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Source: *Ecology*, February 2013, Vol. 94, No. 2 (February 2013), pp. 315-324

Published by: Wiley on behalf of the Ecological Society of America

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Ecology, 94(2), 2013, pp. 315–324
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The relationship between offspring size and fitness: integrating theory and empiricism

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Abstract. How parents divide the energy available for reproduction between size and number of offspring has a profound effect on parental reproductive success. Theory indicates that the relationship between offspring size and offspring fitness is of fundamental importance to the evolution of parental reproductive strategies: this relationship predicts the optimal division of resources between size and number of offspring, it describes the fitness consequences for parents that deviate from optimality, and its shape can predict the most viable type of investment strategy in a given environment (e.g., conservative vs. diversified bet-hedging). Many previous attempts to estimate this relationship and the corresponding value of optimal offspring size have been frustrated by a lack of integration between theory and empiricism. In the present study, we draw from C. Smith and S. Fretwell's classic model to explain how a sound estimate of the offspring size–fitness relationship can be derived with empirical data. We evaluate what measures of fitness can be used to model the offspring size–fitness curve and optimal size, as well as which statistical models should and should not be used to estimate offspring size–fitness relationships. To construct the fitness curve, we recommend that offspring fitness be measured as survival up to the age at which the instantaneous rate of offspring mortality becomes random with respect to initial investment. Parental fitness is then expressed in ecologically meaningful, theoretically defensible, and broadly comparable units: *the number of offspring surviving to independence*. Although logistic and asymptotic regression have been widely used to estimate offspring size–fitness relationships, the former provides relatively unreliable estimates of optimal size when offspring survival and sample sizes are low, and the latter is unreliable under all conditions. We recommend that the Weibull-1 model be used to estimate this curve because it provides modest improvements in prediction accuracy under experimentally relevant conditions.

Key words: clutch size; egg size; fitness function; maternal care; maternal effects; offspring fitness; optimality; optimal offspring size; parental care; parental investment; Weibull-1 model.

INTRODUCTION

Natural selection on body size and size-related traits is ubiquitous and predominantly positive (Kingsolver and Diamond 2011). This is also true of selection during early life, where offspring emerging from larger eggs or seeds typically exhibit greater survival, e.g., bryozoans (Marshall and Keough 2006), fish (Einum and Fleming 2000), amphibians (Altwegg and Reyer 2003), reptiles (Janzen et al. 2000a), birds (Krist 2011), and some plants (Charpentier et al. 2012). Yet, if selection usually favors

large offspring, why do we not observe the evolution of increasingly large eggs and seeds? Current theory was fashioned by the ideas of Lack (1947) and Svårdson (1949), who recognized that selection will act to maximize parental fitness, not offspring fitness, and that an increase in parental fecundity occurs at a cost to investment per offspring (offspring size). These and other concepts were synthesized by Smith and Fretwell (1974) in their classic model of offspring size evolution. Smith and Fretwell proposed that there is an optimal level of investment per offspring that will maximize parental reproductive success in a given environment, but optimal size will differ among environments according to the shape of the relationship between offspring size and offspring fitness (Fig. 1).

Manuscript received 5 April 2012; revised 8 August 2012; accepted 5 September 2012. Corresponding Editor: S. J. Schreiber.

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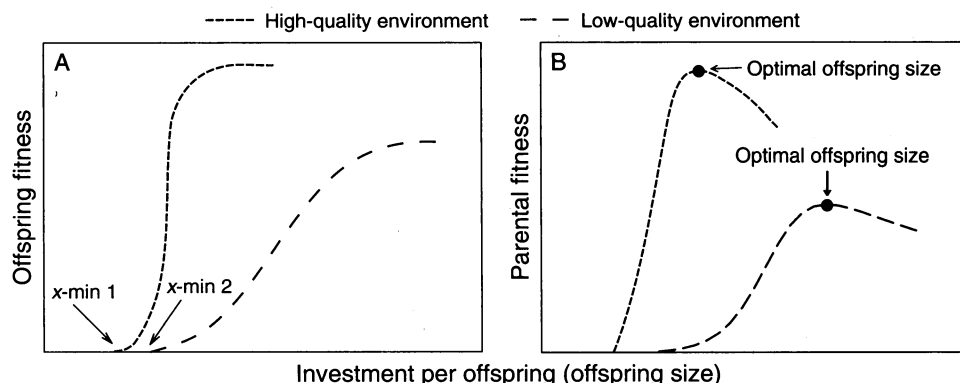


FIG. 1. A possible set of relationships between investment per offspring and fitness. (A) In the high-quality environment, the minimum level of investment needed to produce a viable offspring ($x\text{-min}$) is relatively low, and the fitness curve increases quickly from this minimum to an elevated asymptotic value of offspring fitness. The tail of the function approaches $x\text{-min}$ quickly because optimal offspring size is small and near the limit of viability. In the low-quality environment, $x\text{-min}$ is larger, and offspring fitness increases incrementally with offspring size up to a relatively low asymptotic value of fitness. The tail of the function is longer because low, but stochastic, survival of very small offspring (that are still well above the physiological minimum) compels the curve toward the $x\text{-axis}$ more slowly. (B) The resultant parental fitness curves (the product of offspring fitness at size x and the number of offspring produced at size x) differ in shape by virtue of the shape of the offspring fitness curves. Optimal offspring size is the level of investment per offspring that maximizes parental fitness (see Fig. 2 for further development).

Smith and Fretwell (1974) recognized that the relationship between offspring size and fitness is fundamental to the study of offspring size-number strategies (Fig. 1A). First, it will reveal the value of optimal offspring size in a given environment (Figs. 1

and 2), such that quantitative tests of optimality can be performed with empirical data (Orzack and Sober 1994). Second, this relationship can be used to approximate the fitness consequences for parents that produce offspring that are larger or smaller than the optimal value, and

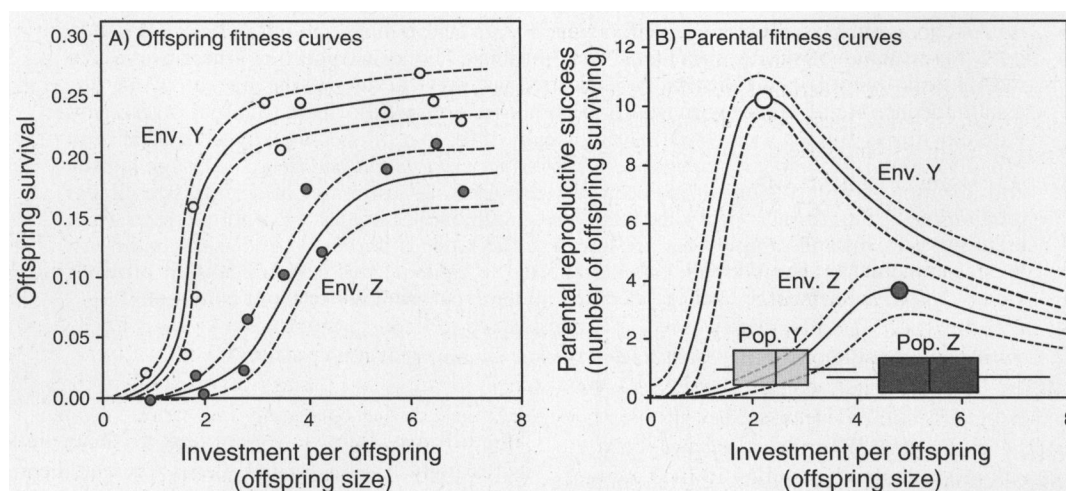


FIG. 2. A hypothetical experiment in which offspring are released into two different environments (Env. Y and Z), and survival (fitness) is subsequently assessed. Values on the $x\text{-axis}$ represent relative parental investment (i.e., "4" means twice the parental investment of "2" as measured by offspring size). (A) Offspring fitness relationships with 95% confidence intervals are fit to the data for survival vs. parental investment. (B) Parental fitness (with 95% CI) is calculated as the product of offspring survival at size x and the number of offspring of size x that can be produced. Box-and-whisker plots just above the $x\text{-axis}$ show the distribution of natural offspring sizes from populations Y and Z that inhabit environments Y and Z, respectively (median, box limits representing the upper and lower quartiles of the hypothetical data, and whiskers depicting the maximum and minimum of all data). Comparing natural variation in offspring size to parental fitness curves constructed with experimental data reveals evidence of selection. Greater natural variation in population Z coincides with small fitness penalties for parents deviating from optimality, and vice versa for population Y. These fitness curves reveal that the strength of stabilizing selection on investment per offspring differs between populations, which explains why offspring size varies more in population Z and less in population Y. Finally, there probably would be quantitative agreement between the value predicted to maximize parental fitness (large circles) and population-averaged offspring size in both populations (e.g., if a one-sample t test were performed). Although this would indicate that selection has contributed to the evolution of offspring size, this general agreement could not be interpreted as evidence that offspring size is in an optimal state, because optimality must be assessed at the level of the individual (for details, see Orzack and Sober [1994]).

TABLE 1. Statistical models that have been used to map a positive relationship between offspring size and offspring fitness.

ID	Common name	Model statement	Type	Source(s)†
1	Asymptotic regression	$1 - (a/x)^b$	E, T	1–8
2	Asymptotic regression†	$1 - \exp[-b(x - a)]$	T	9–16
3	Sigmoidal curve	$[1 + p(\exp[-x/q])]/[1 + m(\exp[-x/q])]$	T	17
4	Logistic regression	$\exp[a + \beta(x)]/(1 + \exp[a + \beta(x)])$	E	18–29
5	Cubic spline	see Schluter (1988)	E	20–21, 30–34
6	Hill equation†	$x^b/(x^b + a^b)$	T	35–36
7	Power function	$a(x)^b$	E	37
8	Linear regression	$\beta(x) + a$	E	38–39
9	Logarithmic regression	$\beta[\ln(x)] + a$	E	40
10	Polynomial regression	$\beta_1(x) + \beta_2(x)^2 + a$	E	41

Notes: “Type” refers to the model’s use in theoretical studies (T) of offspring size–number strategies, or in experimental studies (E). Estimable parameters are: b , a scaling exponent that typically governs the asymptotic shape of the fitness curve; β , the linear slope of y on x ; and a , a constant. See the source publications for a detailed description of these estimable parameters and their roles in particular models. The variable x (not estimable) is any measure of offspring size; \exp indicates exponential notation, $\exp(y) = e^y$; and \ln is the natural logarithm. Some studies have been omitted for brevity, but the list includes every function used to map a positive relationship between offspring size and offspring fitness.

† When slightly different parameterizations of the same model have been used, they are grouped under the most common form. ‡ 1, McGinley et al. (1987); 2, McGinley (1989); 3, Schultz (1991); 4, Einum and Fleming (2000); 5, Hendry et al. (2001); 6, Einum and Fleming (2004); 7, Einum and Fleming (2007); 8, Charpentier et al. (2012); 9, Winkler and Wallin (1987); 10, Parker et al. (1989); 11, Lalonde (1991); 12, Charnov et al. (1995); 13, Lessells (2002); 14, Mock et al. (2005); 15, Guinnee et al. (2007); 16, Marshall et al. (2010); 17, Kindsvater et al. (2011); 18, Hutchings (1997); 19, Mojonier (1998); 20, Janzen et al. (2000b); 21, Janzen et al. (2000a); 22, Altwegg and Reyer (2003); 23, Marshall and Keough (2006); 24, Marshall et al. (2006); 25, Marshall and Keough (2008); 26, Marshall and Keough (2009); 27, Bownds et al. (2010); 28, Monro et al. (2010); 29, Dias and Marshall (2010); 30, Sinervo et al. (1992); 31, Janzen (1993); 32, Carrière and Roff (1995); 33, Congdon et al. (1999); 34, Rankin and Sponaugle (2011); 35, Bonabeau et al. (1998); 36, Fischer et al. (2011); 37, Heath et al. (2003); 38, Hutchings (1991); 39, Sinervo and Doughty (1996); 40, Dziminski et al. (2009); 41, Janzen and Warner (2009).

this may lead to a better understanding of within- or among-individual variation in offspring size (see Fig. 2). Finally, subsequent development of the Smith-Fretwell model has illustrated that different types of offspring provisioning strategies, such as diversified bet-hedging vs. conservative bet-hedging (Einum and Fleming 2004), usually require different functional relationships between offspring size and fitness, such that the shape of the fitness curve can also intimate the type of investment strategy that is viable in a given environment (for more details, see McGinley et al. 1987, Marshall et al. 2008).

Although it is clear that the offspring size–fitness relationship is fundamental to understanding size–number strategies, few experimental studies have provided sound estimates of the offspring size–fitness curve and the corresponding value of optimal size. There are two reasons for this. First, empirical study of size–number strategies is still a developing field. Experimental studies that estimate offspring size–fitness relationships began only recently (Hutchings 1991), and most have appeared since the turn of the 21st century (Table 1). The other reason is methodological. The recent proliferation of experimental research has occurred in the absence of a literature describing how to construct a sound, theoretically defensible estimate of the offspring size–fitness relationship. It is telling that an exceedingly broad array of statistical models has been used to estimate the fitness curve from experimental data, including asymptotic regression (Charpentier et al. 2012), logarithmic regression (Dziminski et al. 2009), linear regression (Hutchings 1991), power regression (Heath et al. 2003), polynomial regression (Janzen and Warner 2009), logistic regression (Marshall and Keough

2008), and cubic splines (Rankin and Sponaugle 2011). Some of these models, on a priori grounds, can be deemed unlikely to accurately describe the fitness relationship. Furthermore, a sound estimate of this relationship requires a metric of offspring fitness that directly links parental reproductive success to investment per offspring, but many different metrics of offspring fitness are currently being used (e.g., Einum and Fleming 2000, Marshall and Keough 2008, Dziminski et al. 2009, Bownds et al. 2010).

The present synthesis has three objectives. The first is to explain why the offspring size–fitness curve and the concept of optimal offspring size are fundamental to understanding the ecological and evolutionary significance of size–number strategies. The second is to evaluate what measures of offspring fitness can be used to generate a sound estimate of the offspring size–fitness curve and the corresponding value of optimal size. Finally, we evaluate which statistical models should and should not be used to estimate offspring size–fitness relationships. Ultimately, we aim to promote an integration of theoretical and empirical research, and we hope that our recommendations will facilitate the comparison and communication of results, which may provide broad insight into the adaptive significance of size–number strategies.

WHY ESTIMATE OPTIMAL SIZE?

The study of optimality focuses on evolutionarily stable phenotypes (Orzack and Sober 1994), and optimality models aim to predict these phenotypic values (Parker and Maynard Smith 1990). In general, a claim of optimality usually implies that strong

selection has overcome local constraints, such as drift or genetic limitations, and that a phenotype has evolved which confers the greatest fitness to the individual, compared to a range of plausible alternatives (for an in-depth discussion, see Orzack and Sober 1994). Under experimentation, an observed phenotype is said to be optimal if there is quantitative agreement between the value predicted by the optimality model and the observed value. If empirical observations do not quantitatively match model predictions but are in the same general direction, one can infer that selection probably played an important role in the evolution of the phenotype, but that other evolutionary forces were also important. In such cases, the phenotypic value is below the adaptive peak (Orzack and Sober 1994). Importantly, Smith and Fretwell's model is based on the premise that any observer can construct an offspring size–fitness relationship and ultimately estimate optimal offspring size, i.e., the phenotype that confers maximum reproductive success to the parent (Fig. 2).

One will probably concede, however, that our understanding of the direct and indirect demographic consequences of variation in most traits is incomplete. For this reason, we generally should not expect optimality models to accurately predict observed phenotypes (Abrams 2001). But this should not discourage the use of optimality models in ecology and evolution: even when we do not expect optimality, comparing the predictions of an optimality model to observed phenotypes can provide valuable insight into ecological and evolutionary processes (Parker and Maynard Smith 1990). For example, a fitness curve that relates offspring size to parental fitness might inform an observer of the expected fitness consequences for parents that deviate from optimality (Fig. 2), and this may help to explain why offspring size varies more in some groups and less in others (Mangel and Ludwig 1992). Optimality models, then, can be best appreciated as guides that help us understand evolutionary processes by providing a knowledge of the trait values that will and that will not maximize individual fitness (Abrams 2001).

ESTIMATING FITNESS OF PARENTS AND OFFSPRING

Smith and Fretwell's model incorporates parental fecundity and offspring fitness components to estimate the level of investment per offspring that maximizes parental reproductive success (Figs. 1 and 2). In practice, a variety of fitness metrics have been used to estimate optimal size and the offspring size–fitness curve (e.g., Einum and Fleming 2000, Marshall and Keough 2008, Dziminski et al. 2009, Bownds et al. 2010), but some of these metrics are unlikely to allow an accurate assessment of optimal size. Smith and Fretwell (1974:505) affirm that: "In most cases, [offspring] fitness will be measured by relative survival." Although size-specific disparities in offspring survival following fertilization or parturition comprise the basis of Smith and Fretwell's thesis, these disparities will be eliminated over

time through processes such as offspring growth and resource acquisition (Einum and Fleming 2000, Nislow et al. 2004, Marshall and Keough 2009). We therefore recommend that size–number researchers measure offspring fitness as offspring survival up to the time at which the instantaneous rate of offspring mortality becomes random with respect to initial size. This provides a simple and reliable estimate of parental reproductive success that is consistent with Smith and Fretwell's thesis, given that parents maximizing the number of offspring surviving up to this point will (on average) leave the most offspring that survive to reproductive maturity. Moreover, it is simple to construct confidence intervals on the optimality estimate when a single metric comprises fitness; this is important, given that confidence intervals are necessary for a quantitative test of optimality (Orzack and Sober 1994), even though confidence intervals are lacking for almost all estimates of optimal size (e.g., Hutchings 1991, Einum and Fleming 2000, Marshall and Keough 2006, 2008). Adopting this metric also means that, for some species, survival need only be measured over a small fraction of an organism's entire life span (e.g., the first 28 of the ~2000 days lived by Atlantic salmon; Einum and Fleming 2000). Ultimately, the parental fitness curve reflects the demographic consequences of variation in investment per offspring, because fitness is expressed in theoretically defensible, ecologically meaningful, and broadly comparable units: *the number of offspring surviving to independence*.

Offspring fecundity can also be useful in size–number studies. Smith and Fretwell (1974:505) acknowledge that "The competitive advantage during early growth resulting from a larger parental investment (e.g., larger seed size) may not be expressed until a seed has grown up to reproduce itself." Indeed, offspring survival and offspring fecundity are multiplicative components of parental reproductive success (Latta 2010), such that parental fitness can be expressed as the *predicted number of grandchildren* (i.e., the number of offspring of size x that a parent can produce \times offspring survival at size $x \times$ offspring fecundity at size x). However, while direct measures of offspring reproduction can be of interest in some systems (e.g., bryozoans; Dias and Marshall 2010), accurate assessments of reproduction can be difficult in other systems (e.g., estimating reproductive success of male offspring), or offspring reproduction may simply be random with respect to initial size. Incorporating offspring reproduction into expressions of parental fitness may therefore complicate matters unnecessarily in many systems.

In this vein, a common practice when estimating optimal size is to treat traits other than offspring survival and reproduction as multiplicative components of parental fitness (e.g., Marshall et al. 2006, Bownds et al. 2010, Monro et al. 2010). Depending on the goals of the study, this may present serious challenges. If the goal is to estimate optimal size *sensu* Smith and Fretwell

(1974), then fitness components must always be defined so that their product gives a direct estimate of parental reproductive success (Arnold and Wade 1984*a, b*). Otherwise, the relationship between offspring size and parental reproductive success is obfuscated, and a quantitative comparison of observed and expected phenotypes may not be meaningful (Houle et al. 2011).

THE SHAPE OF THE OFFSPRING FITNESS CURVE

Smith and Fretwell (1974) suggest that parents should receive decreasing returns on offspring fitness as offspring size increases. This proposition has long been considered reasonable on biological grounds, given that the proportional unit contribution to investment declines as investment per offspring increases (Pianka 1976). Both Lloyd (1987) and Jørgensen et al. (2011) have since derived an asymptotic offspring fitness curve from first principles over a broad range of parameters. Smith and Fretwell also proposed that a minimum level of investment per offspring (x_{\min}) is necessary for offspring to be viable. This minimum will not necessarily be governed by the physiological requirements of the offspring, such as the notion that offspring require x units of energy to complete embryonic development. Rather, various selection pressures will also cause x_{\min} to vary among environments, such as competition for resources after embryonic development is complete (e.g., Allen et al. 2008).

Brockelman (1975:678) remarked that “Smith and Fretwell’s [offspring fitness] curve abruptly intersects the x -axis to the right of the origin, but a sigmoid curve which gradually approaches the x -axis may be more biologically realistic.” In fact, both models are probably realistic, and whether offspring fitness approaches zero quickly (an “ r -shaped” curve) or gradually (an “ s -shaped” curve) could depend on whether selection favors fewer, larger offspring, or many small offspring (e.g., Fig. 1). If selection favors many small offspring, then offspring fitness may approach zero rapidly, simply because selection on parental reproductive success has reduced offspring size to the physiological limit of viability. At the other extreme, when a strategy of fewer, larger offspring is favored, far fewer parents will be producing offspring that are near the limit of physiological viability. Here, low but stochastic survival of smaller offspring might compel the curve toward the x -axis relatively slowly (Fig. 1). In this case, the concept of a clear value of x_{\min} is obnubilated.

Empirical studies often seem most interested in the “slope” or average gradient of the fitness curve. Some authors have even suggested that optimal size will be relatively large when the gradient of the fitness curve is relatively steep (e.g., Allen et al. 2008, Marshall et al. 2010). Others have implied the opposite (e.g., Hutchings 1997). Neither view is very useful. Optimal size is predicted by a nonlinear function, such that a focus on the global properties of the relationship is warranted.

FITTING A MODEL TO THE DATA

Estimating the shape of a univariate fitness curve is usually accomplished by fitting a cubic spline to the data (Schluter 1988). Splines can be invaluable in estimating the form of selection on a quantitative trait, especially because they require no prior information about the shape of the fitness relationship. However, a great deal of research has already focused on capturing the form of the offspring size–fitness relationship (Lloyd 1987, Jørgensen et al. 2011), so fitting a function whose form is restricted to a shape supported by first principles is perhaps a better approach. (Although the terms “fitness curve” and “fitness function” are generally used interchangeably, here we use the term “function” to refer to the functions generated by statistical models to estimate the shape of the offspring fitness curve).

Many statistical models have been fit to experimental data (Table 1), but given the asymptotic shape of the offspring size–fitness relationship, our focus will be restricted to two-parameter models that feature a specifiable asymptotic value of offspring survival (k). We focus on two asymptotic regression models (Fig. 3A, B), logistic regression (Fig. 3C), the Weibull-1 model (Fig. 3D), and the Hill Model (Appendix A). Ritz (2010) provides an exceptional overview of the relationships among generalized linear models, the Hill model, and Weibull models, including alternative parameterizations. Here, we review qualitative properties of these models, and we use simulations to assess how well each of these models can predict optimal offspring size (to within $\pm 5\%$ of the true value) under a series of conditions likely to be encountered by size–number researchers. A detailed simulation methodology can be found in Appendix B, and a deeper exploration of simulation results can be found in Appendix C.

Our simulations assume that the offspring fitness curve will adopt a shape along a continuum ranging from a very fast rise from x_{\min} to a maximum fitness (“fecundity selection”; Fig. 1), and a protracted, s -shaped fitness relationship (“viability selection”; Fig. 1). We created five artificial fitness curves that sample several realistic shapes ranging from pronounced fecundity selection (Appendix B: Figs. B1A and B2A) to strong viability selection (Appendix B: Figs. B1E and B2E). Each artificial fitness relationship maps a known value of offspring fitness (a continuous survival probability between 0 and 1) to a value of offspring size, and each of the five fitness curves therefore features a known value of optimal offspring size. Although the present study assesses model performance using continuous survival probabilities, our approach is nevertheless widely applicable: size–number studies that collect binary survival data typically feature large sample sizes (e.g., Mojonier 1998, Marshall and Keough 2008) such that survival data can be binned into discrete offspring size classes and then modeled as continuous survival probabilities.

We simulated experiments in which offspring of discrete size classes are marked, released into the wild,

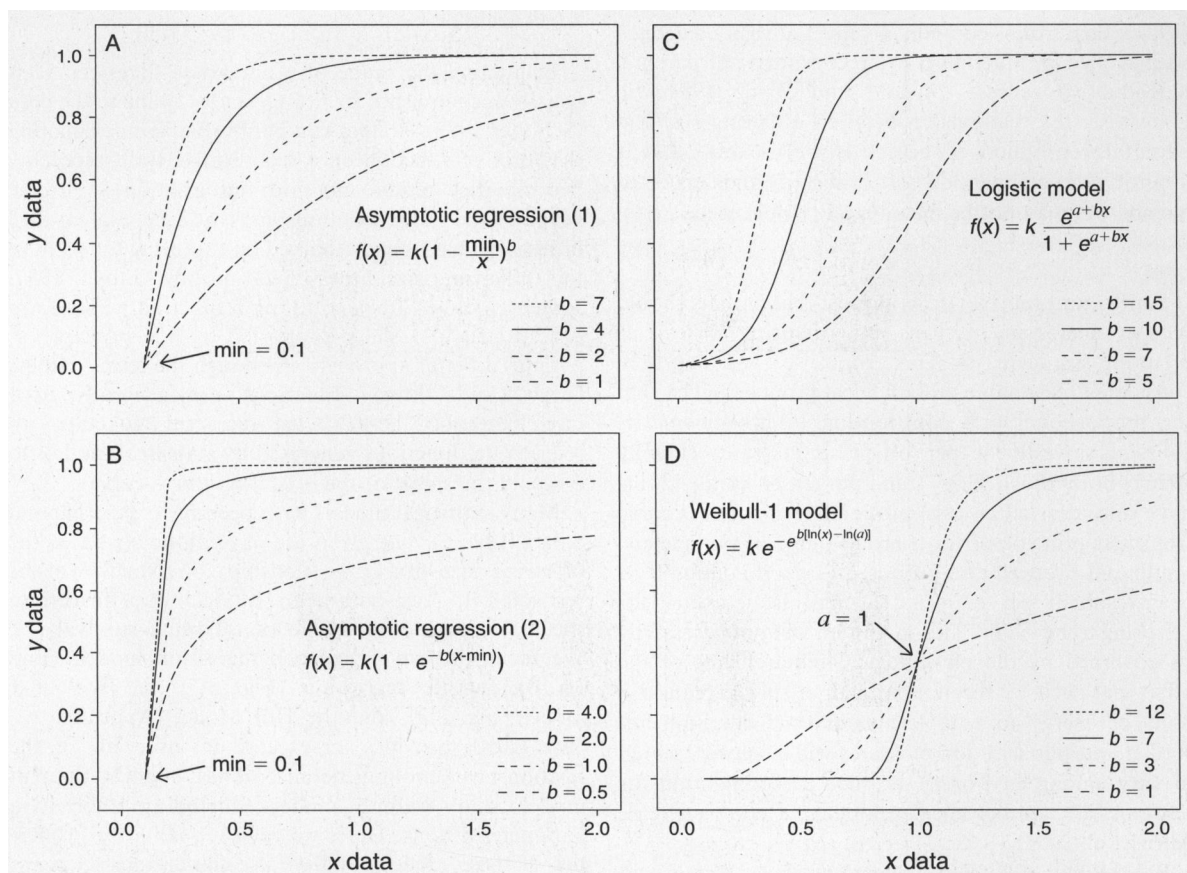


FIG. 3. (A, B) Asymptotic regression models, (C) logistic regression model, and (D) Weibull-1 model fit with different slope values (b); k is the asymptotic offspring survival rate, and here it is always set to 1. Parameter values for the inflection point or y -intercept (a) or the x -intercept (\min) are given in each panel.

and then recaptured after time t . We examined the effect of sample size on experimental estimates of optimal size by varying the number of offspring of a given size that were initially released (i.e., the number of offspring released in a given size class was under the control of the researcher). Concomitantly, we examined how estimates of optimal size are influenced by variation in the mean and asymptotic value of offspring survival (or recapture rate). The effects of sample size and offspring survival rate were examined for each of the five artificial offspring size–fitness curves (Appendix B: Fig. B1A–E), such that each simulation involved one combination of sample size, survival rate, and fitness curve. We generated 50 000 individual data sets in each simulation, and each of our candidate models was fit to each of the 50 000 data sets. First, model fit was assessed using a runs test. Next, maximum parental fitness (which corresponds to optimal size) was estimated for parents where reproductive effort (R) was 1000 units of energy; where investment per offspring (x) varied between 10 and 39 units of energy; and, following Smith and Fretwell (1974), the number of offspring produced by parents (N) was $N = R/x$. These methods allowed us to assess each model's unique ability to emulate the

offspring size–fitness curve and to estimate optimal size over a range of sample sizes, offspring survival rates, and for a range of biologically realistic relationships between size and fitness. In total, three million data sets were generated (5 fitness curves \times 3 levels of sample size \times 4 levels of offspring survival rate \times 50 000 simulations per level). Below, we assess how well the models fit the simulated data and how accurately each model predicted optimal size.

Asymptotic regression

Asymptotic regression functions (Stevens 1951) typically increase from an x -intercept at a decreasing rate toward an asymptote. The unique property of these models is that they feature an estimable minimum viable offspring size, the x -intercept coefficient. The two asymptotic regression models that have been used in offspring size–number research are as follows:

$$f(x) = k \left(1 - \frac{\min}{x} \right)^b \quad (1)$$

$$f(x) = k \left(1 - e^{-b(x-\min)} \right) \quad (2)$$

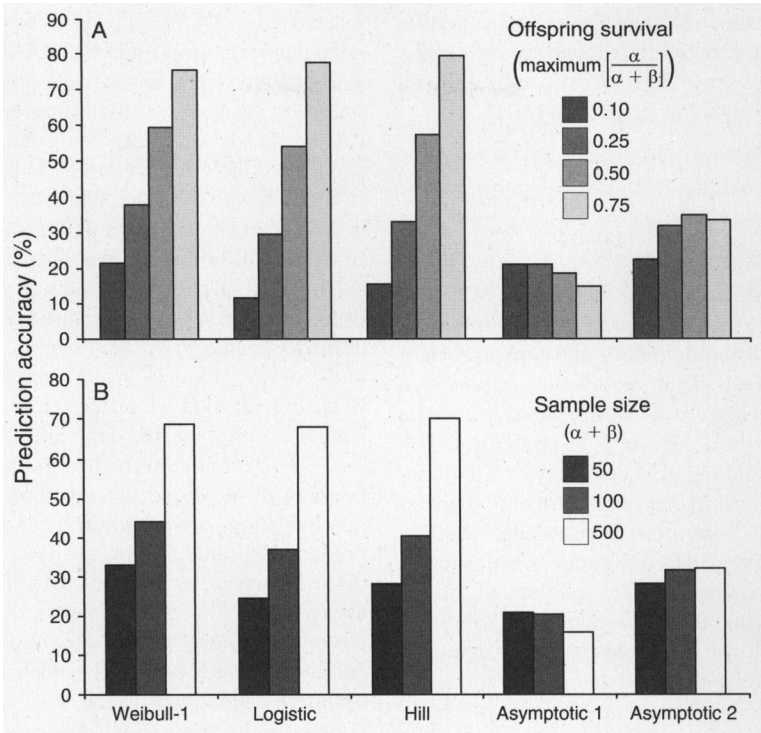


FIG. 4. Results of all simulations are collapsed across all artificial fitness curves to demonstrate the overall effects of (A) asymptotic offspring survival and (B) sample size on each model's unique ability to estimate optimal size. Prediction accuracy (y-axis) is the percentage of simulations in which models estimated optimal offspring size to within $\pm 5\%$ of the true value (also see Appendix C: Tables C1–C5). In panel (A), maximum $[\alpha/(\alpha + \beta)]$ is asymptotic survival; in panel (B), $\alpha + \beta$ is the number of offspring initially released at a given level of offspring size. The Weibull-1 model better predicts optimal size at low values of survival and sample size, but this disparity disappears as survival and sample size increase.

where k is the known value of maximum fitness (e.g., maximum observed survival rate), \min is the x -intercept to be estimated (i.e., minimum viable offspring size), b is the scaling exponent to be estimated, and e is the base of natural logarithms (Fig. 3A, B).

In our simulations, asymptotic regression did not provide adequate estimates of optimal size under the vast majority of conditions (Fig. 4; Appendix C: Figs. C2, C3A, and C4A). Model (1) correctly estimated optimal size in only 19% of all simulations, and this is troubling because Model (1) is often fit to experimental data (e.g., animals, Einum and Fleming 2000; plants, Charpentier et al. 2012). Model (2) provided accurate estimates in only 31% of cases. Both models also produced inaccurate estimates of parental fitness, and the accuracy of Model (2) decreased as sample size and offspring survival increased (Appendix C: Figs. C3B, C4B). Runs tests indicated that Models (1) and (2) did not fit the simulated data well in 30% of all cases. By comparison, a poor fit was observed in no more than 11% of all cases for other statistical models.

The problem with the asymptotic regression models evaluated herein is that they underestimated survival probabilities when offspring size was relatively large (e.g., Fig. 4B; Appendix C: Fig. C3B). Thus, although asymptotic regression incidentally predicted optimal offspring size with accuracy under some conditions,

these models were unable to provide a realistic representation of the true fitness curve. This pattern is not a construct of the artificial fitness relationships that we chose in our simulations, it is systematic: the same problem is also evident in published size–number studies that used asymptotic regression to model optimal offspring size with experimental data. Einum and Fleming (2000), for example, collected mark–recapture data for young Atlantic salmon (*Salmo salar*) and then estimated the relationship between offspring size and survival using Model (1). An inspection of their model predictions, however, suggests that offspring size must be ~ 8.6 standard deviations above their mean phenotypic value when offspring fitness is at 90% of their maximum observed fitness value (assuming a mean offspring size of 0.105 g and standard deviation of 0.0251 g estimated from their Fig. 1A). Akin to the present study, their function approaches the asymptote very slowly, and this generates what appears to be an unreasonable prediction. Our findings suggest that Model (1) and Model (2) should not be used in experimental size–number research.

Generalized linear models

Most empirical studies that estimate the offspring fitness relationships use logistic regression (Table 1). Logistic regression is a form of generalized linear model

that uses a logit link function, and this model generates *s*-shaped or sigmoidal functions bounded by zero and *k* (although *k* is usually set to 1.0; see Appendix D for a case study). The equation can be given by

$$f(x) = k \frac{e^{a+\beta x}}{1 + e^{a+\beta x}} \quad (3)$$

where *k* is the known value of maximum fitness (e.g., maximum observed survival rate), *a* is the *y*-intercept, and β defines the steepness of the slope (Fig. 3C). The ubiquitous use of the logistic model to estimate offspring fitness relationships probably reflects the convenience of using a well-established linear model that happens to exhibit two nonlinear regions when predicted values are back-transformed from logits into probabilities. Although a logistic function might accurately or adequately describe the relationship between offspring size and fitness in some cases, one must acknowledge that by equating a logistic curve with a fitness curve, a particular *a priori* hypothesis has been accepted. Namely, one is assuming that offspring fitness is symmetric about a fitness of 0.5, and that offspring fitness approaches the *x*-axis slowly. Although the logistic model is in widespread use (Table 1), the assumption that offspring fitness approaches an upper asymptote from a value of 0.5 at the same rate as it approaches *x*-min from 0.5 is not based on theory. In fact, no theoretical model has ever used an offspring fitness curve that is necessarily symmetric about a fitness of 0.5 (Table 1), which suggests that a different assumption prevails, at least among theorists.

Under simulation, the logistic model produced accurate estimates of optimal size in 43% of all cases, which makes it the least accurate of the sigmoidal models. Although the logistic model often performed as well as, or better than, the Hill and Weibull-1 models when offspring survival and sample size were highest, it was typically less accurate under other conditions (but see Appendix B: Table B1). The logistic model did not fit the simulated data in about 11% of all cases, which is similar to the rate of 8% generated by the Weibull-1 and Hill models.

Weibull-1 model

Weibull models (Weibull 1951) have been used extensively in ecotoxicological modeling (Ritz 2010), and although they have never been applied in offspring size-number research, it has long been recognized that they are useful for modeling survival in ecology and evolution (Pinder et al. 1978). Here we use a special case of the Weibull-1 model (Ritz 2010) where the lower and upper asymptotes are, respectively, fixed at 0 and *k*:

$$f(x) = ke^{-e^{b[\ln(x) - \ln(a)]}} \quad (4)$$

where *k* is the known value of maximum fitness (e.g., maximum observed survival rate), *b* defines the slope of the curve, and *a* is the *x*-value where the inflection point is

located (Fig. 3D). In many respects, the Weibull-1 function is similar to that produced by the Hill equation: both are *s*-shaped; both increase relatively quickly from zero to the inflection point, *a*; and both approach the upper asymptote, *k*, slowly after surpassing the inflection point. The primary difference between the Hill and Weibull-1 curves is that the slope of the Weibull-1 curve is much more pronounced between zero and *a*, such that the Weibull-1 function must approach the *x*-axis relatively abruptly.

The Weibull-1 model produced accurate estimates of optimal size in 49% of all simulation runs. On average, it correctly predicted optimal size more often than the Hill and logistic models when sample size and overall offspring survival were low, although its accuracy was similar to that of the Hill and logistic models when sample size and survival were high (Fig. 4). When prediction success is averaged across all simulations involving low offspring survival, the Weibull-1 model predicted optimal size between 8% and 10% more often than the logistic model (Fig. 4A). Prediction success was also between 7% and 8% greater than the logistic model when sample sizes were low to modest (Fig. 4B). Over all conditions, we found that values of parental fitness at optimality predicted by the Weibull-1 model were also closest to the true value (Appendix C: Figs. C3A and C4B). Therefore, the Weibull-1 model produced the most accurate estimates of optimal size and parental fitness, on average, largely because it performed best when survival and sample size were low.

WHICH MODEL SHOULD ONE FIT?

An important lesson learned from our simulations is that it can be very difficult to accurately estimate optimal offspring size with experimental data (e.g., Appendix C: Fig. C2), and both large sample sizes and elevated offspring survival will often be necessary to secure an accurate estimate. This is unfortunate because it is typically highly fecund organisms with low offspring survival that are used in size-number studies (e.g., Atlantic salmon), and logistical constraints often have the effect of limiting sample size. With this lesson in mind, our simulations suggest that asymptotic regression should not be used to estimate the shape of an offspring size-fitness curve in experimental studies. Differences in the accuracy of the Hill, logistic, and Weibull-1 models were usually unremarkable when sample sizes and offspring survival were high; however, the Weibull-1 model offered modest improvements over the Hill and logistic models when sample size and offspring survival were low. Given that low sample sizes and survival are often expected in size-number studies, the Weibull-1 model will, on average, provide the most accurate predictions. The Weibull-1 model can also be fit easily in R (R Development Core Team 2011) with the *drc* package (Ritz and Streibig 2011), which features the option of estimating *k*, or having *k* specified by the user. However, although we recommend the Weibull-1 model for experimental research, our simulations show that

there is no silver bullet when it comes to modeling optimal offspring size (Appendix C: Tables C1–C5). The choice of model should always be justified. Only after carefully designing an experiment, thoroughly exploring the data, and then considering carefully which model should be applied can one potentially estimate the relationship between offspring size and fitness with defensible accuracy.

ACKNOWLEDGMENTS

We thank D. J. Marshall, T. Day, H. Kindsvater, R. G. Latta, M. O. Johnston, P. V. Debes, J. Porter, and two anonymous reviewers for commenting on earlier versions of the manuscript. D. Keith helped develop the simulations, and J. C. Pezzullo generously provided statistical insight. Funding was provided by a Killam Trust and an NSERC CGS scholarship to N. Rollinson, and an NSERC Discovery Grant to J. A. Hutchings.

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SUPPLEMENTAL MATERIAL

Appendix A

A description of the Hill model (*Ecological Archives* E094-026-A1).

Appendix B

Extended simulation methodology (*Ecological Archives* E094-026-A2).

Appendix C

Extended simulation results (*Ecological Archives* E094-026-A3).

Appendix D

Case study: estimating offspring size–fitness relationships using binary logistic regression (*Ecological Archives* E094-026-A4).

Supplement

R code used for simulations (*Ecological Archives* E094-026-S1).