

A long life among ruminants: giraffids and other special cases

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Summary

In order to investigate differences in the relative maximum longevity and other life history parameter between ruminant species, we collated data on mean body mass, maximum longevity, gestation period and newborn mass in wild ruminant and camelid species. Among ruminants, giraffids (giraffe *Giraffa camelopardalis* and okapi *Okapia johnstoni*) have particularly high longevities, long gestation periods, and low intra-uterine growth rates. A particularly high absolute and relative longevity is also achieved by the anoa (*Bubalus depressicornis*), a member of the bovinæ (cattle-type ruminants) and an insular dwarf (inhabiting the Indonesian island of Sulawesi). The fact that some (but not all) other small ruminants also achieve surprisingly high longevities leads to the hypothesis that extreme relative longevities in this group are an indication for secondary body size reduction.

Keywords: Longevity, gestation period, metabolism, *Giraffa camelopardalis*, *Okapia johnstoni*, *Bubalus depressicornis*, dwarfism

Ein langes Leben unter Wiederkäuern: Giraffen und andere Spezialfälle

Um Unterschiede in der relativen maximalen Lebensdauer zwischen Wiederkäuer zu untersuchen, wurden Daten zur durchschnittlichen Körpermasse, zur maximalen Lebensdauer, zur Tragzeit und zum Neugeborenenengewicht von wildlebenden Wiederkäuern und Kameliden zusammengestellt. Bei den Wiederkäuern erreichen Giraffiden (Giraffe *Giraffa camelopardalis* und Okapi *Okapia johnstoni*) ein besonders hohes Alter, haben lange Tragzeiten und ein langsames intrauterines Wachstum. Eine besonders hohe absolute und relative Lebenserwartung wird auch vom Anoa (*Bubalus depressicornis*), einem Vertreter der Bovinae (Rinder) und zugleich eine Insel-Zwergform (von der indonesischen Insel Sulawesi), erreicht. Die Tatsache, dass einige (jedoch nicht alle) der anderen kleinen Wiederkäuer ebenfalls ein überraschend hohes Alter erreichen, führt zu der Hypothese, dass extreme relative Lebenserwartungen in dieser Gruppe ein Hinweis auf eine evolutionäre sekundäre Reduzierung der Körpergrösse sind.

Schlüsselwörter: Langlebigkeit, Tragzeit, Metabolismus, *Giraffa camelopardalis*, *Okapia johnstoni*, *Bubalus depressicornis*, Verzweigung

Introduction

When celebrating a birthday, wishes of a long life accompany the congratulations. We consider those who have a high longevity to be blessed individuals. This does not only apply to humans, but also to animals in the wild, and those in our care. In this respect, longevity is not only an attribute of individuals, but also of species. The longevity of a species is one factor that determines its lifetime reproductive output, as most animals reproduce until old

age. For the management of captive wild animals, knowledge of species' longevity potential is important in order to assess husbandry conditions: the closer the mean life expectancy of the individuals in one's care is to the species maximum longevity, the more successful the husbandry regime appears (Müller et al., 2010).

When recently evaluating the mean life expectancy of captive wild ruminants (Müller et al., 2011), we realized that the giraffe (*Giraffa camelopardalis*) can achieve a par-

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ticularly high longevity with a reported record of 38 years for a free-ranging animal (Carey and Judge, 2000). On the one hand, this could simply be an effect of body size. As many other physiological parameters, longevity increases allometrically with body size (Sacher, 1959; Blueweiss et al., 1978; Western, 1979). Blueweiss (1978) found that average life expectancy in mammals scaled with $BM^{0.17}$, Gaillard et al. (2003) found an allometric exponent of 0.19 in an analysis of 78 mammalian species, and Western (1979) calculated that life expectancy in artiodactyls scaled with body mass (BM)^{0.20}. Our own unpublished analyses of data for captive wild ruminants reveal a dichotomy, with average life expectancy of females scaling with $BM^{0.15}$, and of males scaling with $BM^{0.11}$ (as used for Müller et al., 2011). The very high longevity noted for giraffe, the largest extant ruminant (Owen-Smith, 1988), may therefore not be surprising.

On the other hand, however, the only other extant giraffid, the okapi (*Okapia johnstoni*), can also become very old as compared to other ruminants (animals up to 33 years of age were reported in captivity; EAZWV, 2008), although its average adult body mass is far lower than that of the giraffe (250–300 kg). Therefore, we wondered whether the taxonomic group of the giraffids is characterised by a particularly high longevity among the ruminants that

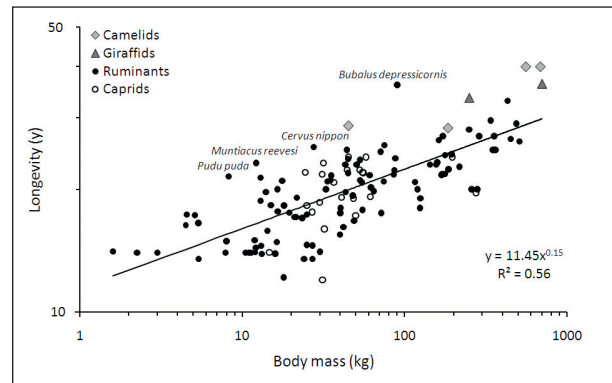


Figure 1: Relationship between body mass and the maximum longevity in 127 ruminant and 4 camelid species.

is independent of their body mass range. In order to test this hypothesis, we collated maximum longevity data for wild ruminants and camelids, and compared these also to data on gestation periods and neonate body masses.

Material and Methods

Literature data on ruminants was collated on a species level for maximum longevity and average female body

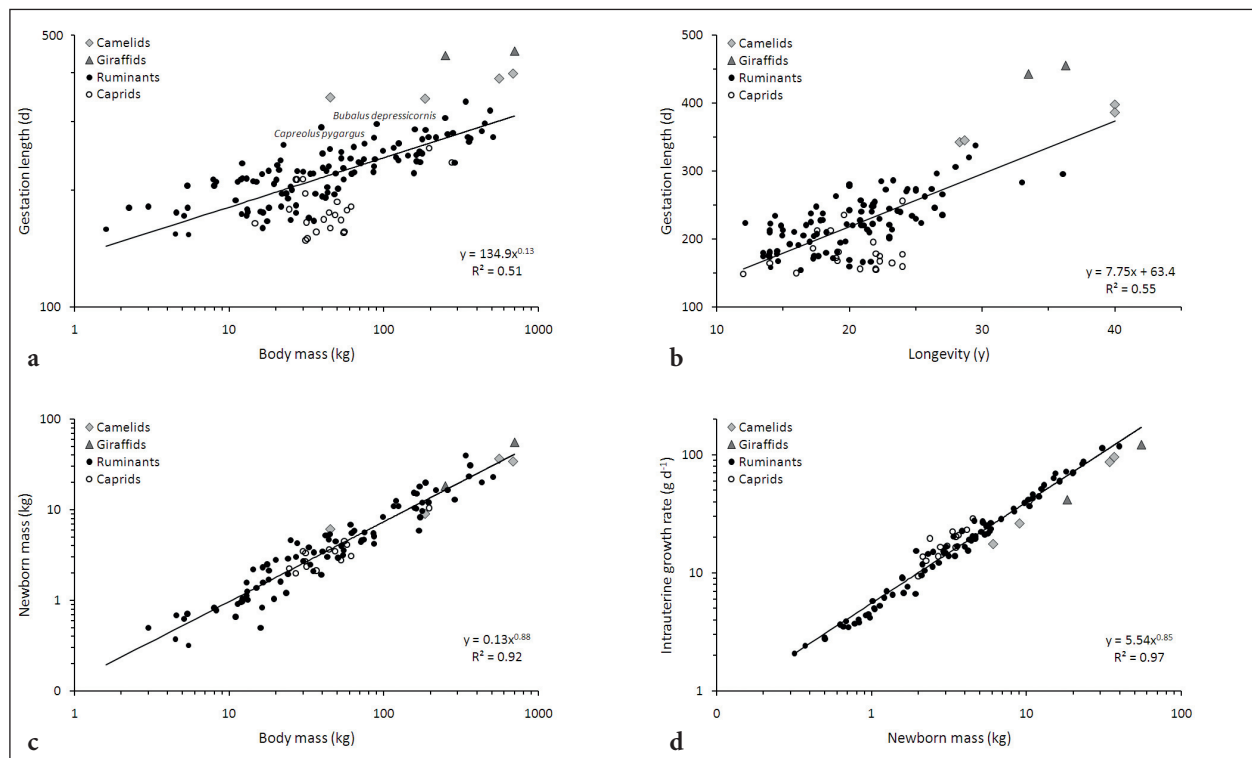


Figure 2: Relationship between a) body mass and gestation period in 151 ruminant and 4 camelid species; b) maximum longevity and gestation period in 120 ruminant and 4 camelid species; c) body mass and newborn mass in 151 ruminant and 4 camelid species; d) newborn mass and intrauterine growth rate in 151 ruminant and 4 camelid species. Note that although giraffids and camelids have comparatively long gestation periods (a), even in relation to their longevity (b), they do not produce comparatively larger offspring (c), which means that the intrauterine growth rate in these species is relatively small (d).

mass (BM) (mostly from Silva and Downing, 1995; Weckerly, 1998; Ernest, 2003); data for gestation periods and neonate body mass was taken from the Pantheria database (Jones et al., 2009). For some species, not all data were available. As a comparative group, the only other ruminating herbivores, the camelids, were included in this study, because camelids are known to have a lower metabolism than most ruminants (Van Saun, 2006; Maloiy et al., 2009), and level of metabolism is one factor that is often referred to in the context of longevity (de Magalhães et al., 2007). Data are presented in log-log plots; allometric regressions (as linear regression on log-transformed values) according to $y = a \text{ BM}^b$ were performed in PASW 18.0 (SPSS Inc., Chicago, IL). The resulting allometric exponent was used to rank species in terms of their relative longevity.

Results

Maximum longevity (in years) among ruminants and camelids scaled to 11.5 (95%CI 10.4–12.5) $\text{BM}^{0.15}$ (95%CI $0.12-0.17$) ($r^2 = 0.56$, $p < 0.001$). Although the giraffids and the camelids were clearly above the regression line (Fig. 1), other individual ruminant species also achieve comparatively high longevities. When expressed as relative longevity (years $\text{BM}^{-0.15}$), the anoa (*Bubalus depressicornis*) achieves the highest longevity, followed not only by the camelids and the okapi but also by several small cervids (Reeve's muntjac *Muntiacus reevesi*, Southern pudu *Pudu puda*, Sika deer *Cervus nippon*).

The gestation period (in days) among ruminants and camelids scaled to 135 (95%CI 124–147) $\text{BM}^{0.13}$ (95%CI $0.11-0.15$) ($r^2 = 0.51$, $p < 0.001$). Although the giraffids and the camelids are clearly above the regression line (Fig. 2a), other ruminant species also achieve comparatively long gestation periods, such as the Siberian roe deer (*Capreolus pygargus*) (where this can be attributed to the peculiarity of delayed implantation, Aitken, 1974) and again the anoa. When gestation period is plotted against longevity (Fig. 2b), it is evident that camels and especially giraffids have very long gestation periods even for their high longevity. In contrast, a group of medium-sized ruminants mostly belonging to the caprids have comparatively short gestation periods. In spite of their long gestation period, camelids and giraffids do not produce larger offspring than other ruminants (Fig. 2c). Consequently, the intrauterine growth rates of camelids and giraffids are lower than those of other ruminants (Fig. 2d).

Discussion

The comparisons of longevity and especially of gestation periods and intrauterine growth rates suggest that giraf-

fids are peculiar among extant ruminants. Ruminant species differ in various physiological adaptations (Clauss et al., 2010) and also in various life history parameters (this study). Life history parameters have often been linked to the level of metabolism; one question under debate is, for example, whether species with a low metabolism achieve higher longevities than species with a higher metabolism (de Magalhães et al., 2007). Among the cetartiodactyls, the hippopotamids, with their comparatively low metabolism (Schwarm et al., 2006), achieve particularly high longevities. The record of 44 years for the pygmy hippopotamus (*Hexaprotodon liberiensis*) (Carey and Judge, 2000) with a body mass of about 220 kg is distinctively longer than that of similar-sized ruminants. The same pattern applies to camelids, for which evidence for a lower metabolism than for ruminants exists (Van Saun, 2006; Maloiy et al., 2009), and which display higher longevities than most similar-sized ruminants (Fig. 1). These findings do not necessarily mean that these principles can be generally transferred to other taxonomic groups. Actually, metabolism-dependent longevity is not evident in most mammalian taxa (de Magalhães et al., 2007). However, transferring these considerations within the ruminants to the giraffids invokes the assumption that that giraffids also have a comparatively low metabolism among the ruminants.

This hypothetical conclusion is further supported by data on intrauterine growth rates. Even more impressive than the giraffids' long lifespans are their extremely long gestation periods (Fig. 2a) and particularly slow intrauterine growth rates (Fig. 2d). Slow intrauterine growth is compatible with a reduced metabolic level, and our findings may thus have important ecological consequences for giraffids. Low reproductive outputs coupled with slow metabolic rates may leave giraffids competitively disadvantaged when interacting with more reproductively efficient species (McNab, 2006). Maybe because of this, giraffids occupy only very peculiar habitats, and have narrow niche breadths: of the two extant species, the okapi is limited in the wild to one small habitat in the Ituri forest (Hart and Hart, 1988), whereas the giraffe occupies, due to its peculiar body shape, a unique dietary/behavioural niche (Cameron and du Toit, 2007). In this way, the scenario we describe may account for the low species richness amongst extant compared with fossil giraffe faunas (Solounias, 2007). A low metabolism could further hinder performance, for instance by contributing to the giraffe's suspected susceptibility to cold spells (Clauss et al., 1999), and the high longevity of giraffids might explain the observation that the abnormal tooth wear reported in captive specimens is more prominent in giraffe and okapi than in any other browsing ruminant (Clauss et al., 2007; Kaiser et al., 2009).

A surprising finding of our analysis was that several other ruminant species achieve longevities that are, in relation to their body mass, even higher than that of the giraffids.

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This leads to the question whether those species with outstanding longevities share some common characteristics, or whether this observation simply has to be considered individually for each species in isolation. The highest relative longevity recorded in the ruminants (i.e., in proportion to body mass) is achieved by the anoa, which is native to the Indonesian island of Sulawesi (Burton et al., 2005). The anoa belongs to the tribe Bovini, the cattle-type ruminants, shares some characteristics of digestive physiology with other cattle-type ruminants (Flores-Miyamoto et al., 2005), and is a typical case of island dwarfism, where descendants of larger-bodied species reduce their body size as a response to their restriction on an island habitat—a phenomenon observed in animals as diverse as cervids, hippos, and elephants (Raia and Meiri, 2006). Insular dwarfism is usually interpreted as an adaptation to the limited resources on the smaller island habitat. It is tempting to speculate that during the evolution of dwarf forms, not only anatomical (Clauss et al., 2009), but also physiological adaptations of the ancestral form are maintained, resulting in comparatively high longevities and long gestation periods in the dwarf forms. In this study, several other small ruminants such as the small cervids pudu and muntjac had particularly high longevities; in these cases, one could speculate that the extreme longevities of these species indicate a similar secondary dwarfing, not because of island habitats, but because of other habitat characteristics that made an evolutionary reduction of body size adaptive. If these speculations could be corroborated, the examples presented here may indicate that the effect of the evolutionary history of species needs to be taken into account when interpreting results of allometric analyses. However, these speculations, as well as the intriguing fact that caprids have particularly short gestation periods that might be an adaptation to the particularly pronounced reproductive seasonality of this group, remain to be further investigated. Whatever the evolutionary implications, advancing knowledge of such species differences is important for the zoo and wildlife veterinarian who has to plan the management of the populations in his or her care.

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References

- Aitken R. J.: Delayed implantation in roe deer (*Capreolus capreolus*). *J. Reprod. Fert.* 1974, 39:225–233.
- Blueweiss L., Fox H., Kudzma V., Nakashima D., Peters R., Sams S.: Relationships between body size and some life history parameters. *Oecologia* 1978, 37:257–272.
- Burton J. A., Hedges S., Mustari A. H.: The taxonomic status, distribution and conservation of the lowland anoa (*Bubalus depressicornis*) and mountain anoa (*Bubalus quarlesi*). *Mammal Rev.* 2005, 35:25–50.
- Cameron E. Z., du Toit J. T.: Winning by a neck: tall giraffes avoid competing with shorter browsers. *Am. Nat.* 2007, 169:130–135.
- Carey J. R., Judge D. S., 2000: Longevity records: life spans of mammals, birds, amphibians, reptiles, and fish. Odense University Press, Odense, Denmark.
- Clauss M., Suedmeyer W. K., Flach E. J.: Susceptibility to cold in captive giraffe (*Giraffa camelopardalis*). *Proc. AAZV* 1999:183–186.
- Clauss M., Franz-Odenaal T. A., Brasch J., Castell J. C., Kaiser T. M.: 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.
- Clauss M., Reese S., Eulenberger K.: Macroscopic digestive anatomy of a captive lowland anoa (*Bubalus depressicornis*). In: *Zoo animal nutrition Vol. IV*. Eds. M. Clauss, A. L. Fidgett, J.-M. Hatt, T. Huisman, J. Hummel, G. Janssen, J. Nijboer and A. Plowman, Filander Verlag, Fürth, 2009, 255–263.
- Clauss M., Hume I. D., Hummel J.: Evolutionary adaptations of ruminants and their potential relevance for modern production systems. *Animal* 2010, 4:979–992.
- de Magalhães J. P., Costa J., Church G. M.: An analysis of the relationship between metabolism, developmental schedules, and longevity using phylogenetic independent contrasts. *J. Gerontol. Biol. Sci.* 2007, 62A:149–160.
- EAZWV: Evaluation of okapi (*Okapia johnstoni*) necropsy reports and studbook data as part of the EAZWV Summer School. *Proc. EAZWV* 2008, 7:323–327.
- Ernest S. K. M.: Life history characteristics of placental nonvolutant mammals *Ecology* 2003, 84:3401.
- Flores-Miyamoto K., Clauss M., Ortmann S., Sainsbury A. W.: The nutrition of captive lowland anoa (*Bubalus depressicornis*): a study on ingesta passage, intake, digestibility, and a diet survey. *Zoo Biol.* 2005, 24:125–134.
- Gaillard J.-M., Loison A., Festa-Bianchet M., Yoccoz N. G., Solberg E.: Ecological correlates of life span in populations of large herbivorous mammals. In: *Life span: Evolutionary, ecological, and demographic perspectives*, vol 29, 1st edn. Eds. J. R. Carey and S. Tuljapurkar, The Population Council Inc., New York, 2003, 39–56.
- Hart J. A., Hart T. B.: A summary report on the behaviour, ecology and conservation of the okapi (*Okapia johnstoni*) in Zaire. *Acta Zool. Pathol. Antverp.* 1988, 80:19–28.
- Jones K. E., Bielby J., Cardillo M., et al.: PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 2009, 90:2648 (Ecological Archives E2090–2184).
- Kaiser T. M., Brasch J., Castell J. C., Schulz E., Clauss M.: Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. *Mamm. Biol.* 2009, 74:425–437.

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Maloiy G. M. O., Rugangazi B. M., Rowe M. F.: Energy expenditure during level locomotion in large desert ungulates: the one-humped camel and the domestic donkey. *J. Zool.* 2009, 277:248–255.

McNab B. K.: The energetics of reproduction in endotherms and its implication for their conservation. *Integr. Comp. Biol.* 2006, 46:1159–1168.

Müller D. W. H., Bingaman Lackey L., Streich W. J., Hatt J.-M., Clauss M.: Relevance of management and feeding regimens on life expectancy in captive deer. *Am. J. Vet. Res.* 2010, 71:275–280.

Müller D. W. H., Bingaman Lackey L., Streich W. J., Fickel J., Hatt J.-M., Clauss M.: (2011) Mating system, feeding type and ex-situ conservation effort determine life expectancy in captive ruminants. *Proc. R. Soc. B* 2001, 278:2076–2080.

Owen-Smith N., 1988: Megaherbivores – the influence of very large body size on ecology. Cambridge University Press, Cambridge.

Raia P., Meiri S.: The island rule in large mammals: paleontology meets ecology. *Evolution* 2006, 60:1731–1742.

Sacher G. A.: Relation of lifespan to brain weight and body weight in mammals. In: *The lifespan of animals*. Eds. G. E. W. Wolstenholme and M. P. O'Connor, J. & A. Churchill Ltd., London, 1959, 115–141.

Schwarm A., Ortmann S., Hofer H., Streich W. J., Flach E. J., Kühne R., Hummel J., Castell J. C., Clauss M.: Digestion studies in captive hippopotamidae: a group of large ungulates with an unusually low metabolic rate. *J. Anim. Physiol. Anim. Nutr.* 2006, 90:300–308.

Silva M., Downing J. A., 1995: CRC handbook of mammalian body masses. CRC Press, Boca Raton.

Solounias N.: Family Giraffidae. In: *The evolution of artiodactyla*. Ed. D. R. Prothero, John Hopkins University Press, Baltimore, 2007, 257–277.

Van Saun R. J.: Nutrient requirements of South American camelids: A factorial approach. *Small Rum. Res.* 2006, 61:165–186.

Weckerly F. W.: Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammal.* 1998, 79:33–52.

Western D.: Size, life history and ecology in mammals. *Afr. J. Ecol.* 1979, 17:185–204.

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