Foraging energetics of arctic cormorants and the evolution of diving birds

Abstract
Efficient body insulation is assumed to have enabled birds and mammals to colonize polar aquatic ecosystems. We challenge this concept by comparing the bioenergetics of cormorants (Phalacrocorax carbo) living in temperate and arctic conditions. We show that although these birds have limited insulation, they maintain high body temperature (42.3 °C) when diving in cold water (1–10 °C). Their energy demand at these times is extremely high (up to 60 W kg⁻¹). Free-living cormorants wintering in Greenland (water temperature −1 °C) profoundly alter their foraging activity, thus minimizing time spent in water and the associated high thermoregulatory costs. They then meet their daily food demand within a single intense dive bout (lasting 9 min on average). Their substantial energy requirements are balanced by the highest predatory efficiency so far recorded for aquatic predators. We postulate that similar behavioural patterns allowed early diving birds (Cretaceous) to colonize cold coastal areas before they evolved efficient insulation.

Keywords
Diving endotherms, energetics, foraging ecology, seabirds, cormorants, Hesperornis, thermoregulation, vertebrate evolution, polar ecosystems.

INTRODUCTION
The polar seas are among the most challenging ecosystems on earth, due to the extreme cooling capacity of their subzero waters. Most extant marine endotherms (sea birds and mammals) diving in these areas show extensive morphological and physiological adaptations to cold in the form of thick insulating layers of fat and feathers (Scholander et al. 1950; Watts et al. 1993). These characteristics are assumed to have evolved soon after the colonization of marine ecosystems by Cretaceous diving birds and Eocene proto-cetaceans, well before these groups spread into polar seas (Berta & Sumich 1999). Cormorants (Phalacrocorax carbo) are a clear exception to this evolutionary route. These diving, fish-eating birds only have partly water-proof plumage and very limited body insulation (Rijke 1968). The species is thought to have originated in warm Australasian coastal areas (Van Tets 1976), but is currently resident from the tropics to the high arctic, where air and water temperatures may be as low as −30 °C and −1.5 °C, respectively. In this paper, we investigate the energetic challenges confronting cormorants from Greenland and identify the key factors that enable them to survive in this harsh climate. We further compare the energy requirements and feeding behaviour of cormorants from temperate Normandy and arctic Greenland. We use these findings to highlight an unsuspected evolutionary pathway to the colonization of aquatic ecosystems by diving warm-blooded animals.

METHODS
All trials were conducted under licence of the local authorities and concerned great cormorants of the subspecies Phalacrocorax carbo carbo, which occurs in western Europe as well as in Greenland and North America (Johnsgard 1993). These populations live in different climate zones, but may all experience cold weather conditions during the winter period.

Bird body insulation
The volume of air trapped in the feathers of five great cormorants from Greenland was determined following Wilson et al. (1992). The volume of this insulating layer was compared with data given by Wilson et al. (1992) for great cormorants from the temperate zone.
Diving energetics

Energy costs of diving were measured in an open respirometry system (Calik et al. 1994) for six great cormorants from western Europe diving voluntarily in a still-water tank (dimensions 2 m × 15 m; 1 m deep). The walls of the tank were V-shaped and the water surface was covered with a flexible liner, to prevent wave reflection and related artefacts (Butler & Jones 1997). At each end of the 15 m long channel the birds were able to surface under a respiratory hood. Each hood had a volume of approximately 120 L. Air was drawn out of each hood using a high volume pump (Electrolux Ltd) at a rate of about 160 L min⁻¹. This airflow was dried using silica gel and metered using an industrial digital gas mass flow meter (Scottish Gas Ltd, accuracy 1%). The excurrent air was then subsampled at a rate of approximately 2 L min⁻¹ using a smaller air-pump (Charles Austen Pumps Ltd) and this subsampled flow directed to a single channel gas analyser (Servomex Ltd, model 1100H) where 150 mL min⁻¹ were passed through the measuring cell. Tests suggested that the washout of the system had a half life of approximately 3 min. Since birds surfaced at much more frequent intervals than this during the course of each measurement it was not possible to resolve the total oxygen consumption into that attributable to individual dives. The respirometry systems were duplicated at either end of the channel. Trials lasted on average 40 min. During this time the birds either rested under one of the two hoods, or they dived between hoods. A total of 98 trials were conducted at water temperatures ranging between 1 and 10 °C. The total oxygen consumption of the birds was calculated from the summed oxygen consumption measured across the two analysers. For each analyser we measured the instantaneous differences at 10-s intervals between observed oxygen contents of the excurrent air from the hood and the ambient oxygen content of the air assuming a linear drift between the initial and final ambient measurements of oxygen content. Because trials were short (less than 1 h), drift was generally negligible (less than 0.02% O₂). We multiplied these instantaneous records by the flow rate reported from the digital flowmeter to obtain a continuous record of oxygen consumption rates (mL min⁻¹) through each trial following Speakman (2000). We did not absorb CO₂ prior to measuring oxygen content as this yields the most accurate estimate of energy demands when the RQ is unknown (Koteja 1996; Speakman 2000). The oxygen consumption rates were summed across all measurements to obtain the total oxygen consumption (mL) for each analyser. The average oxygen consumption rate in each trial was therefore the summed oxygen consumed at each analyser divided by the total time the bird was in the channel (mL min⁻¹). We converted this estimated oxygen consumption to energy expenditure using the equations from Speakman (2000) which are independent of the assumed RQ. Changes in body temperature of the birds were recorded using gastric probes (dimensions 85 mm × 15 mm, mass 18 g) containing a temperature logger (recording range 0–50 °C, 0.4 °C relative accuracy, one measurement every 8 s) enclosed in a titanium housing. The device was fed to the bird in a fish and recovered after each trial when it was naturally regurgitated in pellets along with other undigested food material (Grémillet & Plöes 1994).

Foraging techniques

We located the northernmost wintering site for cormorants near the Southern Disko Bight, Greenland (68°15′N, 52°50′W) and studied their behavioural response to cold in March 2000 (n = 30). We compared these results with two similar summer studies of cormorants breeding on nearby Disko Island (69°30′N, 54°05′W, n = 11) and in Normandy, France (48°55′N, 01°45′W, Grémillet 1997; n = 14). Cormorants forage by foot-propelled, pursuit-diving at all three locations and feed predominantly on bottom-dwelling fish. Feeding behaviour was recorded by radio-tracking following Grémillet et al. (1998) in Normandy and Greenland in summer or direct observations (Greenland winter). Direct observations were possible in the latter case due to the concentration of wintering cormorants in small ice-free areas near to the shore. In all situations we recorded total time spent in the water, average dive time, time spent underwater per dive bout, air and water temperatures. Dive depths were calculated from dive times after Grémillet et al. (1999) and results validated with direct soundings at the feeding sites. Prey capture rates were calculated using time spent underwater and food consumption as measured by automatic weighing of nesting birds (Grémillet et al. 1996) (Normandy, Greenland in summer) or calculated using nominal energy budgets (Greenland winter) after Grémillet et al. (2000).

RESULTS AND DISCUSSION

The average volume of air trapped in the plumage of five arctic cormorants was 0.131 ± 0.063 (10⁻³ m³ kg⁻¹), which is similar to the value recorded by Wilson et al. (1992) for their European conspecifics (0.09 10⁻³ m³ kg⁻¹) and is less than 30% of the mean air volume carried by well-insulated diving birds such as common guillemots (Uria aalge) (Wilson et al. 1992). Cormorants from Greenland and Europe were of similar mass (average 2.93 ± 0.22 kg in Greenland and 2.76 ± 0.12
kg in Normandy, \( t = 0.43, P > 0.05 \) and carried less than 1.5 mm subcutaneous fat [average 1.0 ± 0.4 mm in Normandy, and < 1.5 mm in Europe (Kieckbusch, unpublished data)]. There was thus no evidence that cormorants have evolved specialized morphological adaptations to the Arctic. Such a lack of morphofunctional adaptation could be explained by two potential microevolutionary scenarios: (i) there is a sustained individual exchange and continuous gene flow between great cormorant populations of both the Boreal and Arctic zones, or (ii) this cormorant subspecies recently moved into Arctic regions.

Trials with captive birds diving in water between 1 and 10 °C showed that this activity is energetically extremely demanding for the birds (Fig. 1). Energy costs are negatively correlated with water temperature \( F = 10.65, P = 0.002 \). Using a model which integrates the relationship between energy expenditure and water temperature with the effect of dive depth (Grémillet & Wilson 1999), we calculated that average dive costs in cormorants vary between 28 W kg\(^{-1}\) (c. 6 × Resting Metabolic Rate; RMR, Schmid et al. 1995) for a bird diving in shallow (3 m), warm (25 °C) water and 64 W kg\(^{-1}\) (c. 14 × RMR) for a bird diving in deeper, colder water (10 m deep, -1 °C) (Fig. 2). Abdominal temperatures of diving cormorants remained constant regardless of water temperature and showed one of the highest sustained levels yet measured (average 42.3 ± 0.3 °C, \( n = 6 \), Fig. 1) for nonpasserine birds (Prinzinger et al. 1991). Taken together, these results indicate that diving cormorants use intense central thermogenesis to balance peripheral heat losses. This is a completely different physiological adaptation to that of other extant diving birds, such as penguins, which use peripheral vasoconstriction and marked regional hypothermia to reduce energy costs (Handrich et al. 1997).

Wild cormorants observed at their breeding and wintering sites in Normandy and Greenland responded to lower ambient temperatures by a highly significant decrease in the total time spent diving (less time spent diving in Greenland in summer than in Normandy; \( t = 4.71, P < 0.01 \) and less time spent diving in Greenland in winter than in summer; \( t = 5.77, P < 0.01 \); Fig. 3A), the rest of the day being spent resting ashore. They also significantly reduced their dive depth (and thus heat losses, see Fig. 2) during the Arctic summer \( (t = 6.32, P < 0.01) \), but failed to do so in wintertime \( (t = 1.68, P > 0.05) \); Fig. 3B). This was due to the extensive ice cover at this time which forced the birds to

![Figure 1](image1.png)  
**Figure 1** Energy costs (upper graph) and body temperature patterns (lower graph) in a cormorant diving in a still-water tank at 4.8 °C. The black bar shows the time spent swimming. Note the extremely high body temperature and metabolic rate. Our facilities did not allow birds to dive deeper than 1 m. Field metabolic rates of diving cormorants are thus significantly higher (Fig. 2), as wild individuals usually dive for food at 3–7 m (Fig. 3B) where plumage air is already compressed to c. 50% of its original volume.

![Figure 2](image2.png)  
**Figure 2** Relationship between energy costs of diving, water temperature and water depth in cormorants (*Phalacrocorax carbo*). The impact of varying water temperature was derived from respirometric measurements (this study) and the influence of water depth calculated (Grémillet & Wilson 1999). Note the important impact of water depth which shows that birds should favour warm and shallow waters.
dive farther from the shore, and thus in deeper water along the ice edge. We predicted from the respirometry study that these cormorants wintering in Greenland spend, on average, 49 W kg$^{-1}$ when searching for prey in icy waters. They then reduce their daily fishing period to a single bout lasting on average only 9 min (Fig. 3A), and allocate c. 10% of their daily energy budget to diving costs. During this period they sustain a prey capture rate of nearly 60 g fish per minute spent underwater (Fig. 3B), which is by far the highest value so far recorded for diving endotherms (Grémillet 1997). Thus a simple behavioural adjustment, rather than highly developed morphological or physiological adaptation, allows this species to live year-round in the Arctic. This elevation of foraging efficiency depends critically upon dense, highly predictable prey stocks allowing birds to gain sufficient energy during extremely short dive bouts.

CONCLUSIONS

Our case study clearly demonstrates that sophisticated morphofunctional adaptations are not a prerequisite for the colonization of cold aquatic ecosystems by endotherms. Such secondary colonization is usually exemplified by the evolution of early whales: the cetacean radiation started along tropical shores and estuaries of the Tethys Sea (Bajpai & Gingerich 1998), allowing members of this order to develop efficient body insulation and diving skills as whales gradually colonized colder, deeper oceans (Carroll 1997). Diving birds followed a different route: the flightless, piscivorous Hesperornithiformes which appeared some 50 million years earlier were abundant at high latitudes (Feduccia 1996). The global climate was then markedly milder, but these birds probably encountered water temperatures of less than 10 °C when diving for food (Herman & Spicer 1997). We do not know how well insulated Hesperornithiformes were, but they appeared to have preyed upon particularly dense shoaling prey stocks, just as do cormorants today (Janis & Carrano 1992; Grémillet & Wilson 1999). Thus, we postulate that some early diving birds may have colonized colder areas despite little morphofunctional adaptation to reduce heat losses. They may have done so by constantly commuting between highly productive but cold feeding grounds and thermally less demanding shores. In this scenario, Cretaceous Hesperornithiformes birds take advantage of their endothermic features to spread rapidly through cold, rich coastal ecosystems. By doing so they also move out of the range of ectothermic competitors and predators such as Cretaceous mosasaurs (Lingham-soliar 1995). This pattern is found in modern cormorants (Phalacrocoracidae), which evolved in warm south-east Asia, but subsequently spread through four continents (van Tets 1976). Despite their poor insulation, today’s cormorants are most numerous in cold, highly productive ecosystems at high latitudes and along upwelling systems (Johnsgard 1993).

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REFERENCES


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