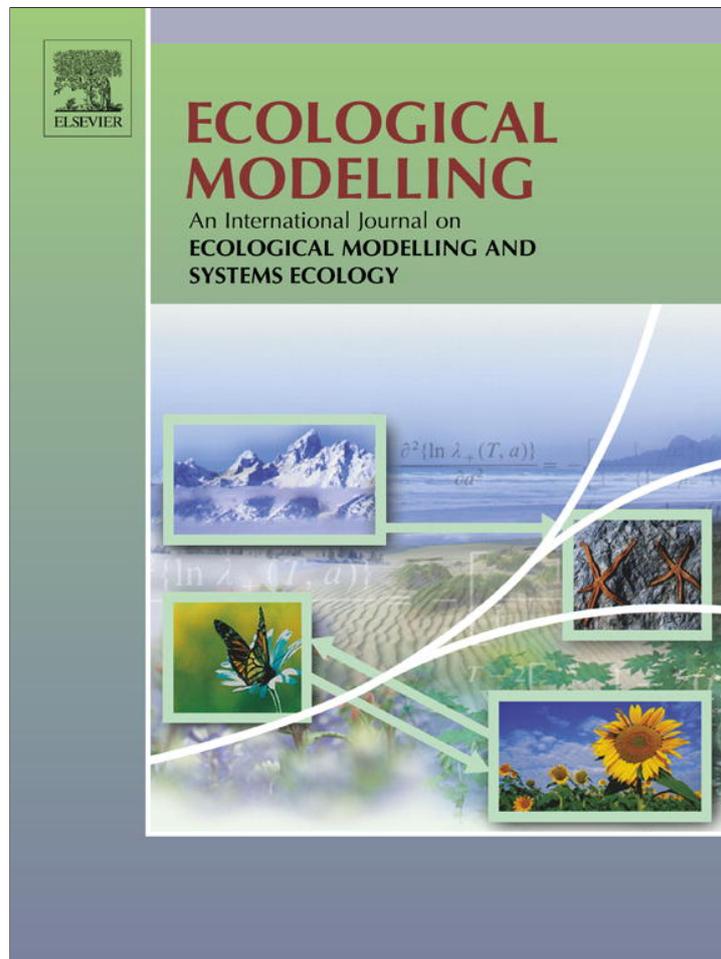


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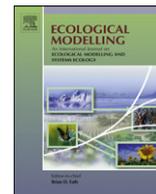
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A model of parental conflict: Predicting provisioning behavior of penguin partners in response to local changes in krill

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ABSTRACT

Understanding direct influences of local prey availability on penguin breeding behavior is limited in part because it is extremely challenging to organize a study that collects detailed data for both simultaneously. Models can help us understand the pattern of interaction between penguins and their prey, bridging holes in the data and helping steer future empirical studies. The main goal of our work is to provide an estimate of the functional response for penguins with respect to local changes in Antarctic krill (*Euphausia superba*) around breeding colonies in the Southern Ocean. We use data from field studies on penguins and krill to characterize a state-dependent life-history model where a breeding pair of penguins forage to provision a chick to fledging. Each parent makes decisions that maximize a measure of reproductive success based on quantified estimates for state dynamics, using a probabilistic distribution of how their partner is behaving (determined by successive runs of the model). We predict that the relationships describing total amount of krill eaten and chick survival versus krill available around a breeding colony approximate a Holling Type III functional response. We also found that quantifying the quality of the prey environment, rather than total quantity was a useful and relatively simple way to test changes in krill availability.

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1. Introduction

Many species of penguin in the Southern Ocean rely on krill, *Euphausia superba*, for their breeding success each summer. Krill biomass on a scale relevant to predators fluctuates widely from year to year (Mackintosh, 1972, 1973; Murphy et al., 1998), with predator populations often linked to krill abundance on a local scale (Croxall et al., 1988, 1999; Atkinson et al., 2001; Reid and Croxall, 2001; Reid et al., 2002). Fluctuations in krill are due to changes in environment, with current strength, ice cover, and water temperature being linked to krill recruitment and abundance in particular regions of the Southern Ocean (Wiedenmann et al., 2008, 2009).

Krill have also been targeted over the last 40 years by a fishery that is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (SC-CCAMLR, 2001; Everson and Goss, 1991; Nicol and Endo, 1997; Kawaguchi and Nicol, 2006). The fishery has operated at a consistent low-level of exploitation to date, but it is set to expand (Nicol et al., 2000), due to increased demand from aquaculture and massive improvements in the way that krill is harvested from the ocean. The Marine Stewardship Council (MSC) has recently certified the Southern Ocean krill

fishery but there is controversy due to concerns about the issue of indirect effects of the fishery on predators (Jacquet et al., 2010) (<http://www.nytimes.com/2010/06/23/science/earth/23krill.html>).

The CCAMLR is moving towards management in Small Scale Management Units (SSMUs, Constable and Nicol, 2002; Hewitt et al., 2004), because of the potential for competition between the fishery and krill predators at a local scale around predator breeding colonies. The management units are located within key areas in the Southern Ocean where krill are abundant around predator breeding colonies and the fishery is present. Among the questions related to management in small scale units are: (a) how should the overall catch limit for an area be subdivided among the SSMUs, (b) how should the development of the fishery be limited until this decision is made, and (c) which of predator demand, krill biomass, or biomass minus demand are most important in effective management of krill? There are a number of management models exploring the potential allocation of catch among the SSMUs (Krill Predator Fisheries Model, Hill et al., 2007a,b). One of the goals of our work is to qualify the component of krill mortality relating to predation from land-based predators, so that this information may be used in a management model, with our focus on two questions: (1) what is the relationship between the abundance of krill and the consumption of krill by penguins (the predator functional response) and (2) what is the relationship between the abundance of krill and

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the reproductive success of penguins (the predator reproductive response).

There are various studies on penguin abundance and population dynamics in different regions of the Southern Ocean. However, there is little understanding of how these dynamics are linked to changes in local prey availability. One way to examine this linkage is through penguin behavior and breeding ecology. Penguins are an altricial species, meaning that the young need nourishment and protection directly after hatching. Breeding success for penguins requires a contribution from both parents to ensure that the chick reaches independence within limited time and resources, for example reaching independence before the onset of winter (Davis et al., 1989), or before parental reserves reach a critical low. Mass loss in altricial species may be necessary, even adaptive (Barlow and Croxall, 2002; Cresswell et al., 2007; Green et al., 2007) down to a threshold point (Robin et al., 1998), to maintain the brooding parent through a period when nestlings require heat, insulation and food (Moreno, 1989). In considering the behavior of both the male and the female during chick rearing, and looking at how this is affected by changes in local prey availability, we are able to better predict how these animals may be affected by a changing prey environment, and can examine fundamental questions about provisioning behavior and parental conflict.

Conflict between parents over care of young arises because the success of the young generally depends on the care from both parents, whereas the cost to a parent depends on its own effort (Trivers, 1972; Parker et al., 2002; Houston et al., 2005). For each parent there is a trade-off between the amount of resources invested in current offspring versus the amount that remains for their survival and future reproductive investment (Williams, 1966; Clutton-Brock, 1991). An inverse relationship between current reproductive success and future parental survival has been a key assumption in life-history theory (Fisher, 1930; Williams, 1966); however, this is not necessarily the case (Bryant, 1979). In many species, individuals show flexibility in the pattern of parental investment in response to both natural and experimental changes in conditions (Varpe et al., 2004; Wright, 1990). Allocation of investment may also change as the demands of the growing chick change (Tinbergen and Verhulst, 2000). Experimental manipulation of breeding birds has been used to answer some of the questions relating to parental conflict. Further, when used in combination with modeling, it is possible to explore the mechanisms behind these observations in greater detail, and to associate different patterns in behavior with different outcomes in breeding. Thus, it may be possible to predict the likely breeding success of a given species in a particular location based on a satellite track of its movements.

Models have greatly enhanced our understanding of reproductive behavior, including mechanisms underlying the evolution of parental conflict (Alonzo and Warner, 2000; Dall and Boyd, 2002; Houston et al., 2005). Many of these models are purely theoretical (Winkler, 1987; Székely et al., 2000), or consider reproductive success in terms of the total number of offspring in a population (Davis et al., 1999), rather than individual fledging weight and survival. Winkler and Adler (1996) investigate chick demands in detail using a state-dependent life-history model, but do not examine parental foraging trips. An individual-based model by Salihoglu et al. (2001) examines mechanisms that potentially underlie observed constancy in fledging weight in Adélie penguin chicks in spite of large variability in Antarctic krill availability. Cresswell et al. (2007) consider the effects of krill depletion, but only during the guard stage and do not consider chick death or parental abandonment. Similarly, a model by Mangel and Switzer (1998) examines the effects of the krill fishery on expected reproductive success and parental survival, but does not consider the foraging behavior of the parents. The main motivation for our work is to use life history theory to gain a better understanding of how fishing-induced changes to the

prey environment near a penguin colony may affect the survival of the chick and of both parents. The aim of our model is to create a game from consecutive runs of a state-dependent life-history model, using krill as currency, that may in the future be applied to a number of different krill-reliant penguin species in the Southern Ocean; we apply it to the Adélie penguin, for which we can reference a large amount of data from many different studies.

2. Methods

There are 17 different penguin species in the world, and similar to most seabirds, all go through three stages of breeding. The first stage is incubation, when parents guard the egg and keep it warm. The second is the guard stage, when the rapidly growing chick needs protection, food and warmth. The final is the crèche stage, when chicks from different parents gather together for protection against predators, while being fed intermittently by the parents. During these distinct stages of breeding, the parents undertake behavioral roles that vary according to sex and species. Out of the combination of tasks that the male and female undertake during the three stages of breeding, there are three main strategies. Adélie penguins use a strategy where the male fasts while the female forages during incubation of the egg, with the male and female alternating tasks (feeding/guarding the chick alternating with foraging) for the guard and crèche stage. We do not predict penguin behavior during incubation, because the male sits alone at the nest for the entire incubation stage while the female forages at sea and does not return to the nest.

The model consists of a smaller prey environment model (the “single-trip” model) within a larger state-dependent life-history model (the “life-history model”). From the single-trip model we obtain multiple probable outcomes for a single foraging-trip, specifically, foraging-trip duration and amount of prey brought back to the nest within a limited overall trip duration. The results from the single-trip model are contained in an array of probable times and prey amounts, which represents the prey environment used in the life-history model.

The life-history model is a game using consecutive runs of a state-dependent life-history model, predicting the behavior of a penguin parent from the beginning of the guard stage to the end of the crèche stage. The algorithm works backward in time to calculate the optimal policy for each state (chick body weight, parent body weight and state of abandonment) at each time step (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). We call the decision-making parent the ‘focal individual’, and the other parent the ‘partner’. The focal individual makes decisions based on a need to maximize fitness, given a probabilistic distribution of the partner’s behavior. In the first run of the life-history model, the probable behavior of the partner is fixed. The optimal policy is determined in the backward run. In the forward run of the model, the focal individual forages within the prey environment determined by the single-trip model and considers the likely behavior of the partner when making decisions. After 1000 forward runs of the model, the behavior of the focal individual is recorded, averaged and used to parameterize the next backward run of the model, in which the partner makes decisions based on the probabilistic distribution of the focal individual. We repeat this process until the model finds an evolutionary stable solution (Fig. 1).

2.1. Single-trip model: simulating the prey environment

In the single-trip foraging model, the focal individual chooses from one of three behavioral decisions each time step. Decisions occur at sea, and we assume that a penguin still making decisions has not yet foraged from a patch of food, i.e. a swarm of krill.

Table 1
Parameters used in the single-trip foraging model.

Symbol	Parameter	Value	Unit
$\Psi(r, t)$	Fitness is the maximum gain in krill from one foraging trip given distance from nest r and time at sea t	–	–
N	Number of individuals in the forward iteration	1000	–
t	Time step of the model	8	min
T	Final time (equal to S in life-history model)	6–36	h
t_p	Time foraging in patch of prey	0 to $(T-2)$	–
r	Distance from nest	0 (nest) to r_{\max}	km
r_{\max}	Maximum possible distance from nest	100	km
r_{int}	Traveling/swimming speed	7.5	km h ⁻¹
$t_c(r)$	Commute time back to nest from distance r	1 to (r/r_{int})	–
$\alpha(r)$	Patches encountered per km on ship transect from acoustic data	0 to ...	patch km ⁻¹
ϵ	Rate of gain from patch	0.002 high or 0.0002 low	–
G_{\max}	Maximum gain (max stomach fullness of penguin)	2000	g
$G(\epsilon, t_p)$	Gain from foraging in a patch of quality ϵ for time t_p	0 to x_{\max}	g
$P_f(r)$	Probability of encountering a patch of prey at distance r	See text	–
$P_z(r)$	Probability that, once encountered, a patch has rate of gain ϵ , depending on quality level z	See text	–

Table 2
Parameters used in the life-history model.

Symbol	Parameter	Value	Unit
$\Phi(f, c, a, t)$	Fitness is the maximum expected body weight of chick and focal individual (FI) given current FI body weight f , chick body weight c , state of abandonment a and time since hatching t	–	–
N	Number of individuals in the forward iteration	1000	–
t	Time step of the model	4	h
T	Final time	60	d
f	Body weight of focal individual	0 to f_{\max}	g
f_{\max}	Maximum body weight of focal individual	4000	g
f_{\min}	Minimum body weight of focal individual	2400	g
c	Body weight of chick	0 to $c_{\max}(t)$	g
$c_{\max}(t)$	Maximum body weight of chick, depends on age	See text	g
$c_{\min}(t)$	Minimum body weight of chick, below which death occurs	See text	g
a	State of abandonment	see Table 4	–
t_s	Time at sea	1 to S	h
S	Upper limit in trip duration	6–36	h
t_n	Wait time at nest (guard stage)	0 to S	h
Δf_{\max}	Maximum contribution to stores each time for FI	28	g krill h ⁻¹
l	Location, used to calculate metabolic costs	1 (at sea) 0 (at nest)	–
$m_f(l)$	Metabolic costs for FI each time step, for location l	$m_f(0) = 16.8, m_f(1) = 28$	g h ⁻¹
$x_f(t_s, t_n)$	Cost of FI metabolism over time $t_s + t_n$	See text	g krill
$y_f(\Delta t)$	Cost of storing maximum amount Δf_{\max} for FI over time Δt	See text	g krill
$x_c(t, \Delta t)$	Cost of chick metabolism from time t to $t + \Delta t$	See text	g krill
$y_c(t, \Delta t)$	Cost of maximum growth of chick from time t to $t + \Delta t$	See text	g krill
k_f	Size of foraging reward for focal individual	0–2000	g
γ	Amount of krill delivered to chick by FI	100–1000	g
k_p	Size of meal delivered to chick by partner	100–1000	g
λ	Fraction of krill converted to growth	0.75	–
β	Assimilation efficiency of krill to metabolic energy	0.8	–

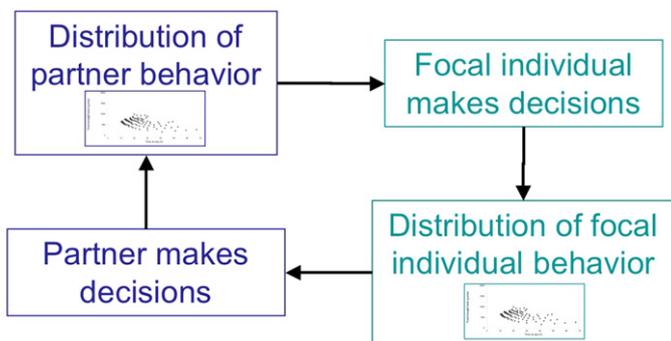


Fig. 1. Explanation of flow of events in the life-history model. In the first run of the model, the focal individual makes decisions based on a probable distribution of the behavior of partner. The behavior of the focal individual is averaged over 1000 forward runs of the model, and this information is used to create a distribution of likely behavior that is used to parameterize the next backward run of the model, where the partner then makes decisions. This process is repeated until we reach an evolutionary stable strategy.

If a patch is encountered, the penguin forages to maximize gain and then returns to the nest. Decisions are to travel further from the nest, to travel back towards the nest, or to hunt for food at the current distance from the nest. We assume that the individual only forages from one patch of food during a foraging trip, similar to single-patch provisioning in Ydenberg and Davies (2010) (see Table 1).

Each unit of time t represents 8 min, in which the penguin can travel 1 km at 7.5 km h⁻¹ (either towards or away from the nest) based on a range of swimming speeds recorded for Adélie penguins of 2 m s⁻¹ (or 7.2 km h⁻¹) (Culik and Wilson, 1991; Culik et al., 1994) to 3.7 m s⁻¹ (or 13.3 km h⁻¹) (Hui, 1987). We vary the final time S from 6 to 36 h, so that the result is a representation of how much food a foraging individual can collect, and how long it forages for, given the maximum time S at sea. This result is used in the game model, where the decision-making individual chooses an upper limit in trip duration S at sea that maximizes fitness. At elapsed time t , the amount of time that the penguin can stay in a patch of prey is at most $S - t_c(r) - t$, where $t_c(r)$ is the commute time back to the nest from distance r .

We set the maximum distance from the nest to be 100 km, which is based on median maximum distances from the colony reached by foraging birds of 60 and 125 km from the nest for guard and crèche stages of breeding respectively for all years (Clarke et al., 2006).

We separate the foraging process into two steps: the probability of encountering a patch of prey $P_f(r)$ in one period of time at distance r from the nest; and the probability that once located, the rate of gain from a given patch is ϵ , specified by probable patch quality $P_g(z, \epsilon)$. There is very little data on patch quality for Antarctic krill, in terms of rate of gain, so we parameterize the model in the simplest way, with the penguin either encountering a low quality patch, $\epsilon = 0.002$, or a high quality patch, $\epsilon = 0.02$.

$$P_g(z, \epsilon) = \Pr(\text{patch once encountered has rate of gain } \epsilon, \text{ depending quality level } z) \quad (1)$$

To test different prey environments, we vary quality level z , which affects the ratio of low to high quality patches in the environment. We test 20 levels of z , affecting the probability that a patch is low quality $\epsilon = 0.0002$, or high quality $\epsilon = 0.002$.

$$P_g(z, 0.002) = 1 - .0025(z - 1) \quad (2)$$

The probability of finding a high quality patch $P_g(z, 0.02)$ is $1 - P_g(z, 0.002)$.

The gain from a patch of prey $G(\epsilon, t_p)$ depends on the rate of gain from a patch ϵ , the amount of time spent in the patch t_p , and the maximum possible gain. We set $G_{\max} = 2000$ g krill. Recorded stomach contents delivered to chicks for Adélie penguins measure up to 1000 g (Trivelpiece et al., 1987), which does not include the parent digesting food at sea. By the time chicks are 2–3 weeks old they can rapidly consume a parent's entire stomach contents and consumption rates are limited by parental delivery rates (Chappell et al., 1993b), with stomach content average around 600 g (Trivelpiece et al., 1987). Parents must be able to hold more than this amount to cover their own metabolic needs. Other studies show seabirds may swallow single prey items in excess of 10% of their own body mass (Wilson et al., 1995), with max stomach capacity around 20% body mass (Trivelpiece et al., 1987) and that maximum stomach volume during chick rearing 800–1200 mL for medium weight Pygoscelid penguin (Peters, 1997). During the period of highest demand, adults need to find around 2.0 kg krill per foraging trip in order to meet the energetic needs of themselves and their brood (Culik and Wilson, 1991). Gain varies according to the following:

$$G(\epsilon, t_p) = G_{\max}(1 - e^{-\epsilon t_p}) \quad (3)$$

Time to a new patch varies depending on the rate of patches encountered per time step $\alpha(r)$ (Fig. 2). We estimate the density of patches in the environment from Klevjer et al. (2010), who measured prey density from a ship at three separate distances from shore. From the Klevjer et al. (2010) data, we approximate how the number of patches encountered per unit time changes with distance from the nest as follows:

$$\alpha(r) = -0.0006r^2 + 0.1261r + 0.0665 \quad (4)$$

The probability of finding a patch of prey in one time step $P_f(r)$ varies with distance from the nest r and the density of patches observed in the Klevjer et al. (2010) study $\alpha(r)$. We convert the swarm encounter rate from Klevjer et al. (2010) into the mean number of patches per time step $\alpha(r)$ for our model using penguin swimming speed at 7.5 km h^{-1} , and then define $P_f(r)$ by the following:

$$P_f(r) = 1 - e^{-\alpha(r)} \quad (5)$$

We now set fitness $\Psi(r, t)$, where

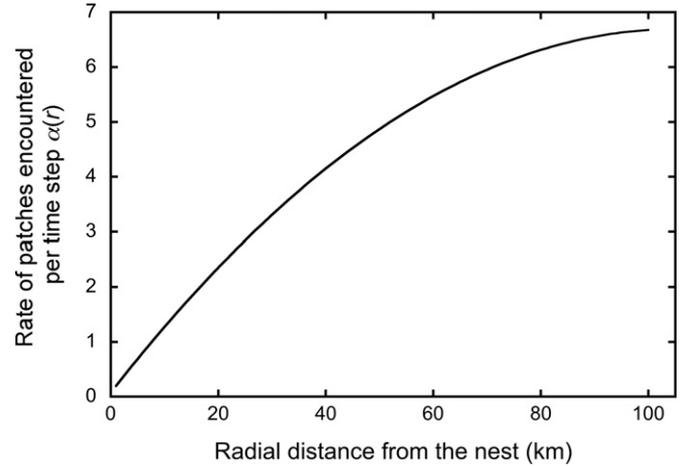


Fig. 2. Rate of patches encountered per time step $\alpha(r)$ changes with radial distance from nest r , and is estimated from Klevjer et al. (2010).

$$\Psi(r, t) = \text{maximum return of krill from one foraging trip, given the current distance from the nest } r \text{ and time at sea } t \quad (6)$$

If the individual chooses to travel away from the nest, the probability of finding a patch during that time step is reduced to $P'_f(r) = 0.6P_f(r)$ because the swimming behavior of the penguin is aimed at traveling rather than searching for prey. The fitness value of this decision $V_{out}(r, t)$ is

$$V_{out}(r, t) = (1 - P'_f(r))\Psi(r + 1, t + 1) + P'_f(r)E_{\epsilon} \times [\max_{t_p} P_g(z, \epsilon)G(\epsilon, t_p)] \quad (7)$$

where E_{ϵ} denotes the expectation over the distribution E_{ϵ} . If the individual encounters a patch of prey, the penguin is still considered to be within the radial distance r rather than $r + 1$, and the rate of gain in this patch is drawn accordingly.

If the individual decides to travel back towards the nest, the probability of finding a patch is again reduced to $P'_f(r) = 0.6P_f(r)$ because the individual is traveling towards a destination rather than searching for prey. The value of this decision $V_{in}(r, t)$ is the same as that for traveling away from the nest, except the distance r decreases by 1 unit if food is not encountered.

$$V_{in}(r, t) = (1 - P'_f(r))\Psi(r - 1, t + 1) + P'_f(r)E_{\epsilon} \times [\max_{t_p} P_g(z, \epsilon)G(\epsilon, t_p)] \quad (8)$$

If the individual decides to hunt for food at the current distance from the nest, the probability of finding a patch is $P_f(r)$, not reduced by travel, and the fitness value $V_{hunt}(r, t)$ is

$$V_{hunt}(r, t) = (1 - P_f(r))\Psi(r, t + 1) + P_f(r)E_{\epsilon} [\max_{t_p} P_g(z, \epsilon)G(\epsilon, t_p)] \quad (9)$$

The optimal decision at each time t and distance r is that which gives maximum fitness

$$\Psi(r, t) = \max[V_{out}(r, t); V_{in}(r, t); V_{hunt}(r, t)] \quad (10)$$

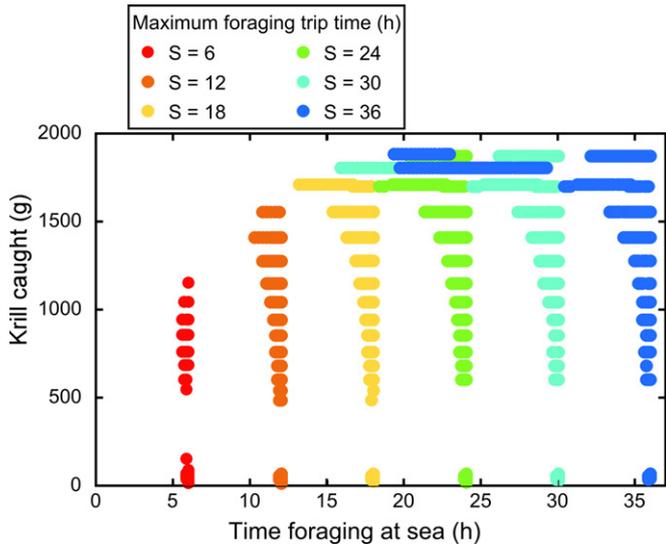


Fig. 3. Amount of krill caught (g) in one foraging trip versus time at sea (h), for 1000 penguins over 12 separate runs of the 'single-trip' foraging model, where each color represents a different maximum foraging trip time S .

We ran this model for 20 different levels of food quality z , affecting the ratio of high to low quality patches, and for 6 maximum foraging trip times ranging from a maximum 6 h trip ($S=1$) to a maximum 36 h trip ($S=6$). The probability of finding a patch $P_f(r)$ varied with distance from the nest but this relationship was kept constant for successive runs of the model. This resulted in a distribution of probable meal sizes brought to the nest and foraging trip times depending on the upper limit in trip length and the probable quality of food in the environment.

A detailed example of all the meals brought back at quality $z=6$ helps us understand the calculation of probable trip times and meal sizes for each quality level and upper limit in trip length S (Fig. 3). Food ingested and trip time are noticeably affected by the upper limit on trip length S at food quality level $z=6$. Simulated penguins with a longer upper limit on their trip length were at sea for longer, but did not necessarily bring back more food than with a shorter maximum trip length. There was also more variability in how long the penguin adult was at sea as the upper limit in trip length increased. We recorded an array of values, such as the above example, for each food quality level $z=1$ through 20. We converted these numbers into probabilities for each of the 20 food quality levels, and used these probabilities to represent the prey environment in the game model. Intuitively from this figure, a penguin foraging in the game model may choose a lower limit in trip length S if it is more optimal to return with a smaller meal in a shorter amount of time, rather than a larger meal in a longer amount of time, i.e. if minimizing time is more valuable than maximizing amount of krill.

2.2. Life-history model: the game

2.2.1. Breeding strategies

We assume that the parents only raise one chick. An Adélie female penguin raises on average 1.3 (Chappell et al., 1993a) to 1.6 ± 0.5 (SD) eggs to crèche, with the majority of egg loss occurring during the incubation stage (Ainley et al., 1983). We assume that the parents only raising one chick based on this average and because the majority of other penguin species only raise one chick to independence, making it easier to compare between the case study and other species.

The possible outcomes of breeding are: that the focal individual may live or die, and if alive, may raise the chick to fledging or may

Table 3
Explanation of probabilities.

Symbol	Explanation
$P_{k_f}(S, t_s, k_f)$	Probability that focal individual returns to nest with k_f g krill after t_s hours at sea given choice of upper trip limit S hours
$P_{k_p}(t_n, k_p)$	Probability that the partner will return at within time t_n with meal size k_p to feed the chick (during guard stage)
$P_a(t, t_s)$	Probability that the partner abandons between time t and $t + t_s$

abandon the chick; the chick may survive or die; and the partner of the focal individual may be present and helping for the entire breeding cycle or may abandon the nest at some stage, for reasons including death. In addition to parent and chick survival there is also a range of possible sizes that either may attain by the time of chick fledging that will affect their respective future survival and fitness.

We now explain the how the life-history model operates, first outlining the decisions that the focal individual can choose at any time. We outline the state dynamics in the model, including details on chick abandonment and death, justify our estimated values for parameters, and finally explain how fitness is calculated.

2.2.2. Decisions

All decisions are made at the nest. During the guard stage, the focal individual must choose to either forage at sea and return with a meal to feed the chick, or to abandon the chick and spend the rest of the breeding season at sea. If the focal individual decides to forage, the optimal upper limit in trip duration S and the amount of stomach contents to feed to the chick γ are chosen. At sea, an expectation of foraging trip time and meal size is drawn from the distribution determined by the single-trip foraging model. After foraging, the focal individual will wait up to 36 h at the nest for the partner to return, after which time it will abandon the nest. Chappell et al. (1993b) recorded total nest wait plus foraging trip time to be around 40 ± 8.6 h during the guard stage, with Wilson et al. recording mean foraging time during guard stage for Adélie to be 30.8 h in 1989 Wilson et al. (1989a) and 24.6 h in 1991 (Wilson et al., 1991), making 36 h a reasonable estimate for the longest wait at the nest. If either parent abandons during the guard stage, the chick dies.

During the crèche stage, the focal individual has the same choice each time step: to forage and feed the chick, or to abandon the chick. The difference is that the focal individual does not have to wait for the partner to return, because the chick no longer needs adult protection, so only stays at the nest to feed the chick. If either parent abandons during the crèche stage, the chick may still die from starvation, but will not die from abandonment alone (see Table 4).

Given a particular upper limit in trip time S , we look up the probability, from the single-trip model, that the focal individual will bring back a meal of size k_f after a time at sea of t_s time units. This probability is $P_{k_f}(S, t_s, k_f)$ (Table 3):

$$P_{k_f}(S, t_s, k_f) = \Pr(\text{focal individual returns after } t_s \text{ hours with } k_f \text{ g} \\ \times \text{krill, given trip limited to } S \text{ hours}) \quad (11)$$

Likewise, there is some probability $P_{k_p}(t_n, k_p)$ during the guard stage or $P_{k_p}((t_s + t_n), k_p)$ during the crèche stage that the partner will return after a particular time t_n or $(t_s + t_n)$ respectively with k_p g krill to feed the chick. The time that the partner forages at sea is t_n during the guard stage, because the partner will either return within time t_n while the focal individual is at the nest, or the chick will die. In contrast, during the crèche stage, the chick is not guarded, so the partner may return at any time while the focal individual is at the nest or at sea. Initially, there is an equal

Table 4
Explanation of state of abandonment a , with implications changing depending on the stage of the model.

a	Abandoned	Consequence: guard stage	Consequence: crèche stage
0	Neither	No effect on chick survival	No direct effect on chick survival
1	Partner only	Chick dies	No direct effect on chick survival
2	Focal individual only	Chick dies	No direct effect on chick survival
3	Both parents	Chick dies	No direct effect on chick survival

probability of close to zero for every possible value of $P_{k_p}((t_s + t_n), k_p)$. On subsequent runs of the model, we use the results from the forward iteration of the model (the behavior of the focal individual) to parameterize the backward iteration for the next run of the model.

2.2.3. State dynamics

Energetic costs for the chick are divided into costs for metabolism $x_c(t, \Delta t)$ and growth $y_c(t, \Delta t)$. First, we describe the amount of krill needed $y_c(t, \Delta t)$ for the chick to grow to maximum weight $c_{\max}(t + \Delta t)$ from its current weight $c(t)$, in time Δt , considering fraction of krill that is converted to growth λ .

$$y_c(t, \Delta t) = \lambda^{-1}(c_{\max}(t + \Delta t) - c(t)) \quad (12)$$

The new body weight of the chick c' after time Δt depends on current chick weight $c(t)$, maximum weight for age $c_{\max}(t + \Delta t)$, size of meal from the partner k_p and focal individual γ , costs of metabolism $x_c(t, \Delta t)$ and maximum growth $y_c(t, \Delta t)$, and the fraction of energy that is converted into growth λ . The chick will only eat as much from the focal individual as it needs to reach maximum body weight. If the total meal is not large enough to cover basic metabolic needs, the chick must cover these costs from its own stores. If the body weight of the chick ever falls below minimum for age $c_{\min}(t)$, the chick dies ($c(t)=0$).

$$c' = \begin{cases} c_{\max}(t + \Delta t) & \text{if } (\gamma + k_p) > (x_c(t, \Delta t) + y_c(t, \Delta t)) \\ c(t) + \lambda(\gamma + k_p - x_c(t, \Delta t)) & \text{if } x_c(t, \Delta t) < (\gamma + k_p) < y_c(t, \Delta t) \\ c(t) - (x_c(t, \Delta t) - \gamma - k_p) & \text{if } (\gamma + k_p) < x_c(t, \Delta t) \\ 0 & \text{if } c' \leq c_{\min}(t + \Delta t) \text{ or } c(t) = 0 \end{cases} \quad (13)$$

The size of the meal delivered to the chick from the focal individual γ is recalculated in γ^* so that excess food is not delivered to the chick if it reaches maximum size for age.

$$\gamma^* = \begin{cases} x_c(t, \Delta t) + y_c(t, \Delta t) - k_p & \text{if } (\gamma + k_p) > (x_c(t, \Delta t) + y_c(t, \Delta t)) \\ \gamma & \text{if } (\gamma + k_p) < (x_c(t, \Delta t) + y_c(t, \Delta t)) \\ 0 & \text{if } \gamma^* < 0 \end{cases} \quad (14)$$

The amount of krill needed to cover total metabolic costs of the focal individual, $x_f(t_s, t_n)$ in g krill, for time t_s hours at sea and t_n hours at the nest is

$$x_f(t_s, t_n) = \beta^{-1}(m_f(1)t_s + m_f(0)t_n) \quad (15)$$

where $m_f(1)$ are metabolic costs at sea, $m_f(0)$ are metabolic costs at the nest, and β is assimilation efficiency of krill into metabolic energy.

The cost of storing fat $y_f(\Delta t)$ for the focal individual is calculated in grams of krill, and is limited by the maximum amount that can be contributed to stores each time step Δf_{\max} .

$$y_f(\Delta t) = \lambda^{-1}(\Delta f_{\max} \Delta t) \quad (16)$$

The size of the focal individual's reserves will increase or decrease depending on whether the amount of krill left in its stomach after feeding the chick ($k_f - \gamma^*$) is enough to cover metabolic costs and storage costs as described in the previous equations. The focal individual cannot grow larger than f_{\max} , or at a rate faster than Δf_{\max} , and will die ($f(t)=0$) if body weight falls below minimum f_{\min} .

$$f' = \begin{cases} \min[f_{\max}; (f(t) + \Delta f_{\max} \Delta t)] & \text{if } (k_f - \gamma^*) > (x_f(t_s, t_n) + y_f(\Delta t)) \\ f(t) + \lambda(k_f - \gamma^* - x_f(t_s, t_n)) & \text{if } x_f(t_s, t_n) < (k_f - \gamma^*) < (x_f(t_s, t_n) + y_f(\Delta t)) \\ +y_f(\Delta t) & \\ f(t) - (x_f(t_s, t_n) - (k_f - \gamma^*)) & \text{if } (k_f - \gamma^*) < x_f(t_s, t_n) \\ 0 & \text{if } f' \leq f_{\min} \text{ or } f(t) = 0 \end{cases} \quad (17)$$

2.2.4. Chick mortality/fledging and abandonment

If either parent abandons during the guard stage, the chick will die (Table 4). If the focal individual chooses to abandon during the crèche stage, survival depends on the current weight of the chick and the probability of the partner abandoning, which both affect whether the chick will starve. If the partner does not abandon, chick survival is calculated by the probable size of total meals delivered to the chick by the partner until the end of the crèche stage.

A chick may die at any time if its energy reserves fall below $c_{\min}(t)$. Likewise, the focal individual may die if its reserves fall below f_{\min} .

In the first run of the model, if the focal individual abandons at time t , we assume that the probability $P_{k_p}((T - t), k_p)$ that the partner brings back a total meal size of k_p g krill over the time $(T - t)$ is zero. In subsequent runs of the model, we adjust this probability based by counting and averaging meal sizes delivered by the partner over this time, creating a cumulative probable total meal size from 1000 forward runs of the model.

The probability that the partner abandons between time t and $t + t_s$ is $P_a(t, t_s)$. For the first run of the model, we set $(P_a(t, t_s) = 0.0001$ for all t and $t_s = 1$ to t . We then record when the focal individual abandons and create a cumulative probable abandonment over time from 1000 forward runs of the model. These values make $P_a(t, t_s)$ for the following run of the model, when the partner is making decisions.

2.2.5. Parameter estimation

We run the model for a total of 60 days, but take results only for the first 46 days. The time considered is the combined time for the guard and crèche stages, approximately 21 and 25 days respectively, or 46 days total (Ainley et al., 1983).

The main prey of Adélie penguins is krill (Trivelpiece et al., 1987; Lishman, 2009) with a mean energy content of 4.35 kJ g^{-1} (Croxall et al., 1984). The assimilation efficiency of penguins eating krill is 0.75–0.8 for each gram of krill ingested (Wiens, 1984; Kooyman et al., 1982), so we use assimilation efficiency $\beta = 0.8$ in the current model. Adult Adélie penguins (4.2 kg) need $17.4 \text{ g krill h}^{-1}$ on land, $21.5 \text{ g krill h}^{-1}$ for resting in water and $31.5 \text{ g krill h}^{-1}$ when traveling at sea (Culik and Wilson, 1991). If Adélie penguins spend 35% of time resting at surface (Wilson et al., 1989b) this equates to $28 \text{ g krill h}^{-1}$ at sea, $17.4 \text{ g krill h}^{-1}$ on land ($x_f(1)$ and $x_f(0)$ respectively in the model see Table 2).

We separate the daily energy requirements of the chick into requirements for growth and maintenance, based on Croll and Tershy (1998). The metabolic requirement $x_c(c(t), \Delta t)$ in g krill for a chick of mass $c(t)$ per model time step of 4 h is

$$x_c(c(t), \Delta t) = \beta^{-1} 32.17 c(t)^{0.947} \Delta t \quad (18)$$

We use the proportion $\lambda = 0.75$ to convert consumed krill into penguin growth, based on the energy content of krill, 4.35 kJ g^{-1} , and the energy content of dry penguin tissue,

23.4 kJ g⁻¹, and the water content in penguin tissue of around 75% ($\lambda = 4.35/23.4/0.25 = 0.744$) (Croll and Tershy, 1998).

Maximum body weight of chicks for age $c_{\max}(t)$ is based on chick weights in the field, where Adélie chicks from single broods grow to around 75% of adult weight, 3500 g, around 40 days after hatching (Volkman and Trivelpiece, 1980; Ainley and Schlatter, 1972). Thus we set

$$c_{\max}(t) = \begin{cases} \frac{t}{40} 3500 & t \leq 40 \\ 3500 & t > 40 \end{cases} \quad (19)$$

2.2.6. Fitness for crèche and guard stages

We define fitness during the crèche and guard stages by

$$\Phi(f, c, a, t) = \begin{cases} \text{maximum expected value of current and expected future} \\ \text{reproductive success for the focal individual} \end{cases} \quad (20)$$

The final time T specifies the time at which the chick fledges. We define the fitness at the final time T to be a combination of current $c(T)$ and expected future $f(T)$ reproductive success as follows

$$\Phi(f, c, a, T) = \frac{c(T)}{c_{\max}(T)} + \rho \frac{f(T)}{f_{\max}(T)} \quad (21)$$

We run different values of ρ to test the relative difference in investing in the growth of the chick ($\rho \leq 1$, invest in current reproductive effort) compared to investing in own growth ($\rho > 1$, invest in future reproductive effort). We test $\rho = 1, 2, 4$ and 8.

There are two decisions to choose from each time step, to abandon V_{abandon} or to continue foraging V_{forage} , with the latter being broken into two further decisions of upper limit in trip length S , and what amount of stomach contents γ to feed the chick.

The focal individual will choose the action which leads to maximum value of fitness for the current set of state variables.

$$\Phi(f, c, a, t) = \max(V_{\text{forage}}; V_{\text{abandon}}) \quad (22)$$

$V_{\text{forage}}(f, c, a, t)$ is the value of foraging during the guard stage given that the partner has not abandoned yet ($a = 0$) for time t_s with foraging reward k_f , returning to the nest, feeding the chick the amount γ from the total available k_f . The focal individual waits at the nest for a maximum time of 36 h, after which, if the partner does not return, the focal individual will abandon. There is a probability that the partner will abandon during the time t to $t + t_s + t_n$, specified by $P_a(t, t_s + t_n)$. The fitness value resulting from this decision depends on how much food is brought back given maximum time away S , and whether or not the partner also returns with a meal in this time. If the partner abandons during the guard stage, the chick dies and therefore the focal individual must abandon $a = 3$.

$$V_{\text{forage}}(f, c, 0, t) = \max_S \sum_{t_s=1}^S \sum_{k_f=1}^{k_{\max}} P_{k_f}(S, t_s, k_f) \max_{t_n} * (P_a(t, t_s + t_n) \times [\max_{\gamma} \Phi(f', 0, 3, t + t_s + t_n)] + (1 - P_a(t, t_s + t_n)) \times [\max_{\gamma} \sum_{k_p=1}^{k_{\max}} P_{k_p}(t_n, k_p) \Phi(f', c', 0, t + t_s + t_n)]) \quad (23)$$

where $f = f(t + t_s + t_n)$ and $c' = c(t + t_s + t_n)$.

Next, we define the value of foraging during the crèche stage given that the partner has not abandoned yet ($a = 0$) for time t_s with return k_f , returning to the nest, feeding the chick γ g krill at the nest for one time step $V_{\text{forage}}(f, c, 0, t)$. There is a probability that the

partner will abandon during the time t to $t + t_s + 1$, specified by $P_a(t, t_s + 1)$. The fitness value resulting from this decision depends on how much food is brought back given upper limit in trip duration S , and whether or not the partner also returns with a meal in this time.

$$V_{\text{forage}}(f, c, 0, t) = \max_S \sum_{t_s=1}^S \sum_{k_f=1}^{k_{\max}} P_{k_f}(S, t_s, k_f) * (P_a(t, t_s + 1) \times [\max_{\gamma} \Phi(f', c', 1, t + t_s + 1)] + (1 - P_a(t, t_s + 1)) \times [\max_{\gamma} \sum_{k_p=1}^{k_{\max}} P_{k_p}(t_s + 1, k_p) \Phi(f', c', 0, t + t_s + 1)]) \quad (24)$$

where $f = f(t + t_s + 1)$ and $c' = c(t + t_s + 1)$.

Next, we define the value of foraging during the crèche stage given that the partner has abandoned ($a = 1$) for time t_s with return k_f , returning to the nest, feeding the chick γ g krill over one time step $V_{\text{forage}}(f, c, 1, t)$. The fitness value resulting from this decision depends on how much food is brought back given max time away. The partner has abandoned and so there is no chance that it will return to feed the chick.

$$V_{\text{forage}}(f, c, 1, t) = \max_S \sum_{t_s=1}^S \sum_{k_f=1}^{k_{\max}} P_{k_f}(S, t_s, k_f) \times (\max_{\gamma} \Phi(f', c', 1, t + t_s + 1)) \quad (25)$$

where $f = f(t + t_s + 1)$ and $c' = c(t + t_s + 1)$.

The value of the focal individual abandoning the chick $V_{\text{abandon}}(f, c, 0, t)$ given that the partner is still foraging ($a = 0$) depends on the probability that the partner will abandon during the time t to T , specified by $P_a(t, T - t)$, and whether the chick has enough food to survive until time T .

$$V_{\text{abandon}}(f, c, 0, t) = P_a(t, T - t) (\Phi(f', c', 3, T)) + (1 - P_a(t, T - t)) \times (\sum_{k_p=1}^{k_{\max}} P_{k_p}(T - t, k_p) \Phi(f', c', 2, T)) \quad (26)$$

where $f = f(T)$ and $c' = c(T)$.

Finally, the value of the focal individual abandoning the chick during the crèche stage given that the partner has already abandoned ($a = 1$) is

$$V_{\text{abandon}}(f, c, 1, t) = \Phi(f', c', 3, T) \quad (27)$$

where $f = f(T)$ and $c' = c(T)$.

2.2.7. Model runs

We designed the model using the C programming language. We run the backward simulation of the model through 20 different levels of food quality level z and different terminal rewards (by adjusting ρ). We run the forward simulation for 1000 individual penguins. For each run of the forward simulation we record number of chicks surviving to fledging, fledging weight, parent weight and survival, abandonment, chick death, and total krill consumed by the focal individual.

Next, we count and average the results of the forward simulation to create a probability of parent abandonment over time. We also average the size of meals and length of foraging trips undertaken

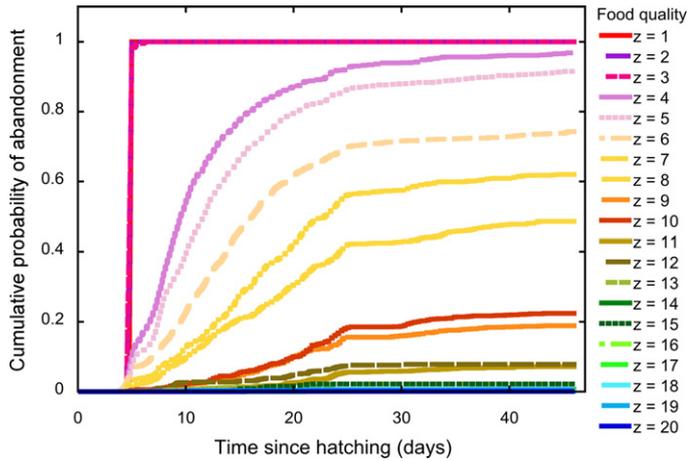


Fig. 4. Cumulative proportion of 1000 parents abandoning over time, where the crèche stage starts at day 22, for different levels of food quality z (see Eq. (2)).

by the focal individual. These averages are converted into probabilities that are used for the next backward run of the life-history model (Fig. 1). This is a type of game simulation, using consecutive runs of the life-history model. We present results after 50 iterations of the model, when the difference between probability of parent abandonment in successive iterations decreased rapidly enough to assure convergence to an evolutionary stable strategy (McNamara et al., 1997).

3. Results

We show the cumulative probability that the focal individual will abandon at any time, given 20 different levels of patch quality, after allowing the model to reach a stable solution (Fig. 4). As the likelihood of finding a high quality patch increases, the probability that the parent will abandon is delayed through time, so that by quality level $z = 12$ and higher there is little chance of abandonment.

The proportion of chicks that survive to fledging as a function of local food availability approximates a sigmoid curve (Fig. 5). We predict that all chicks die before fledging when the probability of finding a high quality patch of food in one time step is below 0.01, and around 100% when the same probability is above 0.03. In addition, chick fledging weight is constant at maximum (3500 g) for

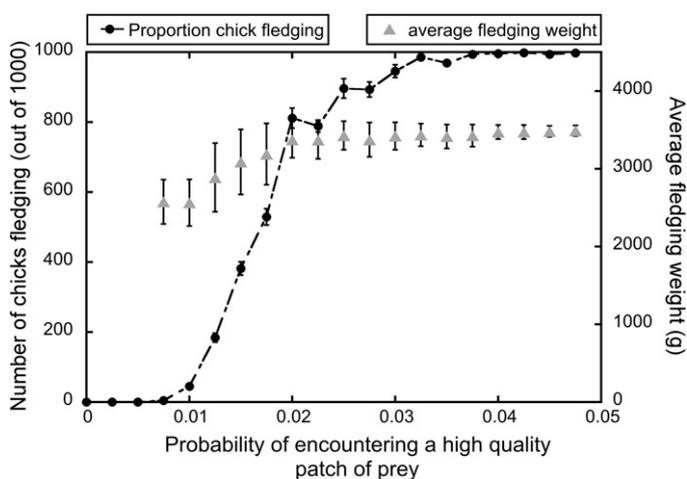


Fig. 5. Proportion of 1000 chicks reaching fledging alive (circles) and average fledging weight in g (\pm SD) of these surviving chicks (triangles) for different levels of food availability, characterized by the probability of encountering a high quality patch while foraging.

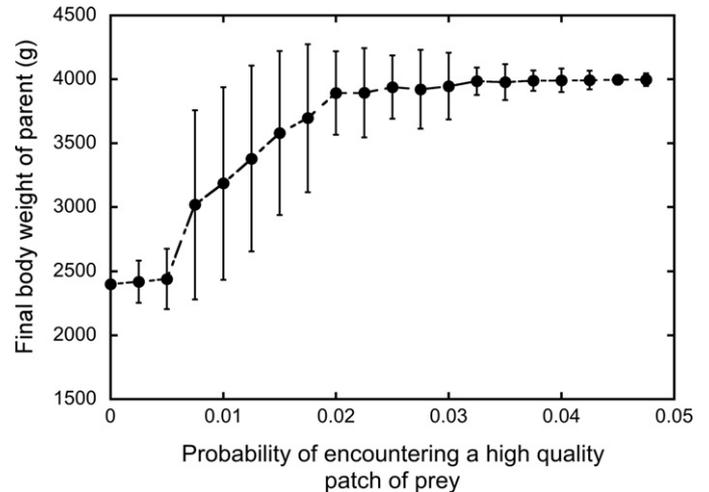


Fig. 6. Final weight of the parent at the end of the crèche stage, day 46, in g (\pm SD) for different levels of food availability, characterized by the probability of encountering a high quality patch while foraging.

probability of high quality food at 0.02 and above, but is more variable and decreases to around 2500 g as food availability decreases.

Average final body weight of the focal individual is lowest when the probability of finding a high quality patch is < 0.01 (Fig. 6). Variability in focal individual body weight is highest for medium levels of prey quality, decreasing when probability of finding a high quality patch is around 0.02. Above this point, body weight is around the maximum of 4000 g and variability is low.

The total amount of krill eaten by the focal individual is close to zero when the prey environment is of lower quality, increasing rapidly to a maximum value with increasing food availability (Fig. 7). Like chick survival and focal individual body weight, this curve is roughly sigmoidal, with high variability for a medium quality prey environment (probability of finding high quality patch is 0.01–0.03).

The effect of parent age, by modifying the terminal reward function, on chick survival has a larger effect in medium levels of food quality (Fig. 8). When the probability of finding a high quality patch is medium (0.01–0.03), the strategy of investing in future reproductive fitness leads to the fewest chicks fledging, although the effect

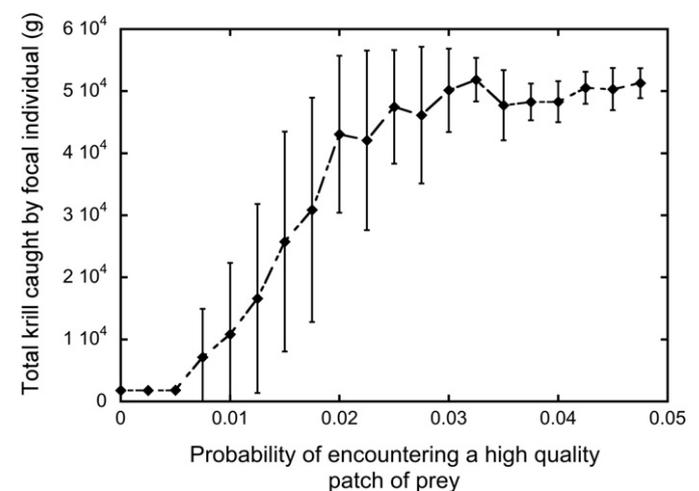


Fig. 7. Total amount of krill consumed in g (\pm SD) by one parent over the guard and crèche stage compared to level of food availability, characterized by the probability of encountering a high quality patch while foraging.

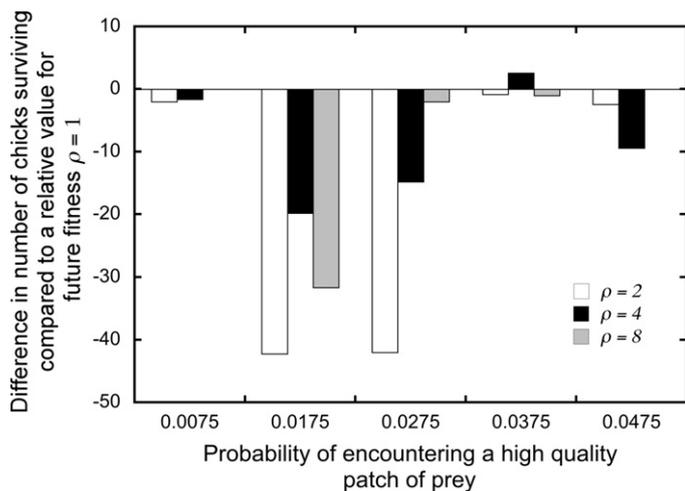


Fig. 8. Difference in chick survival as the relative value for future fitness (ρ) is increased from 1 to 8 (Eq. (21)) for different levels of food availability, characterized by the probability of encountering a high quality patch while foraging.

is not very large (40 out of 1000). In a higher quality prey environment (>0.03 chance of high quality patch) the strategy does not have a noticeable effect.

4. Discussion

One of the main goals of this model was to estimate the response of penguin breeding success to changes in krill availability. At low krill availability, when probability of encountering a high quality patch is low, no chicks survive to fledging. However there is a threshold amount of prey availability above which the survival of chicks to fledging rapidly increases until 100% of chicks survive to fledging. In observational studies of Adélie penguins, Watanuki et al. (1993) found that chicks had poor survival in years of low food availability compared to years of high food availability. Evidence of a threshold in food availability is found in other studies that report consistencies in Adélie chick and adult weight despite large differences in krill availability (Salihoglu et al., 2001; Prévost and Sapin-Jaloustre, 1965; Culik and Wilson, 1991), perhaps indicating that although variable, prey availability during the study years was above the threshold.

We estimate that the average weight of the adult penguin at chick fledging is positively correlated with krill availability, with parents remaining at maximum size for very high krill availability, but dropping to a variable and low weight with decreasing krill availability. Some studies indicate the adult Adélie penguins are quite robust to changes in their prey environment while breeding (Salihoglu et al., 2001; Prévost and Sapin-Jaloustre, 1965; Culik and Wilson, 1991), while other studies suggest that the parents keep up the same level of meal delivery to the chick, at their own cost (Takahashi et al., 2003) even as chick demands increase through the breeding cycle (Chappell et al., 1993a,b). This is the case for other species, with the condition of female fur seals at parturition and average foraging trip duration reflecting prey availability (Costa et al., 1989). We predict that parents will cover their own needs before those of the chick. Although variable, parents maintain a weight that keeps them alive at low krill availability, the same level at which <5% of chicks survive to fledging.

The other main goal of our work was to estimate the shape of the curve describing total amount of krill eaten versus krill available around a penguin breeding colony. We estimate this curve by averaging the sum of the total prey eaten by 1000 individuals over time, simulated during the guard and crèche stage, and find that the shape of the curve approximates a Holling Type III functional

response. This type of response is classically explained by prey switching or because of a higher predator density due to increased prey density. However, in the current model, this response occurs because at low krill availability, the parent lets the chick starve, whereas at high availability, the parent must balance its own needs with those of the chick; the parent must eat enough krill to cover its own daily energy requirements along with the energy requirements for maintenance and growth of a chick (Culik and Wilson, 1991).

The ability of the focal individual to choose abandonment at any time has not been included previously in a predator/prey model with this level of foraging detail. By including the decision to abandon, we were able to examine the mechanism by which a parent may invest relatively in current versus future fitness. We predict that the timing of abandonment is not related to breeding stage, i.e. guard versus crèche stage, but more related to the total time since the chick hatched. No parent abandoned earlier than 8 days after chick hatching. Our results contradict studies that suggest nest abandonment occurs solely when a fasting bird runs out of energy before its mate returns during the guard stage (Ainley et al., 1983; Davis and McCaffrey, 1986; Trivelpiece and Trivelpiece, 1990; Watanuki et al., 1993; Vleck et al., 1980). In our model, abandonment occurred for this reason, but also occurred during the crèche stage, when neither parent needs to fast at the nest to guard the chick. Spurr (1975) noted the tendency for Adélie parents to abandon around 2 weeks prior to fledging, which may possibly due to this being the period of highest demand from the chick.

We found a difference in chick survival due to changes in the relative reward for current versus future reproductive success, but only for medium levels of food availability. Reproductive performance, or competence, improves with age in birds (Forslund, 1995). The many hypotheses on why this may occur can be divided into three main groups: the progressive appearance of a phenotype; age-related improvement in competence; and optimization of reproductive effort (Forslund, 1995). Our model allows us to test the latter two of these hypotheses. We can correlate the effects of an improvement in competence with the results from an increase in prey availability, because a more competent forager would potentially find it easier to locate higher quality patches of prey, leading to increased foraging gain. We tested optimization of reproductive effort by varying the terminal reward, and the relative contribution to fitness for adult versus chick survival and body weight. By decreasing relative optimal value given to parent survival we represent an older parent and vice versa for a younger parent. Younger adults may invest more in themselves at the cost of their offspring, e.g. arctic terns (Monaghan et al., 1989) and puffins (Barrett and Rikardsen, 1992), compared to older adults that may work harder to ensure the survival of a chick (Burger and Piatt, 1990). We found a barely noticeable difference in chick survival due to optimization of reproductive effort, suggesting that larger observational correlations in age and chick survival may be due to other reasons, such as increased competence.

5. Conclusions

We predict that the shape of the curve describing krill eaten versus krill available around a penguin breeding colony approximates a Holling Type III functional response. In all model scenarios, as prey availability increased, a threshold was reached where probability of chick survival increased dramatically. At low krill availability, chicks did not survive because parents were covering their own needs first. Finally, we found that the probability of finding a high quality versus a low quality patch was an extremely useful, and relatively simple, measure of krill availability. Quantifying the quality of a prey environment rather than the overall amount of prey could be useful in future empirical studies.

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