3.3 Factors affecting movements and distribution

3.3.1 Resighting latitude

Variation in the latitude of resighting was explained mainly by the colony at which birds originated, and by the month and year of resighting (Table 7). Age class was much less important in explaining latitudinal variation in resightings, but monthly trends differed between age classes and breeding colonies. The inclusion of a year effect in four of the five significant interaction terms suggests that there was much annual variation in resighting latitude. Note, however, that the total count variance explained by the model was low.

Table 7. ANODEV table for factors explaining the latitude of resighting of cormorants ringed at two inland colonies in England between 1989 and 1998. Minimal adequate model explains 36.0% of count variance.

Parameter	F-value	D.F.	P
$Month^2$	9.41	1, 3089	0.002
Year	8.49	8, 3089	0.000
Colony	1250.71	1, 3089	0.000
Age class	1.17	2, 3087	0.311
$Month^2$ x Year	3.56	8, 3076	0.000
Colony x Year	2.70	3, 3076	0.044
Colony x $Month^2$ x Age class	4.95	2, 3041	0.007
Colony x $Month^2$ x Year	4.27	3, 3041	0.005
$Month^2$ x Year x Age class	4.91	12, 3041	0.000

Besthorpe birds were resighted significantly further north than Abberton birds (Figure 11) even after taking into account the difference in latitude between the two colonies. After excluding resightings at the colonies of ringing (to allow for differences in resighting effort), the difference between resighting latitude and colony latitude was significantly greater for Besthorpe than for Abberton birds (Table 8). This was true for all three age classes, but was not significant for two year old birds. Differences were not significantly different between the three age classes (Kruskal-Wallis One-Way Anova, X^2=2.166, 2 d.f., P=0.339). As the mean difference between resighting latitude and colony latitude was positive for all three age classes at both colonies, birds were generally resighted to the north of their breeding colony.

Figure 11. Latitude of resighting (mean ± 2 SE) of cormorants ringed as pulli at two inland colonies in England, Abberton Reservoir (51.82°N) and Besthorpe Gravel Pits (53.17°N), between 1989 and 1998 in relation to colony of ringing. Data labels are number of resightings.

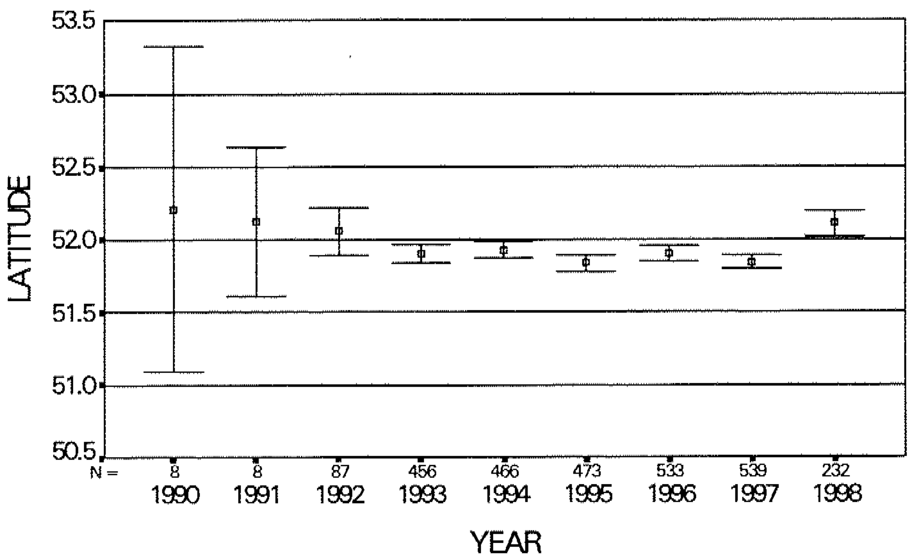
Table 8. Difference between resighting latitude and colony latitude (degrees) for cormorants ringed as pulli at two inland colonies in England, 1989-1998, excluding resightings at colony of ringing.

Colony	N	Mean	S.E.	U	P
First years					
Abberton	642	0.14	0.03	23772	0.001
Besthorpe	94	0.40	0.10		
Total	736	0.17	0.03		
Second years					
Abberton	438	0.10	0.04	6726	0.082
Besthorpe	37	0.34	0.15		
Total	475	0.12	0.04		
Adults					
Abberton	439	0.16	0.03	554	0.046
Besthorpe	5	0.62	0.24		
Total	444	0.16	0.03		
All birds					
Abberton	1519	0.13	0.02	81127	0.000
Besthorpe	136	0.39	0.08		
Total	1655	0.15	0.02		

Cormorants from Abberton showed no marked trends in latitude of resighting over the nine years resighting period (Figure 12), the slight increase in 1998 probably being caused by the incomplete data set for this year. There is much annual variation in the latitude of resighting for Besthorpe birds although no firm conclusions can be drawn from only four years data. Overall, first year birds were resighted further north than second year birds and adults (Figure 13).

Figure 12. Latitude of resighting (mean ± 2 SE) of cormorants ringed as pulli at two inland colonies in England, and, between 1989 and 1998 in relation to year of resighting. Data labels are number of resightings.

a) Abberton Reservoir (51.82°N)



b) Besthorpe Gravel Pits (53.17°N)

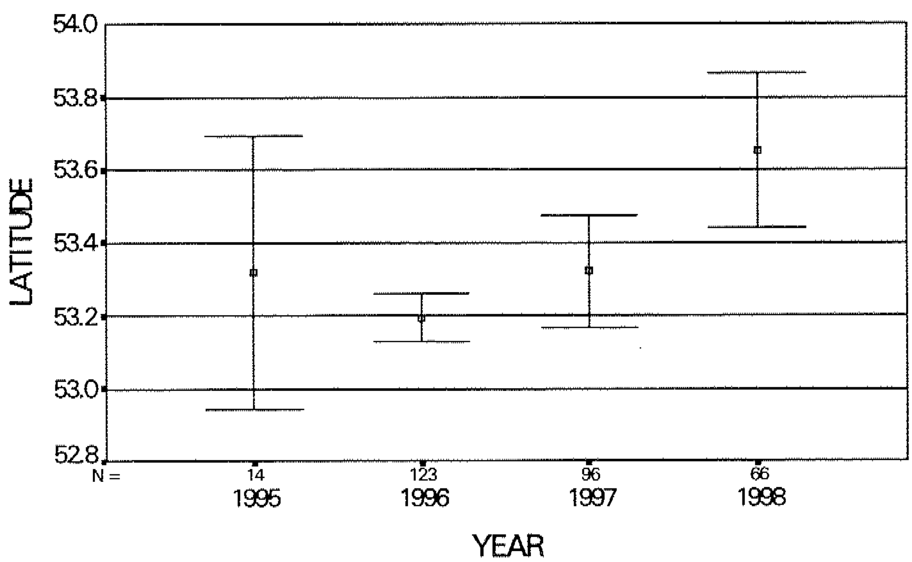
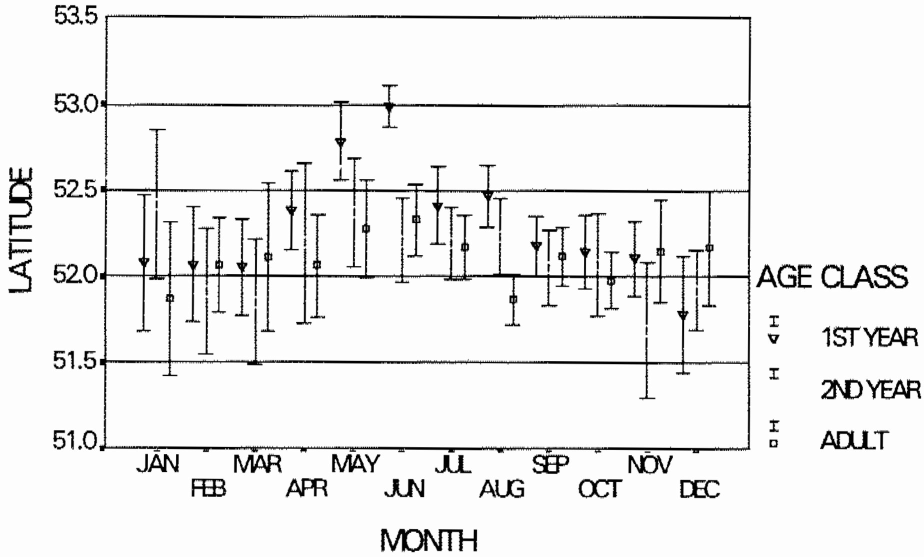


Figure 13. Latitude of resighting (mean ± 2 SE) of cormorants ringed as pulli at two inland colonies in England, Abberton Reservoir (51.82°N) and Besthorpe Gravel Pits (53.17°N), between 1989 and 1998 in relation to age at resighting. Data labels are number of resightings.

Although there is variation between age classes and colonies in the monthly latitude of resighting, birds were generally found further north in summer (Figure 14).

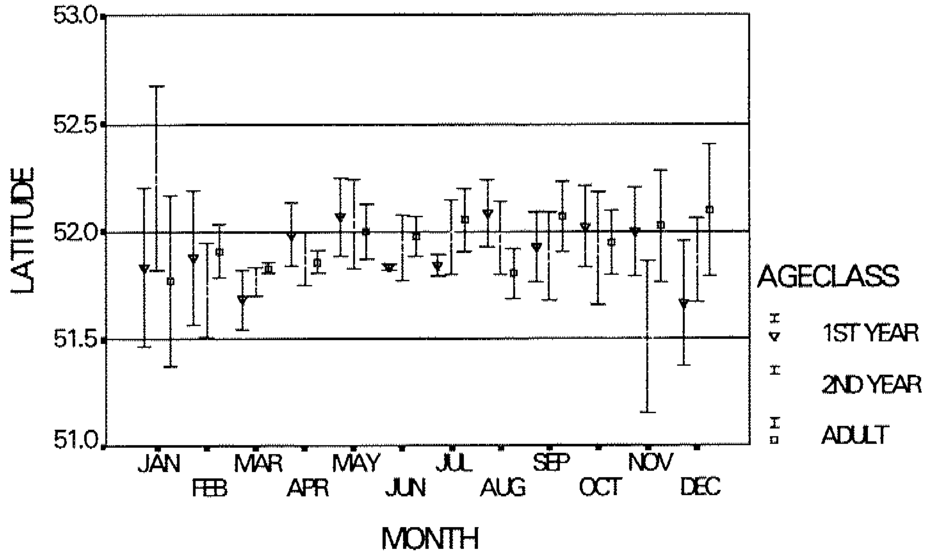
Figure 14. Latitude of resighting (mean ± 2 SE) of cormorants ringed as pulli at two inland colonies in England, Abberton Reservoir (51.82°N) and Besthorpe Gravel Pits (53.17°N), between 1989 and 1998 in relation to age of bird and month of resighting.



Data from Abberton suggest that first and second year birds were found further south than adults during the winter (Figure 15). Overall, first year birds and adults were generally resighted to the north of the Abberton breeding colony and second year birds at about the same latitude as the colony (Figure 16). Although there are relatively few data for Besthorpe, again birds tended to be found further north in summer, although in contrast to Abberton, this appeared to be associated with a specific late summer northward movement in all age classes (Figures 17 & 19).

Figure 15. Latitude of resighting (mean ± 2 SE) of cormorants ringed as pulli at two inland colonies in England between 1989 and 1998 in relation to age of bird and month of resighting.

a) Abberton Reservoir (51.82°N)



b) Besthorpe Gravel Pits (53.17°N)

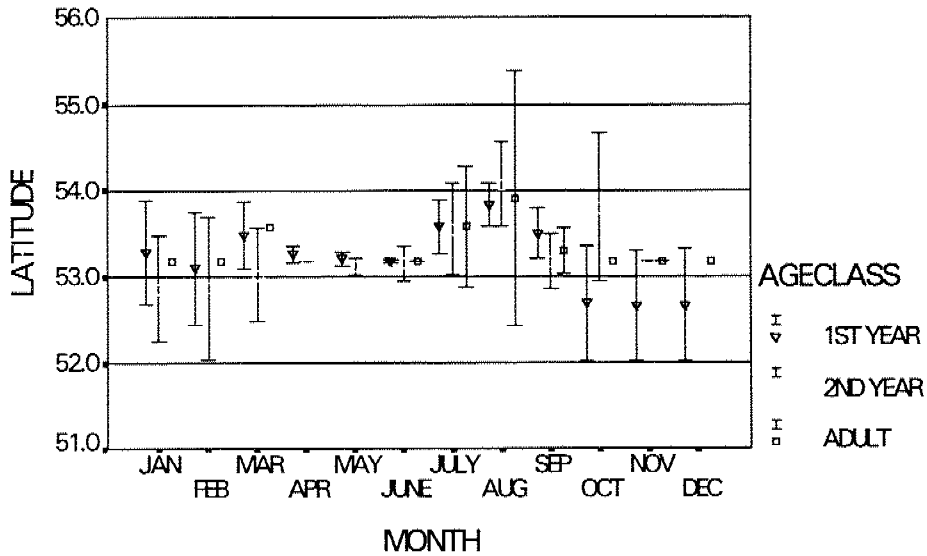
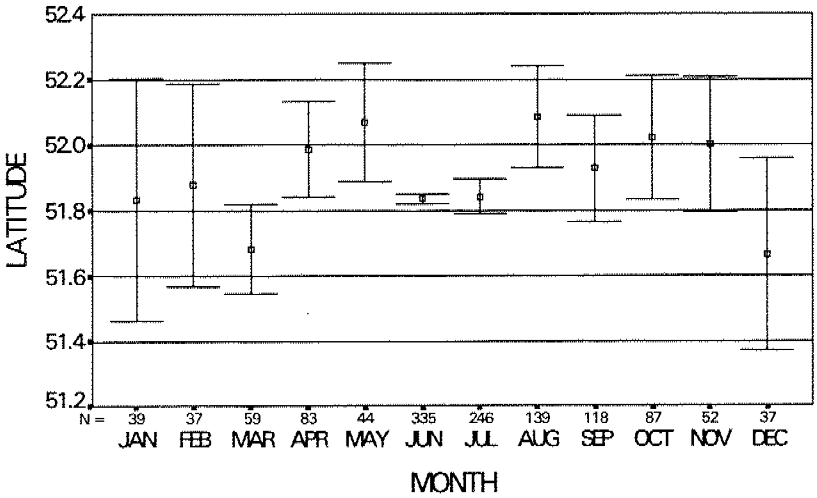
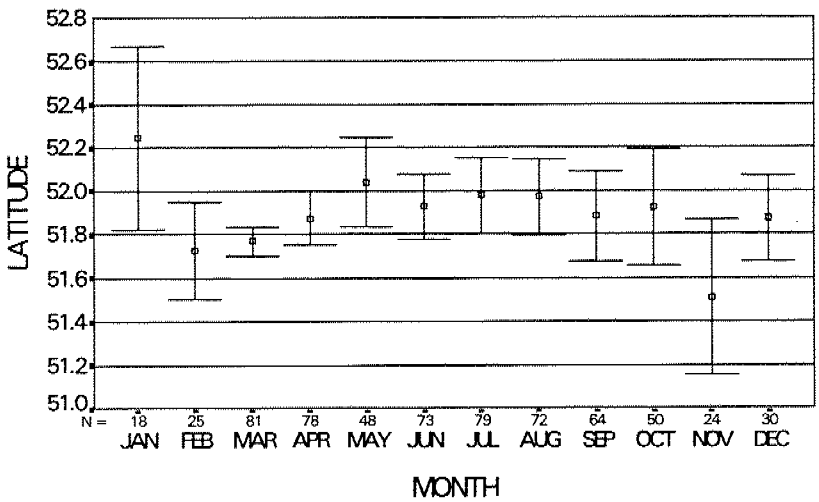


Figure 16. Latitude of resighting (mean ± 2 SE) of cormorants ringed as pulli at Abberton Reservoir, Essex (51.82°N), between 1989 and 1998, in relation to month and age at resighting. Data labels are number of resightings.

a) first years



b) second years



c) adults

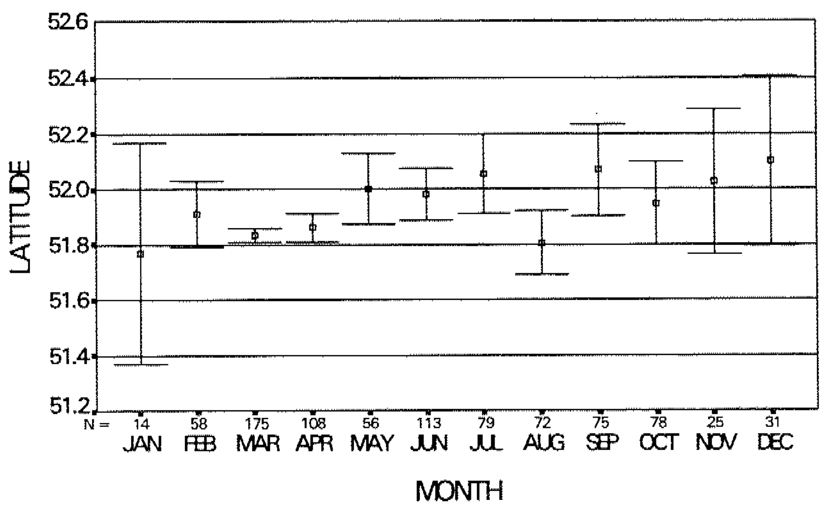
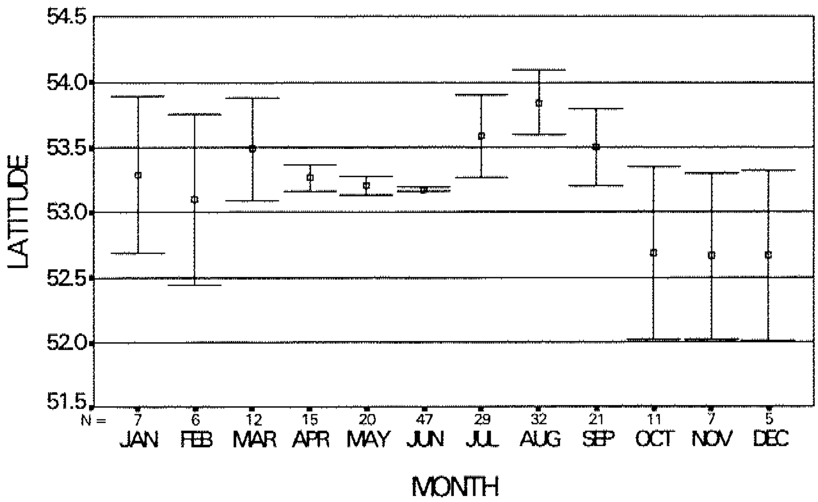
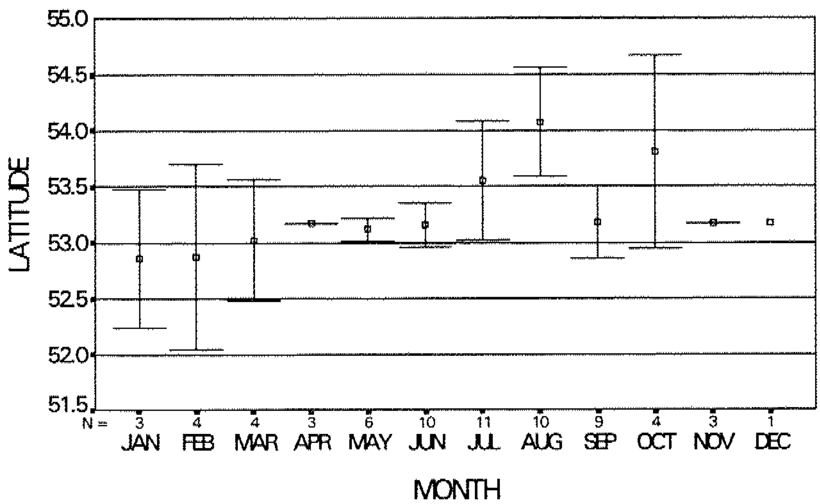


Figure 17. Latitude of resighting (mean ± 2 SE) of cormorants ringed as pulli at Besthorpe Gravel Pits, Nottinghamshire (53.17°N), between 1989 and 1998, in relation to month and age at resighting. Data labels are number of resightings.

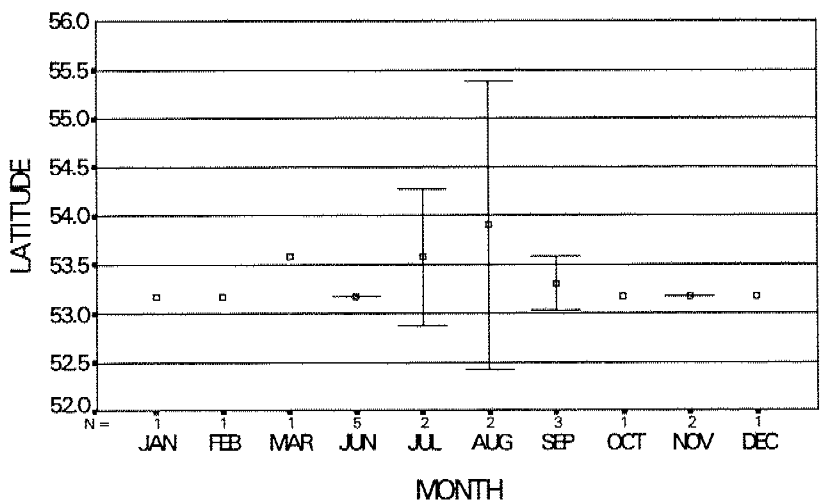
a) first years



b) second years



c) adults



3.2.3 Distance between natal colony and resighting site

The distance between the natal colony and the site of resighting was mainly explained by month of observation and the age class of the birds concerned (Table 9), although there was variation between colonies, and to a lesser extent between years. Note, however, that the total count variance explained by the model was low.

Table 9. ANODEV table for factors explaining the distance between ringing and resighting sites for cormorants ringed at two inland colonies in England between 1989 and 1998. Minimal adequate model explains 27.6% of count variance.

Parameter	F-value	D.F.	P
$Month^2$	165.83	1, 3087	0.000
Year	9.34	8, 3087	0.000
Colony	9.44	1, 3087	0.002
Age class	32.45	2, 3087	0.000
$Month^2$ x Year	6.94	8,3059	0.000
$Month^2$ x Age class	4.46	2,3059	0.012
Year x Age class	3.84	13, 3059	0.000
Colony x Age class	17.72	2, 3059	0.000
Colony x Year	12.52	3, 3059	0.000
$Month^2$ x Year x Age class	3.01	12, 3041	0.000
$Month^2$ x Colony x Age class	8.28	2, 3041	0.000
$Month^2$ x Year x Colony	8.05	3, 3041	0.000

Overall, cormorants were generally resighted further from their natal colony during autumn and winter, on average some 90-120km away (Figure 18). First year birds were resighted significantly closer to their natal colonies than second year birds (U=454827, P=0.000) which were resighted further away than adults (U=257411, P=0.000) (Figure 19). However, examination of monthly trends in distance from natal colony for the three different age classes reveals a somewhat different picture. Adults were found closer to their natal colonies than first or second year birds throughout the year (Figure 20), but first year birds tended to be further from their natal colonies than second year birds over most of the year, with the notable exception of the immediate post-fledging period.

Figure 18. Distance between ringing and resighting sites (mean ± 2 SE) for cormorants ringed as pulli at two inland colonies in England, Abberton Reservoir (51.82°N) and Besthorpe Gravel Pits (53.17°N), between 1989 and 1998 in relation to month of resighting. Data labels are number of resightings.

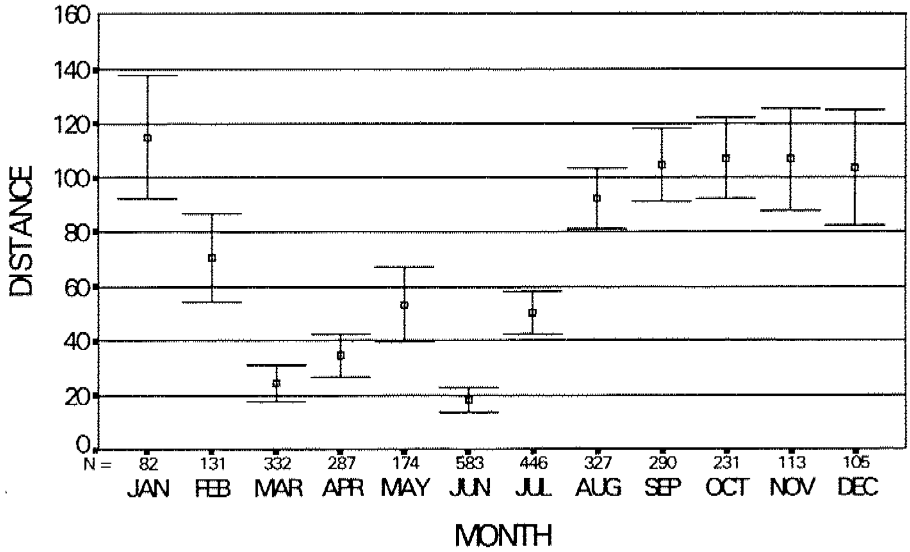


Figure 19. Distance between ringing and resighting sites (mean ± 2 SE) for cormorants ringed as pulli at two inland colonies in England, Abberton Reservoir (51.82°N) and Besthorpe Gravel Pits (53.17°N), between 1989 and 1998 in relation to age at resighting. Data labels are number of resightings.

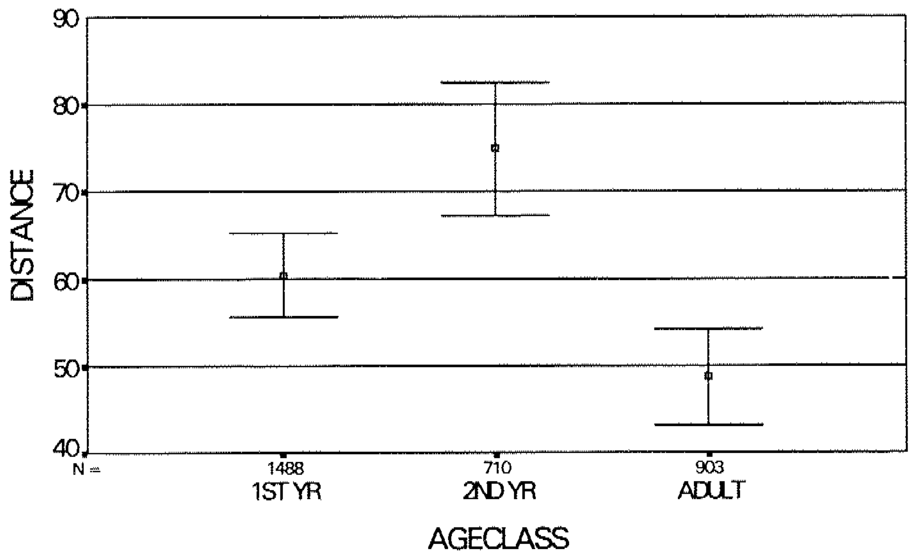
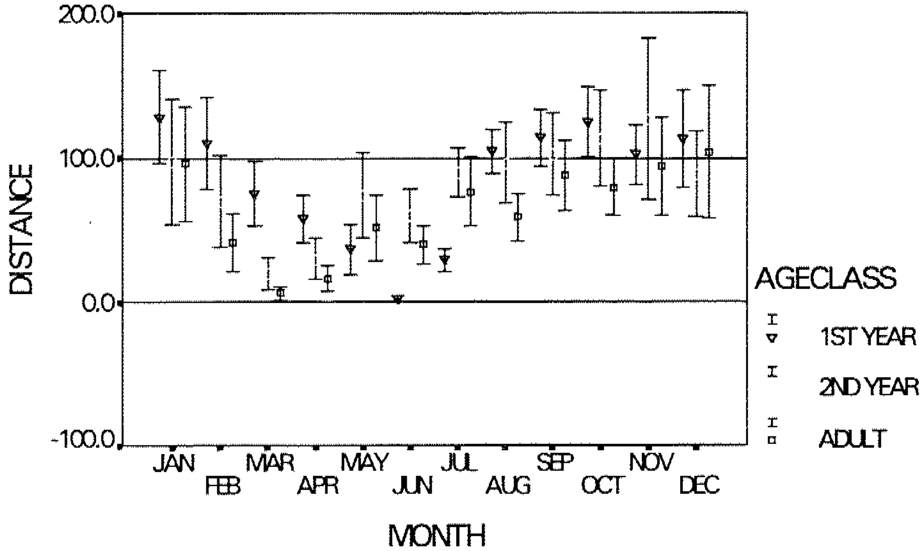


Figure 20. Distance between ringing and resighting sites (mean ± 2 SE) for cormorants ringed as pulli at two inland colonies in England, Abberton Reservoir (51.82°N) and Besthorpe Gravel Pits (53.17°N), between 1989 and 1998 in relation to age of bird and month of resighting.

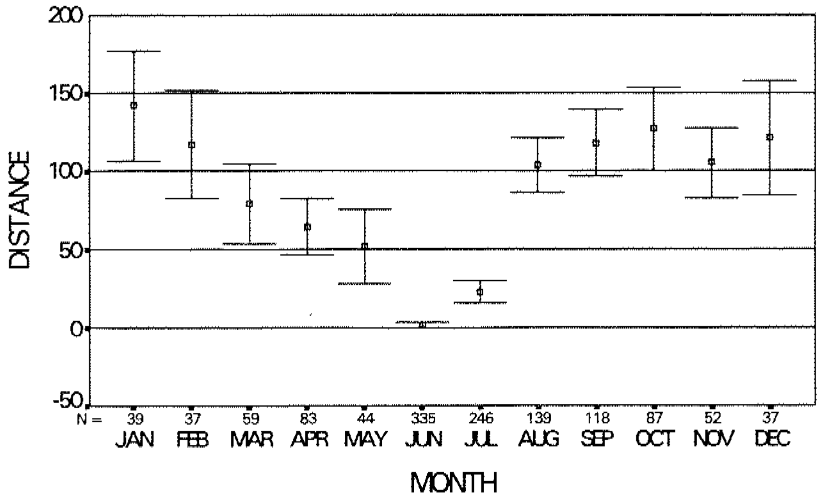


Further insight into the dispersal of the different age classes can be gained from investigating seasonal trends in resighting distances (Figures 21 and 22). Small sample sizes for Besthorpe, especially for older birds, preclude detailed examination, but at Abberton the distance of resighting of first year birds from their natal colony increased rapidly during the first two months following fledging (Figure 21a). By August, resightings of juvenile cormorants were on average over 100km from Abberton. Although sample sizes were small, juveniles from Besthorpe appeared to undergo an equally rapid dispersal to a similar distance from the colony in the same time (Figure 22a). Mean resighting distance of Abberton birds then remained at between 100 and 150km from Abberton until February from when birds gradually moved closer to the colony over the next four months. Nevertheless, most birds apparently did not return to Abberton in their first breeding season with birds on average still over 50km from the site in May.

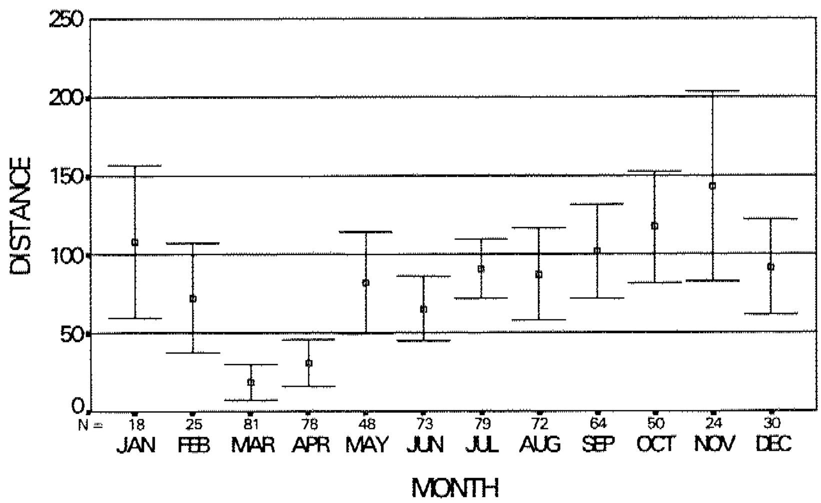
Second year birds did not show the rapid movement away from the breeding colony characteristic of first years. Instead, resighting distances gradually increased between late summer and early winter (Figure 21b). Birds began moving back towards the colony in January with most birds back by March. Adults showed a similar trend in resighting distance as second year birds (Figure 21c), although they appeared to return to the colony earlier in February and March when resighting distances were significantly lower than for second years (February - U=525, P=0.034; March - U=6075, P=0.001).

Figure 21. Distance between ringing and resighting sites (mean ± 2 SE) for cormorants ringed as pulli at Abberton Reservoir, Essex (51.82°N), between 1989 and 1998, in relation to month and age at resighting. Data labels are number of resightings. Note that the first young fledge in June.

a) first years



b) second years



c) adults

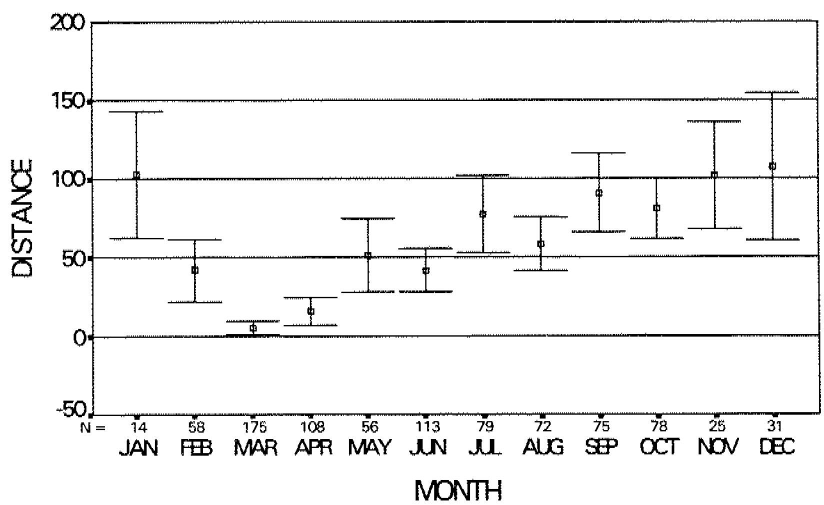
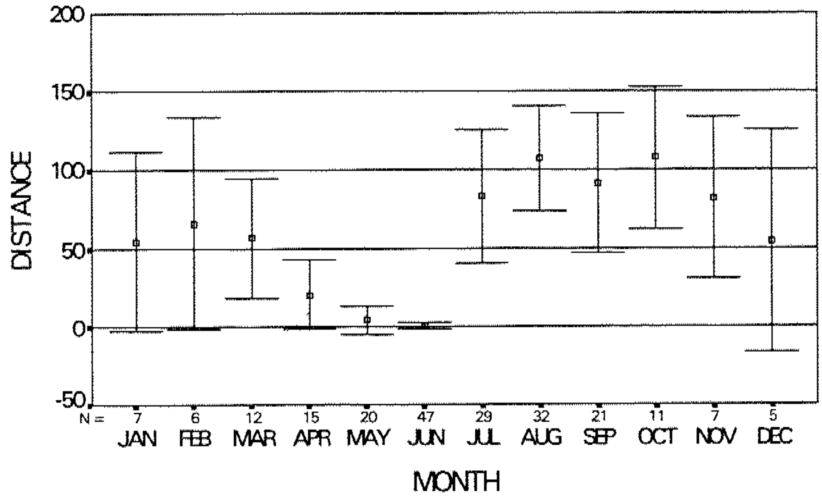
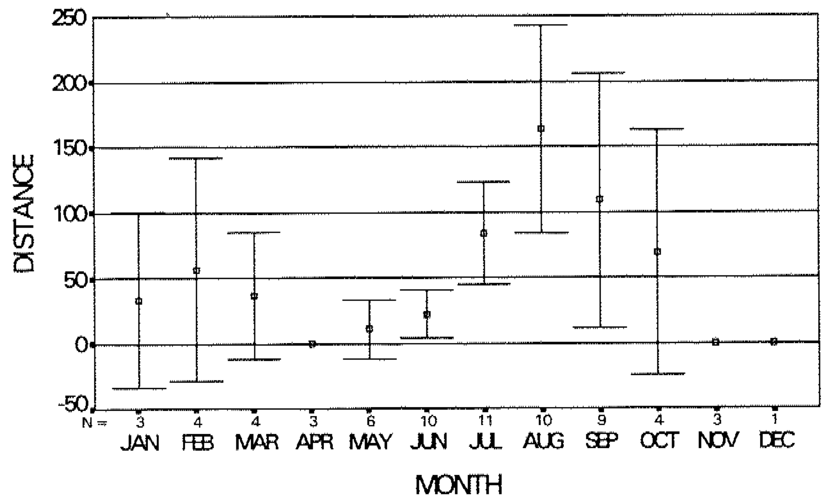


Figure 22. Distance between ringing and resighting sites (mean ± 2 SE) for cormorants ringed as pulli at Besthorpe Gravel Pits, Nottinghamshire (53.17°N), between 1989 and 1998, in relation to month and age at resighting. Data labels are number of resightings. Note that the first young fledge in mid-May.

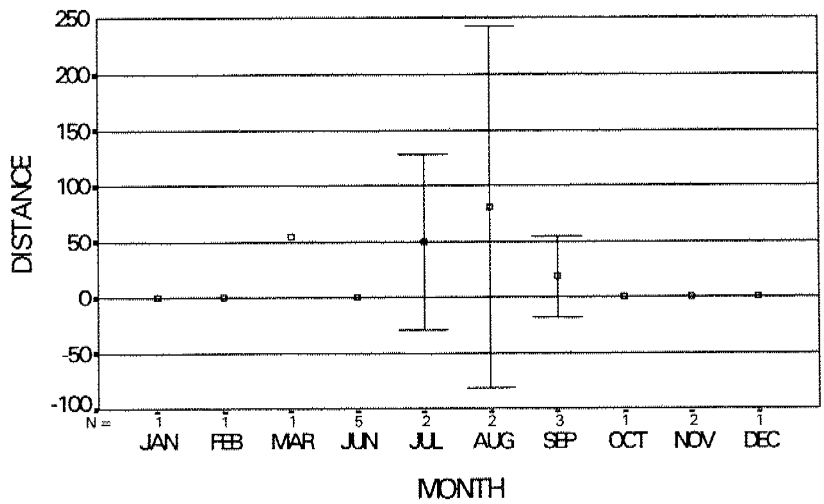
a) first years



b) second years



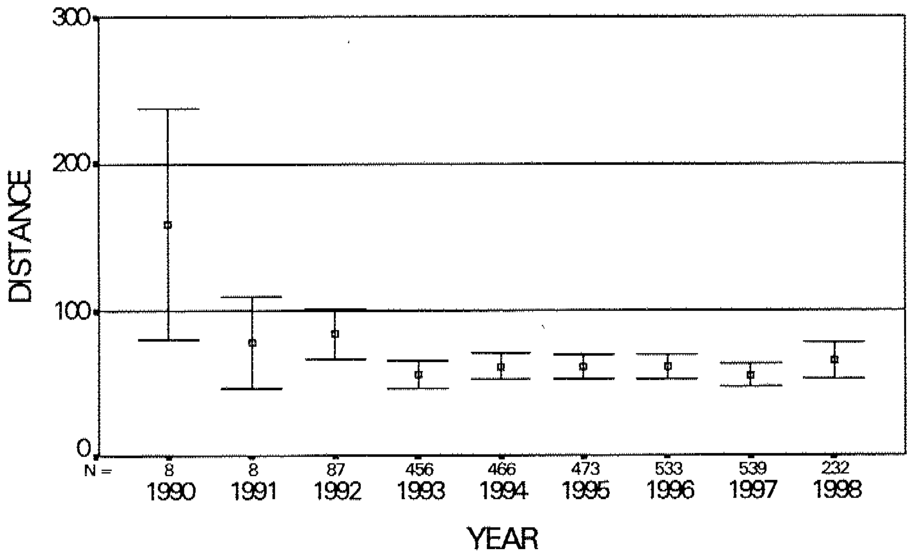
c) adults



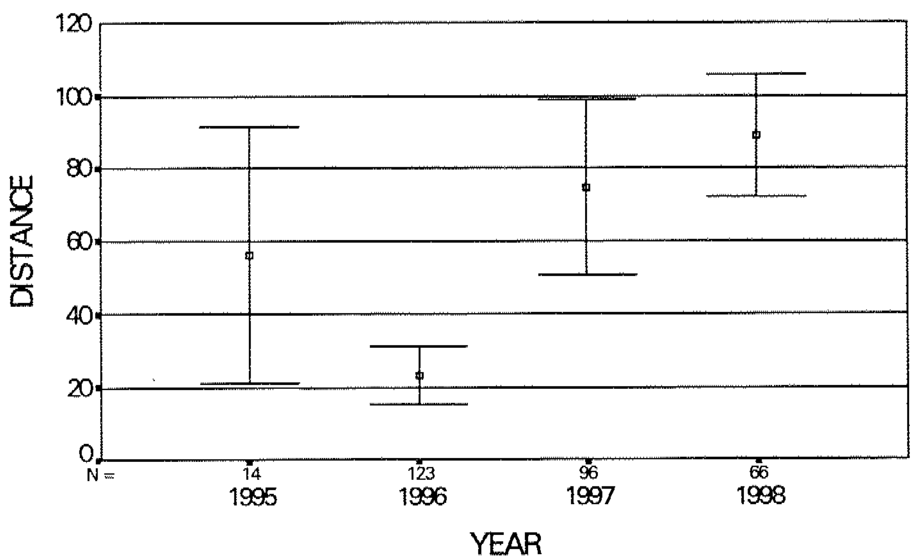
Although there was significant annual variation in resighting distance between colonies (Table 9, Figure 23), this may well have been due to small sample sizes at Besthorpe. The mean resighting distance from Abberton was relatively stable over the course of the study once sufficient birds had been marked.

Figure 23. Distance between ringing and resighting sites (mean ± 2 SE) for cormorants ringed as pulli at two inland colonies in England, and, between 1989 and 1998 in relation to year of resighting. Data labels are number of resightings.

a) Abberton Reservoir (51.82°N)



b) Besthorpe Gravel Pits (53.17°N)



3.3.3 Resightings and recoveries abroad

Most cormorants resighted or recovered overseas originated from Abberton, with a total of 61 birds resighted and 20 birds recovered abroad (Table 10). Most birds were found in The Netherlands and France, but with three birds from Spain and one as far south as Tunisia. Only three (1.5%) Besthorpe ringed cormorants were seen abroad, two in The Netherlands and one in Spain. No cormorants ringed at Paxton Pits or Rutland were recorded abroad.

Overall, 8.6% of Abberton ringed birds subsequently resighted alive were seen abroad (Table 10). This is much lower than the comparable figure calculated from recoveries of dead birds of 26.3% (20 of 76 birds).

Table 10. Numbers of cormorants ringed as pulli at two inland colonies in England, 1989-1998, and resighted or recovered abroad. Figures in parentheses are percentage of overseas recoveries and/or resightings.

COUNTRY	BESTHORPE		ABBERTON			
	RESIGHTINGS		RESIGHTINGS		RECOVERIES	
	No. of birds	%	No. of birds	%	No. of birds	%
Belgium	-	-	8 (12)	1.2	1 (5)	1.2
France	-	-	20 (31)	3.9	8 (40)	9.9
Germany	-	-	7 (11)	1.1	1 (5)	1.2
Netherlands	2 (67)	1.9	30 (46)	5.0	6 (30)	7.4
Spain	1 (33)	0.9	-	-	3 (15)	3.7
Tunisia	-	-	-	-	1 (5)	1.2
TOTAL	3	2.8	61[1]	8.6	20	24.7

[1] Four birds seen in two different countries.

Cormorants seen overseas were predominantly immatures (Table 11), with 90% of overseas recoveries relating to birds of three years and younger. The age distributions of birds resighted in the UK and abroad were significantly different (Table 12) with more second year birds resighted abroad than in the UK. Older birds were resighted mainly in the Netherlands.

Table 11. Age-specific totals of cormorants ringed as pulli at inland colonies in England, 1989-1998, resighted or recovered abroad. Figures in parentheses are percentages. Note that these data include repeat observations of the same individuals at different ages.

Age (years)	Country of Resighting/recovery						Total
	Belgium	France	Germany	Netherlands	Spain	Tunisia	
Abberton Reservoir							
1	6	17	5	20	1	1	50 (47)
2	4	9	3	12	1	-	29 (27)
3	3	5	2	6	1	-	17 (16)
4	-	-	-	4	-	-	4 (4)
5	-	1	-	2	-	-	3 (3)
6	-	-	-	1	-	-	1 (1)
7	-	1	-	1	-	-	2 (2)
8	-	-	-	1	-	-	1 (2)
Total	13	33	10	47	3	1	107
Besthorpe							
1	-	-	-	1	-	-	1
2	-	-	-	1	1	-	2

Table 12. Comparative age distributions of cormorants ringed as pulli at inland colonies in England, 1989-1998, and resighted or recovered in the UK and abroad. Expected values for overseas resightings calculated from frequency distribution of UK resightings.

Age (years)	No. of resightings in the UK	No. of resightings abroad	Expected Value	χ^2	P (d.f.)
1	500	50	50.14	0.000	0.986 (1)
2	189	29	18.95	5.326	0.210 (1)
3	161	17	16.15	0.045	0.832 (1)
4	108	4	10.83	4.308	0.038 (1)
5	68	3	6.82	2.139	0.144 (1)
6	28	1	2.81	1.164	0.281 (1)
7	12	2	1.20	0.527	0.468 (1)
8	1	1	0.10	8.072	0.005 (1)
Total	1067	107	107	21.582	0.003 (7)

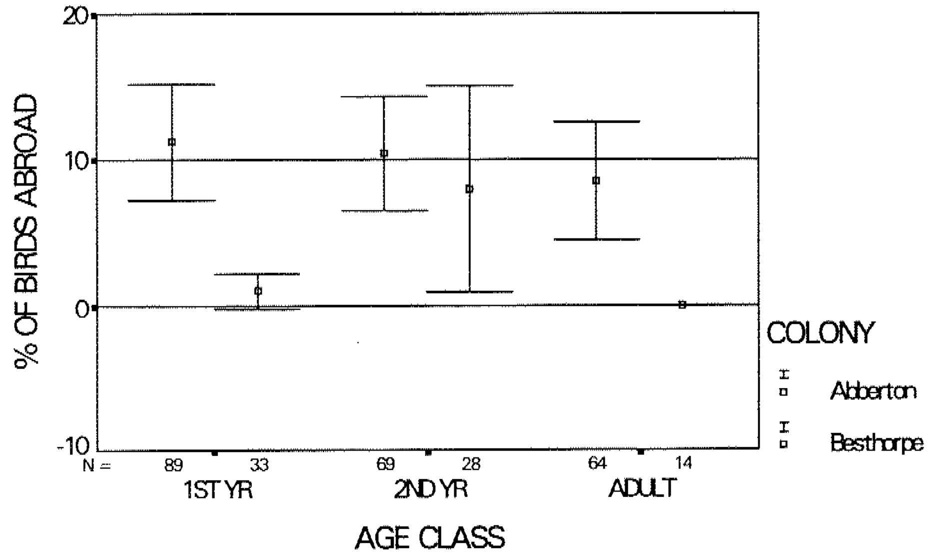
The proportion of inland breeding cormorants resighted abroad was mainly explained by month and year factors and to a lesser extent by differences between age classes and colonies (Table 13). Month and year factors, and the interaction between these two terms were most important, reflecting the cormorant's natural seasonal migration and the annual variation in its timing and extent. Note, however, that the total count variance explained by the model was low.

Table 13. ANODEV table for factors explaining the proportion of cormorants resighted abroad from birds ringed as pulli at two inland colonies in England between 1989 and 1998. Minimal adequate model explains 40.6% of count variance.

Parameter	X^2 value	D.F.	P
Month^2	47.51	1	0.000
Year	28.80	8	0.000
Colony	13.82	1	0.000
Age class	14.28	2	0.001
Month^2 x Year	26.43	8	0.001
Year x Age class	27.11	13	0.012
Colony x Age class	6.87	2	0.032
Colony x Year	13.70	3	0.012

Although the three first order interactions between colony, age class and year all explained a significant amount of variation in the proportion of birds abroad, these relationships may be caused by the small sample sizes involved (especially for Besthorpe) as biological explanations are problematical. For example, a higher proportion of second year cormorants from Besthorpe were resighted abroad compared with first years and adults (Figure 24). This seems somewhat at odds with previous, more detailed analyses (see Sections 3.2.1 and 3.2.2) and the number of actually involved in the sightings was very low (18 sightings of only three different birds). Resightings of Besthorpe cormorants were therefore excluded from further analyses.

Figure 24. Percentage (mean ± 2 SE) of cormorants ringed as pulli at two inland colonies in England, Abberton Reservoir and Besthorpe Gravel Pits, between 1989 and 1998 and resighted abroad in relation to colony of ringing and age at resighting. Data labels are number of months with resightings.



The proportion of Abberton cormorants resighted abroad (all age classes combined) was lowest during the breeding season (2%), and increased gradually to reach 24% of birds in January (Figure 25). First and second year birds predominated abroad, mainly during the winter months (Figure 26), although sample sizes for individual age classes are small.

Figure 25. Percentage (mean ± 2 SE) of cormorants ringed as pulli at Abberton Reservoir, Essex, between 1989 and 1998 and resighted abroad in relation to month of resighting. Data labels are total number of months with resightings.

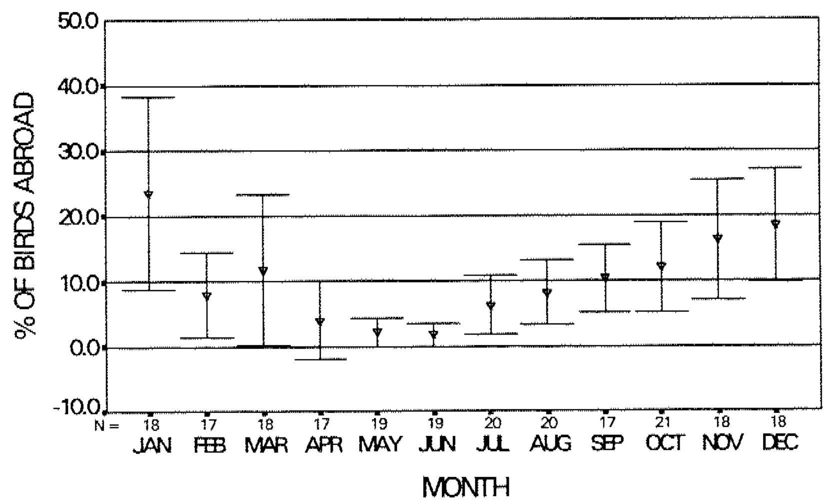
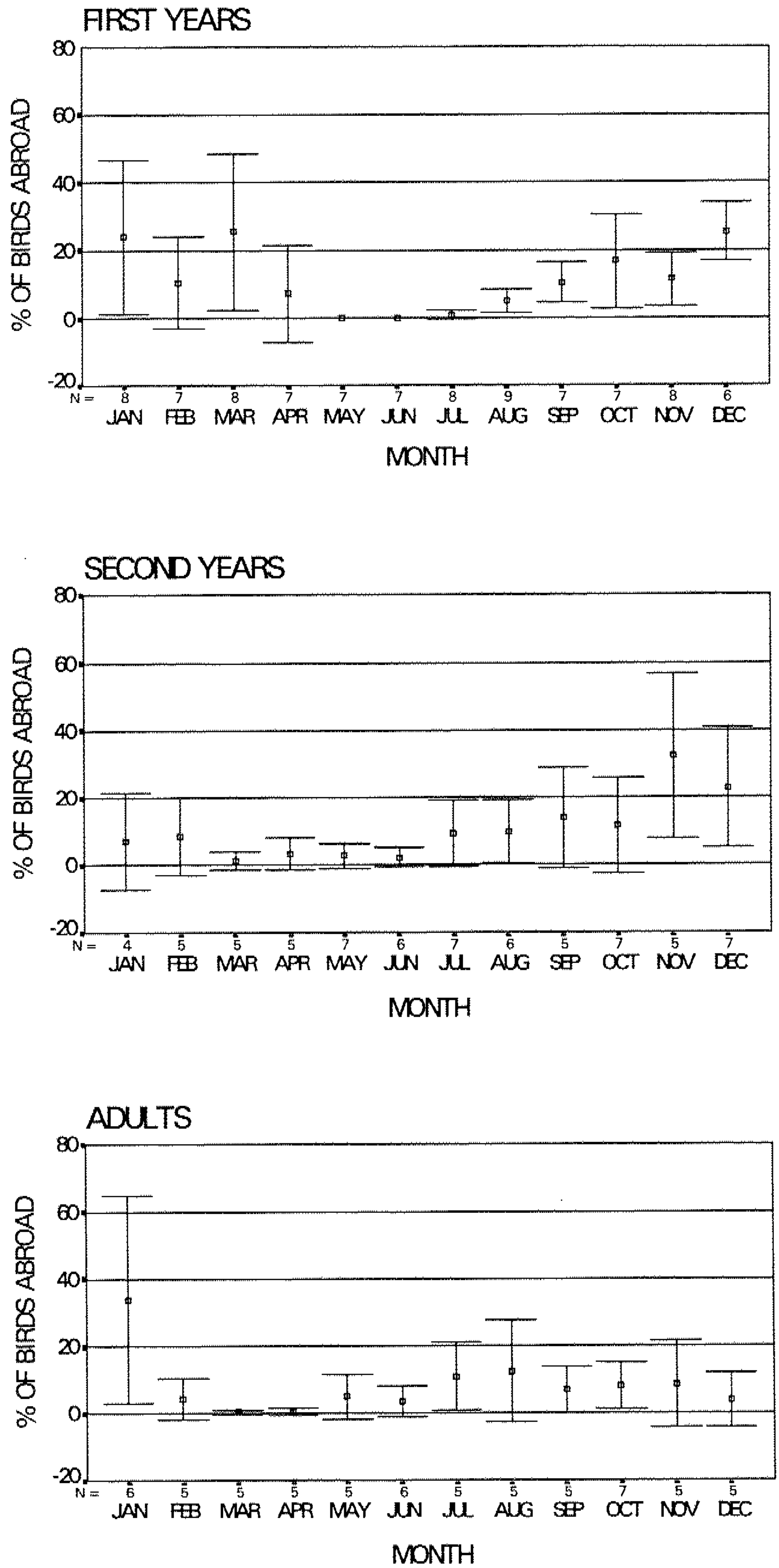


Figure 26. Percentage (mean ± 2 SE) of cormorants ringed as pulli at Abberton Reservoir, Essex, between 1989 and 1998 and resighted abroad in relation to age class and month of resighting. Data labels are total number of months with resightings.



4. Discussion

Many factors cause bias in colour-ringing studies of birds movements and need to be considered during interpretation of results. These include operational factors (eg. geographical variation in observation and reporting rates, and the effects of ring wear and ring loss), biological factors (eg. resighting distribution may be influenced by habitat preference and food availability), genetic factors (different sub-species, ages and sexes may have different migratory strategies) and environmental conditions (eg. cold weather may force birds further south (Marion 1995, Bregnballe *et al.* 1997a, 97b, Van Eerden & Munsterman 1995, Wernham *et al.* 1997). Within the current analysis it was impossible to control for most of these factors. However, whilst recognising that their effect can be considerable, Marion (1995) and Bregnballe *et al.* (1997a) concluded that general patterns in cormorant movements as described by resighting data were probably correct.

4.1 Non-breeding distribution and dispersal

4.1.1 Proportion of English inland breeding cormorants wintering abroad

This study showed that during the non-breeding season, cormorants from English inland breeding colonies were resighted mainly within England, but mostly away from their natal colonies. The majority of winter resightings were still, however, relatively close to breeding colonies, on average within 90 to 120km. Nevertheless, a significant proportion of birds were resighted abroad: some 2-24% of Abberton birds (depending on month) based on resighting data and some 26% based on recoveries of dead birds. The proportion of inland breeding cormorants moving abroad may be underestimated using resighting data if there is a lower observation and/or reporting rate abroad than in the UK. This may indeed be the case as there are active ring readers at most of the main English breeding colonies and roosts, and the reporting rate from France is known to be low due to the cessation of the official ring reporting scheme in 1991 (Sadoul *pers. comm.*). It seems reasonable to assume that a minimum of 25% of Abberton birds are found abroad during mid-winter. The proportion of cormorants from other inland breeding colonies wintering abroad was much lower, however small sample sizes precluded further investigation.

Cormorants resighted overseas were predominantly young birds, with 90% of recoveries relating to birds of three years and younger. Van Eerden & Munsterman (1995) and Bregnballe *et al.* (1997a) also reported that first year *sinensis* generally dispersed furthest from breeding colonies.

4.1.2 Distance, direction and timing of dispersal

Although some Abberton birds dispersed over great distances (the maximum recovery distance being a seven month old bird recovered in Tunisia some 1,800km from Abberton), the mean monthly winter resighting distance over all age classes was 90-120km. Abberton birds recovered dead during winter (September to February) were found at a median distance of 152km from Abberton (n=40). This compares with a median winter recovery distance of 72-111km for *carbo* breeding in the Firth of Forth in Scotland (n=8-58, Summers & Laing 1990) and a mean winter recovery distance of 182km from a complete analysis of recoveries of British and Irish coastal breeding *carbo* (n=1,143 birds, Wernham *et al.* 1997). Winter recovery distances for Norwegian coastal breeding *carbo* were much higher at 400-800km

(Mogstad & Røv 1997). Recovery distances for *sinensis* were even greater: 87% of birds from the Sea of Azov were recovered more than 200km from their breeding areas including 33% more than 600km away (Koshelev *et al.* 1997). Some 80% of *sinensis* cormorants from Denmark wintered more than 300km to the south of their breeding colonies (Bregnballe *et al.* 1997a) with around 55% of first year birds and 42% of adults wintering in the Mediterranean, some 1,500-2,500km from their breeding colonies. Although these recovery and resighting data are presented differently by different authors, it is clear that Norwegian *carbo,* and *sinensis* in general, tend to winter further from their natal colonies than British coastal breeding *carbo* and English inland breeding cormorants.

Norwegian *carbo* and all populations of *sinensis* studied to date disperse (or migrate) south during winter (eg. Mogstad & Røv 1997, Bregnballe *et al.* 1997a, Koshelev *et al.* 1997, Van Eerden & Munsterman 1995). In contrast, dispersal patterns of *carbo* from coastal breeding colonies in the UK have been found to be colony-specific in terms of both distance and direction, with movements of birds from some colonies, such as the Farne Islands (Northumberland), Mochrum Loch (Dumfries and Galloway) and the Lamb (Lothian) having a significant northward component (Coulson & Brazendale 1968, Summers & Laing 1990). In this study, the majority of English inland breeding cormorants were generally resighted to the north of their breeding colonies throughout the year, with a net movement to the south of natal colonies only during certain winter months.

Juvenile dispersal from English inland breeding colonies was rapid: most first year birds left their breeding colonies within two months of fledging. By August, juvenile cormorants were resighted on average over 100km from Abberton. Furthermore, this juvenile dispersal from Abberton is absolute, with very few juveniles remaining at the colony by September (Ekins 1996). The mean resighting distance of juvenile Abberton cormorants remained at 100-150km until February when birds moved closer to Abberton, however many first years apparently did not return to the colony with a mean resighting distance of over 50km in May. Second year birds and adults did not show the rapid post-breeding dispersal characteristic of juveniles. Instead, resighting distances gradually increased between late summer and early winter. These older birds returned to Abberton earlier than first years (between January and March), with adults returning first. This arrival pattern is to be expected as most cormorants usually breed for the first time at three years of age (Bregnballe *et al.* 1997c).

4.1.3 Factors affecting dispersal

Movements and dispersal of cormorants may well be determined mainly by factors not measured during this study, such as sex, temperature, wind strength and direction during dispersal, intra-specific competition for food and other resources, and an innate or learned tendency for site fidelity. Temperature, age and sex have all been found to explain the wintering distribution of *sinensis* (Van Eerden & Munsterman 1995, Bregnballe *et al.* 1997a) although there have been no studies of the effect of prevailing wind strength and direction and few on site fidelity (see below). Adult male *sinensis* were found to winter further north and in colder areas than females and young birds, whilst first year birds migrated over a shorter period of time, arrived earlier in southern wintering areas and left later than adults (Van Eerden & Munsterman 1995, Bregnballe *et al.* 1997a). This study similarly found that adult cormorants were resighted closer to their natal colonies than first or second year birds throughout the year.

Three hypotheses have been suggested to explain differential migration in birds: the body size hypothesis - larger birds are more adapted to colder conditions (Calder 1974); the arrival time hypothesis - when early arrival on the breeding grounds is advantageous, birds winter nearer to breeding colonies so they can return to breed earlier and thus experience higher breeding success (Myers 1981); and the social dominance hypothesis - dominant birds outcompete others for food resources close to breeding colonies thus forcing others to migrate further to find food (Gauthreaux 1978). Van Eerden & Munstermann (1995) suggested that, while recognising that the three theories are not mutually exclusive, the arrival time hypothesis ranked first in explaining the differential migration in this habit in *sinensis*. During the non-breeding period, perhaps cormorants strive to minimise their energy expenditure and maximise their chances of survival to the next breeding season by dispersing from their breeding colonies only as far as is necessary to acquire sufficient food. Adult and male cormorants, being larger, may then outcompete smaller females and young birds at favoured wintering sites closer to breeding colonies thus forcing less dominant birds to winter further from the breeding colonies. Limited data on site fidelity in cormorants (R.M. Sellers *unpublished data*, G.R. Ekins *unpublished data*) do, however, suggest that some cormorants have preferred wintering sites irrespective of distance from their natal colony.

There have been few studies of roost or breeding site-fidelity in cormorants in Europe (Yésou 1995, Reymond & Zuchuat 1995, Bucheim 1997) and none from England although Ekins (1996) presented preliminary results from work at Abberton. Yésou (1995) estimated that although the actual number of cormorants using an inland roost in France over the course of a season was 4-6 times greater than the peak count, the majority of wintering birds were highly site-faithful, especially adults.

Although this study was not designed to investigate site fidelity in cormorants, movement data suggested that birds from individual colonies dispersed widely (eg. Abberton cormorants were resighted at 237 different sites), but individual birds appeared to be site faithful, with 84% of birds resighted at only one or two sites. Only 11 birds (all from Abberton) were seen at five or more sites with a maximum of seven sites used by one individual. Detailed studies of dispersal and site fidelity in individual birds of known age and sex both within and between winters are required.

4.2 Origins of English inland breeding cormorants

Prior to the 1990s, cormorants in Britain were thought to be mainly *carbo*, which bred on the coast and usually remained in coastal waters in winter, but there is growing evidence that *sinensis* now comprise an increasing proportion of both wintering and breeding populations, especially at inland sites (see below). This study suggested that inland nesting cormorants in England show dispersal patterns characteristic of both *carbo* and *sinensis* in that most birds were resighted relatively close to their natal colonies (a *carbo* trait), but a significant proportion of (mainly Abberton) birds wintered inland in continental Europe (a *sinensis* trait). Whilst data on movements and dispersal can be indicative of the origins of inland breeding cormorants in England, more detailed studies are required to provide evidence on the provenance of birds and their sub-specific status.

4.2.1 Ringing studies

Colour and metal ringing studies have proven that cormorants breeding at inland colonies in England originate from both British coastal *carbo* colonies and continental *sinensis* colonies. Between 1985 and 1995 in the UK there were 184 sightings of 71 colour-ringed *sinensis* from six different European countries (Sellers *et al.* 1997). Most were winter observations of immature birds, but 40 records of 18 adults (11 from Denmark and seven from The Netherlands) occurred during the brood-rearing period (April to July). There have been at least six records of *sinensis* attempting to breed in British inland colonies, three of which were successful: a Danish bird at Deeping St. James in 1993, a Dutch bird at Abberton between 1993 and 1995, and a Dutch bird at Besthorpe in 1993 (Sellers *et al.* 1997). Taking into account the different numbers of birds colour-marked, a much higher proportion of Dutch (1.5%) than Danish birds (0.2%) have been resighted in Britain and Dutch colour-ringed birds have been involved in more inland breeding attempts, despite the fact that fewer birds have been ringed.

Sightings and recoveries of British coastally-bred *carbo* are common inland in winter (Ekins 1996, Wernham *et al.* 1997), but records of mature birds during the breeding season are less frequent. For example, at Abberton Reservoir up to 1995 there were 176 sightings of 30 different birds from eight coastal colonies, but only 19 sightings of four of these birds were during the brood-rearing period (April to July). Coastally-bred *carbo* have been recorded nesting at inland colonies in Britain on four occasions: birds from St. Margaret's Island bred at Abberton Reservoir in 1993 and Paxton Pits in 1994, while birds reared at Grune Point, Cumbria, bred at Little Paxton and Deeping St. James in 1995 (Sellers *et al.* 1997).

4.2.2 DNA studies

Microsatellite DNA analysis proved that cormorants at four inland colonies (Abberton, Besthorpe, Paxton Pits and Rutland) were a mixture of *carbo* and *sinensis* (Goostrey 1997, Goostrey *et al.* 1998). Mitochondrial DNA sequencing suggested that most Besthorpe birds (*ca.* 80%) were of *sinensis* origin, but that most Abberton birds (*ca.* 70%) were of *carbo* origin (Winney 1998). Cormorants from Abberton, Rutland and Besthorpe were most similar to *sinensis* cormorants from Danish rather than Dutch colonies (Goostrey 1997), perhaps suggesting that colonies were established by Danish cormorants.

4.2.3 Morphological studies

Recent morphological studies have proven that museum specimens of *carbo* and *sinensis* can be separated on gular pouch angle (Newson *in prep.*), *carbo* having a significantly smaller angle than *sinensis*. Application of the same identification criteria to birds at English inland breeding colonies suggested that *sinensis* predominates in most colonies (Ekins 1996, Newson *in prep.*), although further DNA studies linking morphology to genotype would be needed to confirm this. Sellers (1993) suggested that inland colonies may be founded by *sinensis* with an increasing proportion of wintering *carbo* then remaining to breed. The fact that, based on gular pouch shape, the proportion of *carbo* is higher and the proportion of *sinensis* lower in older inland colonies (Newson *in prep.*) would seem to support this.

Observations of gular pouch shape suggest that hybridisation is occurring between *carbo* and *sinensis* at inland colonies (Sellers *et al.* 1997, Newson *in prep.*). Combined DNA and morphological studies would be required to detect the level of hybridisation between the two subspecies.

4.3 Future population trends

Historically, British cormorants remained mainly in coastal waters during in winter. However, between 1970 and 1985 the numbers of birds wintering inland increased and the proportion of birds recovered inland doubled from 20 to 40% (Wernham *et al.* 1997). Many new inland roosts were formed (Porter 1987) and cormorants re-established themselves as an inland breeder when nine pairs nested at Abberton in 1981. As with roosting birds, cormorants breeding inland usually do so in trees on islands and several inland breeding sites were formerly winter roosts. A 'good' winter roost site is therefore also a potential breeding site (Sellers & Hughes 1997).

In 1997, there were at least 268 cormorant roosts in Great Britain, 168 of which were inland in England (Sellers & Hughes 1997). It is now likely that a minimum of 10,000 cormorants winter inland in England, representing perhaps 40-50% of the total number wintering in Great Britain (Kershaw & Hughes 1997). Since first breeding inland in 1981, the number of inland breeding cormorants increased to 1,437 pairs at 23 different sites in 1998[2]. However, the actual pattern of increase has not been linear - rather there has been a stepwise pattern of expansion, apparently controlled mainly by the formation of new colonies (Figure 27). That is, numbers at existing colonies appear to plateau before new colonies are formed. This has been most obvious in recent years with no new colonies established between 1994 and 1997 then first time breeding attempts at 12 sites in 1998. Four inland breeding colonies in England held more than 100 pairs of cormorants in 1998: Abberton Reservoir (457 pairs); Walthamstow Reservoirs, Greater London (222 pairs); Besthorpe Gravel Pits, Nottinghamshire (210 pairs); and Paxton Pits Nature Reserve, Cambridgeshire (180 pairs). A further site, Deeping St. James in Lincolnshire (where access is restricted) may also have held over 100 pairs.

Cormorants attempting to breed inland in England do so mainly in the south and east of the country (Figure 28) and sites with breeding records show a similar distribution to cormorants from Abberton Reservoir (see Figure 6).

[2] Including a known underestimate of 30 pairs at Deeping St. James, Lincs, where access is restricted and which held 120 pairs in 1995.

Figure 27. Number of cormorants and number of extant breeding colonies inland in England, 1981-1998. Includes known underestimates of 30 pairs for one site in both 1997 and 1998 (Deeping St. James, Lincolnshire) where access is restricted and which held 120 pairs in 1995.

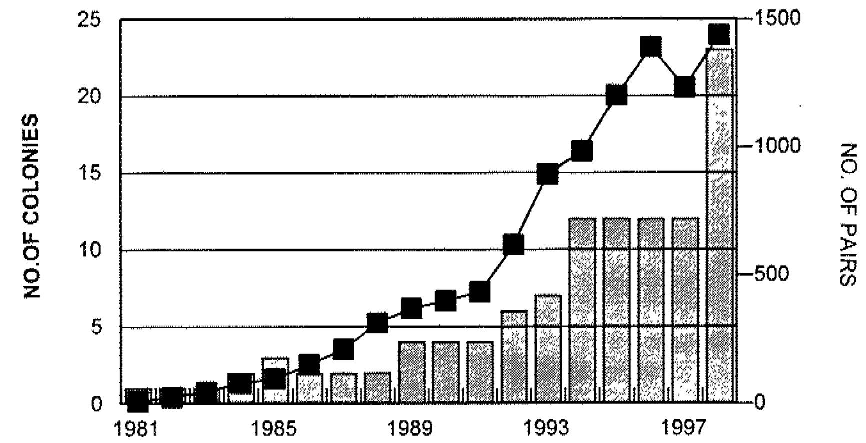
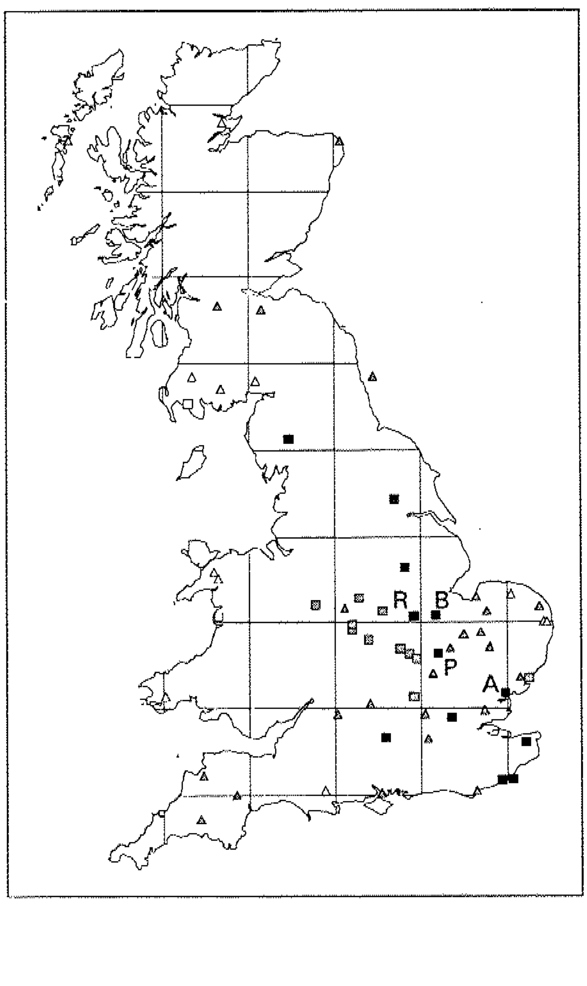


Figure 28. Inland sites in Great Britain with cormorant breeding records. Key: white squares - long-established colonies within 7km of the coast; black squares - inland colonies established since 1981 (A - Abberton Reservoir, B - Besthorpe Gravel Pits, P - Paxton Pits, R - Rutland Water); grey squares - sites with first breeding records in 1998; grey triangles - sites with breeding attempts (display, nest-building and/or chicks reared) since 1981, but without colony formation; white triangles - sites with historical (pre-1981) breeding attempts.



These comparisons of the numbers of inland breeding colonies, the number of inland roosts, and the numbers of cormorants currently wintering inland, suggest that there is much potential for further expansion of range and increase in numbers.

4.4 Implications for management

4.4.1 International issues

This study of the movements of inland breeding cormorants in England has a number of management implications, both politically and practically. The fact that inland breeding cormorants winter abroad suggests that control abroad may affect English populations. Thus, ideally, any population management should take place as part of an international management plan. The management of migratory populations of animals is implemented via the Bonn Convention, and waterbird conservation specifically via the African-Eurasian Waterbird Agreement (AEWA). Within the framework of the AEWA, national and/or international conservation action plans are required for those species which cause conflict with human interests, such as geese and swans which cause agricultural damage and fish-eating birds. The process of producing such an action plan for *sinensis* began in 1993 with the Dutch and Danish governments taking the lead. A review of information on the impact of cormorants on fish stocks was conducted (Veldkamp 1997) and possible management scenarios drawn up based on biological population models (Bregnballe *et al.* 1997a, Van Dam & Asbirk 1997). At the final meeting of experts in Copenhagen in 1997 (Anon. 1997), the aim of the action plan was agreed as:

"*to minimise the conflict between fisheries interests and the great cormorant* Phalacrocorax carbo sinensis *by ensuring that best practice is followed in mitigating, preventing and reducing the reported impacts of the species on fisheries, while maintaining a favourable conservation status for the species. Range States should try to achieve this, in the following order of preference through:*

- *appropriate site specific fisheries management,*
- *local management and control of cormorants and*
- *co-ordinated management and control of cormorants between Range States.*"

Subsequently, individual Range States have addressed cormorant management within this framework, although there appears to have been little overall co-ordination of cormorant control between countries. As DNA analysis, ringing, and observational studies have all suggested that English inland cormorant colonies hold significant numbers of birds of *sinensis* origin and that appreciable numbers of these birds winter abroad, the UK should be involved in any further development and implementation of the African-Eurasian Management Plan for *sinensis*.

4.4.2 National issues

This study of inland breeding cormorants in England highlighted the need for ongoing and substantial colour-ringing effort if the development of inland breeding colonies is to be monitored adequately. To date, most colour-ringing studies have been conducted and funded by volunteers who have thus provided government, through the Country Agencies with unique data on cormorant movements and distribution. However, trends in movements of inland breeding cormorants can only be explained if:

a. sufficient individuals at sufficient colonies continue to be ringed annually and on an ongoing basis. Even at Abberton, where colour-ringing has now taken place for ten years, further data is required to explain trends in movements and distribution;

b. adequate data on factors explaining trends in movements are collected: Most importantly, all ring readers should record the numbers of cormorants checked for rings.

Although this study was not designed to investigate site fidelity, movement data suggested that cormorants breeding in inland colonies in England dispersed widely during the non-breeding season, but individual birds appeared to be site faithful. This suggests that limited winter control of cormorants in England is unlikely to have an appreciable impact on inland breeding colonies. In order to predict the effect of control at sites used by cormorants outside the breeding season, more detailed studies of dispersal and site fidelity in individual birds of known age and sex both within and between winters would be required.

In keeping with the AEWA recommendation that action plans should be produced for species causing conflict with human interests, the UK should now produce a national action plan for cormorants, including both coastal breeding and inland breeding populations. Following on from the extensive, government-funded research programme on the impact of cormorants on fish stocks in the UK which is due to be completed in 1999, this action plan should determine appropriate management measures for cormorants in the UK.