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Revisiting the positive correlation between female size and egg size

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ABSTRACT

Positive correlations between maternal size and propagule (egg, seed, embryo) size could arise for several reasons. One of these is that larger mothers may improve the survival of their offspring during a stage when large propagules typically have lower survival than small propagules. We previously developed an optimality model that incorporated this effect and used it to explain the positive correlation between female size and egg size in some fishes. Our original analysis included the common assumption that large eggs have lower survival than small eggs when dissolved oxygen is low (because of surface-to-volume constraints). Recent empirical work, however, has suggested just the opposite: large eggs actually have higher survival than small eggs when dissolved oxygen is low. Here we re-analyse our original model in the light of this new evidence, showing that the original explanation for positive egg size–female size correlations no longer holds, but that new candidate explanations emerge. Specifically, larger females should produce larger eggs when they provide incubation environments of *lower* quality (i.e. lower dissolved oxygen). One way this might occur is that larger females produce larger clutches, which should have higher total oxygen demand. The re-analysis demonstrates that our theoretical approach can accommodate a variety of assumptions and may prove useful as a general framework for predicting variation in optimal egg size.

Keywords: habitat quality, incubation, maternal effects, offspring survival, survival to emergence, trade-offs.

THE PROBLEM

A common observation in plants and animals is that maternal size is positively correlated with propagule (egg, seed, embryo) size (for a review, see Roff, 1992: 354–355). Many explanations have been proposed for this relationship (e.g. Parker and Begon, 1986; McGinley, 1989; Sakai and Harada, 2001; Einum and Fleming, 2002) and we recently used

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an optimality model to explore one of them. Our analysis suggested that larger females should produce large propagules when (i) large propagules have lower survival than small propagules during a particular life-history stage and (ii) larger females provide better environments for their propagules during that stage (Hendry *et al.*, 2001). It is easy to envision the latter assumption, but the first contradicts much of the conventional wisdom that bigger is better for individual propagules (for a review, see Roff, 1992: 348–352). Nevertheless, a negative relationship between propagule size and offspring survival could arise for several reasons, such as constraints imposed by the size of the reproductive tract (Congdon and Gibbons, 1987; for other examples, see Hendry *et al.*, 2001).

Hendry *et al.* (2001) applied their model to a natural system in which large eggs have long been expected to suffer a selective disadvantage: during incubation in water. The traditional reasoning behind this expectation is that as an egg becomes larger, its volume [$(4/3)\pi r^3$] increases more rapidly than its surface area ($4\pi r^2$). Because an egg's oxygen demand is presumably proportional to its volume, whereas the ability of an egg to acquire oxygen is presumably proportional to its surface area (Krogh, 1959), large eggs should be more likely than small eggs to suffocate when dissolved oxygen is low. Thus, if larger females provide incubation environments with more dissolved oxygen, they should produce larger eggs, which are favoured during other life-history stages (for reviews, see Roff, 1992: 348–352; Heath and Blouw, 1998). Hendry *et al.* (2001) found empirical support for this prediction: positive correlations between female size and egg size were strongest in freshwater fish taxa where mothers had the greatest potential to influence the oxygen available to their eggs.

Soon after the publication of Hendry *et al.* (2001), one of us (A.H.) participated in an experiment designed to test the assumption that large eggs have lower survival than small eggs when dissolved oxygen is low (Einum *et al.*, 2002). The experiment was performed because although the assumption was widely adopted (e.g. Holtby and Healey, 1986; Sargent *et al.*, 1987; Fleming and Gross, 1990; Quinn *et al.*, 1995; Seymour and Bradford, 1995; Jonsson and Jonsson, 1999; Kolm, 2001), it had never been tested empirically. Surprisingly, the experiment provided strong evidence to the contrary: large eggs survived better than small eggs when dissolved oxygen was low (Einum *et al.*, 2002). The reason for this result appears to be that an increase in egg size increases metabolic demand at a slower rate than it increases surface area (Einum *et al.*, 2002). This might occur because an increase in egg volume is mostly caused by an increase in egg yolk, which should respire at a much lower rate than embryonic tissue.

The experimental results of Einum *et al.* (2002) thus directly contradicted the assumption of Hendry *et al.* (2001) that large eggs have lower survival than small eggs when dissolved oxygen is low. Here we incorporate the results of Einum *et al.* (2002) into the model of Hendry *et al.* (2001), showing that the original explanation for positive egg size–female size correlations no longer holds, but that new candidate explanations emerge. In general, we find that larger females should produce larger eggs when larger females provide incubation environments of *lower* quality (lower dissolved oxygen). This could occur in two ways, which for convenience we term 'abiotic' environment quality (dissolved oxygen independent of clutch size) and 'biotic' environment quality (dissolved oxygen as influenced by clutch size, i.e. density dependence). Our analysis should apply to aquatic eggs in general, but it is particularly well suited for salmonid fishes (Hendry *et al.*, 2001; Einum *et al.*, 2002).

THEORETICAL FRAMEWORK

In our model, offspring survival is influenced by egg size during two life-history stages: pre-hatching and post-hatching. Offspring fitness is the product of the probability of survival during these two periods, and maternal fitness is the product of offspring fitness and egg number. Following Hendry *et al.* (2001), as well as others, we assume that post-hatching survival is positively correlated with egg size but is not influenced by maternal phenotype. This last assumption may not always be true (Einum and Fleming, 2002) and our model could be expanded to include such effects. Contrary to Hendry *et al.* (2001), we now assume that pre-hatching survival also increases with increasing egg size (following Einum *et al.*, 2002).

In the model, maternal size can have two effects on pre-hatching survival and, therefore, on offspring fitness. First, maternal size might influence the abiotic quality of the incubation environment through a process we termed 'phenotype/habitat matching' (Hendry *et al.*, 2001). Specifically, larger females may provide incubation environments of higher abiotic quality (van den Berghe and Gross, 1989; Hendry *et al.*, 2001), with the converse also being possible (Holtby and Healey, 1986). Second, larger females produce more eggs (Hendry *et al.*, 2001) and have larger clutches per nest (Fleming *et al.*, 1996; $r^2 = 0.52$, $P < 0.001$, I.A. Fleming, unpublished data), which should increase oxygen demand within the nest and reduce the biotic quality of the incubation environment (i.e. negative density dependence). Hendry *et al.* (2001) focused on total egg production (biomass of all eggs produced), but here we focus on clutch biomass because of its more direct link to density dependence within nests. Regardless, clutch biomass will be strongly correlated with total egg production and with female size. These and other aspects of the model are discussed in more detail by Hendry *et al.* (2001).

The above relationships can be summarized using the fitness function

$$W(s, k(l), E(l)) = F_1(s, k(l), E(l))F_2(s)N(s, E(l)) \tag{1}$$

This equation states that maternal fitness (W) is a function of egg size (s), habitat quality (k) and clutch size (E), with k and E being functions of female size (l). Maternal fitness is thus the product of: (i) the probability of survival to hatching (F_1), which is a function of s, k and E; (ii) the probability of survival after hatching (F_2), which is a function of s; and (iii) clutch size (N), which is a function of s and E. Our model maximizes maternal fitness with respect to egg size (cf. Smith and Fretwell, 1974; Einum and Fleming, 2000) and so optimal egg size will occur when the first derivative of equation (1) with respect to egg size equals zero ($\partial W/\partial s = 0$) and the second derivative with respect to egg size is negative ($\partial^2 W/\partial s^2 < 0$). The first derivative condition can be differentiated with respect to female length (l) to obtain:

$$\left[\frac{\partial^2 W}{\partial s^2}\frac{\mathrm{d}s}{\mathrm{d}l}\right] + \left[\frac{\partial^2 W}{\partial s \partial k}\frac{\mathrm{d}k}{\mathrm{d}l}\right] + \left[\frac{\partial^2 W}{\partial s \partial E}\frac{\mathrm{d}E}{\mathrm{d}l}\right] = 0 \tag{2}$$

The sign of ds/dl (positive or negative) gives the sign of the predicted relationship between egg size and maternal size and, because $\partial^2 W/\partial s^2$ is negative, equation (2) can be simplified to:

$$\frac{\mathrm{d}s}{\mathrm{d}l} \propto \left[\frac{\partial^2 W}{\partial s \partial k}\frac{\mathrm{d}k}{\mathrm{d}l}\right] + \left[\frac{\partial^2 W}{\partial s \partial E}\frac{\mathrm{d}E}{\mathrm{d}l}\right] \tag{3}$$

Thus, the sign of the predicted relationship between egg size and maternal size is given by the sign of the right-hand side of equation (3). In this equation, d*k*/d*l* represents how the abiotic quality of the incubation environment changes with maternal size: positive (negative) when larger females provide incubation environments of higher (lower) abiotic quality. d*E*/d*l* represents how clutch biomass changes with maternal size: positive because larger females produce larger clutches (see above).

In equation (3), $\partial^2 W/\partial s \partial k$ represents how a change in the abiotic quality of the incubation environment influences the relationship between egg size and maternal fitness. When this quantity is positive (negative), an increase in abiotic quality will increase (decrease) the fitness benefits of a given increase in egg size. To obtain a more explicit expression for this function, we first differentiate equation (1) with respect to egg size and then differentiate the resulting equation with respect to abiotic quality. The result is equation (22) of Hendry *et al.* (2001):

$$\frac{\partial^2 W}{\partial s \partial k} = \left[\frac{\partial^2 F_1}{\partial s \partial k} F_2 \frac{E}{s}\right] - \left[\frac{\partial F_1}{\partial k} E \frac{\partial F_1}{\partial s} \frac{F_2}{F_1} \frac{1}{s}\right] \tag{4}$$

where E and s are defined as above, F_1 is the probability of pre-hatching survival, F_2 is the probability of post-hatching survival, $\partial F_1/\partial k$ represents how pre-hatching survival is influenced by abiotic quality (positive, because survival increases with increasing quality) and $\partial F_1/\partial s$ represents how pre-hatching survival is influenced by egg size (positive, because larger eggs have higher survival; Einum *et al.*, 2002). $\partial^2 F_1/\partial s \partial k$ represents how a change in the abiotic quality of the incubation environment influences the relationship between pre-hatching survival and egg size. When this quantity is positive (negative), an increase in abiotic quality will increase (decrease) the positive effects that a given increase in egg size has on pre-hatching survival.

Returning to equation (3), $\partial^2 W/\partial s \partial E$ represents how a change in clutch biomass influences the relationship between egg size and maternal fitness. When this quantity is positive (negative), an increase in clutch biomass will increase (decrease) the fitness benefits of a given increase in egg size. To obtain a more explicit expression for this function, we first differentiate equation (1) with respect to egg size and then differentiate the resulting equation with respect to clutch size. The result is equation (19) of Hendry *et al.* (2001):

$$\frac{\partial^2 W}{\partial s \partial E} = \left[\frac{\partial^2 F_1}{\partial s \partial E} F_2 \frac{E}{s}\right] - \left[\frac{\partial F_1}{\partial E} E \frac{\partial F_1}{\partial s} \frac{F_2}{F_1} \frac{1}{s}\right] \tag{5}$$

where E, s, F_1, F_2 and $\partial F_1/\partial s$ are defined as above. $\partial F_1/\partial E$ represents how pre-hatching survival is influenced by clutch biomass (negative, because an increase in clutch biomass should decrease pre-hatching survival through negative density dependence). $\partial^2 F_1/\partial s \partial E$ represents how a change in clutch biomass influences the relationship between pre-hatching survival and egg size. When this quantity is positive (negative), an increase in clutch biomass will increase (decrease) the positive effects that a given increase in egg size has on pre-hatching survival.

ANALYSIS

Using the above framework, we can now ask how optimal egg size changes with maternal size under phenotype/habitat matching (maternal size influences the abiotic quality of the incubation environment) and density dependence (larger females produce larger clutches, which lower the biotic quality of the incubation environment). To address these questions, we evaluate the sign of each of the quantities in equations (3–5) to determine if $\mathrm{d}s/\mathrm{d}l$ is positive (> 0) or negative (< 0). If $\mathrm{d}s/\mathrm{d}l$ is positive, optimal egg size increases with increasing maternal size. If $\mathrm{d}s/\mathrm{d}l$ is negative, optimal egg size decreases with increasing maternal size.

In the case of phenotype/habitat matching without density dependence, the second term of equation (3) disappears, and $\mathrm{d}s/\mathrm{d}l$ will be positive if $\partial^2 W/\partial s \partial k$ and $\mathrm{d}k/\mathrm{d}l$ are both positive or both negative. $\mathrm{d}k/\mathrm{d}l$ represents the effect of maternal size on the abiotic quality of the incubation environment, and this is customarily assumed to be positive (larger females provide better environments; e.g. van den Berghe and Gross, 1989) but could conceivably be negative (Holtby and Healey, 1986). We can then determine whether $\partial^2 W/\partial s \partial k$ is positive or negative by examining equation (4).

In equation (4), we know that $E > 0$, $s > 0$, $F_1 > 0$, $F_2 > 0$, $\partial F_1/\partial k > 0$ and $\partial F_1/\partial s > 0$. We also now know that $\partial^2 F_1/\partial s \partial k < 0$ because the positive relationship between egg size and pre-hatching survival is weaker in incubation environments of higher abiotic quality (Einum *et al.*, 2002). Thus, $\partial^2 W/\partial s \partial k < 0$ and larger females should produce smaller eggs ($\mathrm{d}s/\mathrm{d}l < 0$) if they provide incubation environments of higher abiotic quality ($\mathrm{d}k/\mathrm{d}l > 0$), but larger eggs ($\mathrm{d}s/\mathrm{d}l > 0$) if they provide incubation environments of lower abiotic quality ($\mathrm{d}k/\mathrm{d}l < 0$). Because we know that larger females typically have larger eggs, especially in salmonids (Hendry *et al.*, 2001), it would appear that larger females somehow provide incubation environments of lower abiotic quality (if the above hypothesis is to explain the observed pattern). One way this might occur is if larger females bury their eggs deeper in the gravel (Steen and Quinn, 1999) and if the dissolved oxygen supply is lower in such locations (suggested by Holtby and Healey, 1986).

In the case of density dependence without phenotype/habitat matching, the first term of equation (3) disappears and $\mathrm{d}s/\mathrm{d}l$ will be positive if $\partial^2 W/\partial s \partial E$ and $\mathrm{d}E/\mathrm{d}l$ are both positive or both negative. $\mathrm{d}E/\mathrm{d}l$ represents the effect of maternal size on clutch biomass and is known to be positive (see above). We can then determine whether $\partial^2 W/\partial s \partial E$ is positive or negative by examining equation (5). In that equation, $E > 0$, $s > 0$, $F_1 > 0$, $F_2 > 0$, $\partial F_1/\partial s > 0$ and $\partial F_1/\partial E < 0$ (because increasing clutch biomass decreases egg survival). We further assume that $\partial^2 F_1/\partial s \partial E > 0$ because the positive effect of egg size on pre-hatching survival should increase as clutch biomass increases (because dissolved oxygen demand increases; Einum *et al.*, 2002). Under these conditions, $\partial^2 W/\partial s \partial E > 0$ and, because $\mathrm{d}E/\mathrm{d}l > 0$ in equation (3), $\mathrm{d}s/\mathrm{d}l > 0$. Thus, under density dependence without phenotype/habitat matching, larger females should produce larger eggs.

When phenotype/habitat matching and density dependence are both present, the predicted relationship between optimal egg size and maternal size can depend on the relative magnitude of different effects. Using the above approach [in this case, both terms of equation (3) are retained], we obtain the following results (see also Table 1). First, when larger females provide incubation environments of lower abiotic quality, they should produce larger eggs regardless of the strength of density dependence. Second, when larger females provide incubation environments of higher abiotic quality, they should produce

Table 1. Expected correlations between maternal size and egg size (positive: $ds/dl > 0$; negative: $ds/dl < 0$) when females influence the abiotic quality of the incubation environment (phenotype/habitat matching) and the biotic quality of the incubation environment (density dependence owing to the larger clutches of larger females)

Correlation between egg size and pre-hatching survival	Effects of maternal size on egg survival owing to phenotype/habitat matching . . .	Larger females provide incubation environments of *higher* abiotic quality[c]	Larger females provide incubation environments of *lower* abiotic quality[d]
Negative (Hendry *et al.*, 2001)[a]	. . . are *stronger* than the effects of density dependence[e]	**A.** $ds/dl > 0$	**C.** $ds/dl < 0$
Negative (Hendry *et al.*, 2001)[a]	. . . are *weaker* than the effects of density dependence[f]	**B.** $ds/dl < 0$	**D.** $ds/dl < 0$
Positive (present paper)[b]	. . . are *stronger* than the effects of density dependence[e]	**E.** $ds/dl < 0$	**F.** $ds/dl > 0$
Positive (present paper)[b]	. . . are *weaker* than the effects of density dependence[f]	**G.** $ds/dl > 0$	**H.** $ds/dl > 0$

Note: Hendry *et al.* (2001) assumed that pre-hatching survival was negatively correlated with egg size and that larger females provided better incubation environments, generating options A and B. In the present paper, we assume that pre-hatching survival is positively correlated with egg size and that larger females might provide incubation environments of higher or lower abiotic quality, generating options E–H.

[a] $\partial F_1/\partial s < 0$. [b] $\partial F_1/\partial s > 0$. [c] $dk/dl > 0$. [d] $dk/dl < 0$. [e] $\left|\left(\frac{\partial^2 W}{\partial s \partial k}\right)\left(\frac{dk}{dl}\right)\right| > \left|\left(\frac{\partial^2 W}{\partial s \partial E}\right)\left(\frac{dE}{dl}\right)\right|$. [f] $\left|\left(\frac{\partial^2 W}{\partial s \partial k}\right)\left(\frac{dk}{dl}\right)\right| < \left|\left(\frac{\partial^2 W}{\partial s \partial E}\right)\left(\frac{dE}{dl}\right)\right|$.

larger eggs when this positive abiotic fitness effect is weaker than the negative biotic fitness effect of their larger clutches.

CONCLUSIONS AND EXTENSIONS

One hypothesis for why larger females produce larger propagules (eggs, seeds, embryos) is that larger females improve offspring survival during a stage when larger propagules have lower survival than small propagules. Hendry *et al.* (2001) modelled this hypothesis and argued that it might explain the positive correlation between female size and egg size in some fishes. Subsequent research, however, revealed that large eggs have higher survival than small eggs when dissolved oxygen is low (Einum *et al.*, 2002). Here, we have re-analysed the model of Hendry *et al.* (2001) after incorporating this new evidence. In doing so, we have demonstrated that the original explanation for why larger females have larger eggs is probably incorrect, but that other explanations are possible.

The results of our new analysis suggest that larger females should produce larger eggs when larger females provide incubation environments of *lower* quality. This might occur in at least two different ways. First, larger females might place their eggs in sites that have lower dissolved oxygen supply; for example, because they dig deeper nests (Steen and

Quinn, 1999). Second, larger females produce larger clutches, which require more oxygen and should reduce dissolved oxygen availability for eggs. Moreover, even if females place their eggs in sites that have a higher oxygen supply, they will still be selected to have larger eggs if this positive abiotic fitness effect is weaker than the negative biotic fitness effect of their larger clutches. A complementary effect not currently considered in our model is that larger eggs will reduce oxygen demand per unit of clutch biomass, which should further favour larger eggs in larger females (Einum *et al.*, 2002).

Although the traditional assumption that larger aquatic eggs have lower pre-hatching survival now appears incorrect, other factors could still select against large eggs before hatching (see Hendry *et al.*, 2001). In these other contexts, the original conclusions of Hendry *et al.* (2001) should hold true, depending on the effects of maternal phenotype (Table 1). Indeed, we can envision several additional selective factors that might constrain egg size in salmonids. For example, juveniles from larger eggs may have more difficulty emerging through fine gravels (Koski, 1981), which might select against large eggs in small females because smaller females tend to construct their nests in finer gravels (van den Berghe and Gross, 1989). This ‘entombment’ effect is one possible explanation for the positive correlation between egg size and gravel size among salmon populations (Quinn *et al.*, 1995).

Some readers might question the value of a model that seemingly predicts the same trend (a positive correlation between egg size and maternal size) even after reversing an assumption supposedly critical to that prediction. In general, our goal is to posit explanations for an observed empirical relationship, and our model identifies several factors that might influence this relationship. Each of these factors has an effect that could theoretically vary in direction – for example, larger females could potentially provide better or worse incubation environments. Thus, a model such as ours can predict the same relationship through different combinations of assumed effects (Table 1). The value of the model is therefore in illustrating which combinations of effects might give rise to a particular observed relationship. Empirical tests can then concentrate on elucidating the nature of the assumed effects, thereby narrowing the range of possible explanations. In this spirit, Hendry *et al.* (2001) initially worked with the standard assumption that large eggs have lower survival than small eggs when dissolved oxygen is low. This led us to consider cells A–D in Table 1, wherein cell A had the only combination of effects predicting a positive correlation between egg size and maternal size. We then tested the assumption and found that it should be inverted (Einum *et al.*, 2002), which now leads us to consider cells E–H in Table 1. In these cells, a positive correlation between egg size and maternal size could arise owing to several different effects (cells F–H). Thus, future empirical research should concentrate on testing the effects that discriminate among these possibilities.

Just as the predictions of a model depend on the nature of its assumed effects, they also depend on whether additional factors might be important. Many such factors have yet to be considered in theoretical treatments of the relationship between optimal egg size and maternal size. For salmonids, such factors might include: (i) the ability of juveniles of different sizes to emerge through gravels of different sizes (Koski, 1981); (ii) the effect of egg size on the rate of oxygen consumption per unit of clutch biomass (Einum *et al.*, 2002); and (iii) the effect of maternal phenotype on the survival of free-swimming larvae (Einum and Fleming, 2002). We suggest that all of these effects could be investigated together using an extension of our theoretical framework.

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