

The effect of inbreeding level and genetic factors on longevity in Arabian oryx (*Oryx leucoryx*)

Paweł Szablewski, Anna Wolc, Tomasz Szwaczkowski

Department of Genetics and Animal Breeding,
The August Cieszkowski Agricultural University of Poznań,
Wołyńska 33, 60-637 Poznań, Poland

(Received June 10, 2006; accepted November 1, 2006)

Pedigree information was analysed of 2106 individuals recorded from 184 zoological gardens. Two single-trait animal models (including inbreeding coefficients as linear or quadratic covariables) were employed. Three data subsets were formed relative to the length of life. Heritability estimates were obtained using the DFREML algorithm. Moreover, phenotypic, genetic and environmental trends were estimated. Mean inbreeding level was 3.8% for all individuals, and 11.2% for the inbred animals. The inbreeding effects (evaluated as partial linear regression) ranged from -93 days (for individuals living longer than 500 days) to 25 days (for all individuals included). Heritability estimates appeared low. Generally, the time trends were non-negative, indicating the high efficiency of the realized breeding strategy.

KEY WORDS: Arabian oryx / inbreeding / restricted maximum likelihood /
heritability / longevity

Arabian oryx (*Oryx leucoryx*) is a small antelope, formerly inhabiting deserts and semideserts of the north-eastern Africa and the Arabian Peninsula. Population had begun to disappear due to over-hunting from the mid XIX century which led to the species extinction in the natural environment in the 1970's [Henderson 1974]. In 1962 the protection programme was started [Spalton *et al.* 1999] using three specimens captured in Oman. Over the next years, several animals (from Arabian countries) were included in the captive breeding. In spite of relatively small initial population size, reproductive abilities of the species led to creation of several subpopulations. First reintroduction of oryx was performed in a stony desert plateau in central Oman. Over

the next years the species was gradually reintroduced to Saudi Arabia, Jordan and other countries of the Middle East.

With a small and more or less closed population the risk of inbreeding is obvious, but very little is known about the current inbreeding level within the species. However, some studies on inbreeding within the population considered have been reported [Marshall and Spalton 2000]. An increase of the inbreeding rate leads to reduction of genetic variation, and in consequence has a negative effect on the adaptation ability [Falconer 1989, Lacy 1994]. A number of authors reported inbreeding depression manifesting itself in weakening of fitness and performance traits, especially in populations of livestock [Brückner 1980, Hagger *et al.* 1989, Boujenane and Chami 1997, Rodriganez *et al.* 1998, Thompson *et al.* 2000].

Length of life is one of the most important characters in wild animals. According to current knowledge, the trait is affected both by environmental and genetic factors. Furthermore, longevity is determined by many *loci*. On the other hand, early mortality in particular can be strongly influenced by chromosomal and gene point mutations [Keightley 1998, Higgins and Lynch 2001]. It is known that the probability of lethal or semilethal genotype expression increases when relatives are mated. Hence, the inbreeding effects can vary in relation to the animals' age.

The objective of this study was to estimate the inbreeding level, its trend over time and its effects on length of life in the captive-bred Arabian oryx population. Moreover, genetic and phenotypic trends of longevity were also estimated.

Material and methods

The data were extracted from International Species Information System [ISIS 2001] resources from the Minnesota Zoological Garden, edition of January 2001. Pedigree information was analysed of 2106 individuals from 184 zoological gardens (from 30 countries). The animals included were born in the years 1900-2000. A single record structure was as follows:

- animal code;
- sire code;
- dam code;
- sex of animal;
- date of birth;
- date of death;
- inbreeding coefficient.

The data were divided into three-year periods of birth groups, except from the first period (Tab. 1). As the breeding programme for the oryx population was introduced in the 1970s, the number of individuals recorded before that time was relatively small. The highest mortality of individuals falls within the first month of life while sexual maturation appears at the age of about 500 days. Therefore, the following three data-sets have been studied: DATA 1 (all individuals), DATA 2 (individuals that survived

more than 31 days), DATA 3 (individuals that survived more than 500 days).

To estimate the inbreeding effects two following linear models were employed.

Model I (including the inbreeding coefficient as a linear covariable):

$$y_{ijk} = m + s_i + p_j + bx_{ijk} + a_{ijk} + e_{ijk}$$

where:

y_{ijk} – length of life (days) of ijk -th individual;

m – overall mean;

s_i – fixed effects of i -th sex;

p_j – fixed effects of j -th birth period;

b – linear regression coefficient;

x_{ijk} – inbreeding coefficient of ijk -th individual included as covariable;

a_{ijk} – random additive genetic effect of ijk -th individual;

e_{ijk} – random error associated with ijk -th observation.

Model II (including inbreeding coefficient as a quadratic covariable):

$$y_{ijk} = m + s_i + p_j + b_1x_{ijk} + b_2x_{ijk}^2 + a_{ijk} + e_{ijk}$$

where:

b_1 and b_2 – quadratic linear coefficients;

other symbols – as for model I.

The fixed and random effects as well as regression coefficients and variance components were evaluated by the use of the derivative-free restricted maximum likelihood algorithm (DFREML) – Meyer [1989]. The DFREML package programme was applied [Meyer 2000]. The mean inbreeding depression was estimated using partial regression coefficients (for average inbreeding level 3.8%). The use of animal model enabled (due to the incorporation of the additive relationship matrix) the inclusion of deep pedigree information, especially for animals born in the last years. Estimates of residual variances were taken as criteria of model adequacy for describing relationships between the inbreeding level and longevity.

Moreover, the phenotypic and genetic trends were estimated. The genetic trends were obtained as averaged additive genetic effects per period of birth.

Results and discussion

Changes in the numbers of inbred and non-inbred individuals over time are shown in Table 1. Mean inbreeding coefficient of the studied population was 3.8%. It might be underestimated due to incompleteness of pedigree information particularly in the beginning of captive breeding. Generally, the proportion of inbred animals in the three data sets was very similar (about 37% – Tab. 1). The ratio of inbred and non-

Table 1. Number of individuals and their inbreeding coefficients within DATA sets

| Year class | DATA 1 | | | DATA 2 | | | DATA 3 | | | | | |
|------------|--------|--------------------|----------------|--------------------|------|--------------------|----------------|--------------------|------|--------------------|----------------|--------------------|
| | n | F _a (%) | n _F | F _i (%) | n | F _a (%) | n _F | F _i (%) | n | F _a (%) | n _F | F _i (%) |
| <1974 | 78 | 1.12 | 5 | 17.5 | 72 | 1.22 | 5 | 17.5 | 67 | 1.12 | 4 | 18.75 |
| 1974-1976 | 57 | 2.19 | 17 | 7.35 | 53 | 2.24 | 21 | 7.42 | 50 | 2.25 | 15 | 7.50 |
| 1977-1979 | 127 | 6.34 | 56 | 14.39 | 113 | 6.30 | 51 | 13.96 | 105 | 6.07 | 47 | 13.55 |
| 1980-1982 | 140 | 3.79 | 56 | 9.47 | 114 | 3.78 | 45 | 9.58 | 96 | 3.51 | 36 | 9.36 |
| 1983-1985 | 203 | 4.15 | 74 | 11.35 | 186 | 4.15 | 66 | 11.69 | 175 | 3.94 | 59 | 11.68 |
| 1986-1988 | 297 | 5.31 | 153 | 10.30 | 282 | 5.17 | 143 | 10.19 | 259 | 5.27 | 134 | 10.19 |
| 1989-1991 | 423 | 3.55 | 199 | 7.55 | 381 | 3.35 | 170 | 07.51 | 322 | 3.52 | 142 | 7.97 |
| 1992-1994 | 336 | 3.21 | 100 | 10.77 | 304 | 3.01 | 83 | 11.02 | 234 | 3.41 | 73 | 10.89 |
| 1995-1997 | 273 | 4.51 | 72 | 17.09 | 251 | 4.24 | 63 | 16.88 | 189 | 5.11 | 52 | 18.59 |
| 1998-2000 | 172 | 5.28 | 60 | 18.55 | 159 | 6.33 | 54 | 18.64 | 104 | 6.01 | 36 | 17.38 |
| Total | 2106 | 3.84 | 792 | 11.22 | 1915 | 3.69 | 696 | 11.26 | 1601 | 4.28 | 598 | 11.26 |

DATA 1 – all individuals. DATA 2 – individuals that survived more than 31 days. DATA 3 – individuals that survived more than 500 days.

n – number of individuals. F_a – inbreeding coefficient for all individuals (%). n_F – number of inbred individuals. F_i – inbreeding coefficient for inbred individuals (%).

inbred animals decreased, while the inbreeding level (especially for inbred individuals) strongly increased. When all the animals were considered the highest inbreeding level (4.2%) was recorded for DATA 3. Lowest inbreeding was observed for DATA 2. The trends in inbreeding level were similar within subclasses. Generally, it corresponds to changes of inbreeding level in milu deer (*Elaphurus davidianus*) and Przewalski's horse (*Equus caballus przewalskii*) – (Szablewski, unpublished data).

From the stock breeder's perspective inbreeding can be used for developing lines for subsequent crossing to make use of the heterosis phenomena. In case of wild species, however, inbreeding depresses fitness traits. The reduction of fitness after close inbreeding can be caused by a number of genetic factors [Crnokrak and Roff 1999], e.g. by an increase of homozygosity and in consequence by unmasking of recessive unfavourable alleles.

Mean length of life was 1175 days (with standard deviation of 1626). Considering genetic and environmental effects on longevity it is worth to pay attention to heritability which reflects the relative impact of both. As shown in Table 2, the heritability estimates (h^2) of longevity obtained in this study were relatively low, ranging from 0.045 (for DATA 3, model II) to 0.074 (for DATA 2, model II). Similar h^2 were found in various wild and domestic species. Vollema [1998] reported very low h^2 estimates (less than 0.1) of longevity in dairy cattle. Similar results were found in red deer [Kruuk *et al.* 2000] as well as in *Drosophila melanogaster* [Baret *et al.* 1995]. By contrast to these data, Herskind *et al.* [1996] and Mitchell

et al. [2001] showed that the estimated h^2 in humans exceeded 0.2. It seems that heritability might be underestimated as the assumption of normality of the distribution was not fulfilled, which may lead to overestimation of error variance [Besbes *et al.* 1993]. Boujenane and Chami [1997] reported that inbreeding depression is deeper for traits of low than of high heritability.

Table 2. Inbreeding effects, heritability estimates and their standard deviations (in parentheses) as well as error variance estimates for length of life.

| Data set | Mean level of inbreeding (%) | Regression coefficients | Estimate of error variance | Mean inbreeding depression (in days) | Heritability estimates |
|-----------------|------------------------------|----------------------------|----------------------------|--------------------------------------|------------------------|
| DATA 1 Model I | 3.8 | -3.3x | 1453890 | -13 | 0.067 (±0.030) |
| DATA 1 Model II | | -6.5x + 43.2x ² | 1454292 | 22 | 0.067 (±0.030) |
| DATA 2 Model I | 3.6 | 3.9x | 1311462 | 14 | 0.073 (±0.034) |
| DATA 2 Model II | | 5.2x - 5.2x ² | 1311655 | -49 | 0.074 (±0.038) |
| DATA 3 Model I | 4.3 | -3.9x | 1253461 | -17 | 0.049 (±0.025) |
| DATA 3 Model II | | 7.5x - 7.8x ² | 1258673 | -84 | 0.045 (±0.026) |

Inbreeding level was relatively low in the three data sets studied. The partial linear regression coefficients of the inbreeding level on longevity appeared negative. In general, negative interrelations were also obtained by the use of partial quadratic regression model (positive b_1 and negative b_2 coefficients). As shown in Table 2, inbreeding in the oryx resulted in negligible depression of the length of life for all individuals (DATA 1) and individuals that survived for more than 500 days (DATA 3). Conversely, the linear regression coefficient for DATA 2 (individuals that survived more than 31 days) was positive. Generally, similar tendencies occurred when quadratic regression equations were employed. Mean square error was applied as a criterion for choosing the best model (including linear or quadratic regression). Error variance estimates for models with linear regression were smaller than those with the quadratic one. Hence, the simpler animal model (including linear partial regression) is preferred for evaluation of inbreeding effects in the studied population. Differences in estimated inbreeding depression among the oryx data sets might have been caused by higher mortality in the first and last period of time. As noted above, longevity is strongly affected by environmental factors (low heritabilities were estimated).

Inbreeding is an important problem in small populations of wild animals. Therefore, special mating systems to reduce the inbreeding rate are still being developed. Over the last three decades, the protection strategy has been realized in the oryx population [Marshall and Spalton 2000]. As previously noticed it resulted in the decreasing ratio of inbred to non-inbred animals (Tab. 1).

The genetic and phenotypic trends are shown in Figures 1 and 2, respectively. In general, the mean genetic value increased, especially over the last two decades when the genetic improvement programme was implemented. It should be stressed

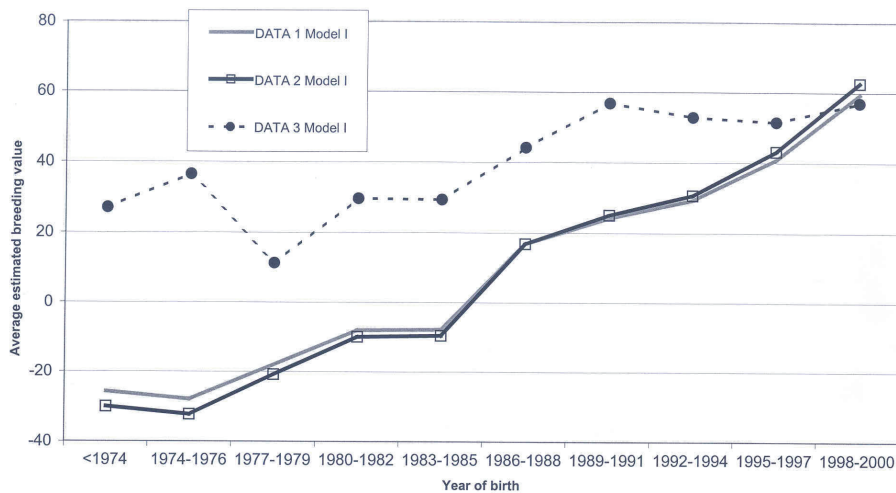


Fig. 1. Genetic trends for longevity in Arabian oryx population.

Longevity in Arabian oryx

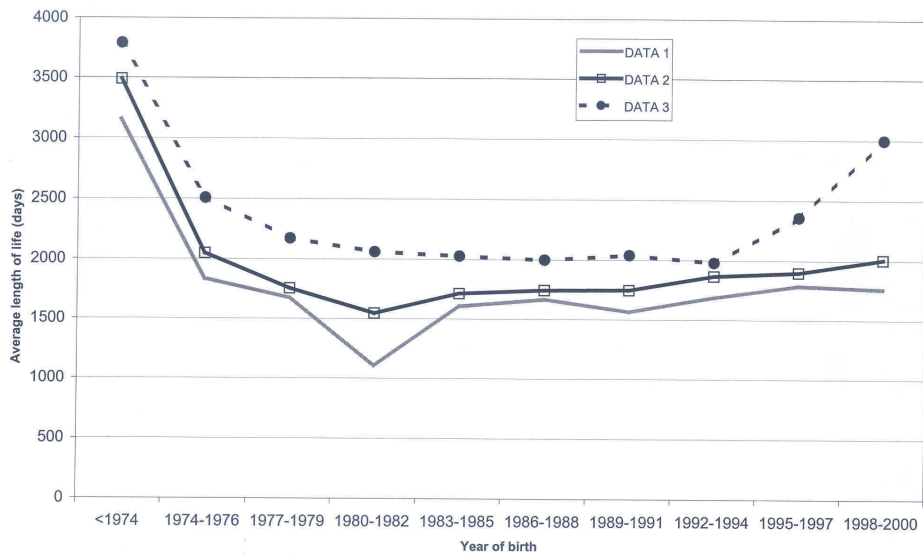


Fig. 2. Phenotypic trends for longevity in Arabian oryx population.

that over the period in question, the mean genetic value increased by 120 days for all individuals (DATA 1) – Figure 1. Smaller differences were observed in two data sets (90 days for DATA 2 and 31 days for DATA 3). This corresponds to the unpublished results got by Szablewski on milu deer and Przewalski's horse where positive genetic trends in longevity were also obtained. Examined were also dependencies between genetic trends and inbreeding level. Within DATA 1 and DATA 2 these relations were positive whereas occurred non-positive for oldest individuals (DATA 3).

The phenotypic trends for longevity (in all three data sets) as illustrated in Figure 2 show two distinct periods. First, from year 1970 to 1980, was marked by a decreasing longevity. The second – from 1980 to 2000 – shows a tendency to stabilize, with an increasing number of individuals. It could be associated with the implementation of the breeding strategy. However, the dependencies between mean phenotypic values and the inbreeding level were positive for inbred animals, but negative when all individuals were considered. Since the residual variances were very high, average environmental effects for all data sets varied over time. As noted earlier, the effects of inbreeding were only slightly affected by the age of individuals.

Analysis of heritability and genetic trend of longevity leads to the conclusion that major role is played by environmental effect. However, consistent increase in breeding value suggests genetic adaptation to captive breeding. It should be kept in mind that from the perspective of conservation of genetic diversity lack of genetic trend would be most favourable. Changes in genetic potential reflect variation in gene frequencies and may be related to loss of some alleles. In general, due to the breeding strategy

employed, inbreeding rate in Arabian oryx seems to be on a safe level, especially over the last decades.

Acknowledgements. The authors are grateful to Headquarters of Minnesota Zoological Garden, US, and Poznan Zoological Garden, Poland, for providing records and to Dr. Karin Meyer for supplying the set of DFREML programmes.

REFERENCES

1. BESBES B., DUCROCQ V., FOULLEY J.L., PROTAIS M., TAVERNIER A., TIXER-BOICHARD M., BEAUMONT C., 1993 – Box-Cox transformation of egg-production traits of laying hens to improve genetic parameter estimation and breeding evaluation. *Livestock Production Science* 33, 313-326.
2. BARET P.V., BECKERS F., LINTS F.A., 1995 – Realized heritability of longevity in *Drosophila melanogaster*. *Gerontology* 41, 82-85.
3. BOUJENANE I., CHAMI A., 1997 – Effect of inbreeding on reproduction, weights and survival of Sardi and Guil sheep. *Journal of Animal Breeding and Genetics* 114, 23-31.
4. BRÜCKNER D., 1980 – Hoarding behaviour and life span of inbred, non-inbred and hybrid honeybees. *Journal of Apicultural Research* 19, 35-41.
5. CRNOKRAK P., ROFF D.A., 1999 – Inbreeding depression in the wild. *Heredity* 83, 260-270.
6. FALCONER D.S., 1989 – Introduction to Quantitative Genetics. 3rd edition. Longman Scientific and Technical, New York.
7. HAGGER C., STEIGER-STALF D., MARGUERAT D., 1989 – Embryonic mortality in chicken eggs as influenced by egg weight and inbreeding. *Poultry Science* 65, 812-825.
8. HENDERSON D.S., 1974 – Were they the last Arabian oryx? *Oryx* 12, 374-350.
9. HERSKIND A.M., MCGUE M., HOLM N.V., SOERENSEN T.I., HARVALD B., VAUPEL J.W., 1996 – The heritability of human longevity: a population-based study of 2872 Danish twin pairs born 1870-1900. *Human Genetics* 97, 319-323.
10. HIGGINS K., LYNCH M., 2001 – Metapopulation extinction caused by mutation accumulation. *Proceedings of National Academy of Sciences of the USA* 27, 2928-2933.
11. ISIS, 2001 – International Species Information System. Minnesota Zoological Garden. <http://www.worldzoo.org>
12. KEIGHTLEY P.D., 1998 – Inference of genome-wide mutation rates and distributions of mutation effect for fitness traits: a simulation study. *Genetics* 150, 1283-1293.
13. KRUIK L.E.B., CLUTTON-BROCK T. H., SLATE J., PEMBERTON J. M., BRATHERSTONE S., GUINNESS E., 2000 – Heritability of fitness in wild mammal population. *Proceedings of the National Academy of Sciences of the USA* 97, 698-703.
14. LACY R.C., 1994 – Managing genetic diversity in captive populations of animals. In: Restoration of Endangered Species. (M.L. Bowles, and C.J. Whelan, Eds.), Cambridge University Press, 63-89.
15. MARSHALL T.C., SPALTON J.A., 2000 – Simultaneous inbreeding and outbreeding depression in reintroduced Arabian oryx. *Animal Conservation* 3, 241-248.
16. MEYER K., 1989 – Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genetics, Selection, Evolution* 21, 317-340.
17. MEYER K., 2000 – DFREML Version 3.0. User's Notes.

18. MITCHELL B.D., HSUEH W.C., KING T.M., SORKI J., AGARWALA R., SCHÄFFER A.A., SHULDINER A.R., 2001 – Heritability of life span in the Old Order Amish. *American Journal of Medical Genetics* 102, 346-352.
19. RODRIGANEZ J., TORO M.A., RODRIGUEZ M. C., SILIO L., 1998 – Effect of founder allele survival and inbreeding depression on litter size in a closed line of Large White pigs. *Animal Science* 67, 573-582.
20. SPALTON J.A., LAWRENCE M.W., BREND S.A., 1999 – Arabian oryx reintroduction in Oman: successes and setbacks. *Oryx* 33, 168-175.
21. THOMPSON, J.R., EVERETT, R.W., WOLFE, C.W., 2000 – Effects of inbreeding on production and survival in Jerseys. *Journal of Dairy Science* 83, 2131-2138.
22. VOLLEMAA.R., 1998 – Selection for longevity in dairy cattle. PhD Thesis, Wageningen Agricultural University, The Netherlands.

Paweł Szablewski, Anna Wolc, Tomasz Szwaczkowski

Wpływy inbrodu i czynników genetycznych na długość życia oryksa arabskiego (*Oryx leucoryx*)

Streszczenie

Zbadano zależności między poziomem inbrodu a długością życia oryksa arabskiego. Wykorzystano informację o 2106 osobnikach ze 184 ogrodów zoologicznych. Wykorzystano dwa jednocechowe modele zwierzęcia (uwzględniając liniowy i kwadratowy wpływ inbrodu). Analizowano trzy podgrupy zwierząt utworzone w zależności od długości życia. Do szacowania odziedziczalności wykorzystano algorytm DFREML. Ponadto oszacowano trendy genetyczne, fenotypowe i środowiskowe długości życia. Średni poziom inbrodu dla wszystkich osobników wyniósł 3.8%, natomiast 11.2% dla osobników zimbredowanych. Efekty inbrodu (oszacowane na podstawie współczynników regresji cząstkowej) zawierały się w przedziale od -93 dni (dla osobników żyjących powyżej 500 dni) do 25 dni (dla wszystkich osobników). Oszacowany współczynnik odziedziczalności był niski. Ogólnie trendy były nieujemne, co wskazuje na skuteczność realizowanej strategii hodowlanej.

