Hydrobiologia **488:** 163–170, 2002.
D.M. Harper, R. Boar, M. Everard & P. Hickley (eds), Lake Naivasha, Kenya.

Population changes in sympatric Great and Long-tailed Cormorants (*Phalacrocorax carbo* and *P. africanus*): the effects of niche overlap or environmental change?

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Key words: Phalacrocorax carbo, *Phalacrocorax africanus*, population changes, niche overlap, sympatric species, resource competition, ecological separation

Abstract

Between January 1993 and January 1995, the number of Great Cormorants (*Phalacrocorax carbo*) using Lake Naivasha, Kenya (00° 45′ S, 36° 20′ E) for foraging and resting increased 56%, while the number of sympatric Long-tailed Cormorants (*Phalacrocorax africanus*) decreased 64%. In 1995 and 1996, we documented habitat changes and conducted monthly population and resource-use surveys of the two species in an attempt to discover the most likely reasons for these changes. The increase in Great Cormorants was probably the result of immigration from nearby Lake Nakuru due to extreme water level reductions there. Lake Naivasha also experienced falling water levels and transparency during this period, but these changes were not as severe and are not considered likely reasons for the decline in Long-tailed Cormorant numbers. Despite some probable dietary overlap, the two species were well separated in terms of foraging locations, foraging methods, resting habitats and breeding timing. The decline in Long-tailed Cormorant numbers may be connected with increased disturbance by fishermen along the lake littoral, this species' primary feeding location.

Introduction

The ranges of the Great and Long-tailed Cormorants substantially overlap in sub-Saharan Africa (Johnsgard, 1993). At Lake Naivasha (00° 45′ S, 36° 20′ E) in the southern part of Kenya's Rift Valley, the two species are sympatric. Between January 1993 and January 1995, the number of Great Cormorants using the lake for foraging and resting increased by 56%, while the number of Long-tailed Cormorants decreased by 64% (Table 1; Nasirwa & Bennun, 1994, 1995). These population changes continued through 1996.

The competitive exclusion principle postulates that ecologically similar species using the same set of limited resources cannot coexist in equilibrium (reviewed in Wiens, 1989). Both prey variety and suitable resting habitat are limited at Lake Naivasha. This lake is unusual for a tropical freshwater lake in having only three abundant fish species (Harper et al., 1990) to support the 45 species in its avian fish-eating guild (Hartley, 1984). However, while the limited number of prey species might indicate a high degree of diet overlap, previous studies have shown that ecologically similar species which exhibit a high degree of overlap on one niche dimension (e.g., prey species), often are able to coexist due to compensating differences on other dimensions such as prey size, or foraging locations or methods (Lack, 1945; Schoener, 1974; Brandl & Utschick, 1985). Further, it has also been shown that two similar sympatric species with a large difference in size, such as the Great and Long-tailed Cormorants (Brown et al., 1982), are not likely to utilise the same resources to any important extent (e.g., Lack, 1971; Furness & Barrett, 1985).

Before 1993, there was a breeding population of approximately 3000 Great Cormorants at Lake Nakuru (Bennun, 1992; Nasirwa, pers. comm.), an alkaline lake about 55 km north-west of Lake Naivasha. The years 1993 and 1994 were relatively dry in this section of the Rift Valley (Nasirwa & Bennun, 1994) and Lake Nakuru evaporated almost completely. Due to the low water level and resulting high alkalinity, fish stocks virtually disappeared, followed by the fish-eating birds (Bennun & Nasirwa, 2000). The Great Cormorant population there declined from 3238 in 1992, to 578 in 1993, and to zero in 1994.

In 1995, Great Cormorants established a new breeding colony on Lake Oloidien in the Lake Naivasha ecosystem. Lake Oloidien (00° 49′ S, 36° 16′ E) is a small (5.5 km^2) alkaline satellite of Lake Naivasha (ca. 130 km^2). This colony, which contained 875 nests in its first year, increased to 925 nests in 1996. No birds in the Lake Nakuru population were marked, and it is therefore not certain where they dispersed. However, it seems probable that the increase in Great Cormorants using Lake Naivasha and the establishment of the new breeding colony were the result of immigration from Lake Nakuru. This does not, however, explain the coincidental decrease in the number of Long-tailed Cormorants using Lake Naivasha. Here we assess two hypotheses, not mutually exclusive, to explain this decline:

- There is extensive niche overlap between the two sympatric species, suitable prey and resting resources are limited, and the Great Cormorant is more successful in competing for these limited resources.
- Declines in lake water level and transparency at Lake Naivasha during the 1990s had a greater negative effect on the Long-tailed Cormorant's ability to meet its needs than on that of the Great Cormorant.

Methods

Between September 1995 and August 1996, we conducted monthly population and resource-use surveys of the two cormorant species on lakes Naivasha and Oloidien. For these surveys, the littoral of the two lakes was divided into 16 sections (Fig. 1), the sections containing approximately equal lengths of shoreline. To facilitate historical analysis, the sections were the same as those used by the Department of Ornithology, National Museums of Kenya for its annual waterbird counts.

Each survey of Lake Naivasha consisted of circumnavigating the lake in an inflatable dinghy, keeping approximately 100 m offshore. Due to the size of the lake (approximately 130 km^2), the high winds and rough waters that often occurred in the afternoons, and the daily movement patterns of the cormorants, the surveys were all conducted between about 07:00 and 13:00 h. Surveys usually took place over two successive days with six or seven sections being completed each day. Each survey was begun in a different section, and the direction of travel was altered to vary the survey times for each section throughout the year. Water transparency was recorded with a Secchi disc at the beginning, middle, and end of each section. Because of its smaller size, Lake Oloidien could be surveyed accurately with ×10 binoculars and a ×20–60 telescope from an elevated point of land along the southern shore. In order to maintain time-of-day consistency, the Oloidien surveys were always conducted mid-morning on the day immediately following the Lake Naivasha survey.

During the surveys, each cormorant sighted was recorded, along with its activity (foraging, resting, or flying), foraging location (lake section and estimated distance from shore), and, if appropriate, resting habitat (mud shore, floating water hyacinth, sedges, rocks, man-made structures). The numbers of birds in flocks (foraging, resting, or flying) were counted with the aid of ×10 binoculars and a tally counter, and recorded along with the foraging location or resting habitat of the flock. The number of individual birds in each flock was counted twice. If the counts were within 5% of one another, the mean of the two counts was recorded. If the counts were more than five percent apart, the flock was counted a third time, and the mean of the three counts was recorded.

In order to obtain an indication of the Great Cormorant diet an analysis was made of the species and size of dropped and regurgitated fish collected under the colony. Between the ages of 5 and 8 weeks Great Cormorant nestlings will frequently regurgitate whatever is in their oesophagus when threatened (RBC, unpubl. data). For a period of approximately 8 weeks in both 1995 and 1996, while the main body of nestlings passed through this age category, all dropped and regurgitated fish were collected, measured, and weighed ($n = 190$). Fish identification was straightforward, since the fish species variety in Lake Naivasha is limited and well known, consisting

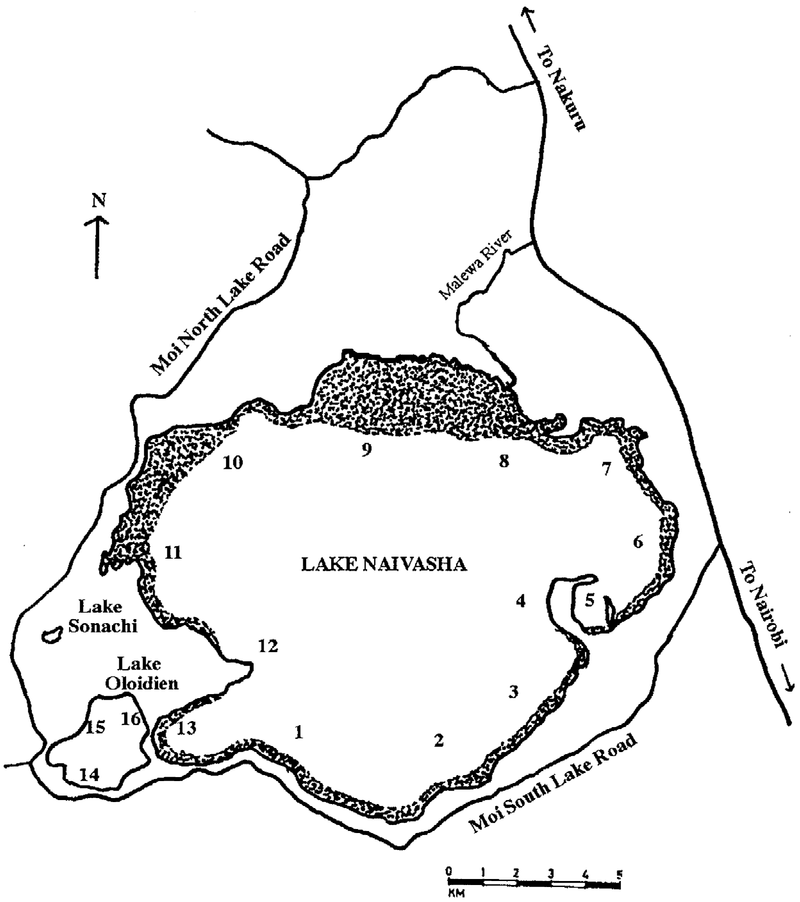

Figure 1. Lake Naivasha population survey map; sources: Hartley, 1984 & Ornithology Dept., National Museums of Kenya; numbers indicate shoreline survey sections.

primarily of two introduced tilapine species (*Oreochromis leucostictus* and *Tilapia zillii*) and the introduced American Black Bass (*Micropterus salmoides*).

These data are believed to represent a random sample of the fish the nestlings were fed during the period when they were between 5 and 8 weeks old. However, because Great Cormorants appear to be opportunistic feeders taking whatever is available, and because 8-week-old nestlings are as large as adults, these data were also used to indicate the diet of adult cormorants during the breeding season.

Results

Cormorant population trends

Between January 1993 and January 1995, the number of Great Cormorants using Lake Naivasha for foraging and resting increased by 56% from 555 to 868, while the number of Long-tailed Cormorants decreased 64% from 1035 to 374 (Table 1).

The population shifts observed in 1993–95 continued through 1996. From a low of 555 in January 1993, the number of Great Cormorants counted using the Lake Naivasha ecosystem for foraging and resting increased by 110% to 1167 individuals in January 1997, after peaking at 2403 individuals in January

Table 1. Counts of cormorants using Lake Naivasha ecosystem* each January, 1993–95

	1993	1994	1995
Great Cormorant	555	861	868
Long-tailed Cormorant	1035	823	374
Both species	1590	1684	1242

*Includes small adjacent lakes Oloidien and Sonachi.

1996. During the same time period, the number of Long-tailed Cormorants using the lakes declined by 77% from the peak of 1035 individuals counted in January 1993 (Fig. 2).

Resource-use comparisons

Prey species and size

Approximately 90% of the Great Cormorant diet during the breeding period consisted of fish weighing ≤150 g. Body shape appears to have had a significant influence on the weight of individual fish eaten and regurgitated (Fig. 3). Mean weights for the more cylindrical-shaped bass (131.6 ± 63.4 g S.D., $n = 73$) were twice as great as for the broader, deeper-shaped *Tilapia* (65.2 ± 39.2 g S.D., $n = 117$; $t = 8.05$, $P < 0.001$; separate variance *t*-test).

We did not document the Long-tailed Cormorant diet. Only 83 individuals were seen foraging during the 12 censuses and they were rarely observed catching anything. Analysis of stomach contents was not attempted, and examination of pellets cast at their day roosts was unsuccessful.

Foraging distance from shore

The Great Cormorant was found foraging most often (62.8%) in open water >100 m from the edge of the lake, while the Long-tailed Cormorant was found foraging most often (88.0%) <100 m of the lake edge (Fig. 4). Long-tailed Cormorants often foraged very close inshore: 44.6% of foraging individuals were recorded <5 m of the lake edge, compared to just 9.8% for the Great Cormorant. The difference between the two species in foraging distance from shore is highly significant ($\chi^2{}_1 = 87.39$, $P < 0.01$; χ^2 test).

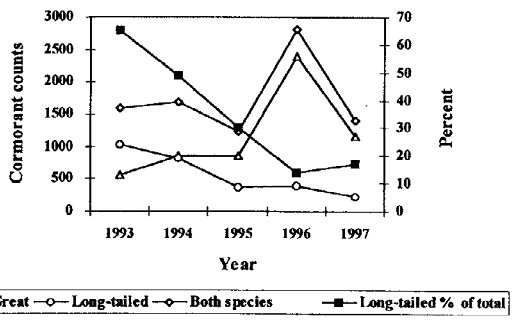

Figure 2. Counts of cormorants using Lake Naivasha ecosystem each January, 1993–97, and the Long-tailed species percentage of the total each year; source: Bennun, 1993; Nasirwa & Bennun, 1994, 1995; Nasirwa personal communication. Includes small adjacent lakes Oloidien & Sonachi.

Foraging methods

The Long-tailed Cormorant was only observed foraging solitarily, while the Great Cormorant usually foraged in flocks. Of 3023 Great Cormorants recorded foraging, only 15% were solitary, the rest being in flocks ranging in size from nine to 407 birds ($n = 28$, mean = 91.7 ± 96.6 S.D.).

Effect of water transparency on Great Cormorant foraging method

When water transparency was <40 cm, Great Cormorant foraging was almost exclusively communal (95.8%). However, when water transparency was ≥40 cm, the relative frequency of solitary foraging increased to 37.4%. There was a highly significant association between communal foraging and water transparency <40 cm, and between solitary foraging and water transparency ≥40 cm ($\chi^2{}_1 = 797.7$, $P < 0.01$, χ^2 test). Long-tailed Cormorants were never observed foraging in groups, so water transparency appeared to have no effect on this aspect of their foraging behaviour.

Effect of water transparency on foraging activity

Long-tailed Cormorants foraged as readily in areas where water transparency was relatively low (<40 cm Secchi disk depth), as in those where it was relatively high (≥40 cm Secchi disk depth) (Fig. 5). However, a disproportionate number of Great Cormorants were recorded foraging in waters where transparency was relatively low (<40 cm). There was a highly significant association between Great Cormorant foraging and water transparency <40 cm ($\chi^2{}_1 = 662.2$, $P < 0.01$, χ^2 test).

Day and night roost locations and habitats

From their night roosts, both species flew to Lake Naivasha to feed just after dawn. Before beginning to forage, however, the Long-tailed Cormorants first flew singly or in small groups of twos and threes to day roosts, large clumps of papyrus or floating water hyacinth located near their foraging areas at various points around the lake. These roosts, which usually accommodated between 10 and 50 birds each, acted as bases for the day's foraging, with birds flying out to forage and then returning to rest throughout the day.

At the end of the day, the Long-tailed Cormorants again gathered at their day roosts before flying off in small groups to their night roost just before sunset. (We were unable to locate their night roost.) The locations of the day roosts varied throughout the

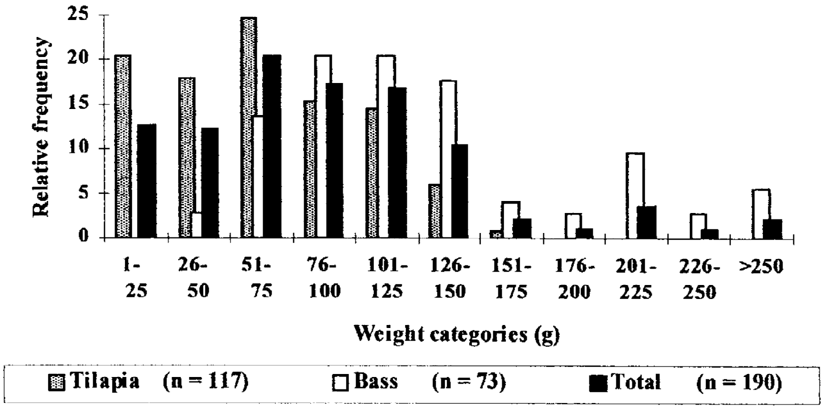

Figure 3. Proportion of Great Cormorant colony diet represented by fish weight category: tilapia (combined species) and American large-mouthed bass, 1995–96.

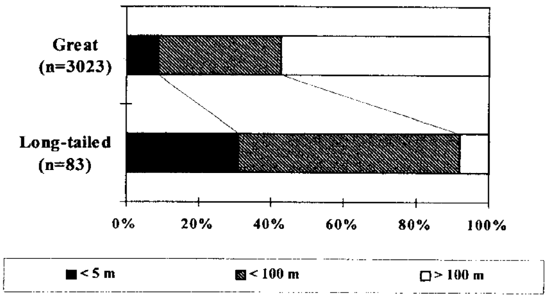

Figure 4. Relative frequency of foraging distance from the lake edge by species.

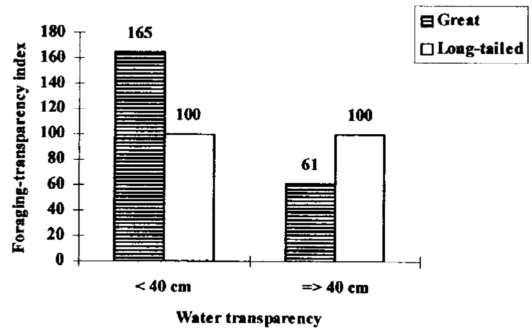

Figure 5. Foraging index (the proportion of individuals recorded foraging at each transparency level divided by the proportion with which that level occurred in the survey). Sample sizes according to water transparency (Secchi disk) depth. Great Cormorant: <40 cm 1611; ≥40 cm 984; total 2595; Long-tailed Cormorant: <40 cm 27; ≥40 cm 45; total 72; survey transparency levels: <40 cm 47; ≥40 cm 78; total 125.

year depending on the foraging locations currently in use. For 6 months of the year (October–March), extensive beds of floating Water Hyacinth *Eichhornia crassipes* became anchored on a large area of submerged macrophytes located north of Crescent Island. During this part of the year, the majority (61.8%) of resting Long-tailed Cormorants were found on these centrally located beds (Table 2). During the remaining 6 months, when these beds were much smaller, the majority (61.0%) rested on sedges around the lake edge (Table 2). The October–March pattern of resting habitat occupation was significantly different from the April–September pattern ($\chi^2_6 = 652.0$, $P < 0.01$).

The Great Cormorants roosted at night in their breeding colony trees at Lake Oloidien. At dawn, they would leave this roost in groups of 15–30 birds, usually flying to Lake Naivasha. Here, they would fly around the edge of the lake. When a group located a shoal of fish, it landed and began foraging. It would soon be joined by other groups of Great Cormorants, and the resulting flock could quickly build to 300–400 birds. As with the Long-tailed Cormorant, the period of most intense foraging occurred between daybreak and about 09:00 h. After completing foraging, the Great Cormorants also began gathering in ones and twos at day roosts. Like the Long-tailed Cormorants, the Great Cormorants rested in large numbers during the day on beds of floating water hyacinth, either the large central beds north of Crescent Island when these were available (October–March), or the beds around the edge of the lake (April–September). At all times of the year, even larger numbers rested during the day on muddy or sandy shoreline (>40%, Table 2).

The differences between the October–March period and the April–September period in the frequency with which different resting habitats were used (Table 2) were statistically significant, even after combining the two water hyacinth categories ($\chi^2_5 = 46.6$, $P < 0.01$, χ^2 test). Likewise, the differences between

Table 2. Seasonal relative frequency of resting habitat use by species

Habitat	Percentage of Long-tailed Cormorants resting		Percentage of Great Cormorants resting*	
	Oct.–March (n = 1930)	April–Sept. (n = 669)	Oct.–March (n = 3743)	April–Sept. (n = 2636)
Central hyacinth beds	61.8	8.2	11.0	0.5
Littoral hyacinth beds	10.5	23.9	22.0	35.8
Sedges	9.9	61.0	0.8	0.2
Mud/sand shore	0.4	1.2	41.5	42.9
Rocks	3.6	4.3	14.1	14.1
Stumps	3.3	1.4	6.9	3.9
Man-made structures	0.5	0.0	3.7	2.6

*Excludes birds in breeding-colony trees.

the resting habitat distributions of the two species were highly significant during both the October–March and April-September periods (October-March: χ^2_6 = 2886.5, P =< 0.01; April–May: χ^2_6 = 2886.5, P < 0.01; χ^2 tests).

Breeding timing and locations

The Great Cormorants nested in a single colony from March to August/September, peaking in April/May. The nest sites of the Long-tailed Cormorants were not found, but this species appeared to breed later in the year, peaking between June and August. This was inferred from the relatively low numbers of adults counted on the lake at that time, presumably being away sitting on nests, and the increase in young birds in immature plumage counted during October–December.

This breeding timing would result in peak prey demand for one species occurring during a period of relatively low prey demand for the other. During 1995–96 the Great Cormorant population in the Lake Naivasha ecosystem was at its lowest between November 1995 and April 1996, the period between the dispersal of the 1995 fledglings and the start of the 1996 breeding effort. This was the same period during which the Long-tailed Cormorant was most numerous (Fig. 6). Similarly, in 1996 the Great Cormorant population peaked with the fledgling of that year's young between May and July, at a time when the Long-tailed Cormorant numbers on the lake were at their lowest level of the year.

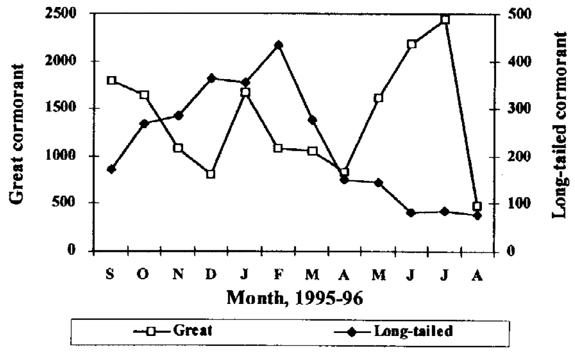

Figure 6. Monthly counts of cormorants (both species) using the Lake Naivasha ecosystem, 1995–96. Includes small adjacent lakes Oloidien and Sonachi.

Environmental changes

Lake water level

The long-term water level trend at Lake Naivasha is downward. During the 6-year period from January 1991 to January 1997, the level fell by 1.48 m, from 1887.9 to 1886.3 m asl (Fig. 7).

Lake water transparency

Between 1990 and 1996, water transparency in Lake Naivasha appears to have declined significantly. We replicated Secchi disk measurements made in 1990 near Hippo Point, the deepest area in the main lake (excluding the small Crescent Island lagoon). The mean decline in transparency at this location between 1990 and 1996 was 44% (Table 3; t-test for differences in means, t = 5.63, P < 0.01, paired t-test). Transparency was consistently lowest in the shallowest areas of the lake along the northern and eastern shores. In 1995–96, mean transparency in this part of the lake (32.5 cm ± 11.5 cm S.D.) was significantly lower than that along the southern, western, and central shores (54.4 cm ± 18.4 cm S.D., t = −8.78, df = 141, P < 0.001; unequal variance t-test).

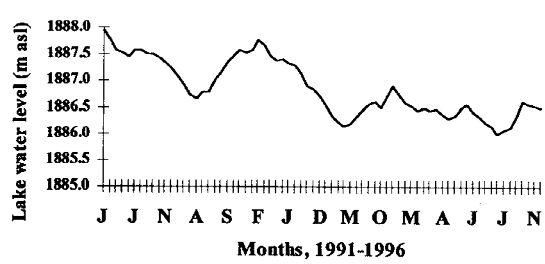

Figure 7. Lake water levels and trend, October 1991–1997; source: Sulmac Company Limited.

Table 3. Comparison of water transparency in centimetres near Hippo Point, Lake Naivasha, in 1996 and 1990. Each monthly value is based on six readings.

Month	Transparency (cm)		
	1990	1996	% Chg.
Feb.	70	55	−21.4%
March	70	44	−37.1
May	80	40	−50.0
June	85	48	−43.5
July	105	53	−59.4
Aug.	115	54	−53.0
Mean	87.5	49.0	−44.0

Effect of lower water level on Long-tailed Cormorant distribution

In 1993, before the substantial reduction in water level and transparency, the shallower northern and eastern shores held over half of the resting and foraging Long-tailed Cormorants (Table 4). By 1997, the population had shifted significantly toward the deeper southern and western sections ($\chi^2{}_2 = 113.3$, $P < 0.01$, χ^2-test). Since the overall Long-tailed population also declined greatly during this period, the southern and western sections in effect lost proportionately fewer birds than the other sections (Table 4).

Discussion

Due to the limited number of suitable prey species in Lake Naivasha, there appeared to be extensive overlap in the diets of the two cormorant species for fish weighing ≤75 g. Approximately 45% of the Great Cormorant's diet during the breeding period appeared to consist of fish of this size, and although we were unable to document the Long-tailed Cormorant's diet in this study, two earlier studies using stomach contents analysis (Bowmaker (1963) and Birkhead (1978)), indicated that prey size ranged from 2.20 cm in length (mean =7 cm) and from under 19 g to 75 g in weight.

This overlap might have been expected to result in substantial competition. However, no evidence was found that such competition occurs. The two species tended to forage in different areas of the lake, using different methods, and were rarely seen foraging close together. Furthermore, their breeding timing appeared to be sufficiently different to reduce competition for prey during the periods of maximum demand (immediately after fledging). Thus, despite probably having substantial dietary overlap, the two species seemed to be well separated on other niche dimensions. Previous studies have shown similar ecological differentiation throughout sub-Saharan Africa where the species are sympatric, such as on lakes Victoria and Malawi in East Africa and Lake Kariba in southern Africa (Benson et al., 1971; Linn & Campbell, 1992; Wanink, 1996). Where only one species is present, such as the Great Cormorant on Lake Abiata in Ethiopia (Urban, 1992) and the Long-tailed Cormorant on Lake Bangweulu in Zimbabwe (Bowmaker, 1963), each retains its restricted habitat utilisation.

Between 1990 and 1996, there were substantial declines in lake water level and transparency at Lake Naivasha. The Long-tailed Cormorant's foraging behaviour did not appear to be affected by lower water transparency, but as the water level declined and large areas of mud flats or very shallow turbid water developed in its favourite feeding areas close to shore along the shallower northern and eastern sections of the lake, this species virtually disappeared from these areas. It also largely disappeared from the Crescent Island lagoon, the deepest and least turbid section of the lake, although the reason for the decline in this section of the lake is less clear.

One reason might be increased disturbance due to fishing activity. During the study period, the numbers of Long-tailed Cormorants declined substantially in all sections of the lake. In 1995 and 1996, virtually the entire littoral zone of the lake was occupied on each day by fishermen. Where the water was deep enough, fishermen set small-mesh gill nets close to and parallel to the floating vegetation fringing the lake edge. This fringing vegetation is the Long-tailed Cormorant's preferred foraging habitat, presumably because the fish use it as cover. The fishermen's nets would block

Table 4. Distribution of Long-tailed Cormorant by lake section, 1997 vs. 1993; data from the Dept. of Ornithology, National Museums of Kenya, annual January waterbird censuses

Lake census sections	Frequency			Relative frequency	
	Jan 1993	Jan 1997	% chg.	Jan 1993	Jan 1997
North and east	571	62	−89.1	53.2	34.7
South and west	164	95	−41.5	15.3	53.6
Central (macrophyte beds and Crescent Island lagoon)	339	21	−93.8	31.5	11.7
Total lake	1074	179	−83.3	100.0	100.0

the movement of fish in and out of the vegetation, and thus the ability of the Long-tailed Cormorants to forage effectively. They would also pose a danger to cormorants of both species, which are easily caught and drowned in the nets (RBC, unpubl. data). In those areas where the water is too shallow for gill nets, the fishermen often fished in pairs with seine nets, moving parallel to the fringing vegetation while making great commotion, both to frighten the fish into the nets and to ward off the many *Hippopotamus amphibius* occupying the lake's edge. Long-tailed Cormorants seemed very sensitive to human disturbance: seldom was it possible to approach within 50 m before a roost would empty or a foraging bird would relocate.

It is unknown whether fishing activity was increasing during the period when the Long-tailed Cormorant population was declining. Many fishermen are unlicensed, and there are no records on their activity. Anecdotal information from local residents suggests the fishing pressure has increased substantially, in parallel with a documented increase in the human population around the lake (Goldson Associates, 1993). If this is so, it is likely that this activity, with its focus in the littoral region of the lake, has affected the Long-tailed Cormorant much more than the Great Cormorant.

Acknowledgements

We thank four colleagues – Matt Prescott, Colin Beale, Steven Windels and Joseph Ojambo – for their invaluable assistance in the field, the Zwager family for allowing access to the study site, and the Department of Ornithology, National Museums of Kenya the use of their survey map and population data. Elsamere Conservation Centre kindly provided boats, outboard motors, office and laboratory facilities, and overnight accommodation for field assistants. The Earthwatch Institute provided support for DH, and some volunteer teams assisted with observations. We thank the Office of the President of the Republic of Kenya for written permission to conduct this study, as part of a larger project understanding the ecology of Lake Naivasha.

References

Bennun, L. A., 1992. Summary results of the 1992 January waterfowl counts. The National Museums of Kenya, Department of Ornithology, Nairobi.

Bennun, L. A. & O. Nasirwa, 2000. Trends in waterbird numbers in the southern Rift Valley of Kenya. Ostrich 71: 220–226.

Benson, C. W., R. K. Brooke, R. J., Dowsett & M. P. S Irwin, 1971. The birds of Zambia. Collins, London.

Birkhead, M. E., 1978. Some aspects of the feeding ecology of the reed cormorant and darter on Lake Kariba, Rhodesia. Ostrich 49: 1–7.

Bowmaker, A. P., 1963. Cormorant predation on two central African lakes. Ostrich March: 2–26.

Brandl, R. & H. Utschick, 1985. Size, ecology and wading birds: a nonparsimonious view. Naturwissenschaften 72: 550–552.

Brown, L. H., E. K. Urban & K. Newman (eds), 1982. The Birds of Africa, Vol. 1. Academic Press, London.

Furness, R. W. & R. T. Barrett, 1985. The food requirements and ecological relationships of a seabird community in north Norway. Ornis Scand. 16: 305–313.

Goldson, J., 1993. A three-phase environmental impact study of recent developments around Lake Naivasha. Lake Naivasha Riparian Owners Association, Naivasha, Kenya.

Harper, D. M., K. M. Mavuti & S. M. Muchiri, 1990. Ecology and management of Lake Naivasha, Kenya, in relation to climate change, alien species' introductions, and agricultural development. Environ. Cons. 17: 328–336.

Hartley, J., 1984. A guide to the Lake Naivasha area. Evans Brothers (Kenya) Ltd., Nairobi.

Johnsgard, P. A., 1993. Cormorants, Darters and Pelicans of the World. Smithsonian Institution Press, Washington, DC.

Lack, D., 1945. The ecology of closely related species with special reference to cormorant (*Phalacrocorax carbo*) and shag (*Phalacrocorax aristotelis*). Ecology 14: 12–16.

Lack, D., 1971. Ecological Isolation in Birds. Blackwell Scientific Publications, Oxford.

Linn, I. J. & K. L. I. Campbell, 1992. Interactions between white-breasted cormorants *Phalacrocorax carbo* (Aves: Phalacrocoracidae) and the fisheries of Lake Malawi. J. appl. Ecol. 29: 619–634.

Nasirwa, O. & L. A. Bennun, 1994. Waterbirds in the southern Kenyan Rift Valley, July 1993 and January 1994. Centre for Biodiversity Research Reports: Ornithology, No. 17: July 1994. Department of Ornithology, National Museums of Kenya, Nairobi.

Nasirwa, O. & L. A. Bennun, 1995. Monitoring of waterbirds in central Kenya, July 1994 and January 1995. Centre for Biodiversity Reports: Ornithology, No. 19: October 1995. Department of Ornithology, National Museums of Kenya, Nairobi.

Schoener, T. W., 1974 Resource partitioning in ecological communities. Science 185: 27–39.

Urban, E. K., 1992. Seasonal and opportunistic nesting of great cormorants *Phalacrocorax carbo* in Ethiopia. pp 475–480. Proceedings of the VIII Pan-African Ornithological Conference.

Wanink, J. H., 1996. Foraging locations of kingfishers and cormorants at Lake Victoria depend on the distribution of harvestable prey. Afr. J. Ecol. 34: 90–93.

Wiens, J. A., 1989. The Ecology of Bird Communities, Vol. 1. Foundations and Patterns. Cambridge University Press, Cambridge.

Zijlstra M. & M. R. Van Eerden, 1995. Pellet production and the use of otoliths in determining the diet of cormorants *Phalacrocorax carbo sinensis*: trials with captive birds. Ardea 83: 123–131.