

# A bioenergetics model for estimating prey consumption by an Adélie penguin population in East Antarctica

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**ABSTRACT:** Quantifying prey consumption by top predators is a crucial component of ecosystem-based management in the Southern Ocean. In this study, we developed a bioenergetics model to estimate prey consumption by a top predator, the Adélie penguin *Pygoscelis adeliae*. Our model predicts prey consumption throughout the breeding season and incorporates uncertainty in model parameters using Monte Carlo simulation. The model was parameterized with data obtained at Béchervaise Island, the site of a long-term monitoring program in East Antarctica. We parameterized the model (1) using 13 yr of penguin population data, (2) for a year in which penguins successfully reared their chicks (2001–2002) and (3) for a year with low breeding success (1998–1999). Daily per capita energy consumption during the breeding season averaged 4269 kJ d<sup>-1</sup> (95% CI: 4187–4352 kJ d<sup>-1</sup>) and 4684 kJ d<sup>-1</sup> (95% CI: 4596–4771 kJ d<sup>-1</sup>) for males and females, respectively. Over the entire breeding season a male breeder consumes 470 MJ (95% CI: 461–479 MJ) compared to 515 MJ (95% CI: 506–525 MJ) for a female. On average, the Béchervaise Island population of 1836 breeding pairs consumes 16 447 MJ d<sup>-1</sup> which amounts to 1 809 224 MJ during the breeding season. On the basis of variable breeding success and the proportion of krill and fish in their diet, we estimate that this population consumes 78 to 406 t of krill and 4 to 46 t of fish each breeding season. Our results demonstrate clear periods of peak consumption associated with the penguins' breeding cycle.

**KEY WORDS:** Southern Ocean · Predator–prey · Uncertainty · Krill · Harvesting · Fisheries

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## INTRODUCTION

Increased exploitation of fisheries around the world has focused attention on the management of ecosystems rather than single target species (Pikitch et al. 2004). Managing fisheries under an ecosystem-based approach aims to ensure the sustainability of not only target species, but also the higher trophic level predators that are dependent on harvested prey (Brodziak & Link 2002, Garcia et al. 2003). To achieve ecosystem-based management, information on both the predator and prey is required; the abundance, spatial distribution, diet and behavioral interactions

contribute to how prey harvesting might affect predators (Croxall & Lishman 1987). Of particular importance to ecosystem-based management is quantifying the amount and rate of prey consumption by predators. Such estimates can be used to develop ecosystem models, can help set catch limits for harvested species and can assist in the development of multi-species management approaches (Daan & Sissenwine 1991, Pauly et al. 2003).

Southern Ocean ecosystems contain species that are important prey items for many top predators, but are also the focus of major fisheries. To reduce potential negative effects of harvesting, fisheries operating

in the Southern Ocean are regulated by the Convention for the Conservation of Antarctic Marine Resources (CCAMLR) (Agnew 1997). The CCAMLR has adopted an ecosystem-based approach to management, whereby catch limits are set to account for the propagating effects that harvesting might have on dependent predators (Edwards & Heap 1981). The CCAMLR's approach follows the precautionary principle: harvesting decisions need to take into account predator–prey interactions and account for uncertainty in the system being managed. Integral to this aim is an understanding of the diet of indicator species in the Southern Ocean, the overlap of their distribution with prey and the rate of prey consumption across space and time (Duffy & Schneider 1994).

Dietary and energetic studies of top predators in the Southern Ocean have been conducted using techniques such as double-labeled water (Nagy & Obst 1992, Chappell et al. 1993a, Culik 1994, Ballance et al. 2009), by measuring stomach contents (Wilson et al. 1992, Ancel et al. 1997), recording foraging behavior (Wilson et al. 1992, Davis et al. 1999, Takahashi et al. 2004, Sala et al. 2012) and measuring changes in stomach temperature. Each of these techniques determines an aspect of prey consumption which can be synthesized with bioenergetic models. Bioenergetic models are a useful tool for estimating prey consumption by free-ranging predators, where data are available for parameterization and because direct observations are difficult. They are essentially mass-balance equations in which ingested energy is partitioned into various compartments such as growth, metabolism and waste products. Bioenergetic models have been developed for many top predators in the Southern Ocean including numerous species of penguins (Brown 1989, Chappell et al. 1993b, Culik 1994, Croll & Tershy 1998, Salihoglu et al. 2001, Green et al. 2007), seals (Boyd 2002, Forcada et al. 2012) and whales (Reilly et al. 2004).

While the bioenergetics models that exist in the literature provide useful insight into prey consumption by top predators in the Southern Ocean, they tend to ignore (1) the timing and rate of prey consumption within stages of the breeding schedule (i.e. day-to-day prey consumption) and (2) parameter uncertainty (Boyd 2002, Forcada et al. 2012). Furthermore, bioenergetic models have tended to focus on individuals or populations in regions where fisheries are currently concentrated. To our knowledge, few estimates of prey consumption exist outside the Antarctic Peninsula or Scotia Sea regions (Woehler 1997) where diet, behavior and phenology of populations, and hence predator–prey interactions, may be differ-

ent (Clarke 2001, Ainley 2002). Estimating prey consumption by top predators at different locations is important because regional differences in behavior, such as foraging times and trip duration, will likely influence the amount, timing and rate of prey consumption. In some locations, a lack of rigorous predator–prey consumption estimation has hampered the development of ecosystem models and limited the scientific basis for taking account of predators' needs in catch limits (Croxall & Nicol 2004).

Adélie penguins are an important top predator in the Southern Ocean due to their wide distribution and high abundance (Croxall & Lishman 1987). As central-place foragers, they are particularly sensitive to prey availability during the breeding season, because breeders must repeatedly return to colonies to feed their offspring, vastly reducing the area in which they can forage. Adélie penguins consume predominantly fish and krill, both of which are the focus of major fisheries in the Southern Ocean (Constable et al. 2000). The composition of prey in the diet of this species is highly variable across space and time (Ainley 2002). Populations in the Scotia Sea and along the Antarctic Peninsula feed almost exclusively on krill (Coria et al. 1995, Lynnes et al. 2004), while those in the Ross Sea and East Antarctica prefer a mixed diet of fish and krill (Watanuki et al. 1997, Ainley et al. 2003, Tierney et al. 2009, Saillely et al. 2013). Estimating the amount and timing of prey consumption by Adélie penguins is crucial to ecosystem-based management in the Southern Ocean.

We developed a bioenergetics model to estimate daily prey consumption by a population of breeding Adélie penguins in East Antarctica. Our model features 3 developments that offer improved estimation of prey consumption by Adélie penguins by (1) estimating daily prey consumption, thus allowing the identification of periods of peak demand by Adélie penguins within a breeding season; (2) incorporating uncertainty in model parameters to prey consumption estimates, thus providing a scientific basis for implementing CCAMLR's precautionary principle; and (3) parameterizing the model if possible with data obtained from a long-term monitoring site in East Antarctica, thus ensuring estimates that are relevant to East Antarctic ecosystems. We estimate upper and lower bounds in prey consumption across breeding seasons from long-term monitoring data at Béchervaise Island and fit our model to 2 specific years of data to compare prey consumption between successful and unsuccessful breeding seasons. Quantifying prey consumption by Adélie penguins in East Antarctica will lead to improved predator–prey and

ecosystem models, particularly during the breeding season in waters adjacent to breeding colonies.

## MATERIALS AND METHODS

### Study species

The Adélie penguin breeds along most of the Antarctic coastline on ice-free land and offshore islands. At Béchervaise Island, males arrive at colonies in late October, establish territories and build nests (Emmerson et al. 2011). Females arrive shortly thereafter to initiate courtship and mating before laying a single clutch of usually 1 to 2 eggs (mean egg laying date 22 November). After egg lay, males incubate the eggs, while females depart nests to forage in waters surrounding the colonies. After several weeks females return to the colony to switch incubation duties with the males (9 December). When chicks hatch in late December, they require regular feeding and constant parental care while small (guard phase) until they can be left unguarded during the crèche phase (16 January) (Clarke et al. 2006). Towards the end of the breeding season, at the beginning of February, adults stop feeding chicks and forage in preparation for their annual molt. Not long after this, chicks leave the colonies for their winter migration (fledging). Thus, the breeding cycle of Adélie penguins can be divided into 6 phases: courtship/mating, incubation, chick guard, chick crèche, pre-molt and molt.

The breeding cycle of Adélie penguins is divided into periods of fasting and foraging during which their body mass fluctuates markedly (Emmerson et al. 2003). During fasting, breeding penguins rely on body reserves to satisfy energetic demands. When foraging, Adélie penguins not only ingest energy (krill and fish) to satisfy activity energy requirements, but they also ingest sufficient energy to sustain themselves during the next fasting period. Adélie penguins lose body mass from the time they arrive at the breeding colonies, throughout the incubation shift, during their nest attendance, during the guard period, in molt and, in some years, during the crèche period, depending on prey availability and sea-ice conditions (Clarke et al. 2006). Considerable body mass is gained during the pre-breeding season hyperphagia prior to their arrival at breeding colonies and during the pre-molt foraging period so that body reserves can maintain their energy requirements during the long fasts of incubation and molt, respectively. This cycle of fasting and foraging and the associated changes in body mass form the basis of our model.

### A bioenergetics model

We developed a bioenergetics model for estimating daily prey consumption for male and female breeding Adélie penguins. Our model accounts for periods of fasting and foraging within their breeding cycle and has 2 sub-models: (1) energy balance of breeding adults and (2) prey consumption by an entire breeding population. We describe each of these sub-models in detail below.

#### Sub-model 1: energy balance for breeding adults

Our model estimates the energy balance of a male and a female breeder for each day of the breeding season by subtracting energetic costs (activity energy requirements and energy delivered to chicks) from ingested energy. Assuming that all food captured was retained by adults or fed to chicks, the daily energy balance of a male and female adult ( $EB_d$ ) was given by:

$$EB_d = IE_d - EA_d - EC_d \quad (1)$$

where  $IE_d$  is daily ingested energy,  $EA_d$  is daily activity energy requirements and  $EC_d$  is daily energy delivered to chicks. The 3 components of Eq. (1) are described below.

#### Ingested energy, $IE_d$

For any day of the breeding cycle, we assumed that the amount of energy ingested by a breeder,  $IE_d$ , was a function of the probability of a breeder being at-sea and the rate at which energy is consumed at-sea, scaled by the assimilation efficiency. We scaled energy consumption by assimilation efficiency because not all food eaten by penguins is available for metabolism due to inefficiencies in the digestive process. It was calculated as:

$$IE_d = F_d \times FS \times AE_{adult} \quad (2)$$

where  $F_d$  is the probability of a male and a female breeder being at-sea for each day of the breeding cycle, foraging success (FS) is the rate of energy consumed when at-sea ( $\text{kJ d}^{-1}$ ) and  $AE_{adult}$  is the assimilation efficiency of an adult breeder. In determining the energy ingested each day by a breeder, we model the probability of a male and female being at-sea (see the Supplement at [www.int-res.com/articles/suppl/m526p183\\_supp.pdf](http://www.int-res.com/articles/suppl/m526p183_supp.pdf)) and specify adult assimilation efficiency from the literature. We do not, how-

ever, have any information on foraging success. To overcome this problem, we convert our predictions of ingested energy to body mass and estimate a value for foraging success so that our predictions of body mass match observations at our study site. This procedure is described below in further detail.

### Activity energy requirements, $EA_d$

Adélie penguins incur energetic costs every day in the breeding cycle, particularly when they are at-sea during activities such as swimming, diving and walking (Nagy & Obst 1992). We assumed that for any day in the breeding cycle, the energetic cost of carrying out activities depended on body mass, basal metabolic rate and the energetic cost of activities. Daily activity energy requirements,  $EA_d$ , of a male and a female breeder was calculated as:

$$EA_d = BMR \times E_d \times BM_{d-1} \quad (3)$$

where BMR is the basal metabolic rate for an adult,  $E_d$  is the daily energy requirement for a breeder (expressed as multiples of BMR), and  $BM_{d-1}$  is body mass of a breeder on the previous day. We grouped modes of locomotion during foraging and assumed that a breeder engages in 2 activities: on-nests and at-sea. We calculated  $E_d$  as:

$$E_d = F_d \times E_{sea} + (1 - F_d) \times E_{nest} \quad (4)$$

where  $F_d$  is the probability of being at-sea,  $E_{sea}$  is the energy required for activities such as foraging, swimming and resting on ice while at-sea ( $\text{kJ d}^{-1}$ ) expressed as a multiple of BMR and  $E_{nest}$  is the energy required while on a nest ( $\text{kJ d}^{-1}$ ) expressed as a multiple of BMR. When the sea-ice is extensive near the breeding colony, the term  $E_{sea}$  also includes the energetic requirements for traversing the sea-ice to reach the open water for foraging.

### Energy delivered to a chick, $EC_d$

Breeding Adélie penguins consume energy to not only satisfy their own energetic costs, but also to provision chicks. For Adélie penguins, this is relevant from the time chicks hatch in late December through to when adults leave breeding colonies to prepare for molt in mid- to late February. To estimate prey consumption by an adult, knowledge of the amount and rate at which energy is delivered to a brood of chicks is required. For any day in the breeding season between hatching and fledging, the amount of energy

delivered to a brood of chicks,  $EC_d$ , by a single parent was equal to:

$$EC_d = \frac{FMR_d + GR_d \times S_d \times P \times NC}{AE_{chick}} \quad (5)$$

where  $FMR_d$  is the field metabolic rate of a chick,  $GR_d$  is the energy required for a gain in body mass,  $S_d$  is the daily survival rate of chicks,  $P$  is the share of provisioning duty by parents,  $NC$  is the number of chicks per breeding pair and  $AE_{chick}$  is the assimilation efficiency of a chick. Daily chick survival,  $S_d$ , was included to account for the mortality of chicks over time. It can be interpreted as the proportion of the chick population surviving up until each day of the breeding season, set to 1 at hatching and declining linearly to 0.37 at fledging. This decline in the proportion of chicks alive, and hence the amount of ingested energy, was based on chick survival data collected at Béchervaise Island: on average 1.88 chicks hatch per nest and 0.71 of these survive to fledge (Clarke et al. 2003, Emmerson et al. 2003), which means the chance of a single chick fledging is 0.37 (i.e.  $0.71/1.88$ ). Therefore, energy delivered by a parent to a brood of chicks is a function of the rate at which chicks increase in body mass and the rate at which chick abundance declines over time.

The field metabolic rate for chicks was scaled linearly with body mass (Culik et al. 1990, Janes 1997) according to the equation  $FMR_d = 910 \times BMC_d$  ( $BMC$ : chick body mass; Janes 1997). Chick body mass was modeled with a logistic growth curve, given a mean hatching date ( $H$ ), hatching weight ( $W$ ), growth rate ( $G$ ) and fledging weight ( $F$ ). We assumed that chicks reached fledging weight after 52 d, which is the mean number of days between hatching and fledging at our study site.

To estimate the energy required for a gain in body mass, we assumed chicks had a constant total body water content of 75% from hatching to fledging (Salihoglu et al. 2001), resulting in a tissue energy density of  $5.325 \text{ kJ g}^{-1}$ . Therefore, the daily energy required for chick growth,  $GR_d$ , was calculated from the daily increment in body mass gain multiplied by the energy density of that mass gain, given by:  $GR_d = (BMC_d - BMC_{d-1}) \times 5.325$ .

### Estimating foraging success, $FS$

To estimate foraging success ( $FS$ ), we followed the procedure outlined by Green et al. (2007) by adjusting  $FS$  to calibrate model predictions with body mass data obtained at Béchervaise Island. Although our model predicted daily change in energy balance, we

could not measure energy balance directly to calibrate our model. We therefore calculated body mass from our predictions of energy surplus given an initial body mass at the start of the breeding season. We then repeatedly ran the model by iteratively varying foraging success FS (with other parameters held constant at their mean) until we found a value of FS that minimized the squared difference between our predictions and observations (see Fig. 1a,b). Foraging success, FS, was allowed to vary between males and females, but was assumed to remain constant throughout the breeding season.

To follow this calibration procedure, we first converted the predicted daily energy balance (Eq. 1) into body mass. We assumed that Adélie penguin tissue contains 37% water, 7% protein, 54% lipid and 2% other materials, which equates to an energy equivalent of 22.7 kJ g<sup>-1</sup> (Green et al. 2007). On days with an energy deficit (IE<sub>d</sub> is less than the sum of EA<sub>d</sub> and EC<sub>d</sub>), the amount of body mass lost by individuals to account for 1 kJ in energy expended was set to 0.044 g, as was assumed by Green et al. (2007) for macaroni penguins. Alternatively, on days when ingested energy exceeded energetic costs (a positive energy balance), we assumed breeders increased in body mass by 0.103 g for each gram of prey consumed (Green et al. 2007).

$$BM_d = \begin{cases} BM_{d-1} + EB_{d-1} \times 0.103 & \text{if } EB_{d-1} > 0 \\ BM_{d-1} - EB_{d-1} \times 0.044 & \text{if } EB_{d-1} < 0 \\ BM_{d-1} & \text{if } EB_{d-1} = 0 \end{cases} \quad (6)$$

where BM<sub>d</sub> is the body mass of an individual penguin on any given day, BM<sub>d-1</sub> is the body mass of an individual penguin during the previous day and EB<sub>d-1</sub> is the energy balance on the previous day calculated using Eq. (1).

### Sub-model 2: prey consumption by a breeding population

We combined per capita ingested energy (Eq. 2) with abundance estimates to calculate ingested energy by an entire breeding population and the amount of prey needed to satisfy this energetic requirement. The amount of prey required was converted to the amount of krill and fish consumed, as these are the most likely prey items to overlap with fisheries in the East Antarctic sector and are large components of their diet in the region (Tierney et al. 2009). The amount of prey consumed by the population, PC<sub>d</sub>, depended on ingested energy, the proportion of each prey type in the diet and the energy content of prey, given by:

$$PC_d = \frac{IE_d \times N \times D_{prey}}{ED_{prey}} \quad (7)$$

where IE<sub>d</sub> is daily per capita ingested energy, *N* is number of breeding pairs, *D*<sub>prey</sub> is the proportion of a prey type in the diet and ED<sub>prey</sub> is the energy density of prey. We assumed that Adélie penguins consume predominantly 2 types of prey: krill (*Euphausia superba* and *Euphausia crystallorophias*) and fish (Tierney et al. 2009). The proportion of fish and krill in the diet of breeders was estimated using diet composition data published by Tierney et al. (2009) (in the Supplement). Tierney et al. (2009) measured the mean mass of krill and fish in the stomachs of males and females during the guard and crèche stage over an 11 yr period (1991–1992 to 2002–2003). We pooled these data across years and gender to calculate the mean percentage of krill and fish in the diet of breeders (Table 1). We ignored any differences in diet between sexes and differences between the energy content of prey consumed by males and females. Such differences will have a slight influence on the relative amount of krill and fish consumed by the male and female populations, but not on overall amount of energy ingested by the population.

### Model parameterization

We parameterized our model using data on body mass, time spent foraging, breeding success, proportion of prey in their diet, population size and phenology (i.e. the timing of the breeding cycle) obtained from the Béchervaise Island (67°35'S, 62°49'E) long-term monitoring site, approximately 2 km from Mawson station in East Antarctica. We defined breeding success as the proportion of eggs laid that hatch and survive to fledging. Adélie penguins have been monitored at Béchervaise Island since 1990. We used data collected primarily from 1990 to 2003. Where data were unavailable from this site, we used published data from other locations. The data collection methodology is described in the Supplement, and parameter estimates and data sources are listed in Table 1.

### Simulation and sensitivity analysis

We ran the model for each day of a breeding season commencing on 1 November until the completion of molt (150 d). Simulations were run using R<sup>®</sup> 3.0.2 (R Development Core Team 2014). Initial body mass (BM<sub>d=1</sub>) of a male and a female breeder was set to 5713 and 5119 g, respectively (Fig. 1a,b), which is the

mean body mass of birds arriving at the island. To determine uncertainty in model predictions, our model was iterated 10 000 times by re-sampling model parameters using Monte Carlo simulation. Total prey consumption was calculated by summing  $PC_d$  across days for both the male and female population.

To demonstrate 3 applications of our model we calibrated predicted body mass of a male and a female breeder to (1) 13 yr of body mass data, (2) body mass data collected during one of the most successful years during this period in terms of chick survival (2001–2002), and (3) body mass data collected during one of the most unsuccessful years in terms of chick survival (1998–1999). In the first instance, we sampled model parameters from their full ranges of inter-annual variation. However, when calibrating our

model to the successful and unsuccessful breeding seasons, we set the survival rate of chicks and the proportion of krill in the diet of breeders to values observed in those years (Tierney et al. 2009). In 1998–1999 the number of chicks per nest and the proportion of krill in the diet of adults were set to 0.35 and 49%, respectively, while in 2001–2002 these values were fixed at 1.03 and 83%, respectively.

We tested the sensitivity of model predictions to each of the input variables. This was done by increasing and decreasing the mean (or upper and lower bounds) of each input variable by 10% while holding all other variables constant. The sensitivity of the model to input variables was then measured as the percentage change in the magnitude of total krill consumption by the Béchervaise Island population.

Table 1. Parameters of the bioenergetics model used to estimate prey consumption by breeding Adélie penguins *Pygoscelis adeliae* at Béchervaise Island. The term 'Norm' indicates parameters sampled from a normal distribution with the mean and standard deviation listed in parentheses. The term 'Uni' indicates parameters sampled from a uniform distribution with lower and upper bounds in parentheses

Parameter	Description	Value	References
FS	Foraging success	Males: 10187; females: 9542	This study
$AE_{adult}$	Assimilation efficiency	Norm (0.729, 0.067)	Green et al. (2007)
$F_d$	Daily probability off-nest	In the Supplement	L. Emmerson (unpubl. data)
BMR	Basal metabolic rate	Norm (275, 29)	Leresche & Boyd (1969), Kooyman et al. (1976), Pinshow et al. (1977), Ricklefs & Matthew (1983), Chappell & Souza (1988), Nagy & Obst (1992), Chappell et al. (1993a)
$BMC_d$	Daily body mass	See Fig. 1	This study, in the Supplement
$E_{nest}$	On-nest energy requirements	Uni (1.3–2) × BMR	Croxall (1982), Adams & Brown (1990), Green & Gales (1990), Nagy & Obst (1992), Chappell et al. (1993a)
$E_{sea}$	At-sea energy requirements	Uni (4.7–5) × BMR	Croxall (1982), Adams & Brown (1990), Green & Gales (1990), Nagy & Obst (1992), Chappell et al. (1993a)
$FMR_d$	Chick activity energy requirements	910 (kJ d <sup>-1</sup> kg <sup>-1</sup> ) × $BMC_d$ (kg)	Culik et al. (1990), Janes (1997), Chapman et al. (2010)
$W$	Chick hatch weight	90 g	Salihoglu et al. (2001)
$F$	Chick fledging weight	Norm (3432, 574)	Irvine et al. (2000)
$G$	Chick growth rate	Uni (0.146–0.148)	Trivelpiece et al. (1987), Janes (1997)
$EG_{chick}$	Chick energy density equivalent	5.325 kJ g <sup>-1</sup>	Salihoglu et al. (2001)
$AE_{chick}$	Chicks assimilation efficiency	Uni (0.75–0.8)	Davis et al. (1989), Salihoglu et al. (2001)
$S_d$	Number of chicks in brood that survive to fledge	Norm (0.71, 0.05)	Clarke et al. (2003), Emmerson et al. (2003)
$P$	Parental provisioning duties	Norm (0.5, 0.05)	Clarke et al. (2003), Emmerson et al. (2003)
$H$	Hatch date	25 Dec	Emmerson et al. (2011)
NC	Number of chicks per breeding pair	Norm (1.88, 0.05)	Culik (1994)
$ED_{krill}$	Energy density of krill (dry)	Uni (3.699–4.987 kJ g <sup>-1</sup> )	Davis et al. (1989), Nagy & Obst (1992), Salihoglu et al. (2001)
$ED_{fish}$	Energy density of fish (dry)	Uni (29.4–34.3 kJ g <sup>-1</sup> )	Lea et al. (2002), Tierney et al. (2002), Van de Putte et al. (2006)
$D_{krill}$	Proportion of krill in diet	Norm (0.62, 0.27)	Tierney et al. (2009)
$N$	Number of breeding pairs	Norm (1836, 130)	Clarke et al. (2003), Emmerson et al. (2003)

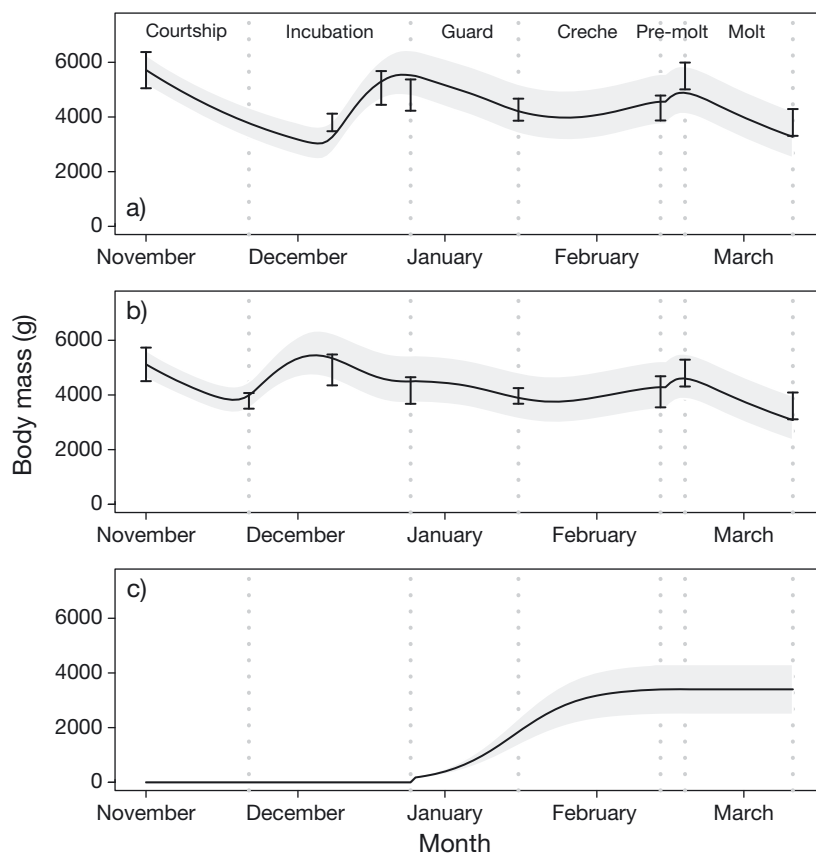


Fig. 1. *Pygoscelis adeliae*. Predicted body mass of a male (a), female (b) and chick (c) during the breeding season. Solid black lines: means of simulations, with grey shading representing 95% confidence intervals; solid black vertical lines in (a,b): observations of body mass ranges observed at Béchervaise Island during key periods of phenology, including arrival at the colony, egg laying, egg hatching, crèche and departure from the colony; dotted grey vertical lines: major phases of the breeding cycle. Body mass during molt was taken from the literature. We calibrated our model to minimize the squared difference between predictions of body mass and the mean of observations

## RESULTS

### Energy consumption by a single chick

Our model estimated daily per capita prey consumption, total per capita consumption, daily prey consumption by the Béchervaise Island population and total population prey consumption by males, females and chicks (Tables 2–4). Assuming a single chick survives from hatching to fledging (52 d), daily per capita ingested energy is equal to 2.774 MJ d<sup>-1</sup> (range: 2.015–3.533 MJ d<sup>-1</sup>) (Table 2). On average, this energetic demand is satisfied by 0.376 kg (0.114–0.651 kg) of krill and 0.036 kg (0.006–0.073 kg) of fish. In total a single chick ingests 144 MJ (105–184 MJ) of energy, composed of 20 kg (6–34 kg) of krill and 1.9 kg (0.3–3.8 kg) of fish during the breeding season.

### Energy delivered to chicks by breeding pairs

Assuming a constant decrease in number of chicks that survive, a breeding pair delivers 3.627 MJ (range: 2.632–4.636 MJ) of energy per day to an average-sized brood, made up of 0.492 g (0.151–0.850 kg) of krill and 0.047 kg (0.008–0.096 kg) of fish (Table 3). A brood of chicks receives 26 kg (8–44 kg) of krill and 2.5 kg (0.4–5 kg) of fish from hatching to fledging (52 d), amounting to 189 MJ (137–241 MJ) of energy. The chick population at Béchervaise Island is delivered on average 6665 MJ d<sup>-1</sup> (4621–8862 MJ d<sup>-1</sup>), comprised of 1.7 t (0.5–3 t) of krill and 0.2 t (0.02–0.33 t) of fish. During a breeding season, 88 t (27–156 t) of krill and 9 t (1–17 t) of fish are delivered to a brood of chicks by breeders, amounting to a total of 346 590 MJ (240 335–460 806 MJ) of energy.

### Energy consumption by an adult

Foraging success was estimated to be 9627 kJ d<sup>-1</sup> for a male and 9125 kJ d<sup>-1</sup> for a female when predicted body mass was calibrated to 13 yr of body mass data at Béchervaise Island (Table 4). Assuming these values, daily per capita ingested energy is equal to 4269 kJ (range: 4187–4352 kJ) for a male and 4684 kJ (4596–4771 kJ) for a female. To satisfy this energy requirement, approximately 579 g (186–949 g) and 635 g (203–1039 g) of krill are consumed by a male and female adult, respectively,

Table 2. *Pygoscelis adeliae*. Results from the chick bioenergetics model for a single Adélie penguin chick assuming survival from hatching to fledging. Values in parentheses represent 95% confidence intervals

	Daily	Total
Ingested energy (MJ)	2.774 (2.015–3.533)	144 (105–184)
Krill consumption (kg)	0.376 (0.114–0.651)	20 (6–34)
Fish consumption (kg)	0.036 (0.006–0.073)	1.9 (0.3–3.8)

per day. A male and female consume approximately 56 g (9–109 g) and 61 g (10–120 g) of fish per day, respectively. When summed over the breeding season, a male ingests 470 MJ (range: 471–479 MJ) of energy, while a female ingests 515 MJ (506–525 MJ). Daily predicted energy balance for a male, female and chick is shown in Fig. 2. Krill consumption totaled 64 kg (20–104 kg) for a male and 70 kg (22–114 kg) for a female, while fish consumption over a breeding season is approximately 6 kg (1–12 kg) and 7 kg (1–13 kg), respectively.

### Prey consumption by the Béchervaise Island population

Daily ingested energy by the Béchervaise Island population under average conditions equaled 7842 MJ (range: 6635–9056 MJ) for males and 8605 MJ (7280–991 MJ) for females, totaling 16447 MJ (13922–18989 MJ) (Table 4). Total daily krill consumption by the population averages 2229 kg (706–3695 kg), of which 1063 kg (337–1762 kg) is consumed by males and 1166 kg (370–1933) kg is consumed by females. Approximately 103 kg (17–201 kg) of fish is consumed each day by the male population, and 113 kg (18–222 kg), by the female population, totaling 215 kg (35–423 kg). During an average breeding season, the Béchervaise Island population ingests a total of 1 809 224 MJ (1 531 502–

Table 3. *Pygoscelis adeliae*. Energy delivered to an average-sized brood of Adélie penguin chicks by a breeding pair, and to the chick population of the colony, assuming 1.88 chicks nest<sup>-1</sup> and that 0.71 of these survive to fledge. Values in parentheses represent 95 % confidence intervals

	Per day	Per season
<b>Single brood</b>		
Energy (MJ)	3.627 (2.632–4.636)	189 (137–241)
Krill (kg)	0.492 (0.151–0.850)	26 (8–44)
Fish (kg)	0.047 (0.008–0.096)	2.5 (0.4–5.0)
<b>Chick population</b>		
Energy (MJ)	6665 (4621–8862)	346590 (240335–460806)
Krill (t)	1.7 (0.5–3.0)	88 (27–156)
Fish (t)	0.2 (0.02–0.33)	9 (1–17)

2 088 701 MJ) of energy; 862 649 MJ (729 902–996 193 MJ) is ingested by males and 946 574 MJ (800 774–1 093 475 MJ) is ingested by females (Table 4, Fig. 3a). Approximately 117 t (37–194 t) of krill and 11 t (2–22 t) of fish are consumed by males. Females consume 128 t (41–213 t) of krill and 12 t (2–24 t) of fish. Total krill and fish consumption by male and female populations is 245 t (78–406 t) and 24 t (4–46 t), respectively (Table 4, Fig. 3b).

Our model predicted the day-to-day demand in prey consumption by the Béchervaise Island population. Not surprisingly, prey consumption by male and female breeders mirrors the probability of being on- or off-nests. Prey consumption by the population increases shortly after egg laying, when females undertake their first foraging trip (Fig. 3a), remaining relatively constant while males and females swap incubation duties. As chicks become more independ-

Table 4. *Pygoscelis adeliae*. Results of the bioenergetics model for a male breeder, a female breeder, and the population of breeders at Béchervaise Island during the breeding season (150 d). Values in parentheses represent 95 % confidence intervals

	Male	Female	Total (male + female)
<b>Daily per capita</b>			
FS (kJ d <sup>-1</sup> )	9627	9125	18752
Energy consumption (kJ)	4269 (4187–4352)	4684 (4596–4771)	8953 (8825–9080)
Krill consumption (g)	579 (186–949)	635 (203–1039)	1214 (388–1988)
Fish consumption (g)	56 (9–109)	61 (10–120)	117 (19–228)
<b>Daily population</b>			
Ingested energy (MJ)	7842 (6635–9056)	8605 (7280–9941)	16447 (13922–18988)
Krill consumption (kg)	1063 (337–1762)	1166 (370–1933)	2229 (706–3695)
Fish consumption (kg)	103 (17–201)	113 (18–222)	215 (35–423)
<b>Annual per capita</b>			
Ingested energy (MJ)	470 (461–479)	515 (506–525)	985 (971–999)
Krill consumption (kg)	64 (20–104)	70 (22–114)	134 (43–219)
Fish consumption (kg)	6 (1–12)	7 (1–13)	13 (2–25)
<b>Annual population</b>			
Ingested energy (MJ)	862649 (729902–996193)	946574 (800774–1093475)	1809224 (1531502–2088701)
Krill consumption (t)	117 (37–194)	128 (41–213)	245 (78–406)
Fish consumption (t)	11 (2–22)	12 (2–24)	24 (4–46)



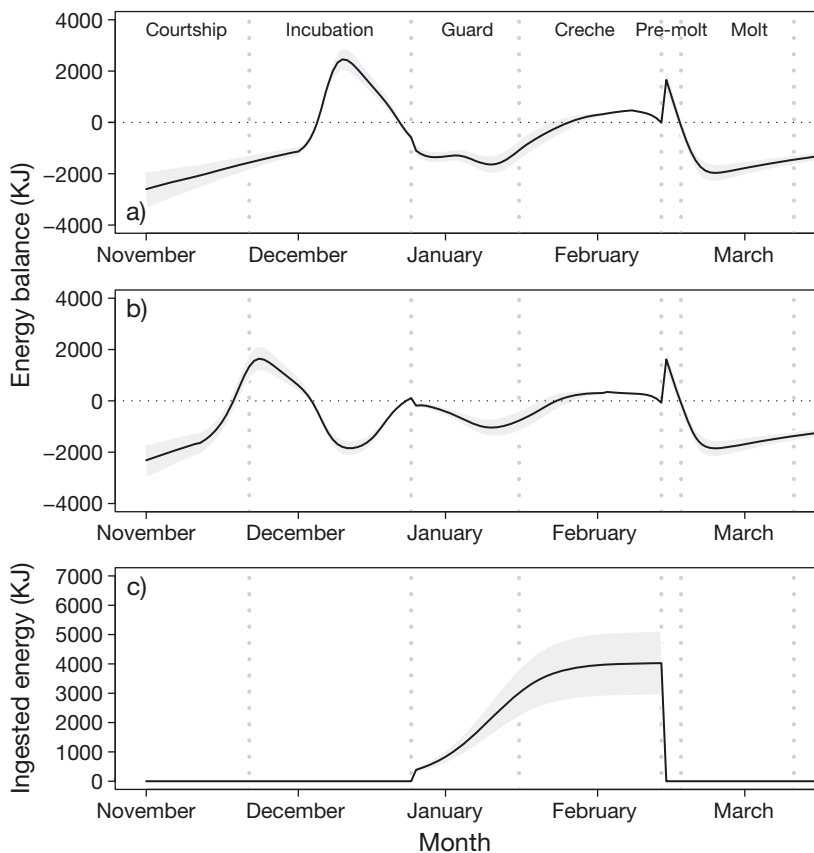


Fig. 2. *Pygoscelis adeliae*. Predicted energy balance for a male (a), female (b) and ingested energy by a chick (c) during the breeding season. Solid black lines: means of 10 000 simulations, with grey shading representing 95 % confidence intervals for inter-annual variation; horizontal lines in (a,b): zero energy balance, which occurs when ingested energy equals energetic costs; dotted grey vertical lines: major phases of the breeding cycle. Adults gain body mass when the energy balance is positive and lose body mass when it is negative

ent during the crèche stage, adults spend less time on their nest and more time at-sea. A peak in prey consumption occurs during pre-molt, as breeders must consume enough prey to gain considerable body mass (Fig. 3a).

### Prey consumption in 1998–1999 and 2001–2002

Per capita ingested energy by a male and a female in 1998–1999 was 4154 kJ (4076–4232 kJ) and 4462 kJ (4377–4545 kJ), respectively. Of this, approximately 472 g (413–540 g) of krill was consumed by a male, and 507 g (444–580 g) by a female per day. Fish consumption was estimated at 67 g (62–72 g) for males and 72 g (67–77 g) for females. Daily krill and fish consumption by the population of breeders in 1998–1999 was lower than consumption averaged over 13 yr (Fig. 3c,d). In 1998–1999 approximately 1 741 840 MJ

(1 476 368–2 002 963 MJ) of energy was consumed by the Béchervaise Island population. During 2001–2002, when the diet of adults was 83 % krill and chick survival was high, a male ingested 4369 kJ (4284–4451 kJ) of energy per day compared with 4802 kJ (4711–4891 kJ) by a female. Daily per capita krill consumption was higher than in 1998–1999, with males and females consuming 840 g (735–965 g) and 923 g (808–1061 g), respectively, while approximately 23 t (22–25 t) of fish was consumed by males and 26 t (24–28 t) by females. Daily krill and fish consumption by the population was consistently higher in 2001–2002 than in 1998–1999 and when averaged over the 13 yr monitoring program (Fig. 3c,d). The Béchervaise Island population consumed 1 853 454 MJ (1 577 293–2 134 531 MJ) in 2001–2002.

### Sensitivity of krill consumption to changes in input variables

Krill consumption by the Béchervaise Island breeding population was most sensitive to abundance estimates, percent krill in diet, energy density of prey and adult assimilation efficiency (Table 5). In general, varying the mean of these parameters by 10 % changed

the final estimate of population krill consumption by 6 to 11 %. Not surprisingly, krill consumption by the Béchervaise Island population was relatively insensitive to the chick model, as well as to the parameters associated with the energetic requirements of breeders at an individual level.

## DISCUSSION

Quantifying prey consumption by predators is crucial to ecosystem-based management of the Southern Ocean. We estimated daily prey consumption by Adélie penguins by calibrating a bioenergetics model to observed changes in body mass at Béchervaise Island in East Antarctica. While the energetic requirements of Adélie penguins have received considerable attention to date (Culik & Wilson 1992, Chappell et al. 1993b, Ballance et al. 2009), the majority of studies

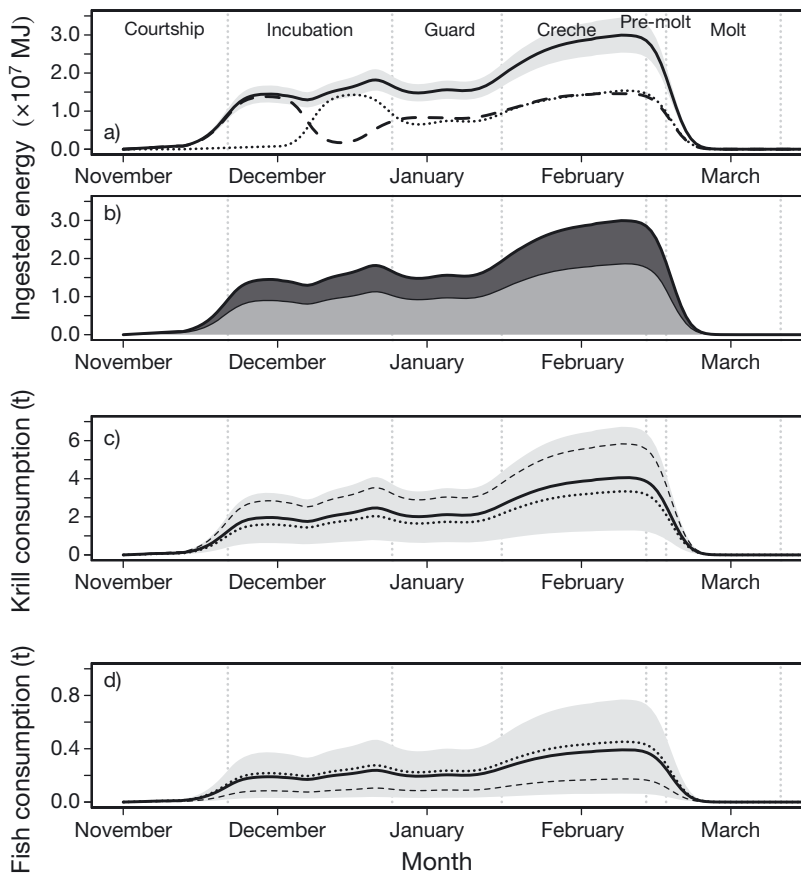


Fig. 3. *Pygoscelis adeliae*. (a) Total daily ingested energy by the Béchervaise Island breeding colony during the breeding season. Solid black line: total daily ingested energy by males and females combined, with grey shading representing 95% confidence intervals for inter-annual variation; dotted line: consumption by males; dashed line: consumption by females. (b) Total daily ingested energy by the Adélie penguin population at Béchervaise Island, partitioned into average amount of krill consumed (light grey) and average amount of fish consumed (dark grey). Total daily (c) krill and (d) fish consumption by the Béchervaise Island population. Solid black line: total daily ingested krill or fish consumption by males and females combined and averaged across years; grey shading: 95% confidence intervals for inter-annual variation; dashed black line: krill or fish consumption in 2001–2002; dotted black line: krill or fish consumption in 1998–1999. Dotted grey vertical lines in (a–d): major phases of the breeding cycle

have focused on populations located on the Antarctic Peninsula and have assumed that individuals have a constant body mass throughout the breeding season, ignoring the timing and rate of prey consumption within activity phases. Here, we quantify prey consumption by a breeding population in East Antarctica, where differences in phenology, diet and foraging behavior will likely influence the timing, rate and amount of prey consumed (Ainley 2002). Unlike previous studies, we account for day-to-day changes in body mass of both chicks and breeders to identify peaks in prey consumption during the breeding season.

Our estimates of energy consumption by breeders at Béchervaise Island are similar to values reported on the Antarctic Peninsula (Green & Gales 1990, Nagy & Obst 1992, Chappell et al. 1993b). Estimates of per capita energy consumption by Adélie penguins on the Antarctic Peninsula are highly variable, ranging from 4120 to 5761 kJ d<sup>-1</sup> (Green & Gales 1990, Nagy & Obst 1992, Chappell et al. 1993b). By comparison, we estimate that males and females consume around 4269 and 4684 kJ d<sup>-1</sup>, respectively (Table 4), which is at the lower end of published estimates. Such differences in daily per capita energy consumption are likely due to our assumptions about body mass, basal metabolic rate, activity energy requirements and the length of the breeding season. We also found a difference in the total amount of energy consumed by males and females. From the time breeders arrive at colonies to the completion of molt, energy consumption totals 470 MJ (461–479 MJ) for males and 515 MJ (506–525 MJ) for females. Differences in energy requirements and foraging strategies by male and female Adélie penguins have been reported in a number of studies (Culik & Wilson 1992, Chappell et al. 1993a, Clarke et al. 1998, Croll & Tershy 1998, Ballard et al. 2010). For example, Croll & Tershy (1998) estimated a male and a female consume 431 and 423 MJ, respectively, during the breeding season. The difference in energy consumption between sexes is likely due to differences in the amount of time males and females forage during

the breeding season. On average, females spend more time foraging than males (Ballard et al. 2010), mainly because they undertake the first foraging trip after courtship and mating and, therefore, consume more energy despite being smaller in size.

Although our estimates of daily per capita energy consumption are similar to values published in the literature, estimates of daily per capita krill consumption were considerably lower. We estimate that males and females consume approximately 579 g (186–949 g) and 635 g (203–1039 g) of krill per day, respectively. Estimates of daily per capita krill consumption

Table 5. Results of a sensitivity analysis for the bioenergetics model

Parameter	Description	Change in output after 10% increase in input (%)	Change in output after 10% decrease in input (%)
$F$	Chick fledging weight	-0.04	0.19
$G$	Chick growth rate	-1.59	1.40
NC	Number of chicks breeding per nest	-1.65	0.04
$AE_{\text{chick}}$	Chick assimilation efficiency	-0.69	1.33
$FMR_{\text{d}}$	Chick activity energy requirements	-1.30	1.70
$AE_{\text{adult}}$	Adult assimilation efficiency	9.19	-11.49
BMR	Basal metabolic rate	1.26	-0.18
$ED_{\text{krill}}$	Energy density of krill (dry)	-9.62	11.76
$ED_{\text{fish}}$	Energy density of fish (dry)	0.50	-0.41
$D_{\text{krill}}$	Proportion of krill in diet	5.68	-6.23
$BM_{\text{d}=1}$	Initial male body mass	1.26	0.25
$BM_{\text{d}=1}$	Initial female body mass	-2.06	2.11
$E_{\text{nest}}$	On-nest energy requirements	-2.21	2.73
$E_{\text{sea}}$	At-sea energy requirements	1.32	-1.05
$N$	Number of breeding pairs	11.01	-10.90

by Adélie penguins on the Antarctic Peninsula range from 800–1000 g d<sup>-1</sup> (Culik 1994) to 1400–1600 g d<sup>-1</sup> (Chappell et al. 1993b). Our estimates of per capita average daily krill consumption were lower than those in both of the Antarctic Peninsula studies, because krill made up on average 62% of the diet of foragers at Béchervaise Island, compared with the 95% used according to Culik (1994) and Chappell et al. (1993b). If we assume that Adélie penguins feed exclusively on krill, daily per capita krill consumption increases to 996 g (871–1142 g) for males and 1088 g (952–1247 g) for females, which is closer to the range of values reported in the studies listed above. Thus, our model suggests that, on average, per capita krill consumption at Béchervaise Island can be lower than that at other locations, but, importantly for this population, due to the variability in the proportion of fish and krill in their diets, can be highly variable between years.

Due to the high variability in the diet of breeders, chicks at Béchervaise Island consume less krill than those of populations at other locations. Assuming survival to fledging, we estimated that a single chick consumes on average 20 kg (range: 6–34 kg) of krill and 1.9 kg (0.3–3.8 kg) of fish, amounting to 144 MJ (105–184 MJ) of energy between hatching and fledging (Table 2). Salihoglu et al. (2001) estimate that 24.12 kg of fresh krill is delivered to chicks over 54 d. Their model was further developed by Chapman et al. (2010) to include a link between environmental conditions (such as temperature and wind speed) and chick growth, increasing krill consumption to 27.8 kg of krill. Trivelpiece et al. (1987) estimated a chick con-

sumes 25 kg of krill based on stomach content analysis combined with feeding rates, while Janes (1997) estimated a chick consumes 33.6 kg. If we assume the diet of chicks is entirely krill, as was assumed in the studies listed above, our estimate of total krill consumption by a chick during the breeding season increases to 33 kg (23–44 kg). Our model suggests that energy consumed by chicks is equal to 72–74% of the energy ingested by an adult. Using double-labeled water to determine activity energy requirements, Chappell et al. (1993b) estimated that approximately 75 to 80% of captured prey fuels the metabolism of breeders, with the remainder allocated towards chicks, while Culik (1994) estimated that 17% of krill consumed by adults is fed to chicks.

The timing and amount of prey consumption by Adélie penguins can be compared with similar or related species that undertake extended periods of fasting and foraging. For example, bioenergetic models have been developed for macaroni, gentoo and chinstrap penguins at various locations in the Southern Ocean. Croll & Tershy (1998) estimated that out of these species, Adélie penguins have the highest estimated individual energy requirement during the breeding season. They found that male and female Adélie penguins require 431 and 423 MJ, respectively, compared with 422 and 423 MJ for male and female gentoo penguins. This compares with 360 and 329 MJ for male and female chinstrap penguins, which is considerably less than our estimate for Adélie penguins. Other studies suggest that macaroni and Adélie penguins consume similar amounts of prey. Boyd (2002) estimated that macaroni penguins consume 1.2 kg of krill per day, while Green et al. (2007) found that 111.7 kg of prey is consumed during the chick-rearing period, 15.3% of which is fed to chicks. The amount of energy delivered to chicks is considerably less than estimated in this study (26–28%). Differences in prey consumption between species are due to differences in the length of the chick-rearing period, the number of chicks per breeding pair, foraging trip duration and the metabolic requirements of adult breeders.

### Model assumptions

Many sources of uncertainty may have contributed to biases in our model. Firstly, we did not include the

effects of temperature and wind (Chapman et al. 2011) in our model, nor did we include the effect of thermoregulation on chick growth, which can account for about 10 to 11% of assimilated energy (Chappell et al. 1990). Secondly, most parameters were held constant over time. In some cases, model parameters will likely change throughout the breeding season. For example, foraging success, FS, may vary between phases of the foraging cycle as sea-ice conditions change. Incorporating methods that allow FS to vary over time would be an interesting area of further work. Thirdly, we grouped activities into 2 categories: on-nests and at-sea. In reality, penguins will participate in a range of other activities when off their nests, such as swimming, walking, resting and diving (Culik & Wilson 1991a,b). Including the energetic costs of these activities separately would require GPS and heart rate data to provide detailed information on foraging activities and energetic requirements (Green et al. 2007). While we could have developed a more detailed model to incorporate these factors, we believe our model strikes a balance between the complexity and generality relevant to prey consumption estimates at a population rather than an individual level. Finally, our sensitivity analysis revealed that energy consumption estimates were most sensitive to abundance estimates. This finding is in agreement with other bioenergetic models (Boyd 2002). When gathering data to estimate prey consumption at the population level, it is wise to invest resources in reducing the uncertainty in this parameter.

### Model limitations

Our estimates of prey consumption do not account for the energy requirements of non-breeders, other Adélie penguin colonies in the region, or other species that feed on krill and fish in the same area. Prey consumption by fledglings after they depart the colony is not included in our model. Hence, our model underestimates prey consumption by the entire Adélie penguin population at Béchervaise Island. Few prey consumption models include both breeding and non-breeding individuals, because it is difficult to determine the abundance and energetic requirements of individuals not constrained to forage close to colonies. Furthermore, prey consumption by other species of seabirds, seals and whales that forage in the vicinity of Béchervaise Island and the offshore waters is likely large (Woehler 1997). Developing multi-species bioenergetics models for all components of these predator populations, in addi-

tion to breeding Adélie penguins, warrants further research.

### Management implications

Although fisheries are currently concentrated in waters surrounding the Antarctic Peninsula, recent development of efficient fishing methods and rising catch limits increase the likelihood that fishing will resume in East Antarctica (Nicol et al. 2012). By estimating day-to-day changes in prey consumption rather than just providing total estimates over the breeding season, we can identify critical periods when prey requirements are high. Fig. 3c,d shows a peak in krill and fish consumption by the Béchervaise Island breeding population towards the end of the breeding season prior to molt, when breeders forage to rapidly improve body condition without the burden of feeding chicks. Similar peaks in estimated prey consumption have been reported for macaroni penguins (Boyd 2002), chinstrap penguins and gentoo penguins (Croll & Tershy 1998). Our model contributes to precautionary management by quantifying the uncertainty around prey consumption estimates. A precautionary approach could be achieved by considering the upper limit of estimated prey consumption when setting catch limits as well as the timing of peaks in prey consumption.

Our model could be used to predict the potential impact of changes in food resource levels on Adélie penguins due to climate change or prey harvesting. We could vary key parameters such as foraging success to assess the potential impacts of reducing the rate of prey consumption on energy balance or body mass. However, modeling the effect of changes in food resource levels may not be simple; there will likely be complex compounding relationships between prey availability and adult behavior. For example, it is thought that adult Adélie penguins preserve their own condition at the cost of their chicks when environmental stress occurs (Watanuki et al. 2002, Takahashi et al. 2003, Ballard et al. 2010). Accounting for such dependencies between prey capture rates and model parameters, such as foraging trip duration, activity energy requirements and chick growth, would be complex, but is an important area of further research.

We could also modify the model to estimate prey consumption by other Adélie penguin colonies, or by other species that experience extended periods of foraging and fasting. In both cases, the most important data requirement to facilitate the calibration process would be observations of body mass during the

breeding season. To run the model for other Adélie populations, data requirements such as diet, abundance and nest attendance would also be important. Nest attendance data are particularly vital in modeling the daily probability of individuals being at-sea. We used daily nest attendance data to model activity schedules; however, we could have easily used observations collected less regularly. Ideally, dataloggers would be attached to individuals, to obtain detailed information on attendance and energetic expenditure (Green et al. 2007). To apply the model to other species, information would also be needed on basal metabolic rate, the energetic cost of activities, assimilation efficiency and chick growth. If information on these parameters is scarce, our method allows for plausible upper and lower bounds to be specified. If no empirical data are available, our model can be parameterized using information from similar or related species or based on expert opinions.

## CONCLUSIONS

We estimated prey consumption by Adélie penguins during the breeding season by calibrating a bioenergetics model to body mass data obtained from a long-term monitoring site in East Antarctica. Day-to-day estimates of prey consumption by populations of Adélie penguins may help the CCAMLR set catch limits for harvested species, which is an important component of ecosystem-based management. The greatest benefit of our model is that it estimates uncertainty in prey consumption, allowing decision-makers to adopt a precautionary approach to management. An understanding of the relationship between prey availability and predator performance is essential when using predators as indicators of marine systems.

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