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Weight loss during breeding is adaptive for female macaroni penguins, *Eudyptes chrysolophus*

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ABSTRACT

Question: How does the female macaroni penguin balance her own needs with those of her chick during breeding?

Features of the model: We model the behaviour of female macaroni penguins during a sensitive life-history stage as a function of the availability of their main prey species, Antarctic krill (*Euphausia superba*), using stochastic dynamic programming. In the model, females maximize accumulated delivery to the chick, accounting for metabolic losses. Chick fullness is included as a state in the model.

Range of key variables: We test three scenarios for krill availability, which changes with distance from the nest. In the first, krill abundance increases with distance from the nest, with no variability in the reward at each distance. In the second, variability increases proportionally with the increasing amount of krill available at each distance from the nest. In the third, the abundance of krill at each distance from the nest is constant, but variability decreases further from the nest.

Conclusions: Natural selection should produce females that sacrifice their own condition to meet the increasing demands of their chicks. We predict a weight loss of 10–20%, which is comparable to the empirical average of 14%. We also predict that females will endure the cost of travelling further from the nest to obtain a more predictable meal of krill, even if the mean reward does not change with distance from the nest.

Keywords: behaviour, chick provisioning, *Eudyptes chrysolophus*, *Euphausia superba*, fitness, foraging, predator, prey, stochastic dynamic programming, variability.

INTRODUCTION

To maximize current and future reproductive success, parents must make decisions based on both their own physiological state and the state of their offspring (Williams, 1966; Clark and Mangel, 2000). This means that parental care is only beneficial when it increases the probable survival

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of the offspring without incurring too great a cost to the parents (Clutton-Brock, 1991). Female macaroni penguins have been shown to lose on average 14% of their body weight during a crucial breeding stage (Barlow and Croxall, 2002a), but there is little understanding of why this happens, the point to which the female can sacrifice her condition to keep up with the needs of the chick, and how changes in prey availability and variability can impact the decisions of the female at this time.

Macaroni penguins breed during the austral summer on a number of sub-Antarctic islands throughout the Southern Ocean (Woehler, 1993; Williams, 1995; Woehler and Croxall, 1997; Barlow and Croxall, 2002b; Brooke, 2004). During breeding, population sizes may exceed several million pairs per island, so their impact on the surrounding ecosystems is great. High food demands also mean that they are sensitive to local changes in the availability of their main prey, Antarctic krill (*Euphausia superba*), at this time (Croxall *et al.*, 1999; Atkinson *et al.*, 2001; Reid *et al.*, 2002). Understanding the behaviour of macaroni penguins during breeding is therefore crucial to managing the consequences of the krill fishery on this krill-dependent species (Trathan *et al.*, 1998a; Barlow and Croxall, 2002b; Green *et al.*, 2005).

One of the island archipelagos where macaroni penguins are most abundant is South Georgia, where an estimated 2.5 million pairs breed each summer (Trathan *et al.*, 1998b; Barlow and Croxall, 2002b). South Georgia is a sub-Antarctic island in the southwest Atlantic Ocean and since its discovery in 1776 by Captain Cook has been recognized as an important biological site, leading to significant research and exploitation in the region (Marr, 1962; Everson and Goss, 1991; Atkinson *et al.*, 2001). The South Georgia region is characterized by a high biomass and productivity of phytoplankton, zooplankton, and vertebrate predators, with a particularly high biomass of Antarctic krill, which make up over half the total zooplankton biomass in the region (Atkinson *et al.*, 2001). During the breeding season, macaroni penguins at South Georgia rely almost exclusively on Antarctic krill for their prey (Croxall *et al.*, 1997). As a resource, krill are notoriously patchy, with the occurrence of 'bad' krill years (years of significantly low krill concentrations) often resulting in nest failure or decreased offspring weight for macaroni penguin chicks and other krill-reliant predators, such as Antarctic fur seals (Croxall *et al.*, 1999; Atkinson *et al.*, 2001; Reid *et al.*, 2002).

There are several reasons why krill availability is so variable. For hourly to daily time periods, krill availability varies as a result of swarming behaviour (Ritz, 1994) and diel vertical migration (Godlewska, 1996). For a larger time scale of months to years, variability in rates of mortality, recruitment, and breeding success impact on local biomass levels (Siegel, 2000; Atkinson *et al.*, 2004). Furthermore, krill can be patchy due to their own swimming behaviour (Cresswell *et al.*, 2007) and transportation by ocean currents (Murphy *et al.*, 2004).

The breeding season for macaroni penguins spans approximately 6 months (Williams and Croxall, 1991). During this time, both parents undertake various duties to raise a single chick to the point of independence, so it can leave the island before the onset of winter (Davis *et al.*, 1989). The guard stage, which lasts 23 days, takes place in January. At this time, the male, which is bigger and more aggressive than the female, sits guarding the newly hatched chick while the female undertakes a number of short foraging trips to bring back meals for the chick (Williams and Croxall, 1991; Barlow and Croxall, 2002b). The female is under significant pressure during this stage, since she must provide regular and constantly increasing meals for the rapidly growing chick (Williams, 1982).

Provisioning behaviour is an important aspect of parental expenditure, which is defined as the resource allocated to offspring care, including time and energy (Barlow and Croxall, 2002a). Natural selection will act on long-lived seabirds such as macaroni penguins to maximize lifetime reproductive success, which includes the trade-off between reproductive expenditure in the present year and potential reproductive output in future years (Barlow and Croxall, 2002a; Green *et al.*, 2002; Varpe *et al.*, 2004). During the guard stage of breeding, the female macaroni penguin is constrained by the need to deliver food to the chick but also to maintain her own body condition. Her foraging behaviour and how she allocates food to the chick and herself is flexible up to a point. There is evidence in the field for variability in foraging trips over temporal and spatial scales, but there is little work examining this flexibility. We use a stochastic dynamic programming (SDP) model to predict the feeding and foraging behaviour of the female for different conditions of krill variability and availability.

Stochastic dynamic programming models are useful in understanding the trade-offs involved with management of energy reserves in general, accounting for the influences of food supply, metabolic costs, predation risk, and social interactions (Mangel and Clark, 1988; Mangel and Ludwig, 1992; Clark and Mangel, 2000). These models are valuable for analysing the effects of environmental stochasticity on life-history strategies (Houston and McNamara, 1999) and have been applied to brood-care (Beauchamp *et al.*, 1991; Winkler and Adler, 1996; Welham and Beauchamp, 1997). Stochastic dynamic programming models have already been applied to foraging decisions of penguins (Alonzo *et al.*, 2003a, 2003b), but chick provisioning, foraging trip distance and duration, and adult energy levels were not considered. In the present study, we build an SDP model that predicts foraging decisions made through consideration of both the state of the parent and the chick, which is a situation far more likely to reflect the full set of trade-offs made during this period of the penguin life cycle.

Through the model, we examine the foraging behaviour of a typical female macaroni penguin during the guard stage at South Georgia. The female responds to variable conditions in terms of krill availability, light intensity, and the increasing demands of the chick. We predict the foraging effort of the female over the guard stage in terms of foraging trip duration and range in response to different scenarios of krill availability.

METHODS

In this section, we describe the model by the behavioural decisions chosen by the female each time step, the state variables that determine and are affected by these decisions, the calculation of fitness in the model, and the dynamic programming algorithm.

The model is an SDP model in which the female chooses from one of four behavioural decisions i each time step (for a list of parameters used in the model, see Table 1). When at sea, she chooses from the first three decisions, to swim or forage, and when at the nest she chooses either to leave the nest ($i = 1$) or feed the chick ($i = 4$).

$$\begin{aligned} &i = 1\text{: to swim away from the nest}\\ &i = 2\text{: to swim back towards the nest}\\ &i = 3\text{: to forage at the current distance from the nest}\\ &i = 4\text{: to feed the chick} \end{aligned} \tag{1}$$

The unit of time t is hours. Any parameter specified in grams of krill is converted from the amount of energy in a meal of krill to its equivalent in how long this would provide metabolic energy to the penguin in hours. The final time T is 552 h, or 23 days, based on the

Table 1. List of parameters used in the model

Symbol	Parameter	Value	Unit
$\Phi(f, c, h_f, h_c, d, t)$	Fitness is the maximum expected net delivery of krill to the chick between t and T, given that $F(t) = f$, $C(t) = c$, $H_f(t) = h_f$, $H_c(t) = h_c$, and $D(t) = d$	—	—
$\Phi(f, c, h_f, h_c, d, T)$	Terminal fitness reward	—	—
i	Behavioural decisions made by female at each time step	1–4	—
N	Number of individuals in the forward iteration	1000	—
t	Number of hours since hatching, time step of the model	1	hours
a	Number of days since hatching	1–23	days
L	Light intensity	0 = night, 1 = day	—
Ψ	Overall krill availability, 1 = low, 2 = medium, 3 = high	1–3	—
T	Final time	552	hours
f	Krill in stomach of female	0 to $f_{\max}$	grams
$f_{\max}$	Maximum stomach contents	2400	grams
Δf	Digestion of krill per hour, from stomach	50	$g \cdot h^{-1}$
$K(d, L, \Psi)$	Krill ingested after 1 h of foraging at distance d, light intensity L, and overall krill availability Ψ	0 to $f_{\max}$	$g \cdot h^{-1}$
c	Krill in stomach of chick	0 to $c_{\max}(a)$	grams
$c_{\max}(a)$	Maximum capacity of chick's stomach, increases daily	0–350	grams
$\Delta c(a)$	Digestion from chick stomach per hour	$0.63a$	$g \cdot h^{-1}$
$Y(t)$	Amount of krill chick needs to fill stomach	0 to $c_{\max}(a)$	grams
$X(t, c, f)$	Food fed to chick	0 to $c_{\max}(a)$	grams
h_f	Time on an empty stomach, for the female	0–120	hours
γ_f	Scaling of time on empty stomach for the female	0–2	—
h_c	Time on an empty stomach, for the chick	0–120	hours
γ_c	Scaling of time on empty stomach for the chick	0–2	—
d	Distance from nest	0 to $d_{\max}$	km
$d_{\max}$	Maximum distance	100	km
$\Delta d/\Delta t$	Travelling speed of female	5	$km \cdot h^{-1}$

approximate length of the guard stage (Williams and Croxall, 1991; Barlow and Croxall, 2002a). It is reasonable to adopt a one-hour decision interval in the model, given that the average length of a foraging trip is approximately 16 h (Barlow and Croxall, 2002b).

State variables

There are five state variables in the model, all of which affect the decision chosen by the female each time step:

$$\begin{aligned} F(t) &= \text{the stomach fullness of the female at time } t \\ C(t) &= \text{the stomach fullness of the chick at time } t \\ H_f(t) &= \text{the number of hours the female has had an empty stomach at time } t \\ H_c(t) &= \text{the number of hours the chick has had an empty stomach at time } t \\ D(t) &= \text{the female's distance from nest at time } t \end{aligned} \tag{2}$$

Dynamics of the state variables

Each of the state variables can change each time step depending on the decision chosen by the female. We now describe those changes.

The stomach contents of the female $F(t)$ are calculated in grams of krill. When the female chooses to swim away from or back towards the nest, decision $i = 1$ and 2, we calculate the new stomach contents $F(t + 1)$ simply by subtracting digestion Δf from the current stomach contents $F(t)$. When the female forages, $i = 3$, we determine the new stomach contents from ingestion of krill $K(d, L, \Psi)$ minus digestion, where the foraging reward $K(d, L, \Psi)$ changes with distance from the nest d, light intensity L, and overall level of krill availability Ψ, where Ψ ranges from 1 to 3 for low, medium, and high availability. If the female feeds the chick, $i = 4$, we subtract digestion and the size of the chick's meal $X(t, C(t), F(t))$ from $F(t)$ to calculate the new stomach contents $F(t + 1)$. $F(t + 1)$ is always non-negative and does not exceed the set value for maximum stomach capacity $f_{\max}$ at any time.

$$F(t+1) = \left\{ \begin{array}{ll} F(t) - \Delta f & ;\ i = 1,2 \\ F(t) - \Delta f + K(d, L, \Psi) & ;\ i = 3 \\ F(t) - \Delta f - X(t, C(t), F(t)) & ;\ i = 4 \end{array} \right\} \tag{3}$$

The maximum stomach capacity of the chick $c_{\max}(a)$ increases with the age of the chick, with age in days a:

$$c_{\max}(a) = 15.12a \tag{4}$$

The hourly digestion rate of the chick $\Delta c(a)$ increases proportionally, as the energetic demands of the chick increase with growth:

$$\Delta c(a) = 0.63a \tag{5}$$

When the female is not feeding the chick, $i \neq 4$, we subtract digested food $\Delta c(a)$ from the stomach contents of the chick $C(t)$ each time step to find the new stomach contents of the chick $C(t + 1)$. When the female is at the nest $d = 0$ and chooses to feed the chick, $i = 4$, we subtract digestion and add ingested meal size $X(t, C(t), F(t))$ to the stomach contents of the chick, so that

$$C(t+1) = \left\{ \begin{array}{ll} C(t) - \Delta c(a) & ;\ i \neq 4 \\ C(t) - \Delta c(a) + X(t, C(t), F(t)) & ;\ i = 4 \end{array} \right\} \tag{6}$$

The amount of food the chick needs to fill its stomach $Y(t)$ is calculated after subtracting digestion from the stomach contents, as follows:

$$Y(t) = c_{\max}(a) - [C(t) - \Delta c(a)] \tag{7}$$

The female feeds the chick either until the chick is full – that is, not exceeding the maximum stomach contents $c_{\max}(a)$ – or until the stomach of the female is empty. Thus the amount of food fed to the chick each time step is

$$X(t, C(t), F(t)) = \left\{ \begin{array}{lll} 0 & ; & i \neq 4 \\ Y(t) & ; & i = 4,\ Y(t) < [F(t) - \Delta f] \\ F(t) - \Delta f & ; & i = 4,\ Y(t) \geq [F(t) - \Delta f] \end{array} \right\} \tag{8}$$

The time in hours that the female has endured an empty stomach H_f increases only when $F(t) = 0$:

$$H_f(t+1) = \left\{ \begin{array}{lll} 0 & ; & F(t) \geq 0 \\ H_f(t) + 1 & ; & F(t) = 0 \end{array} \right\} \tag{9}$$

Similarly, the number of hours the chick has had an empty stomach H_c increases only when $C(t) = 0$:

$$H_c(t+1) = \left\{ \begin{array}{lll} 0 & ; & C(t) \geq 0 \\ H_c(t) + 1 & ; & C(t) = 0 \end{array} \right\} \tag{10}$$

The female's distance from the nest, in kilometres, is one-dimensional. Distance does not change when the female is foraging or feeding the chick $d = 0$, but increases by Δd when swimming out to sea, $i = 1$, and decreases when swimming back towards the nest, $i = 2$:

$$D(t+1) = \left\{ \begin{array}{lll} D(t) & ; & i = 3, i = 4 \\ D(t) + \Delta d & ; & i = 1 \\ D(t) - \Delta d & ; & i = 2 \end{array} \right\} \tag{11}$$

Distance does not exceed the maximum limit $d_{\max}$ or decrease below 0 at any time.

Parameter estimation

In this subsection, we describe our estimations and underlying assumptions for the variables outlined above.

We estimate the female's hourly krill requirement Δf to be 50 g krill $\cdot$ h^{-1} based on macaroni penguin energetic studies and an assumption that breeding macaroni penguins rely almost exclusively on krill during the breeding season (Croxall *et al.*, 1993). During chick rearing, a female weighing 3.8 kg requires 3973 kJ $\cdot$ day^{-1} (Davis *et al.*, 1989). Krill energy content is 4.6 kJ $\cdot$ g^{-1} (Clarke, 1984), and assimilation efficiency of macaroni penguin adults is around 75% (Cooper, 1977; Davis *et al.*, 1989), so that the female has a daily requirement of approximately 1200 g krill $\cdot$ day^{-1}, or Δf of 50 g krill $\cdot$ h^{-1}, as estimated by Croxall *et al.* (1993). We assume an equal demand for energy throughout the day.

We assume that the female's stomach at its maximum capacity $f_{\max}$ can hold 2400 g krill, twice the female's daily requirement of krill. Although the total capacity of the stomach is unknown, Williams (1982) recorded maximum meal sizes of chicks to be as large as 1.2 kg, which suggests that the female can hold more than her own requirement of krill for the day. In addition, there is evidence that some seabirds can remove water from their stomach contents, thereby increasing the amount of krill they can hold in the stomach at any one time (Trivelpiece *et al.*, 2006). We test different values for $f_{\max}$($f_{\max} = 600$, 1200, 1800, 2400, 3000, and 3600 g krill) in the sensitivity analysis.

The macaroni penguin chick has increasing energy demands as it grows, measured in this model by the amount of krill digested each hour $\Delta c(a)$. Estimations for maintenance and energetic requirements of macaroni penguin chicks range from 420 $\mathrm{kJ \cdot day^{-1}}$ in the first week, to 770 $\mathrm{kJ \cdot day^{-1}}$ in the second week and 1250 $\mathrm{kJ \cdot day^{-1}}$ in the third week from hatching, with growth approximately linear (Brown, 1987a; Barlow and Croxall, 2002a). An assimilation rate of 0.75 gives a daily requirement of $1250/0.75 = 1666$ $\mathrm{kJ \cdot day^{-1}}$ as the chick reaches the end of the guard stage (Cooper, 1977). Furthermore, taking into the account the energy content of krill, at 4.6 $\mathrm{kJ \cdot g^{-1}}$ (Clarke, 1984), chicks require on average $1666/4.6 = 362$ g $\mathrm{krill \cdot day^{-1}}$ at this age. Croxall *et al.* (1993) calculated a similar figure for chick energy requirements of 350 g $\mathrm{krill \cdot day^{-1}}$ around this time of year, so we estimate $\Delta c(a) = (350/23)a = 15.2a$ g $\mathrm{krill \cdot day^{-1}} = 0.63a$ g $\mathrm{krill \cdot h^{-1}}$.

The maximum stomach capacity of the chick in the model, $c_{\max}(a)$, at any time does not exceed the energetic requirement for that day. Williams (1982) noted that in the first 10 days after hatching, recently fed penguin chicks had extremely swollen abdomens. He concluded that the female, to reduce foraging time and effort, probably fed as large a quantity to the chick as possible and that the chick probably ate as much food as it could. We therefore test other values for this variable ($c_{\max}(a) = 15.2a$, $30.43a$, $45.7a$, and $60.9a$ g $\mathrm{krill \cdot day^{-1}}$) in the sensitivity analysis.

In the absence of sufficient food intake, both the female and chick must meet daily requirements from their body reserves. We assume that when the female next finds food, the potential delivery to the chick is decreased because of the priority in paying back the depleted reserves. The advantage of this assumption is that we can avoid having additional state variables that characterize the reserves of the mother and chick [for examples with both gut content and reserves, see Chapter 4 in Clark and Mangel (2000)]. The variable H_f indicates the time in hours that the female has endured an empty stomach, ranging from 0, the female has food in her stomach, to 120, her stomach has been empty for 120 h, or 5 days. This variable is scaled by the payback cost γ_f (Table 2). A payback cost of zero means that there is no fitness cost to the female not acquiring enough food to meet her energetic demands for the day. In this case, the female could theoretically starve and there would be no cost in the model. A payback cost of 1 indicates the case where the cost of using up energy/fat reserves is equal to the amount of krill that is missing from the diet – that is, it takes the same absolute amount of energy to build up fat reserves as it took to lose them. A

Table 2. Explanation of the numbers representing the cost to fitness for the female or chick going on an empty stomach

Fitness cost	Explanation
0	No payback for having an empty stomach
1	The payback for 1 h without food is equal to the benefit of being fed 1 h energy requirement
2	The payback for 1 h without food is equal to the benefit of being fed 2 h energy requirement

payback cost of 2 represents the case where there is a greater cost to using up fat reserves. Here we assume it takes twice the energy to build back fat reserves as it took to lose them.

Like the female, time on an empty stomach for the chick h_c means the chick is using stored energy reserves to meet energetic demands when $C(t) = 0$. The magnitude of H_c is varied by the payback cost γ_c. In the best estimate parameterization, we use a payback cost of 1, where we assume that the weight lost is the same weight gained for a given amount of energy either missing from or supplemented to the diet. This is a reasonable assumption, considering that the average growth rate of frequently fed chicks, ~63 $\text{g} \cdot \text{day}^{-1}$ (Croxall *et al.*, 1993), is approximately equal in magnitude to the average mass decrease of unfed chicks, recorded at ~65 $\text{g} \cdot \text{day}^{-1}$ (Williams and Croxall, 1991). Values for H_c have the same range as H_f. We test the effects of varying the payback costs γ_f and γ_c in different combinations for both the female and chick in the sensitivity analysis.

Females appear to follow simple strategies for foraging during the brood-guard period, with highly linear foraging trips (Trathan *et al.*, 2006); we therefore assume two-dimensional foraging in the model. The minimum distance 0 is the female at the nest. Travel speeds are estimated from satellite tracking data in the field and swimming experiments in captivity, with published values ranging from 4 to 8 $\text{km} \cdot \text{h}^{-1}$ (Clarke and Bemis, 1979; Brown, 1987b; Barlow and Croxall, 2002b). We assume a travelling speed of 5 $\text{km} \cdot \text{h}^{-1}$, which gives a maximum distance $d_{\mathbf{max}}$ of 100 km from the nest at 20 h of travelling one way. This is sufficient given that Barlow and Croxall (2002b) estimated most trips during chick rearing to be within 50–60 km from Bird Island for a round trip of 16 h on average.

We assume that the risk of mortality is zero for the female and chick in the model. The male guards the chick during this stage of chick rearing, so we assume the chick is relatively safe from predators. For the female, the only potential threat at Bird Island during January is from leopard seals, and possibly male Antarctic fur seals, though in most areas these predators have little effect on penguin foraging survival (Jansen *et al.*, 1998).

Krill availability

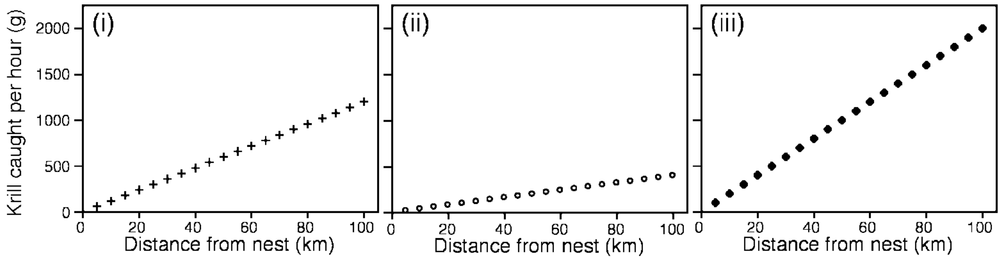
Krill availability $K(d, L, \Psi)$ in the model varies with distance from the nest d, light intensity L ($L = 0$ for night, $L = 1$ for day), and overall food availability through low, medium, and high regimes for krill availability, $\Psi = 1$, 2, and 3 respectively. We describe different scenarios for krill availability changing with distance from the nest in the following subsection. However, the effects of light intensity in the model are constant. Macaroni penguins are visual predators and tend to dive predominantly during the day, with some evidence for a small percentage of foraging dives at night (Croxall *et al.*, 1993; Green *et al.*, 2003). In addition, although visibility is reduced at night, the krill resource is likely to be more dispersed and shallow due to feeding in the shallow layers (Ritz, 1994; Godlewska, 1996; Eiane and Parisi, 2001; De Robertis, 2002; Hays, 2003). We assume krill availability is 10 times less available at night than during the day.

We test different scenarios of krill availability and variability, starting with theoretical constructs and then basing the krill parameter on more realistic scenarios of availability around South Georgia.

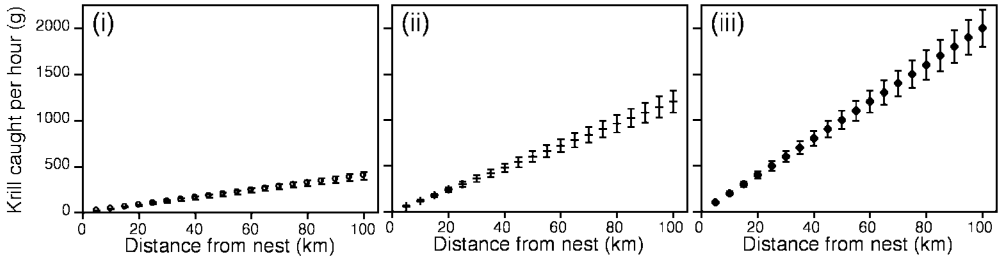
Scenario A

In Scenario A, the availability of krill, $K(d, L, \Psi)$, in grams of krill ingested during one hour of foraging, increases in a linear fashion with distance away from the nest (Fig. 1a). This is

(a) Scenario A



(b) Scenario B



(c) Scenario C

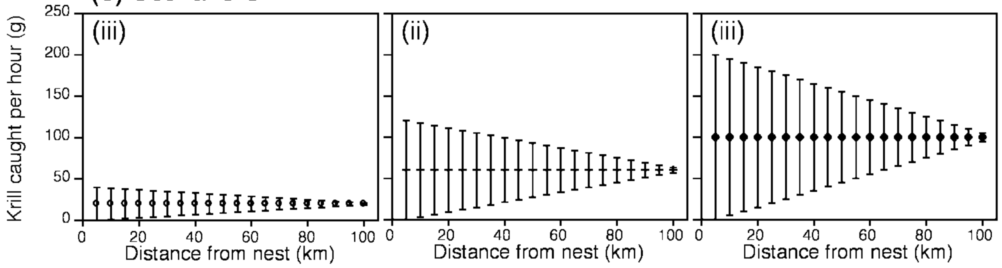


Fig. 1. Foraging reward with distance from the nest for (a) Scenario A, (b) Scenario B, and (c) Scenario C in years of (i) low, (ii) medium, and (iii) high krill availability. Data points represent the mean krill ingested from one hour of foraging during the day, with bars representing the standard deviation. For foraging reward at night, we divide these values by 10.

based on evidence that the concentration of krill increases towards the shelf edge (Witek *et al.*, 1981; Makarov *et al.*, 1988; Trathan *et al.*, 2003) and that resources deplete close to a central foraging place due to inter- and intra-specific competition. Krill is less available at night $L = 0$ and increases as we change the overall food availability through low, medium, and high availabilities, $\Psi = 1$, 2, and 3 respectively. There is no variability in the food reward for this parameterization, which is useful primarily to examine the principal trade-off of distance versus reward.

$$K(d, L, \Psi) = \frac{(4 + (\Psi - 1)d)}{10^{1-L}} \tag{12}$$

Scenario B

In the second scenario, we introduce variability/patchiness into the krill reward. In this scenario, the average availability/density of krill in the water column increases linearly with distance from the nest, where we specify average density as $K(d, L, \Psi)$ in the previous scenario (Table 2). As distance increases, the patchiness – here seen in the standard deviation around the mean density – increases proportionally (Fig. 1b).

At each distance from the nest, there are $j = 20$ possible foraging rewards Y_j equally spaced around the mean krill availability $K(d, L, \Psi)$, such that $[0 \leq Y_j \leq 2K(d, L, \Psi)]$ as follows:

$$Y_j = \frac{K(d, L, \Psi) \cdot j}{10} \tag{13}$$

In this parameterization, we calculate the standard deviation σ around the mean $K(d, L, \Psi)$ by

$$\sigma = 2K(d, L, \Psi) \tag{14}$$

Each of the 20 possible rewards Y_j at each distance from the nest has an associated probability P_j defined by a discrete normal distribution:

$$P_j = c_n \exp\left(- \frac{(Y_j - K(d, L, \Psi))^2}{2\sigma^2} \right) \tag{15}$$

where c_n is the normalization constant, defined as

$$c_n = \frac{1}{\sum_j \exp\left(- \frac{(Y_j - K(d, L, \Psi))^2}{2\sigma^2} \right)} \tag{16}$$

Scenario C

In Scenario C, the mean reward of krill per hour of foraging $K(d, L, \Psi)$ changes with light intensity, but is constant with distance. In this scenario, the variability/patchiness decreases linearly with increasing distance from the nest (Fig. 1c). This represents the case where the krill resource is a lot patchier close to the nest than further away. Locating krill becomes less predictable close to the nest but the rewards for doing so are potentially much higher than at a greater distance from the nest. This scenario is based on observations that krill tend to form denser swarms when over the continental shelf (Hamner and Hamner, 2000), and we propose that this is the most likely representation of krill, given the three scenarios tested here.

For Scenario C, we define the mean availability/density of krill $K(d, L, \Psi)$ at each distance to be

$$K(d, L, \Psi) = \frac{(20 + 40(\Psi - 1))}{10^{1-L}} \tag{17}$$

Again, we have 20 possible foraging rewards Y_j equally spaced around the mean krill availability $K(d, L, \Psi)$, such that $[0 \leq Y_j \leq 2K(d, L, \Psi)]$ as follows:

$$Y_j = \frac{K(d, L, \Psi) \cdot j}{10} \tag{18}$$

In this case, as d increases linearly from 0 to 100 km, the standard deviation σ around the mean decreases linearly from $10K(d, L, \Psi)$ to $0.5K(d, L, \Psi)$, and P_j and c_n are calculated as previously.

Fitness

The fitness function $\Phi(f, c, h_f, h_c, d, t)$ in the model relates linearly to the amount of food fed to the chick. Thus fitness is a compromise between maximizing food reward and minimizing time away from a hungry chick. The condition of the female is also considered in the fitness function, in terms of her accumulated energy. In particular,

$$\Phi(f, c, h_f, h_c, d, t) \tag{19}$$

equals maximum expected net delivery of krill to the chick between t and T, given the state variables f, c, h_f, h_c, and d.

For each of the dynamic programming algorithms, the variables f, c, h_f, h_c, and d represent values for the state variables in the current time step, denoted $F(t)$, $C(t)$, $H_f(t)$, $H_c(t)$, and $D(t)$ respectively in the section describing the dynamics of the state variables. Similarly, the variables f', c', h_f', h_c', and d' represent values for the state variables in the following time step, denoted $F(t+1)$, $C(t+1)$, $H_f(t+1)$, $H_c(t+1)$, and $D(t+1)$ respectively in the section describing the dynamics of the state variables.

At T, there is a final opportunity to feed the chick a meal of size $X(T, c, f)$ only if the female is at the nest and chooses to feed the chick (decision $i = 4$). For all other behavioural decisions at this time, the fitness reward is 0. Thus

$$\Phi(f, c, h_f, h_c, d, T) = \begin{Bmatrix} X(T, c, f) & ; & i = 4 \\ 0 & ; & i \neq 4 \end{Bmatrix} \tag{20}$$

The value $V_i(f, c, h_f, h_c, d, t)$ of action i is the maximum delivery of food to the chick while minimizing time on an empty stomach between t and T given the state variables f, c, h_f, h_c, and d and decision i chosen. The value of the decision chosen is different at sea and at the nest, so we define the dynamic programming algorithm to be

$$\Phi(f, c, h_f, h_c, d, t) = \begin{Bmatrix} \max\limits_{i=1,2,3} [V_i(f, c, h_f, h_c, d, t)] & ; & d = 0 \\ \max\limits_{i=1,4} [V_i(f, c, h_f, h_c, d, t)] & ; & d > 0 \end{Bmatrix} \tag{21}$$

If at sea, $i = 1$–3, given that $F(t) = f$, $C(t) = c$, $H_f(t) = h_f$, $H_c(t) = h_c$, and $D(t) = d$, the new fullness of the female $f_i(f)$ is given by the right-hand side of equation (3), the new fullness of the chick $c_i(c)$ is given by the right-hand side of equation (6), the time that the female $h_{fi}(h_f)$ and chick $h_{ci}(h_c)$ have had an empty stomach is given by the right-hand side of equations (9) and (10) respectively, and distance $d_i(d)$ is given by the right-hand side of equation (11).

For Scenario A, when the female is at sea, she can maximize the food delivered to the chick by maximizing her own ingestion from foraging f_i' and minimizing the time that she or the chick has an empty stomach by paying back these costs $h_{fi}(h_f)$ and $h_{ci}(h_c)$ each time step. If f and c are positive, then there is no payback cost. We therefore find the value from action i for Scenario A when the female is at sea to be

$$V_i = \Phi(f_i', c_i', h_{fi}', h_{ci}', d_i', t+1) \tag{22}$$

If the female or chick has spent time on an empty stomach, if $h_{fi}(h_f)$ or $h_{ci}(h_c)$ is greater than zero, then the female accumulates an energy deficit and the expected delivery to the chick is decreased by the payback cost. Thus

$$V_i = -(h_f\gamma_f + h_c\gamma_c) + \Phi(f_i', c_i', h_{fi}', h_{ci}', d_i', t+1) \tag{23}$$

For Scenarios B and C, food is stochastic, so there are $j = 0$–20 possible food rewards Y_j from foraging, and P_j gives the probability of each, where P_j was defined for different types of krill variability in the previous section.

For Scenario B, when the female is at sea, we define $f_{ij}(f)$ as given by the right-hand side of equation (3) with a probability of P_j from equation (15) for a krill reward of Y_j from equation (13). Similarly, for Scenario C, we define $f_{ij}(f)$ as given by the right-hand side of equation (3) with the krill reward as Y_j from equation (18). There is a possibility that the value from decision i will decrease at any distance from the nest depending on the time that either the female or the chick has endured an empty stomach, h_f and h_c, with the female paying back these costs in any situation where the stomach contents are empty. Therefore, we determine the value of action i when the female is at sea for Scenarios B and C, when f and c are positive, to be

$$V_i = \sum_{j=1}^{21} P_j \Phi(f'_{ij}, c'_i, h'_{fi}, h'_{ci}, d'_i, t+1) \tag{24}$$

If the female or chick has spent time on an empty stomach, $h_{fi}(h_f)$ or $h_{ci}(h_c)$ is greater than zero, then the expected delivery to the chick is decreased by the payback cost. Thus

$$V_i = -(h_f\gamma_f + h_c\gamma_c) + \sum_{j=1}^{21} P_j \Phi(f'_{ij}, c'_i, h'_{fi}, h'_{ci}, d'_i, t+1) \tag{25}$$

At the nest, $d = 0$, the female chooses the one of two decisions that maximizes fitness in the following time step. Here, there is a further opportunity to increase fitness with the size of the meal delivered to the chick X_i. If f and c are positive, then there is no payback cost and we find the value from action i for Scenarios A, B, and C for time $t < T$ to be

$$V_i = \Phi(f'_i, c'_i, h'_{fi}, h'_{ci}, d'_i, t+1) + X_i \tag{26}$$

If either the female or chick has endured an empty stomach, h_f or h_c is greater than zero, then the female accumulates an energy deficit. Therefore, the expected delivery to the chick decreases by the payback cost, such that

$$V_i = -(h_f + h_c) + \Phi(f'_i, c'_i, h'_{fi}, h'_{ci}, d'_i, t+1) + X_i \tag{27}$$

Running the model

The dynamic programming algorithm works backward in time to calculate the optimal policy $i^*(f, c, h_f, h_c, d, t)$ for each state at each time step (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). In the forward iteration, an individual with an initial set of state parameters effectively has a map of the optimal decisions to make at each time step, which will further affect its state and fitness, and therefore the decision made at the subsequent time step. The state of the individual changes according to the rules for the state dynamics defined previously. When foraging, $i = 3$, the krill ingested is deterministic in Scenario A, but determined randomly from the probability distribution defined for Scenarios B and C. The average stomach contents of the female and chick are calculated by recording $F_n(t)$ and $C_n(t)$ for the nth individual ($n = 1, \ldots, N$) at each time step and dividing by the number of individuals N. We also obtain average characteristics of foraging trips by recording the total number of trips, maximum distance reached for each trip, duration of each trip, and duration of time at the nest (resting time) for each individual penguin and averaging.

The sensitivity analysis

We calculate sensitivity as the percentage change in the result divided by the percentage change in the parameter of interest.

In the sensitivity analysis, we examine the effect of different levels of krill availability – low, medium, and high ($\Psi = 1$, 2 and 3) – and different types of krill variability – Scenario A, B and C – on penguin foraging behaviour. We also test the robustness of the model by varying key parameters. We vary the maximum distance the female can travel from the nest $d_{\max}$, the maximum stomach size of the chick $c_{\max}(a)$ and female $f_{\max}$, and the parameter specifying the payback cost of time on an empty stomach for the female γ_f and chick γ_c (see Table 3).

While a parent must consider both its own condition and the condition of the offspring to maximize both current and future reproductive success, it is unknown exactly how the parent balances this decision in terms of maximizing fitness. Given the unique approach used in this model, where there is a payback when the female or chick must use up their stored energy to meet daily energetic demands, it is important to test the variables scaling this payback. We test values of (γ_c, γ_f) ranging from (0, 0) [no payback for either female or chick] to (2, 2) [a scaling of 2 for both female and chick] (Table 2).

RESULTS

Energetic

We predict that krill availability has a non-linear effect on the amount of food fed to the chick for all scenarios tested, with the chick receiving on average around 100% of its energetic requirement for medium to high krill availabilities, but only 10–30% for low krill availability (Table 4). In contrast, the energy state of the female responds more linearly to

Table 3. List of parameters tested in the sensitivity analysis

Symbol	Parameter	Values tested	Unit
$K(d, L, \Psi)$	Krill ingested after 1 h foraging at distance *d*, time *t*	5 different functions in total, described in the text above	g krill · h^{-1}
$d_{\max}$	Maximum distance	50, **100**, 150, 200	km
$F_{\max}$	Maximum stomach contents of the female	600, 1200, 1800, **2400**, 3000, 3600	g krill
$c_{\max}(a)$	Maximum capacity of chick's stomach, changes each day	$r_c\boldsymbol{(a)}$, $2r_c(a)$, $3r_c(a)$, $4r_c(a)$	g krill
(γ_f, γ_c)	Scaling of payback for female and chick depleting energy reserves	(0, 0) (0, 1) **(1, 1)** (2, 1) (2, 2)	—

Note: Values in **bold** are those used in the best estimate parameterization.

Table 4. The average ratio (%) of food eaten per day compared with the daily energetic requirement for both the chick and female for Scenarios A, B, and C with low, medium, and high krill availabilities

	Krill availability	Chick ratio (%)	Female ratio (%)
Scenario A	Low	33.34	80.44
	Medium	98.97	88.99
	High	100.59	90.26
Scenario B	Low	29.64	80
	Medium	102.9	89.92
	High	101.21	105.73
Scenario C	Low	8.39	43.79
	Medium	106.28	92.28
	High	100.2	101.8

krill availability, with her average intake around 90 to 100% of her energetic requirement for simulations with high krill availability, decreasing to around 80% for low krill availability. For the low availability simulations in Scenario C, the female only ingested around 40% of her energetic requirement, much less than Scenarios A and B, probably because the average availability of krill in Scenario C was markedly lower.

Foraging

We first demonstrate some example foraging trips from Scenario A, where krill availability increases linearly with distance from the nest (Fig. 2). The example trips vary in distance and duration even without variability in the krill reward (i.e. the krill reward is constant at each distance from the nest). Tracking the stomach contents of the female and chick alongside the female's distance from the nest demonstrates how both foraging trip duration and range depend on the amount of food in the chick's stomach. The female generally returns to the nest when the chick's stomach is empty, except in the low krill availability simulation, when foraging trips are much longer. The reason for the precise timing is that the female can both maximize the amount of food fed to the chick and minimize its time on an empty stomach by feeding the chick when it has just digested all of its food. However, with low krill availability, trips become longer simply because there is not enough food around that the female can cover her minimal requirements and return to the chick with a meal.

The average results for Scenario B, from 1000 forward simulations of the model, show that foraging trips become closer to the nest with higher krill availabilities (Fig. 3). In addition, the difference between individuals, shown by the standard error, decreases for higher krill availabilities as the female is able to forage closer to the nest with a less variable krill supply. We predict that it is optimal in Scenario B for the female to forage where the krill supply is less variable, even if the mean krill availability is lower, providing there is sufficient krill to meet the energetic demands of both herself and her chick. We predict resting time at the nest to be approximately constant, at around 2–3 h between trips, with a

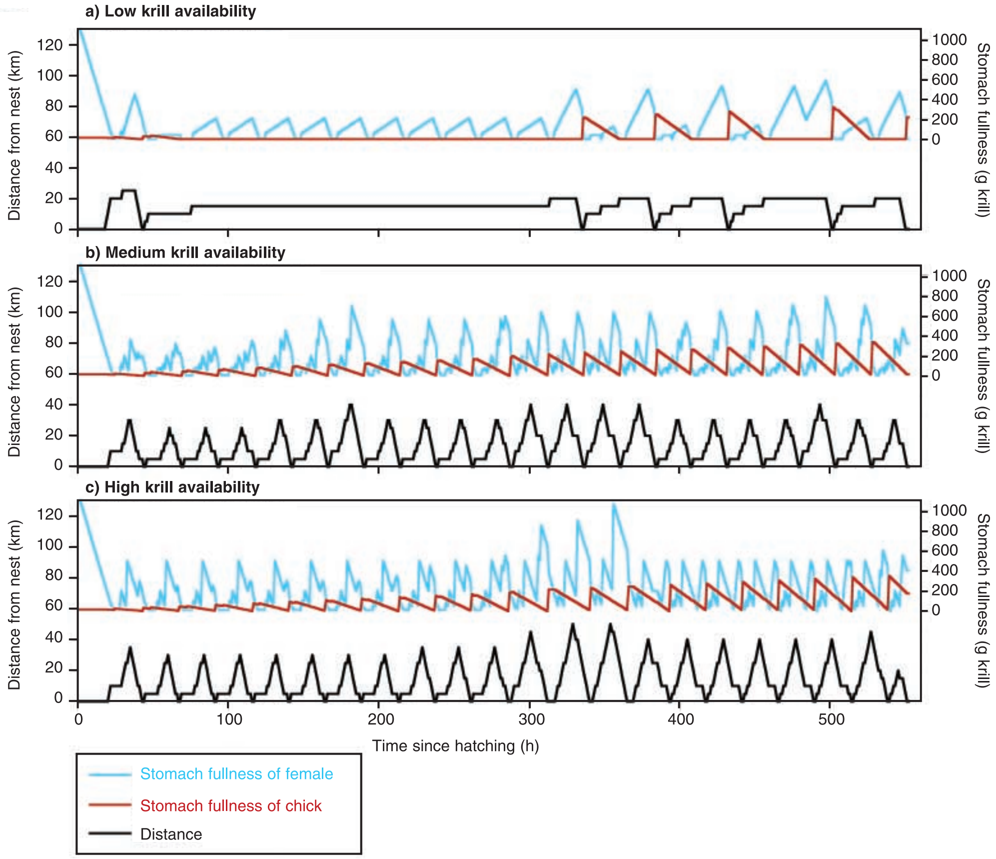


Fig. 2. An example simulated foraging trip record for (a) low, (b) medium, and (c) high food availability in Scenario A. Each graph shows the distance of the female from the nest (black) with time over the guard stage, and the corresponding energy state of both the female (blue) and the chick (red).

few longer rests of 5 h as krill availability increases. Resting times may be shorter than expected because there was no metabolic benefit parameterized in the model.

The average properties of the foraging trips for Scenario C differ markedly compared with the other scenarios (Fig. 4). In contrast to Scenario B, the female tends to forage closer to the nest towards the end of the guard stage, and further from the nest with higher krill availabilities. When krill availability is low, she probably forages close to the nest because there is a chance of a higher reward here, however small. Overall, the female undertakes a larger number of foraging trips than in the other two scenarios, and differences between individuals are much higher. This is probably because variability in krill was highest close to the nest, while it was higher further from the nest in Scenario B.

Comparing performance between the three scenarios (Fig. 5), we predict that a penguin is prepared to swim a considerable distance when the probability of gaining a large reward far from shore is high (Scenario A). However, as soon as prey patchiness is introduced (Scenarios B and C), the distance the penguin is prepared to travel shortens, even when the mean reward increases with distance away from the nest (Scenario B).

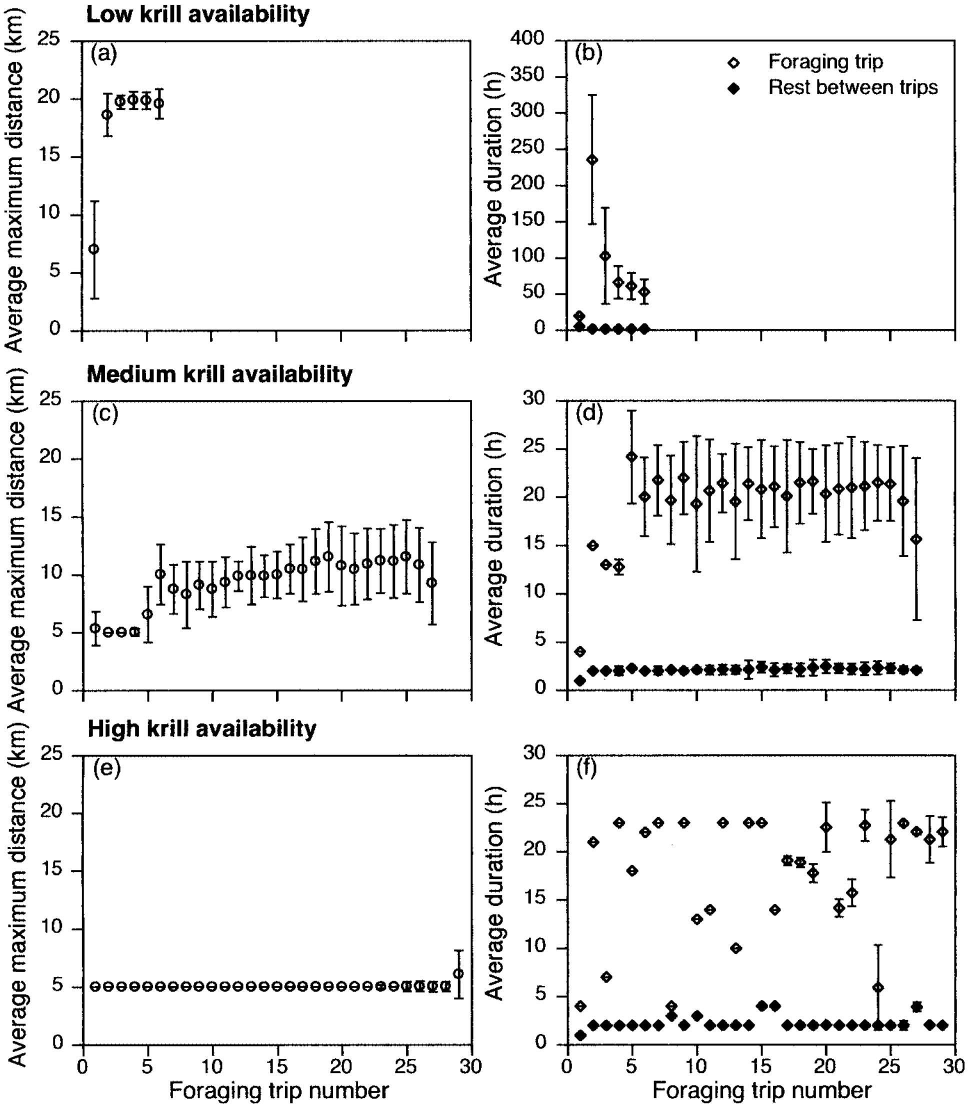


Fig. 3. The mean foraging trip characteristics (± standard deviation) for 1000 simulations of the model with Scenario B type krill availability. We show the maximum distance travelled (a, c, e) and the average duration of foraging trips (b, d, f) with resting time in between for low, medium, and high krill availability.

Sensitivity analysis

The results were most sensitive to changes in the maximum stomach capacity of the chick and changes to the scaling of fitness paybacks, with very low sensitivity to both the maximum distance from the nest and stomach fullness of the female. The maximum distance and duration of foraging trips were most sensitive to changes in $c_{\max}(a)$, while the

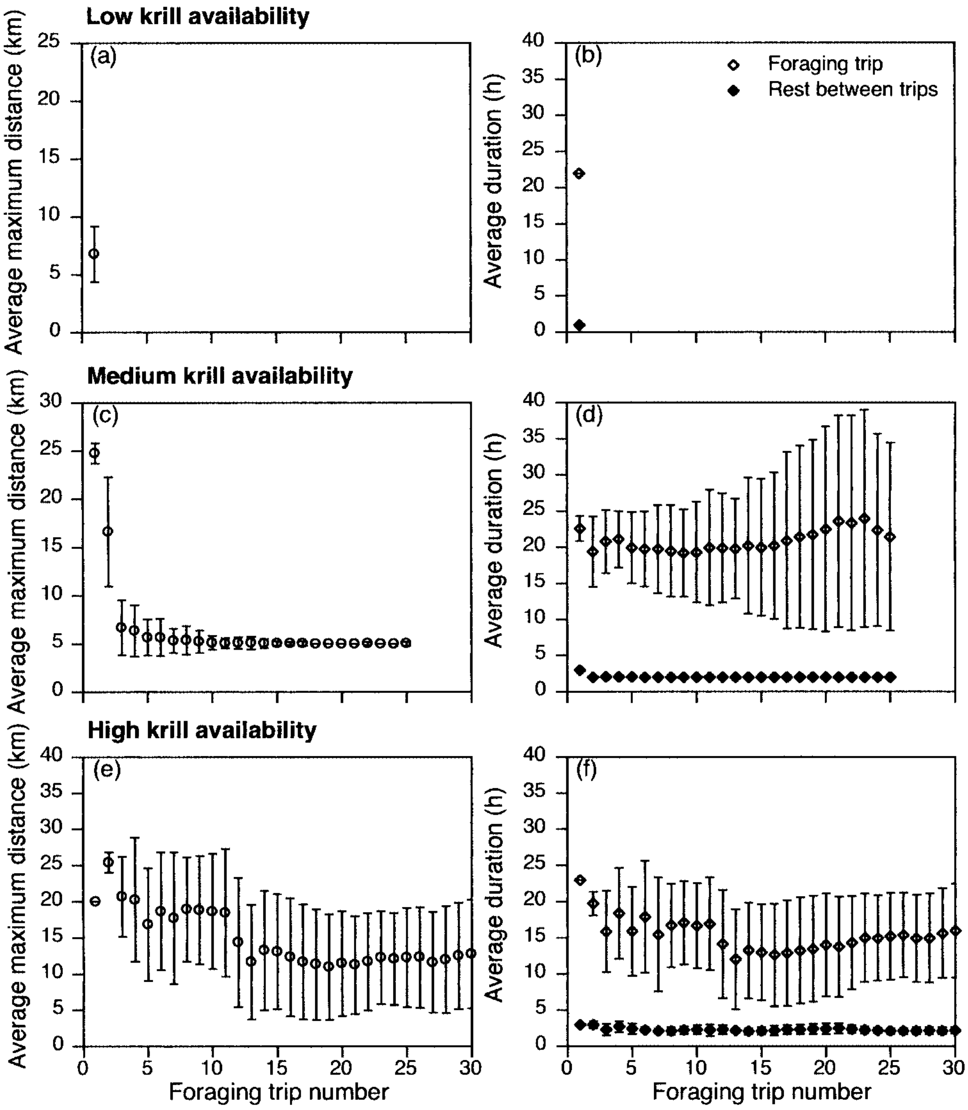


Fig. 4. The mean foraging trip characteristics (± standard deviation) for 1000 simulations of the model with Scenario C type krill availability. We show the maximum distance travelled (a, c, e) and the average duration of foraging trips (b, d, f) with resting time in between for low, medium, and high krill availability.

delivered energy was most sensitive to changes in the scaling of the payback related to the use of energy reserves.

To examine the effect of fitness costs on the energy result further, we calculate a ratio of the energy accumulated each day versus the specified energetic requirement for that day. A ratio of 1 indicates that the individual receives 100% of its energy requirement for that day.

We predict the weight loss of the female and energy intake of the chick for different specifications of the fitness costs (Fig. 6). Without any fitness payback (0, 0), the female received on average much less than her ideal requirement of food for the day, while the chick received around 75% of its requirement. With a fitness payback only for the chick (1, 0), the

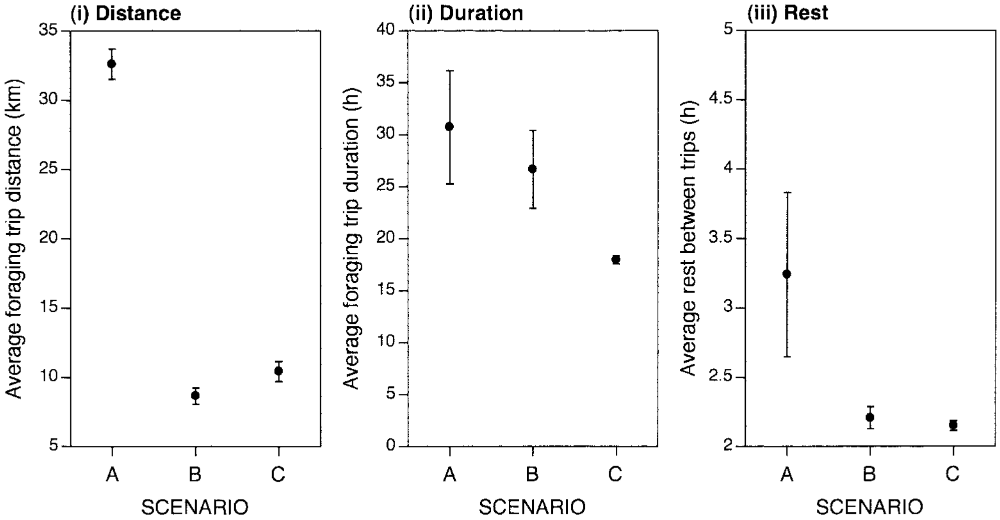


Fig. 5. The mean foraging trip characteristics (± standard error) over all simulations of Scenarios A, B, and C, in average maximum distance, average trip duration, and average resting time.

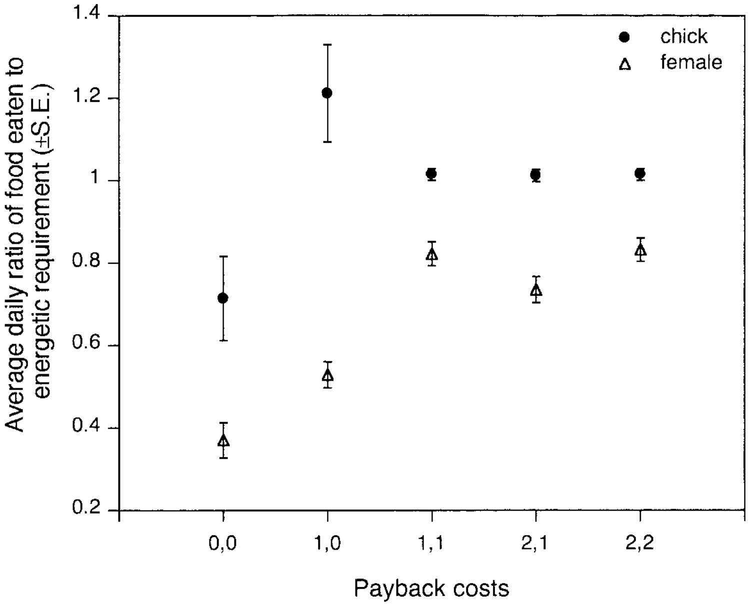


Fig. 6. The average effect (± standard error) of changes in payback costs on the final energy result of the female and the chick for all scenarios. Payback costs of having an empty stomach shown on the x-axis as (γ_c, γ_f) for the chick and female respectively.

chick received around 120% of its ideal amount of krill, but the female still received less than half of hers. With an equal fitness payback for both the female and the chick (1, 1), the best estimate parameterization of the model, and for further changes in this parameter, we predict that the chick receives the ideal amount of krill and the female receives around 80% of her energetic requirement.

DISCUSSION

Overall, we predict that a female will sacrifice her condition up to a certain point so that the chick can receive its full energetic requirement, and therefore that weight loss is adaptive for female macaroni penguins during breeding. We predict that the female ingests on average around 80–90% of her energetic requirement over the guard stage of differing scenarios for krill variability and levels of availability, which is comparable to empirical predictions. For foraging behaviour, we predict that krill variability has an effect on penguin foraging, with notable differences between the three scenarios tested. For Scenario C, which is our best estimate of krill distribution in the field, we predict that the female travels further from the nest in quicker foraging trips when krill availability is higher. In addition, we predict that penguins will travel further from the nest to obtain a more reliable source of krill even if the mean reward does not change with distance from the nest.

Energy and nest failure

In the model, the female received between 80 and 90% of her energetic requirement, which we assume might relate to a weight loss of 10–20% for most conditions except high availability of krill. In contrast, the chick received around 100% of its energy requirement of krill in all conditions except the lowest availability of krill, where we assume the chick would have died. These results indicate that it is an evolutionary strategy for the female to keep up with the needs of the chick at the cost of her condition, down to a threshold level of krill availability, below which the female must forage for herself without meeting the needs of the chick.

We predict that the female will lose 10–20% of her body weight on average over differing conditions to keep up with the energetic needs of the chick. This result is consistent with field studies reporting that female macaroni penguins lose on average around 15% of their body weight during the guard stage (Barlow and Croxall, 2002a; Green *et al.*, 2007). In the field, there are indications of a threshold level of parental expenditure for macaroni penguins, related to prey availability, below which the chick fails and above which there is no significant increase to chick growth (Barlow and Croxall, 2002a; Lynnes *et al.*, 2004). However, there is no record of an adult macaroni penguin dying of starvation during breeding or moult (Williams *et al.*, 1992), so it is likely that there is a threshold point at which the female abandons the chick to maintain her own condition. In addition, there is little understanding of why the female sacrifices her own condition up to this point. We suggest that this is an evolutionary strategy; the best way that the female can maximize her current and future reproductive success is by either fully meeting the needs of the chick to her own cost, or not meeting the needs of the chick so as to avoid her own starvation.

Effect of krill abundance on foraging trips

If mean krill availability increases with distance from the nest with no variability (Scenario A), we predict that the female will take trips shorter in duration and further from the nest for conditions of high krill availability. In these simulations, the female travels further from the nest to secure a meal that satisfies the requirements of both the chick and herself. Because krill availability is high, she is able to obtain a large meal in a shorter amount of time, thereby reducing the foraging trip duration. With medium krill availability, we predict that the female will forage closer to the nest, which means that the chick receives its energy requirement, but the female receives less than her ideal requirement of krill. For medium and low krill availability, the benefit of an increased krill reward further from the nest does not outweigh the cost of travelling time without feeding, hence we predict trips will be made closer to the nest.

Few studies record both foraging trip range and duration for penguins, particularly in relation to prey availability. However, several studies using different techniques provide evidence for inter-annual changes in foraging trips. In the present model, the female only ever extends foraging trip duration when krill availability is low. Some studies support this trend for a number of penguins species, including macaroni and gentoo penguins at South Georgia (Croxall *et al.*, 1999; Barlow *et al.*, 2002), Humbolt penguins, *Spheniscus humbolti*, in Chile (Hennicke and Culik, 2005), and Adélie penguins, *Pygoscelis adeliae*, at Bechervaise Island and Signy Island (Irvine *et al.*, 2000; Lynnes *et al.*, 2002). However, there is also evidence to the contrary – that macaroni penguins appear reluctant to increase foraging trip duration at the expense of meal size (Croxall *et al.*, 1999).

We also predict changes in foraging trip distance: that the female will forage further from the nest in years of high krill availability, due to a change in the relative balance between foraging reward and travelling time. The use of satellite tracking allows for estimates of foraging trip range as well as duration in the field. However, most of these have so far failed to report an inter-annual difference in trips due to changes in krill availability. Trathan *et al.* (2006) found differences in average foraging concentration of macaroni penguins between years but have not yet related this to krill availability. There are a couple of other studies on the foraging range of macaroni penguins in relation to inter-annual variability, and both of these report no differences between years (Barlow and Croxall, 2002b; Green *et al.*, 2005). The lack of an inter-annual effect could be due to krill availability being similar between years, with Barlow and Croxall (2002b) reporting low krill biomass for both years in their study. In addition, macaroni penguins can switch diet in years of low krill availability (Croxall *et al.*, 1999), which could explain a lack of inter-annual difference in foraging effort for field studies.

Effect of krill patchiness on foraging trips

Changes in the variability/patchiness of krill can also have an effect on penguin foraging behaviour. With Scenario C variability (the mean reward constant but variability decreasing further from the nest), we predict that the female will travel to a distance where the krill supply is more reliable (i.e. less variable) at the cost of extended travelling time. This only occurred for simulations of medium to high krill availability, suggesting that the female can only afford the cost of increased travelling time when krill availability is sufficiently high.

Support for penguins preferring a more reliable, or less variable, supply of krill comes from the field, where female macaroni penguins during the guard stage travel directly out to the shelf break each year, where there is likely to be a consistent supply of krill (Trathan *et al.*, 2003, 2006). This type of behaviour is also seen in the closely related rockhopper penguins, *Eudyptes chrysocome*, at the Falkland Islands (Putz *et al.*, 2003). These results suggest that both macaroni and rockhopper penguins (both *Eudyptes* species) head straight to a distant point where krill availability is more reliable, rather than spend time searching for a more patchy krill resource close to the colony. The krill resource is likely to be less reliable on the shelf because, although abundant, they are more likely to be located in tight swarms as a defence mechanism against a higher density of predators (Hunt *et al.*, 1992; Ritz, 1994; Hamner and Hamner, 2000). In the present model, we predict that macaroni penguins will travel to a less variable supply of krill when the mean reward is high enough to offset the cost of travelling further.

Field testing

Technological advances in the last 30 years allow the predictions from the current model to be tested in the field. In particular, we suggest combining satellite-tracking data with local krill density estimates to determine if foraging trip range increases while duration decreases in years of high krill availability. In addition, more detailed analysis of krill swarm data may enable us to determine if penguin foraging trips are affected by prey variability as well as availability, as predicted by this model. Finally, we suggest long-term experiments be conducted to monitor the growth of chicks during the guard stage combined with krill surveys to determine if there is a threshold level of krill availability below which chicks fail. We acknowledge the work of Green *et al.* (2007) on the foraging behaviour and energy expenditure of macaroni penguins during the chick-rearing period, which appeared in print as the current article went to press.

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