

# The risks of parenthood

## II. Parent-offspring conflict

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### Summary

Previous work has demonstrated the value of dynamic programming models for the analysis of parental decision making. In the present paper we extend this approach to analyse conflicts between parents and their offspring, and develop a dynamic ESS model of feeding and fledging of nestling birds. In order to simplify the formulation and solution of the dynamic ESS model, we adopt an assumption of alternating decisions: in each time period the parent first decides whether to continue provisioning the nestling, after which the nestling decides whether to leave the nest. The model takes into account numerous tradeoffs involved in parent-offspring decisions, including differential growth and mortality rates for offspring in and out of the nest, risk of fledging, relation between long-term survival and post-breeding mass of offspring, and parental mortality risk associated with provisioning of offspring. Depending on assumed parameter values, the model is capable of predicting a wide range of feeding-fledging behaviour. The model is applied specifically to the juvenile life history of dovebies (*Alle alle*), and provides a behavioural explanation for the phenomenon of pre-fledging mass recession in this species.

*Keywords:* Parent-offspring conflict; parental risks; evolutionarily stable strategy; game theory (dynamic); fledging behaviour; seabirds; alcids

### Introduction

In two previous papers (Ydenberg, 1989; Clark and Ydenberg, 1990) we studied the optimal age of fledging in birds, using a dynamic modelling approach. As pointed out by Trivers (1974), the optimal fledging age from the offspring's viewpoint will normally differ from that of the parent's. In the present paper we develop a dynamic model of the evolutionary contest between parents and offspring, and show how to determine the dynamic evolutionarily stable strategy (ESS). Simpler static ESS models of parent-offspring conflicts were studied by Trivers (1974), and Parker and McNair (1978, 1979).

In constructing a dynamic model of fledging behaviour, it becomes clear that consideration must be paid to matters other than simply the date of fledging. For example, parents can vary food deliveries over time, eventually reducing or terminating the feeding of nestlings. In some species (e.g. seabirds, oilbirds, etc.) parents actually appear to 'overfeed' their nestlings, in the sense that the nestlings' mass temporarily exceeds their mass at fledging. Sealy (1973) has suggested that pre-fledging mass recession results from exercise of the wing musculature prior to fledging. An

alternative explanation (Harris, 1984) holds that, due to their oily diets, seabird chicks must put on extra fat in order to gain enough protein for growth, and subsequently must pass through a period of starvation in order to lose excess weight before fledging.

One of the purposes of our modelling exercise is to enquire whether such overfeeding and subsequent weight loss could be behavioural adaptations, rather than purely physiological phenomena, as is usually presumed. A dynamic model is obviously required for studying such questions. Dynamic models also permit explicit consideration of important stochastic aspects of breeding behaviour, such as fluctuations in food availability, and risks of predation. Our analysis in fact indicates that stochasticity may be instrumental in the overfeeding phenomenon.

Previous studies of parent-offspring conflict have been largely based on such concepts as parental investment, offspring solicitation costs, and 'fitness units'. While these studies have proved invaluable in conceptualizing the nature of parent-offspring conflicts, they have the disadvantage that these terms do not represent directly measurable quantities. Moreover, the relationship between these concepts and fitness in the sense of expected lifetime reproductive success is often obscure. A further advantage of the dynamic modelling approach used in this paper (cf. Mangel and Clark, 1988) is that fitness can be assessed directly in terms of survival and reproduction, without the necessity of introducing extraneous notions such as costs and investment.

The theory of games has by now assumed a central position in evolutionary and behavioural ecology. Dynamic ESS models have potential advantages analogous to dynamic optimization models. Unfortunately, dynamic game theory is notorious for its mathematical and computational complexity. For example, Houston and MacNamara (1987, 1988) analyse dynamic ESS models in which individuals play against the field. These authors point out that dynamic two-person contests are much more difficult to analyse than dynamic games against the field. In this paper we consider parent-offspring conflict as a dynamic two-person contest; our analysis is based on the simplifying assumption that the participants make *alternating decisions* (cf. Maynard Smith, 1982, p. 137), somewhat as in a chess game. This assumption does not seem unreasonable for the parent-offspring game treated here; our model supposes that in each time period the parent first decides whether to try to provide food for the nestling, and the nestling subsequently decides whether to fledge in the period. A pair of strategies, for the parent and the offspring, is defined to be evolutionarily stable provided that neither participant is able to increase its inclusive fitness by adopting an alternative strategy, given that the other participant continues to employ the ESS. Because of the assumption of alternating decisions, and because each contestant is assumed to be fully aware of the strategy to be used by the other contestant, we need not consider mixed strategies. The ESS can be determined by numerical iterative solution of a system of equations analogous to the dynamic programming algorithm (Mangel and Clark, 1988).

### Seabird biology

The evolutionary interaction that we analyse is that of parent seabirds of the family Alcidae provisioning their dependent offspring. The natural histories of these birds are diverse, but the following features are generally common to all of them, and pertinent to the present discussion. (More detailed discussion can be found in Sealy, 1972; Harris, 1984; Nettleship and Birkhead, 1985; Ydenberg, 1989.)

(1) *Nests are relatively safe from predators*, for both the nestling and the incubating adult. Seabirds nest in burrows, crevices, amongst rubble, or on sheer cliff faces, frequently on islands. Their nests are almost always inaccessible to terrestrial predators, and are often immune to avian predators as well. Thus, while on the nest, seabirds are generally quite safe.

(2) *Leaving or entering the nest, in contrast, is dangerous* because many species are highly colonial and the nesting grounds often attract predators. Eagles and other predators are capable of capturing adults. Some species of seabirds approach and leave their nests only at night, presumably as a defensive measure. When leaving the nest fledglings must face the same predators, as well as others for whom adults are too formidable. Fledging successfully thus often depends upon dodging a heavy concentration of predators. Among the Alcidae, several species flutter or glide on partially-developed wings from the nest into the sea, and are heavily preyed upon at this time (e.g. Daan and Tinbergen, 1979). This fledging journey is doubtless the most dangerous event of the bird's entire life, and selection must act powerfully on any feature giving an advantage at this stage. Many investigators have suggested that a low wing-loading (ratio of body mass to wing area) is advantageous, since it enables a longer and more controlled flight from nest to sea. In some species, such as puffins, fledglings walk from the nest, and must feed themselves once at sea. Since food capture involves diving, it has been suggested (Harris, 1984) that in these species low buoyancy at fledging would be advantageous. In both cases the mass at fledging may influence subsequent survival.

(3) *Seabirds are long-lived*, and once they have survived the juvenile stage they face potentially very long reproductive lives, amounting to decades for some species. Hence the predation risk parents face in order to provision dependent offspring becomes important, even if it is fairly small, since a great deal of future reproduction is at stake.

(4) *Food is often hard to find* for many seabird species, with the consequence that parental foraging excursions are often lengthy, or of unpredictable duration or success.

(5) *Post-fledging survival depends on body mass attained prior to fledging*. The data of Perrins *et al.* (1973) on the Manx shearwater *Puffinus puffinus* indicate a strong linear relationship between fledging weight and survival to breeding, while the study of Harris and Rothery (1985) on the Atlantic puffin *Fratercula arctica* indicates no such relationship within the range of observed fledging weights. At the very least, however, a minimum amount of growth and development must be completed before fledging if the chick is to have any hope of surviving to breed.

(6) *Nest and ocean offer different growth prospects* for the chick. For example, Ydenberg (1989) showed that the ocean growth rate of common murre chicks (*Uria aalge*) is about twice the rate in the nest. In the case of the dovekie (*Alle alle*) outlined below, the nest rate is about 3.5 times the ocean rate.

(7) *Breeding is seasonal at high latitudes* and the chick must complete the minimum amount of growth required during a limited period. At very high latitudes the growing season may be as short as six weeks. This contrasts greatly with tropical areas in some of which there may be no seasonality at all.

These natural history observations indicate that, in seabirds, the parent and chick face a variety of different risks and prospects. We assume in what follows that parents behave so as to maximize their expected lifetime reproductive success. Chicks have the more immediate goal of maximizing their probability of survival to breeding age (as the first essential step in maximizing lifetime reproductive success). Thus the chick's survival is taken into account in calculating the parent's reproductive success, but not vice versa.

### **Seabird case study: the dovekie**

Before developing the model it will be useful to detail a seabird 'case study', to help set the stage for the type of questions that we ask. We stress, however, that the approach we use is much more general than indicated by this specific situation.

The dovekie is a small (approximately 150–180 g) Arctic seabird in the family Alcidae. Dovekies breed in colonies, and each monogamous pair rears a single nestling that fledges in late July to mid-August, at 67–82% of adult body weight and an age of 23–30 days. (Such variability is typical in the Alcidae.) Parents feed their nestlings on zooplankton captured at sea and delivered in the gular pouch in loads of several grammes each (Roby *et al.*, 1981). These prey are captured either near or far from the colony, but due to their vertical migrations are often available only twice per day (dawn and dusk) and may not appear reliably at any one location. Parents deliver, on average, five or six loads per day (apparently the distance to the feeding grounds does not greatly influence this rate of delivery). The nests are located amongst boulders on scree slopes, and parents are at risk from a variety of predators as they fly in or out of the colony, or as they scramble over the rubble. Arctic foxes (*Alopex lagopus*) and gyrfalcons (*Falco rusticus*) are common predators (Evans, 1981).

The dovekie nestling grows rapidly until about day 21–23, at which point skeletal (but not plumage) growth ceases, and body weight begins to fall. (Stempniewicz (1980) details the development on each day of life.) At about the same time the parents reduce the feeding rate, for example from 5.5 to 4.9 feedings day<sup>-1</sup> in an east Greenland colony studied by Evans (1981). Stempniewicz (1980) found on Spitsbergen that 26-day-old young had not recently been fed at all.

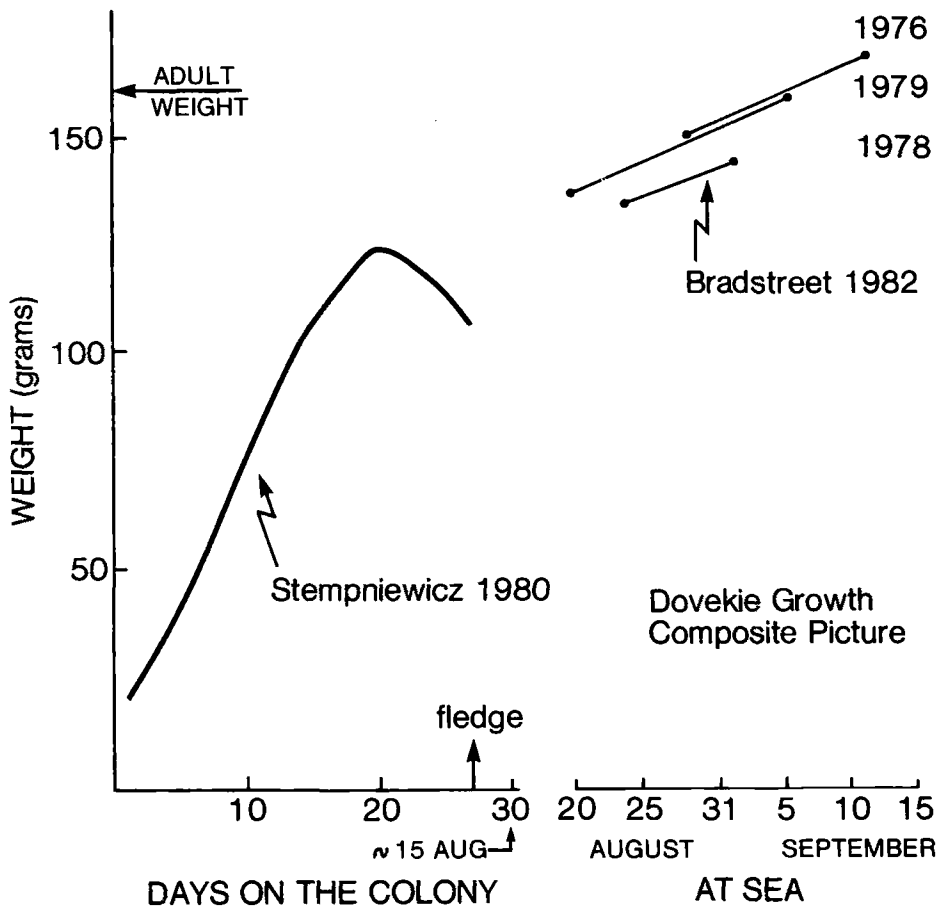


Figure 1. A composite picture of the growth of a young dovekie including growth in the nest prior to fledging, and post-fledging growth on the ocean. The 'pre-fledging mass recession' is clearly visible.

Other such observations show that dovekie nestlings usually lose weight for several days prior to fledging, but that the duration and the magnitude of the 'pre-fledging weight recession' varies greatly, between and within colonies, and between years (Gaston, 1985; Harris and Birkhead, 1985).

After fledging, the young are apparently accompanied at sea for several weeks by their fathers, and during this period continue to grow at about  $1.4 \text{ g d}^{-1}$  (Bradstreet, 1982), until they reach about 90% of their adult body weight of 150–180 g (Roby *et al.*, 1981). They complete their growth the next summer. These facts, combined with the pattern of resource availability and movements of adult birds (Evans, 1981; Bradstreet, 1982), suggest that growth is no longer possible after early or mid-September. A composition picture of dovekie growth is given in Fig. 1.

### The model

We treat parental feeding and offspring fledging behaviour as a dynamic game. In order to avoid a three-player game, we treat the parent as a single decision maker. In other words, care of the nestling is either provided by a single parent, or by two fully cooperating parents. We also assume only a single nestling, as is the case for most species in the Alcidae. A *dynamic evolutionarily stable strategy* (ESS) is defined here as a pair of behavioural strategies, for the parent and its offspring, respectively, such that each participant maximizes its own expected future fitness, at each decision, given current conditions, and given that the other participant employs the ESS.

The structure of our dynamic model is based on the assumption that parental feeding decisions and the nestling's fledging decision alternate. (Once the offspring has fledged parental care ceases and no more decisions are made.) Specifically, in each given time period the parent first decides whether to attempt to feed the nestling; this decision depends upon the current age and mass of the nestling. Dependent on the parent's behaviour, the nestling then decides whether to fledge or to remain in the nest. In a given time period  $t$ , each participant knows both participants' future strategies, and is therefore able to decide on its own present behaviour. The dynamic programming algorithm for computing the ESS operates in the usual way (see Mangel and Clark, 1988; ch. 9), working backwards in time from a terminal horizon  $T$  representing the end of the breeding season.

Our problem is one of 'feedback' control, in which the parent and offspring decisions at any given time depend upon the current state of both participants, as affected by past decisions and by stochastic events. Rather than the parent and offspring competing against each other, it would be more accurate to think of the parents competing against other parents in the population, and offspring competing against other offspring. The two strategies are linked by the feedback between them (Parker, 1984), and the evolutionary contest is between pairs of parent-offspring strategies.

Before specifying the details of our model, it seems worthwhile to outline the various tradeoffs that are involved in the decision problems of parent and nestling. The considerations affecting the nestling are: (a) relative expected growth rates in the nest and outside; (b) the variance in these growth rates; (c) relative mortality risk in the nest and outside; (d) mortality risk incurred in the act of fledging, which may depend on body size; (e) the relationship between terminal body mass (at the end of the current nesting season) and future survival. The parent's decision involves all of these tradeoffs affecting its offspring, and in addition includes (f) the mortality risk incurred in feeding the nestling; (g) future reproductive value. Our dynamic model reflects tradeoffs between all of these considerations.

The basic state variable of our model is  $X(t)$  = offspring's mass at the beginning of time period  $t$ . Time units  $t$  are taken to be days. (Shorter time units, allowing for multiple feeding bouts per

day, could be used instead – see the Discussion.) Additional state variables are  $H(t)$  = offspring’s location at the beginning of day  $t$ , with  $H(t) = 0$  in the nest and  $H(t) = 1$  at sea after fledging, and  $Z(t)$  = parent’s state, with  $Z(t) = 0$  if parent has been killed, otherwise  $Z(t) = 1$ .

The model parameters are:

- $\sigma_{p0}$  = parent’s daily survival probability, if feeding is not attempted
- $\sigma_{p1}$  = parent’s daily survival probability, if feeding is attempted
- $\sigma_{c0}$  = offspring’s daily survival probability in nest
- $\sigma_{c1}$  = offspring’s daily survival probability outside nest
- $p$  = probability that parent obtains food for nestling, per day
- $g_0(x)$  = daily growth of nestling, if fed, as a function of current mass  $x$
- $\alpha(x)$  = daily mass loss of nestling, if not fed
- $g_1(x)$  = daily growth of offspring after fledging
- $\rho(x)$  = probability that offspring survives the act of fledging at mass  $x$
- $\phi(X(T+1))$  = offspring’s terminal fitness, i.e. probability of survival from the end of the breeding season (day  $T+1$ ) to reach maturity.

The zero-one variables in our model are listed in Table 1 for quick reference. The zero or one subscripts to parameters are also consistent with this table.

Table 1. Zero-one variables in the fledging model.

Variable	Meaning	0-value	1-value
$H(t) = h$	offspring’s location	in nest	fledged
$Z(t) = z$	parent’s state	dead	alive
$f$	food offered?	no	yes
$D_p$	parent’s decision	no feeding	attempt feeding
$D_c$	nestling’s decision	stay in nest	fledge

### Dynamic programming algorithm

We now develop the dynamic programming algorithm used to specify, and then to solve the dynamic game between parent and offspring. As in ordinary (non-game) dynamic programming, the algorithm utilizes the ‘lifetime fitness functions’ (Mangel and Clark, 1988) of the decision makers. The offspring makes its decisions on the basis of its own fitness, while the parent considers both its offspring’s and its own fitness. In order to keep track of the alternating decisions (parent, then offspring, in each time period), several lifetime fitness functions need to be specified. First, define

$$F_c(x, z, t) = E\{\phi(X(T+1)) | X(t) = x, Z(t) = z, H(t) = 0\} \tag{1}$$

In words,  $F_c(x, z, t)$  represents the offspring’s expected terminal fitness (ultimate survival to breeding), given that the offspring is in the nest at the beginning of day  $t$ , with mass  $x$ , and that the parent’s current state is  $z$  (i.e. dead or alive). In defining this function, it is assumed that future decisions of the parent and offspring will be as determined by the ESS (specified below).

Next, define

$$S_p(x, h, t) = \Pr(\text{parent survives from } t \text{ to } T+1 | X(t) = x, H(t) = h) \tag{2}$$

This is self-explanatory, but the value of  $S_p$  again depends upon the assumption that both participants act according to the ESS in future time periods. Also let

$$D_p(x,t) = \text{parent's decision (given } H(T) = 0, X(t) = x) \quad (3)$$

where the decision is either  $D_p = 1$ : 'attempt to feed nestling', or  $D_p = 0$ , 'do not attempt feeding'. Thus the parent's decision depends on the current date  $t$ , and state of the offspring,  $X(t) = x$ .

The offspring's fledging decision is made after it has learned whether the parent has offered food that day; define

$$\bar{F}_c(x,z,t;f) = E\{\phi(X(T+1)) | X(t) = x, Z(t) = z, \text{ food offered} = f\} \quad (4)$$

where  $f$  is a zero-one variable indicating whether food has been offered in the present period  $t$ . (Of course  $f = 0$  if  $z = 0$ .) Also let

$$D_c(x,z,t;f) = \text{nestling's decision (given } x,z,t;f) \quad (5)$$

where  $D_c = 1$  corresponds to fledging and  $D_c = 0$  to remaining in the nest. The meanings of the symbols  $f, D_p, D_c$  are also shown in Table 1.

Let  $\psi(x,t)$  denote the offspring's expected fitness if it fledges in period  $t$ , at mass  $x$ ;

$$\psi(x,t) = \rho(x)\sigma_c^{T+1-t}\phi(X(T+1)) \quad (6)$$

where  $X(T+1)$  is computed by following the post-fledging growth, beginning with  $X(t) = x$ . For example, in the case of  $g_1(x) = g_1 = \text{constant}$ , we have simply

$$x(T+1) = x + (T+1-t)g_1$$

The following three equations determine the nestling's fledging decision:

$$\bar{F}_c(x,1,t;1) = \max(\sigma_{c0}F_c(x+g_n(x),1,t+1), \psi(x,t)) \quad (7)$$

$$\bar{F}_c(x,1,t;0) = \max(\sigma_{c0}F_c(x-\alpha(x),1,t+1), \psi(x,t)) \quad (8)$$

$$\bar{F}_c(x,0,t;0) = \max(\sigma_{c0}F_c(x-\alpha(x),0,t+1), \psi(x,t)) \quad (9)$$

These equations are readily understood. For example, in Equation 7 the nestling is offered food. If it accepts the food and remains in the nest, then  $X(t+1) = x+g_0(x)$  and  $Z(t+1) = 1$  (we assume that parental mortality only occurs in the act of proffering food, so that the parent will still be alive at the beginning of period  $t+1$  if it has offered food in period  $t$ ). Hence the nestling's expected fitness equals  $\sigma_{c0}F_c(X(t+1),1,t+1)$  as in Equation 7. On the other hand, if the nestling rejects food and fledges, its expected fitness equals  $\psi(x,t)$ . The nestling maximizes its fitness by choosing the better of these options. A similar argument applies to Equations 8 and 9.

The parent's feeding decision is somewhat more complex, since both parent and offspring fitness are involved. The sequence of events is: first the parent decides whether to attempt to feed the nestling. With probability  $p$  it obtains food, and then with probability  $\sigma_{p1}$  it survives the attempt to provision the nestling. If it fails to find food, or if it decides not to feed, its survival probability equals  $\sigma_{p0}$ . Hence if the parent tries to feed the nestling, then the nestling's expected fitness equals

$$F_c(x,1,t) = p[\sigma_{p1}\bar{F}_c(x,1,t;1) + (1-\sigma_{p1})\bar{F}_c(x,0,t;0)] \\ + (1-p)[\sigma_{p0}\bar{F}_c(x,1,t;0) + (1-\sigma_{p0})\bar{F}_c(x,0,t;0)] \quad (10)$$

We also require an expression for  $S_p(x,t)$ , the parent's survival probability, given that the offspring is still in the nest. We have (still assuming now that the parent attempts to feed the nestling)

$$S_p(x,t) = p\sigma_{p1}\cdot A_1 + (1-p)\sigma_{p0}\cdot A_0 \quad (11)$$

where

$$A_1 = \begin{cases} \sigma_{c0}S_p(x+g_0(x),t+1)+(1-\sigma_{c0})\sigma_{p0}^{T-t} & \text{if } D_c(x,1,t;1) = 0 \\ \sigma_{p0}^{T-t} & \text{if } D_c(x,1,t;1) = 1 \end{cases} \quad (12)$$

$$A_0 = \begin{cases} \sigma_{c0}S_p(x-\alpha(x),t+1)+(1-\sigma_{c0})\sigma_{p0}^{T-t} & \text{if } D_c(x,1,t;0) = 0 \\ \sigma_{p0}^{T-t} & \text{if } D_c(x,1,t;0) = 1 \end{cases} \quad (13)$$

To explain this, observe that the parent finds food and survives the period with probability  $p\sigma_{p1}$ , after which the nestling makes the decision  $D_c(x,1,t;1)$ . If the nestling remains in the nest ( $D_c = 0$ ), it survives with probability  $\sigma_{c0}$  and gains weight  $g_0(x)$ , resulting in future parent survival probability equal to  $S_p(x+g_0(x),t+1)$ . If the nestling dies, the parent's future survival probability from period  $t+1$  to  $T$  is just  $\sigma_{p0}^{T-t}$ . Similarly, if the nestling fledges ( $D_c = 1$ ), then the parent's future survival probability is again  $\sigma_{p0}^{T-t}$ . This explains the term containing the factor  $A_1$  in Equation 11. Factor  $A_0$  in the second term (for the case in which the parent fails to find food) is derived in the same way.

Next, if the parent does not attempt to feed the nestling we have

$$S_p(x,t) = \sigma_{p0} \cdot A_0 \quad (14)$$

where  $A_0$  is again given by Equation 13. The argument for this case is as before; note that we are here assuming that if not fed on a given day (even though the parent is alive), the nestling cannot tell whether or not its parent intended to feed it.

The expression for nestling fitness  $F_c(x,1,t)$  when the parent does not attempt feeding becomes

$$F_c(x,1,t) = \sigma_{p0}\tilde{F}_c(x,1,t;0) + (1-\sigma_{p0})\tilde{F}_c(x,0,t;0) \quad (15)$$

where the first term corresponds to parent survival in period  $t$ , and the second to parent death.

The parent's optimal (ESS) decision maximizes the sum

$$F_c(x,1,t) + RS_p(x,t) \quad (16)$$

(where  $R$  denotes the parent's future reproductive value) with respect to the decision whether to attempt feeding. Here  $F_c$  and  $S_p$  are given by Equations 10 and 11 for the decision to feed and by Equations 15 and 14 for the nonfeeding decision, respectively.

To complete the dynamic ESS algorithm we only need to specify the terminal values at the end of the season,  $t = T+1$ . Equations (1) and (2) imply immediately that

$$F_c(x,z,T+1) = \rho(x)\phi(x) \quad (17)$$

$$S_p(x,T+1) = 1 \quad (18)$$

Equations 7–18 specify the dynamic programming algorithm for determining the dynamic ESS.

## Results

We applied the foregoing model to the feeding and fledging behaviour of dovekeys. Parameter values for this species are summarized in Table 2.

Measures of hatching weight ( $x_0$ ), nestling growth rate ( $g_0$ ), and weight loss rate ( $\alpha$ ) were derived from several sources in Harris and Birkhead (1985) and Gaston (1985). Bradstreet (1982) provides an estimate of the ocean growth rate ( $g_1$ ). The preferred fledging weight ( $x_f$ ) is derived from Stempniewicz (1980), while the critical weight for future survival ( $x_c$ ), and the time horizon ( $T$ ) are guesses based on the biology of the species. Daily survival probabilities ( $\sigma_{c0}$ ,  $\sigma_{c1}$ ,  $\sigma_{p0}$ ,  $\sigma_{p1}$ )



Table 2. Parameter values for the dynamic ESS model applied to the dovekie.

Parameter	Meaning	Value
$g_0$	average daily growth in nest	5.0 g day <sup>-1</sup>
$g_1$	daily growth at sea	1.4 g day <sup>-1</sup>
$\alpha$	daily weight loss in nest if not fed	4.0 g day <sup>-1</sup>
$p$	probability of food delivery per day	(parameter)*
$x_0$	nestling's weight on hatching	20 g
$x_c$	critical weight for future survival	150 g
$x_f$	preferred fledging weight	110 g
$T$	time horizon (end of nesting season)	60 days
$\sigma_{c0}$	offspring daily survival probability in nest	0.999
$\sigma_{c1}$	offspring daily survival probability at sea	0.995
$\sigma_{p0}$	parent's daily survival probability, not feeding	0.99985
$\sigma_{p1}$	parent's daily survival probability, feeding	0.997
$R$	parent's future reproductive value	(parameter)*

\* These parameters are assigned a range of values; see Figures 2 and 3.

are not available for dovekies, and our values are guesses based on our work with other northern alcids (see Ydenberg, 1989; Clark & Ydenberg, 1990).

The model's output is a plot in  $x, t$  space showing regions in which different behavioural choices are optimal. Figures 2 and 3 show the model's predictions under various parameter combinations. The parent's and offspring's strategies are combined in these figures; each contains regions denoted 'Zero fitness', 'Feed', 'Fledge', and 'Nest', in which different behavioural strategies are used, as defined in Table 3.

Table 3. Evolutionarily stable strategies shown in Figures 2 and 3.

Region	Parent's strategy	Nestling's strategy
Zero fitness	Abandon	—
Feed	Attempt to feed	Remain in nest
Fledge	Do not feed	Fledge
Nest	Do not feed	Remain in nest

The base-case dovekie model (Fig. 2) uses the parameter values

$$p = 0.7, R = 1$$

Terminal fitness is given by

$$\phi(x) = \begin{cases} 0 & x < x_c \\ 1 & x \geq x_c \end{cases} \quad (19)$$

and the probability of surviving the act of fledging is

$$\rho(x) = \begin{cases} 1 & x < x_f \\ 1 - 0.1(x - x_f) & x \geq x_f \end{cases} \quad (20)$$

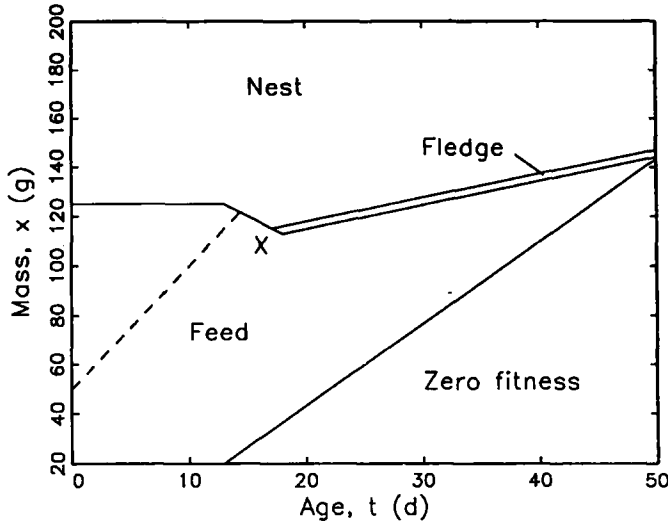


Figure 2. ESS diagram for dovekie parent-offspring behaviour. 'Zero fitness': nestling cannot survive; 'Feed': parent attempts to feed nestling; 'Nest': nestling remains in nest, but parent does not feed; 'Fledge': nestling fledges. The dashed curve depicts an average nestling growth trajectory, exhibiting overfeeding. Fledging occurs at point X. (Parameter values given in Table 2, with  $p = 0.7$ ,  $R = 1.0$ .)

The different regions shown in Fig. 2 are readily explained. First, in the region labeled 'Zero fitness' the nestling is underweight, has little or no hope of attaining the minimal mass for survival ( $x_c$ ), and is abandoned by the parent. When the nestling's mass and age lie in the 'Feed' region the parent feeds the nestling (or attempts to), and the nestling remains in the nest. In this region at least some feeding by the parent is necessary for the nestling to reach the critical weight  $x_c = 150\text{g}$  by day 50, the end of the season.

The lines on the boundaries of the 'Fledge' region have slope equal to  $g_1$  ( $= 1.4\text{ g day}^{-1}$ ). If the nestling's mass-age point  $(x, t)$  enters the region 'Fledge' the nestling immediately fledges, and subsequently grows at  $1.4\text{ g day}^{-1}$ , reaching a terminal weight  $X(T+1) \geq x_c$ , so that  $\phi(X(T+1)) = 1$  (subject to survival during and after fledging).

The dashed curve shown in Fig. 2 represents an average growth curve for a nestling, starting from post-hatching weight  $X(0) = 50\text{ g}$ , corresponding to dovekie nestling weight approximately six days after hatching. (Because of the randomness of food deliveries, an actual weight trajectory would tend to wander, like a random walk, around the average trajectory shown in Fig. 2). When the growth curve intersects the boundary between the 'Feed' and 'Nest' regions, parental feeding is reduced and nestling weight then declines to the point labeled 'X', at which time fledging takes place. Post-fledging growth, at  $1.4\text{ g day}^{-1}$ , follows the boundary between the 'Fledge' and 'Nest' regions, reaching the critical mass  $150\text{ g}$  at  $T = 50$  days.

This overall growth profile (pre- and post-fledging) agrees closely with the observations of Stempniewicz (1980), including in particular the mass recession prior to fledging (see Fig. 1). The period of mass recession is preceded by a period of 'overfeeding' on the part of the parent, in the sense that the nestling's mass temporarily exceeds the level necessary to reach the critical end-of-season mass of  $150\text{ g}$ .

Why does the parent overfeed the nestling? Several tradeoffs are in fact involved in this decision; versions of our model that did not involve all these tradeoffs failed to predict

overfeeding. First, from the nestling dovekie's point of view, remaining in the nest is preferable on two accounts: daily mortality risk is lower, and the rate of growth is greater than it would experience outside the nest. On the other hand, the risk incurred in the act of fledging increases with body weight, so that there is an optimal fledging weight of  $x_f = 110$  g. Nevertheless the parent continues to feed the nestling until its weight reaches about 120 g. This overfeeding allows the nestling to remain in the nest several extra days, after which it fledges at the optimal weight of 110 g. Keeping the offspring in the nest increases its overall survival probability, at the cost of a (slight) increase in parental mortality. With the assumed parameter values, the parent's total fitness is maximized by having the offspring remain in the nest for this additional period.

Still, the offspring could be kept in the nest without actually overfeeding it. The explanation for overfeeding lies in the uncertainty of food availability and of parental survival. By overfeeding, the parent ensures that the offspring will be able to stay in the nest for several additional days in the event that food is not obtained, or that the parent is killed. According to our estimated parameters, the advantage to the offspring of remaining in the nest is about 0.5% per day in terms of mortality risk. Thus, although the model does predict a selective advantage to remaining in the nest, the advantage is rather small. Our post-fledging mortality estimate ( $\sigma_{cl} = 0.995$  per day) is a time-average; it seems likely that mortality risk would actually be at a maximum for young, light-weight fledglings. If so, the advantages of remaining in the nest would be strengthened.

The predictions of our model are of course sensitive to the assumed parameter values. Table 4 indicates how the overfeeding prediction depends qualitatively on certain parameters; the results are all intuitively reasonable. (Given the limited accuracy of our parameter estimates, quantitative sensitivity tests, though possible, would be of little interest here.) For example, an increase in parent's reproductive value  $R$  results in less intensive parental care, i.e. reduced overfeeding of the nestling. Similar predictions were obtained for non-game-theoretic models of parental care, by Clark and Ydenberg (1990) and Hom *et al.* (1990). The sensitivity of overfeeding to other parameters is indicated in Table 4. For example, a reduction in the variance of food supply (corresponding to an increase in the value of  $p$ , in our model) results in a shrinking of the region in  $x, t$  space where 'overfeeding' occurs; zero variance implies no overfeeding.

Table 4. Effects of parameter changes on the prediction of overfeeding of nestlings.

Parameter	Effect of increasing the parameter on the degree of overfeeding
$R$ = parent's reproductive value	reduced
$p$ = daily probability of food delivery	reduced
$x_f$ = optimal fledging weight	increased
$\sigma_{pl}$ = parental mortality risk, while feeding nestling	reduced
$\sigma_{cd}$ = nestling's mortality rate	reduced

Figure 3 shows the effect on the ESS of altering the shape of the fledging survival function  $\rho(x)$ ; in this figure  $\rho = \text{constant}$ , so that there is no advantage in fledging at a mass smaller than  $x_c = 150$ g. Consequently the chick remains in the nest up to the final age considered, 50 days; overfeeding and mass recession prior to fledging are observed.

Figure 2 also provides an explanation for another known feature of dovekie fledging behaviour. Stempniewicz (1980) reports that the pre-fledging weight recession is reduced or

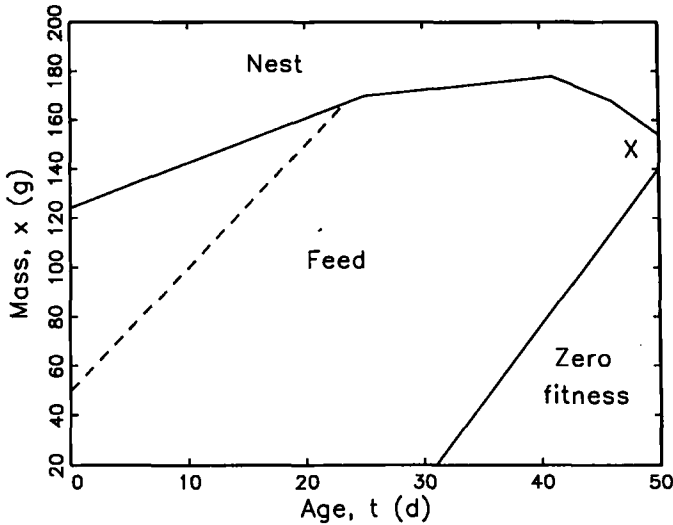


Figure 3. Same as Figure 2, except that risk of fledging does not increase with fledging mass. Nestling is overfed and remains in nest until fledges at  $t = T, X = 150$  g (point X in the figure).

absent in late-season nestlings. The growth trajectory of a late-season (i.e. little time remaining until  $T$ ) nestling can be depicted by moving the dotted line in Figure 2 to the right. As this is done it can be seen that the predicted pre-fledging weight recession shrinks and then disappears entirely. Indeed, the model suggests that late-season chicks should fledge at greater weights than mid-season chicks. The reason is that in order to reach  $x_c$  by  $T$  extra growth must be completed in the nest before going to sea, where growth is slower. A seasonal *increase* in fledging weight has not been reported for dovekies, but the striking seasonal decline in fledging weight observed in most other northern seabirds (see Birkhead and Harris, 1985; Ydenberg, 1989) has not been reported either.

## Discussion

A full understanding of behavioural interactions between parents and their offspring must make allowances for conflicts resulting from the difference between parental and offspring fitness. In this paper we show how traditional static ESS models of parent-offspring conflict can be broadened to include dynamic phenomena; we use feeding and fledging behaviour as an illustration. The dynamic modelling framework also facilitates the analysis of the multiple tradeoffs inherent in any behavioural situation; our model of feeding and fledging behaviour involves tradeoffs between relative growth and mortality rates of nestlings and fledglings, mortality risks to parents, dependence of fledging risk on mass at fledging, and dependence of offspring long-term survival on mass achieved by the end of the breeding season. The key simplification making our dynamic programming model tractable involves the assumption of alternating sequential decisions of parents and offspring. This assumption removes much of the ambiguity inherent in simultaneous decisions; it seems a natural assumption in the setting of parent-offspring conflict, and may also be appropriate for other types of conflicts. For example Enquist *et al.* (1985) use the idea of alternating decisions in their analysis of fighting in fulmar (*Fulmarus glacialis*) contests (see also Enquist and Leimar 1983; 1987).

All variables and parameters in our model possess operational meaning in biological terms and could be measured in the field. By varying the parameter values within reasonable limits we can predict a wide variety of juvenile life histories, from fledging immediately after hatching to reaching near-adult weight in the nest. Stochastic environmental influences on feeding on fledging behaviour can also be investigated. Variation of behaviour within and between species can be thus understood as adaptations to different environmental conditions, regarding food availability and predation risks.

The dovekie case study that we have outlined involves considerable complexity in the form of multiple tradeoffs. Our model involves all of these tradeoffs, and leads to the conclusion that overfeeding may constitute a hedge against uncertain or variable food supplies, allowing the nestling to complete its development in the nest even in the event that the parent is unable to deliver food up to the optimal fledging date. Also overfeeding may increase the nestling's probability of survival in the event that the parent is killed or injured. Thus overfeeding and mass recession may be true behavioural phenomena rather than the consequences of some physiological constraint affecting nestling development.

Most of the tradeoffs considered in this paper are common to the biology of other seabird species. However altering some of the tradeoffs leads to different behavioural patterns. For example, black guillemots (*Cepphus grylle*) differ from dovekies in several aspects of their biology, and nestlings behave differently. Black guillemots are unusual among alcids in nesting in small and scattered groups. Predators do not congregate around these small groups, and feeding visits to the nest are not likely to be as dangerous for black guillemots as for dovekies. Parents can sustain a high delivery rate to the nest as a consequence of their inshore feeding habits. Altering the tradeoffs in this way suggests that parents should not be reluctant to feed their offspring in the nest, and that nestlings should be reluctant to leave the nest. As we would expect, black guillemot chicks do in fact remain in the nest until fully grown. Also as expected, since the tradeoffs leading to overfeeding and mass recession remain intact for this species, black guillemot chicks undergo a pre-fledging mass recession. Thus the framework developed here can readily accommodate and predict the behaviour of species other than dovekies; it could be applied, in principle, to any situation in which parents provision their offspring.

## References

- Bradstreet, M. S. W. (1982) Pelagic feeding ecology of dovekies, *Alle alle*, in Lancaster Sound and Western Baffin Bay. *Arctic* **35**, 126–40.
- Clark, C. W. and Ydenberg, R. C. (1990). The risks of parenthood. I. General theory and applications. *Evolutionary Ecology* **4**, 21–34.
- Daan, S. and Tinbergen, J. (1979) Young guillemots (*Uria lomvia*) leaving their arctic breeding cliffs: a daily rhythm in numbers and risk. *Ardea* **67**, 96–100.
- Enquist, M. and Leimar, O. (1983) Evolution of fighting behavior: decision rules and assessment of relative strength. *J. Theoret. Biol.* **102**, 387–410.
- Enquist, M. and Leimar, O. (1987) Evolution of fighting behavior: the effect of variation in resource value. *J. Theoret. Biol.* **127**, 187–205.
- Enquist, M., Plane, E. and Røed, J. (1985) Aggressive communication in fulmars (*Fulmarus glacialis*) competing for food. *Anim. Behav.* **33**, 1007–20.
- Evans, P. G. H. (1981) Ecology and behaviour of the little auk *Alle alle* in West Greenland. *Ibis* **123**, 1–18.
- Gaston, A. J. (1985) Development of the young in the Atlantic Alcidae. In: *The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Waters* (D. N. Nettleship and T. R. Birkhead, eds), pp. 319–54. London: Academic Press.
- Harris, M. P. (1984) *The Puffin* Calton: Poyster.

- Harris, M. P. and Birkhead, T. R. (1985) Breeding ecology of the Atlantic Alcidae. In: *The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Waters*. (D. N. Nettleship and T. R. Birkhead, eds), pp. 156–204. London: Academic Press.
- Harris, M. P. and Rothery, P. (1985) The post-fledging survival of young puffins, *Fratercula arctica*, in relation to hatching date and growth. *Ibis* **127**, 243–50.
- Hom, C. L., Willits, N. H. and Clark, C. W. (1990) Fitness consequences of nest defense in plethodontid salamanders: predictions of a dynamic optimization model. *Herpetologia* (in press).
- Houston, A. I. and MacNamara, J. M. (1987) Singing to attract a mate – a stochastic dynamic game. *J. Theoret. Biol.* **129**, 57–68.
- Houston, A. I. and MacNamara, J. M. (1988) Fighting for food: a dynamic version of the Hawk-Dove game. *Evolutionary Ecology* **2**, 51–64.
- Mangel, M. and Clark, C. W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton: Princeton University Press.
- Maynard Smith, J. (1982) *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Nettleship, D. N. and Birkhead, T. R. (eds.) (1985) *The Atlantic Alcidae: the Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Waters*. London: Academic Press.
- Parker, G. A. (1984) Evolutionarily stable strategies. In: *Behavioral Ecology*. (J. R. Krebs and N. B. Davies, eds), pp. 30–61. Oxford: Blackwell.
- Parker, G. A. and MacNair, M. R. (1978) Models of parent-offspring conflict. I. Monogamy. *Anim. Behav.* **26**, 97–110.
- Parker, G. A. and MacNair, M. R. (1979) Models of parent-offspring conflict. II. Suppression: evolutionary retaliation of the parent. *Anim. Behav.* **27**, 1201–35.
- Perrins, C. M., Harris, M. P., and Britton, C. K. (1973) Survival of Manx shearwaters *Puffinus puffinus*. *Ibis* **115**, 535–48.
- Roby, D. D., Brink, K. L. and Nettleship, D. N. (1981) Measurement of chick meals and breeding distribution of dovekeys (*Alle alle*) in northwest Greenland. *Arctic* **34**, 241–8.
- Sealy, S. G. (1972) Adaptive differences in breeding biology in the marine bird family Alcidae. Dissertation, University of Michigan, Ann Arbor, MI.
- Sealy, S. G. (1973) Adaptive significance of post-hatching development patterns and growth rates in the Alcidae. *Ornis Scandinavica* **4**, 113–21.
- Stempniewicz, L. (1980) Factors influencing the growth of the little auk *Plautus alle* (L.) nestlings in Spitsbergen. *Ekologika Polska* **28**, 557–81.
- Trivers, R. L. (1974) Parent-offspring conflict. *Amer. Zool.* **14**, 249–64.
- Ydenberg, R. C. (1989) Growth-mortality tradeoffs and the evolution of juvenile life histories in the Alcidae. *Ecology* **70**, 1494–1506.