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Published in:
 Ardea

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Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 1995

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Citation for published version (APA):

Platteeuw, M., & van Eerden, M. R. (1995). Time and energy constraints of fishing behaviour in breeding Cormorants *Phalacrocorax carbo sinensis* at lake IJsselmeer, The Netherlands. *Ardea*, 83(1), 223-234. http://ardea.nou.nu/ardea_search3.php?key=nummer&keyin=83&k2=1

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TIME AND ENERGY CONSTRAINTS OF FISHING BEHAVIOUR IN BREEDING CORMORANTS *Phalacrocorax carbo sinensis* AT LAKE IJSELMEER, THE NETHERLANDS

MAARTEN PLATTEEUW^{1,2} & MENNOBART R. VAN EERDEN¹

ABSTRACT Two Cormorant colonies in The Netherlands (Naardermeer and Oostvaardersplassen), exploiting the same water bodies but situated at different distances from them, were compared with respect to daily variations in exact fishing sites and corresponding variations in time budget and fish consumption. Mean flying distances between colony and fishing site were estimated at 22 and 15 km respectively. Birds from the Naardermeer colony carried out less trips but of a longer duration than birds from Oostvaardersplassen, most markedly so in the chick rearing period (2 trips per day of 185 min vs. 3 trips of 165 min). Daily fluctuations in time spent away from the colony were clearly dependent on daily shifts in main fishing sites. On days when fishing was concentrated at larger distances, individual foraging trips lasted longer, due to the increase in flying time. Neither net fishing time nor daily fish consumption, as estimated by pellet analyses, compensated for the increment in time and energy expenditure on those days. It was estimated that the average daily energy expenditure would amount to about $2.8 \cdot BMR$ (basal metabolic rate) in birds from Naardermeer and to about $2.7 \cdot BMR$ in birds from Oostvaardersplassen. Fish consumption estimates based on pellet analyses led to an estimated *DME* (daily metabolisable energy) of $2 \cdot BMR$ for both colonies. Thus, an overall negative energy balance became apparent, resulting in estimated mass losses throughout the breeding season of on average 980 and 860 g for Naardermeer and Oostvaardersplassen birds, respectively. Mass losses are likely to be higher with increasing travelling distances, indicating that travelling distance may influence reproductive output. This could be one of the factors causing consistently lower reproductive outputs at the Naardermeer throughout the years.

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INTRODUCTION

Members of inland colonies of Cormorants *Phalacrocorax carbo sinensis* are often forced to search for their food at considerable distances from their nests (e.g. Cramp & Simmons 1977). These travelling distances may vary among colonies as well as from day to day, according to feeding conditions (Voslamber & Van Eerden 1991). Since travelling distance is likely to have a considerable influence on timing and duration of the foraging trips of breeding Cormorants, a comparative time budget study was carried out in 1982 in

two large colonies (Naardermeer with 4340 pairs and Oostvaardersplassen with 2500 pairs; Zijlstra & Van Eerden 1991) along the southern edge of lake IJsselmeer, The Netherlands (Fig. 1). Both colonies depended chiefly on the rich fishing grounds in the IJsselmeer area and both were still expanding at that time, but the two colonies differ in the average travelling distance between the colony and the prevailing fishing areas. Because of the reclamation of two large polders in the IJsselmeer area (Oostelijk Flevoland and Zuidelijk Flevoland) the Naardermeer colony, being the older of the two, had become situated at a consid-

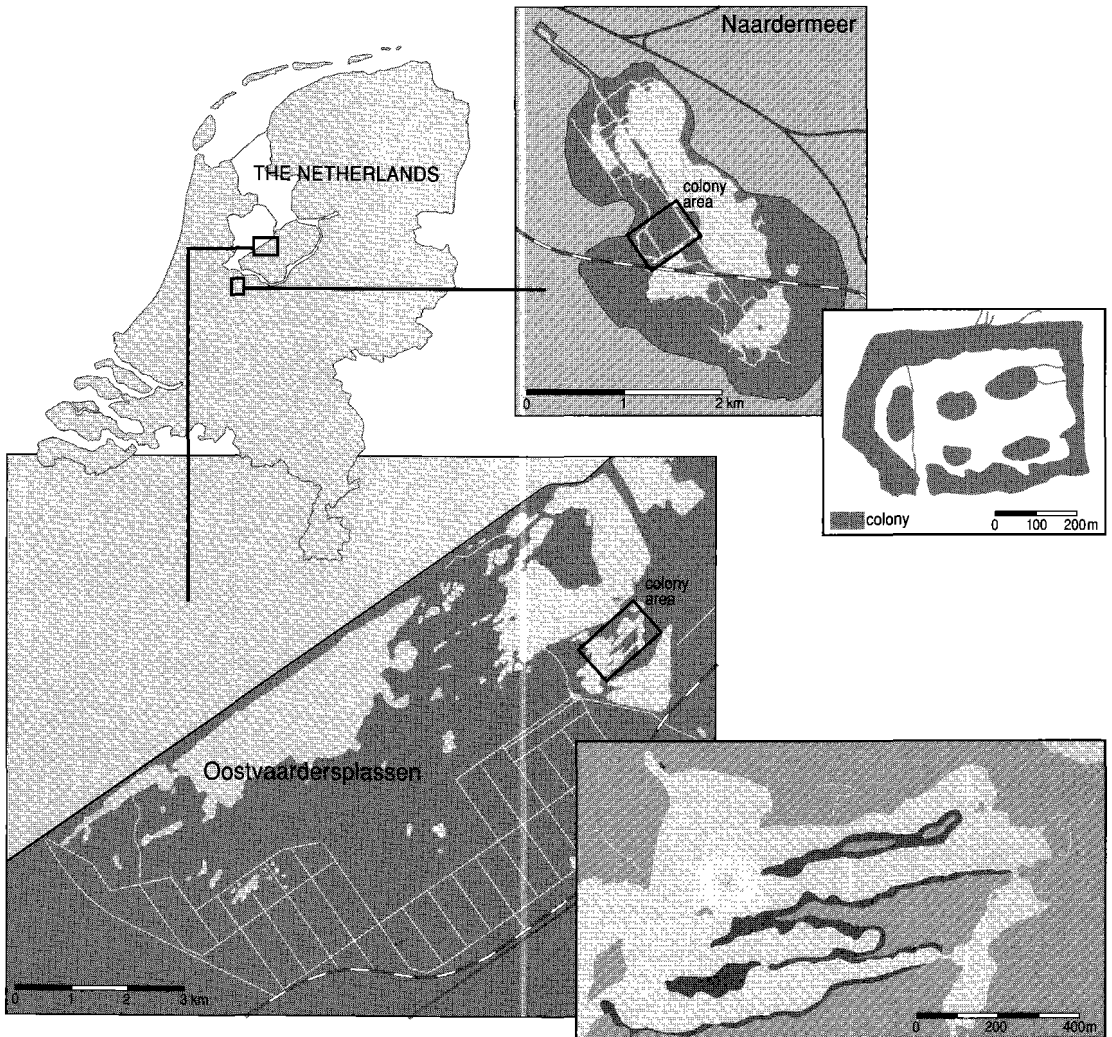


Fig. 1. Map of the IJsselmeer area; the colonies of Naardermeer and Oostvaardersplassen are indicated. Inset shows colony structure in 1982 (occupied area in black) and scale.

erably greater distance from the southern part of the IJsselmeer (Markermeer). This would seem to be a considerable disadvantage. In 1978 the Oostvaardersplassen colony had become established in Zuidelijk Flevoland and had started to grow at a very high rate (Van Eerden & Zijlstra 1985). This was apparently due to a much more favourable site with respect to the proximity of good fishing areas. In the past it had been observed that the reclamation of a yet older polder (Noordoost-

polder) had coincided with the subsequent decline of the formerly equally large colony at Wanneperveen, of which the birds also used to feed at lake IJsselmeer (Van Dobben 1952).

The aim of this paper is to describe the influence of larger travelling distances between colony and feeding site on timing and duration of individual foraging trips by adult breeding Cormorants and to quantify the energetic costs.

METHODS

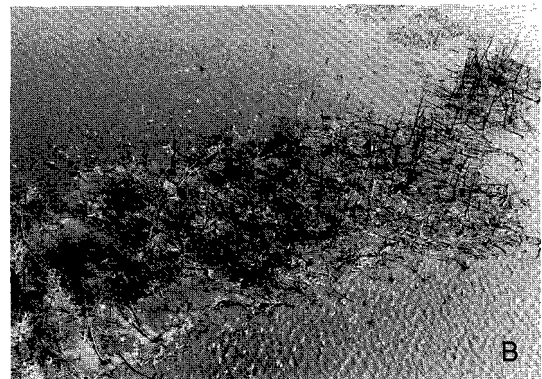
Throughout the breeding season of 1982 daily observations were carried out to locate the main foraging sites of the Cormorants from the two colonies. This was done by following the birds leaving the colony until they reached their fishing site. These observations turned out to be relatively easy because of the birds' habit of foraging in huge social groups (Voslamber & Van Eerden 1991, Van Eerden & Voslamber 1995). The prevalence of social fishing over solitary fishing over a much wider range is a rather recently acquired habit (cf. Van Dobben 1952, De Boer 1972). In both colonies regular observations were made on individual nest attendance throughout the day, in order to determine the number and duration of individual foraging trips (defined as any period of absence of at least half an hour). These observations were carried out during the periods of nest building and/or occupation (only at Oostvaardersplassen), and the periods of breeding and raising the young (at both colonies). We were able to score foraging trips of males and females separately since the sexes are distinguishable (Koffijberg & Van Eerden 1995) within a pair. Eventually, freshly regurgitated pellets were collected the day following the observations and analysed later to obtain both qualitative and quantitative information on the food consumption. Experiments on

captive Cormorants at Amsterdam Zoo (Artis) have shown that each individual produces one pellet every morning (Zijlstra & Van Eerden 1995), containing the remains of the fish consumed the day before. Thus, the freshly regurgitated pellets found on any particular day were assumed to contain the indigestible remains of all the fish eaten by an individual Cormorant the previous day. So estimates were made of daily fish consumption, expressed in grams fresh mass, by identifying and measuring the otoliths retrieved from the pellets. Fish lengths and masses were calculated from otolith lengths, using empirically derived regression equations (cf. Doornbos 1979, Platteeuw 1985, Voslamber 1988, Marteiijn & Dirksen 1991, Platteeuw *et al.* 1992). No correction for possible wear was made. In this way we were able to relate both time spent per day in foraging trips (time budget) and travelling distance from the colony to the main fishing site (field observations) to an estimate of the amount of fish eaten (pellet analysis).

RESULTS

Structure of the colonies

The Naardermeer colony was established in a complex of rather high Alder *Alnus glutinosa* trees, situated in a circle. This had been the result



Colony of Cormorants *Ph.c.sinensis* at Oostvaardersplassen, Flevoland The Netherlands, May 1991. (A) site after 7 years of breeding in trees, (B) after 14 years. (Photographs M.R. Van Eerden)

of the dying off of trees over 40 years. Thus virtually any individual breeding pair could oversee the entire colony (Fig. 1). By contrast, the Oostvaardersplassen colony was distributed over a larger area of rather young (and low) willows (*Salix cinerea*, *S. triandra*, *S. viminalis*), situated on a number of small peninsulas, which were poorly inter-visible (Fig. 1). Furthermore, many nests were situated lower than at the Naardermeer colony (with quite a lot of nests actually on the ground), so it must be assumed that in this colony it was much less easy for individual pairs to be aware of the activities of the other inhabitants of the colony.

Time and frequency of foraging flights

The total amount of time spent by individual breeding Cormorants in foraging trips increased markedly throughout the breeding season, delineating clearly the periods of nest occupation, breeding and raising the young (Fig. 2 A). There was no marked difference in this respect between the two colonies. The first increase in time spent outside the colony (from period of nest occupation to breeding period) was achieved mainly by enhancing the duration of each foraging trip rather than by carrying out more trips (Fig. 2 B, C), while the gradual second increase was caused by the fact that individual birds started to carry out 2-3 trips per day in stead of 1-2 during nest occupation and breeding. At this point the first remarkable difference between the two colonies began to emerge: the Naardermeer Cormorants made on average 1.2 trips a day during the breeding period and 2 trips a day while tending their young, whereas the Oostvaardersplassen birds carried out 2 and 3 trips a day respectively (Fig. 2 B). The mean duration of an individual foraging flight, however, tended to be longer among the Naardermeer birds, especially in the chick rearing period (Fig. 2 C).

Synchronisation of foraging flights

Since the birds from the two colonies generally joined together in huge social fishing groups (Voslamber & Van Eerden 1991, Van Eerden &

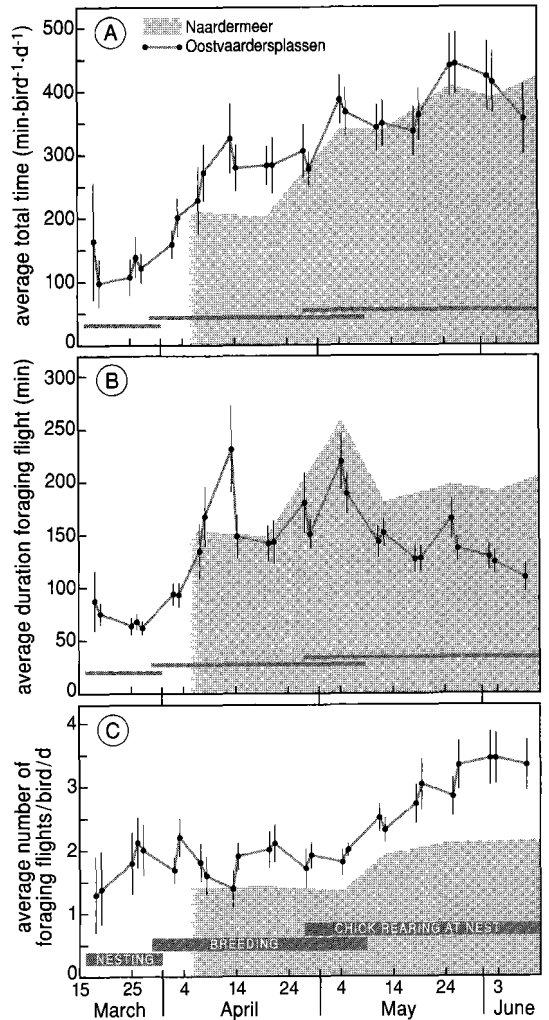


Fig. 2. Seasonal patterns for two colonies in total amount of time spent per day in foraging flights (A), mean length of individual foraging flights (B) and total number of foraging flights per day (C). Indicated are also the 95% confidence limits.

Voslamber 1995), a rather high degree of synchronisation of the foraging flights was to be expected at the two sites. For two days within the breeding period and four days in the young raising period the percentages of parent birds attending the nest site were recorded for the entire daylight period (Fig. 3). It becomes apparent that

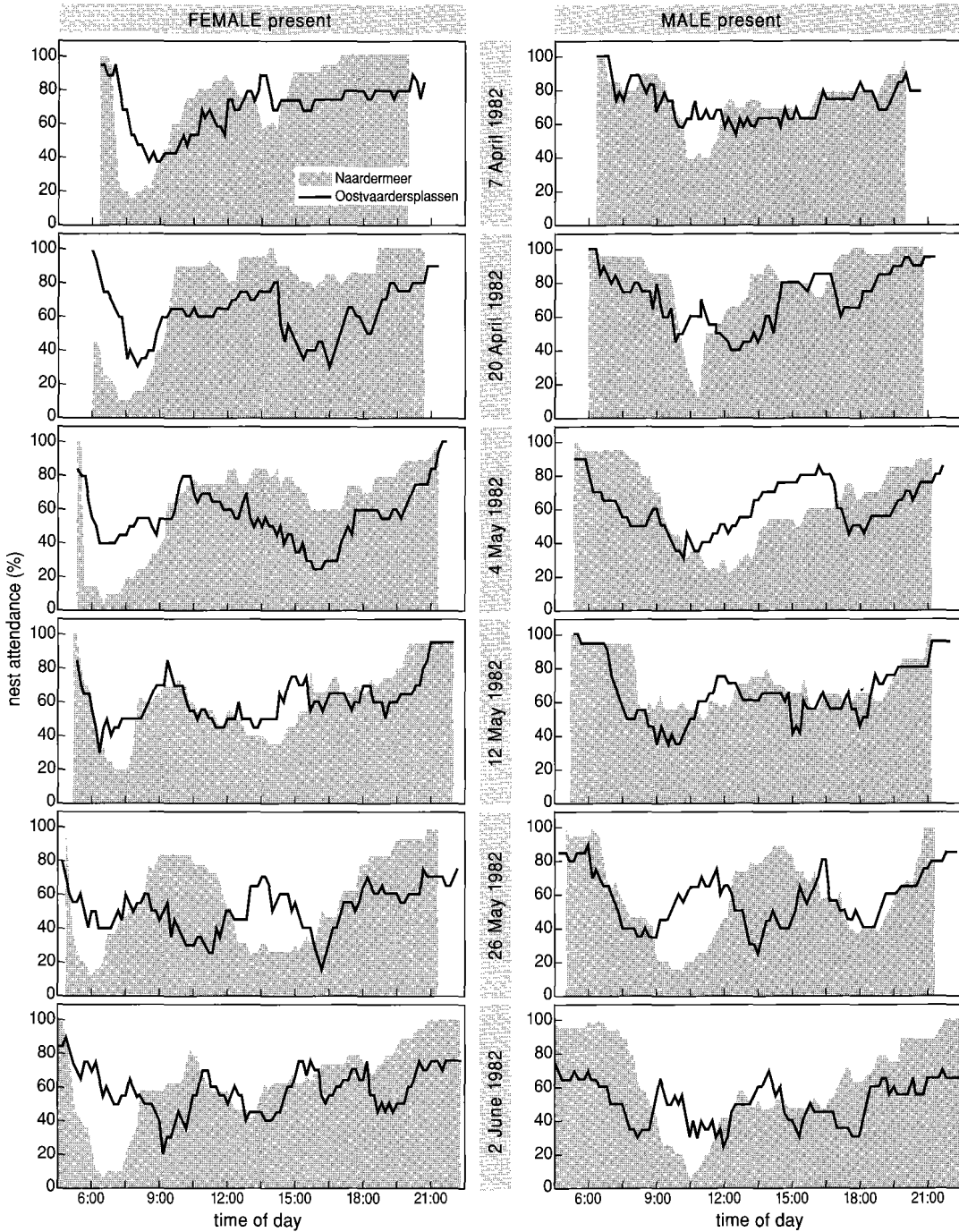


Fig. 3. Nest attendance (in %) at Oostvaardersplassen and Naardermeer of both sexes throughout the daylight period for two days within the breeding period and for four days within the period of rearing young.

both sexes showed rather well synchronised movements to the fishing grounds in both colonies. Nonetheless, the degree of synchronisation was much higher at the Naardermeer colony than at the Oostvaardersplassen colony. In the breeding period, when the Naardermeer birds made only one trip a day, from noon onwards virtually all birds there remained at the nest site until dusk. Furthermore, throughout the entire breeding cycle both males and females from the Naardermeer colony were at any one time of the day present or absent in a markedly higher percentage than birds from Oostvaardersplassen.

A second remarkable feature shown by Fig. 3 is the difference in timing of the foraging flights between males and females. In both colonies the females were generally the first to leave, the males awaiting their return while brooding or keeping the chicks warm before leaving themselves. This feature was even more marked in the Naardermeer birds.

In all periods the females spent 4-16% more time on foraging trips than the males in both colonies. During the night, 57% of the brooding was carried out by the females, while during the day the males took charge of 55%. This meant that both sexes spent about the same amount of time brooding, albeit that the females generally covered the coolest periods.

Daily fluctuations in foraging flights

Rather large daily fluctuations in the mean duration of individual foraging trips were found (Fig. 2 C). There were considerable daily variations as well in the choice of the main foraging site on lake IJsselmeer (Voslamber & Van Eerden 1991). The mean time spent on individual foraging trips on one particular day was related to the distance the birds had to travel that day (Fig. 4). For this analysis only data on the Oostvaardersplassen colony were used. Not surprisingly, 55% of the variance in the average duration of a foraging flight was explained by travelling distance.

Subtracting the time spent in flying to and from the fishing site, calculated on the basis of flight speed measurements (about 50 km/h, Vos-

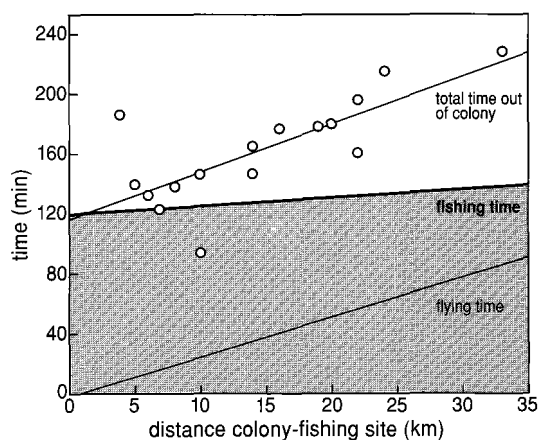


Fig. 4. Relation between travelling distance from the colony to the main fishing site and mean time spent in an individual foraging flight within the same day.

lamber 1988), from the total time spent on a foraging flight, the time spent on the water could be estimated as well (Fig. 4). This actual foraging time hardly increased at all on days with a longer travelling distance, which means that an increase in the distance to be travelled from the colony to the day's main foraging site resulted in longer foraging flights but not in significantly longer foraging times.

Daily fish consumption

The daily fish consumption of adults varied from about 235 g to almost 360 g fresh mass, with a mean value of about 330 g. In both colonies a marked decrease in daily consumption was noted between April and June and there were no consistent differences between the two colonies (Table 1).

For each of the 19 days for which both travelling distance and daily individual food consumption were estimated, Spearman rank correlation coefficients between these factors, as well as between travelling distance and mean mass of an individual prey item were not significantly negative (r_s between -0.09 and -0.56, $p > 0.1$) for both

Table 1. Average daily fish consumption (g fresh mass) per month as derived from reconstruction of species specific fish lengths and masses from otoliths in pellets in 1982.

	Oostvaarders- plassen		Naardermeer		average	
	fish mass/ pellet (g)	<i>n</i>	fish mass/ pellet (g)	<i>n</i>	fish mass/ pellet (g)	<i>n</i>
April	359.8	84	331.6	18	354.8	102
May	322.9	73	366.8	78	345.6	151
June	234.3	7	255.6	66	253.6	73
total	338.0	164	317.8	162	327.9	326

colonies. Clearly, the daily amount of food consumed per individual did not significantly change with the travelling distance. However, an overall tendency to eat somewhat less on days with a greater travelling distance seemed to become apparent.

DISCUSSION

Duration of foraging flights

In 1982 social fishing of breeding Cormorants on lake IJsselmeer took place at average distances of respectively 21.6 km (± 11.8) from Naardermeer and 14.6 km (± 6.9) from Oostvaardersplassen ($n = 81$; Voslamber 1988). From the relationship found between travelling distance and duration of an individual foraging trip (Fig. 4), average trips were estimated to last about 185 minutes in Naardermeer and 165 minutes (i.e. 12% less) in Oostvaardersplassen birds, which coincides very well with the empirical value found at Naardermeer (Table 2). Subtracting the also empirically established flying times (Voslamber 1988), it was found that the actual time spent foraging during each trip was only 3% less in Oostvaardersplassen birds. Thus, it can be understood that Cormorants from the Naardermeer colony, which had to go out further and therefore to spend more time flying than Oostvaardersplassen birds, were more inclined to carry out as few trips as they can. Therefore, since they still remain dependent upon

the social foraging techniques to maximise their efficiency (Voslamber 1988), the need to synchronise their movements may well be stronger in Naardermeer birds in order to ensure a sufficient number of fishing companions in spite of a lower frequency of foraging trips. The high degree of synchronisation achieved by the Naardermeer birds was unlikely to be equalled by Oostvaardersplassen birds, because of the rather chaotic structure of the colony.

The total daily amount of time spent by Cormorants outside their breeding colonies increases between the periods of nest site occupation and incubation and again, gradually, between the periods of incubation and young raising. The first increase could result from making longer trips, while the second increase is brought about by making more trips a day. In terms of time and energy, it may be a disadvantage to carry out more foraging flights instead of making longer ones in order to meet the growing energy needs. A good reason for not increasing the duration of individual foraging flights in the period of chick rearing may be that the birds would tend to stay at the fishing site until the maximum amount of fish is caught, with which they are still able to return to the colony. A very similar mechanism was assumed to exist in determining the timing of foraging flights between colony and feeding sites in Spitzbergen Barnacle Geese *Branta leucopsis* (Prop *et al.* 1978). The fact that the actual foraging time was found to be relatively constant, merely

dependent upon the foraging success to be achieved at a given site, may be explained by this phenomenon. To be able to save on flying movements to and from the colony, the parents should thus have to stay out digesting. This would probably result in absences of more than a day, as found in seabirds, e.g. the Red-footed Booby *Sula sula* (Diamond 1974). The quick day-to-day shifts in main foraging site that are the rule in the IJsselmeer area (Voslamber 1988, Van Eerden & Voslamber 1995), as well as the fact that having to feed up to 3 young requires shorter foraging flights than taking care of a single chick (cf. Diamond 1974) rule out this option.

Sexually linked patterns in timing of foraging

It was found that, generally, female Cormorants were the first to leave the colony for foraging in the morning. By carrying out on average more foraging trips a day they spent more time per day foraging. It was argued before that the growing food demand of the chicks cannot be met by enhancing the duration of the individual trips. Thus, it may be assumed that females are forced to spend more time on foraging, because during the reproductive cycle they are generally under greater pressure than males. The only way for either one of the partners to bring more food to the nest is by making more trips a day (and forcing the other partner to brood or safeguard the chicks, cf. Pierotti 1981). The partner that is the first to leave (probably being most in need of food, cf. Davis 1982) has the option to make one trip more each day. Checking on the few cases in which the males were the first to go foraging, it was indeed found that in these instances they spent more time outside the colony. The duration of consecutive foraging flights only began to diminish significantly from the fourth daily trip onwards. The question as to why female Cormorants should be under greater pressure than males is less easy to answer. Possibly egg production has worn them out and furthermore a 50% share in brooding, and generally covering the more energy-consuming night sessions, may very well represent a larger proportion of parental invest-

ment at this stage because females are slightly smaller and lighter than males (Koffijberg & Van Eerden 1995). The fact that in the Naardermeer colony the females were even more inclined to be the first to leave may thus be an indication for a greater pressure on these birds, caused by the generally larger travelling distances.

Implications on energy budget

It has been shown that Cormorants, when feeding further out, enhance neither their actual foraging time or their daily food consumption. Their average daily intake, some 330 g of fresh fish in both colonies, would provide them with a gross energy intake (*GEI*) of about 1518 kJ (caloric values of fish species consumed are about 4.6 kJ/g fresh mass, Platteeuw 1985). Assuming an assimilation efficiency of 0.8 for piscivorous birds (Castro *et al.* 1988), this amounts to a daily metabolisable energy (*DME*) of about 1214 kJ. Assuming an average body mass of 2.6 kg (Cramp & Simmons 1977), basal metabolic rate (*BMR*) can be estimated at 620 kJ (Aschoff & Pohl 1970). Thus, *DME* would amount to about $2 \cdot BMR$, a remarkably low value in comparison with other species (e.g. Kersten & Piersma 1987). The time budget of an average day, on which the birds make two feeding trips (Oostvaardersplassen and Naardermeer birds to sites at distances of 15 and 22 km respectively), enables us to roughly estimate the energy expenditure as well, using the activity-specific metabolic rates found for Gannets *Sula bassana* and various other seabird species by Birt-Friesen *et al.* (1989; cf. Table 3). It is assumed that of the total fishing time of about 4 h a day, about half is spent swimming and the other half diving (Voslamber 1988). Thus, an overall daily energy expenditure of $65.4/24 = 2.7 \cdot BMR$ emerges for Oostvaardersplassen birds and of $66.3/24 = 2.8 \cdot BMR$ for those of Naardermeer. Although these energy costs remain well below the generalised optimal working level of $4 \cdot BMR$ in bird parents (Drent & Daan 1980, Masman *et al.* 1989), the calculations induce to believe that even at these apparently low costs Cormorants from both colonies suffered a negative energy balance

Table 2. Mean time (in minutes and percentages) spent in foraging flights per bird per day (*t*) in periods of nest occupation, breeding and young raising in Oostvaardersplassen (OVP) and Naardermeer in 1982 (NM) (*n* = number of Cormorant-days).

	Males time spent foraging (minutes)			Females time spent foraging (minutes)		
	<i>t</i>	<i>SD</i>	<i>n</i>	<i>t</i>	<i>SD</i>	<i>n</i>
<i>OVP</i>						
nest occupation	102 42%	96.8	62	140 58%	85.7	62
breeding period	245 45%	123.1	197	297 55%	142.6	197
young period	385 48%	155.4	233	422 52%	148.9	233
<i>NM</i>						
breeding period	193 46%	90.9	40	225 54%	65.2	38
young period	366 48%	141.6	95	398 52%	125.2	96

throughout the 1982 breeding season of 0.7 (= 434 kJ) and 0.8·*BMR* (= 496 kJ) per day respectively. With the breeding season lasting about 75 days (25 days incubating and 50 days before fledging) and the use of fat reserves providing about 38 kJ/g, Oostvaardersplassen birds should have shown an overall mass loss of $75 \cdot 434 / 38 = 857$ g and Naardermeer birds even of $75 \cdot 496 / 38 = 979$ g. Mass losses of 140-150 g over the breeding season have been shown to occur in eastern Germany, but since these birds averaged 620 g less in males and 325 g less in females at the onset of breeding than did Dutch birds (Cramp & Simmons 1977), mass losses of at least 770 g do seem possible. Taking into account that in 1982 feeding conditions close to both colonies were relatively favourable compared to other years (Van Eerden *et al.* 1991), the average travelling distance between colony and fishing site may become rath-

er higher than 15-22 km. In fact, on extreme days Cormorants may find themselves forced to cover up to 60 km to the nearest suitable fishing site. On such a day the energy loss would amount to 1.3·*BMR* (= 806 kJ) and the birds might experience a mass loss of no less than 21 g within a single day.

We must conclude that adult breeding Cormorants do not seem to achieve a mean daily *GEI* high enough to cover the costs of foraging at large distances from the colonies and at the same time maintain their energy balance. At travelling distances of 15-22 km, mean daily energy expenditure (*DEE*) does not exceed values of about 2.7-2.8·*BMR*, which is low in comparison to maximum working levels in birds. The energetic bottleneck therefore seems to be caused by lack of time for foraging rather than by physiological energy constraints. Birds may have to go further afield when feeding conditions nearby become

Table 3. Estimated costs from time budget data for Cormorants on an average day in Oostvaardersplassen (OVP) and Naardermeer (NM) during the 1982 breeding season. Costs estimated according data from Birt-Friesen *et al.* (1989).

activity	costs (kJ·h ⁻¹)	time (h)		costs kJ·d ⁻¹	
		OVP	NM	OVP	NM
feeding/interaction	64.6	1	1	64.4	64.6
sleeping/resting	55.0	17.6	17.3	968.4	951.9
flying (2 trips)	135.6	1.4	1.7	189.9	230.6
swimming	97.7	2	2	195.3	195.3
diving	135.6	2	2	271.3	271.3
total		24	24	1689.4	1713.6
in multiples of BMR				2.7	2.8

worse than in 1982 (Van Eerden *et al.* 1991) and *DEE* may increase until up to 3·*BMR*. In these conditions the parent birds are bound to reduce on the number of fishing trips, which might cause their chicks to starve (cf. Platteuw *et al.* 1994). Indeed, Naardermeer birds have been shown to produce less fledglings per pair in five out of six consecutive years (Van Eerden *et al.* 1991).

ACKNOWLEDGEMENTS

Field observations on fishing sites and fishing behaviour were carried out by Bram Bij de Vaate, Wouter Dubbeldam, Jan Muller, Berend Voslamber and Menno Zijlstra. Berend Voslamber also participated in sorting out the regurgitated pellets and identifying, counting and measuring the otoliths. Willem Dekker and Bruno Ens assisted during the computer processing of the food data. A first draft of this paper was critically examined by Joep de Leeuw. Our sincere thanks are due to all these persons.

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SAMENVATTING

Van twee kolonies Aalscholvers, Naardermeer en Oostvaardersplassen, is onderzocht in hoeverre hun verschillende ligging ten opzichte van de visgronden in IJsselmeer en Markermeer consequenties heeft voor de tijds- en energiebesteding van de vogels. Dagelijkse bepalingen van de exacte visplaatsen van beide kolonies wezen uit dat de gemiddelde afstand tussen kolonie en visplaats voor beide kolonies respectievelijk 22 en 15 km bedroeg. In beide kolonies werd, naarmate het broedseizoen vorderde, meer tijd door de vogels aan fourageervluchten besteed. De twee belangrijkste toenames vonden plaats op het moment van eileg en op het moment van het uitkomen van de jongen. De eerste toename kwam tot stand door het uitvoeren van langere fourageervluchten, de tweede door het maken van meer vluchten.

In het algemeen maakten vogels uit het Naardermeer minder vluchten per dag (1.2 in broedtijd en 2 in jongentijd) dan die uit de Oostvaardersplassen (respectievelijk 2 en 3). Wel was de duur van de gemiddelde fourageervlucht bij Naardermeer vogels langer. Ook binnen één kolonie en binnen de jongentijd bestonden grote dagelijkse verschillen in zowel de totale tijd die aan fourageervluchten werd besteed als in het aantal vluchten. Deze variatie hing vooral samen met de aanzienlijke dagelijkse verschuivingen van de voornaamste visplaatsen. Naarmate deze verder van de kolonies verwijderd waren, duurden de voedselvluchten langer en deze toegenomen duur kwam uitsluitend voor rekening van de toegenomen vliegtijd.

Kwantitatieve analyses van vers gevonden braakballen toonden bovendien aan dat vluchten naar verder verwijderde visgronden evenmin gecompenseerd werden door een hogere voedselopname op dergelijke dagen.

Vogels uit het Naardermeer vertoonden een sterkere synchronisatie van de voedselvluchten dan soortgenoten uit de Oostvaardersplassen. Omdat ze verder weg moeten gaan, maken ze minder vluchten per dag. Om dan toch in samenwerkende groepen te kunnen opereren is de noodzaak tot synchronisatie veel sterker in deze kolonie. De ruimtelijke structuur van de kolonie in het Naardermeer (nesten gesitueerd in een cirkel van hoge bomen rond een min of meer open plek) laat een goede synchronisatie ook gemakkelijker toe dan die van de Oostvaardersplassen. Meestal zijn de eerst vertrekkende vogels vrouwtjes. Door als eerste van een broedpaar te vertrekken stelt een Aalscholver zichzelf in staat om op een bepaalde dag één vlucht meer te maken dan zijn partner. Het is dan ook in het algemeen zo dat vrouwtjes iets meer tijd aan fourageervluchten besteden dan mannetjes.

Een schatting van de energiebesteding op basis van

de vastgestelde tijdsindeling suggereert dat Naardermeer vogels $2.8 \cdot BMR$ (basale metabolisatie snelheid) en Oostvaardersplassen vogels $2.7 \cdot BMR$ per dag besteden. Dit verschil wordt veroorzaakt door het verschil in gemiddeld af te leggen afstand. In beide kolonies kan de gemiddelde *DME* (dagelijks metaboliseerbare hoeveelheid energie) op basis van braakbalanalyses worden geschat op ongeveer $2 \cdot BMR$. De hieruit resulterende negatieve energiebalans zou over de gehele duur van het broedseizoen leiden tot een gewichtsverlies van ongeveer 980 g voor Naardermeer vogels en 860 g voor Oostvaardersplassen vogels. Het zal duidelijk zijn dat toenemende afstanden tussen kolonie en visplaats kunnen leiden tot een dermate groot gewichtsverlies bij de oudervogels dat ze gedwongen worden om de jongen te verwaarlozen, om zelf in conditie te blijven.

In jaren waarin vaak op grote afstand moet worden gevist, mag men dan ook een geringer voortplantingsresultaat verwachten. Eerder is aangetoond dat vogels uit het Naardermeer minder vliegvlugge jongen per paar grootbrengen dan vogels uit de Oostvaardersplassen. Dit suggereert de sterke invloed van de reisafstanden.