

Feeding, fasting and foraging success during chick rearing in macaroni penguins

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ABSTRACT: Foraging behaviour and energy expenditure were measured continuously throughout the chick-rearing period of free-ranging macaroni penguins *Eudyptes chrysolophus*. These data were integrated with values obtained from the literature on body mass, assimilation efficiency, body reserve consumption and deposition rates, chick growth and energy expenditure and energy content of food in a new type of algorithm to predict (with 95 % confidence limits [CL]) foraging success and daily changes in body mass. A successfully breeding pair of macaroni penguins will capture 111.7 kg (95 % CL: 79.4 to 158.0 kg) of prey during the chick-rearing period. The crucial phase of the chick rearing period was around the time that chicks crèche, when prey consumption rates more than doubled as the male assisted in foraging and recovered from a long fast. Female macaroni penguins extracted 2.28 (1.60 to 3.26) and males extracted 2.84 (2.02 to 3.99) g of prey from their environment for every minute spent submerged during foraging. Only 15.3 (14.7 to 15.6)% of all prey consumed was fed to chicks. While food capture rates increase in the middle of the breeding season, this may be more a function of greater food availability than a response to demands from their chick. Male and female macaroni penguins have differing breeding strategies with the male showing the characteristics of a capital then income breeder while the female has a strategy that shows characteristics of both capital and income strategies simultaneously. The high synchronicity and precise timing of the macaroni penguin breeding season and timing of the increase in prey capture rates suggest an influx of prey to their foraging area during the middle of the breeding season. A depletion of prey resources in the foraging area used during the breeding season could affect foraging success and have profound effects on the body condition and composition of this species and its ability to raise chicks successfully.

KEY WORDS: Penguin · Antarctic krill · Foraging · CPUE · Energetics · Diving · Breeding

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INTRODUCTION

Birds vary considerably in their use of internal and external resources during reproduction. For example, during egg formation this variation has been described as the difference between 'capital breeders', which use stored body reserves to form their eggs and 'income breeders', which immediately divert ingested food into egg formation (Drent & Daan 1980). Some attempts have also been made to expand this classification across the rest of the breeding season of birds (Thomas 1988).

While rearing their altricial chicks, seabirds might be considered to be 'income breeders' since they retrieve food from a spatially distant resource and bring it back to the chick in an essentially unmodified state. However, as is often the case with such classifications, in seabirds there is more to their energetic and ecological strategy during breeding than is initially apparent. While some seabirds retain a constant body mass during chick rearing (Hull et al. 2002), others may show a considerable decline in mass, implying that body reserves are used during investment in offspring (Clarke 2001).

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Macaroni penguins *Eudyptes chrysolophus* are the most numerous of the penguins (Woehler 1993), are one of the most abundant consumers of Antarctic krill *Euphausia superba* in the Southern Ocean (Croxall & Prince 1987), and, among all the species of seabirds, are thought to be the single largest consumer of marine resources (Brooke 2004). Like all seabirds, during the breeding season macaroni penguins engage in regular foraging trips to bring back food for their chicks. At South Georgia in the Southern Ocean these foraging trips usually last less than 1 d (Barlow & Croxall 2002a). This high feeding frequency combined with a relatively slow speed of movement means that during the chick rearing period, macaroni penguins must feed relatively close to their breeding site, usually within 50 to 60 km, over the continental shelf (Barlow & Croxall 2002b). Synchronicity of breeding (Williams & Croxall 1991), combined with restricted foraging range (Trathan et al. 2006) and the large populations around South Georgia, means that there is potential for high localised predation pressure by macaroni penguins in late December, January and early February. Furthermore, this intensive foraging is concurrent both spatially and temporally with foraging by other sympatric species such as Antarctic fur seals *Arctocephalus gazella*, gentoo penguins *Pygoscelis papua* and other seabirds (Reid et al. 1999) in the same region, and, to some extent, on the same food resources. Indeed, some evidence suggests that macaroni penguins breeding at South Georgia are losing out in competition with fur seals in particular (Barlow et al. 2002) and both species may come under pressure if commercial fisheries expand in this location.

Despite the constraints of a restricted foraging area, macaroni penguins at South Georgia have a high and relatively stable annual breeding success in raising their single chick to fledging (around 0.5 chicks pair⁻¹ yr⁻¹; Reid et al. 1999). It appears that this success is sustained by an adaptive mass loss strategy where, during the breeding season, female macaroni penguins decreased in body mass by 16% and males by 7% (Croxall 1984). Adaptive mass loss strategies are common among seabirds, for example, to decrease wing loading (Croll et al. 1991) or reduce the time spent foraging during breeding (Gaston & Jones 1989). Clearly, the observed patterns in body mass loss at this critical phase of the annual cycle reflect a delicate balance between providing enough food for the chicks while retaining sufficient body reserves and condition for the parents (Ricklefs 1983). However, such a strategy leaves birds vulnerable to a change in the availability of food resources. If parents are already losing body mass while breeding, they may have little capacity left to buffer a decrease in foraging success. Such a decrease is then likely to lead to a drastic reduction in

the body condition of the adults and, hence, their ability to survive the following winter and/or the abandonment of their chick. Several studies have illustrated the importance of body condition for successful breeding in penguins (Robinson et al. 2005) and other seabird species (Chastel et al. 1995a,b).

Thus, an understanding of the interactions between food resources, parental investment, adult body condition and offspring development is relevant in a variety of studies of marine top predators, ranging in scale and nature from effects on prey species at a population level (Croxall 1995, Priddle et al. 1998) to understanding observed behaviours in the context of life history decision making (Boyd 2000). In this study, we recorded energy expenditure and foraging behaviour in male and female macaroni penguins throughout the chick rearing period. With these data and information extracted from the literature, we were able to derive an algorithm to calculate (1) daily food consumption and (2) changes in body mass throughout the breeding season. This is the first time that it has been possible to construct an accurate day-to-day estimate of energy balance and prey consumption in a free ranging animal. With these data we are able to pinpoint periods of vulnerability to ecosystem change and answer important questions about the allocation of resources between parents and offspring.

We set out to answer 5 key questions at a population level to aid in the understanding of the role of macaroni penguins in the Southern Ocean around South Georgia during their chick rearing period. (1) How much food do the birds extract from their environment during the chick rearing period? (2) Are there any particularly critical points during the breeding chick rearing period in relation to food availability? (3) How is the prey captured apportioned between chicks and adults? (4) What is the prey capture rate during foraging dives? (5) How might changes in prey availability affect this species?

MATERIALS AND METHODS

Study animals. Study animals were captured at the British Antarctic Survey (BAS) base on Bird Island, South Georgia (54° 00' S, 38° 02' W). All birds used in the experiments were randomly selected from the macaroni penguin colony at Fairy Point on the north side of Bird Island. All individuals were mature adults that successfully raised a chick to fledging that season. Although the United Kingdom Animal (Scientific Procedures) Act 1986 does not apply to South Georgia, we followed its provisions, especially those set out by the Home Office in the official guidance on the operation of the Act, and followed guidelines to researchers

using similar methods in the United Kingdom. Our procedures also conformed to the Scientific Committee on Antarctic Research (SCAR) code of conduct for use of animals for scientific purposes in Antarctica.

Heart-rate logger deployments. As described previously (Green et al. 2005a,b), a total of 82 macaroni penguins were equipped with data loggers (DLs) during the austral summers of 2001 to 2002 and 2002 to 2003. The DLs were surgically implanted in the abdominal cavity using previously established techniques (Stephenson et al. 1986, Green et al. 2003). Long-term deployment of these devices has no detectable adverse effects on the behaviour, breeding success and survival of this species (Green et al. 2004). The DLs recorded heart rate every 10 s and dive depth either every 2 s (2001/2002) or 1 s (2002/2003). The mean (\pm standard error of the mean [SEM]) duration of data recorded by the DLs was 207 ± 14 d. As in previous studies (Green et al. 2005b), each day of the deployment for each penguin was assigned to a phase of the annual cycle as well as to a day from the start of that phase for that bird (phaseday). The phases analysed in this study were (1) brood (after chicks hatch, but with one parent in continuous attendance) and (2) crèche (late chick rearing when the chick is left unguarded).

Data were obtained for the brood (13 females, 7 males) and crèche phases (13 females, 11 males) of the 2002 to 2003 breeding season. This season was considered to be a 'normal' year in terms of chick fledging rates and mass when compared with the long-term average (BAS unpubl. data). The duration of the brood and crèche phases varied slightly among individuals. For the purposes of the algorithm and to match literature data, standard durations of 23 and 35 d were used for the brood and crèche phases, respectively, based on the mean duration of these phases in 2002 to 2003 and previous data from the same colony (Williams & Croxall 1991). Data from days in excess of these durations were not used in the analyses.

Data logger analysis. Heart rate was converted to an estimate of mass specific rate of oxygen consumption ($s\dot{V}_{O_2}$; $\text{ml min}^{-1} \text{kg}^{-1}$) using Eqs. (12) and (13) from Green et al. (2005d). These equations were derived from animals from the same population during the same time period (9 January to 3 March, 2003) as this study. The body mass and condition of the penguins spanned the full range observed for this period of the breeding season and were collected while the animals rested, walked and swam (see Green et al. 2005d for full details of the calibration procedure). Mean $s\dot{V}_{O_2}$ was calculated for each animal for each day and converted to average daily mass specific metabolic rate (ADMR_s ; $\text{kJ kg}^{-1} \text{d}^{-1}$) using a conversion factor of $18.87 \text{ kJ (l O}_2\text{)}^{-1}$. This factor was derived from standard values for the metabolism of protein and lipid

(Schmidt-Nielsen 1997) and knowledge of the diet of the penguins (see 'Materials and Methods—Diet'). The standard error of the estimate (SEE) for estimates of ADMR_s was calculated following the method of Green et al. (2001). ADMR_s was converted to average daily metabolic rate (ADMR) by simply multiplying ADMR_s by body mass (M_b) on that day since \dot{V}_{O_2} is isometric with M_b over the range of M_b found in this study (Green et al. 2005c).

Dives with maximum depths of <2.4 m were ignored during analyses. Between the surface and this depth, wave action, recorder noise, and the interaction between temperature and pressure degraded depth accuracy, making it impossible to accurately characterise dives this shallow. Following the methodology of Green et al. (2005b), dives were classified as either foraging (>10 m) or non-foraging (travelling or searching, ≤ 10 m). Only foraging dives were analysed, since in this study we were interested primarily in foraging activity. In total, 404 497 foraging dives were analysed and total number of dives, duration of each dive and, hence, total time spent submerged per day (DTS) were extracted for each day for each penguin. DTS has been used in previous studies as an indicator of seabird foraging activity (Grémillet 1997). The foraging success (FS, mass of prey captured per minute submerged) was assumed to be constant throughout the breeding season within each sex since neither foraging locations (Barlow & Croxall 2002b), meal mass (Barlow & Croxall 2002a) nor diet composition (BAS unpubl. data) change dramatically either within or between breeding seasons. The mean total amount of prey captured per day (DPC) was calculated by multiplying FS by DTS. FS was quantified for both males and females using an iterative procedure (see 'Materials and Methods—Calculation of body mass change and foraging success').

Chicks. While the growth of macaroni penguin chicks has been studied previously at Bird Island (Barlow & Croxall 2002a), energy expenditure and body composition of macaroni penguin chicks has only been studied at Marion Island (Brown 1987). At Marion Island ($46^\circ 52' \text{S}$, $37^\circ 51' \text{E}$), chicks fledge relatively later (70 vs. 58 d) and at a lighter mass (~ 2.3 vs. ~ 3.0 kg) than at Bird Island. However, the total biomass of a chick for the fledging period (sum of mean daily mass from hatching to fledging) was similar at the 2 sites (~ 109 vs. ~ 102 kg). Similarly, the estimated total amount of food delivered to chicks at Marion Island (21.8 kg) was similar to the total amount of food delivered to chicks at Bird Island (22.8 kg) based on a long-term average mass of stomach contents of 394 g (Reid et al. 1999). The mass of stomach contents of adults returning to feed chicks does not change during the breeding season (Barlow & Croxall 2002a). Since mass

is the primary determinant of metabolic rate, it was assumed that the total energy expenditure of a chick was also the same at both sites. As a result, the total energy expenditure for growth and maintenance, which had been calculated for 7 d intervals at Marion Island, was taken to represent a 6 d interval in the faster growing chicks at Bird Island. Since this energy expenditure is sufficient for all of the requirements of the chick, it can be equated to a 'demand' on the parents for food resources. Chick energy requirements were converted to food requirements using a dietary energy content of 5.17 kJ g^{-1} and an assimilation efficiency of 0.729 (see 'Materials and Methods — Diet').

In both monomorphic and dimorphic seabird species, provisioning responsibilities may not be shared equally between the sexes (e.g. Lewis et al. 2002). However, macaroni penguins (and other crested penguins) represent a unique extreme example of this. During the brood phase, the male remains ashore and fasts while guarding the chick continuously. Meanwhile, the female engages in trips of 1 to 2 d in duration, returning with meals to feed to the chick. In the crèche phase, both parents forage at sea and provide food for the chick. However, the division of labour at this time is still not equal. On average, females provide 59% of meals delivered to the chick while males provide only 41% (Barlow & Croxall 2002a). These proportions were used in this study to assess meal delivery by parents.

Diet. During the 2002 to 2003 season the diet of the penguins consisted of (as percentage of wet mass) 54% Antarctic krill *Euphuasia superba*, 8% fish and 38% other crustaceans (BAS unpubl. data). It was assumed that all crustaceans had a nutrient composition and energy density equal to that of Antarctic krill, as previously reported by Croxall et al. (1999). The fish component of the diet was not identified to genera or species level so was assumed to be composed wholly of myctophid fish, as previously found in this population (Croxall et al. 1997).

Macaroni penguins catch male and gravid female Antarctic krill in a 1:3 ratio (Croxall et al. 1997). From the nutritional composition of the different sex and age classes of the krill (Clarke 1980) and myctophid fish caught by macaroni penguins (Clarke & Prince 1980), an average meal during the 2002 to 2003 season would have consisted of 5.5% lipid, 10.9% protein and 83.0% water. As a result, the energy density (ED_{food}) would have been 5.17 kJ g^{-1} . The assimilation efficiency (AE) of penguins feeding on a predominantly crustacean diet (commonly Antarctic krill) has now been studied 6 times in 4 species (see Kirkwood & Robertson 1997 for summary). However, macaroni penguins have not been studied and considerable variation has been noted in AE (range: 0.633 to 0.828) both within and

between the species studied. In the absence of species-specific data on AE from macaroni penguins, we used the mean AE (\pm SD) from all previous studies of 0.729 ± 0.067 .

Body mass and body composition. Unfortunately, it was not possible to weigh the penguins implanted with data loggers regularly during this study as it was thought this might unduly disturb the breeding animals. Croxall (1984) presented data on the mean (\pm SD) body mass of macaroni penguins from the same breeding colony, weighed serially throughout the breeding period from their arrival to breed until their departure for their winter migration. Fig. 25 from Croxall (1984) was scanned and the points on that chart digitised and captured (our Fig. 1) using Engauge Digitizer software (<http://digitizer.sourceforge.net>). Mean masses at the start of the brood phase and end of the crèche phase were used in the iterative process, which, as well as deriving FS, predicted mass for each day of the chick rearing period (see 'Materials and Methods — Calculation of body mass change and foraging success'). Mean masses at the end of the brood and the start of crèche phase and intermediate points during the crèche phase (Fig. 1) were used to assist in validating this procedure.

Fig. 1 shows that the body masses of both male and female penguins changed considerably during the chick rearing period. Male penguins underwent a period of mass loss while they fasted during the brood phase, but then regained mass as they resumed foraging during the crèche phase. Female penguins lost mass steadily during the brood phase, but more slowly during the crèche phase. It is assumed that the penguins lost mass when energy expended was greater than the energy content of the diet, after subtraction of food fed to the chick. In this case it is assumed that

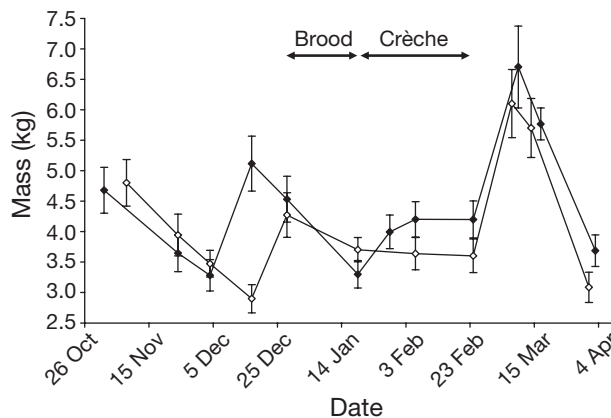


Fig. 1. *Eudyptes chrysolophus*. Mean masses (\pm SD) throughout the breeding season in (\diamond) female and (\blacklozenge) male macaroni penguins. All birds are from an original 'pool' of 20 birds of each sex. Data are taken from Fig. 25 in Croxall (1984). Body mass at the beginning of the brood phase and end of the crèche phase (indicated by arrows) were used in the iterative process

body reserves were catabolised. Mass loss and the change in body composition of penguins have not been studied during active/foraging periods, but have been studied during fasting periods. Water, protein and lipid account for 43, 8 and 47%, respectively, of the total mass lost in king penguins *Aptenodytes patagonicus* during Phase II fasting (Cherel et al. 1994). Consequently, the energy equivalent of body reserve consumption is 19.9 kJ g^{-1} . In emperor penguins *Aptenodytes forsteri*, the relative proportions are 30, 6 and 62%, respectively, during Phase II fasting and the energy equivalent of body reserve consumption is 25.4 kJ g^{-1} (Robin et al. 1988). Macaroni penguins are also well adapted to long fasts and rapid changes in body mass and composition (Fig. 1). This is supported by their relatively high adiposity of 21% before moulting (Williams et al. 1977), which is the second highest level among the 6 penguin species surveyed to date (Cherel et al. 1993). Since macaroni penguins seem to be at least as well adapted to long fasts as king and emperor penguins, a mean energy equivalent of 22.7 kJ g^{-1} was selected for mass loss calculations (equivalent to 0.044 g body mass lost per kJ required). The relative proportions of water, protein and lipid would, therefore, also have been intermediate at 37, 7 and 54%, respectively, with 2% of other materials. As a result, 94% of the energy expended from reserves comes from lipids and 6% from protein, the same as that for similar sized breeding Adélie penguins *Pygoscelis adeliae* (Chappell et al. 1993).

It is assumed that the penguins gained body mass when they consumed more food than was used in metabolism and fed to the chick. Very little data exist on the conversion of constituent components of the diet into body reserves; therefore, some assumptions were made in the derivation of this factor. (1) It is assumed that water, protein and lipid were added to body reserves in the same proportions in which they are catabolised (see previous paragraph). This is reasonable since macaroni penguins remain in Phase II during fasting (Williams et al. 1992), so replacement of reserves will simply match their usage. (2) Since lipid is the primary source of stored energy reserves (Robin et al. 1988, Cherel et al. 1994), it was assumed that all excess lipid was transferred to body reserves, but any protein in excess of the proportion used during reserve consumption was excreted or used in other metabolic pathways. Therefore, since the food consumed by macaroni penguins was 5.5% lipid (see 'Materials and Methods—Diet') and that 54% of reserves utilised were lipid (see previous paragraph), then for each extra gram of krill consumed, it was estimated that the penguins increased in mass by 0.103 g . This increase would consist of 0.056 g of lipid, 0.007 g of protein, 0.038 g of water and 0.002 g of other materials.

Calculation of body mass change and foraging success. The data on chick energy expenditure, and, hence, food demands, anabolic/catabolic factors and foraging effort, were combined in an algorithm designed to calculate the change in body mass of an adult for each day of the chick rearing period. It was assumed that all food captured was retained by the adults or fed to the chicks and there was no wastage during chick feeding. Such losses are uncommon and klepto-parasitism was not commonly observed at this colony (J. A. Green pers. obs.). The calculation was made separately for males and females. Initial masses were 4.27 and 4.53 kg for females and males, respectively; the values at hatching are from Fig. 1. The algorithm was of the form:

$$M_{b(d)} = M_{b(d-1)} + \text{Mass change} \quad (1)$$

Where $M_{b(d)}$ was the mass on a given day and $M_{b(d-1)}$ was the mass on the previous day. Mass change depended on whether there was a surplus or deficit of energy in the food obtained during the previous day where:

$$\text{Deficit/Surplus} = (\text{DTS} \times \text{FS} \times \text{ED}_{\text{food}} \times \text{AE}) - (\text{ADMR}_s \times M_{b(d-1)}) - (c\text{DMR}) \quad (2)$$

DTS was the total time spent submerged the previous day, FS was the foraging success, AE was the assimilation efficiency, ED_{food} was the energy density of the diet, ADMR_s was average daily mass specific metabolic rate for the previous day, and $c\text{DMR}$ was average daily metabolic rate of the chick for the previous day. During the crèche phase, it was assumed that females provided 59% of the food required by the chick and males provided 41% (see 'Materials and methods—Chicks').

If, as calculated above, an energy deficit existed, body reserves to match the shortfall in energy required were consumed at the rate 0.044 g kJ^{-1} , leading to a decrease in mass. If a food surplus existed, this would be converted into body reserves at the rate of $0.103 \text{ g (g krill)}^{-1}$ leading to an increase in mass. All quantities in the algorithm were measured or assumed as described above with the exception of FS. Repeated iterations of the algorithm were run with FS increasing in increments of 0.0001 until calculated M_b on the last day of crèche was within 0.1% of the mean mass measured by Croxall et al. (1984) and shown in Fig. 1. Thus, the algorithm derived foraging success and intermediate values of M_b between chick hatching and fledging. Mean total daily prey capture (DPC) could then be calculated as the product of DTS and foraging success. Total prey consumption (TPC) for the entire breeding season for a breeding pair was calculated as the sum of DPC for each day for males and females.

Sensitivity analysis. To test the robustness of the algorithm and reliability of assumptions made in esti-

mating intermediate M_b , FS, and food consumption, we varied the inputs of the algorithm and repeated the iterative process to obtain a range of values of FS and intermediate M_b . The 8 inputs to the algorithm (AE, EC_{food} , body reserve consumption rate, body reserve deposition rate, M_b at chick hatching and fledging, $c\text{-DMR}$, ADMR_s and DTS) were varied singly and sequentially with a value equivalent to the mean for that day \pm SD or \pm SEE, or where this value was not available, for a standard variability of $\pm 10\%$ (Gremillet et al. 2003). As a result, new values of intermediate mass, FS and, hence, DPC and TPC were generated. The relative importance of each of the inputs could then be assessed by calculating the percentage change in the estimate of FS or TPC attributable to that input. Furthermore, a 'worst case scenario' where the algorithm was rerun with all 8 inputs at their minimum and maximum values provided confidence limits around the estimates of intermediate M_b , FS, DPC and TPC. A similar approach was applied to generate confidence intervals around the estimate of chick food consumption, though in this case only $c\text{-DMR}$, AE and EC_{food} were varied.

RESULTS

Daily metabolic rate and foraging effort

Fig. 2 shows how ADMR_s varied during the chick rearing period for both female and male macaroni penguins. During the brood phase, there was no trend in ADMR_s in relation to the number of days since hatching (DSH) for female ($p = 0.25$, $r^2 = 0.06$) or male ($p = 0.27$, $r^2 = 0.06$) penguins. After the chicks crèched there was a slight but significant decrease in female ADMR_s ($\text{ADMR}_s = 1073 - [2.76 \times \text{DSH}]$, $p < 0.01$, $r^2 = 0.22$). During the brood phase, male ADMR_s was approximately 25 to 30% of female ADMR_s . However, after the chicks crèched, male ADMR_s increased substantially for the first 7 d, as they resumed foraging ($\text{ADMR}_s = [52.2 \times \text{DSH}] - 526$, $p < 0.01$, $r^2 = 0.77$). Thereafter, ADMR_s of males was similar to that of females, but there was no trend in male ADMR_s until the end of the chick rearing period ($p = 0.95$, $r^2 = 0.00$).

Time spent submerged per day (DTS) was used as an index of forag-

ing effort (Fig. 3). For female penguins, DTS increased significantly during the brood phase ($\text{DTS} = 20640 + [765 \times \text{DSH}]$, $p < 0.001$, $r^2 = 0.65$), did not change during the first 17 d of the crèche phase ($p = 0.07$, $r^2 = 0.21$), and decreased significantly during the last 18 d of the crèche phase ($\text{DTS} = 83497 - [1114 \times \text{DSH}]$, $p < 0.001$, $r^2 = 0.88$). After male penguins resumed foraging they had 1 d with a very low DTS, presumably associated with a slow resumption of foraging activity and reduced foraging trip duration. Thereafter, DTS was similar to that in females and did not change during the next 16 d of the crèche phase ($p = 0.4$, $r^2 = 0.05$), although it did decrease significantly during the last 18 d of the crèche phase ($\text{DTS} = 70022 - [856 \times \text{DSH}]$, $p < 0.001$, $r^2 = 0.82$). As such, there was no significant difference in DTS between the sexes during the crèche phase (ANCOVA: $F_{1,67} = 2.59$, $p = 0.112$).

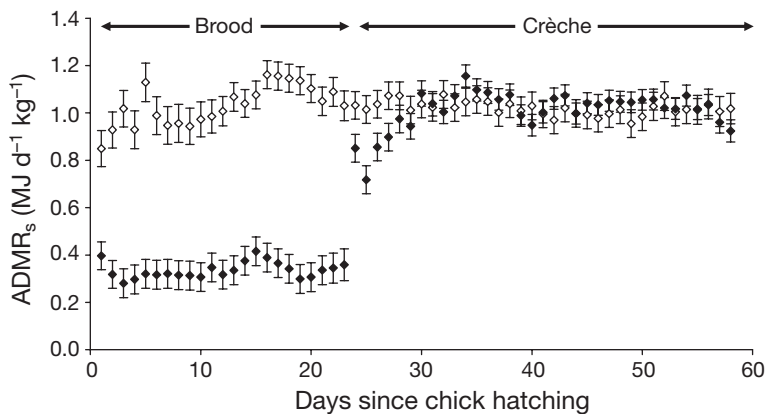


Fig. 2. *Eudyptes chrysolophus*. Average daily mass specific metabolic rate ($\text{ADMR}_s \pm$ standard error of the estimate [SEE]) in (\diamond) female ($n = 13$) and (\blacklozenge) male ($n = 11$) macaroni penguins during the brood and crèche phases of the chick rearing period

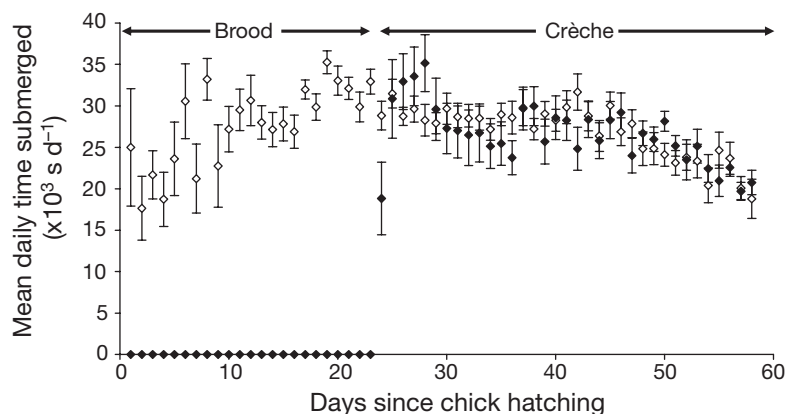


Fig. 3. *Eudyptes chrysolophus*. Mean (\pm standard error of the mean [SEM]) time spent submerged per day (DTS) in (\diamond) female ($n = 13$) and (\blacklozenge) male ($n = 11$) macaroni penguins during the brood and crèche phases of the chick rearing period

Chicks

As might be expected, the food requirements of a chick based on its energy expenditure for maintenance and growth varied throughout its fledging period (Fig. 4). From an initial low level of around 110 g d⁻¹ (approximately equal to chick body mass), food demands increased to around 400 g d⁻¹ (approximately 18% of chick body mass) after crèching at around 32 d of age. Food demands then declined to a low level of around 180 g d⁻¹ (approximately 6% of chick body mass) before fledging. The total amount of food consumed by a chick between hatching and fledging was therefore 17.0 kg (95% CL: 11.6 to 24.6 kg).

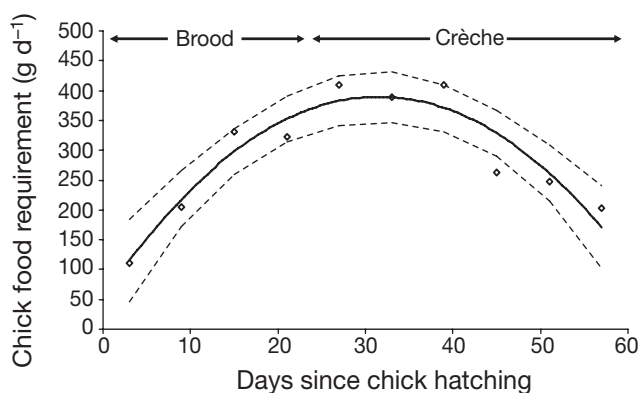


Fig. 4. *Eudyptes chrysolophus*. Calculated food requirements for growth and maintenance for a macaroni penguin chick during the brood and crèche phases of its fledging period. Data are adapted from Brown (1987). The fitted quadratic curve is plotted (—) and described by the equation: food requirement = 54.8 + (21.25 × day) – (0.34 × day²) (p < 0.001, r² = 0.89). The 95% confidence intervals of the regression are also plotted (---)

Foraging success

Repeated iterations of the algorithm were run with varying values of FS until mass at fledging was within 0.1% of the mass in Fig. 1. The estimates of FS derived through iteration were 2.28 and 2.84 g min⁻¹ for females and males respectively. Table 1 shows the results of the sensitivity analysis on the estimates of FS for both males and females. When considered individually, all of the parameters (except DTS) had a minimal effect on the estimate of FS (≤10% in all cases, except one). Notably, despite the assumptions inherent in their derivation, the effects of varying consumption and deposition rates of body reserves were particularly low (<2%). The most dominant influence on the estimate of FS was DTS. This is perhaps not surprising. All of the other parameters could be grouped as relating to 'demand' on food resources and control the amount of prey that must be caught. On the other hand, DTS and FS are intimately linked to providing the 'supply' of these food resources to both the chick and the parents. Furthermore, it is not surprising that DTS had a large influence on FS since there is clearly a great deal of variation between individuals in DTS, leading to large values of SD and standard error of the mean (SEM) (Fig. 3). Importantly then, the large effect of DTS on FS does not represent uncertainty in our measurements of DTS but simply the variability between individuals. So while the confidence intervals of FS including DTS are large, this simply reflects differences between individuals in their foraging success. In this study, we investigated food consumption and energy utilisation of the entire population, so a more meaningful calculation of the 95% confidence intervals can be obtained excluding DTS. These new limits, which are reflective of uncertainties in prediction rather than in individual

Table 1. *Eudyptes chrysolophus*. Sensitivity analysis of the determination of foraging success (FS, g min⁻¹) in male and female macaroni penguins. Minimum and maximum input values were calculated for each parameter as ±SD or standard error of the estimate (SEE) or for ±10% average values. The 'worst case scenario' was computed for the most and least demanding combination of input situations of all parameters. Thus, they provide the maximum range of potential FS values for breeding macaroni penguins

Parameter	Range	Females				Males			
		FS for minimum value	Variation of mean FS (%)	FS for maximum value	Variation of mean FS (%)	FS for minimum value	Variation of mean FS (%)	FS for maximum value	Variation of mean FS (%)
Assimilation efficiency	SD	2.50	9.7	2.09	-8.2	3.07	8.0	2.65	-6.8
Energy content of krill	10%	2.53	10.8	2.08	-8.9	3.09	8.9	2.63	-7.2
Body reserve consumption rate	10%	2.30	1.1	2.26	-1.1	2.89	1.9	2.79	-1.7
Body reserve deposition rate	10%	2.30	1.1	2.26	-0.8	2.89	1.9	2.80	-1.5
Start and end body mass	SD	2.14	-6.1	2.42	6.1	2.67	-5.9	3.01	6.1
ADMR of chick	SD	2.20	-3.4	2.36	3.4	2.79	-1.7	2.89	1.7
ADMR of parent	SEE	2.14	-6.3	2.42	6.3	2.63	-7.2	3.04	7.0
Daily time submerged	SD	3.14	37.6	1.80	-21.1	4.24	49.5	2.14	-24.5
Worst case scenario	All	1.27	-44.5	4.49	97.1	1.52	-46.3	5.94	109.3

variability, were 1.60 to 3.26 g min⁻¹ for females and 2.02 to 3.99 g min⁻¹ for males.

Changes in body mass

Fig. 5 shows calculated M_b throughout the chick rearing period for both males and females. M_b at the beginning and end of the chick rearing period (see Fig. 1) were inputs into the algorithm, but in female penguins, the algorithm correctly predicted the different rates of M_b loss in the brood and crèche phases. Furthermore, the predicted intermediate M_b values at the beginning and mid-way through the crèche phase were within 3% and 1 SD of the measured mean values from Fig. 1. The confidence intervals calculated under the 'worst case scenario' adopt a slightly different shape as the algorithm is cumulative; each day's estimate is dependent on that of the day before. Notably, using the upper confidence limit where body reserve accumulation and deposition rates are at their maximum generates more exaggerated changes in M_b . In male penguins the algorithm also correctly predicts the decline and subsequent recovery in M_b during the breeding season. Interestingly, both the estimated M_b and the confidence intervals of the prediction for males converge at the time of transition from brood to crèche. Predicted intermediate M_b at the beginning and mid-way through the crèche phase were close (within 10%) to

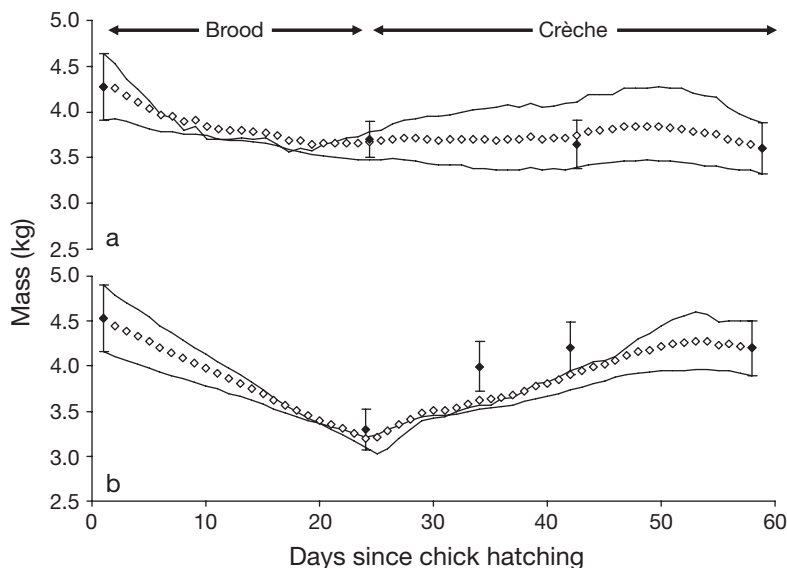


Fig. 5. *Eudyptes chrysolophus*. Calculated body mass (\diamond) with confidence limits (—) for (a) female and (b) male macaroni penguins during the chick rearing period. Closed symbols (\blacklozenge) are the observed mean (\pm SD) masses for macaroni penguins at different stages of the chick rearing period measured from a pool of 20 penguins of each sex (see Fig. 1 for details)

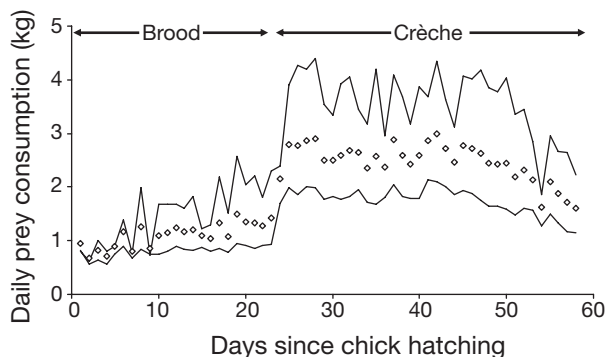


Fig. 6. *Eudyptes chrysolophus*. Predicted daily prey consumption (DPC, \diamond) with 95% confidence limits (—) by a pair of macaroni penguins successfully raising a chick to fledging

the mean values from Fig. 1, though not as close as those for females. In male penguins the confidence intervals deviated less from the predicted values of M_b .

Food consumption

DTS was multiplied by FS to calculate mean daily prey capture (DPC) by both male and female penguins for each day of the breeding period. The sensitivity analysis allowed calculation of confidence intervals of each of these estimates as well as of DPC for a breeding pair (Fig. 6). DPC (by females only) increased significantly during the brood period from approximately 1.0 to 1.5 kg d⁻¹ (DPC = 783 + [26.8 × DSH], $p < 0.001$, $r^2 = 0.64$). DPC (per breeding pair) was stable at around 2.8 kg d⁻¹ for the first 17 d of the crèche phase ($p = 0.64$, $r^2 = 0.01$) before decreasing significantly over the last 18 d of the crèche phase to around 2.0 kg d⁻¹ (DPC = 6041 × [74.7 × DSH], $p < 0.001$, $r^2 = 0.87$). The sum of DPC of both males and females can be used to compute the total prey consumption (TPC) for the chick rearing period of both males and females and of the breeding pair. The sensitivity analysis allowed calculation of confidence intervals around these estimates. Detailed examination of this analysis for TPC of the breeding pair shows how uncertainty in the different parameters influences the estimate of TPC (Table 2). Most parameters had a similar influence as in the sensitivity analysis of FS with AE and EC_{food} hav-

Table 2. *Eudyptes chrysolophus*. Sensitivity analysis of the determination of total prey consumption (TPC, kg) for a successful breeding pair of macaroni penguins. Minimum and maximum input values were calculated for each parameter as \pm SD or \pm SEE or for \pm 10% average values. The 'worst case scenario' was computed for the most and least demanding combination of input situations of all parameters. Thus, they provide the maximum range of potential TPC values for breeding macaroni penguins

Parameter	Range	TPC for minimum value	Variation of mean TPC (%)	TPC for maximum value	Variation of mean TPC (%)
Assimilation efficiency	SD	121.77	9.0	103.21	-7.6
Energy content of krill	10%	122.85	10.0	102.50	-8.2
Body reserve consumption rate	10%	113.25	1.4	110.21	-1.3
Body reserve deposition rate	10%	113.25	1.4	110.48	-1.1
Start and end body mass	SD	104.98	-6.0	118.48	6.1
ADMR of chick	SD	108.66	-2.7	114.70	2.7
ADMR of parent	SEE	104.22	-6.7	119.04	6.6
Daily time submerged	SD	111.35	-0.3	112.41	0.7
Worst case scenario	All	79.44	-28.9	158.00	41.5

ing the most importance (~10%). However, in this case DTS had a very small influence on the confidence of estimates of DPC.

TPC for females and males during the chick rearing period was 65.4 (95% CL: 46.3 to 93.6) kg and 46.3 (33.2 to 64.4) kg, respectively. The total amount caught by the breeding pair was therefore 111.7 (79.4 to 158.0) kg and so the proportion of this fed to chicks was 15.3 (95% CL: 14.7 to 15.5)%. Of the 17.0 kg fed to their chick, 12.3 kg (72.4%) was supplied by the female and 4.7 kg (27.6%) was supplied by the male.

DISCUSSION

Like all breeding animals, macaroni penguins must balance the conflicting demands of their own body condition and future reproductive success with the more immediate demands of their current offspring, in this case a single chick per year. Our data show that while rearing their chicks males and females have different strategies. Females have a mixed capital and income strategy; they feed chicks with food gained during foraging trips, yet also use their own body reserves to sustain their own metabolism. Conversely, males are purely 'capital' breeders during the brood phase, as their contribution to guarding the chick is sustained entirely from body reserves, whereas during the crèche phase, they are purely 'income' breeders, as they assist in provisioning the chick yet obtain sufficient food to increase their own body reserves every day. For the first time we have been able to determine energy balance on a daily basis for a free ranging marine predator. These fine scale findings are particularly valuable for species that forage in a dynamic environment, which may be subject to current and future change. For now, these data enable us to answer 5 key questions about the foraging of macaroni penguins during their breeding season.

Amount of food consumed during the breeding season

The penguins in the present study removed 111.7 (95% CL: 79.4 to 158.0) kg of prey per pair from the shelf waters around South Georgia in 58 d. As a percentage of body mass, daily prey consumption (DPC) varied from 15.7 to 41.2% in females (mean \pm SEM: 29.9 \pm 0.8%) and from 21.1 to 48.2% in males (34.9 \pm 1.2%). Few studies have been able to assess food consumption accurately during foraging by seabirds due to the difficulty of recording the size of prey items and occurrence of feeding events. Some success has been achieved by recording stomach temperature during foraging (Wilson et al. 1992), though this method is fraught with problems (Wilson et al. 1995, Catry et al. 2004). Despite this, DPC has been estimated for some species and was equivalent to ~22% of adult body mass in grey-headed albatrosses *Thalassarche chrysoloma* (Catry et al. 2004). DPC has been assessed in great cormorants *Phalacrocorax carbo*, and European shags *Phalacrocorax aristotelis*, by weighing adults immediately after they return from foraging trips and assessing meal mass and digestion rates of prey remains (Grémillet et al. 1997). This approach is possible for these species since their foraging trips are relatively short in duration when compared with those of other seabirds. Female and male great cormorants consumed prey equivalent to ~32 and ~27% of their body mass each day, respectively, while European shags consumed ~38 and ~25% of their body mass each day, respectively. Grémillet et al. (1997) did not discuss whether their birds were in energy balance, but the differing approaches taken in their study and this study have produced very similar results.

Preliminary data on DPC from the similar sized magellanic penguin *Spheniscus magellanicus* based on measurement of mandibular movement (Wilson 2004) are greater than estimates for the albatrosses des-

cribed by Catry et al. (2004), and instead are similar to the rates of consumption for cormorants and those found in this study. Estimates of DPC made using isotopic techniques suggest that during chick rearing, little penguins *Eudyptula minor* may consume over 60% of their body mass in prey items each day (Gales & Green 1990), whereas African penguins *Spheniscus demersus* consumed 23.9% of their body mass in anchovies on alternate days (Nagy et al. 1984), though these penguins were apparently in negative energy balance. It should be noted that all of the above studies assumed similar energy density of prey items in the range of 4.0 to 5.5 kJ g⁻¹ despite dietary differences among species.

Total prey consumption rates varied substantially during the chick rearing period. For both male and female penguins DPC was correlated with the food requirements of the chick (Fig. 7). However, this increase in prey consumption was not matched by a correlation between food requirements of the chick and ADMR_s for either female ($r = 0.16$) or male ($r = 0.07$) penguins. Neither was ADMR_s well correlated with DPC in either females ($r = 0.03$) or males ($r = 0.17$). As one might expect, therefore, the penguins spend more time submerged and capture more food in the middle of the breeding season when the demands of the chick are highest (Fig. 4). However, this is apparently achieved at no extra energetic cost. While this may seem counter-intuitive, a previous study of macaroni penguins indicated that metabolic rate while at sea is the same during the day and night, despite the fact that the penguins only dive and forage during daylight hours (Green et al. 2002). At night and other times when not foraging, the penguins presumably rest on the water surface or travel between feeding patches. It is, therefore, possible to increase foraging effort (DTS) without increasing ADMR_s. This might instead suggest that there was a greater availability of prey at the time when

the demand from chicks was highest (see 'Critical points in the breeding season' below), allowing an increase in foraging time and a decrease in travelling/resting time at the same energetic cost. Further work would need to analyse the characteristics of macaroni penguin foraging trips at a fine scale, sequentially through the chick rearing period.

Critical points in the breeding season

While prey captured is linked to an increase in food demand by chicks, the largest change occurs at the transition point between brood and crèche phases when males return to sea to assist in foraging, when the prey consumption rate of a breeding pair more than doubles (Fig. 6). For such an important consumer (Brooke 2004) with such a synchronous breeding season (Williams & Croxall 1991), this will undoubtedly have a profound impact on the populations of their preferred prey species and relationships with potential competitors. It would be interesting to examine whether this period coincides with shifts in foraging area or diet in competing species. Alternatively, this massive increase in consumption may be a reflection of an increase in availability of prey at this time. Selection pressure may have acted to synchronise breeding cycles in this species to exploit a boom in krill availability. Unfortunately, while the inter-annual variability of Antarctic krill populations in terms of size and structure is reasonably well understood (e.g. Murphy et al. 1998), there are far fewer data available on intra-annual changes in krill availability. However, several studies have discussed the transport of new populations of krill into the waters around South Georgia during later summer months (e.g. Reid et al. 1999). Perhaps the increase in food consumption by macaroni penguins during late January/early February coincides with the arrival of new populations of krill.

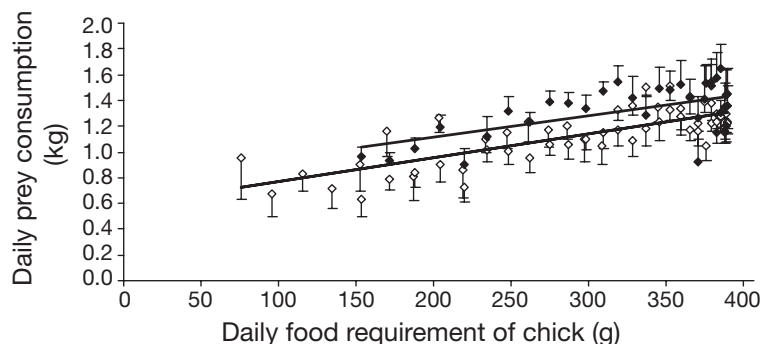


Fig. 7. *Eudyptes chrysolophus*. Correlation between daily food requirements of a macaroni penguin chick and the amount of prey captured per day by both (◇) female ($n = 13$, $r = 0.78$) and (◆) male parents ($n = 11$, $r = 0.60$) during the breeding season. Error bars: SEM

Food share between chicks and parents

Intuitively, one might assume that the greater proportion of the food captured would be fed to the chick at this time of the penguin's annual cycle. However, chick food requirement was only 22.3% of the food caught by females during the entire brood phase and was even less than this during the crèche phase in both females (16.7%) and males (10.2%). In all, 15.3% of all food caught

was fed to the chick. This proportion was slightly less than the 17 to 19.8% of krill caught fed to chicks of 3 species of pygoscelid penguin chicks in Antarctica (Culik 1994). However each of these species has an initial brood of 2 chicks and the data from the Culik (1994) study are based on a large number of assumptions. Energetic costs of provisioning young constitute a positive feedback loop; parents must use energy to catch food to bring back for the chick. This energy expenditure in turn must be fuelled either by further foraging or from body reserves. Unfortunately, therefore, it is not really possible to apportion the energy expended in chick rearing between that used in feeding the chick or that retained by the parent.

Mean (\pm SEM) mass of stomach contents upon coming ashore during the crèche phase was 407 ± 40 g for females and 561 ± 55 g for males during the year of study (BAS unpubl. data), slightly higher than the long-term average for this colony of 394 g (Reid et al. 1999). Mass of stomach contents can be converted to the potential meal size available to a chick per day by multiplying meal size by feeding frequency, which is ~ 0.74 and ~ 0.5 meals d^{-1} , respectively, for female and male macaroni penguins (Barlow & Croxall 2002a). Therefore, the amount of food available for a macaroni penguin chick would be ~ 290 g d^{-1} during brood and ~ 570 g d^{-1} during crèche. Mass of stomach contents (and hence potential chick meal size) remains constant throughout the breeding season (Barlow & Croxall 2002a) despite variation in demands from the chick (Fig. 4). At peak demand, all of the food will be transferred to the chick, whereas at other times the majority of the stomach contents returned ashore will be retained by the adult(s). In contrast to Fig. 7, this may suggest that the parents do not assess the needs of the chick but instead simply obtain as much food as possible while foraging, the amount of which is dependent on local prey availability. Similarly, in Adélie penguins breeding success is dependent on allocation of resources rather than on foraging effort or success (Takahashi et al. 2003).

The constancy of mass of stomach contents may suggest that the penguins fed until their stomach was full. The mean (\pm SEM) stomach contents mass was equivalent to 11.1 ± 1.1 and $14.2 \pm 1.4\%$ of body mass for females and males, respectively, which is at the lower end of the range of meal sizes returned by similar sized species including gannets, albatrosses and petrels (Ricklefs 1983, Phillips & Hamer 2000, Phillips et al. 2005). The mass of the stomach contents was equivalent to 36.1 and 42.4% of estimated mean daily prey consumption for females and males, respectively, so the majority of food captured in any given day is digested and used by the adults to sustain their metabolism before returning ashore.

Digesting the majority of food while at sea could have advantages both in terms of reducing the amount of energy that would be required to carry undigested food during the foraging trip and using the energy required for digestion (specific dynamic action) to substitute for thermoregulatory costs while at sea (Green et al. 2006). This could be particularly important during intervals spent at the surface between dives or diving bouts (Peters 2004). Studies of transit times through the gut, gastric motility and stomach pH in 5 species studied so far suggest that penguins are able to control the timing of digestion while at sea, such that prey items caught later in the foraging trip are fed to the chick essentially undigested (Wilson et al. 1989, Peters 1997, 2004, Thouzeau et al. 2004). Put together, these findings suggest that macaroni penguins feed continuously during a foraging trip, digesting the food caught during the early to mid-part of the trip. When they are ready to return to the colony they cease digestion in the stomach, continue foraging if necessary and return to the colony with their stomachs full of largely undigested food.

Prey capture rate during foraging dives

Several studies have attempted to determine the foraging success of marine predators while diving, often termed catch per unit effort (CPUE). Estimating CPUE or FS is useful as, for example, intra or inter annual changes in this quantity may identify periods when animals are or may become vulnerable to fluctuations in food supply (Grémillet et al. 2004). Despite some recent progress in this area (Ropert-Coudert et al. 2001, Simeone & Wilson 2003), data on specific feeding events and behaviour are difficult to obtain in free-ranging diving animals. This problem is particularly acute in medium- or long-term studies and future work should focus on new techniques and analysis to estimate prey consumption from behavioural data. In this study, we assumed that FS remained constant throughout the breeding period within each sex, but the analysis presented should be extended to year round data so that periods of vulnerability may be identified.

In this study the iterative process determined that male penguins were $\sim 24\%$ more effective foragers than females. Male macaroni penguins are larger than females (our Fig. 1; Williams 1995) and, therefore, have larger oxygen stores and a greater diving capacity. This will lead to sex specific differences in their ability to access the same prey at different depths. Mori & Boyd (2004) suggested that differences in body size between gentoo and macaroni penguins lead to differences in foraging success at different depths, allowing

these 2 species to live sympatrically while both feeding on the same prey resource, Antarctic krill. However, while male macaroni penguins usually dive to greater depths than females, the crèche phase is the only phase of the annual cycle in which females dive more deeply than males (Green et al. 2005b). Perhaps during this crucial phase of the year, which is the only time in which both sexes are constrained to forage sympatrically, males competitively exclude females and force them to forage at greater, less efficient depths. During the crèche phase males tend to travel slightly less far on foraging trips than do females. Furthermore, they travel more directly (i.e. with fewer turns) between the breeding colony and foraging areas and over a larger area (Barlow & Croxall 2002b). This may be indicative of males excluding females from particular profitable prey patches with the females having to undertake more searching activity leading to more sinuous paths during foraging trips. However, body size differences cannot always be invoked in studies of sex specific foraging behaviour of seabirds (Lewis et al. 2002).

Foraging success or CPUE was 2.28 and 2.84 g (min submerged) $^{-1}$ for females and males, respectively, in this study. CPUE has been estimated to be as high as 41 g min $^{-1}$ in the great cormorant (Grémillet et al. 2004), but can vary considerably between populations feeding under different conditions (Grémillet 1997) and between the sexes, with the larger males foraging more efficiently than the smaller females (Grémillet 1997). The little data that exist on CPUE in penguins suggest that the foraging success of macaroni penguins is similar to that of 3.1 g min $^{-1}$ (Nagy et al. 1984) or 1.75 g min $^{-1}$ (Grémillet 1997) in African penguins, but less than that of 7.2 to 9.6 g min $^{-1}$ in Magellanic penguins (Wilson 2004). An earlier analysis of sub-antarctic penguins suggested CPUE values ranging from 2.2 to 7.0 g min $^{-1}$ in chinstrap *Pygoscelis antarctica*, gentoo and king penguins (Croxall & Lishman 1987).

Effect of changes in prey availability

Competition from other consumers or fisheries or depletion in marine resources is most likely to manifest itself as a decrease in the FS of macaroni penguins. If we assume that the food demand from the chicks and all other factors remain constant, then varying FS within our algorithm results in differing body masses at the end of the breeding season (Fig. 8). Even a 10% reduction in FS would result in a 10 and 8% reduction in mass for females and males, respectively, at the end of the breeding season. A reduction in FS of 15 to 20% would result in body mass for both males and females dropping below that at the end of the moult fast (Fig. 1)

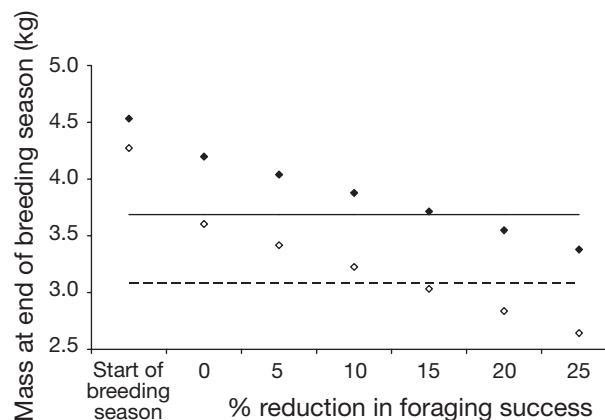


Fig. 8. *Eudyptes chrysolophus*. Effect of a modelled reduction in foraging success on body mass at the end of the chick rearing period for (◇) female and (◆) male macaroni penguins. Also shown is the mass at the start of the chick rearing period and lines representing body mass at the end of the moult fast for (---) females and (—) males

when body mass is at its lowest and the penguins are visibly emaciated and in very poor condition. The alternative to such a sacrifice would be to reduce the proportion of food fed to the chicks, which would undoubtedly affect their fledging mass, chance of survival and recruitment, as is the case in other penguin species (Dann 1988, Olsson 1997, Takahashi et al. 2003). Therefore, while macaroni penguins appear to show considerable flexibility in diet in response to short-term depletion of krill, (Croxall et al. 1999), even a small longer term reduction in the availability of prey could have profound implications on the viability of populations of this species. Similar studies should be conducted on the other major consumers in this ecosystem as a matter of urgency.

Concluding remarks

This study has integrated simultaneously recorded data on energy expenditure and foraging behaviour. By combining these with published data on growth rates, diet and body mass we have been able to estimate prey consumption rates and the allocation of prey caught between offspring and parents and answer several questions about the behaviour of this important species during chick rearing; a critical phase of its annual cycle. Specifically, macaroni penguins only feed 15.3% of all the food they capture to their chicks, while the remainder is retained to support their own metabolism, even though this results in negative energy balance. Further pressure from competing species or fisheries during chick rearing is likely to put this species under great pressure.

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