

Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in Great Cormorants

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Abstract. Aquatic endotherms living in polar regions are faced with a multitude of challenges, including low air and water temperatures and low illumination, especially in winter. Like other endotherms from cold environments, Great Cormorants (*Phalacrocorax carbo*) living in Arctic waters were hypothesized to respond to these challenges through a combination of high daily rate of energy expenditure (DEE) and high food requirements, which are met by a high rate of catch per unit effort (CPUE). CPUE has previously been shown in Great Cormorants to be the highest of any diving bird. In the present study, we tested this hypothesis by making the first measurements of DEE and foraging activity of Arctic-dwelling Great Cormorants throughout the annual cycle. We demonstrate that, in fact, Great Cormorants have surprisingly low rates of DEE. This low DEE is attributed primarily to very low levels of foraging activity, particularly during winter, when the cormorants spent only 2% of their day submerged. Such a low level of foraging activity can only be sustained through consistently high foraging performance. We demonstrate that Great Cormorants have one of the highest recorded CPUEs for a diving predator; 18.6 g per minute submerged (95% prediction interval 13.0–24.2 g/min) during winter. Temporal variation in CPUE was investigated, and highest CPUE was associated with long days and shallow diving depths. The effect of day length is attributed to seasonal variation in prey abundance. Shallow diving leads to high CPUE because less time is spent swimming between the surface and the benthic zone where foraging occurs. Our study demonstrates the importance of obtaining accurate measurements of physiology and behavior from free-living animals when attempting to understand their ecology.

Key words: Arctic; basal metabolic rate; catch per unit effort, CPUE; daily energy expenditure; day length; diving depths; field metabolic rate; foraging efficiency; Great Cormorant; Greenland; *Phalacrocorax carbo*; seasonal variation.

INTRODUCTION

Endotherms living in cold environments have higher maintenance and daily rates of energy expenditure (DEE) than those living in warm environments (Anderson and Jetz 2005, White et al. 2007a). Therefore, because of the general global temperature gradient, animals living at high latitudes tend to have higher energy demands than those living at low latitudes. Diving birds living in cold environments and diving in cold water must additionally deal with the conflicting requirements for insulation and buoyancy, because thermoregulation is facilitated by retaining air in the plumage and this increases buoyancy (Wilson et al. 1992). Cormorants (Phalacrocoracidae) have a partially

wettable plumage that reduces buoyancy at the cost of increased rates of heat loss to the water, particularly during deep dives when the plumage air layer is further compressed by hydrostatic pressure (Grémillet et al. 2005a, Enstipp et al. 2006b). This strategy is intuitively sensible in warm, tropical waters, where cormorants are thought to have evolved (van Tets 1976). However, cormorants now have a global distribution, and the range of Great Cormorants *Phalacrocorax carbo* extends from New Zealand to above the Arctic Circle in Greenland, where during winter they dive in water at subzero temperatures and are exposed to air temperatures below -20°C (Grémillet et al. 2005c, White et al. 2008a).

It has been suggested that Great Cormorants in the Arctic “live life in the fast lane” (Grémillet and Wilson 1999), combining high DEE with high rates of food consumption. Estimates of food consumption in Great Cormorants have been obtained using a variety of indirect approaches. These include laboratory measurements of energy expenditure (e.g., Schmid et al. 1995,

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Grémillet et al. 2001), field measurements of behavior (e.g., Grémillet et al. 2004, 2005c), estimation of mass of stomach contents (e.g., Grémillet 1997), and bioenergetics modeling (e.g., Grémillet et al. 2003). Modeling approaches using such data suggest that Great Cormorants wintering in Greenland will require about 1170 g of fish per day (Grémillet et al. 2005c), which is 75% more than that required by conspecifics of similar mass wintering in Scotland (Grémillet et al. 2003).

To support these estimates of high food requirements, it has been suggested that Great Cormorants are extremely efficient foragers and have a remarkably high catch per unit effort (CPUE, the rate at which prey are captured during foraging dives). A number of studies have suggested that CPUE during foraging of Great Cormorants and other Phalacrocoracidae is an order of magnitude greater than that of other diving seabirds (Enstipp et al. 2007b). However, although CPUE has been evaluated and compared within and between seabird species, it remains a rather elusive quantity, rarely calculated in studies of foraging endotherms, and usually relying on modeled estimates of food requirements (e.g., Enstipp et al. 2006a). If calculated accurately and applied appropriately, CPUE is potentially a very valuable tool in comparative studies of foraging, both within and between species. Great Cormorants are an excellent model for the study of what influences and determines variability in CPUE, as they do not buffer temporal variations in food consumption by the laying down and consumption of body reserves (Grémillet 1997, Grémillet et al. 2003, 2005c). As a result, the DEE of cormorants should be matched by daily prey consumption.

The present study aimed to test the hypothesis generated by indirect methods that Great Cormorants living in Greenland have high DEE and food requirements, as is the case for other high-latitude-dwelling endotherms. The goal was to determine rates of energy expenditure throughout the complete annual cycle of Greenland-dwelling birds at high temporal resolution (5 minutes), and to examine the factors that influence intra-annual variation in energy expenditure. The heart rate technique (Butler et al. 2004) was used to derive the metabolic rate of free-living birds, by converting heart rate measured with implantable heart-rate data loggers into rates of oxygen consumption, with a calibration relationship obtained from captive Great Cormorants resting, walking, and diving in the laboratory. These were converted to DEE, and in turn were used to calculate food requirements throughout the annual cycle. When combined with data for diving behavior of Greenland-dwelling Great Cormorants and the energy density of their food, CPUE during the winter could be estimated. DEE was also decomposed into rate of energy expenditure associated with activity and with maintenance. Variation in these rates was related to a range of environmental and behavioral parameters (water temperature, ambient illumination, day length,

diving depth, and daily time submerged) to evaluate how Great Cormorants are able to thrive in such an apparently hostile environment.

MATERIALS AND METHODS

In June 2002, 10 breeding male Great Cormorants raising young chicks on Disko (69°30' N, 54°05' W), West Greenland, were equipped with heart-rate data loggers (HRDL: 60 × 24 × 7 mm, mass 20 g, ~0.6% of the body mass of the cormorants studied). These HRDLs previously have been shown to have no significant impact on the behavior and physiology of a range of species, including Great Cormorants (Guillemette et al. 2002, Green et al. 2004, Grémillet et al. 2005c). The HRDLs were programmed to record data every second day for a period of one year. On the days during which HRDLs were recording, heart rate and pressure (depth) were stored every 2 s and body temperature was stored every 6 s. All devices were calibrated before and after use (depth resolution 0.1 m, temperature resolution 0.13°C). Loggers were surgically implanted under isoflurane anesthesia following Stephenson et al. (1986); additional details and analyses of this data set are provided elsewhere (Grémillet et al. 2005b, c, White et al. 2008a). Nine birds were recaptured after one year of logger deployment and one bird after two years of deployment, but only seven data loggers recorded valid data.

Data analyses

Data from the free-living birds were classified into three seasons, based on changes in behavioral strategies (White et al. 2008a). These were: (1) late breeding, the first eight weeks from 1 July during the breeding season in which the data loggers were deployed; (2) winter, the period from September to March during which the cormorants move south along the west coast of Greenland, winter at locations in southern Greenland, and return to the breeding grounds (C. R. White, G. R. Martin, P. J. Butler, D. Boertmann, J. A. Green, and D. Grémillet, *unpublished manuscript*); and (3) early breeding, the last eight weeks before 1 July of the subsequent breeding season when the birds were recaptured.

Calculation of energy expenditure.—Mean heart rate (f_H) was calculated every five minutes for each bird and was converted into mass-independent rate of oxygen consumption ($c\dot{V}O_2$, mL O₂·kg⁻¹·min⁻¹, where “c” denotes corrected for mass) using a calibration relationship derived for laboratory birds (for a full description of calibration procedures, see the Appendix). A daily mean was calculated from these values and a grand mean of $c\dot{V}O_2$ was computed for each day of the deployment period and multiplied by the mean body mass of the free-living Great Cormorants (3.5 kg; range 3.3–3.7 kg) to give mean daily rate of oxygen consumption ($\dot{V}O_2$). Mean daily $\dot{V}O_2$ was converted to daily rate of energy expenditure (DEE, kilojoules/day) by multiplying by the energy equivalence of 18.4 J/mL

O₂, assuming a largely proteinaceous diet (Dunn 1975, Schmidt-Nielsen 1997, Grémillet et al. 2004). Estimates of DEE were compared between seasons using *Z* tests, with Bonferroni corrections applied for multiple comparisons. Resting rate of energy expenditure (REE, kilojoules/day) was calculated by the same method, using the grand mean of the lowest 15-minute average of f_H for each bird. Activity rate of energy expenditure (AEE, kilojoules/day) was calculated as the difference between DEE and REE. A model to explain daily variation in AEE was then constructed by relating AEE to a series of environmental parameters: water temperature (°C); ambient illumination during diving (log lux), maximum daily dive depth (meters); day length (hours), and daily time submerged (hours). Water temperature and ambient illumination during diving were estimated from published data for the same population of cormorants obtained during winter 2004–2005 (White et al. 2008a). Day length was obtained for Nuuk, which is near the center of the winter distribution of cormorants in Greenland (Merkel et al. 2002) from The World Clock (2009). Daily time submerged was calculated as we will describe. The best-fit model was estimated using stepwise backward elimination from a full model that included all of the parameters. Parameters were assessed on the basis of Akaike's Information Criterion (AIC; Burnham and Anderson 2001, 2002), and were eliminated from the model if their exclusion increased the value of AIC by less than 2. The relative importance of a parameter was assessed on the basis of its Akaike weight (w_i), which was calculated as the probability that a model without that parameter provided a better fit to the data than a model including that parameter.

Calculation of daily prey consumption (DPC).—Unlike many seabirds (e.g., Green et al. 2009), cormorants do not buffer variations in daily energy expenditure and food consumption by laying down and utilizing energy reserves of body fat (Grémillet et al. 2003). It was therefore possible to convert DEE into daily prey consumption (grams/day) by simply dividing DEE by the digestive efficiency of 0.77 (Brugger 1993) and then dividing this value by the energy density of the prey of 4.0 kJ/g (Grémillet et al. 2005c). This estimate of energy density is based on the average prey consumed by cormorants during summer. The energy density of the various species taken by cormorants in summer ranges from 3.9 kJ/g (capelin *Mallotus villosus*) to 6.8 kJ/g (lesser sand-eel *Ammodytes marinus*), but the majority of their diet consists of sculpin *Myoxocephalus* spp. (62–82% by mass; energy density 4.1 kJ/g) and capelin (13–29% by mass) (Grémillet et al. 2004). In winter, cormorants also forage mainly on sculpin (Grémillet et al. 2001), so an average energy density of 4.0 kJ/g is appropriate for the entire year (Grémillet et al. 2005c).

Calculation of daily time submerged (DTS).—To evaluate diving behavior, DTS (minutes/day) was calculated for each day of the deployment period by

simply summing the amount of time the birds spent at depths deeper than 1 m. Maximum dive depth attained for each day of the deployment was also noted. Changes in DTS were compared between seasons using mixed-model ANOVA with season as a fixed effect and individual ID as a random effect, followed by Tukey post hoc multiple comparisons.

Calculation of catch per unit effort (CPUE).—CPUE (grams/minute submerged) was calculated as DPC/DTS. CPUE could only be calculated for the winter period, because detailed information was not available on the food requirements of nestlings during breeding periods; nestlings can consume up to 35% of the food caught by their male parents (Grémillet et al. 2000). Daily variation in CPUE during winter was explored by consideration of a variety of abiotic environmental parameters: water temperature, maximum illumination during daylight, day length, relative lunar brightness (estimated from lunar phase angle according to Allen [1973]), and maximum dive depth. Water temperature, maximum illumination, and day length were estimated as described previously. Models were compared on the basis of AIC and w_i .

Of the 120 possible combinations of parameters, 16 models for CPUE were specified a priori based on previous studies of the foraging energetics and behavior of Phalacrocoracidae. These explained CPUE in terms of visual or energetic parameters, or a combination of both. Visual models used combinations of ambient illumination (both daylight and moonlight), which influences visual acuity (White et al. 2007b) and foraging behavior (Wanless et al. 1999), and day length, which has previously been suggested as a correlate of CPUE (Grémillet et al. 2005b). Energetic models used water temperature and dive depth, which influence metabolic rate both in the present study (see *Results*) and in studies of other species of *Phalacrocorax* (Enstipp et al. 2005, Enstipp et al. 2006b).

RESULTS

Free-living measurements

The distribution of f_H recorded in free-living Great Cormorants was bimodal, showing peaks at around 100 and 260 beats/min. These peaks coincided with the average heart rates found while captive Great Cormorants rested on a treadmill and while the same birds were active on the treadmill and swim flume, respectively (see Appendix). The distribution also had a long tail in the region of 350–450 beats/min. Visual inspection of raw heart-rate data identified some periods that were likely to be flight (consistently high heart rates immediately before diving bouts). Although it was impossible to identify reliably and unambiguously all periods of flight, these observations suggest that f_H during flight was around 400 beats/min (see Appendix).

Daily rate of energy expenditure (DEE) was relatively invariant during the majority of the study period, usually around 1500–1700 kJ/d (Fig. 1a). However,

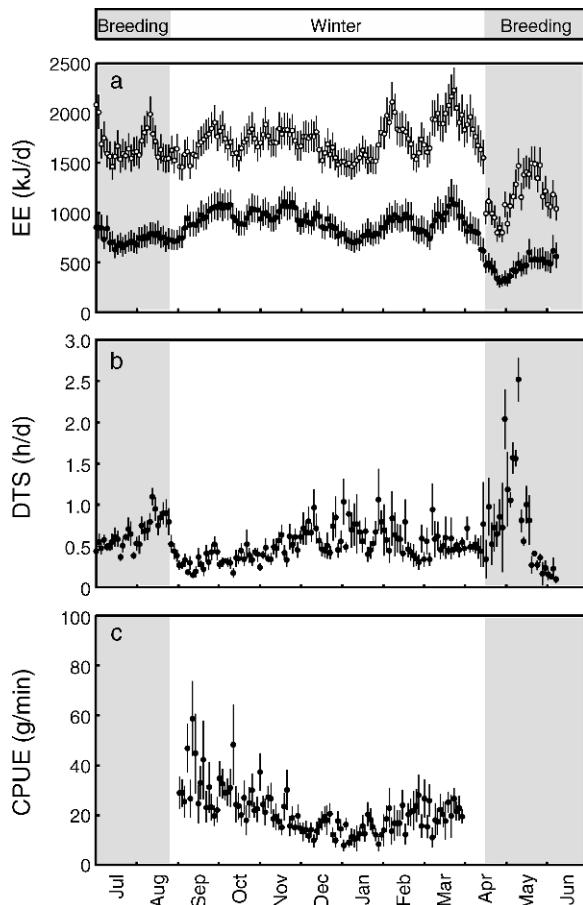


FIG. 1. Changes throughout the annual cycle in free-living Great Cormorants (*Phalacrocorax carbo*) breeding and overwintering in Greenland. (a) Daily rate of energy expenditure (DEE, open circles) and resting rate of energy expenditure (REE, solid circles); (b) daily time submerged (DTS); and (c) catch per unit effort (CPUE). Data are presented as means \pm SEE (for DEE and REE) or SEM (for DTS and CPUE).

DEE was significantly lower during early breeding than it was during both late breeding (Z test: $Z = 3.5$, $P < 0.001$; Table 1) and winter ($Z = 3.3$, $P < 0.001$; Table 1). DEE was significantly positively correlated with resting rate of energy expenditure (REE, $r = 0.84$, $t_{13} = 5.58$, P

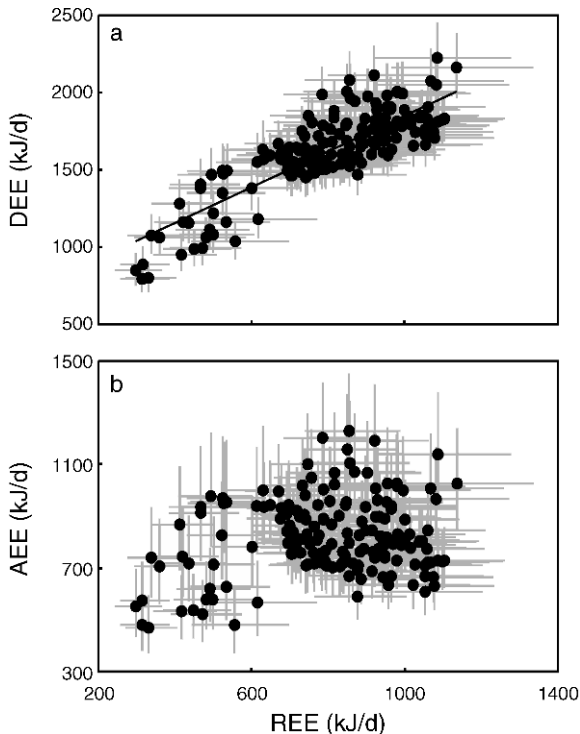


FIG. 2. Correlations between resting rate of energy expenditure (REE) in Great Cormorants breeding and overwintering in Greenland and (a) daily rate of energy expenditure (DEE); and (b) activity rate of energy expenditure (AEE = DEE – REE). Each point represents a single day and is shown \pm SEE. The relationship between DEE and REE is significant ($r = 0.84$, $t_{13} = 5.58$, $P < 0.001$); the relationship between AEE and REE is not ($r = 0.28$, $t_{13} = 1.04$, $P = 0.31$).

< 0.001 ; Fig. 2a), but not with activity rate of energy expenditure (AEE, $r = 0.28$, $t_{13} = 1.04$, $P = 0.31$; Fig. 2b). The best model for AEE included water temperature, maximum dive depth, ambient illumination during diving, day length, and daily time submerged, each of which were significant ($P \leq 0.003$; Table 2).

Daily prey consumption (DPC) showed that the birds consume $\sim 40\%$ less food per day during early breeding than during winter (Table 1). This is presumably a result of the birds spending more time ashore during courtship

TABLE 1. Mean daily rate of energy expenditure (DEE), daily prey consumption (DPC), and daily time spent submerged (DTS) for three periods during the annual cycle in Great Cormorants, *Phalacrocorax carbo*.

Period	<i>n</i>	DEE (kJ/d)	DPC (g/d)	DTS (h/d)	DEE/REE
Late breeding	7	1662 ^a (141/154)	536 ^a (45/49)	0.65 ^a \pm 0.04	2.2
Winter	7	1717 ^a (144/158)	553 ^a (47/51)	0.50 ^b \pm 0.06	1.9
Early breeding	3	1028 ^b (115/129)	331 ^b (37/42)	0.56 ^{ab} \pm 0.05	2.0

Notes: Data are presented with standard error of the estimate, SEE (for DEE and DPC) or standard error of the mean, SEM (for DTS) given in parentheses. SEEs are uneven due to the curvilinear nature of the relationship between heart rate and mass-independent rate of oxygen consumption (see Appendix); two SEE values are presented because SEE is asymmetric when back-transformed. For each variable, seasons connected by the same superscript letter were not significantly different from each other ($P \geq 0.05$). Also shown is DEE/REE for each season, where REE is the resting rate of energy expenditure (kJ/d).

TABLE 2. Parameter estimates for a model explaining variation in activity rate of energy expenditure (AEE; kJ/d) of Great Cormorants in terms of water temperature (T), ambient illumination (IL), daily maximum dive depth (D), day length (DL), and daily time submerged (DTS).

Term	Units	Estimate	SE	<i>t</i>	<i>P</i>	ΔAIC	<i>w_i</i>
Intercept		2377	550	4.32	<0.0001		
T	°C	-67.1	10.5	-6.37	<0.0001	16	0.00
log(IL)	lux	-585	194	-3.02	0.003	2.6	0.17
D	m	-12.9	4.2	-3.05	0.003	2.7	0.16
DL	h	90.1	20.7	4.35	<0.0001	7.2	0.02
DTS	h	275	51	5.39	<0.0001	12	0.00
Full model						0	0.64

Notes: ΔAIC is the increase in Akaike's information criterion (AIC) associated with excluding each parameter from the model, compared to the full model with all parameters included. The Akaike weight (*w_i*) is the probability that a model with a given parameter excluded provides the best fit to the data, compared to the full model. The full model with all parameters included has the lowest value of AIC (ΔAIC = 0) and therefore provides the best fit to the data (*w_i* = 0.64).

in early breeding. Daily time submerged (DTS) showed day-to-day variability both within and between seasons. DTS increased during late breeding, before declining dramatically at the start of the winter migration (Fig. 1b). There was then a systematic increase and then decrease in DTS, with DTS reaching a winter maximum that coincided with the shortest days of mid-winter. At the start of early breeding, DTS was high and variable and then declined to the lowest levels of the annual cycle, also presumably coincident with courtship behavior on land (Fig. 1b). DTS was significantly greater in late breeding than in winter ($F_{2,8} = 6.04$, $P = 0.025$), but there was no difference in mean DTS between early breeding and winter or between early and late winter (Table 1).

Because catch per unit effort (CPUE) was derived by a combination of DEE and the inverse of DTS, and DEE was relatively invariant, CPUE tended to show trends that were the reverse of those noted for DTS, reaching a minimum at mid-winter (Fig. 1c). The model that best explained the daily variation in CPUE during winter included both visual and energetic parameters (Table 3). Models containing exclusively either visual or energetic parameters were more than 700 times less likely to explain daily variation in CPUE than the best model, which incorporated significant effects of day length and maximum dive depth. CPUE increased as day length increased and maximum dive depth decreased (Fig. 3). Mean CPUE for the entire winter was 18.6 g per minute submerged, with a 95% prediction interval of 13.0–24.2 g per minute submerged.

DISCUSSION

The daily rate of energy expenditure (DEE) of free-living, Arctic-dwelling Great Cormorants was considerably lower than previous estimates made using a bioenergetic modeling approach (Grémillet et al. 2003, 2005c). As a result, catch per unit effort (CPUE) was also substantially lower than previous estimates for this population. The bioenergetic modeling approach uses behavioral time budgets recorded from free-living birds,

but relies on metabolic data measured for captive birds at rest and swimming in a 1 m deep static water tunnel under cold conditions, as well as modeled estimates of flight costs, the energy cost of warming ingested fish food, and additional data taken from the literature (Grémillet et al. 2003). In contrast, DEE in the present study is measured continuously for free-living birds using a calibrated relationship between heart rate and metabolic rate. Therefore, the present study demonstrates the importance of obtaining accurate measurements of the behavior and physiology of free-living animals. For example, our data from free-living cormorants reveals a negative relationship between maximum dive depth and activity energy expenditure, AEE (Table 2), so the use of data for captive birds diving to only 1 m for bioenergetic models will tend to overestimate AEE and therefore also DEE. As such,

TABLE 3. Akaike's information criterion (AIC) and Akaike weights (*w_i*) for seven visual, three energetic, and six combined statistical models to explain daily variation in catch per unit effort by Great Cormorants during winter.

Category	Model	AIC	<i>w_i</i>
Visual	LB	-183.2	<0.001
	IL	-212.0	<0.001
	DL	-213.4	0.001
	IL + LB	-210.4	<0.001
	DL + LB	-211.8	<0.001
	IL + DL	-211.8	<0.001
Energetic	LB + IL + DL	-210.1	<0.001
	T	-212.3	<0.001
	D	-208.4	<0.001
Visual and energetic	T + D	-210.7	<0.001
	IL + D	-224.1	0.13
	DL + D	-226.6	0.44
	IL + T	-222.5	0.06
	DL + T	-224.4	0.15
	IL + T + D	-222.4	0.05
DL + T + D	-224.7	0.18	

Notes: Model terms are: LB, log(relative lunar brightness); IL, log(maximum ambient illumination, lux); DL, day length (h); T, water temperature (°C); D, mean maximum dive depth (m). The model with the lowest AIC provides the best fit to the data, and the probability that a given model provides the best fit to the data is represented by its Akaike weight.

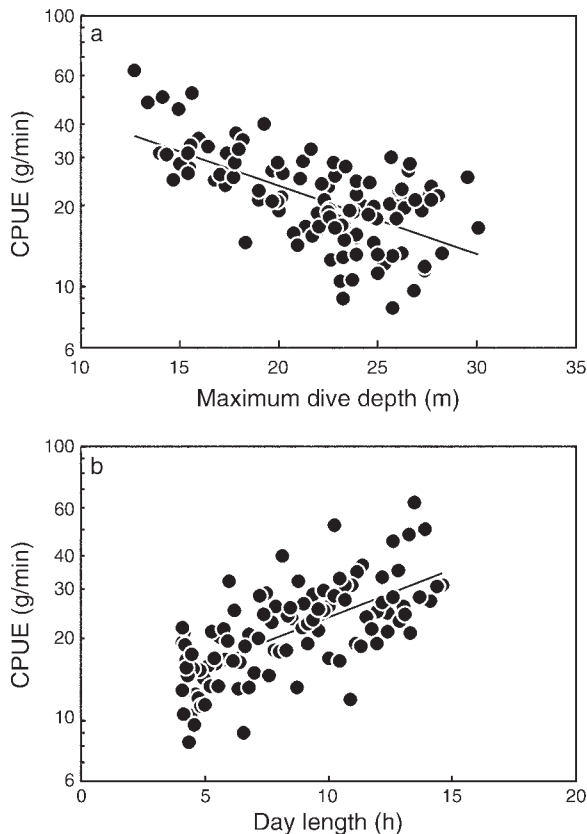


FIG. 3. Significant correlations between catch per unit effort (CPUE) in Great Cormorants breeding and overwintering in Greenland and (a) maximum dive depth and (b) day length. Both correlations were significant and are related to CPUE according to the equation

$$\text{CPUE} = 29.7 \times 10^{0.026(\text{day length}) - 0.017(\text{maximum depth})}$$

which was the best-fit model for describing $\log(\text{CPUE})$ of those presented in Table 3.

measurements of free-living animals can reveal novel strategies for overcoming ubiquitous problems that may not be apparent from laboratory studies. Contrary to the hypothesis that, like other endotherms resident in cold environments (Anderson and Jetz 2005, White et al. 2007a), Greenland-dwelling Great Cormorants would have high rates of energy expenditure associated with their partially wettable plumage (Grémillet et al. 2005a) and diving in cold water (White et al. 2008a), the present study demonstrates that the rate of energy expenditure of these birds is remarkably low.

Daily rate of energy expenditure of Arctic-dwelling cormorants

The DEE was low throughout the annual cycle. DEE was only $2.2 \times \text{REE}$ during late breeding, $1.9 \times \text{REE}$ during winter, and $2.0 \times \text{REE}$ during early breeding (Table 1). Several previous studies have investigated the energetics of Great Cormorants, and estimated DEE and/or daily prey consumption (DPC) using different

methods, at different times of year in captive and wild populations (Table 4). During breeding, the most similar estimate of DEE was from a study that reconstructed diet by analyzing regurgitated pellets, an approach that is notoriously biased (e.g., Jobling and Breiby 1986). A measurement of DEE made using the doubly labeled water technique during winter in Germany was similar to that of the present study, yet if the smaller mass of the German Cormorants is considered, DEE was considerably higher than that in the present study (Keller and Visser 1999). Nevertheless, a comparison between breeding and winter DPC suggests that the present estimates are not unreasonable. Great Cormorants during late breeding in France require ~ 1349 g of fish per day, 41% of which is used by the chicks (Table 4). If the estimate of late-breeding DPC from the present study (536 g/d) is compared to values measured for Greenland cormorants using nest balances that include food consumed by the chicks (878 g/d; Grémillet et al. 2004), it can be estimated that the chicks use 39% of total DPC, which is similar to the percentage of DPC attributable to chicks in France. The present study suggests that energetics modeling overestimated the DPC of Great Cormorants wintering in Greenland, and that both DPC and DEE were less for Great Cormorants breeding in arctic Greenland than in France (Table 4).

Independent of the method selected, it is clear that the DEE of Great Cormorants is relatively low compared with that of other species. Interspecific analyses of DEE and basal metabolic rate (BMR) among seabirds usually report a DEE/BMR ratio during breeding greater than 3 and often approaching 4 (Ellis and Gabrielsen 2002), the optimal limit suggested by Drent and Daan (1980). A broader interspecific comparison indicates that, at least in part, the low ratio of DEE/REE in Great Cormorants is a result of a relatively high REE and BMR (Fig. 4). When compared to all other birds for which comparable data exist, DEE and BMR are relatively low and high, respectively, but very much within the range observed for other species (Fig. 4). The relatively high BMR of cormorants has been noted previously in other studies of the Phalacrocoracidae and has been attributed to the relatively poor insulation provided by their wettable plumage, even when dry (Chappell et al. 1989). However, $\dot{V}\text{O}_2$ of the captive birds remains independent of ambient air temperature at temperatures at least as low as 5°C (the lowest temperature at which measurements were made in the present study; see the Appendix). Thus, the high BMR of cormorants, which is a general characteristic of birds from cold environments (White et al. 2007a), is probably associated with high maximum rates of thermogenesis (Rezende et al. 2002) and cold tolerance (Swanson and Liknes 2006). Similarly, the seasonal variation observed in BMR of captive birds (see the Appendix) and REE of wild birds (Fig. 1a) is presumably also associated with seasonal variation in temperature and thermogenic capacity

TABLE 4. Daily rate of energy expenditure (DEE) and daily prey consumption (DPC) during the winter, and breeding seasons recorded in previous studies of Great Cormorants.

Season and location	Body mass (kg)	Sex†	DEE		DPC (g/d)	Method‡	Source§
			(kJ/d)	DEE/BMR			
Winter (free-living)							
Greenland	3.5	M	1717	1.9	553	HR	A
Greenland	3.5	M	3632	2.5	1170	EM	B
Germany	2.12	ns	2094	2.5	539	DLW	C
Scotland	3.2	ns	2779	2.1	672	EM	D
Winter (captive)							
England	2.4	ns	1560	1.6	335	WFR	E
Germany	2.08	ns	1325	1.6	341	DLW	C
Breeding, early (free-living)							
Greenland	3.5	M	1028	2.0	331¶	HR	A
France	3.2	M	2131	1.8	692¶	EM	F
France	3.2	M	1663	1.4	540¶	NB	F
Breeding, late (free-living)							
Greenland	3.5	M	1662	2.2	536¶	HR	A
France	3.2	M	2435	2.1	791¶/1349#	EM	F
France	3.2	M			1410#	NB	F
Breeding, ns (free-living)							
Greenland	3.5	M			878#	NB	G
France	3.2	M			828#	NB	H
The Netherlands	2.6	ns	1178	1.3	330¶	FP	J

† Where available, data from males (M) were selected; sex was not specified (ns) in some studies.

‡ Key to abbreviations: HR, heart rate; DLW, doubly labeled water; EM, energetics modeling; WFR, weigh food ration; NB, nest balances; FP, food pellet analysis.

§ Source codes: A, present study (data from Table 1); B, Grémillet et al. (2005c); C, Keller and Visser (1999); D, Grémillet et al. (2003); E, White et al. (2008b); F, Grémillet et al. (2000); G, Grémillet et al. (2004); H, Grémillet (1997); J, Platteeuw and Van Eerden (1995).

¶ Does not include food for nestlings.

Includes food for nestlings.

|| Measurements were made during breeding season, but size/age of nestlings and timing of experiments were not specified.

(Swanson and Olmstead 1999, Swanson and Liknes 2006).

In the present study, the activity and resting components of DEE are independent (Fig. 2b), which indicates that AEE and REE (or BMR) can be considered separate contributors to DEE (Ricklefs et al. 1996). The main influence on DEE above BMR will be the amount of time that the birds spend engaged in energetically costly activities, usually those associated with foraging. Flight, swimming, and diving are all energetically expensive activities in comparison to resting on land (Schmid et al. 1995, Bevan et al. 1997, Ancel et al. 2000, Enstipp et al. 2005, Enstipp et al. 2006b). However, when compared to the majority of seabirds, the Phalacrocoracidae are relatively inactive, spending a very small proportion of their time engaged in foraging activity; the Great Cormorants in the present study were no exception. On an average day, Great Cormorants in Greenland spend less than 3% of the day submerged during diving (Table 1) and ~5.5% of their time in flight (Grémillet et al. 2005c). Similarly, during mid-winter in Norway (70° N), Great Cormorants spend <5% of each day at sea (Johansen et al. 2001), whereas individuals breeding in France (49° N) spend ~10% of the day at sea in water (Grémillet et al. 2001). In

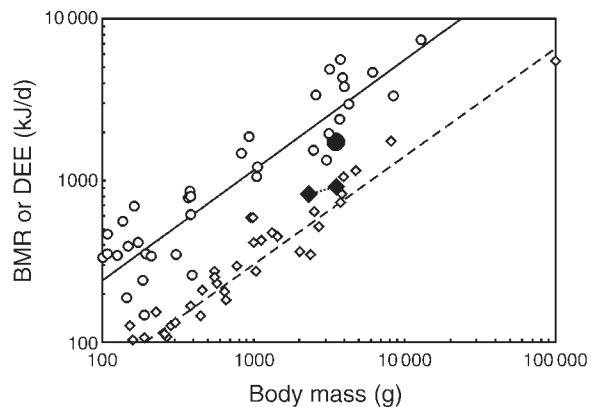


FIG. 4. Basal metabolic rate (BMR) (solid diamonds, measured during July 2005 for captive cormorants weighing 2.3 kg and estimated as resting energy expenditure for free-living 3.5-kg cormorants during winter) and free-living daily rate of energy expenditure (DEE) (solid circle, measured during winter) of Great Cormorants in comparison to similar measurements (DEE: open circles, BMR: open diamonds, respectively) taken from published studies of other bird species and presented as a function of their body mass. Data on BMR are from McKechnie and Wolf (2004). Error bars are obscured by data points for Great Cormorants and are not shown for the other species. Data on DEE are from Nagy et al. (1999).

contrast, Bank Cormorants *Phalacrocorax neglectus* breeding in South Africa (33° S) spend ~17% of their time actively foraging (Wilson and Grémillet 1996), South Georgian Shags (*Phalacrocorax georgianus*) breeding on Bird Island (54° S) spend ~22% of the day foraging (Bevan et al. 1997), and chick-rearing Crozet Shags *Phalacrocorax melanogenis* on Ile de la Possession (46° S) spend ~25% of their time at sea (Cook et al. 2007). Most seabirds spend 50% or more of their time on foraging trips during which they fly, dive, or rest on the water (e.g., Barlow and Croxall 2002, Phillips et al. 2005); previous analyses have also shown that when compared to other birds, Great Cormorants spend relatively little of their day in flight (Pelletier et al. 2008). Because energetic costs increase in proportion with the amount of time spent in flight and away from the breeding colony (Ellis and Gabrielsen 2002), it is not surprising that species that are more active than Great Cormorants will tend to have higher rates of daily energy expenditure.

On a day-to-day basis, DEE of the Great Cormorants showed an interesting pattern of temporal variability. There was no change in DEE between the end of the breeding season and winter, but quite a substantial decrease in DEE between these two seasons and early breeding. During the nonbreeding season, AEE was significantly positively related to day length and daily time submerged, and significantly negatively related to water temperature, ambient illumination, and dive depth. These findings match laboratory measurements that report a similar effect of water temperature (Enstipp et al. 2006b). However, in captive Double-crested Cormorant *Phalacrocorax auritus* diving to depths of up to 10 m, metabolic rate is positively related to dive depth (Enstipp et al. 2006b). A negative relationship between depth and the net cost of diving has also been identified for free-living Macaroni Penguins *Eudyptes chrysolophus* (Green et al. 2005). This suggests that the difference between captive and free-living birds is related to the greater depth attained by free-living animals, the negative relationship between buoyancy and depth (Wilson et al. 1992), and a reduction in the metabolic cost of working against buoyancy at depth (Wilson et al. 2006, Shepard et al. 2009, Cook et al. 2010). The effect of DTS is not surprising, because of the relatively high metabolic rate observed during activity compared to that at rest (see Appendix). The positive relationship between day length and AEE possibly arises because relatively long days provided more foraging opportunities (White et al. 2008a), but the reasons for the negative relationship between AEE and ambient illumination are less clear. Cormorants are able to maintain foraging performance at moderate light levels (Enstipp et al. 2007a), but their visual acuity declines precipitously at the low levels of ambient illumination that they encounter during winter in Greenland (White et al. 2007b, 2008a). Thus, because the foraging behavior of cormorants is visually guided

(Martin et al. 2008), the negative relationship between ambient illumination and AEE probably arises as a consequence of a negative relationship between illumination and foraging efficiency. Indeed, any environmental condition that requires cormorants to increase their time spent in the water will result in an increase in AEE.

High catch per unit effort of Arctic-dwelling cormorants

Results of the present study suggest that Great Cormorants are able to maintain low rates of daily energy expenditure due to extremely efficient foraging: mean catch per unit effort (CPUE) of Great Cormorants during winter was estimated to be 18.6 g/minute submerged. This is less than half of the winter estimate published previously for this population (Grémillet et al. 2005c), but it is still the highest recorded in a free-ranging seabird, with the exception of estimates from the same population during the breeding season (Table 5). However, CPUE has been recorded rather infrequently in free-ranging seabirds. A broader comparative base would clearly be useful, especially in the light of the suggestion that evaluating behavior and performance of marine predators in the prey space is critical to understanding topics as diverse as energy flow between systems and optimal foraging decisions (Wilson et al. 2002).

CPUE is likely to be influenced by a range of parameters, including prey abundance, prey capture abilities, and the energy cost of predation. For Great Cormorants in Greenland, CPUE during winter is driven primarily by variation in day length and dive depth, with CPUE being lowest for days with deep dives and during the shortest mid-winter days (Fig. 3). Although the relationship between CPUE and day length has been reported previously (Grémillet et al. 2005c), it is nevertheless surprising that ambient illumination (both daylight and moonlight) does not contribute to the best model describing variation in CPUE (Table 3). A priori, it was predicted that CPUE will be related to ambient illumination, because Great Cormorants are visually guided foragers (Martin et al. 2008). Although it is possible that day length serves as a better proxy for ambient illumination than the measurements for 2004–2005 used in the present study (for details, see White et al. 2008a), it is at least equally likely that day length serves as a proxy for some other parameter that varies throughout the winter, such as seasonal variation in primary production (e.g., Heide-Jørgensen et al. 2007) and prey availability.

In Greenland, Great Cormorants prey mainly on sculpin, *Myoxocephalus* spp., throughout the year (Grémillet et al. 2001, 2004). Sculpin are a group of benthic fish that are diurnally active predators (Nickell and Sayer 1998, Norderhaug et al. 2005). Surprisingly, Great Cormorants make use of this prey source even when other potential prey species are more abundant (Andersen et al. 2007). For example, unlike other seabirds (Carscadden et al. 2002), Great Cormorants

TABLE 5. Catch per unit effort (CPUE) of diving seabirds.

Species	Season	Location	Sex†	CPUE (g/min submerged)	Method‡	Source§
<i>Phalacrocorax carbo</i>	winter	Greenland	M	18.6	HR	A
<i>Phalacrocorax carbo</i>	breeding	Greenland	M	35–41	NB	B
<i>Phalacrocorax carbo</i>	breeding	France	M	15.2	NB	C
<i>Phalacrocorax carbo</i>	winter	Scotland	ns	7.3	EM	D
<i>Phalacrocorax aristotelis</i>	breeding	Scotland	ns	10.1	EM	E
<i>Phalacrocorax neglectus</i>	breeding	South Africa	ns	1.34	ST	B, F
<i>Uria aalge</i>	breeding	Scotland	ns	2.45	EM	E
<i>Aptenodytes patagonicus</i>	breeding	subantarctic	ns	4.5	DLW	G
<i>Eudyptes chrysolophus</i>	breeding	subantarctic	M	3.19–4.16	HR	H
<i>Eudyptes chrysolophus</i>	pre-molt	subantarctic	M	6.97	HR	H
<i>Eudyptes chrysolophus</i>	winter	subantarctic	M	1.94	HR	H
<i>Pygoscelis antarcticus</i>	breeding	subantarctic	ns	2.2–7.0	DLW	I
<i>Pygoscelis papua</i>	breeding	subantarctic	ns	2.1–4.4	DLW	I
<i>Spheniscus demersus</i>	breeding	South Africa	ns	3.1	DLW	J
<i>Spheniscus demersus</i>	breeding	South Africa	ns	1.75	ST	B, F
<i>Spheniscus magellanicus</i>	breeding	Argentina	ns	6.0–9.3	HS	K, L

† Where available, data from males (M) were selected; sex was not specified (ns) in some studies.

‡ Codes for methods are as for Table 4; ST is stomach temperature.

§ Source codes: A, present study; B, Grémillet et al. (2004); C, Grémillet (1997); D, Grémillet et al. (2003); E, Enstipp et al. (2006a); F, Wilson and Grémillet (1996); G, Kooyman et al. (1992); H, Green et al. (2009); I, Croxall and Lishman (1987); J, Nagy et al. (1984); K, Wilson et al. (2002); L, Wilson (2004).

make limited use of capelin *Mallotus villosus*, which are abundant in West Greenland and migrate inshore to spawn during the Great Cormorant breeding season (Friis-Rødel and Kannevorf 2002). The preference of the Great Cormorants for sculpin over the more numerous capelin probably arises because sculpin represent a stable food resource (Methven et al. 2001, Grémillet et al. 2004), but is also likely to reflect the relatively low costs of hunting sedentary prey (Halsey et al. 2007), as well as the poor visual acuity of Great Cormorants (White et al. 2007b). Nevertheless, although sculpin are a relatively stable prey source, their abundance does vary seasonally (Weslawski et al. 1988, Methven et al. 2001), and this variation could drive the observed association between CPUE and day length. Thus, although the reliability of sculpin as a prey source probably contributes to the high CPUEs of Great Cormorants in Greenland, the likely seasonal variation in this food source probably also contributes to seasonal variation in CPUE.

In addition to the changes associated with day length, CPUE is negatively associated with dive depth (Fig. 3). The influence of depth on CPUE probably acts through the costs of swimming from the surface to the sea bed where Great Cormorants forage for sculpin. Deeper dives are less efficient in terms of the proportion of the dive duration spent at the bottom of the dive where foraging occurs (Grémillet et al. 1999). Thus a lesser proportion of the DTS is available for prey consumption on days where the Great Cormorants dive more deeply. Presumably, the requirement to dive more deeply is driven by the availability and/or behavior of the sculpin. In Little Penguins, another inshore diving forager, the fledging success of different colonies appears to be related to the availability of shallow waters within their foraging range (Chiaradia et al. 2007). In the successful

colonies, penguins dived more shallowly and less frequently, and as a result we might expect them to have a greater CPUE. The change in CPUE with depth in Great Cormorants may therefore occur as a result of utilization of inshore areas with a smaller proportion of shallow depths for benthic foraging or movement to deeper depths of the sculpin.

Conclusion

By measuring the energy use of free-living, Arctic-dwelling Great Cormorants throughout their annual cycle, the present study rejects the hypothesis that the daily energy expenditure of this species is exceptionally high. In fact, it is lower than that of most other birds. This occurs despite the birds' habit of diving in water temperatures below -1°C in winter and their partially wettable plumage. Great Cormorants in Greenland achieve the highest catch per unit effort of any diving bird thus far measured. This ensures that they need to forage for only very short periods, allowing them to minimize their absolute levels of activity and their exposure to cold water. Thus, a suite of physiological, sensory, and behavioral adaptations result in cormorants maintaining a low level of energy expenditure throughout the year.

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APPENDIX

Laboratory calibration of the relationship between heart rate and metabolic rate in Great Cormorants (*Ecological Archives* E092-041-A1).