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Resource Allocation in Offspring Provisioning: An Evaluation of the Conditions Favoring the Evolution of Matrotrophy

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abstract: We used analytic and simulation models to determine the ecological conditions favoring evolution of a matrotrophic fish from a lecithotrophic ancestor given a complex set of trade-offs. Matrotrophy is the nourishment of viviparous embryos by resources provided between fertilization and parturition, while lecithotrophy describes embryo nourishment provided before fertilization. In fishes and reptiles, embryo nourishment encompasses a continuum from solely lecithotrophic to primarily matrotrophic. Matrotrophy has evolved independently from lecithotrophic ancestors many times in many groups. We assumed matrotrophy increased the number of offspring a viviparous female could gestate and evaluated conditions of food availability favoring lecithotrophy or matrotrophy. The matrotrophic strategy was superior when food resources exceeded demand during gestation but at a risk of overproduction and reproductive failure if food intake was limited. Matrotrophic females were leaner during gestation than lecithotrophic females, yielding shorter life spans. Our models suggest that matrotrophic embryo nourishment evolved in environments with high food availability, consistently exceeding energy requirements for maintaining relatively large broods. Embryo abortion with some resorption of invested energy is a necessary preadaptation to the evolution of matrotrophy. Future work should explore trade-offs of age-specific mortality and reproductive output for females maintaining different levels of fat storage during gestation.

Keywords: lecithotrophy, life history, matrotrophy, *Poecilia latipinna*, trade-off, viviparity.

Matrotrophy, the nourishment of developing embryos by a source other than yolk in a viviparous female, has evolved independently from a lecithotrophic viviparous ancestor many times in vertebrate history (Stewart 1992; Wake 1992; Wourms and Lombardi 1992; Blackburn 1998; Hamlett and Hysell 1998). The evolution of placental mammals is the most striking example, but analogous transitions in female reproductive investment are found in many groups (e.g., viviparous plants). Evolution of matrotrophy marks a dramatic shift in the timing of allocation of resources and energy to parental care; lecithotrophic females make a major energetic investment in offspring before fertilization with the deposition of yolk resources, while matrotrophic females spread this investment across gestation. Fishes and squamate reptiles provide excellent models for the evolution of embryo nourishment. In these taxa, the relative mix of lecithotrophic and matrotrophic embryo nourishment forms a continuum of female investment patterns, including species that rely predominantly on either mode (Wourms et al. 1988; Stewart and Thompson 1996; Blackburn 1998). Some species display plasticity in the relative investment in pre- and postfertilization nourishment (Thibault and Schultz 1978; Stewart 1989; Trexler 1997). In spite of this diversity of nourishment strategies and the importance of the transition from lecithotrophy to matrotrophy, there is no well-developed theory of the environmental conditions that would yield higher fitness for a lecithotroph that increases the relative amount of matrotrophic nourishment.

The evolution of matrotrophy by a lecithotrophic species can be treated as a life-history adaptation. The timing and magnitude of allocation of limited energy supplies into offspring nourishment is one dimension of the generalized life-history problem (Schaffer 1983): How do organisms resolve conflicting demands for limited energy supplies in order to maximize fitness? Interestingly, benefits of lecithotrophy have been proposed, but benefits of matrotrophy are less clear. It has been proposed that lecithotrophy is favored in a fluctuating environment because all energy needed for completion of a brood is prepackaged (Thibault and Schultz 1978; Wourms and Lombardi 1992). A benefit

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to matrotrophy may come through enhanced fecundity (Trexler 1997). This suggests that, if the total cost per neonate is comparable, lecithotrophic eggs must initially be more energetically costly (and probably larger) than matrotrophic ones because at the outset they contain the total energy stores of prenatal development. Thus, same-sized females should be able to gestate more matrotrophic eggs than lecithotrophic ones if both are brought to term at the same size and energetic condition. The benefit of matrotrophy may be greater brood size if resources are available to carry them to term. Thus, the total cost per brood may be greater for matrotrophs than lecithotrophs because investing less per egg (perhaps simply by starting with smaller eggs) at the outset of gestation permits greater brood size. Energy storage as fat may serve to buffer matrotrophs from fluctuation of food availability (Jonsson 1997) and extend the conditions where they produce more offspring than lecithotrophs.

Matrotrophic nourishment is a complex adaptation, requiring a diversity of morphological and physiological characteristics to carry out. The evolution of such complex adaptations is generally anticipated by the presence of preadaptations that facilitate transitions from one adaptive system (e.g., lecithotrophy) to another (e.g., matrotrophy). Selective abortion of embryos (Kozlowski and Stearns 1989) and reallocation of energy among progeny (Greeff et al. 1999) are two such characters that may be linked to female reproductive investment and could affect the success of a strategy of manipulating the number of eggs fertilized as a function of their initial size or cost. If environmental conditions change such that an initial investment cannot be sustained until parturition, the inability to diminish brood size and/or recapture some of the previously invested energy may be catastrophic. Thus, these characters may be beneficial or necessary preadaptations to permit the transition from lecithotrophy to matrotrophy (cf. Sillen-Tullberg 1988; discussed in Brooks and McLennan 1991, pp. 146–150).

In this article, we describe two models that simulate the energetic fitness costs and benefits of matrotrophic relative to lecithotrophic reproduction. Our major question concerns what environmental conditions favor evolution of matrotrophy from lecithotrophy. In particular, under what conditions does matrotrophy allow production of more offspring? In these models, we hold terminal offspring quality (often equated with size) constant for all investment strategies to simplify the currency we use to measure fitness. At least for live-bearing fishes, there is no evidence of systematic patterns of offspring size linked to embryo nourishment mode (Thibault and Schultz 1978), and there is evidence that these modes do not yield markedly different sizes of offspring in a species that employs both (Trexler 1997). Hypotheses of plastic solutions to offspring size-number trade-offs have been proposed as adaptive responses to variation in resource availability (Reznick and Yang 1993), and fine-tuning of neonate size in addition to egg size could be explored in future models. We first report a simple analytical model that permits a contrast of the fertility of a female employing lecithotrophic to matrotrophic modes of embryo nourishment in a single reproductive bout. Analytical models have been developed to consider many of the individual trade-offs influencing embryo nourishment (Perrin and Sibly 1993), but the combination of conditions that we wished to consider was complex. Several trade-offs emerge from competing physiological demands to influence the outcome of this contrast on lifetime fitness: the size and number of eggs; age-specific allocation of energy to reproduction, storage, and growth; and body condition and probability of survival through an age class. The complexity of all of these simultaneous energetic demands dictated that we supplement our analytical model with a simulation modeling approach. This modeling approach allowed us to derive general results for the trade-off of offspring number and provisioning mode mediated by the food availability before and during reproduction, and survival costs of slow growth and age-specific depletion of energy stores by allocation of energy to reproduction.

We have chosen to develop our simulation model based on a live-bearing fish, the sailfin molly (*Poecilia latipinna*). Fishes provide an excellent system to consider the evolution of matrotrophy. Female fishes with internal fertilization and retention of embryos leading to the release of precocious young display a diversity of modes of embryo nourishment. Embryos may receive nourishment from yolk supplied to the egg before fertilization (lecithotrophy) or from external sources including maternal secretions (matrotrophy), from unfertilized trophic eggs (oophagy), or from fellow brood mates (adelphophagy; reviewed in Wourms and Lombardi 1992). In the family Poeciliidae, live-bearing fishes that include guppies and other aquarium fishes, there is increasing evidence that lecithotrophy is the ancestral state and that matrotrophy has arisen independently several times (Reznick et al. 2002). We have developed our simulation model around the biology of a fish from this family because it is well studied and provides an excellent basis for generalization. We simulated the energetic fitness costs and benefits of matrotrophic relative to lecithotrophic reproduction in the facultative matrotroph, the sailfin molly (Trexler 1997).

Model Development and Analysis

We first describe a simple analytic model used to illustrate the implications of trade-offs incorporated into the model for fitness as measured by reproductive output. We follow that description with a simulation model that permits us to bring together the complexity of several trade-offs in a demographic context. The latter model simulates an age-structured population, including probabilistic effects of trade-offs between patterns of energy allocation and life expectancy.

Analytic Model

The analytic model describes single reproductive bouts of lecithotrophic and matrotophic fishes and focuses on their relative advantages in producing offspring. The resources available to reproduction from stored and recently consumed food mediate the egg number-size trade-off. In this model we ignore the long-term strategies involved in maximum production over multiple bouts and any trade-offs related to age-specific survivorship.

The lecithotroph is assumed to use all of its initial available energy reserves, $\mathrm{Energy}_{\mathrm{LipidInitial}}$, to create a number of eggs, $\mathrm{EggNumber}_{\mathrm{LecInitial}}$. (Here, $\mathrm{Energy}_{\mathrm{LipidInitial}}$ is defined as the lipids stored at the beginning of the reproductive bout in surplus of what the adult needs to maintain itself, $\mathrm{Energy}_{\mathrm{LipidMinimum}}$; thus, energy that can be allocated to reproduction.) No additional energy is invested in the eggs through the time period, $\mathrm{Time}_{\mathrm{Bout}}$, to their maturation. The matrotroph is assumed to produce a larger number of initially smaller eggs, $\mathrm{EggNumber}_{\mathrm{MatInitial}}$, and is assumed to apportion energy from its stores, as well as energy above its maintenance needs, $\mathrm{Energy}_{\mathrm{AvailablePerDay}} = \mathrm{Energy}_{\mathrm{IntakePerDay}} - \mathrm{Energy}_{\mathrm{AdultNeedsPerDay}}$, on a day-by-day basis to bring its clutch of eggs to maturity. Thus the matrotroph, if it starts with the same $\mathrm{Energy}_{\mathrm{LipidInitial}}$ as the lecithotroph, has the potential to produce more eggs during a bout.

Assume that the average amount of energy needed per egg per day for both matrotroph and lecithotroph to bring the egg to maturity is $\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}$ (although the lecithotroph provides all of this initially). Then the number of eggs that the lecithotroph produces, assuming that all eggs produced initially survive to maturity, can be expressed as

$$\mathrm{EggNumber}_{\mathrm{LecFinal}} = \mathrm{EggNumber}_{\mathrm{LecInitial}} = \frac{\mathrm{Energy}_{\mathrm{LipidInitial}}}{\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}\mathrm{Time}_{\mathrm{Bout}}}, \quad (1)$$

rounded down to the nearest integer. The number of eggs produced by the matrotroph with the same initial store of energy in lipid, $\mathrm{Energy}_{\mathrm{LipidInitial}}$, as the lecithotroph will depend on the amount of energy available to allocate to eggs by the matrotroph per day after its own energy needs are met (i.e., daily surplus energy intake [$\mathrm{Energy}_{\mathrm{AvailablePerDay}}$]). If this quantity is positive, then the matrotroph can produce, at best, a number of eggs given by

$$\mathrm{EggNumber}_{\mathrm{MatFinal}} = \mathrm{EggNumber}_{\mathrm{LecFinal}} + \frac{\mathrm{Energy}_{\mathrm{AvailablePerDay}}}{\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}}. \quad (2)$$

The matrotroph female appears to have an advantage in egg production over the lecithotroph, given its potential to produce a greater number of eggs in a given reproductive bout, assuming the same initial store of energy and the same daily intake of energy. However, there are also energetic disadvantages to the matrotrophic strategy. If the matrotroph creates too many initial eggs, its daily energy intake may not be sufficient to bring all of them to maturity, and, in order to maintain lipid reserves above a critical level, $\mathrm{Energy}_{\mathrm{LipidMinimum}}$, the matrotroph must abort some or all of the eggs. The net result might be a less efficient use of energy by the matrotroph than by the lecithotroph, since some energy will be wasted in eggs that are subsequently aborted. The matrotroph may be able to mitigate some of this loss of energy to aborted eggs through resorption of energy from those aborted eggs.

We use this model to consider two possible cases involving matrotroph reproductive dynamics. First, there is a constant daily intake of energy by the matrotroph, which may or may not be sufficient to maintain the initial number of eggs through the period until egg maturity. A range of feasible values of energy resorption, $\mathrm{Resorb}_{\mathrm{Fraction}}$, from aborted eggs, from $\mathrm{Resorb}_{\mathrm{Fraction}} = 0$ to 1, can be explored. Second, the daily intake of energy is not a constant but fluctuates from day to day, so there is a risk of depletion of lipid reserves below the minimum required, $\mathrm{Energy}_{\mathrm{LipidMinimum}}$, although the energy intake over the whole bout, if distributed uniformly across the gestation period, would be sufficient to supply the eggs and maintain the lipid reserves.

Case 1: Constant Daily Rate of Energy Intake. We assume that a matrotroph produces an initial number of eggs $\mathrm{EggNumber}_{\mathrm{MatInitial}}$. It uses its daily available energy for reproduction, $\mathrm{Energy}_{\mathrm{AvailablePerDay}}$, as well as a percentage each day of the energy from its initial lipid stores, $\mathrm{Energy}_{\mathrm{LipidInitial}}$, to maintain the eggs. If at any time t during the reproductive bout the lipid reserves fall to $\mathrm{Energy}_{\mathrm{LipidMinimum}}$, the matrotroph switches to a tactic of aborting eggs down to a number that it can maintain. It can be shown (see app. A in the online edition of the *American Naturalist*) that the final number of eggs is given by

$$\begin{aligned}\mathrm{EggNumber}_{\mathrm{MatFinal}} &= \\ \mathrm{Energy}_{\mathrm{AvailablePerDay}}/\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}} & \\ + (\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}\mathrm{EggNumber}_{\mathrm{MatInitial}} & \\ - \mathrm{Energy}_{\mathrm{AvailablePerDay}})/\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}} & \\ \times [\mathrm{Energy}_{\mathrm{LipidInitial}}/ & \\ (\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}\mathrm{EggNumber}_{\mathrm{MatInitial}} & \\ - \mathrm{Energy}_{\mathrm{AvailablePerDay}})\mathrm{Time}_{\mathrm{Bout}}]^{1/\mathrm{Resorb}_{\mathrm{Fraction}}}. &\end{aligned} \tag{3}$$

A critical quantity in equation (3) is the ratio in the last factor of the equation, which is raised to the power $1/\mathrm{Resorb}_{\mathrm{Fraction}}$. The importance of that factor is as follows. When

$$\begin{aligned}\mathrm{Energy}_{\mathrm{AvailablePerDay}}\mathrm{Time}_{\mathrm{Bout}} + \mathrm{Energy}_{\mathrm{LipidInitial}} \geq & \\ \mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}\mathrm{EggNumber}_{\mathrm{MatInitialTimeBout}}, &\end{aligned} \tag{4}$$

the intake of available energy over the period $\mathrm{Time}_{\mathrm{Bout}}$ plus the initial energy in lipid storage are together sufficient to meet the needs of all of the eggs produced. When equation (4) is an equality, the ratio in the last factor in equation (3) is equal to 1.0. Since the model assumes that energy intake above the needs of maintaining minimum lipid storage and supplying the eggs cannot be used, only the equality in equation (4) has meaning, permitting the factor to be set equal to 1.0 for all cases in which equation (4) holds. When equation (4) holds, it follows that

$$\mathrm{EggNumber}_{\mathrm{MatFinal}} = \mathrm{EggNumber}_{\mathrm{MatInitial}}. \tag{5}$$

If the inequality (4) is reversed, which occurs when $\mathrm{EggNumber}_{\mathrm{MatInitial}}$ is large enough, it means that there is not enough energy to bring all of the eggs to maturation and that some must be aborted. Then the ratio within the brackets takes some value between 0.0 and 1.0. The fraction of eggs that must be aborted depends on the fraction of the energy per egg that can be resorbed and reused, $\mathrm{Resorb}_{\mathrm{Fraction}}$. Consider first the case that $\mathrm{Resorb}_{\mathrm{Fraction}}$ is 0 or close to 0. It is easy to see in this case that the whole second term of equation (3) approaches 0 for any value of the ratio that is <1.0, and, as a result,

$$\mathrm{EggNumber}_{\mathrm{MatFinal}} = \frac{\mathrm{Energy}_{\mathrm{AvailablePerDay}}}{\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}}. \tag{6}$$

The biological reason for this is as follows. If the energy reserves of the matrotroph fall to $\mathrm{Energy}_{\mathrm{LipidMinimum}}$ (i.e., the initial surplus lipid $\mathrm{Energy}_{\mathrm{LipidInitial}}$ is exhausted), the matrotroph does not have the energy beyond $\mathrm{Energy}_{\mathrm{AvailablePerDay}}$ to support its eggs. Therefore, it must abort all eggs above the number that can be supported by daily available energy in order to prevent further depletion of energy below that critical threshold. We can plot $\mathrm{EggNumber}_{\mathrm{MatFinal}}$ as a function of $\mathrm{EggNumber}_{\mathrm{MatInitial}}$ (*solid line with circles*, fig. 1*A*). This figure illustrates that as long as inequality (4) holds, the number of eggs produced, $\mathrm{EggNumber}_{\mathrm{MatFinal}}$, is equal to $\mathrm{EggNumber}_{\mathrm{MatInitial}}$. However, when the inequality is reversed (at a point denoted by E_2 on the X-axis in fig. 1*A*), $\mathrm{EggNumber}_{\mathrm{MatFinal}}$ can only be the number of eggs that can be maintained with the daily input, $\mathrm{Energy}_{\mathrm{AvailablePerDay}}$. For concreteness in this figure, we considered the situation in which the constant daily energy intake of available energy, when summed over the reproductive bout, is identically equal to the initial lipid energy:

$$\mathrm{Energy}_{\mathrm{AvailablePerDay}}\mathrm{Time}_{\mathrm{Bout}} = \mathrm{Energy}_{\mathrm{LipidInitial}}. \tag{7}$$

Now consider a female that can resorb some energy by aborting eggs. In that case, if the matrotroph runs out of lipid reserves, it does not need to abort all of its eggs beyond what it can maintain on $\mathrm{Energy}_{\mathrm{AvailablePerDay}}$. It can abort a fraction of them and use the energy for its own maintenance needs while continuing to maintain a number of remaining eggs greater than $\mathrm{Energy}_{\mathrm{AvailablePerDay}}/\mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}$. Consider again the situation in which there is a constant daily energy intake of available energy, which, when summed over the reproductive bout, is equal to the initial lipid energy (equation 7). Assume that some fraction, say $\mathrm{Resorb}_{\mathrm{Fraction}} = 0.5$, of the energy in the aborted eggs can be reused. In this case, equation (3), after some manipulations, can be rewritten in a more convenient form. Defining $\mathrm{Energy}_{\mathrm{TotalNeededPerEgg}} = \mathrm{Energy}_{\mathrm{NeededPerEggPerDay}}\mathrm{Time}_{\mathrm{Bout}}$ and using equation (7), we obtain from equation (3) the equation

$$\begin{aligned}\mathrm{EggNumber}_{\mathrm{MatFinal}} &= \\ \mathrm{Energy}_{\mathrm{LipidInitial}}/\mathrm{Energy}_{\mathrm{TotalNeededPerEgg}} & \\ + (\mathrm{EggNumber}_{\mathrm{MatInitial}} & \\ -\mathrm{Energy}_{\mathrm{LipidInitial}}/\mathrm{Energy}_{\mathrm{TotalNeededPerEgg}}) & \\ \times [\mathrm{Energy}_{\mathrm{LipidInitial}}/ & \\ (\mathrm{EggNumber}_{\mathrm{MatInitial}}\mathrm{Energy}_{\mathrm{TotalNeededPerEgg}} & \\ - \mathrm{Energy}_{\mathrm{LipidInitial}})]^2. &\end{aligned} \tag{8}$$

From equation (8) it is possible to plot $\mathrm{EggNumber}_{\mathrm{MatFinal}}$ as a function of $\mathrm{EggNumber}_{\mathrm{MatInitial}}$ (*solid line with squares*, fig. 1*A*). As long as the ratio in the final parentheses is greater than unity (or negative, which means that there is sufficient energy in the daily energy intake alone to main-

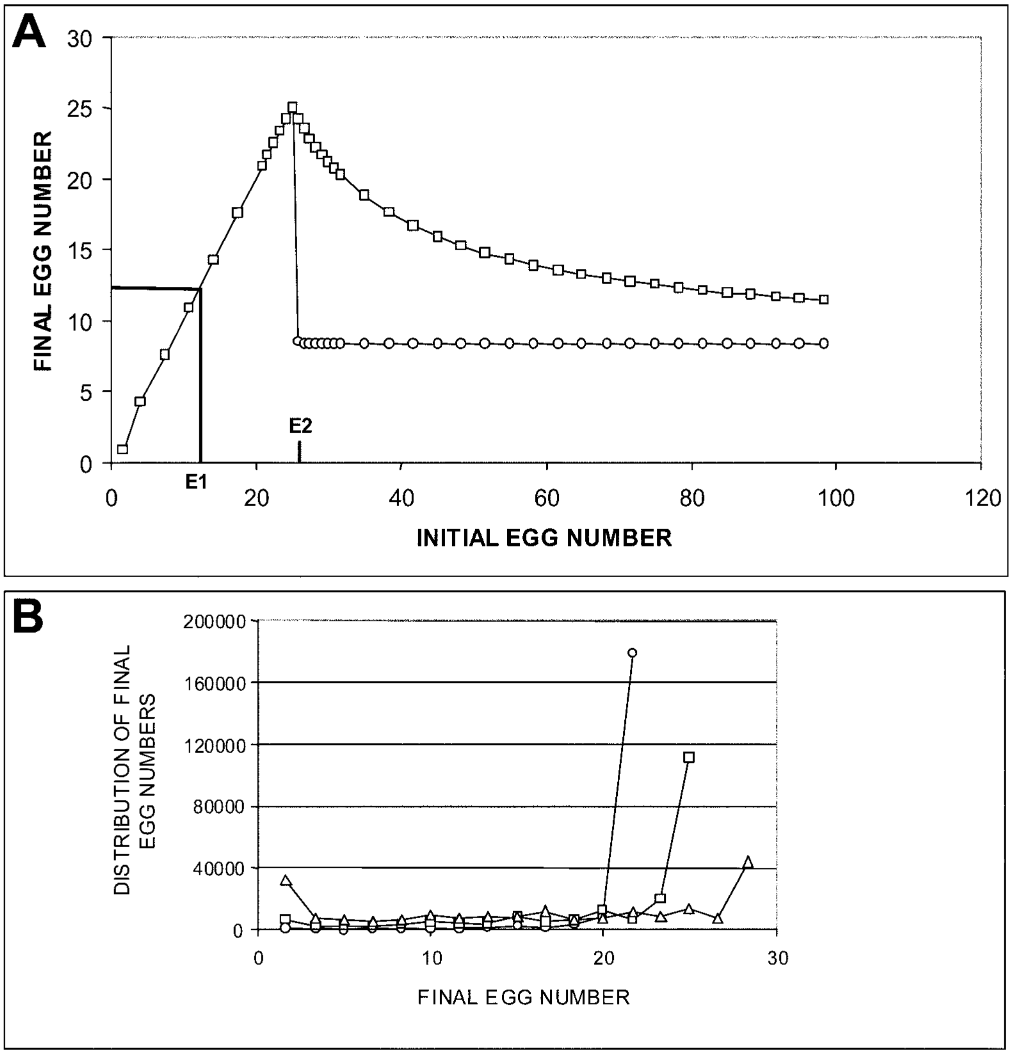

Figure 1: *A*, Total number of matrotrophic eggs brought to maturity, $\mathrm{EggNumber}_{\mathrm{MatFinal}}$, is plotted as a function of the total number of initial matrotrophic eggs, $\mathrm{EggNumber}_{\mathrm{MatInitial}}$, from the analytic model. (Egg units are arbitrary.) The point E_1 along the horizontal axis represents the assumed initial lipid energy in units of mature eggs. The number of final lecithotrophic eggs, $\mathrm{EggNumber}_{\mathrm{LecFinal}}$, which equals $\mathrm{EggNumber}_{\mathrm{LecInitial}}$, is given by the intersection of the line originating at E1 with the vertical axis. The point E_2 represents the $\mathrm{Energy}_{\mathrm{AvailablePerDay}}\mathrm{Time}_{\mathrm{Bout}} + \mathrm{Energy}_{\mathrm{LipidInitial}}$, again in units of mature eggs. Two curves representing $\mathrm{EggNumber}_{\mathrm{MatFinal}}$ as a function of $\mathrm{EggNumber}_{\mathrm{MatInitial}}$ are shown. Here, we assumed that $\mathrm{Energy}_{\mathrm{LipidInitial}} = 12.5$ (arbitrary units), that $\mathrm{Energy}_{\mathrm{TotalNeededPerEgg}} = 1$, and that equation (7) holds. If daily energy ingestion is constant and there is no resorption and the initial number of eggs produced exceeds those that can be maintained, then all are aborted except those that can be supported by the daily energy intake $\mathrm{Energy}_{\mathrm{AvailablePerDay}}$, so there is a maximum at the point E_2 (*solid line with circles*). If daily energy ingestion is constant and if some fraction of resorption occurs (in this case, $\mathrm{Res}_{\mathrm{Fraction}} = 0.5$), then a maximum still occurs at E_2, but the decrease in $\mathrm{EggNumber}_{\mathrm{MatFinal}}$ as a function of $\mathrm{EggNumber}_{\mathrm{MatInitial}}$ is smooth (*solid line with squares*). *B*, Monte Carlo simulation of the model for 10,000 matrotrophs, in which daily energy ingestion fluctuates about the mean and no resorption is assumed. Instead of a fixed number of mature eggs for a number of initial eggs, there is a distribution of final numbers of eggs produced (number of females times number of eggs per female) by the population of matrotrophs, as shown here for $\mathrm{EggNumber}_{\mathrm{MatInitial}} = 22$ (*circles*), 25 (*squares*), and 28 (*triangles*).

tain all eggs through gestation), we assume that it is unity. When $\mathrm{EggNumber}_{\mathrm{MatInitial}}$ is large enough that the ratio is less than unity (there is not enough energy to bring all eggs to maturity), the $\mathrm{EggNumber}_{\mathrm{MatFinal}}$ declines roughly as $1/\mathrm{EggNumber}_{\mathrm{MatInitial}}$ rather than sharply, as in the case where there is no resorption of energy from aborted eggs. In nature, it is probably unrealistic to assume resorption of energy greater than $\mathrm{Resorb}_{\mathrm{Fraction}} = 0.5$, but no data are available at present.

In addition to the matrotrophic egg production, the number of lecithotrophic eggs produced is also shown in figure 1 (signified by E_1). Because the energy ingested by the matrotroph over the reproductive bout (above what is needed for basal metabolism, and so available for reproduction), $\mathrm{Energy}_{\mathrm{AvailablePerDay}}\mathrm{Time}_{\mathrm{Bout}}$, is assumed in this example to equal $\mathrm{Energy}_{\mathrm{LipidInitial}}$, it is possible for the matrotroph to initiate twice as many eggs as the lecithotroph.

The curves of $\mathrm{EggNumber}_{\mathrm{MatFinal}}$ as a function of $\mathrm{EggNumber}_{\mathrm{MatInitial}}$ for other values of $\mathrm{Resorb}_{\mathrm{Fraction}}$ would fall between the curves of $\mathrm{Resorb}_{\mathrm{Fraction}} = 0.0$ and 0.5, shown in figure 1*A*. In all cases, the production of matrotrophic eggs is maximized at the point E_2, where the equality in equation (4) is satisfied. This means that egg production is maximized when the matrotroph can perfectly align its initial number of eggs with the amount of intake energy that will be available to the adult over the reproductive bout. If the matrotroph either underestimates or overestimates the energy that will be available by too much, its production of mature eggs could even fall below that of the lecithotroph.

Case 2: Fluctuating Daily Energy Intake. The above analytic model is deterministic and does not take into account stochastic factors in daily intake of energy. If the intake of energy by the matrotrophic female fluctuates from day to day, then there is some risk of the energy stores of the female falling below $\mathrm{Energy}_{\mathrm{LipidMinimum}}$ even though the mean input over the reproductive bout satisfies inequality (4). The implication of such fluctuations is that the matrotroph might employ a more conservative strategy in the number of eggs initiated than in the case where the daily energy input is constant. There are many possible patterns and intensities that the fluctuations in energy intake can assume, so it is difficult to make generalizations. We calculate the consequences of only one possible scenario.

Suppose that the expected available energy ingested by the individual matrotrophic female during the reproductive bout can vary but has the mean value of $\mathrm{Energy}_{\mathrm{AvailablePerDay}}$ averaged over the whole 30-d reproductive bout. As a specific example, we allowed the probability of feeding on a particular day to be 1 : 3 but the amount of energy in the ingested food to be three times the daily intake of the analytic model above. Even for this simple situation, it does not appear possible to solve analytically for the expected number of matrotrophic eggs, $\mathrm{EggNumber}_{\mathrm{MatFinal}}$. Instead, we performed Monte Carlo simulations using all of the other assumptions of the analytic model. We simulated 10,000 matrotrophs for each starting number of eggs—22, 25, and 28—and found the numbers of eggs brought to maturity in each simulation. We assumed no resorption of eggs.

Contrary to the deterministic model, some of the matrotrophs that started with 22 eggs were unable to bring all eggs to maturity, and there was a distribution of mature eggs that included cases where zero mature eggs were produced (*circles*, fig. 1*B*). Also, contrary to the deterministic case of zero resorption, some matrotrophs starting with 28 eggs were able to bring all to maturity (*triangles*, fig. 1*B*). The reason for this difference is that, in the Monte Carlo simulation, the matrotrophs aborted eggs each day that lipid levels fell below their minimum allowable value, $\mathrm{Energy}_{\mathrm{LipidMinimum}}$. Unlike the deterministic case, in which lipid levels continued to decline below $\mathrm{Energy}_{\mathrm{LipidMinimum}}$ if the female did not abort all of her eggs, in the stochastic case, a female's situation might improve in following days, allowing it to maintain the remaining eggs. Hence, fluctuations in the temporal acquisition of prey can introduce an element of risk for the matrotroph even if the mean level of food availability over the reproductive bout is predictable.

Detailed Simulation Model

Simple models such as the one above can be useful "minimal" models for exploring a few properties of a system by ignoring much of the complexity. The results of such models are a good starting place but must be followed up by analysis of more detailed models, both to test the results of the analytic model and to expand to more complex situations. The analytical model is formulated on an energy budget and does not consider age-specific patterns of mortality that are commonly correlated with energy storage in fishes from natural populations.

We developed a simulation model to examine the difference between lecithotrophic and matrotrophic reproductive strategies in fish experiencing different conditions of food availability and with realistic size-specific mortality schedules (see app. B in the online edition of the *American Naturalist*). We asked what environmental conditions favor either of these strategies based on the average lifetime reproductive output of females. We developed separate models for each strategy that included allocation of energy to growth, storage, and reproduction through time while computing the effects of each on reproductive success. We parameterized the model with data on sailfin mollies *Poecilia latipinna*, though our intent is to use this as a general example of the constraints and trade-offs in viviparous animals. The model follows individual female fish through their lifetime in daily time steps starting from an initial juvenile age. The model tabulates the daily energetics of each fish starting with intake of food. It describes the allocation of this energy through the reproductive season and keeps track of the number of offspring produced in order to calculate the reproductive fitness for each fish (fig. 2).

The fish are assumed to survive for at most one repro-

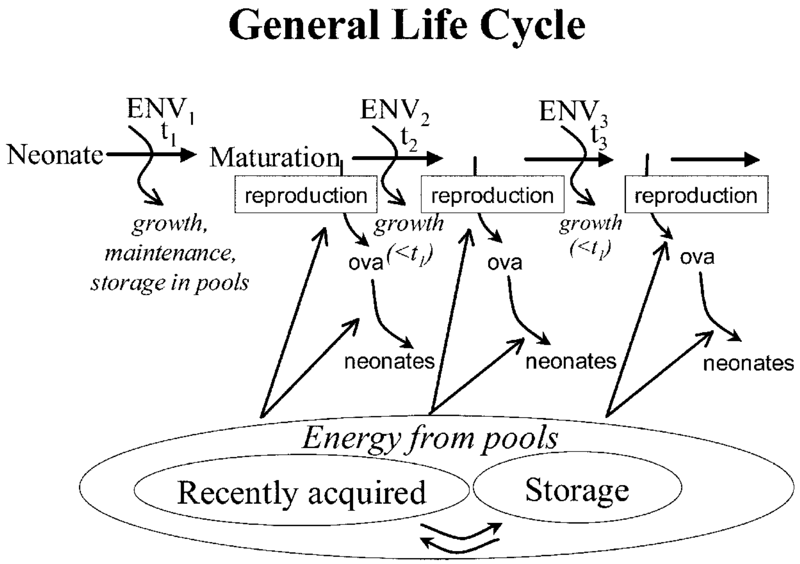

Figure 2: Schematic diagram of the sailfin molly life cycle employed in our models. The cycle begins with the fish as a neonate that experiences one environment as a juvenile before maturation (ENV$_1$) and before her first reproductive bout. Energy is allocated to growth, maintenance, and storage in energy pools (illustrated at the bottom of the figure) as a juvenile. Reproduction requires the allocation of energy to production of ova and, in a matrotroph, to embryos. This energy is drawn from pools of recently acquired and previously stored reserves. Energy not used promptly is shuttled into storage (lipids), forcing a time lag of several days before it can be mobilized when demand increases again. Each female may survive for up to three reproductive bouts in her lifetime, experiencing a particular environment in each brood cycle with assigned energetic costs and survival risks. Survival, growth, and reproductive investment for each bout are mediated by the availability of energy acquired by feeding and stored in the two pools.

ductive season, and the simulations follow each fish until the end of the reproductive season or until its death, if the latter comes first. Because survival is strongly related to the size (Trexler et al. 1992) and condition (McManus 1993; McManus and Travis 1998) of sailfin mollies, the probability of survival per daily time step is modeled as an increasing function of size and stored lipids. Thus, the calculation of reproductive fitness considers survivorship through the reproductive season.

Survival is the lone stochastic element in the simulation model. Each fish can die at any time during the simulation, depending on the pseudorandom number generator. In order to derive statistics for the reproductive fitness of the lecithotrophic and matrotrophic strategies, a Monte Carlo approach was used in which 500 fish employing each strategy were simulated. The mean number of offspring for each strategy was calculated. The specific components of the model are described below.

Model Simulations. Two types of model simulations were performed. The first was to compare the simulation model with the analytic model for the case of a single reproductive bout. Both the lecithotroph and the matrotroph were given a constant rate of resource availability. The model performed Monte Carlo simulations with a number (500) of individual female fish starting at a chosen age and wet weight in grams on a certain day of the year. The assumptions on the starting conditions were the following: starting age of fish was 40 d, starting weight of fish was 0.5 g wet weight, and starting age of reproduction was 100 d. A set of simulations with initial egg numbers from five to 100 was performed.

The second set of simulations was aimed at comparing the lecithotrophic and matrotrophic strategies for a range of values of resource availability, *P*, over an entire season of several reproductive bouts. For each value of *P*, sets of 500 fish each, using lecithotrophic and matrotrophic strategies, were started with the same ages and weights indicated above. Until the start of reproduction, both the lecithotrophs and matrotrophs followed the same strategy of investment of energy in growth and lipid storage. Consequently, they each had exactly the same weight, length, and amount of lipid storage when they were about to start reproduction. In this second set of simulations, we did not allow the matrotroph to produce its maximum capacity of initial eggs but chose the same initial egg production that maximized the number of mature embryos produced.

Simulation Results. The number of eggs brought to ma-

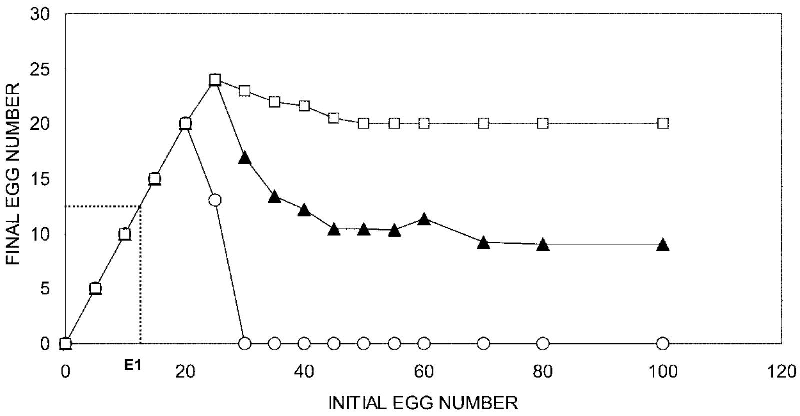

Figure 3: Total number of matrotrophic eggs brought to maturity, EggNumber$_{\mathrm{MatFinal}}$, is plotted as a function of the total number of initial matrotrophic eggs, EggNumber$_{\mathrm{MatInitial}}$, for three values of energy resorption from embryos: 0.0, 0.2, and 0.5 (*circles*, *triangles*, and *squares*, respectively). The lecithotrophic strategy is compared (E1). Results from means of 500 individual fish in our simulation model; the results are similar to the analytic model (fig. 1).

turity for a range of initial values of matrotrophic eggs can be compared for three assumptions for the resorption efficiency of energy from aborted embryos: 0.0, 0.2, and 0.5 (fig. 3). Note that as the initial investment in eggs increases from 0 to about 25, the number of successful eggs increases linearly but then declines as the matrotroph produces a higher number of initial eggs than it is able to provide energy for. This agrees well with the results of the analytic model (fig. 1*A*; the units in the analytic model are arbitrary). An exception to this general agreement is that the production of mature eggs for 0.5 resorption does not decline as rapidly or as much as in the analytic model. The reason for this lies in the discrete-time nature of the simulation model. The simulated matrotrophs make decisions on abortion on daily time steps, whereas in the analytic model behavior occurs on continuous time. This results in the simulated energy-limited matrotroph aborting a higher number of eggs earlier in the reproductive bout than in the analytic model. This initial high abortion rate has a longer-term advantage in preventing the wastage of energy in nourishing eggs that will eventually be aborted. Of course, both the continuous-time and discrete-time assumptions are artifacts of the model. We do not know how the decision for embryo abortion might be made.

The next simulations refer to the whole reproductive season and so demonstrate how additional complexities are brought into play. Here we show only a single pair of simulations (fig. 4) comparing the performances of a lecithotroph and matrotroph individual, respectively, through a season for a particular value of food availability. These were two individuals that managed to survive through the whole season. In these plots, both the number

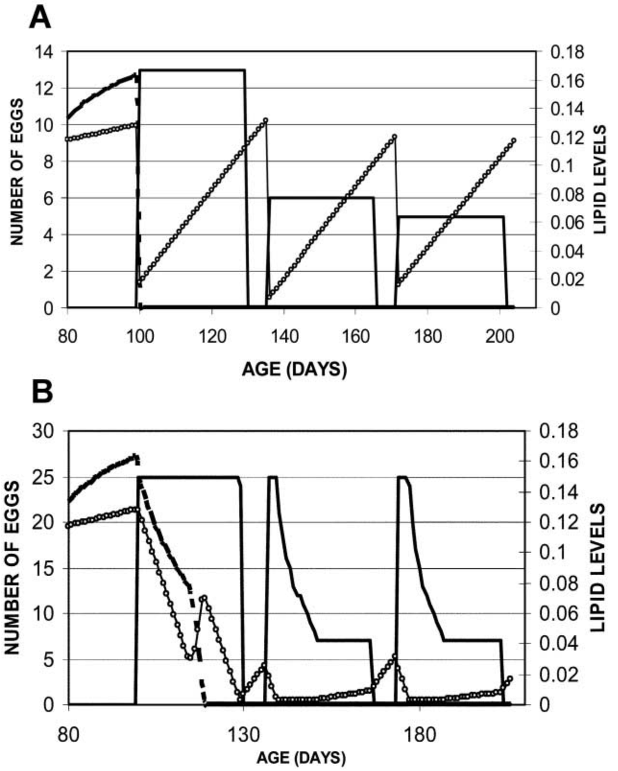

Figure 4: Results of reproductive dynamics for selected individual female fish in the simulation model. These individual fish are ones that survived for the whole reproductive season. The number of surviving eggs is plotted as well as the amount of energy stored in short-term and long-term lipid stores. *A*, Lecithotrophic strategy; *B*, matrotrophic strategy. Egg number is represented by thick solid lines, long-term lipids by dashed lines, and short-term lipids by circles.

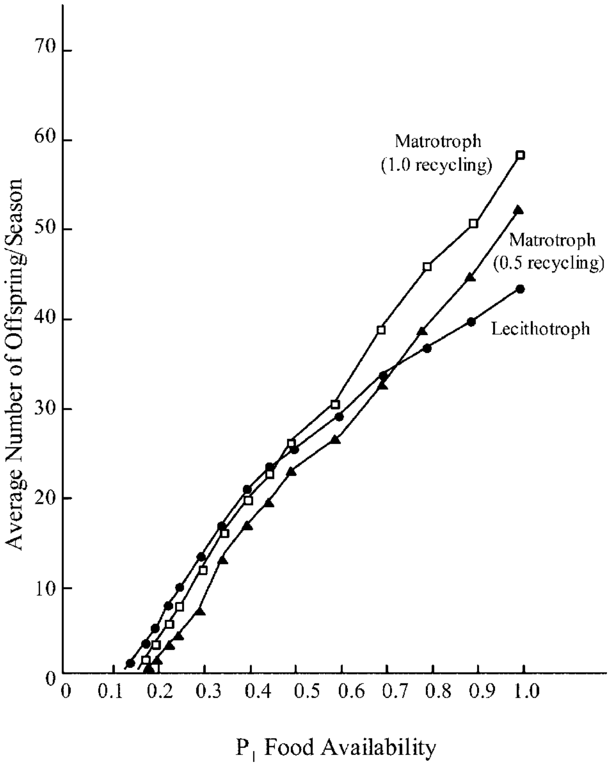

Figure 5: Average number of offspring produced per season relative to food availability as predicted by our simulation model. Lecithotrophs are plotted with solid circles, matrotrophs with 100% resorption of embryo energy are plotted with open squares, and matrotrophs with 50% resorption efficiency are plotted with solid triangles.

of surviving eggs on each day (*solid lines*) and the amounts of stored lipid, both short-term (*circles*) and long-term (*dashes*), are shown. Note that the lecithotroph (fig. 4*A*) had three reproductive bouts, producing 13, six, and five successful eggs, respectively, in these bouts, for a total of 24 offspring. Preceding each of these bouts, it drew its lipid stores down to nearly zero. But the lipid stores recovered at a relatively rapid rate.

The matrotroph, for the case of 0.5 resorption (fig. 4*B*), had three bouts as well, starting with 25, 25, and 25 eggs and ending with 25, seven, and seven successful eggs at the end of the respective bouts for a total of 39 successful eggs. Note that through most of the reproductive season, the lipid stores were drawn down to almost zero as the matrotroph tried to provide for the eggs under energy-limited conditions. As a consequence of the energy limitation, the original number of eggs decreased rapidly as they were resorbed in order to provide maintenance energy for the fish. In the case in which zero resorption was permitted, only 13 matrotroph eggs were brought to maturity: 13, 0, and 0 is the fertility of the three respective bouts. It appears that the matrotrophic strategy may be less advantageous over the whole reproductive season than for the first bout when daily energy intake is not high. An additional disadvantage was that the matrotroph had a slightly shorter expected life span (110.2 d) compared with the lecithotroph (112.8 d).

In all scenarios, the matrotroph and lecithotroph produced similar numbers of offspring at low food levels, but the matrotroph produced more at high food levels (fig. 5). The efficiency of embryo resorption determined the food level where matrotrophy became superior to lecithotrophy: the less efficient resorption, the greater range of food ration where lecithotrophy yielded more offspring than matrotrophy. Lecithotrophs generally had longer life spans than matrotrophs when we incorporated a trade-off between probability of survival and fat storage. Matrotrophs drew on their fat stores throughout gestation and were leaner throughout the reproductive season in simulations using all but the lowest food levels (fig. 6). The difference was generally about 10 d, not enough to yield an extra reproductive cycle (30 d) but possibly important at the population level.

Discussion

If matrotrophy increases the number of offspring a viviparous female can gestate, why is it not more common in

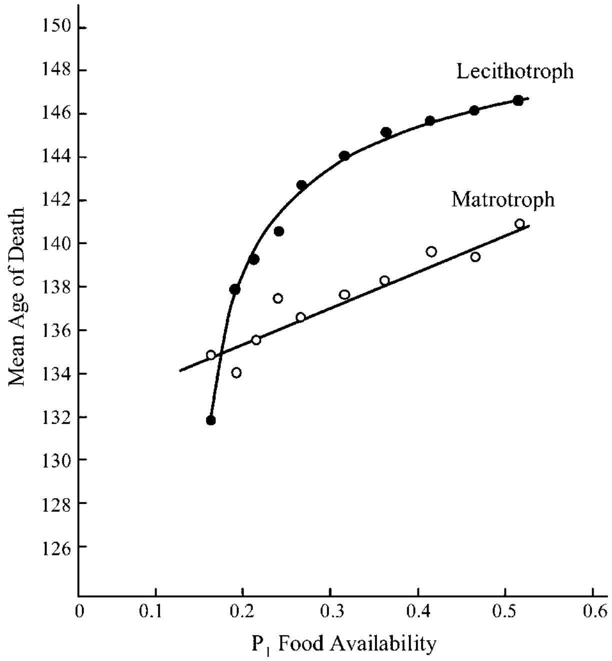

Figure 6: Mean age at death relative to food availability for females in our simulation model. Lecithotrophs are plotted with solid circles and matrotrophs with open circles.

fishes? Our models indicated that trade-offs might limit the advantage of matrotrophic reproduction relative to lecithotrophic in food-limited environments. While the assumptions of our models render the matrotrophic strategy clearly superior when food resources are not limiting, the multiple costs of overproduction can lead to a higher lifetime reproductive production for lecithotrophy if food is limited. Our simulations suggest that matrotrophic embryo nourishment may have evolved in environments where food availability consistently exceeded requirements. Food limitation can diminish fitness through a diversity of mechanisms both physiological (decreasing fertility) and demographic (decreasing life expectancy). Considering both types of demands simultaneously in our simulation model is instructive in illustrating limitations on the apparent benefit of matrotrophy through costs of increased initial fertility. These costs were less apparent when each factor was considered separately. Phylogenetic analysis suggests that matrotrophy has arisen and been lost multiple times within the poeciliid fishes (Reznick et al. 2002); these costs may explain this pattern.

The efficiency of embryo resorption and recycling of energy invested at the outset of the reproductive bout proved to strongly influence the potential benefits of matrotrophy. Bet-hedging and selective abortion hypotheses on the benefits of brood reduction assume that zygotes are relatively cheap (Kozlowski and Stearns 1989) or that resources invested can be reallocated among progeny (Greeff et al. 1999). A key assumption of our models was that matrotrophic reproduction might lead to females investing in reproduction beyond their energetic capacity to complete the brood. In our models, this led to embryo abortion and resorption of various fractions of the energy invested in those aborted embryos. If matrotrophic females cannot recycle the energy invested in a failed or partially failed brood, the benefits of matrotrophy are greatly diminished and the risks greatly enhanced. The frequency of embryo abortion and energy recycling is not established in live-bearing fishes (cf. Meffe and Vrijenhoek 1981; Trexler 1997); our model suggests that this is an important area for future research.

Many other aspects of the lecithotroph/matrotroph trade-off require further exploration, notably the implications of stored lipid and age-specific survival. We expect that since lipid storage is higher in lecithotrophs (because matrotrophy draws more heavily on stored energy at relatively low food levels in order to sustain greater initial reproductive commitment), this could expand the ranges over which lecithotrophy is favored. Thus, the three-way trade-off of current reproductive effort, energy storage, and future survival may play a role in the evolution of matrotrophy as well as other life-history characters. We explored only one potential functional relationship between lipid stores and survival: a simple linear relationship. Other forms of this relationship are feasible, particularly nonlinear relationships (Schaffer 1974; Charnov and Skinner 1984; Bell and Koufopanou 1986) and time lags. Nonlinear relationships would arise if, for example, there were a threshold level of lipid storage needed to sustain routine metabolic costs. Time lags could arise if physiological stress induced by low lipid storage at an early age leads to accelerated senescence and greater age-specific mortality later in life. Finally, both such relationships may vary across environments as a function of metabolic costs of life in each environment (e.g., along a temperature gradient) or the energetic demands of survival (e.g., the intensity and type of predation risks). Such relationships deserve greater empirical and theoretical consideration.

Our models suggest new ways that age-specific patterns of female reproductive investment may emerge. For example, females may be favored that become more matrotrophic later in life as the likelihood of additional reproductive bouts diminishes and the benefits of minimizing future costs become less important. This would be most relevant in environments where food availability is not likely to drop low enough to yield reproductive failure if a female overinvested in a brood initially or for females with the greatest capacity to adjust brood size during gestation.

Seasonal shifts in food availability or maintenance demand may shift the favored reproductive strategy. This observation has two implications. First, this could favor some facultative control of matrotrophic investment in embryos depending on the season of reproduction. Females producing multiple broods across a reproductive season may maximize their fertility by shifting their mode of investment as food availability shifts with seasons. There is some evidence that female sailfin mollies become more matrotrophic as the reproductive season progresses, which is possibly linked to food availability. For cohorts with reproductive cycles coinciding with seasonal cycles (young females reproduce initially in the spring and then survive to produce a second brood in the mid or late summer), female age and size may change in concert with seasonal shifts in food availability. The first brood of such small/young females may be produced with relatively low lipid stores but coincide with a spring flush of food. This may favor lecithotrophic reproduction because of low energy reserves and a high potential for future reproductive bouts. The second brood would then be produced by older females in a relatively low food environment (higher intraspecific competition for food) and with low probability of survival through the winter to the next reproductive season. Second, fluctuating food level may favor lecithotrophy if food-limiting conditions are likely to arise after a brood is initiated, especially if embryo recycling is not efficient.

This can lead to the failure of clutches in matrotrophs in our model and greatly diminish the benefits of matrotrophy in lifetime reproductive success. If recycling efficiency is low enough, the loss can be catastrophic.

The use of simulation modeling has provided us the opportunity to examine multiple trade-offs simultaneously while considering the effects of stochastic survival processes on fitness. It indicated that matrotroph advantage diminished in later reproductive bouts and that the matrotroph's expected life span was slightly smaller than the lecithotroph's. Several topics remain to be explored that may further influence the evolution of matrotrophy. These include the age at first reproduction and potential benefits of earlier reproduction, the effects of different functional relationships of survival and lipid stores, the effects of time-varying or seasonal food supply (P), and variation in neonate size. Each of these topics has been explored in other contexts in analytical models but has not been considered simultaneously, as is possible with our simulation approach. The simulation approach holds out great potential for future explorations in life-history ecology.

Acknowledgments

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Literature Cited

Bell, G., and V. Koufopanou. 1986. The cost of reproduction. Oxford Surveys of Evolutionary Biology 3:83–131.

Blackburn, D. G. 1998. Structure, function, and evolution of oviducts of squamate reptiles, with special reference to viviparity and placentation. Journal of Experimental Zoology 282:560–617.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior: a research program in comparative biology. University of Chicago Press, Chicago.

Charnov, E. L., and S. W. Skinner. 1984. Evolution of host selection and clutch size in parasitoid wasps. Florida Entomologist 67:5–21.

Greeff, J. M., M. G. Storhas, and N. K. Michiels. 1999. Reducing losses to offspring mortality by redistributing resources. Functional Ecology 13:786–792.

Hamlett, W. C., and M. K. Hysell. 1998. Uterine specializations in elasmobranchs. Journal of Experimental Zoology 282:438–459.

Jonsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos 78:57–66.

Kozlowski, J., and S. C. Stearns. 1989. Hypotheses for the production of excess zygotes: models of bet-hedging and selective abortion. Evolution 43:1369–1377.

McManus, M. G. 1993. Differential resource allocation in the sailfin molly, *Poecilia latipina*: laboratory and field experiments. Ph.D. diss. Florida State University, Tallahassee.

McManus, M. G., and J. Travis. 1998. Effects of temperature and salinity on the life history of the sailfin molly (Pisces: Poeciliidae): lipid storage and reproductive allocation. Oecologia (Berlin) 114:317–325.

Meffe, G. K., and R. C. Vrijenhoek. 1981. Starvation stress and intraovarian cannibalism in livebearers (Atheriniformes: Poeciliidae). Copeia 1981:702–705.

Perrin, N., and R. M. Sibly. 1993. Dynamic models of energy allocation and investment. Annual Review of Ecology and Systematics 24:379–410.

Reznick, D. 1983. The structure of guppy life histories: the tradeoffs between growth and reproduction. Ecology 64: 862–873.

Reznick, D., and A. P. Yang. 1993. The influence of fluctuating resources on life history: patterns of allocation and plasticity in female guppies. Ecology 74:2011–2019.

Reznick, D. N., M. Mateos, and M. S. Springer. 2002. Independent origins and rapid evolution of the placenta in the fish genus *Poeciliopsis.* Science 298:1018–1020.

Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. Ecology 5:291–303.

———. 1983. The application of optimal control theory to the general life history problem. American Naturalist 121:418–431.

Sillen-Tullberg, B. 1988. Evolution of gregariousness in aposematic butterfly larvae: a phylogenetic analysis. Evolution 42:293–305.

Snelson, F. F., Jr., J. D. Wetherington, and H. L. Large. 1986. The relationship between interbrood interval and yolk loading in a generalized poeciliid fish, *Poecilia latipinna.* Copeia 1986:295–304.

Stewart, J. R. 1989. Facultative placentotrophy and the evolution of squamate placentation: quality of eggs and neonates in *Virginia striatula.* American Naturalist 133: 111–137.

———. 1992. Placental structure and nutritional provision to embryos in predominantly lecithotrophic viviparous reptiles. American Zoologist 32:303–312.

Stewart, J. R., and M. B. Thompson. 1996. Evolution of reptilian placentation: development of extraembryonic membranse in Australian scinid lizards *Bassiana duperreyi* (oviparous) and *Pseudemoia entrecasteauxii* (viviparous). Journal of Morphology 227:349–370.

Thibault, R. E., and R. J. Schultz. 1978. Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). Evolution 32:320–333.

Trexler, J. C. 1997. Resource allocation and plasticity in offspring provisioning: embryo nourishment in sailfin mollies. Ecology 78:1370–1381.

Trexler, J. C., J. Travis, and M. McManus. 1992. Effects of habitat and body size on mortality rates of *Poecilia latipinna.* Ecology 73:2224–2236.

Wake, M. H. 1992. Evolutionary scenarios, homology and convergence of structural specializations for vertebrate viviparity. American Zoologist 32:256–263.

Wourms, J. P., and J. Lombardi. 1992. Reflections on the evolution of piscine viviparity. American Zoologist 32: 276–293.

Wourms, J. P., B. D. Grove, and J. Lombardi. 1988. The maternal-embryonic relationship in viviparous fishes. Pages 1–134 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology. Vol. 11B. Academic Press, San Diego, Calif.

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