Breeding biology and ecology of the great cormorant (*Phalacrocorax carbo lucidus*) at Lake Naivasha, Kenya

by

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To Sarah

who shares my fascination for birds

Abstract

Breeding biology and ecology of the great cormorant
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This thesis examines breeding season timing and seasonal declines in reproductive success in piscivores nesting inland near the equator. Also explored are the effects of sexual character intensity and nest-site characteristics on breeding timing, fecundity and mate choice, as well as the effects of resource partitioning between two similar piscivores. *P. carbo lucidus* is a relatively common, but little-studied, piscivore of sub-Saharan Africa. Lake Naivasha (0° 46' S) is reputed to be seasonally-constant in fish production. The colony studied was newly-established in 1995, the first year of the two-year study.

At Lake Naivasha, *P. carbo lucidus* bred primarily during April-June. There was no evidence of a consistent increase in prey in the lake during this period, and the timing did not appear to result from any other consistent environmental-response adaptation. However, the onset of the main rains appeared to be an important stimulant. Based on studies by others, this subspecies breeds during April-June throughout sub-Saharan Africa, irrespective of the local rainfall regime or differences in photoperiod trend. While nesting at Lake Naivasha, a large portion of the colony appeared to forage at other locations. It is suggested that breeding timing at Lake Naivasha may be controlled by the combination of an increase in prey abundance generally throughout sub-Saharan Africa during April-June, the subspecies' nearly 12-month endogenous reproductive cycle, and the onset of the main rains.

A significant seasonal decline in reproductive success was observed. Combining the two years, the mean number of chicks fledged by the first third of pairs to start laying (2.9) was significantly greater than that of the last third (1.2). The primary reason appeared to be the greater age (and experience) of the early-breeding pairs. Egg or chick predation did not seem to be an important factor, even for late breeding pairs. Breeding interference by hungry chicks from earlier broods appeared to be an important factor limiting the reproductive success of late-breeding pairs.

In the first year of the new colony, the earliest-breeding pairs (first third) preferentially selected canopy-top nest sites (76%) vs. sites below the canopy (24%). They also built significantly larger nests than later-breeding pairs. Canopy-top locations and larger nests had significant positive effects on brood size and fecundity in the colony's first year but not in its second year.

P. carbo lucidus is monomorphic in its basic plumage and seasonal sexual characters. Individual birds with more intensely developed sexual characters formed pairs significantly earlier than those with less intensely developed characters: 15 days earlier for males and 10 days earlier for females. Pairs which bred earliest had significantly higher fecundity. Males with the darkest cheek, foreneck, and upper breast plumage fledged significantly more chicks (2.9) than males with lower intensity development (1.9). The role of the sexual characters studied in mate choice was not clear.

The great cormorant population increased 56% at Lake Naivasha between 1993 and 1995, most likely as the result of immigration from nearby Lake Nakuru. During the same period, the long-tailed cormorant population declined 64%. These trends continued during the study. The findings indicated that neither niche overlap nor environmental change was the likely cause, and it is suggested that foraging interference by fishermen may be the most likely explanation.

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Chapter 1 Introduction

This thesis examines breeding season timing and seasonal declines in reproductive success in piscivores breeding inland near the equator. Also explored are the effects of sexual character intensity and nest-site characteristics on breeding timing, fecundity and mate choice, as well as the effects of resource partitioning between two similar piscivores. The underlying two-year study was conducted during 1995-96 at Lake Naivasha, Kenya (0° 46' S) with the great cormorant *Phalacrocorax carbo lucidus* (Lichtenstein 1823), a relatively common, but little-studied, colonial piscivore of sub-Saharan Africa. The colony studied was newly-established in 1995, and the questions addressed were:

- Near the equator, what are the most likely proximate factors controlling the breeding timing of piscivores?

- Do piscivores breeding near the equator experience seasonal declines in reproductive success similar to those experienced by piscivorous birds breeding in temperate regions and, if so, what are the most likely reasons?

- Does the intensity of seasonal sexual characters at the time of pair formation have an effect on breeding timing, mate choice, or reproductive success?

- Were the significant opposite shifts in population size of two similar sympatric piscivorous species at the study location the result of niche overlap and competition or environmental change?

As a piscivore breeding in an environment with apparently little seasonal variation in food supply, *P. carbo lucidus* is a good subject with which to examine general theories of avian breeding season timing and seasonal variation in reproductive success. As a monomorphic species with distinctive breeding plumage features, it is also an appropriate subject for testing ideas on the evolution of monomorphic sexual characters. At Lake Naivasha, the great cormorant is sympatric with the smaller long-tailed cormorant (*P. africanus*), providing the opportunity to examine resource partitioning between similar piscivores and its potential effect on breeding timing.

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1.1 Breeding season timing and its control factors near the equator

For the vast majority of birds, breeding is an annual event timed to coincide with seasonal periods of food and nest-site abundance (Lack, 1950, Perrins 1970, Phillips *et al.* 1985). Regardless of whether a certain species times its breeding to coincide with maximum food abundance when the chicks are in the nest (Lack 1950), or when the females are accumulating resources for egg laying (Perrins 1970), food abundance is widely considered to be the most important or "ultimate" factor in determining breeding timing.

The mechanism which enables birds to co-ordinate their breeding timing with the seasonal periods of food abundance is generally believed to involve two elements (Lack 1950, Lofts & Murton 1968, Immelmann 1971, Perrins & Birkhead 1983, Wingfield 1983, Gwinner & Dittami 1985):

- an endogenous cycle which brings each bird into breeding condition generally in phase with the period of abundance in the area where it normally breeds

- one or more modifying signals ("proximate factors") from the environment which enable the bird to synchronise its breeding timing more precisely with the actual period of abundance each year

In temperate climates, the annual period of abundance for most birds (insectivores, frugivores, nectarivores and granivores) coincide with the longer, warmer days of spring and summer when plant growth and insect abundance are at their maximum. These are also the periods when fish availability is increased generally for the piscivores. In temperate regions, the surface of many inland lakes and rivers freezes, denying access to avian piscivores. Also during this period, even if the surface is not frozen, fish tend to retreat to the deepest (and warmest) areas for over-wintering; many actually hibernate in the bottom sediments or burrows (Voslamber *et al.* 1995), making them less available to avian piscivores. Gradual increases in daily temperature and photoperiod following the winter solstice generally predict the arrival of periods of abundance for most birds in temperate regions. It is the gradual increase in photoperiod which is thought to be the main proximate factor used by most birds to synchro-

nise their breeding with periods of food abundance in these regions (Wolfson 1952, Lofts & Murton 1968, Lack 1969, Immelmann 1971).

Near the equator, the situation is different. Daily temperatures and photoperiods are much more uniform than in temperate regions (Thomson 1950), yet there are seasonal periods of relative food and nest-site abundance with which most birds need to synchronise in order to breed most successfully. Here, periods of food abundance for birds which feed on insects, plants, fruits, and seeds are associated in one way or another with the seasonal wet and dry periods which regulate the plant and insect life in these regions. However, this may not be true for some piscivores. While many lakes in the equatorial region of sub-Saharan Africa have marked seasonal patterns in primary production (phytoplankton and zooplankton), and thus in fish spawning cycles (e.g. Lakes Malawi and Victoria), others such as Lake George in Uganda and Lake Naivasha have seasonally constant patterns of primary production (Payne 1986) and continuously spawning fish species (Siddiqui 1977).

Beginning with Rowan (1926), there have been numerous attempts to understand the most likely proximate factors for birds breeding near the equator, (e.g. Moreau 1931, 1936, 1950a, 1950b, Winterbottom 1935, 1963, Baker 1938b, Moreau et al. 1947, van Someren 1947, Miller 1955, 1958, 1960, Skutch 1950, Thomson 1950, Marshall & Disney 1956, Serventy 1957, Ennion & Ennion 1962, Ashmole 1963, Snow & Snow 1964, Ward, 1969, Immelmann 1970, Jones & Ward 1976, Maclean 1976, Snow 1976, Sinclair 1978, Fogden & Fogden 1979, Stiles 1980, Wilkinson 1983, Dittami & Gwinner 1985, Gwinner & Dittami 1985, 1990). From these studies, it has been variously hypothesised that, near the equator, breeding timing in non-piscivores is controlled by:

- seasonal food abundance or quality (e.g. Skutch 1950, Ward 1969, Immelmann 1970, Jones & Ward 1976, Maclean 1976, Snow 1976, Sinclair 1978, Berry et al. 1979, Fogden & Fogden 1979, Stiles 1980)

- seasonal rains (e.g. Moreau 1950a, Serventy & Marshall 1957, Miller 1960, Ennion & Ennion 1962, Brown & Britton 1980, Dittami & Gwinner 1985)

- photoperiod shift (e.g. Marshall & Disney 1956, Gwinner et al. 1983, Gwinner & Dittami 1985)

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- inhibiting effects of the dry season (*e.g.* Fogden & Fogden 1979, Stiles 1980, Dittami & Knauer 1986)

- ambient air temperature (*e.g.* Marshall 1949, Serventy & Marshall 1957, Wilkinson 1983)

- a combination of an endogenous reproductive cycle and signals from the environment which are diverse, habitat-dependent, and often species-specific (*e.g.* Miller 1955, Lofts 1964, Marshall 1959, Lehrman 1965, Gwinner & Dorka 1976, Farner & Gwinner 1980, Dittami 1986, 1987, Gwinner & Dittami 1990)

Although there are published data on breeding timing near the equator for a variety of piscivores, few attempts appear to have been made to explore the most likely proximate factors responsible for this timing.

1.2 The effects of breeding timing and nest-site characteristics on reproductive success near the equator

A seasonal decline in reproductive success is a general phenomenon in birds (Krebs & Davies 1997) and has been observed in a number of colonial piscivores breeding in temperate environments. Pairs breeding early have consistently been shown to be more successful than those breeding late in terms of clutch size, egg volume, hatching success, fledging success, and fledging mass (De Forest & Gaston 1996). This effect has been documented across a wide range of piscivorous species including: black-legged kittiwake (Coulson & White 1958), shag (Snow 1960), herring gull (Davis 1975, Parsons 1975), common guillemot (Birkhead 1977, Hedgren 1979, 1980, Hedgren & Linnman 1979, Wanless & Harris 1988, Hatchwell 1991), thick-billed murre (Birkhead & Nettleship 1981, 1982, De Forest & Gaston 1996), northern fulmar (Ollason & Dunnet 1978), razorbill (Lloyd 1979), puffin (Harris 1980), common tern (Nisbet *et al.* 1984), Antarctic fulmar (Weimerskirch 1990), Cassin's auklet (Ainley *et al.* 1990), chinstrap penguin (Moreno *et al.* 1997), and great cormorant (Bregnballe 1996).

Three hypotheses, which are not mutually exclusive, have been suggested to explain the observed decline in reproductive success over the course of the breeding

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season among colonial piscivores breeding in temperate climates (summarised in De Forest & Gaston 1996). These are:

- 'Synchrony/predation risk' hypothesis: The risk of predation on eggs and chicks of pairs breeding out of synchrony will be substantially higher than for those pairs breeding in synchrony with the main colony (Parsons 1975, 1976, Birkhead 1977, Harris 1980, Wanless & Harris 1988, Hatchwell 1991). For late-breeding pairs, the risk of predation increases as earlier-breeding pairs and their fledged young depart the colony, leaving the late-breeding pairs more isolated and exposed.

- 'Food availability' hypothesis: a natural seasonal decline in food availability and/or quality results in reduced fledging success or lower fledging mass (Birkhead & Nettleship 1981, 1982, Hedgren 1979, Hedgren & Linnman 1979). This hypothesis would also apply to pairs breeding unusually early, before the period of maximum food abundance (i.e. out of synchrony). In temperate environments there is a seasonal cycle of prey availability controlled mainly by photoperiod and water temperature (Sverdrup et al. 1942).

- 'Age and experience' hypothesis: young, inexperienced birds often breed later in the breeding season and have lower reproductive success than older, more experienced birds (Coulson & White 1958, Davis 1975, Ollason & Dunnet 1978, Lloyd 1979, Hedgren 1980, Potts et al. 1980, Ryder 1980, Nisbet et al. 1984, Sæther 1990, Weimerskirch 1990, Pärt 1995, De Forest & Gaston 1996).

Just as there appears to have been little exploration of the proximate factors controlling breeding season timing in piscivores near the equator, there also appears to have been little study of whether colonial piscivores breeding near the equator experience a reduction in reproductive success over the course of the breeding season and, if so, what the reasons for this might be.

Nest-site characteristics have also been shown to have a direct influence on reproductive success across a broad range of colonial piscivores: shag (Snow 1960, Potts et al. 1980), kittiwake (Coulson 1968), adelie penguin (Tenaza 1971), common guillemot (Birkhead & Nettleship 1987), and thick-billed murre (Birkhead et al. 1985). The importance of nest-site characteristics to reproductive success in colonially-nesting piscivorous birds has been studied most often in species and populations

which nest on sea-facing rock ledges, or in burrows; nest-site quality has usually been defined in terms of the density of surrounding nests and, where relevant, height above the water. Little comparative investigation appears to have been made of the importance of various nest-site characteristics in the reproductive success of fish-eating species which nest colonially in trees. Here high densities may often be difficult to achieve due to large nest sizes and open branch configurations.

1.3 Seasonal sexual character intensity and its effect on breeding timing, fecundity, and mate choice

Many species thought to have monogamous mating systems have evolved secondary sexual characters expressed similarly in both sexes. Examples include parrots, pigeons and doves, grebes, penguins, herons, and egrets (Kirkpatrick *et al.* 1990). Darwin (1871) believed that elaborate ornamental characters expressed similarly in both sexes might have evolved through sexual selection involving both male and female mate choice. Huxley (1914), who is credited with first using the term "epigamic characters" for monomorphic seasonal sexual characters used in courtship, also suggested an hypothesis of mutual selection to account for their evolution (Kirkpatrick *et al.* 1990). Experiments by Jones and Hunter (1993) with monomorphic crested auklets (*Athia cristatella*) found support for the hypothesis that 'ornament size is likely to be favoured by sexual selection involving mutual mate choice'.

Kirkpatrick *et al.* (1990) suggested that evolution of epigamic characters through mutual selection (*i.e.* sexual selection involving mutual mate choice) might have occurred in 'monogamous, sexually monomorphic species because good nutritional condition affects the breeding date and fecundity of both sexes'. Their hypotheses were:

- 'females in good condition breed earlier and are more fecund than females in poor condition and healthier males are ready to breed earlier and are more fecund'

- 'within the pool of fecund males and females that are ready to breed early, both sexes choose mates on the basis of an sexual (epigamic) character that is expressed equally in both males and females'

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- 'males and females with more extreme development of the sexual character tend to breed sooner'

- 'birds ready to breed but with less extreme development of the character tend to lag behind and so may pair with later-breeding, less fecund mates'

Great cormorants are, putatively, socially monogamous (Marchant & Higgins 1990) and the subspecies *P. carbo lucidus* is monomorphic (Brown *et al.* 1982). Both males and females develop similar secondary sexual characters prior to breeding. Thus, this subspecies appears to represent an ideal subject for assessing the hypotheses advanced by Kirkpatrick *et al.* (1990) relative to the evolution of monomorphic sexual characters and the effect of breeding timing on reproductive success.

1.4 Population shifts between sympatric great and long-tailed cormorants: the effects of niche overlap or environmental change?

The ranges of great and long-tailed cormorants substantially overlap on inland freshwater lakes and rivers of sub-Saharan Africa (Brown, *et al.* 1982, Johnsgard, 1993). Between 1993 and 1995 the two species experienced significant opposite shifts in sizes of their populations at Lake Naivasha, with the great cormorant population increasing and the long-tailed population decreasing. The increase in great cormorants seems most likely to have been the result of immigration from nearby (approximately 45 km) Lake Nakuru. In 1993-94 Lake Nakuru experienced a nearly complete loss of fish and fish-eating birds, including a breeding population of approximately 3000 great cormorants, as the consequence of unusually low water levels and high alkalinity (Bennun 1992, 1993, Nasirwa & Bennun 1994, 1995, Nasirwa, pers. comm.).

Two hypotheses, not mutually exclusive, to explain the subsequent decline in the number of long-tailed cormorants using Lake Naivasha were assessed. The first hypothesis, which derives from the 'competitive exclusion principle' first suggested by Grinnell (1917, 1924) and later stated more forthrightly by Gause (1934), is that the larger great cormorant (mean weight: 1780g, Brooke *et al.* 1982) was more successful than the much smaller long-tailed cormorant (mean weight: 505g, Bowmaker 1963) in competing for limited prey resources, which became increasingly scarce at Lake Nai-

vasha as the great cormorant population on the lake increased. The "competitive exclusion principle" postulates that ecologically similar species using the same set of limited resources cannot coexist in equilibrium (reviewed in Wiens 1989).

Lake Naivasha is highly unusual for a tropical freshwater lake in having only a limited number of fish species (Harper et al. 1990) to support the forty-five species in its avian fish-eating guild (Hartley 1984). Due to a probable drying up of this lake in the mid-1800s (Harper et al. 1990), the prey species for large fish-eating birds in Lake Naivasha consist almost entirely of three introduced fish species: two tilapia species (Tilapia zillii and Oreochromis leucostictus) and the American large-mouthed bass (Micropterus salmoides), in addition to the introduced Louisiana crayfish (Procambarus clarkii). The only other fish species in the lake are a small barbus (Barbus amphigramma) and a guppy (Lebistes reticulata) (Harper et al. 1990, Muchiri & Hickley 1991), neither of which would seem to be of sufficient size or available in sufficient quantity to be a worthwhile food source for the cormorants.

Although the limited number of prey species might indicate a high degree of diet overlap, and competitive pressure between the two cormorant species, experience has shown that similar sympatric 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: foraging methods and locations, prey size, or breeding timing which would tend to limit direct competition for prey (Lack 1945, Schoener 1974, Brandl & Utschick 1985). Further, it has often been suggested that two species with such a large difference in size as the great and long-tailed cormorants are unlikely to utilise the same resources to any important extent (Lack 1971, Ricklefs & Travis 1980, Reynolds & Meslow 1984, Brandl & Utschick 1985, Furness & Barrett 1985). Elsewhere in sub-Saharan Africa, the two cormorant species also seem to occupy separate niches (Bowmaker 1963, Birkhead 1978, Whitfield & Blaber 1979, Urban 1979, 1992, Campbell 1982, Brown et al. 1982, Linn & Campbell 1992, Johnsgard 1993, Wanink 1996).

The second hypothesis is that the substantial declines in water level and transparency which also occurred at Lake Naivasha between 1990 and 1995 had a greater negative effect on the long-tailed cormorant's ability to meet its resource needs than it did on that of the great cormorant. An examination of how these similar piscivores partition the resources at Lake Naivasha may also shed light on the great cormorant's breeding season timing and seasonal reproductive success.

1.5 Study Aims

The aims of this study, in relation to the overall questions introduced above, were:

1.5.1 Breeding season timing and its control factors near the equator

- to document great cormorant breeding season timing at Lake Naivasha

- to assess the applicability to this piscivore of the environmental proximate factors most commonly hypothesised for non-piscivores near the equator. The environmental factors included in the study were: food abundance (and the potentially related factors of lake water level and transparency), rainfall, photoperiod, and ambient air temperature.

1.5.2 The effects of breeding timing and nest-site characteristics on reproductive success near the equator

- to determine if the seasonal decline in reproductive success observed in colonial piscivores breeding in temperate regions also occurs near the equator

- to evaluate the applicability of the three main hypotheses which have been suggested to explain this phenomenon in temperate environments

- to document the relationships between reproductive success and two conspicuous and obviously variable nest-site characteristics in a new colony: nest size and relative nest height

1.5.3 Seasonal sexual character intensity and its effect on breeding timing, fecundity and mate choice

- to document the variability in intensity of five primary seasonal sexual characters in both sexes of great cormorant at the time of pair formation, along with breeding timing and fledging success

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- to assess the five model assumptions suggested by Kirkpatrick *et al.* (1990) to explain the evolution of epigamic characters by sexual selection involving mutual mate choice

1.5.4 Population shifts between sympatric great and long-tailed cormorants -- the effects of niche overlap or environmental change?

- to describe foraging, roosting, and nesting behaviour, and resource use of the two sympatric cormorant species during 1995-96, as well as environmental changes at Lake Naivasha between 1991 and 1996

- to assess the niche-overlap and environmental change hypotheses in terms of their ability to provide a reasonable explanation for the significant opposite population shifts observed

The hypotheses examined in order to meet these aims are presented in the respective chapters.

1.6 Thesis outline

The remaining six chapters of the thesis are presented in the following ways:

Chapter 2 describes the general biology of *P. carbo lucidus*, the location and characteristics of the study site, and the general research and statistical analysis methods used.

Chapter 3 documents the breeding timing of *P. carbo lucidus* at Lake Naivasha, explores the reported breeding timing of this piscivorous subspecies in other regions of sub-Saharan Africa, and assesses the applicability of the most widely suggested proximate factors for non-piscivores breeding near the equator.

Chapter 4 analyses the effect of breeding early *vs.* late in the breeding season and two nest-site characteristics (nest size and relative nest height) on the reproductive success of *P. carbo lucidus*.

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Chapter 5 presents data on the variability of seasonal sexual character intensity in *P. carbo lucidus* at the time of pair formation and analyses its effect on mate choice, breeding timing, and reproductive success.

Chapter 6 defines the environmental niches occupied by the sympatric great and long-tailed cormorant species at Lake Naivasha, provides data on environmental changes at the lake between 1991 and 1996, and assesses whether niche overlap and competition or environmental change were most likely to have been responsible for the significant opposite population size trends observed during this period.

Chapter 7 discusses of the results of each chapter, places them in context, and suggests future research to explore the findings in more detail.

Chapter 2 Great cormorant biology, study site description, research, and statistical methods

2.1 General great cormorant biology

Present virtually throughout the world, cormorants are members of the family *Phalacrocoracidae* in the order *Pelecaniformes*, which also includes pelicans (*Pelecanidae*), gannets and boobies (*Sulidae*), tropicbirds (*Phaethontidae*), frigatebirds (*Fregatidae*), and darters (*Anhingidae*) (Brooke & Birkhead 1991). The great cormorant *Phalacrocorax carbo*, through its six sub-species, is found on all of the world's continents except South America (del Hoyo *et al.* 1992). The African subspecies *P. carbo lucidus* is the largest of Africa's six resident cormorant species (Johnsgard 1993). It occurs discontinuously on the inland waters of sub-Saharan Africa and along the south-western coast (Brown *et al.* 1982).

Based on their significantly different mean weights and tarsus lengths, Jarvis (1970) and Brooke *et al.* (1982) considered the coastal and inland populations to be discrete. The mean weight of individuals in the inland population is 1780g (n = 7, range = 1470g to 1980g, sd = 184.8; Brooke *et al.* 1982), while that of individuals in the coastal population is 2997g (n = 7, range = 2720 to 3250, sd = 168.6; Brooke *et al.* 1982). Both populations are sexually dimorphic, with males weighing more than females (Brooke *et al.* 1982). However, the inland population appears to be much more dimorphic than the coastal population: inland males weigh approximately 30% more than inland females, while coastal males weigh only about 10% more than coastal females (Brooke *et al.* 1982). Members of the inland population are often seen roosting in large numbers along the shores of rivers and lakes during the day or in nearby trees at night. Adults are easily recognised by their size, and by their plumage, which is highly variable in pattern among individuals but alike in colour for both sexes: overall black with white cheeks, foreneck, and usually upper breast (Figure 2.1).

A gregarious bird when roosting, the great cormorant is usually described as a solitary forager on inland African waters (Brown *et al.* 1982). However, foraging flocks have been reported on East African lakes (Campbell 1982) and in other regions of the world where prey is abundant (Marchant & Higgins 1990) or water transparency low (Dirksen *et al.* 1995, van Eerden & Voslamber 1995). In East Africa, foraging usually

occurs in open water more than 100 m from shore and in waters up to 9 m in depth (Wanink 1996). Prey is most often reported to be small benthic fish in the 10-38 g range (Whitfield & Blaber 1978, Dirksen *et al.* 1995), although prey size may be site-specific, as the norm at Lake Naivasha is much larger (Chapter 6).

Figure 2.1 Great cormorant *Phalacrocorax carbo lucidus*

Prey shape has a direct effect on the size of fish which is taken: long thin shapes enable larger prey to be swallowed than deep-bodied shapes. Prey is pursued underwater and caught between the mandibles before being turned and swallowed head first. It was once thought that all prey was swallowed after the bird has surfaced (Whitfield & Blaber 1978). However, recent studies indicate that in European waters most small prey fish are swallowed underwater, making direct observation of dietary intake difficult (Grémillet *et al.* 1998). Mean daily food intake immediately post-fledging is approximately 285 g or about 16% of body weight (Junor 1972).

The inland great cormorant of sub-Saharan Africa usually breeds in colonies of up to 1000 or more pairs nesting in trees near or surrounded by water (Brown *et al.* 1982, Urban 1992). Prior to breeding, both sexes develop similar seasonal sexual characters, five of which are readily observable: white feathers on the crown and

nape; patches of white filoplumes on both thighs; darker cheek, foreneck and upper breast plumage; olive gular skin; and an orange-red suborbital skin patch (Chapter 5).

Breeding begins with the male selecting a nest site and displaying for a mate (Brown *et al.* 1982). Pair formation and copulation take place at the nest site (B. Childress, pers. obs.). Material for the nest is collected largely by the male, while the nest is assembled and guarded during nest-building periods largely by the female (Brown *et al.* 1982). Although nest-building material continues to be added throughout the incubation period, the primary nest-building period begins immediately after initial copulation and continues for only 3-6 days. Nest-building is not a continuous process but is limited to daily periods of about 1.5 hours in the morning between about 07:30 and 09:00, following the female's return from her usual early-morning foraging trip (B. Childress, pers. obs.).

The mean clutch size is approximately 2.6 eggs (Olver & Kuyper 1978, Brooke *et al.* 1982, Brown *et al.* 1982). The modal clutch is three eggs usually laid at intervals of about 24 hours (Brown *et al.* 1982). Incubation begins with the first egg and the adults share incubation duties more or less equally. The mean incubation period is 28 days (Brown *et al.* 1982, Urban 1979), with eggs hatching about a day apart in laying sequence (Olver & Kuyper 1978). Mean brood size is approximately 2.0 chicks (Olver & Kuyper 1978, Brooke *et al.* 1982). In one study in South Africa, hatching success was 74% (n = 186, Olver & Kuyper 1978). The chicks are altricial, being hatched blind, naked, and unable to control their body temperature. Mean weight at birth is approximately 35g. From hatching until the oldest chick is approximately 28-35 days old (mean = 33d, sd = 9.1d), one parent is always at the nest to protect the nestlings from predation and the effects of weather (B. Childress, pers. obs.).

Both parents participate in feeding the young, although the female spends slightly more time feeding the very young than the male (B. Childress, pers. obs.). Feeding is by regurgitation. For the first three days, the parent regurgitates a liquid into the chick's mouth. When the chick is four days old, it begins to put its head into the mouth of the parent, which regurgitates small pre-digested pieces of fish. As the chick grows, it extends its head deeper and deeper into the parent's gullet, and the food pieces become larger and progressively less digested. Chicks follow a typical sigmoidal growth curve, achieving a mean weight of approximately 1 kg after two weeks, and 2 kg after four weeks, at which point they begin to lose weight slightly as their flight muscles become toned for fledging (B. Childress, unpub. data). The mean fledging period is eight weeks. In Olver & Kuyper's (1978) study, fledging success was

52% of eggs laid (n = 186), and 69% of chicks hatched. (n = 138). The mean number fledged per nest was 1.6 chicks. The main causes of nestling mortality are starvation and falling from the nest (Brown *et al.* 1982, Johnsgard 1993). The youngest nestlings often starve, particularly in years of poor prey availability and with young, inexperienced parents. Most nestling mortality occurs during the first three weeks after hatching (Johnsgard 1993). The marabou stork (*Leptoptilos crumeniferus*), African fish eagle (*Haliaeetus vocifer*), black kite (*Milvus migrans*), and fan-tailed raven (*Corvus rhipidurus*) are reported to prey on eggs and young in the nest (Brown *et al.* 1982), although this was not observed at Lake Naivasha.

Fledglings must teach themselves to forage, and the parents continue to feed the fledglings at their nest site at irregular periods for up to four weeks after fledging. The mortality rate from starvation among the newly-fledged young is very high. In a study of 2567 nestlings ringed over a period of 19 years in South Africa, Skead (1980) found that 57% of nestlings died within one month of their being ringed and 73% died within the first year. At Lake Naivasha, many new fledglings were caught in fishermen's stationary gill nets and drowned, ending up being brought in with the daily fish catch (L. Bennun, pers. comm.). Dispersal among newly fledged young can be quite spectacular; in the same study, Skead (1980) found the mean dispersal distance to be 356 km (range: 4-1045 km). One bird was found 672 km from its ringing site after 50 days, while another was found 985 km away after five months. For adults, the main cause of mortality observed during this study was predation by the African fish eagle (*Haliaeetus vocifer*). Four individuals were seen to be killed and eaten by this predator (B. Childress, pers. obs.). Mean annual mortality has been found to be 55.4% (Skead 1980), heavily weighted toward the one-and-two-year-olds. Maximum life span was reported to be about 12 years, with a mean of 1.9 years.

2.2 The Lake Naivasha ecosystem

Lake Naivasha (00° 46' S, 36° 22' E) is located in the eastern Rift Valley in Kenya, approximately 77 km north-west of the capital Nairobi and 85 km south of the equator (Figure 2.3). In 1995, the Lake Naivasha ecosystem, defined as the area bounded on the north by Moi North Lake Road, on the south by Moi South Lake Road, and on the

east by the Kenya Railways' track (Figure 2.4, S. Higgins, pers. comm.), was officially listed as a wetland of international importance under the Ramsar convention.
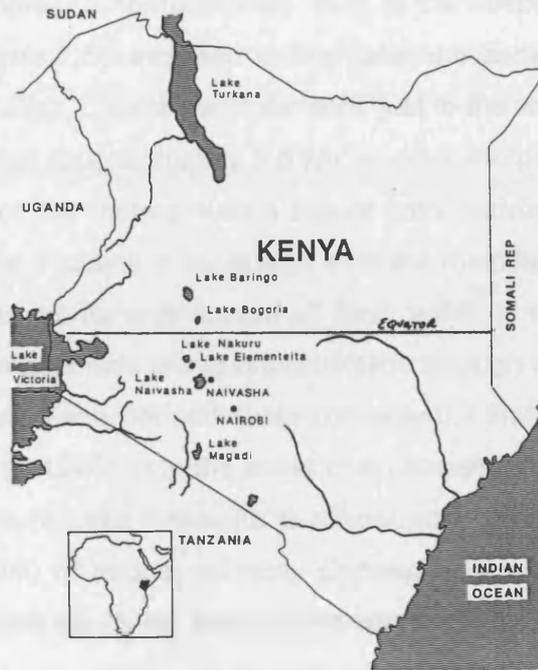
Figure 2.3 Location map of Lake Naivasha; Source: Harper *et al.* 1990

Figure 2.4 The Lake Naivasha ecosystem; Sources: Hartley 1984, D. Harper

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Lake Naivasha is the highest lake in the Rift Valley. During the study period (1995-96), the lake level varied between 1886 and 1887 m asl. At this level, the surface area covered approximately 130 km^2 and the depth ranged from < 1 m along the northern and eastern shores to approximately 16 m at the deepest point in the Crescent Island lagoon (Figure 2.5). Included in the Lake Naivasha ecosystem are two small, shallow, alkaline lakes, Oloidien and Sonachi, just to the west of Lake Naivasha (Figure 2.4). Lake Oloidien (approximately 5.5 km^2 in area, Harper et al. 1990), with a maximum depth of about five metres, was a bay of Lake Naivasha before it was cut off by falling water levels. Today it is separated from the main lake by an isthmus approximately 150 m wide. As its only source of fresh water is rainfall (and probably seepage), Lake Oloidien becomes increasingly alkaline through evaporation as its period of isolation continues. Lake Sonachi (approximately 0.2 km^2 in area and four metres in depth, Harper et al. 1990), is in the crater of an ancient volcano.

The riparian area of Lake Naivasha is almost completely ringed by a narrow band (approximately 50m) of sedge, primarily Cyperus papyrus, although there are also small patches of Cyperus dives. Beyond this narrow band of sedge, most areas have several hundred metres of wetland grasses, short sedges and acacia woodland (Acacia xanthophloea). The riparian areas of the small alkaline lakes are devoid of the fringing band of C. papyrus and C. dives.
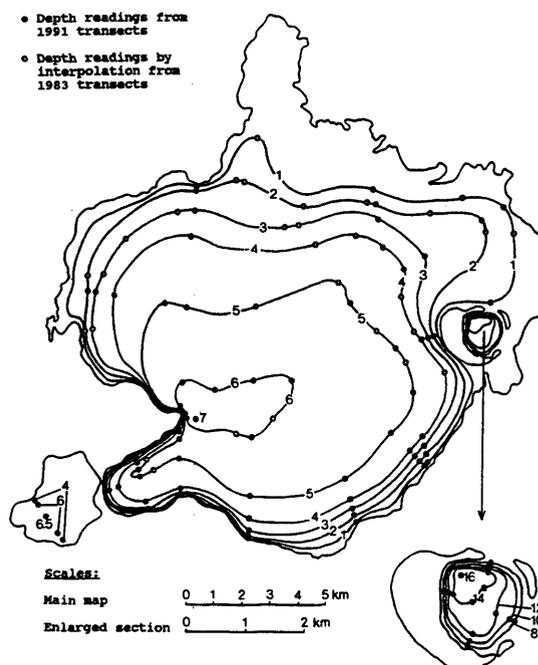
Figure 2.5 Lake Naivasha depth chart; Source: P. Hickley, unpublished data

Although much of the land around the lake is intensively used for human habitation and commercial-scale horticulture, the lake and its immediate environs have always comprised an important ecological site due to the richness and diversity of its associated flora and fauna (Harper *et al.* 1990). As an example, over 450 species of resident and palaearctic migrant birds have been recorded using the lake and its surrounding habitats, including Hell's Gate National Park which is adjacent to the southern shore of the lake (Hartley 1984).

Lake Naivasha is located in a climatic region with a bimodal annual rainfall pattern, typical of equatorial regions. The mean annual rainfall over the six-year period 1991-1996 was 594.6 mm (range: 530.5 to 755.7, se = 35.5), of which approximately 40% occurred during the "long rains" (March-May), 25% during the "short rains" (October-December), and the remainder sporadically in other months. The dates of onset for the main rainy periods and the monthly rainfall totals were highly variable from year to year, which is also typical of equatorial regions (Figure 2.6).
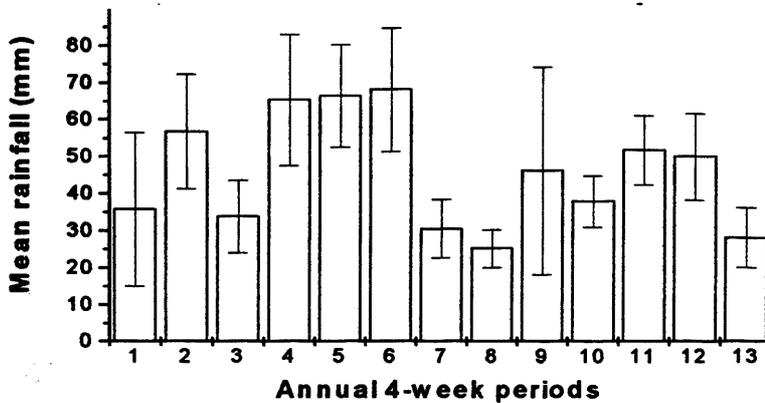
Figure 2.6 Mean rainfall at Sulmac Farm, Lake Naivasha, annual 4-week periods, 1991-1996, in millimetres +/- 1 std. error; Source: Sulmac Company, Ltd., Naivasha, Kenya; monthly figures not available

Lake Naivasha is fed by the Malewa River, a perennial water source, and two seasonal streams, the Karati and Gilgil Rivers. The Malewa River drainage area (1730 km^2) includes the Nyandarua Mountains (formerly the Aberdares) to the north-east, while the Karati River drains the Kinangop Plateau which lies between the these mountains and the valley floor (Figure 2.7, D. Harper, unpublished). The Gilgil River drains the valley floor itself (420 km^2).

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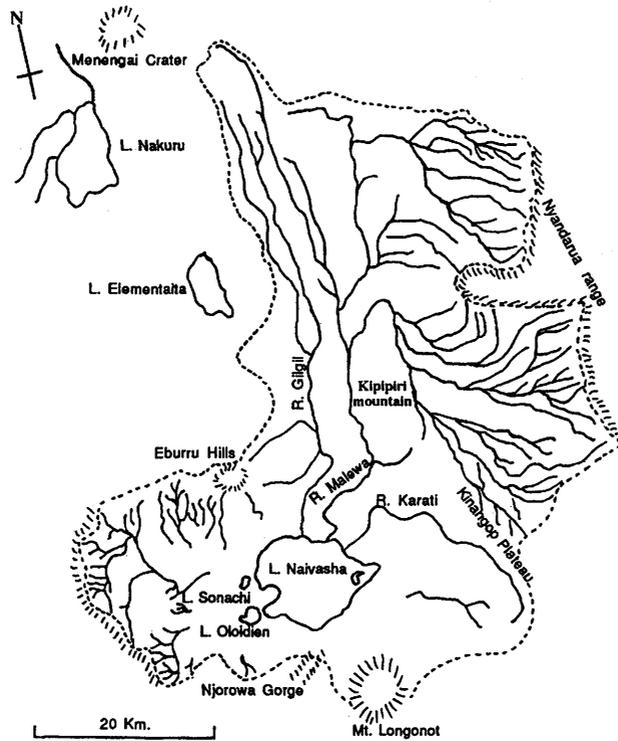
Figure 2.7 Lake Naivasha catchment area; Source: D. Harper, unpublished

The trend of Lake Naivasha's water level since the turn of the century has been primarily downward, although there have been notable periods of heavy rainfall in the early 1960s and late 1970s when this downward trend was reversed for several years (Åse 1987, Figure 2.8). Between 1 January 1991 and 1 January 1997, the historic long-term water level decline continued, falling by an additional 1.5 metres, from 1888.0 to 1886.5 m asl.
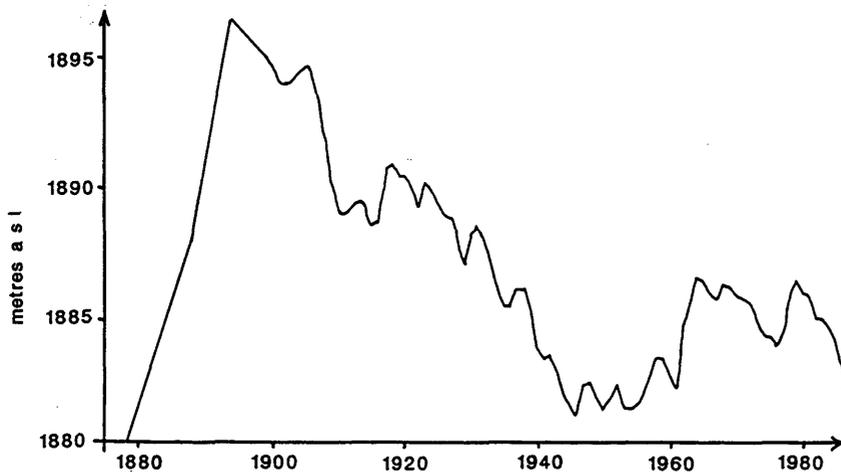
Figure 2.8 Lake Naivasha 100-year water level trend, 1880-1990; Source: Åse 1987

Water transparency in Lake Naivasha, as measured with a Secchi disc, appears to have a definite seasonal pattern (Figure 2.9). In September-October 1995, during the dry sunny period before the onset of the short rains, mean transparency was 64.0 cm (range: 13.5 cm - 101.5 cm, Table 2.1). In March and May 1996, during the long rains, mean transparency was only 35.2 cm (range: 18.0 cm - 68.5 cm, Table 2.1), a statistically significant difference (t = 5.43, P < 0.001; paired t-test).
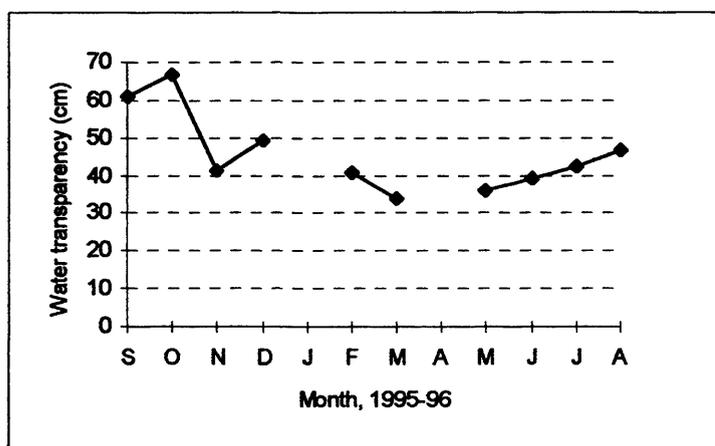
Figure 2.9 Seasonal pattern of water transparency in Lake Naivasha; no observations in January or April

Table 2.1 Seasonal mean water transparency in Lake Naivasha by lake section, 1995-96; section definitions in Chapter 6 Methods

Lake Section	Sep-Oct 95	Mar-May 96	% Difference
1	101.5	45.0	- 55.7%
2	77.5	41.0	- 47.1%
3	63.0	40.0	-36.5%
4	64.0	23.5	-61.7%
5	77.5	68.5	-11.6%
6	39.5	23.5	-40.5%
7	31.5	18.0	-42.9%
8	42.5	21.0	-50.6%
9	13.5	24.0	+77.8%
10	60.0	32.0	-46.7%
11	82.5	35.5	-57.0%
12	92.5	42.0	-54.6%
13	86.0	43.5	-49.4%
Total lake	64.0	35.2	-45.0%

The lake being just 85 km south of the equator, there is very little variation in daily photoperiod as measured by the difference between sunrise and sunset. In Nai-

robi, 77 km south of Lake Naivasha and the nearest location for which official data are available, the daily photoperiod varies by just nine minutes from the shortest to the longest day of the year. (The annual difference in Naivasha, which is closer to the equator, can be expected to be smaller.) However, during the course of the year, the entire photoperiod shifts by 29 minutes, moving sunrise in Nairobi from 06:14 in October-November to 06:43 in February, with sunset moving more or less in tandem (Figure 2.10). These shifts occur with regularity on the same dates each year.
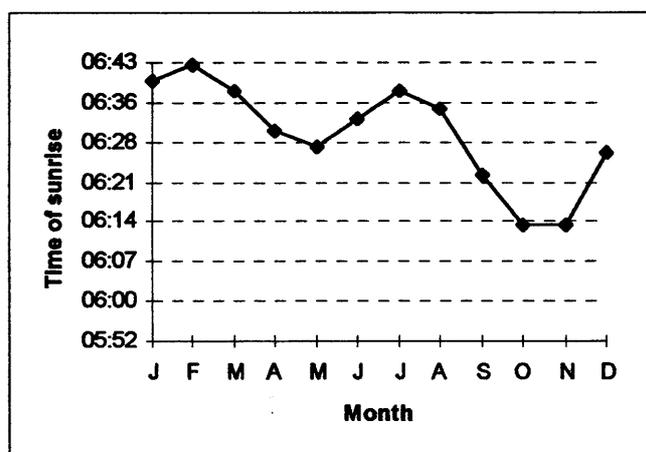
Figure 2.10 Time of sunrise at Nairobi on the 21st of each month; Source: Kenya Meteorological Department

At Lake Naivasha, there is relatively little seasonal variation in the mean ambient air temperature, maximum or minimum. Historically, the highest mean daytime temperatures (27.2° to 27.3° C) occur in January, February, and March, the dry sunny period between the end of the short rains and the beginning of the long rains. The lowest mean daytime temperatures (22.4° to 23.0° C) occur in June, July, and August. The highest mean night-time temperatures (10.6° to 11.0° C) occur in April and May, while the lowest mean night-time temperatures (7.9° to 8.3° C) occur during December, January and February, and again in August (Figure 2.11).
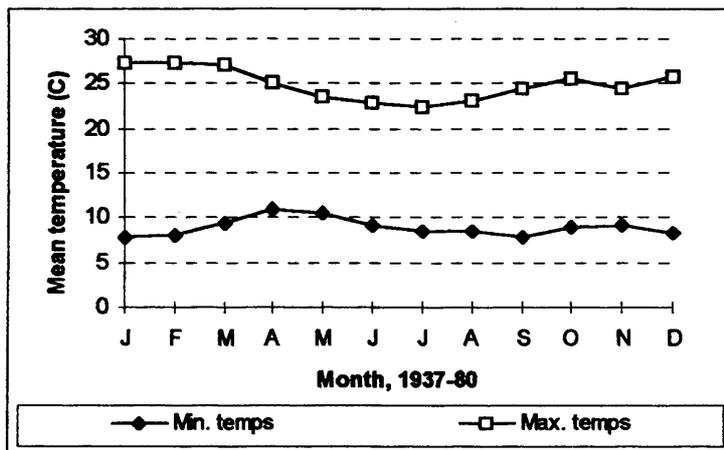
Figure 2.11 Historical minimum & maximum temperatures at Lake Naivasha, 1937-80; Source: Drought Monitoring Centre, Kenya Meteorological Department

2.3 The research site

In April 1995 the great cormorants established a new breeding colony in *Acacia xanthophloea* trees in the south-western corner of Lake Oloidien (00° 49' S, 36° 16' E; Figure 2.12). These trees, which served as the cormorants' night roost during the previous year, were on privately owned land (known as Kongoni Farm) and thus were largely protected from human disturbance. It was this new colony which was the subject of this study. The first nests were built in the trees closest to the water at what would prove to be the eastern end of the colony. Later nests continued to be built in approximately 30 trees which were in a more or less straight line extending approximately 160 m to the west of the initial nesting trees (Figure 2.13). Due to the curve of the lake shoreline in front of the colony, these trees and nests were increasingly farther from the water. Most nests were located between 20 m and 30 m above the ground on smaller, outer branches facing the water (Figure 2.14). Almost all nests were built on the northern side of the trees facing the lake.

Starting at the southern lake edge near the colony, the primary vegetation consisted of 10-15 m of low, grass-like sedge followed by large shrubs and creepers under the colony trees. The most abundant shrubs included: candle bush *Senna* (*Cassia*) *didymobotrya*, sesbania *Sesbana sesban*, candelabra tree *Euphorbia candelabrum*, hibiscus *Hibiscus calyphyllus* and *Hibiscus diversifolius*, along with *Rhus vulgaris*, *Teclea simplicifolia*, *Buddleia polystachya*, and *Psiadia punctulata* (J. Wright,

pers. comm.). The most common creepers included: *Senecio hadiensis, Ipomoea cairica, Cynanchum altiscandens, Rumex usambarensis,* and *Achyranthes aspera* (J. Wright, pers. comm.).
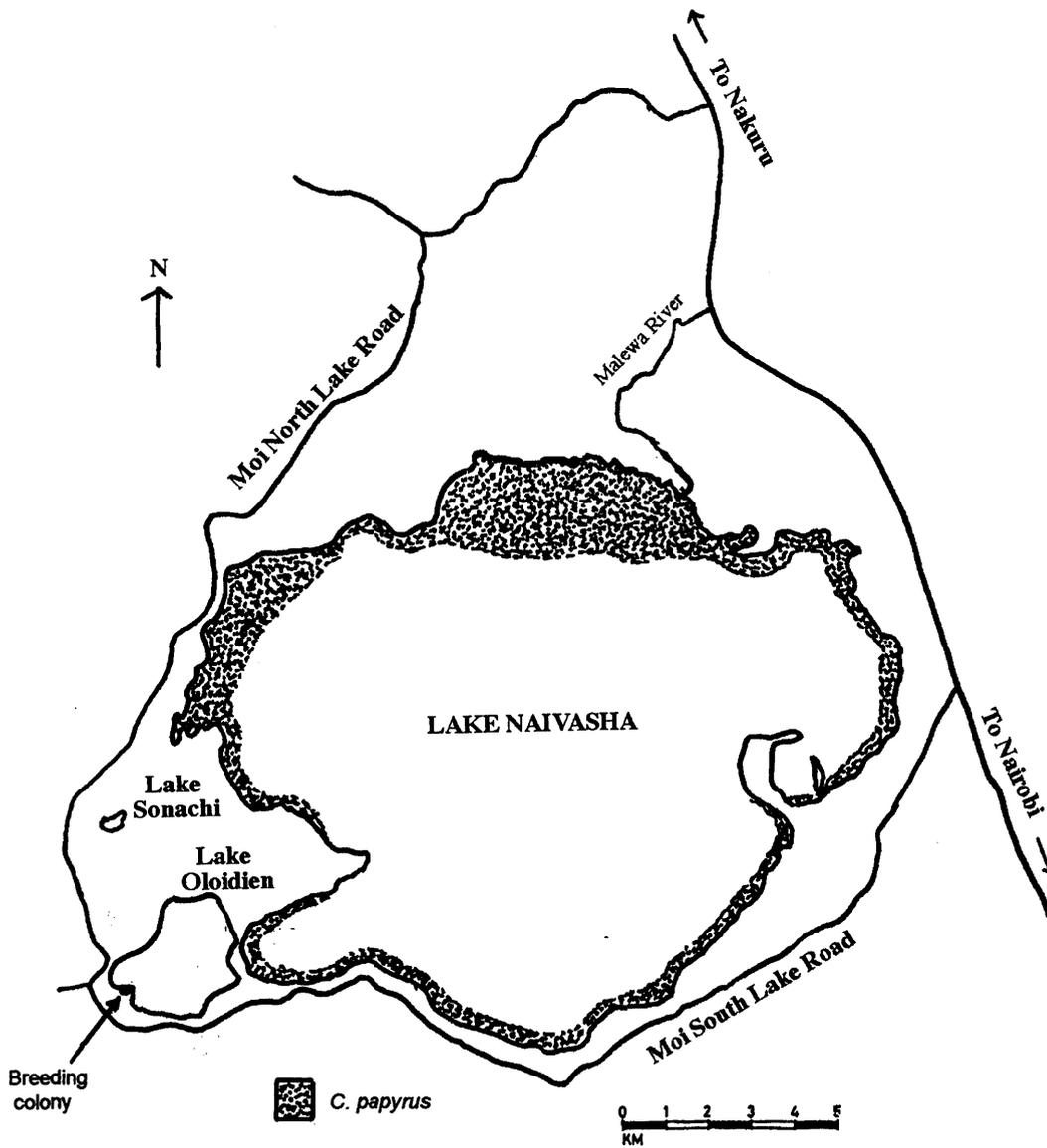
Figure 2.12 Research site map showing the location of the great cormorant breeding colony
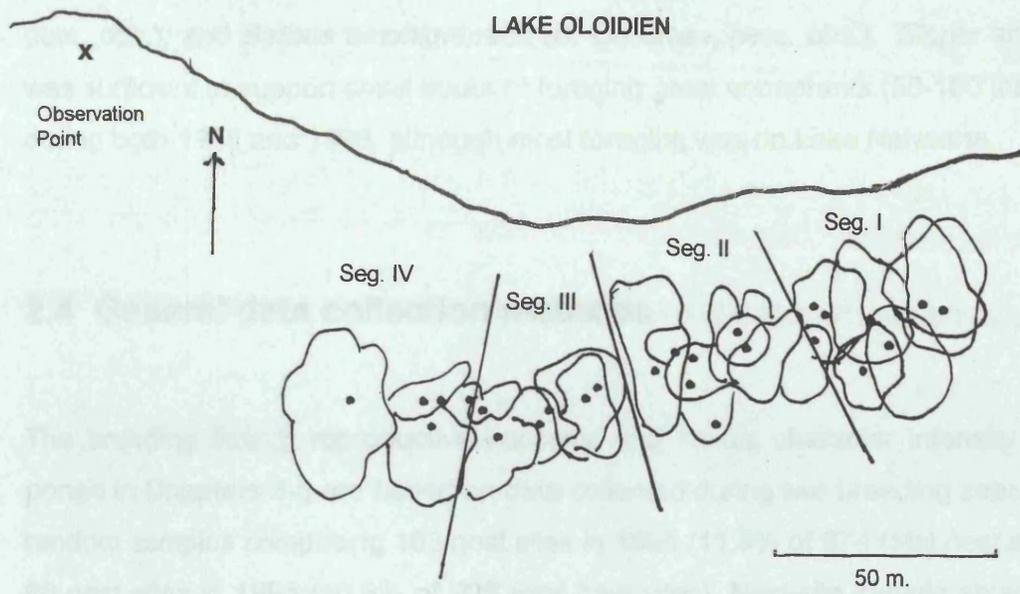
Figure 2.13 Study site layout with approximate tree canopy outlines and tree trunk locations (dots)

Figure 2.14 Breeding colony segments III (left) & IV (right) looking towards the south-east from the research observation point

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Lake Oloidien contains at least two species of fish: *Tilapia zillii* (P. Hickley, pers. obs.), and *Barbus amphigramma* (B. Childress, pers. obs.). *Tilapia* abundance was sufficient to support small flocks of foraging great cormorants (50-100 individuals) during both 1995 and 1996, although most foraging was on Lake Naivasha.

2.4 General data collection methods

The breeding timing, reproductive success, and sexual character intensity data reported in Chapters 3-5 are based on data collected during two breeding seasons from random samples comprising 103 nest sites in 1995 (11.8% of 874 total nest sites) and 98 nest sites in 1996 (10.6% of 928 total nest sites). Nest-site sample selection, observation methods, and schedules are described in this section. Additional chapter-specific methodology is described in the respective chapters.

2.4.1 Nest-sample selection

In selecting the nest sample, there were two primary criteria which needed to be accommodated. First, the sample needed to be representative of the entire colony and be randomly selected. Secondly, each nest in the sample needed to be clearly visible to the researcher throughout the breeding season. Since different selections of nest sites were clearly visible from different observation points, and since there were an almost infinite number of observation points which would have been suitable, the task of selecting a random sample of nest sites was accomplished by randomly selecting an observation point (from which all observations would be made) and then selecting approximately 100 nest sites throughout the colony which were clearly visible from that point. An additional requirement was that the sample include approximately equal numbers of nest sites on the canopy top and below the canopy so that the effect of relative nest height on reproductive success could be evaluated.

The nest sites included in the first-year sample (1995) were selected over a two-day period between four and five weeks after the first eggs are estimated to have been laid in the first nests. The 103 nest sites selected for the sample included nests in all stages of development, from those which were just

being built to those with newly-hatched chicks, and were evenly spread throughout the colony (Table 2.2)

Table 2.2 1995 nest sample characteristics by colony segment

	Seg. I (~40 m)	Seg. II (~40 m)	Seg. III (~40 m)	Seg. IV (~40 m)	Total colony (~160 m)
Total nests	389	184	96	206	875
Sample nests	38	24	19	22	103
Canopy top	20	9	10	13	52
Beneath canopy	18	15	9	9	51

Of the 103 nest sites in the 1995 sample, 22 (21%) were not reoccupied by breeding pairs in 1996. Only 17 suitable replacement sites could be found for the 1996 sample, resulting in a total sample in 1996 of 98 sites, 52 on the canopy-top and 46 below the canopy. The selection criteria for these replacement nests were unobstructed visibility and close proximity to the abandoned 1995 nest site being replaced. Usually, the first nest built near an abandoned 1995 site which was clearly visible from the observation point was selected as its replacement.

2.4.2 Observation method and schedule

The distance from the observation point to the sample nest sites ranged from approximately 100 m to 200 m. All nest-site observations were made with a 20-60x telescope (complete research equipment list in Appendix I). In 1995, the initial research year, regular observations did not begin until 24 May, approximately five weeks after the first eggs are estimated to have been laid in the earliest-starting sample nests, and continued until 25 November when all nestlings were believed to have fledged. The delay in starting observations was due to a delay in locating the breeding colony the first year. Observations were made six days per week with the off-day randomised. Daily observation periods lasted four hours and were scheduled for one of three four-hour day-parts (06:30-10:30, 10:30-14:30, and 14:30-18:30). The principal researcher was present on-site daily and personally made all observations except for a three-week period between 25 September and 18 October, when all observa-

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tions and recordings were made by M. Prescott. Site-mapping assistance was provided by C. Beale in 1995, and observation recording assistance was provided by Earthwatch volunteers in both years of the study.

In 1996 regular observations began on 29 February, the date of pair-formation for the earliest-breeding pair, and continued until 30 July when all nestlings were believed to have fledged. The breeding season was substantially shorter in the second year because an expansion of the colony into several additional trees early in the breeding season reduced the amount of late-season nesting. As the intensity of breeding plumage characters was being ranked in 1996, the observation periods were scheduled as often as possible in the afternoons, when visibility was best (the sun was behind the observer). As in 1995, the principal researcher was present on-site daily and made all observations throughout the entire period. Field assistance in 1996 was provided by J. Ojambo. Earthwatch volunteers also provided recording assistance.

2.5 Statistical analysis methods

A majority of the data generated consists of counts and ranks which are not normally distributed or capable of being transformed satisfactorily. Thus, extensive use is made of non-parametric analytical methods. Where parametric tests are used, F tests were run initially to determine if combined or separate variance tests were required. All tests are two-tailed and corrected for continuity or tied ranks, as appropriate. A probability ≤ 0.05 is used to indicate statistical significance. Where appropriate, least squares linear regression and general linear model analyses are also used. All analysis techniques are identified in the text and described in Sokal & Rohlf (1995) and Fowler & Cohen (1993). Two computer statistical analysis packages were used: Minitab 11.0 (1996) and Unistat 4.5 (1997).

Chapter 3 Breeding season timing and its control factors

3.1 Introduction

Avian breeding is usually timed to coincide with annual periods of local food and nest-site abundance (Thomson 1950, Lack 1950, Perrins 1970). In equatorial regions, periods of food abundance for most birds (insectivores, frugivores, nectarivores and granivores) are associated in one way or another with the seasonal wet and dry periods which stimulate the growth of plants and insects in these regions. For piscivores breeding on inland waters near the equator, prey abundance may not have a seasonal pattern associated in a consistent way with the annual wet and dry periods. For example, Lake Naivasha is reported (Payne 1986) to be non-seasonal in terms of its primary production (phytoplankton and zooplankton), and in terms of the reproductive cycles of *Oreochromis leucostictus*, the most abundant fish species (Siddiqui 1977).

On Lake Victoria and the Rift Valley lakes in Kenya, all of which are near the equator, the great cormorant has been reported to breed in all months of the year (Marshall & Roberts 1959, Brown & Britton 1980, Brown et al. 1982). In the Nyanza region of Kenya on Lake Victoria ($0°\ 20'$ N), Marshall and Roberts (1959) found that year-round breeding was commonly reported. Although their study found a breeding hiatus from January to April, Marshall and Roberts attributed this to strong, potentially nest-destroying storms which were reported to sweep that part of the lake during the hiatus period. They concluded that the great cormorant probably would breed year-round at this location in the absence of these storms.

This chapter examines four hypotheses, the last three of which are not mutually exclusive: at Lake Naivasha ($0°\ 46'$ S), a seasonally-constant lake,

- the great cormorant does not normally breed in all months of the year but has a defined breeding season

- the timing of the great cormorant's breeding season is controlled by one or more of the environmental factors believed to control breeding timing in non-piscivores near

the equator (seasonal changes in food abundance or quality, rainfall, photoperiod shift, and/or ambient air temperature)

- the timing of the great cormorant's breeding season is controlled by seasonal changes in water level or transparency, either singly or in combination

- the timing of the great cormorant's breeding season is controlled by a combination of its endogenous reproductive cycle and proximate signals from the environment

3.2 Methods

3.2.1 Breeding season timing

Biweekly during the main nest-building period and monthly thereafter, all active nests in the colony trees were counted. An "active nest" was one which was being used for incubation, chick rearing, or the feeding of fledglings. Counts were made from the ground beneath the colony trees, with the nests silhouetted against the sky making them relatively easy to count. Each nesting tree in the colony was numbered, and the nest count was first tallied by individual tree and then consolidated.

In addition, the dates on which the first egg was laid, the first chick hatched, and the first chick fledged were estimated for each breeding attempt in randomly selected samples of nests (1995: n = 103, 1996: n = 98). Sample selection and observation methods are described in Chapter 2. Because direct observation into the nests was not possible, as the nests were located between 20 and 30 metres above ground level (Chapter 2), the egg and chick "milestone" dates could only be estimated.

For each breeding attempt, the date on which the first egg was most likely to have been laid was estimated by subtracting the mean incubation period of 28 days from the date on which the first chick was estimated to have hatched. The hatch date was recorded as the first date on which a parent was observed feeding a chick in the nest. (This was usually three days before the chick could actually be seen from the observation point.) If no chicks hatched from a breeding attempt, the estimated first egg-laying date was recorded as

the incubation start-date based on direct observation. The date on which the first nestling was believed to have fledged was recorded as the first day on which the oldest nestling (based on plumage development) was missing from the nest, provided it was at least seven weeks old and therefore old enough to fledge. Prior to the age of seven weeks, missing chicks were presumed to have been predated or to have fallen from the nest. Brood size and number of nestlings fledged were determined for each nest by observation. A sample data collection form is shown in Appendix II-a.

3.2.2 Environmental factors

3.2.2.1 Prey abundance

At Lake Naivasha, great cormorants and commercial fishermen catch the same species (two species of Tilapia and one bass species). During 1995-96, the mean-size Tilapia (both species) caught by the fishermen was 147g, while the mean-size bass was 248g, both at the upper end of the size range utilised by the great cormorants (Table 6.4, Chapter 6). Thus, monthly commercial catch data provided by the Kenya Department of Fisheries were used as a measure of seasonal prey abundance (and as a crude index of prey availability to the cormorants) after a constant-effort transformation. These data, in kilograms and numbers of fish caught by species, were compiled from the fishermen's daily catch reports. The consolidated monthly data along with the mean number of boats reporting each month were obtained for 1989 to 1996. The constant-effort transformation involved putting the raw data on a per-boat basis.

Because these data were based on voluntary reporting, and because the proportion of active fishermen reporting as well as the proportion of their catch actually reported is unknown, the data represent an unknown portion of the actual total catch. Nevertheless, the fishermen who did report daily were licensed and were believed to be the same ones reporting throughout the year. It is also thought that they fish the same areas of the lake in the same manner each month

throughout the year. Therefore, when converted to a unit-of-effort measure, the data are believed to indicate seasonal patterns in fish availability to the cormorants as well as to the fishermen.

3.2.2.2 Rainfall and lake water level

Weekly rainfall (in millimetres) for 1985 through 1996 and daily rainfall for 1995-96 were provided by Sulmac Company Limited, a horticultural subsidiary of Brooke Bond Ltd. Also provided were weekly measurements of the Lake Naivasha water level (in metres above sea level) for 1990-96.

3.2.2.3 Lake water transparency

Lake-water transparency measurements (in centimetres) were taken with a Secchi disc monthly from September 1995 to August 1996. These measurements were taken as part of the monthly population and resource-use surveys described in Chapter 6. The measurements were taken approximately 100 m from shore with a mean separation between measurements of about 2.4 km. They were taken on approximately the same dates and the same time of day, weather permitting, each month. All measurements were taken by the principal researcher for consistency.

3.2.2.4 Daily photoperiod

Daily sunrise and sunset times in Nairobi, approximately 57 km south of Lake Naivasha (the nearest location for which official data are available), were provided by the Kenya Meteorological Department.

3.2.2.5 Ambient air temperature

Daily minimum and maximum air temperatures were recorded at Lake Nai-vasha by the principal researcher from January 1995 through August 1996.

3.2.3 Weekly measures of breeding readiness

In 1996, a general indication of the breeding readiness of the population as a whole was obtained weekly from 23rd January until the start of breeding on 1st March. This was obtained by ranking the intensity of five clearly observable sexual characters, expressed similarly in both sexes, in a randomly selected sample of 100 individuals each Tuesday. Definitions of the sexual characters, intensity ranks and ranking methods are detailed in Chapter 5. The samples were selected from the several hundred individuals roosting in a line along the shore just prior to roosting for the night. The selection method consisted of starting at one end of the line and selecting every third or fourth individual, depending on the total number of individuals gathered along the shore, so that the entire roosting population was included in the sample. A sample data collection form is included as Appendix II-b.

3.3 Results

3.3.1 Breeding timing in 1995 and 1996

The great cormorant had a well-defined breeding season at Lake Naivasha, beginning in March-April and extending through August-September. In 1995, nest-building began in mid-April, with the number of active nests peaking at 875 in mid-July (Figure 3.1). In 1996, nests remaining from the previous year were occupied six weeks earlier, in late February. The number of active nests peaked at 928 in mid-June 1996. During the hiatus between the two breeding seasons (Oct. 1995-Feb. 1996), there was no breeding activity.

Prior to the establishment of this new colony in 1995, the population of great cormorants using Lake Naivasha daily for foraging and roosting was approximately 850 individuals (Chapter 6). The total number of breeding and non-breeding adults at the colony peaked at approximately 2000 individuals in both 1995 and 1996, indicating that over 50% of the birds present at the colony at the peak of breeding came from outside the Lake Naivasha ecosystem.

In the nest samples selected for reproductive success analyses (selection method described in Chapter 2), the first eggs were estimated to have

been laid in mid-April 1995. The first chicks hatched in mid-May and fledged in mid-July (Figure 3.2). The secondary egg-laying period from July to October represented primarily young (based on their plumage) and late-arriving individuals who were unable to secure a nest site during the primary breeding period. A few of the late-nesting pairs had bred successfully during the primary period and were attempting a second brood at the same nest site. The secondary breeding effort may also have included individuals which were unsuccessful in their first breeding attempt, although it is impossible to assess how many since the individuals were not ringed. In 1996, the first eggs were estimated to have been laid on 1 March, with the first chicks hatched in late March and fledged in early June (Figure 3.3).
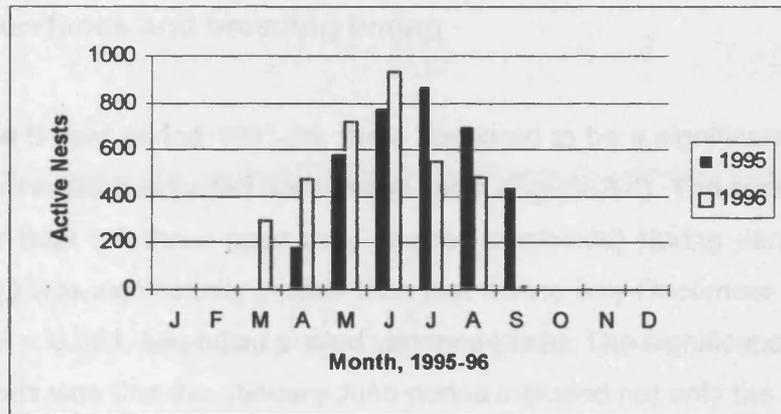
Figure 3.1 1995 & 1996 great cormorant breeding timing based on the number of active nests at mid-month; final counts: 1995: mid-September; 1996: mid-August
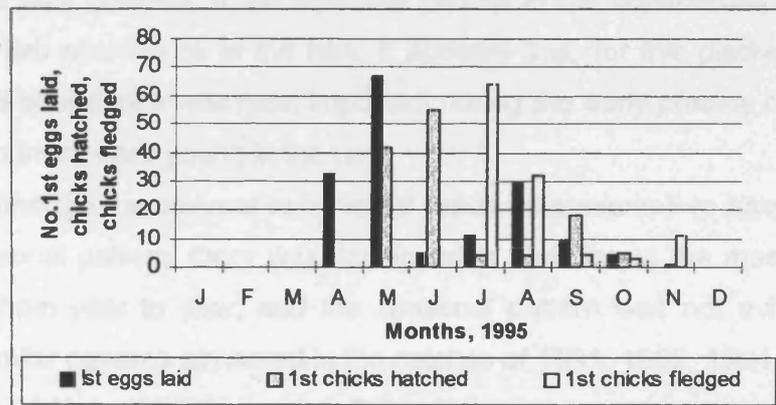
Figure 3.2 Timing of 1st eggs laid, 1st chicks hatched and 1st chicks fledged in 1995 sample nests; all breeding attempts, n = 158

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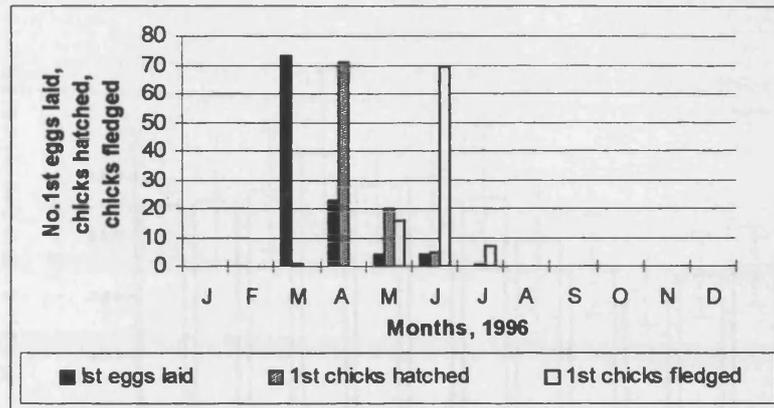
Figure 3.3 Timing of 1st eggs laid, 1st chicks hatched and 1st chicks fledged in 1996 sample nests; all breeding attempts, n = 98

3.3.2 Prey abundance and breeding timing

During the 6-year period 1991-96, there appeared to be a significant seasonal pattern in the effort-adjusted commercial catch (Figure 3.4). The mean monthly catch per boat (all three main prey species combined) during January-June (384.7 kg.) was significantly greater than that during July-December (266.1 kg, t = 4.61, P < 0.001, two-tailed pooled variance t-test). The significance of these time periods was that the January-June period included not only the main egg-laying and chick-rearing periods but also the period prior to egg laying when the females were accumulating the resources required for egg formation. The July-December period includes the main post-fledging period when demand for resources was greatest. If the seasonal pattern in the commercial catch data reflected fish abundance in the lake, it appears that, for this piscivorous species, food abundance was most important during the early phases of breeding and when there were young in the nest.

Although the six-year commercial catch data seemed to have a significant seasonal pattern, there was considerable variation in the mean monthly catches from year to year, and the seasonal pattern was not evident in all years. Similar patterns appeared in the catches of 1991, 1992, 1994, and 1996 but not in 1993 or 1995 (Figure 3.5, Table 3.1)
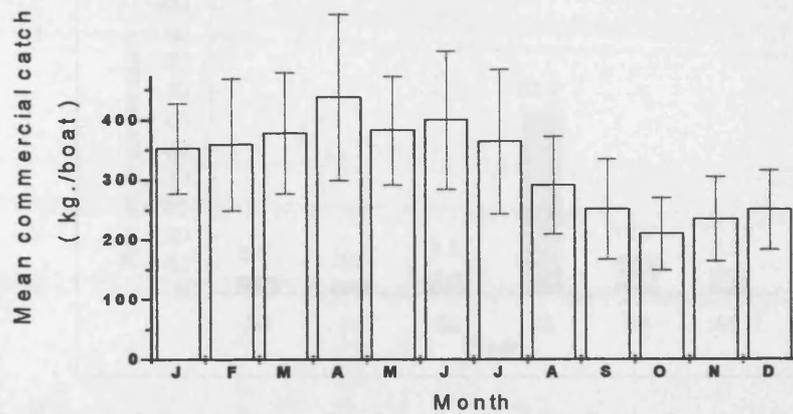
Figure 3.4 Mean monthly effort-adjusted commercial catch in Lake Naivasha, 1991-1996 (kg./boat fishing +/- 1 std. dev.)
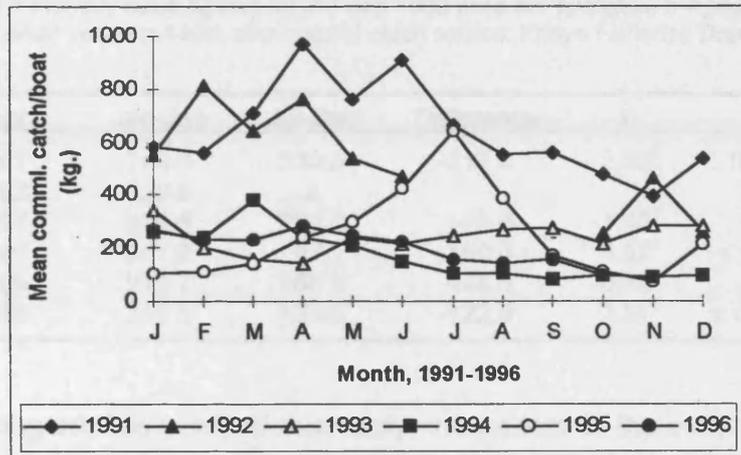
Figure 3.5 Mean monthly effort-adjusted commercial catch per boat fishing in Lake Naivasha, 1991-1996; commercial catch source: Kenya Fisheries Dept.; monthly catch figures for Jul-Sep 1992 were not available

The June-August peak which occurred in 1995 was due almost entirely to an unusual peak in the catch of *Oreochromis leucostictus*. Such a peak was foretold by an unusually high catch of this species in survey gill nets during July-September 1993 (Figure 3.6), as *O. leucostictus* would be predicted to appear in the commercial catch two years after being susceptible to the survey mesh sizes (P. Hickley, unpub. data).

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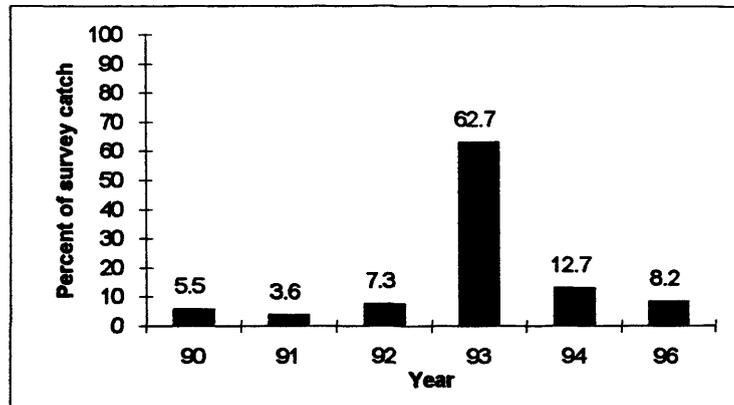
Figure 3.6 Percent of hourly survey gill net catch accounted for by *Oreochromis leucostictus* during Jul-Sep, 1990-1996; number of fish per gill net gang per hour (n): 1990: 0.06, 1991: 0.04, 1992: 0.08, 1993: 0.69, 1994: 0.14, 1996: 0.09; source: P. Hickley, unpublished data

Table 3.1 Mean monthly effort-adjusted commercial catch in kg/boat, Jan-Jun vs. Jul-Dec, 1991-1996; a = monthly catch figures for Jul-Sep 1992 were not available, b = pooled variance t-test, c = separate variance t-test; commercial catch source: Kenya Fisheries Dept.

Year	Jan-Jun	Jul-Dec	Difference	t	P
1991	748.6	530.8	-217.8	2.82^b	0.02
1992	629.5	a			
1993	216.6	263.2	+46.6	-1.48^c	ns
1994	247.2	97.2	-150.0	4.67^c	< 0.01
1995	219.7	268.3	+48.6	-0.48^b	ns
1996	246.5	123.6	-122.9	7.31^b	< 0.001

During the two years of this study, the pattern of the monthly commercial catch per boat varied substantially from year to year. In 1995, the monthly commercial catch was rising when the great cormorant breeding started, peaked when most cormorant chicks were still in the nest, and declined rapidly just when the new fledglings were leaving the nest (Figure 3.7). In 1996, however, the commercial catch was low when breeding started and continued to decline all year (Figure 3.8).

3.3.3 Rainfall and breeding timing

Great cormorant breeding in 1995 was associated with the "long rains" but the onset of the rains did not appear to have stimulated breeding directly. The first substantial rains of the year came during the sixth and seventh weeks (5 - 18 February), when 40 mm fell (Figure 3.9). This was followed by an additional 53

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mm in the ninth week. Based on the hatching dates of the first chicks, the first eggs are estimated to have been laid in the sample nests early in the 16th week (16 - 22 April). This was followed by a substantial period of rainfall with 83 mm falling during weeks 17 and 18.
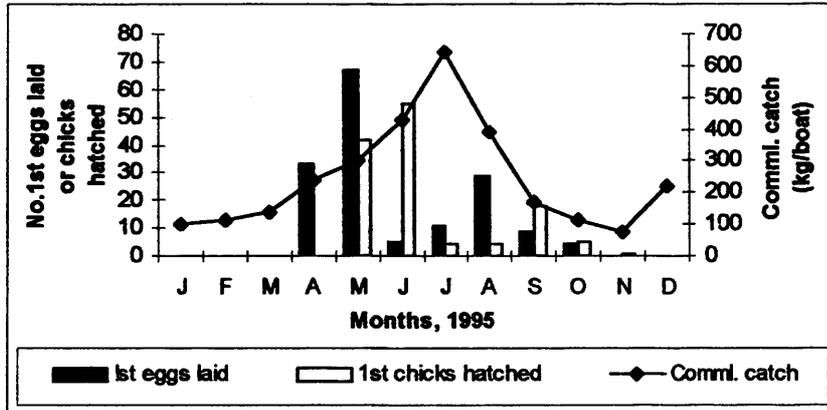
Figure 3.7 1995 breeding timing and mean monthly effort-adjusted commercial catch (kg./boat)
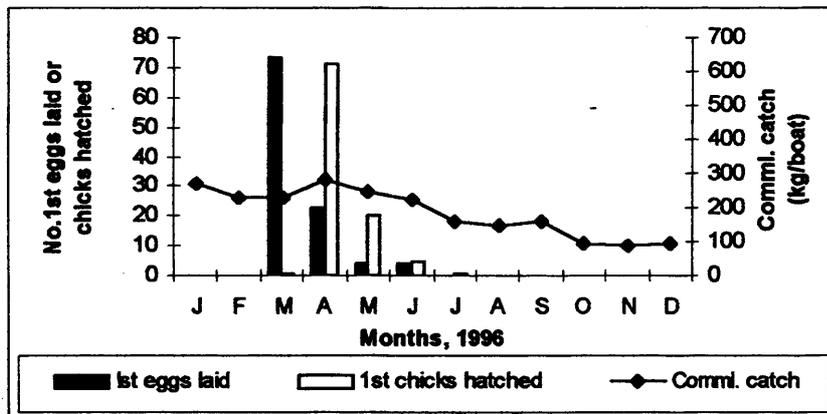
Figure 3.8 1996 breeding timing and mean monthly effort-adjusted commercial catch (kg./boat)

In 1996, the onset of breeding appears to have been somewhat more closely associated with the onset of the rains although, again, the onset of the rains *per se* did not seem to stimulate the onset of breeding. As in 1995, the first substantial rains (85 mm) fell during the sixth and seventh weeks of the year (5 - 18 February). The first eggs are estimated to have been laid in the sample nests two weeks later on 1 March (Figure 3.10).

The pattern of association between rainfall and the onset of breeding is perhaps more clearly seen when looked at on a cumulative rainfall basis. In

both 1995 and 1996, the great cormorants laid the first eggs in the sample nests after cumulative rainfall reached a level of approximately 100 mm (Figure 3.11). Once laying had begun, there was no significant difference between the two years in terms of the weekly pattern of first eggs laid during the 14-week primary breeding period (χ^2_{13} = 8.99, P = ns, two sample Chi-square test).
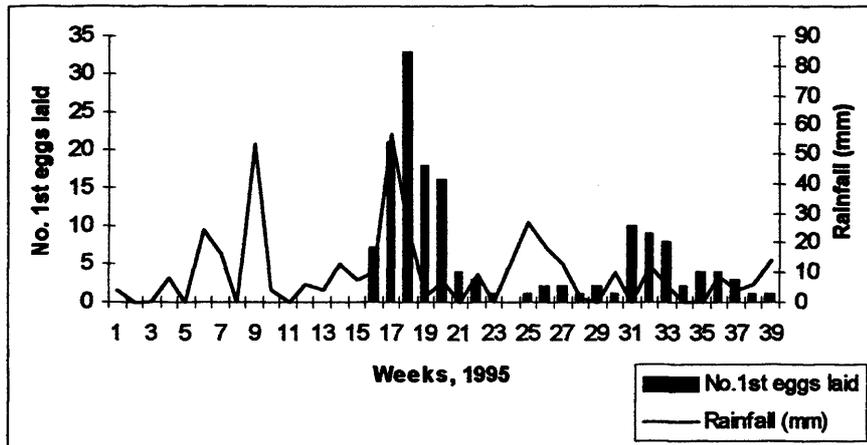
Figure 3.9 Timing of rainfall and first eggs laid in sample nests by week, 1995; all breeding attempts, n = 158. Rainfall source: Sumac Company, Ltd., Naivasha, Kenya
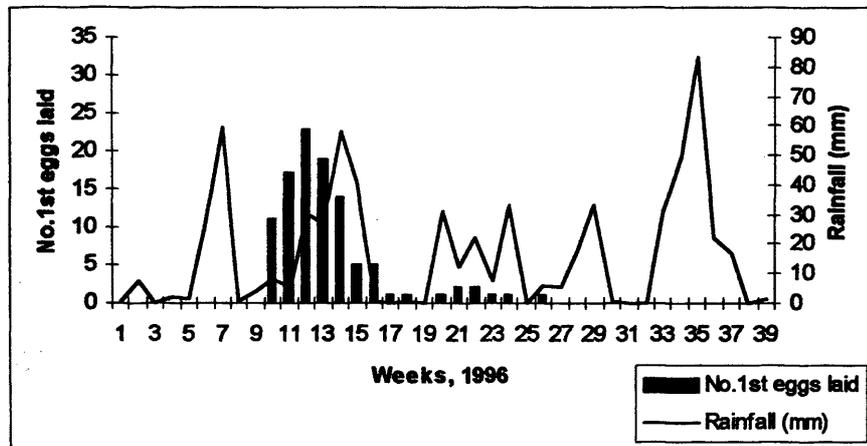
Figure 3.10 Timing of rainfall and first eggs laid in sample nests by week, 1996; all breeding attempts, n = 104. Rainfall source: Sumac Company, Ltd., Naivasha, Kenya

3.3.4 Lake water level and breeding timing

During both 1995 and 1996, the onset of great cormorant breeding coincided with periods of falling water levels (Figure 3.12). In both years, water levels

were relatively high in January and then declined steadily for 6 to 10 months, depending on the year, before recovering.
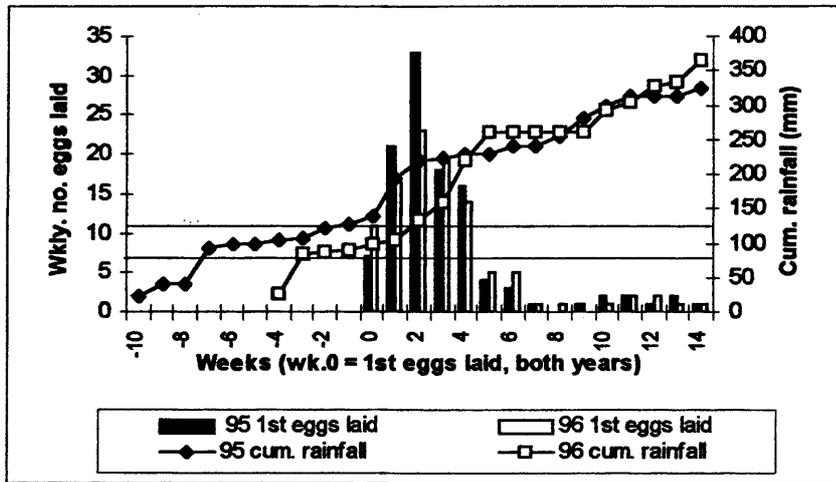
Figure 3.11 Comparison of cumulative weekly rainfall and the number of first eggs laid each week in the 1995 & 1996 sample nests, beginning with the first substantial rains each year: 24.3 mm in week 6 of 1995 and 25.4 mm in week 6 of 1996
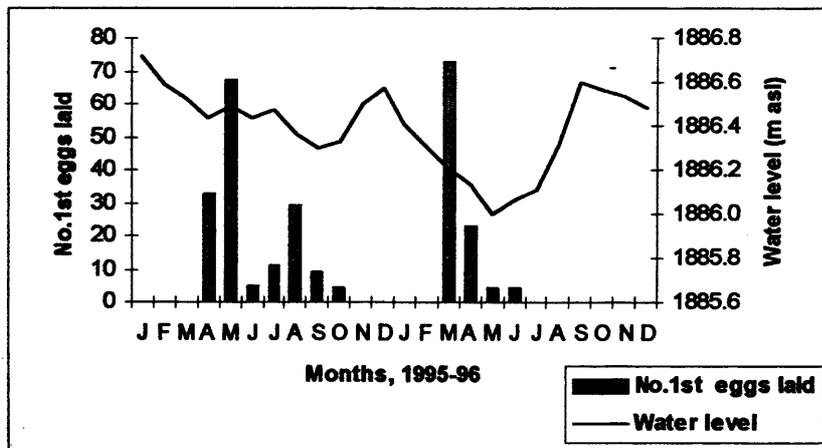
Figure 3.12 Water level & timing of 1st eggs laid in 1995-96 sample nests; all breeding attempts; 1995 n = 158, 1996 n = 104. Water level source: Sulmac Company Ltd., Naivasha

3.3.5 Water transparency and breeding timing

In 1996, breeding onset occurred in March, near the period of lowest water transparency (Figure 3.13). Fledging began 12 weeks later and continued for two months into July, a period of increasing water transparency.
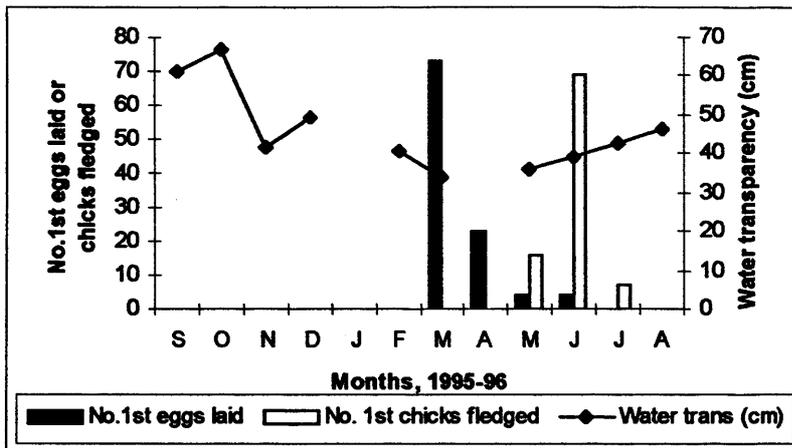
Figure 3.13 Water transparency & timing of 1st eggs laid & 1st chicks fledged in 1996 sample nests; all breeding attempts, n = 104; no transparency measurements taken in January or April

3.3.6 Photoperiod shift and breeding timing

As great cormorant breeding timing was not consistent from year to year at Lake Naivasha, it appeared to have little relationship with the regular variations in photoperiod timing (Figure 3.14).
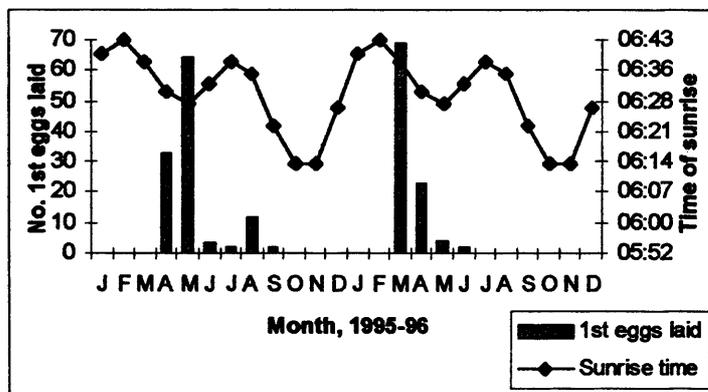
Figure 3.14 1995-96 monthly number of first eggs laid & time of sunrise on the 21st of each month. Photoperiod source: Meteorological Office, Nairobi, Kenya

3.3.7 Ambient air temperature and breeding timing

In both 1995 and 1996, the onset of breeding coincided with the period of highest night-time air temperatures (Figure 3.15). In 1995, breeding began in mid-April when the mean night-time minimum temperature was 14.3° C, and in

1996 breeding began at the beginning of March when the mean night-time minimum temperature was 15.1° C.
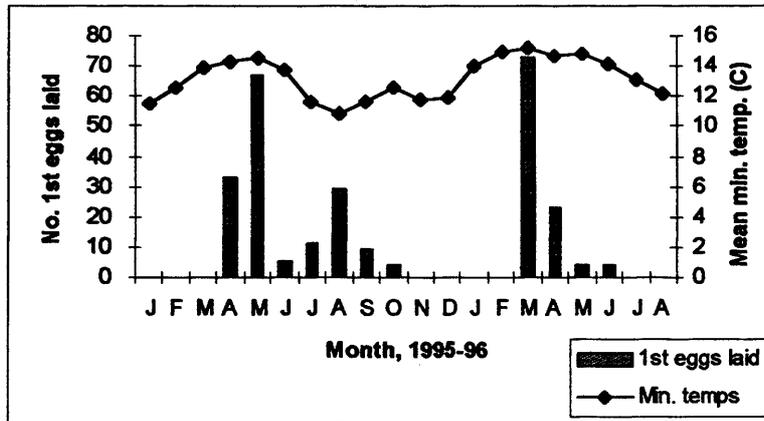
Figure 3.15 1st eggs laid & mean monthly minimum air temperature, 1995-96, all breeding attempts: 1995, n = 158; 1996, n = 104)

3.3.8 Synchronised acceleration of breeding readiness

In 1995, advanced stages of breeding plumage development were first noticed in a few individual birds in early January, 13 weeks prior to the start of breeding. In 1996, advanced stages of breeding plumage development were also first noticed in a few individuals in early January. The rate of change in intensity as evidenced by the proportion of the population exhibiting the most intense sub-orbital patch and gular skin colours, progressed rather slowly from mid-January until mid-February, at which point the rate increased substantially (Figure 3.16).

The results of ordinary least squares regressions of the development slopes of these two seasonal sexual characters before and after 19 February show coefficients before 19 February of 2.5 for suborbital skin patch colour and 2.0 for gular skin development. After 19 February the coefficients are 21.2 for suborbital skin patch colour and 25.4 for gular skin colour development. A heterogeneity of regression test using the Tukey-HSD procedure indicates that while there is no significant difference between the coefficients for the two characters (suborbital skin patch colour and gular skin colour) either before or

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after 19 February, the difference between the coefficients for both characters before and after 19 February is significant (Table 3.2).
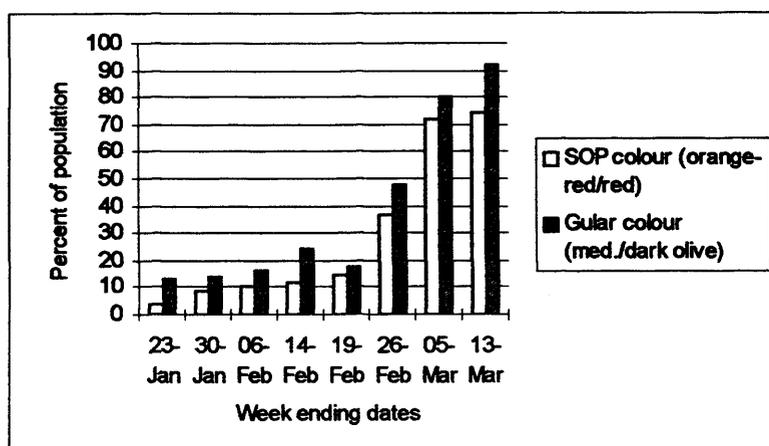
Figure 3.16 Percentage of 1996 adult population exhibiting advanced sub-orbital patch and gular skin colour by week from late January until the median breeding start date; weekly n = 100

Table 3.2 Ordinary least squares regression and heterogeneity of regression test results using the Tukey-HSD procedure for the slopes in Figure 3.16, before and after 19 February, 1996; *Method: 95% Tukey-HSD interval

	Slope Regressions Before 19 Feb (23 Jan - 19 Feb)		Slope Regressions After 19 Feb (19 Feb - 13 Mar)		Signif. Diff.*
	Slope	P	Slope	P	
Adv.suborbital skin colour	2.5	< 0.01	21.2	0.04	yes
Adv.gular skin colour	2.0	0.17	25.4	0.02	yes
Significant difference	no		no		

The proportion of the total population exhibiting thicker filoplumes on the crown, nape, and thigh patches, and more intense plumage colour on the cheeks, foreneck, and upper breast continued to increase at approximately the same rate after 19 February as before (Figure 3.17). This was not unexpected as feathers tend to grow at a fairly steady rate, and it is probably not likely that their growth rates would be affected by environmental or social factors.

The results of ordinary least squares regressions of the slopes of filoplume development (both crown/nape and thigh patch), and cheek, foreneck, and upper breast colour show coefficients prior to 19 February of 4.4 for crown/nape filoplume development, 5.2 for thigh patch development, and 7.0

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for cheek, neck and upper breast colour development. After 19 February the coefficients are 10.2 for crown/nape filoplume development, 13.2 for thigh patch development, and 11.7 for cheek, foreneck, and upper breast colour development. A heterogeneity of regression test using the Tukey-HSD procedure indicates there is no significant difference between the pre- and post-19 February regression coefficients for crown/nape filoplume development or for cheek, foreneck, and upper breast colour development. There is, however, a significant difference between the pre- and post-19 February regression coefficients for thigh patch development (Table 3.3).
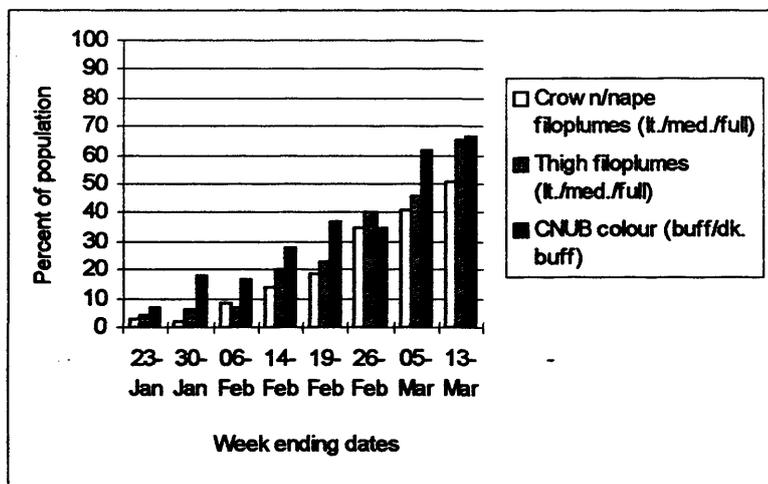
Figure 3.17 The percentage of 1996 adult population exhibiting advanced filoplumes and cheek, foreneck ,and upper breast (CNUB) colour by week from late January until the median breeding start date; weekly n = 100

Table 3.3 Ordinary least squares regression and heterogeneity of regression test results using the Tukey-HSD procedure for the slopes in Figure 3.17, before and after 19 February 1996; *Method: 95% Tukey-HSD interval

	Slope Regressions Before 19 Feb (23 Jan - 19 Feb)		Slope Regressions After 19 Feb (19 Feb - 13 Mar)		Signif. Diff.*
	Slope	P	Slope	P	
Adv. filoplume dev.	4.4	0.01	10.2	0.02	no
Adv. thigh patch dev.	5.2	0.02	13.2	0.02	yes
Adv. cheek, neck & breast colour	7.0	0.01	11.7	0.09	no
Significant differences	no		no		

3.4 Discussion

The great cormorant was found to have a defined breeding season near the equator at Lake Naivasha, despite previous reports of year-round breeding in a number of equatorial locations in East Africa. At Lake Naivasha its breeding season started between March and May, peaked between April and June, and continued into September or October. Seven other independent studies show that this breeding season timing appears to be shared by several other populations of great cormorant throughout sub-Saharan Africa, independent of latitude and local rainfall regime (Table 3.4).

Table 3.4 Breeding seasons of the great cormorant in sub-Saharan Africa; 1. Urban (1992); 2. Marshall & Roberts (1959); 3. Campbell (1982); 4. Benson et al. (1971); 5. Milstein (1975), Farkas (1962), Skead (1980); 6. Berruti (1980), Whitfield & Blaber (1979); 7. Olver & Kuyper (1978)

Country	Lake	Latitude	Rains	Breeding	Peak
Ethiopia [1]	L. Shala	07° 30' N	Mar-Sep	Mar-Aug	Apr-May
Kenya [2]	L. Victoria	00° 20' N	Mar-May	May-Jan	Jun
Malawi [3]	L. Malawi 1979	14° 00' S	Nov-Apr	May-Oct	Jun
	L. Malawi 1980	14° 00' S	Nov-Apr	Mar-Sep	Apr
Zambia [4]	L. Kariba	17° 00' S	Nov-Mar	Feb-Sep	Apr
South Africa	L. Barberspan [5]	26° 35' S	Oct-Mar	Apr-Oct	Jun-Jul
	L. St. Lucia [6]	28° 00' S	Oct-Mar	Mar-Sep	May-Jun
	L. Cedara [7]	29° 32' S	Oct-Mar	Apr-Oct	Jun

This consistent pattern of breeding timing does not mean, however, that year-round breeding does not occur in the inland population or that it has not occurred at Lake Naivasha in the past. Year-round breeding in this subspecies seems to happen opportunistically under certain temporary environmental conditions (usually flooding). For example, Urban (1979, 1992) recorded opportunistic year-round breeding at Lake Abijata in Ethiopia (7° 35' N) between December 1968 and April 1974 when flooding created a new expanded area of nesting sites several kilometres nearer to the colony's primary feeding area. He observed that the majority of out-of-season breeding was accounted for by immature and sub-adult birds breeding outside the normal April-May season. After the water level retreated, the cormorants moved back to their original breeding site at Lake Shala (7° 30' N) and resumed their seasonal breeding pattern. The reasons for this "opportunistic" out-of-season breeding by young birds are not clear. It would seem they could have bred out of season in their normal breeding location on Lake Shala just as easily. The flooding may have had an effect other than

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simply providing an expanded area of safe nest sites. Perhaps the flooding had the effect of increasing fish abundance by providing expanded spawning areas (Lowe-McConnell 1975), or perhaps it resulted in the fish being easier to catch by encouraging them to move out into the shallow, newly-flooded areas to spawn.

Apparent out-of season breeding has also been reported in the past at Lake Naivasha during periods of flooding. During 1980-81, when high water flooded an area along the southern shore known as Marina Bay, great cormorants were photographed with young in the nest in January and February (P. Davey, pers. obs.). In this same area between 1978 and 1981, breeding colonies of 50-75 pairs were recorded from November to February by members of the East Africa Natural History Society. More recently, in the early 1990s when Marina Bay was no longer flooded and the great cormorants were breeding annually on a small platform near the Lake Hotel, January breeding was also reported (L. Bennun & J. Oyugi, pers. comms.). Perhaps the reason for this latter out-of-season breeding was the limited breeding space provided by the small platform. Whatever the reason, out-of season or year-round breeding by this subspecies near the equator appears to occur occasionally as the result of unusual conditions.

The finding that several great cormorant populations at different latitudes throughout sub-Saharan Africa share similar breeding season timing seems most unusual. Based on previous studies of both aquatic and terrestrial species, it would have seemed more likely to find latitudinal variations in breeding timing based on a consistent response by the birds to some environmental factor with a latitudinal variation, such as photoperiod length, ambient air temperature, or rainfall (e.g. Baker 1938a, Miller 1960). However, no consistent response to any of the most likely proximate factors seems to occur. For example in Ethiopia, a region of little annual photoperiod change, the great cormorants breed in the rains at the hottest time of the year, while in South Africa they breed during the austral winter, a dry period when daylight is shortest and ambient air temperatures are coolest.

One possible explanation for the observed consistency of breeding timing across sub-Saharan Africa, despite varying environmental conditions, is that the timing reflects an inherited breeding pattern which has been maintained as the species radiated out from its presumed point of origin in Australia (van Tets 1976), first to southern Africa and then northward throughout the sub-Saharan region. If there is no consistent seasonal variation in prey abundance in the warm inland waters of sub-Saharan Africa and the weather is not prohibitively inclement at that time of the year,

there may have been no reason for the subspecies to shift its breeding timing away from that of its ancestors. Breeding timing for the great cormorant in Australia is similar to that found in sub-Saharan Africa: Queensland, April to August; New South Wales, March to August and September to January; South Australia, April to May (Marchant & Higgins 1990).

The situation may be similar to that found with the black noddy (Anous tenuirostris) on Ascension Island at 8° S in the mid-Atlantic. Ashmole (1962) found that the black noddy bred seasonally in that tropical location despite any evidence of a seasonal pattern in prey abundance. He suggested that the timing might be an inherited pattern. Urban (1992) also suggested that the April-May breeding timing of the great cormorant in Ethiopia might reflect an inherited pattern, although he attributed the historical pattern to ancestors from the Palaearctic which, according to van Tets (1976), is probably not the region from which the subspecies radiated.

If the timing of the great cormorant's breeding season in sub-Saharan Africa is indeed ancestral, the breeding timing of the coastal population in south-western Africa should also correspond. Although breeding timing data for this population, complied from nine different sources and presented in Brooke et al. (1982), does show egg laying in all months of the year, there was a significantly higher level of laying activity during the April-June quarter (Table 3.5; χ^2_3 = 149.7, P > 0.001, Chi-square test). Because of the multiplicity of sources and, presumably, of methodologies, it is difficult to judge the meaningfulness of this compilation. However, the significantly higher level of breeding activity in the April-June quarter is what would be expected under the inherited-timing hypothesis.

Table 3.5 Breeding data for south-western Africa coastal populations of P. carbo lucidus, number of nests in which the first egg was probably laid during each annual quarter; Source: Brooke et al. 1982

Jan-Mar	Apr-Jun	Jul-Sep	Oct-Dec
36	242	138	167

At Lake Naivasha, the timing of great cormorant breeding also did not appear to be associated in a consistent way with the environmental proximate factors traditionally postulated for non-piscivores breeding near the equator. Photoperiod, for example, was almost certainly not an important factor. Daily photoperiod, defined here as the difference between the times of sunrise and sunset, varies by less than nine minutes in a year at Lake Naivasha and is consistent from year to year on a daily ba-

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sis to within one or two minutes. Further, although there is a shift in the photoperiod earlier or later in the day as the sun crosses the equator twice each year, the timing of these shifts is consistent from one year to the next. In this study, the dates on which first eggs were laid in the two years were six weeks apart, indicating that the regular annual changes in photoperiod are probably not an important proximate factor for breeding. Similarly, ambient air temperature is probably not an important factor, as its seasonal pattern was much more consistent from year to year in this study than the great cormorant breeding periods.

Although fish abundance at Lake Naivasha was not measured directly, apparent seasonal patterns of prey abundance, as reflected in the effort-adjusted commercial catch, did not seem to be sufficiently consistent to be an important proximate factor in the breeding timing of the great cormorant. The effort-adjusted commercial catch experienced substantially different seasonal patterns in 1995 and 1996 and yet the great cormorants bred in the April-June quarter in both years. It is acknowledged that seasonal patterns in the effort-adjusted commercial catch data may not accurately reflect seasonal patterns in fish abundance. Not only are there concerns about the completeness and consistency of reporting from one period to the next (Section 3.2), but also the catch appears to be significantly affected by water transparency. In a test of this effect, a significant inverse relationship was found between the level of water transparency and the size of the effort-adjusted commercial catch during the 10-month period between November 1995 and August 1996 (Figure 3.18). This effect apparently results from the lowered ability of fish to see and avoid the fishermen's stationary gill nets when water transparency is reduced (P. Hickley, pers. comm.)
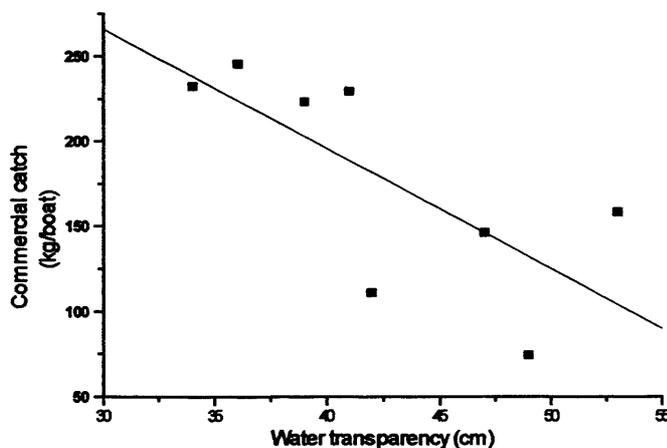
Figure 3.18 Regression plot of relationship between water transparency and commercial catch per boat, Nov 1995 to Aug 1996; regression equation: Y = 477.2 - 7.04X; r^2 = 0.52; P = 0.04

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Cormorants are demersal feeders, usually foraging by pursuing prey near the bottom. Thus, water transparency and water level changes could be expected to have an effect on prey availability for them as well as for the fishermen. Water level changes have been shown to affect fish movements (Bowmaker 1963, Kahl 1966), and Bell-Cross (1974) found that cormorants foraging solitarily in turbid water had a lower percentage of successful dives than those foraging in clear water. Nevertheless, it is doubtful that seasonal variations in prey availability due to changes in water levels or turbidity were an important factor influencing breeding timing of this subspecies at Lake Naivasha, as the great cormorant has developed at least two behaviours which would seem to help compensate for reductions in prey availability.

First, they are strong fliers (Mackworth-Praed & Grant 1952). They can and do fly considerable distances to feed (Olver & Kuyper 1978, Brooke *et al.* 1982, Platteeuw & van Eerden 1995) and thus are not restricted to any one body of water as a food source. For example, each morning during this study, large numbers (uncounted) of great cormorants were observed flying out of the Lake Naivasha ecosystem and returning again late in the afternoon, presumably having foraged at some other location during the day. The main flight directions seemed to be primarily west and north, although some also went south. Monthly surveys (Chapter 6) rarely recorded as many great cormorants foraging and roosting in the ecosystem as were counted roosting there at night. This was particularly true during the breeding season.

Secondly, although commonly described as solitary feeders (*e.g.* Brown *et al.* 1982), this subspecies was frequently observed feeding communally in flocks at Lake Naivasha, a foraging technique which appears to be a successful adaptation for more effective feeding in turbid waters, not only elsewhere in sub-Saharan Africa (Linn & Campbell 1992) but also in Europe (van Eerden & Voslamber 1995).

Water transparency and lake water levels are, of course, related to rainfall, and rainfall may have had an effect on the breeding timing of the great cormorant at Lake Naivasha even though no consistent relationship between the two events has been found across the rest of the subspecies' range. In both years of the study, females in the sample nests started laying when cumulative rainfall had reached a level of 100-150 mm (Figure 3.11). Additionally, there is evidence that rainfall may have played an important role in the acceleration of breeding readiness in the population as a whole and thereby in the breeding timing of the colony. In 1996, the first heavy rainfall of the year (40.5 mm) fell during the two weeks ending 18 February. Immediately thereafter, significant acceleration in breeding readiness, as evidenced by gular

and suborbital skin colour intensity, was observed. As this finding is based on only one year's observation, the reasons for the acceleration are not clear. Perhaps the heavy rainfall was the stimulant. On the other hand, perhaps the acceleration was the result of social stimulation (Darling 1938) or both factors reinforcing each other.

For insectivores, frugivores, nectarivores, and granivores breeding near the equator, the relationships among rainfall and new vegetation growth, increased numbers of nesting sites, and food supplies seem fairly straightforward. Rainfall has been shown to have an immediate stimulative effect on the breeding activities of several species in tropical Africa (Moreau 1950a, Winterbottom 1963, Bennun 1989). However, Stiles (1980) in his study of hummingbirds in a Costa Rican rain forest (where even the driest months receive 100 mm of rain), concluded that for these nectarivores the "dry" period between the periods of heavy rain was an inhibitory factor for breeding and that heavy rainfall was more likely to be an enabling, or permissive, factor rather than the factor which triggered breeding *per se*. Dittami and Gwinner, in their studies of several passerine species (Dittami & Gwinner 1985, Gwinner & Dittami 1985, Dittami & Knauer, Gwinner & Dittami 1990) in the bimodal rainfall regime near the equator in Kenya, came to the same conclusion. For the great cormorant at Lake Naivasha, rainfall may have affected breeding timing by having a stimulative effect on breeding condition development.

Why rainfall may have the suggested stimulative effect, and the nature of the benefits which piscivorous great cormorants gain by breeding in the rains at Lake Naivasha, are not obvious. Perhaps the rains are related to their prey abundance in some way. *Tilapia*, the primary cormorant prey in Lake Naivasha, are reported by Kenya Fisheries Department personnel to be particularly active in spawning during the rainy periods, when lake water levels are often higher than during other times of the year. Hyder (1970) found that the onset of rainfall appeared to stimulate peak breeding activity in *Oreochromis leucostictus* in Lake Naivasha. However, this finding was disputed by Siddiqui (1977) who found a seasonally constant pattern of reproduction at Lake Naivasha. In any event, spawning activity, taking place largely within the fringing beds of *C. papyrus* and water hyacinth (*Eichhornia crassipes*) would seem to reduce availability to the cormorants of suitable adult prey fish, and the new fry would seem to be too small during the first year to be of interest to either the adults or the fledglings. Perhaps the relatively warm night-time temperatures provided by the cloudy, rainy periods benefit nestling survival. Perhaps the birds are programmed to breed at

this time of the year throughout sub-Saharan Africa and it is a coincidence that this is also the time of the "long rains" at Lake Naivasha.

The consistency of great cormorant breeding timing across such a broad geographical area and the apparent lack of consistent response to the traditional environmental proximate factors seem to suggest that perhaps part of the overall regulation for this subspecies may be its endogenous reproductive cycle. The great cormorant's endogenous reproductive cycle appears to require nearly twelve months to complete: three months for reproduction (one month for incubation and two months for fledging), six months for complete post-nuptial moult, and three months for partial pre-nuptial moult (Ginn & Melville 1983). At Lake Naivasha this internal cycle seemed to bring the most advanced individuals into breeding condition in early January as evidenced by the state of their breeding plumage. However, as Ashmole (1963) found with sooty terns, although appearing physiologically ready to breed, something seemed to inhibit these early-developing individuals from breeding until some threshold number of others was also ready to breed. Endogenous reproductive cycles alone are not likely to ensure high levels of breeding synchrony. Individuals hatch over a several-month period each year and reliance on their internal rhythm alone for breeding timing would eventually result in individuals breeding at all times of the year (Ashmole 1963). This does not seem to have happened with the sub-Saharan great cormorant.

Several authors have postulated an important role for social stimulation in the control of breeding synchrony (and thus, timing) in colonial species (Darling 1938, Hickling 1959, Ashmole 1963, Hailman 1964, Brown 1965). The general hypothesis is that in colonial species, where reproductive success is significantly affected by breeding synchrony, mutual responsiveness to the breeding activities of other birds is one of the ways each individual can help insure that it breeds close to the most favourable time (Ashmole 1963). Brown (1965) cited convincing experimental evidence across a wide variety of species that stimuli from other birds of the same species, not necessarily mates, are important to the development of breeding condition in individuals. The importance of social stimulation to breeding has also been shown by several other authors (e.g. Lehrman 1959, 1965, Erickson & Lehrman 1964, Brockway 1964). Field investigations of the breeding timing and synchrony of the kittiwake (Coulson & White 1958) and the swallow-tailed gull (Hailman 1964) show that social stimulation produced a high degree of breeding timing synchrony within subsections of the overall colonies.

Great cormorants are a highly sociable species (Darling 1938). At Lake Naivasha, the resident population not only bred colonially, it also stayed together throughout the year, often foraging in flocks, gathering in large flocks along the shore after foraging, and roosting together at night. Perhaps, in situations where there is little seasonal variation in prey availability, the most favourable time for an individual member of a colonial species to breed is simply when the majority of the other members of the colony are also breeding. However, same-species social stimulation does not appear to be a requirement for great cormorant breeding. A single pair was observed breeding on Navillus Pond near Eldoret, Kenya in March 1995 (B. Childress, pers. obs.). No other waterbirds of any type appeared to be breeding at the time. In April 1995, a single great cormorant pair was observed breeding in a small mixed colony (about 50 nests) of long-tailed cormorants (*Phalacrocorax africanus*) and darters (*Anhinga rufa*) on an island in the outflow of Masinga Dam in Kenya (B. Childress, pers. obs.). Furthermore, different populations of a colonial species with an endogenous reproductive cycle of nearly twelve months and a high degree of social stimulation, but no environmental timing cue, would eventually be expected to develop a year-round pattern of breeding; the more or less restricted breeding period of each population shifting from year to year so that in the course of many years breeding will occur in every month (Immelmann 1971).

Based on the findings of this study, it seems a distinct possibility that there is a seasonal increase in fish abundance in the second quarter of the year generally in sub-Saharan Africa and that the consistent breeding timing of the great cormorant throughout this region may be maintained from year to year by this general increase in prey abundance and the subspecies' nearly 12-month reproductive cycle. Further, it seems likely that breeding onset in *P. carbo lucidus* is stimulated by one or more environmental factors which are specific to each locality. At Lake Naivasha, the stimulating proximate factor appears to be the onset of the major rainy season.

Chapter 4 The effects of breeding timing and nest-site characteristics on reproductive success

4.1 Introduction

Breeding early *vs.* late in the breeding season has been shown to have a direct effect on the reproductive success of many avian piscivores nesting colonially in temperate climates, including the great cormorant. Pairs breeding early in the season have been consistently more successful than those breeding late in terms of clutch size, egg volume, hatching success, fledging success, and fledging mass (Chapter 1). It has been hypothesised that this phenomenon occurs in temperate regions because of a natural decline in food availability, increased exposure to egg and chick predation as early-breeding pairs leave the colony, and/or the increased age and experience of early-breeding pairs relative to later-breeding pairs.

This chapter examines whether piscivorous species nesting near the equator also experience similar seasonal declines in reproductive success and, if so, whether the reasons are similar to those suggested for temperate environments. Lake Naivasha is putatively seasonally-constant in its production of phytoplankton (Payne 1986) and in the reproductive cycle of *Oreochromis leucostictus*, the most abundant fish species (Siddiqui 1977). Thus, it appears to be an ideal environment within which to examine seasonal variation in reproductive success among piscivores.

Nest-site characteristics have been shown to have an effect on the reproductive success of colonial piscivores nesting on rock cliffs and in burrows in temperate regions (Chapter 1). This chapter analyses the effect of nest-site characteristics on reproductive success in tree-nesting piscivores near the equator. Although the great cormorant had bred in colonies of 50 to 100 pairs in various locations around Lake Naivasha for many years (E. A. Natural History Society nest record scheme), 1995 was the first year in which a large tree colony (875 nests) was recorded. As a new colony, it provided an opportunity to study the effects on reproductive success of nest-site selection and nest-size without the confounding factors of previously-used nest-sites and pre-existing nests.

This chapter examines six non-mutually-exclusive hypotheses:

- Great cormorants breeding at Lake Naivasha experience a significant decline in reproductive success over the course of the breeding season.

- Predation of eggs and chicks of pairs breeding out of synchrony is significantly greater than for those pairs breeding in synchrony with the main colony.

- A natural decline in food availability results in reduced fledging success due to increased starvation.

- Young, inexperienced birds tend to breed later in the breeding season and have lower reproductive success than older, presumably more experienced birds.

- Nest height has a positive effect on reproductive success.

- Nest size has a positive effect on reproductive success.

4.2 Methods

During 1995 and 1996, estimated breeding timing (dates of first egg laying, first chick hatching, and first chick fledging) and reproductive success (brood size and number of chicks fledged) were recorded for each breeding attempt in random samples of nest sites, as described in Chapter 3, Methods. Sample selection and observation methods are described in Chapter 2. A sample data collection form is shown in Appendix II-a.

As nest building began in 1995, it was observed that a majority of the earliest nest-sites selected were on the canopy-top; later it was observed that there was substantial variability in the size of the nests built by different pairs. To measure the effect of the apparent preference for canopy-top nest sites on reproductive success, the nest-site sample was stratified to include approximately equal numbers of nest sites located on the canopy-top and below the canopy (Chapter 2). Variability in nest size was documented by ranking each nest in the nest-site sample on a 5-point scale (1-5), "1" being the smallest and "5" the largest. A nest with the rank of "1" consisted of a small collection of sticks only, barely a nest at all, while a nest with the rank of "5" was

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a massive construction. For example, a "5"-ranked nest fell to the ground in a storm: weight, 2.6 kg; width, 500 mm; height, 220 mm; composed of 355 sticks of various sizes, 107 feathers (mostly cormorant), and 835 g (dry weight) of vegetable matter (primarily grass and leaves).

The ranking of nest size was done on 20 June after all of the nests were believed to have reached their maximum size. In this subspecies, males (and occasionally females) continue adding nest-building material, primarily small branches, to the nest throughout the incubation period. After the first egg hatches, the material brought to the nest consists almost exclusively of nest-lining material (live plant material) which does not affect the overall dimensions of the nest. Nest-size research was not carried out in 1996 as the results would have been confounded by the apparent preference of early-breeding males for building on sites with pre-existing nests. In analysing the effect of nest-site characteristics on reproductive success, the analysis has been limited to those pairs which initially selected the sites and built the nests.

4.3 Results

4.3.1 Reproductive success

In 1995, among the 158 breeding attempts observed, mean brood size was 2.1 (range: 0 to 4, SE = 0.10) and the mean number of chicks fledged per attempt was 1.8 (range: 0 to 4, SE = 0.11). The Spearman rank order correlation coefficient (r_s) between brood size and number of chicks fledged per attempt was 0.93 and the proportion of chicks hatched which fledged was 0.88 (Table 4.1). In 1996, among the 104 breeding attempts observed, mean brood size was 2.9 (range 0 to 5, SE = 0.11) and the mean number of chicks fledged per attempt was 2.7 (range: 0 to 5, SE = 0.12), both means being significantly higher than those in 1995. The Spearman rank order correlation coefficient (r_s) between brood size and number of chicks fledged per attempt in 1996 was 0.89, and the proportion of chicks hatched which fledged was 0.92. The primary factors influencing the increase in the number of nestlings fledged per breeding attempt in 1996 appeared to be fewer late-season breeding attempts and a significant increase in brood size in 1996. There was no significant difference in the number of nestlings lost per attempt between the two years.

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Table 4.1 Comparison of mean brood size, number of nestlings lost and chicks fledged per breeding attempt in 1995 and 1996; Mann-Whitney U Test

	1995 (n = 158)	1996 (n = 104)	P
Brood size	2.1	2.9	< 0.001
No. of nestlings lost	0.3	0.2	ns
No. of chicks fledged	1.8	2.7	< 0.001
r_s: No. of chicks fledged: brood size	0.93	0.89	
Ratio: No. of chicks fledged: brood size	0.88	0.92	

4.3.2 Effect of relative breeding date

Pairs breeding early in both years were significantly more successful than pairs breeding late in terms of brood size, number of nestlings lost, and number of chicks fledged per breeding attempt (Table 4.2). Over the 2 years combined, smaller brood sizes later in the season were responsible for 81% of the difference in reproductive success between early and late-breeding pairs, while nestling loss represented only 19% of the difference (Table 4.3). Mean brood size increased significantly overall from 1995 to 1996 due to a significant increase in brood size among late-breeding pairs (Table 4.3). Among early-breeding pairs, there was no significant year-to-year difference in reproductive success Table 4.3).

Table 4.2 Comparison of mean brood size, number of nestlings lost and number of chicks fledged per breeding attempt; first 1/3 vs. last 1/3 to start egg laying in 1995 and 1996

	First 1/3 to breed		Last 1/3 to breed		Mann-Whitney U	
	n	Mean	n	Mean	U	P
1995						
Brood size	54	3.0	54	1.1	339.0	< 0.001
No. of nestlings lost	54	0.2	54	0.4	1791.5	< 0.01
No. of chicks fledged	54	2.8	54	0.7	247.5	< 0.001
1996						
Brood size	33	3.1	34	2.6	420.5	0.05
No. of nestlings lost	33	0.1	34	0.5	424.5	0.02
No. of chicks fledged	33	3.0	34	2.1	359.0	< 0.01
Combined years						
Brood size	87	3.0	88	1.7	1778.5	< 0.001
No. of nestlings lost	87	0.1	88	0.5	2924.0	< 0.001
No. of chicks fledged	87	2.9	88	1.2	1453.0	< 0.001

Table 4.3 Comparison of mean brood size, number of nestlings lost, and number of chicks fledged per breeding attempt, 1996 vs. 1995; first 1/3 and last 1/3 to start egg-laying; Mann-Whitney U Test

	1995	1996	P	Combined years
First 1/3 to breed	(n = 54)	(n = 33)		(n = 87)
Brood size	3.0	3.1	ns	3.0
No. of nestlings lost	0.2	0.1	ns	0.2
No. of chicks fledged	2.8	3.0	ns	2.8
Last 1/3 to breed	(n = 54)	(n = 34)		(n = 88)
Brood size	1.1	2.6	< 0.001	1.7
No. of nestlings lost	0.4	0.5	ns	0.5
No. of chicks fledged	0.7	2.1	< 0.001	1.2
Difference				
Brood size	1.9	0.5		1.3 (81%)
No. of nestlings lost	0.2	0.4		0.3 (19%)
No. of chicks fledged	2.1	0.9		1.6

4.3.3 Patterns of nestling loss

Starvation is presumed to have been the primary cause of nestling loss although nestling mortality was never observed directly. Great cormorant eggs hatch one to three days apart in laying sequence (Olver & Kuyper 1978). Of the 227 pairs with broods observed during 1995 and 1996, 53 pairs (23%) lost at least one nestling during the fledging period. Of these, 47 pairs (89%) lost only one nestling, usually the last to be hatched, while two pairs lost two nestlings, and four pairs lost three nestlings (Table 4.4). The majority of nestlings lost (71%) disappeared within three weeks of hatching (Table 4.5). Pairs which were among the last one-third to breed accounted for a disproportionately high percentage (63.5%) of the total chicks lost (Table 4.6). The frequency of loss among pairs which hatched only one nestling was significantly greater than the expected frequency if losses in this group had been proportionate to the losses in the entire sample (Table 4.4; χ^2_1 = 7.74, P < 0.01; Chi-square test). As the majority of these pairs (60%) were among the last third to breed, lower fecundity and higher loss rate are consistent with the hypotheses that late-breeding pairs may be in poorer condition or have less breeding experience.

The two pairs which lost two chicks each lost their first chick when it was between two and three weeks old and the second chick when it was be-

tween five and six weeks old. Starvation was the suspected cause in both cases. The pattern was similar for two of the four pairs which lost three chicks. However, the other two pairs which lost three chicks lost them all on the same day; predation or threatened predation, causing the chicks to jump from the nest, are suspected as the causes in those cases.

Table 4.4 Frequency of nestling loss by brood size, 1995 & 1996 combined

Brood Size:	1	2	3	4	5	Total
No. of broods:	25	48	100	53	1	227
No. of broods which lost:						
1 chick	13	9	14	11	-	47
2 chicks	-	1	1	-	-	2
3 chicks	-	-	4	-	-	4
Observed frequencies:	13	10	19	11	-	53
Expected frequencies:	5.8	11.2	23.3	12.3	0.2	53

Table 4.5 Nestling loss by age of nestling, 1995 & 1996

Nestling age:	1-3 weeks	4-6 weeks	χ^2	P
1995	29	10	181.0	< 0.01
1996	16	8	32.5	< 0.01

Table 4.6 Nestling loss by relative date of breeding, 1995 & 1996

	First 1/3 to breed	Mid 1/3 to breed	Last 1/3 to breed	df	χ^2	P
1995	(n = 54)	(n = 50)	(n = 54)			
Nestlings lost	11	6	22	2	248.5	< 0.01
Loss/breeding attempt	0.20	0.12	0.41			
1996	(n = 33)	(n = 37)	(n = 34)			
Nestlings lost	3	3	18	2	129.0	< 0.01
Loss/breeding attempt	0.09	0.08	0.53			

4.3.4 Effects of nest-site characteristics

4.3.4.1 Relative nest height

Of the first 33 nests built on the sample nest sites in 1995 (approximately 1/3 of the total), 23 (71%) were on the canopy top, a significant difference from the number which would have been expected if there had been no preference ($\chi^2_1 = 4.36$, $P < 0.05$; Chi-square test). Among all initial breeding attempts in the 103-site sample, mean brood size and number of nestlings fledged were significantly greater in canopy-top nest sites. The higher rate of chick loss from the canopy-top nests was not statistically significant (Table 4.7).

Table 4.7 Comparison of 1995 mean brood size, number of nestlings lost and chicks fledged per breeding attempt by relative nest height; Initial breeding attempts only

	Canopy top	Below canopy	Mann-Whitney U U	P
Breeding attempts	52	51		
Brood size	2.9	2.4	847.5	< 0.01
No. of nestlings lost	0.2	0.1	1221.5	ns
No. of chicks fledged	2.7	2.3	958.5	0.01

At the beginning of the 1996 breeding season, the males faced a situation entirely different from that in 1995: 34 of the sample nest sites (approximately 1/3 of the total) had nests in various states of disrepair remaining from the previous year's breeding effort. In this situation, both canopy-top sites and sites with existing nests were preferentially selected by the first third (33) of males to select sites (Table 4.8), although there was no significant association between the two variables (Table 4.9; $\chi^2_1 = 1.96$, $P = $ ns, Chi-square test).

Of the 98 sample nest sites monitored in 1996, 52 (53%) were on the canopy top, while 46 (47%) were below the canopy. There was no significant difference overall between canopy-top nest sites and those below the canopy in terms of mean brood size, number of nestlings lost, or number of chicks fledged per initial breeding attempt (Table 4.10).

Table 4.8 Comparison of the incidence of canopy-top nest sites & sites with existing nests in the total 1996 sample vs. the first third of nest sites occupied; the total sample was stratified to achieve approximately equal numbers of nest sites on the canopy-top and below the canopy (Chapter 2)

| | Incidence | | | | |
	Total sample n = 98	First third n = 33	df	χ^2	P
Canopy-top sites	52	25			
Below-canopy sites	46	8	1	5.37	< 0.05
Sites with existing nests	34	23			
Sites with newly-built nests	64	10	1	12.25	< 0.01

Table 4.9 Association between canopy-top locations and existing nests in sample nest-sites selected by the first 1/3 to start egg laying in 1996 (χ^2_1 = 1.96, P = ns, Chi-square test)

	Canopy-Top	Below-Canopy	Totals
Existing nest			
Observed frequency:	16	7	23
Expected frequency:	17.4	5.6	
Newly-built nest			
Observed frequency:	9	1	10
Expected frequency:	7.6	2.4	
Observed frequency totals:	25	8	33

Table 4.10 Comparison of 1996 mean brood size, number of nestlings lost, and number of chicks fledged per breeding attempt by relative nest height; initial breeding attempts only

| | Canopy top | Below canopy | Mann-Whitney U | |
			U	P
Breeding attempts	52	46		
Brood size	3.1	3.1	1190.0	ns
No. of nestlings lost	0.2	0.2	1191.5	ns
No. of chicks fledged	2.9	2.9	1189.5	ns

Similarly, although mean brood size and number of chicks fledged were slightly greater overall in sites with newly-built nests, the differences were not significant (Table 4.11). Among the first 33 sample nest-sites occupied, the mean number of chicks fledged per nest appeared to be substantially higher in canopy-top locations with

newly-built nests vs. those with existing nests (Table 4.12). However, the differences are not statistically significant (χ^2_2 = 4.09, P = ns, Chi-square test).

Table 4.11 Comparison of 1996 mean brood size, number of nestlings lost, and number of chicks fledged per breeding attempt between existing and newly-built nests; Initial breeding attempts only

	Existing nest	Newly-built nest	Mann-Whitney U U	P
Breeding attempts	34	64		
Brood size	2.9	3.2	890.5	ns
No. of nestlings lost	0.1	0.2	994.0	ns
No. of chicks fledged	2.8	3.0	964.5	ns

Table 4.12 Comparison of mean no. of chicks fledged among earliest-breeding pairs (first 1/3) by nest location and presence of existing nest, 1996; numbers in parentheses = n

	Canopy-top	Below canopy
Existing nest	2.9 (16)	3.1 (7)
Newly-built nest	3.4 (9)	0.0 (1)

4.3.4.2 Effect of nest size

In 1995, pairs breeding early in the breeding season built significantly larger nests than those breeding late (Table 4.13). Additionally, there was a consistent positive (albeit weak) relationship between nest size and both brood size and the number of chicks fledged in 1995 (Table 4.14).

Table 4.13 Comparison of 1995 mean nest size by egg-laying start date; first third vs. last third

	First 1/3 to breed (n = 33)	Last 1/3 to breed (n = 33)	Mann-Whitney U U	P
Mean nest size rank	3.7	2.7	284.5	< 0.001

For all initial breeding attempts (n = 103), the regression equation for brood size (brood size = 1.94 + 0.22 x nest size) was nearly significant at 0.06 (r^2 = 3.5%), and the equation for number of chicks fledged (no. fledged = 1.76 + 0.22 x nest size) was also nearly significant at 0.07 (r^2 = 3.2%). However, if only those breeding attempts which were successful in hatching at least 1 chick are considered (n = 98), the regression equations for both brood size (brood size = 1.9 + 0.28 x nest size) and number of chicks fledged (no. fledged = 1.72 + 0.28 x nest size) were significant (brood size: P < 0.01, r^2 = 7.8%; no. chicks fledged: P = 0.01, r^2 = 6.3%). This research was not carried out in 1996, as the results would have been confounded by the preference for building on pre-existing nests by early-breeding males.

Table 4.14 1995 mean brood size & no. of chicks fledged per nest by nest size rank

Nest size rank	Brood size		No. fledged	
	All initial attempts (n = 103)	Broods >0 (n = 98)	All initial attempts (n = 103)	Broods >0 (n = 98)
1-2	2.5	2.6	2.2	2.3
3	2.6	2.7	2.4	2.5
4	2.7	2.9	2.6	2.8
5	3.2	3.5	2.9	3.2

4.3.5 Comparative effects of breeding timing, nest location, and nest size on reproductive success

An analysis of variance for number of chicks fledged (reproductive success) using the Minitab (1996) general linear model shows that for all breeding attempts (1995 n = 158, 1996 n = 104) only the relative date of breeding had a significant effect in each year (Tables 4.15 & 4.16). Nest size had no significant effect in 1995, the only year studied, and relative nest height had no significant effect in either year (Tables 4.15 & 4.16). Relative date of breeding accounted for 71% of the variability in the number of chicks fledged per breeding attempt in 1995 (Table 4.15), and 62.5% in 1996 (Table 4.16).

Combining the two years, there was a significant difference in fledging success and the importance of relative nest height between the years (Table

4.17). Relative nest height had a significant effect on reproductive success in 1995 but not in 1996 (Section 4.3.4.1). Relative date of breeding had a significant effect on fledging success for the two years combined.

Table 4.15 General linear model ANOVA for number of chicks fledged per breeding attempt by relative breeding date, relative nest height, and nest size, all attempts 1995 (n = 158); a. each factor fitted after all others in the model; b. based on adjusted sum of squares

Source of variance	df	Seq. sum of squares	Adj. sum of squares[a]	Portion of variability[b]	Variance[b]	F[b]	P[b]
Rel. breed. date	70	200.93	203.69	71.0%	2.91	3.09	< 0.01
Rel. nest height	1	3.11	2.96	1.0%	2.96	3.15	ns
Nest size	4	5.76	5.76	2.0%	1.44	1.53	ns
Within-sample	82	77.25	77.25	26.9%	0.94		
	157	287.04					

Table 4.16 General linear model ANOVA for number of chicks fledged per breeding attempt by relative breeding date, and relative nest height; all attempts 1996 (n = 104); a. each factor fitted after all others in the model; b. based on adjusted sum of squares

Source of variance	df	Seq. sum of squares	Adj. sum of squares[a]	Portion of variability[b]	Variance[b]	F[b]	P[b]
Rel. breed. date	45	97.06	97.80	62.5%	2.17	2.14	< 0.01
Rel. nest height	1	1.58	1.58	1.0%	1.58	1.55	ns
Within-sample	57	57.82	57.82	37.0%	1.01		
	103	156.46					

Table 4.17 General linear model ANOVA for number of chicks fledged per breeding attempt by year, relative breeding date, and relative nest height plus interactions; all breeding attempts 1995-96 (n = 262); a. each factor fitted after all others in the model; b. based on adjusted sum of squares

Source of variance	df	Seq. sum of squares	Adj. sum of squares[a]	Portion of variability[b]	s[2b]	F[b]	P[b]
Year	1	49.57	6.21	1.3%	6.21	5.94	0.02
Rel. breed. date	1	173.42	100.03	20.3%	100.03	95.73	< 0.001
Rel. nest height	1	0.37	0.11	0.0%	0.11	0.11	ns
Year x rel. breed date	1	0.48	0.48	0.1%	0.48	0.46	ns
Yr. x rel. nest height	1	4.73	4.78	1.0%	4.78	4.61	0.03
Rel. date x rel. height	1	0.11	0.11	0.0%	0.11	0.11	ns
Within-sample	255	264.43	264.43	53.6%	1.04		
	261	493.07					

4.4 Discussion

4.4.1 Effect of breeding timing on reproductive success

Great cormorants breeding near the equator at Lake Naivasha experience a decline in reproductive success over the course of the breeding season similar to that found in studies of colonially-nesting piscivores in temperate environments. In both 1995 and 1996, pairs breeding early hatched significantly larger broods, lost significantly fewer chicks during the fledging period and, thus, fledged significantly more chicks per breeding attempt than did pairs breeding late in the season. In the two years combined, 81% of the variability in the number of chicks fledged was attributable to variability in brood size; only 19% was attributable to variability in nestling loss. This finding seems important in evaluating the applicability of the three hypotheses most commonly advanced to explain the seasonal declines in reproductive success in temperate climates as, in general, the three hypotheses would predict different effects on brood size and nestling loss.

4.4.1.1 Synchrony/predation risk hypothesis

In temperate regions, egg and chick predation by gulls and corvids are a common hazard for great cormorants (B. Hughes, pers. com.). However, during the Lake Naivasha study predation did not appear to be an important factor in limiting reproductive success, even for early and late-breeding pairs. Although three known predators of great cormorant eggs and young in sub-Saharan Africa, *i.e.* marabou stork (*Leptoptilos crumeniferus*), black kite (*Milvus migrans*), and fan-tailed raven (*Corvus rhipidurus*) (Brown *et al.* 1982), were not seen at the Lake Naivasha colony during the two years of the study, several other potential predators were observed: African fish eagle (*Haliaeetus vocifer*), tawny eagle (*Aquila rapax*), harrier hawk (*Polyboroides radiatus*), and a small troop of vervet monkeys (*Cercopithecus aethiops*). Clutch sizes were not measured because it was not possible to see into most sample nests from the observation point and impractical to use other methods (*e.g.* climbing the trees, using an observation

tower or pole mirror) due to the height and location of the nests in the trees. However, no egg or chick predation was seen during approximately 875 hours of observation and, during the two study years, there was only one unconfirmed report of a fish eagle eating a young cormorant.

The main predators at Lake Naivasha, an African fish eagle pair, seemed interested exclusively in adult cormorants. They were never seen attacking nestlings, even when the nestlings were without the protection of a parent. However, the adult great cormorant appeared to be a faster, more manoeuvrable flier than the fish eagle. The fish eagle's primary method of attack was to perch in the Acacia trees underneath the colony and attempt to capture an adult cormorant as it left its nest, swooping downward and outward toward the lake, before it had a chance to build up enough speed to escape. Four adults were seen to be captured in this way. None of the other potential avian predators were witnessed attacking the colony, and the troop of vervet monkeys was too small (five to six) to overcome the defensive reactions of the nesting adult cormorants.

Although breeding synchrony did not appear to be important in terms of reducing egg and chick predation during this study at Lake Naivasha, it may be more important at other locations in equatorial Africa or even at this location in future years. Unusually, at Lake Naivasha the nests are located in trees which are not surrounded by water. Potentially, this provides an opportunity for terrestrial predators and, due to their fewer numbers, pairs which nest late in the season might be more negatively affected than those which breed at the same time as the majority of pairs in the colony. In addition, breeding synchrony would seem to be important in reducing breeding interference by conspecific fledglings later in the breeding season.

Late-breeding pairs (both initial pairs attempting a second brood and pairs which were simply late in their initial breeding attempt) appeared to experience substantial interference from fledglings of earlier-breeding pairs. Fledglings continued to be fed by their parents at their nest site for at least four weeks following fledging. As the frequency of feeding became less and less over time, the fledglings be-

came increasingly hungry; many appeared to die of starvation during this period. Any pairs attempting to incubate eggs or brood young chicks in the vicinity of these starving fledglings from earlier broods incurred relentless harassment in the form of continuous aggressive begging for food.

This harassment, which happened primarily when there was extensive late breeding (e.g. 1995), often resulted in the nesting adult being driven off the nest completely. Although inadvertent trampling of any eggs or young nestlings was not witnessed directly, the numbers of broken egg shells and dead young chicks on the ground were substantially greater during the secondary breeding period than during the earlier primary period. Whether this was due to interference from hungry fledglings or the inexperience of the late breeders is not clear. However, interference with late-breeding attempts by hungry fledglings was extensive and pervasive throughout the colony in 1995. Those pairs which were able to breed at approximately the same time as the main body of the colony were largely spared this aggressive begging from the starving fledglings of earlier-breeding pairs.

A second type of conspecific predation, which breeding synchrony does not help to avoid, is the commandeering of single-parent nests and those nests where foraging by both parents is required to feed the growing nestlings. From the time the first egg is laid until the nestlings require the foraging efforts of both parents to survive, when the oldest chick reaches the mean age of 33 days (range = 16d - 58d, sd = 9.1d; B. Childress, unpub. data), one parent is always in attendance at the nest to protect the eggs and chicks from predation and inclement weather, and to protect the nest from destruction by other adults seeking easily-obtainable nest-building material. When the foraging effort of both parents is required to provide sufficient food for the growing brood, or if a parent loses its mate, the nest and its contents (eggs and/or chicks) are, of necessity, left unguarded.

During these absences at Lake Naivasha, an unpaired male without a nest of its own would invariably attempt to take over the unguarded nest. During the incidences observed, the nestlings were old enough to escape onto nearby branches. However, if these nests had

contained eggs or chicks which were not old enough to escape, they would almost certainly have been destroyed by the new male. At single-parent nests, although the nestlings are old enough to escape initially, death often results, as a single parent is able to bring only enough food to keep one chick alive, usually the oldest. Of course, starvation of the younger chicks in a single-parent nest would happen anyway, even if the nest is not taken over by a new male.

4.4.1.2 Food availability hypothesis

Although the cause of any specific nestling mortality was difficult to determine with certainty, starvation appeared to be the likely cause of most nestling losses at Lake Naivasha. Starvation is a major cause of mortality in great cormorant nestlings (Olver & Kuyper 1978, Johnsgard 1993) and most starvation deaths occur within the first three weeks after hatching (Johnsgard 1993). During the two years studied, 71.4% of the nestlings lost in the sample nests were lost during the first three weeks. Individual nestlings would be found dead on the ground in the morning almost always just a few days old and severely underweight. Most were assumed to have died of starvation, their bodies being removed from the nests by the parents during the night. Most pairs (89%) in sample nests which lost a chick lost only one. Of those six pairs which lost more than one chick, only one pair lost more than one chick at a time. The general pattern of loss among pairs which lost more than one chick was one loss at a time, spread two to three weeks apart, suggesting starvation.

Based on the effort-adjusted commercial fishery catch data there seemed to be seasonal variations in prey abundance at Lake Naivasha (Chapter 3). In addition there may also have been seasonal variations in prey availability to the cormorants due to variations in lake-water transparency (Chapter 3). However, these seasonal variations do not seem likely to have been responsible for the seasonal decline in reproductive success observed. Between 1991 and 1996, seasonal variations in the effort-adjusted commercial catch at Lake Naivasha were inconsistent from year to year, providing clear support

for the prey-availability hypothesis in only two years (1991 and 1992). During the other four years, there were vaguely similar commercial catch patterns with peaks during the first six months of the year, followed by declines during the remainder of the year. However, for the four years combined, the difference in mean monthly catch between the first six-months of the year and the second six months was not significant. During the two years studied (1995 and 1996), the commercial catch patterns were completely different (Chapter 3) and supportive of the prey-availability hypothesis only in 1996.

There was a significant negative relationship between water transparency and the effort-adjusted mean monthly commercial catch (Chapter 3). This effect apparently results from the lowered ability of the fish to see and avoid the fishermen's stationary gill nets when water transparency is reduced (P. Hickley, pers. comm.). As cormorants are diving feeders, foraging by underwater pursuit often near the bottom, low water-transparency might be expected to have a similar effect on prey availability by reducing the cormorants' ability to see the fish. Indeed, Bell-Cross (1974) found that cormorants fishing in turbid water had a lower percentage of successful dives than those fishing in clear water. Nevertheless, it is doubtful that seasonal variations in prey availability due to changes in water transparency levels are an important factor in the observed seasonal decline in great cormorant reproductive success.

Great cormorants are strong fliers (Mackworth-Praed & Grant 1952) and they can (and do) fly considerable distances to feed (Olver & Kuyper 1978, Brooke *et al*. 1982, Platteeuw & van Eerden 1995). Thus, they are not limited to any one body of water as a source of food. Further, although commonly described as solitary feeders (*e.g.* Brown *et al*. 1982), this species is flexible in its foraging techniques (Grémillet *et al*. 1998) and was frequently observed feeding in flocks at Lake Naivasha. This foraging technique appears to be a successful adaptation for more effective feeding in turbid waters, not only elsewhere in sub-Saharan Africa (Linn & Campbell 1992) but also in Europe (van Eerden & Voslamber 1995). Finally, the seasonal pattern of water transparency observed at Lake Naivasha during 1995-96 is

not consistent with the prey-availability hypothesis. To support the prey-availability hypothesis, water transparency would be high prior to and during the main breeding period, declining thereafter. However, at Lake Naivasha the observed water transparency pattern was the opposite (Chapter 3).

4.4.1.3 Age and experience hypothesis

The age and experience hypothesis seems to be the most helpful of all the temperate-region hypotheses in terms of explaining the seasonal decline in great cormorant reproductive success observed at Lake Naivasha. Older, more experienced individuals of many species including the great cormorant have been shown to breed earlier in the breeding season and to have higher reproductive success than younger, less experienced individuals. It is commonly believed that the reason older, more experienced individuals are able to breed earlier and to have greater reproductive success is that they often are more efficient foragers and thus better able to acquire the nutritional resources required to breed earlier, lay larger clutches, and successfully feed larger broods (Darwin 1871, Huxley 1914, Kirkpatrick et al. 1990).

In the great cormorant, the extent of seasonal head filoplume development prior to breeding is believed to be positively correlated with age (Witherby et al. 1940, Stokoe 1958, Marion 1995). In the study colony, individuals with more extensively developed head filoplumes at the time of pair formation bred substantially earlier than individuals in which this character was less well developed (Chapter 5). Further, early-breeding pairs were significantly more successful than late-breeding pairs in terms of brood size and fledging success.

Nestling loss was also significantly less among early-breeding pairs. Pairs which were among the last one-third to breed accounted for a disproportionately high 63.5% of total chicks lost during the two-year study period. While most of the chicks lost were presumed to have starved, an undetermined number were observed to have fallen or jumped from their nests to avoid predation. This phenomenon ap-

peared to be much more frequent later in the breeding season than earlier, when the presumed older and more experienced pairs were nesting, which lends additional support for the importance of age and experience in great cormorant reproductive success.

Falling from the nest has previously been reported as a major cause of nestling mortality in other regions of sub-Saharan Africa (Olver & Kuyper 1978). Nestlings, usually the smallest, apparently get pushed out of the nests inadvertently by siblings jostling for position to be fed, and occasionally nestlings jump from their nests to avoid presumed predators (Brown *et al.* 1982). This is assumed to have happened on at least one occasion, when all three nestlings from one nest were found as a group on the ground, and in most of the other cases where a nestling disappeared after the first three weeks of life (28.6% of the total nestling loss).

4.4.2 The effect of nest-site characteristics on reproductive success

Among the initial breeding attempts in 1995, mean brood size and number of chicks fledged were both significantly greater in canopy-top nests than in nests located below the canopy. Additionally, there was a consistent and positive relationship between nest size and both brood size and number of chicks fledged per nest in 1995. In 1996, however, neither canopy-top nest sites nor pre-existing nests were significantly associated with larger broods or greater fledging success. (Nest size was not documented in 1996, due to the potential confounding influence of the pre-existing nests.)

There could be several reasons why pairs with canopy-top locations and larger nests were more fecund. Canopy-top locations may be more sanitary, being above falling excreta from other nests, although most great cormorant nests contain substantial amounts of excreta from their own occupants (B. Childress, pers. obs.). Their full exposure to ultra-violet radiation from the tropical sun may result in their being less infested by certain parasites. Nestlings may be less likely to fall from larger nests. However, it is suggested that the main reason pairs breeding in nest-sites with these characteristics were more

fecund is that generally they appeared to have been older pairs with more breeding experience.

The difference between the two years in terms of the effect of the nest-site characteristics studied on reproductive success may have been due in part to the limitation of canopy-top sites; this may have forced many high-quality males which ordinarily would have preferred a canopy-top site to select a site below the canopy in 1996. Alternatively, because many of the same nest sites were included in the sample in both years (Chapter 2), the improvement in reproductive success in 1996 may have been due to male site fidelity and the increased age and experience of individuals breeding on the sample sites in the second year. This effect might have been particularly strong among those individuals which were among the last to breed in 1995.

Among European shags, a closely related species, nest site fidelity from one year to the next has been reported to be very high (Snow 1960), with 56% of surviving males returning to the same site in consecutive years, and 87% of those which changed sites selecting a new site within 16 metres of their previous site (Aebischer et al. 1995). Assuming the same is true of great cormorants, the fact that primarily the same sample nest sites were used in both 1995 and 1996 suggests that the majority of the birds in the sample would have been a year older with more breeding experience in 1996 (after taking into account mortality and immigration). Increased age and experience may have been an important factor in the improvement in brood size and fledging success from 1995 to 1996, indicated by the fact that the biggest improvement was made by the latest-breeding pairs, those which presumably were young, inexperienced breeders in 1995 and which benefited disproportionately by an additional year's experience. Davis (1975) found a similar age effect in herring gulls (Larus argentatus) on Skokholm Island, Pembrokeshire.

Chapter 5 Seasonal sexual character intensity and its effect on breeding timing, fecundity, and mate choice

5.1 Introduction

Kirkpatrick *et al.* (1990) suggested that seasonal sexual characters, expressed similarly in both sexes, might have evolved in monogamous, sexually monomorphic species through sexual selection involving mutual mate choice. In their proposed model, the authors hypothesised that this might have occurred because individuals of both sexes in good nutritional condition and with more extreme character development would tend to breed earlier with more fecund mates and to select mates on the basis of these characters (Chapter 1). Great cormorants are, putatively, sequentially monogamous (Marchant & Higgins 1990). In *P. carbo lucidus*, the sexes are monomorphic in their non-breeding plumage, and both sexes develop five similar and clearly observable sexual characters (Brooke *et al.* 1982, Brown *et al.* 1982, Figure 5.1):

- white filoplumes on the head and nape
- white feather patches on the outer thighs
- buff/dark buff contour feathers on the normally white/off-white cheeks, foreneck, and upper breast (first described in Brooke *et al.* 1982 as "pinkish brick ")
- darkening of gular skin colour from dull yellow to various shades of olive
- change in colour of the triangular suborbital skin patch from dull yellow to various shades of red

With the exception of gular skin colour, the intensity of these seasonal sexual characters was observed to vary widely among individual birds at the time of pair formation. Using *P. carbo lucidus*, this chapter assesses the Kirkpatrick *et al.* (1990) model assumptions by exploring the following hypotheses:

- Great cormorants which breed early in the season have more intensely developed sexual characters at the time of pair formation than those which breed late.

- Pairs which breed early are more fecund than pairs which breed late.

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- Males and females which breed early select mates on the basis of one or more of the seasonal sexual characters.

Figure 5.1 *P. carbo lucidus* in breeding plumage

5.2 Methods

During the 1996 breeding season, the intensity of the five seasonal sexual characters at the time of pair formation was ranked visually on a 5-point scale (0-4; Table 5.1) for males and females in a randomly-selected sample of 100 nest sites. The intensity of each character was also ranked at the nest site weekly thereafter for 12 weeks. A sample data collection sheet is provided in Appendix II-c.

Nest sample selection and observation methods are described in Chapter 2. Only those pairs for which sexual character intensity had been ranked for both sexes at the time of pair formation (n = 100) were used for this analysis. Pair formation dates and fledging success were based on direct observation. The pair-formation date was recorded as the date of first observed copulation. It was not possible to track development of seasonal sexual character intensity in individuals prior to nest-site selection

and pair formation as it was not possible to identify individual birds away from the nest site.

Table 5.1 Five-point sexual character rating scales; * the male of one breeding pair still had immature plumage, having just moulted out of its first-year plumage

Head Filoplumes & Thigh Patch Feathers (same scale for both)		
	0	none
	1	sparse
	2	light
	3	medium
	4	heavy
Colour of cheek, neck & upper breast plumage	0	immature*
	1	none (white)
	2	light buff
	3	buff
	4	dark buff
Colour of gular skin	0	dull yellow
	1	bright yellow
	2	light olive
	3	medium olive
	4	dark olive
Colour of suborbital skin	0	dull yellow
	1	bright yellow
	2	orange
	3	orange-red
	4	deep red

5.3 Results

5.3.1 Sexual character intensity at pair formation

The mean intensity rank of each character started to decline in both sexes immediately following pair formation and continued to decline steadily for the 12-week measurement period. The rates of decline were similar for both sexes (Figures 5.2 and 5.3).
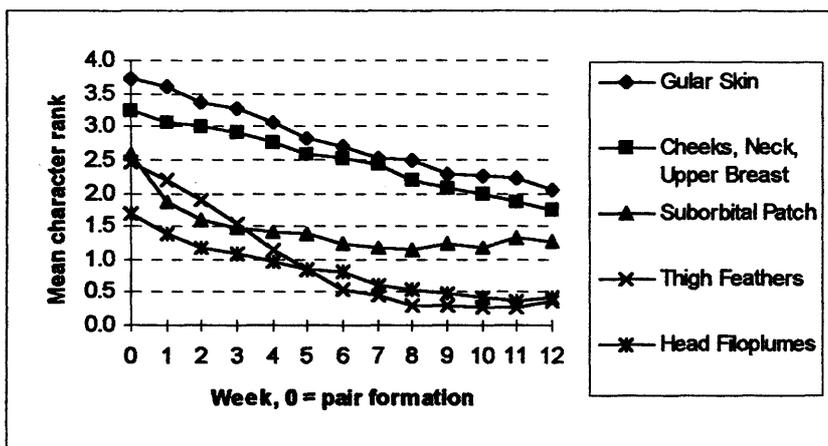
Figure 5.2 Mean rank of male seasonal character intensity by week from pair formation (weekly n range: 63 - 100)
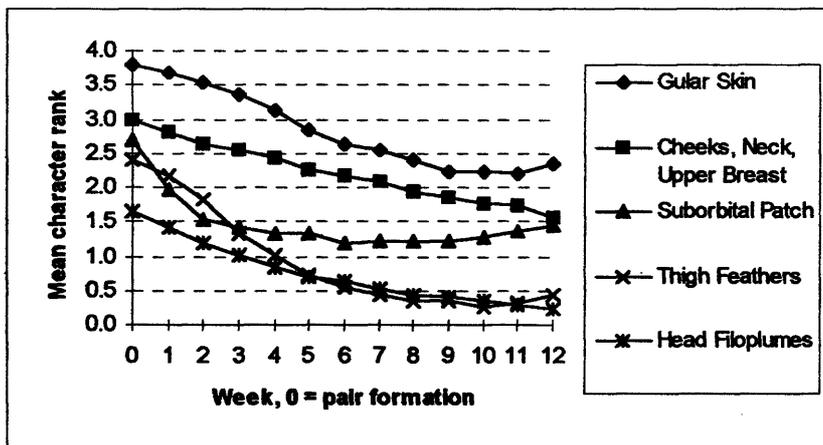
Figure 5.3 Mean rank of female seasonal character intensity by week from pair formation (weekly n range: 62 - 100)

Plumage colour on the cheeks, foreneck, and upper breast was significantly more intense in males. However, no significant difference was found in the frequency of the character intensity ranks between males and females for the other characters (Table 5.2). Thus, it appears that these other characters are expressed similarly in both sexes.

In paired comparisons, correlations between male and female sexual character intensity at pair formation were positive, albeit weak, and significant only in the case of gular and suborbital skin colour (Table 5.3). On an individual bird basis, correlations among the intensities of the different characters indicate that development of the plumage character intensity is probably linked,

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as is development of the skin colour intensity although not to the same extent (Tables 5.4 & 5.5).

Table 5.2 Frequency distribution of 1996 sexual character intensity ranks among males & females at pair formation (Chi-square Test; n = 100); * cells eliminated for chi-square test

Intensity Rank:	0	1	2	3	4	χ^2	df	P
Head Filoplumes								
male	16	32	26	19	7			
female	17	29	30	21	3	2.16	4	ns
Thigh Patch Feathers								
male	6	21	14	34	25			
female	5	21	21	35	19	2.35	4	ns
Cheek, Neck & Upper Breast Colour								
male	1*	3	15	32	49			
female	0*	4	24	43	29	8.82	3	< 0.05
Gular Skin Colour								
male	0*	1*	4	17	78			
female	0*	0*	5	13	82	0.74	2	ns
Suborbital Skin Colour								
male	0*	10	39	33	18			
female	0*	10	30	38	22	1.93	3	ns

Table 5.3 Correlations of character intensity ranks within pairs at pair formation (Spearman Rank Order; n = 100); * P < 0.05; ** P < 0.01

Sexual character	Male-female intensity rank correlation coef. (r_s)
Head filoplumes	0.15
Thigh patch feathers	0.08
Cheek, neck & upper breast colour	0.17
Gular skin colour	0.24*
Suborbital skin colour	0.31**

Table 5.4 Correlations of intensity ranks among characters within individual males (Spearman Rank Order; n = 100); * P < 0.05; ** P < 0.01

Sexual characters	Head filoplumes	Thigh patch feathers	Cheek, neck & up. breast colour	Gular skin colour
Thigh patch feathers	0.69**			
Cheek, neck & upper breast colour	0.41**	0.30**		
Gular skin colour	0.15	0.09	0.26**	
Suborbital skin colour	0.24*	0.22*	0.15	0.33**

Table 5.5 Correlations of intensity ranks among characters within individual females (Spearman Rank Order; n = 100); * P < 0.05; ** P < 0.01

Sexual characters	Head filoplumes	Thigh patch feathers	Cheek, neck & up. breast colour	Gular skin colour
Thigh patch feathers	0.58**			
Cheek, neck & upper breast colour	0.00	-0.13		
Gular skin colour	0.04	0.06	0.10	
Suborbital skin colour	0.22*	0.18	0.12	0.28**

5.3.2 The relationship between sexual character intensity and date of pair formation

Those individuals with the most intensely developed sexual characters overall at the time of pair formation tended to breed earlier, while those with the less intensely developed characters tended to breed later (Table 5.6). This is particularly true of males with more intensely developed head filoplumes and of both sexes with more intensely developed suborbital skin patch colour. Combining data on all five sexual characters by summing their ranks shows that males with more intense character development bred 15 days earlier on average than those with less development (P = 0.001, Mann-Whitney U test), while females with more intense character development bred 10 days earlier on average than those with less development (P < 0.01, Mann-Whitney U test).

5.3.3 The relationship between breeding timing and fledging success

There was a highly significant negative relationship between the number of chicks fledged and the relative date the first egg was laid in 1996 (Figure 5.4). Furthermore, there was a significant difference in the mean number of chicks fledged per nest by the first third of pairs to start breeding (2.88, n = 33) in comparison with the mean number fledged by the last third to start (2.24, n = 33; P < 0.05; Mann-Whitney U test).

Table 5.6 Mean date of pair formation by intensity rank of sexual characters at the time of pair formation; a. intensity ranks consolidated into two groups for convenience of presentation; similar mean and median date trends and probabilities are achieved without consolidation b. median number of days elapsed since date of first pair formation in sample; c. Mann-Whitney U test based on median rel. dates; adjusted for ties

Male characters	Intensity rank[a]	n	Mean pair formation date	Median rel. date[b]	p[c]
Head filoplumes	3-4	24	14 March	8.0	
	0-2	70	25 March	24.0	< 0.01
Thigh patch feathers	3-4	55	19 March	14.0	
	0-2	39	28 March	24.0	ns
Cheek, neck, upper breast colour	3-4	77	19 March	16.0	
	0-2	17	6 April	35.0	ns
Gular skin colour	3-4	89	22 March	16.0	
	0-2	5	1 April	14.0	ns
Suborbital skin patch colour	3-4	48	17 March	8.5	
	0-2	46	28 March	25.5	< 0.001
Combined (sum) male characters	13-20	63	17 March	10.0	
	0-12	31	2 April	30.0	0.001
Female characters					
Head filoplumes	3-4	24	18 March	10.0	
	0-2	70	24 March	20.5	ns
Thigh patch feathers	3-4	52	22 March	12.0	
	0-2	42	23 March	23.0	ns
Cheek, neck, upper breast colour	3-4	70	22 March	17.0	
	0-2	24	- 24 March	16.0	ns
Gular skin colour	3-4	89	23 March	16.0	
	0-2	5	20 March	25.0	ns
Suborbital skin patch colour	3-4	56	19 March	9.0	
	0-2	38	28 March	26.0	< 0.001
Combined (sum) female characters	13-20	60	19 March	10.0	
	0-12	34	29 March	26.0	< 0.01

5.3.4 Fledging success and sexual character intensity at pair formation

The correlation coefficients between the number of chicks fledged and the intensity of the parents' sexual characters at pair formation were, overall, weak and not significant (Table 5.7). However, there was a significant difference between the median number of chicks fledged by males with the darkest plumage on their cheeks, foreneck, and upper breast (rank of "3" or "4") and those with lighter plumage colour (rank of "0", "1" or "2"; P = 0.01, Mann-Whitney U test; Table 5.8).
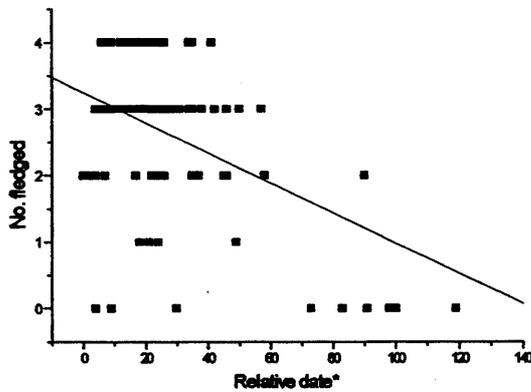
Figure 5.4 Regression plot of the relationship between the number of chicks fledged and the estimated relative date of first egg laid, 1996; (Regression equation: $Y = 3.41 - 0.026X$; $r^2 = 22.7\%$; $P < 0.001$); * For each nest in the sample, the estimated relative date of the first egg laid is the number of elapsed days between the estimated date the first egg was laid in that nest and the estimated date the first egg was laid in the first sample nest to start breeding

Table 5.7 Correlations between the number of chicks fledged and intensity ranks of parents' sexual characters at the time of pair formation (Spearman rank order, n = 100); * Critical values at 0.05 & 0.01 levels of confidence (df = 98): 0.20 & 0.26

	Correlation coef. (r_s) with number of chicks fledged*
Male parent characters	
Head filoplumes	0.10
Thigh patch feathers	0.07
Cheek, neck, upper breast colour	0.16
Gular skin colour	- 0.13
Suborbital skin patch colour	- 0.10
Combined male characters	0.06
Female parent characters	
Head filoplumes	0.08
Thigh patch feathers	0.13
Cheek, neck, upper breast colour	0.16
Gular skin colour	0.05
Suborbital skin patch colour	0.08
Combined female characters	0.19

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Table 5.8 Mean no. of chicks fledged by intensity ranks of parents' sexual characters at pair formation; * Mann-Whitney U test based on median no. fledged, adjusted for ties; n = 100)

	Intensity rank	n	Mean number of chicks fledged	P*
Male characters				
Head filoplumes	3-4	26	2.77	
	0-2	74	2.69	ns
Thigh patch feathers	3-4	59	2.81	
	0-2	41	2.56	ns
Cheek, neck, upper breast colour	3-4	81	2.90	
	0-2	19	1.90	0.01
Gular skin colour	3-4	95	2.68	
	0-2	5	3.20	ns
Suborbital skin patch colour	3-4	51	2.59	
	0-2	49	2.84	ns
Combined (sum) male characters	13-20	67	2.79	
	0-12	33	2.54	ns
Female characters				
Head filoplumes	3-4	24	2.71	
	0-2	76	2.71	ns
Thigh patch feathers	3-4	54	2.85	
	0-2	46	2.54	ns
Cheek, neck, upper breast colour	3-4	72	2.83	
	0-2	28	2.39	ns
Gular skin colour	3-4	95	2.72	
	0-2	5	2.60	ns
Suborbital skin patch colour	3-4	60	2.73	
	0-2	40	2.68	ns
Combined (sum) female characters	13-20	63	2.78	
	0-12	37	2.60	ns

5.4 Discussion

The intensity of sexual characters in birds is thought to be directly reflective of gonadal development and breeding readiness (Witsche 1935 & 1961, Middleton 1991). For example, in members of the European great cormorant subspecies *P. c. carbo* and *P. c. sinensis*, suborbital skin patch colour varies from yellow to bright red. Recent observations of both species in tree-nesting colonies at Abberton Reservoir near Colchester, England, have found that both members of a breeding pair exhibit bright red suborbital skin patch coloration at the start of laying. This has been suggested to indicate that, in these subspecies, suborbital skin patch colour may be a signal for breeding readiness (G. Ekins, pers. comm.).

Of the five sexual characters examined in *P. c. lucidus*, four (head filoplumes, thigh patch feathers, gular and suborbital skin patch colour) were expressed similarly

in both sexes at the time of pair formation, while the cheek, foreneck, and upper breast plumage colour was significantly darker among males. There was substantial variation in the intensity of the various characters among individuals at the time of pair formation and later at the start of egg laying.

5.4.1 Effect of sexual character intensity on breeding timing and fecundity

Consistent with the Kirkpatrick et al. (1990) model (Chapter 1), males and females of P. c. lucidus with more intensely developed sexual characters at the time of pair formation formed pairs significantly earlier than those with less intensely developed characters. Also consistent with the model, those pairs which bred earliest (first third) had significantly higher fecundity. Although the correlations between the number of chicks fledged and sexual character intensity at the time of pair formation were weak overall and not significant, males with the darkest plumage on their cheeks, foreneck, and upper breast (intensity ranks of "3" or "4") fledged significantly more chicks than those with lighter intensity of this character.

It is suggested that the significant relationships observed among sexual character intensity, breeding timing, and fecundity are due at least in part to the honest condition-dependent nature of the characters in this subspecies. Condition-dependency occurs when a physical link exists between the signal and the underlying condition, making the projection of a dishonest signal difficult or impossible (Johnstone 1997). It is one of the two most commonly postulated evolutionary mechanisms for ensuring the usefulness of sexual characters as signals (Andersson 1986). Carotenoid-based coloration as an indicator of general nutritional condition, foraging ability and, perhaps, parasite load are commonly-given examples of condition-dependency. Carotenoid pigmentation accounts for most yellow, orange and red colours in animals (Ralph 1969); however, animals cannot synthesise carotenoids and therefore must obtain them from their diets (Fox & Vevers 1960, Brush 1990, Gray 1996). Hill & Montgomerie (1994) found that, in house finches, carotenoid-based feather coloration was an indicator of nutritional condition during moult. The authors also found that female house finches preferred to mate with more colourful males (Hill 1990, 1991). Although intraspecific studies have provided equivocal results (Dufva & Allander 1995, Bortolotti et al. 1996, Shykoff & Widmer 1996), colour variation in carotenoid-

based pigmentation of the skin and plumage is thought by many to be a reliable indication of the relative presence or absence of parasites, or the level of immunity to certain types of parasites (Brush & Power 1976, Hamilton & Zuk 1982, Kodric-Brown 1984, Dufva & Allander 1995).

The second often-postulated evolutionary mechanism for ensuring the usefulness of sexual signals is the "handicap principle" proposed by Zahavi (1975, 1977). The "handicap principle" postulates that the existence of an exaggerated ornament, requiring extra effort to produce, handicaps the individual through loss of condition and thus provides evidence of quality through the individual's ability to survive in spite of this handicap. Although controversial for many years, there seems to be general agreement today that Zahavi's (1975) principle is plausible in theory (Johnstone 1997). Møller's (1988, 1989) studies showing that female barn swallows prefer males with longer tails, and that natural tail length in male barn swallows reflects their ability to bear the costs of such an elaborate ornament, apparently provides the only empirical evidence that this principle operates in nature (Johnstone 1997).

In the great cormorant, head filoplumes and thigh feather growth appear to be condition-dependent signals of age, survival ability, and breeding experience (Witherby *et al.* 1940, Stokoe 1958). In British populations of *P. c. sinensis,* Witherby *et al.* (1940) noted that filoplume development was non-existent in first-year birds and only sparse in second-year birds. Thereafter, the extent of filoplume and feather growth tended to increase with the age of the individual. Similar observations were made in the Lake Naivasha population of *P. c. lucidus* during the current study. One way (up to a point) for females to ensure that they mate with males carrying good genes for survival is to select older males (Halliday 1978). Older birds commonly have been observed to breed earlier in the season, occupy preferred nest sites, have larger clutches, and achieve higher reproductive success than younger birds. Examples include: kittiwake *Rissa tridactyla* (Coulson & White 1958), gannet *Sula bassana* (Nelson 1964), herring gull *Larus argentatus* (Davis 1975), fulmar *Fulmarus glacialis* (Ollason & Dunnet 1978), shag *Phalacrocorax aristotelis* (Potts *et al.* 1980), California gull *Larus californicus* (Pugesek 1983), common terns *Sterna hirundo* (Nisbett *et al.* 1984), glaucous-winged gull *Larus glaucescens* (Reid 1988), western gulls *Larus occidentalis* (Pyle *et al.* 1991), wandering albatross *Diomedea exulans*

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(Croxall *et al.* 1992), great cormorant *Phalacrocorax carbo sinensis* (Bregnballe 1996), thick-billed murre *Uria lomvia* (De Forest & Gaston 1996).

Rarely mentioned in the literature as an element of breeding plumage in *P. c lucidus*, the growth of darker feathers on the normally white cheeks, foreneck, and upper breast during the pre-nuptial moult appears to be an important sexual character, particularly in males. In the Lake Naivasha population, the colour of this seasonal plumage was buff, varying in intensity from light buff to dark buff by individual. It was the only character which was not expressed similarly in both sexes at the time of pair formation, being expressed significantly more intensely in males. Furthermore, males in which this character was most intensely developed not only formed pairs significantly earlier than males with less intense development but also fledged significantly more chicks. This character is the only one of the five studied which was correlated with fledging success. The finding that it was expressed more intensely in males than in females suggests that this character may be a male-specific, condition-dependent signal. This could be analogous to the black breast stripe of the monogamous great tit, present in both sexes but expressed more intensely in the males and believed to be a male-specific signal of parental quality (Norris 1990). On the other hand, the darker cheek, foreneck, and upper breast plumage in breeding male cormorants may be the result of an age difference in the male and female populations.

Like the other seasonal feather characters (head filoplumes and thigh patch feathers), the intensity of this seasonal plumage on the cheeks, foreneck, and upper breast appears to be related to age. This is indicated by the observation that birds which were presumed to be second-year adults, based on their adult plumage and sparseness of white head filoplumes and thigh feathers, had almost universally bright white plumage on their cheeks, foreneck, or upper breast, with no buff colouring. On the other hand, individuals with more intensely developed filoplumes almost always had darker plumage on their cheeks, forenecks, and upper breasts. Although this correlation was not significant in females, it was highly significant in males, indicating that perhaps darker cheek, foreneck, and upper breast plumage is a male-specific character based on age.

It seems likely that suborbital skin patch colour is also a condition-dependent character. It was previously thought by some that the suborbital skin patch of *P. c. lucidus* became redder in females than in males prior to breeding (Urban 1979, Brown, *et al.* 1982). However, this was not the case in the sample

of breeding pairs at Lake Naivasha in 1996. Because there was a wide variation in suborbital patch colour among individuals at the time of pair formation, from bright yellow through orange to bright red, it does not seem likely that this signal reflects only breeding readiness. If it reflected only breeding readiness, it would seem that there should be little colour variation at the time of pair formation, as observed in the European subspecies (G. Ekins, pers. comm.).

Presuming suborbital skin patch colour is carotenoid-based, perhaps it is more reflective of nutritional health, foraging ability, parasite load and/or level of immunity to certain parasites than of breeding readiness. For example, Hill *et al.* (1994) concluded that the colour variations observed in male and female house finch plumage were most likely the result of variations associated with the uptake of carotenoids, such as foraging ability, diet quality and/or parasite load. Similarly, Sundberg (1995) showed that the intensity of colour in the male yellowhammer (*Emberiza citrinella*) during the breeding season reliably reflected the intensity of parasite infection and that males with heavy parasite loads produced fewer fledglings. However, no direct relationship was found between male colour and fledging success. The nature of the relationship between parasites and plumage colour is complex (Shykoff & Widmer 1996) and may well depend on the specific parasite-host combination being considered. Some parasites are known to impede the ingestion of carotenoids in fishes (Milinski & Bakker 1990), while others are thought to cause carotenoids to be drawn away from signals in favour of the immune system (Shykoff & Widmer 1996). Nematodes, a chronic endoparasite occurring in large numbers in the stomachs of some cormorants, are known to debilitate their hosts and affect plumage brightness in other avian species (Hamilton & Zuk 1982).

5.4.2 The effect of sexual character intensity on mate choice

Kirkpatrick *et al.* (1990) hypothesised that, within the pool of healthier males and more fecund females ready to breed early, both sexes choose mates on the basis of an epigamic character that is expressed equally in both sexes. Pair formation in *P. c. lucidus* begins with the male selecting a nest site and advertising for a mate. This he does by 'wing-waving" (alternately exposing and covering his seasonal growth of white thigh patch feathers). At the same time, he displays

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his white head/nape filoplumes, gular and suborbital skin colour and cheek, foreneck, and upper breast plumage by crouching in the nest and pointing his bill skyward (Kortlandt 1958, Urban 1979, Johnsgard 1993). The male is soon joined at the nest site by a female and, providing she is not rejected by the male, they proceed through ritualised pair-formation behaviour, culminating in copulation at the nest site. Occasionally, a female will be rejected by the male. Kortlandt (1958) found that females of the European subspecies were occasionally rejected by males. He attributed this to the females not being sufficiently submissive to the males during initial contact. Although female rejection also occurred in the Lake Naivasha colony, it was not observed often and when it was, the criteria for rejection were not apparent to the observer. Thus, while it appears the female is primarily responsible for mate choice, the male also seems to exercise an element of choice, consistent with the assumption of Kirkpatrick *et al.* (1990).

In *P. c. lucidus*, males and females provide similar levels of parental investment. The male collects the vast majority of the nest-building and nest-lining material and shares the incubation, brooding, feeding, and nest defence duties approximately equally with the female. Both parents are required for success in fledging the modal brood of three chicks. For example, after the male disappeared from one of the sample nests at Lake Naivasha, the female by herself was able to fledge only one chick of the original three. This reduced reproductive success appears to be fairly typical of avian species in which nestlings are normally cared for by both parents (Sasvari 1986, Lyon *et al.* 1987).

In a sequentially monogamous system such as this, where substantial parental investment is required of both sexes, it would seem that mate choice would be critically important to both sexes, having a direct effect on the fecundity of both. In selecting a mate, the female will maximise her fecundity by selecting a male which not only has "good genes", but also is able to breed early; owns a superior nest site; is a superior forager for nest-building and nest-lining materials as well as for food for the nestlings; is experienced at incubating, brooding and feeding; will be a strong defender of the nest and brood; and is relatively free of parasites. The male, of course, would improve his reproductive success by selecting a female with the same qualities. Female mate choice for parental quality, on the basis of conspicuous male plumage coloration, has been shown in the cactus finch (*Geospiza conirostris*) and the great tit (*Parus major*),

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both seasonally monogamous species (Grant & Grant 1987, Norris 1990). However, Møller (1990) found that in the monogamous swallow *Hirundo rustica*, while females preferred to mate with males having longer tails, they were not able to predict the quality of male parental care from tail length alone.

Reliable signals concerning potential parental quality which could be used in mate selection would seem to be of particular value to *P. c. lucidus* and would be consistent with the assumption in Kirkpatrick *et al.* (1990). However, the effect of sexual character intensity on mate choice in this subspecies is not clear. At the time of pair formation, there were positive and significant correlations between the intensity of male and female suborbital and gular skin colours in paired comparisons. There was also a positive and significant correlation between male and female intensity rankings for all five characters combined. On the other hand, the correlations between male and female intensity rankings for the feather-based characters (head filoplumes, thigh patch feathers or cheek, foreneck, and upper breast plumage colour) at the time of pair formation were not significant. The positive and significant correlations between male and female intensity rankings for the suborbital skin and gular skin colour may indicate that the birds may be using these signals in mate choice. However, since the correlations were weak, and since most individuals had highly-developed gular skin colour at the time of pair formation, the correlations observed may not be related to mate choice.

Given the finding that males and females with more intensely developed sexual characters tended to breed earlier and *vice versa*, it was expected that there might be a stronger level of correlation between the male and female characteristics at the time of pair formation. One possible reason for not finding stronger correlations may be that from both sexes' point of view, it might be more advantageous (in terms of maximising fitness) to breed earlier in the season and accept a mate in less than prime condition rather than delay breeding, waiting for a potential mate in better condition. This might have been particularly true for the many birds which immigrated into the Lake Naivasha ecosystem to breed over the course of the breeding season. In both years studied, a large proportion of the colony consisted of breeding birds from outside the ecosystem. This was evidenced by census findings which indicated that the resident population at Lake Naivasha ranged between 850 and 1050 birds, while the breeding population ranged between 1750 and 1850 birds.

Similarly, this subspecies may not be as generally monogamous during the breeding season as commonly thought. It may be more advantageous for a female to breed earlier with a lower quality male and to seek extra-pair copulations with higher-quality males to improve the genetic quality of her offspring. The females of many species previously thought to be monogamous have been shown to use extra-pair copulations to improve the genetic quality of their offspring (reviewed in Westneat *et al.* 1990 and Birkhead & Møller 1992). Examples include: cactus finch, *Geospiza conirostris* (Grant & Grant 1987); black-capped chickadee, *P. atricapillus* (Smith 1988); blue tit, *Parus caeruleus* (Kempenaers *et al.* 1992); zebra finch, *Poephila castanotis* (Houtman 1992); chaffinch, *Fringilla coelebs* (Sheldon 1994); purple martin, *Progne subis* (Wagner *et al.* 1996); and collared flycatcher, *Ficedula albicollis* (Sheldon *et al.* 1997).

The European shag (*Phalacrocorax aristotelis*), a species closely related to the great cormorant, was also thought to be sequentially monogamous (Johnsgard 1993). However, recent studies of this species by Graves *et al.* (1992, 1993) showed that approximately 14% of male copulations were extra-pair copulations. The authors concluded that the pattern of extra-pair copulations was consistent with the hypothesis that females were soliciting extra-pair copulations to enhance the genetic quality of their offspring. It may be that sexual selection for genetic benefits in the great cormorant operates to some extent through extra-pair copulations and parenthood (*e.g.* Houtman 1992), and perhaps the significance of variations in sexual character intensities will only become clear when these are taken into account (*e.g.* Sheldon *et al.* 1997). Finally, the observed lack of strong correlations between male and female sexual character intensities at the time of pair formation may be because, from the female's perspective, other signals such as the quality of the male's nest site (see Chapter 5), and/or the vitality with which he executes the "wing-waving" display, may be more reliable indicators of his breeding condition and potential parental quality than filoplumes or skin colours.

Chapter 6 Population shifts between sympatric great and long-tailed cormorants: the effects of niche overlap or environmental change?

6.1 Introduction

At Lake Naivasha, and at several other sub-Saharan freshwater rivers and lakes, great and long-tailed cormorants (*Phalacrocorax africanus*) are sympatric. Between 1993 and 1995, the number of great cormorants using the lake for daytime foraging and roosting increased by 56%, while the number of long-tailed cormorants decreased 64% (Table 6.1).

Table 6.1 Counts of cormorants using Lake Naivasha ecosystem in January, 1993-95; source: Nasirwa & Bennun 1994, 1995; includes small adjacent lakes Oloidien & Sonachi

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

Prior to 1993, there was a breeding population of approximately 3000 great cormorants at Lake Nakuru (Bennun 1992, Nasirwa, pers. comm.), an alkaline lake approximately 45 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, a shallow lake, evaporated almost completely. Due to the low water level and resulting high alkalinity at Lake Nakuru, fish stocks disappeared, followed by the fish-eating birds (Nasirwa, pers. comm.). The great cormorant population there declined from 3238 in 1992, to 578 in 1993, and to zero in 1994 (Table 6.2).

Table 6.2 Great cormorant population sizes & trends at lakes Nakuru & Naivasha in January, 1992 - 1995; source: Bennun 1992, 1993, Nasirwa & Bennun 1994, 1995, Nasirwa, personal communication; *includes small adjacent lakes Oloidien & Sonachi

	1992	1993	1994	1995
Lake Nakuru	3238	578	0	4
Lake Naivasha*	662	555	861	868

In 1995, great cormorants established a new 875-nest breeding colony on Lake Oloidien in the Lake Naivasha ecosystem. This breeding colony increased to 925 nests in 1996. Without the Lake Nakuru population having been ringed, it can not be said with certainty what portion may have moved to Lake Naivasha. Nevertheless, it seems a reasonable hypothesis that the large increase in great cormorants using Lake Naivasha and the establishment of the new breeding colony were the result of immigration from Lake Nakuru due to the adverse environmental changes there. This does not, however, explain the substantial coincidental decrease in the number of long-tailed cormorants using Lake Naivasha (Table 6.1).

Two non-mutually-exclusive hypotheses concerning the reasons for the observed decline in the long-tailed population were examined:

- There is extensive niche overlap between the two sympatric species, prey and roosting resources are limited, and the larger great cormorant was more successful in competing for these limited resources.

- Substantial 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 resource needs than on that of the great cormorant.

6.2 Methods

Between September 1995 and August 1996, monthly population and resource-use surveys of the two cormorant species were conducted on lakes Naivasha and Oloidien between the 15th and 30th of each month. For these surveys, the littoral zones of the two lakes were divided into 16 sections (13 on Lake Naivasha and three on Lake Oloidien, Figure 6.1), 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 the African Waterfowl Census conducted annually since 1990 (e.g. Nasirwa & Bennun 1995).
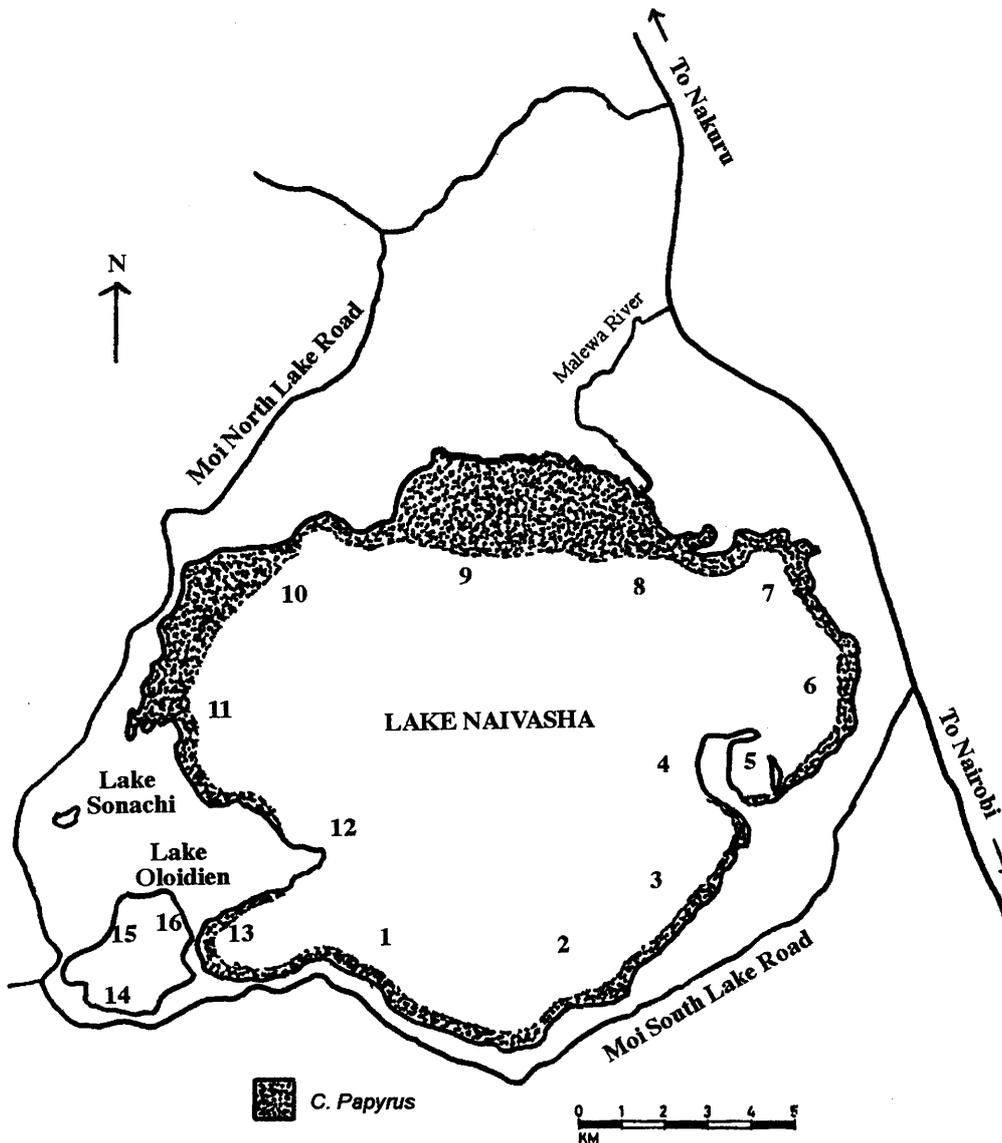
Figure 6.1 Lake Naivasha population survey map; sources: Hartley 1984, Ornithology Dept. National Museums of Kenya; numbers indicate shoreline survey sections

During the surveys, each great and long-tailed cormorant sighted was recorded, along with its activity (foraging, roosting, or flying), foraging location (lake section and estimated distance from shore), and day-roosting habitat (mud shore, floating water hyacinth, sedges, rocks, man-made structures). On Lake Naivasha, the numbers of birds in flocks (foraging, roosting, or flying) were counted with the aid of 10x binoculars and a tally counter, and recorded along with the foraging location or roosting habitat of the flock. The number of individual birds in each flock was counted twice. If the two counts were within five percent of each other, the mean of the two counts was recorded. If the two counts were more than five percent apart, the flock was counted a third time, and the mean of the three counts was recorded. A sample data collection sheet is provided in Appendix II-d.

On Lake Naivasha, each survey consisted of running a transect approximately 100 m off-shore around the entire littoral zone of the lake in an inflatable Avon dinghy. Due to the size of the lake (approximately 130 km^2), the high winds and rough waters which often occurred in the afternoons, and the daily movement patterns of the cormorants, the surveys were conducted almost exclusively in the mornings (from about 7:00 to about 13:00), usually over a period of two days. Six or seven sections were completed during the morning of the first day and the remaining six or seven sections during the morning of the second 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 10x binoculars and a 20-60x telescope from an elevated point of land near the great cormorant breeding colony. In order to maintain time-of-day comparability, the Lake Oloidien surveys were always conducted mid-morning on the day immediately following the Lake Naivasha survey.

In an attempt to define the great cormorant diet, two studies were conducted. First, an analysis was made of recently-regurgitated whole fish collected on the ground under the colony in order to obtain an indication of the size of the fish which were being brought back to the nestlings. Between the age of five and eight weeks (B. Childress, unpub. data), a great cormorant nestling will frequently regurgitate whatever is in its oesophagus when threatened. For a period of approximately eight weeks in both 1995 and 1996, while the main body of nestlings passed through this age category, all recently-regurgitated whole fish were collected from the ground under the colony, measured, and weighed (n = 190). Because the source of these dropped fish is believed to be the nestlings, the summary data technically represent only a sample of the fish the nestlings were fed during the period when they were between five and eight weeks old. On the other hand, because great cormorants are opportunistic feeders, taking whatever is available at any given point in time, and because eight-week-old nestlings are ready to fledge and as large as adults, these data may also represent the diet of adult cormorants during the breeding season at Lake Naivasha.

Additionally, a population diet study based on pellets collected under the colony was conducted in 1996. Cormorant pellets are notoriously inadequate for documenting diet details such as the number and size of fish eaten (Duffy & Laurenson 1983, Johnstone et al. 1990, Zijlstra & van Eerden 1995, Carss 1997). Therefore, since the species variety in Lake Naivasha is limited and well known, the aim of this

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study was to document the relative importance of fish and crayfish in the diet of the population as a whole before, during, and after the breeding period. The purpose was to elucidate an apparent shift in diet observed anecdotally in 1995, from one consisting primarily of fish during the breeding period to one with substantial amounts of crayfish during the post-fledging period.

As the colony trees were aligned in a more or less straight-line transect covering approximately 160 m (Chapter 2), four 64 m^2 study plots were cleared on the ground under the colony trees, one within each 40 m segment of the transect. On Monday evenings, from 15 January to 29 August, these plots were raked clean of debris, and on Tuesday mornings all pellets in each plot were collected, sorted by type (fish only, crayfish only, or a combination), counted, and weighed. Crayfish remains (carapaces and gastroliths) were easily distinguishable from fish remains (gill plates, bones, and otoliths). To ensure that only pellets within the plots were collected each time, the boundaries of the plots were delineated with twine stretched between permanent marker stakes prior to each weekly collection.

6.3 Results

6.3.1 Cormorant population trends

The 1993-95 population shifts continued through 1996. From a low of 555 great cormorants in January 1993, the number of individuals counted using the Lake Naivasha ecosystem (lakes Naivasha, Oloidien & Sonachi) for foraging and roosting during the day increased by 110% to 1167 individuals in January 1997. During the same time period, the number of long-tailed cormorants using the lake declined by 77% from the peak of 1035 individuals counted in January 1993 (Table 6.3).

Table 6.3 Counts of cormorants using Lake Naivasha ecosystem in January, 1993-97; source: Bennun 1993, Nasirwa & Bennun 1994, 1995, Nasirwa personal communication; includes small adjacent lakes Oloidien & Sonachi

	1993	1994	1995	1996	1997
Great cormorant	555	861	868	2403	1167
Long-tailed cormorant	1035	823	374	401	233
Both species	1590	1684	1242	2804	1400

6.3.2 Resource-use comparisons by species

6.3.2.1 Prey species and size

It was not possible to document the diet of the long-tailed cormorant during the study through observation alone (*i.e.* without taking specimens periodically throughout the year and examining stomach contents, which was not attempted). Just 83 individuals were seen foraging during the 12 censuses and rarely were they seen to catch anything. Several attempts to get an indication of their diet by examining pellets cast at their day roosts were also unsuccessful. Thus, for this species, the best prey size description is that obtained in two earlier studies, one in Zambia (Bowmaker 1963) and one in South Africa (Birkhead 1978), both of which utilised stomach content analysis. In these studies, mean bird weight ranged from 505g (Bowmaker 1963; n = 66) to 540g (Birkhead 1978; n = 10) and fish prey size ranged from 2 to 20 cm, with a mean of 7 cm. Prey weight ranged from under 1g to 70-75g.

For the great cormorant, there were two good indications of diet and prey size during the breeding period: a weekly analysis of pellet contents before, during, and after the breeding period in 1996 and an analysis of the "fresh" weights of regurgitated whole fish collected underneath the colony during both 1995 and 1996 (see section 6.3 for a description of the methodology used for these studies and the limitations of the data). Based on these studies, the diet of the great cormorant population at Lake Naivasha varied significantly during the year from a heavy emphasis on fish during the incubation and fledging periods (March-June) to an almost equal emphasis on fish and crayfish later in the year (Figure 6.2). The frequencies of the two types of pellets (pellets containing fish remains only vs. those with some crayfish remains) produced by the colony in March-June were significantly different from the frequencies of the two types of pellets produced during the July-August post-fledging period (χ^2_1 = 229.0, P < 0.01, Chi-square test). Whether this pattern reflected a reliance by

newly-fledged cormorants on the slower crayfish prey or variability in crayfish availability is uncertain.

Table 6.4 contains an analysis of the "fresh" weights of fish presumed to have been regurgitated by five-to-eight-week-old nestlings under threat of attack during the 1995-96 breeding seasons (Section 6.3). Based on these data, approximately 45% of the diet of these nestlings consisted of fish with a "fresh" weight ≤ 75 g. Body shape appears to have had a significant influence on the weight of the fish eaten and regurgitated. The mean "fresh" weight of the bass (131.6 g, n = 73, sd = 63.4 g), was significantly greater than the mean "fresh" weight of the *Tilapia* (65.2 g, n = 117, sd = 39.2 g; W = 9729.5, P < 0.01, Mann Whitney-U). Bass have a more cylindrical shape than *Tilapia,* which presumably makes them easier to swallow even when larger. This relationship is shown graphically in Figure 6.3.
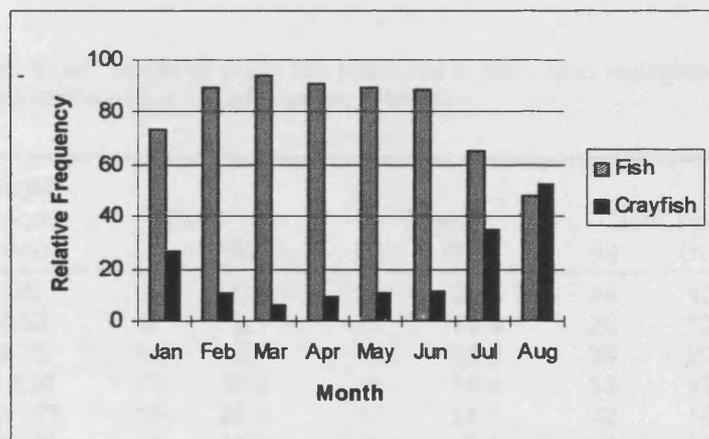
Figure 6.2 Relative frequency of pellets containing remains of fish-only *vs.* those containing some crayfish remains (remains of crayfish-only, or a combination of fish and crayfish, 1996; sample sizes: Jan: 113, Feb: 421, Mar: 422, Apr: 704, May: 565, Jun: 526, Jul: 491, Aug: 228

6.3.2.2 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

(Figure 6.4). Moreover, while only 9.8% of great cormorant foraging recordings were < 5 m from the lake edge, a substantially greater percentage (44.6%) of long-tailed cormorant foraging recordings were < 5 m from the edge of the lake.
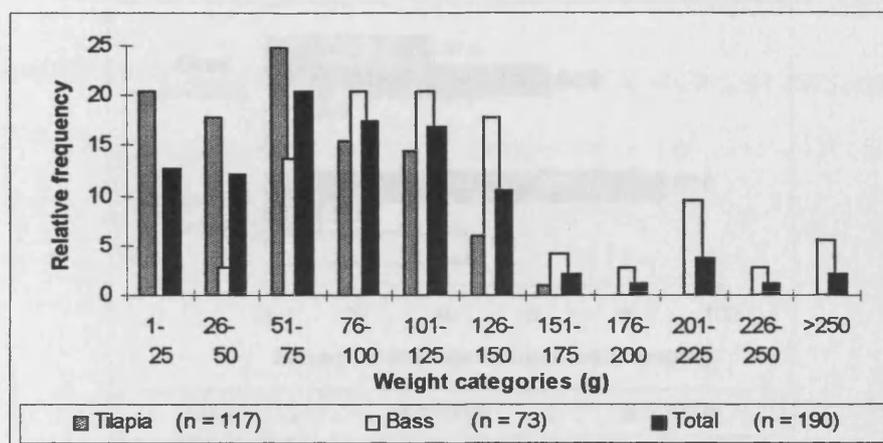
Figure 6.3 Proportion of 5- to 8-week-old great cormorant nestling diet represented by fish weight category; tilapia (combined species) and American large-mouthed bass, 1995-96

Table 6.4 "Fresh" weight of whole fish presumed to have been regurgitated by 5- to 8-week-old cormorants at Lake Naivasha, 1995-96

Weight Category (grams)	Bass		Tilapia		Both Types	
	(n)	(%)	(n)	(%)	(n)	(%)
1-25	0	0.0	24	20.5	24	12.6
26-50	2	2.7	21	17.9	23	12.1
51-75	10	13.7	29	24.8	39	20.5
76-100	15	20.5	18	15.4	33	17.4
101-125	15	20.5	17	14.5	32	16.8
126-150	13	17.8	7	6.0	20	10.5
151-175	3	4.1	1	0.9	4	2.1
176-200	2	2.8	0	0.0	2	1.1
201-225	7	9.6	0	0.0	7	3.7
226-250	2	2.8	0	0.0	2	1.1
>250	4	5.5	0	0.0	4	2.1
Totals	73	100.0	117	100.0	190	100.0

6.3.2.3 Foraging methods

At Lake Naivasha, the great cormorant most often foraged communally in flocks, while the long-tailed cormorant was only observed forag-

ing solitarily. Of the 3023 great cormorants recorded foraging, 84.9% were in flocks (Figure 6.5). The flocks ranged from 9 to 407 birds (n = 28, mean = 91.7, sd = 96.6).
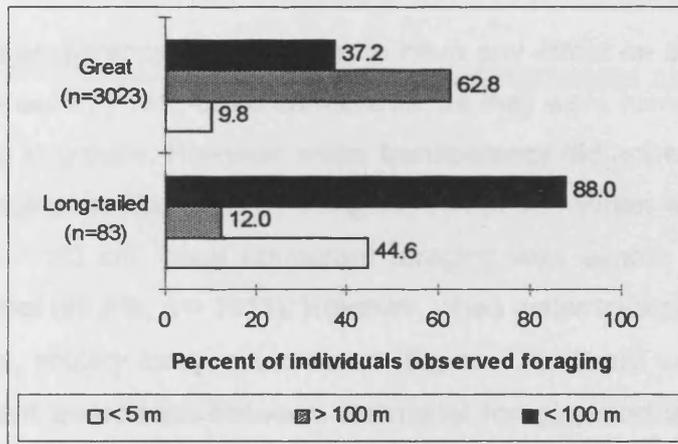
Figure 6.4 Foraging distance from the lake edge by species
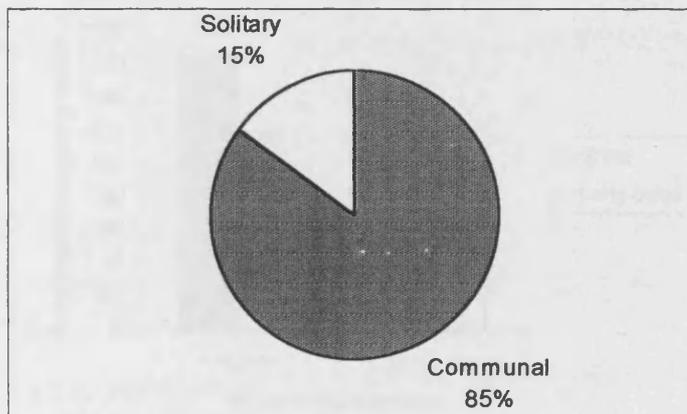
Figure 6.5 Relative frequency of great cormorant foraging by method

6.3.2.4 Effect of water transparency on foraging activity

Water transparency did not seem to have any effect on long-tailed foraging activity. This species appeared to forage just as readily when water transparency   was < 40 cm as when it was ≥ 40 cm, as indicated by the foraging-transparency indices of 100 for both transparency levels in Figure 6.6. On the other hand, the great cormorant was

recorded foraging proportionately much more often in waters where transparency was < 40 cm.

6.3.2.5 Effect of water transparency on foraging method

Water transparency did not seem to have any effect on the foraging method used by long-tailed cormorants, as they were never observed foraging in groups. However, water transparency did appear to affect the foraging method used by the great cormorant. When water visibility was < 40 cm, great cormorant foraging was almost exclusively communal (95.8%, n = 1611). However, when water transparency was ≥ 40 cm, solitary foraging increased (Figure 6.7). There was a highly significant association between communal foraging and water transparency < 40 cm, and between solitary foraging and water transparency ≥ 40 cm (χ^2_1 = 797.7, P < 0.001, Chi-square test).
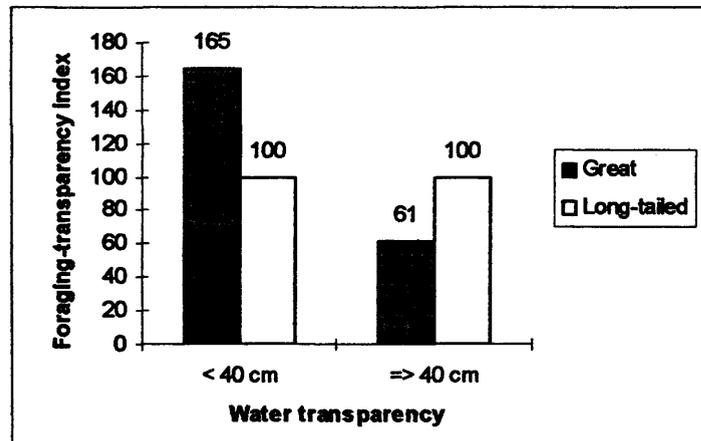
Figure 6.6 Indices of the relative frequency of foraging by each species at each transparency level divided by the relative frequency with which that level occurred in the survey; sample sizes: great cormorant: < 40 cm: 1611, > 40 cm: 984, total: 2595; long-tailed cormorant: < 40 cm: 27, > 40 cm: 45, total: 72; survey transparency levels: < 40 cm: 47, > 40 cm: 78, total: 125

6.3.2.6 Day and night roost locations and habitats

From their night-roosts, both species flew to Lake Naivasha to feed just after dawn (between 06:00 and 06:30, depending on the time of

year). 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 day-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.
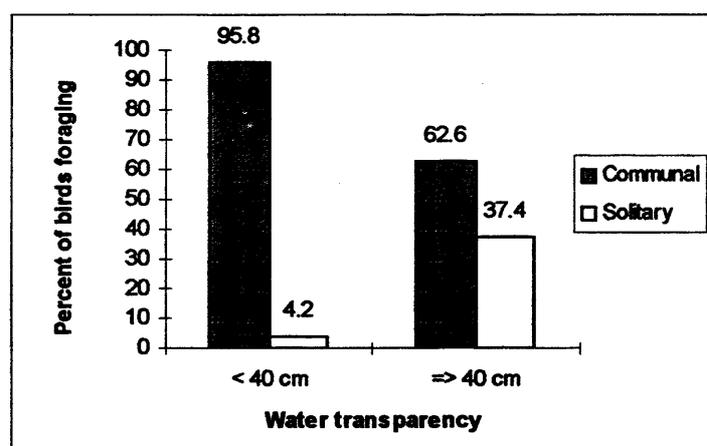
Figure 6.7 Relative frequency of great cormorant foraging by water transparency level, 1995-96; sample sizes: < 40 cm: 1611, > 40 cm: 984

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. (The location of their night roost was not found.) The locations of the day-roosts varied throughout the year depending on the foraging locations currently in use. For six months of the year (October - March), extensive beds of floating water hyacinth plants 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 roosting long-tailed cormorants were found on these centrally-located beds (Table 6.5). During the remaining six months, when these beds are substantially reduced, the majority (61.0%) of roosting long-tailed cormorants were found roosting on the sedges surrounding the lake edge (Table 6.5). The October-March pattern of day-roost habitat occupation was significantly different from the April-September pattern ($\chi^2_6 = 652.0$, P < 0.001).

Table 6.5 Seasonal relative frequency of long-tailed cormorant day-roost habitats

Habitat	Percentage of birds roosting	
	Oct.- March (n = 1930)	April- Sept. (n = 669)
Central hyacinth beds	61.8%	8.2%
Littoral hyacinth beds	10.5	23.9
Sedges	9.9	61.0
Mud/sand shore	0.4	1.2
Rocks	3.6	4.3
Stumps	3.3	1.4
Man-made structures	0.5	0.0

The great cormorants roosted at night in their breeding-colony trees at Lake Oloidien. At dawn, they would leave this night-roost in larger groups (*i.e.* 15 to 30 birds), usually flying to Lake Naivasha. Here, they would fly around the edge of the lake apparently looking for shoals of fish. When a shoal was found, the group which located the shoal would land on the water nearby and begin foraging. It would soon be joined by other groups of great cormorant, 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. After completing their foraging, the great cormorants also began gathering in ones and twos at day-roosts. Like the long-tailed cormorants, the great cormorants roosted in large numbers during the day on beds of floating water hyacinth, either the large central beds north of Crescent Island when they were available (October-March), or the beds around the edge of the lake (April-September).

At all times of the year, the largest number of great cormorants were found roosting during the day on mud/sand shoreline (> 40%, Table 6.6). Between October and March, the central water hyacinth beds north of Crescent Island held on average only 11.0% of the roosting great cormorants, while the mud/sand shore held between 41% and 43% year round (Table 6.6).

Table 6.6 Seasonal relative frequency of great cormorant day-roost habitats; excludes birds in breeding-colony trees

Habitat	Percentage of birds roosting	
	Oct.-March (n = 3743)	April-Sept. (n = 2636)
Central hyacinth beds	11.0%	0.5%
Littoral hyacinth beds	22.0	35.8
Sedges	0.8	0.2
Mud/sand shore	41.5	42.9
Rocks	14.1	14.1
Stumps	6.9	3.9
Man-made structures	3.7	2.6

The differences in roosting habitat distribution between the October-March period and the April-September period (Table 6.6) were highly significant, even after combining the two water hyacinth categories (χ^2_5 = 46.6, P < 0.001, Chi-square test). However, this difference is unlikely to be important biologically. The differences in the relative frequencies are small and are highly significant primarily due to the large sample sizes. During both periods, (Oct-Mar and Apr-Sep) differences between the roosting-habitat distributions of the two species were highly significant (Oct-Mar: χ^2_6 = 2886.5, P = < 0.001; Apr-May: χ^2_6 = 2088.6, P < 0.001; Chi-square tests, Tables 6.7 and 6.8).

Table 6.7 Seasonal relative frequency of day-roost habitat distribution, both species, October-March, 1995-96; excludes birds in breeding-colony trees

Habitat	Percentage of birds roosting	
	great* (n = 3743)	long-tailed (n = 1930)
Central hyacinth beds	11.0%	61.8%
Littoral hyacinth beds	22.0	10.5
Sedges	0.8	19.9
Mud/sand shore	41.5	0.4
Rocks	14.1	3.6
Stumps	6.9	3.3
Man-made structures	3.7	0.5

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Table 6.8 Seasonal relative frequency of day-roost habitat distribution, both species, April-September, 1995-96; excludes birds in breeding-colony trees

Habitat	Percentage of birds roosting great* (n = 2636)	long-tailed (n = 669)
Central hyacinth beds	0.5%	8.2%
Littoral hyacinth beds	35.8	23.9
Sedges	0.2	61.0
Mud/sand shore	42.9	1.2
Rocks	14.1	4.3
Stumps	3.9	1.4
Man-made structures	2.6	0.0

6.3.2.7 Breeding timing and locations

At Lake Naivasha during the two years of the study, the great cormorant typically bred in a single colony from March to August or September, with a peak in April or May. This timing appears to be consistent for the species throughout sub-Saharan Africa (Chapter 3). Although the breeding location of the long-tailed cormorant was not found during the study, its breeding timing appeared to be later in the year: a peak between June and August, based on their low population on the lake at that time and the increase in the number of young in immature plumage observed on the lake during October-December. Generally speaking, the breeding timings of the two species appeared to result in peak prey demand for one species occurring during low prey demand for the other species. For example, during 1995-96 the great cormorant population using the Lake Naivasha ecosystem was at its lowest between November 1995 and April 1996, coinciding with 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 (Figure 6.8). Similarly, in 1996 the great cormorant population peaked with the fledgling of that year's young between May and July, the same period when the long-tailed population on the lake was at its lowest level of the year.
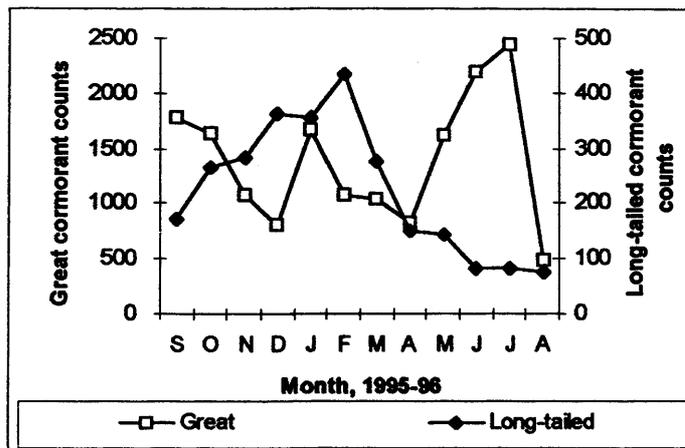
Figure 6.8 Monthly counts of cormorants (both species) using the Lake Naivasha ecosystem, 1995-96; includes small adjacent lakes Oloidien & Sonachi

6.3.3 Environmental changes

6.3.3.1 Lake water level

The long-term lake water level trend at Lake Naivasha is downward (Chapter 2). During the 6-year period from January 1991 to January 1997, the level fell by a further 1.48 metres, from 1887.9 m asl to 1886.3 m asl (Figure 6.9).

6.3.3.2 Lake water transparency

Between 1990 and 1996, water transparency in Lake Naivasha appears to have declined significantly. In 1990, Earthwatch volunteers lead by David Harper took a series of six monthly Secchi disc readings near Hippo Point, the deepest area in the main part of the lake (excluding the small Crescent Island lagoon). As part of the present study, the 1990 measurements were replicated. Based on the two comparable sets of readings, the mean decline in water transparency at this location between 1990 and 1996 was 44% (Table 6.9). There is a significant difference between the two sets of readings (t = 5.63, P < 0.01, paired t-test).
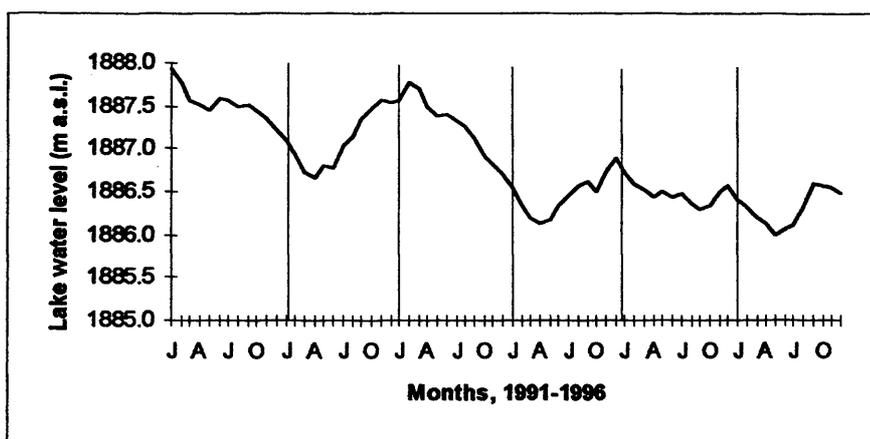
Figure 6.9 Lake water levels and trend, Oct 1991-1997; source: Sulmac Company Limited; months indicated are January, April, July, and October

Water transparency was consistently lowest in the shallowest areas of the lake along the northern and eastern shores (Table 6.10; Chap. 2: Fig. 2.5). In 1995-96, mean water transparency in this part of the lake (32.4 cm.) was significantly lower than the mean water transparency along the southern, western, and central shores (54.2 cm, $t = -3.96$, $P < 0.01$; pooled variance t-test). Furthermore, water transparency along the north shore at the mouth of the Malewa River ranged from 10 to 32 cm. throughout the year, with a mean of only 17.9 cm.

Table 6.9 Comparison of water transparency in centimetres near Hippo Point, Lake Naivasha, 1996 vs. 1990; 1990 data source: D. Harper

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

6.3.3.3 Effect of lower water level and transparency on long-tailed cormorant distribution

Prior to the substantial reduction in water level and transparency along the northern, eastern, and central shores, these areas held a

majority of the roosting and foraging long-tailed cormorants (Table 6.11). The combined effect of these environmental changes seems to have been a significant shift in the relative frequency of long-tailed cormorant occurrence (Table 6.11), away from the northern, eastern, and central sections of the lake shore, toward the southern and western sections (χ^2_2 = 113.3, P < 0.01: Chi-square test).

Table 6.10 Water transparency by lake section, 1995-96; * Section 4: central macrophyte bed; section 5: Crescent Island lagoon

Lake census sections	12-month means (cm)
North & East	
3	45.7
6	35.1
7	27.3
8	31.9
9	22.0
N & E mean	32.4
South & West	
10	43.8
11	54.4
12	59.1
13	58.6
1	62.0
2	50.5
S & W mean	54.7
Central*	
4	37.2
5	68.0
Central mean	52.6
Total Lake mean	45.8

However, this shift in relative abundance by lake shore section did not involve any apparent movement of birds from the northern, eastern and central sections to the southern and western sections. Rather, as the overall long-tailed population declined, the southern and western sections simply lost proportionately fewer birds than the other sections (Table 6.11).

Table 6.11 Long-tailed cormorant distribution by lake section, 1997 vs. 1993; a. Source: Dept. of Ornithology, National Museums of Kenya; b. Macrophyte bed and Crescent Is. lagoon

Lake census sections	Frequency Jan. 1993	Frequency Jan. 1997[a]	Percent Change	Relative frequency Jan 1993	Relative frequency Jan 1997[a]
				(n = 1074)	(n = 179)
North & East					
3	62	25		5.8%	14.0%
6	103	14		9.6	7.8
7	82	17		7.6	9.5
8	207	0		19.3	0.0
9	117	6		10.9	3.4
N & E sub-totals	571	62	-89.1%	53.2	34.7
South & West					
10	25	4		2.3	2.2
11	5	25		0.5	14.0
12	1	0		0.1	0.0
13	1	2		0.1	1.1
1	3	1		0.3	0.5
2	129	64		12.0	35.8
S & W sub-totals	164	96	-41.5%	15.3	53.6
Central[b]					
4	197	21		18.3	11.7
5	142	0		13.2	0.0
Central sub-totals	339	21	-93.8%	31.5	11.7
Total Lake	1074	179	-83.3%	100.0	100.0

6.4 Discussion

Between 1993 and 1995, there was a significant opposite shift in the numbers of great and long-tailed cormorants using Lake Naivasha during the day: the number of great cormorants increased by 56%, the number of long-tailed cormorants declined by 64%. The increase in great cormorant numbers was probably due to immigration from the former Lake Nakuru population as a result of the virtual disappearance of fish from that lake in 1993 and 1994. However, the reasons for the simultaneous decline in the long-tailed population are not clear.

Due to the limited number of suitable prey species in Lake Naivasha, there appeared to be extensive overlap in the diets of the two sympatric species, particularly with fish weighing ≤ 75 g. This overlap might have been expected to result in substantial competition for prey between the two species. However, no evidence was found that such competition occurs. The two species tended to forage in different areas of

Furthermore, their breeding timing appeared to be sufficiently different to lessen competition for prey during periods of maximum demand (immediately after fledging). Their selection of breeding and roosting habitats was also significantly different. Thus, although the two species were assumed to have extensive overlap in their diets, they seemed to be able to tolerate this overlap by virtue of separation on other niche dimensions (foraging locations and methods, and breeding timing).

This separation does not appear to be unique to Lake Naivasha. Previous studies have shown similar separation throughout sub-Saharan Africa, both where the species are sympatric, such as on lakes Victoria and Malawi in East Africa and L. Kariba in southern Africa, and in waters where only one species is present, such as the great cormorant on Lake Abiata in Ethiopia and the long-tailed cormorant on Lake Bangweulu in Zambia (Mackworth-Praed & Grant 1952, 1970, Ansell 1958, Carr 1958, Estcourt 1958, Mitchell 1958, Uys 1958, Bowen et al. 1962, Farkas 1962, Bowmaker 1963, Benson & Pittman 1958, Benson et al. 1971, Birkhead 1978, Olver & Kuyper 1978, Whitfield & Blaber 1979, Urban 1992, Olver 1984, Linn & Campbell 1992, Wanink 1996).

This is not to suggest that the current apparent separation is not the result of competition in the evolutionary past. Cormorants are thought to have evolved initially in Australasia (van Tets 1976), and these two species may have radiated across sub-Saharan Africa from opposite directions, the great cormorant spreading northward from an initial foothold in southern Africa and the long-tailed cormorant spreading southward from the Ethiopian region (van Tets 1976). It is perhaps not unreasonable to speculate that as the ranges of the two species overlapped, competitive interactions enabled each species eventually to accommodate its life history to the presence of the other. On the other hand, the two species may have evolved their niche differences in Australasia before radiating. In any event, niche overlap and competition for resources does not appear to have been an important factor in the recent decline of the long-tailed cormorant population at Lake Naivasha.

There were substantial declines in lake water level and transparency between 1990 and 1996. Although the long-tailed cormorant's foraging behaviour did not appear to be affected by lower water transparency, lower water levels appeared to have a significant effect on its distribution around the lake. As the water level declined, the long-tailed cormorant virtually disappeared from the northern and eastern sections of the lake shore, as well as from the Crescent Island lagoon. The northern and eastern sections of the lake were presumably abandoned because they had become too

shallow for effective foraging. The reasons for the abandonment of the Crescent Island lagoon would not appear to be related to lower water levels, as this area is the deepest in the entire lake. Nevertheless, the birds did not simply move from the more shallow sections of the lake to the less shallow sections but rather their numbers declined in all sections. Thus, it seems that the environmental degradations were only marginally related to the decline observed in the overall long-tailed population.

An alternative hypothesis which might help explain the decline in the long-tailed population during this period, and which might be the subject of a future study, is that increased disturbance due to fishing activity in the littoral zone of the lake has resulted in fewer long-tailed cormorants being able to forage successfully. During the study period, virtually the entire littoral zone of the lake was occupied on a daily basis by fishermen. In those sections where the water was sufficiently deep, the 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. Setting gill nets close and parallel to this vegetation would appear to effectively block fish movement in and out of the vegetation and thus the ability of the long-tailed cormorants to forage effectively. It also creates the danger of cormorants being caught and drowned in the nets. 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 hippopotami 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.

Whether fishing activity was greater during the study period than previously, when there were more long-tailed cormorants using the lake, is not known. However, as the human population around the lake is estimated to have increased substantially in recent years (Goldson Associates 1993), it seems a reasonable hypothesis that fishing activity has also increased substantially. Furthermore, it seems reasonable to believe that this activity, due to its focus in the littoral region of the lake, has affected the long-tailed cormorant much more than the great cormorant.

Chapter 7 General Discussion

This thesis has examined issues relating to breeding season timing and control, and seasonal declines in reproductive success among piscivores nesting colonially on inland waters near the equator, where there is little seasonal variation in temperature or photoperiod and where there may be little seasonal variation in fish abundance. Also studied were the effects of sexual character intensity and nest-site characteristics on breeding timing, fecundity, and mate choice, as well as the effects of resource partitioning between two similar piscivores. The study subject was the great cormorant *Phalacrocorax carbo lucidus* breeding at Lake Naivasha, Kenya (0° 46' S).

The principal findings appear to help in understanding the issues addressed, particularly in relation to the great cormorant breeding at Lake Naivasha; they also seem to raise many new questions which might be addressed in future research. A general limitation of the study, which renders many of the conclusions tentative, is the length of the study period. One or two breeding seasons are simply not sufficient to be able to draw conclusions about the effects of environmental or evolutionary factors. This is particularly true in equatorial regions, where environmental factors may be highly irregular from year to year. Another general limitation is that the results are based largely on behavioural observations and have not been confirmed with experimental studies. This chapter discusses of the main findings, places them in context, and suggests future research to explore them in more detail.

7.1 Breeding season timing and its control factors near the equator

At Lake Naivasha, the great cormorant appeared to have a well-defined breeding season, occurring primarily during the second quarter of the year (Chapter 3). No evidence was found of a consistent seasonal increase in prey abundance or availability during this period, and this general breeding timing did not appear to be the result of any other environmental-response adaptation. Taking into account the results of previous studies by others, this subspecies seems to breed during the second quarter of the year throughout sub-Saharan Africa, from 7° N in Ethiopia to 29° S in South Africa. There appears to be no latitudinal effect, irrespective of local rainfall regime, thought by many to be an important proximate

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factor in equatorial regions, and irrespective of differences in photoperiod trend, thought by many to be the primary proximate factor in temperate regions. The exception to the second quarter breeding timing appears to be occasional opportunistic year-round breeding during periods of unusual environmental conditions (usually flooding).

These findings seem to add a new dimension to the widely-held view that near the equator, if there is no significant seasonal pattern in food supply and predation is not an important factor, a species could be expected to breed year-round. For example, in a study of six passerine species in the equatorial region, Dittami (unpub. data) showed that species with a food supply tied to the primary rainy season tended to co-ordinate their breeding with the rains, while those with a year-round food supply tended to breed year-round. Presumably, colonial piscivores could be predicted to behave in the same manner. However, this study showed that during 1995-96, the great cormorant did not breed year-round at Lake Naivasha, although there did not appear to be a consistent seasonal pattern of prey abundance.

For colonial species, the most advantageous time for an individual to breed is when the majority of the population is also breeding. Birds which breed colonially are believed to do so to enhance predator defence (Birkhead 1977), foraging location information (Ward & Zahavi 1973), and avoidance of conspecific interference during breeding (Immelmann 1971). When food abundance is seasonal, this factor would seem to provide an overwhelming reason for the population to breed during the period of greatest abundance (e.g. Birkhead & Nettleship 1982). However, when the food supply is not seasonal and predation is not a factor, a strong controlling factor for breeding timing does not seem to exist and year-round breeding could be expected to evolve.

A limitation of this part of the study is that prey abundance was not measured independently. Thus, the proposition that prey abundance does not have a significant and consistent seasonal pattern in Lake Naivasha (Siddiqui 1977, Payne 1986, Dadzie & Aloo 1990) was not tested. Apparently, unlike Lake Naivasha, most inland lakes in sub-Saharan Africa do have seasonal patterns of prey abundance (Payne 1986). Perhaps there is a seasonal increase in fish abundance during the second quarter of the year generally throughout much of the sub-Saharan region (e.g. Lake Malawi, McKaye & Stauffer, Jr. 1988), and perhaps such a general pattern of prey abundance controls the breeding timing

of great cormorants throughout the region, including at Lake Naivasha. It does not seem unreasonable to hypothesise that the breeding timing of great cormorants at Lake Naivasha may be controlled by environmental events which are general to the region around the lake, even though they do not occur at Lake Naivasha. Great cormorants are strong fliers and are known to fly long distances each day to feed. Indeed, during this study, large numbers appeared to spend the daytime hours outside the Lake Naivasha ecosystem.

There was limited evidence that local rainfall may have had a stimulating effect on the development of breeding condition, and therefore perhaps on breeding timing, of the great cormorants at Lake Naivasha. The first heavy rainfall of the main rainy season in 1996 coincided with a highly significant increase in the rate of breeding condition development in the population as a whole, as evidenced by a general increase in breeding plumage intensity. Whether this increase in intensity resulted directly from stimulation by rainfall, as it appears, or whether other factors such as social stimulation were also involved, is uncertain. It was reported in 1997 that after several unusually dry months at Lake Naivasha, the great cormorants began to breed in January, one day following a 25 mm. rainfall. That the cormorants should respond to rainfall in the first half of the year and not to the second period of rain later in the year, most likely relates to their endogenous reproductive cycle. However, why they should breed in the rains in Kenya and Ethiopia but during the dry season farther south is unclear.

In the case of the great cormorant breeding at Lake Naivasha, it is suggested that its breeding season timing may be controlled by the combination of a general increase in prey abundance in the surrounding region during the second quarter and the subspecies' nearly 12-month reproductive cycle. It is also suggested that the date of breeding onset each year is controlled by the onset of the major rainy season ("long-rains"), through the acceleration of breeding condition development. To further elucidate these issues, future research might examine the following hypotheses:

- There is a seasonal increase in fish abundance generally during the second quarter in the inland waters of central Kenya. This hypothesis might be explored by determining the seasonal spawning pattern of the main local fish species in a random sample of lakes and dams within 100 km of Lake Nai-

vasha utilising gonosomatic indexing (e.g. Dadzie & Aloo 1990). This research might also be conducted at Lake Naivasha to test the seasonally-constant hypotheses of Payne (1986) and Siddiqui (1977).

- Breeding condition development in inland great cormorants at Lake Naivasha is stimulated by the onset of the seasonal "long rains". This hypothesis could be explored in future years by ranking gular and suborbital skin patch skin colour intensity weekly in the population as a whole, and comparing the trends of the mean ranks with weekly rainfall amounts (e.g. Figure 3.17). These studies, which would replicate the study reported in Chapter 5, would be done during the first half of the year until breeding begins. It should be conducted over several years.

7.2 Effects of breeding timing and nest-site characteristics on reproductive success

In this study, great cormorants breeding near the equator at Lake Naivasha were found to experience a significant decline in reproductive success over the course of the breeding season similar to that experienced by colonially-nesting piscivorous species in temperate regions (Chapter 4). At Lake Naivasha, no evidence was found of a consistent decline in prey abundance during the course of either breeding season studied. Nevertheless, in both years of the study, pairs which bred early in the season hatched significantly larger broods, lost significantly fewer chicks, and fledged significantly more chicks per breeding attempt than pairs which bred toward the end of the season. The primary reason appeared to be the greater age and experience of those pairs breeding early. Predation of eggs or chicks did not appear to be an important factor limiting reproductive success, even for late-breeding pairs. Breeding interference by hungry chicks from earlier broods appeared to be an important factor in reduced reproductive success by late-breeding pairs.

In addition to confirming that reproductive success declines over the course of the breeding season for a colonial piscivore breeding near the equator, these findings also seem to reinforce the 'age and experience' hypothesis often suggested to explain the same phenomenon observed among colonial

piscivores in temperate regions (*e.g.* Potts *et al.* 1980, Nisbet *et al.* 1984, Saether 1990, Weimerskirch 1990, Pärt 1995, De Forest & Gaston 1996).

Limitations of this part of the study include the fact that the sample breeding population was not ringed, so the effects of age could only be surmised from plumage patterns. In addition, due to the nest locations, neither eggs nor chicks less than about four days old could be seen. Thus, losses in the egg stage are not known, and losses of chicks less than four days old may be underreported. These two factors might have affected the conclusions. Prey abundance was not measured directly, so the effect of a possible variation in prey abundance on reproductive success could not be documented. Finally, interference by chicks from earlier breeding attempts was only noted anecdotally, and the extent of their damage to later clutches/broods was not determined because the location of the nests precluded direct observation.

As a result of being able to study a new colony in its first year, it was possible to show that early-breeding pairs preferentially selected canopy-top nest sites and built significantly larger nests than later-breeding pairs. Canopy-top nest locations and larger nests were found to have significant positive effects on brood size and number of chicks fledged in the colony's first year, but not in its second year. Reproductive success was significantly better overall in the second year, irrespective of breeding timing or nest-site characteristics. It is suggested that, because the study samples contained many of the same nests in both years and since this species is thought to be highly site-loyal from one year to the next, the probable reason for the overall improvement in reproductive success was also increased age and experience.

In any follow-up research, it would be ideal to be able to work with a ringed population with known ages of individual members. It would also be ideal if further research could be conducted with a colony in another location where it is practical to access the nests by climbing into the trees (*e.g.* the colony on Boadzulu Island in Lake Malawi, Campbell 1982). If direct access is not possible, it would be important to be able to see into the nests, either from an observation tower or with the use of a pole mirror. Of particular interest would be documentation of early egg and chick losses, and of interference in the reproductive efforts of later-breeding pairs by already-fledged chicks. It appears that this phenomenon may not be severe during most years but may become so when there is a larger than normal amount of late nesting. A ringed population

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of known age and direct access to the nests would enable testing of the following hypotheses:

- Sexual plumage character development is positively correlated with age in *P. carbo lucidus*. This hypothesis might be tested by ranking the intensity of head filoplume and thigh patch feather development and the intensity of cheek, foreneck, and upper breast plumage colour in a random sample of breeding cormorants at the time of pair formation and comparing the mean ranks of different known age groups. The ranking method could be similar to that used for this study.

- Male age is positively correlated with relative date of breeding in this subspecies. This hypothesis could be tested directly with a ringed population of known age.

- Nests located on the canopy-top are warmer and less infested with nest parasites than nests located below the canopy. This hypothesis might be tested by placing thermometers in nests and inspecting nests for parasites during the breeding period.

7.3 Seasonal sexual character intensity and its effect on breeding timing, fecundity and mate choice: an assessment of the Kirkpatrick *et al.* (1990) model assumptions

Kirkpatrick *et al.* (1990) proposed a model to describe the evolution of monomorphic sexual characters through sexual selection involving mutual mate choice (Chapter 1). A central assumption of the model seemed to be that nutritional condition is the primary determinant of relative breeding timing and fecundity among individual birds, rather than any other factor (*e.g.* age). In their model, Kirkpatrick *et al.* (1990) assumed that individuals with better nutritional condition would breed earlier and be more fecund. They also assumed that individuals with more intensely developed sexual characters would breed earlier and that individuals ready to breed early would select mates on the basis of their sexual characters.

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Great cormorants have monomorphic sexual characters, and there is substantial variation in character intensity at the time of pair formation in the African subspecies (Chapter 5). Consistent with the proposed model, male and female great cormorants with more intensely developed sexual characters at the time of pair formation formed pairs significantly earlier than those with less intensively developed characters. Also consistent with the model, pairs which bred earliest had significantly higher fecundity. Darker plumage on the cheeks, foreneck, and upper breast is a signal which appeared to be expressed significantly more strongly in males than in females. Further, males with the darkest plumage coloration in these areas fledged significantly more chicks than males with lighter plumage coloration. However, the role of the five sexual characters studied in mate choice was not clearly elucidated by this study. Several of the paired correlations between male and female character intensity rankings at the time of pair formation were positive and significant but also weak, apparently indicating little assortative mate selection on the basis of these characters.

One possible limitation of this part of the study, in terms of assessing the assumptions in the model, may be that the study did not measure nutritional condition in breeding individuals; however, it is not clear that this is a critical limitation. Kirkpatrick et al. (1990) did not directly link nutritional condition and seasonal character intensity. Perhaps this was intentional: the intensity of several great cormorant sexual characters (i.e. the plumage characters) are believed to be reflective of age rather than breeding or nutritional condition. Furthermore, age appeared to be an important factor in determining relative breeding timing among individual great cormorants, with older more experienced birds breeding earlier (Chapter 4). Older more experienced individuals are believed to be able to breed earlier, because they are often able to acquire the nutritional resources required for breeding earlier than younger, less experienced individuals (Lack 1966). Thus, the fact that nutritional condition was not measured by this study may not be critical to an assessment of the validity of the model assumptions relative to the relationships between sexual character intensity and both relative breeding timing and fecundity in great cormorants.

Another limitation of the current study is that the design enabled only the most cursory look at the factors involved in mate choice. Thus, while it did not appear from the summary correlations that mate choice involved the sexual characters to an important extent, an understanding of other factors which might

be involved in mate selection in this subspecies (*e.g.* nest site quality, male vigour) did not evolve. In future research of mate selection in this subspecies, an attempt might be made to measure these factors. For example, male wing-waves per minute might be a valid indication of male vigour. Nest-site quality might be ranked objectively, taking into account relative height within the colony and perhaps other characteristics not included in this study.

Although not addressed by this study, the effect of endoparasites on sexual character intensity is also an area which may be relevant when discussing the relationships among character intensity, breeding timing, and fecundity in this subspecies (*e.g.* Hamilton & Zuk 1982). Unfortunately, it would not appear possible to test this effect without taking specimens of breeding individuals with varying character intensities at the time of pair formation and measuring their parasite levels by opening their stomachs. This not only may be ethically questionable, it also precludes the ability to compare endoparasite loads with reproductive success.

7.4 Population shifts between sympatric great and long-tailed cormorants -- the effects of niche overlap or environmental change?

The great cormorant population at Lake Naivasha increased 56% between 1993 and 1995, most likely as the result of immigration from nearby Lake Nakuru (Chapter 6). During the same period, the long-tailed cormorant population declined 74%. This study concluded that neither niche overlap nor environmental change was the likely cause of the observed decline and suggested foraging interference by fishermen as a possible explanation. Long-tailed cormorants appeared to be especially sensitive to human disturbance when foraging and/or roosting during the day at the edge of the lake, and local fishermen create substantial disturbance along the edge of the lake as they beat the water surface to scare fish into their nets. However, there has been heavy fishing pressure on Lake Naivasha for many years and yet the long-tailed cormorant population has declined precipitously only recently. According to Kenya Department of Fisheries personnel, the number of fishermen on the lake ebbs and flows from year-to-year in response to the economic situation in the towns and villages surrounding

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the lake. They also reported that fishing pressure was particularly heavy during the two years of this study. However, whether the situation during the study represented a significant increase relative to previous years is not known, and why fishing disturbance did not seem to have had a strong negative effect on the long-tailed population in previous years is not clear.

Although there appears to be extensive diet overlap between the two species, in terms of prey weighing ≤ 75 g, little competition for prey was found. This paradox results from the finding that the two species foraged largely in different areas of the lake, using different foraging methods, which is consistent with the 'ecological guild' hypothesis (Root 1967) that species which exploit the same class of environmental resources in a similar way will achieve niche separation through limiting specialisations which are largely dictated by morphology. The specialisations will be related to the structural features of the habitat and to behavioural and size characteristics of the prey. The finding of little competition between the two cormorant species at Lake Naivasha is also consistent with the hypothesis that similar sympatric species which exhibit a high degree of overlap on one niche dimension are often able to coexist due to compensating differences on other niche dimensions (Schoener 1974, Brandl & Utschick 1985).

The breeding timing of the two species appeared to limit competition during the times of maximum demand, immediately following each species' main fledging period. No competition for either day or night roosts was observed. A substantial fall in water level (1.5 m) occurred during the period in question, with the result that approximately half of the long-tailed cormorant's preferred foraging habitat was too shallow for foraging. However, there appeared to be sufficient suitable foraging habitat remaining to accommodate the small long-tailed population. A significant decrease in water transparency also occurred during this period, but lower water transparency did not seem to affect the foraging behaviour of the long-tailed cormorant. These findings are consistent with the hypothesis that similar sympatric species which are substantially different in size are not likely to utilise the same resources in ways which result in direct competition (Lack 1971, Ricklefs & Travis 1980, Reynolds & Meslow 1984, Furness & Barrett 1985).

A limitation of this part of the study is that it did not document the suspected interference by fishermen in the foraging and roosting activities of the long-tailed cormorant. This missing element might be the focus of any further

studies of this ecological problem. Ideally, such a study would be conducted by excluding fishermen from certain sections of the lake shore and comparing the resulting long-tailed foraging activity with that in areas where fishermen were allowed. However, this probably would be impractical at Lake Naivasha, as voluntary co-operation could not be expected and there could be no enforcement. Another approach might be to attempt to document long-tailed foraging behaviour and interference by fishermen with randomly scheduled observations of study plots established near sections of shoreline and submerged macrophytes frequently used by long-tailed cormorants for foraging and roosting. In addition to the date and time of the observations and the weather conditions, such surveys might record the number of individual birds roosting and/or foraging, length of foraging sessions, elapsed time of dives, presence/absence of fishing gear and/or fishermen, and any obvious signs of disturbance.

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Appendix I Research equipment list

Equipment	Manufacturer/type
Vehicle	Isuzu Trooper, 1983
Inflatable rubber dinghy	Avon Rover 310, 1995
Outboard engine	Evinrude, 15 hp.
Telescope	Kowa TSN-4, Prominar, Fluorite Lens 20-60 X magnification
Tripod	Bogen #3221
Tripod Head	Bogen # 3047
Window Mount	Bushnell
Binoculars	Leica 10x42 BA
GPS Receiver	Magellan Meridian XL
Rangefinder	Rangematic 1200 (range: 45-1500 m)
Compass	Suunto A1000
Clineometer	Suunto
Spring balances	Pesola 50g, 100g, 300g, 1kg Salter 3kg
Wing rules	Technical Sales, London, Stainless Steel 150 mm & 300 mm
Calliper	Measy 2000, Type 5921
Tally Counter	ENM
Min-Max Thermometer	Zeal
Camera	Canon EOS Elan 35mm
Lenses	Canon 28-80mm, 1:3.5-5.6, AF Canon 80-200 mm 1:2.8 L, AF Canon EF 500 mm 1:4.5 L, AF Canon extender EF 1.4X Canon extender EF 2.0X
Computer	NEC Versa V/75 486 processor

Appendix II-a Sample daily nestling census data sheet

Nest No	29/3	30/3	31/3	1/4	2/4	3/4	4/4	5/4	6/4	7/4	8/4	9/4	10/4	12/4
1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1.1 ∆2	—	—	(2ch?)	—	—	—	⊗(X)	F	F	1	F	F	F	HS
1.3	F	F	F	HS/T	HS	F	(tiny) 2	3	3	3	-	3	-	3
1.4	—	—	—	—	—	—	—	⊗(X HS)	.	—	NS	HS	1	1
1.2 1.5	—	—	—	⊗(HS)	—	1	1	F	1	F	-	HS/T	F	1
1.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.0	—	—	—	—	⊗(HS)	F	(days?) F	F	F	-	-	HS/T	HS	1
3.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.2	—	—	—	—	—	—	—	—	—	—	—	⊗(HS)	HS	HS
3.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
3.4	—	—	—	—	—	—	—	—	—	⊗(X)	—	F	-	2
3.5	—	—	—	—	—	—	—	—	—	—	—	⊗(X)	.	F
4.0	—	—	—	—	—	—	(F)	(tiny) 1	F	-	-	HS	1	2
4.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.0	—	—	—	—	⊗(HS)	—	—	HS	—	—	HS	HS	HS	HS
5.1	—	—	—	—	—	—	—	—	⊗(X)	—	F	1	1	
6.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
6.4	—	—	—	—	—	—	—	(F)	HS	-	F	HS	1	
7.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—

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Appendix II-b Sample population breeding plumage data sheet

Date: 5 Mar 96 Species: _____ Lake Section: Kongeni Game Observer: RBC Recorder: SC

Bird No	CNUB	Lores	Gular Skin	Filo-Plume	Thigh Patch	Bird No	CNUB	Lores	Gular Skin	Filo-Plume	Thigh Patch
1	W	3	4	1	1	26	B	1	2	0	0
2	LB	3	4	0	0	27	LB	3	3	1	1
3	B	1	1	1	1	28	LB	4	4	4	3
4	LB	1	2	0	1	29	DB	3	3	1	0
5	LB	1	1	1	1	30	LB	3	4	1	2
6	LB	2	3	0	1	31	LB	4	4	4	4
7	LB	1	1	0	0	32	B	4	4	1	2
8	B	2	2	1	0	33	LB	1	3	0	0
9	B	3	3	2	2	34	DB	4	4	2	2
10	LB	3	3	1	1	35	DB	2	3	0	1
11	LB	1	2	0	0	36	B	2	4	1	1
12	W	2	4	0	0	37	DB	4	4	1	2
13	W	1	1	0	0	38	LB	3	4	2	2
14	DB	4	4	2	4	39	LB	3	3	0	0
15	DB	3	4	2	2	40	DB	4	4	1	0
16	LB	2	2	0	0	41	B	3	3	1	1
17	W	4	4	3	2	42	B	3	4	1	1
18	DB	3	4	1	2	43	LB	3	3	1	2
19	LB	1	1	0	0	44	B	3	4	2	2
20	LB	3	3	1	3	45	W	1	2	1	1
21	LB	3	3	1	1	46	B	4	4	3	3
22	W	4	4	0	0	47	DB	2	2	1	0
23	W	2	1	1	1	48	DB	3	4	1	1
24	DB	3	4	2	2	49	W	1	1	1	0
25	W	2	1	0	0	50	LB	3	3	4	4

LORES
0 = dull yellow
1 = bright yellow
2 = orange
3 = orange-red
4 = red

GULAR SKIN
0 = dull yellow
1 = bright yellow
2 = light olive
3 = med. olive
4 = dark olive

FILOPLUMES
0 = none
1 = sparse
2 = light
3 = medium
4 = full

THIGH PATCH
0 = none
1 = sparse
2 = light
3 = medium
4 = full

Appendix II-c Sample breeding pair plumage data sheet

Day: _Thursday_ Date: _7/3_   Observer: _RBC_ Recorder: _RBC_

Nest No	Sex	Sex Confirm Date	How	CNUB	Lores	Gular	Filo-Plume	Thigh Patch	Other Description
1.3	♂	29/2	BnBm	B	1	4	0	1	
	♀			B/DB	1.	4	0	1	
47.1	♂			B	3	4	3	3	
	♀			G/DB	2	4	2	1	
11.2	♀			B	3	3	0	1	prev.nest. below 11.1
	♂	7/3	AM	DB	4	V	4	4	
1.1	♂	2/3	BnBm	LB	4	4	1	3	(old nest) buffy temples
	♀			DB(CN)	4	4	1	4	
1.4	♂	5/3	BnBm	DB(Cn)	3	4	1	2	(old nest)
	♀			W	3	4	2	4	
3.4	(♀)			(BB(CN))	4	4	3	(4)	(old nest) dk. temples.
	(♂)			LB	3	3	(2)	3	
4.0	♂	5/3	AM	B	2	3	3	3	(old 4) blk. breast streak
	♀			B	3	4	1	3	blk. "v" onto LB near temple
7.5	♂	5/3	BNBM	B(CN)	4	4	3	3	(new) between 7.2 & 7.4
	♀			DB	4	4	2	4	
11.1	♂	7/3	BnBm	DB(CN)	3	4	3	2	(old 11k)
	♀			(DB)	3	4	2		

LORES	GULAR SKIN	FILOPLUMES	THIGH PATCH
0 = dull yellow	0 = dull yellow	0 = none	0 = none
1 = bright yellow	1 = bright yellow	1 = sparse	1 = sparse
2 = orange	2 = light olive	2 = light	2 = light
3 = orange-red	3 = med. olive	3 = medium	3 = medium
4 = red	4 = dark olive	4 = full	4 = full

Appendix II-d Sample monthly census data sheet

Date: 22 Mar 96 Section: 4   Time Start: 9:15   Time Finish: 10:05

Secchi Disk: Start: 69 cm   Middle: 22 cm   End: 45 cm

WHITE-NECKED CORMORANT	Adult	Imm.	Totals
ROOSTING			
Hyacinth (floating or fixed)	THH III	III	11
Sedges (papyrus/dives)	I	III	4
Rocks			
Stumps	I		I
Mud/Sand/Shore/Bar	I		I
Artif.Structures/Hippos			
FORAGING (distance from fringing vegetation)			
<1 m			
1-5 m			
5-30 m			
30-100 m			
>100 m	II (54)	I	57
FLYING	II		2
			(76)

LONG-TAILED CORMORANT	Adult	Imm.	Totals
ROOSTING	(8) (89) (160)		
Hyacinth (floating or fixed)	THH THH (10)(14)(14) THH THH THH	(7) (2) THH THH IIII	181
Sedges(papyrus/dives)	THH	THH I	11
Rocks			
Stumps			
Mud/Sand/Shore/Bar			
Artif.Structures/Hippos	I	I	2
FORAGING (distance from fringing vegetation)			
<1 m			
5 m			
5-30 m			
30-100 m			
>100 m FLYING	II	I	3

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