

1 A state dependent life-history model of provisioning in
2 penguins

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8

9 **Abstract**

10 There is a wealth of information detailing the behavior of penguins in the Southern Ocean
11 during breeding. However, we have less of an idea how their behavior is affected by changes
12 in prey availability. The aim of management models in this region is to allocate catch
13 limits for one of the main prey species for penguins, Antarctic krill (*Euphausia superba*),
14 in defined units around major breeding colonies. Our main goal is to estimate the shape
15 of the functional response of penguins and krill, key information that is currently missing
16 from management. We use data from field studies on penguins and acoustic readings
17 of krill swarms to characterize a state-dependent life-history model where two penguin
18 parents forage to provision a chick to fledging. Each individual parent makes decisions
19 based on quantified estimates of state dynamics, a probabilistic distribution of how their
20 partner is behaving, and a need to maximize fitness. We predict that the shape of the
21 curve describing total amount of krill eaten versus krill available around a breeding colony
22 approximates a Holling Type III functional response. Our broader prediction is that the
23 age of parents can influence chick survival, but only at medium food levels.

24

25 **Introduction**

26 Penguins can provide valuable information about the marine environment they inhabit,
27 and are good subjects for investigations of parental care in monogamous, long-lived
28 species. This is because they are abundant and colonial, generally return to the same
29 place to breed (Lewis et al., 2006), and the adults are easy to individually mark and
30 observe (Chappell et al., 1993a), being large enough to carry technological instruments
31 (Jouventin et al., 1994). In addition, many aspects of their energetics, life history and
32 behavior have been described (Chappell et al., 1993a).

33

34 Many species of penguin in the Southern Ocean rely on krill, *Euphausia superba*, for
35 their breeding success each summer. Krill biomass on a scale relevant to predators fluc-
36 tuates widely from year to year (Mackintosh, 1972, 1973; Murphy et al., 1998), with
37 predator populations often linked to krill abundance on a local scale (Croxall et al.,
38 1988, 1999; Atkinson et al., 2001; Reid and Croxall, 2001; Reid et al., 2002). Fluctuations
39 in krill are due to changes in environment, with current strength, ice cover, and water
40 temperature being linked to krill recruitment and abundance in particular regions of the
41 Southern Ocean.

42

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

50 controversy over this certification because of the issue of indirect effects of the fishery on
51 predators (www.nytimes.com/2010/06/23/science/earth/23krill.html)

52

53 The CCAMLR is moving towards management in Small Scale Management Units (SS-
54 MUs, Constable and Nicol, 2002; Hewitt et al., 2004), because of the potential for com-
55 petition between the fishery and krill predators at a local scale around predator breeding
56 colonies. The management units are located within key areas in the Southern Ocean where
57 krill are abundant around predator breeding colonies and the fishery is present. Among
58 the questions related to management in small scale units are: a) how should the overall
59 catch limit for an area be subdivided among the SSMUs, b) how should the development
60 of the fishery be limited until this decision is made, and c) which of predator demand,
61 krill biomass, or demand minus biomass are most important in effective management of
62 krill? There are a number of models used to explore the question of how to allocate catch
63 among the SSMUs (KPFM, Hill et al., 2007*a,b*). One of the goals of our work is to qualify
64 the component of mortality relating to predation from land-based predators, so that this
65 information may be used in a management model, with our focus on two questions: 1)
66 What is the relationship between the abundance of krill and the consumption of krill by
67 predators (the predator functional responses) and 2) what is the relationship between the
68 abundance of krill and the reproductive success of predators (the predator reproductive
69 response)

70

71 There are various studies on penguin abundance and population dynamics in differ-
72 ent regions of the Southern Ocean. However, there is little understanding of how these
73 dynamics are linked to changes in local prey availability. One way to examine this link-
74 age is through penguin behavior and breeding ecology. Penguins are an altricial species,

75 meaning that the young needs nourishment and protection directly after hatching. In a
76 challenging environment, such as the Southern Ocean, breeding success for penguins re-
77 quires a contribution from both parents to ensure that the chick can reach independence
78 within limited time and resources, for example reaching independence before the onset of
79 winter (Davis et al., 1989), or before parental reserves reach a critical low. Mass loss in
80 altricial species may be necessary, even adaptive (Barlow and Croxall, 2002; Cresswell
81 et al., 2007; Green et al., 2007) down to a threshold point (Robin et al., 1998), to maintain
82 the brooding parent through a period when nestlings require heat, insulation and food
83 (Moreno, 1989). However, many questions arise in relation to how much each parent
84 contributes to rearing the chick, how much weight loss each parent incurs as a cost, and
85 whether the two sexes respond to the provisioning behavior of the other. In considering
86 the behavior of both the male and the female during chick rearing, and looking at how
87 this is affected by changes in local prey availability, we are therefore able to better predict
88 how these animals may be affected by a changing prey environment, and we can examine
89 fundamental questions about provisioning behavior and parental conflict in a putatively
90 monogamous species.

91

92 Conflict between parents over care of young arises because the success of the young
93 generally depends on the care from both parents, whereas the cost to a parent depends on
94 its own effort (Trivers, 1972; Parker et al., 2002; Houston et al., 2005). For each parent
95 there is a trade-off between the amount of resources invested in current offspring versus
96 the amount that remains for their survival and future reproductive investment (Williams,
97 1966; Clutton-Brock, 1991). An inverse relationship between current reproductive success
98 and future parental survival has been a key assumption in life-history theory (Fisher,
99 1930; Williams, 1966); however, this is not necessarily the case (Bryant, 1979). In many

100 species, individuals show flexibility in the pattern of parental investment in response to
101 both natural and experimental changes in conditions (Wright, 1990). Allocation of in-
102 vestment may also change as the demands of the growing chick change (Tinbergen, 2000),
103 and may be fundamentally different for the male and female parent because of divergent
104 interests in reproduction where traits favored by one sex might be costly to the other
105 (Chapman et al., 2003).

106

107 In theory, each sex should generally gain if the other works harder because the evo-
108 lution of increased care by one sex will enable reduced care in the other (Westneat and
109 Sargent, 1996; Wachtmeister and Enquist, 2000; Royle et al., 2002). This raises questions
110 about how the parents negotiate with each other, such as whether one parent compensates
111 for another with a lower provisioning rate and if there are particular rules for negotiation
112 between the parents (Houston and Davies, 1985; Houston and McNamara, 1999; Houston
113 et al., 2005). Barta et al. (2002) theorized that the female may handicap herself to get
114 the male to care, even to the extent that she would desert the nest to trigger a response
115 in the male. Thus, in some circumstances it is possible that the young would have had
116 better care with only a single parent providing for it (McNamara et al., 2003).

117

118 Experimental manipulation of breeding birds has been used to answer some of the
119 questions relating to parental conflict. Experiments have consisted of: (A) increasing
120 the costs of rearing, for example by placing small weights on the legs of Antarctic petrel
121 (Sæther et al., 1993) or European starlings, or; (B) decreasing the costs of rearing, by
122 removing eggs from breeding kittiwakes (Golet and Irons, 1999) to see how chick rear-
123 ing affects body condition, or; (C) increasing costs and reducing brood at the same time
124 (Wright and Cuthill, 1989). Less manipulative observations, such as assessing female con-

125 dition of great tits at different stages of chick rearing (Tinbergen, 2000), can also provide
126 us with key information about parental provisioning. Adélie, penguins show consistent
127 sex differences in foraging trip duration, feeding locality and diet at different locations
128 and breeding seasons (Clarke et al., 1998). Volkman et al. (1980) demonstrated that
129 male gentoo penguins consumed 23 percent more fish than females, despite a lack of sex
130 difference in foraging trip duration. Differences between the behavior of the sexes may
131 also depend on the phase of chick rearing, with female Adélie penguins having longer
132 trips and delivering larger meals than males during the guard stage of breeding (Clarke
133 et al., 1998). These experimental studies are vital, providing us with valuable information
134 about the respective breeding systems that they describe. Further, when used in combi-
135 nation with modeling, it is possible to explore the mechanisms behind these observations
136 in greater detail, and to associate different patterns in behavior with different outcomes
137 in breeding. Thus, it may be possible to predict the likely breeding success of a given
138 species in a particular location based on a satellite track of its movements.

139

140 Models have greatly enhanced our understanding of reproductive behavior, including
141 mechanisms underlying the evolution of parental conflict (Alonzo and Warner, 2000; Dall
142 and Boyd, 2002; Houston et al., 2005). Many of these models are purely theoretical, not
143 relating to any particular species (Winkler, 1987; Székely et al., 2000), or considering
144 reproductive success in terms of the total number of offspring in a population (Davis
145 et al., 1999), rather than at the individual level. Winkler and Adler (1996) investigate
146 chick demands in detail using a state-dependent life-history model, but do not examine
147 parental foraging trips. An individual-based model by Salihoglu et al. (2001) examines
148 mechanisms that potentially underlie observed constancy in fledging weight in Adélie pen-
149 guin chicks in spite of large variability in Antarctic krill availability. The aim of our work

150 is to create a state-dependent life-history model, using energy as currency, that could be
151 applied to a number of different krill-reliant penguin species in the Southern Ocean; we
152 apply it to the Adélie penguin, for which we can reference a large amount of data from
153 many different studies.

154

155 There are 17 different penguin species in the world, and all go through three differ-
156 ent stages of breeding. The first stage is incubation, when parents must guard the egg
157 and keep it warm. The second is the guard stage, when the rapidly growing chick needs
158 protection, food and warmth. The final is the creching stage, when chicks from different
159 parents gather together for protection against predators, while being fed intermittently
160 by the parents. During these distinct stages of breeding, the parents undertake behavioral
161 roles that vary according to sex and species. Out of the combination of tasks that the
162 male and female undertake during breeding, there are three different strategies for all
163 penguins (Table 3), but we focus on the third because it is the Adélie penguin strategy.
164 We do not predict penguin behavior during incubation, because in strategy 3 the male
165 sits alone at the nest for the entire incubation stage while the female forages at sea and
166 does not return to the nest. In addition, we assume that the parents are only raising one
167 chick. An Adélie female penguin raises on average 1.3 (Chappell et al., 1993a) to 1.6
168 +- 0.5 eggs to crèche, with the majority of egg loss occurring during the incubation stage
169 (Ainley et al. 1983). We assume that the parents are only raising one chick because the
170 majority of other penguin species only raise one chick to independence, making it easier
171 to compare between the case study and other species.

172

173 In summary, the main motivation for this work is to use life history theory to gain
174 a better understanding of how a fishery for krill near a penguin colony may affect the

175 survival of the chick and of both parents. In particular we aim to examine how small
176 changes in the timing of fishing, the amount of krill taken, and the distance of the fishery
177 from a colony can affect breeding success. Previous models in this area have addressed
178 this problem, but from different angles. Cresswell et al. (2007) consider the effects of krill
179 depletion, but only during the guard stage and did not consider chick death or parental
180 abandonment. Similarly, a model by Mangel and Switzer (1998) examined the effects of
181 the krill fishery on expected reproductive success and parental survival, but did not con-
182 sider the foraging behavior of the parents. Using a higher level of detail in the behavior
183 of the parents will allow us to tease out any patterns in behavior that consistently lead to
184 scenarios of nest abandonment or death. We can also begin to define rules about how krill
185 depletion affects penguin behavior. For example, are parents likely to work harder when
186 prey is harder to find (invest in current reproductive success), or put in the same amount
187 of foraging effort and feed the chick less (invest in future reproductive success)? These
188 rules allow us to make better predictions about how potential krill depletion will affect
189 breeding success for a particular species of penguin. Through the model we also hope to
190 address some of the broader theoretical questions, such as do parents compensate, and
191 what affects the relative contribution to future versus current reproduction for the parent.
192

193 **Methods**

194 The model is a game using consecutive runs of a state-dependent life-history model to
195 predict the behavior of one of the parents during two stages of breeding. We call the
196 decision-making parent the 'focal individual', and the other parent the 'partner'. The
197 focal individual makes decisions based on a need to maximize fitness, given a probabilis-
198 tic distribution of how the partner is behaving. The focal individual always forages in a

199 prey environment where likely time spent foraging and amount of food brought back is
200 predetermined by a separate 'single-trip' foraging model. In the first run of the model,
201 the probabilistic distribution of the partner is random. The focal individual behaves in
202 response to the probabilistic distribution of the partner. At the end of this run, the be-
203 havior of the focal individual is recorded and used to parameterize the next run of the
204 model, in which the partner makes decisions based on the probabilistic distribution of
205 the focal individual. We repeat this process until the model finds an evolutionary stable
206 solution (Figure 1 A).

207

208 In this section, we first describe the 'single trip' foraging model and then the game
209 model, detailing the behavioral decisions chosen by the focal individual each time step, the
210 state variables that determine and are affected by these decisions, all other parameters in
211 the model, and show how we calculate fitness with the dynamic programming algorithm.
212 The time step of the model is 4 hours.

213

214 **Single trip foraging model**

215 In the single trip foraging model, the focal individual chooses from one of three behav-
216 ioral decisions each time step. Decisions occur at sea, and we assume that a penguin still
217 making decisions has not yet foraged from a patch of food, i.e. a swarm of krill. If a patch
218 is encountered, the penguin forages to maximize the gain and then returns to the nest.
219 Decisions are to travel further from the nest, to travel back towards the nest, or to hunt
220 for food at the current radius from the nest. We assume that the individual only forages
221 from one patch of food during a foraging trip.

222

223 Each unit of time t represents 8 minutes, in which the penguin can travel 1 km at
 224 7.5 km h^{-1} (either towards or away from the nest) based on a range of swimming speeds
 225 recorded for Adélie penguins of 2 m s^{-1} (or 7.2 km h^{-1}) (Culik and Wilson, 1991; Culik
 226 et al., 1994) to 3.7 m s^{-1} (or 13.3 km h^{-1}) (Hui, 1987). We vary the final time T from 6
 227 to 36 hours, so that the result is a representation of how much food a foraging individual
 228 can collect, and how long it forages for, given the maximum time T at sea. This result
 229 is used in the game model, where the decision-making individual chooses a time T at sea
 230 that maximizes fitness. At elapsed time t , the amount of time that the penguin can stay
 231 in a patch of prey is at most $T - t_c(r) - t$, where $t_c(r)$ is the commute time back to the
 232 nest from radius r .

233

234 We separate the foraging process into two steps: the probability of encountering a
 235 patch of prey in one period of time $P_f(r)$; and the probability that once located, the rate
 236 of gain from a given patch is ϵ , specified by $P_g(\epsilon)$. There is very little data on patch
 237 quality, in terms of rate of gain, so we choose to parameterize the model in the simplest
 238 way, with the penguin either encountering a low quality patch, $\epsilon = 0.002$, or a high quality
 239 patch, $\epsilon = 0.02$. We run the model for different levels of food

240

$$P_g(z, \epsilon) = \Pr(\text{patch at radius } r \text{ has rate of gain } \epsilon \text{ depending on food level } z) \quad (1)$$

241

242

243 We vary the probability that once located, a patch is low quality $\epsilon = 0.002$, according
 244 to level of food in the environment z (for 20 levels of food) by the following.

245

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

246

247

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

249

250 The gain from a patch of prey $G(\epsilon, t_p)$ depends on the rate of gain from a patch
251 ϵ , the amount of time spent in the patch t_p , and the maximum possible gain. We set
252 $G_{\max} = 2000$, based on recorded stomach contents delivered to chicks for Adélie penguins
253 of up to 1000g (Trivelpiece et al., 1987), which does not include digestion at sea. Gain
254 varies according to the following

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

255

256

257 The probability of finding a patch of prey in one time step $P_f(r)$ varies with radial
258 distance from the nest r and the rate of the mean number of patches per time step $\lambda(r)$.

259

$$P_f(r) = 1 - e^{-\lambda(r)} \quad (4)$$

260

261

262 Time to a new patch varies depending on $\lambda(r)$. We estimate the density of patches

263 in the environment from Tarling et al. (In Press), who measured prey density at three
 264 radial distances from shore (we assume the fourth value of near zero prey at nest) (Figure
 265 2). From the data, we approximate how the rate of patches encountered per unit time
 266 changes with radial distance from the nest (Figure 3). We convert the swarm encounter
 267 rate from the data into the mean number of patches per time step $\lambda(r)$ using a penguin
 268 swimming speed of 7.5 km h^{-1} .

269

270 We now set

271

$\Psi(r, t)$ = maximum return of krill from one foraging trip, given the
 current radial distance from the nest r and total time at sea so far t

272

(5)

273

274

275 If the individual chooses to travel further from the nest, the probability of finding a
 276 patch is reduced to $P'_f(r) = 0.6P_f(r)$ because the individual is less effective at searching
 277 during travel, and the fitness value of this decision $V_{out}(r, t)$ is

278

$$V_{out}(r, t) = \left(1 - P'_f(r)\right)\Psi(r + 1, t + 1) + P'_f(r)E_\epsilon \left[\max_{t_p} P_g(r, \epsilon)G(\epsilon, t_p) \right] \quad (6)$$

279

280

281 where E_ϵ denotes the expectation over the distribution on ϵ . If the individual encoun-
 282 ters a patch of prey, the penguin is still considered to be within the radial distance r
 283 rather than $r + 1$, and the rate of gain in this patch is drawn accordingly.

284

285 If the individual decides to travel back towards the nest, the probability of finding a
 286 patch is also reduced to $P'_f(r) = 0.6P_f(r)$ because the individual is traveling not search-
 287 ing, and the value of this decision $V_{in}(r, t)$ is the same as that for traveling away from the
 288 nest, except the radius r decreases by 1 unit if food is not encountered

289

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

290

291

292 If the individual decides to hunt for food at the current radius from the nest, the
 293 probability of finding a patch is $P_f(r) = 0.6$, and the fitness value $V_{hunt}(r, t)$ is

294

$$V_{hunt}(r, t) = \left(1 - P_f(r)\right)\Psi(r, t + 1) + P_f(r)E_\epsilon \left[\max_{t_p} P_g(r, \epsilon)G'(\epsilon, t_p) \right] \quad (8)$$

295

296

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

298

$$\Psi(r, t) = \max \left[V_{out}(r, t); V_{in}(r, t); V_{hunt}(r, t) \right] \quad (9)$$

299

300

301 We ran this model for 20 different levels of food availability, and for 6 total foraging
302 trip times ranging from a maximum 6 h trip to a maximum 36 h trip. To test food
303 availability we adjusted the quality of food encountered in each patch, not the probability
304 of finding a patch. This resulted in a distribution of probable food brought back and
305 foraging trip time depending on the maximum time that the model ran and the level of
306 food in the environment. we used this information in the game model, where the foraging
307 parent chooses a maximum trip time S that maximizes fitness according to the probable
308 amount of food brought back and time away. Here, we show an example of how foraging
309 reward and trip time change with S for food level 6 (Figure 4). We converted these
310 numbers into probabilities for each of the 20 food levels, and used these probabilities to
311 represent the foraging grounds in the game model.

312

313 **The main model**

314 **Breeding strategies**

315 We now explain the how the game model operates, first outlining the decisions that the
316 focal individual can choose at any time, then the state dynamics in the model, detailing
317 how chick abandonment and death occurs, we explain how we estimated values for pa-
318 rameters and finally how fitness is calculated.

319

320 **Decisions**

321 All decisions are made at the nest. During the guard stage, each time unit the focal
322 individual must choose to either forage at sea and return with a meal to feed the chick, or
323 to abandon the chick and spend the rest of the time at sea. If the focal individual decides
324 to forage, it must decide the optimal maximum time to forage at sea S and the optimal
325 amount of krill to feed to the chick γ . At sea, the distribution of possible foraging trip
326 times and meal sizes is determined by the single trip foraging model (described above).
327 After foraging, the focal individual will wait up to 36 h at the nest for the partner to
328 return, after which time it will abandon (Figure 5). If either parent abandons during the
329 guard stage, the chick dies.

330

331 During the creche stage, the focal individual has the same choice: to forage and feed
332 the chick, or to abandon the chick. The difference is that the focal individual does not
333 have to wait for the partner to return, so only stays at the nest for one time unit to feed
334 the chick. Also, if the focal individual chooses to abandon during the creche stage, the
335 chick will not necessarily die (see Table 4).

336

337 Given a particular maximum time at sea S , we compute the probability that the focal
338 individual will bring back a meal of size k_f after a time at sea of s time units. This
339 probability is $P_{k_f}(S, s, k_f)$

340

$$P_{k_f}(S, s, k_f) = \Pr(\text{focal individual returns after } s \text{ hours with } k_f \text{ g krill, given max time at sea } S)$$

(10)

341

342

343 Likewise, there is some probability $P_{k_p}(t_n, k_p)$ during the guard stage or $P_{k_p}((s+t_n), k_p)$
344 during the crèche stage that the partner will return after a particular time t_n or $(s + t_n)$
345 respectively with k_p g krill to feed the chick. Initially, there is an equal probability of close
346 to zero for every possible value of $P_{k_p}((s + t_n), k_p)$. On subsequent runs of the model, we
347 use the results from the forward iteration of the model (the behavior of the focal individ-
348 ual) to parameterize the backward iteration for the next run of the model.

349

350 State dynamics

351 First, we describe the total metabolic costs x_f for the focal individual for time s hours at
352 sea and t_n hours at the nest

$$x_f = m_f(1)s + m_f(0)t_n \quad (11)$$

353

354

355 where $m_f(1)$ are hourly metabolic costs at sea and $m_f(0)$ are metabolic costs at the
356 nest.

357

358 The size of the focal individual will increase or decrease depending on whether the
359 amount of krill left in its stomach after feeding the chick $(k_f - \gamma)$ is enough to cover
360 metabolic costs x_f as described in the previous equation (Figure 1 B).

361

362 Metabolic costs for the chick change depending on the chick's size and the time con-
363 sidered.

364

$$x_c(c, (s + t_n)) = 8.043c^{0.947}(s + t_n) \quad (12)$$

365

366

367 We demonstrate the dynamics of chick energetics using the following scenario, where
368 chick stomach contents and size change according to the size of meal from focal individual
369 and potential meal from the partner (Figure 1 C).

370

371 **Chick mortality/fledging and abandonment**

372 When the focal individual chooses to abandon, there is some probability that the chick
373 will survive to fledging (e.g. alive at the final time T) based on its current size, time to the
374 final time ($T - t$) and how often and how much the partner feeds the chick during this time.

375

376 At any time, even if the focal individual is still foraging, a chick of energy reserves c
377 may die after time $(s + t_n)$ from starvation depending on its metabolic rate $m_c(s + t_n)$.

378

379 In the first run of the model, if the focal individual abandons at time t , we assume
380 that the probability $P_{k_p}((T - t), k_p)$ that the partner brings back a total meal size of k_p
381 g krill over the time $(T - t)$ is zero.

382

383 In subsequent runs of the model, we adjust this probability based on how the focal

384 individual behaves (as described previously). If the focal individual chooses to abandon
385 in the guard stage, the chick dies. In the creche stage, the may die of starvation, but does
386 not die because of abandonment (see Table 4).

387

388 The probability that the partner abandons at time t is $P_{pabandon}(t)$. For the first
389 run of the model, we put in arbitrary values ($P_{pabandon}(t) = 0.0001$ for all t). We then
390 record when the focal individual abandons and create a probable abandonment from 1000
391 forward runs of the model. These values make $P_{pabandon}(t)$ for the following run of the
392 model, when the partner is making decisions.

393

394 **Parameter estimation**

395 Total time of the model is based on the combined time for the guard and creche stages,
396 or approximately 21 and 25 days respectively for guard and creche (Ainley and Sladen,
397 1983).

398

399 The main prey of Adélie penguins is krill (Trivelpiece et al., 1987; Lishman, 2009)
400 with a mean energy content of 4.35 kJ g^{-1} (Croxall et al., 1984). The assimilation
401 efficiency of penguins eating krill is 0.75 to 0.8 (Wiens, 1984) for each gram of krill in-
402 gested (Kooyman et al., 1982). Adult Adélie penguins (4.2 kg) need $17.4 \text{ g krill h}^{-1}$
403 on land, an extra $21.5 \text{ g krill h}^{-1}$ for resting in water and an extra $31.5 \text{ g krill h}^{-1}$ when
404 traveling at sea (Culik and Wilson, 1991). If Adélie penguins spend 35% of time resting
405 at surface (Wilson et al., 1989) this equates to $28 \text{ g krill h}^{-1}$ at sea, $17.4 \text{ g krill h}^{-1}$ on land.

406

407 We separate the daily energy requirements of the chick into requirements for growth

408 and maintenance. During the growth phase, we parameterize energy requirements based
409 on Croll and Tershy (1998). The requirement in g krill⁻¹ for a chick of mass c per model
410 time step of 4 h is.

$$x_c(c) = 32.17c^{0.947} \quad (13)$$

411

412

413 Energy requirements for growth depend on the size change, where growth = [(new
414 chick mass) - (old chick mass)]*(% dry tissue 25%)* (energy content of dry tissue 23.4
415 kJ dry mass⁻¹) (Croll and Tershy, 1998). The maximum size change possible is

416

$$\Delta c_{\max} = c_{\max}(t) - c \quad (14)$$

417

418

419 The cost of the size change is

420

$$y_g = 0.25\Delta c 23.4 / 4.35 = 1.34 * \Delta c \quad (15)$$

421

422

423 Conversely, if there is not enough krill to grow the chick to maximum size, we calculate
424 the size change

425

$$\Delta c = \lambda_c(\gamma - y_m(c))/0.25 * 4.35/23.4 \quad (16)$$

426

427

428 or if there is not enough krill to even cover metabolic costs, the chick can use its stores

429

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

433

434 By the time chicks are 2-3 weeks old they can rapidly consume a parent's entire stom-
435 ach contents and consumption rates are limited by parental delivery rates (Chappell et al.,
436 1993b), with stomach content average around 600g (Trivelpiece et al., 1987). Parents
437 must be able to hold more than this amount to cover their own metabolic needs. Other
438 studies show seabirds may swallow single prey items in excess of 10% of their own body
439 mass (Wilson et al., 1995), with max stomach capacity around 20% body mass (Trivel-
440 piece et al., 1987) and that maximum stomach volume during chick rearing 800-1200mL
441 for medium sized Pygoscelid penguin (Peters, 1997). During the period of highest de-
442 mand, adults have to catch up to 2.0-2.5 kg krill per foraging trip in order to meet the
443 energetic needs of themselves and their brood - 50-60% of their body mass which must
444 be assimilated or stored within a 24h period (Culik and Wilson, 1991).

445

446 Maximum size of chicks is based on chick weights in the field, where Adélie chicks from
447 single broods attain 90-108 percent adult minimum weight around day 42 (t_{peak}) and then
448 fall to 75-89 percent at fledging (Ainley and Schlatter, 1972). Thus, chicks reach about

449 80% of adult size, around 3940 g asymptotic size 39-45 days after hatching (Volkman
 450 and Trivelpiece, 1980). Thus we set

451

$$c_{\max}(t) = \begin{cases} t/t_{peak} * 3500 & t \leq t_{peak} \\ 3500 & t > t_{peak} \end{cases} \quad (17)$$

452

453

454 **Fitness for creche and guard stages**

455 We define fitness during the creching and guard stages by

456

$$\Phi(f, c, a, t) = \begin{cases} \text{maximum expected value of current and expected future} \\ \text{reproductive success for the focal individual, given } F(t) = f, \\ C(t) = c \text{ and } A(t) = a \end{cases} \quad (18)$$

457

458

459 The final time T specifies the time at which the chick fledges. We define the fitness at
 460 the final time T to be a combination of current $\psi(c)$ and expected future $\rho(f)$ reproductive
 461 success for chick size c and reserves of the focal individual f as follows

$$\Phi(f, c, a, T) = \psi(c/c_{\max}) + \rho(f/f_{\max}) \quad (19)$$

462

463 We adjust the above values to represent an old versus a young parent, with old parent
464 $\rho = \psi$ and test younger parents with $\rho = 4\psi$ and $\rho = 8\psi$.

465 There are two decisions, to abandon or to continue foraging, with the latter being
466 broken into three other decisions of how long to be at sea and at the nest, and what
467 fraction of meal to feed the chick.

468

469 We then determine the maximum value of fitness for the current set of state variables
470 by comparing the fitness values of foraging or abandoning:

471

$$\Phi(f, c, a, t) = \max \left(V_{forage}; V_{abandon} \right) \quad (20)$$

472

473 $V_{forage}(f, c, a, t)$ is the value of foraging during the guard stage given that the partner
474 has not abandoned yet for time s with return k_f , returning to the nest, feeding the chick
475 γ . The focal individual waits at the nest for a maximum time of 36 hours, after which, if
476 the partner does not return the focal individual will abandon . The fitness value result-
477 ing from this decision depends on how much food is brought back given max time away,
478 whether or not the partner also returns with a meal in this time, and whether the chick
479 survives to the following time.

480

$$\begin{aligned}
V_{forage}(f, c, 0, t) = & \\
\max_S \sum_{s=1}^S \sum_{k_f=1}^{k_{\max}} P_{k_f}(S, s, k_f) \max_{t_n} * & \\
\left(P_a(t, s + t_n) \left[(1 - \beta_c(1)) \left(\max_{\gamma} \Phi(f', c', 1, t + s + t_n) \right) + \beta_c(1) \left(\Phi(f', 0, 1, t + s + t_n) \right) \right] + \right. & \\
\left. (1 - P_a(t, s + t_n)) \left[(1 - \beta_c(0)) \left(\max_{\gamma} \sum_{k_p=1}^{k_{\max}} P_{k_p}(t_n, k_p) \Phi(f', c', 0, t + s + t_n) \right) + \beta_c(0) \left(\Phi(f', 0, 0, t + s + t_n) \right) \right] \right) &
\end{aligned}$$

481

(21)

482

483 If the partner abandons during the guard stage, the chick dies and therefore the focal
484 individual must abandon.

485

486 Next, we define the value of foraging during the creche stage given that the partner
487 has not abandoned yet ($a = 0$) for time s with return k_f , returning to the nest, feeding
488 the chick γ g krill, resting for just one time step $V_{forage}(f, c, a, t)$. The fitness value result-
489 ing from this decision depends on how much food is brought back given max time away,
490 whether or not the partner also returns with a meal in this time, and whether the chick
491 survives to the following time.

492

$$\begin{aligned}
V_{forage}(f, c, 0, t) = & \\
\max_S \sum_{s=1}^S \sum_{k_f=1}^{k_{\max}} P_{k_f}(S, s, k_f) * & \\
\left(P_a(t, s+1) \left[(1 - \beta_c(1)) \left(\max_{\gamma} \Phi(f', c', 1, t+s+1) \right) + \beta_c(1) \left(\Phi(f', 0, 1, t+s+1) \right) \right] + \right. & \\
\left. (1 - P_a(t, s+1)) \left[(1 - \beta_c(0)) \left(\max_{\gamma} \sum_{k_p=1}^{k_{\max}} P_{k_p}(s+1, k_p) \Phi(f', c', 0, t+s+1) \right) + \beta_c(0) \left(\Phi(f', 0, 0, t+s+1) \right) \right] \right) &
\end{aligned}$$

493

(22)

494

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

500

$$\begin{aligned}
V_{forage}(f, c, 1, t) = & \\
\max_S \sum_{s=1}^S \sum_{k_f=1}^{k_{\max}} P_{k_f}(S, s, k_f) * & \\
\left((1 - \beta_c(0)) \left[\max_{\gamma} \Phi(f', c', 1, t+s+1) \right] + \beta_c(1) \left[\Phi(f', 0, 1, t+s+1) \right] \right) &
\end{aligned}$$

501

(23)

502

503 The value of abandoning the chick given that the partner is still foraging ($a = 0$).

504

$$\begin{aligned}
V_{abandon}(f, c, 0, t) = & \\
& P_a(t, T - t) \left((1 - \beta_c(1)) \left[\Phi(f', c', 1, T) \right] + \beta_c(1) \left[\Phi(f', 0, 1, T) \right] \right) + \\
& (1 - P_a(t, T - t)) \left((1 - \beta_c(1)) \left[\sum_{k_p=1}^{k_{\max}} P_{k_p}(T - t, k_p) \Phi(f', c', 1, T) \right] + \beta_c(1) \left[\Phi(f', 0, 1, T) \right] \right)
\end{aligned}$$

505

(24)

506

507 Finally, the value of abandoning the chick given that the partner has already aban-
508 doned ($a = 1$) is

509

$$V_{abandon}(f, c, 1, t) = (1 - \beta_c(1)) \left(\Phi(f', c', 2, T) \right) + \beta_c(1) \left(\Phi(f', 0, 1, T) \right) \quad (25)$$

510

511 Model runs

512 We run the model through 20 different levels of food availability, and record number of
513 chicks fledging, fledging weight, parent weight and survival, abandonment, and total krill
514 consumed by one parent. We also run a sensitivity analysis to test the robustness of
515 the model and sensitivity to any parameters. Finally, we test different terminal rewards,

516 which serves to approximate how younger and older parents value relative future and
517 current fitness differently.

518

519 **Results**

520 We show the cumulative probability that the focal individual will abandon at any time,
521 given 20 different food level runs of the model, and the crèche stage starts at day 22
522 (Figure 6). As the quality of patches in the environment increases, the probability that
523 the parent will abandon is delayed through time, so that by food level 12 and higher there
524 is little chance of abandonment.

525

526 The proportion of chicks that survive to fledging as a function of food availability
527 approximates a sigmoid curve. We predict that all chicks die before fledging when the
528 probability of finding a high quality patch of food is below 0.01, and around 100% chicks
529 survive to fledge when the same probability is above 0.03 (Figure 7). In addition, chick
530 fledging weight is constant at maximum size (3500 g) for probability of high quality food
531 at 0.02 and above, but is more variable and decreases to around 2500 g as food availability
532 decreases.

533

534 Final size of the focal individual starts low with high variability and increases, also
535 similar to a sigmoid shape, reaching maximum size when probability of finding a high
536 quality patch of prey is around 0.02, above which size is around the maximum of 4000 g
537 and variability is low (Figure 8).

538

539 The amount of krill eaten is low at low food availability, and increases rapidly to a

540 maximum value with increasing food availability in the ocean (Figure 9). Variability is
541 high in mid level food simulations.

542

543 The effect of age of the parent on chick survival has a larger effect in medium levels of
544 food availability, where older parents have fewer chicks (Figure 10), however the relative
545 size of the difference in terminal reward does not matter after the value of the parent is
546 more than that of the chick.

547

548 **Discussion**

549 One of the main goals of this model was to estimate the response of penguin breeding
550 success to changes in krill availability. At low krill availability, no chicks survive to fledg-
551 ing. However there is a threshold amount of prey availability above which the survival
552 of chicks to fledging rapidly increases until 100% of chicks survive to fledging. In obser-
553 vational studies of Adélie penguins, Watanuki et al. (1993) found that chicks had poor
554 survival in years of low food availability compared to years of high food availability. Evi-
555 dence of a threshold in food availability is found in other studies that report consistencies
556 in Adélie chick and adult weight despite large differences in krill availability (Salihoglu
557 et al., 2001; Prévost and Sapin-Jaloustre, 1965; Culik and Wilson, 1991), perhaps indi-
558 cating a foraging environment during the study years where prey availability was above
559 the threshold.

560

561 The other main goal of our work was to estimate the shape of the curve describing
562 total amount of krill eaten versus krill available around a penguin predator colony. We
563 estimate this curve by summing the total prey eaten by 1000 individuals simulated during

564 the guard and crèche stage, and we find that the shape of the curve approximates a Holling
565 Type III functional response. However, this does not occur in the current model due to
566 prey switching or because of a higher predator density due to increased prey density.
567 Rather, the shape of the curve is because at low krill densities, the chick dies, in contrast
568 to high krill densities where the chick is alive and therefore the parent must eat enough
569 krill to cover its own daily energy requirements along with the energy requirements for
570 maintenance and growth of a chick (Culik and Wilson, 1991).

571

572 We estimate that the average weight of the adult penguin at chick fledging is posi-
573 tively correlated with krill availability, with parents staying at their maximum sizes for
574 very high krill availability, but dropping to a variable weight around the minimum allowed
575 in the model below a threshold level of krill availability. Some studies indicate the adult
576 Adélie penguins are quite robust to changes in their prey environment while breeding
577 (Salihoglu et al., 2001; Prévost and Sapin-Jaloustre, 1965; Culik and Wilson, 1991), with
578 other studies suggest that the parents keep up the same level of meal delivery to the chick,
579 at their own cost (Takahashi et al., 2003) particularly as chick demands increase through
580 the breeding cycle (Chappell et al., 1993*a,b*). Similarly, this is the case for other species,
581 with the condition of female fur seals at parturition and average foraging trip duration
582 reflecting prey availability (Costa et al., 1989).

583

584 The ability of the focal individual to choose abandonment at any time has not been
585 included previously in a predator/prey model with this level of foraging detail. By in-
586 cluding the decision to abandon, we were able to examine the mechanism by which a
587 parent may invest relatively in future versus current fitness. We predict that the timing
588 of abandonment is not related to breeding stage, i.e. guard versus creche stage, but more

589 related to the total time since the chick hatched. No parent abandoned earlier than 8 days
590 after hatching in the model. Our results are partly contradictory to studies that suggest
591 that unless eggs or chicks are lost to predation, nest abandonment occurs only when a
592 fasting bird runs out of energy before its mate returns (Ainley and Sladen, 1983; Davis
593 and McCaffrey, 1986; Trivelpiece and Trivelpiece, 1990; Watanuki et al., 1993; Vleck et al.,
594 1980), because in our model, the focal individual also chose to abandon during the crèche
595 stage, when it is not necessary to wait for the partner to return to the nest. Spurr (1975)
596 noted the tendency for Adélie parents to abandon around 2 weeks prior to fledging, which
597 may possibly due to this being the period of highest demand. Around this time, chicks
598 are growing rapidly but it is still within the guard stage, so parents must spend a lot of
599 time at the nest rather than foraging for their own requirements (Culik and Wilson, 1991).

600

601 There is evidence, for many species of central place forager, that it is optimal to al-
602 ternate short and long trips during breeding; such breeding is seen in Adélie penguins
603 (Ropert-Coudert et al., 2001), and many other breeding seabird, such as sooty shearwa-
604 ters (Weimerskirch, 1998). The reason often cited is that longer trips account for the
605 body condition of the parent, while shorter trips provide meals for the chick at a maximal
606 rate (Weimerskirch, 1998), but the reason may also be different foraging sites. Weimer-
607 skirch (1998) found the probability of a sooty shearwater starting a short trip depends
608 on adult body weight, with probability increasing in a sigmoidal shape with increasing
609 adult body weight. Other studies support that the duration of trips, i.e. adult petrels,
610 could be related to the energy reserves of the adult and not the nutritional state of the
611 chick (Chaurand and Weimerskirch, 1994; Ricklefs and Schew, 1994; Weimerskirch, 1998).
612 Mangel and Switzer (1998) tested a model that showed degree of self-feeding compared to
613 chick provisioning was ultimately related to krill availability near the colony and whether

614 or not krill biomass was sufficient to cover the energy requirements of both the adult and
615 chick. Our results suggest that the duration of trip may depend on the energy reserves of
616 either the adult or chick, depending on stage of growth, and may be affected by what we
617 represent as "age" of the adult.

618

619 Long-lived seabirds and marine mammals may modify their reproductive investment in
620 a given year according to their future reproductive potential, which is correlated with their
621 age and condition (Drent and Daan, 1980; Pugesek, 1987; Costa et al., 1989; Watanuki
622 et al., 1993; Stearns, 1992). Younger adults may invest more in themselves at the cost
623 of their offspring, e.g. arctic terns (Monaghan et al., 1989) and puffins (Barrett and
624 Rikardsen, 1992), compared to older adults that may work harder to ensure the survival
625 of a chick (Burger and Piatt, 1990). Breeding is a stressful time energetically, with many
626 species losing weight that must be regained after breeding, and yet other species having
627 maximum mortality rates around the end of breeding (Coulson et al., 1983). According
628 to life history theory, we would expect abandonment if risks to survival are too great
629 (Drent and Daan, 1980). In the current study, we found a difference in chick survival due
630 to optimization of reproductive effort, but only for medium levels of food availability.

631

632 Reproductive performance improves with age in birds (Forslund, 1995). The many
633 hypotheses on why this may occur can be divided into three main groups: the progressive
634 appearance of a phenotype; age-related improvement in competence; and optimization
635 of reproductive effort (Forslund, 1995). Our current model allows us to test the latter
636 two of these hypotheses. We tested the improvement in competence by increasing by a
637 percentage both the probability of finding a patch of prey and the gain from a patch of
638 prey once located, representing increased competence in older birds. We tested optimiza-

639 tion of reproductive effort by varying the terminal reward, and the relative contribution
640 to fitness for adult versus chick survival and size, with increased weight given to chick
641 survival representing an older bird and vice versa for a younger bird. We found a small
642 difference in chick survival due to optimization of reproductive effort, suggesting that
643 larger observational correlations in age and chick survival may be due to other reasons,
644 such as increased competence.

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Table 1. Parameters used in the single trip foraging model

Symbol	Parameter	Value	Unit
$\Phi(r, t)$	Fitness is the maximum gain from one foraging trip given radial distance from nest r and time since foraging individual left the nest 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 other model)	24	h
t_p	Optimal time in patch	0 to $(T-t)$	
r	Radial distance from nest	0 (nest) to r_{\max}	km
r_{\max}	Maximum possible distance from nest	300	km
r_{int}	Travelling/swimming speed	10	km h ⁻¹
ϵ	Rate of gain from patch	0.0016 to 0.018	-
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

Table 2. Parameters used in the model

Symbol	Parameter	Value	Unit
$\Phi(f, c, a, t)$	Fitness is the maximum expected size of chick and focal individual (FI) given current FI size f , chick size 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	2	h
T	Final time	60	d
f	Size of focal individual	0 to f_{\max}	g
f_{\max}	Maximum size of focal individual	4000	g
f_{\min}	Minimum size of focal individual	2400	g
c	Size of chick	0 to $c_{\max}(t)$	g
$c_{\max}(t)$	Maximum size of chick, depends on age	see text	g
$c_{\min}(t)$	Minimum size of chick, below which death is likely	see Figure	g
a	State of abandonment	see Table 4	-
s	Foraging trip time	1 to S	h
S	Maximum time at sea for one foraging trip, otherwise abandon	24	h
t_n	Wait time at nest (guard stage)	0 to S	h
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}
$m_c(t)$	Metabolic costs for chick each time step	<i>see text</i>	g h^{-1}
k_f	Size of foraging reward for focal individual	0 to 2000	g
γ	Amount of krill delivered to chick by FI	100 to 1000	g
k_p	Size of meal delivered to chick by partner	100 to 1000	g
λ_f	Fraction of energy stored, rest is wasted, for FI	0.8	-
λ_c	Fraction of energy stored, rest is wasted, for chick	0.8	-
λ_f	Fraction converted from fat to energy, for FI	0.7	-
λ_c	Fraction converted from fat to energy, for chick	0.7	-

Table 3. Behavior for each stage of breeding

Strategy	Incubation	Guard	Creche
1	M and F alternate	M fasts, F forages	M and F alternate
2	M and F alternate	M and F alternate	M and F alternate
3	M fasts, F forages	M and F alternate	M and F alternate

887 Note: We show the behavior for the male (M) and female (F) parent. The behavior
888 'alternate' means that the two parents alternate the takes of guarding the egg/chick at
889 the nest with foraging at sea. This is distinct from when the male stays fasting at the
890 nest for an entire stage of breeding 'M fasts' while the female forages to feed the chick or
891 build her own reserves 'F forages'

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

Value	Abandoned	Consequence: guard stage	Consequence: creche 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

892 Captions for Figures

893

894 Figure 1. Explanation of flow of events in game model and state dynamics, with: (A)
895 how focal individual makes decisions based on behavior of partner; (B) how state of focal
896 individual changes depending on how much krill is eaten and how this is apportioned to
897 self and chick; and (C) state of chick depending on meals from partner and focal individual.

898

899 Figure 2. Densities of swarms - bars show average number of swarms encountered per
900 kilometer track during daytime in the different areas, error bars are 1 standard deviation
901 - from Klevjer and Tarling (In Press).

902

903 Figure 3. The rate of patches encountered per time 8 minute step with radial distance
904 from the nest r (km), approximated from unpublished data in Figure 2.

905

906 Figure 4. Result, amount of krill caught (g) in one foraging trip vs time at sea (h), for
907 12 separate runs of the 'single-trip' foraging model, where each color represents a different
908 final time T , which correlates to a choice of maximum foraging trip time S in the game
909 model. .

910

911 Figure 5. Example of the decision-making process and conceptual explanation of
912 distance and time. Black line shows in theory where focal individual (FI) is, value zero
913 is at nest. Blue line shows conceptual representation of where partner would be depend-
914 ing on location of FI, i.e. one is at the nest while the other is at sea during the guard
915 stage. Time s is the length of a foraging trip for the FI same as time partner waits at

916 nest) and time t_n is time that FI waits at nest for partner (while partner is foraging at sea).

917

918 Figure 6. Cumulative proportion of 1000 parents abandoning over time, where the
919 creche stage starts at time 151, for different levels of food availability, where food avail-
920 ability is described in equation 2.

921

922 Figure 7. Proportion of chicks reaching fledging alive (circles) and average fledging
923 weight in g (\pm SD) of these surviving chicks (triangles) for different levels of food availabil-
924 ity, characterized by the probability of encountering a high quality patch while foraging.

925

926 Figure 8. Final weight of the parent at the end of the creche stage, or at time of
927 chick fledging, in g (\pm SD) for different levels of food availability, characterized by the
928 probability of encountering a high quality patch while foraging.

929

930 Figure 9. Total amount of krill consumed in g (\pm SD) by one parent over the guard
931 and creche stage compared to level of food availability, characterized by the probability
932 of encountering a high quality patch while foraging.

933

934 Figure 10. Difference in chick survival as the relative value for future fitness is in-
935 creased (from TR 2 to TR 16) where TR 16, the final fitness per gram of parent weight
936 is 8 times the fitness per gram of chick weight for different levels of food availability,
937 characterized by the probability of encountering a high quality patch while foraging.

938

939 **Figures**

940

Figure 1

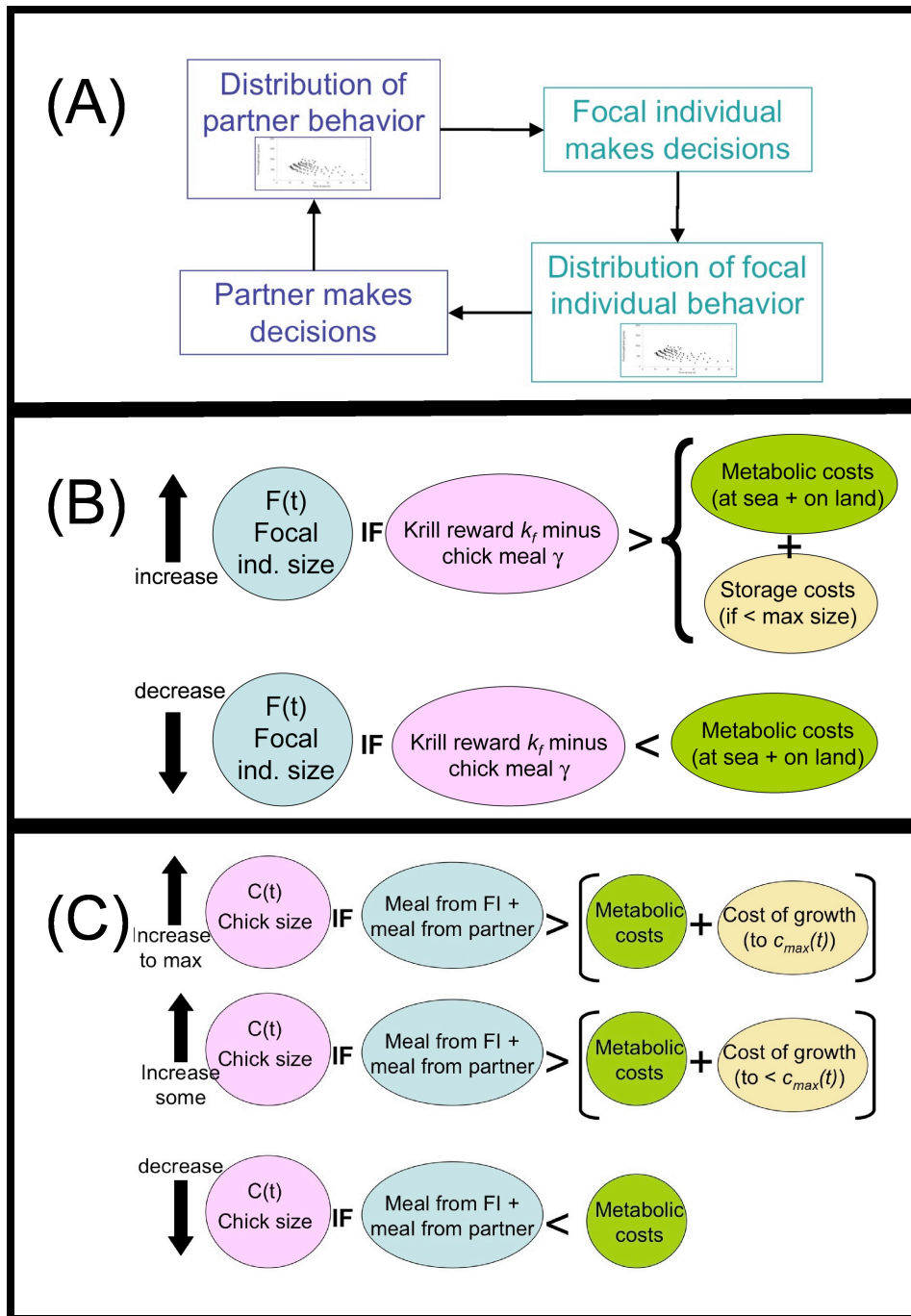


Figure 2

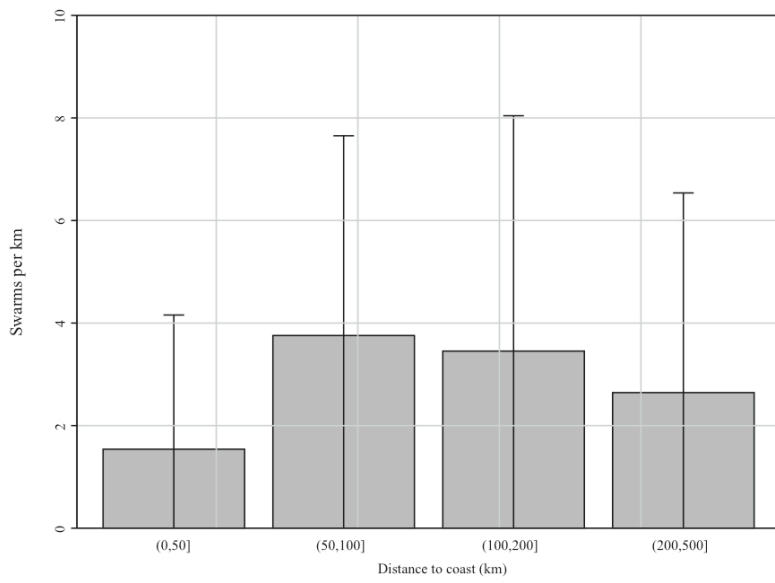


Figure A:

Densities of swarms. Bars show average number of swarms encountered per kilometer track during daytime in the different areas, error bars are 1 standard deviation.

Figure 3

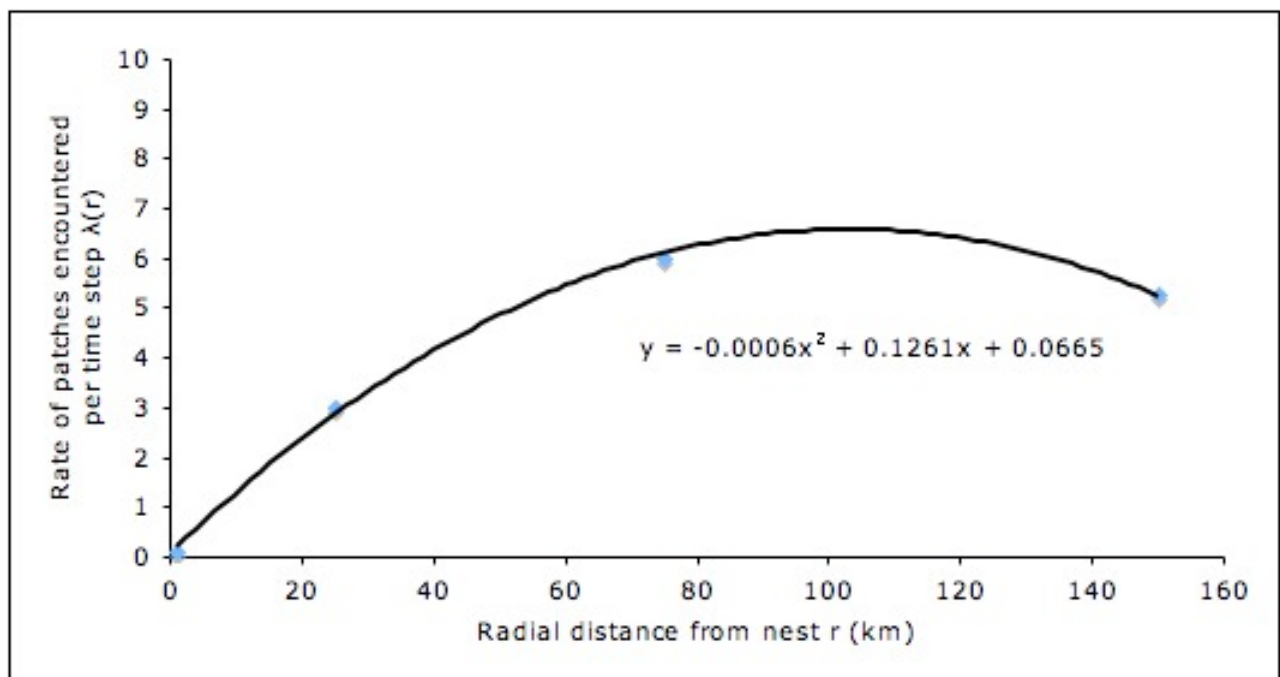


Figure 4

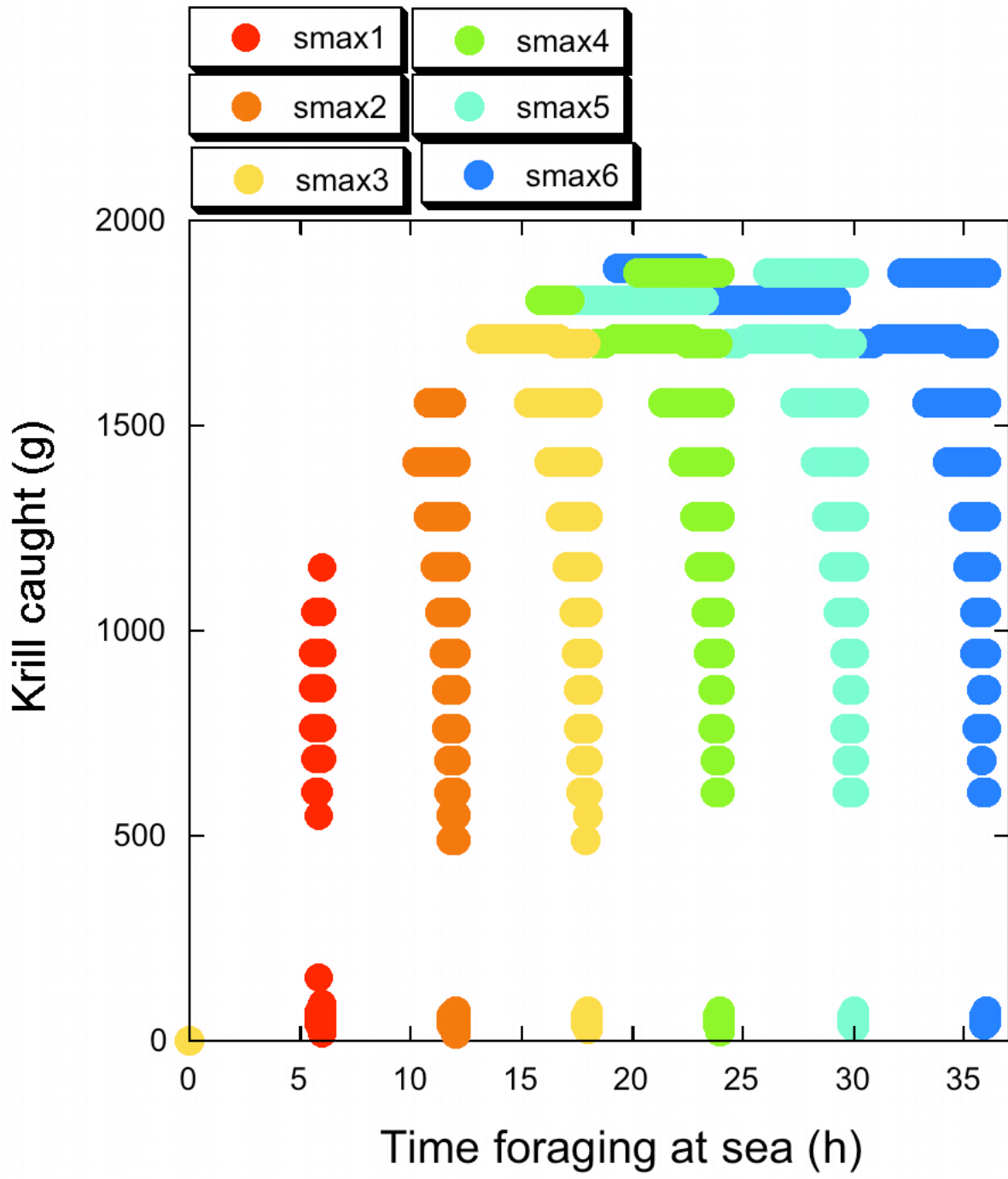
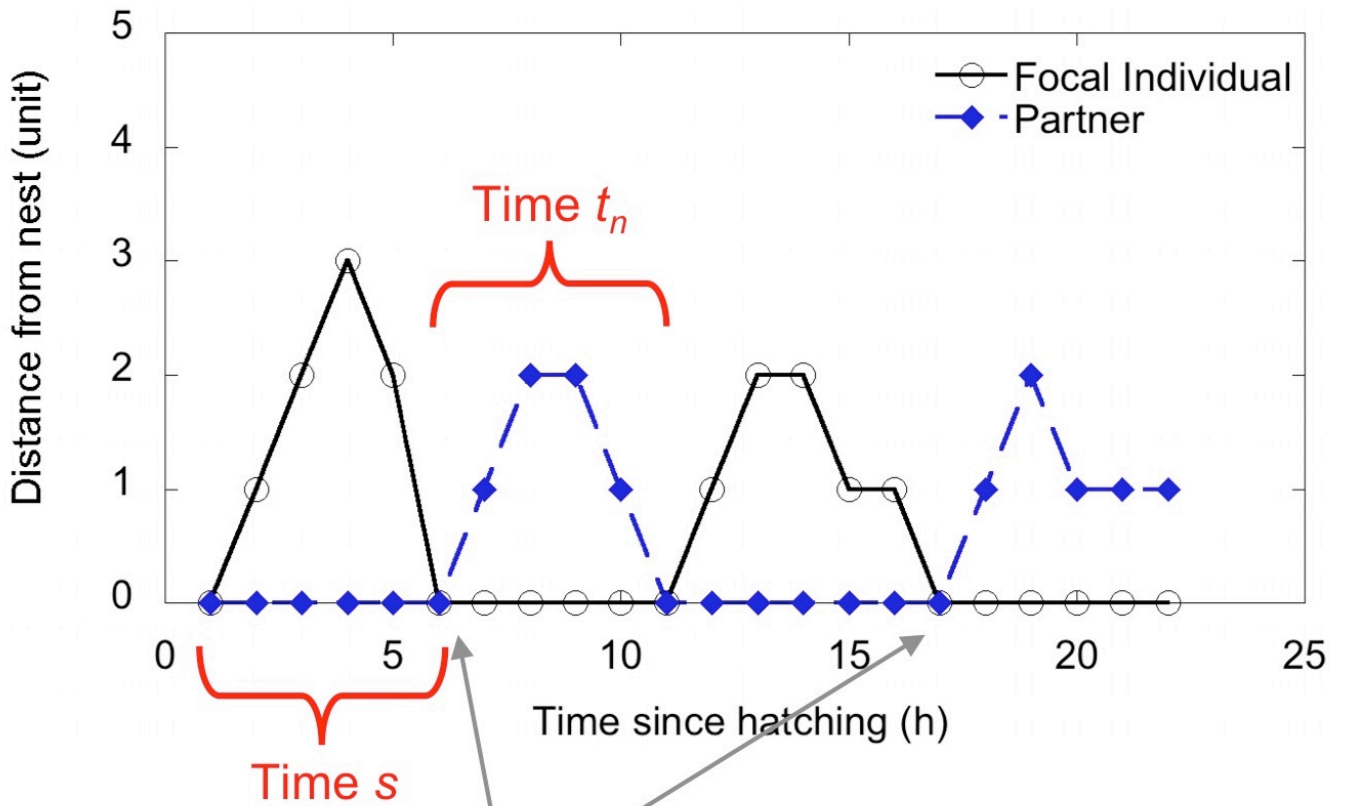


Figure 5



On return to nest:

1. See how much partner has fed chick while at sea for time s
 2. Feed chick and stay at nest for time t_n
- (if no parent present at nest for any time step, abandon $a = 1$)

Figure 6

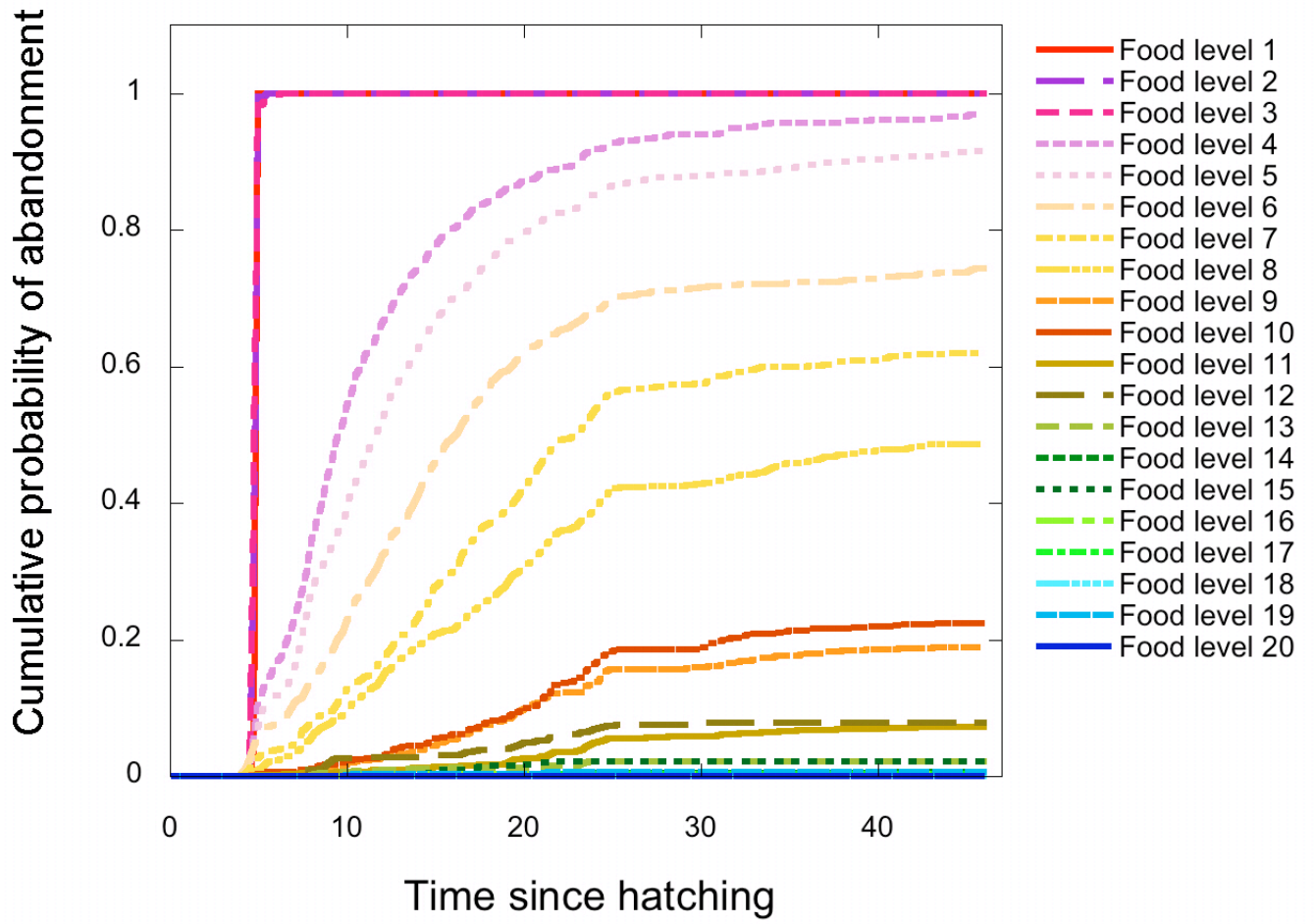


Figure 7

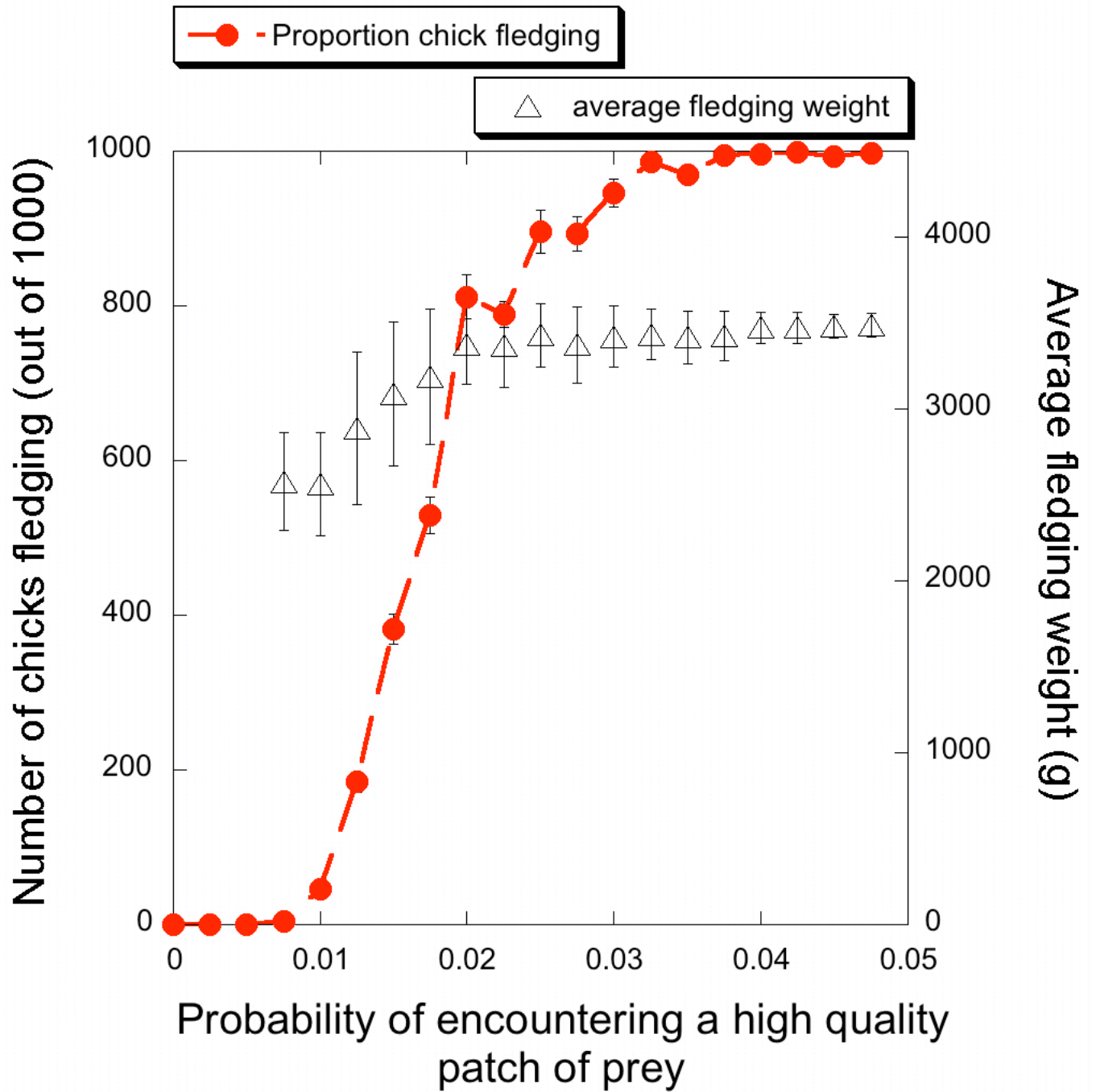


Figure 8

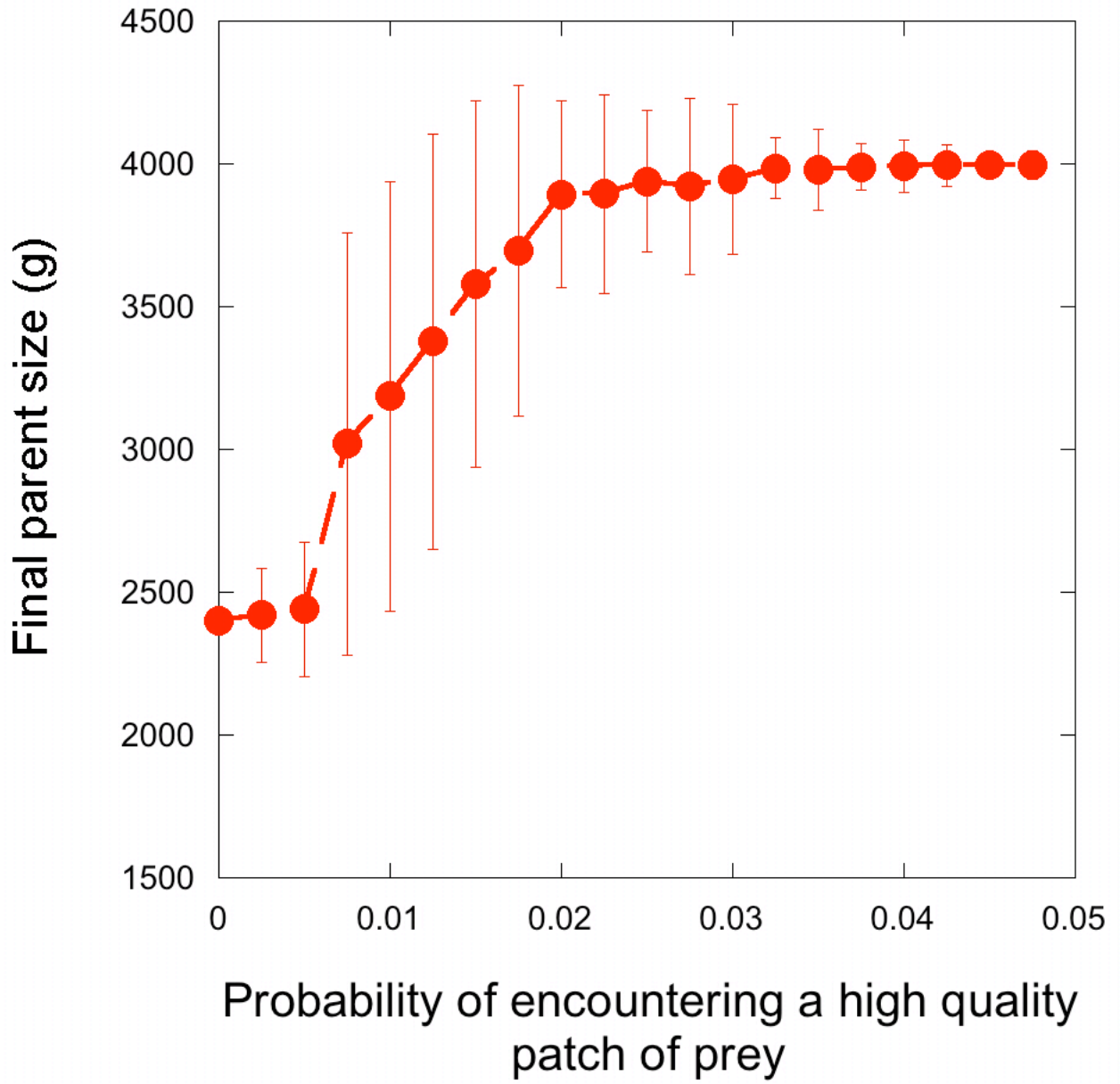


Figure 9

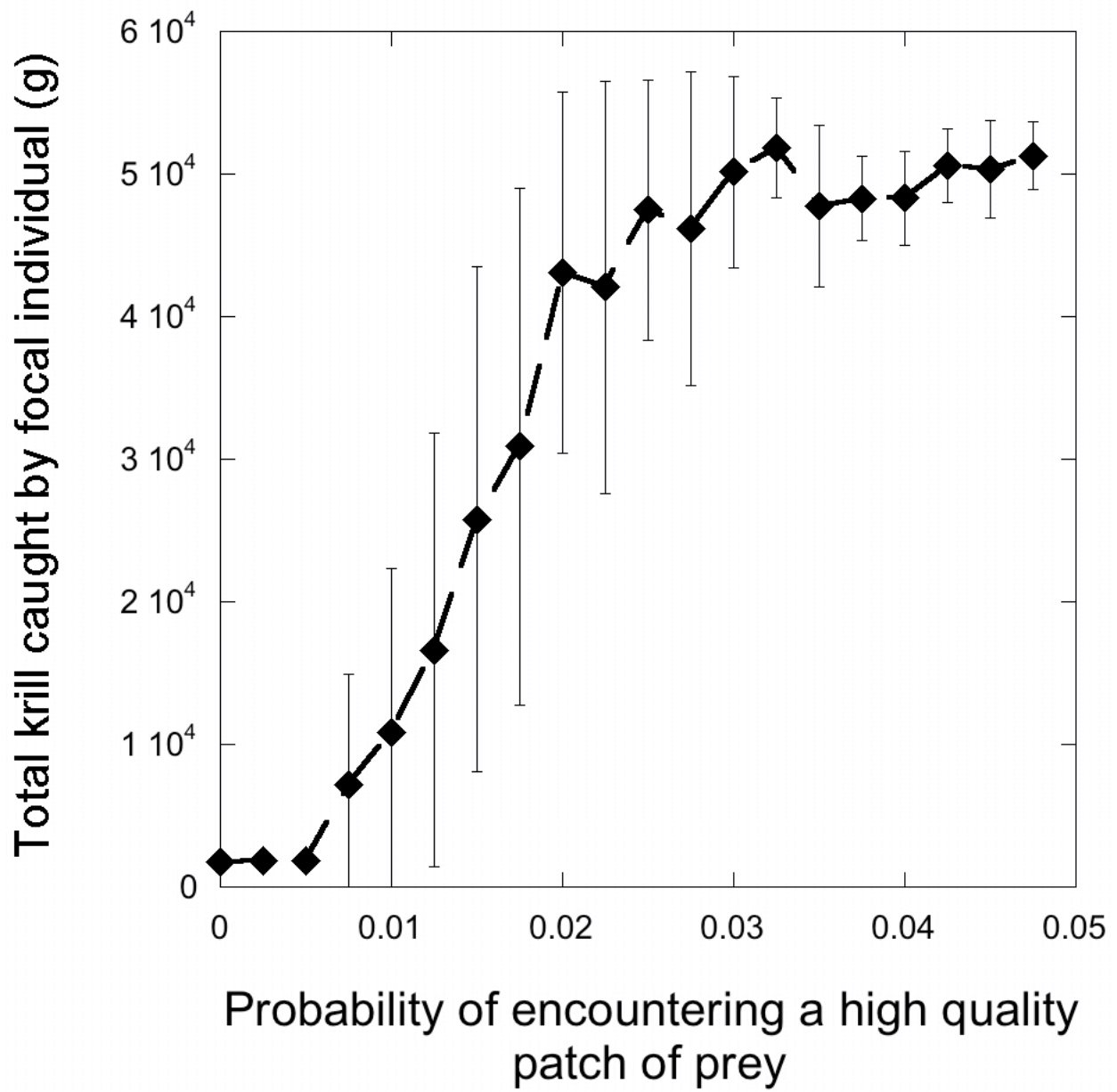


Figure 10

