Migration Strategies of the Great Cormorant Wintering Inland in Spain

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Abstract.—Searches for color-banded Great Cormorants (*Phalacrocorax carbo*) were carried out during 2002-2004 at an inland roost in Spain in order to determine the origin of the birds, to measure the length of stay and within- and between-seasons site fidelity in relation to age. Contrary to expectations, neither the stay duration at the roost nor the site fidelity depended on age. The low stay duration (the majority of the birds were sighted only once) and return rates suggest nomadic behavior of the wintering cormorants. The cormorants that stayed longer at the roost also returned there more times during one season, suggesting that site fidelity may have an adaptive value for wintering cormorants. *Received 26 November 2004, accepted 15 May 2005.*

Key words.—Age-related behavior, Great Cormorant, Iberian Peninsula, migration strategies, *Phalacrocorax carbo*, site fidelity, staging sites.

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Migrant birds usually divide their journey between the breeding and wintering grounds into phases of movements and stopovers. Migratory stopovers are places used for resting and replenishing depleted energy reserves (Restani 2000). Adult birds often have shorter stopovers than juveniles, the latter tending to be in poorer condition and needing additional time to replenish fat reserves before continuing migration (Holmgren *et al.* 1993; Restani 2000 and cited references). The experience gained during previous migrations may also allow older birds to have shorter stopovers (Restani 2000). The need for an early arrival at the breeding sites also causes adults to migrate faster in spring than younger, non-breeding individuals (Spina *et al.* 1994; Bregnballe *et al.* 1997) and, therefore, the stopover duration may decrease with the age.

The fidelity to stopover sites, both within a season and between seasons, seems to increase with several factors: (1) experience, because older birds can use well-known areas to enhance their survival rate (Reymond and Zuchuat 1995b; Kruckenberg and Borbach-Jaene 2004); (2) social status, because subordinate birds are forced toward suboptimal sites and hence their willingness to look for other sites may increase (*op. cit.*); and (3) breeding status, because when reaching breeding age the birds tend to be more sedentary, while non-breeders and young may explore new roosting sites to gain individual experience in preparation for future breeding (Stahl *et al.* 2001; Kruckenberg and Borbach-Jaene 2004). These three factors closely interact, because the greater experience of older birds allows them to have higher success in agonistic interactions, thus increasing their social status (Reymond and Zuchuat 1995b; Galván 2003, 2004). Thus, age might have an important effect on the stopover behavior of birds. These effects may also apply to birds moving between sites in wintering areas. For simplicity, hereafter "staging site" refers to a site with migrating and/or staging birds.

The Great Cormorant (*Phalacrocorax carbo*) is a large-bodied, fish-eating, colonial waterbird. In continental Europe, the inland breeding subspecies *P. c. sinensis* has increased dramatically since the 1970s (van Eerden and Gregersen 1995). This has been followed by an expansion of new inland wintering and breeding grounds (Bregnballe *et al.* 2003). In Iberia, inland wintering cormorants were rare before 1960. By the early 1990s, pairs bred sporadically (Díaz *et al.* 1996), and at present there are about 40 breeding pairs in Spain (Lekuona 2003).

The Great Cormorant uses a repeatable scheme to optimize its migration routes and wintering time, showing a high fidelity to stopovers between years and even to individual perches at particular roosts (Yésou 1995; Reymond and Zuchuat 1995a,b; Frederiksen *et al.* 2002; Paquet *et al.* 2003). Some authors have reported that this fidelity increases with the age (Yésou 1995; Reymond and Zuchuat

1995b), but others have not found differences between age classes (Frederiksen *et al.* 2002; Paquet *et al.* 2003). Furthermore, a substantial proportion of cormorants move to different areas between seasons (Frederiksen *et al.* 2002), and other authors have reported that the majority of the cormorants use a roost briefly, while other individuals make long stays (Yésou 1995; Paquet *et al.* 2003). These studies suggest that the Great Cormorant is not entirely nomadic outside the breeding season, although some individuals exhibit a certain degree of nomadism. This raises questions about the conditions that make cormorants to follow a particular migration strategy (Frederiksen *et al.* 2002).

Bregnballe *et al.* (1997) studied the stopover duration of cormorants in relation to age and found shorter stopovers for first-year birds than for adults during the autumn migration (contrary to what should be expected; see above), but that the opposite occurred during spring passage. Lekuona and Campos (2000) also report longer stopovers in first-year cormorants.

There also seems to be a relation between the stopover duration and date of arrival in cormorants, with shorter stays corresponding to migration periods (Yésou 1995; Buchheim 1997; Paquet *et al.* 2003).

Between seasons, the fidelity to stopover sites may be related to the stopover duration in the Great Cormorant, since birds that stay longer have a better knowledge of the feeding opportunities in the vicinity of the stopover site, which could lead to more days spent there and to a more effective defence of a particular perch inside the stopover roost. Thus birds that stay longer are more faithful to that roost (Yésou 1995; Paquet *et al.* 2003). From this it could be inferred that young birds show a higher fidelity to stopover sites than older birds, because the young tend to stay longer at the stopovers/staging sites. However, the fidelity to these sites should increase with the age (see the three factors listed above), but this would be a contradiction of the findings of most authors. Only Yésou (1995) reported fidelity to the stopover sites increased with the age of the birds.

Although data exist on the ecology and behavior of Great Cormorants wintering in Iberia (Campos and Lekuona 1994; Lekuona, 1999, 2000; Galván 2004), the migration strategies have not been investigated at inland sites (Blanco *et al.* 1994; Díaz *et al.* 1996; Lekuona 2003). The aim of the present study was to determine the origin of the cormorants and to explore possible relationships between the age of the birds and the stay duration and site fidelity at a roost inland in Spain, using data obtained from sightings of color-banded birds.

STUDY AREA AND METHODS

The study was carried out during 2002-2004 at a Great Cormorant roost in Badajoz (SW Spain, 38°53'N, 06°58'W), about 180 km from the coast. In this region, the number of wintering cormorants has increased during the last two decades due, in part, to the proliferation of large reservoirs (Sánchez *et al.* 1991). The roost was situated on an islet in the Guadiana River in Eucalyptus (*Eucalyptus camaldulensis*) trees.

Searches for color-banded cormorants were undertaken at least three times a week from September to March, the period in which the roost is used by the cormorants. The observations began at least three hours before sunset and finished when the light conditions made accurate readings of the band codes and colors impossible. The origin and exact age of the banded cormorants was determined from the banding details.

The minimum stay duration each year (i.e., the time elapsed between first and last sighting) was calculated for these birds. This method underestimates the stay duration because of neglecting the time a bird may have spent at the staging site before the first and last sightings. The near-total lack of leaf cover at the roost (Galván 2004) allowed easy observation of the color-bands, and all the cormorants present at the roost could be examined on each visit. Because of this and of the high frequency of monitoring the roost, cases in which color-banded cormorants were not recorded during their stay at the roost, although unavoidable, were probably uncommon. As found by Reymond and Zuchuat (1995b), the cormorants were often faithful to individual perches inside the roost, and this facilitated the checking of color-banded birds. None of the perches were more visible than others because the roost can be seen from both sides of the river. For each individual, the mean stay duration was calculated taking into account all the sightings of that individual.

To evaluate within-season fidelity of the cormorants, it was considered that when at least three weeks had elapsed between two sightings of a bird, it had left the area and returned again. The roost investigated here is one of three important roosts in Spain, and far larger than others situated in the area (Extremadura region; del Moral and de Souza 2004). The second in importance has only 30% of the number of birds which were recorded in the study roost and was located 70 km away. There are other roosts nearer (less than 20 km away),

but none of them has more than 20% of the cormorants that used the roost of Badajoz (*op. cit.*). Due to the importance of the site, the departures and returns of cormorants to the roost during the same winter indicate the mobility of the birds within the wintering area.

One adult bird was judged to be a statistical outlier because of its extremely long stay duration (it stayed at the roost for the whole study period), and was therefore excluded from the analyses of number of sightings and stay duration. From a total of 190 visits to the roost, this bird was seen on 155 (82%) days, a value that indicates the effectiveness of the searches for color-banded cormorants.

The age of the cormorants was measured in years from the banding date because all were banded as young, but birds over three years old were pooled into a single age class to consider the social hierarchy of the Great Cormorant (Galván 2004). Kolmogorov-Smirnov tests revealed that data on stay duration were not normal distributed, and non-parametric statistics were used. To analyze the frequencies of cormorants coming from different countries, a G-test based on the number of sightings was carried out after applying Williams' correction. Mann-Whitney's U-tests and Kruskal-Wallis tests were used to examine differences between medians. Spearman and Pearson correlation tests were used to investigate relationships between the stay duration and the age of the cormorants. Means are expressed with the corresponding standard errors (Zar 1999).

RESULTS

In all, 36 individuals of known origin and age were recorded at the roost during the study period. The country of origin was determined for another six birds from the type of band, but the code was not identified. In total, 116 sightings were made, 74 of them during 2002-03 and 42 during 2003-04. From these sightings 53 periods of stay were recorded.

The mean age of the cormorants was 3.7 ± 0.6 years, individually ranging up to 17 years. The majority of the birds were in adult plumage.

Origin of the Cormorants

The cormorants came from eight localities in four countries (Table 1). The majority of the sightings were of birds from France (Table 1).

There was evidence of seasonal segregation between cormorants of different origins (Fig. 1). Thus, French birds outnumbered birds from other areas during the autumn and during September only birds coming from France were seen. However, in winter, Danish birds dominated (Fig. 1). The age of the cormorants did not differ between the four different origin countries (H_3 = 5.97, n.s.).

Stay Duration

The mean duration of stay at the roost was 7.0 ± 1.8 days (range: 1-75 days). Stays of only one day were far the most numerous (62%), and 91% stayed lasted less than three weeks (Fig. 2).

Young cormorants did not stay longer at the roost than older birds (r_s = -0.10, N = 46, n.s., Fig. 3). The same results were obtained (H_2 = 0.95, n.s.) when the birds older than three years were pooled into a single age class. The duration of stay did not relate to the arrival month (H_6 = 3.50, n.s., Fig. 4) and this also applied to birds older than three years (H_5 = 2.8, n.s.).

Table 1. Geographical distribution of the banding localities of color-banded Great Cormorants seen during the study. The place of banding of two Danish birds could not be identified. One of the French cormorants was not taken into account when calculating the number of sightings because of being considered an statistical outlier (see Study Area and Methods).

Banding colony	Country	No. individuals	No. sightings
Lake Grand-Lieu	France	27	65
Flevoland	The Netherlands	1	2
Delfzijl	The Netherlands	1	20
Mågeøerne	Denmark	1	10
Yderste Holm	Denmark	4	8
Rønland Sandø	Denmark	2	3
Toft Sø	Denmark	1	1
Øra Naturreservat	Norway	3	5
Total		40	114

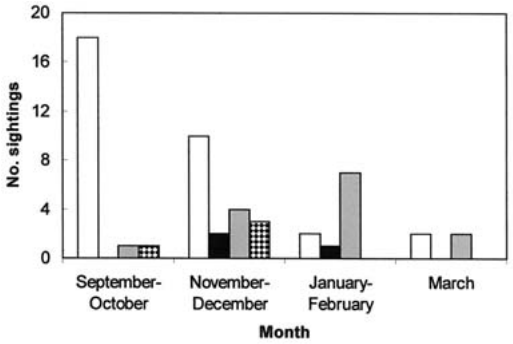

Figure 1. Number of sightings in relation to the month of observation of Great Cormorants of different origins. White: France; black: The Netherlands; gray: Denmark; dotted columns: Norway.

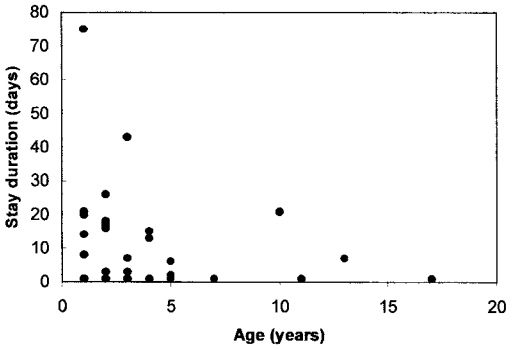

Figure 3. Relationship between the stay duration and the age of Great Cormorants wintering at the roost.

Site Fidelity

Eight (19%) of the cormorants stayed more than once at the roost within the same season. Only five of those (27) seen in the first year were re-sighted during the second year of study. Four of these five birds stayed at the roost more than once during the same winter.

The mean stay duration per visit of the cormorants which visited more than once during the same season was 17 ± 5.1 days, much longer than the stay duration calculated for the birds which stayed only once at the roost (mean 3.2 ± 0.9 days, U = 83.0, P < 0.001). The mean age of these multiple visit birds was 2.7 ± 0.4 years, not different from the age of the rest (U = 131, n.s.). The stay duration of these birds was not significantly correlated with their age (r_{13} = -0.47, n.s., Fig. 5). The mean period of the absence from the roost of the cormorants that stayed more than once during the same season was 40 ± 5.4 days (range: 22-69 days), and thus the re-sightings could not be mainly due to different pre- and post-breeding time of passage.

The mean age in the first season of the five individuals that were re-sighted during the second season of study was 2.4 ± 0.2 years, similar to the age of the other birds (U = 82.5, n.s.). Their stay duration (mean 10 3.8 days) did not differ from the other cormorants (U = 179, n.s.).

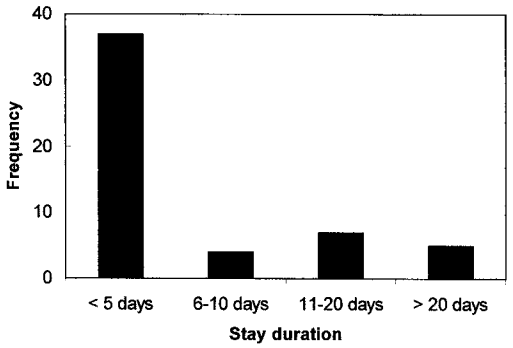

Figure 2. Stay duration of Great Cormorants wintering at the roost, showing the high proportion of short stays.

DISCUSSION

Origin of the Cormorants

The majority of the sightings were of birds reared in France, and these had been banded at a colony on Lake Grand-Lieu, in Loire-

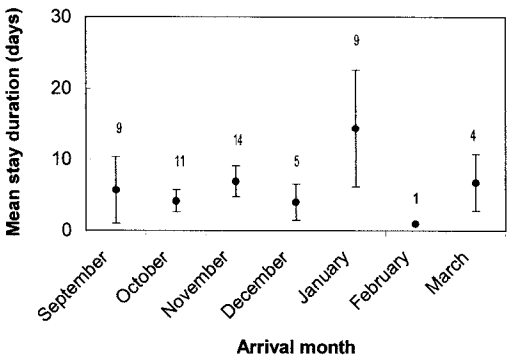

Figure 4. Stay duration of Great Cormorants in relation to month of arrival at the roost. Means are given with corresponding one standard error. The numbers above the bars are sample sizes.

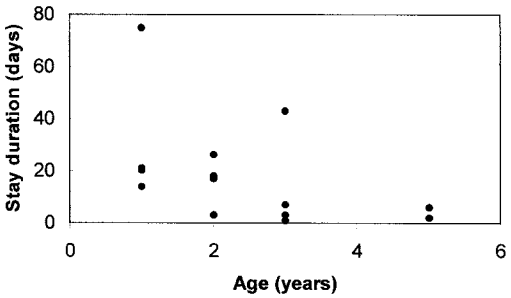

Figure 5. Relationship between stay duration and the age of Great Cormorants seen more than once in a year at the roost.

Atlantique. A comparison between countries of origin is biased toward the countries where large banding efforts are carried out. If the high banding efforts made in countries are taken into account (e.g., Denmark; Yésou 1995 and cited references; Bregnballe *et al.* 1997) there is a relatively low proportion of cormorants from countries other than France, and the geographical segregation becomes significant. Campos and Lekuona (1994) also found that a high proportion of birds in northern Spain came from France, but their study was carried out near the coast. Ibarra and Martín (1996) did not find French cormorants in central Iberia. Marion (1995) reported similar results, concluding that the French cormorants from the Grand-Lieu colony rarely migrated. Furthermore, only a few of these birds used inland areas in winter, and the low proportion of birds which moved to Iberia were limited to the coastal areas of north Spain (Marion 1995). This suggests that a change has occurred in recent years, and the French cormorants are now using inland Iberia in winter.

The differences found in the origin of the cormorants between autumn and winter are probably related to the distance between the roost and the countries of origin, with French birds arriving earlier as a consequence of the proximity to the breeding colony.

Although extensive color-banding programs on Great Cormorants have been carried out in the British Isles, none of the birds sighted in this study came from there, which is in agreement with the findings of Coulson and Brazendale (1968) that British cormorants reaching Iberia tended to winter on the coast and only few individuals went inland.

Stay Duration

The mean stay duration of the Great Cormorant was 40 days at a roost in France (Yésou 1995), and 64 days in northern Spain (Lekuona and Campos 2000), much higher than the value of seven days found here, where the majority of the birds seen on only one day (transients). Although the majority of visits by cormorants recorded by Yésou (1995) lasted less than eight days, a substantial proportion of birds stayed for over three months. Here, 91% of the visits lasted less than three weeks. These results suggest that the Great Cormorant showed a higher degree of nomadism in the interior of Iberia than in traditional wintering areas. It could also support the suggestion of Coulson and Brazendale (1968) that this species exhibits dispersal (i.e., random) movements outside the breeding season rather than migratory movements.

At the roost used in this study, Galván (2004) found that adult cormorants are dominant over first- and second-winter birds. It has been suggested that subordinates are poor competitors, which causes them either to leave densely populated stopover areas quickly, searching for unoccupied areas or to have longer stopovers as they attempt to replace fat reserves (Restani 2000; Kruckenberg and Borbach-Jaene 2004). In spite of the age-related dominance in the Great Cormorant, the adults do not cause subordinates to retreat, as they can make use high quality sites that are vacant (Galván 2004). This could explain the lack of correlation between the stay duration and the age of the birds.

At another cormorant roost, Yésou (1995) found that later arrivals in winter had a shorter stays. Although he did not give an explanation, his results are probably related to the fact that adult cormorants may leave earlier and migrate faster to arrive early at the breeding colony (Bregnballe *et al.* 1997). However, a relationship between the stay duration and the month in which the birds arrived at the roost was not found in this study.

Further investigations are required to determine the causes of this lack of seasonal effect. It is possible that more staging than migratory cormorants are present in inland Spain during the winter.

Site Fidelity

In Yésou's (1995) study, 40% of the cormorants were sighted during at least two seasons, and Frederiksen *et al.* (2002) estimated that about 85-90% of all surviving adults seemed to return to the same roost site from year to year. The low rate of return to the roost found in this study, both between two years or in the same winter, suggested that individual cormorants do not travel according to fixed patterns, contrary to the conclusions of some authors (Yésou 1995; Reymond and Zuchuat 1995a, b; Lekuona and Campos 2000; Frederiksen *et al.* 2002; Paquet *et al.* 2003). However, some of these authors have recognized a capacity for a substantial proportion of the cormorants to make nomadic movements outside the breeding season (Yésou 1995; Frederiksen *et al.* 2002), and that could be the case reported here.

According to Yésou (1995) and Paquet *et al.* (2003), and also in this study, the site-faithful cormorants stayed longer at the roost. Thus, the birds that stay longer may have a better knowledge of the feeding opportunities in the vicinity of the staging site, which encourages them to return. Although Yésou (1995) and Paquet *et al.* (2003) referred to roost-faithful individuals between years, this could be applied to within-season faithful birds. A possible exploration of the wintering area could be involved. The fact that, contrary to expectations, but similar to the results of Paquet *et al.* (2003), the age of roost-faithful cormorants did not differ from the rest is probably due to the failure to exclude subordinate young cormorants from poorer roost sites (Galván 2004).

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