

Modeling the Marine Resources Consumed in Raising a King Penguin Chick: An Energetics Approach

L. G. Halsey^{1,*}

P. J. Butler²

A. Fahlman³

C.-A. Bost⁴

A. J. Woakes²

Y. Handrich⁵

¹School of Human and Life Sciences, Roehampton University, Holybourne Avenue, London SW15 4JD, United Kingdom; ²Centre for Ornithology, School of Biosciences, University of Birmingham, Edgbaston B15 2TT, United Kingdom; ³North Pacific Universities Marine Mammal Research Consortium, University of British Columbia Marine Mammal Research Unit, 2202 Main Hall, V6T 1Z4 Vancouver, British Columbia, Canada; ⁴Centre d'Etude Biologiques de Chizé-Centre National de la Recherche Scientifique (CNRS), Villiers en Bois, 79360 Beauvoir Sur Niort Cedex, France; ⁵Institut Pluridisciplinaire Hubert Curien, Unité Mixte de Recherche 7178 CNRS-Université Louis Pasteur, Département Ecologie, Physiologie et Ethologie, 23 rue Becquerel, F-67087 Strasbourg Cedex 02, France

Accepted 8/26/2008; Electronically Published 10/21/2008

ABSTRACT

Accurate estimates of penguin energetics would represent an important contribution to our understanding of the trophodynamics of the Southern Ocean ecosystem and our ability to predict effects of environmental change on these species. We used the heart rate–rate of oxygen consumption technique to estimate rate of energy expenditure in adult king penguins raising a chick, in combination with data from the literature on changes in adult mass, chick energy requirements, and prey energy density. Our model estimated a variety of energetic costs and quantities of prey consumption related to raising a king penguin chick during the austral summer. The total energy requirements of a king penguin chick at the Crozet Archipelago from hatching until reaching a mass of 8 kg 90 d later is 271 MJ, representing the consumption of 38.4 kg of myctophid fish. A successfully breeding male requires 0.78 kg d⁻¹ of fish

during the entirety of the incubation period and 1.14 kg d⁻¹ during the subsequent 90 d of chick rearing. Assuming the same energy requirements for females, the estimated 580,000 pairs of king penguins that breed successfully at Crozet each year, together with their chicks, consume a total of around 190,000 tons of fish during the incubation and summer rearing periods combined. If, due to depletion of fish stocks, the diet of breeders and chicks during the summer becomes identical to the typical diet of adults during the austral winter, the mass of prey required by both adults and chicks combined (where the chick still reaches 8 kg after 90 d) would increase by more than 25%.

Introduction

In marine ecosystems, seabirds are predators in the upper trophic level and are sensitive indicators of changes in ocean environments (Jenouvrier et al. 2005). Studies in both the Northern and Southern Hemispheres have successfully related changes in seabird demographics to variations in climate that affect marine resources over large timescales (Fraser et al. 1992; Barbraud and Weimerskirch 2001; Croxall et al. 2002). Where interests lie in understanding changes in marine resources, several authors have suggested that these may be achieved more accurately, and certainly more cost effectively, by using seabirds as indicators of changes in prey stocks rather than by using research vessels to sample the prey stocks themselves (Cairns 1992; Bost et al. 1994; Croxall et al. 2002; Piatt et al. 2007).

However, whereas there are now many examples of trends in availability of marine resources being inferred from changes in seabird populations (Croxall 1992; Croxall et al. 2002; Weimerskirch et al. 2003; Jenouvrier et al. 2005), such trends can only be detected after many years (Bost and Le Maho 1993; Weimerskirch et al. 2003). Trends can also be inferred by measuring variables associated with breeding success, such as chick feeding rates, adult and chick masses, and fledging success (Prince and Walton 1984; Wilson 1984; Le Maho et al. 1993; Grémillet et al. 2000; Boyd and Murray 2001; Croll et al. 2006; Durant et al. 2006; Piatt et al. 2007). However, a more accurate and quantified assessment of the marine resources consumed by seabird species can be obtained from modeling their energy needs on the basis of the energy requirements of chicks and their parents and the energy densities of the prey they consume. At the population level, energy requirements can identify the impact of species in an ecosystem (i.e., how much of the pri-

* Corresponding author. E-mail: lhalsey@roehampton.ac.uk.

mary production of an ecosystem is utilized by the populations of those species; Green et al. 2002).

Penguins are key components of the Southern Ocean food web (Brooke 2004). The world population of king penguins (*Aptenodytes patagonicus*) represents the third largest proportion of penguin biomass in the Southern Ocean ecosystem, with nearly 50% of individuals inhabiting the Crozet Archipelago (Woehler 1995). Crozet is an important location in terms of prey consumption and energy and carbon fluxes (Guinet et al. 1996). This means that estimates of marine resources utilized by king penguins in this region would represent an important contribution to our understanding of the trophodynamics of the Southern Ocean ecosystem and of the role of king penguins as consumers within this particular region (Woehler 1995). Such knowledge would also enable predictions of some of the future effects of possible environmental change on king penguin populations (Wikelski and Cooke 2006).

Clearly, model estimates of resource consumption are only as accurate as the data they include and the assumptions on which they are based. Thus, where such estimates are at least in part based on calculations of energy expenditure, it is necessary that those calculations be as exact as possible (Froget et al. 2004). Indeed, uncertainty in energy expenditure can produce particularly large errors in models of population food consumption (Winship et al. 2002), and accurately estimating energetics in the field is still difficult (Brooke 2004). However, the heart rate–rate of oxygen consumption ($f_H \cdot \dot{V}O_2$) technique (Butler 2004) enables metabolic rate to be estimated in terms of $\dot{V}O_2$ from measures of f_H over periods of many months. It is possible for the estimates to be validated by comparing them with directly measured $\dot{V}O_2$ values. Coupled with information on changes in body mass (Le Maho et al. 1993), the energy balances of adult birds can be estimated. Furthermore, recent data in combination with those from previous studies now provide sufficient details to accurately model the total energy requirements of growing king penguin chicks (e.g., Barré 1978; Heath and Randall 1985; Cherel et al. 1993; Verrier 2003; J.-P. Robin, unpublished data).

The penguin breeding cycle consists of four main stages: courtship, incubation and chick rearing, chick creching, and fledging. During the periods of egg incubation and chick rearing, until maximum fat levels are reached by the chick (i.e., approximately through the austral summer), consumption of marine resources by penguins—and thus their impact on the ecosystem—is relatively high (Brown 1987; Chappell et al. 1993; Boyd 2002; Croll et al. 2006). Furthermore, because of the constraints that returning to the colony to relieve the partner imposes on the distances that seabirds can travel in search of prey (e.g., Charrassin and Bost 2001), foraging areas are relatively small at these times of year. This potentially leads to localized depletion of prey. King penguins are the most specialized of the Antarctic and sub-Antarctic seabirds in terms of their diet (Cherel et al. 1996). This is exemplified at Crozet, where king penguins have a diet that consists almost exclusively of mesopelagic fish during the summer months (Cherel and

Ridoux 1992; Bost et al. 1997). These fish have particularly high lipid contents and, therefore, high energy contents (7.0 kJ g^{-1} of wet mass; Cherel and Ridoux 1992). However, king penguins will also hunt other prey when necessary; for example, those breeding at the Falkland Islands have a large proportion of squid in their diet. Squid have a lower energy value; those ingested by king penguins provide, on average, 5.6 kJ g^{-1} (Cherel and Ridoux 1992).

In our study, we used the $f_H \cdot \dot{V}O_2$ technique to estimate rates of energy expenditure in king penguins raising a chick, here defined as egg production, incubation, and rearing the hatched chick, where rearing occurs until the chick obtains maximum fat levels (i.e., at about 3 mo of age). With these data, in combination with data from the literature on changes in adult mass, chick energy requirements, and prey energy density, we modeled the energetic costs and, thus, the quantities of prey consumption related to raising a king penguin chick in a typical year. We were able to answer the following questions (each successive question comprises a progressively broader array of factors): (1) What are the total energy requirements of a chick from conception until maximum fat levels are reached? (2) What is the energy expenditure and, thus, the fish consumption for digestion and absorption of an adult king penguin while incubating an egg and while rearing a chick? (3) What are the total energy requirements to raise a chick (including the cost of egg production, the energy expenditure of the chick, and the energy expenditure of the parents during incubation and rearing)? What quantity of fish does this represent? (4) What is the total consumption of marine resources by the population of king penguins that successfully breed during a typical summer in the Crozet region?

Adjusting variables within the model enabled us to model the marine resources consumed when raising a chick under different environmental conditions and to answer the following questions: (1) How do the growth rates of chicks vary with the amount of fish prey provided to them? (2) How do the amounts of prey provided to the chick and prey digested and absorbed by the adults vary as the types of available prey vary?

Material and Methods

Ethical approval for all procedures was granted by the ethics committee of the French Polar Research Institute (IPEV) and of the Ministère de l'Environnement et du Développement Durable (Paris). We also followed the provisions of the United Kingdom Animal (Scientific Procedures) Act 1986, especially those set out by the Home Office in the Official Guidance on the operation of the act.

Study Birds

Fieldwork was performed on Possession Island ($46^{\circ}25'S$, $51^{\circ}45'E$), Crozet Archipelago, during two field seasons over consecutive austral summers (2002–2003, 2003–2004). Male king penguins were captured and equipped with a data logger.

The selected penguins were incubating eggs at the colony of La Baie du Marin. A total of 32 birds were captured between November 2002 and January 2003 and between December 2003 and March 2004 (mean mass \pm SEM, 14.3 ± 0.1 kg). They were each implanted with a transponder tag and a custom-built heart rate and depth data logger (see Woakes et al. 1995 for the basic design), as described in Froget et al. (2004) and Fahlman et al. (2005). Immediately after surgery, birds were returned to the exact site from where they had been captured and their eggs were returned to them. The implantation was performed at least 2 d after the egg exchange with the female, so that each bird was settled on its egg and therefore continued to incubate after the disturbance of handling and surgery. Females could not be implanted because, shortly after egg laying, the female goes to sea and would not have had time to fully recover from the surgery. The implanted birds each undertook a foraging trip at sea 15–20 d later, after exchanging the egg with the returning female.

To aid in identifying birds, a fish tag was attached to the back of each bird and a picric acid mark was applied to its chest. Twice-daily observations were made of each implanted bird's egg or chick to determine when the implanted birds were onshore and when they were at sea. Recapture of the birds and removal of the data loggers were undertaken either in the same season of deployment or in the following season. The procedures for the removal of the data loggers were similar to those for implantation. Because of failures of the automatic identification system at the colony, only 20 of the 32 implanted birds were located and recaptured. Of the 20 data loggers that were retrieved, heart rate data were recorded and could be extracted from 12. Of these 12, eight data loggers were implanted shortly after egg laying and thus provided data for the majority of the period of incubation, whereas six of these 12 data loggers provided data from the whole period of chick rearing. Date of egg laying for the eight birds ranged from November 22 to December 27, and the range of egg hatching was January 15–February 19.

Data Loggers

The data loggers (30 mm \times 25 mm \times 15 mm; 30 g, <1% of the mean body mass of a king penguin) contained 16–64 MB of memory, were able to record f_H and hydrostatic pressure (to an accuracy of a depth of 1 m), and were programmed to record these measurements at a frequency of 1 Hz. The data loggers were encapsulated in wax and coated with medical-grade silicone rubber. Before implantation, a data logger was bathed in a cold sterilizing solution for 1–2 h and then rinsed thoroughly with sterile saline solution.

Data Analysis

After retrieval, data from all loggers were downloaded onto a computer and extracted, prepared, and analyzed using purpose-written computer programs in Matlab (ver. 6.0, MathWorks).

For each bird, estimated mean $\dot{V}O_2$ was calculated from mean f_H for the two periods of incubation and chick rearing. This was achieved using conversion equation (1) derived in Fahlman et al. (2004), which is suitable for king penguins while they are both on land and at sea (Halsey et al. 2007a). Conversion equation (1) in Fahlman et al. (2004) includes the number of days ashore, t , as a predictor variable, as well as f_H . During periods when the bird is at sea, $t = 0$. Observational data on the presence or otherwise of the implanted birds on shore and the pressure data recorded by the data loggers (indicating when the birds were diving at sea) enabled the calculation of t .

Modeling Energetic Costs

King penguins incubate an egg for 51–54 d (Handrich 1989; Weimerskirch et al. 1992). Shortly after the egg is laid (typically in December or January), the female exchanges the egg with the male and goes to sea to forage and increase body reserves while the male stays ashore and incubates (termed shift 2). While ashore, the male is fasting and is thus losing body mass. The female returns to relieve the male usually approximately 2 wk later. The male now goes to sea to forage while the female incubates the egg (shift 3; Weimerskirch et al. 1992). Typically by the end of shift 4, that is, when the female has relieved the male for a second time, the chick has hatched (Gauthier-Clerc et al. 2000). A chick is brooded for 30–40 d, during which time it is fed regurgitated, undigested prey (hence, prey consumption for digestion and absorption by parents must be distinguished) and protected alternately by each parent. The parents again alternate tending to the chick and foraging at sea. After the brooding period, the chick is left unattended in the colony for part of the time and the parents visit the chick to feed it more briefly than before (Weimerskirch et al. 1992). During this period (usually in March or April; Stonehouse 1956) the chicks form creches, creating groups with other chicks (e.g., Stonehouse 1960; Barrat 1976). The chicks obtain maximum fat levels about 90 d after hatching, losing mass during the subsequent winter months when food provisioning by the parents is scarce.

The energy requirements (E) modeled in our study include those directly involved in egg production, those of the chick, and those of the adult pair during incubation and rearing:

$$E_{\text{total}} = E_{\text{egg}} + E_{\text{chick}} + E_{\text{adults incubation}} + E_{\text{adults rearing}}$$

Energetic Requirements of Egg Production (E_{egg})

The average mass of a king penguin egg is 302 g (Barrat 1976), and therefore, it has a total energy value of 2,013 kJ on the basis of calculations given by Sotherland and Rahn (1987). Assuming an assimilation efficiency of 75% (Adams 1992), the energetic cost of egg production is 2,677 kJ. The cost of courtship, which occurs before mating, is not considered.

Energy Requirements of a Growing Chick (E_{chick})

The total average mass of hatchlings is 226 g (Barrat 1976), which includes the remaining yolk, which is consumed by the chick during the first 2 d after hatching (Adams 1992). Subsequently, the chick is dependent on food provided by the parents. The energetic requirements of the chick can be simplified into two categories, for body maintenance/activity and for growth. Barré (1978) provides estimates of metabolic rate in king penguin chicks in terms of $\dot{V}O_2$ and based on body mass. The mass growth curves of king penguin chicks can vary considerably, depending on location (Barrat 1976), year (Verrier 2003), and time of year of hatching (van Heezik et al. 1993; Verrier 2003). On the basis of studies including body mass data for king penguin chicks at Crozet (Barrat 1976; Barré 1978; Cherel et al. 1993; Verrier 2003) and the average time of year of hatching for the birds in our study, we have assumed that chicks attain a mass of 8 kg by 90 d after hatching. The shape of the growth curve for king penguins is consistent and is typical for seabirds (Cherel and Ridoux 1992). Therefore, we used the growth curve shape for king penguins provided in Stonehouse (1960; Fig. 1a).

Values of metabolic rate represent the energy costs of maintenance/activity and tissue deposition but do not account for the energy value of the deposited tissues (Brown 1987). Body composition of chicks changes as the chicks grow, which means that the energy equivalence per gram of accumulated body tissue also changes. The bodies of chicks at the start of the creche period are composed of, on average, 33.6% fat and 15.1% protein (Cherel et al. 1993), whereas at hatching they are only around 5% body fat and about 20% protein (J.-P. Robin, personal communication, from unpublished data). It was assumed that the proportional changes in body composition in growing chicks were linear over the 90-d period from hatching until maximum fat levels were reached. Energy equivalence of lipids and protein (muscle) were taken to be 38 kJ g^{-1} and 20 kJ g^{-1} , respectively (Brown 1987; Fig. 1b).

Chicks at Crozet are fed a diet of almost exclusively myctophid fish during the summer (Cherel and Ridoux 1992; Bost et al. 1997). The composition of myctophids found in the stomach contents of adults at Crozet over the summer have a similar nutritional content to the anchovies fed to the chicks of jackass penguins (*Spheniscus demersus*; Heath and Randall [1985] report an assimilation efficiency of 0.78 increasing to 0.88 as the chicks develop). Combination of the growth curve with the modeled changes in body composition over time provided an estimate of the energy equivalence of tissue accumulated per day after hatching. The total energy input required by the chick each day during the rearing stage was initially calculated by summing metabolic rate and the energy equivalence of tissue accumulated. Second, an assimilation efficiency was applied (Fig. 2). The values used were those reported by Heath and Randall (1985; 0.78–0.88). These authors did not account for metabolic fecal and endogenous urinary energy in their calculations of assimilation efficiency, although this should rep-

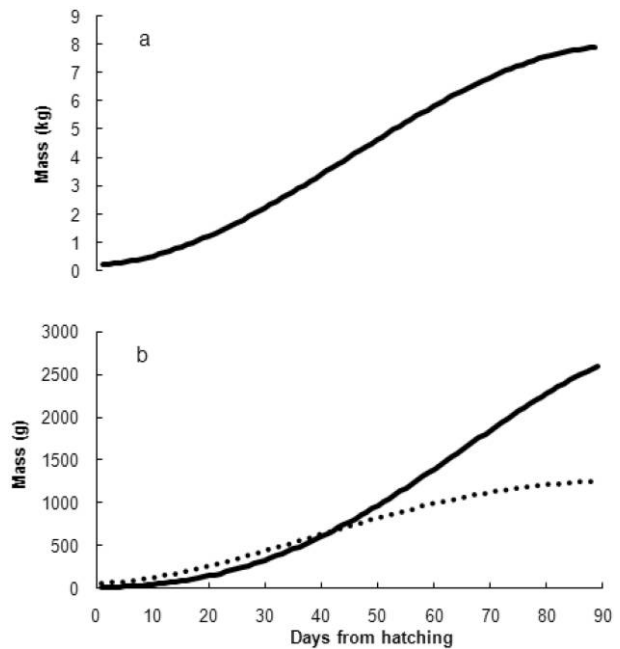


Figure 1. Modeled growth curves of a king penguin chick during the 90 d until maximum fat levels are reached. *a*, Body mass assuming a final mass of 8 kg (based on the growth curve shape of Stonehouse 1960). *b*, Body tissue mass assuming a final mass of 8 kg; solid lines represent lipids; dotted line represents proteins.

resent a small error (Miller and Reinecke 1984). Finally, the amount of myctophid fish required per day to supply these energy requirements was calculated, given that the energy density of the stomach contents of an adult king penguin at Crozet during the summer is 7.0 kJ g^{-1} (Cherel and Ridoux 1992).

Energetic Requirements of Parents ($E_{adults\ incubation} + E_{adults\ rearing}$)

The metabolic rate of adult male king penguins, in terms of $\dot{V}O_2$, was estimated from measurements of heart rate. Standard errors of the estimates were calculated using the procedures described in Froget et al. (2004). Values of $\dot{V}O_2$ were converted to rates of energy expenditure assuming that 1 mL $O_2\ s^{-1} = 19.8\ W$ during time ashore (Culik et al. 1996; Froget et al. 2004) and that 1 mL $O_2\ s^{-1} = 18.9\ W$ during time at sea (Bevan et al. 2002; Froget et al. 2004). Mean rates of energy expenditure for incubation and chick rearing, along with their estimate errors, were included in the calculations of energy required to raise a chick.

To estimate the combined total energy requirements of both parents in raising a chick, it was assumed that, across the entire period of egg incubation and chick rearing together, the male and female expended similar amounts of energy. These assumptions are reasonable given that, over the entire summer breeding season, the activity time budgets of the two parents are similar (Jouventin et al. 1994; Guinet et al. 1997; Descamps et al. 2002; Pütz and Cherel 2005). This is in contrast, for

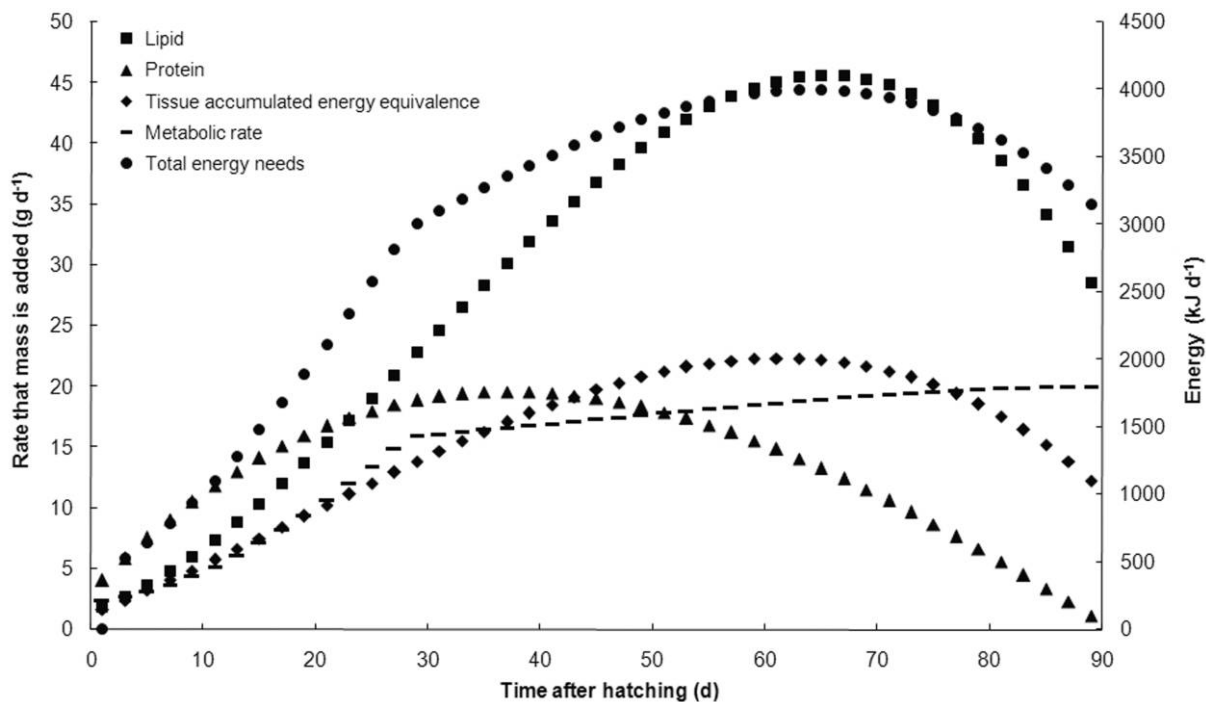


Figure 2. Modeled changes in tissue accumulation and metabolism of a king penguin chick during the 90 d until the chick obtains maximum fat levels. Squares represent estimated mass of lipids added (g d^{-1}); triangles represent estimated mass of muscle protein added (g d^{-1}). The energy equivalence of these accumulated tissues is represented by diamonds (kJ d^{-1}). Horizontal dashes represent metabolic rate (kJ d^{-1}) derived using equations presented in Barré (1978); circles represent estimated total energy needs of the chick from the parents (i.e., after eating the egg yolk; kJ d^{-1}).

example, to macaroni penguins (Green et al. 2002, 2005). Male and female king penguins also have similar feeding ecologies (Cherel and Ridoux 1992; C.-A. Bost, unpublished data). Furthermore, whereas females tend to have slightly lower body masses than males (Handrich et al. 1995; Gauthier-Clerc et al. 2001), there is no difference in the $\dot{V}\text{O}_2$ - f_{H} relationship between male and female king penguins, at least when accounting for mass and fasted duration (Fahlman et al. 2004). Finally, the body masses of females change from month to month in similar proportions to those of males (Handrich et al. 1995).

Body Mass Changes in Adults

King penguins are able to store large quantities of energy as lipids and protein, which are metabolized (predominantly the lipids) during periods of fasting. Changes in body composition of penguins have not been studied during periods of foraging activity, but they have been studied during fasts. Gauthier-Clerc et al. (2001) report the mean body masses of male king penguins at the time of mating when they first return from a foraging trip at sea (12.9 kg) and at the time of their first subsequent departure to sea after having been relieved by the female (10.4 kg). From these data, it is possible to calculate a rate of body mass loss in males during this fasting period ($0.13 \text{ g kg}^{-1} \text{ d}^{-1}$). This value is similar to the rate of body mass loss in males reported by Gauthier-Clerc et al. (2002) and Fahlman

et al. (2004) during fasts in other situations, suggesting that rate of body mass loss is consistent at different times of the year and, thus, the calculated value can be used to estimate body mass at specific times ashore during the summer breeding season. Males are estimated to experience a net loss in body mass of 0.8 kg between the start of incubation and the end of their second incubating period ashore, that is, about the time that the egg typically hatches. Thus, during the incubation period, the adult male does not obtain all of its required energy from digested and absorbed prey, as some is supplied from body reserves.

King penguins also gain mass during certain breeding periods. Indeed, apart from the incubation period for males, breeding king penguins typically exhibit a progressive increase in body mass through the summer from one month to the next (Le Maho et al. 1993), which totals around 1.8 kg between January and April (Handrich et al. 1995). In these cases, estimates of energy intake are evaluated by calculations of metabolism and also by the energy equivalence of the accumulated tissue. As in Green et al. (2007), it was assumed that water, protein, and lipids were added to body reserves in the same proportions in which they were catabolized. Lipids account for 47% of mass lost during periods of fasting in king penguins (Cherel et al. 1994); therefore, it is assumed that protein and water account for the remaining 53% lost. Given that the lipid content of the prey

Table 1: Estimated rate of oxygen consumption (\pm SEE) and energy obtained (with confidence limits) by male king penguins during the 54-d incubation period ($n = 8$) and the subsequent 90 d of chick rearing ($n = 6$)

Parameter	Incubation	Rearing
$\dot{V}O_2$ (mL O ₂ min ⁻¹)	184.4 (+19.7, -17.7)	228.9 (+25.7, -23.1)
Mean amount of fish digested and absorbed per day (kg d ⁻¹)	.78 (.64, .93)	1.14 (.96, 1.34)
Energy obtained from fish per day (MJ d ⁻¹)	5.1 (4.6, 5.6)	6.4 (5.7, 7.1)

eaten by king penguins is 8.8% (Cherel and Ridoux 1992), it is estimated that, for each gram of prey consumed beyond that required for maintenance, the bird experiences an increase in mass of 0.187 g (0.088 g of lipid, plus protein and water, with a combined mass of $0.088/47 \times 53 = 0.099$ g). From this, the amount of prey consumed to provide the mass of tissue accumulation can be estimated.

Thus, the amount of fish digested by an adult over a period of time can be calculated from estimates of metabolic rate by accounting for the change in body mass over this period. The assimilation efficiency of a penguin feeding on myctophid fish is taken to be 0.88 and again to apply a prey energy density of 7.0 kJ g⁻¹ (Heath and Randall 1985; Cherel and Ridoux 1992).

Population Consumption of Marine Resources

The calculated total energy requirements to raise a chick were then combined with estimates of the breeding population at Crozet to estimate resource consumption at the population level. There are large variations in the breeding successes of king penguins each year (Weimerskirch et al. 1992; Viera et al. 2006). However, on the basis of other studies, Brodin et al. (1998) concluded that, on average, king penguins have a 50% rate of breeding success from egg laying to the end of the winter fast in October. King penguins have a hatching success of around 95% (S. Durand, personal communication). Thus, we assume the percentage success rate at incubating and rearing a chick to the creche to be 72.5%; that is, half of the chicks that will die by the end of the winter are lost by this stage. The annual breeding population each year in the Crozet region is about 800,000 pairs (Guinet et al. 1995); therefore, the population that breeds successfully to the end of the winter is estimated to be 580,000 pairs.

Modeling Different Environmental Conditions

The calculated energetic values for breeding pairs and their chicks, as described above, formed the basis of a simple modeling of the effects of variations in the environment on the marine resources extracted by king penguins from that environment. This was achieved, for example, by changing values of prey energy density and assimilation efficiency to represent a change in available prey type.

Statistics

For each set of environmental conditions that were modeled, including for a typical year, three iterations of the model were run. For the first iteration, each variable was set to model that condition. Second, each variable was set at 1 SE or, where this information was not available in the literature from where the variable value had been obtained, at a 10% change from the mean in the direction that resulted in a decreased estimate of overall energy uptake (and, thus, prey uptake). Third, the directions of the variability were reversed for each variable. The minimum and maximum values provided by the second and third iterations represent confidence limits (CL) around the estimates of the energetic costs of raising a chick for each environmental condition modeled (Grémillet et al. 2003; Green et al. 2007).

To look for differences in estimates of mean $\dot{V}O_2$ for adult king penguins, a form of the proximate normal test for comparing the differences between two estimates was used (Green et al. 2001). Differences were considered to be statistically significant when $Z > 1.96$ (i.e., $P < 0.05$).

Results

A Typical Year

The total energy requirement of a king penguin chick at Crozet, which reaches 8 kg in mass within 90 d, is 271 MJ (CL = 227, 320). This includes the cost of egg production by the mother, metabolism, energy equivalence of accumulated tissue, and assimilation efficiency. The mass of fish consumed by such a chick from hatching to reaching maximum fat levels within 90 d is 38.4 kg (CL = 31.6, 46.0).

Because the standard errors around the estimates of $\dot{V}O_2$ for king penguins are fairly large, differences between mean values of $\dot{V}O_2$ can sometimes be large without being significantly different (Halsey et al. 2007b). This is the case for mean $\dot{V}O_2$ of adult king penguins in our study during the incubation period and the rearing period (Z -test, $Z = 1.47$; Table 1). Nevertheless, when taking mass change into account, a breeding male at Crozet requires a total of 42.1 kg (CL = 34.8, 50.4) of fish during the incubation period and a total of 102.8 kg (CL = 86.8, 120.7) during the first 90 d of the chick rearing period. Table 1 provides values of energy expenditure, daily fish consumption (in terms of digestion and absorption), and energy obtained from those fish.

Table 2 provides details of the total and daily amounts of energy metabolized by a breeding pair of king penguins and the fish digested and absorbed to provide this energy, accounting for changes in body mass. The summation of these costs plus the energy requirements of the chick and the cost of egg production (i.e., E_{total} , the total energy involved in raising a chick) is 2,105 MJ (CL = 1,871, 2,343). This equates to a total fish consumption of 328.6 kg (CL = 275.2, 388.5) associated with raising a chick. Figure 3 provides a schematic summary of the model to estimate the energy costs and fish consumption involved in raising a king penguin chick. On the basis of estimates derived from the present model for a typical summer breeding season, 190,606 tons of fish (CL = 159,612, 225,326) are consumed throughout the summer breeding season by the population of king penguins in Crozet that successfully raises chicks.

Different Environmental Conditions

When the mass of the chick after 90 d is set at 6 kg, chicks are estimated to consume 10.0% (CL = 9.8, 10.1) of the fish ingested by their parents, whereas when mass at maximum fat levels is set at 12.2 kg, they consume 15.0% (CL = 14.7, 15.2). If the chicks at Crozet are provided with the same diet in the summer as in the winter, a chick would require 48.8 kg (CL = 40.2, 58.6) of prey over 90 d and adults would digest and absorb 364.1 kg (CL = 304.6, 431.0) of prey during the incubation and rearing periods. Figure 4 shows the changing quantity of prey required by a chick and by a breeding pair while raising a chick as the foraging diet varies.

Discussion

Our study uses a validated method (Fahlman et al. 2004; Halsey et al. 2007a) to obtain estimates of energy expenditure in adult king penguins; these estimates, combined with data on the energy requirements of king penguin chicks, are used to estimate the energy costs of raising a chick through the summer breeding season and the associated amount of prey consumed. From these results, it is possible to estimate the differences in energy expenditure and prey consumption associated with raising a chick under different hypothetical environmental conditions (e.g., certain changes in prey diversity or rates of chick growth). It is also possible to produce estimates of the total consumption of marine resources in the region of Crozet by the population of successfully breeding king penguins. These

are crucial steps toward a quantified understanding of the role of and the pressures exerted by king penguins in the Southern Ocean ecosystem. These calculations also provide a basis for an understanding of the energy balance and resource consumption that might be required of king penguins in the face of certain environmental changes. First, however, it is important to assess the validity of our model on the basis of previous relevant estimates of energetics.

Our study estimates that energy consumption of a breeding king penguin during incubation and chick rearing combined is 5.9 MJ d^{-1} . This agrees with the predictive allometric equation in Nagy et al. (1999) for the field metabolic rate of seabirds living in cold environments (6.3 MJ d^{-1} for a bird of 12.7 kg, the approximate mean mass for a breeding king penguin during the rearing period; Handrich et al. 1995). As would be expected given their larger size (McKechnie and Wolf 2004), the average mass-specific metabolic rate of breeding king penguins is lower than that estimated for breeding macaroni and jackass penguins (71% and 82%, respectively; Nagy et al. 1984; Green et al. 2002). Finally, our findings show that the energy expended per day by the male parent during the incubation period is considerably lower than it is during the rearing period. This is expected for a number of reasons. The first main reason is the large proportion of time that the male spends ashore, and is thus relatively inactive, during the incubation period compared with the rearing period (63.9% and 50.5%, respectively; calculated from data in Weimerskirch et al. 1992). The second main reason is the larger mean mass of the male during the rearing period (Gauthier-Clerc et al. 2001); for example, in the study of Handrich et al. (1995), breeding male birds weighed 12.7 kg on average during rearing from March to April and significantly less (11.9 kg) during incubation from December to January.

Cherel and Ridoux (1992) calculated the mean rate of energy uptake by a king penguin chick between 3 and 4 wk of age to be 2.2 MJ d^{-1} . This was based on direct measurements of the quantity and calorific content of the prey provided by the parents and can thus be assumed to be accurate. This is similar to the value of 2.5 MJ d^{-1} for total energy requirement estimated for the same period in our study. The metabolic rate of king penguin chicks continues to increase throughout the rearing period until the chicks obtain maximum fat levels, after about 90 d (Barré 1978), which is expected given that the chick is constantly growing. However, the modeling of chick body composition in our study predicted that the energy equivalence of tissue accumulation per day would decrease beyond 62 d (and,

Table 2: Estimates of total energy metabolism and total fish consumption for digestion and absorption (with confidence limits) of breeding pairs of king penguins during the 54-d incubation period ($n = 8$) and the subsequent 90 d of chick rearing ($n = 6$)

Parameter	Incubation	Rearing
Energy metabolized per day (MJ d^{-1})	10.2 (9.2, 11.2)	12.8 (11.4, 14.1)
Total energy metabolized (MJ)	550.9 (495.0, 606.7)	1,147.8 (1,025.6, 1,270.1)
Total fish digested and absorbed (kg)	84.3 (69.6, 100.7)	205.6 (173.7, 241.4)

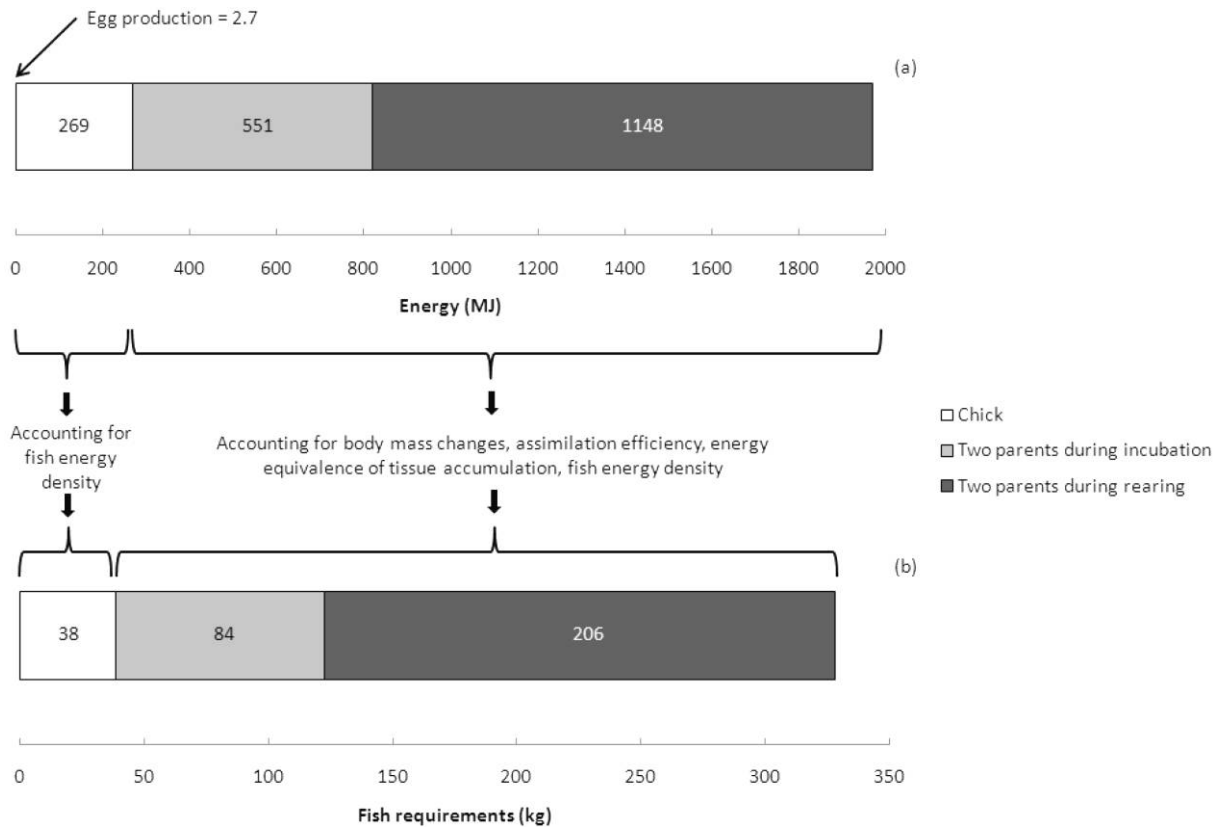


Figure 3. Summary explanation of the model to estimate total energy costs and fish consumption associated with raising a king penguin chick. *a*, Estimated costs of egg production on the basis of egg size, modeled total energy requirements of the chick during incubation and rearing, and total energy expenditure of two parents during incubation and chick rearing estimated from heart rate data. *b*, Estimated quantity of total fish consumption by the chick from total energy requirements, factoring in fish energy density. Estimated quantity of total fish consumption during incubation and chick rearing by two parents from total energy expenditure, factoring in body mass changes, prey assimilation efficiency, energy equivalence of tissue accumulation, and fish energy density.

thus, the predicted rate of food required would decrease soon afterward; Fig. 2). This is in accordance with trends in energy expenditure measured in macaroni and rockhopper penguin chicks (Brown 1987). The energy expenditure and, therefore, the quantity of fish required by a growing king penguin chick from hatching until full fat accumulation is similar to that of a single parent during the same period (Fig. 3). This is surprising, given that the average size of the chick is much smaller than that of an adult and that the former generally behave less energetically than the latter. Figure 2 suggests that it is the energy equivalence of tissue accumulation that increases the energetic costs of chicks to surprisingly high values.

The various energetic values calculated in our study are generally similar to relevant estimates from earlier studies. Given the increased detail and use of the most up-to-date data, our calculations are reasonably the most valid estimates of king penguin energetics and, therefore, of resource consumption by this species during breeding.

Consumption of Marine Resources at the Population Level

For a typical summer breeding season, 190,606 tons of fish are consumed by the population of king penguins at Crozet that

successfully raise chicks. This is about 15% of the total prey consumed over the annual cycle by the 800,000 pairs of king penguins attempting to breed at Crozet each year, according to the predictive calculations in Woehler (1995). In contrast, it is about 24% of the total prey consumed for a similar population size as estimated by Guinet et al. (1996). A percentage of around 29% might be predicted (chick rearing lasts 144 d, which is 40% of a year, $72.5\% \text{ of } 40\% = 29\%$). Thus, 15% is rather low, particularly given that successful breeders are likely to expend more energy in total than are unsuccessful breeders. This most likely suggests that Woehler (1995) overestimated the energy costs of a breeding pair of king penguins, perhaps using estimates from allometric equations and data for other penguin species that cannot be generalized. The percentage associated with the data in Guinet et al. (1996) is also lower but is much closer to the prediction in our study. Guinet et al. (1996) based estimates of annual population food consumption on procedures proposed in Croxall et al. (1984) for calculating energetic costs of individuals. Possibly the most suitable method available for modeling changes in marine resource consumption in response to possible environmental variation

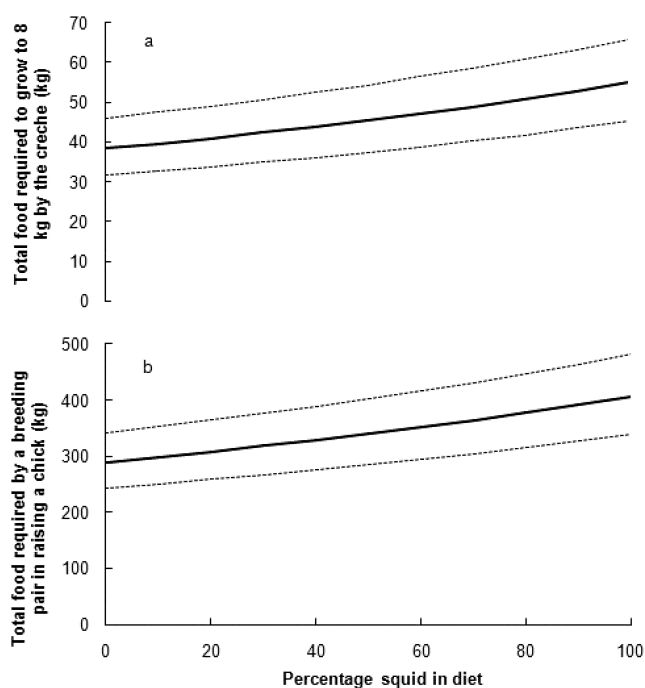


Figure 4. Estimates of the prey required by a king penguin chick (a) during the rearing period to grow to 8 kg and the prey required by a breeding pair (b) to raise a chick (i.e., through the incubation period and the subsequent 90 d of rearing), depending on the proportion of squid in the diet of the parents (otherwise composed of myctophid fish). Dotted lines represent confidence limits.

is an investigation of how changes in some of the variables included in our study affect the calculated energetic values.

Relationship between Growth Rate of Chicks and Amount of Fish Prey Provided to Them

Chick growth rate is driven by parental provisioning; chick food intake has a large effect on final body mass (Boersma 1976; Croll et al. 2006). For example, a chick fed 38.4 kg of fish will grow to 8 kg; in comparison, a chick that finally grew to 12.2 kg after 90 d at South Georgia (Stonehouse 1960), where myctophid fish are also the dominant prey (Woehler 1995), would have required 51.0 kg of food (i.e., 33% more). Chicks that grow larger by the start of the creche period receive a greater allocation of resources; that is, they consume a greater proportion of the fish ingested by their parents. When final mass is 6 kg (which means they are likely just viable enough to survive the winter with continued provisioning), the chicks consume 10.0% of ingested fish compared with 15.0% of fish ingested by the parents when final mass is 12.2 kg. Whether chick growth size is ultimately limited by the ingestion/assimilation capabilities of the chick is unknown.

Relationship of Amount of Prey Provided to Chick and Amount of Prey Digested and Absorbed by Adults, Compared with Types of Available Prey

King penguins at Crozet have a diet that consists almost exclusively of mesopelagic fish during the summer months (Cherel and Ridoux 1992; Bost et al. 1997). However, during winter at Crozet, the diets of adults with chicks consist of only 30% myctophid fish and 70% squid (Cherel et al. 1996). The energy content of myctophid fish is 7.0 kJ g^{-1} , whereas that of squid is 5.6 kJ g^{-1} (Cherel and Ridoux 1992). The assimilation efficiency of squid is also lower (51%–77% vs. 78%–88% for myctophid fish; Heath and Randall 1985). Therefore, if hypothetically, stocks of myctophid fish within the foraging ranges of king penguins at Crozet during the summer were reduced and the breeding birds were only able to provide prey for their chicks in the winter proportions of fish and squid, a chick would require 48.8 kg of prey to grow to 8 kg after 90 d, an increase of 27%. Assuming there were no changes in foraging costs during the summer months (L. G. Halsey and Y. Handrich, unpublished data), adults would consume and digest 364.1 kg of prey, an increase of 26%. Thus, the pressures placed on marine resources around Crozet during the summer by breeding king penguins will increase if those resources are already reduced such that adults respond by foraging in part on squid. Investigations should consider by how much fish availability must decrease to make such a response by king penguins likely.

Future Research Directions

Our model provides the most detailed estimates to date of the total energy costs of a species of breeding seabirds during the austral summer. We now have estimates of the impact of marine resources on successfully breeding king penguins in the southern Indian Ocean, a prerequisite for assessing interactions between marine predators and fisheries (Winship et al. 2002).

Breeding energetics are complex, and our study has shown that insights can be gained using models incorporating bioenergetics and life-history information (Boyd 2002). However, it is the development of such models that highlights relevant areas of research that require further attention if those models are to be fine-tuned for more involved investigations, such as to assess the tolerances of predators to varying energy budgets as a consequence of climate variability (Biuw et al. 2007). A lack of certain information required for a modeled estimate tends to result in an input of estimates and assumptions in lieu of quantified measures. Our model was possible because king penguins are one of the most extensively studied seabird species. Nevertheless, we found that data on certain key aspects of their biology were surprisingly lacking. Most notably, the ontogeny of body tissues has not been studied in the chicks of king penguins, although such data are available for some other penguin species (Brown 1987). Also, records on changes in body mass of adult king penguins during the summer breeding sea-

son and throughout the year are relatively sparse. Detailed information on body mass is vital, in conjunction with measures of energy expenditure, for accurate estimates of prey consumption. A detailed database of body mass changes over time can be developed relatively easily with the use of automatic weighing devices such as those used previously for studies of king penguins (e.g., Le Maho et al. 1993; Handrich et al. 1995).

In the future, we can make simple predictions about possible variations to the pressures imposed by breeding king penguins as their environment changes, and we can evaluate populations in terms of the nutritional stress hypothesis (Winship et al. 2002). This method can be applied to other regions where populations of king penguins exist and can be adapted to other species of penguins. Of course, a more complete picture of the demands on prey by the whole population of king penguins in the region of Crozet would be obtained by including estimates of energy expenditure for both successful breeders and unsuccessful breeders (where presumably the timing of chick abandonment would affect various energy costs) and for periods outside of the summer breeding season. It might be possible to generate useful estimates for the whole Crozet population during the summer via extrapolation of the estimates presented in our study for successful breeders only.

Acknowledgments

This study was mainly funded by a grant from the Natural Environment Research Council, United Kingdom (NER/A/S/2000001074), with financial support also provided by Institut Paul Emile Victor (Plouzané, France). The Company of Biologists and the Society for Experimental Biology awarded funds to support the analysis and writing of this article. We thank J. Green for enlightening us about the possibility of undertaking this study and for his useful input during the development of the analysis and subsequent manuscript. We also thank J.-P. Robin for a number of valuable discussions on the life history of king penguins at Crozet and for his comments on a finalized version of the manuscript. R. Groscolas also kindly commented on the manuscript.

Literature Cited

- Adams N.J. 1992. Embryonic metabolism, energy budgets and cost of production of king *Aptenodytes patagonicus* and gentoo *Pygoscelis papua* penguin eggs. *Comp Biochem Physiol A* 101:497–503.
- Barbraud C. and H. Weimerskirch. 2001. Emperor penguins and climate change. *Nature* 411:183–186.
- Barrat A. 1976. Quelques aspects de la biologie et de l'écologie du manchot royal (*Aptenodytes patagonicus*) des Iles Crozet. *Comité Nationale Française des Recherches Antarctiques* 40: 9–52.
- Barré H. 1978. Dépense énergétique du poussin de manchot royal *Aptenodytes patagonicus* (J.F. Miller) au cours de la croissance. *J Physiol Paris* 74:555–561.
- Bevan R.M., P.J. Butler, A.J. Woakes, and I.L. Boyd. 2002. The energetics of gentoo penguins, *Pygoscelis papua*, during the breeding season. *Funct Ecol* 16:175–190.
- Biuw M., L. Boheme, C. Guinet, M. Hindell, D. Costa, J.B. Charrassin, F. Roquet, et al. 2007. Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proc Natl Acad Sci USA* 104:13705–13710.
- Boersma D. 1976. An ecological and behavioral study of the Galapagos penguin. *Living Bird* 15:43–93.
- Bost C.A., J.Y. Georges, C. Guinet, Y. Cherel, K. Putz, J.B. Charrassin, Y. Handrich, T. Zorn, J. Lage, and Y. Le Maho. 1997. Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser* 150:21–33.
- Bost C.A., P. Koubbi, F. Genevois, L. Ruchon, and V. Ridoux. 1994. Gentoo penguin *Pygoscelis papua* diet as an indicator of planktonic availability in the Kerguelen Islands. *Polar Biol* 14:147–153.
- Bost C.A. and Y. Le Maho. 1993. Seabirds as bio-indicators of changing marine ecosystems: new perspectives. *Acta Oecol* 14:463–470.
- Boyd I.L. 2002. Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *J Appl Ecol* 39:103–119.
- Boyd I.L. and A. Murray. 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *J Anim Ecol* 70:747–760.
- Brodin A., O. Olsson, and C.W. Clark. 1998. Modeling the breeding cycle of long-lived birds: why do king penguins try to breed late? *Auk* 115:767–771.
- Brooke M.D.L. 2004. The food consumption of the world's seabirds. *Proc R Soc B* 271(suppl.):S246–S248.
- Brown C. 1987. Energy requirements for growth and maintenance in macaroni and rockhopper penguins. *Polar Biol* 8: 95–102.
- Butler P.J. 2004. Metabolic regulation in diving birds and mammals. *Respir Physiol Neurobiol* 141:297–315.
- Cairns D.K. 1992. Diving behaviour of black gullmots in northeastern Hudson Bay. *Colon Waterbirds* 15:245–248.
- Chappell M.A., D.N. Janes, V.H. Shoemaker, T.L. Bucher, and S.K. Maloney. 1993. Reproductive effort in Adélie penguins. *Behav Ecol Sociobiol* 33:173–182.
- Charrassin J.-B. and C.-A. Bost. 2001. Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar Ecol Prog Ser* 221:285–297.
- Cherel Y., J.-B. Charrassin, and Y. Handrich. 1993. Comparison of body reserve buildup in prefasting chicks and adults of king penguins. *Physiol Zool* 66:750–770.
- Cherel Y., J. Gilles, Y. Handrich, and Y. Le Maho. 1994. Nutrient reserve dynamics and energetics during long-term fasting in the king penguin (*Aptenodytes patagonicus*). *J Zool (Lond)* 234:1–12.

- Cherel Y. and V. Ridoux. 1992. Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis* 134:118–127.
- Cherel Y., V. Ridoux, and P.G. Rodhouse. 1996. Fish and squid in the diet of king penguin chicks, *Aptenodytes patagonicus*, during winter at sub-Antarctic Crozet Islands. *Mar Biol* 126: 559–570.
- Croll D.A., D. Demer, R. Hewitt, J. Jansen, M.E. Goebel, and B.R. Tershy. 2006. Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (*Pygoscelis antarctica*). *J Zool (Lond)* 269:506–513.
- Croxall J.P. 1992. Southern Ocean environmental changes: effects on seabird, seal and whale populations. *Philos Trans R Soc B* 388:319–328.
- Croxall J.P., C. Ricketts, and P.A. Prince. 1984. Impact of seabirds on marine resources, especially krill, of South Georgia waters. Pages 285–317 in G.C. Whittow and H. Rahn, eds. *Seabird Energetics*. Plenum, New York.
- Croxall J.P., P.N. Trathan, and E.J. Murphy. 2002. Environmental change and Antarctic seabird populations. *Science* 297:1510–1514.
- Culik B.M., K. Pütz, R.P. Wilson, D. Allers, J. Lage, C.A. Bost, and Y. Le Maho. 1996. Diving energetics in king penguins (*Aptenodytes patagonicus*). *J Exp Biol* 199:973–983.
- Descamps S., M. Gauthier-Clerc, J.-P. Gendner, and Y. Le Maho. 2002. The annual breeding cycle of unbanded king penguins *Aptenodytes patagonicus* on Possession Island (Crozet). *Avian Sci* 2:1–12.
- Durant J.M., T. Anker-Nilssen, and N.C. Stenseth. 2006. Ocean climate prior to breeding affects the duration of the nestling period in the Atlantic puffin. *Biol Lett* 2:828–831.
- Fahlman A., Y. Handrich, A.J. Woakes, C.-A. Bost, R.L. Holder, C. Duchamp, and P.J. Butler. 2004. Effect of fasting on the \dot{V}_{O_2} - f_H relationship in king penguins, *Aptenodytes patagonicus*. *Am J Physiol* 287:R870–R877.
- Fahlman A., A. Schmidt, Y. Handrich, A.J. Woakes, and P.J. Butler. 2005. Metabolism and thermoregulation during fasting in king penguins, *Aptenodytes patagonicus*, in air and water. *Am J Physiol* 289:R670–R679.
- Fraser W., W.Z. Trivelpiece, D. Ainley, and S.G. Trivelpiece. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol* 11:525–531.
- Froget G., P.J. Butler, A.J. Woakes, A. Fahlman, G. Kuntz, Y. Le Maho, and Y. Handrich. 2004. Heart rate and energetics of free-ranging king penguins (*Aptenodytes patagonicus*). *J Exp Biol* 207:3917–3926.
- Gauthier-Clerc M., Y. Le Maho, Y. Clerquin, C.-A. Bost, and Y. Handrich. 2002. Seabird reproduction in an unpredictable environment: how king penguins provide their young chicks with food. *Mar Ecol Prog Ser* 237:291–300.
- Gauthier-Clerc M., Y. Le Maho, Y. Clerquin, S. Drault, and Y. Handrich. 2000. Penguin fathers preserve food for their chicks. *Nature* 408:928–929.
- Gauthier-Clerc M., Y. Le Maho, J.-P. Gendner, J. Durant, and Y. Handrich. 2001. State-dependent decisions in long-term fasting king penguins, *Aptenodytes patagonicus*, during courtship and incubation. *Anim Behav* 62:661–669.
- Green J.A., I.L. Boyd, A.J. Woakes, C.J. Green, and P.J. Butler. 2007. Feeding, fasting and foraging efficiency during chick-rearing in macaroni penguins. *Mar Ecol Prog Ser* 346:299–312.
- Green J.A., I.L. Boyd, A.J. Woakes, N.L. Warren, and P.J. Butler. 2005. Behavioural flexibility during year-round foraging in macaroni penguins. *Mar Ecol Prog Ser* 296:183–196.
- Green J.A., P.J. Butler, A.J. Woakes, and I.L. Boyd. 2002. Energy requirements of female macaroni penguins breeding at South Georgia. *Funct Ecol* 16:671–681.
- Green J.A., P.J. Butler, A.J. Woakes, I.L. Boyd, and R.L. Holder. 2001. Heart rate and rate of oxygen consumption of exercising macaroni penguins. *J Exp Biol* 204:673–684.
- Grémillet D., S. Storch, and G. Peters. 2000. Determining food requirements in marine top predators: a comparison of three independent techniques in great cormorants, *Phalacrocorax carbo carbo*. *Can J Zool* 78:1567–1579.
- Grémillet D., G. Wright, A. Lauder, D.N. Carss, and S. Wanless. 2003. Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. *J Appl Ecol* 40:266–277.
- Guinet C., Y. Cherel, V. Ridoux, and P. Jouventin. 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–1985. *Antarct Sci* 8:23–30.
- Guinet C., P. Jouventin, and J. Malacamp. 1995. Satellite remote sensing in monitoring change of seabirds: use of spot image in king penguin population increase at Ile aux Cochons, Crozet Archipelago. *Polar Biol* 15:511–515.
- Guinet C., M. Koudil, C.A. Bost, J.P. Durbec, J.Y. Georges, M.C. Mouchot, and P. Jouventin. 1997. Foraging behaviour of satellite-tracked king penguins in relation to sea-surface temperatures obtained by satellite telemetry at Crozet Archipelago: a study of three austral summers. *Mar Ecol Prog Ser* 150:11–20.
- Halsey L.G., A. Fahlman, Y. Handrich, A. Schmidt, A.J. Woakes, and P.J. Butler. 2007a. How accurately can we estimate energetic costs in a marine top predator, the king penguin? *Zoology* 110:81–92.
- Halsey L.G., Y. Handrich, A. Fahlman, A. Schmidt, C.-A. Bost, R.L. Holder, A.J. Woakes, and P.J. Butler. 2007b. Fine-scale analyses of diving energetics in king penguins *Aptenodytes patagonicus*: how behaviour affects costs of a foraging dive. *Mar Ecol Prog Ser* 344:299–309.
- Handrich Y. 1989. Incubation water loss in king penguin eggs. I. Change in egg and brood pouch parameters. *Physiol Zool* 62:96–118.
- Handrich Y., J.-P. Gendner, and Y. Le Maho. 1995. Breeding penguins as indicators of marine resources: a study with minimal human disturbance. Pages 73–79 in P. Dann, I.

- Norman, and P. Reilly, eds. The Penguins: Ecology and Management. Surrey Beatty, Chipping Norton, UK.
- Heath R. and R. Randall. 1985. Growth of jackass penguin chicks (*Spheniscus demersus*) hand reared on different diets. *J Zool (Lond)* 205:91–105.
- Jenouvrier S., H. Weimerskirch, C. Barbraud, Y.-H. Park, and B. Cazelles. 2005. Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. *Proc R Soc B* 272: 887–895.
- Jouventin P., D. Capdeville, F. Cuenot-Chaillet, and C. Boiteau. 1994. Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the king penguin throughout the breeding cycle. *Mar Ecol Prog Ser* 106:11–19.
- Le Maho Y., J.-P. Gendner, E. Challet, C.A. Bost, J. Gilles, C. Verdon, C. Plumere, J.-P. Robin, and Y. Handrich. 1993. Undisturbed breeding penguins as indicators of changes in marine resources. *Mar Ecol Prog Ser* 95:1–6.
- McKechnie A.E. and B.O. Wolf. 2004. The allometry of avian basal metabolic rate: good predictions need good data. *Physiol Biochem Zool* 77:502–521.
- Miller M.R. and K.J. Reinecke. 1984. Proper expression of metabolizable energy in avian energetics. *Condor* 86:396–400.
- Nagy K.A., I.A. Girard, and T.K. Brown. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annu Rev Nutr* 19:247–277.
- Nagy K.A., W. Siegfried, and R. Wilson. 1984. Energy utilization by free-ranging jackass penguins, *Spheniscus demersus*. *Ecology* 65:1648–1655.
- Piatt J.F., A. Harding, M. Shultz, S. Speckman, T. Van Pelt, G. Drew, and A. Kettle. 2007. Seabirds and indicators of marine food supplies: cairns revisited. *Mar Ecol Prog Ser* 352:221–234.
- Prince P.A. and D.W.H. Walton. 1984. Automated measurement of meal sizes and feeding frequency in albatrosses. *J Appl Ecol* 21:789–794.
- Pütz K. and Y. Cherel. 2005. The diving behaviour of brooding king penguins (*Aptenodytes patagonicus*) from the Falkland Islands: variation in dive profiles and synchronous underwater swimming provide new insights into their foraging strategies. *Mar Biol* 147:281–290.
- Sotherland P.R. and H. Rahn. 1987. On the composition of bird eggs. *Condor* 89:48–65.
- Stonehouse B. 1956. The king penguin of South Georgia. *Nature* 178:1424–1426.
- . 1960. The king penguin *Aptenodytes patagonica* of South Georgia. I. Breeding behaviour and development. Falkland Islands Dependencies Survey Scientific Reports. Colonial Office, London.
- van Heezik Y.M., P.J. Seddon, C. Du Plessis, and N.J. Adams. 1993. Differential growth of king penguin chicks in relation to date of hatching. *Colon Waterbirds* 16:71–76.
- Verrier D. 2003. Croissance et mue chez le poussin de manchot royal (*Aptenodytes patagonicus*): aspects ecophysiologiques. Université Claude Bernard, Lyon.
- Viera V., C. Le Bohec, S. Côté, and R. Groscolas. 2006. Massive breeding failures following a tsunami in a colonial seabird. *Polar Biol* 29:713–716.
- Weimerskirch H., P. Inchausti, C. Guinet, and C. Barbraud. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarct Sci* 15:249–256.
- Weimerskirch H., J.C. Stahl, and P. Jouventin. 1992. The breeding biology and population dynamics of king penguins *Aptenodytes patagonica* on the Crozet Islands. *Ibis* 134:107–117.
- Wikelski M. and S.J. Cooke. 2006. Conservation physiology. *Trends Ecol Evol* 21:38–46.
- Wilson R.P. 1984. An improved stomach pump for penguins and other seabirds. *J Field Ornithol* 55:109–111.
- Winship A., A. Trites, and D. Rosen. 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eurometopias jubatus* in Alaska, USA. *Mar Ecol Prog Ser* 229:291–312.
- Woakes A.J., P.J. Butler, and R.M. Bevan. 1995. Implantable data logging system for heart rate and body temperature: its application to the estimation of field metabolic rates in Antarctic predators. *Med Biol Eng Comput* 33:145–151.
- Woehler E. 1995. Consumption of Southern Ocean resources by penguins. Pages 267–291 in P. Dann, I. Norman, and P. Reilly, eds. The Penguins: Ecology and Management. Surrey Beatty, Chipping Norton, New South Wales.