

## **Survival and hazard functions in the population of David's deer (*Elaphurus davidianus* Milne-Edwards, 1866)**

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Survival and hazard functions supply suitable information concerning changes in the population dynamics, especially in the case of species that are not subjected to artificial selection. One of such species is David's deer (*Elaphurus davidianus* Milne-Edwards, 1866) that underwent a dramatic reduction in the population size in the first years of the XX century, but has been subsequently restored from 18 individuals.

Population dynamics changes were studied on 1221 David's deers kept in zoological gardens in the years 1947-2001. Survival and hazard functions were constructed for all individuals according to sex, and separately for those which died in the first year of life, *i.e.* 14.5% males and 8% females. The hazard function showed similar values for individuals of both sexes in the year 6, 10, 15, 17 and 18 of life. For all males the medians for mortality (hazard function) appeared similar to those for all females. Similar pattern was shown for yearlings. However, between day 40 and 323 shapes of these functions were quite different. Generally, the life span in females was found longer than in males.

**KEY WORDS:** David's deer / mortality rate / survival rate

Variation in the number of individuals occurring along the time is characteristic of a majority of populations, and is determined by many factors [Pielou 1969], especially in wild species. One of such species is David's deer (*Elaphurus davidianus* Milne-Edwards, 1866), that inhabited the mid-eastern China. However, in the course of time the natural

environment of the species had become unfavourably changed [Sternicki *et al.* 2001], and the last hind died there in 1922. The species survived thanks to Duke of Bedford who, at the beginning of XX century, purchased 18 individuals, now considered the founders for the currently existing population [Szablewski 2003]. The reconstruction of a species from a small number of founders naturally leads to an increased inbreeding rate, leading to all well-known negative consequences, and among others to reduction of fitness, including lifespan.

Time-dependent mortality and reproductive ability can be described using the classical mortality tables [Elandt-Johnson and Johnson 1999]. The method is based on the analysis of the age structure of the population at a given time or within a short time interval [Szczepaniak and Wesołowska-Janczarek 2002]. Collection of data for the construction of such tables usually requires a number of generations studied [Begon 1999].

The main advantage of the construction of life tables is the feasibility of their application to populations from different environments. The statistical method applied in this study using information on individuals still alive is a more appropriate way to estimate the population's life expectancy.

Life tables have been constructed for humans [Elandt-Johnson 1985] and livestock [Wallin *et al.* 2000, Arnason and Björnsdottir 2003]. To our knowledge, such tables have been drawn for wild animals neither living at large, nor maintained in captivity.

Hence, the objective of this study was to determine the functions of survival and hazard (determining mortality) for the population of David's deer kept in zoological gardens, as an exemplary species restored from a limited number of individuals.

### Material and methods

Data for the present study were withdrawn from the International Species Information System – January 2001 edition and consisted of records of 1221 individuals born in the years 1947-2000. Censored data (animals living on December 31, 2000) were also included in the analysis. A brief statistical description of the population studied is presented in Table 1.

Numbers of animals born in consecutive years are shown in Figure 1. The data set does not contain complete information on the cause of death. Hence, death cause was not included in the statistical analysis. As shown by Szablewski and Szwaczkowski [2003] the mean inbreeding level of the population was 0.025, exhibiting a rather wide fluctuation over time. However, they reported no upward trend in the last two decades.

As reported by Sternicki *et al.* [2003], considerable mortality of David's deer is observed in the first year of life. Therefore, a respective data sub-set was formed. Additionally, the data were divided according to sex.

In general, the life tables for the population studied can be treated as extended tables of numbers of individuals. Thus, random variable  $X$  is the individual's age (expressed in days or years), whereas  $n_x$  is the expected number of individuals, which survived from birth denoted as point ( $n_0$ ) to current (given) age  $x$ . Distribution of survival time

**Table 1.** Description of the David's deer population studied

Data set	Number of individuals	Average age	Standard deviation
All individuals	1221	5.55 (years)	5.97
Individuals dead in the 1st year of life	338	57.68 (days)	106.49

was divided into intervals (their number depending on the data set used). For each interval, the number and proportion of individuals that survived to  $n_x$  and died at  $d_x$  interval has been given.

The analysis was enriched by information concerning individuals, for which only the date of birth is known, but which later on for various reasons have been lost from the analysis. These cases are called truncated, as although the information about them is incomplete, it somehow better illustrates the whole population. They were quantified

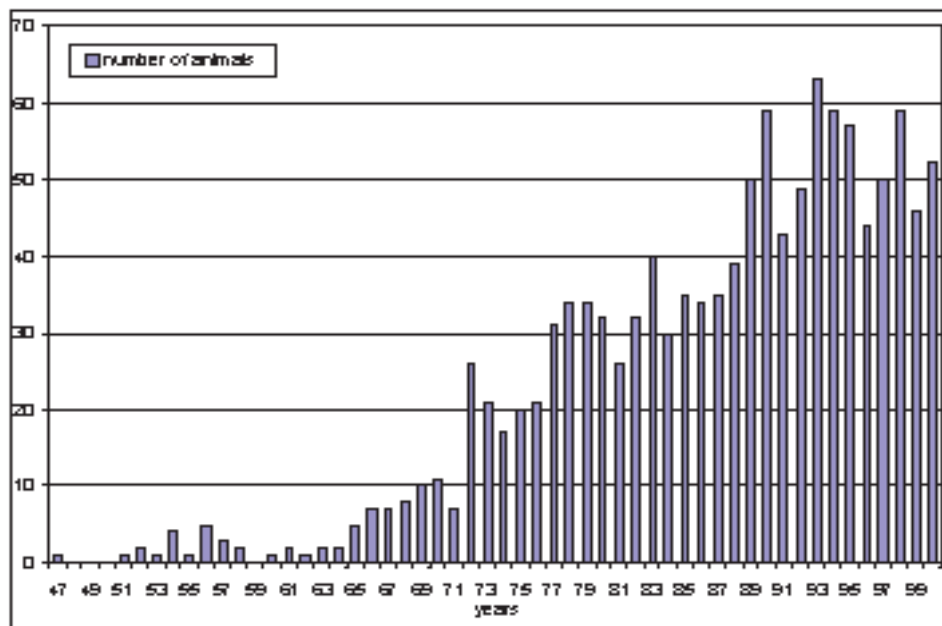


Fig. 1. Number of animals in subsequent years.

according to the formula:

$$r_x = n_x - W_x$$

$$\text{where: } W_x = n_x - n_{x+1} - d_x \quad \frac{1}{2}$$

The number of individuals, which have survived to age  $x$  as  $P_x$  can be denoted as:

$$P_x = \frac{n_x}{n_0}$$

In the present study given is the cumulated proportion of animals which have survived. Putting it more precisely, concerned is the proportion of individuals, which have survived to the beginning of the interval. As the probability of survival in subsequent intervals is independent it can be calculated as the product of probabilities in the preceding intervals. The resulting function is called the survival function.

Therefore  $P_x = p_x P_{x-1}$

The successive function ( $\mu_x$ ) used in the construction of the mortality tables is also defined on a given lifetime interval bounded by  $x$  and  $x+t$ , as follows:

$$\mu_x = P(x < X \leq x+t | X > x) = -\frac{1}{T} \frac{dn_x}{dn_x}$$

This value is interpreted as the conditional probability of mortality within a given interval  $(x, x+t)$  of an individual which has survived until the age of  $x$  [Growder 2001] and is further referred to as the hazard rate. It is estimated as the ratio of the number of individuals which died within the given interval to the average number of individuals which survived the middle of this interval.

Then  $p_x$  is the conditional probability that the individual which has survived until the age of  $x$  will not die within the time interval  $(x, x+t)$  or will not die until the age  $x+t$ :

$$p_x = 1 - q_x$$

Moreover  $q_x$  is the expected mortality within the interval  $(x, x+t)$ . This proportion is estimated as the number of individuals that died within the given interval divided by the number of individuals endangered.

The computations were performed using the STATISTICA 6.0 package programme [2002].

## Results and discussion

Cumulated survival and hazard functions for individuals of both sexes are presented in Figures 2 and 3. The separate analyses for sexes turned out to be justified, as sex factor significantly differentiated the lifespan in the population studied, corresponding with the unpublished data for David's deer obtained by Sternicki. A larger effect on survival rate was shown of the female rather, than of male sex. Although in the literature the reports on David's deer population are limited, the trends shown for the sex effect on lifespan seem to be universal, at least for mammals. This hypothesis corroborates the

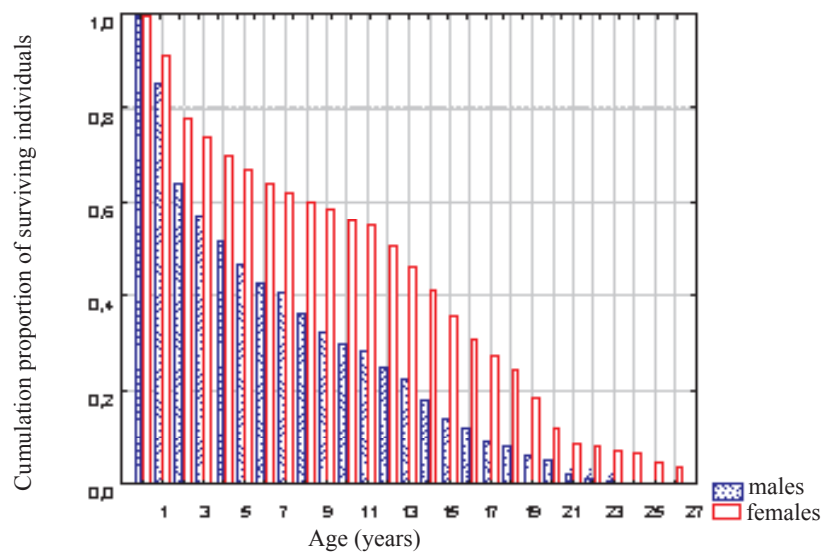


Fig. 2. Cumulated survival function for individuals of both sexes.

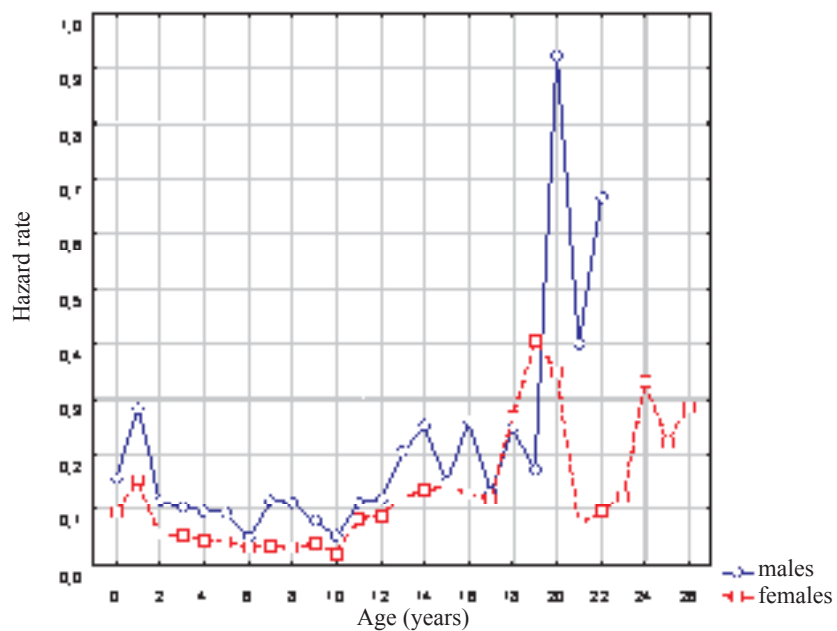


Fig. 3. Hazard function for individuals of both sexes.

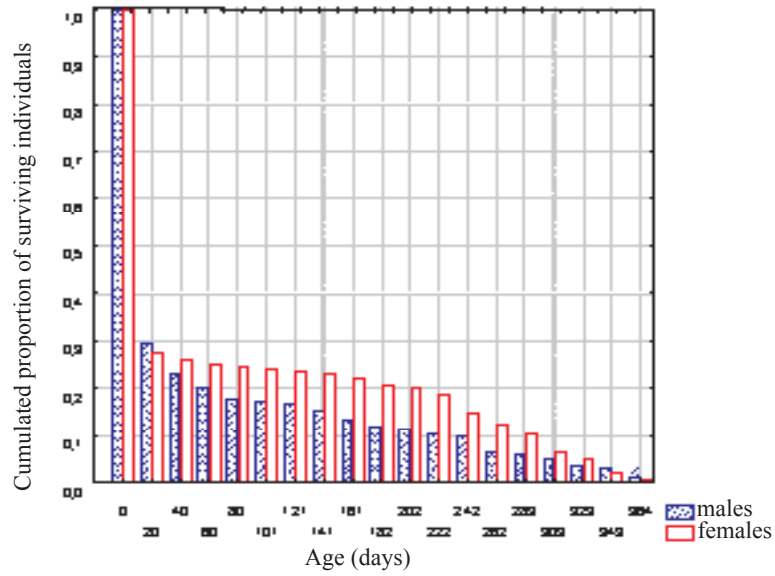


Fig. 4. Cumulated survival function for yearlings of both sexes.

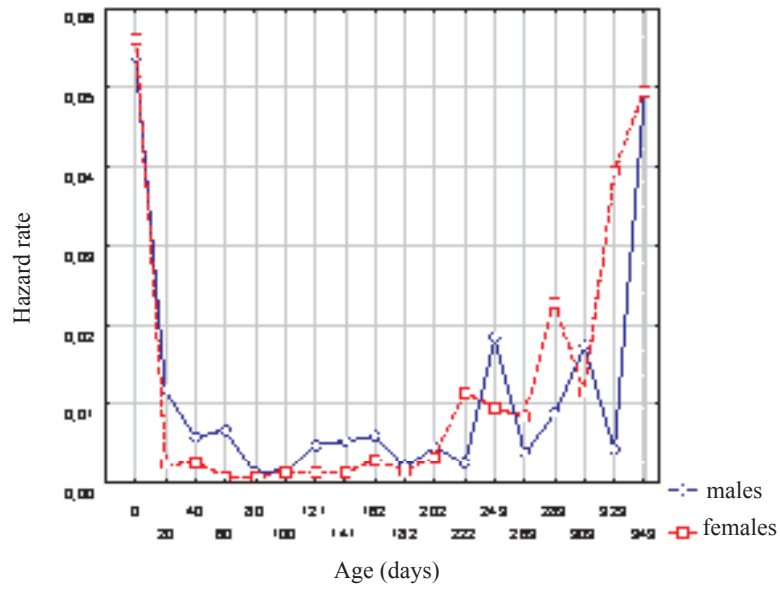


Fig. 5. Hazard function for yearlings of both sexes.

conclusions by Wallin *et al.* [2000] who analysed the survival rate in Swedish warm-blood and cold-blood horses and found, at any time interval, a greater survival rate of females than of males. Langlois [1976] reported that in Thoroughbreds the mean age at death and/or culling was lower in females than in males. In farm animals it is sometimes difficult to determine the true lifespan, as the culling of an individual is not always identified with its natural death.

In the population analysed 14.5% males died already during their first year of life, whereas only 8% females. A similar proportion was maintained for the consecutive years of life. The longest living individuals were females, among which three reached the age of 27 years, while the oldest male died at the age of 23 years. Moreover, mortality rate of females exceeded significantly that of males only in year 19 of life. However, for the age structure of the whole population several years appeared – 6, 10, 15, 17 and 18 – in which the mortality rates in both sexes were comparable (Fig. 3).

The differentiation of survival rate as related to sex could already be observed in the first year of deers' life. In yearlings (Figure 4 and 5), *i.e.* those, which died within the first year of their live, a situation was similar to that observed for the whole population. During the first 20 days of life the rates of mortality in both sexes were high and reached 70% of all animals which died during the first year of life. On day 80, 100, 182, 202 and 343 the mortality rates were comparable in both sexes. However, in the majority of time intervals mortality rates of males significantly exceeded those of females, day 222, 283 and 323 being found the only exceptions (Fig. 5). Olech [2003] and Szablewski [2003] studying small populations of animals living in the wild agree that one of the main factors determining mortality is their level of inbreeding. Another factor significantly affecting the mortality is in the initial period of life, and especially in animal populations at large, is environment, with the unfavourable weather conditions and restricted access to, or total shortage of feed. These factors are especially apparent when animals are kept in conditions unnatural to them, which certainly is the case with David's deer. The data analysed in this study come from zoological gardens where the factor limiting the survival rate is not the lack of food, but rather varying climatic conditions.

Generally speaking, survivability is a trait of low heritability. Considerable convergence is observed in the case of results obtained for the populations of farm animals and animals living in the wild, including those under protection programmes. This is confirmed, among others, by Roxström *et al.* [2003], thus indicating a decisive environmental effect on lifespan.

In general, this study demonstrates that survival analysis can be efficiently used to monitor the variation taking place with time in the size of David's deer population.

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## Funkcje przeżycia i hazardu w populacji jelenia Dawida (*Elaphurus davidianus* Milne-Edwards, 1866)

### Streszczenie

Funkcje przeżycia i hazardu dostarczają cennych informacji o dynamice liczebności populacji, zwłaszcza w odniesieniu do gatunków nie poddawanych sztucznej selekcji. Badaniami objęto 1221 osobników jelenia Dawida, jakie utrzymywano w latach 1947-2001 w ogrodach zoologicznych świata. Gatunek ten przeżył drastyczne załamanie liczebności w pierwszych latach XX wieku, a następnie został odtworzony z 18 osobników uchronionych przed zagładą. Funkcje przeżycia i hazardu skonstruowano w ramach każdej płci dla wszystkich osobników oraz oddzielnie dla osobników padłych w pierwszym roku życia, które stanowiły 14,5% samców i 8% samic. Mediany rozkładu śmiertelności (funkcji hazardu) były podobne u samców i samic. Zbliżone kształty rozkładów (dla obu płci) zanotowano także w przypadku osobników żyjących nie dłużej niż rok. Wykazano jednak znaczące różnice w przebiegu tych funkcji między 40 a 323 dniem życia. Generalnie, samice cechowały się wyższą przeżywalnością niż samce. Aczkolwiek w przypadku osobników będących w 6, 10, 15, 17 i 18 roku życia funkcja hazardu przyjęła dla obu płci wartości podobne, to jednak generalnie samice żyły dłużej niż samce.

