

Survivorship patterns in captive mammalian populations: implications for estimating population growth rates

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Abstract. For species of conservation concern, ecologists often need to estimate potential population growth rates with minimal life history data. We use a survivorship database for captive mammals to show that, although survivorship scale (i.e., longevity) varies widely across mammals, survivorship shape (i.e., the age-specific pattern of mortality once survivorship has been scaled to maximum longevity) varies little. Consequently, reasonable estimates of population growth rate can be achieved for diverse taxa using a model of survivorship shape along with an estimate of longevity. In addition, we find that the parameters of survivorship shape are related to taxonomic group, a fact that may be used to further improve estimates of survivorship when full life history data are unavailable. Finally, we compare survivorship shape in captive and wild populations of the same species and find higher adult survivorship in captive populations but no corresponding increase in juvenile survivorship. These differences likely reflect a convolution of true differences in captive vs. wild survivorship and the difficulty of observing juvenile mortality in field studies.

Key words: captive vs. wild populations; Euler equation; mammalian life history; population growth rates; slow-fast continuum; survivorship.

INTRODUCTION

Life history variation among mammals has been the subject of widespread interest for decades as ecologists search for general models to explain the wide spectrum of observed mammalian survival and reproduction strategies. Recently, the discussion has focused on a suite of allometric relationships that explain much of the variation in life history strategy as a consequence of covariation among different life history traits (Blueweiss et al. 1978, Western 1979, Western and Ssemakula 1982, Millar and Zammuto 1983, Stearns 1983, Harvey and Read 1988, Harvey et al. 1989, Read and Harvey 1989, Promislow and Harvey 1990, Purvis and Harvey 1995, Fisher et al. 2001, Oli 2004, Bielby et al. 2007). Emerging from this approach is a general framework in which mammals are placed along a slow-fast continuum in which larger mammals that mature more slowly and have smaller litter sizes at larger interlitter intervals comprise the “slow” end of the continuum while smaller animals that mature quickly and have larger litters at smaller intervals represent the “fast” end (Read and Harvey 1989, Promislow and Harvey 1990, Oli 2004, Bielby et al. 2007). Even within this framework, there remains disagreement as to the extent to which these differences are driven by body size (the

“allometric constraint” view; Western and Ssemakula 1982, Peters 1983, Calder 1984, Harvey and Read 1988, Lindstedt and Swain 1988), phylogeny (Stearns 1983), the environment (including extrinsic sources of mortality) (Promislow and Harvey 1990, Brommer 2000), or some combination of all three (Stearns 1983, Partridge and Harvey 1988). Life history outliers, such as the bats, and differences between eutherian and metatherian lineages (Austad and Fischer 1991, Fisher et al. 2001, Jones and MacLarnon 2001) continue to provide interesting challenges to this paradigm.

Among the life history traits being studied, one of the most difficult to quantify is survivorship, a key component to estimating population growth rates (r) by way of the Euler equation and an important, but often missing, component to population viability analysis (Beissinger and McCullough 2002). A long line of research in ecology relates to mortality models and their implications for mammalian life history analysis (Deevey 1947, Caughley 1966), although estimates of population growth rate have traditionally used highly simplified survivorship models such as the step function (Cole 1954) or the exponential (Pereira and Daily 2006). Thus far, few attempts have been made to link these two lines of inquiry regarding patterns in life history or to develop a survivorship model flexible enough to be used in a comparative analysis of mammalian life history but simple enough to be used to estimate r when species-specific survivorship is unavailable. Although the ecological literature is rife with confusion over different

Manuscript received 16 July 2009; revised 8 December 2009; accepted 18 January 2010. Corresponding Editor: N. T. Hobbs.

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metrics of population growth rates (Fagan et al. 2010), we emphasize that here we are using data from captive mammals to generate models of survivorship that reflect, as far as possible, intrinsic limits to survivorship that are environmentally independent. An entire literature focuses on allometric scaling of maximum population growth rates, and the estimation of population growth rates approaching this theoretical maximum requires data on survivorship when resources are abundant and external sources of mortality are minimized. We are not aware of an effort to provide general models of survivorship under just these conditions, and in the absence of such empirical evidence, ecologists have been left to use inappropriate, highly simplified models (see Lynch and Fagan [2009] for a comparison among models).

To address this issue, Lynch and Fagan (2009) used a beta distribution function with one scale parameter and two shape parameters to model survivorship in wild populations of mammals and, in doing so, demonstrated that variation in survivorship curves can be parsed into scale, or maximum longevity, and shape, which captures the relative rate of mortality throughout the potential life span of that species. The idea that the “rate of living” is fundamentally different for different organisms is not new (Pearl 1928, Hill 1950), and several authors have suggested that the relevant timescales of life history (gestation time, weaning time, etc.) are best compared when scaled against some standard, such as mean life span (Pearl 1940, Deevey 1947) or maximum longevity (Lindstedt and Calder 1976). As mean life span depends strongly on environmental conditions, maximum longevity represents a more sensible standard timescale against which to compare survivorship curves. In fact, the use of physiological time as a standard has highlighted broad similarities in the “arc of life” among mammals of all sizes that are obscured when life histories are compared using chronological time (Calder 1984, Lindstedt and Swain 1988). Using a survivorship model that explicitly separates survivorship shape from scale, we can analyze differences in survivorship shape that transcend differences in scale that are already known to correlate strongly with body mass (Lindstedt and Calder 1976, 1981).

Despite efforts to understand mammalian life history patterns in the context of ecology, aging (e.g., Gavrillov and Gavrillova 1991, Ricklefs 1998, Ricklefs and Scheuerlein 2002), and statistics (e.g., Pinder et al. 1978, Wilson 1994, Eakin et al. 1995), including efforts specific to survivorship scale (e.g., Sacher 1978), relatively little empirical work has sought to understand survivorship shape, that is, the rate of mortality scaled to an organism’s maximum longevity. This is surprising considering that patterns of mortality are widely recognized as explaining much of the diversity in life history patterns (Charnov and Schaffer 1973, Harvey and Zammuto 1985, Read and Harvey 1989, Harvey et al. 1989, Promislow and Harvey 1990, Charnov 1991).

Traditionally, ecologists have focused on three “classic” survivorship shapes, known as type I (“negatively skew rectangular”), type II (“diagonal”), and type III (“positively skew rectangular”) when survivorship is plotted on a semi-logarithmic scale (Pearl and Miner 1935). Ecology and biology texts are decidedly mixed with respect to their treatment of this topic. Some texts say that only type III survivorship is realistic for mammals (Remmert 1980), whereas others say that most mammals follow a type I survivorship curve (Krohne 1997, Pianka 2000), and some say that all three survivorship curve shapes are possible among mammals (Kormondy 1996). Some specify that a type I curve is characteristic of “large mammals” (MacKenzie et al. 2001), implying some unspecific link between survivorship shape and body size, whereas some texts explicitly contrast type I survivorship for “large mammals” with the type II survivorship expected of “small mammals” (Starr and Taggart 2006, Mader 2007). Pearl (1940) expanded this classification by adding two more categories (“high-low-high” and “low-high-low”) to describe mammalian mortality, although as noted by Caughley (1966), there was, and arguably still is, a dearth of empirical evidence to suggest any such classification of survivorship patterns for either captive or wild mammals. This issue is further complicated by proposals that survivorship shape is actually related to the extent of r vs. K selection in a population (Pianka 1970), a property that is itself linked to body size (Boyce 1984). Textbooks in particular frequently couch discussions of survivorship shape in the context of r vs. K selection, a dichotomy that was popular following its introduction but has more recently been criticized (as reviewed by Boyce [1984] and Reznick et al. [2002]). Although ecologists are now reexamining the utility of r – K theory, the mapping of survivorship shape to body size remains unconfirmed dogma that, like r – K selection theory, needs to be reexamined in light of empirical evidence.

In this paper we focus our attention on the range of survivorship shapes seen in mammals in captivity to explore how strongly mammalian survivorship shape is related to body mass or other life history traits. In developing a model of survivorship that not only captures the average survivorship patterns across all captive mammals but, more importantly, places bounds on the variance in survivorship patterns seen across this group, we provide a mechanism for obtaining reasonable estimates of survivorship even in the absence of species-specific data. We relate the shape parameters of our survivorship model to life history traits previously discussed in terms of the slow–fast continuum of mammalian life history and show that while differences between “slow” and “fast” mammals are only weakly evident in survivorship shape, there are consistent differences in survivorship shape relating to taxonomic order. Although our aim is to develop a generic model of survivorship that can be used in the absence of more

specific information, we demonstrate that additional life history information can be used to improve this model and, subsequently, used to improve estimates of population growth rates.

Finally, for those species for which sufficient data are available, we compare survivorship shape between captive and wild populations to assess the comparability of these two different sources of survivorship data for a given species. This approach highlights the potential limitations of survivorship models based on field studies and extrapolates these differences in survivorship shape to their impacts on estimated population growth rates.

METHODS

Although several different methods can be and have been used to estimate population growth rates from census or life history data (Fagan et al. 2010), we focus here on the use of survivorship and fecundity data to estimate r via the Euler equation:

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

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). To focus our investigation on survivorship, we use a simplified model that assumes constant fecundity:

$$\bar{m} \int_0^{\infty} \sum_{y=0}^{\infty} l(x)\delta(x - y\Delta - \alpha')e^{-rx} dx = 1 \quad (2)$$

where \bar{m} is the number of female offspring per litter, δ is the Dirac delta function, Δ is the interval between litters, α' is the minimum age of reproduction, and r denotes the population growth rate (Pereira and Daily 2006).

To explore survivorship shape, we used a model for survivorship based on the beta distribution that is flexible, includes as special cases other population models of survivorship shape, and represents a good fit to available mammalian survivorship data (Lynch and Fagan 2009, particularly Fig. 1 therein). Specifically, we model survivorship as

$$\ell(x) = 1 - \text{CDF}(\text{Beta}(x/L; \alpha, \beta)) = 1 - I(x/L; \alpha, \beta) \quad (3)$$

where CDF is the cumulative density function, α and β are the nonnegative shape parameters of the beta distribution, and $I(x; \alpha, \beta)$ is the regularized incomplete beta function (Abramowitz and Stegun 1972; see Morris and Doak [2002] for an ecological discussion). The beta function has nonzero support only on the interval $[0, 1]$, and subsequently we scale x by the maximum life span L for each species. 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 moments of the beta distribution (which are directly related to mortality) may be derived from the shape parameters α and β

(Appendix A). Further details regarding the beta function model and its comparison to other mortality models may be found in Lynch and Fagan (2009).

Interpretation of the two beta distribution shape parameters is complicated by the close interrelationship between them. Roughly speaking, the ratio between α and β is related to the skewness of the distribution; small values of α/β are associated with relatively higher mortality early in life. Similarly, the product of α and β relates to the amount of mortality at the extremes of life (very early and very late) as opposed to mortality during intermediate ages; increasing values of the product $\alpha\beta$ are associated with a distribution that is more sharply peaked in the center, whereas small values of $\alpha\beta$ represent a “U-shaped” distribution in which mortality in the population is concentrated at the beginning and end of the species’ potential life span.

As previously noted, it is important to distinguish between survivorship shape (as controlled by the shape parameters α and β) and scale (L), the latter of which has already been demonstrated to correlate with body mass (Sacher 1959). The survivorship model in Eq. 3 allows us to clearly parse survivorship into these two components, and estimates for poorly known species can proceed with independent estimates of these two components. Estimates of r are relatively insensitive to uncertainty in survivorship scale, particularly to overestimates of scale (Lynch and Fagan 2009), and species longevity can often be estimated using allometric considerations (Blueweiss et al. 1978, Western 1979, Calder 1984). Here we focus on understanding patterns of survivorship shape and using the available data to put bounds on shape that may be used to constrain estimates of r from the Euler equation.

We fit beta distribution survivorship curves to survivorship data for 39 captive mammals drawn primarily from International and Regional Studbooks, which are computerized pedigree databases in use around the world to keep track of births, death, and transfers of captive animals among the world’s zoos and aquariums (Appendix B; ISIS/WAZA 2004). We selected species that represented the range of body sizes available in the database and included in our selection all those species for which wild population survivorship data sets were also available. To maximize data quality, we restricted our data to only those individuals in the pedigree database system on or after 1 January 1980. Particularly for the longest-living species, survivorship data for the oldest age classes suffered from small sample sizes, and we considered only those age classes represented by more than 10 individuals. This also filtered out individuals that may have been “lost” in the system and appeared to be living well past their maximum longevity. A second level of data filtering was done to ensure that after the small sample size age classes had been removed, the remaining survivorship curve represented the majority of the cohort mortality. In other words, it would not make sense to fit a

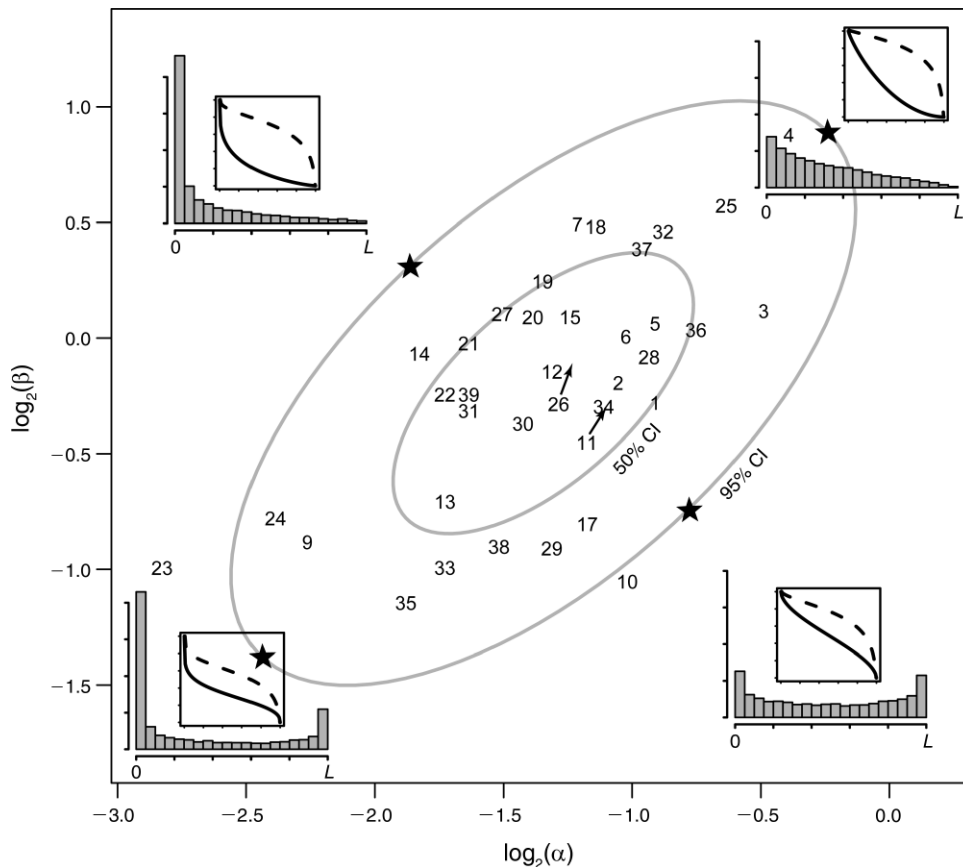


FIG. 1. Distribution of survivorship shapes as described by the two shape parameters of the beta distribution (α and β). For clarity, labels for two species have been displaced (denoted by arrows). Gray elliptical curves represent the 50th and 95th confidence intervals of the multivariate distribution of points in shape space (Table 1). Points at the extremes of the ellipse are marked with a star, and details of the survivorship curves specific to these points are illustrated in the four insets. The histogram indicates the distribution of mortality from birth to maximum longevity (L). The solid and dashed insets to the histograms represent survivorship (1 – cumulative mortality) on the linear scale and semilogarithmic scale, respectively. Species numbers are: 1, Bornean orangutan (*Pongo pygmaeus*); 2, Plains zebra (*Equus burchelli*); 3, blue wildebeest (*Connochaetes taurinus*); 4, Parma wallaby (*Macropus parma*); 5, Asian small-clawed otter (*Aonyx cinereus*, formerly *Amblonyx cinereus*); 6, Addra gazelle (*Gazella dama ruficollis*); 7, Grants gazelle (*Nanger granti*, formerly *Gazella granti*); 8, Florida manatee (*Trichechus manatus latirostris*) (not shown and excluded from analysis [see Results]); 9, gray seal (*Halichoerus grypus*); 10, puma (*Puma concolor*); 11, serval (*Leptailurus serval*); 12, Thomson's gazelle (*Eudorcas thomsonii*, formerly *Gazella thomsonii*); 13, Rodriguez fruit bat (*Pteropus rodricensis*); 14, golden lion tamarin (*Leontopithecus rosalia*); 15, Kirk's dik-dik (*Madoqua kirkii*); 16, Tasmanian devil (*Sarcophilus harrisii*) (not shown and excluded from analysis [see Results]); 17, ocelot (*Leopardus pardalis*); 18, Geoffroy's marmoset (*Callithrix geoffroyi*); 19, cotton-top tamarin (*Saguinus oedipus*); 20, Goeldi's monkey (*Callimico goeldii*); 21, slender-tailed meerkat (*Suricata suricatta*); 22, pied tamarin (*Saguinus bicolor*); 23, aardvark (*Orycteropus afer*); 24, African wild dog (*Lycaon pictus*); 25, Alpine ibex (*Capra ibex*); 26, banteng (*Bos javanicus*); 27, capybara (*Hydrochaeris hydrochaeris*); 28, cheetah (*Acinonyx jubatus*); 29, gelada baboon (*Theropithecus gelada*); 30, gemsbok (*Oryx gazella gazella*); 31, giant panda (*Ailuropoda melanoleuca*); 32, greater kudu (*Tragelaphus strepsiceros*); 33, red wolf (*Canis rufus gregoryi*); 34, sea otter (*Enhydra lutris*); 35, sloth bear (*Melursus ursinus*); 36, Bolivian squirrel monkey (*Saimiri boliviensis*); 37, owl monkey (*Aotus azarai*); 38, slender loris (*Loris tardigradus nordicus*); 39, black-footed ferret (*Mustela nigripes*).

survivorship curve to data that were truncated at $l_x = 0.7$ because the model would be unduly influenced by its extrapolation from $l_x = 0.7$ to 0.0 at its maximum longevity. Therefore, in a balance between data completeness and sample size, we considered only those species for which the last age class (with >10 individuals sampled) had $l_x \leq 0.20$.

To determine what life history traits may be associated with survivorship shape, we used linear regression and principal components analysis (PCA) to

look for correlations between life history traits, such as body mass and litter size, and the shape parameters α and β . Details may be found in Appendix C.

RESULTS

The distribution of mammalian survivorship shapes in the space of the two beta distribution parameters is shown in Fig. 1 (see also Appendix D). To focus on the differences among the majority of species, we have not shown either the Florida manatee or the Tasmanian

TABLE 1. Parameters of the best-fit bivariate normal distribution describing the distribution of mammal species.

Group	$E[\log_2\alpha]$	$E[\log_2\beta]$	$\text{Var}[\log_2\alpha]$	$\text{Var}[\log_2\beta]$	$\text{Cov}[\log_2\alpha, \log_2\beta]$
All species	-1.34	-0.22	0.25	0.26	0.16
Artiodactyla	-1.06	0.11	0.09	0.09	0.00†
Carnivora	-1.50	-0.54	0.19	0.19	0.00†
Primates	-1.30	-0.12	0.16	0.16	0.00†

Notes: Survivorship shape is described by the two shape parameters of the beta distribution (α and β) as described in *Methods*, E is the expectation of the distribution, and Var and Cov are the variance and covariance, respectively.

† The best model for these subsets of the data was a spherical model with no covariance between the two shape parameters.

devil, both of which were found, for reasons not yet understood, to be extreme outliers (see Appendix D) and were not considered in our analyses. We fit a bivariate normal distribution to the distribution of points in shape space using the logged values of the shape parameters α and β as plotted in Fig. 1, and we plot the 50th and 95th percentile confidence intervals of this bivariate distribution (Fraley and Raftery 2002, 2006). We find the bivariate mean to be $\log_2(\alpha) = -1.34$ and $\log_2(\beta) = -0.22$, i.e., the geometric means of the original variables α and β are 0.40 and 0.86, respectively (see also Table 1). The logarithmic transformation of the two shape parameters is consistent with earlier work using this distribution (Lynch and Fagan 2009) and is supported by the maximum-likelihood estimation of the Box-Cox normalizing powers of the bivariate distribution of α and β (Fox 2002).

Underlying our model of survivorship is a statistical distribution (the beta distribution) describing how mortality is distributed between birth and maximum longevity for a species. These distributions and the survivorship curves derived from them are placed at key points along the 95th percentile confidence ellipse to illustrate how survivorship is related to the shape parameters of the beta distribution. We find that the distribution of shape parameter values is clustered along two principal axes (Appendix C: Table C1) that roughly correspond to the two degrees of freedom previously introduced (i.e., skewed toward early vs. late mortality [α/β] and unimodal vs. U-shaped mortality [$\alpha\beta$]; see *Methods*).

Initially, we sought to develop a model to explain a species' position in survivorship shape space as a function of its life history characteristics (longevity, litter size, age to maturity, etc.). We found longevity, age to weaning (relative to longevity), and litter size to be significantly correlated with the position of a species along the first principal component (PCA1) in shape space but found no correspondingly strong covariate to explain variation along the second principal axis (PCA2; details in Appendix C). We also found no statistically significant relationship between the first principal component of life history and either principal component in shape space. However, we do find a relationship between taxonomic group (specifically, order) and

survivorship shape. In Fig. 2 we illustrate how survivorship shapes are roughly grouped by order, with emphasis on the differences among the Artiodactyla, the Carnivora, and the Primates, which together represented 32 of the 37 species in our final sample. We see that the Artiodactyla and the Carnivora inhabit barely overlapping areas in shape space, with the Primates lying between these two extremes. The Artiodactyla tend to have relatively lower juvenile mortality and higher adult mortality relative to the Primates, which in turn have relatively lower juvenile and higher adult mortality than the Carnivora. This variation among orders is best illustrated by comparing the Artiodactyla curves against the Carnivora curves (Fig. 2, lower right inset). In the Artiodactyla, mortality is fairly evenly spread out among all age classes and survivorship is a smoothly decreasing function of age, whereas in the Carnivora, mortality is strongly concentrated in the youngest and oldest age classes (see Fig. 1). In fact, variation of species along PCA1 in "shape space" is best modeled by order alone (i.e., this model has the lowest Akaike information criterion [AIC]; see upper left inset to Fig. 2) and is a better fit to the data than models including PCA1 of the life history traits (either alone or as an additional covariate to order).

Compared with wild populations, survivorship shapes for captive mammals are less variable (Fig. 3; Lynch and Fagan 2009), reflecting both the higher precision of the captive survivorship data and the integration of environmental factors with inherent drivers of survivorship in the wild. As was found for the wild mammal populations, we find that the captive mammal survivorship shapes are largely contained within a triangle in shape space (Fig. 3A). There were seven species for which we had both wild population and captive population data of sufficient quality to allow a comparison (see Fig. 3A inset). Although both chimpanzee (*Pan troglodytes*) and hippopotamus (*Hippopotamus amphibius*) captive data were truncated at $l_x = 0.23$ and 0.21, respectively, and were not considered in the preceding analyses, they have been included here due to the small number of species for which both wild and captive data were available. Of the seven species we considered, five of them showed a shift to smaller values of α and β when moving from the wild population to the

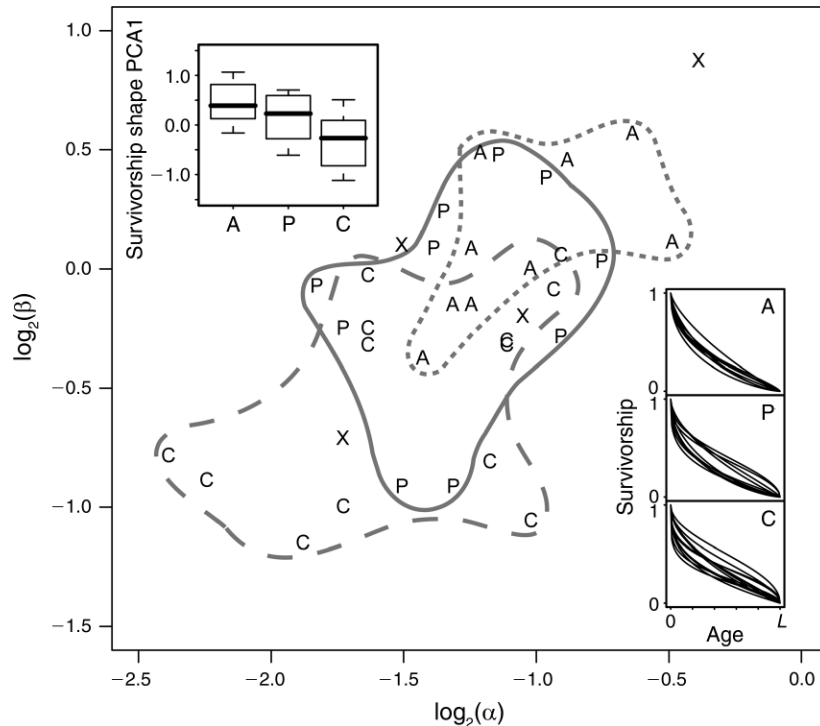


FIG. 2. Distribution of points in shape space (as described by the two shape parameters of the beta distribution [α and β] labeled by the order to which they belong: A, Artiodactyla; C, Carnivora; P, Primates; X, other). Gray shapes containing all the points of a given order have been drawn as a general guide to the distribution patterns of these three orders. Upper left inset: Boxplot representing the distribution of the Artiodactyla, Carnivora, and Primates along the first principal component of survivorship shape space (PCA1). The thick line is the median, the box edges represent the lower and upper quartiles, and the whiskers extend to the data extremes. Lower right inset: Fitted survivorship curves for the Artiodactyla, Carnivora, and Primates in our sample. The x-axis indicates the distribution of mortality from birth to maximum longevity (L).

captive population. This shift is associated with relatively higher juvenile mortality (compared to overall mortality) in captive populations. In Fig. 3B, C we illustrate the survivorship curves associated with those species near to the corners of the wild and captive survivorship triangles. Survivorship patterns in wild populations exhibit greater variation relative to captive populations as environmental factors become integrated with inherent differences in life history strategy.

One of our goals was to put bounds on the survivorship shapes that might be expected in captive mammals so that estimates of maximum population growth rates could proceed without species-specific information. We illustrate the use of our shape space confidence intervals by mapping estimates of r across a large range of survivorship shape space using life history data (litter size, litter interval, etc.) for the Thomson's gazelle (*Eudorcas thomsonii*) (Fig. 4). Overlaid on this map is the 50th percentile confidence envelope (similar to that in Fig. 1) that results from using all of the data except that for the Thomson's gazelle. Using this multispecies confidence envelope, we estimated r for the Thomson's gazelle would lie between 0.26 and 0.38, which does in fact contain the true value of $r = 0.32$. We repeated this method of leave-one-out cross-validation

for each species in the data set (except for Geoffrey's marmoset, for which we had insufficient life history information to estimate r) and found that, remarkably, r estimates for 28 out of the 36 species were bounded by the generic (i.e., not order-specific) model prediction (Fig. 4 inset). Among those 28 species, the upper and lower limits on r were, on average, only 22% above and 21% below the true value, respectively. Model error was unrelated to the absolute size of r . This finding emphasizes that not only are mammalian survivorship shapes quite similar across species, but that that similarity has an important functional consequence in terms of predicting population growth rates across species.

DISCUSSION

The study of survivorship patterns sits at the nexus of several active research areas. The relative rate of mortality across an organism's life span is key to understanding the evolution of life history strategies. Survivorship patterns are also intimately related to our understanding of death, senescence, and the mechanisms of aging from the scale of individuals down to the scale of individual genes. We have focused our analysis on the role that survivorship patterns play in ecology and

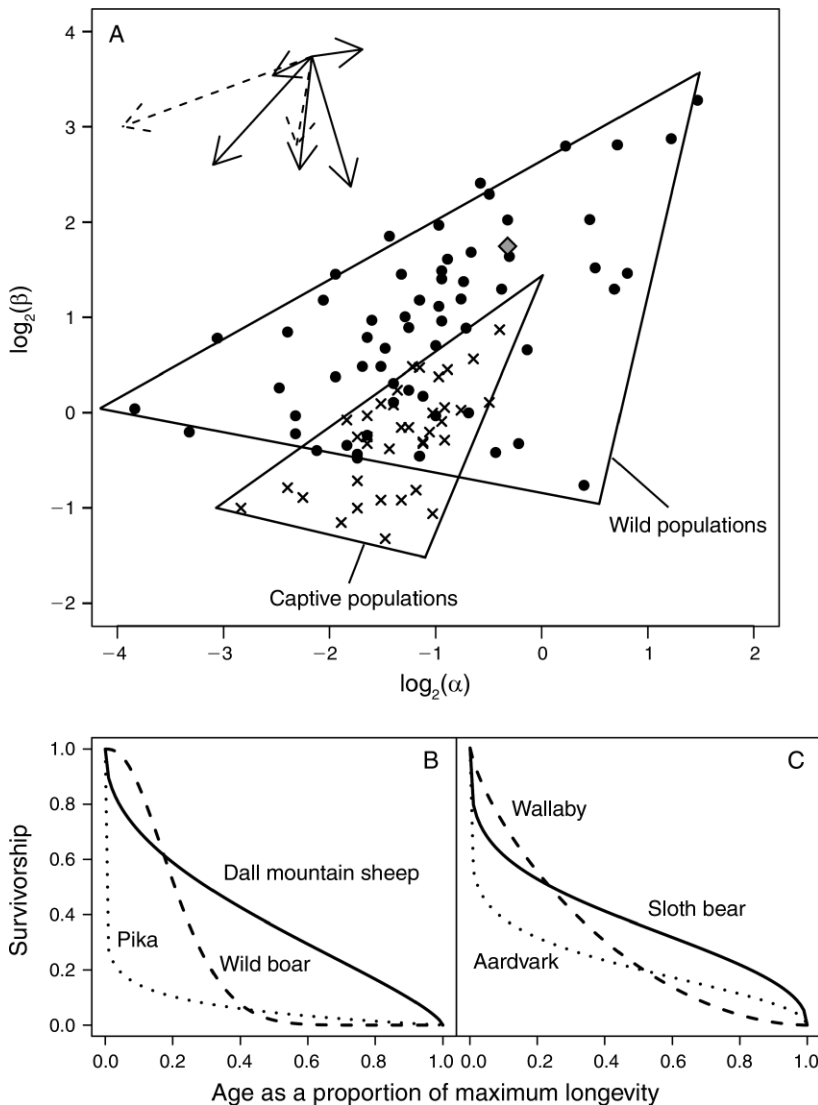


FIG. 3. (A) Comparison of survivorship shapes (as described by the two shape parameters of the beta distribution [α and β]) from wild populations (solid circles) (scaled to maximum life span in the wild; see Lynch and Fagan [2009]) and captive populations (crosses). Triangles have been drawn as a guide to the region in survivorship shape inhabited by each data set. An exponential decay (type II) survivorship shape (in which maximum life span is truncated to five times the mean life span; for details see Lynch and Fagan [2009]) is shown as a gray diamond. A step function (type I) survivorship shape may be approximated by $(\alpha, \beta) = (8, 0.0625)$ but is not drawn. Data from wild populations are extracted from the literature and are cited in Lynch and Fagan (2009). New wild population data, not previously cited, were used for the giant panda (Carter et al. 1999) and the black-footed ferret (Conservation Breeding Specialist Group 2004). Inset: Arrows showing the difference in survivorship between a wild population and a captive population for seven species that had both sets of data available. Arrows point from the wild to the captive survivorship shape, and all arrows have been centered at the origin. The arrows representing the chimpanzee and the hippopotamus are dashed, as these two species were excluded from the rest of the analysis (see *Results*). (B) Survivorship curves for three species that are representative of the wild data triangle. (C) Survivorship curves for three species that are representative of the corners of the captive data triangle.

conservation biology where data, particularly on patterns of survivorship, are often limited.

Differences (and similarities) in survivorship patterns among mammals

We find that captive mammalian survivorship patterns are constrained to a fairly narrow area of

shape space. Previous models of survivorship have either depended on a host of biologically driven parameters (e.g., the Weibull, Gompertz, and Siler models) or have described survivorship in terms of purely phenomenological curve-fitting equations (e.g., Harvey et al. 1989). In all cases, survivorship scale and shape have been convolved, making it difficult to

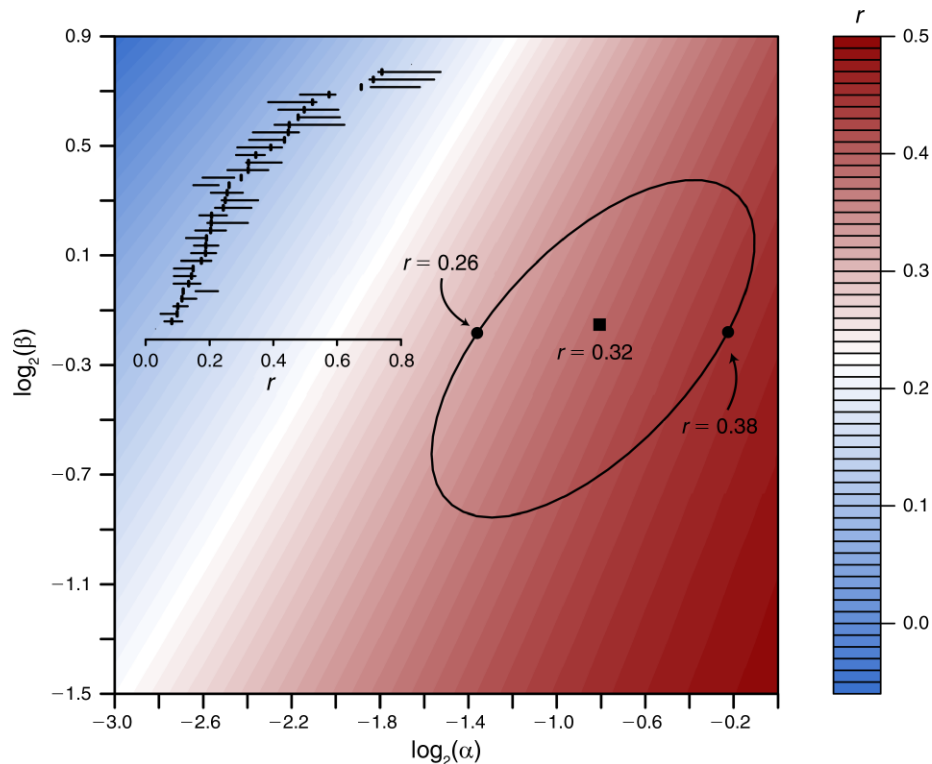


FIG. 4. Contour plot showing the change in population growth rate r (estimated using the Euler equation; Eq. 2) for the Thomson's gazelle (*Eudorcas thomsonii*) associated with a survivorship curve given by shape parameters α and β (Eq. 3). The 50th percentile ellipse of the remaining data set (i.e., when the Thomson's gazelle data are left out) is overlaid, and the maximum and minimum values of r estimated along that curve are plotted. Note that, due to the nontrivial mapping of survivorship shape to population growth rate, the extreme values of r do not lie at the extrema of the ellipse. Inset: Predicted range of r based on the 50th-percentile ellipse (horizontal lines) for the 36 species (Geoffrey's marmoset excluded) for which it was possible to estimate r based on the known life history and survivorship data (vertical lines). The species are ranked vertically according to the magnitude of r .

compare survivorship patterns across taxa. The beta distribution model used here describes the statistical properties of mortality scaled to maximum longevity, a parameter that has already been estimated for a large suite of animals.

Despite all of the textbook dogma and subsequent discussion regarding the three prototypical survivorship curves (types I, II, and III) and the extensive use that has been made of the type I curve in estimating population growth rates (see Lynch and Fagan [2009]), we find that all mammals (in captivity), large and small, short-lived and long-lived, have fairly similar survivorship curves most similar to type II survivorship curves but with varying degrees of type I character (specifically, high rates of mortality among the oldest age classes) and type III character (high rates of mortality among the earliest age classes). We find that survivorship shape is most closely correlated with life history traits relating to reproduction (relative age to weaning and gestation, litter size, litters per year, etc.; Appendix C). Our results explicitly reject the common textbook assertion that survivorship shape is related to body mass (e.g., MacKenzie et al. 2001, Starr and Taggart 2006, Mader

2007). Order was found to be the best predictor of survivorship shape, which is consistent with earlier findings that suggest that order is significantly correlated with life history variation and annual survivorship (even after any effects of adult mass have been removed) (Stearns 1983, McCarthy et al. 2008). The importance of order for the prediction of survivorship patterns emphasizes the role phylogeny plays in understanding life history variation and correlation among life history traits (Stearns 1983, Felsenstein 1985, Purvis and Harvey 1995, Fagan et al. 2010). A better understanding of the evolution of survivorship patterns and maximum population growth rates would allow for continued refinement in the prediction of maximum population growth rates in data-poor situations; this represents a promising direction for future research.

Although early studies on survivorship shapes focused exclusively on log-linear plots of survivorship (e.g., Pearl and Miner 1935, Pearl 1940, Deevey 1947), more recent treatments have considered survivorship on a linear scale (Barlow and Boveng 1991, Clubb et al. 2008). Although convenient for distinguishing constant rate mortality, the logarithmic scale of survivorship com-

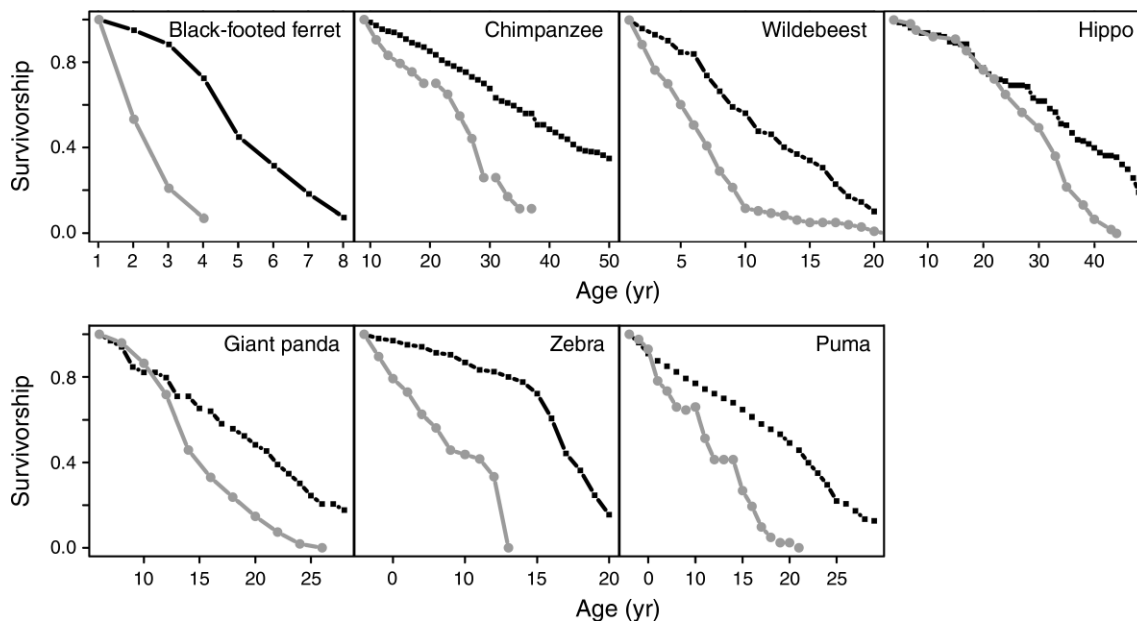


FIG. 5. Adult survivorship for populations in captivity (black squares) and in the wild (gray circles) for the seven species of mammals for which both sets of survivorship data were available. Each survivorship curve is scaled so that $l(x) = 1$ at sexual maturity.

presses juvenile mortality and makes it difficult to distinguish between survivorship curves that differ in this key demographic stage. Because the relative elasticity of juvenile survival vs. adult survival is highly variable across mammals and is correlated with other life history traits such as age at maturity (Heppell et al. 2000), the log-linear plot has the potential to obscure important trends between species that may impact population growth rates. In these contexts, we recommend considering survivorship shape on the linear scale as we have done in this analysis.

From a practical standpoint, it is useful simply to know what survivorship shapes can be expected among mammals in captivity. We believe that by representing the distribution of survivorship shapes among species by a bivariate normal distribution (e.g., Fig. 1), we can place bounds on the range of shapes that might be expected for a species that is relatively unknown. As demonstrated by the leave-one-out cross-validation (Fig. 4), this information can be used in concert with the Euler equation to estimate maximum population growth rates if other basic life history data, such as litter size and litter interval, are known (Fagan et al. 2010). Where species-specific age-specific survivorship data are unavailable, this procedure provides a first estimate of population growth rates that may be used as a guideline for management while more species-specific survivorship data are being collected. As with any cross-taxa comparison there is obviously a concern that a taxonomic bias in the selection of species examined may bias estimates of mean survivorship shape. For that reason we include in Table 1 mean

survivorship shape parameters specific to the Artiodactyla, the Carnivora, and the Primates. We also note that species differ in their sensitivity to different vital rates and that for some species, population growth rates will be more sensitive to estimates of fecundity than survivorship (Heppell et al. 2000, Oli 2004). Predictions regarding the population trajectories of these species will require either detailed species-specific data on fecundity or must rely on estimates of fecundity based on correlations with other life history traits and/or taxonomic relationships (e.g., Stearns 1983, Read and Harvey 1989, Purvis and Harvey 1995).

Survivorship in captive vs. wild populations

We might expect that captive populations would have both higher juvenile and higher adult survivorship as a result of the release from predation, disease, and starvation, although recent evidence suggests that both adult and juvenile mortality are actually higher in captive elephants (Clubb et al. 2008). Direct comparisons of survivorship after sexual maturity show higher adult survivorship among captive populations (Fig. 5) but no clear trend in survivorship to maturity (captive populations may have higher, lower, or indistinguishable rates of survivorship to maturity) compared to populations of the same species in the wild. In other words, gains in survivorship associated with captivity are found predominantly in the adult age classes. Overall, the relative balance between juvenile and adult mortality is shifted in captive populations such that, as a fraction of all mortality, there is greater juvenile

mortality in captive populations (as reflected in a decrease in β [Fig. 3A inset]). On average, expected gains in survivorship among juvenile ages classes in captive populations are offset by other factors. One of the challenges in interpreting relatively greater early mortality in captive populations is the potential for field data to underestimate juvenile mortality. Different methods of assessing survivorship in the field have their own potential biases, but it is generally recognized that juvenile mortality may be underrepresented in field studies because juveniles may die and disappear from the population before being recorded (e.g., Kelly et al. 1998) and smaller carcasses are more quickly consumed by predators and decompose more rapidly (e.g., Spinach 1972, Reimers 1983). We note, however, that results from our comparison of wild and captive populations are consistent with findings by Courtenay and Santow (1989), who found higher infant mortality among captive chimpanzees than among wild chimpanzees, even after the wild data had been adjusted to account for potential misidentification of infant mortality as miscarriage. Courtenay and Santow (1989) suggest that perinatal mortality may be elevated in captive populations as a result of inbreeding and find some tentative support for this hypothesis by comparing perinatal mortality rates between “inbred” and “non-inbred” offspring. More extensive surveys of the cost of inbreeding in mammals also demonstrate a significant increase in juvenile mortality among inbred offspring (Ralls et al. 1979, 1988). The potential for higher infant and/or juvenile mortality in captive populations deserves further consideration, although the challenges of accurately assessing infant and juvenile mortality in the wild must be adequately addressed.

Conclusion

Patterns of survivorship are a critical component of models of population growth and viability, but they are all too often lacking. Should our findings hold true more generally, the estimation of survivorship by means of a few, more easily obtained life history traits will aid the assessment and management of threatened populations. Expanded pairwise comparisons of captive and wild population survivorship patterns will provide deeper insight into the factors that drive survivorship differences, information that may be used to improve management of populations both in the wild and in captivity. Finally, we see that the empirical evidence does not support the connection between body size and survivorship shape that is so frequently presented in ecology texts and that may mislead efforts to characterize broadscale patterns in survivorship shape in data-poor situations.

ACKNOWLEDGMENTS

Support for this project came from the U.S. Department of Defense SERDP Award SI 1475.

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APPENDIX A

Beta distribution moments and parameter estimation (*Ecological Archives* A020-090-A1).

APPENDIX B

Sources for survivorship data (*Ecological Archives* A020-090-A2).

APPENDIX C

Correlation of life history traits and survivorship shape (*Ecological Archives* A020-090-A3).

APPENDIX D

Details of survivorship model fits (*Ecological Archives* A020-090-A4).