

# Survivorship curves and their impact on the estimation of maximum population growth rates

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**Abstract.** Previous efforts to use the Euler equation to estimate maximum population growth rates (variously symbolized as either  $r$ ,  $r_m$ , or  $r_{max}$ ) have used simplified models of survivorship that neglect differences in survivorship schedules among species. In particular, several recent analyses have used either an exponential model of survivorship or a step function model in which all individuals live until a fixed age of death. Using a flexible alternative based on the beta distribution and a compiled data set of mammalian survivorship curves for 58 species, we explore the influence of survivorship shape and scale on the estimation of  $r$ . We show that the Euler equation paired with an exponential model of survivorship can be used to calculate an unbiased estimate of  $r$  over a large range of body sizes, whereas the more commonly used step function survivorship model results in severely inflated estimates of  $r$ , especially for mammals with large maximum population growth rates. Finally, we demonstrate that, despite producing different absolute estimates of  $r$ , the three survivorship models examined yield similar allometric scaling coefficients relating  $r$  to biomass. These allometric scaling relationships are highly sensitive to the inclusion or exclusion of bats (Chiroptera), which exhibit life-history traits (long life spans, small litter sizes, and relatively long litter intervals) inconsistent with their small body size.

**Key words:** allometry; beta distribution; Cole approximation; Euler equation; life history; maximum population growth rate; metabolic theory; survivorship.

## INTRODUCTION

Accurate estimation of population growth rate is critical for diverse problems in ecology, including empirical tests of allometric predictions of the metabolic theory of ecology (Brown et al. 2004, Savage et al. 2004, Duncan et al. 2007), analysis of relative extinction risks among taxa (Calder 2000, Holmes et al. 2007), and exploration of population cycling (Ginzburg and Inchausti 1997, Tkadlec and Zejda 1998). However, the estimation of population growth rate and its scaling with body mass has been complicated by a lack of clarity regarding alternative measures of population growth rate. Here we focus on three metrics that can be estimated using life-history data:  $\bar{r}$  (the per capita population growth rate using empirically derived survivorship for a population under field conditions),  $\hat{r}$  (the per capita population growth rate assuming Type II survivorship), and  $\rho$  (the per capita population growth rate assuming Type I survivorship). The maximum population growth rate for a laboratory or captive population maintained under low-density, high-resource conditions is a fourth metric we designate  $r_{max}$ . These metrics have their origins in demographic theory and empirical estimation using life table data (Caughley 1980), but they are frequently used in inappropriate

contexts without consideration of the assumptions involved in their calculation. The Euler equation,

$$\int_0^{\infty} l(x)m(x)e^{-rx}dx = 1 \quad (1)$$

is frequently used to estimate  $r$  (which could be  $\bar{r}$ ,  $\hat{r}$ ,  $r_{max}$ , or  $\rho$ ) where  $l(x)$  is the survivorship to age  $x$  (i.e., the proportion of individuals that survive to age  $x$ ), and  $m(x)$  is the per capita fecundity of female offspring at age  $x$  (Roughgarden 1996, Kot 2001). Eq. 1 can be used to estimate either  $\bar{r}$ ,  $\hat{r}$ ,  $r_{max}$ , or  $\rho$ , depending on what functions are used for survivorship and fecundity (W. F. Fagan, H. J. Lynch, and B. Noon, *unpublished manuscript*). Because serious difficulties in interpretation arise when alternative measures of population growth rate are combined within a single comparative analysis (e.g., Calder 2000), it is important to be terminologically consistent (Slade and Balph 1974, Caughley 1980, Hayssen 1984). Here we will use the generic symbol  $r$  to represent that quantity that is estimated using the Euler equation (and its various approximations), but we will make clear whenever a particular estimate corresponds to  $\bar{r}$ ,  $\hat{r}$ ,  $r_{max}$ , or  $\rho$ .

As meta-analytic and ecoinformatic analyses continue to proliferate, issues of data completeness and consistency across species become paramount. Comparative analyses of life-history data are no exception, because it is often impossible to find complete survivorship and fecundity schedules specific to each organism. To

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facilitate comparisons across a broad range of organisms, Cole (1954:116) introduced a simplification to Eq. 1 that assumes that all animals in a population live to “some limit characteristic of the species.” This limit has typically been taken to be the physiological maximum life span recorded for animals in captivity (Cole 1954, Hennemann 1983, Schmitz and Lavigne 1984, Robinson and Redford 1986, Thompson 1987, Ross 1992). A recently introduced alternative estimator assumes that survivorship  $l(x)$  is given by an exponential, with a constant mortality rate set by the mean life span (Pereira and Daily 2006). Here we draw on a compiled data set of mammalian survivorship curves from life table data for 58 species to examine the impact of these approximations for survivorship on the estimation of  $r$  and subsequent allometric relationships linking  $r$  and body mass. These data, which come exclusively from wild or free-roaming feral populations, are available in Appendix A. Future cross-taxa analyses of population growth rates or allometric scaling will undoubtedly depend on simplified survivorship models based on easily accessible information regarding life-history characteristics. This analysis explores the impacts of these assumptions on estimates of  $r$  and subsequent allometric scaling and serves as a caution against the use of inappropriate survivorship models in cases for which data are limited.

METHODS

In his classic monograph, Cole (1954) focused on how different assumptions about age-specific fecundity could affect population growth rate, but he did not systematically examine the link between age-specific survivorship and  $r$ . Instead, Cole’s approach was to assume that all individuals in a population survive to a common maximum age (denoted  $L$ ) and then die (i.e.,  $l_x = 1$  for all  $x < L$  and  $l_x = 0$  for  $x \geq L$ ). He also modeled reproduction as occurring annually. With these assumptions, Eq. 1 simplifies to

$$e^{-\rho} + \bar{m}e^{-\rho(\alpha')} - \bar{m}e^{-\rho(\beta'+1)} = 1 \tag{2}$$

where  $\bar{m}$  is the average number of female offspring produced per female per year,  $\alpha'$  is the age of first reproduction, and  $\beta'$  is the age of last reproduction (Cole 1954). In Eq. 2, we use the symbol  $\rho$  to explicitly indicate which version of  $r$  is being estimated using this approximation. The simplicity and minimal data requirements of Cole’s approximation have made it popular, even in analyses for which the original assumptions are inappropriate. This is particularly true among those seeking to understand allometric scaling relationships between  $r$  and body size and/or metabolic rate for cases in which the considerable cross-taxa data requirements encourage the use of the simplest approximation available (McLaren 1967, Hennemann 1983, 1984a, Schmitz and Lavigne 1984, Robinson and Redford 1986, Thompson 1987, Ross 1992, Slade et al. 1998, Duncan et al. 2007). Hennemann (1984a:365) declared the “validity of the Cole method as a means of

estimating  $r_m$ ” on the basis of the similar allometric slopes obtained by Fenchel (1974; using direct estimates of  $r$  from laboratory populations), Blueweiss et al. (1978; using estimates of maximum population growth rate in the literature), and Hennemann (1983; using the Cole approximation). Although Hayssen (1984) objected to the application of Cole’s approximation to estimate maximum population growth rate for many of the same reasons we present here (see also the responses by Hennemann [1984b] and McNab [1984]), no direct comparison of estimation methods has been attempted.

More importantly, even if the Cole approximation were appropriate to assess allometric scaling between  $r$  and body size, it does not follow that the Cole approximation can be used to provide unbiased estimates of  $r$  itself. We return to this critical point in the discussion. In this analysis, we explore the consequences of using Cole’s approximation to estimate  $r$ , with particular focus on his model of step function survivorship. The impact of assuming that reproduction occurs annually is also considered, although unless specifically indicated, comparisons between different models will hold fixed the reproductive schedule of litter size and frequency appropriate to the organism being modeled.

Another simplified model of survivorship functions is that mortality is constant with age, or, equivalently, that the survivorship curve is given by an exponential. Pereira and Daily (2006) substitute an exponential survivorship model into the Euler equation (Eq. 1) to derive

$$\bar{m} \int_0^\infty \sum_{y=0}^\infty \delta(x - y\Delta - \alpha') e^{-(\hat{r} + \mu)x} dx = 1 \tag{3}$$

where  $\bar{m}$  is the number of female offspring per litter,  $\delta$  is the Dirac delta function,  $\Delta$  is the interval between litters,  $\alpha'$  is the minimum age of reproduction,  $\hat{r}$  denotes the variant of population growth rate estimated by this approximation, and  $\mu$  is the mortality rate. Note that this model does not constrain reproduction to occur on an annual basis but does assume constant fecundity.

Large comparative analyses of population growth rates are often limited by a lack of species-specific life-history information, and using simplified survivorship curves based on a minimum of life-history parameters offers clear advantages. Despite the popularity of simplified survivorship schedules such as that used by Cole (1954) and Pereira and Daily (2006), the impact of these assumptions on estimations of  $r$  and resulting allometric scaling relationships has not been examined. To explore this link in a robust way, we develop a generalized model of survivorship that provides excellent fits to each of 58 mammalian survivorship schedules we compiled while also including close approximations to the two preceding survivorship models as special cases. Specifically, we model survivorship as

$$\ell(x) = 1 - \text{CDF}[\text{Beta}(x/L; \alpha, \beta)] = 1 - I(x/L; \alpha, \beta) \tag{4}$$

where CDF is the cumulative density function,  $\alpha$  and  $\beta$

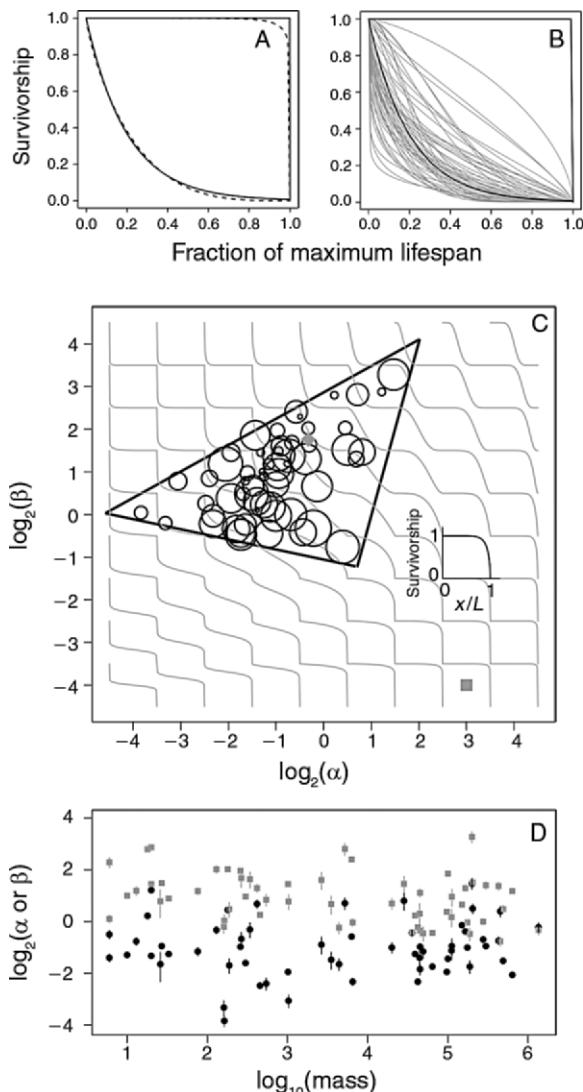


FIG. 1. Using the beta distribution to model mammalian survivorship. (A) Exponential and step function survivorship models (solid line) and their approximations (dashed line) using the beta distribution survivorship (Eq. 4). (B) Gray lines represent the beta function model (Eq. 4) that best fits the empirical survivorship data for each of the 58 mammal species in Appendix A. The exponential and the step function survivorship curves are in black. (C) Location of organisms in survivorship shape space as determined by fitting Eq. 4 to empirical survivorship data for 58 mammal species (Appendix A). The diameters of the circles are proportional to  $\log_{10}(\text{mass})$ . The Cole step function survivorship shape (Cole 1954, Hennemann 1983, Schmitz and Lavigne 1984, Robinson and Redford 1986, Thompson 1987, Ross 1992) is indicated with a gray square, and the exponential survivorship shape (Pereira and Daily 2006) is indicated with a gray diamond. The shapes are illustrated with line plots for all integer values of the beta distribution shape parameters  $\alpha$  and  $\beta$  (Eq. 4) in light gray, and the line plot for  $(\alpha = 8.0, \beta = 0.5)$  is in black. The large outlined triangle represents that portion of shape space in which empirical survivorship shapes fall. (D) Cross-sectional plots of  $\alpha$  (black circles) and  $\beta$  (gray squares) as a function of  $\log_{10}(\text{mass})$ . The 95% CIs are indicated by the vertical error bars.

are the nonnegative shape parameters of the beta distribution, and  $I(x/L; \alpha, \beta)$  is the regularized incomplete beta function (Abramowitz and Stegun 1972). The beta function has nonzero support only on the interval  $[0, 1]$ , and subsequently we scale  $x$  by the maximum lifespan  $L$  for each species. Note the interpretation of the beta distribution in this model; it represents the probability of mortality from the birth of a cohort to the death of its last member, which is by definition bounded between 0 and  $L$ . Fitting survivorship data is complicated by the lack of independence between survivorship at different ages (Ricklefs and Scheuerlein 2001, 2003), and here we estimate model parameters using the nonlinear least squares fitting procedure “nls” found in the statistical computing environment R (R Development Core Team 2007).

The survivorship model in Eq. 4 is a function of both survivorship shape (as controlled by the shape parameters  $\alpha$  and  $\beta$ ) and scale ( $L$ ). This formulation is thus comparable to the “stretched” beta distribution that has seen use in other ecological contexts (Morris and Doak 2002, Calabrese and Fagan 2004). Models of survivorship frequently employ either the Gompertz or the Weibull distributions (Ricklefs 1998, 2000, Ricklefs and Scheuerlein 2001, 2003), particularly where the goal is to test theories of senescence for which these functions are particularly well suited. The model of Eq. 4 has been used in this analysis because it allows us to evaluate the impact of varying survivorship curves on estimates of  $r$  in a continuous shape space that contains as special cases both the step function survivorship and the exponential survivorship used in previous analyses of population growth rates. The former in particular is not easily incorporated into either the Gompertz or the Weibull models since they model mortality as being a continuous function of age. Strictly speaking, the step function survivorship of Eq. 4 is represented by the limit  $\alpha \rightarrow \infty$  and  $\beta \rightarrow 0$ , although we approximate this by  $(\alpha, \beta) = (8, 0.0625)$  to reasonably mimic the step function (see Fig. 1A) on a scale comparable with the parameter values of the empirically fitted survivorship curves. Pereira and Daily (2006) use an exponential survivorship function truncated at five times the mean life span. As seen in Fig. 1A, this is closely approximated by  $(\alpha, \beta) = (0.80, 3.38)$ . Note that, although the beta distribution model used in this analysis was chosen as a convenient tool to explore the impact of survivorship shape and scale on  $r$ , the three-parameter  $(\alpha, \beta, L)$  beta function model (Eq. 4) outperforms, or is statistically indistinguishable from, the three-parameter Weibull model and the two-parameter Gompertz model for 41 of the 58 species in this analysis (model comparisons quantified by the Akaike Information Criteria; see Appendix B).

When needed for parameterization of Eqs. 2–3, we obtained mammalian life-history data from the YOUTHERIA (formerly PanTHERIA) database (Bielby et al. 2007), the AnAge database (de Magalhaes et al. 2005, AnAge 2007), and Nowak and Paradiso (1983). In cases

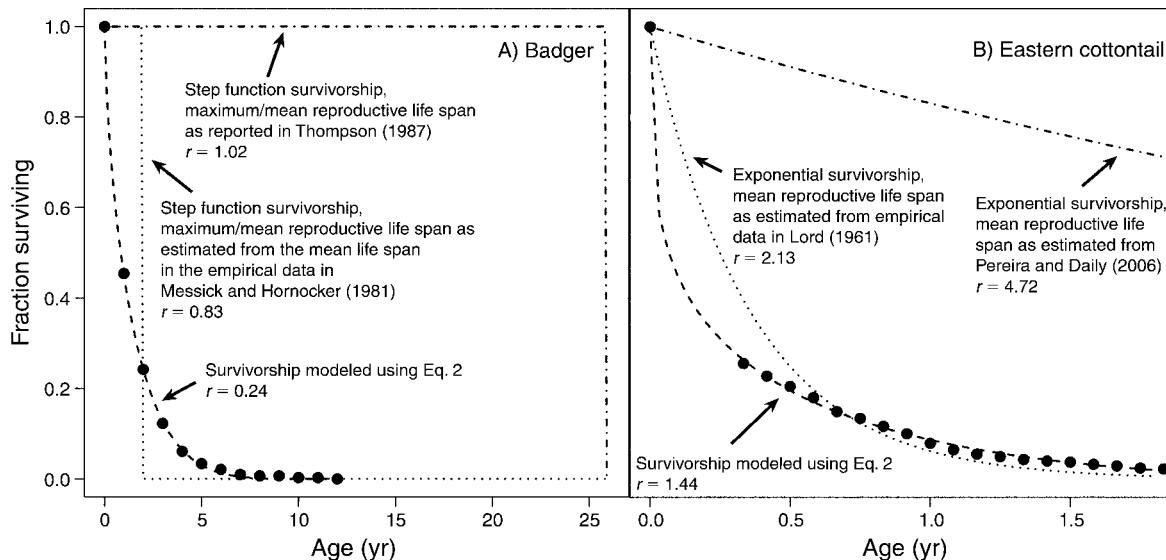


FIG. 2. Survivorship as a function of age for the different survivorship models for (A) the North American badger and (B) the eastern cottontail. Each panel contrasts the survivorship curve used in the original published source with two alternatives. Solid circles indicate the empirical survivorship data (see Appendix A).

in which multiple sources of information were available for a given species-specific parameter, we averaged the values.

#### Estimation of allometric scaling coefficients

In our analysis of the allometric scaling relationship between  $\log_{10}(r)$  and  $\log_{10}(\text{mass})$ , we used standardized major axis (SMA) regression as opposed to the more common ordinary least squares (OLS). As detailed by Warton et al. (2006), SMA, in which the best-fit line minimizes the total distance between the points and the line, is more appropriate than OLS, in which the goal is to summarize a relationship between two variables that contain measurement error as opposed to the use of one independent variable to predict a second dependent variable. This is particularly important in cases in which the goal is to compare the regression slope against a theoretical prediction (Warton et al. 2006, O'Connor et al. 2007). We calculated the allometric slope and its confidence limits using the “smatr” package for R (R Development Core Team 2007, Warton 2007). Note that we do not consider a phylogenetic correction, because our primary goal here is to compare the impact of multiple survivorship models and reproductive schedules across the same set of 58 species.

## RESULTS

### The influence of survivorship shape and scale on estimates of $r$

The wide range of potential survivorship curves that can be modeled by this formulation is illustrated in Fig. 1B, C. We fit Eq. 4 to published survivorship schedules for 58 species (Fig. 1B and Appendix A) and have indicated where these species fall in the two-dimensional

shape space of  $\alpha$  and  $\beta$  (Fig. 1C, D and Appendix A). Each point in Fig. 1C is indicated by a circle whose diameter is proportional to the  $\log_{10}(\text{mass})$ . The special cases of unity survivorship until death (Cole 1954) and an exponential survivorship (Pereira and Daily 2006) are also indicated. We see that survivorship shape varies widely across different mammals but is contained in the triangular area indicated in Fig. 1C. No clear trends in shape space were apparent with regard to mammalian body size (see also Fig. 1D). Although many animals do exhibit roughly exponential survivorship (implicit in Eq. 3), none of the animals approach the more commonly used Cole model of unity survivorship (implicit in Eq. 2).

To evaluate whether these differences in survivorship shape are significant with respect to the estimation of  $r$ , we model survivorship using Eq. 4 to investigate the sensitivity of  $r$  to the details of the survivorship curve, specifically the shape of the survivorship curve (Fig. 1C) and the scale of the curve, which is related to the mean life span of the organism. Fig. 2 illustrates this with two examples, *Taxidea taxus* (North American badger) and *Sylvilagus floridanus* (eastern cottontail), where the original survivorship function used in the literature (badger, Thompson 1987; cottontail, Pereira and Daily 2006) is contrasted with 1) a function having the same shape but a scale that is drawn from empirical survivorship data and 2) the beta distribution model fit to the empirical survivorship data. Both shape and scale play a role in accurately estimating  $r$ . It is important to note that the cottontail was one of the species for which Pereira and Daily (2006) did not have mean life span data and one for which mean life span was estimated using an allometric relationship between mortality and body mass. This illustrates the difficulty of using

allometric relationships to estimate mean life span in cases for which data are not available. More importantly, even when the actual mean life span is used, the exponential model significantly overestimates survivorship in the first six months, which, given that reproduction commences at three months, contributes to an inflated estimate of  $r$ .

To investigate more thoroughly the role of shape and scale, we use the life-history information for two species (*Peromyscus leucopus* [white-footed mouse] and *Equus caballus* [North American wild horse]), which together represent the full range of survivorship shapes, and examine the consequences for  $r$  if we modify shape and scale for these two species over a continuous range that encompasses most reasonable survivorship curves. Fig. 3A, B shows contour plots of estimated  $r$  for the mouse and horse for a wide range of beta distribution shape parameters. Note that here we have only changed the shape of the survivorship curve and have fixed the reproductive schedule at the interval appropriate for that species. The step function approximation, the exponential approximation (Eq. 3), and the best-fit model using the beta distribution (Eq. 4) are indicated on the contour plot at the appropriate points in parameter space. Note that here we wish to consider only the shape of the survivorship curve and have fixed the mean life span as one-fifth the maximum life span so as to replicate the survivorship shape used in Pereira and Daily (2006) while maintaining the same scale as the step function approximation. Here the mean life span is generated artificially from the empirically derived physiological maximum life span, and the estimates of  $r$  thus derived do not reflect directly on estimates that would have been obtained by Pereira and Daily (2006). These analyses demonstrate that  $r$  is highly sensitive to the shape of the survivorship curve, and while the exponential shape model can either inflate or deflate  $r$ , the step function shape model always inflates  $r$ . The impact of using a step function survivorship model on estimates of  $r$  is more significant for the mouse than the horse due to the mouse's highly concave survivorship shape.

In addition to survivorship shape,  $r$  is also sensitive to the scale of the survivorship curve, which is related to the life span of the organism. Fig. 3C, D illustrates the importance of scale for the mouse and the horse. Here we have used all three survivorship models (the step function approximation, the exponential approximation, and the best-fit beta distribution) to model survivorship and have used the Euler equation (Eq. 1) to calculate  $r$ , changing only the scale of the survivorship function. In this analysis,  $r$  is relatively insensitive to the scale of the survivorship curve for the step function survivorship, but is sensitive to scale for the exponential and beta distribution survivorship curves. This occurs because changing the scale of the step function does not change survivorship in the most important early years, whereas the other two functions change everywhere as longevity is extended.

#### *The influence of reproductive schedule on estimates of $r$*

In the above analysis, we held the reproductive schedule of litter size and frequency fixed to explore the influence of survivorship on estimates of  $r$  generated by the Euler equation. The Cole approximation is conditional on an additional assumption that reproduction occurs on an annual basis with reproductive output equal to that of the annual average number of offspring. As an example, consider the bank vole (*Myodes glareolus*), which produces  $\sim 2.1$  females/litter every 30 d starting at age 39 d. The Cole approximation would estimate that 25.2 females are produced when reproduction commences at age 39 d, but in reality those offspring are spread out over the entire year. The exponential discounting of offspring born later in the year is not properly accounted for, a particularly acute issue when reproductive rates are high, as with the bank vole and other small mammals. Relaxing the constraint of annual reproduction reduces the estimate of  $r$  from 30.2 to 11.4. Therefore, accurately capturing the reproductive schedule has a significant impact on the estimation of  $r$  even though the step function model of survivorship ensures that all of the females giving birth at age 39 d will remain alive throughout the year. For this reason, the remainder of our analysis and discussion will contrast four models, the three survivorship models (step function, exponential, and Eq. 4), in which the reproductive schedule is fit to the empirical data, and the Cole approximation, in which a step function survivorship is used along with the constraint of strictly annual reproduction. Note that throughout we have assumed a fixed fecundity with age. The impact of changing reproductive output with age, which was the focus of Cole's original paper (1954), is not considered here.

#### *Allometric scaling for different models of survivorship and reproduction*

Although the different assumptions regarding survivorship shape, survivorship scale, and reproductive schedule together have a large impact on the absolute value of estimated  $r$ , these assumptions make a much smaller impact on the allometric scaling of  $r$  with body size (Fig. 4 and Table 1). In Fig. 4A, we plot the  $r$  estimates obtained by the Cole approximation (step function survivorship with annual reproduction), step function survivorship alone, and exponential survivorship as functions of the  $r$  estimates obtained using the beta distribution (Eq. 4). Ignoring small fluctuations, a 1:1 correspondence exists between the estimates of  $r$  obtained by the exponential model of survivorship and those obtained using the beta distribution fit (Fig. 4A). Moving to a step function survivorship model leads to inflated estimates of  $r$ , particularly for the largest  $r$  values, and these estimates are even more significantly inflated when the additional constraint of annual reproduction is imposed, yielding biologically unrealistic values. Therefore, it is surprising that in plots of  $\log_{10}(r)$  against  $\log_{10}(\text{mass})$  for the four different models (Fig.

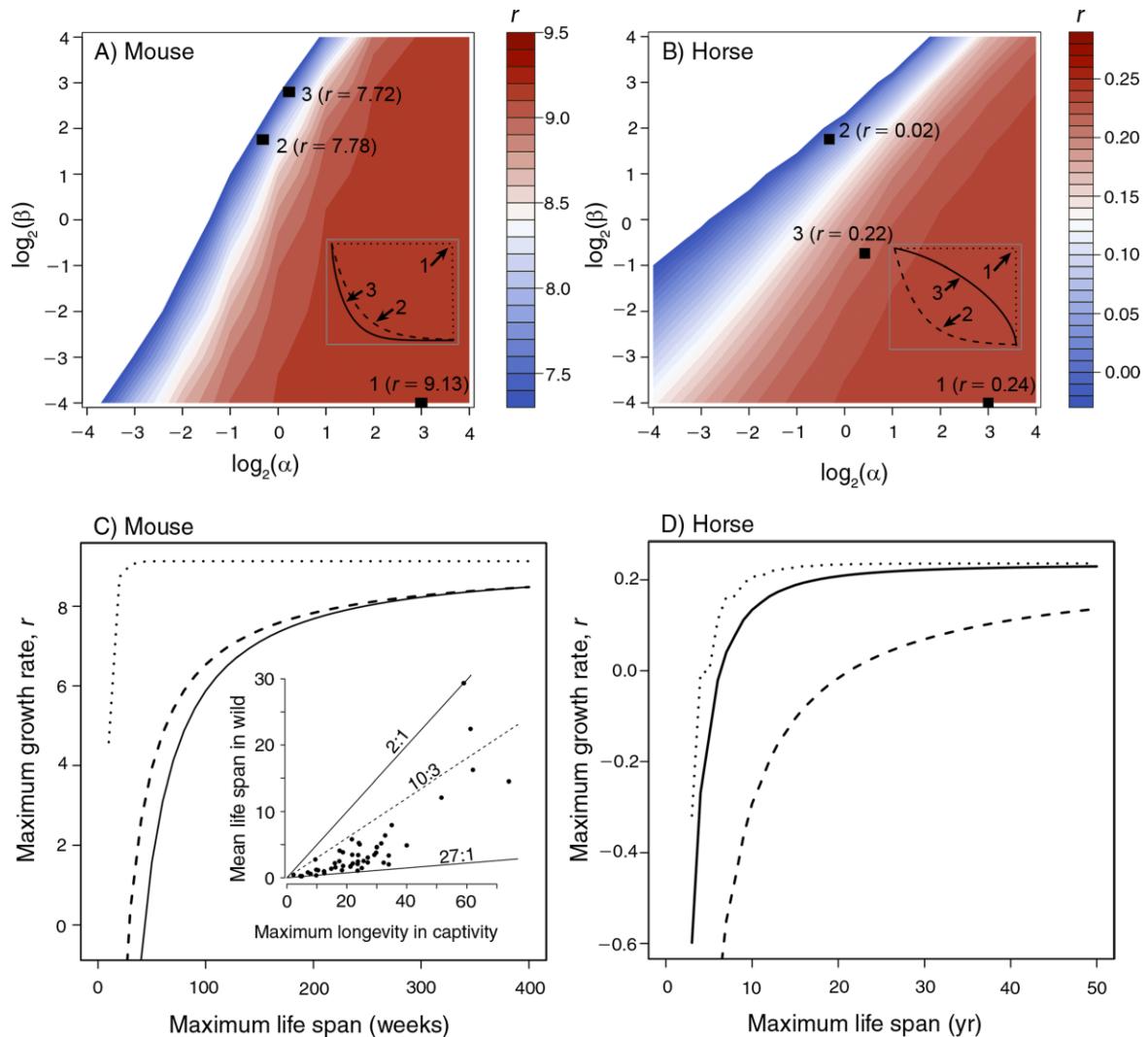


FIG. 3. (A, B) Influence of survivorship shape on the estimate of maximum population growth rate,  $r$ , for (A) the white-footed mouse and (B) the wild horse showing the step function implicit in the Cole approximation, the exponential fit, and the beta distribution fit to data. Each of these survivorship shapes is associated with a different combination of shape parameters  $\alpha$  and  $\beta$  and results in a different estimate of  $r$ . The position of these different curves and the associated  $r$  values are indicated by numbers (1, the step function; 2, the exponential; and 3, the beta distribution) at the appropriate position in “shape space” defined by the beta distribution shape parameters  $\alpha$  and  $\beta$  (Eq. 4). The color scale of the plot has been truncated to preserve the contrast between the areas of interest;  $r$  values for both species decrease precipitously in the upper left portion of the plot, and subsequently these areas are not shown. (C, D) The saturation of  $r$  with maximum life span for (C) the white-footed mouse and (D) the wild horse. The three curves for each species represent the impact of scale on each of the three survivorship models (dotted line, the step function implicit in the Cole [1954] approximation; dashed line, the exponential survivorship used by Pereira and Daily [2006]; solid line, the beta distribution model of Eq. 4 fit to the empirical life-history data). For the step function survivorship, the maximum age along the  $x$ -axis is the age at which all animals die. For the exponential survivorship model, the maximum life span is five times the mean life span as used by Pereira and Daily (2006). For the beta function fit, the maximum life span is the (empirically estimated) scaling factor  $L$  in Eq. 4. Panel C inset: Plot of mean life span in the wild vs. maximum physiological life span ever recorded (Appendix A). Maximum and minimum ratios of maximum physiological life span (years) to mean life span in the wild are indicated (27.2:1.0 and 2.0:1.0, respectively) with solid lines, and the linear regression fit to all the data points (10:3) is shown with the dashed line.

4B), the slopes of SMA regressions (Table 1 and inset to Fig. 4B) have overlapping confidence intervals. Note, however, that the exponential model of survivorship (Type II) used by Pereira and Daily (2006) resulted in a scaling coefficient that was more negative than that produced by the step function model (Type I).

DISCUSSION

In this analysis, we highlight how different survivorship and reproductive schedules impact the estimation of  $r$  when the Euler equation is used. If considering the potential for populations to grow under natural conditions, it is important to use, whenever possible,

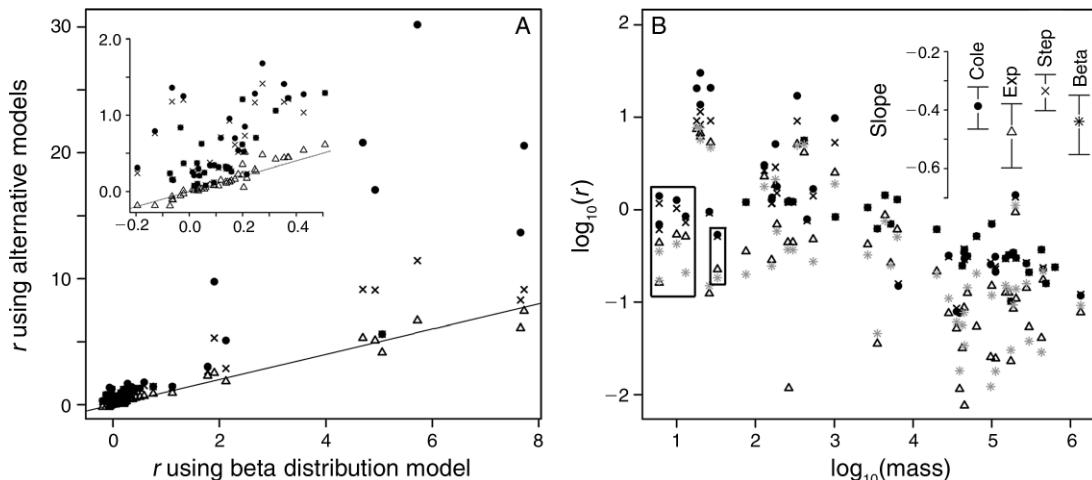


FIG. 4. (A) Estimates of maximum population growth rate,  $r$ , using the Cole (1954) approximation (solid circles), the step function survivorship model (crosses), and the exponential survivorship model (open triangles) plotted as a function of the estimate of  $r$  derived from fitting the beta distribution to the empirical data. The 1:1 line is in black, and the inset shows greater detail for small values of  $r$ . (B) Scatterplot of  $\log_{10}(r)$  vs.  $\log_{10}(\text{mass})$  for all 58 mammal species in the analysis for each of the four estimation methods: the Cole (1954) approximation (solid circles), the step function survivorship model (crosses), the exponential survivorship model (open triangles), and the beta distribution fit to the empirical data (gray stars). Points for the five bat species represented in the sample are boxed. The slope of this plot represents the allometric scaling coefficient studied by other authors (Savage et al. 2004) and used in the metabolic theory of ecology (Brown et al. 2004). The slopes, calculated for each of the four estimation intervals using reduced major axis regression as discussed in *Methods*, are shown in the inset, along with their 95% confidence intervals.

survivorship data from wild populations to estimate  $r$ ; otherwise, the potential for population growth will be overestimated. Even where detailed survivorship data are unavailable, it is important to capture accurately the shape and scale of survivorship. As illustrated in Figs. 1 and 4B, empirical survivorship shapes for mammals show wide variability but are contained within a triangular area in shape space in which the exponential approximation (bounded by the interval  $[0, 5 \times \text{mean lifespan}]$ ) also falls. Although the Cole approximation of a step function survivorship is convenient and commonly used, we have demonstrated that the exponential model of survivorship (which also requires only a single parameter) is a much more realistic model for mammalian survivorship when life-history information is limited.

In addition to survivorship shape, survivorship scale must be chosen appropriately for accurate estimates of  $r$ . As noted by Deevey (1947), and illustrated in the inset to Fig. 3C, small animals live a smaller fraction of their physiological maximum in the wild relative to large animals. This fact is particularly important when

considering the results of those papers, like Hennemann (1983) and Thompson (1987), that use the longest life span ever recorded in captivity as the “potential mean age of females producing their final young” (Thompson 1987:202). For small animals, the physiological life span has little relationship to the actual maximum life span of organisms in the wild, and  $r$  estimated using the physiological life span will inflate  $r$  for wild populations. The appropriate longevity for estimating  $r$  depends on the context. For evaluating the maximum possible rate of population growth (for example, to test allometric scaling relationships as predicted by the metabolic theory of ecology [Duncan et al. 2007]) it is most appropriate to use a longevity that reflects the most benign conditions possible, using data available from captive populations. For understanding the rate at which a real population in its natural environment could grow, it is important to use a longevity suited to populations experiencing mortality characteristic of their environment, which will inevitably be significantly shorter than for a similar captive population. Both

TABLE 1. Allometric scaling slopes (and upper and lower 95% confidence interval limits) of  $\log_{10}(r)$  vs.  $\log_{10}(\text{mass})$  for the species listed in Appendix A for four different models (see *Results*).

Survivorship model	Slope with bats	Slope without bats
Step function (Type I)	-0.34 (-0.40, -0.28)	-0.39 (-0.45, -0.33)
Cole approximation†	-0.39 (-0.47, -0.32)	-0.44 (-0.52, -0.38)
Exponential (Type II)	-0.48 (-0.60, -0.38)	-0.55 (-0.69, -0.44)
Beta distribution (Eq. 4)	-0.44 (-0.55, -0.35)	-0.51 (-0.64, -0.42)

† Step function plus annual reproduction.

shape and scale of the survivorship curve impact the estimation of  $r$  when using the Euler equation.

For conservation-related applications, it is important to consider the details of the organisms' particular life-history characteristics to estimate maximum population growth rates accurately. The Cole approximation will inflate under all circumstances the estimated maximum population growth rates, and management scenarios constructed using these inflated estimates will be inappropriate and potentially harmful. It is absolutely critical that when the interest is in the actual magnitude of the estimate  $r$  (and not on the scaling of  $r$  with body size), survivorship be modeled with a shape and scale that is appropriate to the organism and its current environment. Our results suggest that a "shortcut" of sorts between mammalian life-history traits and population growth rate does exist, but it is not the commonly used one. When survivorship schedules are not available, the approximation of Pereira and Daily (2006) should be used instead of that of Cole (1954).

Although the four survivorship models investigated provide different estimates of  $r$ , they produce similar allometric scaling relationships between  $r$  and body size (Table 1). Across all 58 mammal species studied, the slopes of  $\log_{10}(\text{mass})$  vs.  $\log_{10}(r)$  (Table 1) yielded a scaling relationship of  $-0.44$  ( $-0.55$ ,  $-0.35$ ). However, the small mammals fall into two distinct clusters. One of these clusters contains all the bats studied (Fig. 4), which feature much lower  $r$  estimates than would be predicted by the overall trend (Fig. 4). If bats are excluded from the analysis, the scaling coefficient for  $r$  (estimated from the beta distribution model) drops to  $-0.51$  ( $-0.64$ ,  $-0.42$ ). Bats are well known to exhibit life-history strategies (e.g., exceptionally long life spans, small litter sizes) inconsistent with their small size when compared to other mammals (Austad and Fischer 1991). Although bats represent only five out of 58 species in our sample, they have a profound influence on the allometric results, and the results of other large mammal surveys are likely to be influenced by the inclusion or exclusion of this unusual group. Marsupials have also been singled out as having life-history characteristics that differ from eutherian mammals (Thompson 1987, Austad and Fischer 1991, Fisher et al. 2001), although we did not have sufficient survivorship information to include a representative sample of marsupials in our study.

The meaning of the maximum reproductive rate depends on the context of the analysis. Where survivorship information is drawn from wild populations in their natural environment, the maximum rate of population growth estimated using the Euler equation will reflect both the intrinsic reproductive capacity of the organism and the particular details of the environment in which the sample was taken. Because only the former is of interest when drawing conclusions in a large comparative study of scaling relationships, it is important to exercise caution when using natural population data to understand fundamental scaling relationships across

taxa. In our analysis, the allometric scaling relationship linking  $r$  and body size was similar when using both the empirical survivorship of natural populations and when using the step function survivorship model, which has been used by other authors as a context-independent measure of reproductive potential. In this analysis, we used the beta distribution model fit to empirical data as a null model against which we compared various alternative estimators of  $r$ . Estimates of true maximum reproductive potential  $r_{\max}$  (i.e., the maximum per capita reproductive rate of a population under the most benign conditions) would require extensive life-history information from captive populations; such data are currently unavailable for most mammals. In this analysis, we have illustrated the impact of various approximations that rely on less extensive data.

#### CONCLUSIONS

The estimation of maximum population growth rate using the Euler equation depends sensitively on the shape and scale of the survivorship curve  $l(x)$  and the frequency of reproduction. We use a model of survivorship based on a beta distribution of mortality to explore the impact of different survivorship models on estimates of  $r$  and subsequent allometric scaling of  $r$  with body size. We find that the popular step function survivorship model leads to estimates of  $r$  that are inflated, particularly for high values of  $r$ . These estimates are further inflated by the constraint of annual reproduction that was used, along with the step function survivorship, to derive the Cole approximation. In contrast, the exponential model of survivorship, which also requires only a single parameter (mean life span), provides an unbiased estimate of  $r$  over the entire range of body sizes sampled. Despite the impact of survivorship and reproductive frequency on the absolute values of  $r$ , all the models examined produced similar allometric scaling relationships. For the  $r$  values estimated from the beta distribution fits, the scaling relationship was  $-0.44$  for all mammals vs.  $-0.51$  when considering only non-volant mammals. Bats appear to violate many of the mammalian allometric scaling relationships, and their inclusion or exclusion from allometric scaling studies can significantly impact results.

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#### APPENDIX A

Survivorship data for the 58 mammal species considered in survivorship analysis (*Ecological Archives* E090-072-A1).

#### APPENDIX B

Survivorship model comparison (*Ecological Archives* E090-072-A2).