

S29-4 The relative importance of physiological and behavioral adaptation in diving endotherms: a case study with great cormorants

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Abstract Extensive morphological and physiological adjustments are assumed to underpin the adaptations of diving birds to high thermoregulatory costs. However, the role of behavioral adaptations has received little consideration. We have assessed the relative importance of physiological and behavioral adjustments in aquatic endotherms by studying the case of the poorly insulated great cormorant (*Phalacrocorax carbo*) in two contrasting thermal environments: Normandy (water temperature 12°C) and Greenland (water temperature 5°C). Major differences were found in the feeding behavior of birds breeding in the two regions. Greenland birds showed a 70% reduction in time spent swimming relative to those in Normandy. Reduction in Greenland was achieved first by reducing time spent on the surface between dives and secondly by returning to land in between intensive bouts of diving. Total daily energy intake of cormorants was similar in both areas but prey capture rates in Greenland were 150% higher than those in Normandy. Our study shows that in a cold foraging environment, poorly insulated great cormorants significantly increase their foraging efficiency. To do this they rely on ecological adaptive patterns (minimization of time spent swimming in cold water and increased prey capture rates) far more than physiological adaptations (minimizing instantaneous costs). This finding supports predictions by Grémillet and Wilson (1999) that great cormorants can cope with a wide range of abiotic parameters despite their morphological handicaps, provided they can adjust their distribution to exploit dense prey patches.

Key words Diving endotherms, Great cormorant, Behavioral adaptation, Physiological adaptation, Energetics, Foraging behavior

1 Introduction

Although diving seabirds colonized the oceans rather recently (less than 100 million years ago), they possess highly developed and diverse morphological and physiological adaptations for diving (Kooyman, 1989). These attributes enable them to play a major role at the top of aquatic food chains (Ainley et al., 1994; Croll et al., 1998; Pauly et al., 1998). As endotherms, they also experience much greater heat losses to water than to air, such that their thermoregulatory mechanisms are more developed than those of land birds. Such capabilities have motivated numerous studies of warm-blooded diving animals, with at least 2 200 articles published since 1981 (SCI, 2000). Few of these studies, however, have considered the capacity of marine endotherms to compensate for high living costs via food intake (Guillemette et al., 1992).

The aim of the present paper is to assess the relative importance of physiological and behavioral adaptations in a poorly insulated endotherm diving in cold water, namely the great cormorant (*Phalacrocorax carbo carbo*), which

has wettable plumage (Rijke, 1968; Wilson et al., 1992) and which experiences particularly high heat losses to water (Schmid et al., 1995; Grémillet et al., 1998a). Great cormorants were considered more likely than any other diving endotherm to display specific strategies enabling them to deal with such constraints.

The great cormorant additionally has a wide breeding range (Johnsgard, 1993). We used this characteristic to compare the foraging energetics of birds breeding in temperate (Normandy, water temperature 12°C) and polar (Greenland, water temperature 5°C) environments using radio tracking, qualitative and quantitative dietary analysis, stomach temperature records and time-budget analysis. Previous investigations showed that, despite the colder aquatic environment, daily food intake of Greenland birds was similar to that in Normandy (Grémillet et al., 1999). This finding suggests that Greenland birds have developed specific physiological and/or behavioral adaptations which enable them to compensate for increased heat losses. What those are is investigated here.

Table 1 Comparison of foraging parameters for great cormorants breeding in Greenland ($n = 6$ males, 5 females) and Normandy ($n = 8$ males, 6 females)

	Foraging trips per day	Duration of foraging trip (min)	Foraging range (km)	Time in water per trip (min)	Time in water per day (min)	Mean dive time (s) ($n=5$)	Food load (g fish/ foraging trip)	Catch per unit time (g fish/min underwater)
Males Greenland	3.1±0.8	140 (85–200)	7.4±2.0	13.9± 6.1	43.1	25.5±3.6	305±40	35.1 (0–770)
Males Normandy	2.4±0.7	165 (110–226)	9.7±6.0	52.2±16.7	125.3	38.2±9.4	430±120	15.2 (0–820)
Females Greenland	3.1±0.8	155 (80–185)	6.0±3.0	15.8±10.2	49.0	24.2±3.7	340±140	24.8 (0–480)
Females Normandy	2.3±0.3	180 (130–325)	17.1±10.0	74.5±18.6	171.4	38.8±10.5	425±75	9.0 (0–1060)

Means are given with \pm standard deviation, and medians with range values. Time in water per day is the product of the time in water per foraging trip and the number of foraging trips per day.

2 Materials and methods

Our two study colonies of the great cormorant are located on inshore islands: Chausey in Normandy, France, at 48°55'N, 01°45'W (346 pairs in 1996) and Qeqertaq, Disko in Greenland at 69°30'N, 54°05'W (179 pairs in 1998). Normandy birds bred between March and July when water temperature averaged 12°C and Greenland birds bred between April and August (average water temperature 5°C; Grémillet et al., 1999). We studied adult birds raising young chicks in April and May 1995 and 1996 (Normandy) and in June and July 1998 (Greenland). Due to discrepancies in body mass and foraging patterns, males and females were considered separately. Statistical tests were performed using Minitab 11; means are \pm one standard deviation.

2.1 Greenland study

Foraging behavior: eleven adult cormorants were caught at the nest site and equipped with VHF transmitters (TW3 transmitters, Biotrack, 52 Furzebrook Road, Wareham, BH20 5AX, UK; mass 18 g). Individual birds were subsequently radio-tracked for at least 10 foraging trips chosen at random. Foraging data recorded were location of foraging area, time and duration of each dive plus subsequent recovery phase on the surface, and total time spent swimming per foraging trip in comparison with nest attendance. This gave an estimate of the total time spent on water per day. To compare dive/pause ratios, radio-tracking data (Grémillet, 1997) were pooled as follows: for 5 individuals of each sex and each location, a set of 5 dive bouts was analyzed, within which 5 dive times and ensuing recovery times were pooled. Individuals, dive bouts and dive cycles were chosen at random.

Food intake: using automatic nest balances, adult body mass and food intake rates were determined concurrently with foraging patterns in the same 11 adult birds (after Grémillet et al., 1996, 1999). Food loads were then corrected for the effect of digestion (Grémillet et al., 1996) using radio-tracking data and assuming a mean prey mass of 108 g calculated from stomach temperature measurements. Predation efficiency was assessed by calculations of catch per unit effort (CPUE), where CPUE values are expressed in

grams of fish taken per minute spent underwater (after Grémillet, 1997).

Body temperature patterns: stomach temperature patterns and concurrent activity data (via radio-tracking) were recorded in 6 birds for a total of 10 days using gastric probes (SICUP, Grémillet and Plös, 1994; Wilson et al., 1998). Deployment of such stomach temperature loggers is not detrimental in any way (Wilson et al., 1998). Recorded stomach temperatures were analyzed following Grémillet and Plös (1994) and Wilson et al. (1995) to calculate the mass of individual prey items to an accuracy of 15%. Potential body cooling in diving birds was assessed following Grémillet et al. (1998a), using these stomach temperature records (after Grémillet et al., 1996, 1999).

Diet: prey spectrum was determined and identified via pellet analysis following Harris and Wanless (1993) and from fish regurgitated at the nest site. A total of 52 pellets containing 1 490 otoliths were analyzed. The average energy values of the different prey species were obtained from literature. Using frequency of occurrence of the main prey species in diet, their average specific mass and calorific content, we then calculated the average calorific values of food taken.

2.2 Normandy study

All data for Normandy birds were derived from previous studies performed during the same breeding phase (early to mid chick rearing) and using the same methodology as that used in Greenland (Grémillet et al., 1996; Grémillet, 1997; Grémillet et al., 1998b).

2.3 Modeling

We used respirometric measurements by Schmid et al. (1995) and a thermo-energetics model developed by Grémillet and Wilson (1999) to predict energy costs as a function of water temperature and dive depth. The poor body insulation of great cormorants, and the resulting relationship between water temperature and dive costs, has been recently confirmed experimentally (Grémillet et al., 2001). The calculations were performed for mean water temperatures of 12°C and 5°C, and a mean dive depth of 8 m and 3 m at respective Normandy and Greenland study sites (Grémillet

et al., 1999). Dive depths of Normandy birds were measured by time-depth recorders; and those of Greenland birds were derived from mean dive times presented in Table 1 using a relationship given in Grémillet et al. (1998b).

The increase in the energy costs of diving for Greenland birds was determined as follows. Because cormorants in Normandy and Greenland take similar quantities of similar energy value (Grémillet et al., 1999) and maintain a constant body mass throughout the breeding season (Grémillet, 1997), comparison of the time-energy budgets in the two areas should indicate that energy requirements are similar. If the total daily energy budget for each location is then calculated as if the energy costs of diving are the same in both, the difference should represent the additional energy allocated to diving in Greenland birds.

To determine this, we used the behavioral data presented in Table 1 and the energetics data from Grémillet et al. (2000). We assumed that all activities performed at the nest site had similar energetic costs at both locations. This

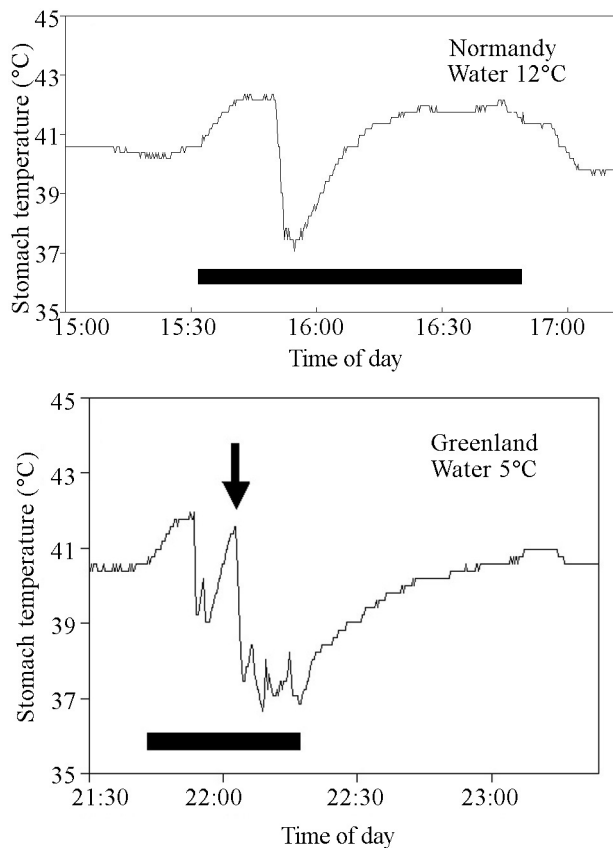


Fig. 1 Examples of stomach temperature patterns in individual great cormorants foraging off Normandy (top) and Greenland (bottom)

The black bar shows the time spent in the water. The initial temperature increase comes from heat generated by diving activity. Precipitous drops in stomach temperature are caused by the ingestion of fish. Note that birds in Normandy keep high, stable body temperature for long periods when swimming and after warming ingested fish. Greenland birds stayed in water for shorter periods, and, while swimming, also rapidly warmed ingested prey to temperatures higher than resting values (arrow).

assumption is valid as long as the temperature regimes are similar, which is not the case when the Greenland colony is shaded by nearby cliffs. To correct for this effect, we applied data recorded by Storch et al. (1999), which predict an increase of 63% in resting metabolic rate (RMR). Differences in flying time periods and brood biomass were also taken into account.

3 Results

3.1 Foraging behavior

Radio-tracking data show that for both sexes, the total times spent swimming per foraging trip and per day were significantly lower in Greenland than in Normandy (average decreases 73% and 65% respectively in males, and 79% and 71% in females, Table 1). Foraging bouts of Greenland birds were not only shorter, but also organized differently. Their recovery times were significantly shorter, and they further reduced contact with cold water by performing significantly briefer dives (Table 1). Great cormorants sometimes rest in the middle of a foraging trip, leaving the water to stand on nearby rocks. In Normandy, males and females have an average of 0.26 ± 0.14 and 0.59 ± 0.19 breaks per foraging trip respectively, i.e. no breaks at all or just one. In Greenland, the mean number of breaks per trip is greater at 1.9 ± 0.64 and 1.8 ± 0.35 in males and females respectively, the birds making up to three breaks per trip.

3.2 Diet and food intake

Although fish mass intake is similar in Normandy and Greenland (Grémillet et al., 1999), the two populations prey upon different species. In Normandy, great cormorants feed on 22 different fish species, mainly labrids, and in Greenland 14, mainly sculpins. The average calorific of the intake was calculated as 4.0 kJ g^{-1} in Greenland (Table 2), and is the same in Normandy (Grémillet and Argentin, 1998). Combining dietary and behavioral data to estimate CPUE (mass prey taken per time spent underwater) showed clearly that, for both sexes, predation efficiency was significantly higher in Greenland than Normandy: twice as high in males and nearly three times as high in females (Table 1).

3.3 Body temperature patterns

Previous studies detected no abnormally low body temperature levels in great cormorants diving off Normandy (Fig. 1, top), even during prolonged periods in the water of up to 158 minutes (Grémillet et al., 1998a). In Greenland, where dive bouts were much shorter (Table 1), cormorants have similar temperature patterns (Fig. 1, bottom). In both groups, body temperature rises rapidly at the start of swimming and then is kept stable until the ingestion of cold prey, which initiates a precipitous drop in temperature (Wilson et al., 1992). Ingested food is subsequently warmed, and stomach temperature returns to initial, high levels.

3.4 Modeling

The algorithm proposed by Grémillet and Wilson

Table 2 Diet of great cormorants breeding in Greenland, from 52 regurgitated pellets containing 1 490 otoliths

Main prey species	Mean calculated mass (g±SD)	Proportion in diet (% of total fish number)	Proportion in diet (% of total fish mass)	Mean energy value (kJ.g ⁻¹)
Sculpins	185±8.0	39.4	79.6	3.8*
Capelin	45±4.0	15.2	7.4	4.1**
Gadids	90±6.5	12.8	12.6	4.9§
Sand eels	2.8±0.2	10.8	0.4	7.1§§
Others		15.7		
Undetermined		6.1		
Mean total calorific value (kJ.g ⁻¹)				4.0

See material and methods for calculations. Mean calorific values are taken from * Grant (1984), ** Van Pelt et al. (1997), § Brekke and Gabrielsen (1994) and §§ Hislop et al. (1991).

(1999) predicts increases of 28% and 36% in the energy costs of diving for male and female cormorants in Greenland. In theory then, the overall costs of diving in Greenland should be 169 W in males and 146 W in females (Fig. 2). However, present calculations based on the time-energy budgets of birds from Normandy and Greenland (Table 3a and b) show that the field energy costs of diving off Greenland may be as high as 257 W in males and 250 W in females. The actual heat losses experienced by birds diving in Greenland may thus be 50%–70% higher than the predicted values, and 98% and 165% higher than in Normandy for male and female cormorants, respectively (Fig. 2).

4 Discussion

Great cormorants have not evolved specific morpho-

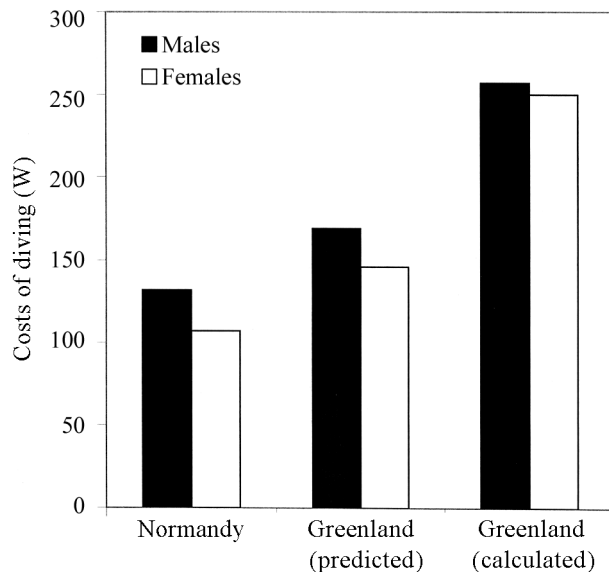


Fig. 2 Comparison between the energy costs of diving in great cormorants

Comparisons based on gas respirometry data from Schmid et al. (1995) for Normandy in 12°C water, on the costs of diving predicted by Grémillet and Wilson (1999) in Greenland in 5°C water (Greenland predicted), and on the energy costs of diving determined *in vivo* for Greenland birds in this study (Greenland calculated).

logical adaptations for diving in cold water (Rijke, 1968; Johnsgard, 1993; Grémillet et al., 2001). Our estimations suggest that the energy costs of diving off Greenland may be as high as 95 W kg⁻¹, more than six times those of Adélie penguins (*Pygoscelis adeliae*) foraging in a similar thermal environment (Culik et al., 1994; Schmid et al., 1995) and comparable with average flight costs (calculated after Pennycuik, 2001). Despite this, our empirical data on prey quantity and quality indicate that the daily energy intake of birds breeding in Greenland does not differ from those breeding in temperate Normandy (Grémillet et al., 1999; Table 2). Taken together these findings suggest that the allocation of energy resources must differ in the two regions. The relative importance of physiological and behavioral adaptations within this unexpected strategy is discussed below.

4.1 Physiological adaptation

Heat loss experienced by diving endotherms is critically influenced by the temperature differential between body and surrounding medium. For Greenland great cormorants, then, a straightforward solution would be to reduce the differential by dropping body temperature. Other diving birds and mammals respond by cooling extremities or larger parts of the body (Butler and Jones, 1997); and hypothermia, which has been claimed to increase foraging efficiency, has been found recently in two cormorant species, the bank cormorant *Phalacrocorax neglectus* (Wilson and Grémillet, 1996) and the blue-eyed shag *Phalacrocorax atriceps* (Bevan et al., 1997). But do great cormorants use these pathways to reduce diving costs?

Grémillet et al. (1998a) showed that this was not the case for great cormorants in Normandy, which kept a constant body temperature for long periods when swimming in water at 12°C (Fig. 1, top). Even at the lower water temperatures experienced by Greenland birds there was no evidence of drastic body cooling (Fig. 1, bottom). Food intake rates calculated for Normandy and Greenland birds using stomach temperature levels confirm these findings, because these estimates are similar for both groups. We thus conclude that hypothermia is unlikely to play a major role in minimizing heat loss in great cormorants diving off Greenland. Our

Table 3a Nominal time-energy budget for male great cormorants breeding in Normandy and Greenland

Activity	Costs per second (W)		Duration (h)		Total costs (kJ d ⁻¹)	
	Normandy	Greenland	Normandy	Greenland	Normandy	Greenland
Overnight resting*	11.9	19.6	7.90	9.16	338	647
Daytime activities on land**	16.4	16.6	13.50	13.70	798	821
Flight***	252	258	0.50	0.38	454	353
Diving§	130.3	132.0	2.08	0.72	977	341
Reproduction§§					536	616
Total (kJ d ⁻¹)					3 103	2 778
Difference between total costs for Greenland / Normandy (kJ d ⁻¹)						325
Related potential increase in dive costs (W and % costs at 12°C)						125 (95%)

Calculations were performed assuming that the energy costs of diving were the same in both regions. The difference between total costs in the two locations thus allows calculation of the potential increase in diving cost in Greenland (see Results).

Table 3b Nominal time-energy budget for female great cormorants breeding in Normandy and Greenland

Activity	Costs per second (W)		Duration (h)		Total costs (kJ d ⁻¹)	
	Normandy	Greenland	Normandy	Greenland	Normandy	Greenland
Overnight resting*	8.6	15.9	7.9	9.17	245	525
Daytime activities on land**	11.9	13.5	12.37	13.70	530	666
Flight***	148	180	0.88	0.32	469	207
Diving§	94.5	107.0	2.85	0.82	970	315
Reproduction§§					536	616
Total (kJ d ⁻¹)					2 750	2 329
Difference between total costs for Greenland / Normandy (kJ d ⁻¹)						421
Related potential increase in dive costs (W and % costs at 12°C)						143 (134%)

Calculations were performed assuming that the energy costs of diving are the same in both regions. The difference between total costs for both locations thus allows calculation of the increase in diving cost in Greenland (see Results).

* Night time in Normandy and time when the colony was in shade in Greenland. ** All these activities have similar energy costs, range 5 to 7 W kg⁻¹ (Storch et al., 1999). *** Flight costs calculated for body masses according to procedures in the Methods; input values for cormorants stated in Pennycuik (2001), using the computer program available on <http://detritus.inhs.uiuc.edu/wes/pennycuik.html>. § Diving costs for great cormorants diving in water at 12°C (Schmid et al., 1995). §§ Calculated from Grémillet et al. (2000) for 1.5 chicks in Normandy and 1.7 chicks in Greenland.

field measurements have been corroborated in recent trials with captive great cormorants, which showed that birds kept constant, high body temperature even when swimming in water at 1°C for 30 min (Grémillet et al., 2001).

4.2 Behavioral adaptation

Great cormorants breeding in Greenland face increases of more than 100% in metabolic costs over those in temperate Normandy while diving for prey, yet eat no more food (Grémillet et al., 1999). To remain in energy balance, then, they have to either drastically reduce the metabolic costs of activities other than diving or increase the energy gained (prey capture) per unit time spent underwater. Except for their diving rhythms, the time-energy budgets of Normandy and Greenland cormorants were very similar (Table 2). Only two significant differences were recorded. First, females spent less time flying in Greenland than in Normandy due to a short foraging range. Secondly, Greenland cormorants raised 30% more chicks than in Normandy (Grémillet, unpubl. data). These effects are in-

cluded in the overall energy budget discussed below.

In contrast, there were major differences between Normandy and Greenland cormorants in diving behavior. In particular, Greenland birds spent much less time foraging both per bout and per day (Table 1). Furthermore, the dive/pause ratios in Greenland birds were significantly higher, indicating that they spent less time in recovery between dives, thereby maximizing foraging time underwater. In addition, dives series made by Greenland birds were more likely to be interrupted by periods spent ashore when the birds were presumably resting, digesting and/or recovering from a potential oxygen debt accumulated during series of intense dives (Ydenberg and Clark, 1989; Butler and Jones, 1997). Dive durations in Greenland birds were also significantly shorter, suggesting that they were shallower (Wilson and Wilson, 1988). By searching for prey in shallow waters, Greenland cormorants avoid increased compression of plumage air volume and consequent increased heat loss to the water as well (Wilson et al., 1992).

In combination, these behavioral strategies allow Greenland birds to catch the same amount of fish of similar calorific value as Normandy birds in only a third of the time. Greenland great cormorants, in fact, have the highest feeding efficiency recorded so far for a marine predator of its size: 35 and 25 g fish caught per minute spent underwater in males and females respectively (Grémillet, 1997).

4.3 Relative importance of physiological and behavioral adaptations

This case study on great cormorants demonstrates that the capacity of diving endotherms to acquire energy and compensate for a costly way of life via specific, flexible foraging techniques should not be underestimated. Our field data and subsequent modeling highlight the major role played by behavioral adaptations in shaping the energy budgets of great cormorants foraging in cold water, especially in comparison with both morphological and physiological adaptations. Knowing that cormorants from both Normandy and Greenland have similar daily energy intakes, it follows that birds from Greenland are likely to lose even more energy when diving than previously thought.

This confirms that great cormorants in Greenland do not have particular morphological or physiological energy saving features. Further modeling presented in Wilson and Grémillet (1996) and Bevan et al. (1997) for bank cormorants and blue-eyed shags also shows why hypothermia is not a good option. These theoretical relationships show that a 3.2 fold increase in prey density at the feeding site (and a proportional increase in bird CPUE values) in great cormorants allows them to fully compensate for a decrease in water temperature from 12°C (Normandy) to 5°C (Greenland). A decrease in body temperature from 41°C to 22°C throughout the time spent swimming, on the other hand, would be necessary to save the same amount of energy. This is not possible for great cormorants diving in Greenland, whose lowest recorded stomach temperature was 25.0°C, an effect due in any case to the ingestion of cold food and not hypothermia (Fig. 1, top).

Our results also indicate that great cormorants from boreal and arctic regions, which have the highest foraging rates so far recorded for any group of diving birds, are nonetheless unlikely to deplete local prey stocks because they can only operate when prey densities are above a certain threshold. Fish resources have to be both abundant and reliable for this energy-maximizing process (Schoener, 1987; Guillemette et al., 1992). This may explain why great cormorants breeding in Greenland feed on sedentary, bottom-dwelling sculpin, a predictable resource rather than on shoaling capelin of higher density per unit area but of more erratic occurrence (Montevecchi and Piatt, 1984). Individual birds are also likely to adjust their distribution patterns then in order to exploit dense prey patches.

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References

- Ainley D, Ribic CA, Fraser WR, 1994. Ecological structure among migrant and resident seabirds of the Scotia-Weddell Confluence region. *J. Anim. Ecol.* 63: 347–364.
- Bevan RM, Boyd LL, Butler PJ, Reid K, Woakes AJ, Croxall JP, 1997. Heart rates and abdominal temperatures of free-ranging South Georgian Shags, *Phalacrocorax georgianus*. *J. Exper. Biol.* 200: 661–675.
- Brekke B, Gabrielsen GW, 1994. Assimilation efficiency of adult Kittiwakes and Brünnich's guillemots fed capelin and Arctic cod. *Pol. Biol.* 14: 279–284.
- Butler PJ, Jones DR, 1997. Physiology of diving of birds and mammals. *Physiol. Rev.* 77: 837–899.
- Croll DA, Tershy BR, Hewitt RP, Demer DA, Fiedler PC, Smith SE, Armstrong W, Popp JM, Kiekhefer T, Lopez VR, Urban J, Gendron D, 1998. An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Res. II* 45: 1 353–1 369.
- Culik BM, Wilson RP, Bannasch R, 1994. Under-water swimming at low energy cost by Pygoscelid penguins. *J. Exper. Biol.* 197: 65–78.
- Grant DAD, 1984. S.I.S. III Industrial Training Report. Banchory: Unpubl. ITE Report.
- Grémillet D, 1997. Catch per unit effort, foraging efficiency and parental investment in breeding cormorants (*Phalacrocorax carbo*). *ICES J. Mar. Sci.* 54: 635–644.
- Grémillet D, Argentin G, 1998. Cormorants, shags and fisheries in the Chausey Islands area. *Le Cormoran* 10: 196–202.
- Grémillet D, Plös A, 1994. The use of stomach temperature records for the calculation of daily food intake in cormorants. *J. Exper. Biol.* 189: 105–115.
- Grémillet D, Wilson RP, 1999. A life in the fast lane: energetics and foraging strategies of the great cormorant. *Behav. Ecol.* 10: 516–524.
- Grémillet D, Dey R, Wanless S, Harris MP, Regel J, 1996. Determining food intake by great cormorants and European shags with electronic balances. *J. Field Orn.* 67: 637–648.
- Grémillet D, Tuschy I, Kierspel M, 1998a. Body temperature and insulation in diving great cormorants and European shags. *Funct. Ecol.* 12: 386–394.
- Grémillet D, Argentin G, Schulte B, Culik BM, 1998b. Flexible foraging techniques in breeding cormorants *Phalacrocorax carbo* and shags *Phalacrocorax aristotelis*: Benthic or pelagic feeding? *Ibis* 140: 113–119.
- Grémillet D, Wilson RP, Wanless S, Peters G, 1999. A tropical bird in the Arctic (the cormorant paradox). *Mar. Ecol. Progr. Ser.* 188: 305–309.
- Grémillet D, Storch S, Peters G, 2000. Determining food requirements in marine top-predators: a comparison of three independent methods in great cormorants *Phalacrocorax carbo*. *Can. J. Zool.* 78: 1 567–1 579.
- Grémillet D, Wanless S, Carss DN, Linton D, Speakman JR, Harris MP, Le Maho Y, 2001. Foraging energetics of Arctic cormorants and the evolution of diving birds. *Ecol. Lett.* 4: 180–184.
- Guillemette M, Ydenberg RC, Himmelman JH, 1992. The role of energy intake rate in prey and habitat selection of common

- iders *Somateria mollissima* in winter: a risk-sensitive interpretation. *J. Anim. Ecol.* 61: 599–610.
- Harris MP, Wanless S, 1993. The diet of shags *Phalacrocorax aristotelis* during the chick-rearing period assessed by three methods. *Bird Study* 40: 135–139.
- Hislop JRG, Harris MP, Smith JGM, 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed upon by seabirds. *J. Zool., London* 224: 501–517.
- Johnsgard PA, 1993. *Cormorants, Darters, and Pelicans of the World*. Washington, DC: Smithsonian Institution Press.
- Kooyman GL, 1989. *Diverse Divers*. Berlin: Springer-Verlag.
- Montevocchi WA, Piatt J, 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. *Comp. Biochem. Physiol.* 78A: 15–20.
- Pauly D, Trites AW, Capuli E, Christensen V, 1998. Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* 55: 467–481.
- Pennycuik CJ, 2001. Speeds and wingbeat frequencies of migrating birds compared with calculated benchmarks. *J. Exper. Biol.* 204: 3 283–3 294.
- Rijke AM, 1968. The water repellency and feather structure of cormorants *Phalacrocoracidae*. *J. Exper. Biol.* 48: 185–189.
- Schmid D, Grémillet D, Culik BM, 1995. The energetic costs of under-water swimming in cormorants. *Mar. Biol.* 123: 875–881.
- Schoener TW, 1987. A brief history of optimal foraging ecology. In: Kamil AC, Krebs JR, Pulliam HR ed. *Foraging Behavior*. New York: Plenum Press, 5–67.
- Storch S, Grémillet D, Culik BM, 1999. The telltale heart: a non-invasive method to determine the energy expenditure of incubating great cormorants *Phalacrocorax carbo carbo*. *Ardea* 87: 207–215.
- Van Pelt TI, Piatt JF, Lance BK, Roby DD, 1997. Proximate composition and energy density of some North Pacific forage fishes. *Comp. Biochem. Physiol.* 118A: 1 393–1 398.
- Wilson RP, Wilson M-P, 1988. Foraging behaviour in four sympatric cormorants. *J. Anim. Ecol.* 57: 943–955.
- Wilson RP, Hustler K, Ryan PG, Burger AE, Nöldecke EC, 1992. Diving birds in cold water: do Archimedes and Boyle determine energetic costs? *Amer. Nat.* 140: 267–275.
- Wilson RP, Pütz K, Grémillet D, Culik BM, Kierspel M, Regel J, Bost C-A, Lage J, Cooper J, 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *J. Exper. Biol.* 198: 1 115–1 135.
- Wilson RP, Grémillet D, 1996. Body temperatures of free-living African penguins (*Spheniscus demersus*) and bank cormorants (*Phalacrocorax neglectus*). *J. Exper. Biol.* 199: 2 215–2 223.
- Wilson RP, Peters G, Regel J, Grémillet D, Pütz K, Kierspel M, Weimerskirch H, Cooper J, 1998. Short retention time of stomach temperature loggers in free-living seabirds. Is there hope in the spring? *Mar. Biol.* 130: 559–566.
- Ydenberg RC, Clark CW, 1989. Aerobiosis and anaerobiosis during diving in the western grebes: an optimal foraging approach. *J. Theor. Biol.* 139: 437–449.