

Behavioural and evolutionary ecology of fishes: conflicting demands during the breeding season

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During the breeding season, fishes may be confronted with the conflicting demands of avoiding predators, feeding, mating, and providing parental care. I constructed a series of three stochastic dynamic-programming models that explore these conflicting demands in terms of tradeoffs between present and future reproduction. The state variables were parental state (i.e. energy reserves) and nest state (i.e. number and age of offspring). The tradeoffs were built in as behaviour dependent coefficients that reduce parental and offspring survival, and as behaviour dependent increments or decrements to parental energy reserves. I found that as parental energy reserves increase, courtship and parental care both increase; whereas, feeding decreases. However, as offspring number or age increases, parental care increases, and mating and feeding both decrease. Thus, with respect to parental state, feeding is traded off against reproduction (i.e. mating and caring); however, with respect to nest state, mating and caring are traded off against each other. These results may provide insights into such phenomena as van Iersel's parental phase (1953); that is, after some combinations of clutch number and age, parental male fishes cease courtship and show heightened levels of parental care.

1. Introduction

Although zoologists have long realized the utility of examining animal behaviour within an adaptive framework (e.g. Darwin 1859, 1871), the widespread use of such an approach is relatively recent (e.g. Tinbergen 1963, Wilson 1975, Krebs & Davies 1978, 1984). Students of the adaptive or functional approach (*sensu* Tinbergen 1963) to

studying animal behaviour assume that at least part of an animal's behavioural repertoire is the result of natural selection, and functions in survival or reproduction. Early models in behavioural ecology usually examined a limited set of behaviours over a narrow part of an animal's lifetime, and used different currencies, depending on the situation at hand. For example, early foraging strategy models examined feeding behaviour,

and often used the currency of net energy per unit time (e.g. Charnov 1976); whereas, early mating strategy models examined mating behaviour, and often used the currency of offspring produced per unit time (e.g. Parker & Stuart 1976).

Implicit in the functional approach is that an animal is confronted with behavioural options that each contribute to some aspect of overall fitness, but that there are constraints that prevent an animal's being able to optimize all of its options simultaneously. For example, conflicts may exist between feeding and predator avoidance (e.g. Sih 1980, Werner & Gilliam 1984, Milinski 1986), or between parental care of current offspring and future reproduction (e.g. Williams 1966, Sargent & Gross 1986). With the advent of dynamic optimization models, behavioural ecologists have been able to examine broader sets of behavioural phenomena (e.g. McFarland & Houston 1981, McFarland 1982), and have been able to incorporate behaviours associated with survival and behaviours associated with reproduction into one theoretical framework (e.g. Gilliam 1982; Mangel & Clark 1986, 1988; McNamara & Houston 1986, Houston & McNamara 1988). This new class of models in behavioural ecology is similar to many traditional models in evolutionary ecology (e.g. Stearns 1976, Charlesworth 1980, Pianka 1988). Both examine phenotypic traits associated with survival versus reproduction, and both use mean population fitness (i.e. the Malthusian parameter, r , or the net replacement rate, R_0) as the currency being maximized by natural selection.

Thus, there has been a convergence between behavioural and evolutionary ecology, both in the phenomena being examined and in analytical approach. Perhaps the most promising of the newly adopted analytical tools in these fields is stochastic dynamic programming (Mangel & Clark 1986, 1988; McNamara & Houston 1986, Houston & McNamara 1988). This technique offers numerical solutions to complex problems of dynamic optimization.

There are three reasons why fishes represent an ideal system for the joint approach of behavioural and evolutionary ecology. First, they exhibit enormous phylogenetic diversity in their life histories, which facilitates a comparative approach. Second, they can be readily studied in the field and laboratory, which facilitates an ex-

perimental approach. Third, there is a vast literature on their behavioural and evolutionary ecology (e.g. Potts & Wootton 1984, Pitcher 1986), which provides the basic knowledge for the construction of mathematical models.

In this paper, I use the approach of stochastic dynamic programming and develop a set of three simple models to examine the dynamics of behavioural tradeoffs that may confront fishes during the breeding season. I start with a simple model, and build toward more complex cases. The tradeoffs that I examine are:

- 1) feeding versus mating,
- 2) feeding versus parental care, and
- 3) feeding versus mating versus parental care.

I use these models to address two phenomena.

- 1) In species of fishes with parental care the amount of care that a parent provides initially increases with increasing offspring age, and then decreases as the offspring mature and become independent (e.g. Sargent & Gross 1986).
- 2) In some species of fishes with exclusive male parental care, males appear to cease courtship voluntarily, and switch into a parental phase (*sensu van Iersel 1953*) until most or all of the offspring are hatched and free swimming.

I illustrate how both phenomena can be explained as dynamic shifts in the tradeoff between present and future reproduction.

2. The approach

2.1. Dynamic optimization

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).

Oster & Wilson (1978) identify five essential components of dynamic optimization models (for a lucid discussion, see Mangel & Clark 1988, Chapter 8). These are:

- 1) *Optimization criterion*: the currency being maximized.
- 2) *The strategy set*: the set of behavioural options available to an animal.
- 3) *State space*: all combinations of magnitudes of variables that depend cumulatively on past decisions, and that determine the present optimal policy.
- 4) *Constraints*: the limitations on the state space.
- 5) *State dynamics*: the rules for moving through the state space.

To this list I add a sixth component:

- 6) *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, one needs to explicitly specify each of these components.

2.2. Stochastic dynamic programming

Stochastic dynamic programming models find numerical solutions, usually with the aid of a computer. The algorithms for solving these models are relatively simple, and within the realm of any "computer literate" empirical behavioural ecologist. 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." Put another way, the optimal trajectory from some initial time, t , to some final time, T (also known as the time horizon), contains the optimal trajectory from time $T-1$ to T . Thus, to find the optimal trajectory from t to T , one first

finds the optimal trajectory from $T-1$ to T , then the optimal trajectory from $T-2$ to $T-1$, and so on back to t . The basic task of constructing a dynamic programming model is in specifying the dynamic programming equation, or *DPE*. Specifying the *DPE* first requires specifying the state dynamics. In the models that follow, I will use either one or two state variables. These are:

- 1) parental state (i.e. energy reserves), and
- 2) nest state (i.e. a combination of number of clutches and their ages within a parent's nest).

Dynamic programming with one state variable. At each time t , for each parental state $x(t)$, we can find a behaviour $B^*(t, x(t))$ that maximizes fitness, $F(t, x(t))$, where the maximum is written as F^* . This requires that we know $F^*(t+1, x(t+1))$, for all possible $x(t+1)$. $B^*(t, x(t))$ and $x(t)$ jointly determine $x(t+1)$. The recursions for the state variable and for fitness, in general form, are:

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

and

$$F(t, x(t)) = f_2[t, B(t, x(t)), x(t), F^*(t+1, x(t+1))], \quad (2)$$

where f_1 and f_2 represent functions. Equation (1) specifies the state dynamics. Substituting (1) into (2) gives the general form of a *DPE* with one state variable.

Dynamic programming with two state variables. This is a similar process, except that we need to incorporate the state dynamics of the second state variable, which in our case is nest state, $y(t)$. The recursions for the two state variables and for fitness, in general form, are:

$$x(t+1) = f_3[t, B(t, x(t), y(t)), x(t), y(t)], \quad (3)$$

$$y(t+1) = f_4[t, B(t, x(t), y(t)), x(t), y(t)], \quad (4)$$

and

$$F(t, x(t), y(t)) = f_5[t, B(t, x(t), y(t)), x(t), y(t), F^*(t+1, x(t+1), y(t+1))], \quad (5)$$

where f_3 , f_4 , and f_5 represent functions. Equations (3) and (4) specify the state dynamics, and equation (5) is the *DPE* for two state variables.

To solve the *DPE* (i.e. equation (2) or (5)), 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 is positive, and represents future reproduction after time T . Also, terminal fitness may be either dependent or independent of the state variables. In the models that follow, I assume that terminal fitness is an increasing function of energy reserves. Then starting at $T-1$, we 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 $t=0$.

The resulting solution is a function of the parameter values, which are chosen from knowledge of the system being modeled (Mangel & Clark 1986, 1988). To examine the robustness of the solution, one performs a sensitivity analysis. For each model, I have manipulated each parameter plus and minus a small amount relative to its default value and convinced myself that the qualitative trends are not artifacts of the parameter values. To save space I do not present these sensitivity analyses. Although it would be desirable to examine the optimal solution over all combinations of parameter values (over discrete intervals), this task is impossible to complete within a reasonable amount of time due to the dimensionality of the models.

Nevertheless, these models may be useful in identifying important ecological variables that affect animal behaviour. My approach is as follows. First, I construct a model whose default solution qualitatively mimics known fish behaviour. Then I manipulate one or more of a model's parameters and examine whether the resulting change in optimal policy qualitatively mirrors what happens in a natural system under similar manipulations. If so, then I may have gained some insights into the mechanisms that regulate animal behaviour. If not, then one or more of the model's assumptions are false, which is also useful information. For each model, I present an example of such a manipulation.

3. The models

During the breeding season, fishes may be confronted with the problems of predator avoidance, feeding, mating, and parental care. In the past, these sorts of phenomena have been modeled with static resource allocation models (e.g. Pressley 1976, Carlisle 1982, Sargent & Gross 1985, 1986). In these models, an animal is assumed to be able to vary continuously the proportion of resources it invests in each of its behavioural options, subject to the constraint that any resource invested in one option cannot be invested in another. There have been relatively few dynamic resource allocation models (but see Oster & Wilson 1978, Mangel & Clark 1986, 1988 (Chapter 6)), probably because the state dynamics of such models can be prohibitively complex. Therefore, as a first approximation to dynamic resource allocation, I have based the following models on Mangel & Clark's simple patch selection model (1988, chapter 2). That is, rather than have continuous decision variables, I assume that an animal must choose from a discrete menu of behavioural options. In spite of this assumption, I nevertheless found dynamics that resemble those of resource allocation models.

I build in tradeoffs in two ways. These are behaviour dependent increments or decrements to parental energy reserves, and behaviour dependent multiplicative probability reducing coefficients, which are decimal fractions. These coefficients impose costs to parental survival and offspring survival, depending on the behaviour chosen. One might also include costs of doing one behaviour to success at another behaviour; for example, attempted feeding may reduce the probability of successful mating. However, to keep the presentation simple, I chose not to examine this second set of costs.

Within a time step, I assume the following general sequence of events:

- 1) choose the behaviour for that time step,
- 2) tally reproduction and/or offspring survival,
- 3) update parental energy reserves,
- 4) tally parental survival.

The models that follow were compiled in QuickBASIC 4.0 or Turbo Pascal 5.0, and analyzed numerically on an 80286 based microcomputer.

3.1. Feed or Mate?

Imagine that a fish has just entered the beginning of the breeding season, and is confronting a trade-off between feeding and mating (assume no parental care). I define the time horizon, T , as the end of the breeding season.

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

- 1) Optimization Criterion, maximizing remaining lifetime reproductive success. The model assumes a stationary population and maximizes the sum of all matings this season plus a terminal fitness function at the end of the season.
- 2) Strategy Set, $B(t, x(t))$. A fish may choose one of the following four behaviours:
 - a) do *Nothing*, which represents passive predator avoidance (e.g. hiding);
 - b) *Feed*, which yields a unit of energy with probability L
 - c) *Mate*, which yields one unit of fitness with probability G ;
 - d) *Feed & Mate*; the probability that the fish is successful at both is $L \cdot G$ (i.e. the events are assumed to be independent); the probability that the fish is only successful at feeding is $L(1-G)$; the probability that the fish is only successful at mating is $G(1-L)$; the probability that the fish is not successful at feeding or mating is $(1-L)(1-G)$.
- 3) State Space: $x(t)$ = parental energy reserves. These are incremented or decremented depending on the behaviour chosen.
- 4) Constraints. The state space is constrained such that parental energy reserves lie between zero and some maximum value; i.e. $0 \leq x(t) \leq Capacity$.
- 5) State Dynamics, $x(t+1) = x(t) + \Delta x(B(t, x(t)))$; parental energy reserves at time $t+1$ depend on the behaviour chosen at time t , i.e. $B(t, x(t))$. I assume that a fish who does nothing pays a metabolic cost of 1 unit of energy reserve. A

fish who attempts to *Feed* and is successful gains +2 energy units, which when added to the metabolic cost yields a net gain of +1; a fish who attempts to feed but is unsuccessful simply pays the metabolic cost of 1. A fish who attempts to *Mate*, whether or not it is successful, pays a cost of 1 energy unit, which when added to the metabolic cost yields a net loss of 2. A fish who attempts to *Feed & Mate* has its energy reserves adjusted for feeding, mating and metabolism, which yields a net gain of 0 in its energy reserves if it finds food; otherwise it pays a net cost of 2 energy units.

- 6) Tradeoffs. The tradeoffs are imposed by behaviour dependent probability reducing coefficients of parental survival, which are p_f for *Feed*, p_m for *Mate*, and the product of the two for *Feed & Mate*, and as behaviour dependent state dynamics for parental energy reserves (see State Dynamics, above).

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

$$F_B(t, x(t)) = Pr(mating \text{ in } t) + Pr(surviving \ t) \cdot \left\{ \sum_{j=1}^{15} Pr[(x(t+1) = j) \cdot F^*(t+1, j)] \right\}. \quad (6)$$

The first additive term on the right hand side of (6) tallies any mating that occurs in time step t , whether or not the parent survives until $t+1$, and whether or not the parent also finds food. The second additive term on the right hand side of (6) tallies expected future reproductive success if the parent does survive until $t+1$. This term sums over all parental state transition probabilities between t and $t+1$, which depend on $x(t)$ and on $B(t, x(t))$. These parental state transition probabilities are then multiplied by their respective F^* 's at $t+1$, for

$$x(t+1) = x(t) + \Delta x[B(t, x(t))].$$

For any given time step, the optimal behaviour is the one that maximizes F_B .

Thus, equation (6) is the *DPE*. To solve the *DPE*, one begins by initializing terminal fitness at the time horizon, T . I decided to make terminal

fitness arbitrarily small and positive, which represents a small probability of a future breeding season. Moreover, I assumed that terminal fitness increases with increasing $x(T)$; i.e.

$$\phi(x(T)) = 0.001x(T).$$

Then starting at $T-1$, one iterates (6) backward over time over all levels of parental state, to the beginning of the breeding season. The results of the default run are presented in Table 3 and Fig. 1.

An interesting property of dynamic programming models is the phenomenon of stationarity. If the parameters are independent of time, and if the distance between t and T is sufficiently large, then the optimal behaviour is independent of time, and independent of the terminal fitness function, provided it is nonzero (McNamara & Houston 1982, Mangel & Clark 1988). In this model, the breeding season was arbitrarily set at 30 time steps. Stationarity was maintained until $T-8$ (i.e. $t=22$).

The basic results of the model are the following. Fitness increases with increasing energy reserves. This is because as energy reserves increase, the parent has more energy to invest in reproduction, and because the parent can afford to avoid the risks associated with feeding. Fitness also increases with increasing time before the end of the breeding season, because the longer the breeding season, the more opportunities there are for mating. At low energy reserves, the parent *Feeds*; at intermediate energy reserves the parent *Feeds & Mates*; at high energy reserves the parent *Mates*. Thus, during the breeding season, the more

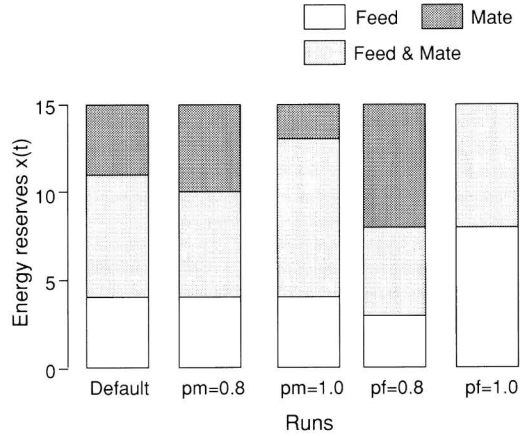


Fig. 1. A graphical representation of the results of *Feed or Mate?* from Table 3. Along the vertical axis is level of parental energy reserves. The individual runs are depicted along the horizontal axis.

energy reserves a parent has, the more likely it is willing to invest in reproduction.

We can examine the effects of the tradeoff between feeding and mating by manipulating p_f and p_m . In Table 1 and Fig. 1, I present the results of manipulating these parameters ± 0.1 with respect to their default values. The qualitative trends of these manipulations mirror those of the default run; however, two interesting patterns appear. As the cost of either feeding or mating decreases (i.e. as p_f or p_m increases), the distribution of *Feed & Mate* among levels of energy reserves increases. Thus, the intensity of the tradeoff between feeding

Table 1. Parameters of *Feed or Mate?*, and their default values.

$T=30$	time horizon or length of breeding season in discrete time steps
$Capacity=15$	maximum level of energy reserves
$G=0.6$	probability of mating within a time step
$L=0.6$	probability of feeding within a time step
$P=0.99$	probability of surviving a time step
$p_m=0.9$	survival coefficient due to mating
$p_f=0.9$	survival coefficient due to feeding

Table 2. *Feed or Mate?* The four possible behaviors, and their consequences for parental energy reserves and parental survival.

Behaviour state	Change in parental state	Parental survival
Nothing	-1	P
Feed	+1 with $Pr(L)$, else -1	Pp_f
Mate	-2	Pp_m
Feed & Mate	0 with $Pr(L)$, else -2	$Pp_f p_m$

and mating determines the distribution of *Feed & Mate* among levels of energy reserves. Although these results are not surprising, they are useful for constructing and understanding the third model below: *Feed, Mate or Care?*

3.2. Feed or Care?

In fishes with parental care, the amount of care that a parent provides is known to depend on two components of the state of a parent's nest:

- 1) offspring number, and
- 2) offspring age (e.g. Sargent & Gross 1986).

Parental care increases with increasing offspring number. In addition, the level of parental care covaries with offspring age. Early in the nesting cycle, parental care increases as offspring age increases; however, after some point, parental care decreases as the offspring mature and become free swimming larvae. We constructed a simple static resource allocation model to investigate these patterns (Sargent & Gross 1986), and found that the optimal level of parental care increases as the rate of return on investment in current offspring increases. We used this result to explain both the dependence of parental care on offspring number, and on offspring age.

To explain the positive correlation between parental care and offspring number, we (Sargent & Gross 1986) argued that for fishes, the predominant form of parental care is guarding, which is a divisible resource (Wittenberger 1981). The benefit of one unit of guarding to offspring survival should be largely independent of offspring number; therefore as offspring number increases, so does a parent's rate of return on defending those offspring.

To explain how parental care covaries with offspring age, we constructed a series of static resource allocation models, whose tradeoffs changed with offspring age (Sargent & Gross 1986). We assumed that early in the nesting cycle that offspring survival without care is constant, and independent of offspring age. Therefore, early in the nesting cycle, as offspring age increases, the rate of return on investment in offspring defense increases, simply because older offspring are closer to independence. We assumed that late in the nesting cycle offspring survival without care increases as offspring age increases, because the offspring are now becoming more able to care for themselves. As offspring survival without care approaches offspring survival with maximal care, the rate of return on investment in offspring defense decreases as offspring age increases. We hypothesized that this decrease in the rate of

Table 3. *Feed or Mate?* The results of the default run, and of the runs that manipulate p_m and $p_i \pm 0.1$ with respect to their default values, evaluated at $t=1$. B^* represents the optimal behaviour, and F^* represents maximum fitness. F is *Feed*, M is *Mate*, and FM is *Feed & Mate*.

Energy Reserves	Default		$p_m = 0.8$		$p_m = 1.0$		$p_i = 0.8$		$p_i = 1.0$	
	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*
1	0.53	F	0.47	F	0.62	F	0.32	F	1.55	F
2	0.81	F	0.70	F	0.94	F	0.52	F	2.27	F
3	1.00	F	0.87	F	1.16	F	0.68	F	2.68	F
4	1.16	F	1.00	F	1.36	F	0.89	FM	2.87	F
5	1.33	FM	1.16	FM	1.54	FM	1.07	FM	2.99	F
6	1.50	FM	1.30	FM	1.76	FM	1.21	FM	3.15	F
7	1.64	FM	1.40	FM	1.96	FM	1.31	FM	3.23	F
8	1.76	FM	1.49	FM	2.13	FM	1.41	FM	3.31	F
9	1.87	FM	1.57	FM	2.29	FM	1.55	M	3.44	FM
10	1.98	FM	1.64	FM	2.45	FM	1.68	M	3.50	FM
11	2.07	FM	1.71	M	2.60	FM	1.77	M	3.58	FM
12	2.17	M	1.78	M	2.75	FM	1.86	M	3.69	FM
13	2.27	M	1.84	M	2.88	FM	1.99	M	3.75	FM
14	2.36	M	1.90	M	3.02	M	2.09	M	3.81	FM
15	2.45	M	1.95	M	3.18	M	2.17	M	3.91	FM

return on investment in offspring defense with increasing offspring age late in the nesting cycle is the cause of the observed decline in the level of parental care late in the nesting cycle that is observed in nature.

Now, I will illustrate how both patterns can be understood with an explicit stochastic dynamic programming model. Imagine that a fish has just mated and has either one or two clutches in its nest. Assume that further mating is impossible, and that our hypothetical fish is confronted with a tradeoff between feeding and parental care. An example of such a system is paternal care in the bluegill sunfish, *Lepomis macrochirus*; females are only available for spawning with males for the first one or two days of the nesting cycle (Coleman et al. 1985). I define the time horizon, T , as the time at which all offspring are hatched and independent of parental care.

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

- 1) Optimization Criterion, maximizing remaining lifetime reproductive success. The currency being maximized is the number of clutches alive at time T (the end of the nesting cycle) plus a terminal fitness function at time T .
- 2) Strategy Set, $B(t,x(t),y(t))$. The behavioural options are four behaviours:
 - a) Do *Nothing*,
 - b) *Feed*,
 - c) *Care*, or
 - d) *Feed & Care*.
- 3) State Space, $(x(t),y(t))$. The state variables are parental energy reserves, $x(t)$, and the number of clutches in the nest, $y(t)$.
- 4) Constraints. Parental energy reserves are constrained as follows: $0 \leq x(t) \leq Capacity$. Clutch number is constrained as follows: $y(t) = 0, 1, \text{ or } 2$ clutches.
- 5) State Dynamics.
 - a) Parental energy reserves:
 - $x(t+1) = x(t) + \Delta x[B(t,x(t),y(t))]$.
 - The behaviour dependent changes in parental energy reserves are essentially those of the previous model: *Feed or Mate*?
 - b) Clutch number: the survival of each clutch is independent of the survival of other clutches. A parent with 0 clutches at time t will have 0 clutches at time $t+1$; a parent with 1 clutch at time t may have either 1 or 0 clutches at time $t+1$; a parent with 2 clutches at time t may have 2, 1, or 0 clutches at time $t+1$.
- 6) Tradeoffs. The tradeoffs are produced by multiplicative probability reducing coefficients, and by behaviour dependent state dynamics for parental energy reserves (see State Dynamics, above). Parental survival is reduced by p_f for *Feed*, by p_c for *Care*, and by the product of the two for *Feed & Care*. Offspring survival is increased from u to w if the parent *Cares*. Offspring survival with care is reduced by q_f if the parent *Feeds*.

Table 4. Parameters of *Feed or Care?*, and their default values.

$T=6$	time horizon or length of nesting cycle in discrete time steps
$Capacity=10$	maximum level of parental energy reserves
$L=0.6$	probability that feeding within a time step is successful
$u=0.3$	probability that a clutch survives a time step without care
$w=0.9$	probability that a clutch survives a time step with care
$P=0.99$	probability that the parent survives a time step
$p_c=0.9$	parental survival coefficient due to caring
$p_f=0.9$	parental survival coefficient due to feeding
$q_f=0.9$	clutch survival coefficient due to feeding

Table 5. *Feed or Care?* The four possible behaviors, and their consequences for parental energy reserves, parental survival, and clutch survival.

Behaviour	Change in parental state	Survival parental clutch	
<i>Nothing</i>	-1	P	u
<i>Feed</i>	+1 with $Pr(L)$, else -1	Pp_f	u
<i>Care</i>	-2	Pp_c	w
<i>Feed & Care</i>	0 with $Pr(L)$, else -2	$Pp_f p_c$	wq_f

the strategy set, and its consequences for parental energy reserves, parental survival, and clutch survival. The fitness that a fish would enjoy from choosing any behaviour can now be written as:

$$F_B(t, x(t), y(t)) = Pr(\text{parent dies in } t) \cdot Pr(\text{clutch survival until } T) \cdot y(t) + Pr(\text{parent surviving } t) \cdot \left\{ \sum_{j=1}^{10} [Pr(x(t+1) = j) \cdot \sum_{k=0}^2 Pr(y(t+1) = k) \cdot F^*(t+1, j, k)] \right\}. \quad (7)$$

The first additive term on the right hand side of (7) tallies clutch survival if the parent dies at the end of t . Clutch survival during t depends on $B(t, x(t), y(t))$; clutch survival from $t+1$ to T equals $u^{(T-t)}$. The second additive term on the right hand side of (7) tallies future reproductive success if the parent survives to $t+1$. This term sums over all independent parental state by nest state transition probabilities between t and $t+1$, which depend on $x(t)$, $y(t)$, and $B(t, x(t), y(t))$ (Table 4). These transition probabilities are then multiplied by their respective F^* 's evaluated at $x(t+1)=j$ and $y(t+1)=k$. Equation (7) is the *DPE*.

To solve the *DPE*, we first set the terminal fitnesses at T . I set terminal fitness as follows:

$$\phi(x(T), y(T)) = y(T) + 0.15 \cdot x(T).$$

We then iterate (7) backward through time over all levels of parental state and nest state. The default parameters are rough approximations based on unpublished data in past studies with fishes with paternal care (i.e. *Gasterosteus aculeatus*, Sargent & Gebler 1980; *Lepomis macrochirus*, Coleman et al. 1985; *Pimephales promelas*, Unger & Sargent 1988; *Etheostoma flabellare*, Knapp & Sargent 1989). In the first run of the model, clutch survival without care was assumed to be constant in time, and always less than clutch survival with care (which is also constant in time). In the second run of the model, clutch survival without care was assumed to be constant in time until the eggs hatched, and to then increase linearly toward clutch survival with care as t approaches T .

The results of the default run are presented in Table 6 and Fig. 2. A fundamental difference between this model and the last one is that here we

are most interested in the optimal behaviour as t approaches T . In the previous model, we were most interested in the optimal behaviour when the interval between t and T was sufficiently large that stationarity was achieved. In this model, the stationary solution is to *Feed* for energy levels 1 to 9, and to do *Nothing* at energy level 10. Note that the stationary solution is the only solution when the parent has no clutches; i.e. when $y(t)=0$.

In the first run, clutch survival without parental care (u) was constant in time. Here we see that the incidence of parental care increases as clutch number increases, and as clutch age increases (Table 6, Fig. 2). Note that it was not necessary to assume that the need for care increases with increasing clutch number or age. Had we made this assumption, by making u a decreasing function of increasing clutch number or age, then we would have seen an even stronger tendency for care to increase with clutch number or age. Finally, note that the incidence of parental care does not decrease to zero as the clutches approach independence.

In the second run, u was constant in time from $t=1$ to $t=3$, after which u increased linearly toward w as t approached T (Fig. 3). Again, the incidence of parental care increases as clutch number increases, and as clutch age increases, but only up to point. At $t=5$, $u=w$, and parental care is no longer observed. Thus an improvement in offspring survival with increasing offspring age near the end of the nesting cycle could be responsible for the decrease in parental care that is observed in nature under similar circumstances.

3.3. Feed, Mate or Care?

Now, let us consider the case of fishes with exclusive paternal care, which is the most common form of parental care in fishes (Blumer 1979, 1982, Gross & Shine 1981, Gross & Sargent 1985). 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 the number of female clutches in the nest through additional matings. An interesting phenomenon in some of these species is that after the eggs are a certain age, or after the male has a certain number of clutches, he

Feed or Care? (u constant)

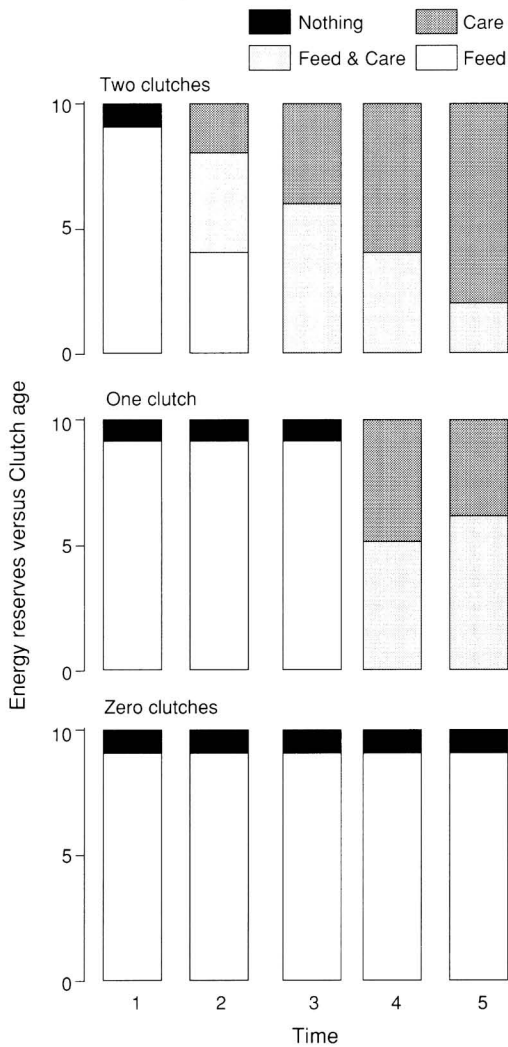


Fig. 2. A graphical representation of the results of the default run of *Feed or Care?* from Table 6. Clutch survival without care is assumed to be constant in time (i.e. $u=0.3$). Along the horizontal axis is time, which equals clutch age. Along the vertical axis is level of parental energy reserves. The three nest states, i.e. 0, 1, or 2 clutches are stacked vertically. For ease of presentation in this graph, and in Figs. 3, 4, 5, and 6, discretization artifacts have been eliminated. These discretization artifacts appear as discontinuities or reversals in the optimal behaviour with increasing parental state, and are found to depend on assumed behaviour dependent increments or decrements to parental energy reserves. In Table 6, the discretization artifacts are at $x(t)=2, y(t)=1, t=4$; $x(t)=6, y(t)=2, t=2$; $x(t)=2, y(t)=2, t=3, 4$.

Feed or Care? (u increases after $t=3$)

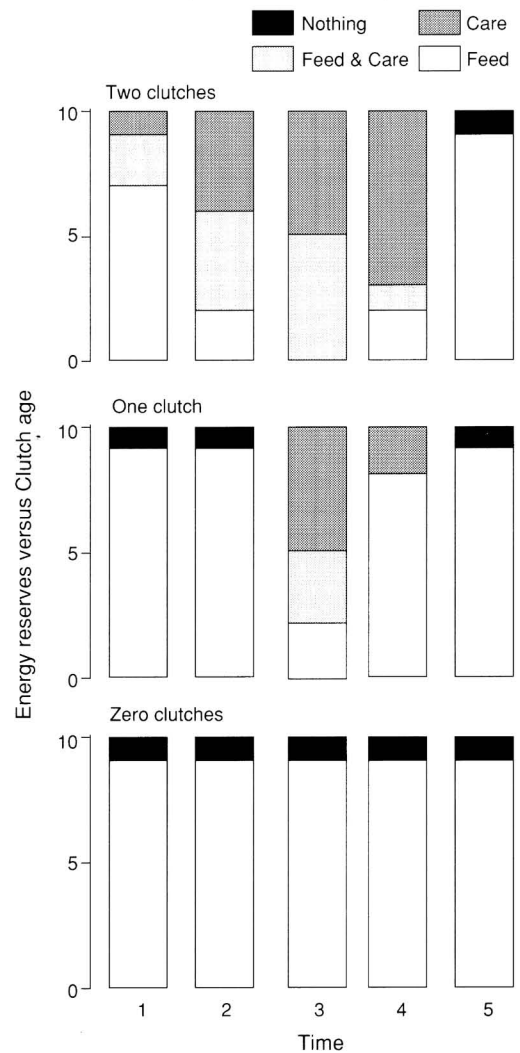


Fig. 3. *Feed or Care?* Offspring survival without care is constant in time until $t=3$, after which offspring survival without care increases to equal offspring survival with care. $u(1)=0.3, u(2)=0.3, u(3)=0.3, u(4)=0.6, u(5)=w=0.9$.

will cease courting females and exhibit a heightened level of parental care. The best documented example of this phenomenon is van Iersel's (1953) work on the "parental phase" in the threespine stickleback, *Gasterosteus aculeatus*.

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

Table 6. *Feed or Care?* The results of the default run, evaluated from $t=1$ to $t=5$ ($T=6$), and over nest states, $y(t)=0$, $y(t)=1$, and $y(t)=2$. Offspring survival without care, u , is constant in time (i.e. $u=0.3$). $x(t)$ represents parental energy reserves; B^* represents the optimal behaviour, and F^* represents maximum fitness. N is *Nothing*, F is *Feed*, C is *Care*, and FC is *Feed & Care*.

$y(t)$	$x(t)$	$t=1$		$t=2$		$t=3$		$t=4$		$t=5$	
		F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*
0	1	0.14	F	0.14	F	0.15	F	0.16	F	0.16	F
	2	0.24	F	0.26	F	0.27	F	0.29	F	0.29	F
	3	0.33	F	0.36	F	0.38	F	0.40	F	0.43	F
	4	0.42	F	0.45	F	0.49	F	0.52	F	0.56	F
	5	0.51	F	0.55	F	0.59	F	0.64	F	0.69	F
	6	0.59	F	0.64	F	0.70	F	0.76	F	0.83	F
	7	0.61	F	0.73	F	0.81	F	0.88	F	0.96	F
	8	0.75	F	0.83	F	0.90	F	1.00	F	1.10	F
	9	0.83	F	0.91	F	1.01	F	1.11	F	1.23	F
	10	0.90	N	1.01	N	1.09	N	1.22	N	1.34	N
1	1	0.14	F	0.16	F	0.18	F	0.31	FC	0.62	FC
	2	0.25	F	0.27	F	0.33	F	0.45	F	0.69	FC
	3	0.34	F	0.38	F	0.44	F	0.68	FC	1.07	FC
	4	0.43	F	0.47	F	0.57	F	0.76	FC	1.19	FC
	5	0.51	F	0.57	F	0.67	F	0.93	FC	1.32	FC
	6	0.59	F	0.66	F	0.78	F	1.04	C	1.44	FC
	7	0.68	F	0.75	F	0.88	F	1.15	C	1.57	C
	8	0.75	F	0.85	F	0.98	F	1.25	C	1.70	C
	9	0.83	F	0.93	F	1.08	F	1.37	C	1.84	C
	10	0.90	N	1.02	N	1.17	N	1.49	C	1.97	C
2	1	0.14	F	0.17	F	0.25	FC	0.56	FC	1.17	FC
	2	0.25	F	0.29	F	0.41	C	0.62	C	1.24	FC
	3	0.35	F	0.40	F	0.66	FC	1.18	FC	1.93	C
	4	0.43	F	0.51	F	0.73	FC	1.27	FC	2.07	C
	5	0.52	F	0.62	FC	1.01	FC	1.63	C	2.20	C
	6	0.60	F	0.71	F	1.10	FC	1.74	C	2.33	C
	7	0.69	F	0.86	FC	1.35	C	1.86	C	2.47	C
	8	0.77	F	0.94	FC	1.45	C	1.98	C	2.60	C
	9	0.85	F	1.13	C	1.55	C	2.10	C	2.74	C
	10	0.93	N	1.22	C	1.68	C	2.22	C	2.87	C

found that the level of male courtship (i.e. zigzags) decreases as clutch age increases, and as clutch number increases. Here, I illustrate how van Iersel's parental phase can be explained within the framework of conflicting demands in a dynamic optimization problem. I 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, maximizing remaining 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) The strategy set, $B(t,x(t),y(t))$. The alternatives are eight behaviours:

- a) Do *Nothing*,
- b) *Feed*,
- c) *Mate*,
- d) *Care*,
- e) *Feed & Mate*,
- f) *Feed & Care*,
- g) *Mate & Care*,
- h) *Feed, Mate & Care*.

To keep our model manageable on a micro-computer, I made feeding deterministic; however, mating is stochastic.

3) State Space, $(x(t),y(t))$. The state variables are parental male energy reserves, and the number and ages of clutches in his nest.

4) Constraints.

- a) Paternal energy reserves are constrained as follows: $0 \leq x(t) \leq Capacity$.
- b) 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 age 1,
 2 , one clutch age 2,
 3 , one clutch age 3,
 12 , two clutches ages 1 and 2,
 23 , two clutches ages 2 and 3,
 13 , two clutches ages 1 and 3, and
 123 , three clutches ages 1, 2, and 3.

5) State dynamics.

- a) Parental energy reserves: parental energy reserves at $t+1$ depend deterministically on the behaviour chosen:

$$x(t+1) = x(t) + \Delta x[B(t,x(t),y(t))].$$

- b) 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.

6) Tradeoffs. The tradeoffs are produced by multiplicative probability reducing coefficients, and by behaviour dependent state dy-

namics for parental energy reserves (see State Dynamics, above). Parental survival is reduced by p_f for feeding, p_m for mating, p_c for caring, and by the products of these coefficients for the combined behaviours. Offspring survival is increased from u to w if the parent cares for its offspring. Offspring survival with care, w , is reduced by q_f if the parent feeds, and by q_m if the parent attempts to mate.

Table 7 lists the model's parameters and their default values, and Table 8 lists each behaviour in the strategy set and its consequences for parental energy reserves, parental survival, and offspring survival. The fitness that a parental male fish

Table 7. Parameters of *Feed, Mate or Care?*, and their default values.

$T=30$	time horizon or length of breeding season in discrete time steps
$Capacity=20$	maximum level of parental energy reserves
$u=0.3$	probability that a clutch survives a time step without care
$w=0.9$	probability that a clutch survives a time step with care
$G=0.6$	probability that the parent mates successfully within a time step
$P=0.9$	probability that the parent survives a time step
$p_m=0.9$	parental survival coefficient due to courting females
$p_f=0.9$	parental survival coefficient due to feeding
$p_c=0.9$	parental survival coefficient due to caring for eggs
$q_m=0.9$	clutch survival coefficient due to a male's courting females. Courtship may attract predators to a male's nest; therefore, q_m affects u and w
$q_f=0.9$	clutch survival coefficient due to feeding. This only affects w , when a male combines feeding and caring

would enjoy from choosing any behaviour can now be written as:

$$F_B(t, x(t), y(t)) = Pr(\text{age 3 clutch hatches in } t) + Pr(\text{male dies in } t) \cdot \sum_{i=1}^3 Pr(\text{clutches hatch in } t+i) + Pr(\text{male survives } t) \cdot \{ \sum_{j=1}^8 [Pr(y(t+1) = j) \cdot F^*(t+1, x + \Delta x(B(t, x(t), y(t))), j))] \} \quad (8)$$

The first additive term on the right hand side of (8) accounts for any age 3 clutch that hatches in time step t , which depends on the behaviour chosen, $B(t, x(t), y(t))$.

The second additive term on the right hand side of (8) tallies the expected reproductive success if the male dies during t . If the male dies, his state is set to zero. 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 probability of hatching in $t+3$ is the probability that the male mated in t , multiplied by u^3 .

The third additive term in the right hand side of (8) 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 $x(t)$ and $B(t, x(t), y(t))$.

Table 8. *Feed, Mate or Care?* The eight possible behaviors, and their consequences for parental energy reserves, parental survival, and clutch survival.

Behaviour	Change in parental state	Survival parental	Survival clutch
Nothing	-1	P	u
Feed	+1	Pp_i	u
Mate	-2	Pp_m	uq_m
Care	-2	Pp_c	w
Feed & Mate	0	$Pp_m p_i$	uq_m
Feed & Care	0	$Pp_i p_c$	wq_i
Mate & Care	-3	$Pp_m p_c$	wq_m
Feed, Mate & Care	-1	$Pp_m p_i p_c$	$wq_m q_i$

These nest state transition probabilities are then multiplied by their respective F^* 's at $t+1$, and for

$$x(t+1) = x(t) + \Delta x[B(t, x(t), y(t))].$$

These nest state transition probabilities can be obtained from the following simple algorithm.

Let us consider the most complex case, 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 G be the probability of mating; $0 \leq G \leq 1$ if $B(t, x(t), y(t))$ incorporates mating; otherwise, $G=0$. To find all possible transition probabilities we expand the expression:

$$(G + (1 - G)) \prod_{a=1}^3 (A_a + D_a)$$

where each term in the expansion represents a different nest state transition probability. For simpler nest states with one or more missing clutch age classes, we simply let $A_a = 0$ and $D_a = 1$ for each missing age class.

Equation (8) is the *DPE*. To solve the *DPE*, we begin by initializing the terminal fitness function at the end of the breeding season. Terminal fitness was set as follows:

$$\phi(x(T)) = 0.001x(T).$$

Then, starting from $T-1$, we iterate backward in time, over all combinations of parental state and nest state, to the beginning of the breeding season.

Table 9 and Fig. 4 present the results of the default run for $t=1$, which nicely illustrates van Iersel's parental phase (1953). The breeding season was set at $T=30$, and a stationary solution was maintained until $T-14$. Thus, we can use Table 5 or Fig. 4 to move through time for the first 15 time steps.

Starting at a nest state of zero clutches and maximum parental energy reserves (i.e. $y(t)=0$ and $x(t)=20$), we see that the optimal behaviour is *Mate*. If the male mates successfully, we then re-enter the figure at $y(t)=1$ and $x(t)=18$. Here the optimal behaviour is *Mate & Care*. Now, let us 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 has survived, then we re-enter the figure at $y(t)=12$ and $x(t)=15$. Here the optimal

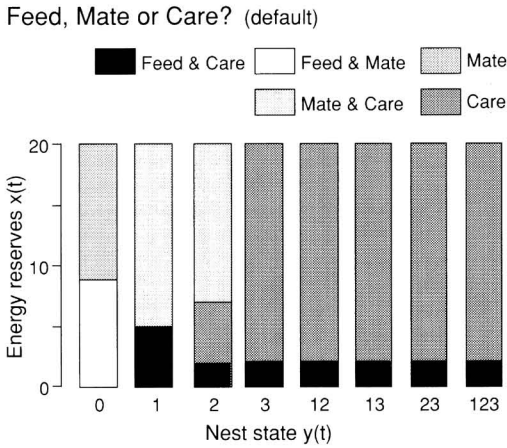


Fig. 4. *Feed, Mate or Care?* The results of the default run from Table 9. Along the horizontal axis are the eight nest states, and along the vertical axis is level of parental energy reserves.

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 we re-enter the figure at $y(t)=2$ and $x(t)=15$. 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.

Thus, we have found two characteristics of van Iersel's (1953) parental phase. These are, the tendency for courtship to decrease to zero increases with

- 1) increasing clutch age and
- 2) increasing clutch number.

Presumably, the parental phase in the model is due to one or both of our mating costs, which are reflected in reduced offspring survival due to q_m , or reduced parental survival due to p_m . We can test

Table 9. *Feed, Mate or Care?* The default run at $t=1$, evaluated over all levels of Male State (i.e. energy reserves) and Nest State. B^* represents the optimal behaviour; F^* represents maximal fitness. F is *Feed*, M is *Mate*, C is *Care*, FM is *Feed & Mate*, FC is *Feed & Care*, MC is *Mate & Care*, FMC is *Feed, Mate & Care*. Time Horizon = 30, Time Step = 1.

Male state	Nest state															
	000		100		200		300		130		230		123		120	
	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*	F^*	B^*
1	0.307	FM	0.487	FC	0.719	FC	1.033	FC	1.297	FC	1.529	FC	1.831	FC	1.021	FC
2	0.335	FM	0.532	FMC	0.735	FC	1.054	FC	1.310	FC	1.545	FC	1.844	FC	1.034	FC
3	0.354	FM	0.564	C	0.830	C	1.148	C	1.464	C	1.730	C	2.100	C	1.200	C
4	0.387	FM	0.617	FMC	0.847	C	1.171	C	1.478	C	1.747	C	2.113	C	1.213	C
5	0.407	FM	0.649	C	0.917	C	1.187	C	1.549	C	1.817	C	2.248	C	1.348	C
6	0.446	FM	0.712	MC	0.936	C	1.213	C	1.564	C	1.836	C	2.263	C	1.363	C
7	0.455	FM	0.727	MC	0.950	C	1.229	C	1.617	C	1.850	C	2.316	C	1.416	C
8	0.497	FM	0.795	MC	0.976	MC	1.261	C	1.634	C	1.872	C	2.332	C	1.432	C
9	0.508	FM	0.812	MC	0.995	MC	1.268	C	1.645	C	1.884	C	2.343	C	1.443	C
10	0.550	M	0.836	MC	1.019	MC	1.303	C	1.667	C	1.911	C	2.362	C	1.462	C
11	0.562	M	0.856	MC	1.041	MC	1.311	C	1.682	C	1.917	C	2.372	C	1.472	C
12	0.587	M	0.866	MC	1.048	MC	1.346	C	1.703	C	1.945	C	2.394	C	1.494	C
13	0.601	M	0.883	MC	1.068	MC	1.355	C	1.720	C	1.953	C	2.400	C	1.500	C
14	0.614	M	0.894	MC	1.080	C	1.376	C	1.727	C	1.980	C	2.422	C	1.522	C
15	0.627	M	0.906	MC	1.096	MC	1.387	C	1.743	C	1.988	C	2.429	C	1.529	C
16	0.636	M	0.915	MC	1.106	MC	1.398	C	1.752	C	2.004	C	2.450	C	1.550	C
17	0.646	M	0.927	MC	1.115	MC	1.408	C	1.765	C	2.013	C	2.457	C	1.557	C
18	0.654	M	0.935	MC	1.125	MC	1.415	C	1.773	C	2.022	C	2.469	C	1.569	C
19	0.663	M	0.946	MC	1.132	MC	1.423	C	1.781	C	2.030	C	2.477	C	1.577	C
20	0.669	M	0.952	MC	1.141	MC	1.430	C	1.789	C	2.036	C	2.484	C	1.584	C

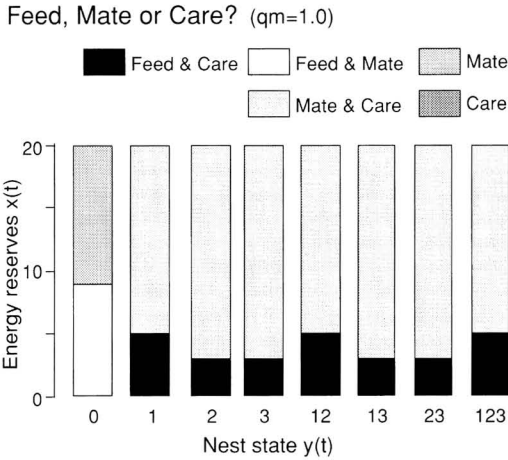


Fig. 5. *Feed, Mate or Care?* In this run, the cost of mating to offspring survival has been eliminated by setting $q_m=1.0$. Note that mating is now observed in all nest states; thus, the parental phase has been eliminated.

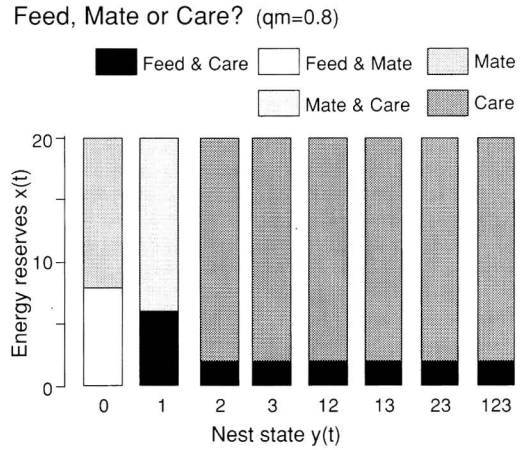


Fig. 6. *Feed, Mate or Care?* In this run, the cost of mating to offspring survival has been increased by setting $q_m=0.8$. Note that males with one clutch stop courting females after that clutch is age 2; in the default run (Fig. 4), males with one clutch stop courting females when that clutch was age 3.

the effect of q_m on our observed parental phase by varying it ± 0.1 with respect to its default value. If $q_m=1.0$, which eliminates any cost of mating to offspring survival, then we eliminate the parental phase (Fig. 5). Mating is observed in all levels of nest state. Alternatively, if $q_m=0.8$, which increases the cost of mating to offspring survival, then males with one clutch cease courtship after that clutch is age 2 (Fig. 6), which is one time step earlier than in the default run (Fig. 4). Thus q_m has a profound affect on van Iersel's parental phase in the model; now it would be interesting to examine this phenomenon in natural systems. A more complete analysis of this model is now in preparation (Sargent et al. unpublished).

4. Discussion

During the breeding season, fishes may improve their overall fitness by avoiding predators, feeding, mating, and providing parental care for their offspring. Although each of these behavioural options is associated with overall fitness, there may be tradeoffs among fitness components that constrain a fish's ability to optimize all of its op-

tions simultaneously. To explore these tradeoffs, I constructed a set of three simple, stochastic dynamic programming models. The tradeoffs were built in as behaviour dependent coefficients that reduce parental and offspring survival, and as behaviour dependent increments or decrements to parental energy reserves.

The behaviour dependent survival reducing coefficients had a large effect on the optimal behaviour. If the cost of doing a particular behaviour is reduced, then the likelihood of that behaviour being combined with another increases. In the model *Feed or Mate?*, as p_f or p_m increases, the incidence of *Feed & Mate* increases among the levels of energy reserves (Fig. 1). Similarly, in the model *Feed, Mate or Care?*, as q_m increases, the incidence of *Mate & Care* increases (Figs 4–6). These results suggest that ecological factors such as behaviour dependent predation risk on parents or offspring may have profound effects on a parent's optimal allocation of behaviour in nature.

The parental energy reserve state dynamics were such that when a parent had maximum energy, no behaviour depleted the reserves within a single time step. In all three models, as the level of energy reserves increases, behaviour that enhances

reproduction (i.e. mating and caring) increases, and behaviour that enhances parental survival (i.e. feeding) decreases. Thus, with respect to energy reserves, feeding is traded off against mating and caring. Mating and caring represent investment in present reproduction; whereas feeding represents investment in the future survival of the parent and offspring.

A third pattern to emerge in those models that involve parental care (i.e. *Feed or Care?* and *Feed, Mate or Care?*), is that the optimal behaviour depends on both offspring number and offspring age. Basically, I assumed that offspring survival between time steps is higher with care than without care, and that both survivals are independent of offspring number and age. I found that the incidence of parental care increases with both the number and age of the offspring. As offspring number/age increases, feeding decreases, mating decreases, and caring increases. Thus, with respect to offspring number/age, mating and feeding are traded off against caring. Here caring represents investment in present reproduction; whereas, feeding and mating represent investment in future reproduction. Caring increases the survival of present offspring; mating is an investment in obtaining future offspring relative to those already in the nest; and, feeding is an investment in parent and offspring survival in future time steps.

In summary, there are two main conclusions from these models.

- 1) With respect to the state of the parent, feeding is traded off against reproduction, i.e. mating and caring.
- 2) With respect to offspring number or age, however, mating and caring are traded off against each other.

Overall, I find the analysis of these models to be very encouraging. They have already provided insights into the conflicting demands and behavioural options that fishes experience during the breeding season. Their further analysis, and experimental tests of their predictions should continue to be profitable. The main advantage that these dynamic optimization models have over their static precursors (e.g. Sargent & Gross 1986), is that they explicitly address the time dependence in parental energy reserves, offspring number,

and offspring age. Thus, we can investigate optimal behavioural trajectories, rather than limit ourselves to optimal solutions that are static in time. Additional directions for future models include the following three areas:

- 1) resource allocation,
- 2) more realistic parental state variables, and
- 3) dynamic games.

Resource allocation

Real fishes do not choose from a discrete menu of behavioural options; rather, they appear to vary their behaviour continuously (e.g. Sargent & Gross 1986). Mangel & Clark (1986, 1988) provide an example of a dynamic programming resource allocation model. Although the analysis of such models is considerably more complicated than for the models presented here, dynamic resource allocation models may well yield new insights into the diversity of animal behaviour.

More realistic parental state variables

In the models in this manuscript, I assumed that the level of energy reserves was the only important parental state variable, and that the state dynamics of energy reserves versus behaviour could be specified by a very simple relationship. Mangel & Clark (1988) present more complex models that break down energy reserves into two components:

- 1) gut contents, and
- 2) fat reserves.

The inclusion of this complexity in future models should yield interesting insights. Moreover, there is evidence that body size is also an important state variable in fish behavioural and evolutionary ecology (e.g. Werner & Gilliam 1984, Sargent et al. 1987). A model that combines energy reserves with body size, via growth, could be very illuminating.

Dynamic games

The models in this manuscript all assume that maximizing individual fitness is independent of what other animals are doing. If the optimal tactic depends on what other animals do, then the appropriate model is a dynamic game. As an example,

consider female choice in the third model, Feed, Mate or Care? Using Fig. 4, imagine that a female has a choice of mating with a male with one clutch versus a male with zero clutches. The female that mates with a male with one clutch puts that male into the parental phase; thus her clutch does not pay any costs to offspring survival for additional male mating. On the other hand, the female that mates with the male with zero clutches does not put that male into the parental phase; he continues to attempt to mate. This female's clutch would suffer survival costs due to the male's continued mating. Thus, a female should prefer the male with one clutch over the male with zero clutches. The problem with this scenario, is that we have not optimized male and female behaviour simultaneously. It is possible that female preference for males with eggs may lead to more mating and less care by males with eggs, thus thwarting the adaptive basis for the female preference. It will likely require a dynamic game to sort this out.

All of these suggested improvements are much easier said than done. The problem is dimensionality. As we add more biological reality, we increase a model's complexity geometrically. What started as a simple model may suddenly explode into something intractable. Nevertheless, as theoreticians develop computational shortcuts, and as supercomputers become more commonplace, I suspect that we will see more and more complex models. For the short term, however, I suggest that simple models such as those presented here, will provide us with new and valuable insights, and will stimulate new experimental research.

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