

Relevance of management and feeding regimens on life expectancy in captive deer

Dennis W. H. Müller, DVM; Laurie Bingaman Lackey, MA; W. Jürgen Streich, Dr rer nat; Jean-Michel Hatt, Prof Dr med vet; Marcus Clauss, PD, Dr med vet

Objective—To establish a demographic approach to facilitate the comparison of husbandry success for deer species in zoos and to test for factors that influence the performance of deer species in captivity.

Sample Population—Data collected from 45,736 zoo-kept deer that comprised 31 species.

Procedures—Data had been collected by the International Species Information System during the last 3 decades on zoo-kept deer around the world. The relative life expectancy (rLE) of a species (ie, mean life expectancy as a proportion of the maximum recorded life span for that species) was used to describe zoo populations. The rLE (values between 0 and 1) was used to reflect the husbandry success of a species.

Results—A significant positive correlation was found between the rLE of a species and the percentage of grass in the natural diet of the species, suggesting that there are more problems in the husbandry of browsing than of grazing species. The 4 species for which a studbook (ie, record of the lineage of wild animals bred in captivity) was maintained had a high rLE, potentially indicating the positive effect of intensive breeding management.

Conclusion and Clinical Relevance—The rLE facilitated the comparison of husbandry success for various species and may offer the possibility of correlating this quotient with other biological variables. Ultimately, identifying reasons for a low husbandry success in certain species may form the basis for further improvements of animal welfare in captivity. (*Am J Vet Res* 2010;71:275–280)

Zoo animal husbandry includes a constant quest for the improvement of husbandry conditions, veterinary care, reproduction, longevity, and animal welfare.^{1–3} An important aspect of this challenge is the problem of evaluating these aims objectively. Although breeding success can be easily examined by analysis of birth rates and infant mortality rates,^{4,5} an objective variable to examine husbandry quality is still lacking. So far, opinions on husbandry success are based mainly on personal communication among zookeepers, subjective observation, personal intuition, necropsy report analysis, and analysis of studbook data (ie, records of the lineage of wild animals bred in captivity).^{6–10}

The mean life expectancy of zoo animals might be a promising value for an objective husbandry evaluation. Several reports^{11–13} indicate that there are major differences in life expectancies among species of wild

ABBREVIATIONS

DOB	Date of birth
ISIS	International Species Information System
rLE	Relative life expectancy

animals in captivity. It is assumed that these differences can be explained by certain biological characteristics (eg, body weight, social behavior, or feeding strategies). To investigate such correlations, analyses of the mean life expectancies of species of wild animals in captivity are required; to date, these are rare.¹⁴

For captive wild animals, the ISIS maintains a database of stock data for zoological institutions. This database includes data for more than 2 million animals of almost 10,000 species kept in approximately 750 zoos in 74 countries. The DOB and, where applicable, the date of death of every animal is documented, if known, which allows calculation of lifespans.

In ecological and demographic research, various variables and methods are available to describe and analyze population data. The life expectancy of an individual is defined as the mean lifetime remaining at a given age and depends on the mortality rate of the population. The life expectancy is an empirical value and can be used to compare various populations of the same species, which is often done in demographic studies. In a study by Clubb et al,¹⁵ the life expectancy was signifi-

Received February 3, 2009.

Accepted April 8, 2009.

From the Clinic for Zoo Animals, Exotic Pets, and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr 260, CH-8057 Zurich, Switzerland (Müller, Hatt, Clauss); International Species Information System, 2600 Eagan Woods Dr, Ste 50, Eagan, MN 55121-1170 (Lackey); and Leibniz-Institute for Zoo and Wildlife Research, Alfred-Kowalke-Strasse 17, 10315 Berlin, Germany (Streich).

Supported by grants of the World Association of Zoos and Aquariums, Georg and Bertha Schwyzer-Winiker-Stiftung, and Vontobel-Stiftung.

Address correspondence to Dr. Müller (dmueller@vetclinics.uzh.ch).

cantly shorter for female adult elephants kept in zoos, compared with that of female adult elephants in wild or semiwild populations. An examination of improvements and regressions in life expectancy is possible by analyzing the development of life expectancy over time. A typical example is the observation of the continuing increase in human life expectancy during the last 2 centuries.¹⁶ A second method is the determination of the age-related mortality rate (or survivorship) as a function of time, which is often used in ecological studies.^{17,18} Various mathematical nonlinear functions are established to describe the resulting graphs of the age-related mortality rates.^{19–21} However, variables of these growth functions have to be estimated.²² Estimation of these factors, and the simplification of data by use of a model, may result in an imperfect reflection of the empirical statistics (ie, loose fit). Furthermore, populations of various species, and even the sexes of the same species, may be best represented by differing functions,¹⁷ making comparisons among species difficult.

Longevity records of various species vary widely even in the same taxonomic groups.^{23,24} A life expectancy of 15 years may be a desirable result in a species with a maximum recorded life span of 20 years, but less so in a species that could achieve a life span of 35 years. Therefore, it is essential to consider the maximum life span in comparative evaluations. Because the maximum life span of a species is not part of demographic models, a new approach is required to address problems inherent in the use of standard mathematical models. The logical step is to calculate the rLE of a population by expressing the mean life expectancy as a proportion of the maximum life span that a species could theoretically achieve.

Ruminants have been traditionally classified into feeding types (ie, browsers, grazers, and intermediate feeders) according to the botanical composition of their diet. There has been an ongoing debate as to whether these different feeding strategies are reflected in morphological and physiologic differences of the digestive system²⁵ and hence relevant for the practical feeding of zoo animals. Experience from wild animal husbandry indicates that several browsing species held in captivity, such as roe deer (*Capreolus capreolus*), moose (*Alces alces*), or giraffe (*Giraffa camelopardalis*) have a high nutrition-related mortality rate, whereas similar problems in grazing species are less frequently observed.^{26,27} The purpose of the study reported here was to establish a demographic approach that facilitates the comparison of the husbandry success in different species by comparing their life expectancies in zoos and to test for factors that influence the performance of deer species in captivity.

Materials and Methods

Data source—The data set contained information on 45,736 deer that comprised 31 species (family Cervidae) as recorded between 1980 and 2007 by the ISIS. Information included the following for each deer: taxon, identification number, sex, DOB and date of death, origin (born in the wild or in captivity), and country of birth and death (or last known residence). Notably, the reason for death was not given in the data set.

Data processing—For the demographic approach used in this study, the exact life span of each animal was required and animals that were still alive (ie, those for which the exact life span had not been determined) were excluded. Thus, records of deer born in the wild, deer for which the DOB or date of death was only estimated to the closest year, or deer without a date of death (ie, that might still be alive or for which a date of death was not recorded) were deleted from the initial data set. Ages at death of the remaining 20,512 deer were calculated and presented in years, with days interpreted as a proportion of the full 365-day year to 2 fractional digits. Single birth cohorts were created, ensuring that all members died within the observation interval (ie, 1980 to 2007).

The number of records for some deer species became too small for further investigation; at least 45 deer/birth cohort were required for analysis. Data on the remaining 20 deer species were examined by calculating the rLE for each species as the arithmetic mean of the life spans of all deer (l_x) within the species' birth cohort (with n deer) divided by the longevity recorded for this species (a_{\max}) as follows:

$$rLE = \frac{\sum_{i=1}^n l_x}{n \times a_{\max}}$$

The longevity records of the species were obtained from published reports.^{23,24} When the maximum age recorded in the ISIS was higher than the reported ages in the literature, calculations were determined on the basis of the maximum age recorded by the ISIS. Resulting rLE values ranged from 0 to 1. Theoretically, an rLE of 0 indicated that all deer died at birth, whereas an rLE of 1 indicated that all deer reached the maximum life span.

The rLE was calculated under various conditions to exclude human influence on the population structure (eg, culling). Assuming that animals are usually culled before they achieve sexual maturity and that more males than females (as most species are kept in harem systems) are culled, the rLE of females that lived ≥ 2 years from DOB was considered most relevant and was calculated for each species in addition to the rLE for all deer (ie, males and females combined). This followed the assumption of Clubb et al,¹⁵ which is that life expectancy of females is most relevant to population viability. In evaluation of the rLE of females that lived ≥ 2 years from DOB, the life expectancy was interpreted as total mean life span measured from birth and not as the remaining life span.

Swiss deer park data—To demonstrate the possibility of comparing the housing success of an individual facility to the overall mean rLE of a species, records for red deer (*Cervus elaphus*) and moose from a Swiss deer park from the last 43 years, which were not part of the ISIS data, were analyzed. Because reasons for death and culling measures were documented in these records, an rLE of deer and moose that were definitely not culled could be determined. This allowed testing assumptions of the typical culling regimes.

Statistical analysis—Analyses were performed on ISIS data for the 20 remaining deer species. Mean rLE for all deer and mean rLE of males or females that lived ≥ 2 years from DOB, respectively, were compared by use of a repeated-measures ANOVA and a subsequent Sidak correction post hoc test. Within species, the mean rLE for males was compared with the corresponding mean rLE for females by use of a paired *t* test. To test for biological and management factors potentially influencing life expectancy, correlations of the rLE of females that lived ≥ 2 years from DOB with body weight, preferred habitat, social behavior, percentage of grass in the natural diet (ie, percentage of grass in the diet the deer are naturally adapted to), and existence of an international studbook were analyzed. For this purpose, a stepwise procedure was performed. A Pearson correlation coefficient (*r*) was used to evaluate whether the rLE of females that lived ≥ 2 years from DOB was correlated with body weight or the percentage of grass in the species' natural diet. A *t* test was performed to evaluate the effect of social behavior, habitat, or existence of a studbook on the mean rLE of females that lived ≥ 2 years from DOB. In the next step, only factors that had a value of $P < 0.1$ were included in an ANOVA or regression analysis approach. To achieve normality, body weight was ln (ie, natural logarithm) transformed and percentage of grass was logit transformed. Values were reported as mean \pm SD. All analyses were performed by use of a commercially available software program.^a A value of $P < 0.05$ was considered significant.

Results

Evaluation by use of rLE—The rLE for 20 deer species included in the ISIS data was analyzed for the whole population, for all deer (male and females) that lived ≥ 2 years from DOB, for females that lived ≥ 2 years from DOB, and for males that lived ≥ 2 years from DOB (Table 1).^{23,24,28–35} The rLE of red deer and moose of the Swiss deer park were within the range recorded for these species within the ISIS database (Table 2). The rLE (0.46) of nonculled red deer that lived ≥ 2 years from DOB in the Swiss deer park was especially close to the rLE (0.48) of red deer that lived ≥ 2 years from DOB recorded in the ISIS. Of the red deer in the Swiss deer park that were culled, most (211/239; 88%) culling events occurred before deer reached the second anniversary of their DOB; other culling events were spread evenly across age classes to correct the age structure of the population or to destroy overly aggressive males.

Data analysis—The mean rLE (0.20 ± 0.07) of all deer was significantly ($P < 0.001$) different from the mean rLE (0.41 ± 0.07) of deer that lived ≥ 2 years from DOB. Differences between the rLE of all deer and the rLE of females that lived ≥ 2 years from DOB or the rLE of males that lived ≥ 2 years from DOB, respectively, were also significant ($P < 0.001$). The mean rLE (0.25 ± 0.08) of females and the mean rLE (0.43 ± 0.07) of females that lived ≥ 2 years from DOB were significantly ($P < 0.001$) higher than the mean rLE (0.16 ± 0.07) of males and the mean rLE (0.37 ± 0.08) of males that

Table 1—The rLE of 20 deer species that lived ≥ 2 years from DOB along with data on maximum age, body weight, social behavior, habitat, percentage of grass in natural diet, and existence of an international studbook.

Species	Cohort (n)	Maximum age (y)	Body weight of females (kg)	Social behavior ³⁰	Habitat ³⁰	Grass (%) ³¹	Stud-book ²⁸	rLE2	rLE2 females	rLE2 males
Moose (<i>Alces alces</i>)	154	27.0 ²⁴	375 ²⁹	A	1	2	No	0.27	0.27	0.27
Mule deer (<i>Odocoileus hemionus</i>)	113	23.0 [*]	56 ²⁹	B	1	11	No	0.29	0.30	0.24
Reeves' muntjac (<i>Muntiacus reevesi</i>)	228	23.2 [†]	16 ²⁹	A	1	10 ³²	No	0.33	0.36	0.29
White-tailed deer (<i>Odocoileus virginianus</i>)	257	23.0 [†]	71 ²⁹	B	1	3	No	0.36	0.37	0.38
Sika deer (<i>Cervus nippon</i>)	161	25.4 ²³	40 ²⁹	B	1	50	No	0.34	0.39	0.28
Sambar deer (<i>Cervus unicolor</i>)	65	26.4 ²³	162 ²⁹	B	2	50 ³³	No	0.38	0.41	0.34
Fallow deer (<i>Dama dama</i>)	290	25.0 ²⁴	97 ²⁹	B	1	46	No	0.37	0.42	0.28
Reindeer (<i>Rangifer tarandus</i>)	319	21.8 [†]	107 ²⁹	B	1	36	No	0.39	0.42	0.32
Red brocket (<i>Mazama americana</i>)	112	17.1 [†]	40 ³⁰	A	2	1	No	0.41	0.44	0.37
Pampas deer (<i>Ozotoceros bezoarticus</i>)	56	15.0 [†]	40 ³⁰	A	2	80 ³³	Yes	0.45	0.44	0.46
Indian muntjac (<i>Muntiacus muntjak</i>)	48	23.2 [*]	27 ²⁹	A	2	10	No	0.48	0.46	0.52
Southern Pudu (<i>Pudu puda</i>)	87	18.3 [†]	9 ³⁰	A	1	3 ³⁴	Yes	0.46	0.46	0.46
Axis deer (<i>Axis axis</i>)	714	20.8 ²⁴	80 ²⁹	B	2	70	No	0.40	0.46	0.30
Chinese water deer (<i>Hydropotes inermis</i>)	436	12.7 [†]	17 ²⁹	A	1	50	No	0.47	0.47	0.48
Roe deer (<i>Capreolus capreolus</i>)	139	17.0 ²⁴	52 ²⁹	A	1	9	No	0.39	0.47	0.28
Barasingha (<i>Cervus duvaucelii</i>)	245	21.3 ²³	189 ³⁰	B	2	75 ³⁵	Yes	0.43	0.48	0.36
Eld's deer (<i>Cervus eldii</i>)	171	21.3 [*]	79 ²⁹	B	2	65	Yes	0.45	0.49	0.38
Red deer (<i>Cervus elaphus</i>)	153	26.8 ²⁴	273 ²⁹	B	1	47	No	0.48	0.50	0.41
Père David's deer (<i>Elaphurus davidianus</i>)	159	23.3 ²⁴	150 ³⁰	B	1	75	Yes	0.50	0.51	0.47
Hog deer (<i>Axis porcinus</i>)	71	20.9 [†]	35 ²⁹	A	2	50	No	0.48	0.52	0.43
Mean \pm SD	ND	ND	ND	NA	NA	ND	NA	0.41 \pm 0.07	0.43 \pm 0.07	0.37 \pm 0.08

The rLE (values between 0 and 1, where 0 indicates that all deer died at birth and 1 indicates that all deer reached their maximum life span) reflects the husbandry success of a species; species are listed in an ascending order by rLE of females that lived ≥ 2 years from DOB.
^{*}Estimated value according to related species, as sufficient data for this species are not available. [†]New longevity record data were found in the ISIS.^{23,24,28–35}
1 = Temperate zone habitats. 2 = Subtropical and tropical habitats. A = Predominantly solitary behavior. B = Predominantly social behavior. NA = Not applicable. ND = Not determined. rLE2 = rLE of all deer (males and females) that lived ≥ 2 years from DOB. rLE2 females = rLE of females that lived ≥ 2 years from DOB. rLE2 males = rLE of males that lived ≥ 2 years from DOB.
Superscript numbers are reference citations for source of data.

Table 2—Comparison of rLE of red deer and moose as recorded in the ISIS and from the Swiss deer park.

Species	ISIS data			Swiss deer park data		
	Cohort (n)	rLE	rLE2	Cohort (n)	rLE _{nc}	rLE2 _{nc}
Moose (<i>A alces</i>)	154	0.14	0.27	48	0.11	0.25
Red deer (<i>C elaphus</i>)	153	0.24	0.48	87	0.20	0.46

rLE_{nc} = rLE of deer and moose that were definitely not culled. rLE2_{nc} = rLE of deer and moose that lived ≥ 2 years from DOB and were definitely not culled.
See Table 1 for remainder of key.

lived ≥ 2 years from DOB, respectively. Mean difference between rLE of females and rLE of males was 0.09 ± 0.04 , and mean difference between rLE of females that lived ≥ 2 years from DOB and rLE of males that lived ≥ 2 years from DOB was 0.07 ± 0.07 . Mean difference between the rLE of females that lived ≥ 2 years from DOB and the rLE of males that lived ≥ 2 years from DOB of all social species was 0.09 ± 0.05 and was higher, but not significantly ($P = 0.059$), than the mean difference for the same comparison in solitary species (0.04 ± 0.08).

Regression analysis revealed that only the percentage of grass in a species' natural diet remained a significant ($R^2 = 0.271$; $P = 0.019$) predictor of rLE of females that lived ≥ 2 years from DOB. The inclusion of a second independent variable never led to an improvement of fit. There was no correlation between rLE of females that lived ≥ 2 years from DOB and maximum body weight of females ($r = 0.104$; $P = 0.662$). Species from tropical habitats, compared with those from temperate habitats, had a higher rLE of females that lived ≥ 2 years from DOB, but this finding was not significant ($P = 0.053$). The rLE of females that lived ≥ 2 years from DOB was positively correlated ($r = 0.521$; $P = 0.019$) to the percentage of grass in the natural diet (ie, the rLE increased with a higher percentage of grass in a species' natural diet). The mean rLE of females that lived ≥ 2 years from DOB of 5 species (Table 1) for which a studbook was maintained was higher than that of species without a studbook, but this difference was not significant ($P = 0.093$).

Discussion

The rLE is used to describe the development of captive animal populations and can be defined as the mean life expectancy of a species as a proportion of the maximum recorded life span for that species. It is an empirical value that can be easily calculated for any demographic data set for the whole population or any subpopulation (eg, only females or only adult animals). The following characteristics of the rLE facilitate comparative studies among species: first, the rLE is a single value describing a given cohort in a precise manner, which is deduced from the life spans of the individual animals; second, the relation to the longevity record of a species (the interpretation of mean life expectancy as a proportion of the longevity record) eliminates problems associated with the fact that various species have different maximum life spans.

It is important to exclude human influences (eg, culling) on the population structure to examine the

mean life expectancy as a variable of a species' husbandry success in captivity. It is assumed that most animals are culled before they achieve sexual maturity and that more males than females are culled.³⁶ In the present study, this led to the hypothesis that the rLE of females that lived ≥ 2 years from DOB is most relevant in terms of analyzing rLE of a captive species. To test this hypothesis, data on red deer and moose of a Swiss deer park with a known culling management were compared with data on the same species included in the ISIS data set. Most (88%) culling events of red deer in the Swiss deer park were completed before deer reached the second anniversary of their DOB. In the present study, the rLE values between the 2 groups of red deer that lived ≥ 2 years from DOB (rLE of 0.46 for nonculled deer in the Swiss deer park vs rLE of 0.48 for deer recorded in the ISIS) were close, supporting the fact that culling usually takes place within the first 2 years of life or before animals achieve sexual maturity.

In the study reported here, females had significantly higher rLE values than males by use of both rLE approaches (ie, use of rLE of all deer and use of rLE of deer that lived ≥ 2 years from DOB). These findings may reflect differences in culling practices for males and females or differences in mortality patterns between males and females. Polygynous deer species are usually kept in harem groups consisting of 1 male and several females, whereas primarily solitary species are mostly kept in pairs (1 male and 1 female). As a result of a smaller demand and less available space for males of polygynous species, differences in culling practices for males and females should be more evident in these species. The difference in the rLE between males and females that both lived ≥ 2 years from DOB was higher (but not significantly) for social species than for solitary species. This finding suggests that more males than females were culled. Additionally, it is a common finding in natural mammalian populations that juvenile and adult males have higher mortality rates than do females. Reasons for this phenomenon in free-ranging populations, such as expression of deleterious recessive alleles on the X chromosome, smaller parental investment in male offspring, lower resistance to food shortage as a result of higher growth rates with higher energy demand of males, sexual size dimorphism, and an intense intrasexual competition in polygynous species, are discussed in the literature.^{37–41} The culling management in zoological institutions and the higher mortality rate in newborn and young nonadult males indicate that adult female

life expectancy is the most useful measure for demographic analysis of zoo populations.

The calculated rLE of captive-born animals of 20 deer species from the ISIS data set mirrors the husbandry success in zoos during the last 27 years. By ranking the rLE of various deer species, it is possible to identify those species that may have special husbandry requirements and therefore need special care. Assuming that an rLE of females that lived ≥ 2 years from DOB of > 0.41 (reached in 15/20 deer species in this report) is a comparatively good value, special efforts are required to improve the husbandry success of moose, mule deer (*Odocoileus hemionus*), Reeves' muntjac (*Muntiacus reevesi*), white-tailed deer (*Odocoileus virginianus*), and sika deer (*Cervus nippon*). Especially in the case of moose, numerous reports on the difficulties that occur in the husbandry of this species have been published, as reviewed by Clauss et al.⁹

For the deer populations reported here, only the percentage of grass in the natural diet of the species was significantly associated with the rLE of females that lived ≥ 2 years from DOB. The percentage of grass in a species' natural diet allows for classification of animals as browsers (low percentage of grass in its natural diet) or grazers (high percentage of grass in its natural diet).²³ In the step-up procedure, only the percentage of grass remained a significant predictor of rLE of females that lived ≥ 2 years from DOB, which demonstrates that species adapted to browse (small amounts of grass in its natural diet) do not perform as well in captivity. This conclusion is supported by a study by Müller et al.⁴² that found a shorter life expectancy of captive roe deer (a browser), compared with that of 2 free-ranging populations of these deer. By comparison, mixed-feeding reindeer (*Rangifer tarandus*) and red deer had longer life expectancies in captivity. It has been suggested that 1 typical characteristic of several browsing ruminants held in captivity is their reluctance to ingest grass hay or even lucerne hay-forages in adequate amounts,²⁶ which are the major components of ruminant diets in most zoos. Reasons for the general reluctance to ingest such feeds could lie in a rumen that is not equipped to handle the degree of stratification these forages induce when ingested in large quantities⁴³ or a dentition that is not adapted to a proper comminution of these roughages.^{13,44,45} Whatever the cause, a reduced forage intake will automatically result in a higher proportion of concentrates in the ingested food, thus enhancing the danger of an ensuing acidosis. Comparative investigations on acidosis in captive ruminants are rare.²⁶ Nevertheless, the trend of increasing fiber content in pelleted feeds marketed for browsing wild ruminant species in captivity²⁷ indicates that fiber intake in these species via the usually offered roughage is not guaranteed. Findings of the study reported here should be considered as an incentive to improve current feeding practices in zoos, especially in the diets of large browsing species like moose, by offering more varied roughage sources, high-fiber compound feeds, and more browse.^{27,46}

Several international studbooks are maintained for deer species (Table 1) and certain subspecies (Vietnamese sika deer [*Cervus nippon pseudaxis*]). In the study reported here, the mean rLE of females that lived ≥ 2

years from DOB for 5 deer species with a studbook was higher than that of species without a studbook, although this difference was not significant. A potentially higher husbandry success of species for which a studbook is maintained may reflect the higher attention provided to more valuable species, compared with more common hoofstock. It is also possible that adherence to explicit husbandry guidelines usually provided in studbook updates, or the avoidance of crowding conditions caused by more frequent translocation of individuals to other facilities, has a positive effect on the rLE of a species.

Most zoos that contribute data to the ISIS are located in North America or Europe within the temperate climate zone. In the study reported here, a higher rLE in deer derived from temperate climates was expected, compared with that of species that originate from subtropical and tropical habitats, as the latter ones may be more prone to infectious diseases and climate stress. The finding that deer species from subtropical and tropical climates had a higher (although not significantly higher) rLE than that of species from temperate climates was surprising and may be an effect of heated housing during winter, which is usually not offered for deer species from temperate zones.

On the basis of the findings of this study, conclusions on differences in the husbandry success between wild-caught and captive-born deer are not possible. Because the exact life span of each deer was required for the rLE approach, information on wild-caught deer (for which a DOB, and hence the exact age, was not available) had to be excluded from the analysis. Further investigations are necessary to prove the common suggestion that animals born in captivity have a higher life expectancy, compared with wild-caught animals, because of better adaptation to the zoo environment. Clubb et al.¹⁵ disproved this assumption for Asian elephants, as captive-born Asian elephants had a poorer adult survivorship than their wild-born conspecifics.

a. SPSS, version 16.0, SPSS Inc, Chicago, Ill.

References

1. World Association of Zoos and Aquariums. WAZA code of ethics and animal welfare, in *Proceedings. 58th Annu Meet World Assoc Zoos Aquariums*, 2003.
2. Hinshaw KC, Amand WB, Tinkelman CL. Preventive medicine. In: Kleiman DG, Allen ME, Thompson KV, et al, eds. *Wild mammals in captivity principles and techniques*. Chicago: The University of Chicago Press, 1996;16–24.
3. Mench JA, Kreger MD. Ethical and welfare issues associated with keeping wild mammals in captivity. In: Kleiman DG, Allen ME, Thompson KV, et al, eds. *Wild mammals in captivity principles and techniques*. Chicago: The University of Chicago Press, 1996;5–15.
4. Wiese RJ. Asian elephants are not self-sustaining in North America. *Zoo Biol* 2000;19:299–309.
5. Anderson HB, Thompson ME, Knott CD, et al. Fertility and mortality patterns of captive Bornean and Sumatran orangutans: is there a species difference in life history? *J Hum Evol* 2008;54:34–42.
6. Clauss M, Rose P, Hummel J, et al. Serous fat atrophy and other nutrition-related health problems in captive giraffe—an evaluation of 83 necropsy reports. *Proc Eur Assoc Zoo Wildl Vet* 2006;6:233–235.
7. Carlstead K, Fraser J, Bennett C, et al. Black rhinoceros (*Diceros*

- bicornis*) in US zoos: II. Behavior, breeding success, and mortality in relation to housing facilities. *Zoo Biol* 1999;18:35–52.
8. Carlstead K, Brown JL. Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. *Zoo Biol* 2005;24:215–232.
 9. Clauss M, Kienzle E, Wiesner H. Importance of the wasting syndrome complex in captive moose (*Alces alces*). *Zoo Biol* 2002;21:499–506.
 10. European Association of Zoo and Wildlife Veterinarians. Evaluation of okapi (*Okapia johnstoni*) necropsy reports and studbook data as part of the EAZWV summer school. *Proc Eur Assoc Zoo Wildl Vet* 2008;7:323–327.
 11. Thomas WD, Barnes R, Crotty M, et al. An historical overview of selected rare ruminants in captivity. *Int Zoo Yearb* 1985;24:77–99.
 12. Jurando OM, Clauss M, Streich WJ, et al. Irregular tooth wear and longevity in captive wild ruminants: a pilot survey of necropsy reports. *J Zoo Wildl Med* 2008;39:69–75.
 13. Kaiser TM, Brasch J, Castell JC, et al. Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. *Mamm Biol* 2009;74:425–437.
 14. Wiese RJ, Willis K. Calculation of longevity and life expectancy in captive elephants. *Zoo Biol* 2004;23:365–373.
 15. Clubb R, Rowcliffe M, Lee P, et al. Compromised survivorship in zoo elephants. *Science* 2008;322:1649.
 16. Oeppen J, Vaupel JW. Broken limits to life expectancy. *Science* 2002;296:1028–1031.
 17. Wilson DL. The analysis of survival (mortality) data: fitting Gompertz, Weibull, and logistic functions. *Mech Ageing Dev* 1994;74:15–33.
 18. Ricklefs RE, Scheuerlein A. Comparison of aging-related mortality among birds and mammals. *Exp Gerontol* 2001;36:845–857.
 19. Gompertz B. On the nature of the function expressive of the law of human mortality, and a new mode of determining the value of life contingencies. *Phil Trans Roy Soc* 1825;182:513–585.
 20. Weibull W. A statistical distribution function of wide applicability. *J Appl Mech* 1951;18:293–297.
 21. Ricklefs RE, Scheuerlein A. Biological implications of the Weibull and the Gompertz models of aging. *J Gerontol A Biol Sci Med Sci* 2002;57:B69–B76.
 22. Mueller LD, Nusbaum TJ, Rose MP. The Gompertz equation as a predictive tool in demography. *Exp Gerontol* 1995;30:553–569.
 23. Jones ML. Lifespan in mammals. In: Montali RJ, Migaki G, eds. *The comparative pathology of zoo animals*. Washington, DC: Smithsonian Institution Press, 1980;495–509.
 24. Carey JR, Judge DS. *Longevity records: life spans of mammals, birds, amphibians, and fish*. Odense, Denmark: Odense University Press, 2000.
 25. Clauss M, Kaiser T, Hummel J. The morphophysiological adaptations of browsing and grazing mammals. In: Gordon IJ, Prins HHT, eds. *The ecology of browsing and grazing*. Heidelberg, Germany: Springer, 2008;47–88.
 26. Clauss M, Kienzle E, Hatt J-M. Feeding practice in captive wild ruminants: peculiarities in the nutrition of browsers/concentrate selectors and intermediate feeders. A review. In: Fidgett A, Clauss M, Ganslofer U, et al, eds. *Zoo animal nutrition*. Fürth, Germany: Filander Verlag, 2003;27–52.
 27. Clauss M, Dierenfeld ES. The nutrition of browsers. In: Fowler ME, Miller RE, eds. *Zoo and wild animal medicine: current therapy* 6. 3rd ed. St Louis: Saunders Elsevier, 2008;444–454.
 28. International studbooks for rare species of wild animals in captivity. *Int Zoo Yearb* 2007;41:426–448.
 29. Silva M, Downing JA. *CRC handbook of mammalian body masses*. New York: CRC Press Inc, 1995.
 30. Heinemann D. Achte Kapitel Hirsche. In: Grzimek B, ed. *Grzimeks Tierleben Säugetiere* 4. Munich, Germany: DTV, 1980;154–254.
 31. Hofmann RR, Streich WJ, Fickel J, et al. Convergent evolution in feeding types: salivary gland mass differences in wild ruminant species. *J Morphol* 2008;269:240–257.
 32. Jackson JE, Chapman DI, Dansie O. A note on the food of muntjac deer (*Muntiacus reevesi*). *J Zool (Lond)* 1977;183:546–548.
 33. Pérez-Barbería FJ, Gordon IJ. Gregariousness increases brain size in ungulates. *Oecologia* 2005;145:41–52.
 34. Eldridge WD, Macnamara MM, Pacheco NV. Activity patterns and habitat utilization of pudus (*Southern Pudu (Pudu puda)*) in south-central Chile. In: Wemmer CM, ed. *Biology and management of the cervidae*. Washington, DC: Smithsonian Institution Press, 1987;352–369.
 35. Wegge P, Shrestha AK, Moe SR. Dry season diets of sympatric ungulates in lowland Nepal: competition and facilitation in alluvial tall grasslands. *Ecol Res* 2006;21:698–706.
 36. World Association of Zoos and Aquariums. Responsible reproductive management: guiding principles, in *Proceedings*. Rigi Symp Ramifications Reprod Management Anim Zoos, 2003.
 37. Clutton-Brock TH, Albon SD, Guinness FE. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 1985;313:131–133.
 38. Toïgo C, Gaillard J-M. Cause of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactic or environment harshness? *Oikos* 2003;101:376–384.
 39. Clutton-Brock TH, Isvaran K. Sex differences in ageing in natural populations of vertebrates. *Proc R Soc Lond B* 2007;274:3097–3104.
 40. Owen-Smith N. Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *J Anim Ecol* 1993;62:428–440.
 41. Promislow DEL. Costs of sexual selection in natural populations of mammals. *Proc R Soc Lond B* 1992;247:203–210.
 42. Müller DWH, Gaillard JM, Bingaman Lackey L, et al. Comparing life expectancy of three deer species between captive and wild populations [published online ahead of print Nov 17, 2009]. *Eur J Wildl Res* doi:10.1007/s10344-009-0342-8.
 43. Clauss M, Lechner-Doll M, Streich WJ. Ruminant diversification as an adaptation to the physicochemical characteristics of forage. A reevaluation of an old debate and a new hypothesis. *Oikos* 2003;102:253–262.
 44. Clauss M, Franz-Odenaal TA, Brasch J, et al. Tooth wear in captive giraffes (*Giraffa camelopardalis*): mesowear analysis classifies free-ranging specimens as browsers but captive ones as grazers. *J Zoo Wildl Med* 2007;38:433–445.
 45. Hummel J, Fritz J, Kienzle E, et al. Differences in fecal particle size between free-ranging and captive individuals of two browser species. *Zoo Biol* 2008;27:70–77.
 46. Hummel J, Nogge G, Clauss M, et al. Energy supply of the okapi in captivity: fermentation characteristics of feedstuffs. *Zoo Biol* 2006;25:251–266.