

# Can macaroni penguins keep up with climate- and fishing-induced changes in krill?

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**Abstract** Macaroni penguins have evolved to cope with the highly variable conditions of the Southern Ocean. However, changes in prey supply and patchiness potentially associated with changes in climate and krill fishing activity may be occurring too rapidly for the penguins to adapt. We use a stochastic dynamic programming model to examine how changes in both the mean and patchiness of krill supply may affect the foraging decisions, and therefore breeding success, of female macaroni penguins at South Georgia. We predict that rapid changes in the mean supply of prey will have more of an effect on the condition of the female and chick than changes in prey patchiness, and that changes in foraging behavior compensate for changes in prey up to a threshold point, beyond which breeding success is likely impacted. In particular, we predict that the location of the threshold is affected by whether or not the penguins are adapted to the prey environment in which they are foraging, with the female and chick receiving on average 20% less of their daily energetic requirement if the female is not foraging optimally.

**Keywords** *Eudyptes chrysolophus* · *Euphausia superba* · Behavior · Foraging · Climate change · Fishing · Predator · Prey · SDP · Provisioning · Fitness

## Introduction

The fauna of the Southern Ocean have adapted to cope with strong variability (Clarke et al. 2007). Mobile, long-lived predators such as penguins integrate the effects of variability in the physical and biological environment over large spatial and temporal scales (Fraser et al. 1992). For example, macaroni penguins (*Eudyptes chrysolophus*), during breeding at South Georgia, deal with a large range of variation in the supply and distribution of their main prey, Antarctic krill (*Euphausia superba*). In turn, krill have evolved to cope with seasonal, interannual and larger changes in temperature, sea-ice habitat, predation pressure, and currents. It is unknown, however, how either of these species will cope with the current rate of climate change and predicted increases in fishing activity in the Antarctic.

The fishery for krill is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) and has been operational for over 30 years, with a steady, low-level of exploitation to date (SC-CCAMLR, 2001; Everson and Goss 1991; Nicol and Endo 1997; Kawaguchi and Nicol 2006). However, recent improvements in krill processing suggest that the annual catch is likely to increase, which may be cause for concern given that the maximum allowable catch is set at over 20× the current catch. In addition, demand for krill is increasing as manufactured products from krill are becoming widely available (Nicol et al. 2000b). The threat from krill fishing to land-based predators lies not in the absolute fraction of krill removed from the Southern Ocean, which is likely to be low, but in the distribution and timing of krill fishing activity in relation to predator colonies (Croxall and Nicol 2004). The distribution of the krill fishery and land-based predators tends to overlap because both prefer areas of high productivity in krill biomass (Murphy et al. 1997). Krill

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abundance correlates significantly with bathymetry, with krill often abundant around shelf-break regions (Trathan et al. 2003). Furthermore, most fisheries for krill are operational in the Austral summer, when land-based predators are breeding, although the fishery at South Georgia is currently a winter fishery. In addition to potentially reducing the density of krill around predator colonies, fishing for krill may affect the patchiness of krill in a local region based on evidence that krill swarm more densely in the presence of predators (Swadling et al. 2005), based on principles of the selfish herd (Hamilton 1971; Clark 1974), and assuming that krill react to the fishery as a predator.

Changes in climate may affect the availability of krill to macaroni penguins at South Georgia through a number of possible mechanisms. Krill at South Georgia are not self-sustaining, and are most likely supplied from their extensive breeding grounds around the Antarctic Peninsula, which is experiencing some of the fastest warming in the world (King 1994). The first major threat from climate change is decline in the sea-ice habitat, as small temperature differences can have large effects on the extent and thickness of sea ice (Smetacek and Nicol 2005). There is evidence that krill recruitment is positively correlated with ice cover. Sea-ice provides shelter and food for juvenile krill over the winter, with evidence for years of low ice-cover decreasing krill availability to predators and affecting predator foraging success (Loeb et al. 1997; Fraser and Hofmann 2003; Atkinson et al. 2004; Nicol 2006). Changes in climate may also affect krill availability to predators through possible increases in the frequency of events such as the El Niño Southern Oscillation (ENSO) (Clarke et al. 2007). There is evidence that ENSO years may affect the currents that transport krill from their breeding grounds to South Georgia, since ENSO years are correlated with years in which the availability of krill at South Georgia is abnormally low, with significant effects on the breeding success of predators (Croxall et al. 1999; Atkinson et al. 2001; Reid et al. 2002). Changes in climate can, therefore, affect krill survival and transport, which may impact the overall abundance of krill from year to year. Increases in the frequency of bad krill years may also increase the expected variability, or patchiness, of krill in local areas.

While there exists some evidence for a link between land-based predator breeding success and krill availability, a number of factors potentially contributing to this interaction remain largely unstudied. Years in which krill are scarce around South Georgia lead to reduced penguin breeding success (Croxall et al. 1999; Atkinson et al. 2001; Reid et al. 2002), but we have little idea of how changes in the frequency of these years affects the penguins. Further, while we understand that krill are extremely variable in time and space (Ritz 1994; Godlewska 1996; Siegel 2000), we do not know how changes in this variability may affect

penguin behavior and condition during breeding. We even lack a coherent way to characterize the variability of the krill resource itself (Mangel 1994).

In this paper, we examine how penguins respond if the rate of change in krill availability is too rapid for a simulated evolutionary adaptation. In particular, we ask what happens if penguins have adapted to a particular landscape of krill availability and variability, and are we changing this landscape too quickly for them to keep up (Clark and Mangel 2000). To address this question, we use a stochastic dynamic programming (SDP) model to examine how changes in both the mean and variability of krill supply may affect the foraging decisions, and therefore breeding success, of macaroni penguins at South Georgia. There is little evidence on how climate change and krill fishing may quantitatively affect krill density and variability around predator colonies; so, we test a number of scenarios and do not separate for the effects of climate change and krill fishing in the results. We present the results in terms of the female's stomach fullness and distance from nest change at crucial decision points, and how changes in krill availability affect the overall condition of the female and chick. In particular, we ask if penguins can compensate for alterations in their habitat through their behavior (Roitberg and Mangel 1997).

## Methods

We use a previously tested SDP model from Cresswell et al. (2007) to test different scenarios for krill density and patchiness, changing with distance from the foraging female penguin's nest. We also modify the structure of this model to test what might happen if the simulated female experiences conditions different from those that the species has adapted to. We briefly summarize the state variables and their dynamics, described in detail in the previous version of this model (Cresswell et al. 2007), outlining the chief differences between this and the previous model. The parameters and their description are outlined (Table 1).

We model the time in which the female is foraging to feed the rapidly growing chick (typically in January). In the model, a female penguin chooses one of four behaviors at each time step: to swim away from the nest, to swim back towards the nest, to forage, or to feed the chick. We assume that the female is not foraging while she is traveling, which is consistent with observations that macaroni penguins tend to travel straight to their main feeding grounds during the guard stage, not stopping to search for krill during transit (Trathan et al. 2006). The unit of time is hours, and the model simulates 23 days, the approximate length of the guard stage at South Georgia, which takes place in January. At this time, the male, bigger and more aggressive than the

**Table 1** List of parameters

Symbol	Parameter	Value	Unit
$k$	Overdispersion parameter relating to krill patchiness	0.2 to 5	–
$d$	Distance from the nest	0 to 20	5 km
$L$	Time of day	$L = 0$ , night; $L = 1$ , day	–
$m(d, L)$	Mean number of packets at distance $d$ and time of day $L$	See Eq. 1	–

female, sits guarding the newly hatched chick while the female undertakes a number of 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).

#### State variables and their dynamics

There are five state variables in the model. The stomach fullness of both the female and chick are affected by ingestion from foraging, digestion, and the female feeding the chick. Two other state variables record the amount of time that the stomach has been empty. The final state variable is the female's distance from the nest, which changes as she swims back towards or further from the nest. The dynamics of the state variables are described in detail in Cresswell et al. (2007) along with estimates of parameter values and their justification. We summarize the dynamics here.

The stomach contents of the female are calculated in grams of krill. While macaroni penguins can eat other prey items, there is evidence that they rely heavily on krill, particularly during the breeding season (Croxall et al. 1993). When the female chooses to swim away from or back towards the nest, we calculate the new stomach contents simply by subtracting digestion, estimated at 50 g krill  $\text{h}^{-1}$  (Croxall et al. 1993), from the current stomach contents. When the female forages, we determine the new stomach contents from ingestion of krill minus digestion, where the foraging reward changes with distance from the nest, light intensity, and overall level of krill availability. If the female feeds the chick, we subtract digestion and the size of the chick's meal to calculate the new stomach contents of the female.

The hourly digestion rate of the chick increases proportionally as the energetic demands of the chick increase with growth, based on estimates for maintenance and energetic requirements of macaroni penguin chicks, with

growth in mass approximately linear up to 23 days (Brown 1987a; Barlow and Croxall 2002a). When the female is not feeding the chick, we subtract digested food from the stomach contents of the chick at each time step. When the female is at the nest and chooses to feed the chick, we subtract digestion and add ingested meal size to the stomach contents of the chick, with the female feeding the chick until it is full or until the stomach of the female is empty.

The time in hours that the female has endured an empty stomach increases only when her stomach content is zero, and likewise for the chick. When time on an empty stomach is positive, the female or chick is using stored energy reserves to meet energetic demands, and this has an equivalent payback cost in the calculation of fitness. 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 Clark and Mangel 2000).

Females appear to follow simple strategies for foraging during the brood-guard period, with highly linear foraging trips (Trathan et al. 2006); therefore, we assume 2-dimensional foraging in the model. The minimum distance 0 is the female at the nest. We assume a travel speed of 5 km  $\text{h}^{-1}$ , within the range of travel speeds estimated from satellite tracking data in the field and swimming experiments in captivity, from 4 to 8 km  $\text{h}^{-1}$  (Clarke and Bemis 1979; Brown 1987b; Barlow and Croxall 2002b).

#### Krill availability

The current model differs from Cresswell et al. (2007) in the parameterization of krill availability. In the previous model, we tested three different simple scenarios of krill availability: krill density increasing linearly with distance from nest with no variability/patchiness or with increasing variability; and krill density constant with patchiness highest close to the nest, decreasing further from the nest. In the current version of the model, we use a negative binomial distribution to describe the availability of krill with distance from the nest. Using a negative binomial distribution is advantageous because it is a versatile probability distribution (Mangel 2006). We were able to independently modify the mean number of krill packets ingested and the over-dispersion parameter, relating to krill patchiness, to test the effects of each of these factors.

The mean increases linearly with distance from the nest based on evidence that the concentration of krill increases toward 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. We define  $m(d, L)$  as the mean number of packets of krill available from 1 h of foraging at distance  $d$ , and time of day  $L$ , where each packet contains 100 g krill (Table 1). We double and halve the mean at each distance to represent years of high and low krill density. The mean  $m(d, L)$  for medium krill density during the day,  $L = 1$ , is  $m(d, 1) = 0.2d$

with the mean density of krill at night  $m(d, 0) = 0.1 m(d, 1)$ . Macaroni penguins are visual predators and tend to dive predominantly in daylight; however, it is possible that they have some success at night (Croxall et al. 1993; Green et al. 2003).

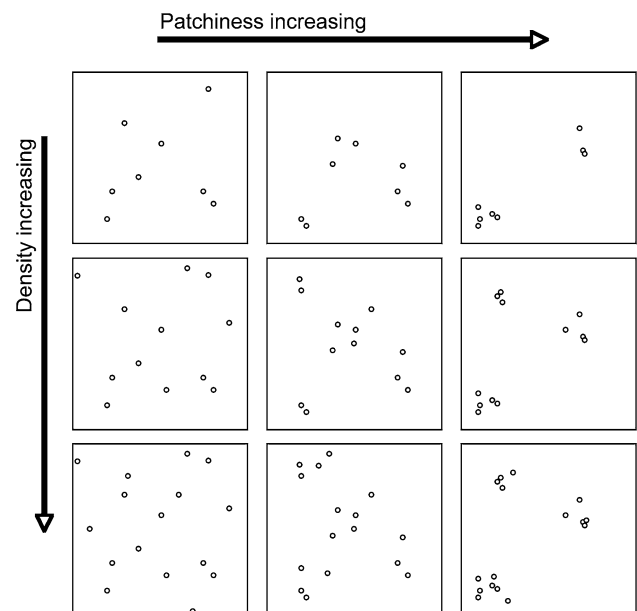
The over-dispersion parameter  $k$  affects how skewed the probability distribution is, but does not change the mean density of krill at a specified distance from the nest. For the negative binomial, variance in the number of packets is

$$\text{Var} = m(d, L) + \frac{m(d, L)^2}{k} \quad (2)$$

In the model, we test different values for  $k$  and for the mean number of packets of krill a penguin can encounter in an hour of foraging, for a given distance from the nest and time of day. For example, we can imagine different scenarios for krill availability where the mean number of packets, or krill density, increases from top to bottom, and the over-dispersion parameter  $k$  decreases, while krill patchiness increases, from left to right (Fig. 1). We compute the probability of finding a given amount of krill using the iterative process described in Mangel (2006).

### Running the model

The second major difference between the current model and the previous model stems from a modification of the forward iteration. In an SDP model, the dynamic programming algorithm works backward in time to calculate the optimal policy, an optimal set of decisions for each state at each time step, for a given range of conditions, such as krill availability (Mangel and Clark 1988; Houston and McNamara 1999; Clark and Mangel 2000). In the forward iteration, the decision-making individual (the female) refers to the optimal policy and behaves accordingly. If there is a probabilistic distribution of food, the optimal decision determined from the backward iteration is that which maximizes fitness over all possible food outcomes within the distribution. In the forward iteration, the actual food reward is chosen randomly from the same probability distribution. We modify this approach by changing the probability distribution of the krill reward in the forward simulation of the model so that the female is now choosing decisions based on the “old” optimal



**Fig. 1** An example of how the prey field per unit foraging varies with krill patchiness and density, where each circle represents a 100 g packet of krill. The patchiness or variability in the number of packets ingested per unit foraging increases from left to right as the value for the over-dispersion parameter  $k$  decreases. Similarly, the density or mean number of packets ingested per unit foraging increases from top to bottom. Both mean number of packets and values for  $k$  are hypothetical

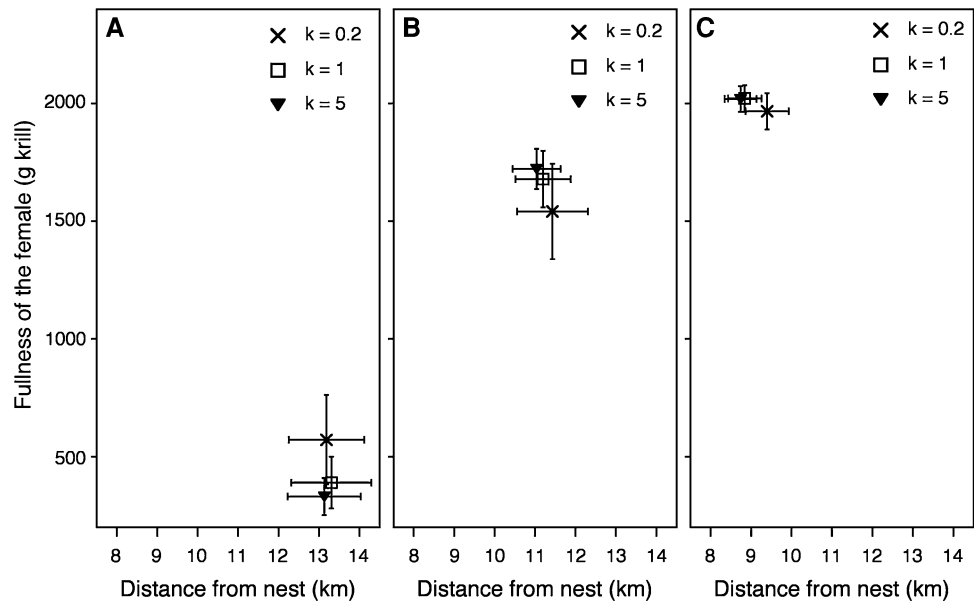
policy, a map of optimal decisions that does not apply to the current landscape.

In the current model, we determine one optimal policy from the backward iteration based on average conditions (medium krill density, with an over-dispersion parameter  $k = 1$ ) and examine the success of the female’s behavioral strategy if the conditions in the forward simulation are the same as those shaping the optimal policy (medium krill density, with an over-dispersion parameter  $k = 1$ ). This represents the situation where we assume that the penguins are adapted to their environment. We compare these results with a situation where conditions in the forward iteration are different to those shaping the optimal policy, with different levels of krill availability/density (low, medium, and high) and krill patchiness ( $k = 0.2, 1, \text{ and } 5$  for high, medium, and low variability/patchiness, respectively) in the forward iteration. This represents the altered situation where we assume that the penguins have not yet adapted to rapid changes in the krill supply brought about by changes in climate and increases in krill fishing effort (sensu Clark and Mangel 2000).

### Results

Changing the mean number of packets ingested per unit foraging, or the overall density of the krill, has a greater

**Fig. 2** The average distance and stomach fullness of the female ( $\pm$ SD) when she stops foraging and heads back to the nest for 1,000 forward simulations of the model: **a** low mean krill density, **b** medium mean krill density, and **c** high mean krill density, in the forward iteration for overdispersion values of  $k = 0.2, 1,$  and  $5$  (high, medium, and low patchiness, respectively). Medium krill density and  $k = 1$  were used in the backward simulation of the model

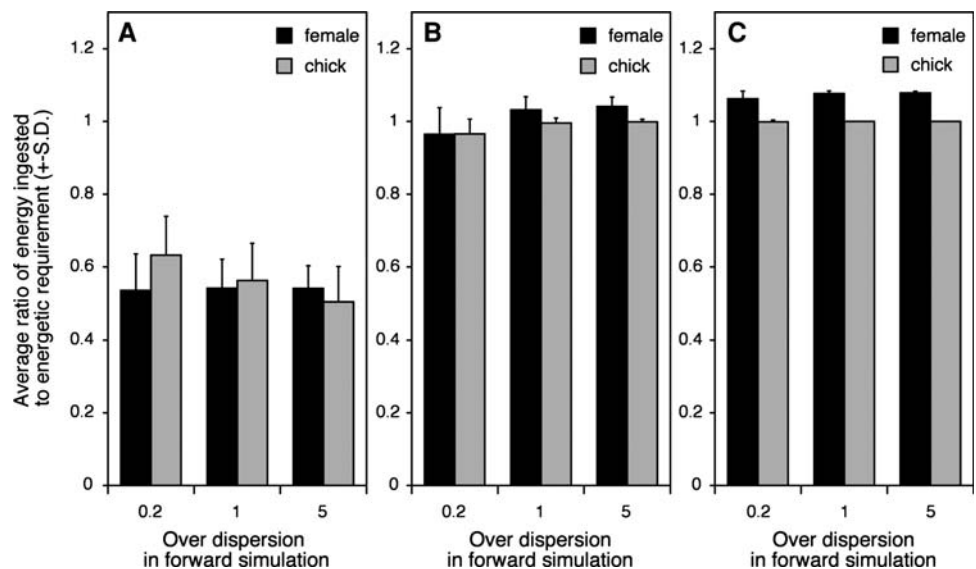


effect than changing the patchiness in krill supply, although both have a noticeable effect on the point at which the female heads back to the nest. Generally, if krill density is lower (Fig. 2a), the female turns back to the nest further from home with an emptier stomach. In addition, at lower krill density there is more variability between penguin behaviors than with higher krill density (Fig. 2c). Increasing the patchiness (decreasing  $k$ ) has the same effect on behavior as decreasing the density of krill, but is more noticeable at medium (Fig. 2b) and high (Fig. 2c) krill densities.

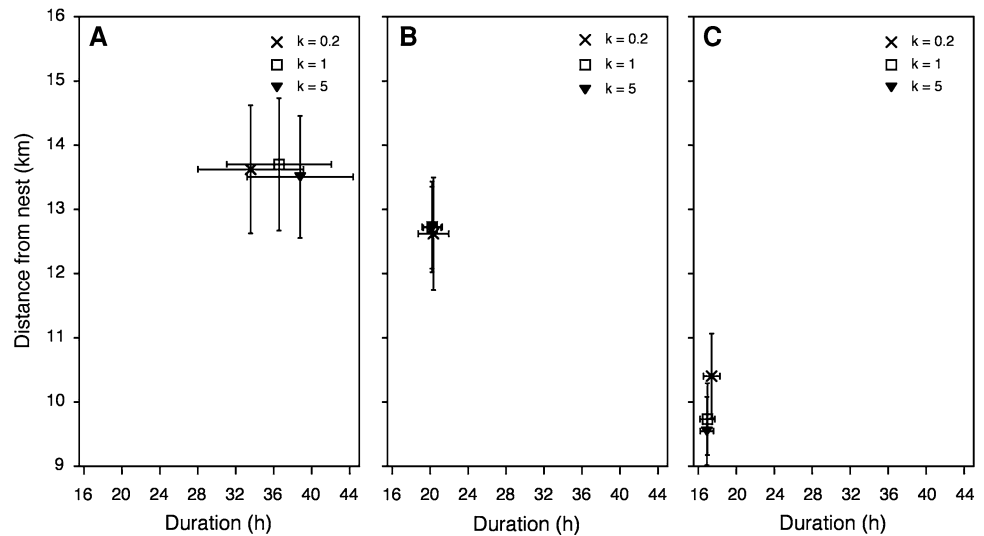
Changes to the density and patchiness of krill in the forward run of the model have a noticeable effect on energy ingested (Fig. 3). If the female encounters a prey density that is similar (Fig. 3b) or greater (Fig. 3c) than

the prey field that she is adapted to, both the female and chick receive around 100% of their energy requirements for the guard stage. However, if she encounters a prey density that is half the density of the prey field that she is adapted to (Fig. 3a), there is a noticeable loss in condition for both the female and chick, who receive only around 50–60% of their energetic requirements. The effect of changes in patchiness become more noticeable at low prey densities, but only for the condition of the chick, which receives less of its energy requirement as prey patchiness decreases ( $k$  increases). This is in contrast to the effect of patchiness at average prey density (Fig. 3b) where decreases in patchiness (increases in  $k$ ) lead to slight increases in condition for both the female and chick.

**Fig. 3** Average energy ingested ( $\pm$ SD) compared to energy requirement for 1,000 forward simulations of the model where the density and variability of krill are: **a** low krill density, **b** medium krill density, and **c** high krill density for overdispersion values of  $k = 0.2, 1,$  and  $5$  (high, medium, and low patchiness, respectively). Medium krill density and  $k = 1$  were used in the backward simulation of the model



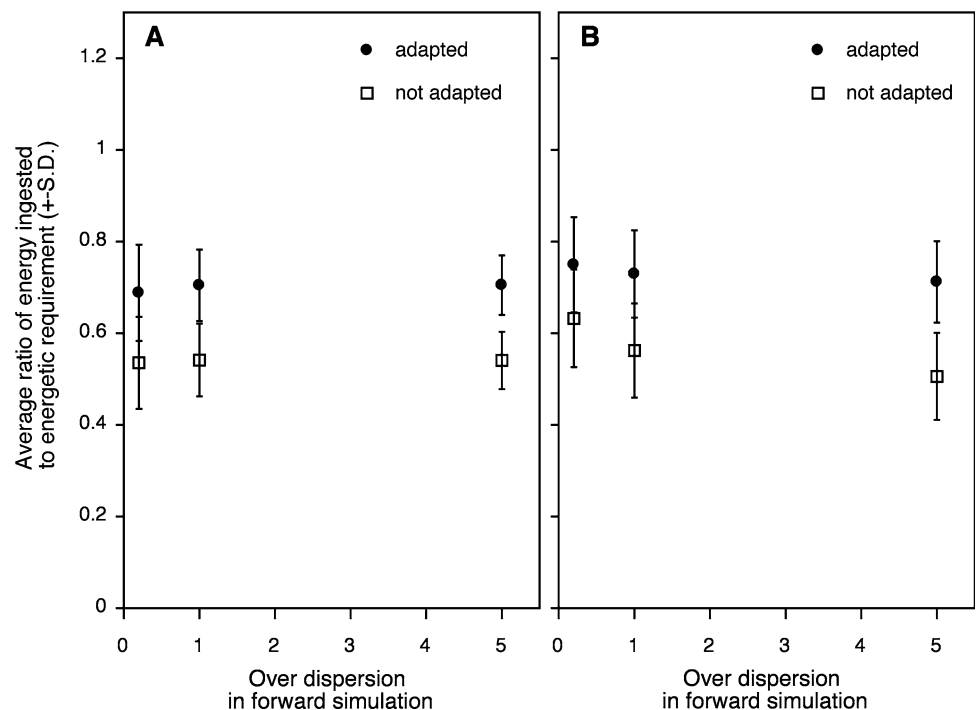
**Fig. 4** Average maximum distance and duration of foraging trips ( $\pm$ SD) for 1,000 forward simulations of the model where both the density and patchiness of krill are changed: **a** low krill density, **b** medium krill density, and **c** high krill density for overdispersion values of  $k = 0.2, 1,$  and  $5$  (high, medium, and low patchiness, respectively). Medium krill density and  $k = 1$  were used in the backward simulation of the model



Changes in krill density and patchiness also have a noticeable effect on the average maximum distance and duration of foraging trips (Fig. 4). At low krill density (Fig. 4a), the difference between individual penguin foraging trips is more variable than at medium (Fig. 4b) and high (Fig. 4c) krill density. Generally, the distance and duration of trips decreases with increasing krill patchiness at low krill density and increases with increasing krill patchiness at high krill density. There is little difference between simulations with low to medium patchiness ( $k = 5$  and  $k = 1,$  respectively) throughout.

We further explore the region of low krill density by comparing a simulation where the prey density that generated the optimal behavior rules for the penguins is the same as the prey density that they encounter in the forward simulation of the model (adapted) with a simulation where the prey density that the penguins encounter is half the density that they have adapted to (not adapted) (Fig. 5). This example is different to the previous situation in that we test the effect of krill density alone, assuming that the female is adapted to the encountered variability in the prey field, and that we average the effect over three different

**Fig. 5** Average energy ingested ( $\pm$ SD) compared to energy requirement for 1,000 forward simulations of the model at low krill density and different levels of variability for: **a** the female penguins and **b** the chick. Low krill density and  $k = 1$  were used in the backward simulation of the model for “adapted” with medium krill density and  $k = 1$  for “not adapted”



levels of krill patchiness. There is approximately a 20% loss of condition for both the female and chick over all levels of patchiness if the female is not adapted to the encountered prey density.

## Discussion

We predict that macaroni penguins can compensate for changes in the density of krill through their foraging behavior, but only up to a point. Generally, we predict that the female will take longer, further trips from the nest with low krill density, and shorter, closer trips with high krill density. If the female encounters a prey density that is half of the prey density the species has adapted to, we predict a noticeable loss in condition for the female and chick. Changes in prey patchiness have less of an effect, with decreases in patchiness resulting in a loss of chick condition at low krill density, but an increase in chick and female condition at medium krill density. This may be because at low krill density, the only way the female can obtain enough krill to return to the nest is if she finds a patch of very high krill density, the chances of which are higher when patchiness is high.

Many authors have observed acoustic changes in krill density on different scales (Hewitt and Demer 2000; Nicol et al. 2000a; Siegel 2000; Trathan et al. 2003) and others have recorded interannual foraging trip characteristics for macaroni penguins (Barlow and Croxall 2002b; Trathan et al. 2006); however, the only studies to relate the two factors make only general observations, such as that trip duration increases with decreasing prey availability (Croxall et al. 1999; Barlow et al. 2002; Hennicke and Culik 2005). These general observations are consistent with our predictions that the female will forage further from the nest in years of low krill density. In addition, while patchiness in krill supply is widely recognized, there is very little work on patchiness in prey affecting the foraging penguin (but see Cresswell et al. 2007), probably because we currently lack a consistent technique to quantify the patchiness in krill supply in a given area and particular time, and particularly in the context of behavior (Mangel 1994).

We predict a threshold in krill density, consistent with findings from the field (Barlow and Croxall 2002a; Lynnes et al. 2004), below which there is a noticeable loss in the condition of the female and chick. This likely leads to reduced breeding success. In particular, we predict that the location of the threshold is affected by whether or not the penguins are adapted to the prey environment in which they are foraging. In the field, females may buffer the effects of low krill density by switching to different prey items (Croxall et al. 1999). While we did not include prey choice in the model, years of low krill availability are still likely to

result in a lower energy intake, as alternate prey sources, such as amphipods, are less nutritious than krill. In the current model, if the female encounters a prey field with low krill density, she and the chick receive on average 20% less of their daily energetic requirement if her foraging rules are not adapted to this environment, i.e., if she is not foraging optimally. A loss of condition is likely to have noticeable effects on the breeding success of the macaroni penguins in a number of ways. First, in the field, female desertion is most likely during the guard stage, with years of low krill density often resulting in nest failure or decreased offspring weight for macaroni penguin chicks and other krill-reliant predators, such as Antarctic fur seals failure (Croxall et al. 1999; Atkinson et al. 2001; Barlow and Croxall 2002a; Reid et al. 2002). Macaroni penguins have a shorter breeding season than other penguins, and need to rear the chick to fledging so that the birds can migrate before the onset of winter (Williams and Croxall 1991). If the chicks are not receiving their daily energetic requirement for maintenance and growth, they will either die, not fledge in time for the onset of winter, or fledge at a significantly lower weight, which may lower their chance for survival (Barlow et al. 2002). While there is no evidence for an adult macaroni penguin dying of starvation during breeding (Williams et al. 1992; Barlow et al. 2002), the female does sacrifice her own condition during the guard stage, and it is possible that this may affect her future breeding success.

A growing number of studies indicate that global climate changes are not just a future concern, but also a current threat to species and ecosystems (McCarty 2001; Clarke et al. 2007). Although, for some species, evolutionary change may occur rapidly (Rice and Emery 2003; Stockwell et al. 2003; Berteaux et al. 2004; Bradshaw and Holzapfel 2006), penguins are long-lived and have a low reproductive output. Macaroni penguins, therefore, may not be able to keep up with potential changes in prey induced by climate, in addition to predicted increases in krill fishing effort. Our work shows that if macaroni penguins do not have a chance to adapt to conditions of density in krill, their condition, and potentially breeding success, will be adversely affected.

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