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

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Running header: Prey consumption by Adélie penguins

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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 years 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 (95% CI 4187 – 4352) and 4684 KJ/d (95% CI 4596 – 4771) for males and females respectively. Over the entire breeding season male breeders consume 470 (95% CI 461 – 479) MJ compared to 515 (506 – 525) MJ for females. In 1998/1999 and 2001/2002, total ingested energy averaged 1,741,840 MJ and 1,853,454 MJ respectively. On average, the Béchervaise Island population of 1,836 breeding pairs consumes 16,447 MJ per day 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 - 406 T of krill and 4 - 46 T of fish each breeding season. Our results demonstrate clear periods of peak consumption associated with the penguins breeding cycle.

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 between predators and prey contributes 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 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). 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). CCAMLR's approach follows the precautionary principle: harvesting decisions need to take into account predator-prey interactions and to 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

65 can be synthesized with bioenergetic models. Bioenergetic models are a useful tool for
66 estimating prey consumption by free-ranging predators where data are available for
67 parameterization and because direct observations are difficult. They are essentially mass-
68 balance equations in which ingested energy is partitioned into various compartments such
69 as growth, metabolism and waste products. Bioenergetic models have been developed for
70 many top predators in the Southern Ocean including numerous species of penguin
71 (Brown 1989, Chappell et al. 1993b, Culik 1994, Croll & Tershy 1998, Salihoglu et al.
72 2001, Green et al. 2007), seals (Boyd 2002, Forcada et al. 2012) and whales (Reilly et al.
73 2004).

74 While the bioenergetics models that exist in the literature provide useful insight into prey
75 consumption by top predators in the Southern Ocean, they tend to ignore: 1) the timing
76 and rate of prey consumption within stages of the breeding program (i.e. day-to-day prey
77 consumption), and; 2) parameter uncertainty (Boyd 2002, Forcada et al. 2012).
78 Furthermore, bioenergetic models have tended to focus on individuals or populations in
79 regions where fisheries are currently concentrated. To our knowledge, few estimates of
80 prey consumption exist outside of the Antarctic Peninsula or Scotia Sea regions (Woehler
81 1997) where diet, behavior and phenology of populations, and hence predator-prey
82 interactions, may be different (Clarke 2001, Ainley 2002). Estimating prey consumption
83 by top predators at different locations is important because regional differences in
84 behavior, such as foraging times and trip duration, will likely influence the amount,
85 timing and rate of prey consumption. In some locations, a lack of rigorous predator-prey
86 consumption estimation has hampered the development of ecosystem models and limited
87 the scientific basis for taking account of predators' needs in catch limits (Croxall &
88 Nicol 2004).

89 Adélie penguins are an important top predator in the Southern Ocean due to their wide
90 distribution and high abundance (Croxall & Lishman 1987). As central-place foragers,
91 they are particularly sensitive to prey availability during the breeding season because
92 breeders must repeatedly return to colonies to feed their offspring, vastly reducing the
93 area in which they can forage. Adélie penguins consume predominantly fish and krill,
94 both of which are the focus of major fisheries in the Southern Ocean (Constable et al.

2000). The proportion of this 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, Sailley et al. 2013). Estimating the amount and timing of prey consumption by Adélie penguins is crucial to ecosystem 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 three 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 where 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 two 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 after to initiate courtship and mating before laying a single clutch of usually 1-2 eggs (average 22nd 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 (9th December). When chicks hatch in late December, they require regular feeding and constant parental care by one or other of the parents while small (guard phase) until they can be left unguarded during the crèche phase (16th 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 six 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 the 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 forms 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 two 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 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 three components of equation 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 that is 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 the probability of a male and female breeder being at-sea for each day of the breeding cycle, foraging success (*FS)* is the rate of energy consumed when at-sea (KJ/d) 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 supplementary material) and specify adult assimilation efficiency from the literature. We do not, however, 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 for Adélie penguins. This procedure is described below in further detail.

178 **Activity energy requirements EA_d**

179 Adélie penguins incur energetic costs any day in the breeding cycle particularly when
180 they are at-sea during activities such as swimming and diving, and walking (Nagy & Obst
181 1992). We assumed that for any day in the breeding cycle, the energetic cost of carrying
182 out activities depended on body mass, basal metabolic rate and the energetic cost of
183 activities. Daily activity energy requirements EA_d of a male and female breeder was
184 calculated as:

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

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

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

189 where F_d is the probability of being at-sea, E_{sea} is the energy required for activities such
190 as foraging, swimming and resting on ice while at-sea (KJ/d) expressed as a multiple of
191 *BMR* and E_{nest} is the energy required while on a nest (KJ/d) expressed as a multiple of
192 *BMR*. When the sea-ice is extensive near the breeding colony, this term also includes the
193 energetic requirements for traversing the sea-ice to reach the open water for foraging.

194 **Energy delivered to a chick EC_d**

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

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

where FMR_d is the field metabolic rate of a chick, GR_d is 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. We assumed the daily survival rate of a chick S_d decreased linearly from one at hatching to 0.37 at fledging. This is based on chick survival data collected at Bechervaise Island: on average 1.88 chicks hatch per nest and of these 0.71 survive to fledge (Clarke et al. 2003, Emmerson et al. 2003). This meant that prey consumption by the chick population was influenced by two factors: 1) the rate at which chicks increased body mass, and; 2) the rate at which the chick population declined throughout the breeding season.

Field metabolic rate for chicks was scaled linearly with body mass (Culik et al. 1990, Janes 1997) according to the equation $FMRd = 910 \times BM_d$ (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 days, which is the mean number of days between hatching and fledging at our study site.

To estimate energy required for a gain in body mass we assumed chicks had constant total body water content of 75% from hatching to fledging (Salihoglu et al. 2001), resulting in a tissue energy density of 5.325 KJ/g. 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: $GR_d = (BM_d - BM_{d-1}) \times 5.325$.

Estimating Foraging success (*FS*)

To estimate foraging success (*FS*), we followed the procedure outlined by Green (2007) by adjusting *FS* to calibrate model predictions of body mass against 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 (Figure 1 a, 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 predicted daily energy balance (Equation 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 (Green et al. 2007). On days with an energy deficit (IE_d is less than the sum of EA_d and EC_d), 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 0.103g for each gram of krill consumed (Green et al. 2007).

$$\mathrm{BM}_d = \begin{cases} BM_{d-1} + \mathrm{EB}_{d-1} \times 0.103 & if\ \mathrm{EB}_{d-1} > 0 \\ BM_{d-1} - \mathrm{EB}_{d-1} \times 0.044 & if\ \mathrm{EB}_{d-1} < 0 \\ BM_{d-1} & if\ \mathrm{EB}_{d-1} = 0 \end{cases} \quad (6)$$

where BM_d is the body mass of an individual penguin on any given day, BM_{d-1} is body mass of an individual penguin during the previous day and EB_d is the energy balance on the given day calculated using Equation 1.

Sub-model 2: Prey consumption by a breeding population

We combined per capita ingested energy (Equation 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 2009). The amount of prey consumed by the population PC_d depended on ingested energy, the proportion of each prey type in the diet and the energy content of prey, given by:

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

where $\mathrm{IE_d}$ is daily per capita ingested energy, N number of breeding pairs, D_{prey} is the proportion of a prey type in the diet and ED_{prey} is the energy density of prey. We assumed that Adélie penguins consume predominantly two 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) (Supplementary information). Tierney et al. (2009) measured the mean mass of krill and fish in the stomach of male and females during the guard and crèche stage over an 11 year period (1991/92 – 2002/03). 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 or 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 population, but not on total 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 (67º35'S; 62º49'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 – 2003. Where data were unavailable from this site, we used published data from other locations. Data collection methodology is described in the Supplementary material 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 the 1st November until the completion of molt (150 days). Simulations were run using R© 3.0.2 (R Development Core Team 2014). Initial body mass of a male and female breeder was set

283 to 5713 g and 5119 g respectively (Figure 1 a, b) which is the mean body mass of birds
284 arriving to the island. To determine uncertainty in model predictions, our model was
285 iterated 10,000 times by re-sampling model parameters using Monte Carlo simulation.
286 Total prey consumption was calculated by summing PC_d across days for both male and
287 females respectively.

288 To demonstrate three applications of our model we calibrated predicted body mass of a
289 male and female breeder to: 1) 13 years of body mass data; 2) body mass data collected
290 during one of the most successful years during this period in terms of chick survival
291 (2001/02), and; 3) body mass data collected during one of the most unsuccessful years in
292 terms of chick survival (1998/99). In the first instance, we sampled model parameters
293 from their full ranges of inter-annual variation. However, when calibrating our model to
294 the successful and unsuccessful breeding seasons, we set the survival rate of chicks and
295 the proportion of krill in the diet of breeders to values observed in those years (Tierney et
296 al. 2009). In 1998/99 the number of chicks per nest and the proportion of krill in the diet
297 of adults were set to 0.35 and 49% respectively, while in 2001/02 these values were fixed
298 at 1.03 and 83% respectively.

299 We tested the sensitivity of model predictions to each of the input variables. This was
300 done by increasing and decreasing the mean (or upper and lower bounds) of each input
301 variable by 10% while holding all other variables constant. The sensitivity of the model
302 to input variables was then measured as the percentage change in the magnitude of total
303 krill consumption by the Béchervaise Island population. While we chose to measure
304 model sensitivity by comparing predictions of krill consumption, we could have just as
305 easily conducted the sensitivity analysis by measuring changes in fish consumption.

306 **RESULTS**

307 **Energy consumption by a chick**

308 Our model estimated daily per capita prey consumption, total per capita consumption,
309 daily prey consumption by the Béchervaise Island population and total population prey
310 consumption by males, females and chicks (Table 2 – 4). Assuming no mortality, daily
311 per capita ingested energy by a chick was equal to 2774 (2015 – 3533) KJ/d from

hatching to fledging (52 days) (Table 2). On average, this energetic demand is satisfied by 376 (114 – 651) g of krill and 36 (6 – 73) g of fish. In total a single chick ingests 144 (105 – 184) MJ of energy, composed of 20 (6 – 34) kg of krill and 1.9 (0.3 – 3.8) kg of fish. If all chicks survive to fledge, the Béchervaise Island chick population requires 9581 (6658 – 12699) MJ of energy per day. Assuming the diet of chicks is the same as adults, this is equivalent to 1.3 (0.4 – 2.3) T of krill and 0.13 (0.02 – 0.26) T of fish. From hatching to fledging, a population of 1400 chicks requires 4.9×10^5 ($3.4 \times 10^5 – 6.6 \times 10^5$) MJ of energy, which on average is satisfied by 68 (20 – 119) T of krill and 7 (1 – 13) T of fish.

Energy delivered to chicks by a breeding pair

Assuming a constant decrease in the survival rate of chicks, a breeding pair delivers 3627 (2632 – 4636) KJ of energy to a two chick brood. Assuming chicks receive the same diet as adults, this is equivalent to 492 (151 – 850) g of krill and 47 (8 – 96) g of fish (Table 3). A brood of chicks receive 26 (8 – 44) kg of krill and 2.5 (0.4 – 5) kg of fish from hatching to fledging (52 days), amounting to 189 (137 – 241) MJ of energy. The chick population at Béchervaise Island is delivered on average 6665 (4621 – 8862) MJ per day, comprised of 1.7 (0.5 – 3) T of krill and 0.2 (0.02 – 0.33) T of fish assuming a decrease in survival over time. During a breeding season 88 (27 – 156) T of krill and 9 (1 – 17) T of fish is delivered to a brood of chicks by breeders, amounting to a total of 3.4×10^5 ($2.4 \times 10^5 – 4.6 \times 10^5$) MJ of energy.

Energy consumption by an adult

Foraging success was estimated to be 9627 KJ/d for a male and 9125 KJ/d for a female when predicted body mass was calibrated to the average of body mass observations made at Béchervaise Island (Table 4). Assuming these values, daily per capita ingested energy was equal to 4249 (4187 - 4352) KJ for a male and 4684 (4596 – 4771) for a female. To satisfy this energy requirement, approximately 579 (186 – 949) g and 635 (203 – 1039) g of krill is consumed by a male and female adult daily. A male and female consume approximately 56 (9 – 109) g and 61 (10 – 120) g of fish per day respectively. When summed over the breeding season, a male ingests 7842 (6635 – 9056) MJ of energy,

while a female ingests 8605 (7280 – 9941) MJ. Krill consumption totaled 1063 (337 – 1762) kg for a male and 1166 (370 – 1933) kg for a female, while fish consumption over a breeding season was approximately 103 (17 – 201) kg and 113 (18 – 222) kg respectively.

Prey consumption by the Béchervaise Island population

Daily ingested energy by the Béchervaise Island population under average conditions equaled 470 (461 – 479) MJ for males and 515 (506 – 525) MJ for females, totaling 985 (971 – 999) MJ (Table 4). Total krill consumption by the population averaged 134 (43 – 219) kg, of which 64 (20 – 104) kg was consumed by males and 70 (22 – 114) kg is consumed by females. Approximately 6 (1 – 12) kg of fish is consumed each day by the male population and 7 (1 – 13) kg by the female population, totaling 13 (2 – 25) kg. During an average breeding season, the Béchervaise Island population ingest a total of 1809224 (1531502 – 2088701) MJ of energy; 862649 (729902 – 996193) MJ is ingested by males and 946574 (800774 – 1093475) MJ is ingested by females (Figure 3a). Approximately 117 (37 – 194) T of krill and 11 (2 – 22) T of fish is consumed by males. Females consume 128 (41 – 213) T of krill and 12 (2 – 24) T of fish. Total krill and fish consumption by the male and female population is 245 (78 – 406) T and 24 (4 – 46) T respectively (Figure 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 mirrored 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 (Figure 3a), remaining relatively constant while male and females swap incubation duties. As chicks become more independent during the crèche stage, adults spend less time on their nest and more time at-sea. A peak in prey consumption occurs between fledging and molt as breeders must consume enough prey to gain considerable body mass (Figure 3a).

Prey consumption in 1998/99 and 2001/02

Per capita ingested energy by a male and female in 1998/99 was 4154 (4076 – 4232) KJ and 4462 (4377 – 4545) KJ respectively. Of this, approximately 472 (413 – 540) g of krill

370 was consumed by a male and 507 (444 – 580) g by a female per day. Fish consumption
371 was estimated at 67 (62 – 72) g for males and 72 (67 – 77) g for females. In 1998/99
372 approximately of 1,741,840 (1,476,368 – 2,002,963) MJ of energy was consumed by the
373 Béchervaise Island population, which is slightly lower than average energy consumption
374 averaged over 13 years (Figure 3c). During 2001/02, when the diet of adults was 83%
375 krill and chick survival was high, a male ingested 4369 (4284 – 4451) KJ of energy per
376 day compared with 4802 (4711 – 4891) KJ by a female. Daily per capita krill
377 consumption was higher than in 1998/99, with males and females consuming 840 (735 –
378 965) and 923 (808 – 1061) g respectively, while approximately 23 (22 – 25) T of fish was
379 consumed by males and 26 (24 – 28) T by females. The Béchervaise Island population
380 consumed 1,853,454 (1,577,293 – 2,134,531) MJ in 2001/02, which is significantly
381 greater than the average amount of energy ingested by this population (Figure 3c).

382 **Sensitivity of krill consumption to changes in input variables**

383 Krill consumption by the Berchervaise Island breeding population was most sensitive
384 abundance estimates, percent krill in diet, energy density of krill and fish, and adult
385 assimilation efficiency (Table 5). In general, varying the mean of these parameters by
386 10% changed the final estimate of population krill consumption by 6 – 11%. Not
387 surprisingly, krill consumption by the Béchervaise Island population was relatively
388 insensitive to the chick model as well as parameters associated with the energetic
389 requirements of breeders at an individual level.

390 **DISCUSSION**

391 Quantifying prey consumption by predators is crucial to ecosystem-based management of
392 the Southern Ocean. We estimated daily prey consumption by Adélie penguins by
393 calibrating a bioenergetics model to observed changes in body mass at Béchervaise Island
394 in east Antarctica. While the energetic requirements of Adélie penguins have received
395 considerable attention to date (Culik & Wilson 1992, Chappell et al. 1993b, Ballance et
396 al. 2009), the majority of studies have focused on populations located on the Antarctic
397 Peninsula and have assumed that individuals have a constant body mass throughout the
398 breeding season, ignoring the timing and rate of prey consumption within activity phases.

399 Here, we quantify prey consumption by a breeding population in east Antarctica, where
400 differences in phenology, diet and foraging behavior will likely influence the timing, rate
401 and amount of prey consumed (Ainley 2002). Unlike previous studies, we account for
402 day-to-day changes in body mass of both chicks and breeders to identify peaks in prey
403 consumption during the breeding season.

404 Our estimates of energy consumption by breeders at Béchervaise Island are similar to
405 values reported on the Antarctic Peninsula (Green & Gales 1990, Nagy & Obst 1992,
406 Chappell et al. 1993b). Estimates of per capita energy consumption for Adélie penguins
407 on the Antarctic Peninsula are highly variable, ranging from 4120 – 5761 KJ per day
408 (Green & Gales 1990, Nagy & Obst 1992, Chappell et al. 1993b). By comparison, we
409 estimate that males and females consume around 4210 KJ and 4520 KJ per day
410 respectively (Table 4), which is at the lower end of published estimates. Such differences
411 in daily per capita energy consumption are likely due to our assumptions about body
412 mass, basal metabolic rate, activity energy requirements and the length of the breeding
413 season. We also found a difference in the total amount of energy consumed by males and
414 females. From the time breeders arrive at colonies to the completion of molt, energy
415 consumption totals 463 (454 – 472) MJ for males and 496 (487 – 506) MJ for females.
416 Differences in energy requirements between male and female Adélie penguins have been
417 reported in other studies. Croll (1998) estimated a male and female consumes 431 MJ and
418 423 MJ respectively during the breeding season. The difference in energy consumption
419 between sexes is likely due to differences in the amount of time males and females forage
420 during the breeding season. On average, females spend more time foraging than males,
421 mainly because they undertake the first foraging trip after courtship and mating, and
422 therefore consume more energy despite being smaller in size.

423 Although our estimates of daily per capita energy requirements are similar to values
424 published in the literature, estimates of daily per capita krill consumption were
425 considerably lower. We estimate that males and females consume approximately 565
426 (179 – 925) g and 606 (192 – 992) g of krill per day respectively. Estimates of daily per
427 capita krill consumption by Adélie penguins on the Antarctic Peninsula range from 800 –
428 1000 g per day (Culik 1994) to 1400 – 1600 kg per day (Chappell et al. 1993b). Our

429 estimates of per capita average daily krill consumption were lower than either of the
430 Antarctic Peninsula studies because krill Béchervaise made up on average 62% of the
431 diet of foragers at Béchervaise Island krill, compared with the 95% used by Culik (1994)
432 and Chappell (1993). If we assume that Adélie penguins feed exclusively on krill, daily
433 per capita krill consumption increases to 976 (854 – 1117) g for males and 1053 (922 –
434 1206) g for females, which is closer to the range of values reported in the studies listed
435 above. Thus, our model suggests that on average, per capita krill consumption at
436 Béchervaise Island can be lower compared with other locations, but importantly for this
437 population, due to the variability in the proportion of fish and krill in their diet, can be
438 highly variable between years.

439 Due to the high variability in the diet of breeders, chicks at Béchervaise Island consume
440 less krill than for populations at other locations. Assuming survival to fledging, we
441 estimated that a single chick consumes on average 18 (6 – 32) kg of krill and 1.8 (0.3 –
442 3.6) kg of fish, amounting to 136 (98 – 174) MJ of energy between hatching and
443 fledging. Salihoglu et al. (2001) estimate that 24.12 kg of fresh krill is delivered to chicks
444 over 54 days. Their model was further developed by Chapman et al. (2010) to include a
445 link between environmental conditions (such as temperature and wind speed) and chicks
446 growth, increasing krill consumption to 27.8 kg of krill. Trivelpiece et al. (1987) also
447 estimated a chick consumes 25 kg of krill based on stomach content analysis combined
448 with feeding rates, while Janes (1997) estimated a chick consumes 33.6 kg. If we assume
449 the diet of chicks is entirely krill, as was assumed in the studies listed above, our estimate
450 of total krill consumption by a chick during the breeding season increases to 32 (22 – 41)
451 kg. Our model suggests that energy consumed by chicks is equal to 72 – 74 % of energy
452 ingested by an adult. Using double-labeled water to determine activity energy
453 requirements, Chappell et al. (1993b) estimated that approximately 75 – 80% of captured
454 prey fuels the metabolism of breeders, with the remainder allocated towards chicks, while
455 Culik (1994) estimated that 17% of krill consumed by adults is fed to chicks.

456 The timing and amount of prey consumption by Adélie penguins can be compared with
457 similar or related species that undertake extended periods of fasting and foraging. For
458 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 MJ and 423 MJ respectively, compared with 422 MJ and 423for male and female gentoo penguins. This compares with 360 MJ and 329 MJ for male and female chinstrap penguins, which is considerably less than our estimate for Adélie penguins. Other studies suggest that macaroni penguins consume similar amounts of prey to Adélie penguins. Boyd (2002) estimated 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, of which 15.3% is fed to chicks. The amount of energy delivered to chicks is considerably less than what was found in this study (26 – 28%). Differences in prey consumption between species is due to differences in the length of 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 in our model (Chappell 1989), nor did we include the effect of thermoregulation on chick growth, which can account for about 10 - 11% of assimilated energy (Chappell 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 allows *FS* to vary over time would be an interesting area of further work. Thirdly, we grouped activities into two 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 obtain detailed information on foraging activities and energetic requirements (Green 2006). While we could have developed a more detailed model to incorporate these factors, we believe our model strikes a balance between complexity and generality relevant to prey consumption estimates at a

489 population rather than individual level. Finally, our sensitivity analysis revealed that
490 energy consumption estimates were most sensitive to abundance estimates. This finding
491 is in agreement with other bioenergetic models (Boyd 2002). When gathering data to
492 estimate prey consumption at the population level, it is wise to invest resources to reduce
493 uncertainty in this parameter.

494 **Model limitations**

495 Our estimates of prey consumption do not account for the energy requirements of non-
496 breeders, other Adélie penguin colonies in the region, or other species that feed on krill in
497 the same area. Prey consumption by fledglings after they depart the colony is not
498 included in our model, nor is prey consumption by non-breeders or intermittent breeders.
499 Hence, our model underestimates prey consumption by the entire Adélie penguin
500 population at Béchervaise Island. Few prey consumption models include both breeding
501 and non-breeding individuals because it is difficult to know the abundance and energetic
502 requirements of individuals not constrained to forage close to colonies. Prey consumption
503 by other species of seabirds, seals and whales that forage in the vicinity of Béchervaise
504 Island and the offshore waters, is likely be large (Woehler 1997). Developing multi-
505 species bioenergetics models for all components of these predator populations in addition
506 to breeding Adélie penguins warrants further research.

507 **Management implications**

508 Although fisheries are currently concentrated in waters surrounding the Antarctic
509 Peninsula, recent development of efficient fishing methods and a rising catch limits,
510 increases the likelihood that fishing will resume in east Antarctica (Nicol et al. 2012). By
511 estimating day-to-day changes in prey consumption rather than just providing total
512 estimates over the breeding season, we can identify critical periods when prey
513 requirements are high. Figure 3c,d shows a peak in krill and fish consumption by the
514 Béchervaise Island breeding population towards the end of the breeding season prior to
515 molt when breeders forage to rapidly improve body condition without the burden of
516 feeding chicks. Similar peaks in estimated prey consumption have been reported for
517 macaroni penguins (Boyd 2002), chinstrap penguins and gentoo penguins (Croll &

518 Tershy 1998). Our model contributes to precautionary management by quantifying the
519 uncertainty around prey consumption estimates. A precautionary approach could be
520 achieved by considering the upper limit of estimated prey consumption when setting
521 catch limits as well as the timing of peaks in prey consumption.

522 Our model could be used to predict the potential impact of changes in food resource
523 levels on Adélie penguins due to climate change or prey harvesting. We could vary key
524 parameters such as foraging success (*FS*) to assess the potential impacts of reducing the
525 rate of prey consumption on energy balance or body mass. However, modeling the effect
526 of changes in food resource levels may not be simple: there will likely be complex
527 compounding relationships between prey availability and adult behavior. For example, it
528 is thought that adult Adélie penguins preserve their own condition at the cost of their
529 chicks when environmental stress occurs (Tveraa 1998; Watanuki 2002; Takahashi
530 2003). Accounting for such dependencies between prey capture rates and model
531 parameters such as foraging trip duration, activity energy requirements and chick growth
532 would be complex, but is an important area of further research.

533 We could also modify the model to estimate prey consumption by other Adélie penguin
534 colonies, or by other species that experience extended periods of foraging and fasting. To
535 run the model for other Adélie populations, the most critical data requirement is diet,
536 abundance and nest attendance. Nest attendance data are particularly important for
537 modeling the daily probability of individuals being at-sea. We used daily nest attendance
538 data to model activity schedules; however we could have easily used observations
539 collected less regularly. Ideally, data loggers would be attached to individuals to obtain
540 detailed information on attendance and energetic expenditure (Green et al. 2007). To
541 apply the model to other species, information would also be needed on basal metabolic
542 rate, the energetic cost of activities, assimilation efficiency and chick growth. If
543 information about these parameters is scarce, our method allows for plausible upper and
544 lower bounds to be specified. If no empirical data are available, our model can be
545 parameterized using information from similar or related species or with expert opinion.
546 The most important data requirement, however, is observations of body mass during the
547 breeding season to facilitate the calibration process.

CONCLUSION

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 can help 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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Table 1: Parameters of the bioenergetics model used to estimate prey consumption by breeding Adélie penguins at Béchervaise Island

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	Supplementary material	Unpublished 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)
BM_d	Daily body mass	See Figure 2	Supplementary material; this study
E_{Nest}	On-nest energy requirements	Uni(1.3 – 2) x BMR	(Chappell et al. 1993a) (Nagy & Obst 1992) (Green & Gales 1990) (Nagy & Obst 1992) (Croxall 1982, Adams & Brown 1990)
E_{Sea}	At-sea energy requirements	Uni(4.7 – 5) x BMR	(Chappell et al. 1993a) (Nagy & Obst 1992) (Green & Gales 1990) (Nagy & Obst 1992) (Croxall 1982, Adams & Brown 1990)
FMR_d	Chick activity energy requirements	910 (KJ/d/kg) * BM (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	(Salihoglu et al. 2001)
AE_{Chick}	Chicks assimilation efficiency	Uni(0.75-0.8)	(Davis et al. 1989, Salihoglu et al. 2001)
S_d	Daily chick survival rate	Norm(0.71, 0.05) per breeding pair	(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	25th 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)	(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)	(Lea et al. 2002, Tierney et al. 2002, Van de Putte et al. 2006)
D_{Krill}	Proportion of krill in diet	Norm(0.62, 27)	(Tierney et al. 2009)
N	Number of breeding pairs	Norm(1836, 130)	(Clarke et al. 2003, Emmerson et al. 2003)

Table 2: Results from the chick bioenergetics model assuming no mortality. Values in brackets represent 95% confidence intervals

Daily per capita	
Ingested energy (KJ)	2774 (2015 – 3533)
Krill consumption (g)	376 (114 – 651)
Fish consumption (g)	36 (6 – 73)
Total per capita	
Ingested energy (MJ)	144 (105 –184)
Krill consumption (kg)	20 (6 – 34)
Fish consumption (g)	1.9 (0.3 – 3.8)
Daily population	
Ingested energy (MJ)	9581 (6658 – 12699)
Krill consumption (T)	1.3 (0.4 – 2.3)
Fish consumption (T)	0.13 (0.02 – 0.26)
Total population	
Ingested energy (MJ)	498227 (346205 – 660390)
Krill consumption (T)	68 (20 – 119)
Fish consumption (T)	7 (1 – 13)

Table 3: Energy delivered to chicks by breeding pairs assuming average chick survival (0.71 chicks per nest) from hatching to fledging. Values in brackets represent 95% confidence intervals.

Daily per capita	
Energy delivered by parents to a brood (KJ)	3627 (2632 – 4636)
Krill delivered by parents to a brood (g)	492 (151 – 850)
Fish delivered by parents to a brood (g)	47 (8 – 96)
Total per capita	
Energy delivered by parents to a brood (MJ)	189 (137 – 241)
Krill delivered by parents to a brood (kg)	26 (8 – 44)
Fish delivered by parents to a brood (kg)	2.5 (0.4 – 5.0)
Daily population	
Energy delivered by parents to a brood (MJ)	6665 (4621 – 8862)
Krill delivered by parents to a brood (T)	1.7 (0.5 – 3)
Fish delivered by parents to a brood (T)	0.2 (0.02 – 0.33)
Total population	
Energy delivered by parents to a brood (MJ)	346590 (240335 – 460806)
Krill delivered by parents to a brood (T)	88 (27 – 156)
Fish delivered by parents to a brood (T)	9 (1 – 17)

Table 4: Results of the bioenergetics model for male breeders, female breeders and chicks at Béchervaise Island during the breeding season (150 days). Values in brackets represent 95% confidence intervals.

	male	female	Total (male + female)
Daily per capita			
FS (KJ/d)	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)
Daily population			
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)
Annual per capita			
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)
Annual population			
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)

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 per nest	-1.65	0.04
AE_{Chick}	Chick assimilation efficiency	-0.69	1.33
FMR_d	Chick activity energy requirements	-1.30	1.70
AE_{Adult}	Adult assimilation efficiency	9.19	-11.49
BMR	Basal metabolic rate	1.26	-0.18
ED_{Krill}	Energy density of krill	-9.62	11.76
ED_{Fish}	Energy density of fish	0.50	-0.41
D_{Krill}	Percent diet krill	5.68	-6.23
BM_d	Initial male body mass	1.26	0.25
BM_d	Initial female body mass	-2.06	2.11
E_{Nest}	Energy requirements on nest	-2.21	2.73
E_{Sea}	Energy requirements at sea	1.32	-1.05
N	Number of breeding pairs	11.01	-10.90

Figure 1: Predicted body mass of a male (a), female (b) and chick (c) during the breeding season. Solid black lines represent the mean of simulations, with grey shading representing 95% confidence intervals. Solid black vertical lines in (a) and (b) are observations of body mass made at Béchervaise Island during key periods of phenology, including arrival to the colony, egg laying, egg hatching, crèche and departure from the colony. Grey dotted vertical lines indicate 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 the observations.

Figure 2: Predicted energy balance for a male (a), female (b) and ingested energy by a chick (c) during the breeding season. Solid black lines represent the mean of 1000 simulations, grey shading is 95% confidence intervals representing inter-annual variation. The horizontal lines in (a) and (b) is zero energy balance, which occurs when ingested energy equals to energetic costs. Grey dotted vertical lines indicate major phases of the breeding cycle. Adults gain body mass when the energy balance is positive and lose body mass when it is negative.

Figure 3: a) Total daily ingested energy by the Béchervaise Island breeding colony during the breeding season. The solid black line represents total daily ingested energy by males and females combined, with grey-shaded areas area 95% confidence intervals representing inter-annual variation. The dotted line is consumption by males, the dashed line consumption by females. b) Total daily ingested energy by the Adélie penguin population at Béchervaise Island, partitioned into the average amount of krill consumed (light grey) and the average amount of fish consumed (dark grey). c) Total daily krill consumption by the Béchervaise Island population. d) Total fish daily fish consumption by the Béchervaise Island population. The solid black line represents total daily ingested energy consumption by males and females combined and averaged across years, and grey-shaded areas represent 95% confidence intervals related to inter-annual variation. The black dashed line represents krill consumption in 2001/2002. The black dotted line represents krill consumption in 1998/1999. Grey dotted vertical lines indicate major phases of the breeding cycle.

SUPPLEMENTARY MATERIAL

Field data collection: Data in the energetics model from Béchervaise Island include mass changes, foraging probability, breeding success, proportion of prey types in their diet, population size and phenology. Each of these are described briefly below with reference to detailed studies if they were used for parameter estimates.

Body mass: Body mass of male and female breeders at key phenological dates (i.e. arrival, hatching, crèche, fledging) were extracted from an Automated Penguin Monitoring System (APMS), installed at Béchervaise Island. Values were used from across breeding seasons presented in Emmerson et al. (2003) and specifically extracted for 1998/99 and 2000/01 for this study. The APMS consists of a weighbridge, a tag detector, direction sensors and computer microprocessor and records the direction of travel, sex and body mass of tagged breeders that arrive to and from the colony (Kerry et al. 1993, Clarke et al. 1998). Data on body mass at the start and of molt was not recorded by the APMS and was taken from the literature (Penney 1967). Body mass changes are shown in Figure 2a, b.

Foraging probability and phenology: The probability of male and female breeders being on and off nests and the phenology of different breeding events were attained from daily nest census data. Nest censuses on up to 300 nests began from 13th November when females departed their nests after egg lay until 5th February when chicks had crèched and were no longer present on the nest and adults departed in preparation for moult. Daily records of the presence of males, females, eggs and chicks at each study nest were recorded.

To determine the probability that a male or female breeder was at-sea for each day of the breeding cycle F_d (equation 4), we fitted generalized additive models (GAMS) (Hastie & Tibshirani 1990) to nest attendance data collected at Béchervaise Island during two breeding seasons. In this dataset, the attendance of males and females was recorded at 268 nests in 1998/99 and 318 nests in 2001/02.

To determine the probability that a male or female breeder was at-sea for each day of the breeding cycle F_d within the dates of the survey, we fitted generalized additive models (GAMS) (Hastie & Tibshirani 1990) to the nest attendance data (Figure 1). Figure 1 shows the results of model fitting. The solid line represents the probability of

a female being at-sea, while the dotted line represents the probability of a male foraging at-sea. The vertical dotted lines represent the start and end of the nest attendance surveys. To extend our model to the start of November, before the start of the attendance surveys, we assumed that the probability of adults being at-sea was 0. This assumption is reasonable since breeders participate in courtship and mating activities during this period. To extend our model past the last day of nest attendance data (5th February), we assumed that males and females forage at-sea with a probability of 1 until the start of molt, which occurs on 20th February (SD = 5). Adults are then assumed to remain on land with a probability of 1.

Breeding phenology events were taken from Emmerson & Southwell (2011), except for the data for 1998/99 and 2000/01 which were calculated separately for this model.

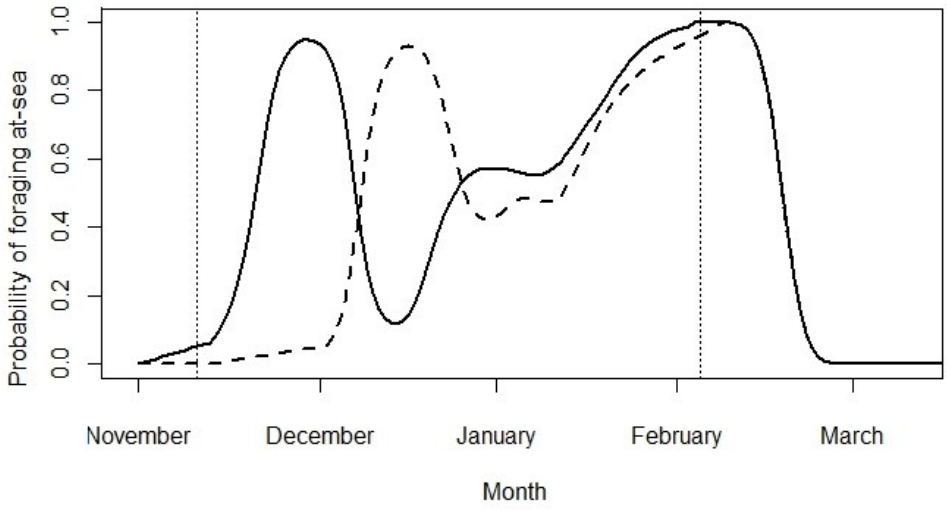
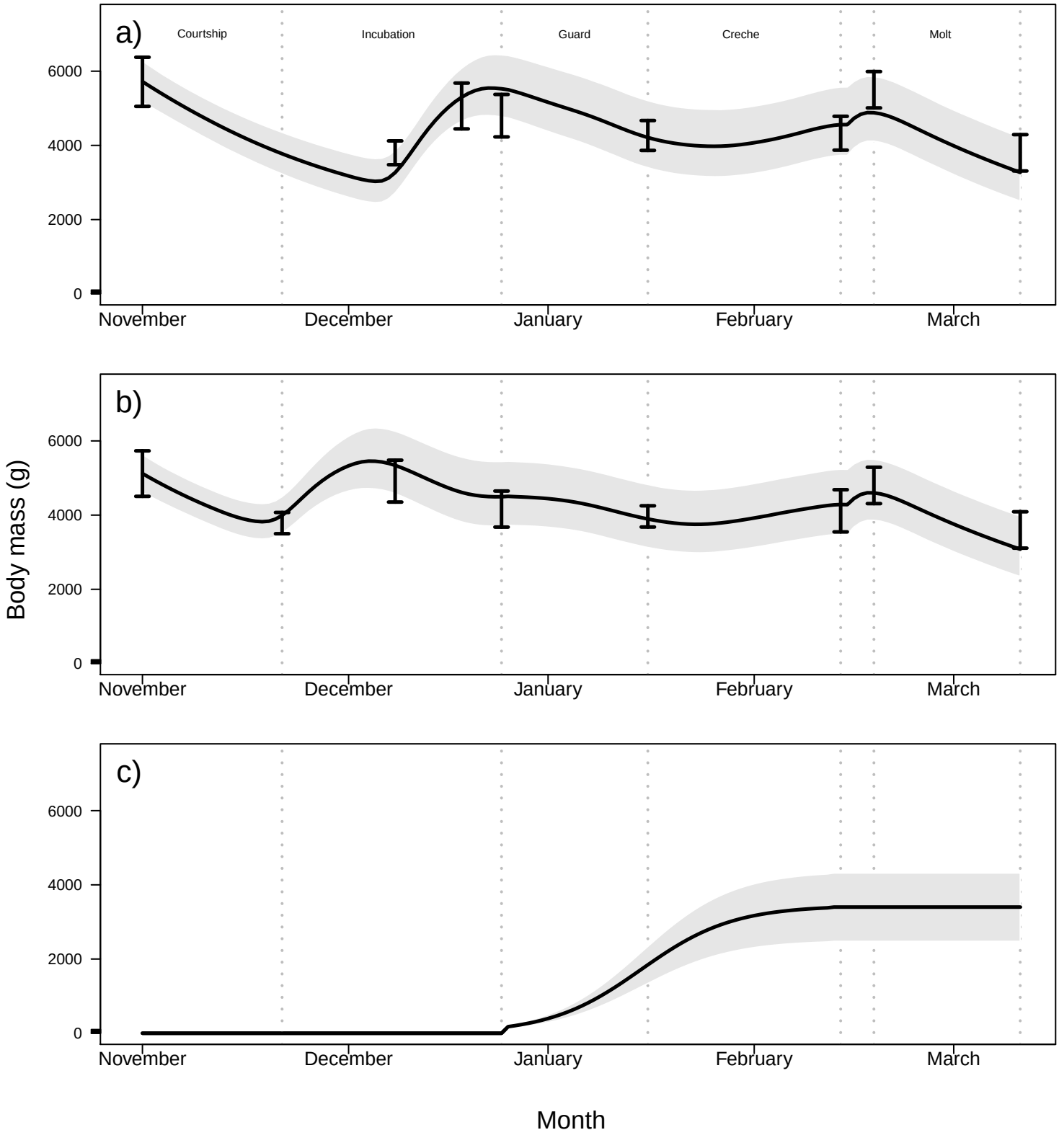


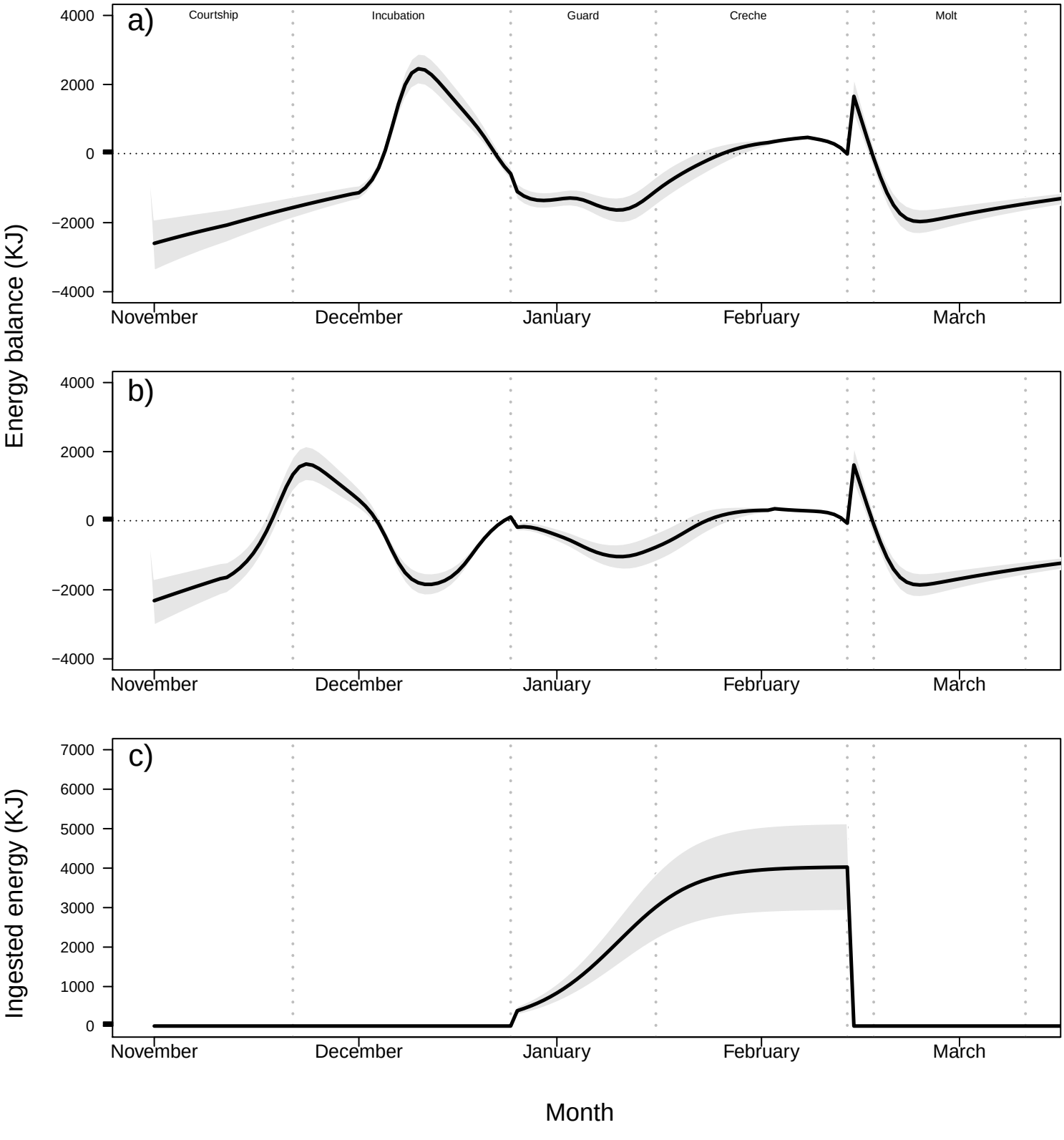
Figure 1: The probability of a male (dashed line) and female (solid line) at-sea for each day of the breeding season. The models were developed by fitting two seasons of nest attendance data with generalized additive models (GAMS). The two vertical dashed lines represent the start and end of the survey period.

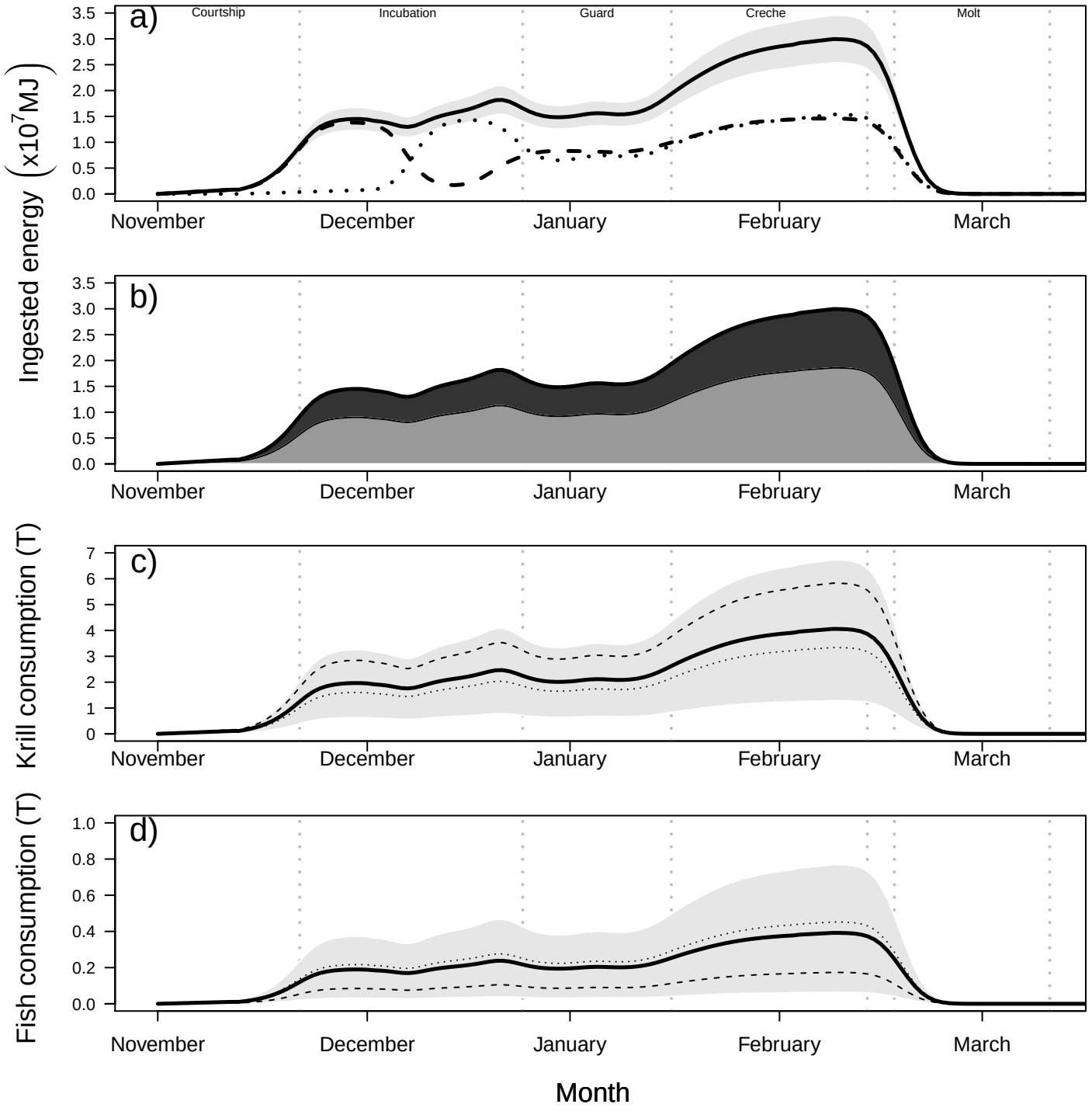
Breeding success and population size: Breeding success was measured as the number of chicks surviving to the time when two-thirds of the chicks have crèched (around mid-January) in relation to the number of nests occupied by breeding adults at the commencement of incubation (in early December). Population size related to the the number of occupied nests at the commencement of incubation.

Proportion of prey type in diet: Approximately forty stomach content samples were collected during the guard and crèche stages of the chick rearing period in each year (except 1994/95) using the water-offloading technique described in Tierney et al. (Tierney et al. 2009). Stomach samples were stored in 70% ethanol for later analysis. Each sample was drained and excess liquid gently squeezed out before being weighed. Samples were sorted and prey species identified to the lowest taxonomic level possible (Tierney et al. 2009). Generally, krill (*E. superba* and *E. crystallorophias*) were identifiable to species level (unless highly digested). The wet mass of each component of the diet including krill was weighed separately. Total proportion of krill and fish in the diet were determined across years and in the 1998/99 and 2000/01 breeding seasons separately. Penguin diet at Béchervaise Island is summarized in Tierney et al. (2009).

Estimates of error associated with parameters: We specified probability distributions wherever possible to account for uncertainty in model parameters using normal distributions where means and standard deviation of measurements were available, or from a uniform distribution representing the maximum and minimum of published estimates. We were able to specify probability distributions for all of the parameters in our model, with the exception of foraging success *FS* (equation 2).


a)
Courtship
Incubation
Guard
Creche
Molt
6000
4000
2000
0
November
December
January
February
March
b)
6000
4000
2000
0
November
December
January
February
March
c)
6000
4000
2000
0
November
December
January
February
March
Body mass (g)
Month


a)
Courtship
Incubation
Guard
Creche
Molt
4000
2000
0
−2000
−4000
November
December
January
February
March
b)
c)
Energy balance (KJ)
Ingested energy (KJ)
7000
6000
5000
4000
3000
2000
1000
0
Month


a)
Courtship
Incubation
Guard
Creche
Molt
Ingested energy (x10^7 MJ)
b)
c)
Krill consumption (T)
d)
Fish consumption (T)
November
December
January
February
March
Month