

REPRODUCTIVE SUCCESS IN THE GREAT CORMORANT *PHALACROCORAX CARBO CARBO* IN RELATION TO COLONY NEST POSITION AND TIMING OF NESTING

BROEDSUCCESS BIJ DE AALSCHOLVER IN RELATIE MET DE POSITIE VAN HET NEST EN HET TIJDSTIP VAN BROEDEN

D.J. ANDREWS¹ & K.R. DAY²

¹*The National Trust, Strangford Lough Wildlife Scheme, Rowallane, Saintfield, BT24 7LH, Northern Ireland, UK;* ²*Environment Research Group, University of Ulster, Coleraine BT52 1SA, Northern Ireland, UK.*

Great Cormorant *Phalacrocorax carbo carbo* breeding success was studied at two colonies on small islands in Strangford Lough, Northern Ireland in 1993 and 1994. Mean clutch sizes were 3.71 on Bird Island and 3.76 on Black Rock in 1993, and 3.4 on Bird Island in 1994. Total productivity on Bird Island in 1993 was calculated as 1.79 young fledged per nesting attempt. Reproductive success was measured on Bird Island in 1993 using data collected from 121 marked nests, and included clutch size, the number of eggs hatched and the number of young fledged. These data were related to the timing of nesting and the position of the nest within the colony. Early nests tended to be located more centrally in the colony than later nests, which were progressively further from the centre. There was a progressive decline in mean values for each reproductive parameter between early and late nesting birds and with increasing distance from the colony centre.

Andrews D.J. & Day K.R. 1999. Reproductive success in the Cormorant *Phalacrocorax carbo carbo* in relation to colony nest position and timing of nesting. *Atlantic Seabirds* 1(3): 107-120.

INTRODUCTION

Great Cormorant *Phalacrocorax carbo carbo* numbers in Ireland have increased significantly during the last thirty years as a result of a reduction in persecution and increases in carrying capacity (Macdonald 1987; Kennedy & Greer 1988; Warke *et al.* 1992). On Strangford Lough, Great Cormorants began breeding in 1980 at a time when numbers at the main colony in Northern Ireland (Sheep Island) had peaked. Since then, the colony, centred on two small islands, grew at a mean annual rate of 17% until 1994 before levelling off at a population of around 200 pairs between 1994 and 1998. The presence of this breeding population is of concern to local fishery managers and a clear understanding of

the processes involved in colony dynamics is therefore important to the conservation management of this species.

Cormorants, like other long lived seabirds, adopt a low risk reproductive strategy (Drent & Daan 1980). Variations in the number of eggs laid and hatched, and prolonged egg laying ensure asymmetric competition within and between broods (Williams & Cooper 1983; Shaw 1985), and together with constraints on fishing efforts by parents (Plateeuw *et al.* 1995) lead to differences in fledging rates among nests.

Many seabird studies have demonstrated that not only are there asymmetries in survival within a family but there is also asymmetry in reproductive performance within a colony. This may be related to the age and experience of nesting birds (Coulson 1968), the quality of the nest site (Potts *et al.* 1980), or the timing of nesting, with earlier arrivals to the colony occupying more central positions (Leger & McNeil 1987; Siegel-Causey & Hunt 1986). On Strangford Lough, the main Great Cormorant colony is on Bird Island, a low lying grassy island with a wide rocky intertidal fringe. Most of the nests are located on the upper shore grouped in a roughly circular pattern, thus providing an ideal opportunity to examine the spatial relationships between nests and their corresponding productivity. This paper describes asymmetries in reproductive performance related to spatial and temporal aspects of breeding.

METHODS

The main study was carried out on Bird Island, Strangford Lough between early March and mid-July 1993, when sixteen visits were made to mark nests and record details of clutch size, numbers of eggs hatched and number of young fledged. As young Great Cormorants tend to leave their nests, particularly when disturbed but also apparently naturally for a time before fledging (Cramp & Simmons 1977), an attempt was made to mark all young birds before they exhibited this behaviour. In practice, this involved ringing the pulli between the age of 10 and 18 days old and resulted in 187 young being ringed (83% of the estimated number of young fledged). This enabled the fate of the young to be determined after they left their nests and before fledging. As the island is also occupied by a Herring Gull *Larus argentatus* colony (31 pairs in 1993), care was taken not to cause opportunistic predation during visits to the colony; survey time was kept to a minimum and retreat was made to an appropriate distance on completion of the survey in order to allow the birds safe return to their nests. No predation was seen to take place during colony visits.

When the last young had left the colony, the positions of 121 nests were recorded using measurements taken from two fixed points. The flattened diameter of 12 nests selected at random was also measured. These data enabled

Table 1. Details of egg laying periods and of distance from colony centre categories.
 Tabel 1. Perioden van eileg en afstandcategorieën naar het centrum van de kolonie.

period	date of first egg laid	category	distance from colony centre (m)
1	≤ 16 April	1	0 - 3.0
2	17 - 21 April	2	3.1 - 4.0
3	22 - 27 April	3	4.1 - 5.0
4	28 April - 4 May	4	5.1 - 6.0
5	≥ 5 May	5	6.1 - 7.0
		6	>7.1 m

a map of the colony to be drawn and the central point of the colony determined (by halving the distances along both the north-south and east-west axes). The distance between each nest and its nearest neighbour was calculated as well as the six nearest neighbours to a random selection of five nests.

The nesting data were analysed in their entirety and mean values calculated for clutch size, number of eggs hatched and number of young fledged per nest. Nests were also separated into groups corresponding to five egg laying periods determined by the appearance of the first eggs in the nest (Table 1). For the purposes of further analysis, nests were also divided into six categories determined by the distance of the nest from the centre of the colony (Table 1). The reproductive parameters detailed above were examined for each data-set and differences in the calculated mean values were statistically tested using one-way analysis of variance.

Mean clutch size was also calculated on Black Rock, the other Strangford Lough colony, in 1993 and also on Bird Island in 1994.

RESULTS

The colony nest map (Fig. 1) illustrates that the Great Cormorant colony on Bird Island in 1993 was roughly circular in shape (diameters approximately 14.5 m east-west and 12.5 m north-south) with the majority of nests constructed on the shore (93%). The mean (\pm SD) diameter of the flattened nests was 0.58 ± 0.03 m, $n = 12$) and the mean distance between nearest neighbour nests (measured edge to edge) was calculated as 0.34 ± 0.24 m, $n = 118$, range zero (nests touching) to 2.12 m). The mean distance between five nests selected at random and their six nearest neighbours was 0.7 ± 0.2 m, $n = 30$, range = 0.42 to 1.13 m. These distances are much closer than those recorded by Debout (1988) at St. Marcouf, Normandy where nearest neighbour distances were around 1 m.

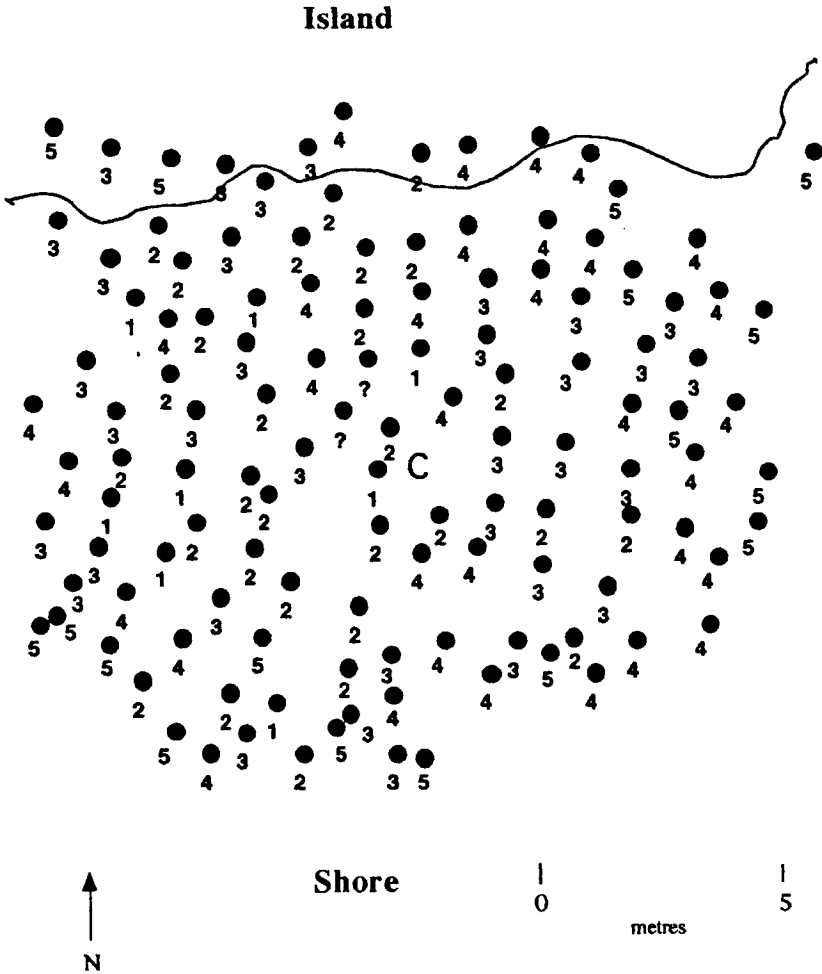


Figure 1. Locations of nests in the Great Cormorant colony on Bird Island, indicating egg laying periods (cf. Table 1). C = the centre of the colony.

Figuur 1. Posities van aalscholvernesten op Bird Island onder vermelding van de periode van eileg (=ie Tabel 1). C= is het midden van de kolonie.

Table 2 shows the mean clutch size for nests on Bird Island in 1993 and 1994 and for Black Rock in 1993. There was little difference in clutch size in 1993 (3.71 on Bird Island and 3.76 on Black Rock) and a small decrease to

Table 2. The total number of nests, mean clutch sizes and relative frequency of number of eggs in completed clutches on Bird Island and Black Rock Great Cormorant colonies in 1993 and 1994. Productivity (number of young fledged per successful nest) of the Bird Island colony in 1993 is also presented.

Tabel 2. Aantal nesten, legselgrootte en frequentie (%) van gecompleteerde nesten met verschillende legselgroottes op Bird Island and Black Rock in 1993 en 1994. Het broedsucces van de kolonie op Bird Island (aantal uitgevlogen jongen per succesvol nest) is eveneens gegeven.

	Bird Island 1993	Bird Island 1994	Black Rock 1993
Total number of nests	126	58	58
Mean (\pm SD) clutch size	3.71 \pm 0.74	3.40 \pm 0.76)	3.76 \pm 0.82)
% with 1 egg	0	1.7	1.7
% with 2 eggs	6.3	8.6	3.4
% with 3 eggs	24.6	41.4	25.9
% with 4 eggs	60.3	41.4	56.9
% with 5 eggs	8.7	6.9	10.3
% with 6 eggs	0	0	1.7
Mean (\pm SD) number of young fledged	2.16 \pm 0.83)	-	-

3.4 on Bird Island in 1994. Three nests with no eggs were recorded on Bird Island in 1993; taking these into account reduces the mean clutch size for all nests to 3.62.

The number of eggs recorded in completed clutches on Bird Island and Black Rock is also shown in Table 2. On Bird Island in 1993, nests with four eggs accounted for 60.3% of clutches and nests containing three or four eggs accounted for 84.9% of clutches. On Bird Island in 1994, nests with four eggs accounted for 41.4% of clutches and nests with three or four eggs accounted for 82.8%. On Black Rock in 1993, nests with four eggs accounted for 56.9% of clutches and nests containing three or four eggs accounted for 82.8% of clutches. Total productivity for the colony in 1993 was estimated at 225 young fledged from 126 nests, a mean of 1.79 young fledged per nesting attempt. In those nests from which young fledged, the mean number fledged was 2.16 \pm 0.83, $n = 92$). This represents a nesting success of 73%, while 27% of birds failed to rear any young.

Egg laying periods The location of nests with respect to each egg laying period is shown in Fig. 1. Period 1 included eight nests; period 2, 30 nests; period 3, 36 nests; period 4, 34 nests; and period 5, 18 nests. The mean distance of nests from the colony centre within each egg laying period is shown in Fig. 2. The pattern that emerges is one with new nests in each successive period being situated further from the colony centre (the mean distance from the centre for

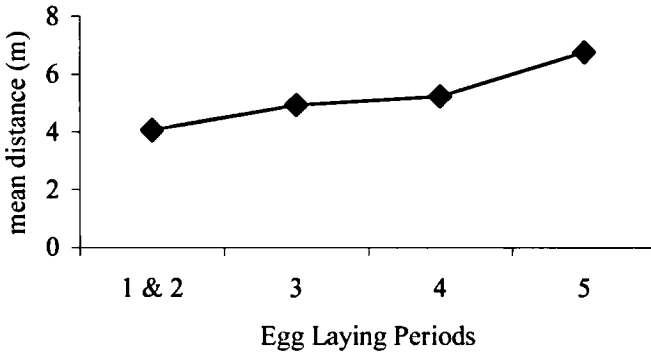


Figure 2. The mean distance from the colony centre for nests in each egg laying period.
 Figuur 2. Gemiddelde afstand tot het koloniemiddelpunt voor elke eilegperiode.

nests in periods 1 and 2 combined is 4.05 m and in period 5 is 6.75 m). This was not an entirely orderly process in concentric circles from the centre out; nests were sometimes built at some distance to others within the same period, the gaps then being available for nests in later egg laying periods.

The mean completed clutch size, mean number of eggs hatched and young fledged for nests in each egg laying period are shown in Fig. 3. With the exception of mean clutch size and mean number of eggs for period 2, there is a clear pattern of progressively smaller mean values between periods 1 and 5 (mean clutch size decreasing from 3.75 to 3.11; mean number of eggs hatched decreasing from 2.67 to 0.89; and the mean number of young fledged per nest decreasing from 2.62 to 0.44). These differences are statistically significant (one-way ANOVA): mean clutch size ($F_{4, 121} = 3.59, P < 0.05$); mean number of eggs hatched ($F_{4, 120} = 8.97, P < 0.01$); and mean number of young fledged ($F_{4, 119} = 9.43, P < 0.01$).

The relationship between egg laying period and nest outcome is further illustrated in Figs 4a and 4b. Fig. 4a shows the marked decrease in eggs hatched as a percentage of eggs laid from 70% in period 1 to 18% in period 5. Again, in Fig. 4b there is a progressive decrease in both young fledged as a percentage of eggs laid (from 70% in period 1 to 14% in period 5), and young fledged as a percentage of eggs hatched (from 100% in period 1 to 50% in period 5).

Distance from colony centre For nests in each of the six distance from colony centre categories, the mean values for completed clutch size, number of eggs

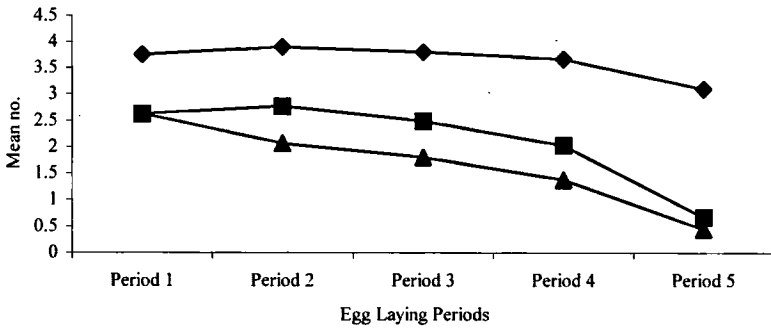


Figure 3. The mean completed clutch size (◆), the mean number of eggs hatched (■) and the mean number of young fledged (▲) for nests in each egg laying period.
 Figuur 3. Gemiddelde, gecompleteerde legselgrootte (◆), gemiddeld aantal uitkomende eieren (■) en gemiddeld aantal uitgevlogen jongen (▲) voor elke eilegperiode.

hatched and number of young fledged are shown in Fig. 5. This shows a progressive decrease in mean values for each reproductive parameter between central nests and those successively further from the colony centre: mean clutch size decreases from 4.1 to 3.4; mean number of eggs hatched from 2.9 to 1.5; and mean number of young fledged decreases from 2.6 to 1.2. These differences are statistically significant (one-way ANOVA) for completed clutch size ($F_{5, 113} = 7.60$, $P < 0.05$) and for the number of young fledged ($F_{5, 115} = 2.50$, $P < 0.01$).

The progressive decline in reproductive success with increasing nest distance from the colony centre is further illustrated in Figs 6a and 6b. The number of eggs hatched as a percentage of eggs laid (Fig. 6a) decreases from 71.8% in the most central category to 37.8% in the outermost, with only the next nearest to the most central category deviating from the trend (73.4%). Both the number of young fledged as a percentage of eggs hatched and the number of young fledged as a percentage of eggs laid show a similar trend (Fig. 6b), decreasing from the central to the outer category from 89.3% to 64.3% and 64.1% to 24.3% respectively; both data-sets indicate that nests in the fourth category (5.1 to 6.0 m from the centre) fare better than predicted.

Fig. 7 shows the locations of the 22 nests that failed at the egg stage, all of which were on the periphery of the colony and presumably more vulnerable to predation. Eggs in most of these nests ($n = 16$, 72.7%) were laid in egg laying periods 4 and 5. Predated Great Cormorant eggs were occasionally found away from the colony, possibly taken by Herring Gulls or Hooded Crows *Corvus corone* [cornix] which were frequently seen in the vicinity of the colony.

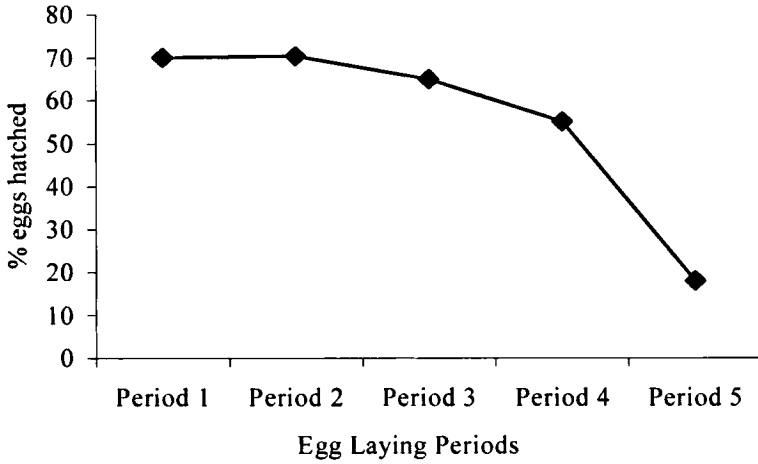


Figure 4a. The proportion of eggs laid that hatched in each egg laying period.
 Figuur 4a. Percentage uitkomende eieren voor elk van de perioden van eileg.

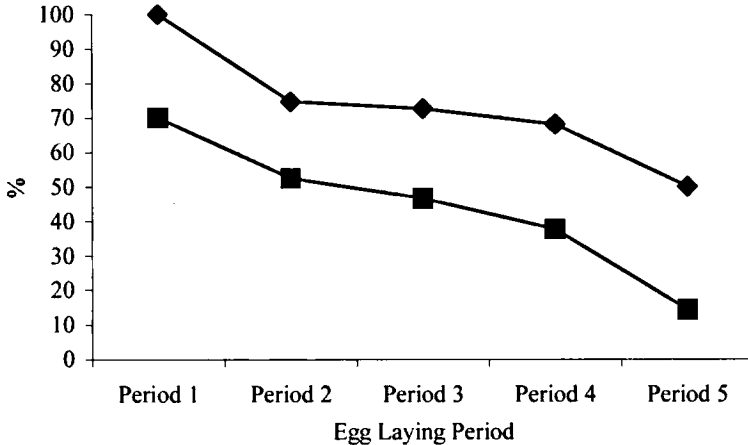


Figure 4b. The proportions of eggs laid (■) and hatched (◆) that fledged young in each egg laying period.
 Figuur 4b. Percentage gelegde eieren (■) en uitkomende eieren (◆) met uitvliegende jongen in elke eilegperiode.

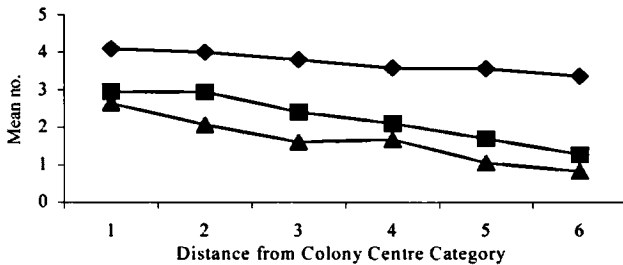


Figure 5. The mean completed clutch size (◆), the mean number of eggs hatched (■) and the mean number of young fledged (▲) for nests in each distance from colony centre categories.

Figuur 5. Gemiddelde legselgrootte (◆), gemiddeld aantal uitkomende eieren (■) en het gemiddeld uitvliegende aantal jongen (▲) voor nesten in elk van de afstandscategorieën naar het midden van de kolonie.

DISCUSSION

The Great Cormorant breeding biology data gathered for this study are similar to those described in other studies. The mean clutch size on Bird Island was 3.71 in 1993 and 3.4 in 1994, and 3.76 on Black Rock in 1993. These values are higher than those recorded for Sheep Island, County Antrim (N. Ireland) where the mean completed clutch size recorded between 1988 and 1993 was 3.13 including nests in which no eggs were laid (Warke 1994). Data collected at two Great Cormorant colonies in England and Wales indicate a range of clutch sizes in these areas between 2.6 and 3.7; at St. Margaret's Island in Wales, mean clutch sizes of 3.1 in 1989, 2.6 in 1990, 2.7 in 1992, and 3.7 in 1996 were reported (Debout *et al.* 1995; Sellers & Hughes 1996), and at Grune Point, England, Carrier & Baker (1991) recorded mean clutch sizes of 3.2 and 3.6 in 1983 and 1984 respectively. In colonies in Norway, Røv (1984) recorded mean clutch sizes of 3.2 and 3.6 in 1983 and 1984 respectively.

Nests containing three or four eggs accounted for 84.9% and 82.8% of clutches on Bird Island in 1993 and 1994 respectively, and 82.8% of clutches on Black Rock in 1993. Warke (1994) found similar clutch sizes in 1991 when 80.5% of nests on Sheep Island contained 3 or 4 eggs, although in both 1992 and 1993 this figure was reduced to 54.8% and 54.6% respectively, with nests containing 2 eggs accounting for proportionately more.

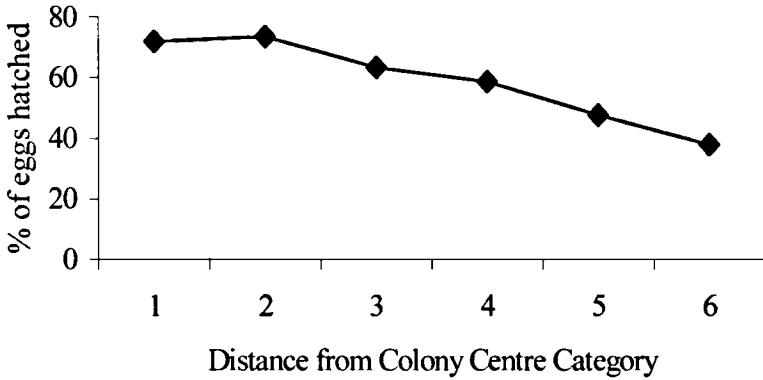


Figure 6a. The proportion of eggs laid that hatched in relation to distance from colony centre.

Figuur 6a. Het percentage uitkomende eieren in relatie tot de afstand tot de kolonie.

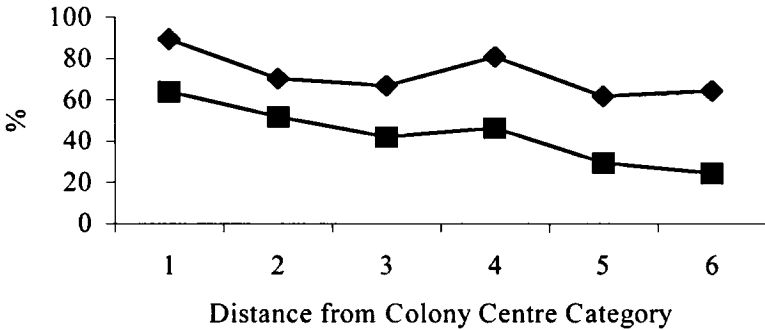


Figure 6b. The proportions of eggs laid (■) and hatched (◆) that fledged young in relation to distance from colony centre.

Figuur 6b. Percentage gelegde eieren (■) en uitkomende eieren (◆) met uitvliegende jongen in relatie tot de afstand naar het midden van de kolonie.

The nesting success of the Bird Island colony of 74% in 1993 was higher than that reported by Sellers & Hughes (1996) for colonies in Wales in 1996 where nesting success was 65% at St. Margaret's Island and 69% at Blockhouse Stack.

The reproductive success of breeding Great Cormorants on Bird Island, Strangford Lough has been shown to be related to the location of the nest within the colony and the timing of breeding. The mean completed clutch size, mean number of eggs hatched and the mean number of young fledged declined progressively from the colony centre to the colony edge and between early and late season. There was also a relationship between the timing of nesting and nest site selection with, in general, earlier nesting birds adopting more central nest sites and later nests being more peripheral within the colony.

Such asymmetry in reproductive success has been explained by a number of factors including the relative age of breeding birds and the effects of predation. Relatively poor breeding performances of young birds have been established in virtually every species studied (Potts *et al.* 1980) including the Great Cormorant (Kortlandt 1942). Other studies have shown that for some species, centre nesting birds are generally older, more experienced birds, whereas young and inexperienced birds are more likely to be found at the edge of the colony (Kharitonov 1971; Veen 1977; Siegel-Causey & Hunt 1986). Peripheral nests may also be subject to greater predation pressure (Leger & McNeil 1987), and may contain fewer eggs or young than central nests (DesGrange & Reed 1981). Lower reproductive effort may be an adaptation whereby young birds gain valuable breeding experience without incurring the higher cost of a large brood which may jeopardise future chances of reproduction (Aebischer & Coulson 1990).

Wooller *et al.* (1989) argue that reproductive success depends on the fitness of the breeding birds and the quality of nest site. Coulson (1968) suggested that the intense pressure for central nests sites in the Kittiwake *Rissa tridactyla* results in very high selection for vigorous males with less severe selection towards the colony edge.

Fretwell & Lucas (1970) proposed a mechanism by which colonial birds could assess and choose optimal breeding sites from among a range of choices. They suggested that as nest density in the optimal nesting habitat increases a density dependent factor such as neighbour conflict or predator awareness results in a decrease in the expected breeding success. At a certain density, reproductive success in the optimal habitat will equal that in an unoccupied but suboptimal habitat. New, incoming birds should then occupy both habitats at an equivalent rate rather than saturate the optimal habitat. This model was tested by Siegel-Causey & Hunt (1986) for a colony of Double-crested Cormorants *P. auritus*. They selected nest sites as predicted, although it

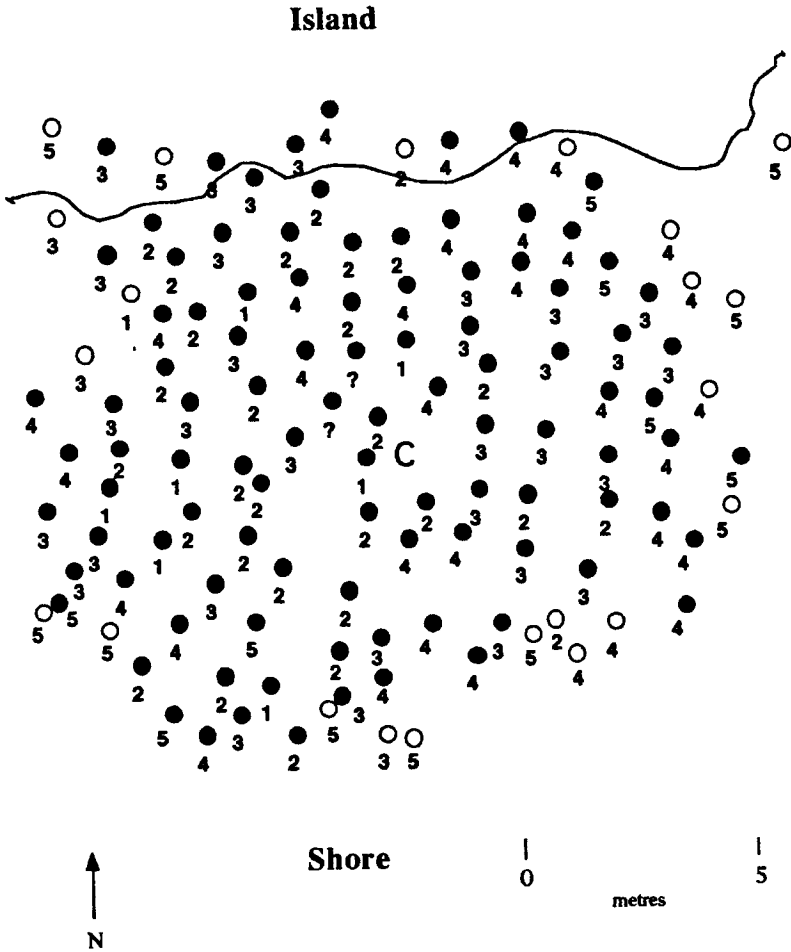


Figure 7. Nest map of the Great Cormorant colony on Bird Island. Circles indicate those nests that failed during the egg stage.

Figuur 7. Nestenkaart van Aalscholvers op Bird Island. Cirkels geven de in de eifase mislukte nesten weer.

was not clear by which mechanism new arrivals were able to assess the suitability of a particular habitat. A similar mechanism may be applicable to the Bird Island data, which show that the colony did not develop from the centre outwards in a progressive manner but that new nests continued to appear in the central (optimal) area up until the fourth egg laying period.

On Bird Island, nests are usually completely washed away during the winter and although the colony is in a similar location each year, it is not known if birds return to occupy the same area on the ground. It is evident, however, that whereas the timing of breeding is in the control of the individual bird, the relative position of the nest in the colony is, to some extent, a matter of chance unless the dynamics of colony formation determine that earlier nesting birds will ultimately also be in the centre of the colony.

Birds that return early to the colony are likely to be experienced males which therefore establish their nest sites first, later arrivals perhaps selecting their nest sites in response to stimuli provided by those nesting birds already present. This may explain why the colony on Bird Island assumes a roughly circular shape. This process is clearly dependent on the topography of the colony location but may also be affected by the proximity of available nest sites to the land or to the sea, as the perceived predator threat from the former and safety provided by the latter are likely to be strong factors in nest site selection; otherwise the entire colony would move landward where it would be at least safe from the effects of high tides.

The relatively high density of nests (compared with Debout 1988) may also be a direct response to a perceived threat from the adjacent Herring Gull colony. It is clear that neither timing of nesting nor position of nest site within the colony were the sole factors determining breeding success. Nor is it clear which is the more powerful influence, but it is likely that both act in combination with a number of environmental factors to result in earlier, more centrally nesting birds being more successful than later, more peripherally nesting birds.

ACKNOWLEDGEMENTS

We wish to thank Robin Sellers and Reami Mathers for their comments on earlier drafts and their encouragement throughout the project. Thanks also to Maarten Platteeuw for his comments.

SAMENVATTING

Het broedsucces van de Aalscholver Phalacrocorax carbo werd onderzocht op twee kleine eilandjes in Strangford Lough, Noord-Ierland, in 1993 en 1994. De gemiddelde legselgrootte was 3.71 op Bird Island en 3.76 op Black Rock in 1993 en 3.4 op Bird Island in 1994. Het broedsucces op Bird Island werd geschat op 1.79 uitgevlogen jongen per broedpoging. Het broedsucces werd bepaald in 121 gemerkte nesten en kon vervolgens worden gerelateerd aan het tijdstip van nestbouw en eileg en aan de positie in de kolonie. 'Vroege' legfels werden vooral in de buurt van het centrum van de kolonie aangetroffen, latere legfels vooral aan de randen. Berekend vanuit het centrum van de kolonie werd een gestage afname in broedsucces gevonden bij een toenemende afstand tot het centrum van de kolonie.

REFERENCES

Aebischer N.J. & Coulson J.C. 1990. Survival of the Kittiwake in relation to sex, breeding experience and position in the colony. *J.Anim.Ecol.* 59:1063-1071.

- Carrier M. & Baker G. 1991. Breeding birds in the Solway. *Birds in Cumbria*, 76-78.
- Coulson J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature (London)* 217: 478-479.
- Cramp S. & Simmons K.E.L. 1977. *The Birds of the Western Palearctic*, 1. Oxford University Press, Oxford.
- Debout G. 1988. La biologie de reproduction du Grand Cormoran en Normandie. *L'oiseau et R.F.O.* 58: 1-17.
- Debout D., Røv N. & Sellers R.M. 1995. Status and population development of Cormorants *Phalacrocorax carbo carbo* breeding on the Atlantic coast of Europe. *Ardea* 83: 47-59.
- DesGranges J.L. & Reed A. 1981. Disturbance and control of selected colonies of Double-crested Cormorants in Quebec. *Colonial Waterbirds* 4: 12-19.
- Drent R.H. & Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.
- Fretwell S.D. & Lucas H.L. Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoret.* 19: 16-36.
- Kennedy G.J.A. & Greer J.E. 1988. Predation by Cormorants *Phalacrocorax carbo* (L.) on the salmonid populations of an Irish river. *Aquaculture and Fisheries Management* 19: 159-170.
- Kharitonov S.P. 1971. The formation of micro-colonies in the Black-headed Gull *Larus ridibundus*. *Zool. Zh.* 50: 540-547.
- Kortlandt A. 1942. Levensloop, samenstelling en structuur der Nederlandsche Aalscholverbevolking. *Ardea* 31: 175-280.
- Leger C. & McNeil R. 1987. Choix de l'emplacement des nids de Cormorans a Aigrettes (*Phalacrocorax auritus*) aux îles de la Madeleine, Quebec. *Can. J. Zool.* 65: 24-34.
- Macdonald R.A. 1987. The breeding population and distribution of the Cormorant in Ireland. *Irish Birds* 3: 405-416.
- Platteeuw M., Koffijberg K. & Dubblelam W. 1995. Growth of Cormorant *Phalacrocorax carbo sinensis* chicks in relation to brood size, age ranking and parental fishing effort. *Ardea* 83: 235-245.
- Potts G.R., Coulson J.C. & Deans I.R. 1980. Population dynamics and breeding success of the Shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *J. Anim. Ecol.* 49: 465-484.
- Røv N. 1984. Clutch size and hatching time in colonies of Cormorant *Phalacrocorax carbo carbo* in Central Norway 1982-1984. *Fauna norv. Ser.C. Cinclus* 7: 124-126
- Sellers R.M. & Hughes B. 1996. Status and breeding success of Cormorants *Phalacrocorax carbo* in Wales in 1996: the effect of the *Sea Empress* oil spill. *Sea Empress Environmental Evaluation Committee Report No. 231*.
- Shaw P. 1985. Brood reduction in the Blue-eyed Shag *Phalacrocorax atriceps*. *Ibis* 127: 476-494.
- Siegel-Causey D. & Hunt G.L. Jr. 1986. Breeding-site selection and colony formation in Double-crested and Pelagic Cormorants. *Auk* 103: 230-234.
- Veen J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern *Sterna s. sandvicensis* Lath. *Behav. Suppl.* 20: 1-193.
- Warke G.M.A. 1994. The ecology and diet of the cormorant *Phalacrocorax carbo* (L.) in Northern Ireland. Unpublished D.Phil. thesis, University of Ulster, 252pp.
- Warke G.M.A., Day K.R., Greer J.E. & Davidson R.D. 1992. Cormorant populations and patterns of abundance at breeding and feeding sites in Northern Ireland, with particular reference to Lough Neagh. *Hydrobiol.* 279/280: 91-100.
- Williams A.J. & Cooper J. 1983. The Crowned Cormorant; breeding biology, diet and offspring reduction strategy. *Ostrich* 54: 213-219.
- Wooler R.D., Bradley J.S., Skira I.J. & Serventy D.L. 1989. Short-tailed Shearwater. In: Newton, I. (ed.) *Lifetime Reproduction in Birds*. pp. 405-417. Academic Press, London.