Viviparous Fishes II

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Modeling the Evolution of Complex Reproductive Adaptations in Poeciliid Fishes: Matrotrophy and Superfetation

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Abstract

▼ We report a simulation model developed to generate hypotheses about environmental conditions favoring the evolution of maternal adaptations in viviparous fishes. Poeciliid fishes display a continuum of adaptations related to embryo nourishment and packing that represent a complex system of co-evolved traits. Lecithotrophic females produce large eggs that develop with little additional nourishment from maternal sources, while matrotrophic females produce relatively smaller eggs that require supplemental nourishment to complete development. Female poeciliids may harbor one brood of offspring per reproductive bout, or two or more broods overlapping in their development, termed superfetation. We evaluated the selective effects of food level and temporal variability in food level on fitness of simulated female fish expressing an array of these reproductive traits, and with different levels of energy investment in reproduction or post-maturation growth. Matrotrophy, a high energy investment in reproduction, and superfetation were favored in stable environments with high food availability. Lecithotrophy, a less energetic investment in reproduction and no superfetation were favored in variable low food environments. Mode of embryo nourishment and energy investment in reproduction evolved rapidly to their final value in our models, while superfetation level responded to selection more slowly. The presence of superfetation may facilitate the evolution of matrotrophy in stable high-food environments. These results suggest that field studies should observe a tighter matching of environmental conditions to embryo nourishment modes and energy allocation than to superfetation level; embryo nourishment and superfetation should covary, though not tightly. Temporal constancy of food availability relative to demand may be an important mechanism selecting for reproductive strategies in poeciliid fishes.

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Modeling the Evolution of Complex Reproductive Adaptations in Poeciliid Fishes: Matrotrophy and Superfetation

Explaining the origins of multi-character traits remains a hallmark challenge for evolutionary biology. Complex traits such as the vertebrate eye derive from multiple components that must function in concert. Darwin identified understanding the origins of such traits as a major challenge for evolutionary biology and this challenge remains today (Futuyma, 1998; Ayala, 2007). Recent discussion by Reznick *et al.,* (2002) pointed out that the vertebrate placenta is an example of a complex trait that may be more accessible to study than some classic examples, such as the eye (see also Enders and Carter, 2004). They point out that maternal nourishment of embryos by a secretive organ has evolved multiple times in poeciliid fishes and that many extant species present are apparently intermediate stages in the evolution of this adaptation (see also Reznick *et al.,* 2007). Understanding the strategies related to the allocation of energetic investment to reproduction are also a fundamental challenge in evolutionary biology (Lack, 1954; Stearns, 1992). The timing of allocation within and among clutches, including clutch overlap (Burley, 1980), is a complementary dimension to the mode of nourishment that collectively represent major contributors to fitness. In addition to a range of placentation, poeciliid fishes also exhibit a diversity of patterns of timing of allocation to individual clutches, including simultaneous brooding of two or more clutches, termed superfetation (Turner, 1937). Thus, poeciliid fishes provide excellent opportunities for comparative studies seeking to untangle the evolutionary origins of integrated adaptations, both structural and strategic, comprising a complex trait.

We have developed a model that treats viviparous reproduction as the co-evolutionary product of several life history elements that yield a complex trait. Oviparous fish, ancestral to all viviparous ones (*e.g.,* Mank *et al.,* 2005), produce eggs that are placed in the environment prior to fertilization and parental care, if present, is focused on developing embryos and post-hatch larvae exposed to predation and environmental conditions exogenous to the mother's body. Viviparous fishes must accommodate internal fertilization and retention of developing embryos for some or all of gestation. If embryonic development is fueled solely from pre-fertilization maternal provisioning (yolk), development is termed lecithotrophic. Maternal care of this form still protects embryos from predation and buffers environmental variation at a cost to the mother both from increased predation risk (Ghalambor *et al.,* 2004; Evans *et al.,* 2007) and reduction in future reproduction (*e.g.,* Henrich, 1998; Reznick *et al.,* 2006). Viviparous females may provide additional nutrition to developing embryos prior to parturition, termed matrotrophy. There is considerable variation in the relative contribution of pre- and post-fertilization nourishment in matrotrophic species, which can be considered a continuous trait in poeciliid fishes (Thibault and Schultz, 1978; Wourms *et al.,* 1988). Thus, it is appropriate to evaluate the 'degree' of matrotrophy in such species, which is a trait that may be plastic (Trexler, 1987).

Superfetation has evolved multiple times in the family Poeciliidae (Hrbek *et al.,* 2007; Reznick *et al.,* 2007) and several workers have noted an association between the degrees of superfetation and matrotrophy (Turner, 1941; Thibault and Schultz, 1978), suggesting that the evolution of one trait may facilitate the evolution of the other (*e.g.,* Emerson *et al.,* 1990; Brodie, 1992; Huey and Sinervo, 2003). Furthermore, Reznick *et al.* (2007) have recently documented a similar association in the Hemirhamphidae, demonstrating independent evolution of livebearing traits tied to matrotrophy and superfetation. However, there are species that provide intriguing outliers to this pattern (*e.g.,* Arias and Reznick, 2000), possibly serving as beacons to the nature of this association (or as exceptions that will help to clarify the rule).

A formal theory of environmental conditions favoring the evolution of maternal provisioning and superfetation of viviparous embryos is not well developed. However, a theoretical framework for analysis of embryo nourishment is desirable because it provides a common basis for hypothesis testing research. We have contributed to developing such a theoretical framework by use of an individual-based model to evaluate environmental conditions that would favor persistence of a matrotrophic mutant in the presence of a lecithotrophic ancestor (Trexler and DeAngelis, 2003). To conduct that work, we simplified the

life history of viviparous fishes by assuming that all offspring are brought to term at a common size with no overlap of developing embryo clutches. In this paper, we discuss a model that incorporates overlapping broods of offspring, while retaining our simplifying assumption of a single size at birth. Future work will relax the assumption of a common size at birth, to create a more complete life history perspective. However, challenges created by model complexity demand that we proceed in a stepwise fashion as we consider the complex mix of adaptations comprising female reproduction in poeciliid fishes.

We have treated the evolution of maternal investment in offspring as an example of the General Life History Problem discussed by numerous authors (Schaffer, 1983; Stearns, 1992). This approach considers the life history as a collection of traits that trade off each other under a constraint of limited resources. Offspring size and number illustrate a typical trade off addressed by such an analysis and trait values are expected that maximize fitness by optimizing allocation of energy or other resources. In general, investment in one aspect of female reproductive function should be balanced by a loss of future reproductive options. We consider embryo retention and nourishment in viviparous fishes as an adaptation to decrease mortality early in life, spread the investment in individual offspring over gestation, and yield precocious offspring. Viviparous female fishes experience a potential cost to future reproduction compared to oviparous fishes, for example if food resources decrease and energy storage is inadequate to complete gestation (Reznick and Yang, 1993; Trexler and DeAngelis, 2003). Ideally, females will delay investment in offspring as late in gestation as possible in order to start as large a number of offspring as possible, while delaying commitment as late as possible in case environmental conditions change. This permits a strategy of optimal packing of embryos in the female's ovary to increase the number of offspring in a limited space. Past workers have suggested that superfetation may be a further adaptation to permit optimal packing (Travis *et al.,* 1987; Zúñiga-Vega *et al.,* 2007).

The life history ecology of female reproduction in poeciliid fishes is remarkably complex. Numerous potential trade-offs between and among traits can be identified, and theoretical analysis of life history evolution typically consider such trade-offs in a pair-wise fashion. When reproduction is considered as a system of interacting components, multi-way trade offs and synergies of evolving traits are possible, if not likely. Developing a theoretical basis for hypothesis testing in such complex life histories using a system of continuous equations can be limiting. As an alternative, we used a simulation approach based on a 'genetic' framework to permit multiple traits to be selected simultaneously. As with all theoretical analyses, the complexity and flexibility of our simulations are still only shadows of real biological systems and ecological complexity. Therefore, our goal in their use and in this paper is in developing and presenting hypotheses to provide recommendations for directions of future empirical research.

Overview of the Model

Our model begins with a collection of the genotypes arrayed along a single axis with pure matrotrophy at one end and pure lecithotrophy at the other. In 'pure' lecithotrophy, all of the investment of embryos occurs 'upfront', whereas in 'pure' matrotrophy, there is an equal amount of investment in embryos each day until maturation of the embryos. There are 20 strategies, with 5%, 10%, 15%, ..., 95%, 100% upfront investment. In addition, we consider different options for how the female invests its surplus energy (the energy beyond which is immediately needed to nourish a brood). She can put some fraction of that energy into storage for later use in reproduction, and the rest into growth in biomass. There are 10 strategies, ranging from 5%, 10%, 20%, ..., 80%, 90% investment in growth, with the remainder going to storage for later use in reproduction. Since all combinations of the two strategies are possible, this adds up to 200 genotypes so far. Finally, it is possible for any of these 200 genotypes to have one further differentiation; one of three levels of superfetation. *1)* No superfetation, so that a new brood can only be started after the last one has matured. *2)* Ability to start a new brood any time (*i.e.,* when energy conditions are right) 24 days after the last one started (weakly superfetatious). *3)* Ability to start a new brood any time 16 days after the last brood has started (strongly superfetatious). In total, there are a total of 600 possible genotypes.

Each of the 4 000 (this number is quite arbitrary, but simulation time increases with additional fish) fish simulated is assigned one of the 600 genotypes. The 4 000 fish in Generation 1 are divided roughly evenly among these genotypes. All 4 000 fish start at the same age and size (the units are a bit arbitrary, but that does not affect the simulations), and grow at the same maximum rate, governed by an allometric relationship between weight

and daily growth. Depending on their strategies along the matrotrophy/lecithotrophy spectrum, fish begin investment into reproduction at different ages. Reproduction is triggered individually in each fish by 'checking' its daily intake of energy. As soon as the daily energy intake rate is high enough to sustain the requirements of providing its clutch of eggs on a daily basis, the fish starts diverting some fraction of their energy (depending on their allocation strategy) either directly or indirectly into reproduction. Directly means the energy immediately goes to embryos, while indirectly means that the energy first goes into storage lipids and then goes into reproduction when needed.

The reproductive modes (matrotrophy/lecithotroph spectrum) vary in the timing and level of energy allocation into embryo nourishment and growth. The extreme matrotroph can already produce eggs at the time of switching and start provisioning them. So it starts putting energy directly into brood provisioning immediately. What is left over goes partly to growth and partly to storage for later use in reproduction (that is, the energy is used indirectly for reproduction). The other strategies along the matrotroph/lecithotroph spectrum must store up some energy before they can produce embryos. As soon as they have enough stored energy for the 'upfront' investment in eggs, they produce a clutch. At that point they also have enough energy for daily provisioning the eggs (although the extreme lecithotrophs do not need to provide any more provisioning). Egg clutch size is a function of female size based on an estimate of ovary size, and the body size to ovary size relationship is the same for all fish. Energy remaining in storage is available to fuel continued growth during the reproductive phase of the life cycle.

The adult fish are allowed to reproduce over a growing season of a certain number of days, ranging from 90 to 250 days, and generations do not overlap. Offspring mature and start reproducing in the year after they are born in this model. The number of offspring of each genotype is computed by summing over the reproductive output of all of the fish of that genotype. The simulations are carried out over 350 generations. This is not always enough to narrow down to one genotype, but it gives an idea of which genotypes are the fitter. While it is theoretically possible for balanced polymorphism to occur (*i.e.,* for more than one genotype to have nearly equal fitness), we have not pushed the simulations to exhaustively explore this possibility.

We have incorporated simple approaches for mortality and resource ecology. The model includes adult mortality at a constant rate that the modeler can adjust. All adults die at the end of the year. Food supply is not assumed to be depleted by consumption by fish, so there is no competition for food. With only 4000 fish divided among 600 genotypes, there is plenty of opportunity for demographic stochasticity to play a role. Some genotypes may go to extinction very early, even if they would have been dominant. We have run repeated simulations to evaluate the stability of our results; stochasticity could be reduced by increasing the population size, but at the cost of increasing computer time and reducing the number of runs evaluated. Furthermore, we feel that some level of stochasticity is relevant to natural populations, where population sizes are not infinite and periods of relatively consistent environments (as occur within each simulated environment) do not persist indefinitely.

There are three parameters built into the model that are particularly important in determining the relative success of the genotypes:

Food: the measure of the maximum amount of food available per day per adult fish.

Var: a measure of the variability of food to the adult fish following the start of reproduction (this can lower the actual amount of food available) to a greater or lesser degree.

S: daily mortality rate.

In the simulations reported here, only the first two vary; S is fixed at a very low 0.002 probability of mortality per day for all simulations.

Energy Investment and Starting of Broods

Before starting reproductive investment, on each day each individual takes in an amount of food:

ADD = HFOOD*WGT**(0.67)

where

HFOOD is an indicator of food availability.

WGT is weight of the fish.

All of this goes to growth in the early life history of the fish.

In this paper, we report three (and in one case four) levels of food availability:

Food = 12: Abundant food availability

Food = 9: Moderate food availability

Food = 6: Low level of food availability

Food = 3: Very low level of food availability

Each female is preprogrammed to start dividing its energy intake between growth and reproduction

at some age TSWITCH (to be determined below). Starting at that time, Genotype_i will put

ADDREPi = (1 – ALLOCATEi)*ADD
to reproduction per day and

ADDGROWTHi = ALLOCATEi*ADD
to growth per day. ALLOCATEi is the fraction of energy intake that is allocated to growth (*versus* reproduction).

The switch from pure growth to an allocation between both reproduction and growth occurs when the time TSWITCH is reached. This TSWITCH occurs as soon as the daily energy that the fish is taking in is enough to meet its own needs plus the daily needs of its brood, ENEEDYi. On TSWITCH, the female does not take into account variability of the energy intake (for simplicity, variability is not taken into account in the model until reproduction actually starts –since that's when it is critical). Of course, the value of ENEEDYi depends on what the female's strategy is along the lecithotrophy-matrotrophy axis. The more matrotrophic the fish is, the larger ENEEDYi will be.

At the time TSWITCH, the female starts to put an amount of energy ADDREPi aside for reproduction each day. This does not necessarily immediately go into nourishing a brood, unless the female is a pure matrotroph. In general, the actual starting of a brood will occur as soon as an amount of energy has been stored to provide the upfront energy. So the time before this happens is:

T_REPRODUCTION = UPFRONTi / ADDREPi

where
UPFRONTi = the amount of upfront energy a female needs to start its brood.

Of course, the larger the upfront energy is, the smaller the daily needs, ENEEDYi.

Variability in Available Energy

As soon as a brood is actually started, energy is assumed to be variable

ADDvar = (1 – VAR*RANDOM)*ADD

where
RANDOM = uniform random number on interval (0, 1).
VAR = a measure of variability of the food availability.

Within each set of simulations reported here, different points represent the variability of food availability (variability). The measure is just the upper limit on random decreases in food availability that can occur each day.

Energy Deficiency

If on a particular day a female does not have energy to meet its own needs and that of its brood, it sacrifices whatever portion of its brood it needs to keep its own intake sufficient. Resorption is not included here (*cf.* Trexler and DeAngelis, 2003), although it could be added. Recent work has failed to support abortion and resorption of nutrients from developing embryos (Banet and Reznick, 2008), though the fitness benefits are clear if a mechanism were to evolve; further work on this topic may be warranted.

Superfetation

There are three strategies for superfetation: *1)* no superfetation, *2)* moderate superfetation (theoretical capability of starting a brood after current brood is 24 days old), and *3)* high superfetation (theoretical capability of starting a brood after current brood is 16 days old). Before a new brood is started the female calculates whether its current stored energy and expected daily energy intake (based on current energy intake) is enough to maintain its current brood for 6 or 14 days, respectively, and a new brood for 30 days. Here, we report three levels of superfetation: Level 1 with no superfetation; Level 2 with up to two broods coexisting, and Level 3 with up to three broods coexisting.

Results

In all cases, the degree of lecithotrophy increased as variation in food level increased (Fig 1); stable food level favored more matrotrophy for all levels of superfetation. Furthermore, higher average food levels favored a greater energy investment into reproduction, though the effect was diminished at the highest level of temporal variability (Fig. 1). This result was also little effected by the level of superfetation. The relative investment into somatic growth, as opposed to reproduction, was relatively insensitive to change in each of the environmental variation or superfetation. The primary effect of superfetation was in stable environments, where an increase in the number of simultaneous broods was associated with an increase in matrotrophy (Fig. 1). Thus, the model predicts highly matrotrophic

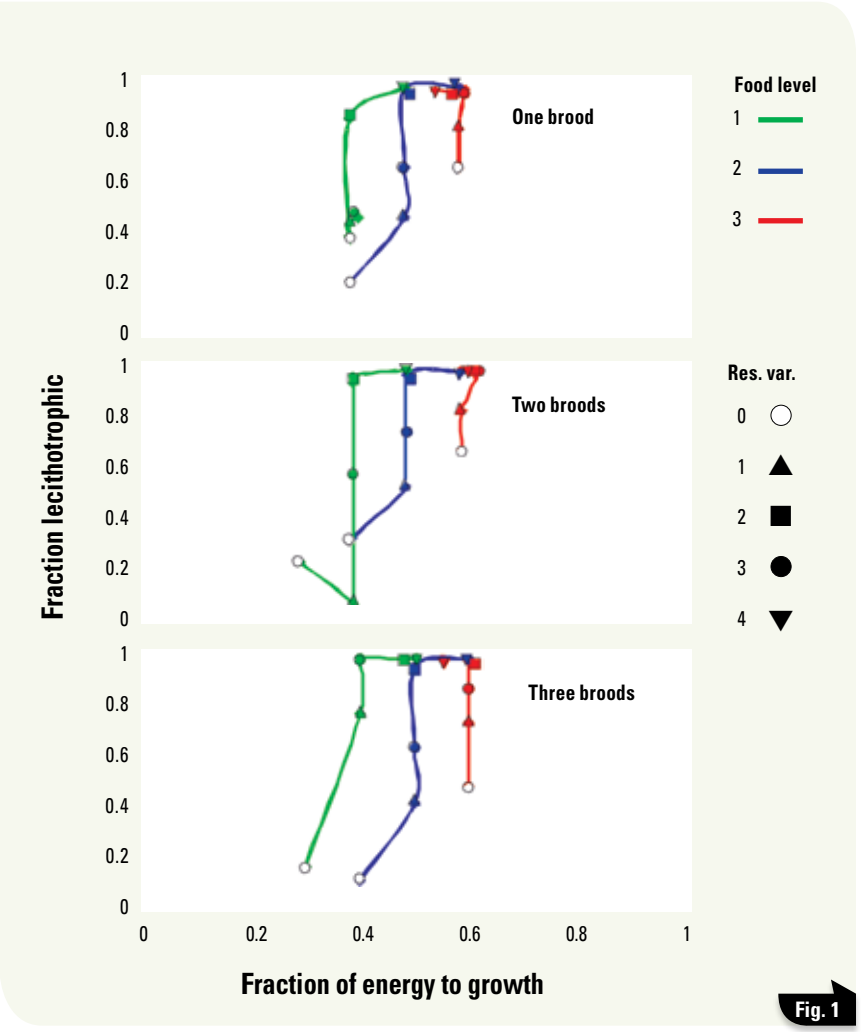

Figure 1.
Model results for allocation of energy to growth and reproduction and embryo nourishment strategy. The relative lecithotrophic investment is plotted on the Y-axis, with 0 being fully matrotrophic and 1 being fully lecithotrophic. The relative investment in growth after sexual maturation is plotted on the X-axis, with 0 being no further growth after maturation and 1 being no energy invested in reproduction. Three food levels (1 is lowest, 3 is highest) and five levels of environmental variability (0 is no variation, 4 is highest) are illustrated

fishes with maximum superfetation to be found in stable environments, particularly with relatively high availability of food resources. In contrast, lecithotrophic strategies were predicted to dominate in fluctuating food-level conditions; these lecithotrophic fishes could be expected to express any level of superfetation we explored.

The strength of selection on individual traits, or the degree to which each trait contributes to fitness, can be inferred by the rate at which that trait evolved to fixation. We explored the rate of trait evolution by plotting the frequency of each trait as a function of generation time in the model runs. Strategies for the relative investment of energy into growth or reproduction stabilized relatively quickly at both low and high levels of variation in food level (generally within 50 generations), as did the mode of embryo nourishment (Figs. 2a, 3a). In contrast, level of superfetation often did not come to fixation until late in most simulations (Figs. 3a, b), and all three strategies often remained for some time. We interpreted this as indicating weak selection on superfetation compared to embryo nourishment mode and energy investment.

Food variability affected the mixture of strategies that emerged. In both stable and variable environments, the winning embryo nourishment strategy (or mixture of strategies) emerged relatively quickly, while the winning superfetation strategy took longer to become fixed (Figs. 2b, 3b). In the variable environment, no single clutch-overlap strategy emerged after 350 generations (Fig. 3b) suggesting selection on this trait is weak in this environment, in contrast to embryo nourishment mode.

Discussion

Our new model simulates a population starting with a diverse mix of strategies underlying two complex reproductive adaptations that appear in poeciliid fishes: matrotrophy and superfetation. We have created a physiologically based life history for each fish in the model and tracked the fate of their lineages under different environmental conditions. The 'winning' strategies that emerge from the genetic algorithm employed by our simulation approach are evolutionarily stable (ESS).

Our simulations support empirical work by Pires (2007; as well as Thibault and Schultz, 1979) that superfetation and matrotrophy should be favored in high resource and stable environments. Superfetation and matrotrophy tended to co-evolve in our models, though the relationship was not as strong as one may have expected based on published works (*e.g.,* Constanz, 1989). This is best illustrated in figure 1, where the fraction of lecithotrophy was highest for females restricted to one brood and lowest in simulations with the highest superfetation we simulated (Level 3). In a stable environment (resource variability = 0), the relative lecithotrophy ranged from 0.2 to 0.6 across the three food levels when one brood was permitted, 0 to 0.6 when up to two broods were permitted, and 0.1 to 0.4 when up to three broods were possible. Stochasticity in individual simulations probably explains the variable results for the high food level, also suggesting that selection for co-evolution of superfetation and matrotrophy was not particularly strong under these conditions. However, the presence of superfetation facilitated evolution of a higher level of matrotrophy (less lecithotrophy) in a stable high-food environment. Though species are known with superfetation but little matrotrophy, and vice versa, these cases are less common than species with lecithotrophy and no superfetation or matrotrophy and superfetation (Reznick and Miles, 1989).

Future work should permit more variation in age at maturity of females by adjusting minimum brood size. Age at maturity currently varies based on acquisition of the minimum energy necessary to produce broods of a given size, which are determined by female size, but more realistic constraints may be imposed by considering morphological limitations leading to different size to fecundity relationships. Also, we plan to consider variation in size at birth and a size-quality trade off by inflicting a juvenile mortality function weighted by the size of neonates. Variation in size of neonates has been hypothesized to be a part of adaptive maternal investment strategies of female livebearing fishes (*e.g.,* Henrich, 1988; Reznick and Yang, 1993; Schrader and Travis, 2005). Reznick *et al.* (1996) proposed that lecithotrophic species responded to variation in food level by modifying the size and energy stores of offspring produced (low food treatments yielded larger offspring, see also Reznick and Yang, 1993; Marsh-Matthews and Deaton, 2006). In contrast, the matrotrophic species they studied displayed little plasticity in offspring size in response to varying maternal food level, which they proposed to be the result of a maladaptive constraint imposed by matrotrophy. While life-history models lacking explicit consid-

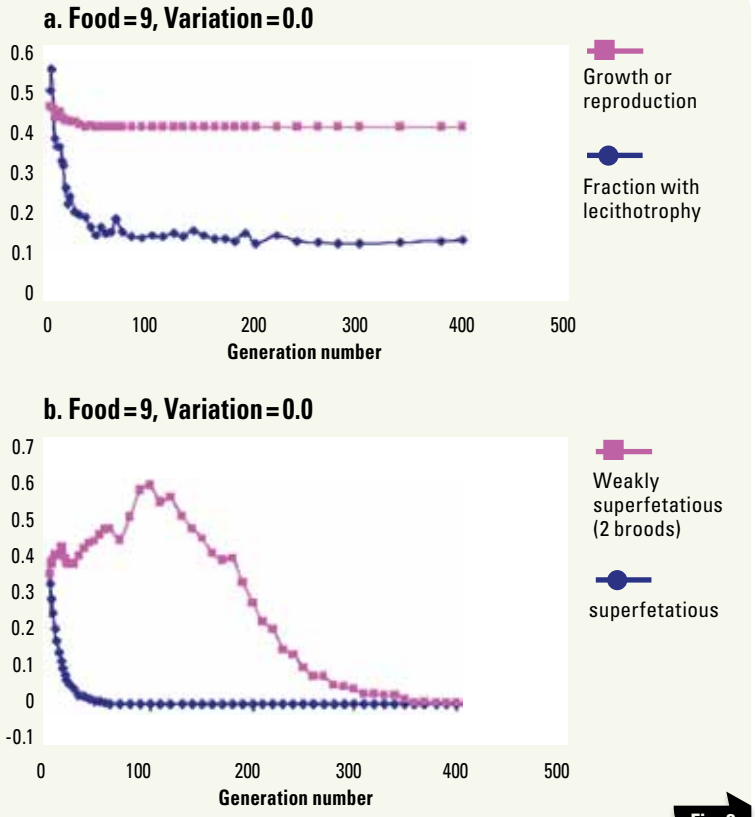

Fig. 2

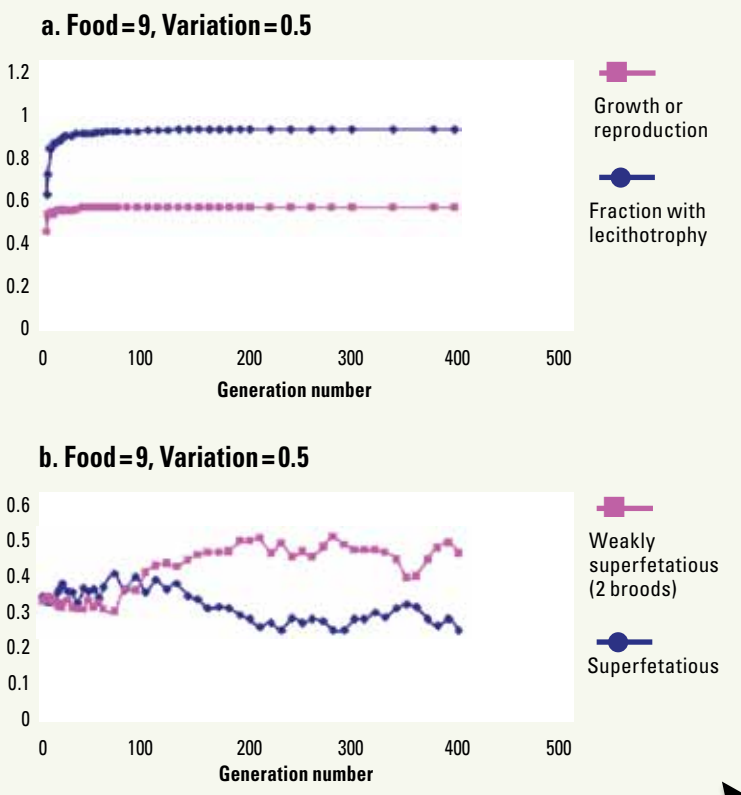

Fig. 3

Figure 2.
Change in composition of populations as the simulations unfold with high food level that does not vary. The relative frequency of two traits over four-hundred generations are illustrated in each graph. *a*) Y-axes are allocation of energy to growth or reproduction after sexual maturity (0 is all energy invested in reproduction and 1 is all energy invested in reproduction) and the relative level of lecithotrophy (0 is fully matrotrophic and 1 is fully lecithotrophic). *b*) Y-axes are the frequency of weakly superfetatious individuals (2 broods carried simultaneously) and non-superfetatious individuals (1 brood carried per reproductive cycle). In this graph, strongly superfetatious individuals (3 broods carried simultaneously) are not plotted, but are the fraction unaccounted for by the two strategies that are plotted (only three strategies were possible in these simulations). Thus, by the end of the simulation, only highly superfetatious females remained

Figure 3.
Change in composition of populations as the simulations unfold with high food level that varies. The relative frequency of two traits over four hundred generations are illustrated in each graph. *a*) Y-axes are allocation of energy to growth or reproduction after sexual maturity (0 is all energy invested in reproduction and 1 is all energy invested in reproduction) and the relative level of lecithotrophy (0 is fully matrotrophic and 1 is fully lecithotrophic). *b*) Y-axes are the frequency of weakly superfetatious individuals (2 broods carried simultaneously) and non-superfetatious individuals (1 brood carried per reproductive cycle). In this graph, strongly superfetatious individuals (3 broods carried simultaneously) are not plotted, but are the fraction unaccounted for by the two strategies that are plotted (only three strategies were possible in these simulations). Thus, by the end of the simulation all three strategies remained

eration of genetic architecture cannot evaluate the existence such constraints, future work incorporating offspring size can permit evaluation of the cost of such constraints.

Predictions for Ecological Studies

A goal of our modeling effort is to generate hypotheses that can be pursued by empirical research. Our model predicts a greater diversity in levels of superfetation at the intra- and inter-specific levels than is seen in embryo nourishment. Also, there should be more strongly matrotrophic species without superfetation than superfetatious species without matrotrophy. Finally, there should be a strong matching of embryo nourishment mode to environmental conditions (*e.g.,* Zúñiga-Vega *et al.,* 2007), and a weaker matching in superfetation.

This work, as well as our previous study (Trexler and DeAngelis, 2003), indicates that temporal fluctuation in food supplies can contribute to determining the fitness relationships of alternative reproductive life histories. These models can be considered as evaluating a form of bet hedging as a possible mechanism driving evolution of viviparous reproductive adaptations. Bet hedging presents an attractive framework to explain evolution of life histories, but one that is challenging to evaluate with prospects to reject should that be appropriate because it does not yield unique predictions. Furthermore, ecological work evaluating resource variability in nature is challenging because resource consumption must be evaluated relative to demand from an organism's energy budget. Comparative studies of levels of fat storage among populations and through time are one way to obtain relevant field information, when gathered while simultaneously tracking resource levels and population size (McNab, 2002:338-342). Coupling this with laboratory studies of energy demands could yield temporal estimates of food limitation. Food level *per se* is less important than consistency of availability at intra- and inter-generational time scales with respect to demand.

Future Directions

This work produced predictions based on maximization of maternal fitness, but other selection schemes are possible. In particular, Crespi and Semeniuk (2004) have proposed a model that examines the outcome of parent-offspring conflict and raising the interesting prospect that maternal fitness is (at least some times) not the appropriate target for evolutionary maximization (see also Wilson *et al.,* 2005). Banet *et al.* (2008) have reported results inconsistent with predictions made by our earlier model, with one possible explanation being that maternal fitness is not maximized by selection. Comparing predictions of our models to data, potentially leading to rejection of our working assumptions, is a powerful research paradigm and one we hope to further by the work reported here. Of course, the rejection of one model does not constitute support for alternatives and, as we noted, our models, though complex, are highly simplified views of nature. Thus, rejection of our model maximizing maternal fitness does not reject all such models. Progress toward understanding the evolution of complex reproductive adaptations will probably continue to resist simple analysis, but it appears that poeciliid fishes will continue to provide exciting insight into rich evolutionary dynamics.

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