

## DETERMINING FOOD INTAKE BY GREAT CORMORANTS AND EUROPEAN SHAGS WITH ELECTRONIC BALANCES

DAVID GRÉMILLET AND RICKMER DEY

*Institut für Meereskunde  
Düsternbrooker Weg 20  
D-24105 Kiel, Germany*

SARAH WANLESS AND MIKE P. HARRIS

*Institute of Terrestrial Ecology  
Banchory Research Station  
Hill of Brathens, Banchory  
Kincardineshire AB31 4BY, Scotland*

JANA REGEL

*Institut für Meereskunde  
Düsternbrooker Weg 20  
D-24105 Kiel, Germany*

Abstract.—The masses of 302 food loads delivered to the nest by 10 Great Cormorants (*Phalacrocorax carbo*) and 6 European Shags (*P. aristotelis*) rearing chicks at the Chausey Islands, France, were assessed to an accuracy of  $\pm 10$  g using automatic weighing units. We present a model based on time budget and published data that transforms these weighings into the total amount of food taken at sea. Based on this model, the daily mean fresh mass of food acquired by adults, including food brought back to their chicks, was 890 g ( $n = 16$ , SD = 361) and 800 g ( $n = 21$ , SD = 292) for adult male and female cormorants, and 478 g ( $n = 14$ , SD = 207) and 583 g ( $n = 13$ , SD = 268) for adult male and female shags.

### DETERMINANDO LAS CARACTERÍSTICAS DE INGESTIÓN DE *PHALACROCORAX CARBO* Y *P. ARISTOTELIS* CON BALANZAS ELECTRÓNICAS

Sinopsis.—Las masas de 302 cargas de alimentos llevadas al nido por 10 *Phalacrocorax carbo* y de 6 *P. aristotelis* con crías en las Islas Chausey en Francia se estimaron con una exactitud de  $\pm 10$  g usando unidades de pesaje automáticas. Presentamos un modelo basado en un presupuesto de tiempo y en datos publicados que transforman estos pesos en la cantidad total de alimento tomado en el mar. Basándose en este modelo, la masa promedio diaria de alimento fresco adquirido por adultos, incluyendo alimento traído a sus crías, fué de 890 g ( $n = 16$ , SD = 361) y de 800 g ( $n = 21$ , SD = 292) para machos y hembras adultos de *P. carbo* respectivamente, y de 478 g ( $n = 14$ , SD = 207) y 583 g ( $n = 13$ , SD = 268) para machos y hembras de *P. aristotelis* respectivamente.

Great Cormorants (*Phalacrocorax carbo*) and European Shags (*P. aristotelis*) feed mainly on fish caught in coastal waters (Géroudet 1959, Steven 1933). Data on the food loads brought back to the nest during the breeding season by these central place foragers (sensu Orians and Pearson 1979) allow the assessment of foraging efficiency and of parental effort (Cairns 1992). Calculating daily food intake is also of applied interest because these species often interact with human fisheries. Daily food intake cannot be assessed by direct observations because these birds often feed out of sight and may swallow prey underwater (Wanless et al. 1991, 1993a). In some dietary studies, birds have been shot at the feeding

sites and their stomach contents analyzed (e.g., Rand 1960, Steven 1933). Diet studies have also been based on prey remains in regurgitated pellets or stomach flushings (Duffy and Jackson 1986, Wanless *et al.* 1993a). Although these methods give useful qualitative information, they are inadequate for quantifying total prey intake (Duffy and Laurenson 1983, Grémillet and Plös 1994).

Electronic balances placed under nests have been deployed in studies of many bird species to determine their time budgets, variations in body mass, or amounts of food brought to the nest (Frank and Becker 1992, Jones 1987, Kerry *et al.* 1993, Le Maho *et al.* 1993, Mulder and Swaan 1992, Moreno 1989, Prince and Walton 1984, Sibly and McCleery 1980). The purpose of this study is to describe an automatic balance and its use in breeding Great Cormorants and European Shags. We show how weighing data from this device can be corrected to determine satisfactorily the daily food intake of Great Cormorants (hereafter cormorants) and European Shags (hereafter shags). Various factors that can influence the reliability of this method are presented, with special reference to digestion rates.

#### METHODS

Field work was conducted between 5 Apr.–7 Jun. 1994 on ground-breeding cormorants and shags with chicks at the Chausey Archipelago (48°55'N, 01°45'W), France and between 6–24 Jul. 1994 at the Isle of May (56°11'N, 02°33'W), Scotland on ground-breeding shags with chicks.

*Weighing data.*—Variations in body mass were assessed using an automatic weighing system consisting of electronic balances, a laptop computer, and a 12v battery. Each of the two balances (Soehnle-Waagen GmbH + Co. Postfach 1265, D-71535 Murrhardt) had a metal weighing platform measuring 350 × 295 mm and was accurate to 5 g over the weight range 0–30 kg (US\$1400). Each balance was connected to a portable computer via a triaxial cable (maximum length 150 m; US\$70). Power for the balances and computer was supplied by a 12v battery; each balance required approximately 200 mA and the computer required approximately 1 A. After being enclosed in a plastic bag containing packages of silica gel, the balance was placed on a plywood board (50 × 50 cm) under a nest. A second plywood board (50 × 50 cm) was placed between the nest and the metal platform to ensure that the nest edges would not touch the ground. Balances were installed under nests of birds rearing newly hatched chicks. Cormorants and shags from Chausey and shags from the Isle of May build basket-like nests directly on the ground. These nests were simply lifted from the ground and placed on the balance. Balance installation can be carried out in less than 15 min. Computer and battery were kept in a watertight housing outside of the breeding colony. Mass data were sent to the computer once per second and the arithmetic mean of every 30 weighings was stored in a file together with the time. Data were analyzed using the program WAAGE (US\$700, Jensen Software, Am Schutterrain 31, D-77694 Kehl, Germany).

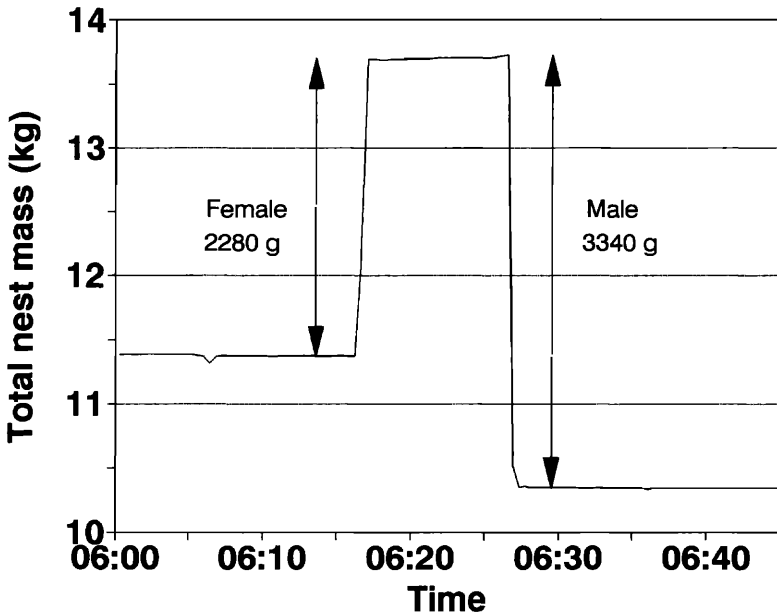


FIGURE 1. Example of weighing data registered during a changeover at a cormorant nest. The female landed on the nest and the male left to forage 10 min later. The body mass of both adults was determined as the mass difference shown by the arrows.

In cormorants and shags, an adult returning from the sea normally lands on the nest, pair members exchange places and, after a variable time, the off-duty bird flies away. Such behavior results in a typical step event in the total nest mass, such that the mass of each adult can be calculated from mass differences (Fig. 1). Because neither cormorants nor shags feed at night (Johngard 1993), a bird's mass in the early morning was assumed to be equal to its mass with an empty stomach (Fig. 1). The masses of food brought back by the parents during each day were calculated relative to this empty mass (Fig. 2).

At the Chausey Islands, weighing data for five cormorant and three shag pairs were used for determination of load masses brought back to the nest. On the Isle of May, tests were performed on four shag nests. Effects of weather conditions on nest mass were investigated by installing the balances under two shag nests where breeding had failed and that were no longer being occupied by the pair. A defined mass (2000 g) was used to test whether the position of a bird on the nest affected the mass reading. The balances were also deployed under two active shag nests that could be observed from hides 10 m away. Observations were made from dawn to 1600 h on three days and allowed changes in total nest mass to be related directly to the activity of the adults and chicks.

*Radio tracking.*—At the Chausey Islands, four additional cormorants

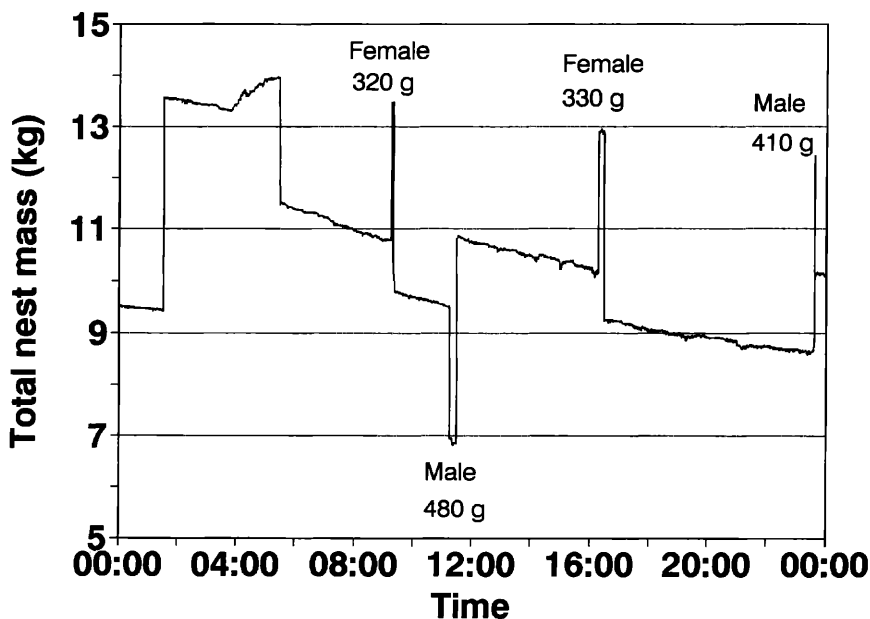


FIGURE 2. Example of the determination of the total amount of food brought back by a cormorant pair during a day. The sexes can be identified by their different body masses. Sharp changes in total nest mass are due to changeovers as described in Figure 1. The mass of food brought back by the incoming bird is indicated for each changeover. The male joined the female shortly before 0200 h (one of the adults usually stands near the nest during the night) and both birds were on the nest between 0200–0600 h. The female left the nest just before 0600 h. The marked rise in total nest mass between 0400–0600 h was due to heavy rain. The nest dried out during the day, which resulted in a gradual reduction in total nest mass.

and five additional shags were radio-tracked. Shags were caught by hand and cormorants with a special net trap (Grémillet, unpubl. data). Nine birds were fitted with TW3 two-stage transmitters (Biotrack, 52 Furzebrook Road, Wareham, BH20 5AX, United Kingdom; mass = 18 g [0.5% to 1% of body mass]; 30-mm long, cross section 20 mm; main and secondary aerials 280-mm and 230-mm long, respectively). The devices were attached on the ventral side of rectrices with cable ties. The transmitter was completely covered by the tail with the antenna directed upwards and backwards through the tail to minimize drag. Foraging behavior was recorded with a system consisting of two pairs of six-element Yagi aerials mounted on a 4-m mast and connected through a null peak combiner (Telonics, 932 E. Impala Ave., Mesa, Arizona 85204) to a FT-290 RII Yaesu receiver (Yaesu musen Co., LTD. C.P.O. Box 1500, Tokyo, Japan). The two tracking stations were situated at distances of 1–2.5 km from the breeding colonies and 1.75 km apart, at a height of 38 m and 42 m above sea level.

Activity data of the birds were collected from dawn to dusk and recorded by hand on a Husky Hunter II field computer. A bird was assumed to leave the colony for a foraging trip when the bearing changed by more than 1°. Total trip length was defined as the time between departure and return to the colony, outward travel time as the time between departure from the colony and first dive of the diving sequence (characterized by sudden, repeated interruptions in the signal), and inward travel time as the time between the last dive of the diving sequence and return to the colony.

*Corrected food loads.*—The food brought back to the nest by a cormorant or a shag is unlikely to represent the total amount of food taken at sea, since some of the ingested prey will be digested and excreted before the bird returns to its nest. To correct for this effect we developed a model that predicts the mean mass loss per unit time in the food loads of cormorants and shags by using the evacuation rate of the food, prey size, trip length, and travel times of the birds. Values for the evacuation rate are from Jackson (1992), who measured the percentage of dry mass excreted per unit time in captive Cape Gannets (*Morus capensis*) fed with pilchard (*Sardinops ocellatus*). In her study, the percentage of the total dry mass fed that was excreted per unit time followed an exponential function, but was approximately linear for the first 8 h after ingestion. None of our birds stayed away from the nest for this long, so we assumed (after Jackson 1992) the excretion rate in cormorants and shags to be

$$Y = 9.75X - 0.17 \quad (1)$$

Where Y is the percentage of food excreted per unit time X (in hours). Furthermore, Jackson (1992) notes that aqueous excretion is high during the first phase of digestion, whereas more solid digesta are excreted later. The proportion of liquid to solid mass excreted is thus constant within the first 8 h following digestion and Jackson's data can be used to assess wet mass excretion as well as dry mass excretion.

At Chausey, shags mainly feed on sandeels (*Ammodytes marinus*) and cormorants on rock cook (*Centrolabrus exoletus*), respectively (Grémillet and Argentin, unpubl. data). Mean mass of sandeels taken by shags on the Isle of May was 3 g (Harris and Wanless 1993). The mean mass of rock cook taken by cormorants breeding on Chausey was 45 g (Grémillet and Argentin, unpubl. data). We assumed that cormorants and shags caught prey at a constant rate during dives. Time spent fishing (trip length minus travel time to and from the feeding area, which includes roosting) was therefore divided into time periods of constant length, at the end of which a fish weighing 3 g in shags and 45 g in cormorants was expected to be caught. Food loads brought back to the nest were corrected as follows. Food mass was divided by the mean mass of the prey to estimate the number of prey captured. Time spent fishing was then divided by the number of prey captured to give the average time elapsing between successive prey captures. The interval between the ingestion of each prey and the arrival of the bird on the balance was then determined as well as the mass loss

through digestion according to Jackson (1992). Finally, the calculated masses allowing for digestion of each prey item at the end of the foraging trip were summed. The complete procedure is described by:

$$M = \sum_{i=0}^n m - [m/100] \times [a(H - i\Delta H) - b] \quad (2)$$

Where  $M$  is the calculated mass of food brought back to the nest (g),  $n$  is the number of prey caught during the foraging trip,  $m$  is the mean mass of a prey item (g),  $H$  is the period between the first dive and arrival at the nest (h),  $\Delta H$  the mean interval between successive prey captures, and  $a$  and  $b$  are the parameters from equation (1) ( $a = 9.75$  and  $b = -0.17$ ). The load mass calculated from weighings upon the bird's return cannot be taken as the input mass in this model because some digestion will have occurred during the trip. The actual amount of food ingested was calculated iteratively whereby the starting load increased until the calculated load corresponded to the mass determined in the field by the weighing system.

All comparisons were made using  $t$ -tests (Sokal and Rohlf 1981).

#### RESULTS

*Assessment of the methodology.*—Dry masses of two empty shag nests from the Isle of May were 5 and 12 kg, respectively. Nest mass varied due to absorption of water, with increases of up to 10% of dry mass occurring within 2 h of the onset of rain and during humid nights. During daytime, nest mass gradually decreased with evaporation of 45g/h ( $n = 2$ ,  $SD = 10$ ). The mass of a dummy could be determined to an accuracy of  $\pm 10$  g ( $n = 10$ ,  $SD = 4.7$ ) irrespective of whether it was placed in the center or on the edge of the nest.

Field observations of the balances deployed under two active shag nests from the Isle of May showed that variations in nest mass logged by the weighing unit were caused by several activities. Arrival or departure of an adult caused mass variations of at least 1500 g (the body mass of a small female shag). All birds arrived at the nest with dry plumage, so that masses of a bird arriving and leaving should be directly comparable. During nest building, typically one of the pair (usually the male) left the nest and brought back a twig or seaweed to the female. The mean mass of the nest material brought back in two shag nests was 29 g ( $n = 13$ ,  $SD = 20$ ). Variation in total nest mass could also occur due to neighbors stealing nest material. This behavior was not, however, recorded during the observation period. Finally, both adults and chicks usually defecated over the edge of the nest. In four adults, droppings had a mean mass of 22 g ( $n = 16$ ,  $SD = 15$ ).

*Estimation of food loads.*—Five cormorant and three shag pairs were monitored on Chausey using the automatic weighing system for 5–20 consecutive days. Four other cormorants and five shags were radiotracked for 3–12 consecutive days. All birds had small chicks at the start of the mon-

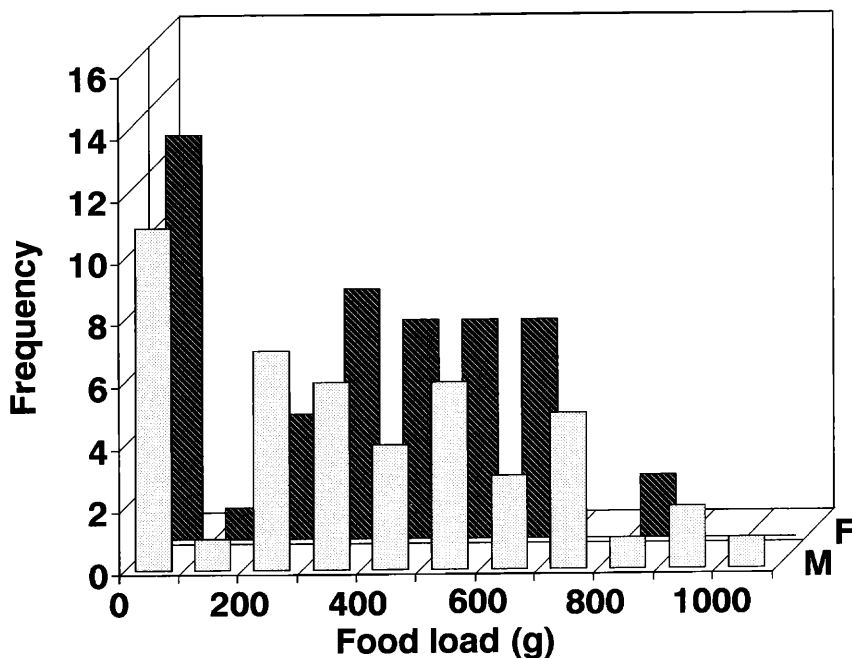


FIGURE 3. Frequency distribution of the food loads brought back to the nest by male (M) and female (F) Great Cormorants.

itoring period (mean brood mass = 500 g,  $n = 3$ ,  $SD = 346$  for the shags and 690 g,  $n = 5$ ,  $SD = 598$  for the cormorants). All birds returned to the nest within 20 min of the balance being installed. The weighings allowed us to calculate the masses of 143 and 156 food loads from cormorants and shags, respectively. Mean mass of food loads was 307 g ( $n = 70$ ,  $SD = 214$ ) in female cormorants, 352 g ( $n = 73$ ,  $SD = 251$ ) in male cormorants (Fig. 3), 164 g ( $n = 76$ ,  $SD = 114$ ) in female shags and 148 g ( $n = 80$ ,  $SD = 113$ ) in male shags (Fig. 4).

*Activity at sea.*—On Chausey, mean length of foraging trips as determined by radio tracking were 195 min ( $n = 37$ ,  $SD = 102$ ) in four cormorants and 121 min ( $n = 23$ ,  $SD = 77$ ) in five shags. Mean lengths of foraging trips determined from automatic nest weighing did not differ significantly from these values (cormorant: 209 min,  $n = 85$ ,  $SD = 124$ ,  $P > 0.05$ ; shag: 163 min,  $n = 135$ ,  $SD = 82$ ,  $P > 0.05$ ). This result indicates that on Chausey during chick rearing, cormorants and shags returned directly to the nest after arriving at the breeding colony. The mean travel time to the feeding area was 10.4 min ( $n = 34$ ,  $SD = 7.2$  min) in cormorants and 4.0 min ( $n = 22$ ,  $SD = 3.7$  min) in shags. The mean return time from the feeding area to the nest was 66.9 min ( $n = 45$ ,  $SD = 64.6$  min) in cormorants and 23.8 min ( $n = 46$ ,  $SD = 29.3$  min) in shags. Differences in outward and inward travel time are due to

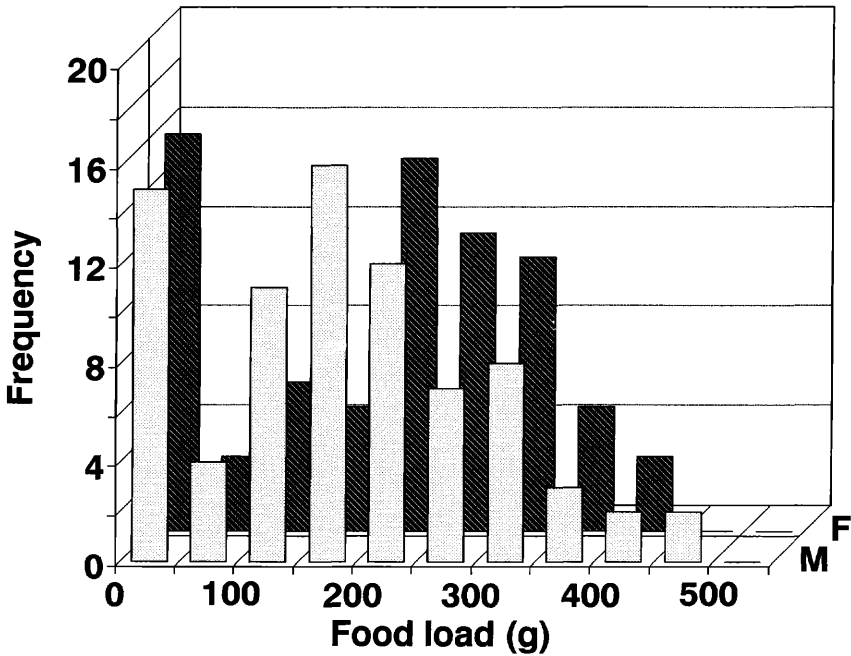


FIGURE 4. Frequency distribution of the food loads brought back to the nest by male (M) and female (F) European Shags.

the fact that birds flew directly to the feeding areas but may have been resting before flying back to their nests.

*Estimation of daily food intake.*—In cormorants, daily food intake based on corrected food loads was 890 g/d ( $n = 16$ , SD = 361) and 800 g/d ( $n = 21$ , SD = 292) in males and females, respectively (Table 1). Male shags had a daily food intake of 478 g/d ( $n = 14$ , SD = 207) and female shags of 583 g/d ( $n = 13$ , SD = 268) (Table 1).

TABLE 1. Mean body mass, brood size, and daily food intake of ten Great Cormorants and six European Shags monitored with electronic nest balances.

|            |         | Body mass (g)                 | Brood biomass (g)            | Daily food Intake (g)         |
|------------|---------|-------------------------------|------------------------------|-------------------------------|
| Cormorants | Males   | 3250<br>( $n = 5$ , SD = 240) | 690<br>( $n = 5$ , SD = 598) | 890<br>( $n = 16$ , SD = 361) |
|            | Females | 2490<br>( $n = 5$ , SD = 175) | 690<br>( $n = 5$ , SD = 598) | 800<br>( $n = 21$ , SD = 292) |
| Shags      | Males   | 1940<br>( $n = 3$ , SD = 23)  | 500<br>( $n = 3$ , SD = 346) | 478<br>( $n = 14$ , SD = 207) |
|            | Females | 1520<br>( $n = 3$ , SD = 91)  | 500<br>( $n = 3$ , SD = 346) | 583<br>( $n = 13$ , SD = 268) |



## DISCUSSION

*Practical aspects.*—The automatic weighing unit used in this study was relatively easy to install for ground-nesting species. Both the laptop computer and the balances are sturdy, and the system can be deployed easily. Disturbance to the birds is confined to installation and recovery of the balance. There is no need to catch the birds and pairs appear to adjust rapidly to the change at their nests. Accurate mass measurements can be registered for periods of several weeks and easily analyzed to determine daily food intake of individual birds. This weighing system has two main technical drawbacks. First, substantial lengths of cable are required between the balance and the control station for both data transmission and the power supply. This can make installation and recovery of more than one balance in the same part of the colony difficult. Additionally, the use of a personal computer as a recording station increases power requirements and necessitates a daily battery change. Both problems could be solved by the use of a new data-acquisition system based on radio transmission of the weighing data directly to a powered research base. This would reduce power requirements of the system in the field.

*Accuracy of the weighings.*—The main source of variation in total nest mass was the activity patterns of the adult birds (Fig. 1). Although several other factors may also have an effect (e.g., meteorological conditions, defecation of adults and chicks, nest building, or removal of nest material), under normal circumstances they should not affect body-mass calculations. An exception to this would occur if a bird returning from a feeding trip also brought in nest material. This behavior was not observed in shags breeding on the Isle of May, nor in cormorants and shags from Chausey. We therefore assume that in this study food loads were calculated with an accuracy of  $\pm 10$  g.

*Assessment of the daily food intake.*—The accuracy of the above calculations depends heavily on the quality of the data concerning the excretion rate. Jackson's data (1992) refer to non-breeding captive Cape Gannets, which may well have different digestion rates than breeding and free-living cormorants and shags. This may have different causes. First, flying birds like cormorants and shags should also minimize their body mass due to substantial flight costs (see Grémillet et al. 1995). Wanless et al. (1993a) found that on the Isle of May shags with young did not return immediately to the nest after a feeding trip but spent some time on the sea rocks below the breeding colony. Wanless et al. (1993a) speculated that during this time the adults were digesting their own requirements and that the load taken to the nest was principally for the brood. Second, the stomach temperature of free-living Bank Cormorants (*Phalacrocorax neglectus*) foraging at sea has been shown to increase initially by 1.6 C before dropping at a rate of 0.12 C/min after an intervening stable period of 9 min (Wilson and Grémillet, in press). Similar patterns have also been recorded for cormorants and shags from Chausey (Grémillet et al., unpubl. data). Following the Q10 rule (see Schmidt-Nielsen 1990), enzyme

activity and digestion are thus expected to vary correspondingly in cormorants and shags swimming in cold water. Third, the size of prey-items can vary between years (Wanless et al. 1993b) and with foraging range (Wanless et al. 1993a). Finally, the gannets studied by Jackson (1992) were fed pilchard, which have a lower surface to volume ratio than the sandeels caught by the shags, but a higher surface to volume ratio than the Labridae taken by the cormorants (Muus and Dahlström 1988). Assuming similar digestive processes, shags should digest their meal relatively quicker than cormorants.

*Comparison with other methods.*—Daily food intake in Phalacrocoracidae have been determined using five further methods: feeding experiments (du Plessis 1957), stomach content analysis (Van Dobben 1952, Rand 1960), pellet analysis (Worthmann and Spratte 1990), time-energy budgets (Grémillet et al. 1995) and stomach temperature records (Grémillet and Plös 1994). The first three methods have been shown to be inadequate for quantitative studies (Duffy and Laurenson 1983, Grémillet and Plös 1994). The last two methods have been used in cormorants, and results concerning this species are thus suitable for comparison. In cormorants rearing downy chicks, Grémillet et al. (1995) used a time-budget model to calculate a mean daily food intake of 588 g. Compared to this, a mean daily food intake of 845 g (this study) appears to be overestimated. However, recent stomach temperature data recorded in four breeding cormorants at the Chausey Islands allowed us to calculate a mean daily food intake of 852 g (Grémillet et al., unpubl. data) and thus to validate to some extent the results presented above. Time-energy budgets are particularly attractive because they allow the calculation of daily food intake using literature data. However, energetic costs of flight as well as the influence of weather conditions on the resting metabolic rate of adults and chicks are difficult to assess precisely. Additionally, because of their particular plumage, cormorants and shags are likely to experience considerable heat losses when diving in cold water. Swimming costs were determined directly by Schmid et al. (1995) via respirometric measurements and these data included in the energy budget by Grémillet et al. (1995). However, stomach temperature measurements have also shown that birds may experience decreasing body temperature and are likely to use wing-flapping and shivering to increase their body temperature again after having foraged. We postulate that these extra costs may be responsible for high daily food intake in cormorants and shags (30% of body mass). Nevertheless, it is important to consider that all results have been collected during the breeding season and likely to represent maximum amounts of food taken for both species, as these data include the requirements of the parents and those of their brood.

#### ACKNOWLEDGMENTS

This study was supported by the Institut für Meereskunde, the Groupe Ornithologique Normand, the Direction Regionale de l'Environnement de Normandie, and the Scottish Natural Heritage. Grateful thanks are due to D. Adelung, G. Debout, C. Wirnham, J. Calla-

dine, and G. Clouet for their help. We also thank L. Marion, M. Kierspel, K. Puetz, G. Peters, R. Wilson, H. Mempel, K. Voß, S. Rehfeuter, S. Lischka, G. Argentin, B. Schulte, L. Huyet, L. Demongin, S. Grémillet, Y. and C. Grall, and P. de Saint Front for their extensive support at all stages of this work and C. Ray Chandler, D. C. Duffy, and D. Cairns for useful comments on the first version of the manuscript.

## LITERATURE CITED

- CAIRNS, D. K. 1992. Population regulation of seabird colonies. *Curr. Ornithol.* 9:37–61.
- DUFFY, D. C., AND L. J. B. LAURENSEN. 1983. Pellets of Cape Cormorants as indicators of diet. *Condor* 85:305–307.
- , AND S. JACKSON. 1986. Diet studies of seabirds: a review of methods. *Colonial Waterbirds* 9:1–17.
- DU PLESSIS, S. S. 1957. Growth and daily food intake of the White-Breasted Cormorant in captivity. *Ostrich* 28:197–201.
- FRANK, D., AND P. H. BECKER. 1992. Body mass and nest reliefs in Common Terns *Sterna hirundo* exposed to different feeding conditions. *Ardea* 80:57–69.
- GÉROUDET, P. 1959. Les Palmipèdes. Delachaux and Niestlé, Neuchâtel. Pp. 58–64.
- GRÉMILLET, D. J. H., AND A. L. PLÖS. 1994. The use of stomach temperature records for the calculation of daily food intake in cormorants. *J. exp. Biol.* 189:105–115.
- , D. SCHMID, AND B. CULIK. 1995. Energy requirements of breeding Great Cormorants *Phalacrocorax carbo sinensis*. *Mar. Ecol. Progr. Ser.* 121:1–9.
- HARRIS, M. P., AND S. WANLESS. 1993. The diet of Shags *Phalacrocorax aristotelis* during the chick-rearing period assessed by three methods. *Bird Study* 40:135–139.
- JACKSON, S. 1992. Do seabird gut sizes and mean retention times reflect adaptation to diet and foraging method. *Physiol. Zool.* 65:674–697.
- JOHNSGARD, P. A. 1993. Cormorants, darters, and pelicans of the world. Smithsonian Inst. Press, Washington, D.C. 445 pp.
- JONES, G. 1987. The use of precision electronic balances to monitor short-term changes in the body-weight of birds. *Comp. Biochem. Physiol. A* 87:287–293.
- KERRY, K., J. CLARKE, AND E. GRANT. 1993. The use of an automated weighing and recording system for the study of the biology of Adélie Penguins (*Pygoscelis adeliae*). *Proceedings of the National Institute of Polar Research symposium on polar biology* 6:62–75.
- LE MAHO, Y., J.-P. GENDNER, E. CHALLET, C.-A. BOST, J. GILLES, C. VERDON, C. PLUMERÉ, J.-P. ROBIN, AND Y. HANDRICH. 1993. Undisturbed breeding penguins as indicators of changes in marine resources. *Mar. Ecol. Progr. Ser.* 95:1–6.
- MORENO, J. 1989. Body-weight variation in breeding Northern Wheatears: a field experiment with supplementary food. *Condor* 91:178–186.
- MULDER, J. L., AND A. H. SWAAN. 1992. Body-weight changes of egg-laying Curlews *Numenius arquata*, as monitored by an automatic weighing system. *Ardea* 80:273–279.
- MUUS, B. J., AND P. DAHLSTRÖM. 1988. Sea fishes of Britain and north-western Europe. Collins, London. 244 pp.
- ORLIANS, G. H., AND N. E. PEARSON. 1979. On the theory of central place foraging. Pp. 154–177, in D. J. Horn, R. D. Mitchell, and G. R. Stairs, eds. *Analysis of ecological systems*. Ohio State University Press, Columbus.
- PRINCE, P. A., AND D. W. H. WALTON. 1984. Automated measurement of meal size and feeding frequency in albatrosses. *J. Appl. Ecol.* 21:789–794.
- RAND, R. W. 1960. The biology of guano-producing seabirds, Chapter 3: the distribution, abundance and feeding habits of the Cormorants Phalacrocoracidae off the south-western coast of the Cape Province. Division of Fisheries, Investigational Report 42. 32 pp.
- SCHMID, D., D. GRÉMILLET, AND B. CULIK. 1995. Energetics of underwater swimming in the Great Cormorant (*Phalacrocorax carbo sinensis*). *Mar. Biol.* 123:875–881.
- SCHMIDT-NIELSEN, K. 1990. Animal physiology. Adaptation and environment. Cambridge University Press, Cambridge, United Kingdom. 602 pp.
- SIBLY, R. M., AND R. H. MCCLEERY. 1980. A balance for weighing ground-nesting birds. *J. Appl. Ecol.* 17:323–327.

- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*. 2nd ed. W. H. Freeman and Company, New York. 859 pp.
- STEVEN, G. A. 1933. The food consumed by Shags and Cormorants around the shores of Cornwall (England). *Mar. Biol. Ass. UK* 14:277-291.
- VAN DOBBEN, W. H. 1952. The food of the Cormorant in the Netherlands. *Ardea* 11:1-34.
- WANLESS, S., M. P. HARRIS, AND J. A. MORRIS. 1991. Foraging range and feeding locations of Shags *Phalacrocorax aristotelis* during chick rearing. *Ibis* 133:30-36.
- , ———, AND A. F. RUSSELL. 1993a. Factors influencing food-load sizes brought in by Shags *Phalacrocorax aristotelis* during chick rearing. *Ibis* 135:19-24.
- , T. CORFIELD, M. P. HARRIS, S. T. BUCKLAND, AND J. A. MORRIS. 1993b. Diving behaviour of the Shag *Phalacrocorax aristotelis* (Aves: Pelecaniformes) in relation to water depth and prey size. *J. Zool. Lond.* 231:11-25.
- WILSON, R. P., AND D. GRÉMILLET. In press. Body temperatures of free-living African Penguins (*Spheniscus demersus*) and Bank Cormorants (*Phalacrocorax neglectus*). *J. exp. Biol.*
- WORTHMANN, H., AND S. SPRATTE. 1990. Nahrungsuntersuchungen an Kormoranen vom grossen Plöner See. *Fisch. Teichwirt.* 41 (1).

Received 27 Nov. 1995; accepted 31 Jan. 1996.