Energy requirements of breeding great cormorants *Phalacrocorax carbo sinensis*

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ABSTRACT: Cormorants and humans are purported to compete for fish resources. Recent increases in cormorant populations in western Europe have led to new conflicts between fishermen and nature conservationists, a situation which has stimulated research into the food requirements of these seabirds. However, most dietary studies are based on stomach content or pellet analysis. Both these methods are biased. We used a time-budget model to calculate the energy requirements of great cormorants *Phalacrocorax carbo sinensis* breeding in Schleswig-Holstein, Germany. The time budgets of the birds were recorded for different breeding phases and the energetic costs of the different activities determined through respirometric measurements or by using values derived from the literature. The food requirements of great cormorants during incubation were calculated to be 238 g adult^{-1} d^{-1} These requirements rise to 316 g d^{-1} during the rearing of young chicks and to 588 g d^{-1} during rearing of downy chicks. Human disturbance causing great cormorants to fly off their nests entails an additional consumption of 23 g fish per bird or ca 23 kg per disturbance event for a typical colony.

KEY WORDS: *Phalacrocorax carbo sinensis* · Time/energy budget · Food requirements · Breeding season · Disturbance

INTRODUCTION

The great cormorant *Phalacrocorax carbo* occurs on all the world's continents and is considered by some to be a major competitor with humans in certain areas (Deufel 1986). This apparent competition resulted in the destruction of most European colonies of the great cormorant *P. carbo sinensis* at the end of the last century (Dif 1982). Persecution has decreased since World War II, after which cormorants became protected. The enhanced protection and, to a lesser extent, the general eutrophication of coastal and freshwater ecosystems have recently led to a rapid increase in the European population of this bird (Hashmi 1988, Suter 1989). This development has been followed by a conflict between nature conservationists and fishermen concerning the influence of cormorants on coastal and freshwater fish populations (Knief & Witt 1983). Consequently, cormorant research has focused on the feeding ecology of these seabirds with the aim of better understanding of their position in the aquatic ecosystem (see Müller 1986, Worthmann & Spratte 1990,

Marteijn & Dirksen 1991). In most studies that directly concern *P. carbo sinensis*, daily food intake has been calculated from pellet or stomach content analyses. However, both of these methods have been shown to be biased (Grémillet & Plös 1994). In the present study we determined the daily energy requirements of great cormorants breeding in Schleswig-Holstein (Germany) using a time budget analysis as described by Weathers et al. (1984). This method allowed us to calculate the theoretical food intake per bird per day for the different breeding phases.

METHODS

Time budgets. Time budgets of great cormorants breeding at Lake Selent (54° 25′ N, 10° 30′ E; Fig. 1), Germany, were determined during June 1993. Ground-breeding birds were observed from dawn to dusk from a hide set 5 m from the nests. Bird activity patterns were recorded using a manual field computer (Husky Hunter II). Activities such as resting, preening, nest
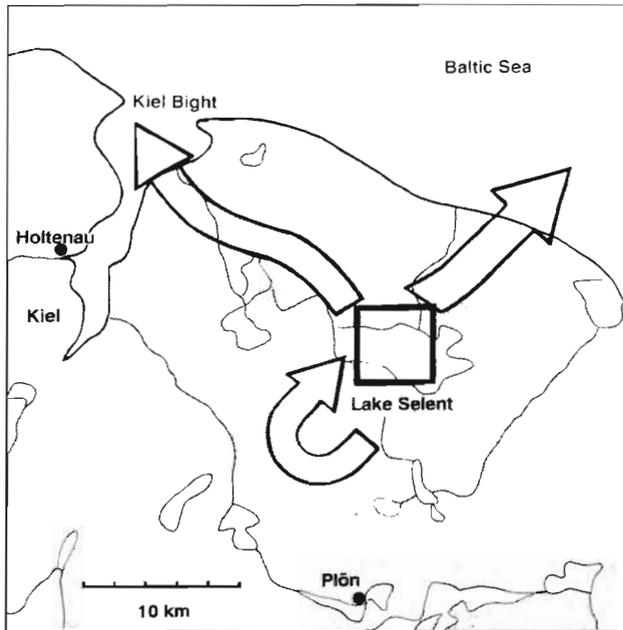
Fig. 1. The study area near Kiel, Germany. Arrows show flight routes of the cormorants to the different fishing grounds (Kieckbusch & Koop 1992). Locations of weather stations are also indicated (●)

building, and chick feeding were registered for incubating birds and for birds raising small (<10 d) or downy chicks. The duration of the foraging trips and their incidence per day were also recorded. Minor activities such as nest defence, walking, wing stretching, and shivering were grouped in a single category.

Great cormorants outside the colony may swim, stretch their wings, preen, and rest. The swimming time per foraging trip was determined during June 1993 by direct observation (binoculars 10 × 50; maximum distance 300 m) of great cormorants fishing along the coast of the Baltic Sea. The observed birds were identified as breeding adults by their dark black body feathers and the white patches on their upper legs.

The flight time per foraging trip was calculated using observations from Menke (1986) and Kieckbusch & Koop (1992) of the flight routes of cormorants breeding at Lake Selent. The areas in which these cormorants usually feed are the lake itself, the outer Kiel Fjord and the Kiel Bight (Fig. 1). Assessment of the diet of the birds by Kieckbusch & Koop (1993) showed that they consume nearly 50% marine and 50% freshwater fish. We thus assumed that the cormorants use the sea for a fishing ground half of the time and the lake the other half of the time. The birds were assumed to fly the shortest route from the colony to the feeding site to avoid flight other than this while at sea, to feed only once during each trip, and to have comparable swimming times when feeding on Lake Selent and at sea. Recent radio-tracking data (Grémillet unpubl.) and direct observations (Menke 1986) confirm these assumptions. The duration of wing stretching was derived from Menke (1986). Resting and preening times outside the colony were assumed to be equal to foraging time as derived from observations at the colony, minus flight, swimming and wing-stretching time.

Energy costs. The resting metabolic rate (RMR) and the energy costs of preening were determined through measurement of oxygen consumption. All respirometric measurements were performed during September 1993 at the Heimattierpark Neumünster, Germany. Five fasting great cormorants were kept for at least 2 h in a 100 l respiration chamber in the dark within their thermoneutral zone, their oxygen consumption was measured using an open respirometric system and an Oxygor 6N oxygen analyser (Maihak, Hamburg; for details see Culik et al. 1990). The birds were particularly tame and thus quickly became accustomed to the respiration chamber. They typically first preened, after which they stood quietly. We used data from standing birds as this is the normal resting position in cormorants, even during the night. The RMR was calculated from the lowest measured oxygen consumption, which was in general attained after 60 min. The RMR at night or during periods of sunshine was assumed to be 75% or 90%, respectively, of the RMR measured in the respiration chamber (Aschoff & Pohl 1970, Dunn 1976). The lower critical temperature in great cormorants is 9°C, calculated after Kendeigh et al. (1977). Since field temperatures of below 9°C occurred for less than 5% of the total breeding time, birds were assumed to be within their thermoneutral zone for the entire breeding season.

Great cormorants usually reuse old nests (Kortlandt 1991). Nest building therefore mainly consists of the reorganisation of nest material. This activity pattern involves head and beak movements which are similar to the movements of preening. We thus assumed that the energy costs of nest building were the same as for preening

The energy costs of egg production can be derived from the energy content of the eggs (Kendeigh et al. 1977). Cooper (1987) additionally showed that the energy content of eggs from the bank cormorant *Phalacrocorax neglectus* was linearly related to their fresh weight. We therefore used the relationship between fresh egg weight and egg energy content given by Cooper (1987) to determine the energy content of great cormorant eggs. The mean fresh weight was taken to be 46 g (Dif 1982). We also considered an efficiency of 70% for egg production (King 1973) and a mean clutch size of 3 (Menke unpubl.) for great cormorants breeding at Lake Selent.

The energy costs of incubation were determined according to Kendeigh et al. (1977) using a mean clutch size of 3, a mean egg weight of 46 g and mean egg and nest temperatures of 33.4 and 28°C respectively (Cooper 1987). A mean egg coverage of 80% (Ackerman & Seagrave 1984) and a constant incubation were also assumed. The energy costs of brooding were also calculated according to Kendeigh et al. (1977) assuming a mean brood size of 2 chicks (Gregersen 1991), a mean chick weight of 165 g (Platteeuw et al. in press), a mean chick body temperature of 40°C (Grémillet unpubl.), and a constant mean coverage of 80%.

Further energy expenditure occurs while parents feed chicks. This activity was determined to cause RMR to rise up to 1.10 in Adélie penguins and to 1.53 in Adélie penguin chicks (Culik 1995). As both regurgitation in adults and begging in chicks are very similar in penguins and cormorants, we consider that the energy requirement of cormorants for this activity can be derived from the measurements made by Culik (1995) in Adélie penguins.

The energy requirements of great cormorant chicks were derived from respirometric measurements made by Dunn (1976) on chicks of double-crested cormorant *Phalacrocorax auritus*. Growth curves of great and double-crested cormorant chicks are very similar Additionally, the species live under comparable meteorological conditions (Schleswig-Holstein and New Hampshire, USA). Thus, according to Klaassen & Drent (1991), the energy requirements of great cormorant chicks can be derived from Dunn (1976).

As in the case of the adult birds, we assumed chicks incur a reduction in RMR of 25% during the night (Aschoff & Pohl 1970) and of 10% during sunny conditions (Dunn 1976). This last assumption was considered valid only for chicks older than 10 d, as younger chicks are constantly covered by their parents.

Flight costs were determined according to Pennycuick (1989) for a body mass of 2230 g (Dif 1982), a wingspan of 136 cm (Géroudet 1959) and a flight speed of 70 km h^{-1} (Van Dobben 1952, Géroudet 1959). Different 'parasitic' food loads were also considered.

The costs of underwater swimming and of resting on the water surface were determined through respirometic measurements using methods described in Culik & Wilson (1991). These measurements were also conducted at the Heimattierpark Neumünster, using the same analytic system as for the determination of RMR and metabolic costs of preening. Five tame great cormorants were trained to voluntarily enter a 13 m long canal (1 m wide and 1 m deep) and to swim from one end of the enclosure to the other. The canal was equipped with a respiration chamber at each end, whereas the rest of the surface was entirely covered

with transparent PVC plates. This guaranteed that the birds could breathe only in the chambers. Each experiment was conducted for 40 to 72 min (mean: 56 min), during which the activity patterns of the birds and their position in the canal relative to colour marks on the PVC plates were recorded by an observer with a walkman with quartz-based time speed. The birds were removed when they stopped swimming and remained for longer than 5 min in one of the chambers.

The energy requirements of wing stretching were determined using a relation given by Hennemann (1983). We assumed a mean body weight of 2230 g (Dif 1982), a mean body temperature of 40°C (Grémillet & Plös 1994) and a mean air temperature of 12.4°C (meteorological station Kiel-Holtenau).

Additional energy costs are required for food warming (Wilson & Culik 1991). These were calculated using a standard thermodynamic relation:

$$E = m \times SHC \times (T_1 - T_2)$$

where E is the energy required to warm the food in joules, m the mass of the food ingested in grams, SHC the specific heat capacity of the food (taken to be 4 J g^{-1} °C^{-1}), T_1 the stomach temperature of the bird (taken to be 40°C based on Grémillet & Plös 1994) and T_2 the temperature of the prey, i.e the water temperature for fish (taken to be 11.3°C; Schweimer 1978).

A literature review by Grémillet & Schmid (1993) showed that the mean daily food intake in great cormorants as determined by pellet and stomach content analysis is 358 g. We thus assumed that the birds from Lake Selent had to warm this quantity of fish every day. Some of this energy can be provided by the bird during hard exercise since 75% of the energy metabolised is liberated as heat (Schmidt-Nielsen 1983). cormorants need about 45 min to warm 358 g of food (calculated from Grémillet & Plös 1994). We noted that, post ingestion, birds usually stretched their wings for a few minutes and then divided their time between resting and preening. Knowing the energetic costs of each of these activities, it is possible to calculate how much heat the bird will be able to reuse for prey warming, assuming that all heat produced will be used to warm the stomach contents. The real energetic costs of eating cold food will be then equal to the costs of warming, minus the heat produced immediately after fishing. Substantial amounts of heat are also generated while flying. However, it is difficult to predict how much heat can then be used for food warming as the birds also lose much heat due to air cooling effects.

No data concerning body weight variations in breeding great cormorants were available. We thus assumed that all energy requirements of breeding birds have to be covered by their food intake during the breeding season and are not taken from fat reserves.

Following Brugger's (1993) calculations for double-crested cormorants, the assimilation efficiency of great cormorants was taken to be 77%. Kieckbusch & Koop (1993) determined by pellet analysis that great cormorants breeding at Lake Selent feed on a very wide range of prey items including perch *Perca* sp., white fish, cod *Gadus morhua* and other marine fish such as sandeel *Ammodytes* sp., whiting *Merlangius merlangus*, herring *Clupea harengus*, plaice *Pleuronectes platessa* and viviparus blenny *Zoarces viviparus*. Cormorants may also take shore crabs *Carcinus maenas*. The mean energy content of their food was thus calculated to be 4.0 kJ g^{-1} (taken from Kieckbusch & Koop 1993, Hislop et al. 1991 and Sidwell 1981, where mass refers to fresh mass of food).

Weather conditions, especially air temperature and wind speed, have been shown to influence the metabolism of free-living birds so as to make the use of respirometric measurements inadequate for the calculation of the daily energy budget (Kendeigh & Blem 1974) We consequently recorded meteorological conditions, such as air and water temperature and wind speed and light intensity, at the breeding site and at the zoo. These measurements were made every 10 min at a height of 1.5 m using a portable micrometeorological station (Grant Instruments). Mean weather data over the complete breeding season (April to July) at the feeding grounds and at the breeding colony were taken from the weather stations Kiel-Holtenau and Plön respectively (Fig. 1). Water temperatures at the fishing areas were taken from Schweimer (1978).

Air temperature in the respiration chambers was also recorded using an independent temperature probe (Single Channel Unit Processor; Driesen & Kern).

RESULTS

Activities outside the colony

Our observations at the breeding colony show that during the day the time spent foraging rises from 44% for incubating birds to 58% for birds with small chicks and to 65% for birds with downy chicks (Figs. 2 to 4). This corresponds to 425, 555 and 623 min spent every day outside of the colony for incubating birds and birds tending small and downy chicks respectively (for a mean day length of 16 h). We also observed that the number of foraging trips per day was higher for birds with chicks than for incubating birds, i.e. a mean of 0.75 d^{-1} (SD = 0.7, n = 2) for incubating birds, 1.81 d^{-1} (SD = 0.8, n = 26) for birds with small chicks and 2.81 d^{-1} (SD = 1.1, n = 16) for birds with downy chicks.

The mean flight distance for a foraging trip to the sea is 30 km, whereas the birds fly only 5 km during a trip
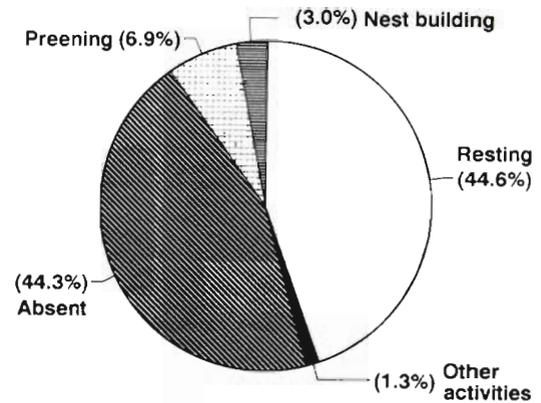
Fig. 2. *Phalacrocorax carbo sinensis*. Time budget of incubating great cormorants as observed at Lake Selent from dawn to dusk

on the lake. This results in a mean flight distance of 17.5 km per foraging trip. Considering the different numbers of foraging trips for the different breeding phases, a mean daily flight distance of 13.1 km for incubating birds (0.75 foraging trips d^{-1}), 31.7 km for cormorants raising small chicks (1.81 trips d^{-1}) and 49.2 km for cormorants with downy chicks (2.81 trips d^{-1}) was calculated. The flight speed of great cormorants is 70 km h^{-1} (Van Dobben 1952, Géroudet 1959), which gives a daily flight time of 11 min for incubating birds, 27 min for birds with small chicks and 42 min for birds with downy chicks. Wind influence on flight time was ignored due to practical difficulties.

The cormorants observed feeding swam for a mean of 28 min (n = 21, SD = 5.3). Considering this time as the mean swimming time for 1 foraging trip, we calculated that incubating birds swim a mean of 21 min d^{-1}, cormorants with small chicks consequently swim 51 min and cormorants with downy chicks 79 min.
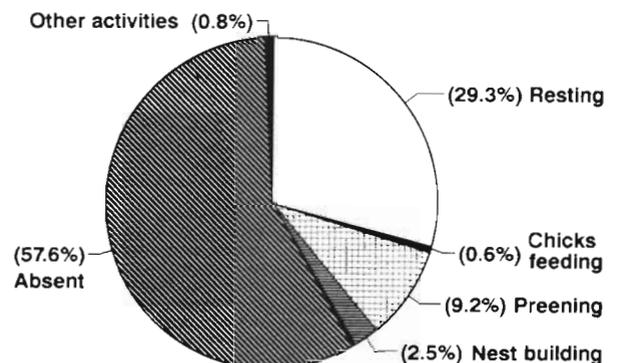
Fig. 3. *Phalacrocorax carbo sinensis*. Time budget of great cormorants with small chicks as observed at Lake Selent from dawn to dusk
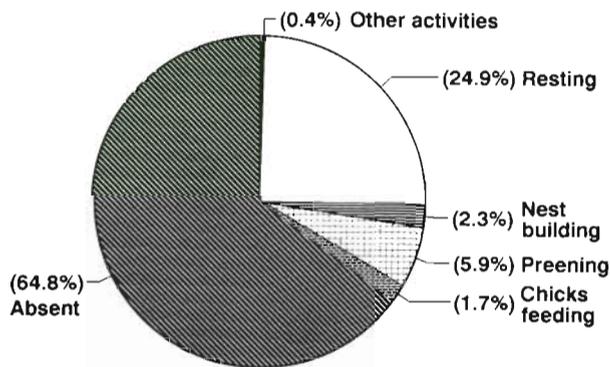
Fig. 4. *Phalacrocorax carbo sinensis*. Time budget of great cormorants raising downy chicks as observed at Lake Selent from dawn to dusk

Great cormorants stretch their wings for 6 min after each foraging trip (Menke 1986). We can thus predict a mean daily wing-stretching time of 5 min for incubating birds, and of 11 and 17 min for parents of small and downy chicks, respectively.

Flight, swimming and wing stretching only account for part of the time that great cormorants spend outside the colony (37, 89 and 138 min daily for birds with eggs and small and downy chicks, respectively), the bulk of this time being spent resting and preening on sand banks near the fishing grounds (388, 466 and 485 min daily for the different breeding phases). Assuming that cormorants spend 75% of this time resting and 25% preening (as observed at the colony), we can predict that they will rest outside the colony for 291, 350 or 363 min d^{-1} according to breeding phase, and correspondingly preen outside of the colony for 97, 117 and 121 min.

Activities within the colony

A total of 833 h of observations and 49 cormorant-days at the colony were recorded. The observed birds rested most of the time when on the nest (Figs. 2 to 4). Total daily resting time (in and outside of the colony) was thus calculated to be 718 min for incubating birds, 632 min for birds with small chicks and 602 min for birds with downy chicks. Additional observations at night showed that the cormorants always rested (480 min per 24 h in June) on the nest.

Total daily preening time (in and outside of the colony) was calculated to be 163, 205 or 178 min for cormorants with eggs or raising small or downy chicks, respectively.

Nest building was calculated to occupy 29 min of every day for incubating birds, 24 min for birds with small chicks and 22 min for those with downy chicks.

Small chicks were fed for 6 min every day, whereas downy chicks were fed for 16 min daily.

Chicks were active only when feeding and remained the rest of the time in the 'energy conserving sleeping posture' described by Nelson (1978) in gannets.

Weather data

Mean air temperature recorded at the breeding site was 15.5°C (range 10.5 to 26.3°C), which is very similar to the 15.3°C recorded at Plön (20 km distant) for the same period. We therefore consider that these localities have comparable climates and that the mean air temperature between April and July as recorded in Plön (12.5°C, range 6.6 to 16.5°C) is a good indicator of the air temperature at the breeding site. This temperature also differed only slightly from the mean air temperature at the zoo (12°C, range 4 to 21°C) and at the feeding areas (12.4°C, range 6.7 to 16.3°C). Additionally, air temperature in the respiration chamber at the zoo never differed by more than 0.4°C from the outer temperature (due to the high flow rate).

Wind speed at the Plön station was stable over the breeding season ($\bar{x}$ = 2.9 m s^{-1}, SD = 0.2) and we thus assume that the wind speeds measured at the colony represent those over the complete breeding season. Wind speeds were low (mean 1.6 m s^{-1}) due to the location of the breeding colony in a small bay sheltered from wind by high trees. Wind was thus considered to play a minor role in the metabolism of birds sitting on the nest. Conversely, winds at the fishing grounds, especially along the coast of the Baltic Sea, which have a mean speed of 3.9 m s^{-1} (April to July; weather station Kiel-Holtenau) presumably significantly influence the metabolism of cormorants resting on a sand bank. Finally 44% of the days during the breeding season were considered 'sunny' (more than 120 W m^{-2}) and 56% overcast.

Mean water temperature in the swimming canal was 12°C (11 to 13.1°C), whereas the mean water temperature at the fishing ground during the breeding season is 11.3°C (5 to 17°C between April and July).

Energy costs

The daily energy budgets of adult great cormorants incubating or raising small or downy chicks are shown in Tables 1 to 3. The mean RMR of the 5 great cormorants from the zoo was 24.7 kJ h^{-1} (SD = 2.3). Our weather data show that during the breeding season (April to July) the sun shines for 42% of the daylight hours. We thus use a RMR of 23.7 kJ h^{-1} for daytime. At night, a reduction of 25% in the RMR as measured at

Table 1. *Phalacrocorax carbo sinensis*. Daily energy budget (DEB) of an incubating great cormorant from Lake Selent. Three eggs per clutch are assumed. See text for further explanation

Activity	Total d^{-1}	Energy costs (kJ h^{-1})	Energy required (kJ d^{-1})
Resting (night)	8 h	18.5	148.0
Resting (day)	11 h 58 min	23.7	284.0
Preening & nest	3 h 12 min	53.8	172.2
Flying	11 min	189.7	34.8
Swimming	21 min	231.0	80.9
Wing stretching	05 min	55.4	4.6
Food warming	358 g fish	35.3 kJ d^{-1}	35.3
Incubating	12 h	0	0
Egg laying		286.8 egg^{-1} (30 d)$^{-1}$	28.7 (3 eggs)
DEB males: 100% efficiency			759.8
77% efficiency			934.6
Daily food requirement (4 kJ g^{-1} food)			233.6 g
DEB females: 100% efficiency			788.5
77% efficiency			969.9
Daily food requirement (4 kJ g^{-1} food)			242.5 g
Average daily food requirement			238 g

the zoo results in a RMR of 18.5 kJ h^{-1}. The energy costs of feeding small and downy chicks are 27.2 kJ h^{-1} (1.10 RMR) and 37.8 kJ h^{-1} (1.53 RMR) respectively.

The energy costs of preening and nest building were calculated to be 53.8 kJ h^{-1} (n = 5, SD = 7.0) and thus correspond to 2.18 RMR.

Flight costs without 'parasitic load' were calculated to be 189.7 kJ h^{-1}. Incubating birds foraging less than once a day consequently spend extended periods resting and preening near the feeding areas (388 min). This time is sufficient to digest all the fish eaten. We thus consider that there is no parasitic load for incubating birds, and take mean flight costs to be 189.7 kJ h^{-1}. Cormorants with small chicks spend less time resting and preening before they return to their nests and certainly have to carry part of the ingested food back to the brood. We thus assumed a general parasitic food load of 100 g for birds returning to the colony when raising chicks, which results in mean flight costs of 195.1 kJ h^{-1}.

Swimming costs in great cormorants as measured in the zoo varied according to swimming speed. The mean swimming speed in the canal was 1.53 m s^{-1} (SD = 0.23, range 0.5 to 3 m s^{-1}), with usual speeds of between 1.3 and 1.7 m s^{-1}. These results are related to the mean swimming speed of great cormorants in the wild which is considered to be 1.5 m s^{-1} (Johnsgard 1993). We thus assumed mean swimming costs of 231 kJ h^{-1}, which is the mean energy cost for swimming speeds between 1.3 and 1.7 m s^{-1}.

An amount of 54.8 kJ is required to warm 358 g fish caught at 11.3°C to the body temperature of cormorants. We also calculated that birds produce 19.5 kJ of heat during the 45 min after fishing when incubating. This amount rises to 21.3 and 23 kJ when the birds have small and downy chicks, respectively. Cormorants are therefore predicted to have an overall energy expenditure of 35.3 kJ d^{-1} for food warming when incubating and of 33.5 and 31.8 kJ when raising small and downy chicks, respectively.

The cost of laying eggs was calculated to be 286.8 kJ egg^{-1} and consequently 860.4 kJ for a clutch of 3. These costs were considered to be incurred over the total incubation period (30 d; Dif 1982) and thus represent daily energy costs of 28.7 kJ for female great cormorants.

Incubation costs calculated according to Kendeigh et al. (1977) are 678 J h^{-1} and the costs of brooding chicks 8.6 kJ h^{-1}. However, we considered that incubating cormorants metabolise 27.7 kJ h^{-1} (resting, preening and nest building) and consequently produce 20.7 kJ heat h^{-1}. This amount of energy is sufficient to keep eggs or chicks warm. We consequently assume that no additional energy costs are required for these 2 activities.

Energy budget of chicks

The RMR of small chicks as determined by Dunn (1976) is 4.3 kJ h^{-1}. The daily energy budget (DEB) of 1 of these chicks consequently involves 25.6 kJ for rest at

Table 2. *Phalacrocorax carbo sinensis*. Daily energy budget (DEB) of a great cormorant from Lake Selent while raising small chicks. Two chicks per brood are assumed. See text for further explanation

Activity	Total d^{-1}	Energy costs (kJ h^{-1})	Energy required (kJ d^{-1})
Resting (night)	8 h	18.5	148.0
Resting (day)	10 h 32 min	23.7	249.6
Preening & nest	3 h 49 min	53.8	205.3
Flying	27 min	195.1	87.8
Swimming	51 min	231.0	196.4
Wing stretching	11 min	55.4	10.2
Food warming	358 g fish	33.5 kJ d^{-1}	33.5
Brooding	12 h	0	0
Chick feeding	6 min	27.2	2.7
DEB chick			94.5
DEB chick + DEB parent			1028.1
77% efficiency			1264.6
Daily food requirement (4 kJ g^{-1} food)			316 g

Table 3. *Phalacrocorax carbo sinensis.* Daily energy budget (DEB) of a great cormorant from Lake Selent while raising downy chicks. Two chicks per brood are assumed. See text for further explanation

Activity	Total d⁻¹	Energy costs (kJ h⁻¹)	Energy required (kJ d⁻¹)
Resting (night)	8 h	18.5	148.0
Resting (day)	10 h 02 min	23.7	237.8
Preening & nest	3 h 20 min	53.8	179.3
Flying	42 min	195.1	136.6
Swimming	1 h 19 min	231.0	304.2
Wing-stretching	17 min	55.4	15.7
Food warming	358 g fish	31.8 kJ d⁻¹	31.8
Brooding	12 h	0	0
Chick feeding	16 min	37.8	10.1
DEB chick			853.9
DEB chick + DEB parent			1913.3
77% efficiency			2353.3
Daily food requirement (4 kJ g⁻¹ food)			588 g

night (with an RMR of $0.75 \times 4.3 = 3.2$ kJ), 68.4 kJ for rest during the day and 0.54 kJ for feeding activities (with an RMR of $1.25 \times 4.3 = 5.4$ kJ). This results in a DEB of 94.5 kJ per chick and of 189.1 kJ for a brood of 2 chicks.

The DEB of 1 downy chick can be calculated in a similar manner: 599.7 kJ is used at rest during the day (with an RMR of 39.9 kJ h⁻¹), 239.2 kJ for rest at night (with an RMR of $0.75 \times 39.9 = 29.9$ kJ h⁻¹) and 15 kJ for feeding activities (with an RMR of $1.25 \times 39.9 = 49.9$ kJ h⁻¹). The DEB of a brood of 2 downy chicks is consequently $2 \times 853.9 = 1707.8$ kJ.

The energy requirements of the brood are assumed to be equally divided between the 2 parents.

Assuming that the birds incubate for 30 d (Dif 1982) and then raise their chicks for 50 d, during which time the chicks are small for 10 d and downy for 40 d, the mean food intake of 1 breeding great cormorant can be calculated to be 428 g fish d⁻¹. In 1993, 503 great cormorant nests were counted at the breeding site at Lake Selent. Assuming a population of $2 \times 503 = 1006$ birds, a daily fish consumption of 428 g and a breeding period of 80 d, we can predict that the entire colony may need ca 34 metric tons of fish every breeding season, of which ca 17 t is likely to be taken from the lake and ca 17 t from the Baltic Sea.

DISCUSSION

Direct quantification of the daily food intake in cormorants through pellet or stomach content analysis has been shown to be problematic (Grémillet & Plös 1994). There are 5 further methods available to solve this problem: (1) The use of stomach temperature probes as first described by Wilson et al. (1992) can deliver information about the mass of single prey ingested with an accuracy of 80% (Grémillet & Plös 1994). However, the price of the devices and their high rejection rate by cormorants at sea reduces sample size and thus makes predictions about the food consumption of an entire population difficult. (2) The DEB can also be determined by using doubly labeled water (DLW). This method has an accuracy of 92% (Nagy 1989) but also involves substantial financial costs and has several drawbacks: in particular, the birds have to be caught twice within a short period of time which is very difficult in the case of great cormorants. Additionally, Wilson & Culik (in press) have shown that injection of DLW may significantly alter foraging parameters. (3) Records of heart rate can also be used to determine the energy requirements of free-living birds; however, this method requires that recording devices be implanted, with associated trauma. (4) Allometric relationships, which have already been used in order to determine the DEB of free-living great cormorants (Reichholf 1990, Voslamber & Van Eerden 1991, Wißmath et al. 1993), have an accuracy of only 60% (Weathers et al. 1984). (5) Different studies, in which both DLW and time budget methods have been deployed, show that, under certain conditions, a time budget analysis may also deliver highly accurate results. Weathers et al. (1984) and Buttemer et al. (1986) show for example that the DEB of loggerhead shrikes *Lanius ludovicianus* and budgerigars *Melopsittacus undulatus* as determined by DLW injection and time budget analysis differ only by 8 and 4%, respectively. Nagy (1989) noted that deviation between the results of these 2 methods should be smaller in larger birds as they are less sensitive to weather conditions. This was the case in Adélie penguins studied by Culik (1995) who found a difference of only 1% between the results of the DLW study and the time budget analysis, and in the jackass penguin where DLW estimates of the energy budget (Nagy et al. 1984) were within 3% of previous bioenergetic estimates (Furness & Cooper 1982).

The energy budget presented here is a first attempt at a quantification of the daily food intake in great cormorants using a time/energy budget. Important assumptions had to be made concerning the timing of certain activities or their costs. In particular activity patterns of the birds outside the colony and the influence of environmental factors such as wind speed on the metabolism are not sufficiently known.

Nevertheless, we consider that the energy expended by breeding great cormorants for activities within the colony, reproduction, swimming in cold water and eating cold food have been accurately determined; these costs, as shown in Fig. 5, represent 75.9% of the DEB in breeding adults. A sensitivity analysis shows that a doubling of the daily flight costs, which could result from higher flight costs or longer flight times, would lead to an increase in daily food intake of only 30 g. A doubling of the daily swimming costs, which could arise as a result of birds foraging more than once per trip, or longer when feeding on Lake Selent, leads to an increase in daily food intake of 60 g.

A daily ration of 500 g is traditionally assumed necessary for great cormorants (Bauer & Glutz 1966, Müller 1986, Deufel 1987, Zimmermann 1989). In the present study the mean food consumption over the complete breeding season was calculated to be 423 g bird^{-1} d^{-1}. This is little different from the 500 g assumed by most authors; however, such fish consumption has to be seen as a maximum which occurs during less than one-third of the year. The rest of the time food requirements of non-breeders under the same meteorological conditions should be very similar to the requirements of incubating birds. These were calculated to be 238 g d^{-1}, less than half of the assumed 500 g.

The time budget used for the present determination of the daily food intake in great cormorants does not include activity patterns resulting from disturbances at the breeding or the resting sites. This kind of intervention usually causes the birds to leave the colony for about 30 min (Grémillet pers. obs.). During this time, the cormorants stay for about 10 min on the water surface several hundred metres away from the colony (Menke 1986, authors' pers. obs.), after which they return to the breeding site, flying around for at least 15 min before landing. This results in energy costs of 63.2 kJ for flight and 18.8 kJ for resting on the water surface. The overall costs are, therefore, 82 kJ bird^{-1}, an increase of 69.7 kJ above those for resting. This converts to 23 g fish which must be additionally eaten per disturbed cormorant. In a colony of 1000 birds, a single disturbance may result in an additional fish consumption of 23 kg, enough to feed a breeding cormorant during the entire breeding season. This confirms the fact that human presence at resting or breeding sites is not an efficient way of reducing the predation of cormorants on fish stocks (see also Kieckbusch & Koop 1992)
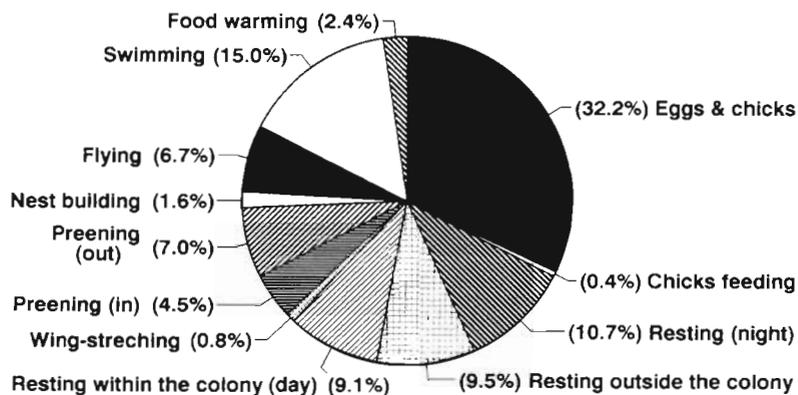
Fig. 5. *Phalacrocorax carbo sinensis.* Mean daily energy budget of a breeding great cormorant and its brood for the period from egg laying to chick fledging

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