INDIVIDUAL MIGRATION STRATEGIES IN CORMORANTS
Phalacrocorax carbo PASSING THROUGH OR WINTERING IN
WESTERN FRANCE

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ABSTRACT The attendance of individually recognisable Cormorants has been studied at a roost site in western France together with the overall use of this roost. Only first and second year birds arrived at the roost before mid-October and almost only 1st-year birds did so after February. In the meantime birds of any age arrived at any time, and the arrival dates of birds of different geographical origin did not vary significantly. A majority of stays (58%) were less than 8 days, and 21% of the stays lasted for more than three months (mean duration 139 days) but there are indications that the true proportion of birds performing long stays, probably elsewhere, must be higher. The mean duration of stays was 27 days, hence the number of birds using the roost during the season was 3.9 to 6.2 times higher than the highest mid-month count. Short-stayers did not tend to return to the area in consecutive years, although part of them remained faithful to their overall migration route. Long-stayers were markedly site-faithful: 48% of the first year birds among them returned at the same wintering site in their second winter; the return rate thereafter was c. 76%, i.e. close to the survival rate of these birds, indicating that site-fidelity was the rule for them. The presented data disagree with an earlier statement that Cormorants are 'nomadic' outside the breeding season. It is suggested that the strategy of long-staying and site-faithful individuals is of adaptive value.

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INTRODUCTION

Nearly 8000 Cormorants Phalacrocorax carbo overwintered in western France at the end of the 1980s (Marion 1991) while further birds stopped over in this area en route to and from more southern wintering places. In western France the Cormorants take advantage of a variety of coastal and inland habitats; they fish mainly in shallow bays, coastal marshes and large rivers and lakes, and concentrate on roosts of which the size rarely exceeds 1000 individuals (Pasquet 1981, Marion 1983, 1991).

Seasonal patterns as established by regular surveys of roosts seem to be reasonably predictable from one year to another. The question arises whether this predictability could be due to an individual tendency to follow more or less the same migration routes according to more or less fixed time schedules. This would mean that, contrary to the opinion expressed by Cramp & Simmons (1977), most individual Cormorants cannot be considered 'nomadic' outside the breeding season.

The existence in recent years of several extensive colour-ring programmes in several breeding colonies all over NW Europe (e.g. in Denmark, Gregersen 1991; The Netherlands, Van Eerden & Zijlstra 1988; Wales, Sellers & Sutcliffe 1987) has offered opportunities to study the attendance of individually recognisable Cormorants at a regular roost at Marais d'Olonne (western France) together with the overall use of this roost. The description of the observed seasonal and yearly patterns of individual arrivals, stays and departures of colour-ringed birds is bound to provide
clues as to whether and to what extent fixed individual migration strategies might exist.

**STUDY AREA AND METHODS**

Cormorants overwintering in the Olonne area fish in various habitats, including open sea, harbours, inland freshwater lakes and ponds. The majority of birds remains within the 1200 ha of Marais d'Olonne, an area of brackish marshes consisting of disused salines and thousands of very small fish ponds, i.e. a rather closed habitat as the ponds' surface area averages less than 0.25 ha. Also, up to 200-300 Cormorants move daily to foraging grounds situated at a distance of up to c. 25 km (Fig. 1). For a long time the Cormorants used to roost on a lighthouse 2 km off at sea, most of them perching on a helicopter platform erected on top. Up to 100-150 birds also gathered at a day roost on the Reserve de Chanteloup (38 ha), the only protected area within the marshes (Builles *et al.* 1986). The helicopter platform was dismantled in 1986, leaving room for only 100 birds or so on the remaining superstructure. The others now spend the night in the Réserve, where they roost on bare islets and a large dike. Both the lighthouse and the Réserve, as well as four other sites within the area, are also used as daytime roosts (Fig. 1).

Birds roosting in the Réserve have been counted just before sunset at least once a week in the years 1986-1992. Using an 89 mm Questar mirrorlens, extensive checks for colour-ringed birds were carried out 1-3 times a week from October 1982 to May 1992, with further, more casual observations made almost daily: a total of 1452 controls (not including repeated controls of the same bird on the same day) referring to 102 different individuals were realised. The origin of all these birds is known, but the date of ringing is known for only 86 of them as some codes were incompletely read or, more often, birds had lost one or more rings from their original combination.

Although the local situation allows easy observation of the birds' legs, it is uncommon for all the Cormorants actually present to be checked for rings on a given date. The chance of a marked individual being controlled is partly linked to the time it spends in the area. Some of the shorter stays - presumably up to a week or so - can remain unnoticed, and the observed length of a stay can be shorter than its true duration. Also, in the few cases when a bird was seen in week 1, not seen in week 2 but controlled again in week 3, it was considered more likely that it has just been missed, although the possibility that it has been away for one week cannot be ruled out. However, the extensive coverage carried out on Marais d'Olonne nevertheless allows a detailed description of the attendance pattern by colour-ringed Cormorants.

**RESULTS**

**Total number at roost**

The seasonal pattern of birds roosting at
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Fig. 2. Annual number of Cormorants roosting at Marais d'Olonne, based on mid-month counts, 1986-92. Note the marked decline in 1991/92 as a result of scaring off activities (see text).

Fig. 3. Individual stays of Cormorants, 1986-1992. Data refer to individual stays recorded each autumn, winter and spring.

Marais d'Olonne throughout the non-breeding seasons 1986-1987 to 1991-1992 is depicted in Fig. 2. From year to year there was a tendency for the birds to arrive sooner and, to a lesser degree, to depart later, while their numbers increased with a peak at c. 590 individuals in December 1990 and January 1991. The particular pattern in 1991-1992 was due to human inference: because of their predation on fish-ponds, the Cormorants were scared off in December-January both on the marshes and on the roost itself.

Fig. 3 depicts the arrivals of individually recognisable birds, along with the duration of their stay. Among them, 4 long-stayers were seen only intermittently in 1991-1992 as they deserted the roost during the scaring operations but soon returned to it once the trouble ended. There was
only one other case of intermittent attendance, that of RED 510 discussed below.

The comparison of Fig. 2 and 3 shows that the pattern of arrivals of individual birds coincided very well with the overall seasonal pattern. The departure dates did not follow so closely the overall pattern, as the duration of stays varied considerably, with many short-time stayers just passing through the area. The frequency of these short-time stayers, which arrived at all times of the year, also indicates that the total number of birds using the roost at any time was far larger than the mere counts would predict.

**Individual stays**

The duration of individual stays varied from 1 to 259 days. The average duration was 40.2 days (SD 56.6) when the multiple stays of birds returning for successive years are all taken into account, but only 26.9 days (SD 42.8) when the mean duration of their stays is used for these returning individuals. A majority of stays lasted less than 8 days (58%), including 39 one-day-only observations (30.2%). At the opposite, 27 stays lasted for over 3 months (20.9%) for an average duration of 139.4 days (SD 38.1); these very long stays concerned 13% of the marked birds, some of them returning for two years or more (see below).

These fluctuations in the duration of stays did not depend closely on the arrival date in autumn, as the mean expected duration did not vary significantly throughout the season, being of 57.4 days for a bird arriving in August (n = 10), 49.4 in September and October (n = 5 and 31 respectively), and 66.5 in November (n = 31). Later arrivals lead to shorter stays, with a mean expected duration of 22.3 days in December (n = 19), 17.7 in January (n = 9), and 6.8 from February to April (n = 22, pooled). The last figure can help understanding the discrepancy in the number of arrivals observed in October-December (n = 89) compared to February-April (n = 22): the shorter duration of their stay gave less opportunities to spot the birds stopping over during the return migration, the speed of which is further illustrated by two marked females that for three years were sighted at their breeding sites in The Netherlands and in Denmark (c. 835 and c. 1350 km to the north-east) only 5-8 and 5-6 days respectively after their last control at Marais d’Olonne (Table 1). Only 8 birds arrived in January: 5 of them were on 17-19 January 1987 when a cold spell obviously induced Cormorants to leave northern wintering spots.

The analysis of individual stays according to the origin of the birds showed that the rise in number in the early season was mainly due to the post-breeding dispersal from the growing colony at the lake of Grand-Lieu, c. 100 km to the north: 13 out of 17 individuals controlled in the period 25 July-30 September originated from this colony. Thereafter, the main movements involved marked birds of various origin (Ireland, England, Wales, NW France, The Netherlands, northern Germany, Denmark) arriving together: no geographic segregation was found in the arrival date of birds of different origin, neither in autumn nor during spring migration.

![Fig. 4. Year to year return by long-staying individuals. A definitive lack of record is shown as -. Possible return after the end of the study is indicated by ?](image-url)
Age-related differences in the arrival pattern appeared to be limited to the predominance of young birds in early and late season. Only first year birds were controlled before mid-September, and individuals over 2 years old were not seen before mid-October. Thereafter Cormorants of any age class arrived at any time up to the end of February. Out of 9 birds recorded in March-April, one was 8 years old while 6 (67%) were in their first year of life.

Site-fidelity
Twenty birds seen for the first time during the last season of study (14 1st-year birds and 6 of unknown age) cannot help in the study of site-fidelity in migrating and overwintering Cormorants. Among the 82 remaining individuals, 42 (51.2%) stopped over only briefly (1 to 7 days, mean 2 days, SD 1.6): none of these short-stayers was spotted again on the study area in a subsequent season.

Among the 40 birds which stayed over one week, 16 (40%) were controlled again during at least another season (Fig. 4). The percentage of birds controlled in one season and again the following season was 47.8% in first year birds (n = 23), 75% in second year (n = 12), 55.6% in 3rd year (n = 9), 100% in 5th to 7th year (n = 2) and 50% in 8th year (n = 2). Thus there was 75.8% chance (SD 23.4) for a 2-8 year old bird staying more than a week to be spotted again during the next season. The site tenacity shown by these long-staying individuals returning from year to year is further exemplified by the rapid return of 4 of them to the study area after the scaring in December 1991-January 1992. At least two of these birds were back there in the autumn of 1992 despite the disturbance they experienced the previous year.

Three of the Cormorants which were seen during only one season nevertheless gave useful information on site fidelity, or the lack of it. One Dutch first year bird visited the study area on 4-30 October 1987 and was controlled during the same winter c. 200 km to the south at a locality where it returned and died the next year, thus being faithful to its overall migration route if not to a precise stopover. Conversely, another first year bird from The Netherlands which overwintered at Marais d’Olonne from 14 November 1985 to 6 February 1986 was found dead the next January in Lincolnshire, eastern England, c. 800 km northeast. A third Dutch bird was located in Camargue, southern France, during its first winter, then was not reported up to seven years later when it turned up for one day in the study area.

Individual schedule of returning long-stayers
The year to year variation in the observed arrival dates of returning birds did not usually show any particular trend, seeming ‘erratic’ within a range of up to a month or so, as exemplified by the case of WHITE 715 (Table 1). One bird which arrived very early in its first year thereafter arrived later every year (Table 2), while another arrived sooner every year (1 December 1989, 9 November 1990, 30 October 1991). However, it remains unclear whether these trends will be continued in the forthcoming years, or these birds too are already adopting the usual ‘erratic’ trend. Similarly, the departure date of most long-stayers varied each year without an obvious trend (Tables 1, 2).

A unique case is that of RED 510. In most years this male arrived erratically in November and stayed for a longer duration every year; then
Table 2. Recorded stay at Marais d'Olonne for VIOLET TH (assumed female), ringed as nestling at St. Margaret’s Island, Co. Dyfed, Wales, 18 June 1988.

<table>
<thead>
<tr>
<th>Winter</th>
<th>Stay at Marais d’Olonne</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988/89</td>
<td>19.08 - 02.05</td>
</tr>
<tr>
<td>1989/90</td>
<td>27.09 - 19.04</td>
</tr>
<tr>
<td>1990/91</td>
<td>18.10 - 05.04</td>
</tr>
<tr>
<td>1991/92</td>
<td>09.10 - 06.12, 27.02 - 25.03</td>
</tr>
</tbody>
</table>

Table 3. Recorded stay at Marais d’Olonne for RED S10, ringed as nestling at Brændegårds Sø, Denmark, 5 June 1982.

<table>
<thead>
<tr>
<th>Winter</th>
<th>Stay at Marais d’Olonne</th>
</tr>
</thead>
<tbody>
<tr>
<td>1982/83</td>
<td>no records</td>
</tr>
<tr>
<td>1983/84</td>
<td>no records</td>
</tr>
<tr>
<td>1984/85</td>
<td>02.11 - 08.11, 13.01</td>
</tr>
<tr>
<td>1985/86</td>
<td>21.11 - 29.11, 21.01</td>
</tr>
<tr>
<td>1986/87</td>
<td>09.11 - 25.11, 22.01</td>
</tr>
<tr>
<td>1987/88</td>
<td>09.11 - 28.11, 28.01 - 03.02</td>
</tr>
<tr>
<td>1988/89</td>
<td>01.12 - 09.01</td>
</tr>
<tr>
<td>1989/90</td>
<td>15.01 - 18.01</td>
</tr>
<tr>
<td>1990/91</td>
<td>30.11 - 06.12, 17.01 - 24.01</td>
</tr>
<tr>
<td>1991/92</td>
<td>no records (possibly dead ?)</td>
</tr>
</tbody>
</table>

it departed for a probably southern place but re­appeared briefly on the way back in January­February. During two winters however, it apparently chose Marais d’Olonne as its final mid­winter stop-over (Table 3).

**DISCUSSION**

The overall seasonal pattern of attendance at the roost of Marais d’Olonne is the result of the combination of a number of individual stays , the duration of which varies greatly. More than half of the Cormorants frequenting the roost use it only briefly, and the average duration of an individual stay is close to one month. This allows turnover to be estimated by dividing the annual total number of bird-days by 30 days. It appears that the true number of birds roosting at Marais d’Olonne a given year is 3.9 to 6.2 times (mean 4.5, SD 0.8, n = 6 years) the highest mid-month count for that year.

A minority of the observed stays lasted for a much longer period: three months or more in the case of 13% of the marked individuals. This figure very probably underestimates - maybe considerably - the proportion of birds which perform long stays, as part of the Cormorants that stopped over briefly at Marais d’Olonne during the autumn migration may later on have stayed for a long time at a more southerly wintering place. The fact is that long-stayers, some of them returning for many years, are a regular feature of individual attendance at any roost surveyed in western France, i.e. in the Loire valley (D. Muselet pers. comm.), at L’Aiguillon in southern Vendée (Yésou 1989, 1991, M. Fouquet pers. comm.), at Ile de Ré (H. Robreau pers.‘ comm.) and near Bassin d’Arcachon (C. Feigné pers. comm.). Still, a certain proportion of the short-stayers visited the study area at dates which imply that they cannot have stayed for a long period anywhere. A larger set of data, preferably combining records from different roosts, would be helpful in estimating the proportion of long-staying and short-staying individuals among the entire population. This would also help understanding the strategy of those birds which obviously are not so site-faithful within one season.

Although some individuals have possibly been overlooked during their return migration in spring, due to the short duration of their stay, it appears that as a rule the birds stopping over briefly during migration are not site-faithful in the study area from one year to another. It is suggested that they may stop over here or there according to the particular conditions they are facing when on the move. The situation is markedly different for the long-staying individuals. Among the birds staying for a long time in their first winter, 48% return to the study area in their second winter: this figure coincides with Gregersen’s (1991) estimate of the proportion of birds returning to the colony in their second
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calendar year, i.e. 35-50%. What happens to the other 50-65% remains speculative. While 8% are reported dead in their first year, Gregersen (1991) estimated that actually 25% of the Cormorants are dying during this period. If this figure were correct (Gregersen’s estimate is not supported by a proper study of the species’ demography), the non-philopatric part of the population of first winter birds could be estimated at at least 25%. The return rate of older birds (c. 76% on average) is certainly closer to their survival rate, as unpublished information on the average age of death (J. Gregersen pers. comm.) suggests a survival rate of 70-80%. Thus, returning every year to the same locality appears to be the rule for those adult Cormorants that stay a long time at one place in the course of the non-breeding season.

It must be stressed, however, that not all the Cormorants are long-stayers. Some already undertake their return migration in winter while others stay until early spring. Others are more mobile in mid-winter and fit better the ‘nomadic’ behaviour proposed by Cramp & Simmons (1977) as being the rule for the species. There is little doubt that these varying individual schedules have adaptive value with respect to for example an early return to the breeding colonies, especially for males that must occupy and defend a nest site, or returning in optimal physical condition, particularly for the females. Although not sufficient to prove it, some of our data agree well with this hypothesis (including site-faithful long-staying females returning late while a male was regularly migrating early). It is likely that birds that stay longer have a better knowledge of the feeding opportunities in the roost’s vicinity, and may thus enhance their foraging efficiency. This, in its turn, may lead to a higher amount of time actually spent at the roost and, consequently, to a more effective defense of their own spot there. Long-staying individuals may thus force other birds to move further south. About the factors that cause an individual Cormorant to be a long-staying and site-faithful bird at a given latitude in the non-breeding season, speculations have been made by Munsterman & Van Eerden (1991) and Reymond & Zuchuat (1995). Sex, age and individual ‘experience’ seem to be important, but a true understanding of this matter requires a thorough evaluation of the circumstances met by birds with a fixed migration pattern and by birds with a more ‘nomadic’ strategy and of the way they cope with them.

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REFERENCES


SAMENVATTING

Regelmatige tellingen en ringaflezingen op een slaapplaats van Aalscholvers in West-Frankrijk (Marais d’Olonne) in de jaren 1986-1992 laten zien dat het patroon van het bezoek - een snelle toename in september/oktober, maximale aantallen in december/januari en een snelle afname in februari/maart - tot stand komt door een combinatie van individuele verblijven van sterk uiteenlopende tijdsduur. De meeste verblijven (58%) duren minder dan 8 dagen, terwijl slechts 21% van de verblijven (betrekking hebbend op 13% van de gemerkte vogels) drie maanden of langer duurt. De gemiddelde verblijftijd is ongeveer een maand, zodat wordt geschat dat het aantal vogels dat gemiddeld per seizoen de slaapplaats bezoekt 4.5 maal hoger is dan het dat jaar getelde maximum.

De vogels die korte bezoeken doorbrachten, zullen gedeeltelijk verder zuidwaarts trekken waar ze mogelijk in een ander gebied wel langduriger verblijven. Een ander deel van de kort verblijvende vogels verscheen echter op data die het onaannemelijk maken dat ze waar dan ook langer dan een week geweest zijn. Van de vogels die meer dan een week achtereen werden gesignaleerd bleek onder de eerste winter exemplaren 48% ook in hun tweede winter gezien te worden. Van de 2-8 jaar oude vogels onder de ‘lange verblijvers’ werd zelfs zo’n 76% in een opeenvolgend seizoen teruggezien, hetgeen ongeveer overeenkomt met de geschatte jaarlijkse overleving.

Aalscholvers die een overwinteringsgebied voor langere tijd bezoeken, vertonen in de regel dus ook van jaar tot jaar plaatsstrouw. Verder onderzoek, waarin gegevens over meer winterslaapplaatsen moeten worden betrokken, zal moeten aangeven welk aandeel van de totale populatie bestaat uit deze langverblijvende en plaatsstrouwe individuen. Tenslotte worden enkele redenen voor verschillende individuele trek- en overwinteringsstrategieën besproken.