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SOLITARY FORAGING IN SAND PITS BY BREEDING CORMORANTS Phalacrocorax carbo sinensis: DOES SPECIALISED KNOWLEDGE ABOUT FISHING SITES AND FISH BEHAVIOUR PAY OFF?

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ABSTRACT Though most Cormorants from the colonies exploiting the lake IJsselmeer area in The Netherlands nowadays have taken up the habit of fishing in large groups, some individuals are still observed fishing solitarily. This phenomenon occurs predominantly during the coldest months at well-defined patches, often located in sand pit regions. A case study in a sand pit in the early spring of 1982 revealed that Cormorants from Oostvaardersplassen took advantage of the fish located at their winter refuges inside the pit by specifically diving along the pit's steepest slopes. Thus, they were able to achieve a more than average daily ration of about 475 g of fish within a mere 15 minutes of foraging in the second half of March. Later on, the site became less profitable and the birds gradually left. The importance of high intake rates in early spring is stressed, in view of time consuming activities like nest site occupation, pair formation and accumulation of body reserves for egg-laying, incubation and chick feeding. It is suggested that only the 'higher quality' birds may have the experience and skill required to use solitary fishing techniques as a profitable alternative to social fishing in early spring.

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INTRODUCTION

Although social foraging appears to be the rule now in birds of the large Cormorant *Phalacrocorax carbo sinensis* colonies along the Dutch lake IJsselmeer area (Van Eerden & Voslamber 1995), throughout the breeding season some individuals choose a solitary approach. This way of feeding is particularly frequent in early spring, in the period of courtship and nest site occupation. This solitary fishing behaviour has been extensively described in an earlier period by De Boer (1972) for birds from the Naardermeer colony, but in those days social fishing was still an exceptional phenomenon (cf. Van Eerden & Voslamber 1995). Good opportunities for studying the solitary fish-

ing technique as an alternative for social foraging were offered in the early spring of 1982, when several birds from the Oostvaardersplassen colony regularly visited a well-defined fishing site in the harbour of Lelystad-Haven (Fig. 1).

METHODS

During the period 1982-1992 fishing sites which regularly attracted solitary birds were mapped. Observations were made from the shore as well as from vessels. The locations of these birds were recorded using buoys, marks on the shore or the ship's Trident navigation system, which allowed an accuracy of c. 5 m.

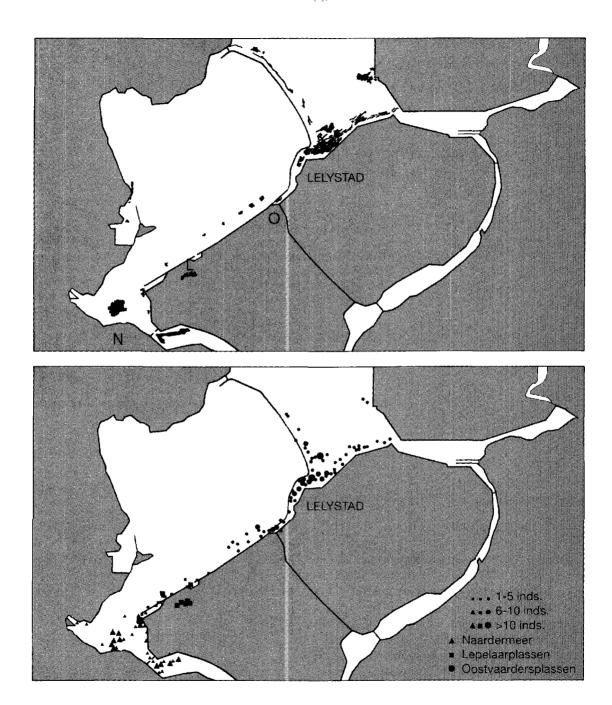


Fig. 1. Southern fringe of lake IJsselmeer showing areas with a depth below 10 m and location of the three main Cormorant colonies (O = Oostvaardersplassen, L = Lepelaarplassen and N = Naardermeer) (above) and locations of solitary feeding birds from these colonies (below). Notice the little overlap between colonies.

From 19 March to 17 April 1982 the fishing site at Lelystad-Haven, situated above and around a former sand pit of a depth to over 20 m. was regularly surveyed for solitarily feeding Cormorants. From their fishing behaviour the following parameters were registered as often as possible; exact locations of individual dives (by means of a range-finder), diving times, between-diving intervals (both to the nearest 0.05 minute) and durations of individual stays at the site. Thus, it proved possible to construct time budgets for individual birds and, assuming the birds dived towards the bottom in a virtually right angle (Portielje 1927, Kortlandt 1942), diving depth of the Cormorants exploiting this fishing site. Since the prey items caught were generally brought up to the surface to be swallowed, the visible success of each individual dive could be scored and related to both diving time and diving depth. By identifying the prey species and estimating their sizes whenever possible, we were able to estimate the intake of the individual birds exploiting the pit. The intake rates thus found could be slightly underestimated, because some small prey items may have been swallowed under water. Fish sizes were registered in three length classes, using the Cormorant's bill length as a reference: small (about 10 cm), average (about 15 cm) and large (about 25 cm). Fish distribution with respect to water depth and location in the pit was recorded using sonar (Atlas Elektronik, 40 dB).

RESULTS

Distribution of solitary feeders

Figure 1 shows the distribution of solitarily feeding Cormorants early in the season, lumped for January-March 1982-1991. Birds from different colonies do not show much overlap in foraging area. For each of the three colonies well defined centres of foraging activity exist, well associated with areas over 10 m water depth. Within a radius of 10 km from each colony this apparent choice for deeper water is highly significant (χ^2 test, p < 0.0001) (Table 1).

In late January, February and early March, the solitary feeders were often observed in areas where previously sand had been removed (Fig. 1). Birds from Naardermeer visited the Gooimeer and Pampus pit, both over 25 m deep. Smaller pits near Pampushaven were also frequently visited by single birds from this colony. Birds from the colony Lepelaarplassen chose sand pits close to their colony situated in the polder itself (up to 19 m deep). Single birds from this colony were also frequently seen fishing in rather deep water near the pumping station De Blocq van Kuffeler (up to 9 m). Birds from Oostvaardersplassen were seen in areas with deep water at Lelystad-Haven (" 20 m), in an extensive area of sand pits north of the sluices at Lelystad and around the power plant Flevocentrale. Few birds went to isolated areas of deep water further away, along the Houtribdijk and in the neighbourhood of Urk.

In the course of the season the preference for deep water becomes less prominent and by April

Table 1. Observed dive locations of solitary foraging Cormorants (January-March 1982-1991) and occurrence of different classes of water depth (in $\rm km^2$) for colonies of Oostvaardersplassen (OVP), Lepelaarplassen (LEP) and Naardermeer (NME), within a range of 10 km from each colony. I, II and III represent water depth, 0-5 m, 6-10 m and 11-20 m respectively. *** p < 0.0001

	observed dives			on offer in lake			χ^2
	I	П	III	I	II	III	
OVP	42	164	203	82	19	20	631.7***
LEP	15	18	62	85	11	4	901.2***
NME	29	28	75	95	8	9	474.0***

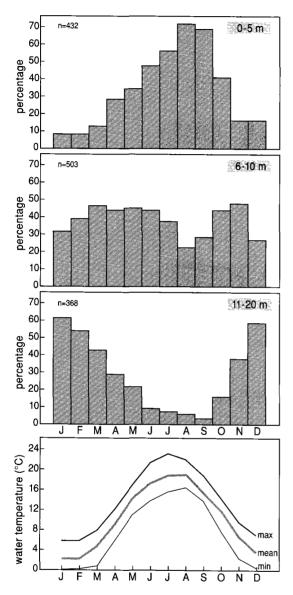


Fig. 2. Occurrence of solitarily feeding Cormorants from Oostvaardersplassen at different water depths within 15 km from the colony throughout the year. Foraging depths over 11 m coincide with the coldest months. Water temperatures are average values and range from 5 stations at the surface (1966-1989).

the birds are no longer associated with sand pits (Fig. 2). In autumn the habit of sand pit-foraging is not apparent until November. Due to the pres-

ence of few birds then, which are not connected to colonies, only scattered observations were made. For Oostvaardersplassen birds the log-transformed percentage of dive locations at depths of 11-20 m was correlated negatively with water temperature throughout the year ($r^2 = 0.86$, p < 0.001). On the contrary Cormorants dove over shallow water (0-5 m) more often at times of higher water temperatures ($r^2 = 0.92$, p < 0.0001). The combined observations over the years show a gradual course of attendance to different water-depths (Fig. 2).

Distribution of fish in winter and early spring

From a series of surveys using sonar along depth gradients in various sand pits in the southern part of lake IJsselmeer, it became clear that during the winter months fish assemble in huge concentrations at depth. Figure 3 depicts a typical cross section through one of the deeper sand pits.

Diving behaviour

The surveys at the Lelystad-Haven sandpit showed that the numbers of feeding Cormorants at this site decreased as the breeding season progressed. From the mean numbers of birds present and the mean duration of individual visits, it was estimated that from 19-28 March the sandpit received some 900 visits per day against a mere 300 in the period 2-17 April. The mean duration of a visit, based on those individuals that could be followed from the moment of arriving until the time they left, was 13.56 minutes (SD = 12.10, n = 41) in the first period and 11.14 minutes (SD = 7.89, n = 31) in the second. This 2.4 minute difference was statistically significant (t = 3.17, p < 0.005). Because of the decrease in both number of visits and time spent per visit, the two periods (19-28 March and 2-17 April) were treated separately in most further analyses.

All diving places recorded were plotted on a map with the depth profile of the sand pit (Fig. 4). Most dives occurred in the depth class of 10-15 m in the areas of the slopes. Birds were seen diving with their tails perpendicular to the surface, indicating an almost vertical descent. Especially the



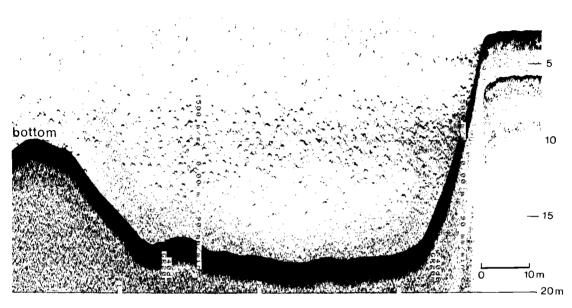


Fig. 3. Example of typical fish distribution in late winter (25 February 1993) along a gradient in water depth, as registered by sonar. Notice the concentration of coarse fish between 8-12 m water depth and along the SE slope of the pit. Echoes of smaller fish are dispersed over the water column but also concentrated along the edge and at the bottom of the pit, 15-18 m deep.

successful dives were concentrated along the steepest slopes of the sand pit (Fig. 4). The numbers of dives per depth class differed in both periods significantly from random (Fig. 5; $\chi^2 = 69.27$, p < 0.005 and $\chi^2 = 95.07$, p < 0.005 respectively). In the second period, a shift towards the shallower areas became apparent, although most dives still took place at depths of 10-15 m (Fig. 5 C).

The percentage of successful dives was higher during the first period than during the second: 53.5% (n = 114) and 37.4% (n = 131) respectively. Generally, dives were more successful at greater depths (Fig. 5 B, C). This difference was most pronounced in the first period, when 64.1% (n = 64) of the dives at depths over 10 m were successful against 40.0% (n = 50) of the dives at less than 10 m. In the second period these figures dropped to 43.4% (n = 53) and 33.3% (n = 78), respectively.

Dive duration and subsequent between-dive

intervals increased slightly with water depth, but only significantly in the successful dives (Spearman $r_s = 0.527$ (n = 7), not significant and 0.943(n = 6), p < 0.05 for diving time, $r_s = 0.125$, not significant and 1.0, p < 0.05 for subsequent between-dive interval in unsuccessful and successful dives respectively; Fig. 6). Between-dive intervals following a successful dive averaged 0.08 minutes longer than those following an unsuccessful one (t = 7, p < 0.05). Based on diving time, subsequent between-dive interval and percentage of successful dives, the mean time needed to catch a fish was calculated for each depth class (Table 2). In the first period the best opportunities for catching fish increased with depth, while in the second period these remained rather similar among depths of over 5 m (Fig. 7). Furthermore, catching success was rather lower in the second period.

During both periods different species, num-

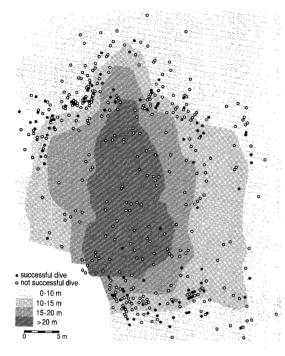


Fig. 4. Detailed map of the sand pit at Lelystad-Haven with isobaths; exact dive locations of Cormorants are plotted, as well as an indication of foraging success per dive.

bers and sizes of fish were caught (Table 3). On average 9 fishes per visit were caught in the first

Table 2. Time (in seconds) needed to catch one fish, per depth class. Period I: 19-28 March, period II: 2-17 April.

depth (m)	period I	period II	overall
3 - 4	154	-	223
4 - 5	112	208	167
5 - 7.5	86	101	94
7.5-10	104	106	105
10 -15	67	118	81
15 -20	89	85	87
>20	-	125	167

Table 3. Estimated size distribution (in %) of the fish caught in the two observation periods. Period I: 19-28 March (n = 33), period II: 2-17 April (n = 63).

	period I	period II
small, about 10 cm	63.6	74.6
average, about 15 cm	21.2	15.9
large, about 25 cm	15.2	9.5

period and 5 fishes in the second. The largest difference in prey choice between the two periods consisted in the proportion of Eel *Anguilla anguilla*, 30.4% (n = 79) and 3.1% (n = 65) respectively. By multiplying the average number of fish

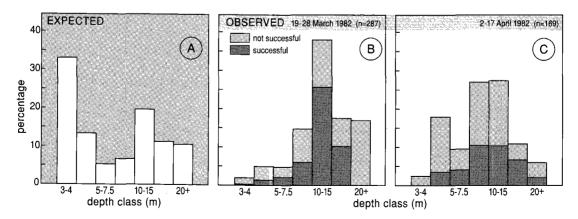


Fig. 5. Frequency distribution of dives according to water depth for: (A) an assumed random distribution of dives over the foraging patch, (B) the observed location of dives over the period from 19-28 March 1982 and (C) the period from 2-17 April 1982. In (B) and (C) the proportion of successful dives is shaded.

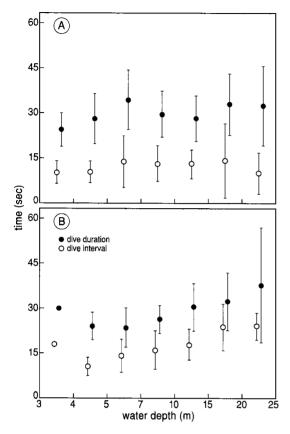


Fig. 6. Dive durations and subsequent dive intervals according to water depth; (A) unsuccessful dives, (B) successful dives.

with the fish mass derived from the estimates of prey size (cf. Voslamber 1988), it was possible to estimate the biomass intake per visit for both periods. Thus, during the first period about 475 g of fish was caught per visit, while during the second period birds had a yield of about 215 g per visit.

DISCUSSION

In the shallow lake IJsselmeer many fish winter in the deepest (and warmest) areas they can find, so the larger depths of former sand pits (of up to 30 m or more) are very attractive in comparison to the 3-4 m depth zone predominating over most of the lake's surface (Beekman & Platteeuw

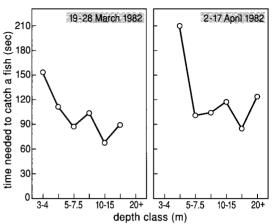


Fig. 7. Time needed to catch a fish in relation to water depth for the period from 19-28 March 1982 and the period from 2-17 April 1982.

1994). In early spring, when water temperatures start rising, fish begin to move out of their winter refuges and often concentrate along the edges of these pits (Fig. 3). As the season progresses, these concentrations dissolve and the fish spread out over a much larger area and become harder to find for solitary feeders (cf. Van Eerden & Voslamber 1995). Eel usually dig themselves in in the bottom substrate during the winter months and since it shows a clear preference for either the coarsest or the finest sediments (Lecomte-Finiger & Prodon 1979), the fine sediments of the deepest parts further increase the attraction of the bottom of the pits to Eel (e.g. Platteeuw 1985). Eel also becomes more active when water temperatures rise and then leave their burrows to spread out over the lake. This would explain the considerable Eel catches in the first period, dropping to almost nil in the second. Eel may have been moving towards the shallows mainly during the second half of March. It is also possible that depletion of the patch occurred.

Solitarily fishing Cormorants as observed in early spring seem to take advantage of the concentration of fish in sand pits by that time. Social fishing as a means to push the fish up into the clear higher water layer (Van Eerden & Voslam-

ber 1995) is not possible at great depths. Moreover, the disruptive behaviour of a group of fishing Cormorants at a relatively small patch like a sand pit is more likely to disperse any existing fish concentration than to drive dispersed fish together in harvestable clumps. Fish concentrations like those found in the pits are probably best exploited by a more subtle approach, which takes advantage of detailed knowledge on bottom relief and fish behaviour.

The question is to what extent visual cues play a role in detecting fish at greater depths. Given local Secchi depth values of a maximum of 2 m during winter, the levels of 1% and 0.1% of surface light occur at depths of 5 and 7.5 m respectively. According to the fish's depth distribution (Fig. 3) and the recorded locations of the diving Cormorants well below 10 m, it seems reasonable to conclude that Cormorants may locate prey by touch. Such a detecting technique can only be successful when prey density is sufficiently high and/or when fish is relatively immobile as is the case in hibernating aggregations. The observed drop in rate of success as the season progresses as well as the general tendency to abandon sand pits by April are probably the result of a combined effect of fish moving out of the pit as well as a greater fish swimming speed as temperatures rize.

At least in early spring, this way of specialised solitary fishing seems a good alternative for joining the socially fishing group. In the period from 19-28 March a mean meal size of some 475 g of fresh fish per visit was caught by Cormorants which visited the sand pit. This is well above the estimated average daily intake of 355 g in this period as determined by pellet analysis (Voslamber 1988) and was achieved within less than a quarter of an hour. Thus, an absence of a mere 20 minutes from the colony (including the time necessary to fly to the sand pit and back) was all the time it took to feed and catch even more fish than did the average Cormorant in the colony in foraging trips of well over 100 minutes (Platteeuw & Van Eerden 1994). Indeed, it was observed that in the first period 91.5% (n = 47) of the birds visiting the sand pit arrived directly from the colony and flew back there again after their visit. Quick provisioning of the daily ration required is especially important at this time of the year for the males that are occupying nests or nest sites. Any absence from the colony may result in a rival taking over the nest site or robbing nest material. In the period from 2-17 April, however, the birds visiting the pit did no longer catch a full daily ration within a single visit. During this period more birds appeared to combine fishing in the sand pit with other areas within the same foraging trip: 21% (n = 38) of the birds either arrived from another site than the colony or left for another site after their visit.

It is suggested that the birds using sand pits were among the 'better quality' birds of the breeding colonies. Being able to catch a more than average amount of fish in a very short time, they might occupy and maintain the most attractive nest sites, dedicate more time to pair formation and, last but not least, might start the breeding season earlier with a higher amount of body reserves than most of their socially fishing conspecifics. The latter factor seems to be of utmost importance for eventual reproductive success, since a considerable loss of body mass is bound to occur in adult breeding Cormorants throughout the breeding season (Platteeuw & Van Eerden 1995). The question of whether or not parent birds succeed in raising their chicks until fledging largely depends on the amount of fishing effort (working level) and the foraging efficiency they are able to achieve (Platteeuw et al. 1995). Birds in better body condition will probably be better prepared for higher working levels later on. Part of above average parental 'fitness' may result directly from the knowledge and experience that enable some birds to carry out this way of fishing in the earliest phase of the reproductive cycle, taking advantage of a concentration of their prey occurring at the same time. On the other hand, diving to greater depths for high quality prey like Eel (rich in fat and protein, cf. Platteeuw 1985) may only be an alternative for individuals that were in better physical shape already. Other even higher daily intake rates have been found at wintering sites, but invariably occurred just before the breeding season (e.g. Marteijn & Noordhuis 1991, Dirksen *et al.* 1995, Keller 1995). This fact may also indicate that individual birds try hard to start the breeding season as well-fed as possible. Obviously, since most birds fish socially even in March, exploiting fish at the greater diving depths is not a choice open to each individual, in spite of the close proximity of some sand pits to the colonies.

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SAMENVATTING

Hoewel tegenwoordig de meeste Aalscholvers rondom het IJsselmeergebied in het broedseizoen in grote, sociaal opererende groepen vissen, zijn er, met name in het winterhalfjaar, nog altijd exemplaren die voor een solitaire aanpak kiezen. Uit alle drie de kolonies langs de zuidrand van het IJsselmeer (Naardermeer, Lepelaarplassen en Oostvaardersplassen) blijken in de winter solitair vissende vogels vooral op diep water (meer dan 10 m) voor te komen.

Waarnemingen aan vogels afkomstig uit de Oostvaardersplassen bij een voormalige zandwinput nabij Lelystad-Haven in maart en begin april 1982 lieten zien dat op dergelijke wijze fouragerende exemplaren vooral langs de steilste hellingen van de put actief waren. Ook werd op deze plekken het hoogste aandeel succesvolle duiken uitgevoerd. Eind maart werd de plek door meer vogels bezocht dan in begin april, terwijl individuele Aalscholvers in eerstgenoemde periode eveneens iets langer aanwezig bleven en vaker na afloop van de fourageerperiode direct naar de kolonie terugkeerden. Dit hing ongetwijfeld samen met een afgenomen aantrekkelijkheid van de fourageerplaats: terwijl in maart de gemiddelde bezoeker zo'n 475 g verse vis bemachtigde in minder dan een kwartier (ruim meer dan een gemiddeld dagrantsoen), werd begin april gemiddeld slechts 215 g vis in iets meer dan 10 minuten verschalkt. Tevens werd vastgesteld dat de vogels begin april boven iets geringere diepte doken.

Gesuggereerd wordt dat in het winterhalfjaar het solitair vissen langs hellingen een goed alternatief is voor sociaal vissen. Hierbij zouden ervaren vogels een zinvol gebruik maken van hun terreinkennis door scholen overwinterende vis te exploiteren die zich ophouden langs deze gradiënten in diep water.

Juist in het vroege voorjaar, waarin balts en concurrentie om de beste nestplaatsen een premie legt op zo kort mogelijke fourageervluchten en maximale aanwezigheid in de kolonie, is het bemachtigen van een meer dan gemiddeld dagrantsoen in een zeer korte tijd van fundamenteel belang. Het lijkt dan ook aannemelijk dat deze vismethode in het vroege voorjaar een goede keuze is voor de 'beste' Aalscholvers met de meeste ervaring. Deze specialistische manier van vissen is dan een beter alternatief voor het meegaan met de grote massa. De hoge kosten van het fourageren (diep water) en/of het ontbreken van de specifieke kennis en vaardigheden beletten mogelijk veel vogels om volgens deze strategie te werk te gaan.