WINTERING CORMORANTS *Phalacrocorax carbo carbo* IN THE YTHAN ESTUARY, SCOTLAND: NUMERICAL AND BEHAVIOURAL RESPONSES TO FLUCTUATING PREY AVAILABILITY

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ABSTRACT Throughout an entire winter season numbers of roosting and foraging Cormorants were surveyed along the Ythan Estuary, Scotland. In this study both bird numbers present and proportion of foraging birds have been related to season, time of day, tidal cycle and section of estuary. An earlier study had revealed Flounder to be the Cormorant's main prey species in the area. A sharp decrease in bird numbers from October to January coincides with lower Flounder abundance, while higher Cormorant numbers in the mornings might reflect the fact that small 'catchable' size classes of Flounder only visit intertidal mudflats at night. Furthermore, the only significant effect of the tidal cycle was that a higher proportion of birds foraged during the ebbing tide. This too is considered to be a behavioural response to prey habits, since Flounders are most likely to be detected by Cormorants at low water levels, while moving from the mudflats into the mid-water channel.

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INTRODUCTION

The Ythan Estuary (Scotland) is a well studied estuarine habitat, where good fish abundance favours the wintering of various piscivorous birds, such as Grey Heron Ardea cinerea, Red-breasted Merganser Mergus serrator, Cormorant Phalacrocorax carbo carbo and Great Black-backed Gull Larus marinus. As part of a study on these piscivorous birds (Richner 1986, 1988), regular counts of Cormorants were carried out during the winter season with the aim of determining the dependence of their numbers and foraging activity on a series of seasonal, diurnal and tidal variables. Fish abundance in such intertidal habitats shows distinct seasonal, diurnal and tidal patterns (Gibson 1982) and it can be expected that these are of influence on abundance and behaviour of piscivorous birds.

The Cormorant is a winter visitor to the Ythan Estuary, arriving in August from the breeding grounds and leaving in March or early April, with the population reaching a peak in October. The abundance of Cormorants is examined with respect to time of day, month, daily tidal cycles and tidal range and the spatial distribution of the birds within the estuary is analysed.

Earlier studies have shown the main prey of the Cormorant in this area to be 1-2 year old Flounder *Platichthys flesus* (10-20 cm long) that make up 85% of the prey items identified (Summers 1974). Seasonal as well as diurnal, spatial and tidal fluctuations in Flounder numbers in the Ythan Estuary have been thoroughly studied by Summers (1974) and Raffaeli *et al.* (1989), thus providing a background against which fluctuations in the occurrence and behaviour of the wintering Cormorants in the area can be considered.

MATERIAL AND METHODS

The Ythan Estuary is situated on the northeastern coast of Scotland, 20 km north of Aberdeen. The estuary receives a large influx of fresh water from the Ythan river at its upper end, then widens and

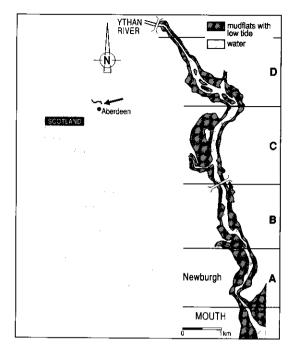


Fig. 1. The Ythan Estuary, NE Scotland. The 4 counting sections (A to D) are indicated.

connects 8 km further downstream with the North Sea. Due to tidal effects the water level in this relatively narrow estuary varies over a range of several meters. The estuary has an extensive intertidal zone, dominated by mud, sand and gravel substrate. A more detailed description of its physical characteristics can be found in Leach (1971), and a description of its general topography and history in Walton (1966).

Foraging and roosting Cormorants were counted on the Ythan estuary between October 1983 and March 1984. Each of a total of 53 counts was completed within 30 minutes. In order to correct for tidal effects on bird numbers due to the time lag between the beginning and the end of a count, the direction of the count was regularly alternated. The behaviourial category 'roosting' included sleeping, resting and preening, the category 'foraging' included diving, submerging the head in search of prey or consuming prey. In order to analyse spatial patterns of bird distribution, the estu-

ary was divided into four sections, each approximately 2 km long (Fig. 1). The number of birds was recorded for each of the sections A to D. After grouping the data into sections A to D, the median of the birds' location was computed and used as an expression of the centre of location of the birds for each count. For a statistical comparison of the mean numbers in each section, a log-transformation of the original values was performed in order to remove the dependence of the variance on the mean, and to render the variances homogeneous. Data are given as mean values (\pm SE), significance values are two-tailed.

RESULTS

Temporal variation

The mean number of Cormorants visiting the estuary was highest in October (43.8 \pm 4.6) and then dropped significantly by 73% (r_{47} = -0.65, P < 0.001) to a minimum in January (11.9 \pm 1.8) and February (13.5 \pm 2.3) before it increased again at the beginning of March (26.3 \pm 2.7) (Fig. 2). Despite the decline in total number, the number of birds observed feeding did not decrease significantly throughout the winter (r_{47} = -0.22, n.s.), so the proportion of birds feeding in-

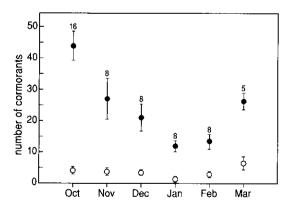


Fig. 2. Mean number (± SE) of Cormorants in the Ythan Estuary during winter. Number of birds present and number of birds foraging are shown. Figures above the symbols indicate the number of counts each month.

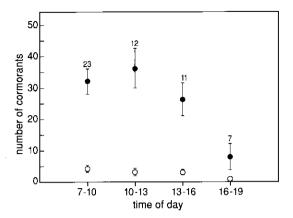


Fig. 3. Mean number (± SE) of Cormorants in the Ythan Estuary during the day. Number of birds present and number of birds foraging are shown. Figures above the symbols indicate the number of counts each time period.

creased from 9% to 23% ($r_{47} = 0.31$, P = 0.03) between October and February, showing that individual birds spent more time feeding later in winter than at the beginning of the season.

The total number of Cormorants was highest in the morning (Fig. 3) and then declined significantly in the afternoon until no bird was left by 17.30 h ($r_{52} = -0.34$, P = 0.013). The total number of feeding birds showed the same pattern ($r_{52} = -0.36$, P = 0.009). There was no significant decrease throughout the day in the proportion of Cormorants feeding ($r_{50} = -0.19$, n.s.), indicating that the feeding activity of the birds that are present remains constant throughout the day. In a multiple regression model with stepwise inclusion procedure, the two variables 'month' and 'time of day' explained 54% of the total variance in numbers of roosting Cormorants and 10% of the variance in feeding Cormorants.

Tidal variation

Daily tidal cycles had no effect on the total number of Cormorants in the estuary: the number of birds remained constant both during the ebbing and the rising tide. A significant increase was found, however, in the number of feeding birds during the ebbing tide ($r_{25} = 0.39$, P = 0.044). The

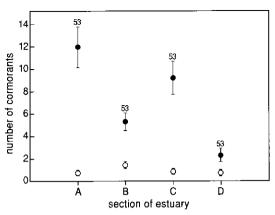


Fig. 4. Mean number (± SE) of Cormorants in the Ythan Estuary counted in each counting section A to D. Number of birds present and number of birds foraging are shown. Figures above the symbols indicate the number of counts.

28 counts around low tide (within three hours before and three hours after) showed that on average $28.1 (\pm 3.8)$ Cormorants were present in the estuary and on average $4.1 (\pm 0.7)$ of these birds were observed feeding. In the 25 counts around high tide (within three hours before and three hours after) on average 29.6 (\pm 4.1) Cormorants were present in the estuary and on average 2.6 (\pm 0.7) of these birds were observed feeding. When the effects of time of day and month on bird abundance were controlled for, there was no significant difference in the total number of birds present around high tide as compared to the birds around low tide (F-test; P = 0.83), but significantly more birds fed around low tide than around high tide (F-test; P = 0.025).

The tidal range, which is expressed as the difference between water levels at high tide and low tide, is greatest at full and new moons (spring tides) and lowest at quarter moons (neap tides). The tidal range of the days when Cormorants were counted varied from 0.8 m to 4.0 m. The counts for which tidal range was less than 2.4 m (midvalue between the two extremes) were considered neap-tide counts, and the remaining counts taken as spring-tide counts. In the 20 spring-tide counts an average of 33.6 (± 4.4) birds was counted,

compared to an average of 25.9 (\pm 3.6) birds noted during the 33 neap-tide counts. This difference is not significant ($t_{51} = 1.37$, P = 0.18). At the higher tidal differences an average of 4.4 (\pm 1.0) birds was observed feeding, compared to an average of 2.8 (\pm 0.5) birds at the lower tidal differences. Again, the difference is not significant ($t_{29.1} = 1.42$, P = 0.17). Thus, neither spring nor neap tides affected the total number or the number of feeding Cormorants in the estuary.

Spatial patterns in bird distribution

Section A of the estuary, which is closest to its mouth, was the preferred site by roosting Cormorants, followed by sections C, B and D (Fig. 4). For feeding activities, however, section B was the preferred part of the estuary. It was used by more than twice the number of Cormorants than any of the other sections. The differences between the means of the log-transformed numbers of both roosting (one-way ANOVA: F = 11.6, P < 0.0001) and feeding (F = 3.1, P = 0.03) Cormorants in each section A to D were significant.

Of the four variables studied, time of day and tidal range had a significant effect on the location of Cormorants within the estuary. In the morning a higher proportion of birds roosted in the lower sections (A and B) of the estuary, in the afternoon a higher proportion was found in the upper sections (C and D). This upward shift of the median location is significantly correlated with time of day for both roosting ($r_{48} = 0.45$, P = 0.001) and feeding Cormorants ($r_{37} = 0.32$, P = 0.05). A downward shift of the median location of roosting Cormorants was recorded with increasing tidal range ($r_{48} = 0.33$, P = 0.02). For feeding birds, however, the median location was not significantly affected ($r_{38} = 0.29$, P = 0.07) by tidal range.

DISCUSSION

The Ythan Estuary Flounder population starts to decline in October and reaches a low from January to March (Summers 1974). In the present study, the decline in the number of Cormorants from

the beginning to the end of winter may be attributed to the decline in the numbers of Flounder during the winter. The proportion of feeding birds increased over the same time period, probably because the birds remaining behind had to devote more time to feeding activities as prey abundance decreased. It is interesting to note that over this time period the number of Grey Herons also decreased (own obs.), while the Red-breasted Merganser population strongly increased (Richner 1988). Flounder forms an important part of the diet of wintering herons, but are only rarely seen as food items of the Red-breasted Merganser.

More Cormorants were present and observed foraging in the morning than in the afternoon. This may simply be because a bird could meet its daily food needs already in the morning and then roost elsewhere, or it may be that the estuary is a more attractive feeding site in the morning. In a study on the feeding and activity of Flounder in the Ythan Estuary, a significant difference was found between the size of the fish feeding on the mudflats at day high tides and those at night (Raffaeli *et al.* 1989). The Flounders in the size range that could be handled efficiently by a Cormorant (5-20 cm) visit the mudflats exclusively at night high tides and may consequently be available only in the mornings.

Daily tidal cycles only correlated with an increase in foraging Cormorants during the ebbing tide. This may be because the bottom feeding Flounder is accessible with less effort at lower water levels. Furthermore, this prey is likely to be more readily spotted by its predators before low tide, when it moves back from the mudflats into the mid-water channel. In herons numbers as well as foraging activity increased during the ebbing tide and then decreased during the rising tide (Richner 1986). In contrast to the Cormorants, most herons which visited the estuary occupied a feeding territory at a neighbouring stream, and left the estuary as soon as it became less profitable than their stream feeding site (Richner 1986). Cormorants did not seem to have alternative feeding sites, so during the rising tide their numbers remained constant, while their foraging activity decreased.

Since many fish use tidal currents as a means of transport to move into the estuary at rising tide and out of the estuary at ebbing tide (Arnold 1989), more fish may enter the estuary at spring tides when a larger mass of water flows into the estuary than at neap tides. It was therefore surprising to find that the cycle of spring and neap tides had no noticeable effect on the number of roosting and foraging Cormorants. This may again be related to the behaviour of Flounder. Summers (1974) noted that many always remain in the estuary: during ebbing tide they only move to the mid-water channel of the estuary, and therefore make little use of tidal currents to leave and enter the estuary. Their number will consequently be little affected by the spring and neap tide cycle and the number of Cormorants, as a Flounder predator, will not change either. This is different from the situation in Red-breasted Mergansers where numbers were significantly higher during spring tides (Richner 1988). Since the estuary is a main feeding site for piscivorous birds, a better knowledge of prey ecology and behaviour would shed light on the factors influencing bird abundance and distribution.

ACKNOWLEDGEMENTS

I thank Prof. G.M. Dunnet and Dr I.J. Patterson for their encouragement and for the facilities provided at Culterty Field Station. The study was financed by a grant from the Swiss National Science Foundation.

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SAMENVATTING

Gedurende een heel winterseizoen zijn aantallen rustende en fouragerende Aalscholvers geteld in het Ythan estuarium in Schotland. Er is gezocht naar verbanden tussen de totale aantallen en het percentage vissende vogels enerzijds en tijd van het jaar, tijd van de dag, getijcyclus en exacte locatie anderzijds. In een eerdere studie was gebleken dat Bot de voornaamste prooi was van Aalscholvers in het gebied. Een sterke afname in aantallen vogels tussen oktober en januari valt samen met geringere hoeveelheden Bot, terwijl de grotere aantallen vogels in de ochtend waarschijnlijk voortkomen uit het feit dat de kleinere, 'vangbare' Bot alleen 's nachts bij vloed op de dan overspoelde ondiepten komt. Verder was het enige significante effect van de getijcyclus dat een hoger percentage vissende Aalscholvers werd aangetroffen bij afgaand water.

Dit alles weerspiegelt waarschijnlijk een gedragsaanpassing van de predator aan zijn prooi, omdat Bot het gemakkelijkst detecteerbaar is bij lage waterstanden wanneer de vis zich van de ondiepten naar de centraal gelegen stroomgeul verplaatst.