# Site fidelity of wintering cormorants Phalacrocorax carbo sinensis in Europe

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# ORIGINAL ARTICLES

# Site fidelity of wintering cormorants *Phalacrocorax carbo sinensis* in Europe

**Morten Frederiksen, Thomas Bregnballe, Mennobart R. van Eerden, Stef van Rijn & Jean-Dominique Lebreton**

The breeding population of cormorants *Phalacrocorax carbo sinensis* has expanded more than twenty-fold in continental Europe since 1970, and these large piscivorous birds cause conflicts with human fishery interests in large parts of Europe, including areas outside their breeding range. Culling aimed at reducing local population size takes place in some wintering areas, particularly in France and Switzerland. The effectiveness of such management actions is unknown and depends on how high cormorant site fidelity is. We use winter resightings from the period 1980-2000 of 24,000 cormorants colour-ringed in Denmark and The Netherlands to estimate site fidelity. Year-to-year fidelity to single sites (typically lakes) was 85-90%. For cormorants that changed site mean distances moved from year to year were typically between 10 and 50 km, depending on geographical location. However, long-distance movements (maximum observed was 1,891 km) also occurred regularly. For larger parts of the winter range, exemplified by France, about 3% of all birds left the area from year to year. A mathematical model showed that the observed levels of movement among wintering areas were sufficiently high to sustain a wintering population in France at levels of culling which would drive it to extinction in the absence of immigration. Although cormorants are not nomadic outside the breeding season, as previously believed, site fidelity is sufficiently low and movement among wintering areas sufficiently high that it must be taken into account in management programmes.

*Key words: cormorant, local survival, management, mathematical model, Phalacrocorax carbo sinensis, site fidelity, wintering ecology*

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Since 1970, the population of cormorants of the continental subspecies *Phalacrocorax carbo sinensis* breeding in northern Europe has increased dramatically from less than 5,000 to more than 100,000 pairs (Bregnballe 1996, Trolliet 1999). Cormorants are large piscivorous birds, and conflicts with human fishery and aquaculture interests have become widespread over the same period (Kirby, Holmes & Sellers 1996, van Dam & Asbirk 1997). Some of the most important conflicts occur in areas in central and southern Europe where cormorants occur only or mainly during the non-breeding season. In response to demands from fishery interest groups, governments in several countries in the wintering range have introduced culling as a measure intended to limit numbers of cormorants and the damage they cause at a local scale (e.g. Keller, von Lindeiner & Lanz 1998). The local effect of these culls depends on the degree of exchange of birds among various wintering populations: the more closed the local 'population' is, the greater effect will be expected from local culls. In the extreme case of absolute site fidelity, population control could be efficiently carried out at e.g. single lakes even though no measures were taken at neighbouring locations. At the other extreme, if birds redistribute themselves randomly from winter to winter, effects of culling will only be apparent at the scale of the total range, and quite large culls may be necessary to cause a measurable reduction in local numbers of cormorants. Both of these cases are very unlikely, but they serve to illustrate the fact that information about the extent of winter site fidelity is highly relevant for population management.

Measuring site fidelity at non-breeding locations requires information from individually marked birds. In some species with a low number of traditional wintering areas, high probabilities of observation can be achieved and direct estimation of probabilities of inter-site movement is possible using capture-recapture analysis (e.g. geese; Hestbeck, Nichols & Malecki 1991, Warren, Fox, Walsh, Merne & Wilson 1992, Reed, Cooch, Goudie & Cooke 1998). Cormorants, on the other hand, winter over most of Europe, spread over thousands of locations, and more indirect methods have to be used. Large numbers of cormorant chicks have been ringed with coloured darvic rings, readable from a long distance, in several European countries, and repeated resightings

of these birds provide valuable information on winter site fidelity. Here, our aim is to extract as much information as possible on winter site fidelity from resightings and dead recoveries of approximately 24,000 cormorants colour-ringed in Denmark and The Netherlands during 1977-1998. To achieve this, we employ several different methods.

Repeated resightings of colour-ringed individuals at single sites have shown that cormorants often use the same wintering or staging sites in several consecutive years (Yésou 1995, Reymond & Zuchuat 1995b). This type of data can be subjected to capture-recapture analysis, and the estimated local winter-to-winter survival can then be compared with an estimate of 'true' survival, i.e. not confounded by emigration (Clobert & Lebreton 1991), to provide information on site fidelity. Such an analysis requires regular observation of a fair number of marked birds over several years and can at present only be carried out for a few well-covered sites. More information becomes available when all winter resightings are included, i.e. resightings from the many sites with more sporadic coverage and/or a low number of birds seen per season are also included. Probabilities of changing site and mean distances of movement can then be estimated. Estimated probabilities of changing site will tend to be biased because the probability of being resighted at the same location will generally be higher than at other locations, i.e. the probability of changing site will thus be underestimated. Information less likely to be biased in this respect is also provided by winter recoveries of dead birds previously resighted in winter, although the sample size is inevitably small for this type of analysis.

In order to integrate the results from our analyses and to show how the degree of interchange of birds between two areas with different culling practices can influence the effect of the culls, we developed a simple mathematical model. Because this question has been raised particularly in a French context, we attempt to illustrate how the effect of culls in a small part of the total range (France) can be 'diluted' by exchange of birds with a larger pool which is not subject to culling (Lebreton & Gerdeaux 1996). To provide input for this model, we first estimate the probability that a cormorant will change its wintering site from France to other areas or *vice versa*.

Table 1. Total sample sizes of cormorants for analyses of winter site fidelity. The total numbers of birds colour-ringed during 1977-1998 in Denmark and The Netherlands are 20,374 and 3,374, respectively.

| Time window | Denmark | | The Netherlands | | Total | |
|---|---|---|---|---|---|---|
| | Resightings | Birds | Resightings | Birds | Resightings | Birds |
| November-February | 6663 | 1819 | 1161 | 310 | 7824 | 2129 |
| December-February | 4593 | 1459 | 781 | 238 | 5374 | 1697 |

## Methods

### Selection of data

In this article, we use data from the Danish and Dutch ringing programmes, in which large numbers of chicks have been colour-ringed since 1977 and 1983, respectively. Table 1 shows total sample sizes for the two data sets. The definition of which winter 'time window' to use was not obvious, since cormorants can show migratory movement as late as mid-November and as early as late February (van Eerden & Munsterman 1986, Yésou 1995, Bregnballe, Frederiksen & Gregersen 1997). In order to check for the influence of the length of the time window, we ran most analyses with data from both November-February and December-February.

### Local survival

Three sites with regular resightings of large numbers of colour-ringed cormorants over a number of years were selected; all three were lakes in the Alpine region. The largest data set came from the roost Les Grangettes de Noville at Villeneuve at the eastern end of Lake Geneva (Lac Léman), Switzerland (46°23'N, 6°54'E). The other sites with sufficient data were Risch, Lake Zug (Zugersee), Switzerland (47°08'N, 8°28'E), and the eastern end of Lake Constance (Bodensee, ca 47°30'N, 9°40'E), where data from both the German (Lindau) and the Austrian part (Bregenz) of the lake were used. Sample sizes for all three sites are shown in Table 2; in all cases the data came almost exclusively from birds ringed in Denmark, since few Dutch cormorants winter so far east (Reymond & Zuchuat 1995a).

For each site, the resightings were collated into individual capture histories, indicating whether a bird was seen in a given winter or not. These were then analysed using standard capture-recapture methods (Lebreton, Burnham, Clobert & Anderson 1992) in program MARK (White & Burnham 1999) to give estimates of local survival and resighting probabilities. Initial goodness-of-fit tests in program U-CARE (Choquet, Reboulet, Pradel & Lebreton 2001) indicated that an excess number of birds disappeared following the first observation (transient effect); this was expected both because the individuals were a mixture of juveniles and adults, with juveniles showing higher mortality, and because some migrants passing through may inadvertently have been included in the data sets. Accordingly, we used models with two age classes for survival (Pradel, Hines, Lebreton & Nichols 1997), and took survival of the second age class as an estimate of local survival of adults. This estimate was then compared with values from the literature for adult survival of cormorants ringed in Denmark (Frederiksen & Bregnballe 2000) to give an estimate of site fidelity F: $F = \phi/S$, where $\phi$ denotes local survival and S true survival. Frederiksen & Bregnballe (op. cit.) used the approach developed by Burnham (1993) to estimate 'true' survival, i.e. without an emigration bias, from a combination of dead recoveries and live resightings.

### Resightings in multiple winters

For each winter a colour-ringed bird was observed, we calculated mean geographical coordinates in radians (if a bird was seen at more than one site), and subsequently orthodromic distances D between mean coordinates in successive winters using the formula:

$$D(km) = 12800 \arcsin\left(\sqrt{\frac{1 - \cos(lat_b)\cos(long_b - long_a)\cos(lat_a) - \sin(lat_a)\sin(lat_b)}{2}}\right),$$

Table 2. Sample sizes, models selected and estimates of local survival of cormorants at the three alpine lake sites, Les Grangettes, Risch and Lindau/Bregenz.

| Site | Time window | Period | Sample size (observations/birds) | Model structure | Estimated local survival |
|---|---|---|---|---|---|
| Les Grangettes | November-February | 1984-1990 | 430/222 | Time | 0.52 - 0.94 (mean: 0.77) |
| | December-February | 1984-1990 | 271/147 | Constant | 0.76 |
| Risch | November-February | 1984-1990 | 145/ 94 | Constant | 0.99 |
| | December-February | 1984-1988 | 98/ 66 | Constant | 1 |
| Lindau/ Bregenz | November-February | 1986-1992 | 178/117 | Constant | 0.76 |
| | December-February | 1986-1992 | 113/ 65 | Constant | 0.78 |

where $lat_a$, $long_a$, $lat_b$ and $long_b$ are mean coordinates for the two winters involved. This formula assumes the Earth to be a perfect sphere, but the bias introduced by this assumption is very small over the limited geographical scale considered here. The total sample sizes were 1,218 (representing 630 birds) for November-February and 854 (482 birds) for December-February. About 60% of the calculated D were equal to zero, and the distribution of the remaining distances was strongly skewed to the right, i.e. towards longer distances. We therefore performed the analysis in two stages.

Because the probability of detecting colour-ringed cormorants was <1, and more importantly because the detection probability was expected to vary over time and space in an unpredictable way, we could not directly estimate the probability that a bird would change its wintering site. The first stage of the analysis thus consisted of a logistic regression of the probability P of being observed at a different site, given that the individual was observed at all, (D > 0) as a function of age (juvenile or adult), origin (Denmark or The Netherlands), birth cohort, year, geographical position (country or geographical coordinates), lag (number of years between two subsequent observations of a bird) and lag$^2$ (to account for non-linearity). For this analysis, we used SAS PROC GENMOD.

In the second stage, we log-transformed all D > 0 (N = 498 for November-February and N = 324 for December-February) in an attempt to achieve normality. Transformed distances were approximately normally distributed, although somewhat platykurtotic (Fig. 1). We then ran general linear models (SAS PROC GLM) with the same
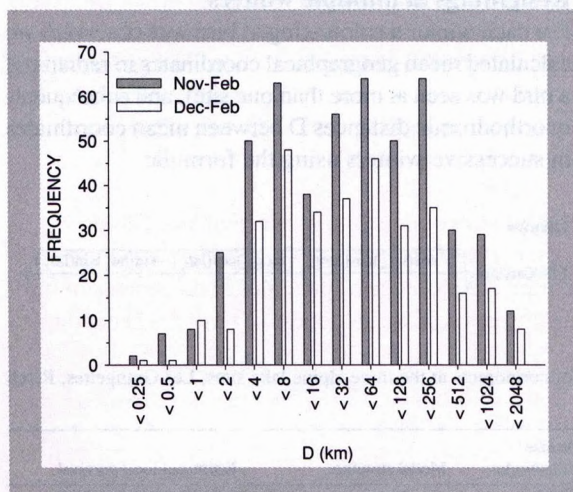


Figure 1. Frequency distribution of D, the distance between mean locations in two subsequent winters in which a cormorant was observed, for the data sets November-February (N = 498) and December-February (N = 324). The number of cases in which D was 0 was 720 and 530 in the two data sets, respectively.

factors and covariates as in the logistic regression above.

We predicted that both P and D would increase in a non-linear fashion as the number of years between subsequent observations (lag) increased. This prediction was made because undetected return movements, cases of which were known from individuals observed in several consecutive winters, would be more likely to have occurred when several years had elapsed between two observations.

## Winter recoveries

Some cormorants resighted in winter were later found dead in the same or a subsequent winter. For these individuals, we calculated distances $D_{rec}$ between the location of the last winter resighting and the recovery site with the above formula. A few birds were recovered at the resighting site (six and two in the two data sets), but generally the distribution of $D_{rec}$ was skewed to the right. We therefore calculated $\ln(D_{rec} + 1)$; this quantity was approximately normally distributed. Sample sizes were 85 for November-February and 55 for December-February; both resighting and recovery were required to occur within the respective time windows. General linear models were run with the following factors: year, country, age and lag (recovered in the same winter as the last resighting or later).

## Model selection

In all the analyses, we selected the most appropriate model to describe the data using $AIC_c$, Akaike's Information Criterion adjusted for small sample size (Burnham & Anderson 1998). This quantity selects a model that has an optimal balance between bias and precision, or in other words, the minimal adequate model (Crawley 1993), where all important effects, but no others, are included. $AIC_c$ is defined as:

$$AIC_c = Deviance + 2K + \frac{2K(K+1)}{n - K - 1}$$

(Burnham & Anderson 1998), where n is the sample size and K is the number of parameters in the model. For capture-recapture analysis and logistic regression, the deviance is provided by the software used (MARK and SAS, respectively; MARK even calculates $AIC_c$). For general linear models, the deviance must first be calculated as:

$$Deviance = -\frac{n}{2} \ln\left(\frac{RSS}{n}\right)$$

(Burnham & Anderson 1998), where RSS is the residual sum of squares.

In general linear models, K includes the intercept and the number of estimated slopes plus an additional parameter for the estimated $\sigma^2$ (Burnham & Anderson 1998).

## Probability of leaving/entering France

The probability $\psi$ of moving between two areas, in this case France and the rest of Europe, can be estimated from the log odds ratio (LOR) between faithful and non-faithful individuals:

$$LOR = \ln(\frac{n_{11}n_{22}}{n_{12}n_{21}}),$$

where $n_{ij}$ is the numbers of individuals seen in area i in one year and in area j in the next year. The expected LOR is:

$$LOR = \ln(\frac{(1-\psi_{12})Sp_1(1-\psi_{21})Sp_2}{\psi_{12}Sp_2\,\psi_{21}Sp_1}),$$

where S is survival (assumed independent of area), $p_1$ and $p_2$ resighting probability in the two areas, and $\psi_{12}$ and $\psi_{21}$ transition probabilities in the two directions. S, $p_1$ and $p_2$ cancel out, so this simplifies to:

$$E(LOR) = \ln(\frac{(1-\psi_{12})(1-\psi_{21})}{\psi_{12}\psi_{21}})$$

$$= - (logit(\psi_{12}) + logit(\psi_{21})).$$

Assuming for the sake of simplicity that transition probabilities in the two directions are equal, i.e. $\psi_{12} = \psi_{21} = \psi$, then $LOR = -2logit(\psi)$; $\psi$ can then be estimated by taking the inverse logit:

$$\hat{\psi} = \frac{e^{-LOR/2}}{1+e^{-LOR/2}}.$$

The variance of LOR is estimated as:

$$var(LOR) = \sum \frac{1}{n_{ij}} \text{ (Everitt 1992)}.$$

Confidence limits of LOR can then be calculated and back-transformed into confidence limits of $\psi$ using the formula above. We applied this estimator to all repeat resightings with a lag of one year (N = 836). The estimator is in principle insensitive to differences in resighting probabilities between the two areas, but will be affected by the geographical distribution of the resighting effort; if the resighting effort is concentrated to areas close to the border, $\psi$ will tend to be inflated because birds changing area are more likely to be detected. The assumption that transition probabilities are equal in the two directions is unlikely to hold - see Discussion.

## A 'dilution' model

We built a simple two-compartment matrix model, which allows logistic population growth within each compartment, culling in one compartment, and exchange of individuals between the two compartments. The general structure of the model was:

$$\begin{bmatrix} N_1^{t+1} \\ N_2^{t+1} \end{bmatrix} = \begin{bmatrix} pe^{\ln(\lambda_1)(1-N_1^t/K_1)} & (1-c)(1-q)e^{\ln(\lambda_2)(1-N_2^t/K_2)} \\ (1-p)e^{\ln(\lambda_1)(1-N_1^t/K_1)} & (1-c)qe^{\ln(\lambda_2)(1-N_2^t/K_2)} \end{bmatrix} \begin{bmatrix} N_1^t \\ N_2^t \end{bmatrix},$$

where N is population size, K is carrying capacity, $\lambda$ is the maximum population multiplication rate, p and q are fidelity probabilities to the two compartments (equivalent to $1-\psi$), c is the proportion culled in compartment 2, and the subscripts 1 and 2 refer to the two compartments. In order to simulate the French situation, which includes a lower observed growth rate of the French wintering population than of the total breeding population, $\lambda_1$ was set at 1.18, $\lambda_2$ at 1.15, and the model was initiated with $N_1 = 300,000$ and $N_2 = 60,000$. $K_1$ and $K_2$ were set at 360,000 and 120,000, respectively. For simplicity, q was assumed to be equal to p. The parameters c and p were then varied, and the equilibrium population sizes $N_1$ and $N_2$ noted.

## Results

The maximum number of winters in which any individual was observed was nine. This was achieved by Yellow 401, a bird ringed in Denmark, which was observed a total of 23 times in winter between 27 January 1986 and 27 January 1994 at Orbetello in central Italy, and never anywhere else. White E|W, which was ringed in The Netherlands, was seen 10 times in winter between 17 January 1989 and 9 December 1997 at Marismas del Odiel in southwestern Spain, but it was not observed in two of the 10 winters. The longest recorded move between two winters was performed by Blue L59, a bird ringed in Denmark, which was seen on 28 December 1988 at Ammersee in southern Germany, and again on 14 January 1992 at Coto de Doñana in southern Spain, a distance of 1,891 km. There were 12 cases of moves of more than 1,000 km and 42 cases of moves of more than 500 km (see Fig. 1).

### Local survival as an estimate of site fidelity

After accounting for the two-age-class structure, indicating the presence of juveniles and/or transient birds in the data sets, the goodness of fit of the general mod-

Table 3. Model selection for logistic regression. The selected model is indicated in italics.

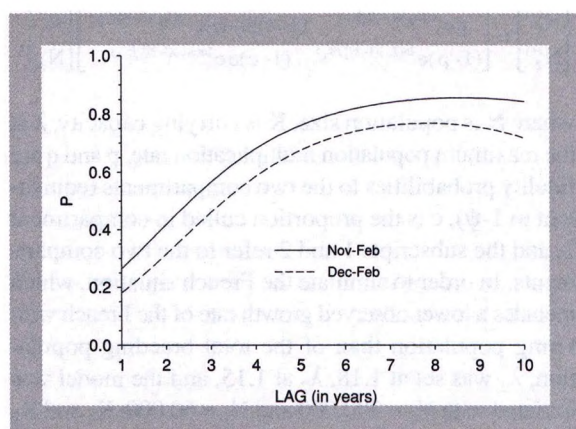| Model | ΔAIC$_c$ | |
|---|---|---|
| | November-February | December-February |
| *lag lag² country year* | 0 | 0 |
| lag lag² country year age | 2.11 | 1.81 |
| lag country year | 7.46 | 13.02 |
| lag lag² country | 15.85 | 9.16 |
| lag lag² lat long year | 131.81 | 77.67 |

Figure 2. The estimated probability (P) of being detected on a different site, given detection, as a function of the lag (in number of years) between two observations for the data sets from November-February and December-February. The example in the figures shows results concerning cormorants observed in France in 1990. Since the model contains no interaction terms, the pattern is the same for all countries and years.



Figure 4. The estimated probability (P) of being detected on a different site, given detection (see Fig. 2), as a function of year of observation. The example in the figure shows results concerning birds observed in France with a lag of one year. Since the model contains no interaction terms, the pattern is the same for all countries and values of lag.

el with time-dependent parameters was acceptable for all six data sets (three sites, two time windows). We attempted to simplify the model by setting survival and/or recapture probabilities constant; this was acceptable in some cases for survival, as judged from $AIC_c$. The estimated values for local survival in the second age class are shown in Table 2; most of these were in the range 0.75-0.80, but at Risch local survival was surprisingly estimated as 1. Disregarding this aberrant estimate, and taking into account that adult survival of Danish cormorants in the years concerned was approximately

0.90 (Frederiksen & Bregnballe 2000), site fidelity F at the local scale could be estimated as approximately 0.85-0.90.

## Resightings in multiple winters

For both time windows, the logistic regression resulted in selection of a model that expressed P, the probability of being observed at a different site given observation (D > 0), as a function of lag, lag², country and year (Table 3). $R^2$ for this model was 18.7% for November-February and 18.8% for December-February. P increased non-linearly with an increasing number of years between two observations (Fig. 2), and varied among countries (Fig. 3) and years (Fig. 4). In most years, P was lower for the shorter time window.

The general linear model selected differed slightly between the two time windows (Table 4). For November-February, a model with lag, lag² and country explained 18.9% of the variation in ln(D), whereas for December-February, a model with lag, lag² and geo-
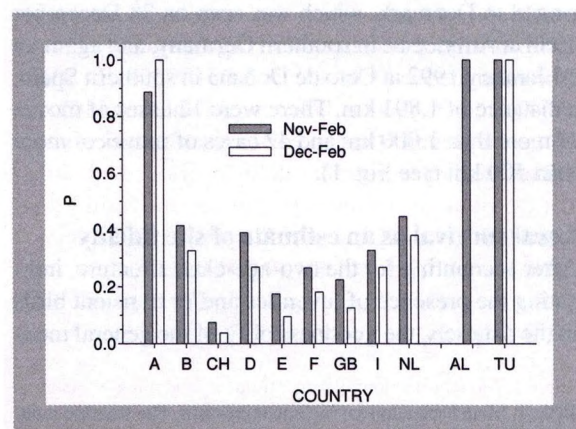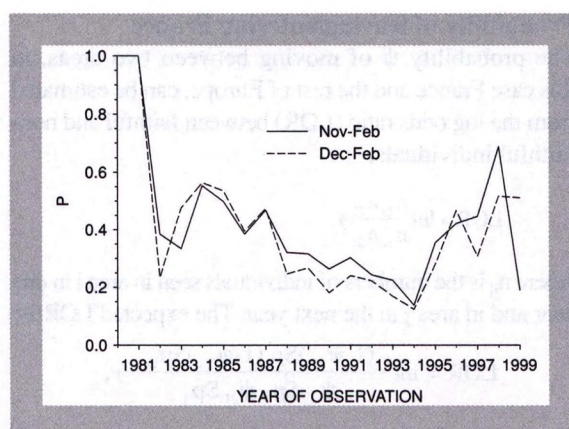


Figure 3. The estimated probability (P) of being detected on a different site, given detection, as a function of which country the bird was observed in. Country codes are A: Austria, B: Belgium, CH: Switzerland, D: Germany, E: Spain, F: France, GB: Great Britain, I: Italy, NL: The Netherlands, AL: Algeria, TU: Tunisia. The example in the figure shows results concerning birds observed in 1990 and again in 1991 (lag = 1). Since the model contains no interaction terms, the pattern is the same for all years and values of lag.

Table 4. Model selection for general linear modelling of distances between successive resightings. The selected models are indicated in italics.

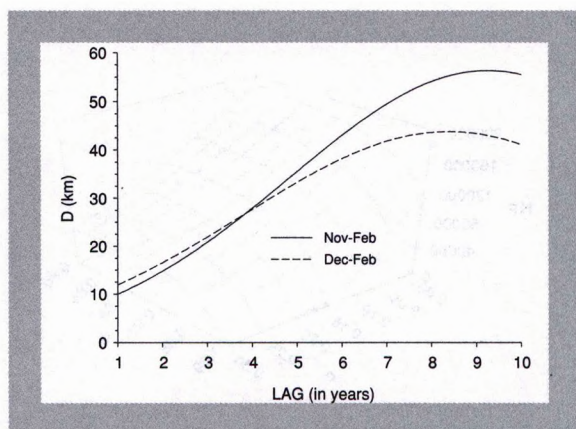| Model | ΔAIC_c | |
|---|---|---|
| | November-February | December-February |
| *lag lag² country* | 0 | 5.92 |
| lag lag² country age | 1.12 | |
| lag country | 3.13 | |
| lag lag² | 48.89 | 29.18 |
| lag lag² lat long age | | 1.86 |
| lag lat long | | 2.38 |
| *lag lag² lat long* | 0.26 | 0 |

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Figure 5. Back-transformed mean distance moved (D) between two subsequent observations of an individual cormorant that changed site as a function of the lag (in number of years) between two observations for the data sets from November-February and December-February. The example in the figure shows results from France for November-February, and for the position 47°N, 3°E (centrally in France) for the December-February data set.

graphical coordinates was selected; this model explained 14.7% of the variation. The model with coordinates was also a strong competitor for the November-February data set ($\Delta AIC_c = 0.26$). The back-transformed mean of ln(D), which is equivalent to the geometric mean of D, increased non-linearly with lag (Fig. 5), and tended to be higher for more easterly areas (Austria, Switzerland, Germany, Italy; Figs. 6 and 7) and for the countries in North Africa. Residuals from the selected models followed a normal distribution.
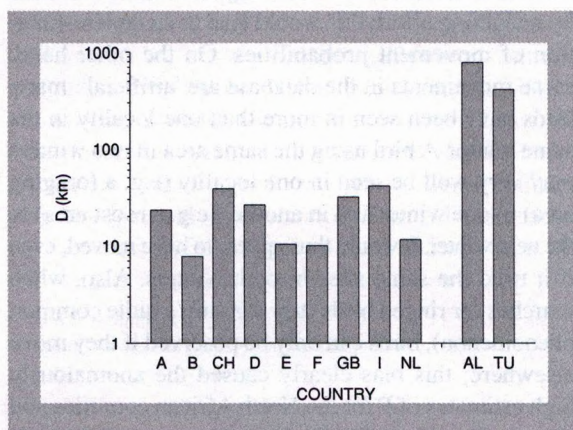


Figure 6. Back-transformed mean distance moved (D) between two subsequent observations of an individual cormorant that changed site (November-February data set) as a function of which country the bird was observed in. Country codes are A: Austria, B: Belgium, CH: Switzerland, D: Germany, E: Spain, F: France, GB: Great Britain, I: Italy, NL: The Netherlands, AL: Algeria, TU: Tunisia. The example in the figure shows results for a lag of one year.
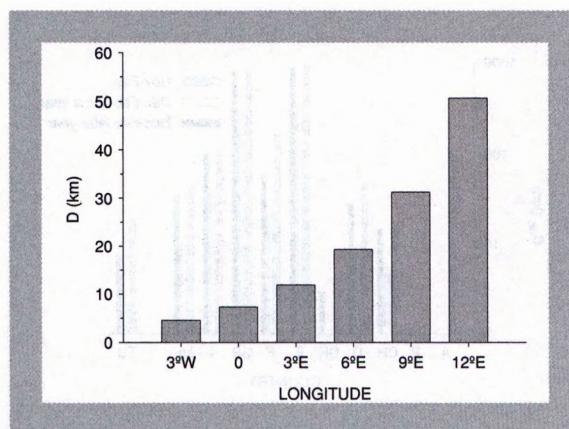
Figure 7. Back-transformed mean distance moved (D) between two subsequent observations of an individual cormorant that changed site (December-February data set), as a function of longitude (latitude held fixed at 47°N). The example in the figure shows results for a lag of one year.

### Winter recoveries

For the November-February data set, the selected model contained only the effect of country (Table 5), which explained 27.8% of the variation. The selected model for December-February included country and lag (recovery in same winter or later) and explained 44.0% of the variation. Residuals from the models were normally distributed. Median $D_{rec}$ was shorter for birds recovered in the same winter as the final resighting, and varied irregularly among countries (Fig. 8). For most countries, median distances moved were shorter for December-February than for November-February.

### Probability of leaving/entering France

The estimated value of ψ was 0.031 (95% CL: 0.020-0.047), indicating that 3% of birds wintering in France leave the country from year to year and *vice versa*. When the data were split into two periods with different distributions of resighting effort, the results were 1980-1990 (N = 422): ψ = 0.057 (0.035-0.092) and 1990-2000 (N = 414): ψ = 0.011 (0.004-0.030).

Table 5. Model selection for general linear modelling of distances between resighting and recovery. The selected models are indicated in italics.

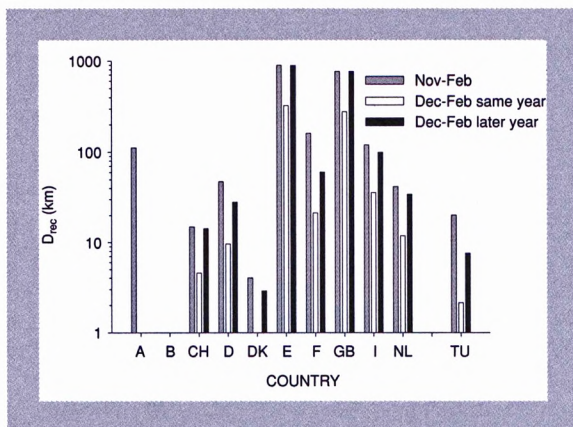| Model | $\Delta AIC_c$ | |
| --- | --- | --- |
| | November-February | December-February |
| *country* | 0 | 0.25 |
| *country lag* | 2.75 | 0 |
| country age | 1.75 | 3.39 |
| lag | 5.64 | 3.5 |
| no effects | 3.51 | 8 |

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Figure 8. Back-transformed mean distance moved ($D_{rec}$) between last resighting and recovery for the data sets from November-February and December-February. Country codes are A: Austria, B: Belgium, CH: Switzerland, D: Germany, DK: Denmark, E: Spain, F: France, GB: Great Britain, I: Italy, NL: The Netherlands, TU: Tunisia.



Figure 9. Modelled equilibrium winter population size in France as a function of the proportion culled, c, and the probability of entering/leaving France, p.

## The 'dilution' model

The model demonstrated that even quite low levels of interchange of birds (p = 0.96-0.98) could sustain a winter population in France under heavy culling (c = 0.3; Fig. 9). At the same time, the response to culling depended strongly on the value of p, particularly at realistically high values (p > 0.95, corresponding to $\psi$ < 0.05).

## Discussion

The various approaches used to estimate winter site fidelity of cormorants provided reasonably consistent results. About 85-90% of all surviving adults seemed to return to the same site from year to year; of the remaining 10-15%, most birds moved less than 100 km, but long-range movements also occurred regularly. At a larger scale, fidelity to large parts of the winter range (e.g. France) could be estimated as approximately 97% (1-$\psi$). These results may, however, be affected by numerous biases, and we will discuss each in turn before concluding on what can be learned from this study.

### Local survival

The analyses of local survival should be free from serious biases, and the results should thus be reliable. However, they are based on data from three sites within the same region and on a short run of years (1984-1990), so it is unclear how far the conclusions can be generalised. A large number of factors could be expected to influence fidelity to a given site, including the extent of year-to-year variations in weather and food availability and frequency and intensity of human disturbance.
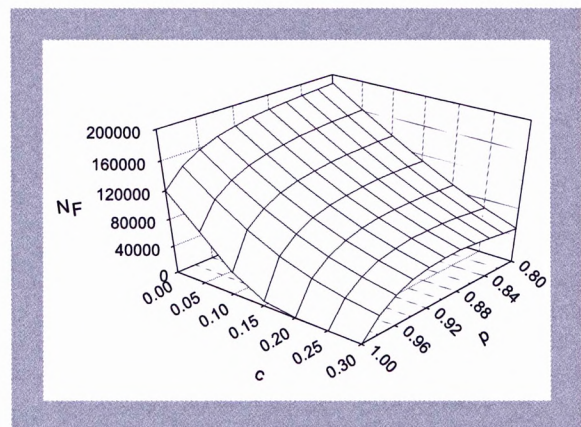
Yésou (1995) estimated a year-to-year return rate of 75.8% at Marais d'Olonne in western France, a site which is used during both autumn and winter; this value is consistent with our estimates of local survival in the Alpine lakes (0.75-0.80).

### Repeated winter resightings

Because of the complex variation in detection probability over space and time, it is quite difficult to draw firm conclusions about how these results may be affected by various biases. On the one hand, one would certainly assume that the probability of being resighted again at the same site was higher than if the bird had moved to another site, since most wintering sites are not covered by resighting effort; this would lead to an underestimation of movement probabilities. On the other hand, some movements in the database are 'artificial': many birds have been seen in more than one locality in the same winter. A bird using the same area in two winters may very well be seen in one locality (e.g. a foraging area) in one winter and in another (e.g. a roost area) in the next winter. It would thus appear to have moved, even if it used the same sites in both winters. Also, when searches for ringed birds stop at a site (a quite common phenomenon), birds can only be observed if they move elsewhere; this bias clearly caused the anomalously high estimates of P for the North African countries and Austria (P = 1; see Fig. 3). How these potential biases balance out is very difficult to evaluate.

Another possible bias, which also occurs for the analysis of recoveries of previously resighted birds, is the inclusion of migratory movements. Some of the medium- and long-range movements observed could be part of

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the regular annual cycle of migration. Against this as an important bias counts the fact that results from the two time windows are not very different; including data from November did lead to higher estimates of movement, but the difference was rather small.

## Probability of entering/leaving France

It is most likely that the difference in $\psi$ found between the 1980s and the 1990s is caused by different geographical distribution of resighting effort outside France. During the 1980s, many resightings were made on the German side of the Rhine, and several of the birds moving between France and areas outside of France were discovered this way. The area had a very low resighting effort in the 1990s. We find it likely that $\psi$ was overestimated for the 1980s and underestimated for the 1990s, and we here take the overall value of 0.031 as a fairly robust estimate.

The assumption of equal $\psi$ in both directions is unlikely to hold, simply because the areas have quite different sizes. A higher site fidelity should be expected for the areas outside of France than for France, because birds wintering outside France would have to move further on average (up to 1,000 km or more) in order to cross the border than those wintering in France (maximum ca 450 km). However, France is centrally located in the wintering area of Danish and Dutch cormorants, and the bias associated with assuming equal probabilities of entering or leaving France is probably small.

## Are cormorants nomadic or site-faithful?

Cramp & Simmons (1977) stated that cormorants show individual nomadism outside the breeding season. This view has been challenged by several authors (Yésou 1995, Reymond & Zuchuat 1995b, Wernham, Armitage, Holloway, Hughes, Hughes, Kershaw, Madden, Marchant, Peach & Rehfisch 1999), who have shown that individual cormorants often return to the same wintering site year after year. Our results, based on a much larger data set, confirm that year-to-year site fidelity is common in continental cormorants, and go some way towards quantifying the balance between site fidelity and nomadism. It appears that a large majority of birds return to the same wintering site year after year, but also that a substantial proportion, perhaps 10-15%, move to another site. Among the latter, the majority move only short distances (less than 50 km), to localities that they may have visited briefly during previous years. Many factors can be imagined that may provoke such movements; among these, ice conditions and human disturbances may be the most obvious. The tendency towards longer moves in the more easterly parts of the wintering range may be a reflection of generally colder winters in this area, which makes some lakes completely unsuitable for wintering cormorants in some winters.

It is much less clear what makes a small proportion of birds change to sites far away, at least up to 1,891 km. Juvenile cormorants generally winter further south than adults (van Eerden & Munsterman 1995, Bregnballe et al. 1997), and one could imagine that individuals winter progressively further north as they grow older; some, but far from all, of the long-distance movements observed conform to this pattern. Furthermore, in none of our analyses did age (juvenile vs adult) explain a significant part of the variation in either probability of changing site or distance moved. Thus, cormorants are capable of what seems to be nomadic movements, and at present we have no clear indications of why a small minority actually change to completely different wintering areas.

The factors that cause individual cormorants to either remain at the same wintering site or move to another site are of wide-ranging interest in both fundamental and applied contexts. For instance, are some individuals more likely to move than others, and is such a propensity linked to e.g. age, sex or the existence of alternative migration strategies? Does fidelity to a given site change with e.g. cormorant density or other aspects of quality, and if so, are some birds forced into less suitable wintering areas - and which ones? The large database we have used here may be useful in answering some of these questions, but more reliable answers could come from intensive local studies, either observational or experimental, involving radio-tracking or other techniques allowing researchers to follow individuals closely. Indeed, very little is known about how individual cormorants exploit wintering areas within one winter, and further insight into this subject is necessary if we are to understand why some individuals change from one wintering site to another.

## Relevance for management

The results obtained using our model clearly demonstrate that in the presence of even quite low levels of movements among wintering areas, the effects of culling within a site or region cannot be predicted reliably without taking such movements into account. The predicted effects of a given intensity of culling in France depend strongly on whether movement is included in the model or not, and also on the value assumed for p (see Fig. 9). It is thus clear that information about the extent of site fidelity and about the factors affecting it can be very important when predicting the effects of local management actions. This question is explored in more detail by Frederiksen, Lebreton & Bregnballe (in press).

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