Mating system, feeding type and ex situ conservation effort determine life expectancy in captive ruminants

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Zoo animal husbandry aims at constantly improving husbandry, reproductive success and ultimately animal welfare. Nevertheless, analyses to determine factors influencing husbandry of different species are rare. The relative life expectancy (rLE; life expectancy (LE) as proportion of longevity) describes husbandry success of captive populations. Correlating rLE with biological characteristics of different species, reasons for variation in rLE can be detected. We analysed data of 166,901 animals representing 78 ruminant species kept in 850 facilities. The rLE of females correlated with the percentage of grass in a species' natural diet, suggesting that needs of species adapted to grass can be more easily accommodated than the needs of those adapted to browse. Males of monogamous species demonstrate higher rLE than polygamous males, which matches observed differences of sexual bias in LE in free-living populations and thus supports the ecological theory that the mating system influences LE. The third interesting finding was that rLE was higher in species managed by international studbooks when compared with species not managed in this way. Our method facilitates the identification of biological characteristics of species that are relevant for their husbandry success, and they also support ecological theory. Translating these findings into feeding recommendations, our approach can help to improve animal husbandry.
Mating system, feeding type and ex-situ conservation effort
determine life expectancy in captive ruminants

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Zoo animal husbandry aims at constantly improving husbandry, reproductive success, and ultimately animal welfare. Nevertheless, analyses to determine factors influencing husbandry of different species are rare. The relative life expectancy (rLE; life expectancy as proportion of longevity) describes husbandry success of captive populations. Correlating rLE with biological characteristics of different species, reasons for variation in rLE can be detected. We analysed data of 166,901 animals representing 78 ruminant species kept in 850 facilities. The rLE of females correlated with the percentage grass in a species’ natural diet, suggesting that needs of species adapted to grass can be more easily accommodated than of those adapted to browse. Males of monogamous species demonstrate higher rLE than polygamous males, supporting the ecological theory that the mating system influences LE, which subsequently explains observed differences of sexual bias in LE in free-living populations. The third interesting finding was that rLE was higher in species managed by international studbooks compared to species not managed in this way. Our method facilitates the identification of biological characteristics of species that are relevant for their husbandry success, and they also support ecological theory. Translating these findings into feeding recommendations, our approach can help to improve animal husbandry.

Key words: animal husbandry; browser; artiodactyls; life expectancy; sexual bias; zoo
Introduction

In 2003, the international zoo community claimed “to exercise the highest standards of animal welfare” [1]. The importance of this aim cannot be overvalued, as ethical considerations of zoo critics conclude that keeping animals in zoos is only acceptable if their welfare is guaranteed [2,3]. Important questions arise from the call for “highest standards of animal welfare” in zoos: How can we measure welfare, and how can husbandry success be improved [4]? Even though an increasing number of articles have been published in this field, most articles are theoretical [5]. Behavioural patterns (occurrence of stereotypies), metabolic parameters (blood and faecal corticosteroid concentrations), health status (prevalence and incidence of diseases) and life history data (breeding success, life expectancy) were discussed as feasible indicators of wellbeing in zoos [6,7].

In their collaborative effort to manage self-sustaining populations, the zoo community started pooling their population data in a common database, managed by the International Species Information System (ISIS). ISIS collected individual animal data from approximately 850 member institutions in over 80 countries since 1973. Considering all single zoo populations of one species as parts of one metapopulation, ISIS data allow calculations of parameters characterising the average zoo population. To estimate the development of a metapopulation, calculations of life history parameters (e.g. annual mortality, life expectancy) are required. For example, Clubb [8] calculated that adult female elephants (*Elephas maximus* and *Loxodonta africana*) had shorter life expectancies in zoos compared with wild and semi-wild reference populations.

Comparative analyses of different species’ performance in captivity are particularly valuable to detect factors influencing husbandry success. Unfortunately, such analyses are relatively rare. Clubb and Mason [9,10] demonstrated that frequencies of stereotypies and the
extent of infant mortality in captive carnivores was higher in wide-ranging species compared
to species with smaller home range sizes. As LE of different species correlates generally with
the body mass of the species (allometric principle [11]), such comparative analyses of LE
require a correction for this factor. In one survey of life history data from 20 deer species held
in captivity, the relative LE (rLE; average LE as proportion of maximum LE) of adult females
correlated positively with the percentage of grass in a species’ natural diet (%grass) [12].
These examples demonstrated that interspecies comparisons of behavioural measures or life
history data allow the detection of biological characteristics that are relevant for the
adaptability of species to live under the conditions in captivity.

Here, we use such a comparative approach (rLE of metapopulations) to analyse
biological factors correlated to husbandry success in 78 ruminant species. We expect that not
only browsing deer, but browsing ruminants in general, perform less successfully in captivity
compared to mixed feeders and grazers. Species from the tropics and subtropics should have
more problems coping with climatic conditions in the temperate zone (where the majority of
ISIS zoos are located), and thus should display a lower rLE compared to species originating
from the temperate zones. Compared to wild populations, captive zoo animals are confronted
with much higher population densities. Density-dependent influences on LE (social stress,
contact with pathogens) should have a higher impact in solitary and pair-living species, which
are less adapted to crowded conditions (as in zoos). Males that defend a harem have a higher
investment in reproduction compared to monogamous species, so that males of polygamous
species may have a lower LE. Additionally, we test the hypothesis that species intensively
managed by an international studbook perform better than those unmanaged, assuming that
husbandry of such focus species is performed with particular care.

Material and methods
For this investigation, data from app. 150,000 animals, representing 78 species held in captivity (suborder Ruminantia) were analysed. The data were collected by the International Species Information System (ISIS). Data preparation followed the same procedure as described by Müller and others [12]. Life expectancy of a species’ birth cohort separately for both sexes was expressed as relative life expectancy (rLE: life expectancy of a cohort as a proportion of the record longevity of the species) to exclude allometric influences. Only animals that lived two years from date of birth were included, to exclude a bias due to the culling of surplus young animals. Ranging from 0 to 1, an rLE of 0 would denote the death of all individuals at birth, whereas an rLE of 1 implies that all individuals reached the maximum lifespan.

To analyse the influence of biological and husbandry factors on the relative life expectancy, literature data on body mass, geographical origin, social behaviour (in case of females), mating system (in case of males), percentage of grass in the natural diet of a species, as well as the existence of an international studbook, was included in a step down linear regression approach as independent variables (separately for both sexes; see supplements for details). To achieve normality, some of the variables were log-transformed in advance. In order to avoid the false interpretation of ancestry based correlations in these models as adaptation [13,14], the raw data were controlled for phylogenetic influences using the “Phylogenetic Generalized Least-Squares” method [PGLS; 15,16; see supplements for details and phylogenetic tree]. This procedure estimates a covariance matrix of the species due to their ancestral roots and includes these interrelationships in a generalized least squares algorithm to determine the model parameters. For comparison purposes, respective GLM’s without phylogenetic control were set up. The statistical calculations were performed with SPSS 16.0 (SPSS Inc., Chicago, IL) and COMPARE 4.6 program [17]. The significance level was set to $\alpha<0.05$. 
Results

Within species, rLE of females was significantly higher than rLE of males (paired t-test, p < 0.001, n=78 species/ (see supplements for details). In females, the step-down procedure identified %grass (Fig. 1) and the presence of an international studbook as the only significant factors influencing rLE. In males, we identified mating type (Fig. 2) and also the presence of an international studbook as the only significant factors influencing rLE (Tab. 1). The resulting models were identical for analysis with raw data and Phylogenetic Generalized Least-Squares.

Discussion

Our study identified biological characteristics of species that had an influence on husbandry success in the past, allowing suggestions for improvements in husbandry. The data on relative life expectancy (rLE) generated in this study (see supplements for details) can serve as global averages, against which a zoo can compare their populations, in the form of an in-house quality control and warning system.

So far, the effect of particular husbandry measures is rather assessed by approaches of single species, than by comparative analysis between species. Different studies demonstrate that environmental enrichment, feeding management, or exhibition to the public influence the excretion of corticoids, indicating different stress responses [18]. Our analysis does not test for such husbandry-related factors, but identifies biological characteristics that describe the adaptability of a species to live under captive conditions. The results allow two different conclusions whether species with a low rLE should be kept: either try to optimise husbandry, or focus on species in which a higher husbandry success can more easily be achieved.
Contrary to our prediction that social behaviour of a species (measure to live under crowded conditions) influences rLE of female ruminants, such a correlation could not be detected. It is conceivable that the common practice of keeping solitary species in pairs in large enclosures prevents a negative impact on rLE. Additionally, no relation between the geographic origin of a species and rLE was observed, indicating that climatic stress in (sub-)tropic species that are kept in the temperate zone does either not play an important role, or that winter housing in heated stables eliminates the influence on rLE.

In adult female ruminants, the percentage of grass in a species’ natural diet was positively correlated to the relative life expectancy in captivity. This parameter characterises the diet a species is physiologically adapted to (not the one fed in zoos), and indicates whether a species is a browser (very low percentage of grass in the natural diet), mixed feeder, or grazer [19]. Our results corroborate the subjective experience that browsers demonstrate a higher nutrition-related mortality in captivity and are more challenging to keep when compared to grazing species, due to the complex logistics of providing browse [20]. In captivity, browsers are often offered grass hay and/or lucerne hay as surrogate roughage sources. The reluctance of browsers to ingest such roughage sources in larger amounts, as either their teeth or their stomachs are not adapted to the physical properties of these materials [21,22], leads to an increased proportion of concentrate feeds in the ingested diet. This will cause chronic forestomach acidosis, which in turn leads to a higher incidence of a variety of diseases [23] and ultimately to a shorter average LE.

The diet a species is naturally adapted to was not a predictor of LE in male ruminants. Instead, mating type had a significant influence on LE, with males of monogamous species demonstrating a higher LE than territorial males, or males defending a harem. Lower annual survival rates in males compared to females are a common characteristic in population dynamics of free-living wild ungulates [24]. The here-described lower rLE of male ruminants
in captivity proves that this pattern can also be observed in captive populations. This is particularly interesting, as the pressure of the rut is expected to be much lower in captivity, where usually only one adult male is kept in a harem, when compared to the situation in the wild, where several males compete for the females. In one experimental study on wild-living soay sheep (*Ovis aries*), castrated males demonstrated a prolonged life expectancy compared to intact males and even females [25]. Both findings together support speculations that not only an intensive intraspecific competition for the females during the rut, but reproductive behaviour per se has a negative influence on male life expectancy. In free-living mammal populations, the degree of male-biased adult mortality correlates positively to the degree of sexual size dimorphism [26]. Sex differences in adult longevity are more pronounced in polygynous (degree of sexual dimorphism correlates with degree of polygyny [27]) as compared to monogamous species [28]. Two results of our analysis support the theory that sexual dimorphism and mating system explain the pattern of sexual bias in adult life expectancy of ungulates: (1) Relative life expectancy in captive males of ruminant species with lower male reproductive investment (monogamous species) was higher compared to species with higher investment (polygynous species), and (2) the difference between the rLE of females and males of monogamous species was significantly smaller than the difference between female and male rLE in polygynous species. Nevertheless, an influence of culling measures on the observed sexual bias of adult life expectancy with respect to mating systems cannot be completely excluded, although recommendations for population management of the World Association of Zoos and Aquariums [29] and the results of Müller et al. [12] suggest that culling is performed before animals are sexually mature.

One major past achievement of zoos was the conservation of species that extinct in the wild, including Przewalski's horse (*Equus caballus przewalskii*) and Père David's deer (*Elaphurus davidianus*). A major key to this success was the breeding coordination of many
zoos with international studbooks. Nowadays, endangered species’ conservation by ex-situ breeding programs is one of the most important aims of zoological institutions [1], and over 150 international studbooks have been established. The principle aim of such studbooks is to maintain a broad genetic diversity by reducing inbreeding to a minimum. Additionally, detailed husbandry recommendations including spatial requirements, housing facilities, group composition, and feeding regimes are often an integral part of these studbooks. In both, male and female ruminant, relative life expectancy was higher in species managed with the help of an international studbook. Newborn mortality of several species in captivity was higher in inbreed compared to not-inbreed individuals [30-32], suggesting that inbreeding may also have an influence on adult life expectancy. It is possible that either the effort to reduce inbreeding in studbook managed populations (as compared to not-managed species), or the implementation of the detailed husbandry guidelines resulted in the higher rLE values of the relevant species. The success of such an intensive population management should encourage more intensive use of studbook coordination in additional species.

Further analyses will demonstrate, whether factors like inbreeding, or geographical distribution of zoo populations also influences LE in captivity, and whether analysis of other taxa identify more parameter that are relevant for the husbandry success of wild species in captivity.

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Table 1. Results of final General Linear Models

Independent variables remained after a step-down procedure starting with %grass, studbook, mating system (or social system, alternatively), habitat, ln(body mass). Results given for raw data (ANOVA) and Phylogenetic Generalized Least-Squares (PGLS) (likelihood ratio test).

<table>
<thead>
<tr>
<th>Dependent variable: rLE_{2f}</th>
<th>raw data</th>
<th>PGLS</th>
</tr>
</thead>
<tbody>
<tr>
<td>%grass</td>
<td>F(1,75)=19.84, p&lt;0.001</td>
<td>$\chi^2 = 8.28$, df=1, p=0.004</td>
</tr>
<tr>
<td>studbook</td>
<td>F(1,75)=7.69, p=0.007</td>
<td>$\chi^2 = 8.80$, df=1, p=0.003</td>
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</table>

<table>
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<th>Dependent variable: rLE_{2m}</th>
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<th>PGLS</th>
</tr>
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<tbody>
<tr>
<td>mating system</td>
<td>F(2,74)=6.719, p=0.002</td>
<td>$\chi^2 = 9.92$, df=2, p=0.007</td>
</tr>
<tr>
<td>studbook</td>
<td>F(1,74)=6.745, p=0.011</td>
<td>$\chi^2 = 5.52$, df=1, p=0.019</td>
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</table>

<table>
<thead>
<tr>
<th>Dependent variable: rLE_{2m}</th>
<th>raw data</th>
<th>PGLS</th>
</tr>
</thead>
<tbody>
<tr>
<td>social system</td>
<td>F(2,74)=5.420, p=0.006</td>
<td>$\chi^2 = 9.76$, df=2, p=0.008</td>
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<tr>
<td>studbook</td>
<td>F(1,74)=5.177, p=0.026</td>
<td>$\chi^2 = 4.34$, df=1, p=0.037</td>
</tr>
</tbody>
</table>

*Independent variables assessed: body mass, percentage of grass in the natural diet, social system or mating system (alternatively), natural habitat (temperate vs. subtropical/tropical), presence of an international studbook.
**Figure 1.** Positive correlation of the relative life expectancy of females that lived two years from date of birth (rLE$_f$) with the percentage grass in a species’ natural diet (%grass). Note that species with low %grass (browsers) demonstrated lower rLE$_f$ compared with species with medium and high %grass (intermediate feeding type and grazers). Relation was significant (see Tab. 1).
Figure 2. Range, arithmetic mean and quartiles of the relative life expectancy of males that lived two years from date of birth (rLE\textsubscript{m}) according to mating type. Note that males of monogamous species had a higher relative life expectancy compared with polygamous species. Relation was significant (see Tab. 1).