

Year-round recordings of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter

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Summary

Warm-blooded diving animals wintering in polar regions are expected to show a high degree of morphological adaptation allowing efficient thermal insulation. In stark contrast to other marine mammals and seabirds living at high latitudes, Arctic great cormorants *Phalacrocorax carbo* have very limited thermal insulation because of their partly permeable plumage. They nonetheless winter in Greenland, where they are exposed to very low air and water temperatures. To understand how poorly insulated diving endotherms survive the Arctic winter, we performed year-round recordings of heart rate, dive depth and abdominal temperature in male great cormorants using miniature data loggers. We also examined the body composition of individuals in the spring. Abdominal temperatures and heart rates of birds resting on land and diving showed substantial variability. However, neither hypothermia nor significantly lower heart rate levels were recorded during the winter months. Thus our data show no indication of general metabolic depression in great cormorants wintering in Greenland. Furthermore, great cormorants did not reduce their daily swimming time during the coldest months of the year to save energy; they continued to forage in sub-zero waters for over an hour every day.

As birds spent extended periods in cold water and showed no signs of metabolic depression during the Arctic winter, their theoretical energy requirements were substantial. Using our field data and a published algorithm we estimated the daily food requirement of great cormorants wintering in Greenland to be 1170 ± 110 g day⁻¹. This is twice the estimated food requirement of great cormorants wintering in Europe. Great cormorants survive the Arctic winter but we also show that they come close to starvation during the spring, with body reserves sufficient to fast for less than 3 days. Lack of body fuels was associated with drastically reduced body temperatures and heart rates in April and May. Concurrent, intense feeding activity probably allowed birds to restore body reserves. Our study is the first to record ecophysiological parameters in a polar animal on a year-round basis. It challenges the paradigm that efficient thermal insulation is a pre-requisite to the colonization of polar habitats by endotherms.

Key words: body temperature, data logger, diving, ecophysiology, great cormorant, *Phalacrocorax carbo*, heart rate, polar night.

Introduction

Living at high latitudes is a challenge for many organisms. Strongly varying light levels throughout the year and associated low temperatures, especially during winter, limit the diversity, distribution and abundance of plants and animals in polar regions (for a review, see Grémillet and Le Maho, 2003). Under such conditions, selection pressure is particularly marked for endothermic animals because of the temperature differential between their bodies and the environment, which can result in high heat losses unless balanced by increased insulation. This effect is further enhanced in diving endotherms, as these potentially lose 30 times more heat to their environment (water) than their terrestrial relatives do (Denny, 1993).

Seabirds and marine mammals are nonetheless successful apex predators in Arctic and Antarctic food webs for two reasons. (1) They show extensive morphological adaptation enabling them to reduce heat losses. Polar marine mammals are large and accumulate subcutaneous fat layers, whereas polar seabirds are protected by their waterproof plumages (Wharton, 2002). (2) They exploit highly profitable food resources and easily balance their costly way of life (van Franeker et al., 1997).

Arctic great cormorants *Phalacrocorax carbo* do not conform to this evolutionary mainstream. Great cormorants are diving, fish-eating birds that originate from the tropics (van Tets, 1976). They have a partially permeable plumage and the

highest metabolic costs of diving among endotherms (Grémillet et al., 2003, 2005a). Despite these handicaps, great cormorants have colonized a wide range of climatic zones ranging from equatorial Africa to northwest Greenland. In Greenland a small population breeds and over-winters along the West coast, north of the polar circle (Boertmann and Mosbech, 1997; Lyngs, 2003). Recent findings indicated that this population feeds on both quantitatively and qualitatively modest prey resources (Grémillet et al., 2004). We studied Greenland great cormorants as a model species of a polar diving endotherm, which does not minimize its heat losses to the water, nor exploits highly rewarding prey patches. This bird nonetheless copes with very low temperatures for extended periods.

Former studies showed that Greenland great cormorants do not have abnormally high food requirements during the summer period (Grémillet et al., 1999a). They compensate for their high foraging costs by reducing the total time spent in the water (temperature $\sim 5^{\circ}\text{C}$) and this strategy seems to be based upon a predatory performance (the amount of food gathered per unit time) that is 10–30 times higher than that of other diving birds (Grémillet et al., 2001). During the winter period they are thought to employ the same strategy, i.e. a drastic reduction of time spent diving when the water is cold. However, field observations were only performed towards the end of the winter (Grémillet et al., 2001), so how the birds survive during the coldest months of the year, during which they are routinely exposed to water temperatures less than 0°C and air temperatures less than -20°C , was unknown.

Using miniature data loggers, we performed year-round recordings of diving activity, heart rate and abdominal temperature in free-ranging male great cormorants from Greenland. We also determined the body composition of individuals at the end of the winter phase.

These empirical data and the output of an energetics model allowed us to test the hypotheses that Greenland great cormorants survive the Arctic winter because of (1) physiological adjustments: they adopt a lower metabolic state, expressed by markedly lower body temperatures and heart rates levels; (2) behavioural adjustments: they reduce the time spent searching for fish in cold water.

Materials and methods

Acquisition of ecophysiological data

We studied male great cormorants *Phalacrocorax carbo* L. in West Greenland, where a small population is present throughout the year (Boertmann and Mosbech, 1997). In June 2002, ten breeding males raising young chicks on Disko ($69^{\circ}30'\text{N}$, $54^{\circ}05'\text{W}$) were equipped with heart rate data loggers (HRDL; Woakes et al., 1995), $60\text{ mm}\times 24\text{ mm}\times 7\text{ mm}$, mass 20 g, i.e. 0.6% of the body mass of the cormorants studied. The HRDLs were programmed to record data every second day for a period of 1 year. On the days during which HRDLs were recording, heart rate was stored every 2 s, depth every 2 s and abdominal temperature

every 6 s. All devices were calibrated before and after use (temperature accurate to $\pm 0.13^{\circ}\text{C}$, time constant 90 s, depth accurate to $\pm 0.05\text{ m}$). After the initial calibration, HRDLs were coated in medical grade silicon (MED 1037, Nusil technology, Carpinteria, CA, USA) and sterilized with a mixture of 70% alcohol (90%) and 5% chlorhexidine (10%). They were implanted into the abdominal cavity of the cormorants following Stephenson et al. (1986), after the male birds had been caught at the nest site and anaesthetized with an isoflurane– O_2 mixture. All birds implanted with a HRDL were also fitted with a transponder to allow individual recognition. The nesting behaviour and breeding performance of the implanted birds were closely monitored following implantation (direct observations using 10×40 binoculars at 50 m distance). In June 2003 and 2004 all data loggers were retrieved, following the same procedure as for implantation.

All experiments were conducted by trained veterinary personnel under permits of the ethics committee of the French Polar Institute, The Arctic Station Godhavn (Copenhagen University), the Danish Polar Center, the Danish veterinary administration, and the Greenland Home rule Government.

Analysis of ecophysiological data

Recorded heart rate, depth and temperature data were visualized and analysed using Multitrace (Jensen Software Systems, Laboe, Germany). The recordings provided information about the behavioural and the physiological status of the birds. We discarded the first month of recordings to ensure that the implanted cormorants had fully recovered from the surgery. We then performed a general analysis using the entire data set (data recorded every second day), and a more detailed analysis using data for every eighth calendar day (i.e. every fourth recorded day). Daily averages were calculated for different variables using the individual birds as the sampling unit.

General analysis

We assessed two variables every second calendar day.

(1) Average total time spent in the water. Great cormorants only stay in the water when they are actively diving, hence time in the water was defined as the time period between the beginning of the first dive (sharp increase of recorded pressure values) and the end of the last dive in a dive bout (Grémillet et al., 2003). A dive bout was defined as a succession of dives interrupted by resting periods at the surface (Fig. 1). If a resting period was longer than 5 min we assumed that the bird did not stay in the water, and that the bout had ended (bout-end criterion, calculated after Gentry and Kooyman, 1986). Birds usually conducted more than one dive bout per day. Total time in the water per day was calculated as the sum of the durations of all dive bouts and this will be termed 'foraging effort' hereafter.

(2) Average total time spent flying. A flight period was defined as a period during which pressure recordings were stable and heart rate values increased to values well above $200\text{ beats min}^{-1}$ (Fig. 1). This threshold value was defined

using direct observations of birds implanted with HRDLs as they flew away from and/or landed onto their nests. A time period not spent either diving or flying was defined as a resting period. Such periods can contain true resting as well as low-cost activities such as preening (Storch et al., 1999).

Detailed analysis

We assessed 12 variables every eighth calendar day. (1) Average duration of the dives. (2) Average depth of the dives. (3) Average dive/pause ratio. We assumed that great

cormorants have an anticipatory diving strategy (Grémillet et al., 1999b), therefore dive/pause ratios were calculated using the duration of each dive and the duration of the resting period prior to the dive. (4) Average heart rate while resting during the low-activity phase. Despite the fact that they experience continual daylight in summer and continual darkness during the polar night, great cormorants in Greenland are far less active between 02:00 h and 05:00 h throughout the year (Grémillet et al., 2005b). We therefore defined this phase as the low-activity phase, for which resting heart rates were determined when neither diving, nor flying activities occurred (i.e. birds were ashore). (5) Average heart rate while resting during the high-activity phase. Similarly, Greenland great cormorants are usually more active between 10:00 h and 15:00 h. Resting heart rates for the high-activity phase were therefore calculated for this time period when the birds were not flying or diving (birds ashore). (6) Average heart rate at the maximum depth of each dive (Fig. 1B), which is also the lowest heart rate during a dive. (7) Average heart rate at the water surface inbetween dives (Fig. 1B). (8) Average abdominal temperature during resting for the low-activity phase (defined above). (9) Average abdominal temperature during resting for the high-activity phase (see above for definition). (10) Average abdominal temperature while diving. (11) Average difference in abdominal temperature (ΔT) between the beginning and the end of a dive bout (Fig. 1C). (12) Preliminary analysis of the temperature traces revealed that the lowest temperature levels were typically reached after completion of a dive bout (Fig. 1C). This minimum temperature level was therefore also recorded.

Body composition analysis and estimation of fasting endurance

Five great cormorants that had accidentally drowned in gill nets off Disko in April 2000 were weighed (± 1 g) and stored in sealed plastic bags at -18°C until analysis. After thawing, the birds were plucked and weighed again (± 1 g). Leg and pectoral muscles, liver and abdominal fat deposits were dissected and weighed (± 0.01 g). These body compartments and the remaining carcass were freeze-dried to constant mass and then ground under liquid nitrogen. Prior to biochemical analysis, powdered samples were freeze-dried again to eliminate traces of water. Protein concentrations were obtained using the Kjeldahl method (Campbell and Leatherland, 1980) and total lipids according to a gravimetric method using a chloroform/methanol solution (2/1, v/v) as the extraction mixture (Folch et al., 1957). Reproducibility between duplicate measurements was $1.1 \pm 0.2\%$ (proteins) and $0.7 \pm 0.1\%$ (lipids).

Fasting endurance was estimated by first calculating the amount of available energy from body

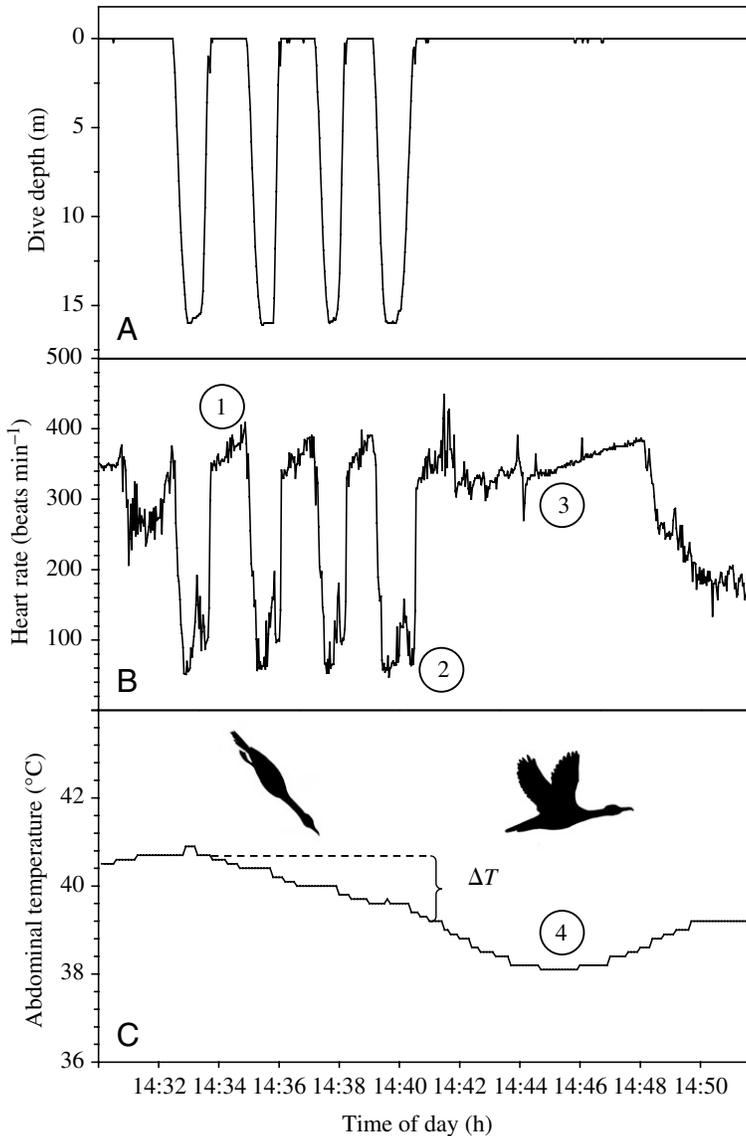


Fig. 1. (A) Dive patterns, (B) heart rate and (C) abdominal temperature of a male great cormorant on Christmas Day 2002 in West Greenland (i.e. during the polar night). Heart rate is maximum when the bird is at the water surface (1), but decreases sharply during dives (2). Sustained heart rates >200 beats min^{-1} in the absence of diving activity occur during flight (3). Note that the abdominal temperature of the bird decreases gradually during the dive bout (ΔT), to reach a minimum after completion of the dive series (4). This short-term temperature drop is probably linked to combined effects of diving in cold water and of ingesting cold fish.

lipid and protein masses that could be metabolized during a prolonged but reversible fast in lean animals (95% and 25%, respectively; Belkhou et al., 1991) and from their caloric equivalents (39.3 and 18.0 kJ g⁻¹, respectively; Schmidt-Nielsen 1990). Secondly, the maximal sustainable duration of fasting was estimated in each bird using an iterative procedure integrating daily body component losses according to Boos et al. (2005). To achieve this, we assumed that the field metabolic rate averaged 12 W kg⁻¹ (Grémillet et al., 2003); that in such fasting lean animals, lipids and proteins accounted for 75 and 25% of the energy expenditure until $\frac{3}{4}$ of lipid reserves were used and for 63 and 37%, respectively, when the fast was further prolonged (Belkhou et al., 1991; Cherel and Groscolas, 1999); and that the hydration of the lean mass was 76±1% (this study).

Energetics modeling

Using an algorithm detailed in Grémillet et al. (2003) we calculated (1) the theoretical daily food intake of the great cormorants studied, and (2) the theoretical catch per unit effort (CPUE, expressed as gram fish caught per minute spent underwater) required to achieve this daily food intake. This theoretical CPUE therefore does not reflect the actual foraging performance of the bird, but the minimal foraging success that is required to balance the energy budget. Calculations were only performed for the periods during which birds were not breeding and we assumed that the birds' body reserves were in a steady state. Data recorded by the HRDLs provided most input values. Day lengths were downloaded from http://aa.usno.navy.mil/data/docs/RS_OneYear.html#formb. Water temperatures were taken from the Arktisk Station database (<http://www.nat.ku.dk/as/indexuk.htm>). Birds were assumed to weigh 3.5 kg (the average body mass of birds when they were implanted) while the average calorific value of the fish was assumed to be 4.0 kJ g⁻¹ (Grémillet et al., 2004). Assimilation efficiency, swim speed and time spent wing-spreading per day were assumed to be as specified in Grémillet et al. (2003).

Abdominal temperatures of resting birds showed a limited, yet significant decline during the winter phase (see Results, Fig. 4A). To estimate the amount of energy saved through this decrease in body temperature, we calculated the thermal conductance (W m⁻² °C⁻¹) of great cormorants resting in air using input data from Storch et al. (1999). Heat losses (W) were then determined: (1) for a bird with stable body temperature equivalent to the average abdominal temperature in September; and (2) for the actual abdominal temperatures measured throughout the winter months. The difference between (1) and (2) gives the amount of energy (W) that might be saved *via* a reduction of body temperature during the winter months. Calculations were performed for birds resting during the active and the non-active phases. Using time budget information, assimilation efficiency of the birds, and calorific value of their prey, output values were then converted into the amount of energy (kJ day⁻¹) and fish (g day⁻¹) saved per day.

Statistical analysis

Summary statistics were computed for the entire sample using individual birds as the sampling unit. Values are means ± s.d. The effect of the time of the winter period on all recorded variables, as well as potential links with day lengths, were analysed using residual maximum likelihood analyses (REML, Patterson and Thompson, 1971). In all analyses, day or day length were entered as fixed factors and bird as a random factor. This method accounted for the fact that we were dealing with time series of different lengths. In all REMLs, the effects of day or day length were determined by comparing Wald statistics (expressed as χ^2 throughout the results) with *F*-distributions (with a 5% significance threshold).

Results

All males implanted in June–July 2002 bred normally (with 2.9±0.9 chicks per nest *vs* 3.1±0.9 chicks for 50 control nests). Nine birds were re-trapped in June 2003, the tenth in June 2004. All birds bred successfully after removal of the HRDLs. 80% of the implanted birds were resighted while breeding in June 2004. This two-year resighting rate is higher than for 15 non-implanted control birds marked with metal rings (60%).

All devices were recovered, but only seven provided recordings on all three channels. The retrieved units were surrounded by a very limited volume of scar tissue, indicating that thermal insulation of the loggers did not vary through time. Three data loggers ran for a whole year, while the four others recorded data for 10, 9, 8 and 7 months. We analysed the 210 million data points recorded by all seven devices. Fig. 1 shows examples of depth, heart rate and abdominal temperature traces.

Behaviour

Knowledge of the breeding phenology (Salomonsen, 1967; Lyngs, 2003) and winter observations (Grémillet et al., 2001) allowed us to set four temporal phases (Fig. 2): (1) July–August, which is the chick-rearing phase at the breeding site on Disko; (2) September to April, which is the non-breeding phase, spent south of the Disko Bight (Grémillet et al., 2001); (3) May, which is when the birds return to Disko to mate; (4) June, which is the incubation period during which the work is shared by both partners.

Great cormorants showed some diving activity during each day for which we had recordings (i.e. every second day), strongly suggesting that they dived for food every day throughout the study period. Foraging effort varied markedly (Fig. 2); until late August 2002 birds provisioned their chicks and spent extended periods in the water. Their foraging effort fell sharply from ~120 min day⁻¹ to 40 min day⁻¹ as they moved from their breeding to their wintering grounds in early September (Fig. 2). During the winter period foraging effort varied according to day length ($\chi^2=49.7$; d.f.=1,6; *P*<0.001): from September to mid-December this effort increased gradually to reach average levels of 73±19 min day⁻¹ between mid-December and early February (during the polar night).

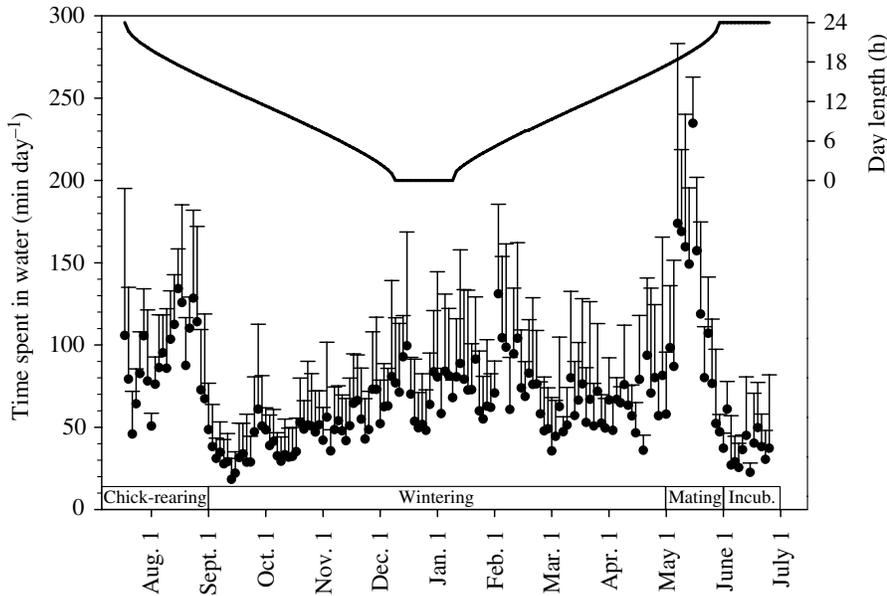


Fig. 2. Daily foraging effort of Greenland great cormorants throughout the annual cycle., showing one data point every second day; values are means + s.d. ($N=3-7$). The continuous line shows day length (h). The four phases of the year cycle (chick-rearing, wintering, mating and incubating) were defined after Salomonsen (1967) and Lyngs (2003).

Foraging effort subsequently decreased with increasing day lengths until the end of April (to $\sim 50 \text{ min day}^{-1}$). As birds moved back from the wintering quarters to the breeding site, foraging effort increased suddenly to over 150 min day^{-1} during the mating phase (May), to fall again to less than 50 min day^{-1} during the incubation period (June, Fig. 2).

Average dive depth increased gradually from $\sim 6 \text{ m}$ to $\sim 18 \text{ m}$ between July and April ($\chi^2=158.7$; d.f.=1,6; $P<0.001$), falling rapidly during May 2003, to reach 2–3 m in early June 2003 (Fig. 3). Dive duration (average $42\pm 13 \text{ s}$, range 10–60 s) followed a similar upward trend ($\chi^2=33.5$; d.f.=1,6; $P=0.001$), from $\sim 20 \text{ s}$ to $\sim 60 \text{ s}$ between July and April. Dive to pause ratio was consistently >1.0 , demonstrating that birds were spending more time underwater than at the water surface when foraging

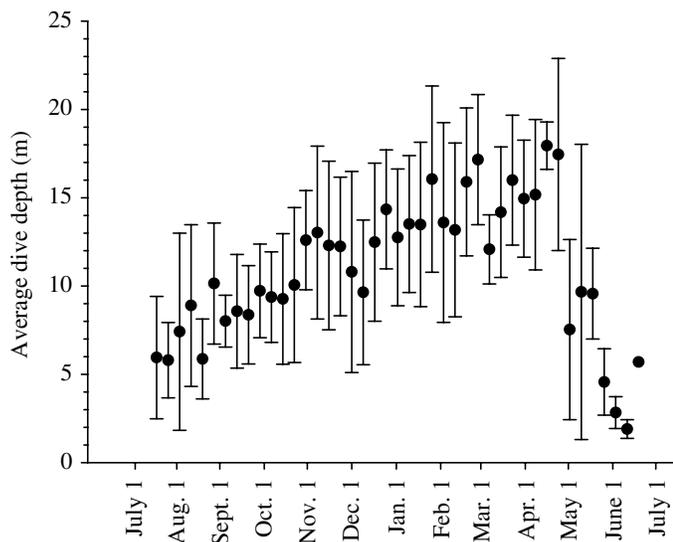


Fig. 3. Dive depths of Greenland great cormorants throughout the year cycle, showing one data point every eighth day; values are means \pm s.d. ($N=3-7$).

(average 1.36 ± 0.25 , range 1.0–2.1). This ratio decreased significantly throughout the winter period from 1.9 to 1.1 ($\chi^2=21.3$; d.f.=1,6; $P=0.003$), as dive depth increased.

Daily flight time varied between 25–160 min day^{-1} (average $78\pm 28 \text{ min day}^{-1}$), with flight activity being highest during chick provisioning ($124\pm 28 \text{ min day}^{-1}$) and lowest during the polar night ($55\pm 8 \text{ min day}^{-1}$) and the incubation period ($38\pm 9 \text{ min day}^{-1}$). Between September and April there was, therefore, a significant, positive relationship between daily flight time and day length ($\chi^2=18.7$; d.f.=1,6; $P=0.005$).

Physiology

Average abdominal temperatures of birds resting on land during the active (10.00–15.00 h) and the non-active (02.00–05.00 h) phases (Fig. 4A) decreased gradually between September and March ($\chi^2=52.5$; d.f.=1,6; $P<0.001$ and $\chi^2=53.4$; d.f.=1,6; $P<0.001$, respectively). The average temperature decrease between the beginning and the end of this period was 0.78°C for resting during both the non-active and active phases. Following this slow, minor decline, resting temperatures dropped markedly in April and May (Fig. 4A). Original temperature levels were restored in June (Fig. 4A). Mean abdominal temperatures of diving birds followed a similar pattern and decreased on average 0.65°C between September and March ($\chi^2=18.1$; d.f.=1,6; $P=0.005$). Markedly lower values were only observed in May (Fig. 4B). In diving birds the lowest abdominal temperatures were recorded immediately after a dive bout (see Fig. 1). These temperatures also decreased gradually between September and April ($\chi^2=34.1$; d.f.=1,6; $P=0.001$), with an average change of 1.22°C between the beginning and the end of the period (Fig. 4B). Mean drop in abdominal temperature while diving (ΔT , calculated between the beginning and the end of a dive bout, see Materials and methods) ranged from 0.4°C to 1.9°C (Fig. 4C). ΔT increased significantly throughout the winter months ($\chi^2=15.4$; d.f.=1,6; $P=0.008$), and there was a

significant, positive correlation between ΔT and average dive depth ($\chi^2=27.0$; d.f.=1,6; $P=0.002$).

Mean heart rate at the bottom of dives (the lowest heart rates during the dives) varied between 90–190 beats min^{-1} (Fig. 5A), and was negatively correlated with dive depth, therefore decreasing throughout the winter phase ($\chi^2=28.6$; d.f.=1,6; $P=0.002$). Mean heart rate at the water surface ranged from 330–380 beats min^{-1} (Fig. 5A), with no significant variation during the winter period ($\chi^2=2.3$; d.f.=1,6; $P=0.182$). Mean heart rate during resting on land varied between 50–100 beats min^{-1} for non-active phase and between

47–152 beats min^{-1} for the active phase (Fig. 5B). Neither level changed significantly during the winter period ($\chi^2=5.6$; d.f.=1,6; $P=0.056$ and $\chi^2=3.0$; d.f.=1,6; $P=0.134$, respectively), but fell abruptly during the second half of April 2003 (Fig. 5B).

Body composition

Body composition of the five great cormorants carcasses gathered off Disko in April 2000 revealed that birds were extremely lean, with average lipid proportion of only $4.6\pm 1.6\%$ ($4.1\pm 0.9\%$ lipid for the liver, $3.0\pm 0.4\%$ for the muscles and $17.3\pm 8.5\%$ for abdominal fat pads). The lipid/protein ratio averaged $25.2\pm 9.1\%$. Leg muscle proteins accounted for $13.9\pm 0.4\%$ of the total protein mass and pectoral muscles for $16.1\pm 0.6\%$. Mobilisable energy reserves were of 7802 ± 2081 kJ, in which proteins represented $33.8\pm 7.8\%$. The estimated fasting endurance based upon these reserves was 2.8 ± 0.8 days (range 2–4 days).

Food intake and foraging efficiency

Theoretical daily food intake for great cormorants wintering in Greenland was 1170 ± 110 g (range 950–1460 g between September and April). To gather this quantity of food, birds required a theoretical foraging efficiency of 41 ± 15 g fish min^{-1} spent underwater (range 22–80 g min^{-1}). Foraging efficiency was positively correlated with day length ($F_{1,28}=15.7$, $P<0.0001$, Fig. 6), with lowest average foraging performances achieved during the polar night (28 ± 4 g min^{-1}). The theoretical amount of energy saved *via* lower abdominal temperatures at rest was between 1–25 kJ, which represents between 0.3–8 g of fish (i.e. less than 1% of the average theoretical food intake).

Discussion

This study is, to our knowledge, the first to detail the behavioural and physiological status of an endotherm wintering in polar regions, and one of the first to perform such long-term recordings in a free-ranging animal (Block et al., 2001; Guillemette et al., 2002; Green et al., 2004). Current technological developments enable investigations of the ecophysiology of numerous wild animals but these studies typically proceed over short time periods, ranging from a few

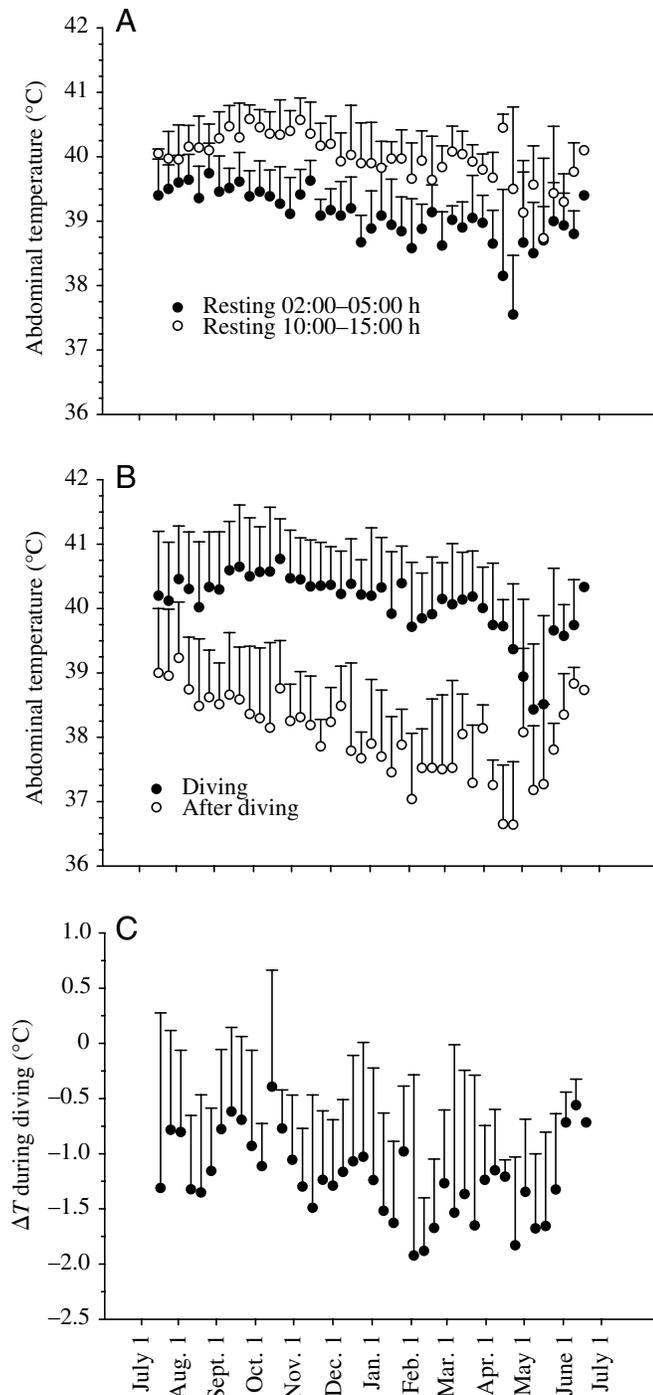


Fig. 4. (A) Abdominal temperatures in resting Greenland great cormorants throughout the year cycle. Filled circles, abdominal temperatures of animals resting during the non-active phase (02:00–05:00 h); empty circles, abdominal temperatures of animals resting during the active phase (10:00–15:00 h). One data point is shown every eighth day; values are means + s.d. ($N=3-7$). (B) Abdominal temperatures of foraging Greenland great cormorants throughout the year cycle. Filled circles, abdominal temperatures of diving animals; empty circles, abdominal temperatures of animals after a diving sequence. One data point is shown every eighth day; values are means + s.d. ($N=3-7$). (C) Effect of diving on the abdominal temperature of Greenland great cormorants throughout the year cycle. ΔT was measured between the moment of the first and the last dive within the dive series. One data point is shown every eighth day; values are means + s.d. ($N=3-7$).

seconds to several days (Boyd et al., 2004; Cooke et al., 2004). The insights gained reveal stunning performances, especially in diving animals (Costa and Sinervo, 2004). However, because of their inherently short time frame, they provide us with a biased perception of the biology of free-ranging animals. Most marine predators, for instance, have been studied during the reproductive phase, which often only corresponds to a fraction of their total annual cycle, and represents a very specific trophic status (Croxall et al., 2005).

Even if highly relevant, year-round recordings of ecophysiological parameters are particularly challenging in diving animals because of technical constraints and, more importantly, because of the potential handicap caused to the animal. For instance, archival tags attached externally to diving

predators disrupt their hydrodynamic properties, and therefore jeopardize energy balance and survival (Ropert-Coudert et al., 2000). External data loggers deployed in polar areas can also initiate icing on the body of the animals, and create an additional handicap (Kooyman and Ponganis, 2004). In order to study the adaptations of great cormorants to the Arctic winter, we therefore chose to equip them with miniature data loggers placed inside the abdominal cavity.

All birds bred normally after being implanted, as well as in the subsequent year after the devices had been removed. 2-year resighting success was also higher than in control birds marked with metal rings. Arctic winter conditions put high selection pressure on great cormorants (see later), so the fact that all birds studied survived the winter phase and reproduced successfully, indicates that our method did not create a significant handicap. Recent studies in eider ducks *Somateria mollissima* and macaroni penguins *Eudyptes chrysolophus*, which used similar technology, came to a similar conclusion (Guillemette et al., 2002; Green et al., 2004).

Unlike most diving birds, great cormorants have a partly permeable plumage and therefore do not appear to be morphologically designed to survive the Arctic winter (Grémillet et al., 2005a). We hypothesized that they show specific physiological and behavioural adjustments to this thermal challenge, either in the form of a depressed metabolism (expressed by lower body temperatures and lower heart rates), or through a decrease of the time spent in cold water. Interestingly, our field data do not support either of these hypotheses.

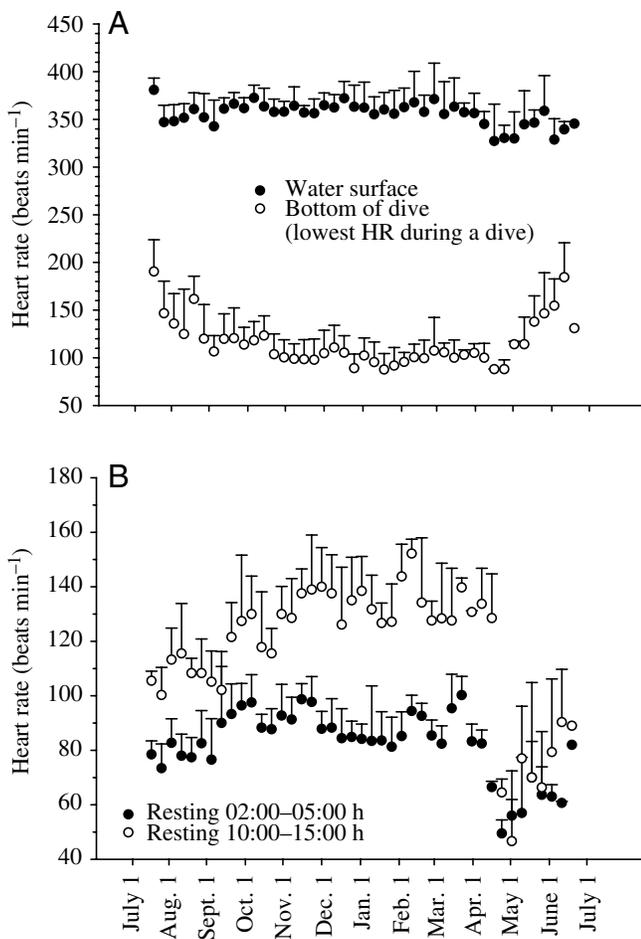


Fig. 5. (A) Heart rate of foraging Greenland great cormorants throughout the year cycle. Filled circles, heart rate (HR) of birds at the water surface in-between dives; empty circles, heart rate of birds in the deepest section of dives. The latter are also the lowest heart rates during the dives. One data point is shown every eighth day; values are means + s.d. ($N=3-7$). (B) Heart rate of resting Greenland great cormorants throughout the year cycle. Filled circles, heart rates of animals resting during the non-active phase (2:00–5:00 h); empty circles, heart rates of animals resting during the active phase (10:00–15:00 h). One data point is shown every eighth day; values are means + s.d. ($N=3-7$).

Physiological adaptation?

To reduce energy expenditure when facing thermoregulatory stress, endothermic animals can allow their body temperatures

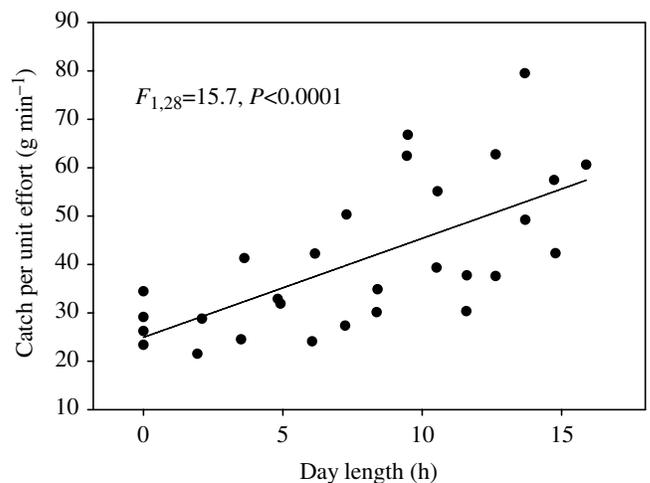


Fig. 6. Positive relationship between theoretical foraging efficiency [Catch per unit effort (CPUE) in g fish caught min⁻¹ spent underwater] and day length in great cormorants wintering in Greenland (September to April). CPUE was modelled after Grémillet et al. (2003) using field data collected during this study as time budget input values. $y = 2.04x + 24.95$.

to fluctuate and follow that of the environment. By so doing they decrease the temperature differential between their bodies and surrounding media, therefore minimizing thermoregulatory costs (McKechnie and Lovegrove, 2002). Theoretically, great cormorants wintering in Greenland could display metabolic depression expressed by lower heart rates and hypothermia when resting on land and/or when diving at sea. On land this phenomenon would be the equivalent of torpor or hibernation, depending on its magnitude and duration (Lyman et al., 1982; Kortner et al., 2000). At sea, birds could also allow their body temperature to drop during dive bouts to save energy, as shown in bank cormorants *Phalacrocorax neglectus* (Wilson and Grémillet, 1996) and South Georgian shags, *Phalacrocorax georgianus* (Bevan et al., 1997). Higher body temperatures could be subsequently restored using heat dissipated by muscular activity (e.g. wing-flapping, flight).

Heart rates of resting great cormorants did not vary significantly during the winter phase (Fig. 5B). However, the abdominal temperatures of birds resting on land decreased gradually during this period (Fig. 4A). The overall temperature drop between July and the following April was $<1^{\circ}\text{C}$, and average abdominal temperatures remained similar to those recorded for great cormorants wintering in Europe ($\sim 40^{\circ}\text{C}$ for resting during the active phase, and $\sim 39^{\circ}\text{C}$ for resting during the non-active phase; see Grémillet et al., 2003). Moreover, energetics modelled revealed that the theoretical amount of energy saved through a temperature drop of 0.78°C (i.e. the drop in abdominal temperature between September and March recorded in resting birds) is 25 kJ, which is equivalent to 8 g of fish, and is less than 1% of the average theoretical daily food intake. We conclude that great cormorants wintering in Greenland do not save significant amounts of energy *via* hypothermia and show no metabolic depression while resting on land. Substantial adjustments nonetheless occurred in the spring (see later in Discussion).

The abdominal temperatures of great cormorants while diving and after each diving session, as well as their heart rates at the bottom of the dives, decreased significantly during the winter period (Figs 4B, 5A). However, as for abdominal temperatures and heart rate at rest, these variables were not at their lowest levels during the most challenging period (November to February). Instead, they showed a minor, gradual decrease throughout the winter period (Figs 4B, 5A). Markedly lower levels were only reached for a short period in the spring (Figs 4B, 5A). Decreased abdominal temperatures in diving birds can be caused by the cooling effect of water and/or the cooling effect of food in the stomach. During deeper dives the body insulation of great cormorants (plumage air) is compressed, and heat losses to the water are higher (Grémillet et al., 1998; Grémillet et al., 2005a). The fact that abdominal temperature of diving great cormorants is lower in the spring than during the winter period could therefore be caused by deeper dives (Fig. 3).

The ingestion of cold food adds to the overall cooling effect. This is probably why abdominal cooling is more pronounced after a dive bout than during a dive bout: this latency

corresponds to the time required for the cooling effect of cold food to reach from the stomach into the rest of the abdomen. Re-examination of abdominal temperature recordings performed in gentoo penguins *Pygoscelis papua* (fig. 1 in Bevan et al., 2002) and in macaroni penguins *Eudyptes chrysolophus* (fig. 1 in Green et al., 2002) revealed similar patterns, whose true cause (ingestion of cold food) might have been previously overlooked. In diving birds feeding on ectothermic prey it is consequently difficult to tell whether abdominal cooling corresponds to actual body cooling towards the water, or towards the stomach. Let us nonetheless assume that in Greenland great cormorants this cooling affects the whole of the bird's body, and is entirely dedicated to energy saving by reducing the difference in temperature between the bird's body and the water.

The average abdominal temperature of great cormorants diving in Greenland was 0.65°C lower in April than it was in September. A thermodynamics model (Grémillet et al., 1998) indicates that such body cooling results in energy savings of ~ 2 W. Assuming that our bird spends 60 min per day in the water (this was the overall average in this study), this converts into an energy saving of 7.2 kJ. Assuming an assimilation efficiency of 78%, and an average calorific value of the prey of 4 kJ g^{-1} (see Materials and methods), this means that a drop of 0.65°C in body temperature while diving allows the bird to save ~ 2.2 g of fish per day (less than 0.5% of the theoretical daily food requirements). Great cormorants wintering in Greenland are thus unlikely to save substantial amounts of energy *via* body cooling when they are in the water. This conforms to former studies of captive great cormorants, which showed that birds kept high, stable abdominal temperatures even when diving in 1°C water, as long as they were not fed with cold fish (Grémillet et al., 2003).

We therefore conclude that Greenland great cormorants showed no sign of metabolic depression during the coldest months of the year, thus excluding this mechanism as a means of making significant energy savings.

Behavioural adaptation?

The great cormorants that breed on Disko Island (70°N) winter south of the Disko Bight ($69^{\circ}30'\text{N}$; Salomonsen, 1967; Lyngs, 2003). As they move from their breeding sites to their wintering quarters in early September, birds seem to encounter favourable feeding conditions. They show limited foraging effort (and therefore high theoretical foraging yield) at depths of less than 10 m (Fig. 3) and spend only ~ 30 min in the water every day (Fig. 2). Reduced foraging effort is also possible because they have stopped providing their chicks with food (they were still spending 1–2 h in the water every day in August, the late rearing-phase, see Fig. 2). High foraging efficiencies and relatively brief swimming periods are also observed towards the end of the winter phase (March–April, see Fig. 2). Data collected over these limited time periods could therefore support the prediction that these poorly insulated endotherms maximize their foraging efficiency and minimize their foraging effort to survive the Arctic winter

(Grémillet et al., 2001). Our recordings performed throughout the winter phase show that this assertion is not correct. Indeed, foraging effort increased markedly between September and December, to reach its maximum levels during the coldest and darkest months of the year (December to February). Time spent swimming averaged 73 ± 19 min day⁻¹ during that phase, and was therefore similar to the foraging effort of birds provisioning small chicks in July (Fig. 2; Grémillet et al., 2001).

Hence, we demonstrate that great cormorants wintering in Greenland do not reduce their foraging time to compensate for heat losses to the colder water. Foraging effort rather seems to be conditioned by varying light levels, with foraging efficiency being lowest during the polar night (Fig. 6; see also Grémillet et al., 2005b), resulting in an increase in foraging time (Fig. 2). Birds also had to work harder to catch sufficient fish during that period, because of greater foraging depths (Fig. 3). Increased dive depth, which could be due to gradual prey depletion, results in higher diving effort due to increased transit costs, while the elevated hydrostatic pressure reduces plumage air volume and thermal insulation in diving birds, causing even more pronounced heat losses to the water (Grémillet and Wilson, 1999).

On the edge of starvation

During the Arctic winter, great cormorants are under considerable environmental stress, for which they do not compensate by way of major physiological adjustments (Figs 4, 5) or by a decrease in their daily foraging time (Fig. 2). Their theoretical daily food intake is consequently very high (1170 g day⁻¹), twice as much as for great cormorants wintering in Europe (Grémillet et al., 2003). Birds could partly cover their energy requirements using body reserves. We nonetheless think that the input due to body fuels is relatively limited because: (1) surgical procedures performed during the summer period revealed that birds had very low adiposity; (2) individuals wintering in Greenland showed regular foraging activity (Fig. 2), indicating that they could not rely on fasting to overcome difficult periods such as the polar night (Grémillet et al., 2005b); (3) discussions with local Inuit hunters also suggested that the great cormorants hunted within our study zone remain lean year-round. Limited fat deposits might nonetheless have been used to subsidize their energy budgets and allow their survival. Thus, our daily food intake estimates must be treated with caution, and further investigations are required to determine the adiposity of Greenland great cormorants throughout the winter period.

The present study shows that great cormorants are running out of body reserves towards the end of the Arctic winter (April). Their adiposity is then well below published values for other bird species at their annual minimal adiposity (Johnston, 1970; Piersma, 1988). The overall physiological status (adiposity, lipid/protein ratio) of great cormorants is then comparable to that of a fasting animal in between phase II and phase III of the fast (as defined by Belkhou et al., 1991; Chérel et al., 1994), and their remaining body reserves would

only allow them to survive for approximately 3 days without food.

Just as their body reserves are presumably at their lowest level (in late April), the birds show drastic physiological changes in the form of low body temperatures when diving and resting, and of markedly lower heart rate levels when resting (Figs 4, 5B). These modifications indicate a depressed metabolism, which can either be seen as a state of metabolic stress caused by the exhaustion of body reserves (see above), and/or as a physiological state permitting the fast accumulation of new body reserves *via* reduced energy expenditure (Butler and Woakes, 2001). Such major changes occur just before/as birds move back to their breeding sites on Disko Island, where they start to mate in May (see Results and Fig. 2). This seems to be a particularly challenging time for male great cormorants, maybe even more challenging than the polar winter itself. Beyond the physiological shifts described above, birds in May show the highest foraging effort ever recorded for this species, with up to 4 h spent in the water per day (Fig. 2). Such hyperactivity relates well with the potential accumulation of new body reserves at the onset of the breeding season. This behaviour might be favoured by the occurrence of vast capelin *Mallotus villosus* stocks within the foraging zone of the birds. Millions of capelin aggregate in coastal waters off Disko Island in May and spawn along gravel beaches in June (Friis-Rødel and Kannevorff, 2002). The foraging depths of great cormorants in May (~8 m) and June (~3 m) correspond to the distribution of capelin during these periods (E. Friis-Rødel, personal communication), suggesting that birds might benefit from this bounty to restore their body reserves at the onset of the breeding season.

Conclusions

Year-round recording of ecophysiological variables in great cormorants from Greenland have allowed us to end the speculation concerning their potential physiological or behavioural adaptations to the Arctic winter and to define their energetic strategy. When facing very low air and water temperatures between November and March, birds did not respond by way of major physiological adjustments (i.e. low metabolism and associated low body temperatures). Nor did they minimize the time spent swimming in cold water. Birds probably metabolised their limited body reserves to cope with winter conditions, getting into a physiological status comparable to the end of phase II of a fast. However, more than anything else, they survived by sustained high feeding activity, with an estimated catch of 1170 g of fish per day. Previous investigations indicated that great cormorants wintering in Northern Europe require ~670 g of food per day (range 440–1100 g day⁻¹; Grémillet et al., 2003). It appears therefore that birds from Greenland routinely ingest the quantity of fish, which was, up to the present, supposed to be the maximum food intake for wintering great cormorants or great cormorants raising large chicks (Grémillet et al., 2003). These very high feeding regimes occur throughout the winter phase, even during the polar night (December and January).

With respect to the management of the expanding European great cormorant populations, which have been accused of depleting valuable freshwater stocks (Carss, 2003), two important conclusions can be drawn. (1) Even when facing some of the most drastic weather conditions on earth, great cormorants do not seem to require more food to survive than the maximum food intake predicted for aquatic birds; (2) contrary to previous suggestions, however, birds do not reduce their foraging effort as ambient conditions deteriorate (Grémillet et al., 2001). Rather, they respond to environmental constraints *via* an increase in their daily food intake. By doing so they might ingest a third of their body mass of fish every day for prolonged periods.

Our study underlines the original adaptation of great cormorants to the high Arctic environment. These unusual birds survive particularly harsh winter conditions despite their limited body insulation and body reserves, thereby breaking the paradigm that efficient thermal insulation is a prerequisite to the colonization of polar ecosystems by endotherms (Grémillet et al., 2001). Our measurements also demonstrate the great variability of the behavioural and the physiological responses of a free-ranging animal during the annual cycle (Figs 2–6), and underline the limitations of field investigations conducted during limited time frames, e.g. during the breeding period.

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