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SHORT COMMUNICATION

Comparing life expectancy of three deer species between captive and wild populations

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Abstract Life in zoological gardens provides a number of benefits to captive animals, resulting in an artificial reduction of the "struggle for life" compared to their free-ranging counterparts. These advantages should result in a higher chance of surviving from 1 year to the next, and thus in longer average life expectancies for captive animals, given that the biological requirements of the species are adequately met. Here, we compare the life expectancy of captive and free-ranging populations of three deer species (reindeer *Rangifer tarandus*, red deer *Cervus elaphus*, and roe deer *Capreolus capreolus*). Whereas captive reindeer and red deer had life expectancies equal to or longer than free-ranging individuals; the life expectancy of captive roe deer was shorter than that of free-ranging animals. These results support the impression that roe deer are difficult to keep in zoos, whereas reindeer and red deer perform well under human care. We suggest that the mean life expectancy of captive populations relative to that of corresponding free-ranging populations is a reliable indicator to evaluate the husbandry success of a species in captivity.

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Introduction

It is often thought that wild animals in captivity live longer than their free-ranging conspecifics. This could be due to a number of reasons: a sufficient amount of adequate food provided consistently throughout the year, the absence of predators, a lower risk of injuries due to intraspecific aggressions (especially among males), a minimum of (intraspecific) competition, and the provision of veterinary care. This assumption is supported by the fact that longevity records are most often held by zoo animals (Carey and Judge 2000). In contrast, there are only few reports of species displaying longevity records under free-ranging conditions. One popular example is the moose *(Alces alces)*, reported to live up to 17 years and 11 months in captivity (Jones 1980), whereas a maximum longevity of 27 years has been reported in the wild (Carey and Judge 2000). Problems occurring in husbandry management are most likely to account for the poorer performance of moose in captivity (reviewed in Clauss et al. 2002).

However, maximum longevity is only one measure of the lifetime performance of animals and strongly depends on the sample size (Krementz et al. 1989). Moreover, the maximum longevity of a given species is reached by only one individual, so that extrapolating the measure to assess the conditions experienced by the entire population is disputable. Measurements based on annual survival, such as the mean life expectancy (expected remaining lifespan at a certain age, e.g. at birth), better reflect these conditions and is the measure generally used in comparative analyses (Gaillard et al. 1989; Clutton-Brock and Isvaran 2007;

Clubb et al. 2008). Here, we compare the life expectancy of free-ranging and captive populations of three deer species, the reindeer (*Rangifer tarandus*), the red deer (two subspecies: red deer, *Cervus elaphus elaphus*; wapiti, *Cervus elaphus nelsoni*), and the roe deer (*Capreolus capreolus*) to test the common prediction that the life expectancy is generally longer in captive populations than in their free-ranging counterparts.

Methods

We calculated the life expectancies of captive deer populations from the dataset of the International Species Information System (ISIS). ISIS has collected stock data of participating zoos (approximately 750 worldwide) over the last 35 years. Using all available data of one species, data on captive populations thus represent the average zoo population. As both the date of birth and the date of death are generally provided, the exact lifespan of each individual was calculated. Birth cohorts were created, ensuring that all members died within the observation interval (1980–2007). We calculated the life expectancy separately for males and females, according to standard life-table analyses (e.g. Caughley 1977). Life expectancy is defined as the number of years an individual is expected to live and can be determined for each age class. At age x, the life expectancy is measured as:

$$e_x = \frac{\sum_{y=x}^{\infty} ly}{lx}$$

where l_y is the cumulative probability of surviving to each remaining age class beyond x, and l_x is the probability of surviving from birth to age x. Thus, at birth the life expectancy is simply the cumulative probability of surviving to each possible age. To exclude a bias due to high neonate losses, we used the life expectancy of animals that reached the mean age of first female parturition in this comparison (i.e. animals that died before mean age of first female parturition were excluded). As comparable data for males (mean age when first fathered offspring is born) are not available, this definition of life expectancy was used for both sexes. Accordingly, the life expectancy was measured at 2 years of age in roe deer (Gaillard et al. 1992), wapiti (only for the free-living population, Houston 1982), and reindeer (Leader-Williams 1988), and 3 years for red deer (Clutton-Brock et al. 1982). As the ISIS dataset did not separate between different subspecies, the captive red deer data included the European red deer and the North American wapiti. The life expectancy of captive red deer thus has to be interpreted as the average of all kept subspecies. The captive roe deer cohort consisted of 62 males and 73 females born between May 1980 and June 1993, the captive reindeer cohort consisted of 132 males and 175 females born between January 1980 and May 1985, and the captive red deer cohort of 59 males and 91 females born between January 1980 and September 1983.

We used or computed the sex-specific life expectancies of free-ranging deer populations collected from published population studies including survival analyses performed in absence of hunting and predation by large carnivores. These included the reindeer population of South Georgia (Leader-Williams 1988), the red deer population on the Island of Rum (Clutton-Brock and Isvaran 2007), the wapiti population of Yellowstone National Park (Houston 1982), and the two roe deer populations of Chizé and Trois Fontaines (Gaillard et al. 2003a; Gaillard et al. 2004). The age-specific survival estimates of roe deer at Chizé and Trois Fontaines were based on the monitoring of 418 and 630 males, and 379 and 624 females, respectively. Sex-specific life expectancy at age of first parturition of reindeer, wapiti, and red deer was directly taken from Clutton-Brock and Isvaran (2007; see their electronic appendix). For roe deer, the data came from long-term capture-mark-recapture (CMR) monitoring (>30 years). Age- and sex-specific survival estimates were obtained from CMR modelling (Gaillard et al. 2003a, 2004) and the life expectancy was directly calculated from CMR estimates.

Table 1 Life expectancy at the age of first female parturition (in years) for males and females of three deer species for captive and free-living populations

Population	Life expectancy					
	Rangifer tarandus		*Cervus elaphus*		*Capreolus capreolus*	
	Male	Female	Male	Female	Male	Female
Captive	5.5	7.7	9.3	12.0	3.6	6.7
Free-living 1	2.2[a]	4.6[a]	8.0[b]	10.6[b]	5.7[d]	9.3[d]
Free-living 2			7.6[c]	16.1[c]	5.0[e]	7.4[e]

Literature source: life expectancies of free-living populations were taken from Clutton-Brock and Isvaran (2007)

[a] Calculations of life expectancy based on published population data of South Georgia (Leader-Williams 1988)

[b] Calculations of life expectancy based on published population data of Island of Rum (Clutton-Brock et al. 1982)

[c] Calculations of life expectancy based on published population data of Yellowstone National Park (Houston 1982)

[d] Calculations of life expectancy based on published population data of Chizé (Gaillard et al. 2004)

[e] Calculations of life expectancy based on published population data of Trois Fontaines (Gaillard et al. 2003a)

Results

As expected from our prediction, the adult life expectancy of captive male and female reindeer was markedly higher than that of their free-ranging conspecifics (Table 1). Captive reindeer males' life expectancy exceeded that of free-ranging conspecifics by 3.3 years (+150%); the life expectancy of captive reindeer females was 3.1 years (+67%) greater than the life expectancy of the free-ranging females. While captive males also had a greater life expectancy than free-ranging males in red deer (+16% and +22% compared to red deer on Rum and Yellowstone wapiti, respectively), the life expectancy of captive red deer females was within the range of values reported in free-living populations (+13% and −25% compared to red deer and wapiti, respectively).

In contrast, captive roe deer of both sexes had shorter life expectancies than free-ranging animals. The difference in life expectancy between the captive and the free-ranging roe deer was −2.1 (−37%) and −1.4 (−28%) years for males and −2.6 (−28%) and −0.7 (−9%) years for females at Chizé and Trois Fontaines, respectively.

Discussion

As would be expected, the adult life expectancy of captive reindeer and red deer populations was within the range or higher than that of free-ranging deer, irrespective of gender. These findings support the positive effect of human care on the quality of life of animals in captivity as well as the use of life expectancy as a relevant measure of animal welfare in zoological institutions (Broom 1991). The high life expectancy of female wapiti in Yellowstone Park relative to captive red deer might represent differences of survival among red deer subspecies. Indeed, wapiti are much larger than red deer and the higher adult life expectancy of wapiti can simply reflect allometric constraints, because life expectancy increases with increasing body mass in mammals (Gaillard et al. 2003b).

On the contrary, captive roe deer had consistently lower life expectancy than their free-living counterparts. This result is surprising at first sight but might illustrate difficulties occurring in the husbandry of roe deer previously reported in the zoo literature (Tschiderer 1973; Heinemann 1979; Wiesner 1987). When comparing several different deer species, Müller et al. (2010) observed that the relative life expectancy of different species was correlated to their natural diet, with relatively lower values for browsing species. On the continuum of diet types going from browsers to grazers, roe deer are classified as browsers (Hofmann 1985), consuming a high diversity of plant species, but only small amounts of grass (Tixier and Duncan 1996; Tixier et al. 1997). In contrast, reindeer and red deer are mixed feeders that both graze and browse (Nieminen and Heiskari 1989; Gebert and Verheyden-Tixier 2001). One might thus expect that reindeer and red deer cope better with grass-hay and lucerne-hay which constitutes the main part of ruminant diets in most zoos. The decreased survival of roe deer under captive conditions might thus reflect the difficulties in providing them with adequate food (Dissen 1983; Clauss et al. 2003; Clauss and Dierenfeld 2008; Kaiser et al. 2009). Interestingly, the other deer that has often been reported to perform less well in captivity is the moose (see "Introduction"), which is also a browser.

An alternative but non-exclusive explanation could involve between-species differences in the ability to live under crowding conditions. Both red deer and reindeer often occur in large groups in the wild and might suffer less from crowding than more solitary roe deer or moose. Higher stress levels in crowding conditions, or higher incidence of parasite infections and other diseases (Dollinger 1981; Clauss et al. 2002; Besselmann et al. 2008; Maublanc et al. 2009) would then be the most likely mechanisms, and could counterbalance the positive influence of protection on life expectancy in zoos. Tschiderer (1973) reported that roe deer in captivity seem to thrive only on an extensive husbandry regime. In contrast, very high adult survival rates (up to 100% per year) were reported for a free-ranging, un-hunted roe deer population under favorable environmental conditions (Cobben et al. 2009). Considering all above mentioned studies and our own results, an improvement of roe deer management may be possible by a constant provision of browse throughout the year, keeping roe deer in pairs in large enclosures, and by deworming all animals regularly.

The difference between the life expectancy of female roe deer in the two free-ranging populations indicates that the life expectancy can differ considerably between wild populations. Therefore, results of life expectancies should ideally be corroborated by a comparison against several free-ranging populations of the same species.

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