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## Population density and intra- and interspecific competition of the African Fish Eagle *Haliaeetus vocifer* in Kyambura Game Reserve, southwest Uganda

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Population density and intra- and interspecific competition of the African Fish Eagle *Haliaeetus vocifer* were studied in Kyambura Game Reserve, southwest Uganda. Density varied significantly between 1.75 and 3.25 individuals per km of shore for the breeding biotopes along the Kazinga Channel and crater lakes and between 0.45 and 0.58 for unsuitable biotopes such as the Kyambura Gorge or the bush grassland. The age-class distribution showed extremely high percentages of immatures in these unsuitable biotopes (50–95%) as a consequence of intraspecific competition for space and food. Some immatures survived in the bush grassland, feeding on lion and leopard kills and very possibly on birds. Each territory was up to five times larger than breeding pair territories along the Kazinga Channel (5.1 km<sup>2</sup> in comparison with 0.9 km<sup>2</sup>). Interspecific competition for space was likely between immature African Fish Eagles and other species of raptors. Ecological segregation with regard to space was assessed between these species in the bush grassland.

The African Fish Eagle *Haliaeetus vocifer* is widespread and well known in East Africa on the seashore, lakes, rivers and swamp areas and has been studied by many ornithologists in the past. Surveys on the breeding behaviour, territory size and population structure were undertaken by Brown (1952, 1960, 1980), Green (1964), Brown and Cade (1972), Brown and Hopcraft (1973), Eltringham (1975) and Sumba and Hebrard (1988). All of these studies defined the territory size by the length of shore occupied by a pair or a single eagle. No information suggested the possibility of African Fish Eagles in the savannah, presumably because it seemed unlikely that this species feeds on anything other than fish. Interspecific competition has also been neglected although the African Fish Eagle is the raptor which shows the greatest level of territorial behaviour with intraspecific neighbours (Brown 1980).

During a 2-month period of investigation between 12 July and 14 September 1994, a study on the African Fish Eagle was carried out in Kyambura Game Reserve with four main objectives: (1) to assess the population density and age-class distribution in different habitats; (2) to survey the territory size of African Fish Eagles along shores and determine how far into the savannah they defend their territories; (3) to assess the population density and territory size of African Fish Eagles living in the savannah and (4) to reveal interspecific relationships with other birds of prey in the Reserve.

Eltringham (1975) reported that the African Fish Eagle was very common in the Queen Elizabeth National Park as it is in Kyambura Game Reserve. The Kazinga Channel, which separates the national park from the game reserve, seems to be an ideal habitat for the species. Brown (1960)

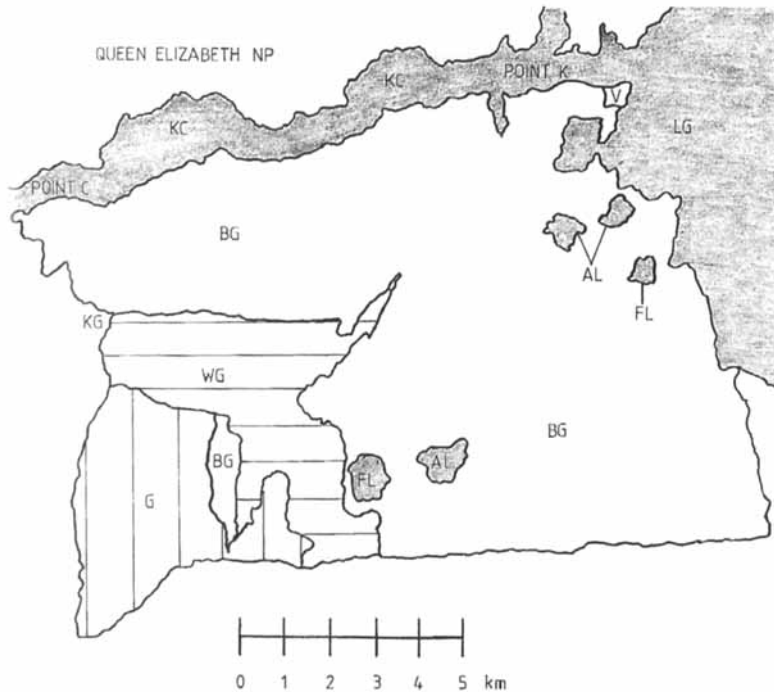
reported that the cichlid fish *Tilapia esculenta* is an important prey, and this species is most often caught by the fishermen in the small villages along the channel.

### STUDY AREA AND METHODS

Kyambura Game Reserve (30°08'E, 0°09'S; Fig. 1) is located in southwest Uganda and serves as a buffer zone for the Queen Elizabeth National Park (formerly Rwenzori National Park). The national park forms the western boundary, across the Kyambura Gorge. The gorge varies between 50 m and 100 m deep and between 100 m and 1000 m wide. The vegetation is riverine forest, consisting mainly of fig trees *Ficus* sp., *Cynometra* sp. and *Diospyros abyssinicus*. At the bottom of the gorge, the river is 5–30 m wide.

The Kazinga Channel is the northern boundary of the reserve. It connects Lake Edward to Lake George, which is the eastern boundary. The channel is 1–2 km wide and has moderate slopes 1–10 m high. The shores mainly support Papyrus *Cyperus papyrus* and are often lined by a tall grass *Vossia cuspidata*. Small groups or single acacias *Acacia sieberiana* and *A. gerrardii* are found near the shore. Their number decreases from the western part to the eastern part of the reserve. To the south of the reserve are plantations and villages.

The dominant habitats in the reserve are the bush grassland, wooded grassland and open grassland. The survey concentrated on the bush grassland because African Fish Eagles were observed only in this habitat and around the lakes. It is covered by groups of *Capparis tomentosa* thickets.



**Figure 1.** Kyambura Game Reserve (KG = Kyambura Gorge, KC = Kazinga Channel, LG = Lake George, BG = bush grassland, WG = wooded grassland, G = grassland, FL = freshwater lake, AL = alkaline lake, V = village).

The Candelabra Tree *Euphorbia candelabrum* is also very common. The main species of grass are *Themeda triandra* and *Sporobolus pyramidalis*. In the bushland and bushthicket, the proportion of bushes is much higher.

The reserve contains five lakes, all of them crater lakes. Three are alkaline and two are freshwater. Their size varies between 50 ha and 200 ha.

Along the Kazinga Channel, the African Fish Eagles were counted on occasional boat trips but mostly from transects along the shore. These transects were normally 5 km long and binoculars (10 × 50) were used to classify the individuals into adults or immatures. The transects were walked on the top of the slopes to make sure that no individuals sitting near the shore were missed. To determine the density around the lakes, the numbers of African Fish Eagles were counted on several occasions by walking around the perimeters of the lakes.

In the bush grassland and the gorge, it was more difficult to obtain data. The density of African Fish Eagles was much lower in the bush grassland; many transects were walked without making any contacts, despite the visibility being greater. Transects were walked from the shore of the channel through the bush grassland to the wooded grassland on random bearings. With these transects, it was possible to assess the size of territories of the eagles along the channel and how deep into the bush grassland they defended them. In the gorge, visibility was the main problem. The transects were walked on the edge of the gorge to identify individuals sitting on the tops of trees or circling over the gorge.

The walking speed in the transects fluctuated between 2 and 4 km per h, depending on the number of observations.

The classification of African Fish Eagles was simplified in

comparison with Brown and Cade (1972). I distinguished only between adults and immatures to avoid misclassification (for detailed description of the different plumage characters, see Brown & Cade 1972). To test the significance of the age-class distribution in the different habitats and interspecific relationships, the  $\chi^2$ -test and *U*-test were used. To calculate the longevity of the adults, I used the following formula, derived by Lack (1954) and Fry (1980):

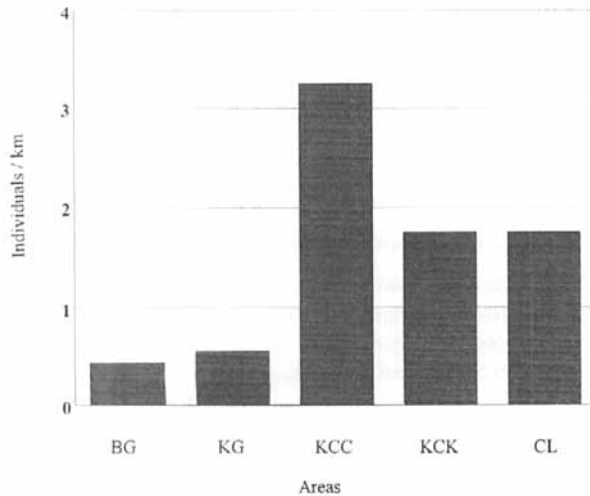
$$Y = \frac{2 - M}{2M}, \quad (1)$$

where *Y* is the mean longevity of the population and *M* is the proportion of annual mortality, in this case estimated by the proportion of immatures in the population.

## RESULTS

### Population density of the African Fish Eagle in different habitats

The population density varied significantly between the different habitats (Fig. 2). Along the channel, the density varied most between point C (3.25 individuals/km) and point K (1.75 individuals/km). There are many trees around C which are absent around K, where only the Candelabra Tree occurs. There is also a fishing village at K and, as a consequence, much more disturbance. The density at the crater lakes was as high as at K. The freshwater lakes had a density of 2.2 eagles per km of shore, and around the alkaline lakes there were 1.3 individuals per km of shore. In the gorge, the density was much lower (0.58 individuals/km) because



**Figure 2.** Population density of the African Fish Eagle in different areas (individuals/transect km) in Kyambura Game Reserve (BG = bush grassland, KG = Kyambura Gorge, KCC = Kazinga Channel [point C], KCK = Kazinga Channel [point K], CL = crater lakes).

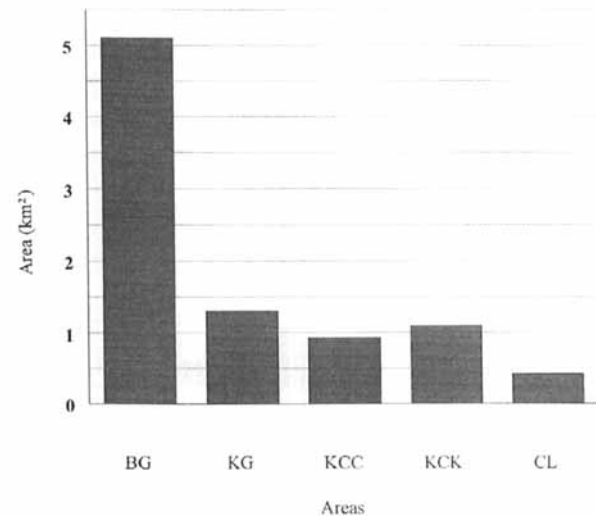
there is only a small river and suitable breeding biotopes are rare. The most interesting information in Figure 2 is the fact that there were African Fish Eagles in the bush grassland. The density was low (0.45 individuals/km of transect), but there were some eagles surviving in the bush grassland relatively far away ( $\geq 2$  km) from water, their typical hunting biotope.

### Territory size and territorial behaviour

The territory size varied between the different habitats because of the densities. Around point C at the channel, one breeding pair occupied a mean of 0.6 km of shore, whereas around point K, the mean was 1.1 km. The mean was 0.9 km per breeding pair for the freshwater lakes and 1.5 km for the alkaline lakes. Along the river in the gorge, a territory had a mean length of 3.4 km. In the bush grassland, no breeding pairs were observed, and the territories seemed to belong to single individuals. According to the transect results, one eagle had a territory with a mean size of *c.* 5 km<sup>2</sup>.

During the survey it became obvious that the breeding pairs along the channel, lakes and the river defended not only the shore but also an inland area. The width of this area varied between 0.2 km and 1.1 km for the pairs along the channel, but around the lakes, this area extended only 0.1 km from the shore. In the bush grassland, only a few territories were surveyed because of the low density. The mean size of the territories in the different habitats is shown in Figure 3.

In addition to the inland area, a part of the lake or channel belonged to the territories as a hunting site. This part was between 0.2 km (some lakes) and 0.75 km (channel) wide. These three parts contributed to the territory. The size



**Figure 3.** Mean territory size of the African Fish Eagle in different areas in Kyambura Game Reserve (single territories for the bush grassland and breeding pair territories for the other areas; BG = bush grassland, KG = Kyambura Gorge, KCC = Kazinga Channel [point C], KCK = Kazinga Channel [point K], CL = crater lakes).

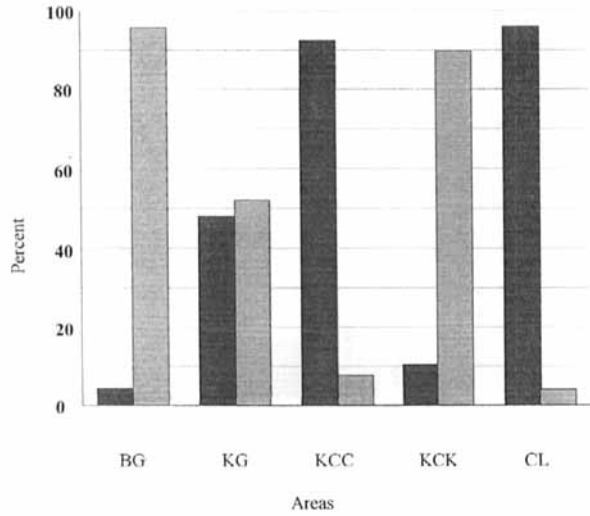
did not vary much between the habitats with the exception of the bush grassland, in which territories were much bigger (mean = 5 km<sup>2</sup>). The very limited food supply presumably led to this size, although the territories were occupied by single birds.

The breeding pairs and the individuals defended their territories rigorously against intraspecific neighbours. Circling over the territory and calling in the air or from single trees were observed often, and fights between neighbouring pairs were seen.

### Age-class distribution in the habitats

The age-class distribution fluctuated widely between the habitats (Fig. 4). In the breeding habitats along the channel at point C and at the crater lakes, the percentage of immatures was low (7.6%,  $n = 79$  and 4.0%,  $n = 25$ , respectively). These values are in line with the mean replacement rate of the African Fish Eagle, estimated as 4–6% (Brown & Cade 1972). In the gorge and around point K along the channel, the percentages were significantly higher (52%,  $n = 25$ ,  $P < 0.001$  for the gorge and 90%,  $n = 29$ ,  $P < 0.001$  for K). In comparison to the normal rate of 6%, these rates indicated that in unsuitable biotope the percentage of immature birds was much higher. The result from the bush grassland further stresses this (96%,  $n = 46$ ,  $P < 0.0001$ ). Nearly all of the birds in the bush grassland consisted of immatures. Some of these individuals tried to occupy a part of the shore of the channel but were attacked by adults. The adults in the gorge attacked every immature trying to fish in the river. The immatures were ousted into less suitable biotopes by the adults.

Using the percentage of immatures around point C and



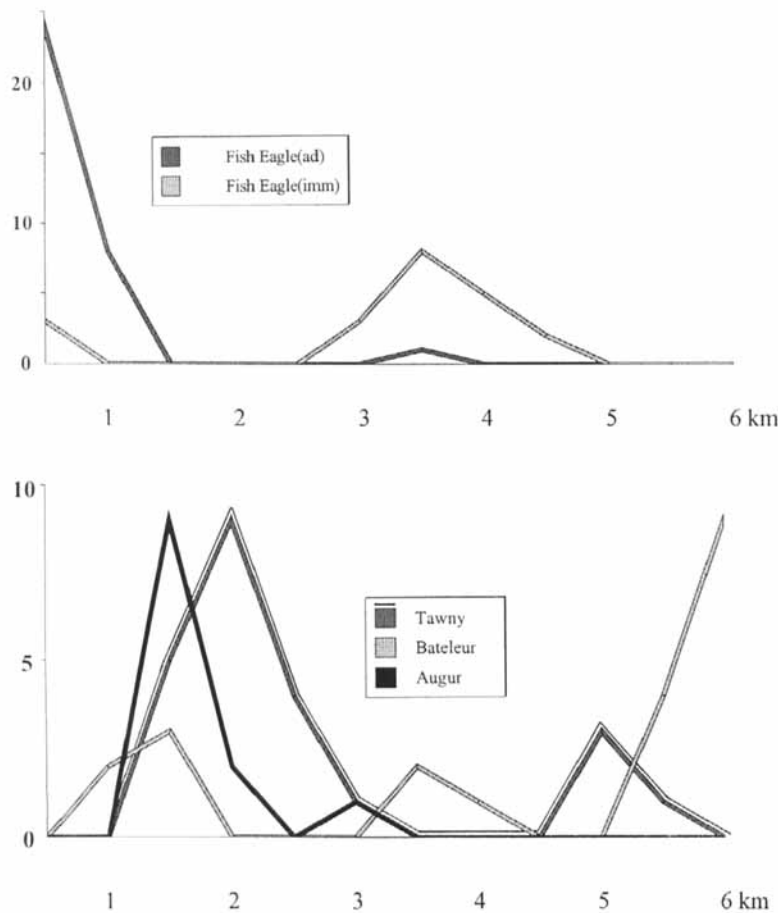
**Figure 4.** Proportion of adult (dark beams) and immature (light beams) African Fish Eagles in different areas in Kyambura Game Reserve (BG = bush grassland, KG = Kyambura Gorge, KCC = Kazinga Channel [point C], KCK = Kazinga Channel [point K], CL = crater lakes).

the crater lakes, the longevity of the adults can be assessed by Lack's formula (Eq. 1). The average life span was 16.8 years for the Kyambura population. The birds in other habitats cannot be included because those habitats are not normally breeding biotopes. Brown and Hopcraft (1973) assessed the life span as 20–28 years at Lake Naivasha, Kenya.

**Intra- and interspecific competition**

The age-class distribution in the different habitats revealed that intraspecific competition took place in the African Fish Eagle. Interspecific interaction was also observed between African Fish Eagles and Tawny Eagles *Aquila rapax*, Bateleurs *Terathopius ecaudatus* and Augur Buzzard *Buteo rufofuscus*. The results of the transects are shown in Figure 5. The plots for the adult and immature African Fish Eagles show the ecological segregation between the age classes ( $P < 0.001$ , *U*-test). There was at least 1 km between the territories along the channel and the immature territories in the bush grassland. Vocalization was used to define the territories.

The plots of the other species show peaks at different distances from the channel. The immature African Fish Eagles



**Figure 5.** Observation numbers of the African Fish Eagle, Tawny Eagle, Bateleur and Augur Buzzard in the bush grassland transects in correlation to the distance to the Kazinga Channel.

probably influenced the other species because Tawny Eagles and Augur Buzzards were not observed with equal frequency, although the habitat did not change ( $P < 0.001$  for the Tawny Eagle and  $P < 0.0001$  for the Augur Buzzard). Some fights between African Fish Eagles and Tawny Eagles were observed. The Bateleur was also influenced significantly ( $P < 0.001$ , but no attacks by African Fish Eagles were observed).

## DISCUSSION

The density of the African Fish Eagle along the Kazinga Channel has been nearly constant for 20 years. Eltringham (1975) reported a density of 3.5 eagles per km of shore for the channel and Sumba and Hebrard (1988) 2.4 eagles per km of shore. The values in this study (1.75–3.25 eagles/km of shore) are similar. Green (1964) stressed that the steepness of the slopes influenced the density, and Eltringham (1975) reported that the distribution was related to the availability of trees as perches. This could explain the lower density around K along the channel. Remarkably, the density along the channel was significantly higher than the density around Lake Edward (1.9–2.6 eagles/km of shore) and Lake George (1.0–1.1; cf. Eltringham 1975, Sumba & Hebrard 1988).

At the crater lakes, the density was much lower in comparison with those reported by Sumba and Hebrard (1988), who found 5.4 eagles per km of shore for the larger crater lakes in Queen Elizabeth National Park. Brown and Hopcraft (1973) reported that breeding pairs in lagoons were more successful than breeding pairs with access only to open water. This could be an explanation for the high density around the crater lakes in the national park but does not fit with the results for the crater lakes in Kyambura Game Reserve, although the low density around Lakes Edward and George, in comparison with the channel, also agrees with this theory.

The low percentage of immatures along the channel at point C (7.6%) is nearly the same (7%) as that obtained by Eltringham (1975). Brown and Cade (1972) reported 14.4–17.8% for a growing population at Lake Naivasha, Kenya. The low percentage of immatures, in addition to the constancy of the numbers, makes a long-term increase in the population very unlikely. The high percentages of immatures in the other habitats were probably a consequence of the stable and high population along the channel. Where breeding sites were missing (channel at point K, gorge, bush grassland), the immatures found their ecological niche. The increasing percentage of immatures indicates a hierarchy of habitats, from the optimal channel and the crater lakes to the gorge and bush grassland. The immatures were ousted from the optimal habitats by the adults because of competition for food between adults and immatures (Eltringham 1975). Adults attacked immatures whenever the immatures tried to fly through the territories of the adults.

There is no doubt that some immatures were living in the

bush grassland. At Lake Malawi, immatures were observed in the savannah far away from any water (K. Newman, pers. comm.). Similar observations were made in Toro Game Reserve, Uganda (J. Graham, pers. comm.). What they feed on could not always be assessed, but they were competing with vultures for Lion *Panthera leo* and Leopard *Panthera pardus* kills. For example on 31 July 1994, four immature African Fish Eagles were observed near a fresh leopard kill together with 12 White-backed Vultures *Gyps africanus*. Brown (1960) stressed that the African Fish Eagle is more a bird-killer than supposed, and Eltringham (1975) reported that African Fish Eagles attacked Egyptian Geese *Alopochen aegyptiacus*. The African Fish Eagle is the most important predator of Lesser Flamingos *Phoenicopterus minor* at Lake Elmenteita and Lake Nakuru (Brown 1958). Kyambura Game Reserve supports a colony of Lesser Flamingos, fluctuating between 3000 and 15,000 in the dry season, and the adult African Fish Eagles around the alkaline crater lakes sometimes prey upon them (cf. Krueger 1996).

Interspecific competition seems to take place between immature African Fish Eagles, Tawny Eagles and Augur Buzzards. Eltringham (1975) reported that an African Fish Eagle drove away a Tawny Eagle but stressed that this was a single observation. Schmutz *et al.* (1980) have studied the coexistence of hawks and found competition for space. Other studies have revealed similar results (James 1984, Dobler 1990, Krueger 1994, 1995). The plots in Figure 5 support the supposition of ecological segregation with regard to space. Many more observations will have to be made to determine if this is a universal effect in the interspecific relations among birds of prey.

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