata. African Wildlife Leadership Foundation News 10(3): 3-6.

VAN LAWICK- GOODALL, J. (1971). In the Shadow of Man. Collins, London.

VAN ORSDOL, K. G. (1979). Uganda's National Parks. Swara 2(4): 14-16.

VAN ORSDOL, K. G. (1981). Lion predation in Rwenzori National Park, Uganda . Ph.D. Thesis. University of Cambridge.

VOOUS, K. H. (1950). The breeding seasons of birds in Indonesia. Ibis 92: 279-287.

WARD, P. (1965). The breeding biology of the Black-faced Dioch Quelea queleain Nigeria. Ibis 107: 326-349.

WHITFIELD, A. K. & BLABER, S. J. M. (1978). Feeding ecology of piscivorous birds at Lake St. Lucia: Part 1. Diving birds. Ostrich 49: 185-198.

WILLGOHS, J. F. (1961). The white-tailed eagle Haliaeetus albicilla albicilla (Linne) in Norway. Norwegian University Press, Bergen.

WILLSON, M. F. (1966). Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr. 36: 51-77.

WINTERBOTTOM, J. M. (1963). Avian breeding seasons in Southern Africa. Int. Orn. Congr. 13: 640-648.

WOODFORD, M. H. (1972). Tuberculosis in the African Buffalo Syncerus caffer in Queen Elizabeth National Park, Uganda. Dr. Med. Vet. Thesis, University of Zurich.

WORTHINGTON, E. B. (1929a). A report on the fishery survey of Lakes Albert and Kyoga. London Crown Agents for the Colonies.

WORTHINGTON, E. B. (1929b) New species of fish from the Albert Nyanza and Lake Kyoga. Proc. Zool. Soc. Lond. Pt. 3: 429-440.

WORTHINGTON, E. B. (1932). A report on the Fisheries of Uganda. London Crown Agents for the Colonies.

WORTHINGTON, S. & WORTHINGTON, E. B. (1933). Inland waters of Africa. MacMillan & Co., London.

WYNNE-EDWARDS, V. C. (1959). The control of population density through social behaviour: a hypothesis. Ibis 101: 436-441.

WYNNE-EDWARDS, V. C. (1962). Animal dispersion in relation to social behaviour. Hafner Publ. Co., New York.

WYNNE-EDWARDS, V. C. (1963). Intergroup selection in the evolution of social systems. Nature 200: 623-626.

YOACIEL, S. M. & VAN ORSDOL, K. G. (1981). The influence of environmental changes on an isolated topi (*Damaliscus lunatus jimela* Matchie) population in the Ishasha Sector of Rwenzori National Park, Uganda. Afr. J. Ecol. 19: 167-174.

YOUNG, H. (1963). Age-specific mortality in the eggs and nestlings of Blackbirds. Auk 80: 145-155.

ZAR, J. H. (1974). Biostatistical analysis. Prentice-Hall, N. J.

WORTHINGTON, S. & WORTHINGTON, E. B. (1933). Inland waters of Africa. MacMillan & Co., London.

WYNNE-EDWARDS, V. C. (1959). The control of population density through social behaviour: a hypothesis. *Ibis 101:* 436-441.

WYNNE-EDWARDS, V. C. (1962). Animal dispersion in relation to social behaviour. Hafner Publ. Co., New York.

WYNNE-EDWARDS, V. C. (1963). Intergroup selection in the evolution of social systems. *Nature 200:* 623-626.

YOACIEL, S. M. & VAN ORSDOL, K. G. (1981). The influence of environmental changes on an isolated topi (*Damaliscus lunatus jimela* Matchie) population in the Ishasha Sector of Rwenzori National Park, Uganda. *Afr. J. Ecol. 19:* 167-174.

YOUNG, H. (1963). Age-specific mortality in the eggs and nestlings of Blackbirds. *Auk 80:* 145-155.

ZAR, J. H. (1974). Biostatistical analysis. Prentice-Hall, N. J.

WORTHINGTON, S. & WORTHINGTON, E. B. (1933). Inland waters of Africa. MacMillan & Co., London.

WYNNE-EDWARDS, V. C. (1959). The control of population density through social behaviour: a hypothesis. *Ibis 101:* 436-441.

WYNNE-EDWARDS, V. C. (1962). Animal dispersion in relation to social behaviour. Hafner Publ. Co., New York.

WYNNE-EDWARDS, V. C. (1963). Intergroup selection in the evolution of social systems. *Nature 200:* 623-626.

YOACIEL, S. M. & VAN ORSDOL, K. G. (1981). The influence of environmental changes on an isolated topi *(Damaliscus lunatus jimela* Matchie) population in the Ishasha Sector of Rwenzori National Park, Uganda. *Afr. J. Ecol. 19:* 167-174.

YOUNG, H. (1963). Age-specific mortality in the eggs and nestlings of Blackbirds. *Auk 80:* 145-155.

ZAR, J. H. (1974). Biostatistical analysis. Prentice-Hall, N. J.