

LIFE HISTORIES OF MAMMALS: AN ANALYSIS OF LIFE TABLES¹

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Abstract. We quantitatively test theoretical predictions concerning mammalian life histories, using published data on survival, reproduction, and body mass for 29 eutherian mammals. Larger mammals have a greater age at maturity, greater generation length, greater life expectancy, lower reproductive value at maturity, and smaller litters than do smaller mammals. Residual reproductive value at maturity is not correlated with adult body mass or survival. Litter size varies inversely with generation length and adult survival. Age at maturity is positively correlated with life expectancy. Twenty-seven of 29 mammals display a generation length longer than their life expectancy at birth, and the same proportion shows a greater life expectancy at maturity than at birth. A fairly high proportion (76-82%) of the variation in these dependent variables is attributable to adult mass.

Many life table characteristics of mammals are interrelated, although not necessarily in the ways predicted by theory. Design constraints may preclude significant differences in life history patterns among mammals, so that the life table characteristics of only a few species may depict the pattern of life table evolution in most eutherian mammals.

Key words: age at maturity; body mass; life expectancy; life history; life table; litter size; mammal; reproductive value.

INTRODUCTION

Many morphological and physiological traits appear interrelated, so that a single trait can be used to predict many others. Adult body mass is such a trait among mammals, since many authors have documented the relationships between morpho-physiological traits and body size (Sacher 1959, Kleiber 1961, Bonner 1965, Gould 1966, Stahl 1967, Calder 1974, Schmidt-Nielsen 1975, Millar 1977, Blueweiss et al. 1978, Western 1979, Tuomi 1980). In addition, several recent reviews have discussed the relationships among life history traits and have made theoretical predictions as to what we should expect to find in nature (Hirshfield and Tinkle 1975, Pianka and Parker 1975, Giesel 1976, Pianka 1976, Stearns 1976, 1977, Blueweiss et al. 1978, Western 1979, Bell 1980), but no study has specifically examined the relationships among mammalian life history traits found in life tables.

The objective of this study was to examine the relationships among life table derivatives and body mass for mammals in order to test theoretical predictions quantitatively.

METHOD

Survivorship, litter size (number born), age at maturity, and adult body mass data were obtained from the literature for 29 mammal species. As far as we know, we used only unbiased data sets. Survivorship data that did not appear representative of females and

a stationary age distribution were not used (i.e., hunted populations, small samples). For each mammalian age structure in the literature meeting our criteria, the number of females reported surviving to the beginning of each age-class (1, 2, 3 . . .) was multiplied by one-half the litter size (or the author's own m_x , if available), and these products were summed over all age-classes. Assuming a 1:1 sex ratio, the same mortality schedules for both sexes, and a stationary population, this summation is an estimate of the average number of females born into the population each year and thus represents ℓ_0 in the survival series of the life table (Caughley 1977). The number of females reported surviving to the beginning of each age-class was divided by this ℓ_0 to create a survival series for females. This provided a net reproductive rate ($R_0 = \sum \ell_x m_x$) that approached unity. Life expectancy (expectation of further life; Deevey 1947, Pianka 1974, 1978) was calculated as:

$$e_x = \frac{\sum_{y=x}^{\infty} \ell_y}{\ell_x}, \quad (1)$$

where ℓ_y is the summation of ℓ_x for all ages successive to and including that of age x . The reproductive value (age-specific expectation of future offspring; Pianka 1974, 1978) was calculated as:

$$v_x = \sum_{t=x}^{\infty} \frac{\ell_t}{\ell_x} m_t, \quad (2)$$

where ℓ_t/ℓ_x is the probability of living from age x to age t , and m_t is the average number of females born to a female of age t . Residual reproductive value (reproductive value in the next age-interval with respect

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TABLE 1. Life table and body mass characteristics for 29 mammals.

| Species | Source | Approximate mass (kg) | Litter size | Age of maturity (yr)* | e_0^\dagger | e_m^\dagger | v_m^\dagger | $v_m^{*\dagger}$ | T_c^\dagger |
|----------------------------------|--|-----------------------|-------------|-----------------------|---------------|---------------|---------------|------------------|---------------|
| <i>Castor canadensis</i> | Larson (1967) | 18 | 6.6 | 2 | 1.52 | 2.22 | 5.63 | 4.03 | 4.87 |
| <i>Clethrionomys glareolus</i> ‡ | Pucek et al. (1971) | 0.025 | 5 | 0.11 | 0.16 | 0.48 | 7.90 | 5.42 | 0.33 |
| <i>Peromyscus leucopus</i> ‡ | Snyder (1956) | 0.02 | 5 | 0.15 | 0.21 | 0.28 | 4.52 | 2.03 | 0.27 |
| <i>P. maniculatus</i> ‡ | Howard (1949) | 0.02 | 3.6 | 0.15 | 0.23 | 0.43 | 5.04 | 3.22 | 0.35 |
| <i>Sciurus carolinensis</i> | A. R. Bisset (personal communication)§, Mosby (1969), Barkalow et al. (1970) | 0.6 | 2.9 | 1 | 1.37 | 2.17 | 5.95 | 3.55 | 2.07 |
| <i>Spermophilus armatus</i> | Slade and Balph (1974) | 0.35 | 5.3 | 1 | 1.38 | 1.72 | 4.52 | 2.23 | 1.78 |
| <i>S. beldingi</i> | Costain and Verts (in press), Morton and Sherman (1978) | 0.25 | 7.4 | 1 | 1.30 | 1.78 | 5.89 | 2.79 | 1.56 |
| <i>S. lateralis</i> | Bronson (1977, 1979) | 0.155 | 5.2 | 1.3 | 1.47 | 2.12 | 5.08 | 2.65 | 2.45 |
| <i>S. parryi</i> | Kiell (1977) | 0.7 | 7.3 | 1 | 1.28 | 1.71 | 6.17 | 2.61 | 1.59 |
| <i>Tamias striatus</i> ‡ | Tryon and Snyder (1973), Smith and Smith (1972) | 0.1 | 4.2 | 1 | 1.24 | 1.63 | 6.84 | 2.64 | 1.59 |
| <i>Tamiasciurus hudsonicus</i> | Kemp and Keith (1970) | 0.189 | 4 | 1 | 1.50 | 2.45 | 4.90 | 2.90 | 1.95 |
| <i>Ochotona princeps</i> | Millar and Zwickel (1972), Smith (1974) | 0.13 | 2.8 | 1 | 1.37 | 2.33 | 6.51 | 3.67 | 2.07 |
| <i>Sylvilagus floridanus</i> | Rose (1977) | 1.25 | 5 | 1 | 1.48 | 1.25 | 2.62 | 0.57 | 1.29 |
| <i>Lutra canadensis</i> | Stephenson (1977) | 7.2 | 2 | 3 | 2.88 | 3.79 | 3.79 | 2.79 | 5.07 |
| <i>Lynx rufus</i> | Crowe (1975) | 7.5 | 2.8 | 1 | 1.72 | 2.48 | 3.48 | 2.08 | 2.87 |
| <i>Mephitis mephitis</i> | Casey and Webster (1975), Verts (1967) | 2.25 | 6 | 1 | 1.33 | 1.90 | 5.71 | 2.71 | 1.78 |
| <i>Taxidea taxus</i> | Messick and Hornocker (1981) | 7.15 | 2 | 1 | 1.45 | 2.33 | 2.48 | 1.63 | 1.24 |
| <i>Equus burchelli</i> | Klingel (1969), Spinage (1972) | 270 | 1 | 4 | 3.84 | 7.95 | 4.00 | 3.49 | 8.74 |
| <i>Aepyceros melampus</i> | Kayanja (1969), Spinage (1972) | 44 | 1 | 2 | 3.44 | 4.80 | 2.42 | 1.90 | 4.36 |
| <i>Cervus elaphus</i> | Lowe (1969) | 175 | 1 | 4 | 4.90 | 3.85 | 1.73 | 2.85 | 5.70 |
| <i>Connochaetes taurinus</i> | Watson (1970) | 165 | 1 | 3 | 3.84 | 4.79 | 2.56 | 2.14 | 6.29 |
| <i>Hemitragus jemlahicus</i> | Caughley (1966) | 100 | 1 | 3 | 3.97 | 4.71 | 2.12 | 1.68 | 5.43 |
| <i>Hippopotamus amphibius</i> | Laws (1968), Laws and Clough (1965) | 2390 | 1 | 10 | 7.62 | 16.40 | 3.98 | 3.85 | 19.82 |
| <i>Kobus defassa</i> | Spinage (1970) | 200 | 1 | 2 | 3.35 | 5.87 | 2.94 | 2.44 | 5.08 |
| <i>Ovis canadensis</i> | Deevey (1947), Geist (1968) | 55 | 1 | 4 | 3.81 | 5.48 | 2.74 | 2.24 | 6.52 |
| <i>Phacochoerus aethiopicus</i> | Clough (1969), Spinage (1972) | 87 | 4.8 | 2 | 1.60 | 2.82 | 6.76 | 4.36 | 4.28 |
| <i>Sus scrofa</i> | Jeziarski (1977) | 85 | 5 | 2 | 1.79 | 1.91 | 4.82 | 2.32 | 3.15 |
| <i>Syncerus caffer</i> | Pienaar (1969), Spinage (1972) | 490 | 1 | 4 | 4.47 | 4.82 | 2.41 | 1.91 | 6.98 |
| <i>Loxodonta africana</i> | Laws (1966) | 4000 | 1 | 15 | 17.90 | 19.10 | 2.24 | 1.76 | 25.80 |

* First age at which >50% of the females give birth.

† Based on stable, stationary age distribution where e_0 was calculated on the basis of a 1:1 sex ratio, the same mortality schedules for both sexes, and approximate litter size. The proportion of females participating was assumed 100% unless otherwise known. e_0 = mean expectation of life at birth (in years), e_m = mean expectation of life at maturity (in years), v_m = reproductive value at maturity, v_m^* = residual reproductive value at maturity, T_c = generation length (in years).

‡ Based on live-trapping data; therefore, dispersal bias possible.

§ Based on 226 squirrels aged by annual lines in the lower jaw.

to the probability of surviving to that interval; Williams 1966) was calculated as:

$$v_x^* = \frac{\ell_{x+1}v_{x+1}}{\ell_x} \quad (3)$$

Generation length (the average age of females giving birth to all offspring) was approximated from the stable age distribution after Birch (1948) and Pianka (1978) as:

$$T_c = \frac{\sum_{x=0}^{\infty} x \ell_x m_x}{\sum_{x=0}^{\infty} \ell_x m_x} \quad (4)$$

where the denominator equals 1. Since little variation existed between life tables when more than one life table was available in the literature for a given species (i.e., *Ochotona princeps*, *Sciurus carolinensis*, or *Spermophilus lateralis*), we used mean values for these parameters in the analysis.

Associations between adult body mass, age at maturity, generation length, life expectancy at birth and maturity, litter size, reproductive value at maturity, and residual reproductive value at maturity were tested with multiple correlation and regression analyses. Comparisons concerning adult body mass were made using allometric equations after both independent and dependent variables were transformed to natural logarithms.

RESULTS AND DISCUSSION

The life table and body mass characteristics for the 29 mammals (Table 1) are not expected to be exact values but are expected to indicate some general patterns common to most species. For example, generation length (T_c) is longer than life expectancy at birth (e_0) in 27 of 29 species. Generation length is the average age of females when giving birth to offspring (Pianka 1978), but most females die before giving birth to offspring. Reproductive value at maturity (v_m) is greater than residual reproductive value at maturity

TABLE 2. Allometric equations relating life history variables to adult body mass (kg) among 29 mammals. Y = dependent variable listed, M = independent variable (adult body mass), a = Y intercept, and b = slope of nonlinear regression.

| Dependent variable | $Y = aM^b$ | Coefficient of determination† (%) |
|---|----------------------|-----------------------------------|
| Age at maturity (yr) | $Y = 0.92 M^{0.27}$ | 79*** |
| Generation length (yr) | $Y = 1.74 M^{0.27}$ | 82*** |
| Life expectancy at birth (yr) | $Y = 1.19 M^{0.24}$ | 76*** |
| Life expectancy at maturity (yr) | $Y = 1.75 M^{0.23}$ | 76*** |
| Litter size | $Y = 3.43 M^{-0.16}$ | 54*** |
| Reproductive value at maturity | $Y = 4.57 M^{-0.08}$ | 41*** |
| Residual reproductive value at maturity | $Y = 2.59 M^{-0.02}$ | 2 |

† Levels of significance determined by F statistics; *** $P < .001$.

(v_m^*) in 28 of 29 species. This indicates that a daughter in an average female's first litter is more likely to replace her mother (as defined by $R_0 = 1$) than daughters in each subsequent litter.

Most life table characteristics are related to adult body mass (Table 2). Age at maturity, generation length, life expectancy at birth, and life expectancy at maturity all increase approximately as the 0.25 (range = 0.23–0.27) power of adult mass. A fairly high proportion (76–82%) of the variation in these dependent variables is attributable to adult mass. Litter size and reproductive value at maturity decrease with increasing adult mass, while residual reproductive value at maturity is not significantly ($P > .05$) related to adult mass.

Table 3 contains the interrelationships among life history traits. Although significant correlations between some trait pairs are expected simply because the traits are calculated as functions of each other (for example e_0 and e_m) or are related similarly to adult mass (for example, litter size and v_m), the magnitude of these relationships is not necessarily anticipated. Age at maturity, T_c , e_0 , e_m , and v_m were all significantly interrelated. Litter size was significantly correlated with all traits except v_m^* , while v_m^* was significantly correlated only with v_m .

In general, these data indicate that large mammals are characterized by having a greater age at maturity,

greater life expectancy, greater generation length, and, although variable, a lower reproductive value at maturity and smaller litter size than are small mammals. Four of these traits (age at maturity, adult mass, litter size, and e_m) should be true independent variables yet vary together. Further research could elucidate why this particular combination of traits exists. At present, the strong correlations between body mass and other life history traits indicate that selection favoring a change in body mass will likely result in concomitant changes in several life history traits (or the converse).

Theoretical considerations suggest that repeated reproduction will be favored if the success of prereproductive individuals is uncertain or if adults have a greater probability of surviving to the next breeding season than do their offspring (Cole 1954, Murphy 1968, Charnov and Schaffer 1973, Stearns 1976). In 27 of 29 species the life expectancy of newborn animals (e_0) is considerably less than that of adults (e_m) (Table 1) so that mammals should be (and are) iteroparous.

Our data also support Stearns' (1976) contention that age at maturity should be positively correlated with life expectancy. Age at maturity is positively correlated with e_0 and e_m ($r = .97$; $P < .001$ for both). Our data do not support Williams' (1966) suggestion that residual reproductive value should be positively correlated to adult survival. We found no significant correlation between these traits ($r = -.04$; $P > .05$).

TABLE 3. Linear correlation coefficients among life history traits from 29 mammalian life tables.

| | Age at maturity | Generation length (T_c) | Life expectancy at birth (e_0) | Life expectancy at maturity (e_m) | Reproductive value at maturity (v_m) | Residual reproductive value at maturity (v_m^*) |
|---|-----------------|-----------------------------|------------------------------------|---------------------------------------|--|---|
| Generation length (T_c) | .99*** | | | | | |
| Life expectancy at birth (e_0) | .97*** | .95*** | | | | |
| Life expectancy at maturity (e_m) | .97*** | .99*** | .92*** | | | |
| Reproductive value at maturity (v_m) | -.43* | -.41* | -.50** | -.43* | | |
| Residual reproductive value at maturity (v_m^*) | -.09 | -.04 | -.21 | -.06 | -.71*** | |
| Litter size | -.51** | -.52** | -.53** | -.57** | .71*** | .21 |

* $P < .05$; ** $P < .01$; *** $P < .001$.

Several authors have theorized expected relationships between reproductive effort and other life history traits. Hirshfield and Tinkle (1975) proposed that reproductive effort (litter size) should be inversely related to generation length, and Stearns (1976) suggested that reproductive effort should be negatively correlated with adult survival. Our data support both these contentions. Reproductive effort as indicated by litter size is negatively correlated with adult survival ($r = -.57$; $P < .01$) and generation length ($r = -.52$; $P < .01$). Our data do not support Pianka and Parker's (1975) suggestion that reproductive effort (litter size) should vary inversely with residual reproductive value due to feedback between them. No significant relationship is evident between these variables ($r = .21$; $P > .05$).

In general, many life table characteristics of mammals are interrelated, although not necessarily in the ways predicted by theory. It is of interest, therefore, to consider why these traits appear to be interrelated. Three main reasons come to mind. First, proper mammalian life tables are available for only a few taxa (11 rodents, 2 lagomorphs, 4 carnivores, 1 perissodactyl, 10 artiodactyls, 1 proboscidean), which may cause spurious correlations. Second, some traits are related because they are numerically dependent (for example, e_0 and e_m). Third, design constraints may preclude significant differences in life history patterns among mammals. Most life history traits of mammals appear bound within narrow physiological constraints (McNab 1980). Therefore, life table characteristics of only a few species most likely depict the pattern of life table evolution in most eutherian mammals. The highly predictable nature of life table characteristics indicates there is limited ability for change in mammalian life table traits.

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