

## PARENTAL CARE AND THE EVOLUTION OF EGG SIZE IN FISHES

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Naturalists have long realized, or at least suspected, a positive correlation among taxa between egg size and the presence of parental care (for review, see Shine 1978). Gross and Sargent (1985) found that egg size apparently increases with the quality of parental care within four families of oviparous fishes: Cichlidae, Percidae, Salmonidae, and Centrarchidae. Within the Centrarchidae, the correlation between the length of parental care and egg size is particularly striking (fig. 1). Members of the sunfish family, Centrarchidae, are characterized by males that establish breeding territories, mate with females, and alone guard the offspring. Paternal care ranges from about 1 day in the Sacramento perch (*Archoplites interruptus*) to about 4 wk in the largemouth bass (*Micropterus salmoides*). Van den Berghe (1984) recently found a similar positive correlation between egg size and the quality of parental care *within* a species, the coho salmon (*Oncorhynchus kisutch*). In salmonids, not only do larger females produce more eggs, but they also produce larger eggs (e.g., fig. 2). Van den Berghe found in coho salmon, however, that larger females compete for better oviposition sites, guard their nests more successfully, and thus have higher rates of egg survival.

Although egg size appears to co-vary continuously with the quality of parental care in many organisms, there have been few testable evolutionary models to explain this correlation. The purpose of this paper, therefore, is to provide such a model. We begin with working definitions of parental care and egg size and with our assumption of how egg size is optimized by natural selection. Reviewing three recent models of the trade-off between quantity and quality of offspring (Smith and Fretwell 1974; Shine 1978; Taylor and Williams 1984), we show why they are inadequate to explain the evolution of egg size under parental care. Using features of all three models, we construct a new evolutionary model to explain the relationship between egg size and parental care in nature. Finally, we conclude with a discussion of how the model may be tested experimentally.

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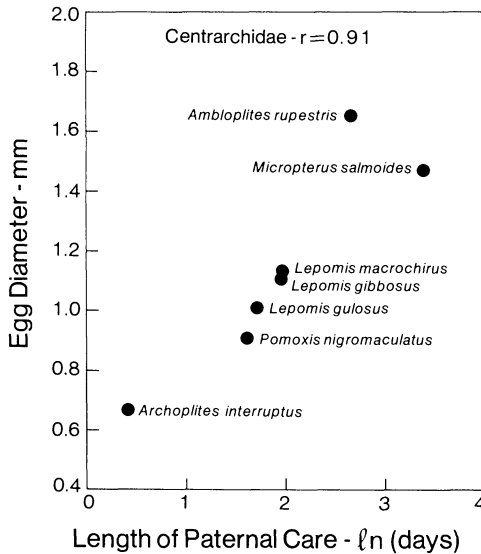


FIG. 1.—Egg size is positively correlated with the length of paternal care in the Centrarchidae (Gross and Sargent 1985). We treated the data as five independent points and used the bivariate mean for the three species of *Lepomis*;  $r = 0.91$ ,  $df = 3$ ,  $p < 0.01$ . The length of paternal care on the abscissa is transformed to natural logarithms (i.e.,  $\ln$  [days]). The correlation among species between egg size and female body size at reproduction is not significant;  $r = -0.13$ ,  $df = 3$ ,  $p > 0.50$ .

#### PARENTAL CARE AND THE OPTIMIZATION OF EGG SIZE

For the purposes of this paper, we define *parental care* as any investment by a parent, other than egg yolk, that increases the survival of the offspring until they are independent of all parental resources. Thus, parental care includes the selection or building of an oviposition site and any guarding or feeding that may occur after fertilization. Note that although parental care is generally defined as investment in offspring after fertilization (e.g., Gross and Sargent 1985; Sargent and Gross 1986), we have broadened our definition of parental care here to include investment before fertilization that affects offspring survival after fertilization (see also Blumer 1982).

Following Shine (1978), we divided offspring survival into two episodes: the egg stage and the juvenile stage. In fishes, the egg stage ends and the juvenile stage begins when the offspring are independent of all parental resources. The juvenile stage ends when the offspring reach reproductive maturity. For most fishes with external fertilization, the egg stage ends when the offspring have resorbed their yolk sacs. Shine (1978) recognized that in viviparous species, and in species in which parental care extends beyond the stage of yolk-sac resorption, "propagule size" (i.e., size at the beginning of the juvenile stage) may experience stronger selection than "egg size." In this paper, however, we restrict our attention to those oviparous species in which the egg stage ends at yolk-sac resorption. We

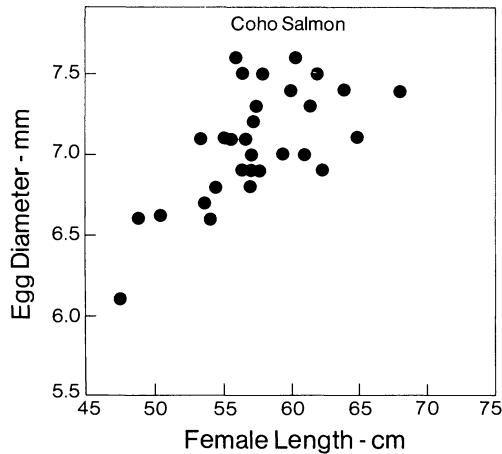


FIG. 2.—Mean egg size is positively correlated with female body size for 30 wild female coho salmon collected from the Chilliwack River, British Columbia, in January 1984 (Sargent and Gross, unpubl. data;  $r = 0.65$ ,  $p < 0.001$ ).

assume that egg size determines initial juvenile size, and we illustrate how parental care may favor the evolution of larger initial juvenile size, and thus larger egg size.

We define *egg size* as the amount of maternal yolk reserves allotted per offspring (in units of mass). Although other factors may contribute to egg size variation (e.g., chemical composition of yolk, oil droplets, hydration), we assume that these factors are constant in our subsequent analyses. We further assume that natural selection maximizes maternal fitness and that egg size is “optimized” with respect to maximizing the number of offspring that survive to maturity. This measure of fitness assumes that a mature individual’s reproductive success is independent of the size of the egg from which it hatched. Our approach is to assume an optimal egg size and to analyze how this optimum depends on one variable, the quality of parental care. In our models, parental care subsumes all parental behaviors that reduce instantaneous mortality during the egg stage.

We consider two potential trade-offs that may affect the evolution of egg size. First, there is the trade-off between egg size and egg number. Assuming a finite amount of resources, the larger a female makes her eggs, the fewer she can produce. If offspring survival increases with increasing egg size, then a female trades offspring quantity against offspring quality (e.g., Svårdson 1949). Smith and Fretwell’s (1974) model of this trade-off forms the basis of most current theory on the evolution of egg size. According to their model, egg number, not egg size, varies with the amount of resources available for reproduction (see also Maynard Smith 1978); thus, each population should have a single optimal egg size.

A second trade-off against increasing egg size occurs if mortality during the egg stage increases with egg size. This may happen if development rate during the egg stage depends on egg size or if instantaneous egg mortality depends on egg size.

First, consider the potential effects of egg size on development rate. If larger

eggs or embryos have proportionately lower respiratory and metabolic rates (see, e.g., Schmidt-Nielsen 1984), then they would have slower development. The result would be that larger eggs, or their hatchlings, would take more time to reach the juvenile stage (for review, see Steele 1977). Assuming that instantaneous egg mortality is constant in time, the longer an offspring remains in the egg stage, the less likely it is to reach the juvenile stage. Shine (1978) recognized that the overall offspring survival, from fertilization to the age of reproduction, depends on the instantaneous egg and juvenile survival and on the relative lengths of time that an offspring spends in each stage. He proposed that a female resolves the trade-off between egg number and overall offspring survival by adjusting egg size, and thus adjusting the relative lengths of the egg and juvenile stages.

Although there is considerable evidence among species that larger eggs have slower development rates (e.g., Balon 1984; Paine 1985), we know very little about the relationship between egg size and development rate within species or within populations, where natural selection is more likely to act. Preliminary evidence, however, suggests that offspring from larger eggs do take longer to resorb their yolk sacs and enter the juvenile stage within species in four families: salmonids (*Salmo salar*, Privol'Nev 1960; *S. gairdneri*, Escaffre and Bergot 1984; *Oncorhynchus tshawytscha*, Rombough 1985); clupeids (*Clupea harengus*, Blaxter and Hempel 1963); gadids (*Gadus morhua*, Knutsen and Tilseth 1985); cyprinids (*Leuciscus leuciscus*, Mann and Mills 1985).

Larger eggs also may experience lower egg-stage survival if they have larger instantaneous mortalities. Preliminary evidence for salmonids suggests that this may be the case under hatchery conditions (*Oncorhynchus tshawytscha*, Fowler 1972; *O. keta*, Beacham and Murray 1985) and in the field (*O. kisutch*, van den Berghe 1984), perhaps because larger eggs are more limited by available oxygen. We examine the effects of each of these trade-offs in a series of models.

#### THE TRADE-OFF BETWEEN EGG SIZE AND EGG NUMBER

Smith and Fretwell (1974) assumed that a female has a finite amount of energy to devote to egg yolk and that natural selection favors a female that allocates her investment in each egg so as to maximize the number of her offspring that survive to reproduce. Thus,

$$W_F = (M/s)P(s), \quad (1)$$

where  $W_F$  is maternal fitness;  $M$  is maternal investment in egg production (in units of mass);  $s$  is egg size (investment per egg, in units of mass); and  $P$  is the probability that an offspring will survive to reproduction, which is assumed to be an increasing function of egg size,  $s$  (fig. 3). Thus,  $M/s$  is the total number of eggs that a female produces, which decreases with increasing egg size. To solve for the optimal egg size,  $s^*$ , we differentiate  $W_F$  with respect to  $s$ , and set it equal to zero:  $dW_F/ds = (dP/ds)M/s - P(M/s^2) = 0$ . Thus, at  $s^*$ ,

$$dP/ds - P/s = 0, \quad (2)$$

$$d^2W_F/ds^2 = (M/s)d^2P/ds^2. \quad (3)$$

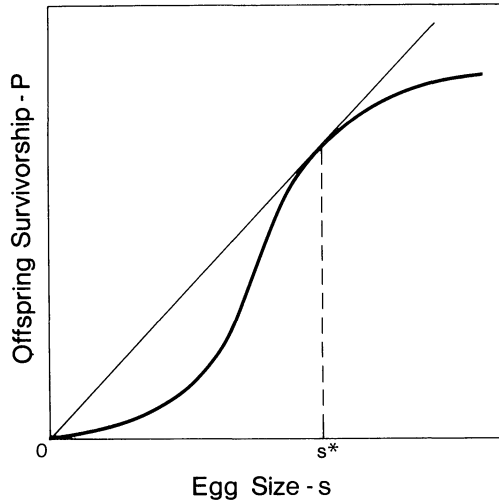


FIG. 3.—Overall offspring survival,  $P$ , versus egg size,  $s$ ; modified from Smith and Fretwell (1974). Straight lines through the origin define fitness isoclines of the form  $P = (W_F/M)s$ . Because fitness is proportional to the slope of the isocline, that isocline with the steepest slope intersecting  $P(s)$  indicates maximal fitness at the point of intersection.

Thus, whether  $s^*$  is a maximum or minimum depends on whether  $d^2P/ds^2$  is positive or negative at  $s^*$ . We assume that  $P(s)$  is sigmoid; that is,  $d^2P/ds^2$  is positive for small values of  $s$ , and negative for large values of  $s$ . In figure 3,  $W_F$  is at a maximum at the point where a straight line drawn from the origin is tangent to the function  $P(s)$ , at which  $d^2P/ds^2 < 0$ . According to this model, the optimal egg size,  $s^*$ , is independent of maternal investment in egg production,  $M$ . This model and similar ones (e.g., Parker et al. 1972; Brockelman 1975; Bell 1978; Maynard Smith 1978) suggest that there should be a single optimal egg size for all females in a population. In order to address the problem of egg size variation, we need an explicit algebraic formulation for offspring survival as a function of egg size,  $P(s)$ .

#### PARENTAL CARE, EGG MORTALITY, AND THE OPTIMAL EGG SIZE

Our model of the relationship between parental care, egg mortality, and egg size has the following form. We divide offspring survival,  $P$ , into egg and juvenile stages (in the sense of Shine 1978), and we allow egg-stage survival to depend explicitly on egg size,  $s$ , and on instantaneous egg mortality,  $\mu_0$ . For simplicity, we assume that  $\mu_0$  is independent of  $s$ . Thus, offspring survival,  $P$ , has the form

$$P(s, \mu_0) = \exp[-\mu_0\tau(s)] L(s), \quad (4)$$

where  $\tau(s)$  is time to yolk-sac resorption;  $\exp(-\mu_0\tau)$  is egg-stage survival; and  $L$  is juvenile-stage survival.

At this point we make three assumptions. First, we assume that  $\tau(s)$  is an

increasing function of  $s$ ; that is, offspring from larger eggs take a longer period of time before entering the juvenile stage. Second, we assume that  $L(s)$  is an increasing function of  $s$ ; that is, offspring hatched from larger eggs have higher survival during the juvenile stage. Third, we assume that for fixed  $\mu_0$ , offspring survival as a function of egg size,  $P(s, \mu_0)$ , has the sigmoid form of figure 3. To examine the dependence of  $s^*$  on  $\mu_0$ , we substitute equation (4) into equation (1) and compute the derivative,  $ds^*/d\mu_0$ , from the defining condition for  $s^*$ , which is

$$\partial P/\partial s - P/s = 0. \quad (5)$$

We differentiate equation (5) with respect to  $\mu_0$  and use the chain rule to take account of the dependence of  $s^*$  on  $\mu_0$ :

$$\begin{aligned} \partial(\partial P/\partial s - P/s^*)/\partial \mu_0 + [\partial(\partial P/\partial s - P/s^*)/\partial s^*] ds^*/d\mu_0 &= 0 \\ \partial^2 P/\partial \mu_0 \partial s - (\partial P/\partial \mu_0)/s^* + [\partial^2 P/\partial s^2 - (\partial P/\partial s)/s^* + P/s^{*2}] ds^*/d\mu_0 &= 0. \end{aligned}$$

Substituting equation (5) gives

$$ds^*/d\mu_0 = [(\partial P/\partial \mu_0)/s^* - \partial^2 P/\partial \mu_0 \partial s]/(\partial^2 P/\partial s^2). \quad (6)$$

From equation (4) we have  $\partial P/\partial \mu_0 = -\tau P$ ; thus, the expression in brackets in (6) becomes  $-\tau(P/s^*) - \partial(-\tau P)/\partial s = -\tau(P/s^*) + P(d\tau/ds) + \tau(\partial P/\partial s)$ . This resolves to  $P(d\tau/ds)$  by again substituting (5). Thus, equation (6) becomes

$$ds^*/d\mu_0 = P(d\tau/ds)/(\partial^2 P/\partial s^2). \quad (7)$$

Because  $d\tau/ds$  is assumed to be positive (larger eggs take longer to resorb their yolk sacs and enter the juvenile stage) and because  $\partial^2 P/\partial s^2$  is negative at  $s^*$ ,  $ds^*/d\mu_0 < 0$ . Under this model, the optimal egg size,  $s^*$ , is at its upper limit when parental care is completely effective, that is, when  $\mu_0 = 0$ . As  $\mu_0$  increases,  $s^*$  decreases. In other words, lower instantaneous egg mortality corresponds to a larger optimal egg size. As illustrated in figure 4, if parental care can reduce instantaneous egg mortality, then parents who provide such care will be selected to produce larger eggs. A shortcoming of this model is that we have not specified under what conditions  $P(s, \mu_0)$  is sigmoid, nor have we specified explicitly how or why juvenile-stage survival,  $L$ , should be an increasing function of egg size.

#### THE EFFECT OF FIXED AGE OF REPRODUCTION

Shine (1978) was the first to combine explicit formulations for the dependence of egg-stage and juvenile-stage survival on egg size. He reasoned that if parental care increases survival of the egg, then it may be to a parent's advantage to increase the proportion of time that an offspring spends in the "safe harbor" of the egg stage. He assumed that the age of reproductive maturity,  $T$ , is fixed and independent of egg size,  $s$ . Thus, if  $\tau(s)$  is the length of the egg stage, then time spent as a juvenile is  $T - \tau(s)$ . Shine also assumed that instantaneous juvenile mortality,  $\mu_1$ , is constant and independent of  $s$ . Thus, his equation for juvenile-stage survival would be

$$L(s) = \exp\{-\mu_1[T - \tau(s)]\}, \quad (8)$$

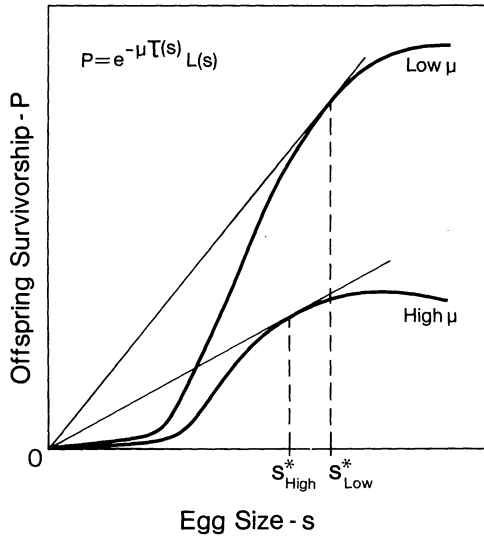


FIG. 4.—A graphical representation of the solution in equation (5). The curves were generated by assuming the same logistic form for  $L(s)$ , and by varying  $\mu_0$ . Because  $\mu_0$  is in an exponential term separate from  $L(s)$ , any increase in  $\mu_0$  both lowers the  $P(s)$  curve and shifts it to the left. As  $\mu_0$  increases,  $s^*$  decreases, and  $\partial P/\partial s$  decreases; thus, parental fitness,  $W_F$ , decreases.

and from equation (4), overall offspring survival,  $P$ , would be

$$P(s, \mu_0) = \exp[(\mu_1 - \mu_0)\tau(s) - \mu_1 T]. \quad (9)$$

(We remark that Shine works with instantaneous survival,  $l$ , which is related to our instantaneous mortality,  $\mu$ , by  $l = e^{-\mu}$ .) Shine's  $P(s, \mu_0)$  in equation (9) may not have the sigmoidal form of figure 3. Indeed, if  $\tau$  is proportional to  $s$  (i.e.,  $\tau(s) = Cs$ , where  $C$  is a constant), as assumed by Shine, then  $\partial^2 P/\partial s^2 = [C(\mu_1 - \mu_0)]^2 P$ , which is always positive; that is,  $P$  is concave up for all  $s$ . Thus, the equilibrium point given by equation (5) is, in fact, a minimum of the fitness function,  $W_F$  (see eq. 3, above), and the maximum is attained at one extreme or the other of feasible egg sizes.

Shine found that the smaller the value of  $\mu_0$ , the more probable it is that having large eggs is advantageous. This can be illustrated as follows. Let  $s_0$  and  $s_1$  be the minimum and maximum possible egg sizes, and set  $W_F(s_0) = W_F(s_1)$ . Then we get  $\mu_0 = \mu_1 - A$ , where  $A = (\ln s_1 - \ln s_0)/[\tau(s_1) - \tau(s_0)]$ . If  $\mu_0 > \mu_1 - A$ ,  $W_F$  is maximized at  $s_0$ ; if  $\mu_0 < \mu_1 - A$ ,  $W_F$  is maximized at  $s_1$ . Thus, the smaller the value of  $\mu_0$ , the more likely that large eggs will be favored.

Shine clearly specified why juvenile-stage survival,  $L$ , might be an increasing function of egg size. Larger eggs produce longer egg stages, resulting in shorter juvenile stages and thus higher juvenile-stage survival. Nevertheless, there are two basic problems with the predictions of Shine's model. First, it predicts that if  $\mu_0 > \mu_1$  (indeed, even if  $\mu_0 > \mu_1 - A$ ), a female should always make her eggs as

small as possible. In other words, egg size should increase with parental care only if parental care can make the egg stages substantially "safer" than the juvenile stage. Second, it predicts a bimodal egg size distribution. Females should be observed to make their eggs as large or as small as possible, which does not explain the continuous egg size variation observed in nature. Both of these predictions appear to be unrealistic, and they can both be shown to depend on Shine's assumption that instantaneous mortality during the juvenile stage is independent of egg size. Under Shine's model, offspring hatched from larger eggs have higher juvenile-stage survival only because they have shorter juvenile stages. Larger eggs, however, should produce larger juveniles with higher survival and faster growth (see, e.g., Gall 1974; Pitman 1979; Beacham et al. 1985). Therefore,  $\mu_1$  should depend on  $s$ , and time spent in the juvenile stage should depend on growth rate (see, e.g., Taylor and Williams 1984). In the next section we combine an assumption of size-dependent mortality and growth during the juvenile stage with Shine's formulation for egg-stage survival.

#### SIZE-DEPENDENT JUVENILE MORTALITY AND GROWTH

To further explore egg size evolution under parental care, we build on a life history model of Taylor and Williams (1984). Taylor and Williams assumed that a species' adaptations enable instantaneous juvenile growth to exceed instantaneous juvenile mortality over a range of body sizes,  $x$  to  $w$  (fig. 5). Mathematically, they assumed that a juvenile of size  $z$  (in units of mass) grows with a size-dependent instantaneous growth rate,  $g(z)$  (i.e.,  $dz/dt = zg(z)$ ; see Ricker 1979), and suffers size-dependent instantaneous mortality,  $\mu_1(z)$ . Within the size range  $x$  to  $w$ , growth exceeds mortality and cohort biomass increases; outside this size range, mortality exceeds growth and cohort biomass decreases. Taylor and Williams solved this model for the optimal size at birth and at maturity. They demonstrated that a species' entire life history should occur within the size range  $x$  to  $w$ . Specifically, they found that the optimal size at birth is  $x$  and that the optimal size at maturity is the value of  $z$  that maximizes the quantity  $z[g(z) - \mu_1(z)]/\mu_1(z)$ , which lies between  $x$  and  $w$ . Their model, however, did not include an egg stage separate from the juvenile stage of an offspring's life history.

#### *A More General Model*

We now extend Taylor and Williams' model to include an egg stage, and we ask how the optimal initial juvenile size depends on parental care. Again, we restrict our analysis to those species in which offspring are independent of all parental resources when they have resorbed their yolk sacs. Assuming a constant instantaneous egg mortality (independent of egg size), we solve our model for the optimal initial juvenile size.

Let a juvenile that hatches from an egg of size  $s$  have an initial size  $ks$ , where  $0 < k < 1$ . Thus,  $k$  allows for energetic costs of development and metabolism during the egg stage. We assume that growth ceases at size of maturity  $m$ , which we assume to be independent of  $s$ . During the juvenile stage, let  $l(z_1, z_2)$  denote



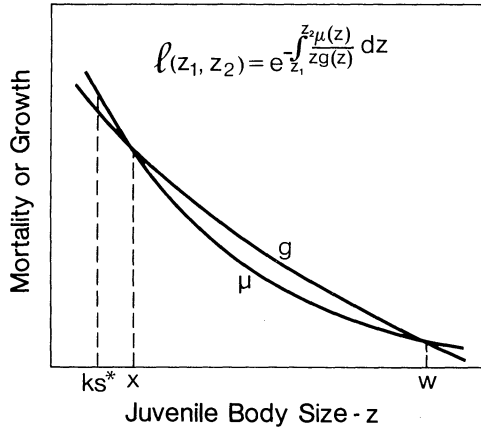


FIG. 5.—Plots of instantaneous growth and instantaneous mortality versus body size. Following Taylor and Williams (1984), we assume that instantaneous growth exceeds instantaneous mortality,  $g > \mu$ , for some range of body sizes  $x$  to  $w$ , and that  $g < \mu$  outside this range. When there is no egg mortality (i.e.,  $\mu_0 = 0$ ), the optimal initial juvenile size is  $x$ . If, however, we assume positive instantaneous egg mortality (i.e.,  $\mu_0 > 0$ ), the optimal initial juvenile size at yolk-sac resorption,  $ks^*$ , is less than  $x$ . As  $\mu_0$  increases,  $ks^*$  decreases; thus,  $s^*$  decreases.

survival over the size range  $z_1$  to  $z_2$ . Then,

$$l(z_1, z_2) = \exp - \int_{z_1}^{z_2} \frac{\mu_1(z)}{zg(z)},$$

where instantaneous mortality depends on body size, which in turn depends cumulatively on absolute growth rate,  $dz/dt$  (Gilliam 1982; Werner et al. 1983; Taylor and Williams 1984). Our expression for juvenile survival as a function of egg size is

$$L(s) = l(ks, m). \quad (10)$$

Maternal fitness, from equations (1), (4), and (10), is

$$W_F = (M/s) \exp[-\mu_0\tau(s)]l(ks, m). \quad (11)$$

Taking the natural logarithm of both sides,

$$\ln W_F = \ln M - \ln s - \mu_0\tau(s) + \ln l(ks, m) \quad (12)$$

and differentiating  $\ln W_F$  with respect to  $s$  gives

$$(1/W_F)dW_F/ds = -1/s - \mu_0(d\tau/ds) + \mu_1(ks)/sg(ks). \quad (13)$$

The optimal egg size,  $s^*$ , occurs when the right-hand side of equation (13) is zero. Therefore, the equilibrium equation for  $s^*$  is

$$\mu_1(ks)/g(ks) = 1 + \mu_0s(d\tau/ds). \quad (14)$$

If parental care is completely effective (i.e.,  $\mu_0 = 0$ ), then from equation (14),  $\mu_1(k_s)/g(k_s) = 1$ , and the optimal initial juvenile size is  $k_s^* = x$  (as in Taylor and Williams 1984). Thus, the optimal egg size is  $s^* = x/k$ . An examination of the sign of  $dW_F/ds$  on either side of  $s^*$  shows that this does indeed give maximum  $W_F$ . If, however, parental care is *not* completely effective (i.e.,  $\mu_0 > 0$ ), and if we were to set  $k_s = x$  in equation (13), then we would get  $dW_F/ds = -W_F\mu_0(d\tau/ds)$ , which is negative. Thus, as  $\mu_0$  increases above zero,  $k_s^*$  decreases below  $x$  (fig. 5). Assuming an initial condition of high instantaneous egg mortality, as parental care reduces instantaneous egg mortality, the optimal egg size increases toward an upper limit of  $s^* = x/k$ . In our model, the juvenile stage will begin at a size for which  $\mu_1(z) > g(z)$ ; however, the optimal size at maturity,  $m$ , is the same as that found by Taylor and Williams.

Our model assumes that the length of the egg stage increases with increasing egg size. Had we assumed instead that the length of the egg stage,  $\tau$ , is independent of egg size but that larger eggs have higher but constant instantaneous mortalities (see, e.g., Fowler 1972; van den Berghe 1984; Beacham and Murray 1985), then our equation (14) would become

$$\mu_1(k_s)/g(k_s) = 1 + \tau s(d\mu_0/ds). \quad (15)$$

If parental care reduces  $\mu_0$  by a constant amount at each egg size, then the right-hand side of equation (15) decreases and  $k_s^*$  increases, as in our analysis of equation (14). In either case, larger eggs impose offspring survival costs over the egg stage (and reduced egg number); however, these costs are exceeded by maternal fitness gains in offspring survival over the juvenile stage.

#### *Testing the Model*

The ultimate usefulness of our model will be determined by testing its assumptions and predictions. Although it is tempting to examine the model against comparative data from an array of taxonomic groups, there are limitations inherent in this approach. First, we designed the model to explain patterns observed among taxa; thus, comparative tests may lack independence. Second, without knowing the underlying phylogeny of the taxa used in a comparative test, it is difficult to determine the true correlations between characters, or between a character and an environmental variable (Felsenstein 1985). Phylogeny is less of a problem, however, if the species being compared are all closely related. Third, developmental rates of eggs and juveniles may evolve independently of egg size, thus adding considerable noise or bias to comparative data. Therefore, we suggest that the most powerful tests of our model will come from artificial-selection experiments.

If a population has heritable variation for egg size (i.e., allotment of yolk per offspring), it should be possible to vary the parameters of equation (14) (or 15), and effect evolution of egg size. The three following general predictions can be obtained from an analysis or inspection of equation (14); each prediction contains the assumption of "other things being equal" (*ceteris paribus*).

1. *As parental care reduces instantaneous egg mortality, the optimal egg size increases.*—This prediction has two implications. First, if a species exhibits a

negative genetic correlation between egg number and egg size, then increasing egg survival should result in the evolution of fewer, larger eggs. Second, if maternal size-dependent parental care is at least partially responsible for the positive correlation between female body size and egg size in such species as coho salmon, then we would expect this correlation to be relatively weak in populations in which egg survival is less dependent on maternal body size.

2. *As the ratio of juvenile mortality rate to juvenile growth rate increases among populations, the optimal egg size increases.*—If the ratio  $\mu_1/g$  in equation (14) were multiplied by a constant greater than one, the optimal initial juvenile size,  $ks^*$ , would increase. This result holds even if the length of the egg stage,  $\tau$ , and instantaneous egg mortality,  $\mu_0$ , were independent of egg size,  $s$ . In biological terms, as the juvenile stage is made less safe, it behooves a parent to produce larger juveniles, who then pass through the juvenile stage more quickly. Thus, we expect juvenile survival and egg size to be negatively correlated among populations.

3. *If there is positive instantaneous egg mortality, then the biomass of the juvenile-stage cohort will initially decrease.*—In Taylor and Williams' model (1984), cohort biomass for a species increases throughout its life history. This can be demonstrated as follows. A cohort starting at body size  $z_0$  has the relative biomass  $C(z_1) = l(z_0, z_1)z_1/z_0$  when it has reached body size  $z_1$ . Because body size is a function of time, the rate of change of cohort biomass over time is

$$\begin{aligned} dC/dt &= 1/z_0 [z_1(dl/dt) + l(dz_1/dt)] \\ dC/dt &= 1/z_0 (-\mu_1lz_1 + lgz_1) \\ dC/dt &= l(z_1/z_0)(g - \mu_1). \end{aligned} \tag{16}$$

In Taylor and Williams' model, at the optimal initial juvenile size instantaneous mortality equaled instantaneous growth for the first time (i.e., at size  $x$  in fig. 5). Thus, for the entire juvenile size range (i.e.,  $x$  to  $m$ ) cohort biomass increases over time. In our model, however, the optimal initial juvenile size lies in a region where mortality exceeds growth ( $ks^* < x$ ). Thus, we predict that instantaneous egg mortality and the rate of change of cohort biomass over time (i.e.,  $dC/dt$ ), evaluated at initial juvenile body size, will be negatively correlated among populations.

#### DISCUSSION

Previous models of the trade-off between quantity and quality of offspring fail to predict the apparent positive correlation between the quality of parental care and egg size that is observed in nature. Smith and Fretwell's model (1974) does not contain an explicit formulation of how offspring survival depends on egg size; thus, it does not address variation among females in their ability to affect offspring survival. An interesting feature of Smith and Fretwell's model, however, is that the optimal egg size is unaffected if offspring survival is multiplied by a constant. This result has been used as a general explanation for what appeared to be an overall lack of egg size variation within populations (e.g., Maynard Smith 1978).

We combined Shine's (1978) formulation for egg-stage survival with Taylor and

Williams' (1984) formulation for size-dependent juvenile mortality and growth. We assumed that larger eggs take longer to become juveniles and that larger eggs produce larger juveniles with a lower ratio of size-dependent juvenile mortality to growth rates. Under these assumptions, our new model offers an explanation for the evolution of egg size under parental care; moreover, we can now address the two shortcomings of Shine's model.

1. Under Shine's model, unless the egg stage is safer than the juvenile stage, a female should make her eggs as small as possible. Under our model, however, instantaneous survival during the egg stage need not exceed instantaneous survival during the juvenile stage for parental care to favor increased egg size. Indeed, the term "safe harbor" may be a misnomer for some species. In our model, a female with parental care who produces larger eggs benefits by producing larger juveniles with higher survival and faster growth. The longer egg stages associated with larger eggs impose a survival cost over the egg stage; moreover, the female who makes larger eggs pays the additional cost of making fewer eggs. These costs of making larger eggs, however, are exceeded by the benefits of increased survival during the juvenile stage.

2. Shine's model predicts that as the quality of parental care varies among populations, or among females within a population, one should observe a bimodal egg size distribution, with females making their eggs as small or as large as possible. His model produces an interior minimum of fitness on egg size, with fitness being maximized at the upper or lower extreme of possible egg sizes. A small shift in instantaneous egg mortality either has no effect on the optimal egg size or shifts the optimal egg size from one extreme to the other. In contrast, our model produces an interior maximum of fitness on egg size; small shifts in instantaneous egg mortality produce small shifts in the optimal egg size. Thus, we can explain continuous covariation between the quality of parental care and egg size.

Our model has limitations, however. We assumed that initial juvenile size is a simple function of egg size. In viviparous species, and in species with extended parental care, this assumption may not be true.

For example, in many viviparous species, not all of the resources for offspring are provisioned in eggs. Developing embryos may take up nutrients directly from the maternal environment. In fact, the tendency in viviparous chondrichthyan fishes is for a reduction in egg size over that observed in related oviparous species (Wourms 1977). The subject of selection in our model is initial juvenile size, and unless this initial juvenile size depends on egg size, parental care will not affect egg size. Nevertheless, our model does make a prediction about initial juvenile size in viviparous as opposed to oviparous fishes. Inasmuch as viviparous fishes must have lower instantaneous egg mortalities than oviparous fishes (Gross and Shine 1981), our model predicts that initial juvenile size will be larger in viviparous fishes. This pattern is observed in nature (Amoroso 1960; Wourms 1977).

Oviparous fishes with extended parental care (e.g., Cichlidae) present another difficulty for our model. In such species, the offspring probably experience two different size-dependent mortality and growth schedules, before and after the termination of parental care. Thus, the offspring life history may consist of three

episodes: egg, larva, and juvenile. The mathematics of such a life history model are considerably more complicated than in the model we have presented, and further research is needed.

Finally, our model is deterministic and independent of density. We chose such a formulation for mathematical convenience and as a logical next step in approximating the relationship between egg size and parental care. In doing so, however, we may be ignoring potentially important evolutionary responses to density-dependent population dynamics in variable environments. Both density dependence (see, e.g., Ware 1975) and environmental uncertainty (see, e.g., Cooper and Kaplan 1982; Kaplan and Cooper 1984) have been incorporated into models of the evolution of egg size, yielding noteworthy results. Thus, it may be useful to include these factors in future models of the evolution of egg size under parental care.

#### SUMMARY

The quality of parental care appears to correlate positively with egg size, both *among* and *within* species of fishes. Past models of the trade-off between quantity and quality of offspring have been inadequate in explaining this correlation. Using features of models by Smith and Fretwell (1974), Shine (1978), and Taylor and Williams (1984), we constructed a model to explain continuous covariation between the quality of parental care and egg size. Our model contains three major assumptions about the dependence of offspring survival on egg size: offspring from larger eggs develop more slowly and take longer to resorb their yolk sacs and become juveniles; egg size determines initial juvenile size; and larger juveniles, which hatch from larger eggs, have lower mortalities, experience faster growth, and take less time to become adults. Under these assumptions, as parental care reduces instantaneous egg mortality, the optimal egg size increases. This increase is expected both among and within populations. Thus, the general conclusion that each population should have a single optimal egg size (see, e.g., Smith and Fretwell 1974; Maynard Smith 1978) may be incorrect.

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