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Age-related shapes of the cost of reproduction in vertebrates

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The shape of the association between age and the cost of reproduction varies across species. However, it is unclear whether there are any general patterns in the way the cost of reproduction varies with life history, taxon or ecological function. Using a simple theoretical method, we identified three characteristic patterns to describe the age-related survival cost of reproduction. The most frequent pattern is an approximately exponential decay (ED) with increasing age. Two additional u-shaped patterns were identified, where the cost of reproduction was higher for young and old individuals compared with intermediate-aged individuals. The majority of these u-shaped curves suggested higher costs of reproduction at older ages (RQ), with the rest suggesting a higher cost at young ages (LQ). While predators were most likely to exhibit ED-shaped cost curves, herbivores were equally likely to exhibit ED and RQ curves; birds were likely to exhibit ED-shaped curves and mammals were split equally between ED and RQ curves. These findings suggest that there may be predictable differences in the age-related shape of the cost of reproduction between species, but further research is required to identify the mechanisms generating such differences.

Keywords: trade-off; life history; reproductive effort; Leslie matrix; diet

1. INTRODUCTION

Costs of reproduction encompass evolutionary trade-offs that constrain the evolution of life histories. These costs may vary with age or stage according to life history and environmental conditions. Although they have proven difficult to measure (Reznick 1992), there is mounting evidence that the strength of the cost of reproduction varies between species. For example, in ungulates the cost tends to be high at young and old ages but low at prime ages, probably due to the superior physiological condition of prime age adults (Clutton-Brock 1984). Studies on other species describe various patterns—an abrupt increase in the cost in passerine birds (McCleery *et al.* 1996), continuously increasing cost with age in humans, or age-invariant cost in pinnipeds (Pistorius *et al.* 2004). Such variation in the pattern of association between age and the cost of reproduction might be attributed to phenotypic aspects such as body size or foraging

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behaviour. This issue is currently unclear, but is important to life-history theory because the extent and pattern of variation in the cost define the margins within which life histories evolve.

Previous attempts to identify the cost of reproduction and measure its intensity with age have focused on comparative and manipulative studies. However, these methods are complex and often yield equivocal results due to insufficient demographic data and confounding effects of individual quality and environmental variation (Reznick 1992; Schwarzkopf 1993). An alternative theoretical method for predicting the costs of reproduction is based on the mathematical properties of a population transition matrix (Leslie matrix). Assuming optimal life history and a stable age distribution, the expected age-dependent survival cost of reproduction can be estimated from the left eigenvector associated with the dominant eigenvalue of a Leslie matrix (Caswell 1982). This vector corresponds to the level of resources left for future reproduction (reproductive value). While this method has been demonstrated as an adequate tool for predicting variation in the survival cost of reproduction in several case-study species (Caswell 1982, 2001), it has not been widely implemented.

Here we employ this method to describe the predominant patterns of variation in the survival cost of reproduction in vertebrates. We then investigate whether specific patterns of the cost are associated with particular foraging behaviours (herbivores or predators) and taxonomic classes (mammals or birds).

2. MATERIAL AND METHODS

(a) Datasets

The literature was searched for studies of vertebrates that provided estimates of survival and fecundity rates. These estimates were used to construct Leslie matrices, under the assumption that there is no age-specific bias in estimated survival and fecundity rates. Most studies reported age-specific demographic rates (electronic supplementary material), although some reported stage-specific demographic rates. These data were used if the average number of years a female spent in each stage was reported, so that stage-specific rates could be approximated to age-specific rates. Species for which there was considerable variation between estimates were included in the analysis if there were at least two consistent estimations of demographic rates in two independent studies. The data represent species from various taxonomic groups (electronic supplementary material). This reduces but does not eliminate the risk of having a large number of species from the same phylogenetic group (pseudoreplication).

(b) Characterizing the cost of reproduction

Age-specific demographic rates were combined into a Leslie matrix,

$$L = \begin{bmatrix} F_0 & F_1 & \dots & F_{i-1} & F_i \\ S_0 & 0 & \dots & 0 & 0 \\ 0 & S_1 & \dots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \dots & S_{i-1} & 0 \end{bmatrix}, \quad (2.1)$$

where L is a matrix with age-specific fecundity rates, F_i , in the first row, and age-specific survival rates, S_i , in the subdiagonal and zeros in the rest of the matrix entries. The left eigenvector (a non-zero row vector of L whose direction is not changed by transformation), v , is scaled to the first element, and the right eigenvector (a non-zero column vector of L whose direction is not changed by transformation), w , is scaled to sum to 1. v and w are respectively the reproductive value and the stable age distributions of the population (Caswell 1982). The predicted survival cost of reproduction was estimated from the reproductive value distribution as

$$C_i = \frac{v_1}{v_{i+1}}, \quad (2.2)$$

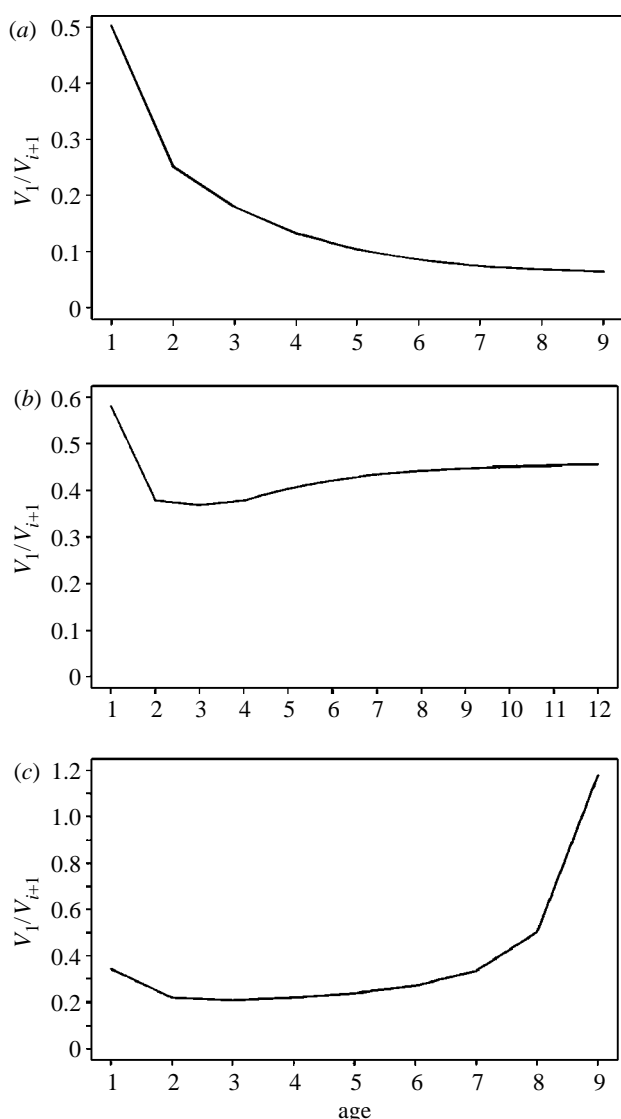


Figure 1. Examples of the three most frequently observed curves of the survival cost of reproduction in 68 vertebrate species. (a) Exponential decay (ED) curve, shown for the Atlantic herring, *Clupea harengus*; (b) left-skewed u (LQ) curve, shown for the red cockaded woodpecker, *Picoides borealis* and (c) right-skewed u (RQ) curve, shown for the grey wolf, *Canis lupus* (sources in electronic supplementary material).

where C_i is the survival cost of reproduction at age i (Caswell 1982), and assuming that the only life-history constraint is the age-specific reproduction–survival trade-off (Schaffer 1974). The values in vector C are not equal to the cost of reproduction because they are scale free, but they can be compared across ages to reflect the relative changes in the cost with age. C was calculated and plotted for each species. Equation (2.2) is based on mean population values but does not reflect variance within age-specific classes. The age-specific shape of the resultant curve was visually characterized into one of three categories. These curves describe the hypothetical cost if an individual reproduces at a particular age.

Differences in the frequencies of the shapes of the cost curves were examined as a function of diet (herbivore or predator) and taxonomic class (bird or mammal) using Fisher's exact test.

3. RESULTS

The survival cost of reproduction curve was calculated for 68 species (electronic supplementary material). Of these, 44% were mammals, 38% birds and the rest reptiles, fishes and amphibians. Based on its diet, each species was classified either as a herbivore (38% of all

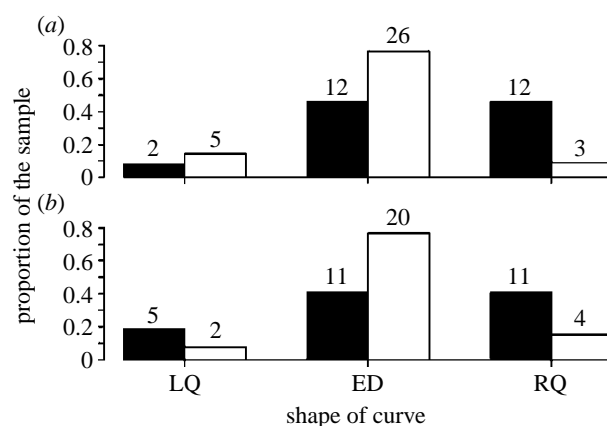


Figure 2. Incidence of different shapes of the survival cost of reproduction curve for (a) herbivores (filled bars) and predators (open bars), and (b) mammals (filled bars) and birds (open bars) (data in electronic supplementary material). Curve notations: ED, exponential decay; LQ, left-skewed u; RQ, right-skewed u. The sample size is given above each column.

species), a predator (50%) or an omnivore (12%); 94% of the cost of reproduction curves in the dataset fell into one of three categories. The most frequent curve, found for 58% of the species, resembles an exponential decay (ED) function which continuously declines from age 1 onwards (figure 1a). The other frequently observed curves resemble u-shaped functions with the lowest cost at intermediate ages. Twenty-four per cent of the species exhibited u-shaped curves with the highest costs of reproduction at younger ages (LQ, figure 1b). Twelve per cent of the species had u-shaped curves with the highest costs at older ages (RQ, figure 1c). The remaining curves did not resemble a consistent pattern and were excluded from further analysis.

The shape of the cost of reproduction curves varied significantly between herbivores and predators (Fisher's exact test, $p < 0.01$). The distribution of predators was skewed towards ED-shaped curves ($\chi^2 = 28.7$, $p < 0.001$), observed for over 75% of the species (figure 2a). Herbivores were skewed towards ED and RQ curves ($\chi^2 = 7.7$, $p < 0.05$), each observed for 46% of species. Taxon also affects the shape of the cost curves (Fisher's exact test, $p < 0.05$). Birds were skewed towards ED curves ($\chi^2 = 22.5$, $p < 0.001$), observed for 77% of the species (figure 2b). In contrast, the distribution of mammals was not significantly skewed towards a particular shape ($\chi^2 = 2.67$, $p > 0.05$). These effects of diet and taxon on the cost of reproduction curves do not interact ($\chi^2 = 3.6$, $p > 0.05$).

4. DISCUSSION

We employed a simple method to characterize the shape of the association between age and the survival cost of reproduction, assuming that survival is only affected by reproduction in the preceding season. We identified three frequently observed shapes that differed from one another in the duration of their initial decline and behaviour as the animals age; the curve may level off, increase a little, or increase beyond the cost observed at young ages. The shapes of the cost curve differed between herbivores and predators, and

independently between birds and mammals. Age-related changes in the cost curve reflect age-specific changes in the strength of the negative effect reproductive effort has on survival (Hirshfield & Tinkle 1975). These may vary between species as a function of developmental, physiological and/or behavioural factors. An ED-shaped cost curve reflects a rapid increase in reproductive value at young ages resulting from age-related improvements in reproductive success until an asymptote is reached. This pattern may characterize species that exhibit substantial size differences between young and adult stages, because a fully grown female incurs lower reproductive costs by investing proportionally fewer resources in reproduction than a younger and smaller female. It may also characterize species with age-related improvements in reproductive success and/or survival due to learning and experience (Forslund & Pärt 1995). The increase in the cost at old ages seen in u-shaped curves reflects an increase in reproductive effort per offspring produced, which is often associated with deleterious senescent effects (Hutchings 1994).

Diet is an important characteristic affecting growth rates and reproduction. The results suggest that while predators are likely to experience an ED curve, in herbivores there is no clear tendency towards a particular cost curve. Studies on long-lived herbivores suggest that increased reproductive effort reduces survival in young but not in adult females (Ericsson *et al.* 2001). This pattern has been linked to low and variable juvenile survival and high adult survival (Gaillard *et al.* 1998). However, the cost in other species may remain substantial and even increase with age, depending on the extent to which changes in reproductive effort and body functioning are driven by state or age (Berube *et al.* 1996; McNamara & Houston 1996). While there is a scarcity of information on age-related variation in the costs of reproduction in predators, our findings are supported by studies on predators that suggest a continuous decline in the cost of reproduction from maturity until adulthood, when it tends to be age invariant (Reiter & Le Boeuf 1991). A possible mechanism for these results is the tendency of predators for short gestation period, which results in the production of heavily dependent (altricial) offspring that require extended parental care (Gittleman 1985). Extended parental care enables the offspring to gradually learn essential hunting skills, but imposes high parental cost because offspring growth in the post-natal stage is on average more energetically demanding *per capita* growth than the embryonic stage (Millar 1977; May & Rubenstein 1985).

The findings also indicate that while birds tend to experience ED cost curves, mammals show a range of cost curves. Some empirical studies on birds support these findings (Gustafsson & Sutherland 1988), but others suggest that state rather than age determines reproductive effort (Weimerskirch 1992). Additionally, comparative studies have indicated that phylogeny is often coupled to energetic constraints and consequently influences reproductive costs (Gittleman & Thompson 1988). Raising a bird offspring from conception to independence is on average less energetically demanding

than raising a mammalian offspring (Wieser 1985), suggesting that birds may have a greater tendency to exhibit reduced reproductive costs with age.

This paper demonstrates how straightforward Caswell's method is for studying patterns in the costs of reproduction. We have identified general patterns of the shape of the association between age and the survival cost of reproduction and, for the first time, linked them to broad taxonomic and diet categories. The association we report between the ED-shaped cost of reproduction curves and predators and birds is an important insight for life-history theory which requires further investigation. In particular, future research should focus on testing hypotheses regarding the mechanisms that underpin the shape of the cost curve, and their association with particular categories of species.

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