Breeding performance and timing of breeding of inland and coastal breeding Cormorants *Phalacrocorax carbo* in England and Wales

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Capsule Breeding performance was higher at inland colonies than on the coast due to higher nestling survival during late development.

Aims To compare breeding performance of inland and coastal breeding Cormorants in England and Wales and to provide breeding performance data for Cormorants for future demographic studies.

Methods Breeding performance and timing of breeding was monitored at six inland and four coastal colonies during 1997 and 1998. We compare clutch and brood size and egg and nestling survival.

Results Breeding performance was higher at inland colonies because of higher nestling survival during the later stages of nestling development, from 15–56 days.

Conclusions Greater and earlier food availability at inland colonies, resulting in earlier and more protracted breeding is the most probable explanation for differences in breeding performance. A more protracted breeding season would reduce competition for food and enhance breeding performance, which may be especially apparent during late chick development when energy demands are greatest.

Whilst the coastal breeding population of Cormorants in England and Wales has been relatively stable to declining in some parts of its range, the inland breeding population has increased by 15% per year between 1990 and 2001 (Wernham *et al.* 1999, Mitchell *et al.* 2004). Although a substantial part of this increase has been accredited to immigration from the continent and, to a lesser extent, higher first year survival (Goostrey *et al.* 1997, Winney 1998, Newson 2000), the importance of breeding performance and timing of breeding on the population dynamics of inland and coastal populations is unknown.

For England and Wales, data on breeding performance and timing of breeding of Cormorants are extremely sparse (Wernham *et al.* 1999). Abberton Reservoir, Essex is the only inland tree-nesting colony represented in any detail in the literature (Ekins 1983, 1989, 1997), while recent data for coastal colonies exist from Wales (Sellers & Hughes 1996, Newson *et al.* 1997) and for parts of Scotland and southwest England (Sellers & Hughes 1997, Budworth *et al.* 2000).

Unfortunately, these data are not very suitable for use in population dynamics work because: (1) mean colony brood sizes are calculated using broods at different stages of development and often collected several weeks prior to fledging; (2) complete nesting failures are not taken into account; and (3) corrections are not made to account for loss of young before or after observations are made. The result of this is to overestimate breeding performance (Mayfield 1961, 1975).

We compare breeding performance and timing of breeding between inland and coastal Cormorant colonies in England and Wales and provide data for future demographic studies.

STUDY AREAS AND METHODS

This study was carried out during the breeding seasons of 1997 and 1998 at six inland and four coastal colonies in England and Wales (Fig. 1 & Table 1). The selected inland colonies constituted approximately 85% of the inland tree-nesting population during this period, while coastal colonies represented only a small proportion of the total with little geographical spread.

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Figure 1. Location of inland and coastal Cormorant *Phalacrocorax carbo* study sites in England and Wales.

Monitoring nests

Each colony was visited prior to the expected egg-laying period to assess the timing of breeding in each year. After this, second visits were made to coincide with the earliest pairs being midway through incubation. Further visits were then made at least once every two weeks until the last chicks fledged. On each visit, nest distribution was mapped to identify individual nests, and nest contents were recorded for all nests.

At inland colonies, trees were climbed for nest inspection purposes and where this was not possible, a mirror mounted on the end of a pole was used. Cliff-nesting coastal colonies were monitored from neighbouring viewpoints or by direct access to nests on offshore islands. On entering a colony, the parent bird departs the nest, leaving eggs and chicks open to potential predators and exposure to the elements. At coastal colonies, where egg and small chick predation by gulls may be a problem (Sellers & Hughes 1996), nest contents were covered with grass to provide concealment. To prevent chilling or heat stress, visit times were kept to a minimum, with adults being kept from their nests for a maximum of 30 minutes. Cormorant chicks were aged to the nearest week by their size and feather development where hatch dates were unknown (G.R. Ekins unpubl. data).

Due to an asynchrony in the timing of breeding in many colonies, early nesters could be up to 12 weeks more advanced than late nesters. Thus some nests in a colony had large chicks while others were still at the egg stage. If disturbed, chicks of four weeks old may wander from their nests, potentially forcing premature fledging. To prevent this, where older chicks were present, nest inspections were carried out from a distance using a telescope. If such observations were impossible, data on older broods were not collected to avoid driving young from nests.

Table 1. Breeding site characteristics and colony size of Cormorants *Phalacrocorax carbo* at inland and coastal study sites in England and Wales in 1997 and 1998. Number of nests monitored in brackets. GI, ground-nesting on island; GC, ground-nesting on coastal cliff; TI, tree-nesting on island; TL, tree-nesting on lake shore.

Inland colonies				Coastal colonies			
		Number of AON[a]				Number of AON[a]	
Location	Habitat	1997	1998	Location	Habitat	1997	1998
Haweswater	GI (1997) TI (1998)	41 (33)	48 (39)	St Margaret's Island	GI	187 (57)	200 (112)
Besthorpe Gravel Pits	TI	173 (33)	178 (47)	Green Scar	GI	36 (30)	32 (15)
Rutland Water	TL	27 (15)	51 (31)	Little Ormes Head	GC	371 (85)	320 (100)
Paxton Pits	TI	235 (33)	210 (33)	Thorn Island	GI	34 (23)	42 (38)
Walthamstow Reservoir	TI	235 (39)	222 (91)				
Aldermaston Pits	TI	9 (9)	14 (13)				

[a]AON, apparently occupied nests, i.e. nests apparently in use or only recently abandoned, but excluding nests remaining from previous seasons.

Breeding performance and timing of breeding

Breeding performance was analysed as clutch size and brood size. Clutch size was the maximum number of eggs recorded in each nest; this could not be recorded at the inland colonies at Paxton Pits and Aldermaston Gravel Pits due to logistic difficulties. Brood size was the maximum number of nestlings aged four weeks or over in each nest. The mean chick age per nest was calculated to the nearest week either using known hatch dates or from chick development. Complete nest failures during the egg or chick stage were rare, but when found were included as zero broods. Complete nest failures not observed were accounted for using Mayfield estimates (see below).

Timing of breeding was described in relation to hatch date, estimated to the nearest week from direct observation or by back calculation from chick ages.

Estimating egg and nestling survival

Differences in survival rates were identified between incubation, hatching to 14 days and 15–56 days using a simple graphic display according to Bart & Robson (1982). It was believed that partial brood failures were important, so instead of examining survival or failure at the entire brood level, we adapted the Mayfield method (Mayfield 1961) to use egg and nestling days rather than nest days.[a]

We calculated 95% confidence intervals for Mayfield estimates according to Johnson (1979) and Hensler & Nichols (1981) and presented them in preference to standard errors for visual purposes. Survival rates were only calculated for colonies where samples of greater than 20 nests for each breeding period were available, as estimates based on a smaller sample than this do not provide the 0.05 level of precision required (Hensler & Nichols 1981).

Statistical methods

Repeated measures ANOVAs were performed on hatch date, clutch size and brood size to examine whether there was a difference between colony types or years within colony types. Colonies were considered as independent statistical units to avoid pseudoreplication (Hurlbert 1984). Where significant results were found, these were followed by Tukey's test with Kramer's modification for unequal sample sizes (Day & Quinn 1989) or chi-squared goodness-of-fit tests (Zar 1996). All statistical tests were performed in the Minitab package (Minitab

1991). Means are presented ± se, unless otherwise stated.

Spearman's rank correlations were used to test for the relationship between hatching synchrony (sd of hatch dates) and the onset of hatching (first nest hatched) and to investigate whether there was a linear seasonal trend in either mean clutch or brood size.

Tests of hypotheses comparing Mayfield estimates of egg and nestling survival were conducted using the computer program CONTRAST (Hines & Sauer 1989). This allowed paired and multiple comparisons of Mayfield estimates to be made using chi-squared contrasts (Sauer & Willliams 1989).

RESULTS

Variation in clutch and brood size

Clutch sizes from one to five eggs were recorded during the study at both inland and coastal colonies (Fig. 2). Mean clutch size per colony was not significantly different between inland and coastal colonies ($F_{1,6} = 0.62$, $P = 0.46$) and did not vary significantly between the two years within colony types ($F_{1,6} = 1.48$, $P = 0.27$) (Table 2).

Brood size of nestlings aged four weeks or older similarly ranged from one to five at both inland and coastal colonies (Fig. 3). However, mean brood size was significantly different between inland and coastal colonies ($F_{1,8} = 7.19$, $P = < 0.05$), with inland colonies having a higher mean brood size in both 1997 and 1998 (Table 3). This was a result of inland colonies having significantly more nests with four and three chicks (χ^2 goodness-of-fit test = 52.03, df = 2, $P < 0.001$) than coastal colonies (Fig. 3). No significant difference in
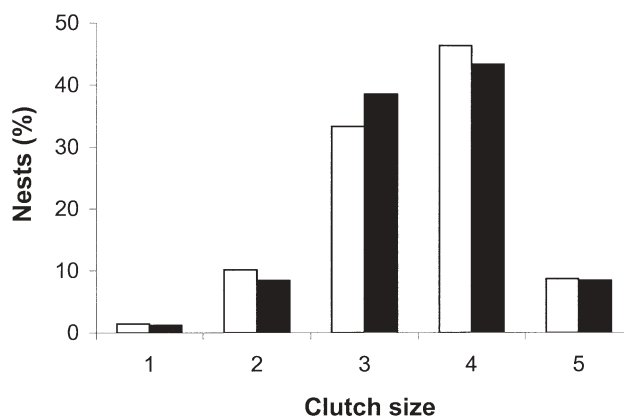
Figure 2. Size frequency distribution of clutch size for inland and coastal breeding Cormorants *Phalacrocorax carbo* in England and Wales for 1997 and 1998 combined. □, Inland colonies (*n* = 138); ■, coastal colonies (*n* = 83).

Table 2. Mean clutch size (± se) of inland and coastal breeding Cormorants *Phalacrocorax carbo* in England and Wales in 1997 and 1998.

	Inland colonies			Coastal colonies	
Location	1997	1998	Location	1997	1998
Walthamstow	3.1 ± 0.2	3.2 ± 0.2	St Margaret's Island	3.8 ± 0.2	3.2 ± 0.1
Rutland Water	3.3 ± 0.2	3.6 ± 0.2	Green Scar	3.6 ± 0.1	3.5 ± 0.3
Haweswater	3.9 ± 0.1	3.7 ± 0.1	Little Ormes Head	2.5 ± 0.3	2.3 ± 0.3
Besthorpe	3.6 ± 0.2	3.6 ± 0.3	Thorn Island	3.6 ± 0.1	3.4 ± 0.2

brood size between years was found within colony types ($F_{1,8} = 1.07$, $P = 0.33$).
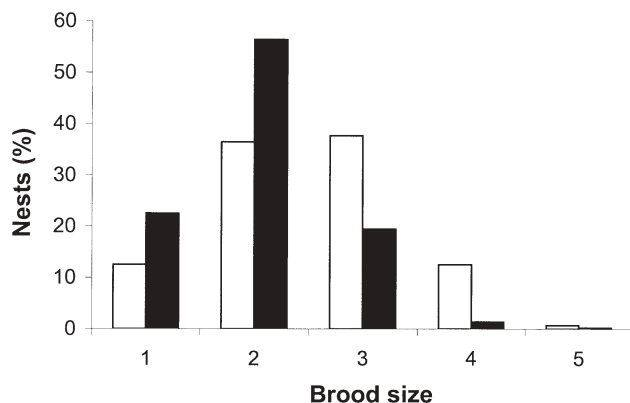
Variation in hatch date

Cormorants showed a considerable variation in hatch date, ranging from mid-February to early July (Fig. 4). Although hatch dates varied widely at both colony types, there was an earlier onset of breeding and consequently earlier mean hatch date at the majority of inland colonies than at coastal colonies ($F_{1,8} = 6.02$, P

Figure 3. Size frequency distribution of brood size of nestlings aged four weeks or older for inland and coastal breeding Cormorants *Phalacrocorax carbo* in England and Wales for 1997 and 1998 combined. □, Inland colonies (*n* = 422); ■, coastal colonies (*n* = 431).

< 0.05) (Fig. 4 & Table 4). To illustrate this point further, in mid-May some 90% of inland nests had hatched compared with only 50% at coastal colonies. In addition, mean hatch date was significantly different between years for inland colonies ($F_{1,8} = 10.27$, $P < 0.05$), due to earlier breeding at the majority of colonies in 1998 than in 1997 (Fig. 4), although no consistent difference was found for coastal colonies (Fig. 4).

Seasonal trends

Brood size decreased with advancing hatch date at inland and coastal colonies, although this was significant at inland colonies in 1998 only (inland colonies: 1997, $r_s = -0.14$, df = 148, $P = 0.09$; 1998, $r_s = -0.28$, df = 235, $P = < 0.001$; coastal colonies: 1997, $r_s = -0.13$, df = 215, $P = 0.06$; 1998, $r_s = 0.002$, df = 214, $P = 0.97$) (Figs 5 & 6). The relationship between clutch size and hatch date for inland and coastal colonies was not examined due to inadequate sample sizes.

Nest initiation was more asynchronous in earlier breeding inland colonies in both 1997 and 1998 ($r_s = 0.94$, df = 5, $P = < 0.01$; $r_s = 0.83$, df = 5, $P = < 0.05$ (Fig. 7), whilst no significant relationship was found for coastal colonies (1997, $r_s = 0.60$, df = 3, ns; 1998, $r_s = 0.60$, df = 3, ns). However, the non-significant finding may be the result of a small sample size.

Table 3. Mean brood size (± se) of inland and coastal breeding Cormorants *Phalacrocorax carbo* in England and Wales in 1997 and 1998.

	Inland colonies			Coastal colonies	
Location	1997	1998	Location	1997	1998
Walthamstow	2.4 ± 0.1	2.8 ± 0.1	St Margaret's Island	2.3 ± 0.1	1.7 ± 0.1
Rutland Water	2.1 ± 0.2	2.4 ± 0.2	Green Scar	2.3 ± 0.1	2.1 ± 0.2
Haweswater	2.8 ± 0.2	2.3 ± 0.1	Little Ormes Head	1.9 ± 0.1	2.0 ± 0.1
Besthorpe	2.4 ± 0.2	2.4 ± 0.1	Thorn Island	2.4 ± 0.2	2.3 ± 0.3
Aldermaston	3.2 ± 0.2	3.0 ± 0.1			
Paxton Pits	2.4 ± 0.1	2.6 ± 0.1			
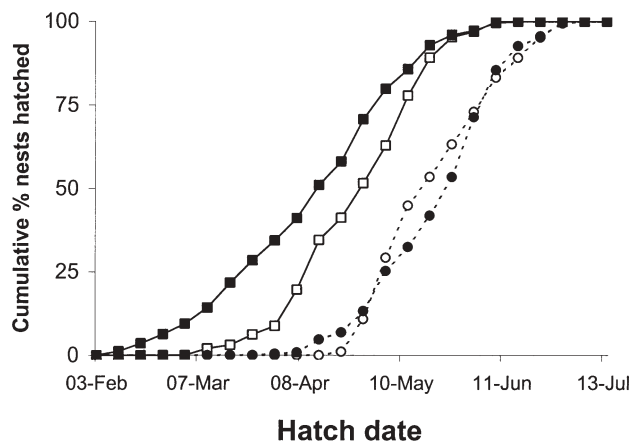
Figure 4. Cumulative percentage of nests hatched against date for inland and coastal breeding Cormorants *Phalacrocorax carbo* in England and Wales. □, inland 1997 (*n* = 198); ■, inland 1998 (*n* = 224); ○, coastal 1997 (*n* = 184); ●, coastal 1998, (*n* = 257).

Egg and nestling survival

No significant difference in survival was observed between inland colonies within years during incubation, hatching to 14 days or 15–56 days so data were pooled across colonies. Similarly for coastal colonies there was no significant difference within years for hatching to 14 days (1997, χ^2 = 2.65, df = 3, *P* = 0.45; 1998, χ^2 = 0.18, df = 3, *P* = 0.98), 15–56 days (1997, χ^2 = 3.43, df = 3, *P* = 0.33; 1998, χ^2 = 2.99, df = 3, *P* = 0.39) or during incubation in 1997 (χ^2 = 3.60, df = 3, *P* = 0.31), although a highly significant difference for incubation in 1998 (χ^2 = 18.42, df = 3, *P* = < 0.001) was observed due to significantly lower survival at Green Scar in 1997 (χ^2 = 19.43, df = 1, *P* = < 0.001). Excluding Green Scar in 1997 during incubation, data were pooled across colonies.

Nest survival, defined as the percentage survival of nest contents for the period through incubation to fledging was 42% and 36% at inland colonies in 1997 and 1998 compared with 27% and 26% at coastal colonies in the two years (Mayfield estimates) (Table 5)

excluding Green Scar in 1997. Daily survival rates were not significantly different for incubation between inland and coastal colonies in either 1997 or 1998 (1997, χ^2 = 0.97, df = 1, *P* = 0.32; 1998, χ^2 = 0.94 , df = 1, *P* = 0.33) or for the period of hatching to 14 days (1997, χ^2 = 0.01, df = 1, *P* = 0.90; 1998, χ^2 = 0.01, df = 1, *P* = 0.89). However, survival in 15–56 day old chicks was significantly higher at inland than coastal colonies in both years of the study (1997, χ^2 = 18.18, df = 1, *P* = < 0.001; 1998, χ^2 = 7.31, df = 1, *P* = < 0.05) (Table 5).

Comparisons within colony types between years showed no significant difference for the incubation period for inland colonies (χ^2 = 1.15, df = 1, *P* = 0.28). However, a significant difference was found for coastal colonies (χ^2 = 7.32, df = 1, *P* < 0.01) due to significantly lower survival during incubation at Green Scar in 1998 (χ^2 = 22.91, df = 1, *P* < 0.0001). No significant difference was observed between years within colony types for either hatching to 14 days (inland, χ^2 = 0.21, df = 1, *P* = 0.64; coastal, χ^2 = 0.03, df = 1, *P* = 0.86) or 15–56 days (inland, χ^2 = 0.14, df = 1, *P* = 0.71; coastal, χ^2 = 0.28, df = 1, *P* = 0.60).

DISCUSSION

This study provides the first detailed breeding performance data for Cormorants in England and Wales for use in future demographic studies. Previous estimates of Cormorant breeding performance in the literature for England and Wales are mainly based on a single colony visit and the mean number of young per successful brood approximated across broods regardless of age (Wernham *et al*. 1999). Because estimates derived from single colony visits are a reflection of brood size for successful nests only, they should not be used in population modelling processes, without correction for unsuccessful nests. Estimates of brood size from a single colony visit will be strongly dependent on the stage of nestling development during which the visit was made,

Table 4. Mean hatch date (± se in days) of Cormorants *Phalacrocorax carbo* at inland and coastal colonies in England and Wales in 1997 and 1998.

| Inland colonies			Coastal colonies		
Location	1997	1998	Location	1997	1998
Walthamstow	27 April ± 2.8	30 March ± 2.4	St. Margarets Is.	15 May ± 1.1	23 May ± 1.6
Rutland Water	26 May ± 2.4	6 May ± 2.1	Green Scar	9 June ± 2.4	19 June ± 2.3
Haweswater	24 May ± 1.6	24 May ± 1.8	Little Ormes Head	6 June ± 1.0	7 June ± 1.8
Besthorpe	25 April ± 2.3	11 April ± 3.8	Thorn Island	6 May ± 1.8	1 May ± 2.1
Aldermaston	20 April ± 5.0	9 April ± 5.4			
Paxton Pits	22 April ± 3.5	12 April ± 3.7			
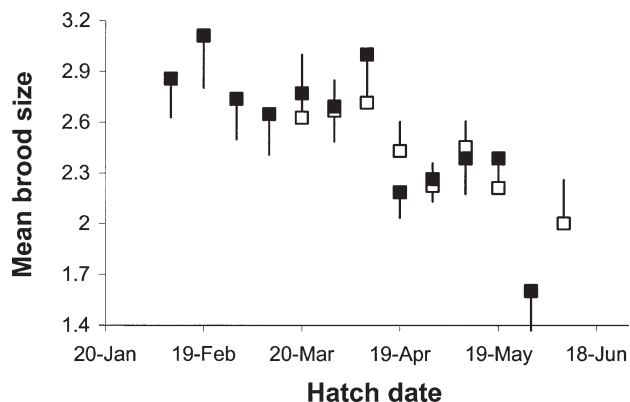
Figure 5. Seasonal decline in mean brood size in inland breeding Cormorants *Phalacrocorax carbo* in England and Wales in 1997 (□) and 1998 (■). Standard errors of the means are indicated by vertical lines extending above (1997) and below (1998) the symbol.
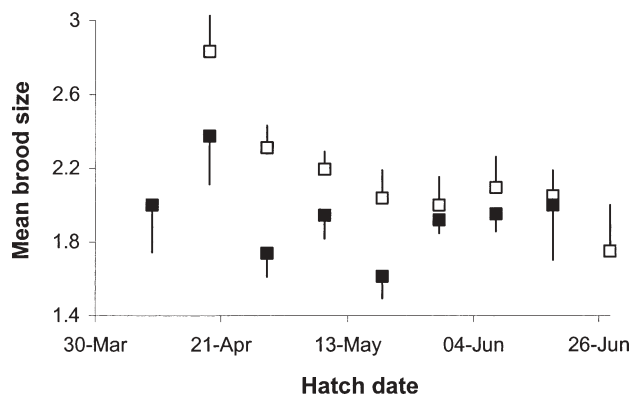
Figure 6. Seasonal decline in mean brood size in coastal breeding Cormorants *Phalacrocorax carbo* in England and Wales in 1997 (□), and 1998 (■). Standard errors of the means are indicated by vertical lines extending above (1997) and below (1998) the symbol.

making it difficult to produce comparable estimates. Obviously if the colony is visited close to fledging, the best estimate of fledgling production for successful nests can be obtained. However, the earliest chicks within a brood may have fledged and have left the nest at the time the visit is made. Furthermore, monitoring nests at an advanced stage may be difficult at coastal colonies where older chicks are likely to wander from their nests making estimation of brood size difficult. The advantage of making multiple visits to a colony, as in this study, is that nest failures can be identified and included in the calculations. This produces estimates that are a good reflection of reproductive output per nest or clutch and as such are most important for population modelling purposes and for comparing between years and between colonies.
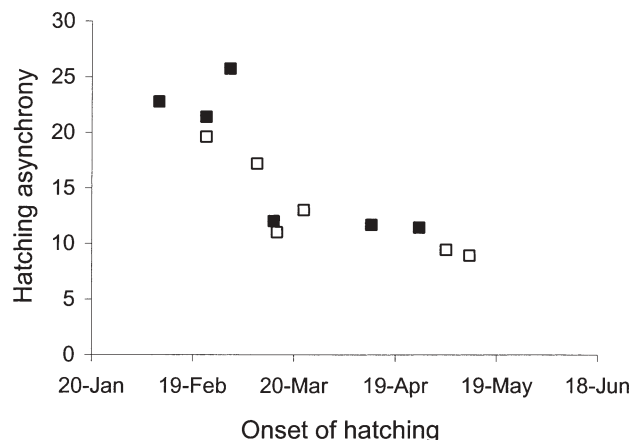
Figure 7. The relationship between hatching asynchrony (sd of hatch date) and onset of hatching (day first nest hatched) for the six studied inland breeding colonies of Cormorants *Phalacrocorax carbo* in England and Wales for 1997 (□) and 1998 (■).

The selected inland colonies constituted about 85% of the total inland breeding population at this time, and are therefore likely to be representative of inland breeders. Coastal colonies represented only a small proportion of the total English and Welsh population with little geographical spread. Although the representativeness of coastal colonies in this study may be questioned, mean fledging production per initiated clutch across colonies was about 1.2-times higher in the six inland colonies than in the four coastal ones. This difference was similar for both years of our study. We therefore believe that the higher fledgling production at inland compared with coastal colonies is important in driving the observed growth of inland breeding Cormorants in England.

Similar levels of Cormorant population increase have been observed on the continent with comparable fledgling production. For example, a breeding population in Denmark increased by 26% per annum for 20 years, despite little net immigration (Bregnballe & Gregersen 1995, Bregnballe 1996a). The production of young in this population was estimated to be approximately 2.3 young per pair per year during the population growth phase (Bregnballe 1996b). Population models have verified that growth rates of 22% can be reached with an average fledgling production of 2.3 young per pair and survival probabilities as observed in one large Danish *P. c. sinensis* colony (Frederiksen *et al.* 2001).

Whilst brood size at fledging in this study was higher at inland tree-nesting colonies than at coastal colonies, clutch sizes were similar. The difference in brood size at fledging is mainly a result of higher nestling survival during the later stages of development from 15–56 days.

Table 5. Estimates of percentage survival (*S*) and 95% confidence interval (95% CI) of Cormorant *Phalacrocorax carbo* contents through incubation, hatching to 14 days old and 15–56 days old in 1997 and 1998 at inland and coastal colonies in England and Wales.

Colony type	Year	Incubation			Hatching–14 days			15–56 days			Incubation to 56 days	
		n	*S*	95% CI	*n*	*S*	95% CI	*n*	*S*	95% CI	*S*	95% CI
Inland	1997	91	73.5	66.3–81.3	83	72.7	67.5–78.4	64	78.4	67.4–91.1	41.9	30.2–58.1
	1998	42	61.6	51.3–73.9	43	69.0	60.7–78.3	62	84.9	76.7–94.0	36.1	23.9–54.4
Coastal	1997	41	79.5	71.8–88.5	67	71.7	64.6–79.6	91	46.6	39.9–54.3	26.6	18.5–38.3
	1998	45	69.4	60.1–80.8	36	70.2	62.3–79.1	45	53.0	40.1–69.9	25.8	17.4–41.0

Survival, S^a (%)

$^a S =$ (Daily survival rate)$^{period\ length}$ × 100.

Examining breeding performance of Cormorants at a European level, fledging production appears to be higher at inland and shallow-water coastal breeding colonies in the UK and inland and coastal parts of continental Europe than at deep-water coastal colonies in England, Wales, Scotland, Iceland, Norway and northwest France (Røv 1994, Bregnballe 1996b, Wernham *et al.* 1999, Kopciewicz *et al.* 2003). Deep-water coastal breeders are likely to face harsher feeding conditions (e.g. higher energetic costs, lower food availability), than inland breeders and shallow-water coastal breeders (such as populations on the Baltic Sea coasts).

In this study, later breeding by coastal-breeding Cormorants may have been caused by restricted food availability early in the season. This would result in an increased breeding synchrony later in the season compared with inland breeders, hence increasing food competition among parents and causing lower breeding performance. At inland colonies, higher food availability, enabling earlier breeding and lower reproductive synchrony, may buffer inland breeders against intense food competition during chick rearing and thereby allow for a higher breeding success. Other less plausible explanations that may explain the higher inland breeding performance include differences in nesting site quality, lower disturbance or levels of inbreeding or disease. Whatever the reason, if this difference is consistent between colonies and years within inland and coastal colonies, this will have important implications for our understanding of Cormorant populations in England and Wales.

ACKNOWLEDGEMENTS

ENDNOTES

a. The assumption of intrabrood independence in survival does not bias survival estimates calculated according to this method, but causes underestimation of the variance (Ringelmann & Longcore 1982, Pollock *et al.* 1989, Mauser *et al.* 1994). To correct for this, standard errors were calculated according to Flint *et al.* (1995), which allows for intrabrood correlation. As visits were made to each site at least once every two weeks, corrections to the estimates discussed by Miller & Johnson (1978) were not needed.

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