

A DYNAMIC PROGRAM FOR MALE PARENTAL CARE IN FISHES: BROOD CYCLING AND FILIAL CANNIBALISM

by

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(With 2 Figures)
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Summary

We constructed a dynamic programming model to investigate the phenomena of brood cycling and filial cannibalism in fishes with paternal care. We assumed that parents behave so as to maximize their total expectation of hatching clutches during a breeding season plus a small probability of breeding in future seasons. We further assumed ecological tradeoffs among fitness components such that investment in one component of fitness results in a reduction in other fitness components. We found that the pattern of brood cycling was most strongly affected by mating costs to survival of the parent and survival of the eggs in the nest. Filial cannibalism was most strongly affected by feeding costs to parent and nest survival. Brood cycling appeared to be independent of feeding costs, and filial cannibalism appeared to be independent of mating costs.

Introduction

During the breeding season, animals may be confronted with the conflicting demands of avoiding predators, feeding, mating, and caring for offspring. Fishes with exclusive male parental care (*i.e.* paternal care) are particularly interesting in this regard, because a male fish that is defending his offspring faces all of these conflicting demands simultaneously. In 1953, VAN IERSEL conducted a classic series of experiments on the conflicting demands that affect the parental behaviour of the threespine stickleback, *Gasterosteus aculeatus*. VAN IERSEL discovered an interesting phenomenon, which he termed the 'parental phase' of the male stickleback

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breeding cycle. After the eggs are a certain age, or after the male has a certain number of clutches, he will cease courting females and exhibit a heightened level of parental care, until all of the eggs have hatched. Then the male may rebuild his nest and initiate another brood cycle. VAN IERSEL (1953) found that male sticklebacks switch into the parental phase after the eggs are roughly 3-6 days old, even if the male only has one female's clutch of eggs in his nest. He also found that the level of male courtship (*i.e.* zig-zags) decreases as clutch age increases, and as clutch number increases.

Brood cycling in fishes with paternal care can be highly variable among species. At one end of the spectrum is the smallmouth bass, *Micropterus dolomieu*, in which males typically care for a single females brood per season (RAFFETTO *et al.*, 1990; MACKERETH, 1995; RIDGWAY, pers. comm.). At the other end of the spectrum are Mediterranean blennies, *Aidablennius sphyinx*, in which males are never known to enter a parental phase (KRAAK & VIDELER, 1991; KRAAK, 1994). Between these two extremes lie fathead minnows, *Pimephales promelas*, in which males acquire eggs over a period of several days, cease courtship for one or two days while the older eggs hatch, and then resume courtship again before the younger eggs have hatched (SARGENT, unpubl.).

SARGENT (1990) presented a preliminary version of a dynamic-programming model for fishes with paternal care. The time horizon was an entire breeding season, and a hypothetical fish was allowed to choose its behaviour so as to maximize its total expectation of hatching clutches over the whole breeding season. A preliminary run of the model yielded nest-state dynamics very similar to those described by VAN IERSEL (1953) for the threespine stickleback. One of the models assumptions was that the survival of eggs in a males nest is lowered if he courts additional females. This assumption appears to be justified, because threespine stickleback nests (*e.g.* SARGENT, 1982) and fathead minnow nests (SARGENT, unpubl.) are very vulnerable to nest raiding and egg predation during courtship. This cost of mating for clutch survival was shown to have a major impact on when males shift into the parental phase in SARGENT's (1990) model. What was not addressed in SARGENT's (1990) preliminary analysis of his model was the relative importance of different ecological parameters to the pattern of brood cycling, nor whether the

model could address the interspecific diversity of brood cycling in fishes with paternal care that is observed in nature.

In a very interesting paper, ROHWER (1978) proposed his theory of filial cannibalism for fishes with paternal care, where filial cannibalism is defined as a parent eating its own offspring. ROHWER made two basic assumptions. (1) Nesting male fishes are food limited and forced to fast; and, (2) a male's own offspring may be an alternative source of food. ROHWER proposed that a filial cannibal trades off present offspring against an energetic investment into some future component of reproductive success. ROHWER's verbal model can be condensed to four basic predictions (SARGENT, 1992). (1) Filial cannibalism should decrease as clutch age increases, because older clutches are closer to hatching, and thus of higher value to the parent. (2) Filial cannibalism should decrease as energy reserves increase. Parents should eat their own offspring only as a last resort, which would be more likely when the parent is low on energy reserves. (3) If filial cannibalism represents an investment into future brood cycles, then total filial cannibalism (*i.e.* a male consuming all of his eggs) may be favored. The likelihood of total filial cannibalism should increase as clutch size decreases, because a clutch's value to a parent increases as its size increases. (4) If filial cannibalism represents an investment into the current brood cycle (*e.g.* if the parent needs to feed in order to complete its brood cycle), then partial filial cannibalism (*i.e.* a male consuming some, but not all, of his eggs) may be favored. The likelihood of partial filial cannibalism should increase as clutch size increases. This is because the effects of partial filial cannibalism should be more dilute in larger clutches.

SARGENT (1992) constructed a dynamic-programming model to investigate the adaptive bases for filial cannibalism. The state variables were parental energy reserve and clutch number. All clutches were the same age, and the time horizon was a single brood cycle. As in previous dynamic-programming models for parental care (SARGENT, 1990), parental care increases, and feeding decreases, as clutch number increases, as clutch age increases, and as parental energy reserve increases. Each of the four predictions on filial cannibalism was corroborated by SARGENT's (1992) model. Moreover, there is also empirical evidence for each prediction (DEMARTINI, 1987; HOELZER, 1992; MROWKA, 1987; PETERSON & MARCHETTI, 1989; SARGENT, 1988, 1989). What was not addressed in

SARGENT's (1992) model is filial cannibalism in nests where clutches vary in age, and where the time horizon is an entire breeding season.

We constructed a dynamic-programming model to address the following questions.

- (1) What ecological parameters affect brood cycling and filial cannibalism, and what is the relative importance of each parameter?
- (2) What explains the diversity of brood cycling that is observed in nature?

The model: feed, eat eggs, mate or care?

In order to investigate the phenomena of brood cycling and filial cannibalism in fishes with paternal care, we constructed a stochastic dynamic-programming model (*e.g.* see HOUSTON & McNAMARA, 1988; MANGEL & CLARK, 1988), which is an elaboration of the model, *Feed, mate or care?*, of SARGENT (1990). Dynamic programming is a dynamic-optimization technique. Dynamic optimization in behavioural ecology uses a state-space approach to model behaviour and ontogeny (McFARLAND & HOUSTON, 1981; McFARLAND, 1982). With this approach, behavioural ecologists can model several kinds of behaviour simultaneously, and examine their consequences in terms of a common currency such as lifetime reproductive success. Dynamic optimization allows decision variables (*e.g.* the particular behaviour chosen from the strategy set) to depend on state variables (*e.g.* hunger, energy reserves, body size, offspring number, offspring age), which in turn depend on past behavioural decisions. Dynamic optimization finds behavioural trajectories through an individual's lifetime (STEPHENS & KREBS, 1986).

There are six essential components of dynamic optimization models (OSTER & WILSON, 1978; MANGEL & CLARK, 1988; SARGENT, 1990). These are: i. *the optimization criterion*: the currency being maximized; ii. *the strategy set*: the set of behavioural options available to an animal; iii. *the state space*: all combinations of magnitudes of variables that depend cumulatively on past decisions, and that determine the present optimal policy; iv. *the constraints*: the limitations on the state space; v. *the state dynamics*: the rules for moving through the state space; vi. *the tradeoffs*: the biotic or abiotic factors that constrain an animal's ability to maximize all of its options simultaneously. In order to construct and solve a dynamic optimization model, we need to explicitly specify each of these components.

Dynamic-programming models are solved by iterating backward through time, following BELLMAN's (1957) principle of optimality: "An optimal policy has the property that, whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision". Another way to think of this is that the optimal trajectory from some initial time, t , to some final time, T (the time horizon), contains the optimal trajectory from time $T-1$ to T . Thus, to find the optimal trajectory from t to T , we first find the optimal trajectory from $T-1$ to T , then the optimal trajectory from $T-2$ to $T-1$, and so on back to $t = 0$. The basic task of constructing a dynamic-programming model is in specifying a recursion equation known as the dynamic-programming equation, or *DPE*. Specifying the *DPE* first requires specifying the state dynamics. In our model, we use two state variables: i. parental state (*i.e.* energy reserves), and ii. nest state (*i.e.* a combination of number of clutches and their ages within a parent's nest).

At each time t , for each level of parental state, $X(t)$, and nest state, $Y(t)$, we can find a behaviour $B^*(t, X(t), Y(t))$ that maximizes fitness, $F(t, X(t), Y(t))$, where the maximum is written as F^* . This requires that we already know $F^*(t+1, X(t+1), Y(t+1))$, for all possible $X(t+1)$ and $Y(t+1)$. $B^*(t, X(t), Y(t))$, $X(t)$, and $Y(t)$ jointly determine $X(t+1)$ and $Y(t+1)$. The recursions for the two state variables and for fitness, in general form, are:

$$X(t+1) = f_1[t, B(t, X(t), Y(t)), X(t), Y(t)], \quad (1)$$

$$Y(t+1) = f_2[t, B(t, X(t), Y(t)), X(t), Y(t)], \text{ and} \quad (2)$$

$$F(t, X(t), Y(t)) = f_3[t, B(t, X(t), Y(t)), F^*(t+1, X(t+1), Y(t+1))], \quad (3)$$

where f_1 , f_2 , and f_3 represent functions. Equations (1) and (2) specify the state dynamics, and equation (3) is the dynamic programming equation (*DPE*).

To solve the *DPE*, we begin by initializing our terminal fitnesses at the time horizon, T . Terminal fitness is zero if the animal is dead at the time horizon; otherwise it may be positive, and represents future reproduction after time T . In our model, we assume that terminal fitness is an increasing function of energy reserves. Starting at $T-1$, we then iterate backward over time over all combinations of our state variables, and find the optimal behaviour for each time step. We begin by finding the optimal behaviours and the associated fitnesses for all combinations of the state

variables for $T-1$. Once this is achieved, we now have a new set of terminal fitnesses. We then repeat the process for $T-2$, and so on back to $t = 0$.

Within a time step, we assume the following general sequence of events: i. choose the behaviour for that time step; ii. tally reproduction and/or offspring survival; iii. update parental energy reserves; iv. tally parental survival.

Now, let us consider the case of fishes with exclusive paternal care. Male fishes who are guarding eggs may be confronted with the conflicting demands of avoiding predators, feeding, caring for eggs already in the nest, and increasing the number of female clutches in the nest through additional matings. Here, we illustrate how brood cycling and filial cannibalism can be explained within the framework of conflicting demands in a dynamic optimization problem. We let the time horizon, T , represent the end of the breeding season.

The six components of the dynamic-programming model are as follows:

1. Optimization criterion, $F(t, X(t), Y(t))$. We assume that an animal behaves so as to maximize its total expectation of lifetime reproductive success. The model maximizes the sum of all clutches hatched during the breeding season plus terminal fitness at the end of the season.
2. Strategy set, $B(t, X(t), Y(t))$. The alternatives are sixteen behaviours and behaviour combinations: i. *Hide*, ii. *Feed*, iii. *Eat eggs*, iv. *Mate vs care*, vi. *Feed & eat eggs*, vii. *Feed & mate*, viii. *Feed & care*, ix. *Eat eggs & mate*, x. *Eat eggs & care*, xi. *Mate & care*, xii. *Feed, eat eggs & mate*, xiii. *Feed, eat eggs & care*, xiv. *Feed, mate & care*, xv. *Eat eggs, mate & care*, and xvi. *Feed, eat eggs, mate & care*.
3. State space, $(X(t), Y(t))$. The state variables are parental male energy reserves ($X(t)$), and the number and ages of clutches in his nest ($Y(t)$).
4. Constraints. Paternal energy reserves are constrained as follows: $0 \leq X(t) \leq N$, where N is the upper limit of energy reserves. Nest state is constrained as follows. It takes a male one time step to obtain one clutch, and it takes a clutch three time steps to hatch and be independent of paternal care. Thus, there are eight possible nest states: 0 , no clutches; 1 , one clutch of age 1; 2 , one clutch of age 2; 3 , one of clutch age 3; 12 , two

clutches of ages 1 and 2; 23, two clutches of ages 2 and 3; 13, two clutches of ages 1 and 3; 123, three clutches of ages 1, 2, and 3.

5. State dynamics.

i. Parental energy reserves: parental energy reserves at $t+1$ depend deterministically on the behaviour chosen; $X(t+1) = X(t) + \Delta X(B(t), X(t), Y(t))$. The behaviour-dependent changes in male state are based on the following rules. Each time step, a male pays a baseline metabolic cost of 1 unit of energy reserves (*i.e.* the cost of *Hiding*). To this baseline metabolic decrease one adds the increment or decrement for each individual behaviour. *Feeding* increments male state by +2 (*i.e.* $+2+(-1) = +1$); *Eating eggs* increments male state by +3, *Mating* decrements male state by -1; *Caring* decrements male state by -1. The male state changes for behaviours that represent combinations of individual behaviours are obtained by adding up the increments and decrements (*e.g.* *FMC*: -1 for basal metabolism, +2 for feeding, -1 for mating, -1 for caring, yields a total of -1). Note that we assume that *Eating eggs* increments male state more than *Feeding*. We make this assumption because our experience indicates that feeding opportunities for a guarding male are limited, and may require travel outside his territory. However, the eggs within a male's nest require no travel costs, and can represent a substantial food resource.

ii. Nest state: the number and ages of clutches in a male's nest depend stochastically on the behaviour chosen. Nest state may change due to the acquisition of one clutch through mating, the loss of one or more clutches due to predation or disease, the aging of one or more clutches to older age classes, and the hatching of an age 3 clutch. We further assume that if a male commits filial cannibalism, that he only eats one clutch per time step, and that he eats the youngest clutch in his nest.

6. Tradeoffs. The tradeoffs are produced by multiplicative probability-reducing coefficients, and by behaviour-dependent state dynamics for parental energy reserves (see above). Parental survival is reduced when multiplied by the decimal fraction p_f for *Feeding*, p_m for *Mating*, p_c for *Caring*, and by the products of these coefficients for the combined behaviours. Clutch survival is increased from u to w if the parent provides care. Clutch survival with care, w , is multiplied by the fraction q_f if the parent

Feeds, by q_m if the parent attempts to *Mate*, and by the product of these coefficients if the parent *Feeds & mates*.

Table 1 lists the model's parameters and their default values, and Table 2 lists each behaviour in the strategy set and its consequences for parental energy reserves, parental survival, and clutch survival. The fitness that a parental male fish would enjoy from choosing any behaviour can now be written as:

$$\begin{aligned}
 F(t, X(t), Y) = & \Pr(\text{age 3 clutch hatches in } t) + \\
 & \Pr(\text{male dies in } t) \sum_{i=1}^3 (\text{clutches hatch in } t + i) + \\
 & \Pr(\text{male survives } t) \sum_{j=1}^8 [\Pr(Y(t + 1) = j) F^* \\
 & (t + 1, X + \Delta X(B(t, X(t), Y(t))), j)] \}. \tag{4}
 \end{aligned}$$

A parent is assumed to choose the behaviour that maximizes equation (4). The first term on the right hand side of (4) tallies any age 3 clutch that hatches in time step t , which depends on the behaviour chosen, $B(t, X(t), Y(t))$.

The second term on the right hand side of (4) tallies the expected reproductive success if the male dies during t . Hatching in $t+1$ or $t+2$ assumes that the male obtained clutches in $t-2$ and $t-1$, respectively, and that these clutches have survived until t . The probability that these clutches survive through t depends on $B(t, X(t), Y(t))$. Their survival beyond t , after the male is dead, is the product of the u 's up until hatching.

The third term on the right hand side of (4) tallies expected reproductive success if the male survives through time step t . This term sums over all possible nest state transitions between t and $t+1$, which depend on $X(t)$, $Y(t)$, and $B(t, X(t), Y(t))$. These nest-state transition probabilities are

TABLE 1. The models parameters and their default values

$T = 30$	The time horizon or length of the breeding season in discrete time steps.
$N = 20$	The number of levels of parental energy reserves.
$P = 0.9$	Male survival through a time step.
$S = 0.6$	Probability that a male mates within a time step, given that he courts females.
$u = 0.3$	Clutch survival through a time step, without care.
$w = 0.9$	Clutch survival through a time step, with care. Generally $w \geq u$.
$p_m = 0.9$	Male survival coefficient if he courts females.
$p_f = 0.9$	Male survival coefficient if he feeds.
$p_c = 0.9$	Male survival coefficient if he cares.
$q_m = 0.9$	Clutch survival coefficient if the male courts females.
$q_f = 0.9$	Clutch survival coefficient if the male feeds.

TABLE 2. The sixteen behaviours in the strategy set, and their effects on parental energy reserve, parental survival, and clutch survival

Behaviour	Change in male state	Male survival	Clutch survival
<i>H (Hide)</i>	-1	<i>P</i>	<i>u</i>
<i>F (Feed)</i>	+1	<i>Pp_f</i>	<i>u</i>
<i>E (Eat eggs)</i>	+2	<i>P</i>	<i>u</i>
<i>M (Mate)</i>	-2	<i>Pp_m</i>	<i>u</i>
<i>C (Care)</i>	-2	<i>Pp_c</i>	<i>w</i>
<i>FE</i>	+4	<i>Pp_f</i>	<i>u</i>
<i>FM</i>	0	<i>Pp_fp_m</i>	<i>u</i>
<i>FC</i>	0	<i>Pp_fp_c</i>	<i>wq_f</i>
<i>EM</i>	+1	<i>Pp_m</i>	<i>u</i>
<i>EC</i>	+1	<i>Pp_c</i>	<i>w</i>
<i>MC</i>	-3	<i>Pp_mp_c</i>	<i>wq_m</i>
<i>FEM</i>	+3	<i>Pp_fp_m</i>	<i>u</i>
<i>FEC</i>	+3	<i>Pp_fp_c</i>	<i>wq_f</i>
<i>FMC</i>	-1	<i>Pp_fp_mp_c</i>	<i>wq_fq_m</i>
<i>EMC</i>	0	<i>Pp_mp_c</i>	<i>wq_m</i>
<i>FEMC</i>	+2	<i>Pp_fp_mp_c</i>	<i>wq_fq_m</i>

then multiplied by their respective F^* s at $t+1$ for $X(t+1) = X(t)+\Delta X(B(t,X(t),Y(t)))$ and $Y(t+1) = j$. These nest state transition probabilities can be obtained from the following simple algorithm described in SARGENT (1990).

Consider nest state 123. For $a = 1$ to 3, let A_a be the probability of survival (aging) of a clutch of age a , and D_a be the probability of death of a clutch age a ; $0 \leq A_a \leq 1$ and $D_a = 1-A_a$. Let S be the probability of mating and N be the probability of not mating (*i.e.* $N = 1-S$); $0 \leq S \leq 1$ if $B(t,X(t),Y(t))$ incorporates mating; otherwise, $S = 0$. The values for S and A_a (and thus for N and D_a) depend on the behaviour chosen from the strategy set, and can be calculated from the parameters in Table 1. To find all possible transition probabilities we expand the following expression:

$$(S + N) \prod_{a=1}^3 (A_a + D_a) = SA_1A_2A_3 + SA_1A_2D_3 + SA_1D_2A_3 + SA_1D_2D_3 + SD_1A_2A_3 + SD_1A_2D_3 + SD_1D_2A_3 + SD_1D_2D_3 + NA_1A_2A_3 + NA_1A_2D_3 + NA_1D_2A_3 + NA_1D_2D_3 + ND_1A_2A_3 + ND_1A_2D_3 + ND_1D_2A_3 + ND_1D_2D_3. \tag{5}$$

For the case of nest state 123, the sixteen terms on the right hand side of equation (5) can be combined to give the eight nest state transition probabilities. For example, the first two terms sum to the probability that

123 is the nest state in the next time step, where S is the probability that the parent mates and gains a new age 1 clutch; A_1 and A_2 are the probabilities that age 1 and age 2 clutches survive to age 2 and age 3, respectively; A_3 is the probability that an age 3 clutch hatches, and D_3 is the probability that an age 3 clutch dies. Similarly, the remaining seven pairs of terms give the transition probabilities to the following nest states, respectively: 12 , 13 , 1 , 23 , 2 , 3 , and 0 .

For nest states at time t with one or more missing clutch age classes, we simply let $A_a = 0$ and $D_a = 1$ for each missing age class. For example, let us assume that at time t that the nest state is 1 . Then there are four possible nest states at time $t+1$: 0 , 1 , 2 , and 12 . The first two pairs of terms on the right hand side of equation (5) sum to the transition probability to nest state 12 ; the third and fourth pairs of terms sum to the transition probability to nest state 1 ; the fifth and sixth pairs of terms sum to the transition probability to nest state 2 ; and, the last two pairs of terms sum to the transition probability to nest state 0 . In a similar manner, equation (5) can be used to determine the nest state transition probabilities at time $t+1$ for each initial nest state at time t .

Equation (4) is the *DPE*. To solve the *DPE*, we initialized the terminal fitness function at the end of the breeding season. Terminal fitness was set as follows: $\phi(X(T)) = 0.001X(T)$. This terminal fitness function assumes a small probability of future breeding seasons, which is an increasing function of energy reserves remaining at the time horizon. Then, starting from $T-1$, we iterated backward in time, over all combinations of parental state and nest state, to the beginning of the breeding season.

Figure 1 presents the results of the default run for $t = 1$, which illustrates VAN IERSEL's (1953) parental phase rather nicely. The breeding season was set at $T = 30$, and a stationary solution (see MANGEL & CLARK, 1988) was maintained from $t = 1$ to $t = 15$. Thus, we can use Fig. 1 to move through time for the first 15 time steps.

Let us assume that a parental male fish begins his breeding season with a nest state of zero clutches and maximum parental energy reserves (*i.e.* $Y(1) = 0$ and $X(1) = 20$). Here, the optimal behaviour is *Mate*. If the male mates successfully, then in the next time step his nest state and energy reserves are $Y(2) = 1$ and $X(2) = 18$ (see Table 2). Here the optimal behaviour is *Mate & care*. Now, consider two possibilities: the male either does or does not mate successfully; we will also assume that the first clutch survives. If the male is again successful in mating, and if his first clutch

The Default Run

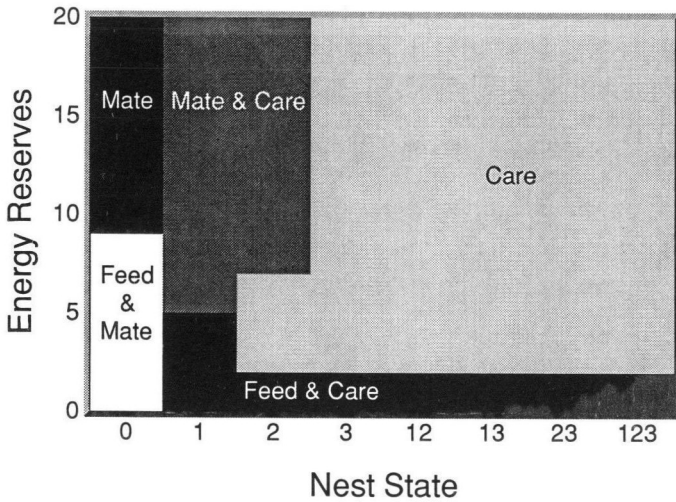


Fig. 1. *Feed, Eat eggs, Mate or Care?* The results of the default run for $t = 1$. Along the horizontal axis are the eight nest states, along the vertical are the levels of parental state, or energy reserves. This distribution of optimal behaviours was stationary and independent of time for the first 15 time steps of the 30 time-step breeding season. The likelihood of the parental phase increases as clutch number and clutch age both increase.

has survived, then in the next time step his nest state and energy reserves are $Y(3) = 12$ and $X(3) = 15$. Here the optimal behaviour is *Care*, and assuming no clutch mortality, *Care* remains the optimal behaviour until both clutches hatch. If the male fails to obtain the second clutch, and the first clutch has survived, then in the next time step his nest state and energy reserves are $Y(3) = 2$ and $X(3) = 15$. Here the optimal behaviour again is *Mate & care*. In fact, males with one clutch do not enter the parental phase until that clutch is age 3.

An alternative representation of the brood cycling produced by the default run is given in Fig. 2. We define a *target brood cycle* as the brood cycle that a male would achieve if he mates successfully every time step that he courts females, and if all of his clutches survive until hatching. In our default run, the target brood cycle is 0-1-12-23-3-0. However, if the male fails to mate given courtship, or if clutches die, then many alternative pathways are possible (Fig. 2).

Brood Cycling In The Default Run

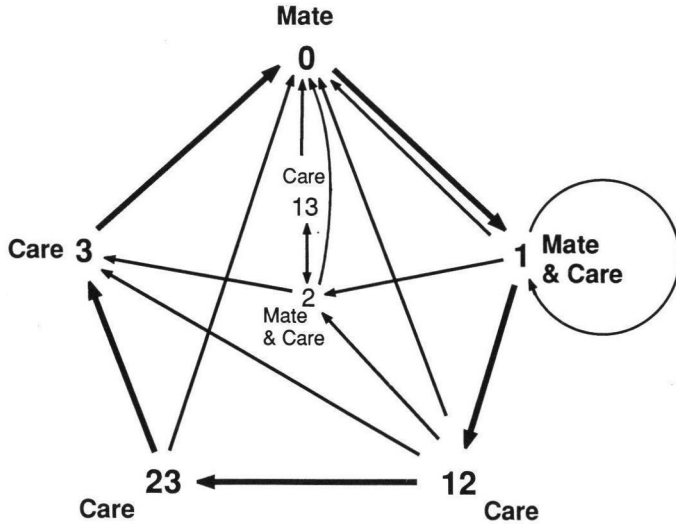


Fig. 2. Brood cycling in the default run. The target brood cycle is defined as the brood cycle that would be achieved if all courtship resulted in successful mating, and if all clutches survive until hatching. The target brood cycle is given in bold arrows; all alternative brood cycles are given in thin arrows. The optimal behaviour is given for each level of nest state.

Thus, we have found two characteristics of VAN IERSEL'S (1953) parental phase. Courtship decreases to zero as clutch age increases, and as clutch number increases. We hypothesized that van Iersel's parental phase is a special case of a larger phenomenon of brood cycling, and that brood cycling can be varied by varying our model's parameters. In order to test this hypothesis, we conducted a sensitivity analysis, where we manipulated each parameter over its entire range in units of 0.1. Although filial cannibalism (*i.e.* *Eat eggs*, alone, or in combination with other behaviours) was not observed in the default run (Fig. 1), we did find it in several runs of our sensitivity analysis. The results of our sensitivity analysis are summarized in Table 3.

Brood cycling

Most of the parameters in the model affect which nest states are in the parental phase, and thus the pattern of brood cycling. As a parameter is varied, nest states in the parental phase are accumulated in the following order: 123, 23, 13, 12, 3, 2, 1. Among our runs, we observed the entire

TABLE 3. Sensitivity analysis: nest states in the parental phase and with filial cannibalism

Parameter	Parental phase	Filial cannibalism
Adult survival - P		
0.0	2,3,12,13,23,123	none
0.1	2,3,12,13,23,123	none
0.2	2,3,12,13,23,123	123
0.3	2,3,12,13,23,123	123
0.4	2,3,12,13,23,123	123
0.5	2,3,12,13,23,123	123
0.6	2,3,12,13,23,123	123
0.7	3,12,13,23,123	none
0.8	3,12,13,23,123	none
0.9*	3,12,13,23,123	none
1.0	3,12,13,23,123	none
Mating probability - S		
0.0	1,2,3,12,13,23,123	none
0.1	1,2,3,12,13,23,123	none
0.2	1,2,3,12,13,23,123	none
0.3	2,3,12,13,23,123	none
0.4	2,3,12,13,23,123	none
0.5	3,12,13,23,123	none
0.6*	3,12,13,23,123	none
0.7	12,13,23,123	none
0.8	23,123	none
0.9	23,123	none
1.0	123	none
Clutch survival with care - w		
0.4	2,3,12,13,23,123	12,13,123
0.5	2,3,12,13,23,123	13,123
0.6	2,3,12,13,23,123	123
0.7	2,3,12,13,23,123	123
0.8	3,12,13,23,123	none
0.9*	3,12,13,23,123	none
1.0	3,12,13,23,123	none
Clutch survival without care - u		
0.0	2,3,12,13,23,123	123
0.1	2,3,12,13,23,123	123
0.2	3,12,13,23,123	none
0.3*	3,12,13,23,123	none
0.4	12,13,23,123	none
0.5	12,13,23,123	none
0.6	23,123	none
0.7	23,123	none
0.8	123	none

TABLE 3 (continued)

Parameter	Parental phase	Filial cannibalism
Male survival coefficient due to mating - p_m		
0.0	1,2,3,12,13,23,123	none
0.1	1,2,3,12,13,23,123	none
0.2	1,2,3,12,13,23,123	none
0.3	1,2,3,12,13,23,123	none
0.4	1,2,3,12,13,23,123	none
0.5	1,2,3,12,13,23,123	none
0.6	1,2,3,12,13,23,123	none
0.7	1,2,3,12,13,23,123	none
0.8	2,3,12,13,23,123	none
0.9*	3,12,13,23,123	none
1.0	123	none
Male survival coefficient due to feeding - p_f		
0.0	3,12,13,23,123	1,12,123
0.1	3,12,13,23,123	1,12,123
0.2	3,12,13,23,123	1,12,123
0.3	3,12,13,23,123	1,12,123
0.4	3,12,13,23,123	12,123
0.5	3,12,13,23,123	12,123
0.6	3,12,13,23,123	12,123
0.7	3,12,13,23,123	12,123
0.8	3,12,13,23,123	123
0.9*	3,12,13,23,123	none
1.0	3,12,13,23,123	none
Male survival coefficient due to caring - p_c		
0.0	2,3,12,13,23,123	none
0.1	2,3,12,13,23,123	none
0.2	2,3,12,13,23,123	123
0.3	2,3,12,13,23,123	123
0.4	2,3,12,13,23,123	123
0.5	2,3,12,13,23,123	123
0.6	2,3,12,13,23,123	123
0.7	2,3,12,13,23,123	123
0.8	3,12,13,23,123	none
0.9*	3,12,13,23,123	none
1.0	12,13,23,123	none
Clutch survival coefficient due to mating - q_m		
0.0	1,2,3,12,13,23,123	none
0.1	1,2,3,12,13,23,123	none
0.2	1,2,3,12,13,23,123	none
0.3	1,2,3,12,13,23,123	none
0.4	1,2,3,12,13,23,123	none
0.5	1,2,3,12,13,23,123	none
0.6	1,2,3,12,13,23,123	none
0.7	2,3,12,13,23,123	none
0.8	2,3,12,13,23,123	none
0.9*	3,12,13,23,123	none
1.0	none	none

TABLE 3 (continued)

Parameter	Parental phase	Filial cannibalism
Clutch survival coefficient due to feeding - q_f		
0.0	3,12,13,23,123	1,12,13,123
0.1	3,12,13,23,123	1,12,13,123
0.2	3,12,13,23,123	1,12,13,123
0.3	3,12,13,23,123	1,12,13,123
0.4	3,12,13,23,123	1,12,13,123
0.5	3,12,13,23,123	1,12,13,123
0.6	3,12,13,23,123	1,12,13,123
0.7	3,12,13,23,123	1,12,13,123
0.8	3,12,13,23,123	12,13,123
0.9*	3,12,13,23,123	none
1.0	3,12,13,23,123	none

The results of the sensitivity analysis. Relative to the default run, each of the models parameters was varied over its entire range in units of 0.1. Nest states that do not include mating but do include caring (*i.e.* C , FC , EC , FEC) are tallied under the parental phase. Nest states that do include eating eggs (*i.e.* E , FE , EM , EC , FEM , FEC , EMC , $FEMC$) are tallied under filial cannibalism. * 's refer to a parameter's value in the default run.

range of nest states in the parental phase from none to all but nest state \emptyset . Thus, our model generated eight different combinations of nest states in the parental phase, which in turn yielded six different target brood cycles (Table 4).

These target brood cycles ranged from mating once and caring until the clutch hatches to mating in every time step (Table 4). The typical stickleback brood cycle, of mating one or more times, and then going into a parental phase until all of the clutches have hatched, is at one end of the spectrum. At the other end, are target brood cycles that may go into a short parental phase after three clutches are accumulated, but resume courtship again before all of the clutches have hatched (Table 4).

As one would expect, mating costs to clutch survival (reflected in q_m) and to parental survival (reflected in p_m) have strong effects on the pattern of brood cycling (Table 3). Generally, as mating costs increase (*i.e.* as q_m or p_m decrease), the number of nest states in the parental phase increases.

Relative to our default run, as clutch survival with and without care (w and u , respectively) decrease, the number of nest states in the parental phase increases; however, the effect of clutch survival without care is stronger (Table 3). As clutch survival without care, u , increases toward clutch survival with care, w , there are fewer nest states in the parental phase, because the relative costs of mating while clutches are in the nest

TABLE 4. Brood cycles *versus* nest states in the parental phase

Nest states in parental phase	Target brood cycle
1,2,3,12,13,23,123 (bass)	0-1-2-3-0
2,3,12,13,23,123	0-1-12-23-3-0
3,12,13,23,123 (stickleback)	0-1-12-23-3-0
12,13,23,123	0-1-12-23-3-1
13,23,123	0-1-12-123-23-3-1
23,123 (minnow)	0-1-12-123-23-3-1
123	0-1-12-123-23-13-12
None (blenny)	0-1-12-123-123

The combinations of nest states in the parental phase that were generated by the model and the corresponding target brood cycles. The target brood cycle is defined as the brood cycle that would be achieved if all courtship leads to mating, and if all clutches survive until hatching. The first three target brood cycles in the table cycle through nest state 0; mating resumes after all of the clutches in the nest have hatched. The rest of the target brood cycles resume mating before all of the clutches have hatched.

are decreasing. As clutch survival with care, w , decreases toward clutch survival without care, u , the number of nest states in the parental phase increases slightly, because the relative costs of mating while clutches are in the nest are increasing.

The number of nest states in the parental phase also increases as the probability of mating (S) decreases; as adult survival (P) decreases; and, as the cost of care to parent survival increases (as p_c decreases).

To examine the relative importance of mating costs for the appearance of the parental phase, we set these costs to zero (*i.e.* we set $q_m=1$ and $p_m=1$), and manipulated each of the other parameters known to affect the parental phase in Table 3 (*i.e.* P , S , u , w , and p_c), independently of one another. With zero mating costs we only found the parental phase when the probability of mating, S , was zero. Thus, p_m and q_m appear to have the strongest effects on the parental phase in our model.

Finally, we point out that our sensitivity analysis contains a diversity of target brood cycles, from mating once per cycle and caring until the offspring are independent, to mating in every time step. It will be interesting to see if the interspecific diversity of brood cycling can be explained by our model.

Filial cannibalism

Although we did not find filial cannibalism in our default run, we did find

it in several of the runs of our sensitivity analysis (Table 3). We only observed filial cannibalism when energy reserves were low (*i.e.* $N \leq 2$), and when the youngest clutch in the nest was age 1 (*i.e.* nest states 1, 12, 13, and 123). As conditions favoring filial cannibalism increase, nest states exhibiting filial cannibalism accumulate in descending order of clutch number (Table 3). We found that clutch survival with care, and feeding costs to clutch survival and to parental survival had the strongest effects on filial cannibalism. The likelihood of filial cannibalism increases as clutch survival with care (w) decreases, as feeding costs to clutch survival increase (*i.e.* as q_f decreases), and as feeding costs to parental survival increase (*i.e.* as p_f decreases). However, if there are no feeding costs (*i.e.* if $p_f = 1$ and $q_f = 1$), then we would only expect filial cannibalism to appear in our model when clutch survival with and without care approach zero. Under these conditions, the parent would gain more by committing filial cannibalism and investing in future breeding seasons than it would by providing care during the current breeding season. When we set feeding costs and offspring survival with and without care all to zero, then we observed filial cannibalism; although, with zero offspring survival with and without care, we might not expect animals to be mating in the first place.

Discussion

Our analysis of the model suggests that the pattern of brood cycling most strongly depends on mating costs to clutch survival and to survival of the male parent. Unless these costs are built in, males court females in all levels of nest state (see also SARGENT, 1990, Figs 5 and 6). Assuming default values for these costs (*i.e.* $q_m = .9$ and $p_m = .9$), then the probability of mating given courtship (S) and clutch survival without care (u) have strong effects on the pattern of brood cycling; whereas, adult survival (P), the adult survival coefficient for caring (p_c , which reflects the cost of care), and egg survival with care (w) all have relatively weak effects on the pattern of brood cycling. The pattern of brood cycling seemed to be independent of feeding costs to adult survival and to clutch survival (reflected in p_f and q_f respectively). We suggest that these predictions may be testable through experimental manipulation of these parameters, or by examining natural variation (*e.g.* geographical or seasonal variation) in these parameters in the field.

Our analysis generated relatively little filial cannibalism; however, it appears that the incidence of filial cannibalism is most strongly affected by feeding costs to adult and clutch survival (reflected in p_f and q_f respectively), and then by clutch survival with care (w). The other parameters had little or no effect on filial cannibalism. Our results do tend to support the predictions generated by ROHWER (1978) and SARGENT (1992). (1) Despite our assumption that males eat the youngest clutch in their nest, we still found that filial cannibalism depends on clutch age. Only age 1 clutches were eaten. (2) Filial cannibalism only occurred when energy reserves were low. (3) The likelihood that males ate an age 1 clutch was in descending order of the number of clutches in his nest; $123 > 12$, $13 > 1$. Thus, males in this model only commit total filial cannibalism when they have a single clutch of age 1. Although SARGENT (1992) found total filial cannibalism of more than one clutch (over time steps within a brood cycle) when all clutches within a nest are the same age, we did not find similar behaviour in this model where all clutches within a nest differ in age. (4) Males only commit partial filial cannibalism if they have more than one clutch, and the likelihood that they do so increases with increasing clutch number.

From our sensitivity analysis, it appeared that mating costs affect brood cycling independently of filial cannibalism, and that feeding costs affect filial cannibalism independently of brood cycling. To examine this pattern further, we varied mating and feeding costs to clutch survival independently of one another, and examined their effects on brood cycling and filial cannibalism. We examined high and low mating and feeding costs by setting q_m and q_f to 0.6 and 1.0, in all four possible combinations. All other parameters were set at their default values (Table 1). We found that q_m affected brood cycling, and that its effects were independent of the value of q_f . Nest states in the parental phase are none for $q_m = 1.0$; 1, 2, 3, 12, 13, 23, and 123 for $q_m = 0.6$. We found that q_f affected filial cannibalism, and that its effects were independent of the value of q_m . Nest states with filial cannibalism are none for $q_f = 1.0$, and 1, 12, 13, and 123 for $q_f = 0.6$. Thus, it appears that q_m affects brood cycling independently of q_f and q_f affects filial cannibalism independently of q_m . It would be interesting to look for potential fine-scaled interactions between these parameters in future studies of the model; however, this simple analysis illustrates

that the model can generate high and low levels of brood cycling and filial cannibalism independently of one another.

Overall, we find the models qualitative behaviour to be very encouraging. Despite its simple assumptions, it is able to generate a diverse array of brood cycling and filial cannibalism behaviours. Although nature is always much more complex than any model, we suggest that this model may provide interesting insights into the dynamics of parental care and filial cannibalism that is observed in nature.

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