Demographic Research a free, expedited, online journal
of peer-reviewed research and commentary
in the population sciences published by the
Max Planck Institute for Demographic Research
Konrad-Zuse Str. 1, D-18057 Rostock · GERMANY
www.demographic-research.org

DEMOGRAPHIC RESEARCH

VOLUME 15, ARTICLE 14, PAGES 413-434
PUBLISHED 17 NOVEMBER 2006
http://www.demographic-research.org/Volumes/Vol15/14/
DOI: 10.4054/DemRes.2006.15.14

Research Article

Comparative mortality levels among selected species of captive animals

Iliana V. Kohler

Samuel H. Preston

Laurie Bingaman Lackey

Table of Contents

Demographic Research – Volume 15, Article 14
research article

Comparative mortality levels among selected species of captive animals

Iliana V. Kohler [1]

Samuel H. Preston [2]

Laurie Bingaman Lackey [3]

Abstract

We present life tables by single year of age and sex for groups of animals and for 42 individual mostly mammalian species. Data are derived from the International Species Information System. The survivorship of most of these species has never been mapped systematically. We demonstrate that, in most of the groups, female survivorship significantly exceeds that of males above age five. Wild-born animals do not have mortality that differs significantly from captive-born animals. While most species have mortality that rises with age above the juvenile stage, there are several groups for which the age pattern of mortality is nearly level.

---

[1] Corresponding author; Postdoctoral Fellow and Research Associate, Population Studies Center, University of Pennsylvania, 3718 Locust Walk, Philadelphia, PA 19104-6299, USA; *Tel.*: +1-(215)-898-7990; *Fax*: +1-(215)-898-2124; *Email:* iliana@pop.upenn.edu.

[2] Fredrick J. Warren Professor of Demography, 3718 Locust Walk, University of Pennsylvania, Philadelphia, PA 19104-6299, USA; *Email:* spreston@sas.upenn.edu.

[3] International Species Information System - ISIS, 2600 Eagan Woods Dr. Suite 50, MN 55121-1170, USA; *Email:* laurie@isis.org.

1. Introduction

Authoritative accounts of survivorship and length of life exist for very few species. In the wild, uncertainty about the survival status of animals lost to follow up and imprecision of age assignment are important hurdles to the accurate mapping of survival. Both in the wild and in captivity, the small number of animals typically under observation entails substantial variability in estimates. Because so few data exist for any single species, comparisons of mortality across species are virtually non-existent.

The present study is an effort to begin addressing the deficiency of systematic data on species survival. This collection of life tables can also enrich data sets aimed at compiling life history characteristics for various species (e.g. Ernest, 2003). The study utilizes a large international data set, the International Species Information System (ISIS). ISIS was founded in 1973 as a network of approximately 50 North American and European zoos. The ISIS data base currently contains reports from approximately 650 zoos and aquaria from over 70 countries on six continents. The database contains records of over 2 million individual zoo specimens. The selection of species for the present investigation was based upon the specimens collection in the Smithsonian's National Zoo in Washington D.C., whose comparative mortality levels for recent years were examined in an unpublished analysis.

A species' mortality profile in captivity can be expected to differ systematically from that in the wild. Courteney and Santow (1989) note that animals in captivity have the benefits of veterinary care, a lack of predators, and a regular supply of food. On the other hand, captive animals may suffer from higher levels of obesity (Taylor and Poole, 1998; Ward et al., 2003), injuries from exhibits (Leong et al., 2004), poor adaptation to captivity or to a zoo's climate (Karstad and Sileo, 1971; Gozalo and Montoya, 1991) and from inbreeding that results in higher perinatal mortality (Wielebnowski, 1996). In addition, close quarters may facilitate the spread of infections, including those derived from other species (Ward et al., 2003; de Wit, 1995). These relative risks will vary from species to species and from age to age, although the process of senescence may be similar in wild and captive populations of the same species (Hill et al., 2001).

2. Description of data and analytic scheme

We have selected 51 species for investigation. An individual animal is included in the data set if it were a member of one of these species and if it were living or born in one of the reporting zoos at any time during a recent period January 1, 1998—December 31, 2003. Altogether, 35,229 animals are included in the data set. The record for each animal includes fields for date of birth, date of arrival at the zoo, date of death, and date of departure from the zoo. It also includes information about sex, whether the animal was born in the wild or in captivity, and an assessment of the quality of information about birth date.

The life tables that will be constructed are 'period' tables based upon age-specific mortality rates observed during the period from January 1, 1998 to December 31, 2003. Rather than following an actual cohort of births throughout life, a period life table follows a synthetic cohort of births and assumes that they are subject at each age to the age-specific death rates observed during a particular period (Preston et al., 2001).

Although the number of observations available on each species is larger than in nearly all other studies, it is small enough that the estimation of age-specific death rates is subject to substantial random error. Accordingly, we begin by creating large groups of species based on order. We then examine how the mortality of each species relates to the average mortality of the group. In our analyses, we treat species as independent statistical units. Species, however, are part of hierarchically structured phylogeny, and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution (Felsenstein, 1985). Some methods have been proposed to circumvent this problem if adequate information on the phylogeny is available (Felsenstein, 1985). These analyses, however, are beyond the scope of the present paper. Any potential nonindependence resulting from species sharing the same phylogeny in our analyses results in an underestimation of the standard errors, and an overestimation of the statistical significance of differences between species. The key findings of this paper that pertain to the general mortality patterns of species, however, are unlikely to be affected by this nonindependence.

Table 1 identifies the species under study, the number of individual animals contributing observations to the analysis of survivorship, and the groupings that we have constructed.

There are three types of entrance to the observational frame: birth in a reporting zoo during the period January 1, 1998—December 31, 2003; migration into a reporting zoo during this period; and survival in a reporting zoo past the beginning of the observational period. Likewise, there are three sources of exit from the observational frame: death during the period; out-migration during the period; and survival past the terminal date of the observational period (censoring). The events are reported according to the day, month, and year that they occurred, so that the exact number of animal-years contributed by each individual animal can be calculated. Age-specific death rates are constructed in a conventional fashion by counting the number of deaths in a particular age-time bloc and dividing that number by the exact number of animal-years lived in that age-time bloc.

Although detailed dates are reported for each event, they are not always accurate. The greatest risk of error pertains to birth date for animals born in the wild or whose origins were not recorded. Birth dates and ages typically must be estimated for these

Table 1: Species and groups of species investigated.

Group name	Species included	Number of animals
Apes	Gorilla (Gorilla gorilla)	868
	Orangutan (Pongo pygmaeus)	675
	Siamang (Hylobates syndactylus)	357
	White-cheeked gibbon (Hylobates leucogenys)	169
	Total	2,069
Small primates	Ring-tailed lemur (Lemur catta)	2,545
	Ruffed lemur (Varecia variegata)	1,873
	Pygmy marmoset (Callithrix pygmaea)	1,310
	Colobus monkey (Colobus guereza)	960
	Geoffroy's marmoset (Callithrix geoffroyi)	840
	Golden lion tamarin (Leontopithecus rosalia)	774
	Goeldi's monkey (Callimico goeldi)	638
	Brown lemur (Eulemur fulvus)	576
	Golden-headed lion tamarin (Leontopithecus chrysomelas)	533
	Lion-tailed macaque (Macaca silenus)	507
	Sulawesi crested macaque (Macaca nigra)	348
	Howler monkey (Alouatta caraya)	269
	Dusky titi monkey (Callicebus moloch)	10
	Total	11,183
Carnivores	Lion (Panthera leo)	1,939
	Tiger (Panthera tigris)	1,626
	Cheetah (Acinonyx jubatus)	1,065
	Fennec fox (Vulpes zerda)	430
	Serval (Leptailurus serval)	422
	Bobcat (Lynx rufus)	406
	Fishing cat (Prionailurus viverrinus)	283
	Leopard cat (Prionailurus bengalensis)	257
	Caracal (Caracal caracal)	230
	Mexican grey wolf (Canis lupus baileyi)	227
	Spectacled bear (Tremarctos ornatus)	176
	Sloth bear (Melursus ursinus)	105
	New Guinea singing dog (Canis lupus hallstromi)	70
	Giant panda (Ailuropoda melanoleuca)	16
	Total	7,252

(Continued)

Table 1 (Continued): Species and groups of species investigated.

Group name	Species included	Number of animals
Hoofstock	North American bison (Bison bison)	1,810
	Arabian oryx (Oryx leucoryx)	1,079
	Reeves’s muntjac (Muntiacus reevesi)	954
	Przewalski’s wild horse (Equus caballus przewalskii)	666
	Grevy’s zebra (Equus grevyi)	552
	Dorcas gazelle (Gazella dorcas)	491
	Eld’s deer (Cervus eldi)	445
	Speke’s gazelle (Gazella spekei)	140
	Total	6,137
Kangaroos	Red kangaroo (Macropus rufus)	1,988
	Western grey kangaroo (Macropus fuliginosus)	581
	Total	2,569
Crocodilians	American alligator (Alligator mississippiensis)	1,914
	Johnston’s crocodile (Crocodylus johnstoni)	188
	Cuban crocodile (Crocodylus rhombifer)	67
	Indian gavial (Gavialis gangeticus)	33
	Total	2,202
Ratites	Greater rhea (Rhea americana)	1,383
	Common emu (Dromaius novaehollandiae)	1,207
	Cassowary (Casuarius casuarius)	213
	Darwin’s rhea (Pterocnemia pennata)	150
	Total	2,953
Raptors	Bald eagle (Haliaeetus leucocephalus)	649
	King vulture (Sarcorhamphus papa)	215
	Total	864
Total Number of Animals		35,229

animals based upon age-characteristic behavior and morphology. When an animal with an uncertain birthdate enters a zoo, its birthdate will often be recorded as January 1. Table 2 shows the proportion of animals in each group with a stated birthdate of January 1. Overall, about one in every 24 animals is credited with a January 1 birth date. Clearly, the dating is least precise for crocodilians, where one in five is assigned a January 1 birth date. Apes and small primates have the lowest percentage in this category, suggesting that age assignment is unusually precise for them.

Table 2: Number of cases (N) and percentage of animals with birthdays reported as January, 1st.

Group Name	N	Percentage
Apes	49	2.37
Small primates	193	1.73
Carnivores	196	2.70
Hoofstock	200	3.26
Kangaroos	114	4.44
Crocodilians	412	18.71
Ratites	208	7.04
Raptors	75	8.68
Total	1,447	4.11

A second area of data ambiguity also relates to the beginning of life. Analysis of human longevity almost invariably begins with a live birth, typically defined following World Health Organization criteria as an infant who shows any sign of life ([WHO] World Health Organization, 1977). Fetal mortality is studied as a separate process. The requirements of animal husbandry in zoos do not always admit a fine distinction between live births and stillbirths, and there are group-specific conventions regarding how to record the reproductive effort of different species. Among mammals, it is customary to include stillbirths among the births, with no distinction between live-born and stillborn offspring. Among birds and crocodilians, on the other hand, a birth is typically not counted until an egg is hatched. There are many instances in the ISIS database in which deaths are recorded at age 0.00, a group that probably includes a mixture of stillbirths and live births. Life expectancy estimates are very sensitive to the estimation of the probabilities of death among the very young. In order to account for this sensitivity and to effect a partial distinction between stillbirths and live births, we include in all life tables information on survivorship from age zero to age one week as well as survival beyond one week.

3. Results

3.1 Life tables for groups of species

To draw a preliminary picture of the characteristic mortality profiles of various large groups of animals, we combine species in the fashion shown in Table 1. The calculation of life tables for these groups is technically straightforward once a decision is made about how to 'complete' the life table by adopting an estimate of life expectancy at the oldest ages. A standard procedure is to invoke a relation characteristic of a stationary population according to which life expectancy at the beginning of the open-ended age interval is the reciprocal of the death rate above that age (Preston et al., 2001). One problem with this approach in the present circumstance is that relatively few animals contribute observations at very high ages and as result, the estimate of life expectancy at the oldest ages is subject to considerable sampling variability. In addition, the mortality rates at the oldest ages may be biased by measurement problems such as age misreporting or the improper presence in the data set of animals whose death at an earlier age was not registered.

An alternative approach to estimating mortality in the highest age interval is to fit a statistical model to data at younger ages and extrapolate the value of that function into the oldest age interval. The most common statistical function used for this purpose is the Gompertz curve ($\mu(x) = ae^{bx}$), which specifies an exponential increase in the mortality hazard with age. In our case the data are too sparse to allow us to distinguish confidently among various competing mortality models. The Gompertz model is chosen because of its simplicity (having only a level and a slope parameter), its familiarity, and the fact that it does a good job of representing adult mortality levels in a wide variety of species (Carnes et al., 1996).

We have applied both approaches to estimate life expectancy at the age that begins the open-ended interval. We select that age to be the lowest integer age above which fewer than 2% of recorded deaths occur. The Gompertz function was fit to the individual-level animal data by using a standard maximum likelihood estimation procedure in STATA. The coefficient of correlation between the two series (N=7) is .89. This value is reassuringly high in view of the fact that the methods of calculation are entirely independent of one another. Except for raptors, for whom the Gompertz model estimates a negative slope of the age-specific death rates, we use the Gompertz values hereafter because the model is parsimonious and provides accurate fit to the data.

Table 3 shows selected values from the life tables of these groups. Apes have the highest life expectancy (expected number of additional years of life) at all ages and kangaroos the lowest. Mortality levels in the first week of life are highly variable across groups. Small primates and carnivores lose nearly 30% of births during this period, while crocodilians lose only 2.5%. As noted above, some of the differences in first-week mortality among the groups are probably attributable to different ways of recording stillbirths. Nevertheless, the effect of variation in mortality during the first week of life on the rank ordering of life expectancy is small. The ranking of groups from highest to lowest life expectancy at one week of age is nearly the same as the ranking at age zero. By age one, however, ratites have vaulted upwards in the life expectancy rankings as they escape infancy and their exceptionally high infant mortality rate.

Table 3: Selected life table parameters for groups of animals.

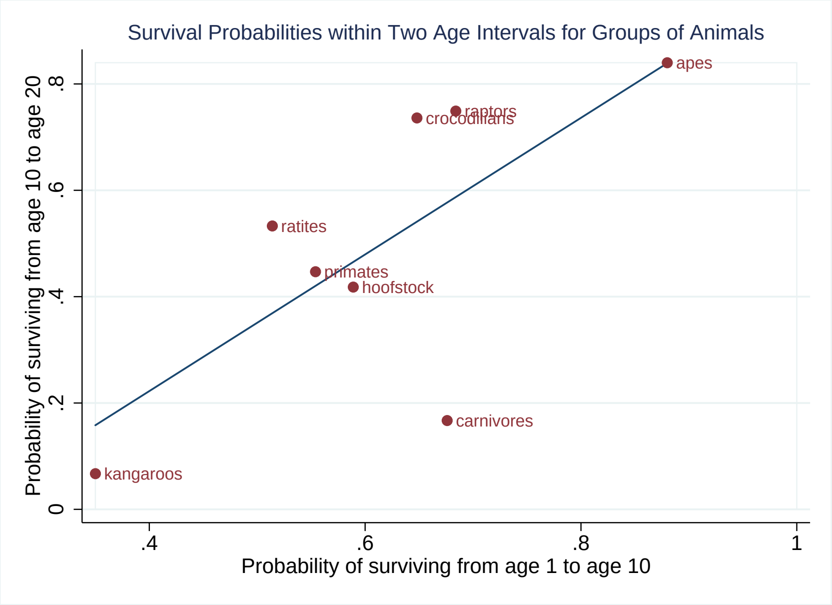
		Number of animals (per 1,000 births) surviving to different ages							
		1 week	*1 year*	*2 years*	*5 years*	*10 years*	*15 years*	*20 years*	*25 years*
Apes		837	747	727	700	657	602	552	473
Small Primates		715	614	574	475	340	234	152	
Carnivores		713	568	534	480	384	211	64	
Hoofstock		862	732	672	577	431	295	180	
Kangaroos		936	762	666	485	267			
Crocodilians		975	836	751	634	542	470	399	314
Ratites		870	525	463	382	270	205	144	94
Raptors		778	689	663	590	471	393	353	315
		Life expectancy (in years) at selected ages							
	age 0	*1 week*	*1 year*		*5 years*	*10 years*	*15 years*		
Apes	24.20	28.88	31.33		29.30	26.06	23.23		
Small Primates	8.45	11.80	12.70		11.84	10.58	9.29		
Carnivores	7.39	10.34	11.87		9.72	6.50	4.73		
Hoofstock	10.05	11.63	12.63		11.59	9.68	7.92		
Kangaroos	6.23	6.64	7.06		6.09	4.07	3.08		
Crocodilians	19.00	19.47	21.63		24.09	22.77	20.91		
Ratites	7.76	8.90	13.45		13.88	12.21	11.59		
Raptors	16.57	21.27	22.97		22.77	22.64	21.76		

The age-pattern of mortality clearly differs among the groups. Beyond age 5, raptors show little sign of an increase in mortality. Life expectancy at 15 years is nearly the same for them as it is at ages 1, 5, or 10. Crocodilians also show a slow diminution of life expectancy with age. Other groups show a more conventional fall-off in life expectancy as age advances.

Groups that have high mortality at one age tend to have high mortality at other ages. Figure 1 plots the probability of surviving from age 1 to age 10 against the probability of surviving from age 10 to age 20 for the various groups. The coefficient of correlation between the two series is .71. Kangaroos, for whom the probability of survival to age 20 is derived from the Gompertz model, are lowest on both indicators and apes are highest.

Other groups generally fall in an orderly intermediate position with the exception of carnivores, who have moderate mortality between ages one and ten and quite high mortality between ages 10 and 20.

Figure 1: Scatterplot of survival probabilities within two age intervals for groups of animals



As theory predicts and as will be demonstrated below, mortality in these heterogeneous groups rises less rapidly with age than it typically does in the individual species that make up the groups. The most longevous species become relatively more prevalent with age, imparting a downward bias to the age-slope of mortality for the group as a whole (Vaupel and Yashin, 1985).

3.2 Mortality variation by species, sex, and birth type

In order to identify how mortality varies by species within groups, we assume that the effect of a particular covariate such as sex or taxonomy has the same proportional effect on the hazard of death at all ages beyond five within the group. We estimate a nonparametric piecewise-constant proportional hazard model, with the mortality hazard at age x specified as

$$\mu(x) = h_0(x)\exp(\beta z_i), \tag{1}$$

where $h_0(x)$ is the piecewise-constant specification of the baseline hazard with constant mortality risks within one year age intervals, and z_i are binary variables for sex, birth type or taxonomy of the animal.

The proportional hazard approach enables us to identify how the mortality of each species relates to that of all other species within the group. Other covariates available in the data set that can also be examined are sex and animal's place of birth (i.e., wild, captivity or unknown place of birth). We estimate the hazard models from age 5 because the proportionality assumption seems less likely to hold across younger ages.

The reference categories that we choose for this analysis (the categories to which all other categories will be compared) are males, animals born in captivity, and the species that contributes the largest number of observations within a group. Animals of unknown sex are excluded from the analysis by sex, but included in other model specifications.

Table 4 shows the coefficients pertaining to sex. Four of the eight groups—apes, hoofstock, crocodilians, and kangaroos—demonstrate significant sex differences in mortality beyond age five. In each of these cases, females have mortality that is lower than that of males by 33-40%. Sex differences are smaller and insignificant in the remaining groups. Previous studies of sex differences in mortality have typically been based upon fewer observations and indirect indicators, such as the sex ratio of the living population (Taylor and Poole, 1998; Hill et al., 2001; Promislow, 1992). Our results offer partial support to a generalization that has emerged from this literature that males typically have higher mortality among mammals (Promislow, 1992).

There are several reports in the literature of animals who suffer excess mortality when brought into a zoo, relative to animals born and reared in the zoo (Wallace et al., 1987; Tocidlowski et al., 1997; Gozalo and Montoya, 1991). Emotional trauma and exposure to new diets and disease environments are among the causes cited. Table 4 also presents the mortality levels of wild-born animals relative to those of captive-born animals. In none of the groups is the effect of being wild-born statistically significant, and in four of the eight groups the mortality of wild-born animals is lower than that of zoo-born animals. Excess mortality of wild-born animals brought to zoos does not appear to be a general phenomenon. Nevertheless, it should be noted that many of the wild-born animals were brought to a zoo well before the period of observation began. For these animals, any immediate momentary trauma associated with the move would not be reflected in the results.

Figures 2 and 3 show the coefficients expressing the level of mortality at ages 5 and beyond for each species, relative to the species chosen as the reference category within a certain group. The hazard ratios are plotted on a logarithmic scale to reflect the relative

Table 4: Hazard ratios for sex and birth type obtained from piecewise-constant hazard models for groups of animals.

Reference category	**Hazard ratio for Females** males	**Hazard ratio for Birth Type** born in captivity	
		Unknown	**Wild born**
Apes	0.662** (0.097)	1.522 (0.538)	1.469 (0.350)
Small primates	1.088 (0.057)	1.026 (0.182)	1.110 (0.170)
Carnivores	0.945 (0.054)	0.912 (0.131)	0.887 (0.096)
Hoofstock	0.620** (0.048)	1.058 (0.281)	1.294 (0.418)
Kangaroos	0.670** (0.078)	0.340** (0.141)	0.948 (0.219)
Crocodilians	0.609* (0.142)	0.961 (0.276)	1.035 (0.318)
Ratites	1.255$^+$ (0.154)	1.186 (0.218)	0.811 (0.328)
Raptors	0.953 (0.233)	0.768 (0.360)	0.638 (0.222)

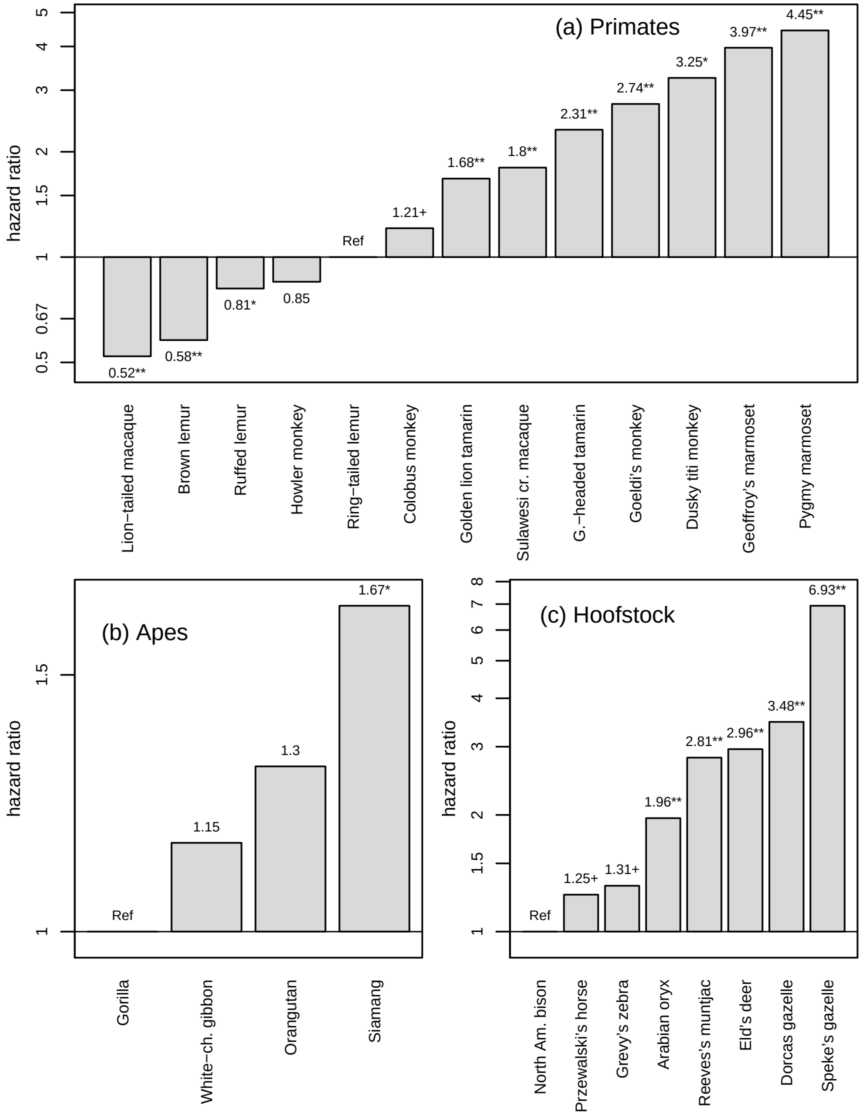
Notes: Standard errors in parentheses. *p-values:* $^+$ $p < 0.05$; * $p < 0.01$; ** $p < 0.001$.

size of bars corresponding to coefficients larger and smaller than 1. Figure 2 shows that mortality variation is enormous within the group of smaller primates. Mortality rates vary by a factor of nearly eight between brown lemurs at the low extreme and pygmy marmosets at the high. Tamarins are intermediate between the lemurs and the marmosets.

In contrast, apes show relatively little differentiation in their post-5 mortality levels, although siamangs have significantly higher mortality than gorillas. Orangutans have mortality that exceeds that of gorillas by 30% but the difference is not statistically significant. The range of variation is also small among hoofstock. North American bisons, the reference category, have the lowest mortality and gazelles the highest. The group of carnivores shown in Figure 3 also presents a highly varied picture, with bears having very low mortality and cheetahs very high compared to the reference category tigers. Lions and tigers are virtually identical to one another in their post-5 mortality levels.

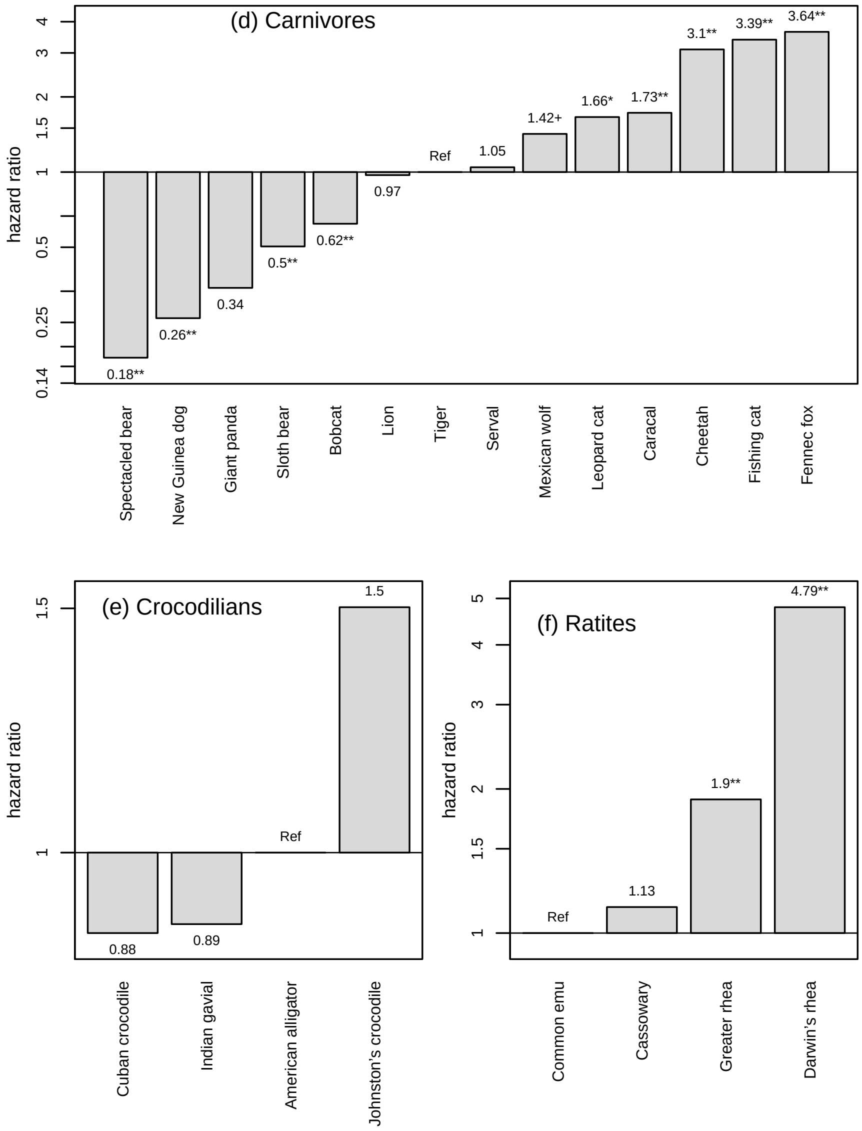
Significant differences in mortality are found also among kangaroos (not shown here) with grey kangaroos having about 33% lower risk of death than red kangaroos. Differ-

Figure 2: Hazard ratios obtained from piecewise-constant model for primates, apes and hoofstock.



Note: p-values: $^{+}\ p < 0.10$; * $p < 0.05$; ** $p < 0.01$.

Figure 3: Hazard ratios obtained from piecewise-constant model for carnivores, crocodilians and ratites.



Note: p-values: $^+ p < 0.10$; * $p < 0.05$; ** $p < 0.01$.

ences in mortality persist also by species among ratites and raptors. Among the non-flying birds (ratites), rheas have the highest mortality levels, and among raptors (not shown here) king vultures have much lower mortality than bald eagles. In summary, significant differences in mortality persist between species within nearly all groups except crocodilians.

3.3 Life table parameters for individual species

In this section we present life table functions for 42 species. This number is lower than the number of species considered in previous sections for the following reasons: *a)* Crocodilians do not show significant inter-species mortality variation, so the four species have been combined into one life table; *b)*, there were too few observations among pandas, New Guinea singing dogs, and dusky titi monkeys (N below 75 in each case) to permit reliable tables to be constructed; *c)*, 98% of the specimens of Darwin's rhea died before reaching age one, and *d)*, king vultures and howler monkeys had too few observations at older ages to allow life tables to be properly terminated.

Below age five, the life tables that we construct are based upon directly observed death rates for a species in single years of age (with the first week of life distinguished in infancy). Beyond age five, we used one of two strategies for constructing a life table: conventional application of directly observed death rates in single years of age for the species (i.e., the same approach used below age five); or use of the hazard model results for the species. The hazard model approach was employed for the 15 species identified in Table 5 for which the direct use of death rates produced erratic age-patterns of mortality. When direct data were used, life tables were terminated in the conventional fashion by estimating life expectancy as the reciprocal of the age-specific death rate in the open-ended interval (Preston et al., 2001). When the hazard model was used, a species' estimated hazard was assumed to apply in the open-ended interval as well as in all other ages beyond five. In this case, the shape of the hazard was estimated for the group of which the species was a member, and the level of the hazard for the species in question was estimated through the hazard model approach described above. Although results beyond age five are shown in five-year intervals, all calculations are performed in single-year age intervals.

Table 5 presents two life table functions for each species: *a)* the probability of surviving from birth to various subsequent ages (or between any pair of ages displayed); *b)* and the expected number of years of additional life for animals who have reached a particular age. Among the species shown in Table 5, the North American bison has the longest life expectancy at birth (15.1 years) followed by the lion-tailed macaque (13.4 years) and the bald eagle and the common emu (both 13.2 years). The fennec fox has the shortest life exepctancy at birth among the species shown in Table 5 (2.6 years). By one week of age, the spectacled bear (life expectancy of 23.9 years) has replaced the North American bison as the most longevous species. The spectacled bear is, however, characterized by a very

Table 5: Life expectancy and survival functions for various species.

		Age												
		0	1 week	1	2	3	4	5	10	15	20	25	30	35
Small Primates														
Goeldi's monkey*	e_x	6.0	8.5	8.4	8.3	7.9	7.4	6.9	5.3	4.1				
(Callimico goeldi)	l_x	1.00	0.70	0.63	0.57	0.53	0.49	0.46	0.26	0.12				
Geoffroy's marmoset	e_x	4.3	6.1	6.7	6.4	6.1	5.8	5.6	4.7					
(Callithrix geoffroyi)	l_x	1.00	0.71	0.55	0.50	0.44	0.39	0.34	0.15					
Pygmy marmoset*	e_x	3.6	5.6	6.0	5.9	5.5	5.2	5.0	4.1					
(Callithrix pygmaea)	l_x	1.00	0.65	0.50	0.44	0.39	0.34	0.29	0.12					
Colobus monkey	e_x	10.1	12.4	12.8	12.5	12.0	11.6	11.5	9.6	7.4	5.0	2.5		
(Colobus guereza)	l_x	1.00	0.82	0.73	0.69	0.66	0.63	0.59	0.44	0.31	0.20	0.09		
Brown lemur*	e_x	12.9	18.2	20.4	19.6	18.6	17.6	17.2	14.0	11.1	8.5	5.9		
(Eulemur fulvus)	l_x	1.00	0.71	0.60	0.60	0.60	0.60	0.58	0.51	0.43	0.34	0.24		
Ring-tailed lemur	e_x	12.1	14.3	15.3	15.0	14.8	14.3	13.7	11.9	9.9	8.6			
(Lemur catta)	l_x	1.00	0.84	0.73	0.71	0.67	0.65	0.62	0.49	0.37	0.25			
Golden-h. lion tamarin	e_x	5.4	8.3	8.5	8.2	8.3	7.9	7.8	5.4	4.2				
(Leontopithecus chrysomelas)	l_x	1.00	0.65	0.57	0.52	0.46	0.42	0.38	0.25	0.11				
Golden lion tamarin	e_x	5.1	10.6	11.0	10.9	10.9	10.6	10.2	6.6	3.9	2.1			
(Leontopithecus rosalia)	l_x	1.00	0.47	0.42	0.39	0.35	0.33	0.31	0.26	0.17	0.06			
Sulawesi cr. macaque*	e_x	7.6	10.7	11.1	10.3	10.0	9.7	9.2	7.2	5.5	4.0	2.6		
(Macaca nigra)	l_x	1.00	0.71	0.62	0.61	0.57	0.53	0.51	0.35	0.21	0.10	0.03		
Lion-tailed macaque	e_x	13.4	19.2	20.0	19.2	19.4	18.9	18.4	14.7	12.4	9.3	5.1	6.7	4.7
(Macaca silenus)	l_x	1.00	0.69	0.64	0.63	0.59	0.58	0.56	0.52	0.43	0.36	0.33	0.09	0.04
Ruffed lemur	e_x	10.8	16.6	17.5	17.2	16.6	16.2	15.3	12.6	10.6	8.8			
(Varecia variegata)	l_x	1.00	0.65	0.58	0.56	0.55	0.53	0.52	0.44	0.34	0.25			
Carnivores														
Cheetah	e_x	6.4	8.1	9.1	8.5	7.6	7.0	6.4	3.3	1.4				
(Acinonyx jubatus)	l_x	1.00	0.79	0.63	0.60	0.59	0.56	0.53	0.35	0.08				
Mexican grey wolf	e_x	8.4	11.8	12.5	11.5	10.5	9.5	8.9	5.4	8.8				
(Canis lupus baileyi)	l_x	1.00	0.71	0.62	0.62	0.62	0.62	0.59	0.48	0.11				
Caracal*	e_x	7.0	9.6	11.4	10.4	9.5	9.1	8.3	4.9	2.8				
(Caracal caracal)	l_x	1.00	0.72	0.55	0.55	0.55	0.52	0.50	0.39	0.17				
Serval*	e_x	9.5	12.4	13.2	12.2	11.7	11.0	10.2	6.4	3.7	2.4			
(Leptailurus serval)	l_x	1.00	0.77	0.67	0.67	0.64	0.63	0.61	0.53	0.32	0.09			
Bobcat	e_x	11.5	14.0	15.9	15.1	14.5	13.5	12.8	8.6	5.1	2.9			
(Lynx rufus)	l_x	1.00	0.82	0.67	0.67	0.65	0.65	0.63	0.59	0.46	0.20			
Sloth bear*	e_x	8.2	16.3	18.1	17.1	16.1	15.1	14.1	10.0	6.9	5.6	4.7	3.8	0.8
(Melursus ursinus)	l_x	1.00	0.50	0.43	0.43	0.43	0.43	0.43	0.40	0.31	0.17	0.08	0.04	0.02
Lion	e_x	6.4	9.0	11.2	11.9	11.9	11.0	10.5	6.9	3.9	1.7			
(Panthera leo)	l_x	1.00	0.71	0.52	0.45	0.41	0.41	0.39	0.33	0.22	0.07			
Tiger	e_x	9.6	13.3	13.4	12.8	12.0	11.4	10.6	6.5	3.6	2.7			
(Panthera tigris)	l_x	1.00	0.72	0.66	0.64	0.63	0.61	0.60	0.54	0.35	0.08			
Leopard cat	e_x	5.3	7.0	9.4	9.3	8.7	8.7	8.7	5.5	3.5				
(Prionailurus bengalensis)	l_x	1.00	0.75	0.49	0.45	0.43	0.38	0.34	0.26	0.13				
Fishing cat	e_x	6.1	8.5	9.4	8.4	7.9	7.2	6.2	2.7	1.1				
(Prionailurus viverrinus)	l_x	1.00	0.71	0.58	0.58	0.54	0.52	0.52	0.37	0.04				

(Continued)

Table 5 (Continued): Life expectancy and survival functions for various species.

		Age												
		0	1 week	1	2	3	4	5	10	15	20	25	30	35
Spectacled bear	e_x	12.8	23.9	24.8	23.8	22.8	21.8	20.8	15.8	11.8	7.2	3.5	4.1	
(Tremarctos ornatus)	l_x	1.00	0.53	0.49	0.49	0.49	0.49	0.49	0.49	0.46	0.44	0.34	0.06	
Fennec fox	e_x	2.6	5.4	8.3	7.8	7.2	6.4	5.7	2.6					
(Vulpes zerda)	l_x	1.00	0.48	0.27	0.25	0.24	0.23	0.22	0.13					
Hoofstock														
North American bison*	e_x	15.1	16.6	17.4	18.0	17.5	17.6	16.9	14.4	12.4	11.7			
(Bison bison)	l_x	1.00	0.91	0.82	0.75	0.73	0.68	0.67	0.57	0.46	0.32			
Eld's deer*	e_x	5.1	8.3	9.4	9.1	8.6	8.4	7.7	5.9	4.0				
(Cervus eldi)	l_x	1.00	0.61	0.48	0.45	0.42	0.38	0.37	0.23	0.12				
Przewalski's wild horse*	e_x	12.9	15.0	14.5	15.2	14.6	13.9	13.2	10.5	8.1	6.3	4.3	3.2	
(Equus caballus przewalskii)	l_x	1.00	0.86	0.83	0.74	0.72	0.71	0.69	0.57	0.43	0.27	0.16	0.05	
Grevy's zebra*	e_x	11.0	13.4	14.2	14.3	14.1	13.5	12.8	10.2	7.8	6.1	4.2	3.1	
(Equus grevyi)	l_x	1.00	0.82	0.72	0.67	0.63	0.61	0.60	0.48	0.36	0.22	0.13	0.04	
Dorcas gazelle*	e_x	5.3	6.3	8.0	7.7	7.6	7.1	7.3	5.8					
(Gazella dorcas)	l_x	1.00	0.84	0.58	0.53	0.47	0.44	0.37	0.21					
Speke's gazelle*	e_x	5.2	5.5	5.4	5.5	5.0	4.4	4.4	3.7					
(Gazella spekei)	l_x	1.00	0.94	0.80	0.66	0.59	0.55	0.44	0.15					
Reeves's muntjac*	e_x	8.2	9.6	10.4	10.2	10.0	9.3	8.6	7.1	6.1				
(Muntiacus reevesi)	l_x	1.00	0.85	0.71	0.66	0.61	0.59	0.57	0.37	0.19				
Arabian oryx	e_x	10.1	10.8	11.7	11.4	11.0	10.5	9.9	6.9	4.4				
(Oryx leucoryx)	l_x	1.00	0.93	0.78	0.74	0.70	0.67	0.64	0.50	0.32				
Ratites														
Cassowary	e_x	11.6	17.4	19.4	18.9	18.3	17.6	16.6	14.7	12.1	10.1	6.8	3.5	
(Casuarius casuarius)	l_x	1.00	0.66	0.56	0.55	0.54	0.53	0.53	0.43	0.36	0.28	0.23	0.16	
Common emu	e_x	13.2	14.1	18.1	18.7	18.4	18.1	17.5	15.5	13.8	11.3	11.0	9.1	
(Dromaius novaehollandiae)	l_x	1.00	0.94	0.69	0.63	0.61	0.58	0.57	0.48	0.38	0.31	0.21	0.15	
Greater rhea	e_x	5.5	6.4	10.8	11.4	11.4	11.2	11.1	9.2	8.6				
(Rhea americana)	l_x	1.00	0.85	0.45	0.39	0.35	0.33	0.30	0.22	0.14				
Raptors														
Bald eagle	e_x	13.2	17.3	19.0	18.9	19.0	19.0	18.8	18.8	17.3	14.2	10.8	8.7	7.6
(Haliaeetus leucocephalus)	l_x	1.00	0.76	0.66	0.63	0.59	0.56	0.54	0.41	0.34	0.31	0.27	0.20	0.12
Kangaroos														
Western grey kangaroo*	e_x	7.3	7.8	8.5	8.7	8.2	7.9	7.7	5.5	4.8				
(Macropus fuliginosus)	l_x	1.00	0.93	0.76	0.66	0.62	0.57	0.52	0.33	0.15				
Red kangaroo	e_x	6.0	6.4	6.8	6.7	6.5	6.2	5.9	4.0					
(Macropus rufus)	l_x	1.00	0.94	0.76	0.67	0.59	0.53	0.47	0.25					

Notes: * Parameters after age 5 are based upon piecewise-constant hazard model.

high mortality at or shortly after birth and only 53% of the animals survive to one week of age. A similar pattern is observed for the sloth bear and the fennec fox among whom only half of the born cubs survive the first week of their life. Among small primates, the golden-lion tamarin is characterized by the highest mortality between birth and one week of age. Lions and tigers have very similar mortality beyond age three although lions have higher death rates below that age.

Not all remaining species are shown in Table 5 because several important species do not exhibit enough deaths at older ages during the period under study to enable the life table to be properly completed. This pattern is observed among crocodilians and apes. In these species, the recorded death rates during the 1998-2003 period imply that large numbers would survive to older ages. However, in the zoo collections during the period under investigation, there are too few deaths at those older ages to allow the life table to be confidently closed out. For example, the life table for gorillas indicates that 31% will survive to age 40, but in the populations and period under study there were only 146 years of exposure and 9 deaths recorded above age 40.

There are several possible explanations of this anomaly: *a)* Death rates for a species were unusually low during the period 1998-2003; the shortage of very old specimens during this period is a result of higher death rates during earlier periods. *b)* Deaths are underrecorded; *c)* The number of specimens is overestimated. This latter problem would be particularly serious if specimens who had died or out-migrated were erroneously maintained on a zoo’s books. In this case, the fraction of estimated years at risk that consisted of absent animals would grow as age advances, and death rates at older ages would be progressively biased downwards.

We consider it unlikely that deaths in these species were underrecorded because four of the five species affected by the problem are apes who are often among the most visible and important species in a collection. In the case of gorillas, it seems more likely that the ISIS data base includes inaccurate records of survivors. Gorillas are assigned multiple studbook numbers in various regions around the world, which is a source of confusion in the record system (Flesness et al., 1995). One analysis argues that "...the mish mosh of studbook IDs that presently permeates the ISIS database for gorillas does not permit either genetic or demographic analyses for one of the highest profile and most charismatic megavertabrates in captivity." (Earnhardt et al., 1995).

Rather than discarding all information for these important species, we have chosen an age at which to terminate the life table and present survival information up to that age. Thus, rather than the conventional life expectancy values, we present ‘partial’ life expectancy values that refer to the expected number of years to be lived before the selected terminal age. That age is 40 in the case of gorillas and orangutans, 35 for siamangs, and 30 for gibbons and crocodilians. The fact that there is an internal inconsistency between the recorded survival for these species and the number of older specimens in collections means that the results, shown in Table 6, are less reliable than for other species presented.

Table 6: Partial life expectancy and survival functions for Apes and Crocodilians.

		Age													
		0	1 week	1	2	3	4	5	10	15	20	25	30	35	40
Apes															
Gorilla	e_x	23.3	27.2	29.1	28.7	28.1	27.1	26.4	22.7	19.1	15.3	12.1	8.3	4.4	0*
(Gorilla gorilla)	l_x	1.00	0.86	0.77	0.76	0.75	0.75	0.74	0.70	0.65	0.61	0.54	0.48	0.40	0.31*
White-ch. gibbon	e_x	15.3	20.4	21.9	22.8	21.8	20.8	20.5	16.6	12.8	8.7	4.7	0*		
(Hylobates leucogenys)	l_x	1.00	0.75	0.67	0.61	0.61	0.61	0.59	0.56	0.51	0.47	0.41	0.36		
Siamang	e_x	19.5	22.2	23.7	23.0	22.3	21.3	21.0	17.7	14.6	11.1	8.2	4.4	0*	
(Hylobates syndactylus)	l_x	1.00	0.88	0.79	0.78	0.77	0.77	0.74	0.68	0.60	0.54	0.43	0.36	0.26*	
Orangutan	e_x	19.0	23.6	26.3	26.0	25.3	25.5	24.5	21.0	17.8	14.3	11.4	7.9	4.3	0*
(Pongo pygmaeus)	l_x	1.00	0.80	0.69	0.67	0.67	0.64	0.64	0.59	0.54	0.50	0.42	0.36	0.28	0.20*
Crocodilians	e_x	14.6	14.9	16.4	17.2	17.9	17.7	17.1	14.6	11.5	8.1	4.5	0*		
	l_x	1.00	0.97	0.84	0.75	0.68	0.65	0.63	0.54	0.47	0.40	0.31	0.25*		

Notes: * By assumption; The group of crocodilians includes American alligator, Johnston's crocodile, Cuban crocodile and Indian gavial.

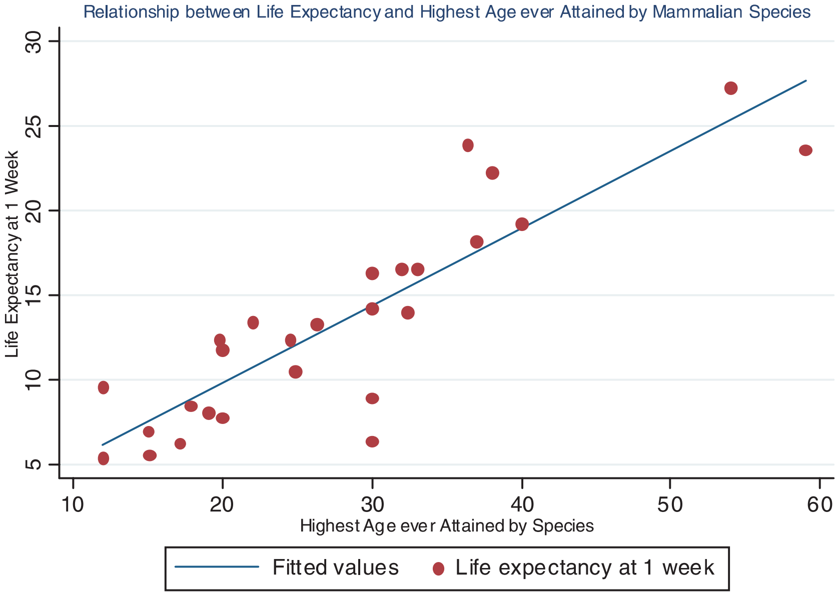
Despite the assumption that no years would be lived beyond age 40 by a cohort of newborn gorillas, the gorilla life expectancy at birth, 23.3 years, is the highest of any species considered. Likewise, orangutans, gibbons, and siamangs achieve a higher life expectancy at birth than any other species under review despite having their survivorship artificially truncated. These species of apes also provide four out of the five highest life expectancies at one week of age (with spectacled bears). Clearly, apes appear to live longer in captivity than the other species that we have reviewed, but data inconsistencies add uncertainty to this conclusion.

4. Discussion

It is useful to compare the estimates of life expectancy that we have produced to other estimates of longevity. The largest collection of longevity records for vertebrate species/subspecies is contained in Carey and Judge (2000). Rather than tabulating the average length of life for a species, Carey and Judge tabulated the highest age recorded to have been attained by a member of that species. Unlike the values presented in this paper, the highest observed age will depend systematically upon the number of animals observed, which introduces noise into the Carey and Judge estimates.

Figure 4 compares our estimates of life expectancy at age one week for mammalian species to estimates of the highest age attained by that species (N=37). Life expectancy at age one week is used rather than at age zero in order to minimize the influence of fetal mortality. The relationship is tight, with a coefficient of correlation between the two series of .87. The line fitted on the graph indicates that the average length of life of a species is approximately equal to half of the highest age attained by that species. For the many mammalian species not included in this analysis and for whom no reliable life table has been constructed but for whom a maximum attained age has been estimated, this rule of thumb may prove useful.

Figure 4: Relationship between life expectancy and highest age ever attained by mammalian species.



However, non-mammalian species show a much poorer fit between these two variables, with a correlation of only .55 (N=5). It is possible that the fit is poorer because Carey and Judge were unable to observe as many members of these species as of mammals, adding greater variability to their estimates. For mammals and non-mammals combined, the correlation coefficient is .77.

Having a large group of species for whom life tables have been prepared using comparable data and methods has enabled us to investigate a number of issues that cannot be considered when one species is considered in isolation. These include questions of the generality of sex differences in mortality and of the excess mortality of wild-born compared to zoo-born animals. The comparative design has also enabled us to generalize about the relation between the life expectancy of a species and the highest age attained by that species. Although we have not pursued the connections here, the estimates can also be used as the basis for studying the relation between longevity and age at sexual maturity, length of the reproductive period, length of juvenile dependency, and patterns of physical growth. The data base of the International Species Information System is an extremely valuable resource for investigations of the life cycle within and across species.

References

Carey J R, Judge D S. 2000. Longevity Records: Life Spans of Mammals, Birds, Amphibians, Reptiles, and Fish. *Odense: Monographs on Population Aging* 8, Odense University Press.

Carnes B A, Olshansky S J, Grahn D. 1996. Continuing the search for a law of mortality. *Population and Development Review* 22:231–264.

Courteney J, Santow G. 1989. Mortality of wild and captive chimpanzees. *Folia Primatologica* 52:167–177.

de Wit J J. 1995. Mortality of rheas caused by a synchamus trachea infection. *Veterinary Quarterly* 17:39–40.

Earnhardt J M, Thompson S D, Willis K. 1995. Reply to Flessness et al. *Zoo Biology* 14:519–522.

Ernest, S K. Morgan 2003. Life History Characteristics of Placental Nonvolant Mammals. *Ecology* 84:3402.

Flesness N R, Lukens D R, Porter S B, Wilson C R, Grahn L V. 1995. ISIS and studbooks, very high census correlation for the north american zoo population: a reply to Earnhardt, Thompson, and Willis. *Zoo Biology* 14:509–517.

Felsenstein, J. 1985. Phylogenies and the Comparative Method. *The American Naturalist* 125:1-15.

Gozalo A, Montoya E. 1991. Mortality causes of the moustached tamarin (Saguinus mystax) in captivity. *Journal of Medical Primatology* 21:35–38.

Hill K, Boesch C, Goodall J A, Pusey A, Williams J, Wrangham R. 2001. Mortality rates among wild chimpanzees. *Journal of Human Evolution* 40(5): 437–450.

Karstad L, Sileo L. 1971. Causes of death in captive wild waterfowl in the Kortright Waterfowl Park, 1967-1970. *Journal of Wildlife Diseases* 7:236–241.

Leong K M, Terrell S P, Savage A. 2004. Causes of mortality in captive cotton-top tamarins (Saguinus oedipus). *Zoo Biology* 23:127–137.

Preston S H, Heuveline P., Guillot M. 2001. Demography: Measuring and Modeling Population Processes. *Oxford: Blackwell Publishers*.

Promislow D E L. 1992. Costs of sexual selection in natural populations of mammals. *Proceedings: Biological Sciences* 247:203–210.

Taylor V J, Poole T B. 1998. Captive breeding and infant mortality in Asian elephants; A comparison between twenty Western zoos and three Eastern elephant centers. *Zoo Biology* 17:311–332.

Tocidlowski M E, Cornish T E, Loomis M R, Stoskopf M K. 1997. Mortality in captive wild-caught horned puffin chicks (Fratercula Corniculata). *Journal of Zoo and Wildlife Medicine* 28:298–306.

Vaupel J W, Yashin A I. 1985. Heterogeneity's ruses: Some surprising effects of selection on population dynamics. *American Statistician* 39:176–185.

Wallace R S, Bush M, Montali R J. 1987. Deaths from exertional myopathy at the National Zoological Park from 1975 to 1985. *Journal of Wildlife Diseases* 23:454–462.

Ward M P, Ramer J C, Proudfoot J, Garner M M, Juan-Sallès C, Wu C C. 2003. Outbreak of salmonellosis in a zoologic collection of Lorikeets and Lories (Trichoglossus, Lorius, and Eos spp.). *Avian Diseases* 47:493–498.

[WHO] World Health Organization. 1977. Manual of Mortality Analysis. *Geneva: Division of Health Statistics*, World Health Organization.

Wielebnowski N. 1996. Reassessing the relationship between juvenile mortality and genetic monomorphism in captive cheetahs. *Zoo Biology* 15:353–369.