THE TELLTALE HEART: A NON-INVASIVE METHOD TO DETERMINE THE ENERGY EXPENDITURE OF INCUBATING GREAT CORMORANTS PHALACROCORAX CARBO CARBO

SANDRA STORCH, DAVID GRÉMILLET & BORIS M. CULIK


We studied the energetics of incubating Great Cormorants Phalacrocorax carbo carbo via heart rate and respirometric measurements performed in captive and free-living animals. We applied a modified heart beat frequency (HR) monitor built for use in human athletics as well as respirometry for measurements in four captive-bred cormorants at Neumünster Zoo, Germany. The obtained data were used to model the relationship between HR and metabolic rate (MR). The resulting correlations were MR (W kg\(^{-0.723}\)) = 4.76 + 0.01 HR (bpm) during daytime and MR (W kg\(^{-0.723}\)) = 2.33 + 0.03 HR (bpm) at night. Furthermore, the heart beat frequencies of 5 free-living, incubating cormorants at the Chausey Islands, France, were measured acoustically using artificial eggs while the activities at the nest were observed via video. HR-MR models established in the captive animals were used to determine the activity-dependent energy expenditure in these free-living cormorants. The Median MR was 5.08 W kg\(^{-0.723}\) at night, 6.06 W kg\(^{-0.723}\) while resting and sleeping during daytime, 6.20 W kg\(^{-0.723}\) during preening, gular flutter and unrest and 6.47 W kg\(^{-0.723}\) during nest building. In resting birds we found a nocturnal reduction in the energy expenditure of 16 %. Our method for measurement of heart beat frequency appears promising as a technique for determination of HR with minimal restraint to the animal.

Key words: Phalacrocorax carbo - energetics - metabolic rate - breeding - HR-measurements - respirometry

Institut für Meereskunde, Düsternbrooker Weg 20, D-24105 Kiel, Germany, E-mail storch@ifm.uni-kiel.de

INTRODUCTION

Seabirds are warm-blooded top-predators that are abundant in all climatic zones and play a major role within the marine and coastal pathways of energy flux (Croxall 1987). The food intake of the Great Cormorant Phalacrocorax carbo carbo has been the subject of particular debate by the European public (Im & Hafner 1984; Deufel 1987; Linn & Campbell 1992) because of the perceived competition for food resources between man and these piscivorous birds. To date, however, there still is a lack of data on overall fish-consumption of Great Cormorants. Different methods are used to determine the food requirement of birds, one of them being the time-energy-budget (TEB). Through the combination of information on the duration of specific activities (time-budget) with data on respective metabolic rates a TEB of the observed animals can be obtained and the resultant energy consumption calculated (e.g. Kendeigh et al. 1977; Weathers et al. 1984; Whittow 1986). The objective of this study was to determine the energetic requirements of incubating free-living Great Cormorants during defined activities with minimal disturbance to the animals in order to enhance calculations of TEBs for these birds. The approach performed in this study comprises the follow-
ing steps: (1) determination of the relationship between metabolic rate (MR) and heart beat rate (HR) in captive cormorants, (2) HR measurement in free-living breeding cormorants, (3) monitoring of the activities of free-living incubating cormorants, and (4) calculation of MR of the animals while performing different monitored activities.

**METHODS**

The experiments were conducted under licence and in accordance with the principles and guidelines of the German laws on animal welfare (Bundesgesetzblatt, 1993, Teil 1) at two different study sites. The HR-MR relationship was determined at Neumünster Zoo, Germany, in June and July 1996. The four adult cormorants (mean body mass 2062 ± 390 g) used in our measurements were captive-bred and housed in a ca. 30 m² outside enclosure. The cormorants were fed with fish (mostly herring Clupea harengus) ad libitum twice per day (11 a.m., 3 p.m.). The measurements of heart beat rates of free-living, breeding cormorants and the monitoring of activities were performed from April to June 1996 at the Chausey Archipelago in France (48°55'N, 1°45'W). The field station was situated on the main island, Grande Ile, whereas the monitored breeding colonies of the cormorants were scattered on 6 different smaller islands of the archipelago. The distance of these islands to the field station was between 1000 and 5000 m. A total of 346 pairs of Great Cormorants bred at the Chausey Archipelago in 1996. We obtained data from five animals. The mean body mass of breeding cormorants at Chausey is approx. 2750 g (male 3200 g, female 2325 g, Grémillet et al. 1996).

**Heart beat frequency of captive cormorants**

To measure HR of captive cormorants with minimum influence on their behaviour or physical well-being a new non-invasive method was developed. We modified a wireless HR monitor (transmitter and receiver, POLAR Sport-Tester Profi, POLAR Elektro Oy, Finland). In its original form the system is used for sport and training in humans. The transmitter (14 x 3 x 1 cm, 50 g) was removed from the original breast-belt and new electrodes were built using round-tipped metal pins that fitted the press-stud bearings at the bottom side of the transmitter without need for any wires (Fig.1). When the transmitter was taped to the feathers at the back of the cormorant (Wilson et al. 1997), the electrodes were pressed onto the skin at two prepared, down-free patches (ca. 5 x 5 mm) that were wetted with gel (Aquasonic Hypoallergenic Gel, Parker, New Jersey, USA). Attachment took about 10 min and the device did not appear to affect the animal afterwards. During the experiments the attached device transmitted the impulses of the detected heart beat over a maximum distance of ca. 1.5 m to the receiver, which computed and displayed the actual beat rate at 5 s intervals. The receiver recorded the displayed HR once per minute (maximum possible storage 33 h).
At the end of an experiment the stored data were transferred to a PC using an interface (POLAR Interface Advantage) and special software (POLAR HR Analysis 5.02). Measurements were taken during daylight hours as well as at night. For further analysis the HR data was categorised in classes of 10 bpm.

Metabolic rate of captive cormorants

To determine MR in captive cormorants in parallel to HR measurements the O$_2$ consumption and CO$_2$ production were measured using an open-flow system (Withers 1977). After attaching the heart beat transmitter the animal was placed in a respiration chamber. We used a 70 l plexiglass box that was darkened with black sheets. The respirometric system and the gas analysers used were the same as previously described by Allers & Culik (1997). The air flux through the system was set to a rate of 6 to 8 l min$^{-1}$ to match the oxygen consumption of the animals and to keep oxygen levels within the chamber close to 20%. A small van was placed at the inner side of the lid of the chamber to ensure fast mixing of exhaled and fresh air. Gas consumption and flow data were sampled every minute by an IBM-compatible 386SX computer. The periods of successful data recording lasted between 4 and 20 hours. Daytime and night-time experiments were conducted between 12 pm and 17 pm, 18 pm and 7 am, respectively.

Measurements were conducted under environmental temperatures that ranged from 12 to 20°C (mean 14.8°C at night and 17.4°C during daytime). The season for the experiments on captive cormorants was chosen such that the temperature conditions were similar to those encountered at Chausey. All data on gas volume and partial pressure derived from the respirometric measurements were recalculated to meet STPD conditions (standard temperature and pressure, dry). The ratio between the rates of CO$_2$ production and O$_2$ respiration by the animal (respiratory quotient, RQ) was calculated for every individual treatment. The mean RQ (0.71, SD 0.06) was similar to the RQ given by Schmidt-Nielsen (1990) for uric acid-producing animals digesting protein. The measured RQ and the data on partial pressure of O$_2$ within the air in the respiratory chamber were used to calculate the O$_2$ consumption rate according to Withers (1977).

Using the caloric equivalent of 18.4 kJ l$^{-1}$ O$_2$ given by Schmidt-Nielsen (1990) for uric acid-producing animals digesting protein, we calculated the MR of the birds in the chamber over the time of the experiment. To take into account the different size of the individuals, energy expenditure is given per kg body mass. Furthermore, to correct for the basic natural differences in metabolic rates of smaller and larger animals we used the exponent 0.723 for non-passerine birds according to Schmidt-Nielsen (1984), therefore
giving $W \text{ kg}^{-0.723}$ as a unit for energy consumption rate.

**Analysis of parallel HR and MR data**

HR and MR were measured simultaneously at 1 min intervals. When plotted against time the trends of HR and MR were clearly parallel, but slightly shifted with respect to time. By overlaying well-defined peaks both data sets were synchronised (Fig. 2), compensating for the time lag of MR data caused by the respiratory system. To eliminate the influence of the attachment procedure, data from the first 30 minutes of each experiment were not considered. Data obtained during day and night (day = photoperiod between 6 am and 9 pm) was analysed separately.

**Heart beat frequency of free-living cormorants**

Artificial eggs, such as those developed for field studies in penguins (Nimon et al. 1996; Ecks unpubl. data), were built and used to monitor the heart beat rate of breeding cormorants. The epoxy and fibreglass shells of the eggs were built to match a cormorant's egg (ca. 7 by 4 cm, Geroudet 1988) in shape, colour and size. Before the two halves of an egg were closed a miniature microphone was attached behind a hole (8 mm in diameter) drilled into one of the halves and a miniature pre-amplifier placed onto the other side. The wires connected to the electronics for power supply and signal transmission left the egg through a second hole and were sealed with silicon. The hole in front of the microphone was covered by a membrane and a fine wire weave to protect the inner parts against moisture and pecks. The artificial egg was placed in a nest already containing one to three eggs (no chicks) in addition to the natural clutch. As natural clutch sizes of up to 4 eggs are not rare in cormorants breeding at Chausey (Debout & Demongin 1996) this was considered non disruptive. The egg was fixed in a central position within the nest cup by threading the wires through the bottom of the nest, thus keeping the microphone located dorsally. The acoustic output of the artificial eggs was transmitted via a video transmitter (described below) and recorded on the sound track of the videotapes used to monitor bird activity. The recorded heart beats were counted per 15 s intervals and calculated to bpm. Mean ambient temperatures during the measurements were 10°C at night and 13°C during day.

**Activities of free-living cormorants**

During the field studies at the Chausey archipelago a video system was used to monitor the activities of free-living cormorants during incubation. The system consisted of 4 small black-and-white video cameras (12 x 9 x 6 cm) (Conrad Elektronik, Hirschau, Germany), a video splitter (Conrad Elektronik, Hirschau, Germany) to show all 4 images simultaneously on one screen, a transmitter and receiver (VSE-1, VEM-1, Remesch Hochfrequenztechnik, Kürten, Germany) to transmit the image data to the field station (frequency 2.414 GHz), a time-lapse video recorder (AG-6040, Panasonic) and a standard TV-monitor. Each camera was attached to a short metal pole (ca. 80 cm) close to the nest to be monitored and adjusted to show a breeding adult bird in full frame on the transmitted images of the birds. Local time and date were displayed by the recorder and recorded within the frame. During daylight hours (from approx. 6:00 am to 9:00 pm) these pictures were recorded in time-lapse mode (ca. 1 frame s⁻¹). To analyse the activities of the cormorants, video tapes were played back at a speed that allowed rapid but reliable registration of behaviour (approx. twice as fast as real time). The following activities were observed in incubating birds and defined: sleeping (head under wing), resting (sitting quietly, head upright), preening, nest building (breeding cormorant rearranges the material or uses material brought to the nest by the partner), gular flutter (as thermoregulatory behaviour) and unrest (obvious unrest, stretched neck, nervous movements of the head).

**Analysis of activity-dependent heart beat frequency**

HR of 5 cormorants derived from the artificial eggs were correlated with the activities recorded on video. For statistical analysis the total data set
for each defined activity from individual birds was reduced by random-selection to the lowest number of observations per bird that occurred in a particular category, thus precluding bias caused by different sample sizes. Data obtained during day and night (day = photoperiod between 6 am and 9 pm) was analysed separately.

Statistical analysis
Kolmogorov-Smirnov and Lilliefors Test were used to test for normal distribution of the HR data. Where data were not normally distributed Medians and 10th and 90th percentiles are given. Linear regressions were performed using a general linear model allowing for correction of a potential ‘bird effect’. T-Tests were used to test the significance of the slopes of the regression functions and an ANCOVA was used to examine the differences between regressions. The activity-dependent HRs were compared using a one way ANOVA (non-parametric Dunn’s Test). The threshold of significance was \( P < 0.05 \).

RESULTS
Parallel plotting of HR and MR data (Fig. 2) showed that the mean lag time of the respiratory system was ca. 2 min and ranged from 1 to 3 min. Differences in lag between individual experiments were due to different air flows. Throughout the experiments the cormorants stood or laid quietly within the respiratory chamber. Median energy expenditures derived from gas respirometry and Median HR were 6.4 W kg\(^{-0.723}\), 155 bpm during daytime and 5.1 W kg\(^{-0.723}\), 115 bpm at night, respectively. For further analysis MR was plotted against HR for diurnal and nocturnal data (Fig. 3a and b, respectively). MR was highly correlated with HR both during day and night (day: \( F = 172.65, P < 0.01 \), night: \( F = 2275.7, P < 0.01 \)). The two best fit regressions were \( MR(W \text{kg}^{-0.723}) = 4.76 + 0.01HR(\text{bpm}) \) during day and \( MR(W \text{kg}^{-0.723}) = 2.33 + 0.03HR(\text{bpm}) \) at night. The regressions are significantly different from each other (ANOVA, \( F = 130.0376, P < 0.001 \)).

HR of free-living cormorants was documented during the following activities performed by incubating birds; nest building (a total of 38 min from each one of 3 birds), unrest (35 min, 5 birds), gular flutter (21 min, 4 birds), preening (21 min, 4 birds), resting (83 min, 4 birds), sleeping (34 min, 5 birds), at night (79 min, 5 birds). Nocturnal acoustic observations indicated that activities of the incubating bird during the dark phase were limited (turning of the eggs, changes in sitting position), rare (about 3-5 times per night) and of very short duration (seconds to 1 min). Night data are therefore referred to as HR of inactive birds.
expenditure of an animal is calculated from its oxygen consumption rate, \( \text{VO}_2 \) (Schmidt-Nielsen 1990). It is, however, difficult to standardise the status of the animal during measurement (Bligh & Johnson 1973) and to define the relevance of the measured data with regard to free-living individuals (Bevan et al. 1994). Following the descriptions summarised by Bligh & Johnson (1973) we defined our data obtained through respirometry as resting metabolic rates (RMR) with the experimental animal resting in a thermoneutral environment, but not in a postabsorptive state. The cormorants involved in respirometric measurements were captive-bred and used to the presence of people as well as to being handled. Furthermore, by carrying out all measurements under natural temperatures we avoided temperature-induced stress. According to Kendeigh et al. (1977) the lower critical temperature (LCT) of cormorants corresponding in mass to our experimental animals is \( 11.8 \pm 1.4^\circ C \). The free-living cormorants at Chausey have, in accordance to their higher body mass, a LCT of \( 11.3 \pm 1.4^\circ C \). During the measurements in Neumünster and Chausey the temperatures encountered by the animals laid within the thermoneutral zone, i.e. no additional energetic costs for thermal regulation were required. None-the-less, we were obliged to use data obtained from captive cormorants to evaluate field data, a procedure which is likely to lead to some inaccuracies because e.g. captive birds may not be as fit as free-living birds. The alternative, however, of using wild animals for respirometric calibration of the HR-MR correlation, would have had the drawback of individuals being extremely stressed during the measurement, and therefore very likely compromising the data (e.g. Regel 1997). Thus reliability and evidence of data would be questionable. Therefore, the drawback included in our methodology was accepted.

\[ \text{VO}_2 \text{ as measured during respirometry, is in general proportional to HR, the cardiual stroke volume (SV) and tissue oxygen extraction. As reviewed e.g. by Hüppop (1988) and Bevan et al. (1994), stroke volume only varies slightly in birds under moderate strain such as was the case for the} \]

### DISCUSSION

#### Methodological considerations

Through direct respirometry the energy expenditure of an animal is calculated from its oxygen consumption rate, \( \text{VO}_2 \) (Schmidt-Nielsen 1990). It is, however, difficult to standardise the status of the animal during measurement (Bligh & Johnson 1973) and to define the relevance of the measured data with regard to free-living individuals (Bevan et al. 1994). Following the descriptions summarised by Bligh & Johnson (1973) we defined our data obtained through respirometry as resting metabolic rates (RMR) with the experimental animal resting in a thermoneutral environment, but not in a postabsorptive state. The cormorants involved in respirometric measurements were captive-bred and used to the presence of people as well as to being handled. Furthermore, by carrying out all measurements under natural temperatures we avoided temperature-induced stress. According to Kendeigh et al. (1977) the lower critical temperature (LCT) of cormorants corresponding in mass to our experimental animals is \( 11.8 \pm 1.4^\circ C \). The free-living cormorants at Chausey have, in accordance to their higher body mass, a LCT of \( 11.3 \pm 1.4^\circ C \). During the measurements in Neumünster and Chausey the temperatures encountered by the animals laid within the thermoneutral zone, i.e. no additional energetic costs for thermal regulation were required. None-the-less, we were obliged to use data obtained from captive cormorants to evaluate field data, a procedure which is likely to lead to some inaccuracies because e.g. captive birds may not be as fit as free-living birds. The alternative, however, of using wild animals for respirometric calibration of the HR-MR correlation, would have had the drawback of individuals being extremely stressed during the measurement, and therefore very likely compromising the data (e.g. Regel 1997). Thus reliability and evidence of data would be questionable. Therefore, the drawback included in our methodology was accepted.

\[ \text{VO}_2 \text{ as measured during respirometry, is in general proportional to HR, the cardiual stroke volume (SV) and tissue oxygen extraction. As reviewed e.g. by Hüppop (1988) and Bevan et al. (1994), stroke volume only varies slightly in birds under moderate strain such as was the case for the} \]

#### DISCUSSION

#### Methodological considerations

Through direct respirometry the energy expenditure of an animal is calculated from its oxygen consumption rate, \( \text{VO}_2 \) (Schmidt-Nielsen 1990). It is, however, difficult to standardise the status of the animal during measurement (Bligh & Johnson 1973) and to define the relevance of the measured data with regard to free-living individuals (Bevan et al. 1994). Following the descriptions summarised by Bligh & Johnson (1973) we defined our data obtained through respirometry as resting metabolic rates (RMR) with the experimental animal resting in a thermoneutral environment, but not in a postabsorptive state. The cormorants involved in respirometric measurements were captive-bred and used to the presence of people as well as to being handled. Furthermore, by carrying out all measurements under natural temperatures we avoided temperature-induced stress. According to Kendeigh et al. (1977) the lower critical temperature (LCT) of cormorants corresponding in mass to our experimental animals is \( 11.8 \pm 1.4^\circ C \). The free-living cormorants at Chausey have, in accordance to their higher body mass, a LCT of \( 11.3 \pm 1.4^\circ C \). During the measurements in Neumünster and Chausey the temperatures encountered by the animals laid within the thermoneutral zone, i.e. no additional energetic costs for thermal regulation were required. None-the-less, we were obliged to use data obtained from captive cormorants to evaluate field data, a procedure which is likely to lead to some inaccuracies because e.g. captive birds may not be as fit as free-living birds. The alternative, however, of using wild animals for respirometric calibration of the HR-MR correlation, would have had the drawback of individuals being extremely stressed during the measurement, and therefore very likely compromising the data (e.g. Regel 1997). Thus reliability and evidence of data would be questionable. Therefore, the drawback included in our methodology was accepted.

\[ \text{VO}_2 \text{ as measured during respirometry, is in general proportional to HR, the cardiual stroke volume (SV) and tissue oxygen extraction. As reviewed e.g. by Hüppop (1988) and Bevan et al. (1994), stroke volume only varies slightly in birds under moderate strain such as was the case for the} \]

#### DISCUSSION

#### Methodological considerations

Through direct respirometry the energy expenditure of an animal is calculated from its oxygen consumption rate, \( \text{VO}_2 \) (Schmidt-Nielsen 1990). It is, however, difficult to standardise the status of the animal during measurement (Bligh & Johnson 1973) and to define the relevance of the measured data with regard to free-living individuals (Bevan et al. 1994). Following the descriptions summarised by Bligh & Johnson (1973) we defined our data obtained through respirometry as resting metabolic rates (RMR) with the experimental animal resting in a thermoneutral environment, but not in a postabsorptive state. The cormorants involved in respirometric measurements were captive-bred and used to the presence of people as well as to being handled. Furthermore, by carrying out all measurements under natural temperatures we avoided temperature-induced stress. According to Kendeigh et al. (1977) the lower critical temperature (LCT) of cormorants corresponding in mass to our experimental animals is \( 11.8 \pm 1.4^\circ C \). The free-living cormorants at Chausey have, in accordance to their higher body mass, a LCT of \( 11.3 \pm 1.4^\circ C \). During the measurements in Neumünster and Chausey the temperatures encountered by the animals laid within the thermoneutral zone, i.e. no additional energetic costs for thermal regulation were required. None-the-less, we were obliged to use data obtained from captive cormorants to evaluate field data, a procedure which is likely to lead to some inaccuracies because e.g. captive birds may not be as fit as free-living birds. The alternative, however, of using wild animals for respirometric calibration of the HR-MR correlation, would have had the drawback of individuals being extremely stressed during the measurement, and therefore very likely compromising the data (e.g. Regel 1997). Thus reliability and evidence of data would be questionable. Therefore, the drawback included in our methodology was accepted.

\[ \text{VO}_2 \text{ as measured during respirometry, is in general proportional to HR, the cardiual stroke volume (SV) and tissue oxygen extraction. As reviewed e.g. by Hüppop (1988) and Bevan et al. (1994), stroke volume only varies slightly in birds under moderate strain such as was the case for the} \]
activities monitored in this study, while oxygen extraction and HR increase with \( V_{O_2} \). After calibration of the relationship between HR and MR in laboratory experiments, HR of free-living birds can therefore be used to determine their mean energy expenditure (Bevan et al. 1994; Woakes & Butler 1983). This method was compared to others by Bevan et al. (1995) who found that modeling energy expenditure of Tufted Ducks by using the data of four individuals led to the same accuracy as the calculations based on the data derived from the doubly labelled water method used on six animals. To eliminate one of the major drawbacks of previous methodologies based on HR-measurements, i.e. being invasive due to necessary surgery to implant transmitters or loggers, we used two non-invasive methods for HR-measurements. Therefore we avoided post operative trauma and ensure rapid recovery of the birds after manipulation.

**Artificial eggs**

Artificial eggs with enclosed microphones have been used to count heart beats acoustically in penguins (Nimon et al. 1996; Ecks unpubl. data) and our work confirms the applicability of this method for cormorants. This method is, however, limited to incubating birds since the acoustic transmission of the heart beat is only possible while the bird is on eggs. Even so, substantial movements or vocalisations by monitored adults or chicks disturb transmissions so that HR can only be determined for specific activities. Nonetheless, good data were obtained during resting, sleeping, preening, gular flutter, nest-building and obvious unrest, as long as the bird did not stand up. A major advantage of artificial eggs is that birds remain undisturbed during measurements. After placing the egg in a natural clutch it can be left in place for the full incubation period (without disturbances apart from occasional checks), therefore allowing measurements of HR of a free-living bird over a time span of days to weeks. The apparent acceptance of the fibreglass egg was demonstrated by a cormorant pair which incubated an artificial egg for a week after having lost the rest of the clutch to a Herring Gull Larus argentatus.

**POLAR HR-monitor**

As opposed to the artificial egg, use of the POLAR HR-monitoring device necessitates the capture and handling of the bird. Although handling of captive cormorants was relatively short (10-15 min) and non-invasive, the procedure would entail a much more serious disturbance to free-living birds than deployment of artificial eggs. HR-measurements via POLAR transmitter can, however, be conducted on non-breeding birds that would not sit on an artificial egg. This method is therefore not limited to incubation. Furthermore, since no wires or harnesses are necessary, the bird is not particularly hindered by the device. In an earlier experimental stage in February 1996 we tested an elastic harness to attach the HR transmitter and electrodes with short wires to one of the captive cormorants, this method having been successfully used to fit external devices to shags (Wanless et al. 1991). However, our harnessed animal appeared to be unable to stand upright and continually lost its balance. The behaviour of a cormorant equipped using tape did not show any differences to other, unequipped individuals. We thus exclusively used this attachment method throughout our study. While using the POLAR HR-monitor, the receiver can either be close (up to approx. 1.5 m distance) to the transmitter-bearing bird, as in this investigation, or it can be attached to the bird together with the transmitter as done by Regel (1997) for penguins. This latter approach enables the HR of free-living birds to be monitored as has been done by other investigators (Regel 1997; Weimerskirch unpubl. data) as long as the animals stay on land or close to the surface of the water, and provided the receiver can be recovered.

**Significance of our data**

We found a differences in the relation between HR and MR during night and day, respectively. The overall range of HR is lower during night than during daytime. Furthermore, the mean
metabolic rate associated with a specific HR category is lower during night. These differences indicate, that for the calculation of the metabolic rate of cormorants, if it is based on HR measurements, different models should be used for diurnal and nocturnal data. This fact is compatible with the findings of Aschoff & Pohl (1970), who described a distinct diel pattern of oxygen consumption in birds. In the calculations for a TEB in incubating Great Cormorants, Grémillet et al. (1995) assumed that the energy expenditure during nest building is the same as for preening. This was based on the similarity of neck and beak movements performed during these two activities. Our data indicate that this assumption is incorrect because the Median HR during nest building is much higher than during preening (142 bpm and 120 bpm, respectively). In the same study Grémillet et al. (1995) assumed the MR of incubating cormorants at night to be 75% of the RMR during day, based on a study by Aschoff & Pohl (1970). Our investigation shows, however, a nocturnal reduction in MR in free-living incubating Great Cormorants of only 16%. Thus a TEB for cormorants calculated under the quoted assumptions by Aschoff and Pohl would lead to an underestimation of the overall energy expenditure. Although this error only concerns the activity with the lowest energy demands it is still significant since at the latitude of Chausey the nocturnal phase accounts for a major part of a 24 hour budget (ca. 40% at this time of the year, pers.obs.). In TEB calculations the errors of each-assumption add up to the overall error of the budget, so it is desirable to correct for every single error as meticulously as possible. By using methods for HR-measurements that can be deployed with limited disturbance to the animals we were able to supply good data on activity dependent energy expenditure that will prove valuable for future TEB calculations in Great Cormorants.

ACKNOWLEDGEMENTS

This work was funded by the Deutsche Forschungsgemeinschaft through a grant to B. Culik (DFG Cu 24/4), and supported by the Groupe Ornithologique Normand, Université de Caen. We thank the Société Civile Immobilière des Îles Chausey and the Mairie de Granville for allowing research to be conducted on the islands under their control. Grateful thanks are due to G. Debout, G. Argentin, I. Bergner, L. Demongin, Y. Gary, G. Hecke meier and M. Kierspel for their extraordinary support. We would like to thank C. Reimesch for making radio transmission of pictures and sounds possible and helping us throughout the project. We are grateful to P. Drüwa and the staff of the Tierpark Neumünster for their support. Special thanks to G. Luna-Jorquera and S. Garthe for their help with statistical questions and to R.P. Wilson for constructive comments on the manuscript.

REFERENCES

Hüppop O. 1988. Aktivität und Energieumsatz bei

SAMENVATTING

In het hier beschreven onderzoek werd het energieverbruik van broedende Aalscholvers Phalacrocorax carbo berekend. Allereerst werd hiertoe bij Aalscholvers in gevangenschap de relatie tussen het metabolisme en de hartslagfrequentie vastgesteld: MR (W kg\(^{-0.723}\)) = 4.76 + 0.01 HR (bpm) overdag en MR (W kg\(^{-0.723}\)) = 2.33 + 0.03 HR (bpm) 's nachts (MR = metabolic rate, HR = hartslag in aantal slagen per minuut). Vervolgens werden vrijlevende, nestelende Aalscholvers opgetuigd met een hartslagmeter, zoals die ook in de atletiek wordt gebruikt en werden de activiteiten van de broedende vogels geprotocolleerd. Het veldmetabolisme werd vervolgens berekend voor elk van de waargenomen activiteiten (rusten of slapen, poetsen en veren schudden, nestbouw), door toepassing van de eerder gevonden relatie tussen hartslag en metabolisme. Het energieverbruik bedroeg 5.08 W kg\(^{-0.723}\) 's nachts, 6.06 W kg\(^{-0.723}\) tijdens rust of slaap overdag, 6.20 W kg\(^{-0.723}\) tijdens het poetsen of veren schudden (onrust) en 6.47 W kg\(^{-0.723}\) tijdens de nestbouw. Het gebruik van een hartslagmeter is veelbelovend en veroorzaakt slechts minimale stress bij de 'behandelde' vogels. (CJC).

Received 9 October 1998, accepted 28 April 1999

Corresponding editor: Kees (C.J.) Camphuysen