STATUS, PRODUCTIVITY, MOVEMENTS AND MORTALITY OF GREAT CORMORANTS *PHALACROCORAX CARBO* BREEDING IN CAITHNESS, SCOTLAND: A STUDY OF A DECLINING POPULATION

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This paper describes the results of a study of the Great Cormorant Phalacrocorax carbo *breeding in Caithness, Scotland, with particular emphasis on its recent status and distribution based on annual surveys carried out between 1992 and 1998, its breeding productivity, diet, mortality and movements. Breeding numbers declined from 842 apparently occupied nests in 1969, to c. 230 in 1985-93, and 90-180 in 1994-98, an overall reduction of 80-90% in 30 years. Over the same period, the number of colonies declined from 12 to five. Breeding productivity varied between 2.18 and 3.20 chicks per successful nest, which is within the normal range of variation found elsewhere in Britain. Nestling diet consisted mainly of sandeels* Ammodytes *spp., according with earlier studies in Caithness. Ringing recoveries show the main winter quarters to be the coasts of the Moray Firth and the rivers that flow into it; fewer numbers move further south along the east coast of Scotland, mainly to the Firths of Tay and Forth but some birds reach southern England. A secondary route extends down the Great Glen (or possibly across the Central Lowlands) to wintering areas along the west coast of Scotland and north-west England, with a few birds crossing to Northern Ireland. Ringing recoveries also show that adult Cormorants from Caithness suffer rather higher mortality rates than birds elsewhere in Britain. The reasons for the declines in breeding numbers are discussed, the most likely cause being reduced adult survival, possibly caused by excessive shooting, although emigration of some birds to other areas to breed is a potential contributory factor.*

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INTRODUCTION

The western European breeding population of the Great Cormorant *Phalacrocorax carbo* has grown dramatically over the past 30 or so years. The

increases have been greatest in Denmark, Germany and the Netherlands, where growth rates of up to 30% *per annum* have been sustained more or less throughout this period (van Eerden & Gregersen 1995). The position in Britain is more complicated, with increases being apparent in some areas, little net change in others and decreases in yet others (Kirby & Sellers 1997). The main areas exhibiting decline are all in Scotland and include the Western Isles, the Northern Isles and Caithness. The population in Caithness declined by 72% between the first national survey of Britain's seabirds in 1969/70 (Operation Seafarer) and the second in 1985-87 (the Seabird Colony Register), the largest decline in any part of Britain between these dates (Lloyd *et al.* 1991). This paper reports the results of an investigation into the causes of these changes, drawing on surveys of breeding Cormorants and study of their productivity in Caithness between 1992 and 1998, and on information on movements and mortality based on ringing recoveries.

METHODS

Complete surveys of all Cormorant breeding colonies in Caithness were undertaken in the seven breeding seasons 1992-98 inclusive; the locations of the colonies are shown in Fig. 1. Counts were made from the shore below the colony at Ord Point (southern section), from the cliff top above the colonies at Ord Point (northern section), Neuk Mhor and Ceann Leathad, and from mainland cliffs at the remainder of the extant colonies, all of which are on stacks 30-50 m offshore. All colonies were counted in late June, when nestlings were mostly well grown, and, if possible, in late May or early June when the nests contained hatching eggs or small young. The Cormorant has a fairly protracted breeding season and although some nests will undoubtedly have failed before the counts were made, others may not have been started. Our counts are likely to be slight underestimates of the actual number of apparently occupied nests (AON), but this will be true of all earlier counts so all counts should be directly comparable. In order to check that no colonies had been overlooked, an aerial survey was undertaken on 25 June 1992. All cliffs from Duncansby Head to the Ord of Caithness, as well as Stroma, Dunnet Head and Holborn Head on the north coast, were checked. The aerial survey also showed that all colonies could be counted accurately from land (i.e. there were no nests on the seaward sides of stacks that could not be seen from land). Historical counts were obtained from the Cormorant Colony Register (Sellers 1997), which draws on the Seabird Colony Register, the results of the Cormorant Breeding Colony Survey (Sellers 1996, 1997) and other published records.

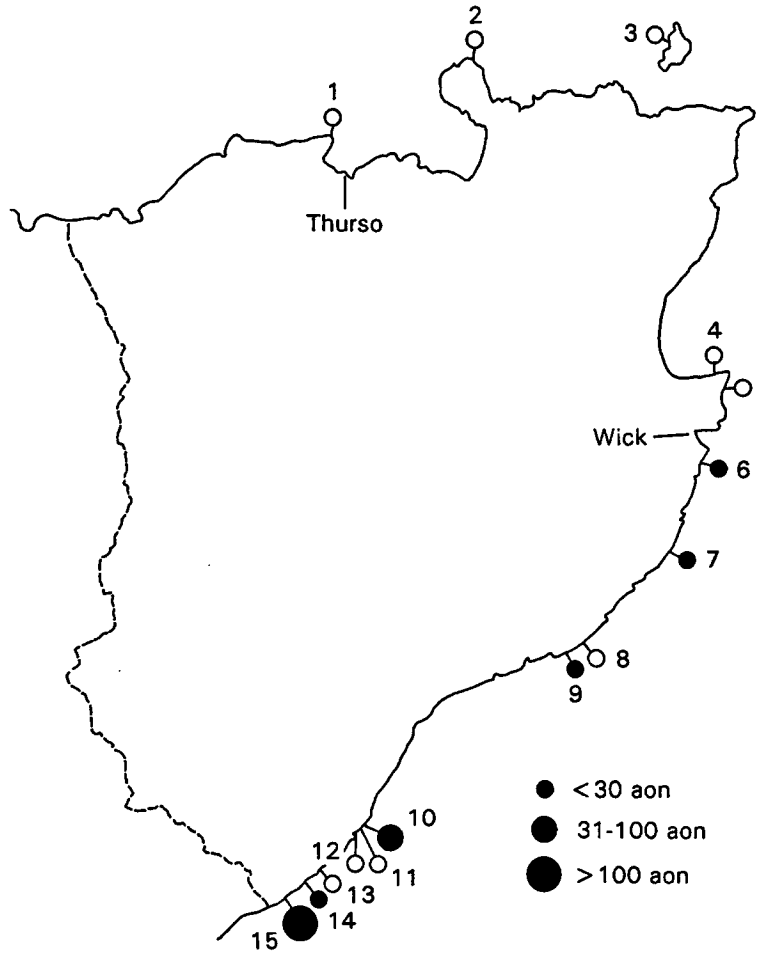

Figure 1. Distribution of Great Cormorant breeding colonies in Caithness: 1 Holborn Head, 2 Dunnet Head, 3 Stroma, 4 Noss Head North, 5 Noss Head East, 6 Stack O'Brough, 7 Stack of Ulbster, 8 Stack of Mid-Clyth, 9 Stacks of Occumster, 10 Ceann Leathad, 11Traigh Bhuidhe, 12 Berriedale Ness, 13 Traigh Muidhe Cleite, 14 Neuk Mhor, 15 Ord Point. Filled symbols are colonies used in the 1990s; open symbols show sites at which Cormorants have bred in the past.

Information on movements and mortality was derived from ringing recoveries of birds marked as nestlings at the Ceann Leathad and Ord Point colonies at which ringing has been carried out regularly for the past 15 years, and intermittently before that. A list of ringing recoveries from these two colonies was obtained from the British Trust for Ornithology and updated from our records, yielding a total sample of 189 recoveries for analysis. In view of the comparatively limited ringing recovery data we estimated survival rates by fairly crude methods. Breeding performance was determined from observations of nest contents at the end of June or in early July, approximately 1-2 weeks before most nestlings fledge. Information on food was derived from chick regurgitates collected during ringing operations at Ceann Leathad and Ord Point in June 1993, each food bolus being classified with respect to principal fish type.

RESULTS

Distribution of colonies The distribution of all 15 sites known to have been used by breeding Cormorants in Caithness is shown in Fig.1. Two of these, Stroma and Stack of Mid-Clyth, appear not to have been used within the past 40 years or so, but the remaining 13 sites have all been used at one time or another since the late 1960s. A total of 12 colonies was found during the first complete survey in 1969, falling to five by the time of the most recent survey in 1998; only three colonies (Stack of Ulbster, Ceann Leathad and Ord Point) were occupied in each of the 11 complete surveys carried out to date. Of the sites no longer in use, breeding seems to have ceased at four in the 1970s (Dunnet Head, the two Noss Head colonies and Berriedale Ness) and at one in the 1980s (Traigh Muidhe Cleite); the situation at two others (Holborn Head and Traigh Bhuidhe) is unclear but neither seems to have been in regular use within the past 30 years. Nearly all the colonies are (or were) located on the east coast, the main concentration being on the cliffs in the south of the county between Ceann Leathad and the county boundary near Ord Point. Seven of the colonies are (or were) on the tops of stacks, and the remainder on broad rocky ledges or rocky promontories on or associated with cliffs.

Breeding numbers A summary of the 11 complete surveys of Cormorants breeding in Caithness is shown in Table 1. Since the first survey in 1969 the number of breeding birds has fallen from about 842 AON to a current figure of 90-180 AON, a decrease of 80-90%. The trends in the counts at individual colonies have mostly been negative (Fig. 2), although the timing of the downturn varies, and at Ceann Leathad increased somewhat in the 1970s to a peak in 1993.

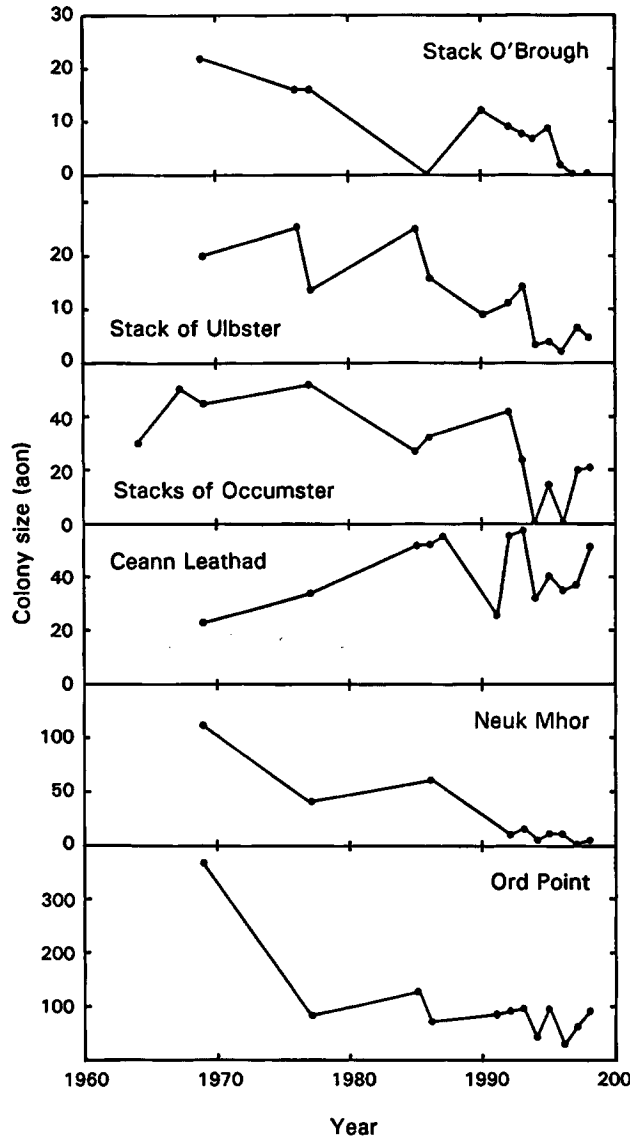

Figure 2. Trends in breeding numbers at selected Caithness Great Cormorant colonies.

Table 1. Summary of censuses of Great Cormorants breeding in Caithness, 1969-98.

Colony	1969	1977	1985	1986	1992	1993	1994	1995	1996	1997	1998
Holborn Head	5	-	1	-	0	0	-	-	-	-	-
Dunnet Head	2	-	-	-	0	-	-	-	-	-	-
Noss Head North	20	0	-	-	0	-	-	-	-	-	-
Noss Head East	31	0	-	-	0	-	-	-	-	-	-
Stack O'Brough	22	16	0	0	9	8	7	9	2	0	0
Stack of Ulbster	20	14	25	16	11	14	3	4	2	7	5
Stacks of Occumster	46	51	28	32	41	23	0	15	0	20	21
Ceann Leathad	22	34	52	52	56	58	32	40	35	37	52
Traigh Bhuidhe	0	0	-	5	0	0	0	0	0	0	0
Berriedale Ness	22[a]	0	0	-	0	0	0	0	0	0	0
Traigh Muidhe Cleite	152-172	46	0	-	0	0	0	0	0	-	-
Neuk Mhor	117-137	42	[b]	62	18	33	8	15	17	0	4
Ord Point	338-388	81	129	65	95	97	42	94	38	58	93
Total	797-887[c]	284	235	232	230	233	92	177	94	122	175
No. Colonies	12	7	6	6	6	6	5	6	5	4	5

[a] colony listed as Berriedale-Traigh Bhuidhe (see text also)
[b] included in total for Ord Point
[c] mean 842 AON; however, Lloyd *et al.* (1991) give the total as 825 AON.
'0' indicates that the colony was checked and no birds were present
'-' indicates that the colony was not checked but it was assumed that no birds were present

Table 2. Breeding productivity estimates (brood size 1, 2, 3, or 4) for Caithness Great Cormorants.

Colony	Year	1	2	3	4	*n*	mean	SE
Ord Point	1993	1	2	10	4	17	3.00	0.19
	1994	2	4	4	0	10	2.20	0.25
	1995	0	1	3	0	4	2.75	0.25
	1998	1	7	10	1	19	2.58	0.16
Neuk Mhor	1993	0	1	7	3	11	3.19	0.18
Ceann Leathad	1993	1	13	17	10	41	2.88	0.28
	1994	1	2	2	0	5	2.20	0.37
	1995	3	13	7	0	23	2.17	0.14
	1996	2	3	9	1	15	2.60	0.21
	1997	3	9	6	1	19	2.26	0.18
	1998	2	17	18	4	41	2.58	0.12
Stacks of Occumster	1993	0	4	5	1	10	2.70	0.21
	1995	1	5	4	1	11	2.45	0.25
Stack of Ulbster	1993	0	1	5	2	8	3.13	0.23
	1994	0	0	3	0	3	3.00	0
Stack O'Brough	1993	0	1	3	1	5	3.00	0.32
	1994	0	4	0	1	5	2.40	0.40
All combined		17	87	113	30	247	2.63	0.05

[a] Based mainly on broods 4-5 weeks of age

Breeding performance Estimates of the numbers of nestlings fledged per active nest were made for all occupied colonies in 1993 and at selected colonies thereafter (Table 2). Brood sizes varied between 1 and 4, with broods of 3 and 2 being the most common. No broods of 5 chicks were recorded. The mean number of chicks per successful pair varied between 2.17 and 3.19, typical of the values found elsewhere in Britain (Sellers & Hughes 1996; Sellers 1997; Newson *et al.* 1997).

No systematic estimates of breeding performance have previously been made in Caithness, but from the data quoted by MacKay (1987) a figure of 2.64 chicks per successful brood (n = 45) can be calculated for the Ceann Leathad colony in 1987, and from brood sizes recorded during ringing at Ord Point from 1962-72, a figure of 2.17 chicks per successful nest (n = 14) can be determined. We have, in addition, consulted a number of ringers and counters who have visited Caithness Cormorant colonies during the past 30 years or so, none of whom recorded unusual numbers of chicks per nest. On the basis of this, albeit anecdotal, evidence we conclude that Caithness Cormorants have shown no substantial change in breeding productivity in the recent past.

Diet During ringing at the Ceann Leathad and Ord Point colonies in June 1993 we collected 24 chick regurgitates. Of these, 22 (92%) contained only sandeels *Ammodytes* spp. and two (8%) flatfish *Pleuronectidae*. Similar results were obtained by MacKay (1987) at Ceann Leathad in 1987 and by Mills (1969) at Ord Point in the 1960s; we conclude that there is no evidence for a recent marked change in the diet of nestling Cormorants in Caithness.

Movements About 40% of recoveries (n = 189) were from within 100 km of the colonies, 70% within 200 km of the colonies, and 85% within 300 km. However, a small number of birds travelled much greater distances (Fig. 3), the longest movement recorded being 1133 km (a bird recovered in Finistère, France). Most recoveries were on the east coast of Scotland especially around the Moray Firth (40% of recoveries) and between Rattray Head and the Scottish Borders (33%; Fig. 4). Around 8% moved further south along the east coast into England but there were only a few recoveries south of the River Humber. A further 16% of birds possibly followed a different route south along the Great Glen to winter quarters along the shores of Argyll and around the Firth of Clyde, with lesser numbers further south along the Solway Firth, north-west England and Northern Ireland (although it is possible that some of these may have taken an alternative route via the Firth of Tay or the Firth of Forth, the Central Lowlands and the Clyde Estuary). In addition, a small number of recoveries (3%) were from north of Caithness - three from Orkney, one from North Rona and one from Foula, Shetland.

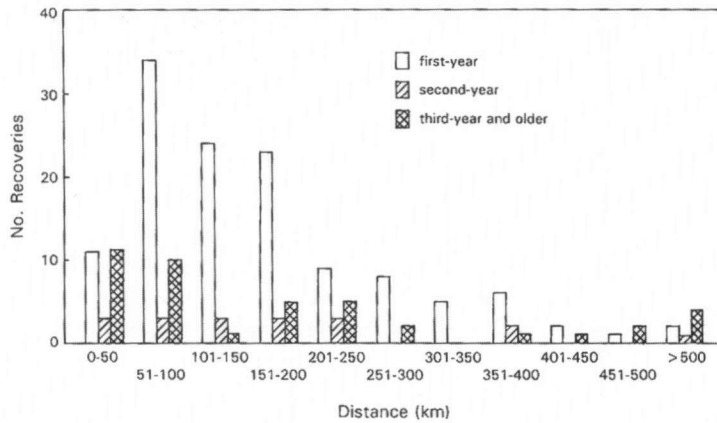

Figure 3. Frequency distribution of distances moved by Great Cormorants ringed in Caithness.

Most birds were recovered from the coast, but about 23% were recovered inland, mostly on rivers rather than still water (Table 3). Slightly more first-year birds were found inland after 1980 than earlier, consistent with the national trend (Kirby *et al.* 1995; Wernham *et al.* 1999), but the differences were not statistically significant ($\chi^2_1 = 0.75$, $P > 0.05$).

There were no obvious differences between age groups in terms of distance moved from the natal colony, but birds may have been recovered closer to breeding colonies in the summer than in the winter (Table 4).

Birds begin to move away from the breeding colonies very shortly after the young fledge and by the time the first ringing recoveries appear approximately 50 days after ringing the majority have departed. It is also worth remarking that there are very few recoveries in Caithness itself and none after mid-September (about 75 days after ringing). A few Cormorants do occur in Caithness in the non-breeding season and from the seven available recoveries it seems that these originate mainly from Orkney (2 recoveries), Shetland (4) and north-west Sutherland (1).

Causes of death and mortality rates The recovery data provide only limited information on the cause of death; most birds were reported simply as 'found dead' (Table 5). The other main categories were shot, oiled and caught in fishing nets. The percentage of recoveries reported as shot decreased from 24% before 1980 to 7% thereafter. These results are similar to those found for birds from the Lamb, Firth of Forth (Summers & Laing 1990).

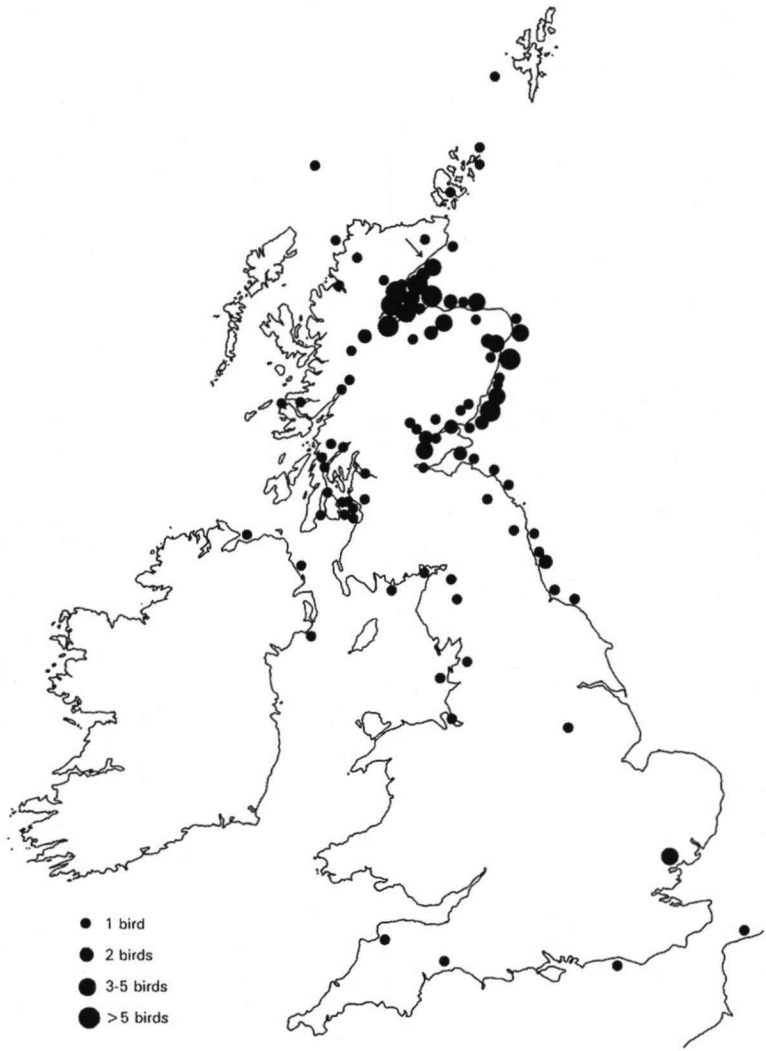

Figure 4. Geographical distribution of ringing recoveries of Great Cormorants ringed in Caithness (not shown, one recovery in Finistère, France). Arrow indicates location of natal colonies.

Table 3. Recovery habitat of Great Cormorants ringed in Caithness.

Age (yr)	No. (%) of recoveries *n*	coast	inland (river)	inland (still water)
1 (ringed before 1980)	38	31 (82%)	5 (13%)	2 (5%)
1 (ringed after 1980)	87	63 (72%)	18 (21%)	6 (7%)
2	21	17 (81%)	3 (14%)	1 (5%)
>3	43	35 (81%)	3 (7%)	5 (12%)
all	189	146 (77%)	29 (15%)	14 (7%)

Table 4. Median distances (km) moved by Caithness Great Cormorants of different ages.

Season of recovery	Median distance moved 1 yr	2 yr	>3 yr
winter (Nov -Feb)	170 (n = 55)	200 (n = 8)	223 (n = 19)
summer (May-Jun)	80 (n = 14)	140 (n = 7)	46 (n = 8)

Table 5. Recovery circumstances of Great Cormorants ringed in Caithness.

Cause of death	Age (yr) 1	2	>3	Total	%
Birds ringed before 1980 (n = 65)					
unknown	22	6	14	42	65
shot	11	4	0	15	23
nets	5	0	0	5	8
oil	0	0	3	3	5
Birds ringed after 1980 (n = 124)					
unknown	66	10	20	96	77
shot	9	1	1	11	9
nets	7	0	0	7	6
oil	1	0	0	1	1
tangled	1	0	1	2	2
hit wires	1	0	0	1	1
field record	2	0	4	6	5

Second-year and older birds were found more or less evenly throughout the year, but first-years were more likely to be recovered in the autumn or winter (September to February inclusive; Fig. 5). Most birds were recovered in their first year of life with much smaller numbers in each year thereafter (Fig. 6). The oldest bird recovered was 11 years old. Survival rates based on recoveries of birds ringed before 1988 (i.e. including all those years for which there are unlikely to be any further recoveries) were rather crudely estimated as 0.39 per annum for first-year birds, 0.68 p.a. for second-years and 0.64 p.a. for third-year and older birds.

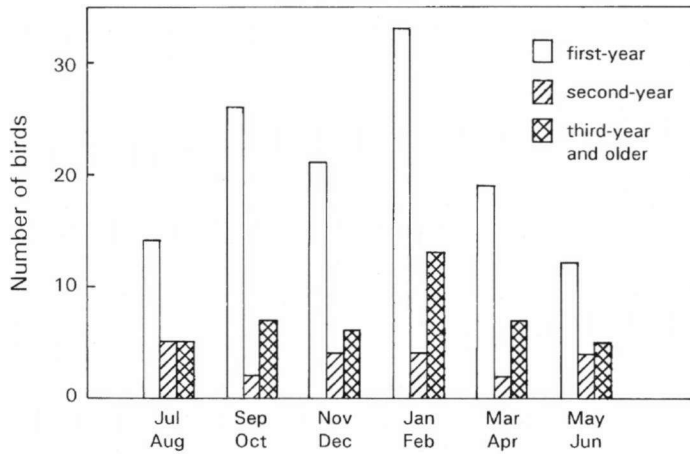

Figure 5. Timing of recovery of Great Cormorants ringed in Caithness in relation to age.

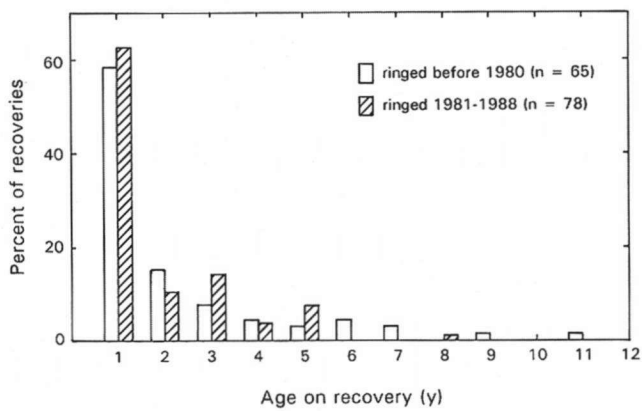

Figure 6. Age on recovery of Great Cormorants ringed as nestlings in Caithness.

DISCUSSION

Status and distribution Cormorant breeding colonies in Caithness are confined primarily to the east coast. There have been occasional records of breeding on the north coast, but they have not bred here regularly in the recent past. In part, this reflects the shortage of breeding sites, but it is more likely to be due to a

shortage also of suitable feeding areas. Cormorants typically are bottom feeders and seek food in water up to about 10 m deep (Debout *et al.* 1995), and there is very little shallow water along the shores of the Pentland Firth. Even on the east coast there is comparatively little shallow water and this probably accounts for the fact that, except for the cluster of colonies south of Ceann Leathad, colonies are mostly small and distributed well apart. The waters off east Caithness are, however, very productive and support some of the largest concentrations of seabirds in Britain (Lloyd *et al.* 1991). There are no suitable breeding areas south of Caithness on the east coast of Sutherland and this is probably why there is a cluster of colonies in the south of the county and why the most southerly one (Ord Point) is the largest, birds here exploiting the shores of the Moray Firth.

Between 1969 and 1998 the number of birds breeding in Caithness decreased by 79% and the number of colonies by 58%. This is the largest decline suffered by any Cormorant population anywhere in Britain over this period and has occurred against a generally increasing population throughout continental Europe. The only other areas showing decreases are Shetland (54% between 1969 and 1995), the Western Isles (33% between 1969 and 1985) and to a lesser extent Orkney (3% between 1969 and 1985, but 31% between 1985 and 1994). It is perhaps significant that the declines are clustered geographically, and likely that some common factor is responsible. The differences in the timing of the declines should be noted, however.

With the exception of the Herring Gull *Larus argentatus* and the Puffin *Fratercula arctica*, other seabirds breeding in Caithness either have not shown such marked declines or have not declined at all. Thus, between the Operation Seafarer survey in 1969/70 and the Seabird Colony Register survey in 1985-87 the following changes were recorded: Fulmar *Fulmarus glacialis* (+25%), Shag *P. aristotelis* (+71%), Herring Gull (-55%), Great Black-backed Gull *L. marinus* (+11%), Kittiwake *Rissa tridactyla* (-15%), Guillemot *Uria aalge* (+158%), Razorbill *Alca torda* (+1%), Black Guillemot *Cepphus grylle* (+161%) and Puffin (-94%). Whatever is causing Cormorant numbers to decrease is not obviously affecting all these other species, and is probably specific to the Cormorant. As many of these species rely on sandeels during the breeding season, it seems reasonable to conclude that the breeding season food supply is not the factor responsible, unless there is some feature of the way in which Cormorants seek their food (say as in-shore or bottom feeders) that renders them more susceptible to changes in sandeel abundance than these other species. However, the available evidence does not suggest that Caithness Cormorants have experienced any significant difficulty in provisioning chicks with sandeels over the past 30 years, or that food has limited breeding success to any significant extent.

Causes of population decline The decline in the Cormorant population in Caithness has occurred progressively over the past three decades, though apparently somewhat faster between 1969 and 1977 (66% in 8 years) than between 1977 and 1998 (38% in 20 years). The decline has thus not been caused by one catastrophic event, but rather is the result of a chronic problem continuing over several decades. Detailed monitoring over the past seven breeding seasons shows that the population has fluctuated quite markedly between years. In particular, 1994 and 1996 seem to have been difficult seasons for the Cormorant, and probably represent responses to cold springs which are known to depress breeding numbers and in the most extreme cases can result in relatively high numbers of birds failing to produce any young (e.g. Debout *et al.* 1995; Sellers & Hughes 1996). By themselves, however, such events are unlikely to account for the changes recorded. Rather, the long-term decline of Cormorants in Caithness appears fundamentally to be a failure of recruitment to the breeding population to match adult mortality. There are five ways in which this might have happened:

a) low breeding productivity;
b) low immature survival;
c) low adult survival;
d) increase in the age of first breeding; and
e) increased emigration.

Breeding success in Caithness has generally been good and the productivity data in Table 2 are within the range of variation seen elsewhere in Britain (1.8 - 3.2) and mostly in the upper half of this range (see Debout *et al.* 1995; Sellers & Hughes 1996; Newson *et al.* 1997). Low breeding productivity may therefore be eliminated as a likely cause of population decline in Caithness.

Our crudely estimated survival rates for first and second-year Caithness birds are quite high but are similar to those found elsewhere in Britain (e.g. Wernham *et al.* 1999). Adult survival, however, is around 20% lower (Sellers 1989), at a rate that is sufficient to account for the population declines observed. Furthermore Wernham *et al.* (1999) suggest that first and second-year Scottish birds may also have lower survival than those in other parts of Britain. The reasons for this are unknown but shooting is an obvious possibility. There is no doubt that Cormorants continue to be subject to a considerable degree of both legal and illegal shooting in Scotland, especially on the salmon rivers of north-east Scotland, one of the wintering areas used by Caithness Cormorants (Kirby *et al.* 1996). In the period 1984-87 an estimated 936-2884 Cormorants, around 20% of the population, were shot in Scotland (Carss 1994) so shooting could well be a cause of excess mortality leading to breeding population decline in Caithness. Shooting probably affects all age groups, and the fact that we have been unable to determine any discernible effect on the mortality rates of

immatures might reflect the fact that these already suffer relatively high mortality from other causes.

Usually, age at first breeding might be deferred in increasing rather than decreasing population (Furness & Monaghan 1987; Newton 1998), so it is unlikely that age of first breeding is increasing in Caithness Cormorants. Although we have no direct information on the age of first breeding in Caithness, third year and older birds are recovered nearer the natal colony in the breeding season than first or second year birds, suggesting that most birds breed around three years of age. However, it should be noted that in a population initially at equilibrium, an increase in the average age of first breeding by one year would cause the population to decline by an amount approximately equivalent to the adult mortality rate. Thus, the declines observed in Caithness could be accounted for by average increases of only a few months in the age of first breeding; such changes would be difficult to detect.

If emigration were the cause of population decline in Caithness over the past 30 years then around 660 pairs must have moved from Caithness to breeding colonies elsewhere in the winter range. In fact there are few such colonies, the chief ones being North Sutor at the mouth of to the Cromarty Firth in Easter Ross and the colonies of the Firth of Forth (Car Craig, Haystack, Inchkeith, Eyebroughty, the Lamb, Craigleith), at the southern end of the main part of the winter range. At all of these colonies there has been a growth in numbers, although at North Sutor there has been a decline in the past few years (Swann 1997). However, the increase at North Sutor (*c.*200 pairs at most) can at best account for only a part of the Caithness declines and the same is true of those in the Firth of Forth colonies (*c.*250 pairs). Furthermore, if substantial numbers of birds had moved to breed at these distant colonies, one would expect there to have been recoveries close by in the breeding season. In fact there have been none in the Firth of Forth nor on the west coast of Scotland, and only three in Easter Ross. What causes birds to shift between colonies is uncertain but generally British Cormorants show high natal site fidelity. Cases are known, however, of birds moving to breed in colonies other than the natal colony, usually to the next nearest colony, but movements up to about 400 km are on record (R.M.Sellers, unpublished results). We note also that movements of this kind could explain both the differences in the timing of the declines at individual colonies in Caithness and the difference in the timing of declines across northern Scotland. However, emigration cannot by itself account for all the declines observed.

In summary, we tentatively suggest the most likely cause of the decline in the Caithness breeding population of the Cormorant is excess adult mortality, perhaps as a consequence of control measures such as shooting in the wintering areas. Emigration to breed in colonies outside Caithness may be a contributory

factor, but cannot solely account for the declines. An explanation based on an increase in the age of first breeding seems unlikely but cannot be eliminated. Breeding productivity is similar to that found elsewhere in Britain and is not a credible causative factor for the declines.

These conclusions account for the observation that it is Cormorants and not other seabirds that are declining and that the declines pertain to Cormorant populations across the north of Scotland and not just Caithness. They also suggest that an obvious action to halt the population declines might be to limit the number of licences granted to control Cormorants in the northern half of Scotland or to restrict licences, say, to the shooting of first-year birds. There is clearly scope for further work on these declining populations. In particular, breeding numbers and other population parameters should be monitored carefully and there needs to be continued and concerted ringing effort in order to monitor mortality and help in the development of a better understanding of the factors that control Cormorant populations. Further research on emigration and the relationship between breeding numbers and food supply would also be merited.

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SAMENVATTING

STATUS, REPRODUCTIE, TREKBEWEGINGEN EN STERFTE VAN AALSCHOLVERS *PHALACROCORAX CARBO* BROEDEND IN CAITHNESS, SCHOTLAND: EEN STUDIE VAN EEN AFNEMENDE POPULATIE

Dit artikel beschrijft de resultaten van een onderzoek naar de Aalscholvers Phalacrocorax carbo *die broeden in Caithness, Schotland, met bijzondere aandacht voor de recente afname van het aantal broedparen en de jaarlijkse veranderingen in de verspreiding in de jaren 1992-98, de jongenproductie, de voedselkeuze, jaarlijkse sterfte en trekbewegingen. De broedpopulatie nam af van 842 'kennelijk bezette nesten' in 1969 tot ongeveer 230 in 1985-93 en 90-180 in 1994-98; een totale afname van 80-90% over een periode van 30 jaren. In dezelfde jaren nam het aantal kolonies af van 12 tot vijf. De productiviteit varieerde van 2.18 tot 3.20 kuikens per succesvol nest, hetgeen als 'normaal' beschouwd mag worden in vergelijking met de resultaten van Aalscholvers die elders op de Britse Eilanden nestelen. De jongen kregen hoofdzakelijk zandspiering* Ammodytes *spp. aangevoerd, hetgeen ook al gebleken was uit eerder onderzoek in Caithness. Ringmeldingen laten zien dat de meeste Aalscholvers uit deze provincie overwinteren langs de kust van de Moray Firth (NO Schotland) en langs de rivieren die daarin uitmonden. Kleinere aantallen overwinterden verder*

zuidelijk langs de Schotse kust, zoals in de Firth of Tay en in de Firth of Forth. Enkele exemplaren bleken naar Zuid-Engeland door te trekken. Een tweede trekroute, klaarblijkelijk van geringere betekenis, bracht Aalscholvers via de Great Glen (of misschien dwars over de centrale laaglanden) naar overwinteringsgebieden langs de westkust van Schotland en naar Noordwest-Engeland, met een enkeling die zo Noord-Ierland bereikte. Ringmeldingen wezen uit dat adulte vogels van Caithness te lijden hadden van een aanmerkelijk hogere sterfte dan vogels van andere kolonies op de Britse Eilanden. De mogelijke oorzaken voor de achteruitgang worden bediscussieerd, met intensieve jacht en bestrijding als meest voor de hand liggende oorzaak van de lage overlevingskansen. De afname kan ook door emigratie veroorzaakt zijn.

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