

The effect of packing constraints on optimal investment in offspring

Christopher W. Beck^{1*} and Robert E. Beck²

¹*Department of Biology, Emory University, Atlanta, GA 30322 and*

²*Department of Computing Sciences, Villanova University, Villanova, PA 19085, USA*

ABSTRACT

Problem: In some taxa, females retain their entire clutch internally and face a packing constraint, which may lead to a correlation between egg size and total allocation (egg size \times clutch size).

Hypotheses: In species with packing constraints (e.g. turtles and copepods), linear measures of egg size will be negatively correlated with total reproductive allocation, but egg volume will be positively correlated with total reproductive allocation. By contrast, in species without packing constraints (e.g. passerine birds), the correlations, if present, can be either positive or negative. However, both will be in the same direction.

Data: Egg length, egg width, egg volume, clutch size and body size in turtles, copepods and North American passerine bird species.

Methods: We calculated independent contrasts separately for each taxonomic group, using composite phylogenies and ignoring branch lengths. We used Smith and Fretwell's (1974) optimality model of egg size. We modified it by assuming a correlation between total reproductive investment and investment in individual offspring.

Conclusions: The data agreed with the hypotheses. Suppose that total reproductive investment increases rapidly with increases in investment in individual offspring. Then, optimal investment in offspring increases greatly.

Keywords: clutch size, life-history evolution, morphological constraints, optimal egg size, reproductive allocation, reproductive effort, reproductive investment.

INTRODUCTION

Most models of optimal offspring size and optimal clutch size have assumed that total allocation of resources to reproduction is fixed and not influenced by either clutch size or offspring size (Smith and Fretwell, 1974; Brockelman, 1975; Lloyd, 1987; McGinley *et al.*, 1987). However, some models have explored the relationship between optimal clutch size and optimal offspring size, and thus the relationships between offspring size, clutch size and total allocation to

* Author to whom all correspondence should be addressed. e-mail: christopher.beck@emory.edu
Consult the copyright statement on the inside front cover for non-commercial copying policies.

reproduction. For example, Parker and Begon (1986) showed that larger females, who are assumed to invest more in reproduction, should produce larger offspring than smaller females, when larger offspring are more successful in competition. McGinley (1989) found a similar relationship between female size and offspring size if larger clutch sizes result in increased offspring fitness, as might occur if predators can kill only a fixed number of offspring. Yet, neither of these models explicitly examined the relationship between offspring size and allocation to reproduction.

The only model that has examined explicitly the relationship between optimal offspring size and allocation to reproduction was proposed by Winkler and Wallin (1987). In their model, they determined optimal total allocation to reproduction and optimal offspring size, based on the assumptions that parental survival is a function of total allocation to reproduction and that offspring production is a function of both total allocation to reproduction and investment in each offspring (i.e. offspring size). Their model predicts that optimal total allocation to reproduction should be inversely related to optimal offspring size.

Despite the common assumption that allocation of resources to reproduction is independent of the division of those resources into individual offspring, recent empirical evidence suggests that offspring size and total allocation to reproduction are indeed correlated in some species (Caley *et al.*, 2001; Czesak and Fox, 2003; but see Hendry *et al.*, 2001). In the seed beetle *Stator limbatus*, egg size (measured linearly as both egg width and egg length) and reproductive effort are positively correlated, although the strength of the correlation depends on the host plant species used by the beetles (Czesak and Fox, 2003). By using a half-sib analysis, Czesak and Fox (2003) were able to show that the relationship between egg size and allocation to reproduction in *S. limbatus* was due to a significant genetic correlation between the two traits. In contrast to seed beetles, egg width and total allocation to reproduction (estimated as egg width times clutch size) are negatively correlated across species of copepods (Caley *et al.*, 2001). It is unclear why this trade-off occurs in copepods.

Previous research has shown that morphological constraints might have important effects on egg size (Congdon and Gibbons, 1987) and trade-offs between egg size and clutch size (Glazier, 2000). Therefore, we were interested in whether the constraints of packing eggs into a body cavity or egg sac might lead to a negative correlation between egg width and reproductive allocation, as found in copepods (Caley *et al.*, 2001). We developed an algorithm that optimized the amount of egg material that could be packed into a body cavity of a given size and shape (C.W. Beck and R.E. Beck, unpublished manuscript). Specifically, we varied the number of eggs being packed into the body cavity and the algorithm maximized the size of those eggs for a given clutch size. By considering a large range of clutch sizes, we were able to determine the relationship between clutch size and maximum egg size, as well as the relationship between egg size and allocation to reproduction (clutch size times maximum egg size).

The results of our packing algorithm show that the maximum diameter of eggs that can be packed into a body cavity decreases exponentially as clutch size increases (Beck and Beck, unpublished manuscript). As a result, maximum egg diameter and allocation to reproduction (clutch size times maximum egg diameter) are negatively linearly related on a log-log plot. However, maximum egg volume and allocation to reproduction (clutch size times maximum egg volume) are positively linearly related on a log-log plot.

Based on the results of our packing algorithm, we hypothesize that total allocation to reproduction as estimated by the product of egg size and clutch size will be correlated with

egg size in taxa in which females maintain their entire clutch within their body cavity or external egg sac [as in copepods (Dussart and Defaye, 2001)] for at least a short period of time, because in these taxa total volume of a clutch will be limited. Specifically, we predict that (1) linear dimensions of egg size (i.e. egg width and egg length) will be negatively correlated with total allocation to reproduction, and (2) egg volume will be positively correlated with total allocation to reproduction in species with packing constraints. In taxa in which females produce and lay their eggs sequentially, packing constraints will not affect the relationship between egg size and total allocation to reproduction. As a result, in species without packing constraints such as birds, we predict that the direction of the relationship between egg size and allocation to reproduction will be the same, independent of whether linear dimensions or egg volume are used as estimates of egg size. It is important to note that our hypothesis makes no predictions with respect to the relationship between the mass of individual eggs and allocation to reproduction, as packing constraints are due to the geometry of packing eggs into a body cavity or egg sac.

The results of Caley *et al.* (2001) for copepods are consistent with the first prediction for species with packing constraints. To test our hypothesis further, we examined the relationship between total allocation to reproduction and egg size (egg width, egg length, egg volume) in turtles and North American passerine birds and between total allocation to reproduction and egg volume in copepods. We chose to use comparative data to test our hypothesis for several reasons. First, we were able to compare our results directly with those of Caley *et al.* (2001). Second, although some species exhibit substantial variation in egg size and clutch size among individuals within a population (e.g. turtles, fish), egg size and clutch size show little variability in other taxa (e.g. birds). Therefore, it was necessary to use comparative data to test all of the predictions generated by our hypothesis. However, further tests of specific predictions of our hypothesis with data from individuals within a population would be warranted if individuals within the population vary substantially in egg size and clutch size.

Since turtles and copepods should exhibit packing constraints, we expected to find a negative relationship between linear dimensions of egg size and total allocation to reproduction in turtles and a positive relationship between egg volume and allocation to reproduction in turtles and copepods. In contrast, since packing constraints should be absent in passerines, we expected to find the direction of the relationship between egg size and allocation to reproduction to be the same when using egg width, egg length or egg volume as estimates of egg size.

METHODS

For all taxa, we determined phylogenetically independent contrasts on log-transformed values of body size, egg size (egg length, egg width, egg volume), and total allocation to reproduction estimated as the product of egg size and clutch size. For North American passerine birds, the data on egg width, egg length and clutch size were compiled for 288 species from Ehrlich *et al.* (1988) and Harrison (1975). Egg volume was calculated from egg width and egg length following Hoyt (1979). In no case was the clutch size equal to one such that total allocation to reproduction would be equal to egg size. Body mass data were taken from Dunning (1993). We constructed a composite phylogeny based on published phylogenies (see Fig. S1 in Online Supplementary Material). For turtles, body size (carapace length) and clutch size data for 150 species were taken from a comparative study on the relationship

between latitude and reproductive traits in turtles by Iverson *et al.* (1993). J.B. Iverson (personal communication) also provided egg size data (egg length, egg width, egg mass) for the turtle species included in his original study. Egg volume was calculated from egg width and egg length following Rose *et al.* (1996). For species for which there were multiple trait values, we used the mean of the values. We constructed the composite phylogeny for the turtle data set based on published phylogenies (see Fig. S2 in Online Supplementary Material) and a maximum likelihood tree for the Testudinoidea based on 12S rRNA sequences published in GenBank (AF175326–AF175341). Data and phylogeny for 70 taxa of copepods were taken from Poulin (1995). Egg volume was calculated from egg width based on the assumption that copepod eggs are spherical.

We calculated independent contrasts using CAIC 2.6.9 (Purvis and Rambaut, 1995). Because branch lengths were unknown, we used equal branch lengths, which assumes a model of punctuated equilibrium (Purvis and Rambaut, 1995). In addition, because the phylogenies were not completely resolved for any of the groups, we used clutch size as the independent variable in determining contrasts using Pagel's method for independent contrasts for unresolved phylogenies (Harvey and Pagel, 1991).

Following Caley *et al.* (2001), in our analysis of the relationship between egg size and total allocation to reproduction, we first controlled for effects of body size, because reproductive traits often covary with body size (Roff, 1992; Stearns, 1992). To control for effects of body size, we calculated the residuals from the regression of contrasts of body size on either contrasts of egg size or contrasts of total allocation to reproduction. In all cases, the regressions were forced through the origin (Pagel, 1993). We then determined the correlation between the residuals of the contrasts of egg size and total reproductive effort. As suggested by Caley *et al.* (2001), egg size and total allocation to reproduction may be correlated to a certain degree because total allocation to reproduction was estimated as the product of egg size and clutch size. Therefore, we followed Caley *et al.* (2001) and determined the significance of the correlation by using a randomization test that determined the correlation between the residuals of the contrasts of egg size and total allocation to reproduction for 1000 randomizations of the data.

RESULTS

Our results supported the predictions of our packing constraints hypothesis both for species with packing constraints (turtles and copepods) and species without packing constraints (passerines). For turtles, we found a significant negative relationship between both linear measures of egg size (egg length and egg width) and total allocation to reproduction (i.e. product of egg size and clutch size) (egg length: $r = -0.38$, $P < 0.001$; egg width: $r = -0.19$, $P = 0.011$) (Fig. 1a). In addition, we found a significant positive relationship between egg volume and total allocation to reproduction ($r = 0.58$, $P < 0.001$) (Fig. 2a). Previously, Caley *et al.* (2001) demonstrated a significant negative correlation between egg width and allocation to reproduction for copepods. Using the same data, we found a significant positive correlation between egg volume and allocation to reproduction ($r = 0.50$, $P = 0.001$) (Fig. 2c). For birds, we found a consistent positive correlation between egg size and total allocation to reproduction, independent of whether we used egg length ($r = 0.18$, $P = 0.005$) (Fig. 1b), egg width ($r = 0.12$, $P = 0.01$) or egg volume ($r = 0.52$, $P < 0.001$) (Fig. 2b).

For both egg length and egg width in turtles, there are several data points with large positive residual values for total allocation to reproduction (Fig. 1a) that may represent

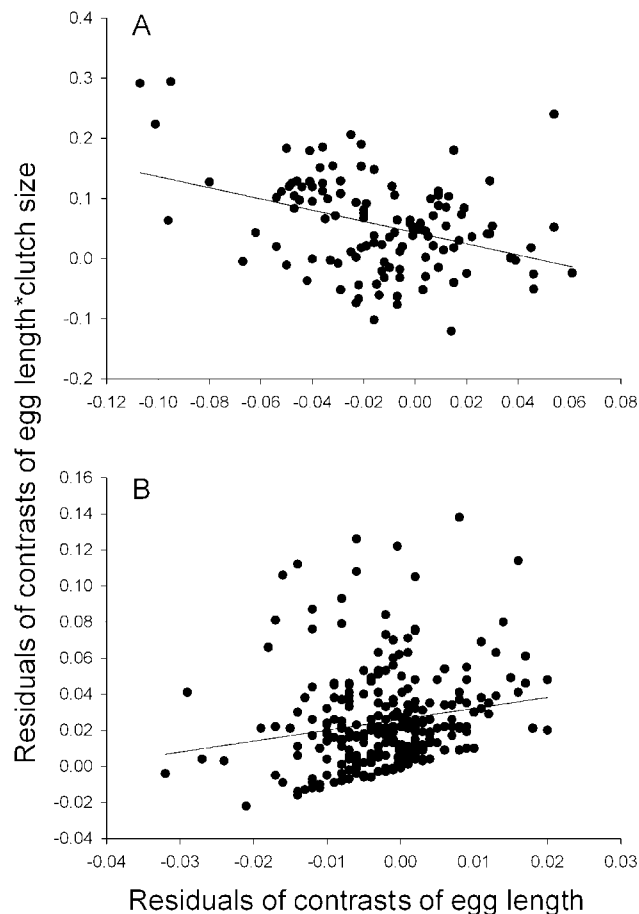


Fig. 1. The relationship between independent contrasts of egg length and total allocation to reproduction (product of egg length and clutch size). Effects of body size were removed by using residuals from regressions of independent contrasts of body size on contrasts of either egg size or total allocation to reproduction. The significance of correlations was determined using a randomization test (see text for details). (A) For turtles, total allocation to reproduction was significantly negatively correlated with egg length ($r = -0.38$, $P < 0.001$). (B) For passerines, total allocation to reproduction was significantly positively correlated with egg length ($r = 0.18$, $P = 0.005$).

statistical outliers. If these data points are removed from the analysis, egg length and total allocation to reproduction are still significantly negatively correlated ($r = -0.23$, $P = 0.008$); however, the relationship between egg width and allocation to reproduction is no longer significant ($r = -0.042$, $P = 0.66$). Although these values may represent statistical outliers, from a biological perspective they are real data and therefore should be included in the analysis. Furthermore, egg width may be constrained in turtle eggs due to the size of a female's pelvic opening (Congdon and Gibbons, 1987), which suggests that egg length might be a more appropriate linear measure of egg size with which to test for packing constraints.

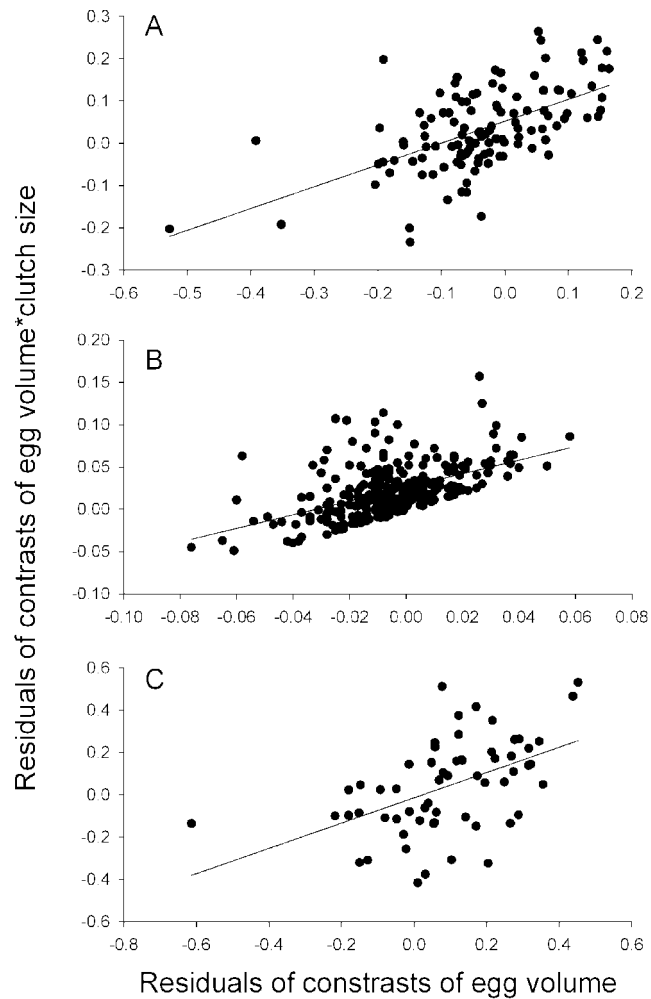


Fig. 2. The relationship between independent contrasts of egg volume and total allocation to reproduction (product of egg volume and clutch size). Effects of body size were removed by using residuals from regressions of independent contrasts of body size on contrasts of either egg size or total allocation to reproduction. The significance of correlations was determined using a randomization test (see text for details). (A) For turtles, total allocation to reproduction was significantly positively correlated with egg volume ($r = 0.58$, $P < 0.001$). (B) For passerines, total allocation to reproduction was significantly positively correlated with egg volume ($r = 0.52$, $P < 0.001$). (C) For copepods, total allocation to reproduction was significantly positively correlated with egg volume ($r = 0.50$, $P = 0.001$).

DISCUSSION

In both turtles and copepods, which retain all of their clutch in their body cavity or an egg sac, we found significant negative correlations between linear measures of egg size (i.e. egg width and egg length) and total allocation to reproduction (Fig. 1) (Caley *et al.*, 2001), as well as

significant positive correlations between egg volume and total allocation to reproduction (Fig. 2). In contrast, in passerine birds, which lay their eggs successively, both linear measures of egg size and egg volume were positively correlated with total allocation to reproduction (Figs. 1, 2). All of these results are consistent with the hypothesis that packing constraints will result in a relationship between egg size and total allocation to reproduction in species that retain their eggs in their body cavity or in an egg sac (Beck and Beck, unpublished manuscript). As a result, in these species, egg size and clutch volume cannot evolve independently due to constraints imposed by geometry. However, even in species in which packing constraints do not occur, such as birds, egg size and clutch volume are not independent. This suggests that the allocation of resources to reproduction and the division of those resources into individual offspring are not sequential allocations, but simultaneous allocations (Caley *et al.*, 2001). Because the allocations are simultaneous, total allocation to reproduction could influence egg size or egg size could affect total allocation to reproduction. The direction of the causal relationship between these allocations depends on whether packing constraints are present. In species with packing constraints, maximum clutch volume is determined by egg size. In contrast, in the absence of packing constraints, the causal arrow could be in either direction.

Integral to the conclusion that total allocation to reproduction and allocation to individual offspring are not independent are the assumptions that linear measures of egg size or egg volume are good estimates of energy allocation to individual offspring and that the product of egg size and clutch size is a good estimate of total allocation to reproduction. In some taxa, investment in individual eggs does vary linearly with linear measures of egg size (e.g. Berg *et al.*, 2001) and egg volume (e.g. McEdward and Morgan, 2001). Therefore, in these taxa, the assumptions appear valid and total allocation to reproduction and allocation to individual offspring are not independent. Thus, models of reproductive allocation and optimal egg size need to be considered simultaneously. When considering the effect of packing constraints on the relationship between egg size and total allocation to reproduction in these taxa, it is important to determine whether linear measures of egg size or egg volume correlate more closely with allocation to individual offspring, because linear measures of egg size are negatively correlated with total allocation to reproduction (Fig. 1a), whereas egg volume is positively correlated with total allocation to reproduction (Fig. 2). Based on independent contrasts from the data we compiled on turtles, we found that egg width, egg length and egg volume were positively correlated with egg mass, but that egg volume explained more of the variation in egg mass ($R^2 = 0.94$) than the linear measures of egg size (egg width: $R^2 = 0.89$; egg length: $R^2 = 0.79$). Therefore, egg volume may be a better estimate of egg quality than linear measures of egg size. Furthermore, egg volume and egg shape may be more important in determining packing constraints than linear measures of egg size.

Although some taxa exhibit a strong relationship between egg size and allocation to individual offspring, in many other taxa egg size is not a good proxy for egg quality in terms of energy content or subsequent juvenile size and survival (Bernardo, 1996). As a result, packing constraints will not lead to constraints on total reproductive effort. Indeed, in some cases, females have been found to adjust egg quality (i.e. lipid content) in response to their own quality or the quality of their environment without adjusting egg size (e.g. Arnold *et al.*, 1991; Royle *et al.*, 1999; Nager *et al.*, 2000). If egg quality is not correlated with egg size, packing constraints will not necessarily result in a correlation between total allocation to reproduction and allocation to individual offspring. However, even in these species, the allocations may still be correlated.

Model of optimal investment in offspring

Since total allocation to reproduction and allocation to individual offspring may not be independent both in species in which packing constraints are present (e.g. turtles and copepods) and in species in which packing constraints are absent (e.g. passerine birds), we modified the Smith-Fretwell model of optimal egg size (Smith and Fretwell, 1974) to include the relationship between total allocation to reproduction and allocation to individual offspring (see Appendix). Because the model is for optimal investment in individual offspring, we assume that allocation to individual offspring affects total reproductive allocation and not the reverse. The model predicts the optimal investment in individual offspring (which may or may not be correlated with egg size) and total investment in offspring for different relationships between these investments (b), different minimum investments in offspring (I_0), and different relationships between investment in individual offspring and offspring fitness (k) (Fig. 3). Winkler and Wallin's (1987) model examines similar parameters, but differs from the model presented here in that it did not consider a functional or genetic correlation between total allocation to reproduction and allocation to individual offspring. Any correlation between these two allocations in their model is due to their effect on determining offspring production, rather than an assumed causal linkage between the two.

Similar to Winkler and Wallin (1987), we found that optimal investment in individual offspring (I^*) is independent of maximal offspring fitness (\hat{W}). In addition, both models predict that I^* increases with increases in the minimum investment in offspring (I_0) (Fig. 3a). However, we found that the rate at which offspring fitness increases with investment in offspring (k) has little effect on I^* , except for large values of b (Fig. 3a). In contrast, in Winkler and Wallin's model, I^* increases exponentially with decreases in k at low values of I_0 .

The relationship between total allocation to reproduction and allocation to individual offspring (b) had the greatest effect on I^* (Fig. 3a). Between $b = 0$ (i.e. the allocations are unrelated) and $b = 1$, I^* increases exponentially with increases in b (Fig. 3a). In other words, we would expect females to invest more in individual offspring in taxa in which total allocation to reproduction increases rapidly with increases in allocation to individual offspring, as compared to taxa in which total allocation to reproduction changes little with allocation to individual offspring. Although I^* increases with increases in b for all values of k and I_0 , the increase in I^* with respect to b is greater when offspring fitness increases less rapidly with increases in investment (i.e. lower values of k). Overall, the greatest investment in individual offspring should occur when minimum investment (I_0) is large, the rate of increase of offspring fitness with increased investment (k) is low, and the rate of increase in total investment with increased investment in individual offspring (b) is high.

Although our model and that of Winkler and Wallin (1987) in general make the same predictions with respect to allocation to individual offspring, the models make strikingly different predictions about the effects of I_0 and k on total allocation to reproduction. In our model, since total allocation to reproduction is exponentially related to allocation to individual offspring (see equation A6), I_0 , k and b all affect total allocation to reproduction in a similar fashion to the way in which they influenced allocation to individual offspring (Fig. 3). In contrast, in the absence of a functional or genetic relationship between total allocation to reproduction and allocation to individual offspring, Winkler and Wallin's model predicts that total allocation to reproduction should decrease with increases in I_0 rather than increase, and should increase with increases in k rather than be unaffected by k .

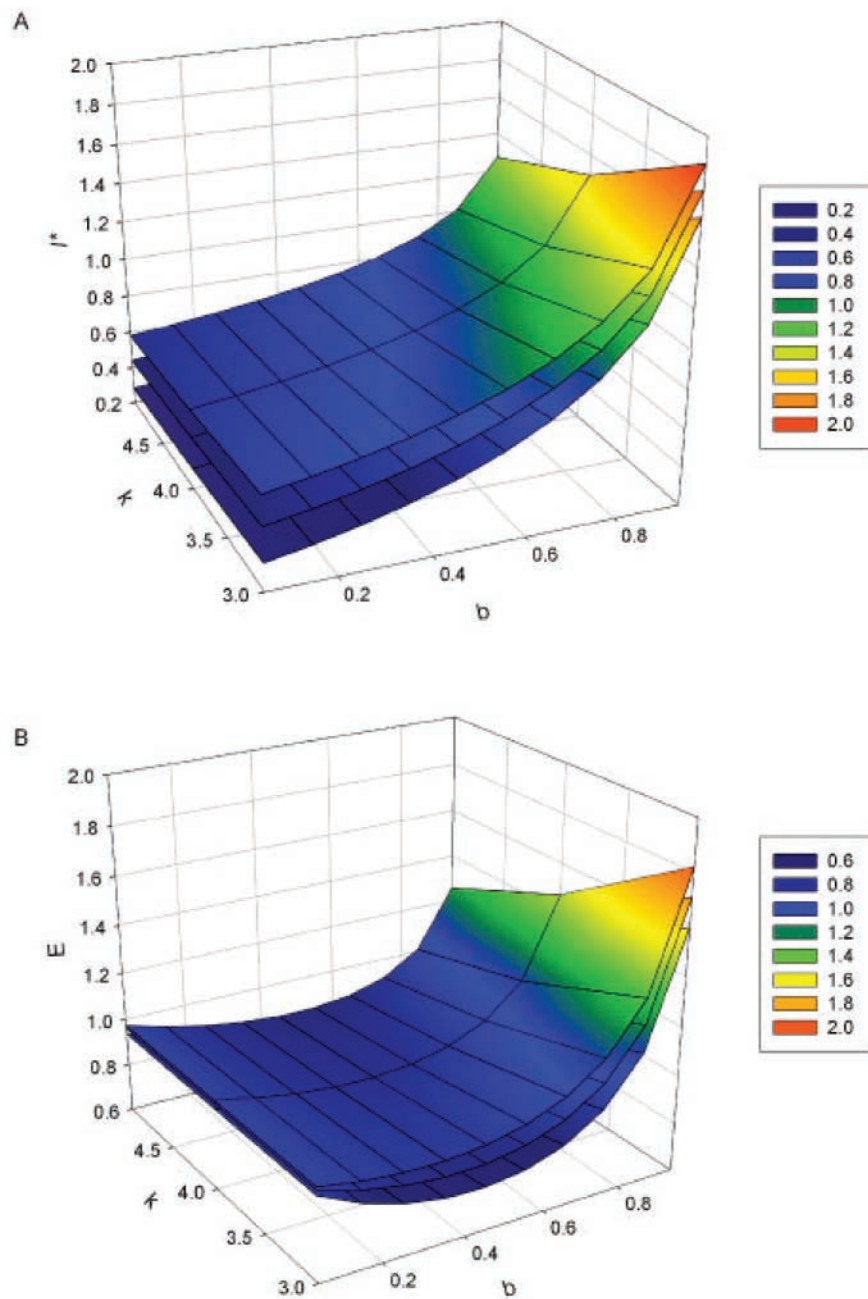


Fig. 3. The effect of the rate of increase in offspring fitness of allocation to offspring (k) and the relationship between total allocation to reproduction and allocation to individual offspring (b) (see equation A6) on (A) optimal allocation to individual offspring (I^*) and (B) total allocation to reproduction (E). Each surface is for a different minimum allocation to offspring (I_0) (top: $I_0 = 0.3$; middle: $I_0 = 0.2$; bottom: $I_0 = 0.1$).

The differences in the predictions of the two models in terms of total allocation to reproduction suggest that how total investment and investment in individual offspring are related is important in determining optimal reproductive investment.

Conclusions

Both packing algorithms (Beck and Beck, unpublished manuscript) and comparative data across a range of taxa (current study) suggest that total allocation to reproduction may be affected by allocation to individual offspring in many taxa due to packing constraints. Furthermore, optimal allocation to offspring and the resulting total allocation to reproduction are influenced mostly by the extent to which total allocation to reproduction increases with increases in allocation to individual offspring. In contrast, the minimum allocation to individual offspring and the relationship between allocation to offspring and offspring fitness have only limited effects on optimal allocation to offspring. As a result, future empirical studies of reproductive allocations should be certain to examine how investment in individual offspring influences total reproductive investment.

ACKNOWLEDGEMENTS

We thank J. Iverson for supplying the turtle data set and A. Hendry for his comments on an earlier version of the paper that greatly improved our thinking on this topic.

REFERENCES

- Arnold, T.W., Alisauskas, R.T. and Ankney, C.D. 1991. Egg composition of American Coots in relation to habitat, year, laying date, clutch size, and supplemental feeding. *Auk*, **108**: 532–547.
- Berg, O.K., Hendry, A.P., Svendsen, B., Bech, C., Arnekleiv, J.V. and Lohrmann, A. 2001. Maternal provisioning of offspring and the use of those resources during ontogeny: variation within and between Atlantic salmon families. *Funct. Ecol.*, **15**: 13–23.
- Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.*, **36**: 216–236.
- Brockelman, W.Y. 1975. Competition, fitness of offspring, and optimal clutch size. *Am. Nat.*, **109**: 677–699.
- Caley, M.J., Schwarzkopf, L. and Shine, R. 2001. Does total reproductive effort evolve independently of offspring size? *Evolution*, **55**: 1245–1248.
- Congdon, J.D. and Gibbons, J.W. 1987. Morphological constraint on egg size – a challenge to optimal egg size theory. *Proc. Natl. Acad. Sci. USA*, **84**: 4145–4147.
- Czesak, M.E. and Fox, C.W. 2003. Evolutionary ecology of egg size and number in a seed beetle: genetic trade-off differs between environments. *Evolution*, **57**: 1121–1132.
- Dunning, J.B.J., ed. 1993. *CRC Handbook of Avian Body Masses*. Boca Raton, FL: CRC Press.
- Dussart, B.H. and Defaye, D. 2001. *Introduction to the Copepoda*. Leiden: Backhuys.
- Ehrlich, P.R., Dobkin, D.S. and Wheye, D. 1988. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds, Including All Species that Regularly Breed North of Mexico*. New York: Simon & Schuster.
- Glazier, D.S. 2000. Smaller amphipod mothers show stronger trade-offs between offspring size and number. *Ecol. Lett.*, **3**: 142–149.
- Harrison, H.H. 1975. *Eastern Birds' Nests* (The Peterson Field Guide). New York: Houghton Mifflin.
- Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. New York: Oxford University Press.

- Hendry, A.P., Day, T. and Cooper, A.B. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *Am. Nat.*, **157**: 387–407.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *Auk*, **96**: 73–77.
- Iverson, J.B., Balgooyen, C.P., Byrd, K.K. and Lyddan, K.K. 1993. Latitudinal variation in egg and clutch size in turtles. *Can. J. Zool.*, **71**: 2448–2461.
- Lloyd, D.G. 1987. Selection of offspring size at independence and other size versus number strategies. *Am. Nat.*, **129**: 800–817.
- McEdward, L.R. and Morgan, K.H. 2001. Interspecific relationships between egg size and the level of parental investment per offspring in echinoderms. *Biol. Bull.*, **200**: 33–50.
- McGinley, M.A. 1989. The influence of a positive correlation between clutch size and offspring fitness on the optimal offspring size. *Evol. Ecol.*, **3**: 150–156.
- McGinley, M.A., Temme, D.H. and Geber, M.A. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *Am. Nat.*, **130**: 370–398.
- Nager, R.G., Monaghan, P. and Houston, D.C. 2000. Within-clutch trade-offs between the number and quality of eggs: experimental manipulations in gulls. *Ecology*, **81**: 1339–1350.
- Pagel, M. 1993. Seeking the evolutionary regression coefficient: an analysis of what comparative methods measure. *J. Theor. Biol.*, **164**: 191–205.
- Parker, G. and Begon, M. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. *Am. Nat.*, **128**: 573–592.
- Poulin, R. 1995. Clutch size and egg size in free-living and parasitic copepods – a comparative analysis. *Evolution*, **49**: 325–336.
- Purvis, A. and Rambaut, A. 1995. Comparative analysis by independent contrasts (CAIC) – an Apple-Macintosh application for analyzing comparative data. *Comp. Appl. Biosci.*, **11**: 247–251.
- Roff, D.A. 1992. *The Evolution of Life Histories: Theory and Analysis*. New York: Chapman & Hall.
- Rose, F.L., Simpson, T.R. and Manning, R.W. 1996. Measured and predicted egg volume of *Pseudemys texana* with comments on turtle egg shape. *J. Herpetol.*, **30**: 433–435.
- Royle, N.J., Surai, P.F., McCartney, R.J. and Speake, B.K. 1999. Parental investment and egg yolk lipid composition in gulls. *Funct. Ecol.*, **13**: 298–306.
- Smith, C.C. and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.*, **108**: 499–506.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.
- Winkler, D.W. and Wallin, K. 1987. Offspring size and number – a life-history model linking effort per offspring and total effort. *Am. Nat.*, **129**: 708–720.

APPENDIX

Here, we modify the classical optimal egg size model (Smith and Fretwell, 1974) to allow for the total energy investment in offspring by a female to be affected by the investment per offspring. Following Smith and Fretwell (1974),

$$W_p = W \cdot N \quad (\text{A1})$$

where W_p is parental fitness, W is offspring fitness, which is assumed to be equal for all offspring, and N is the number of offspring. If E is the total energy invested in offspring by a parent and I is the investment in each offspring, assuming equal investment in all offspring,

$$N = E/I \quad (\text{A2})$$

Like Smith and Fretwell (1974), we assume that offspring fitness is a function of investment in each offspring ($W = g(I)$). However, we also assume that total energy invested in offspring is a function of investment in each offspring ($E = f(I)$). Therefore, from (A1) and (A2)

$$W_p(I) = g(I)f(I)/I \quad (\text{A3})$$

To determine the optimal investment in each offspring I^* , we want to maximize parental fitness W_p with respect to I , the investment in each offspring. We assume f and g are differentiable, and differentiating (A3) we find that

$$W'_p = \frac{I(g'f + gf') - gf}{I^2} \quad (\text{A4})$$

The local maxima for W_p of interest to us occur when $W'_p(I) = 0$ and $I > I_0$, where I_0 is the minimum energy investment needed to produce successful offspring. To find these values, we solve

$$I = \frac{gf}{g'f + gf'} \quad (\text{A5})$$

Above, we have shown that, based on comparative data, after controlling for differences in female body size,

$$\log E = \log f(I) = b \log I + c \quad (\text{A6})$$

Note that if $b = 0$, which is the assumption of constant total investment in offspring assumed by Smith and Fretwell (1974), then $\log f(I) = c$ or $E = f(I) = e^c$. We normalize so that in the classical case $E = 1$, by setting $c = 0$. Therefore, differentiating (A6) with respect to I ,

$$f' = bf/I \quad (\text{A7})$$

Substituting (A7) into (A5), and simplifying, we get

$$g'I + (b - 1)g = 0 \quad (\text{A8})$$

since $f \neq 0$ and $I \neq 0$.

Because g is positive and increasing (i.e. $g' > 0$) on the interval $I > I_0$, then $b < 1$ for (A8) to hold.

To examine the dynamics of optimal investment in offspring, we use the classical assumption from Smith and Fretwell (1974) and Equation 7 in Winkler and Wallin (1987) that

$$W = g(I) = \hat{W}(1 - e^{-k(I - I_0)}) \quad (\text{A9})$$

where \hat{W} is the asymptotic maximum offspring fitness, and k is the coefficient that determines the rate of increase of W with an increase in I . Differentiating (A9) with respect to I ,

$$g' = k\hat{W}e^{-k(I - I_0)} \quad (\text{A10})$$

Substituting (A9) and (A10) into (A8) and simplifying, we have

$$\frac{b - 1}{b - 1 - kI} = e^{-k(I - I_0)} \quad (\text{A11})$$

The optimal investment in each offspring I^* can be found by solving for I in (A11) for known values of b , k , and I_0 . Total energy investment in offspring by the female can be determined for a given optimal investment in each offspring I^* by substituting into (A6).