# *Ecological Archives* E084-093-D1

# S. K. Morgan Ernest. 2003. Life history characteristics of placental non-volant mammals. *Ecology* 84:3402.

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## INTRODUCTION

Understanding the patterns and processes of the evolution of life history strategies is a major theme in evolutionary biology. The study of life histories often involves comparing and contrasting life history characteristics of groups of species, taking into account phylogeny and sometimes ecology. Because of the time and effort required to collect life history data from the literature, many studies that compare across gross taxonomic groups, such as orders, have relatively low sample sizes within each group. As with many studies attempting to find general patterns by comparing across species, large data sets for a diversity of species from numerous continents, habitats, and taxonomic groups are useful for addressing these questions. This data set was collected to facilitate addressing questions on general patterns of mammalian life history characteristics.

This data paper documents the development of a life history data set created for the purpose of exploring general patterns of non-volant placental mammalian life history. Information on nine life history characteristics was collected from the literature for 17 orders within the Class Mammalia. Orders not represented in this data set include Chiroptera and non-placental mammals. Chiroptera was not included because an extensive, high quality database has recently been published (K. E. Jones, A. Purvis, J. L. Gittleman. 2003. American Naturalist **161**:601–614). Non-placental mammals were not included because of their radically different life history. While there is a taxonomic restriction in the data set, there is no geographic restriction. Terrestrial and aquatic species are both heavily represented in this data set, as are all major continents. Species represent a variety of trophic levels, habitats, and ecologies.

One of the challenges in compiling a life history data set for mammals is that life history characteristics can change with environmental conditions. Here, I attempted to create a general life history for each species by drawing from a variety of sources for each life history variable. Therefore, the life histories in this data set are not integrated life histories of a population but should be considered a general life history of the species.

## METADATA CLASS I. DATA SET DESCRIPTORS

### A. Data set identity:

**Title**: Life History Characteristics of Placental Non-Volant Mammals

### B. Data set identification code

**Suggested Data Set Identity Code**: Mammal_lifehistories_v2.txt

### C. Data set description

**Principal Investigator**: S.K. Morgan Ernest, Department of Biology, University of New Mexico, Albuquerque, NM, USA, 87131

**Abstract:**

The purpose of this dataset was to compile general life history characteristics for a variety of mammalian species to perform comparative life history analyses among different taxa and different body size groups. Data were collected from the literature and data sources are documented for each species within the data file. Since life history characteristics will show minor variation with environmental conditions (resource availability, climate, competitive environment, and predation pressure) a general life history for each species was sought to average over minor differences in local populations. To create a general life history for each species, life history values are often an average from several literature sources. Life history variables included in the data set are: Maximum life span (months), Age of First Reproduction (months), Gestation time (months), Weaning age (months), Weaning Mass (grams), Litter size (months), litters per year, new born mass (grams), and adult body mass (grams). Since these data were collected with the intent to examine general life history patterns, these data are good for examining large-scale patterns, specifically in comparing life history characteristics for different orders or families of mammals. All orders of placental mammals, except Chiroptera (bats) are represented in this data set: Artiodactyla (161 species), Carnivora (197), Cetacea (55 species), Dermoptera (2 species), Hydracoidea (4 species), Insectivora (91 species), Lagomorpha (42 species), Macroscelidea (10 species), Perissodactyla (15 species), Pholidota (7 species), Primates (156 species), Proboscidea (2 species), Rodentia (665 species), Scandentia (7 species), Sirenia (5 species), Tubulidentata (1 species), and Xenarthra (20 species). There are two caveats on this data set, however. First, these data are not appropriate for asking population-level questions where the integration of life history parameters with specific environmental conditions is important. Second, while this data set is extensive, it is not exhaustive. The creation of an exhaustive data set is the ultimate goal, but that goal is still several years from completion. In the meantime, researchers utilizing the data set are urged to conduct their own search for data not reported within the current dataset. Researchers are also encouraged to contact the author of the dataset and alert her to literature sources containing data for missing variables or species. The updated data set will be made available to *Ecological Archives* periodically.

**D. *Key words:*** *Non-volant mammals; life history; maximum life span; age of first reproduction; gestation time; weaning age; litter size; litters per year; newborn mass; adult mass*.

## CLASS II. RESEARCH ORIGIN DESCRIPTORS

### A. Overall project description

**Identity:** Life History of Non-volant placental Mammals

**Originator:**

S. K. Morgan Ernest
Department of Biology
University of New Mexico
Albuquerque, NM 87131

**Period of Study:** 1998–indefinite

**Objectives:** To understand general patterns of life history evolution, comparing life histories of species of various taxa and body sizes.

**Abstract:** same as above. This data set is not a subset of larger program of study.

**Source(s) of funding:** S. K. M. E. has been supported by various sources of money while compiling this data set. Recent support has been received from a Biocomplexity grant from NSF (DEB-0083422).

## B. Specific subproject description

**Site description:** Data were obtained from species from a variety of habitats, geologies, hydrologies, etc. This is a worldwide data set, including species from all continents and all major habitat types.

**Experimental or sampling design:** Data were obtained from published sources written by mammalogists.

**Research Methods:**

Field/Laboratory:

*Data Sources*: Data were collected from published sources written by experienced mammalogists. References for data sources are found in Class IV Data Structural Descriptors, Section B. These sources are numerically indexed in the references column of the data set. Reference numbers refer to the order in which these data sources were entered into the dataset.

*Data Collection:* Each life history variable in the data set is a compilation from many data sources. The use of multiple sources reduces the influence of erroneous data points and yields an overall average for the species across environmental conditions. The original data set is in MSExcel format and each life history cell is set up with the Average function which continually recalculates the average as new data is entered into the cell. The resulting average across all sources entered is what is available in the text data file Mammal_lifehistories_v2. This method was not used for Maximum Life Span (see *Life History Variables* in this section)

Different data sources contain different forms of data, ranging from raw data from numerous individuals, to summarized data in the forms of averages and ranges. If averages were available these were entered preferentially. Raw data were used to calculate an average which was then used in the dataset. If only ranges were available, the midpoint of the range was entered. Ranges were only used if no other data were available for that life history variable in that data source. Due to the size and complexity of the database, each source is treated as an independent estimate and sample sizes are not factored into the average.

Since most data came from other compilations, it is very difficult to ensure that the same primary literature source was not used multiple times. However, data were not used if the citation for it matched a reference already in the reference list for the data set. Since many species have only a

couple of citations and the number of numerically identical entries for a life history variable is small, this is unlikely to have a major influence on the results.

After the entry data from reference 26, a new rule was implemented for data collection. Since time and resources are limited, continuing to collect data for species with well-characterized life history variables (i.e., 10 or more estimates for a life history variable) lead to decreased efficiency. Therefore, after any specific life history variable for a specific species reaches 10 entries, it is determined to be well characterized and data collection for that variable for that species stops. This number was chosen because after 10 entries, the average changes very little with each new entry and when there are more than 10 entries the probability of duplicating a source increases. Since this rule was not implemented until the entry of reference 26, there are still a number of species with life history variables characterized by >10 entries.

*Life History Variables*: Nine life history variables were collected. This section contains the specific definitions used in collecting these data.

Maximum life span: Maximum life span (months) is the oldest age recorded for a member (male or female) of that species. Maximum life span, unlike the other variables, represents a single datapoint *not an average*. If a longer maximum life span is found than the number currently in the database, then the previous datapoint is replaced with the new value.

Age of First Reproduction (AFR): AFR is the age (months) at which a female individual of the species first breeds and could potentially conceive. By definition, this is only recorded for females. This variable does not include gestation. If the age of first birth is given by a data source then gestation length was subtracted from the value to yield an estimate of first breeding.

Gestation length: Gestation (months) is the length of active gestating of a fetus. Gestation length does not include the period of delayed implantation.

Weaning length: Weaning length (months) is the time from the birth of an offspring to the independence of that offspring from milk.

Weaning mass: Weaning mass (grams) is the weight of a single offspring at the time of independence from milk.

Litter size: The number of offspring birthed in a single litter. If a data source indicated that its litter size estimate was based on embryo counts or reproductive scars, it was excluded since it is relatively common for a subset of embryos in a litter to be resorbed.

Litter frequency: The number of litters birthed by a female in a 12-month period. Captive studies attempting to maximize litter production were excluded as possible.

Neonate mass: The weight (grams) of a single newborn offspring. If a data source indicated that the mass of the newborn was taken > 12 hours after birth it was excluded.

Adult mass: The weight (grams) of a reproductive adult. If strong sexual dimorphism exists in a species, then only data sources specifying female weight were included. References 16 and 18 were only used for body masses. Furthermore, these references were only used if other body mass

estimates were not available from the sources which supplied life history data.

*Taxonomy*: Taxonomy follows Wilson, D. E., and D. M. Reeder, editors. 1993. Mammal species of the world, Second Edition. Smithsonian Institution Press, Washington, D.C., USA.

**Project Personnel:** S. K. Morgan Ernest

## CLASS III. DATA SET STATUS AND ACCESSIBILITY

### A. Status

**Latest Update:** 25 August 2003

**Latest Archive date:** n/a

**Metadata status**: 25 August 2003, metadata is current

**Data verification:** data has undergone initial data quality and assurance checking, though this is an on-going process.

### B. Accessibility

**Storage location and medium:** Original data file exists on author's personal computer in MSExcel format. A copy in text format resides on the Sevilleta Long-term ecological site mainframe on the author's account.

**Contact person:** S.K. Morgan Ernest, Department of Biology, University of New Mexico 87131, phone: 505.277.6437, fax: 505.277.0304, email: mernest@unm.edu

**Copyright restrictions:** None

**Proprietary restrictions:** None

**Costs:** None, author believes scientific data should be free for scientific use.

## CLASS IV. DATA STRUCTURAL DESCRIPTORS

### A. Data Set File

**Identity:** Mammal_lifehistories_v2.txt

**Size:** 1440 records, not including header row.

**Format and Storage mode:**Ascii text, tab delimited. No compression schemes used.

**Header information:** Headers are given here as header name followed by more information such as measurement units or other basic descriptor. More information on the variable definitions can be found in Section B, variable information. Order, Family, Genus, Species, Adult Mass (grams), Gestation time (months), Newborn mass (grams), Weaning Age (months), Weaning Mass (grams),

Age of First Reproduction (months), Maximum life span (months), Litter size, Litters per year, reference list.

**Alphanumeric attributes:** Mixed

**Special characters/fields:** -999 denotes lack of information on that life history character for that species.

**Authentication procedures:** The following are sums for the numeric columns:

Adult mass=552350473.58; Gestation length=-413634.01; Newborn mass=9652529.75; Weaning age=-615124.25; Weaning mass=23110460.38; Age of First Reproduction =

-587698.17; Maximum life span=-705968.00; Litter size=-80112.72; Litter frequency=

-687082.61

**B. Variable definitions**

| Variable name | Variable definition | Units | Storage type | Range numeric values (-999 not incl.) | Missing value codes |
|---|---|---|---|---|---|
| Order | Taxonomic order of species | N/a | Character | N/a | N/a |
| Family | Taxonomic family of species | N/a | Character | N/a | N/a |
| Genus | Genus to which species belongs | N/a | Character | N/a | N/a |
| Species | Species epithet | N/a | Character | N/a | N/a |
| Adult mass | Average mass of a non-pregnant adult female | Grams | Floating point | 2.1-149000000 | -999 |
| Gestation length | Average length of time for the gestation of a live offspring. Delayed implantation not included in gestation length | Months | Floating Point | 0.49-21.46 | -999 |
| Newborn mass | Average mass of a newborn immediately after birth | Grams | Floating point | 0.21-2250000 | -999 |
| Weaning age | Average age (measured from birth) when offspring begins eating solid food | Months | Floating point | 0.30-48 | -999 |
| Weaning mass | Average mass of one offspring when offspring begins eating solid food | Grams | Floating point | 2.09-19075000 | -999 |
| Age of First Reproduction | Average age when female typically conceives her first offspring | Months | Floating point | 0.7-210 | -999 |
| Maximum life span | Maximum length of time a member of either sex has been | Months | Integer | 12-1368 | -999 |

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|---|---|---|---|---|---|
| | observed to live | | | | |
| Litter size | Average number of live offspring produced in one litter | N/a | Floating point | 1-14.18 | -999 |
| Litter frequency | Average number of litters per year that a female produces | $Year^{-1}$ | Floating point | 0.14-7.5 | -999 |
| Reference list | Index numbers for the data sources used for that species. See Section C, below for cross-reference for citations and reference numbers | N/a | Comma delimited integers | 1-29 | N/a |

*Notes*: Missing values are indicated by the number "-999". There are no text fields with missing data. N/a indicates a category which is not applicable for that variable.

## CLASS V. SUPPLEMENTAL DESCRIPTORS

### A. Data acquisition

Data forms: n/a

Location of completed data forms: n/a

### B. Quality assurance/quality control procedures

Data were entered directly from source material into the computer file and values were double checked upon entry. After complete entry of data, data points were randomly selected and checked against original source material until approximately 60% of points had been checked against source material. After the initial data-checking phase was complete, regressions were created for each variable and compared against published regressions. All regressions matched published regressions closely for both slope and intercept. Outliers were re-examined against source material to determine if values in data set were correct. If data values matched source material an attempt was made to find another data source to confirm that value was not a mistake in the source material.

### C. Related material: n/a

### D. Computer programs and data processing algorithms: n/a

### E. Archiving: n/a

### F. Publications and results:

*Reference list for data set*: Data sources used for each species are indexed in the final column of the data set: Mammal_lifehistory_v2.txt.

| Reference number | Citation |
|---|---|
| 1 | Hayssen,V., and A. Van Tienhoven. 1993. Asdell's patterns of mammalian |

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| | reproduction. Comstock Publishing Associates, Ithaca, New York, USA. |
| 2 | Nowak, R. M. 1999. Walker's Mammals of the World. Volume 1 and 2. John Hopkins University Press, Baltimore, Maryland, USA. |
| 3 | Eisenberg, J. F. 1989. Mammals of the Neotropics. Vol. 1. University of Chicago Press, Chicago, Illinois, USA. |
| 4 | Redford, K. H., and J. F. Eisenberg. 1992. Mammals of the Neotropics. Vol. 2. University of Chicago Press, Chicago, Illinois, USA. |
| 5 | Murie, J. O., and G. R. Michener, editors. 1984. The Biology of Ground-Dwelling Squirrels. University of Nebraska Press, Lincoln, Nebraska, USA. |
| 6 | Verts, B. J., and L. N. Carraway. 1998. Land Mammals of Oregon. University of California Press, Berkeley, California, USA. |
| 7 | Millar, J. S. 1977. Adaptive features of mammalian reproduction. Evolution **31**:370–386. |
| 8 | Purvis, A., and P. H. Harvey. 1995. Mammal life-history evolution: a comparative test of Charnov's model. Journal of Zoology **237**:259–283. |
| 9 | Saether, B. E., and I. J. Gordon. 1994. The adaptive significance of reproductive strategies in ungulates. Proceedings of the Royal Society of London **256**:263–268. |
| 10 | Gittleman, J. L., editor. 1989. Carnivore behavior, ecology, and evolution. Comstock Publishing Associates, Ithaca, New York, USA. |
| 11 | American Society of Mammalogists. Mammalian Species Accounts. |
| 12 | Symonds, M. R. E. 1999. Life histories of the Insectivora: the role of phylogeny, metabolism, and sex differences. Journal of Zoology **249**:315–337. |
| 13 | Parker, S. P., editor. 1989. Grzmek's Encyclopedia of Mammals. McGraw-Hill, New York, New York, USA. |
| 14 | Hoffmeister, D. F. 1986. Mammals of Arizona. University of Arizona Press, Tucson, Arizona, USA. |
| 15 | Strahan, R. 1995. Mammals of Australia. Smithsonian Institution Press, Washington, D.C., USA. |
| 16 | Silva, M., and J. A. Downing. 1995. CRC Handbook of Mammalian Body Masses. CRC Press, Boca Raton, Florida, USA. |
| 17 | McDonald, J. N. 1984. The reordered North American selection regime and late Quaternary Megafaunal Extinctions. *In* P. S. Martin, and R. G. Klein, editors. Quaternary Extinctions. University of Arizona Press, Tucson, Arizona, USA. |
| 18 | Smith, F.A., S. K. Lyons, S. K. M. Ernest, K. E. Jones, D. M. Kaufman, T. Dayan, P. A. Marquet, J. H. Brown, and J. P. Haskell. Body mass of late Quaternary mammals. Ecological Archives E084-094. |
| 19 | Heptner, V. G., A. A. Nasimovich, and A. G. Bannikov. 1961. Mammals of the Soviet Union. Vol. 1. VysshayaShkola Publishers, Moscow, USSR. |
| 20 | Emmons, L. H. 1990. Neotropical rainforest mammals. University of Chicago Press, Chicago, Illinois, USA |
| 21 | Garbutt, N. 1999. Mammals of Madagascar. Yale University Press, New |

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| | Haven, Connecticut, USA. |
| 22 | Harvey, P. H., and T. H. Clutton-Brock. 1985. Life-history variation in primates. Evolution **39**:559–581. |
| 23 | Wootton, J. T. 1987. The effects of body mass, phylogeny, habitat, and trophic level on mammalian age at first reproduction. Evolution **41**:732–749. |
| 24 | Kappeler, P. M., and M. E. Pereiva, editors. 2003. Primate life histories and sociology. University of Chicago Press, Chicago, Illinois, USA. |
| 25 | Delany, M. J., and D. C. D. Happold. 1979. The ecology of African mammals. Longman Press, London, UK. |
| 26 | Wilson, D. E. and S. Ruff, editors. 1999. The Smithsonian Book of North American Mammals. Smithsonian Institution Press, Washington, D.C., USA. |
| 27 | Keltie, R. A. 1988. Gestation as a constraint on the evolution of seasonal breeding in mammals. Pages 257–258 in M. S. Boyce, editor. Evolution of Life Histories of Mammals. YaleUniversity Press, New Haven, Connecticut, USA.. |
| 28 | Swihart, R. K. 1983. Body size, breeding season length, and life history tactics of lagomorphs. Oikos **43**:282–290. |
| 29 | Eisenberg, J. F. 1981. The Mammalian Radiations: an analysis of trends in evolution, adaptation, and behaviour. University of Chicago Press, Chicago, Illinois, USA. |


*Publications citing the data set*: These data have been used in three publications.


Charnov, E. L. 2001.Evolution of mammal life histories. Evolutionary Ecology Research **3**:521–535.

Moses, M. M., and J. H. Brown. 2003.Allometry of human fertility and energy use. Ecology Letters **6**:295–300.

Ernest, S. K. M.**,** B. J. Enquist, J. H. Brown, Eric L. Charnov, J. F. Gillooly, V. M. Savage, E. P. White, F. A. Smith, E. A. Hadly, J. P. Haskell, S. K. Lyons, B. A. Maurer, K. J. Niklas, and B. Tiffney. *In Press*. Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecology Letters.


## G. History of data set usage

*Data request history*: A limited number of people have requested usage of this data set and while many projects are currently underway, few are as yet published. A list of people and their purposes are as follows:

| **Person** | **Purpose** |
|---|---|
| Dr. Eric L. Charnov, University of New Mexico | Used one variable for illustrative figure in published paper |
| Dr. Han Olff, University of Groeningen | Used one variable for illustrative figure in potential manuscript |
| Melanie Moses and Dr. James H. Brown, | Used in analysis comparing human life history |

| | |
|---|---|
| University of New Mexico | traits with primates and other mammals |
| Lisa Schwanz, University of New Mexico | General exploration of life history characteristics of mammals |

**H. Data set update history:**

A major overhaul of the life history data set, which was formerly known as AFR3.xls, occurred over the summer of 2002. The current version reflected an addition of a new life history variable, weaning mass, and many species not represented in AFR3.xls. The paper published by E. L. Charnov (2001) used data from AFR3.xls. The manuscript by M. E. Moses and J. H. Brown uses the previous data set Mammal_lifehistories_v1. (See publications and results).

**Review history**: n/a

**Questions and comments from secondary users**: n/a

**ACKNOWLEDGMENTS**

Special thanks to Eric Charnov for challenging me to explore mammalian life histories and for consultation during the development of the data set (though any errors are mine, not his!), K. E. Jones for extensive discussions on life histories and databases, and to S. K. Lyons for allowing me to raid her library.

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