



Original Investigation

No inbreeding effects on body size in two captive endangered gazelles

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ABSTRACT

Selection for body size is intricate, involving trade-offs between energy costs, reproductive output, foraging efficiency, and interaction with other community members. In dimorphic, polygynous ungulates, body size is highly correlated with reproductive success in both sexes. Body size has been proposed as a potential phenotypic indicator of genetic change, in wild and in captive populations. We analysed the relationship between adult body size and inbreeding in two captive populations of endangered gazelles. Two estimates of inbreeding were used: individual inbreeding coefficient (F_i) and individual increase in inbreeding (ΔF_i). Six cranial traits and eight post-cranial bones were measured in 87 Cuvier's gazelles and 97 Mohor gazelles. The average level of individual inbreeding found for the alive population of Cuvier's gazelle was 0.236 and for Mohor gazelle 0.260. Our study demonstrated that within our populations most variability in body size is explained by sex, but we have not found any evidence of inbreeding depression in this morphological trait. Our results are surprising in the light of a widely held belief that from an evolutionary point of view close inbreeding has deleterious effects. The great diversity of factors acting on the effects of inbreeding on trait values make difficult to provide a simple framework to understand them all, hence, we suggest fitness consequences of inbreeding has to be assessed considering the conditions under which one should expect inbreeding depression.

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Introduction

A wide range of genetic and environmental factors in complex processes affect body size diversification. Selection for body size is intricate, and involves trade-offs between energy costs, reproductive output, foraging efficiency, and interaction with other community members (Wisely et al., 2002). In wild polygynous animals, body size is highly correlated with female social rank (Holand et al., 2004) and with male fighting ability, which influences access to receptive females (Mysterud et al., 2004), as male sexual competition is strong. Body size has been proposed as a potential phenotypic indicator of genetic change (Frankham et al., 1986; Fredrickson and Hedrick, 2002), and some authors have demonstrated that body size is affected by inbreeding in domestic and laboratory animals (Wright, 1977), and captive-born wild species (Laikre, 1999).

One of the most important problems of endangered species is that their populations are small, leading to loss of genetic variability from inbreeding (Bonnell and Selander, 1974; Wayne et al., 1991; Stangel et al., 1992). Thus inbreeding changes the frequency of genotypes in a population, increasing homozygote frequency

(Charlesworth and Charlesworth, 1987; Wright et al., 2008), and may lead to a decline in the value of a trait. Such decline in a trait as a direct consequence of inbreeding is called inbreeding depression (Wright, 1977). This may be the result of either of two mechanisms. The dominance hypothesis states that inbreeding depression leads to the expression of recessive deleterious alleles as homozygosity increases, whereas the overdominance hypothesis states that inbreeding depression arises from the loss of favourable heterozygote combinations when heterozygotes are more frequent than homozygotes (Charlesworth and Charlesworth, 1987; Wright et al., 2008). Inbreeding depression has been found in a large proportion of species (Ralls et al., 1988; Lacy, 1997). Many traits, such as juvenile survival (Ralls et al., 1979, 1988), fecundity, mating success, development and health (Lerner, 1954; Falconer and Mackay, 1996; Roff, 1998; Bijlsma et al., 2000; Cassinello, 2000; Gomendio et al., 2000), are affected by inbreeding depression. But the effect of inbreeding depression on different traits depends on the genetic structural design of such traits (number of loci influencing a trait and the nature of interactions between alleles within and between loci; Merila and Sheldon, 1999; Bolund et al., 2010), and is more likely to occur for life-history traits (closely related to fitness) than for morphological traits (DeRose and Roff, 1999).

Morphological traits (i.e. body size, cranial size) have been shown to be useful features for unveiling the effects of inbreeding depression in mammalian species (Leamy et al., 2001; Fredrickson

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and Hedrick, 2002; Pertoldi et al., 2006; Wisely et al., 2008). For example, in highly inbred captive wolf females, mean body size was significantly smaller than females with little or no inbreeding (Fredrickson and Hedrick, 2002). In a study of *in situ* populations of the endangered Iberian lynx, divergent morphological traits were found in isolated populations, and reduced cranial size was found in a highly inbred population (Pertoldi et al., 2006). Loss of genetic variation can lead to decreased fitness traits, which in the long term can decrease the evolutionary potential of species, increasing their risk of extinction in the face of a changing environment (Franklin, 1980; Wisely et al., 2008).

Mohor gazelle (*Nanger dama mhorh*, Bennett, 1833) and Cuvier's gazelle (*Gazella cuvieri*, Ogilby, 1841) captive breeding programmes have been underway at "La Hoya" Experimental Field Station (EEZA-CSIC), in Almería, Spain, since 1971 and 1975, respectively. After death, the skeletons of these individuals are kept in the scientific collections of the Estación Experimental de Zonas Áridas institute (EEZA-CSIC) offering an excellent opportunity for a morphometric study of these two species to find out whether increased inbreeding in their populations during their captive breeding history has had any effect on a phenotypic trait such as body size.

It has been suggested (González-Recio et al., 2007; Gutiérrez et al., 2008) that assessment of phenotypic effects from inbreeding depression based on inbreeding may not be appropriate, because (a) inbreeding accumulation is nonlinear, and (b) its effects may depend on the pedigree depth. That is, the negative effects of inbreeding are expected to appear if inbreeding has been reached very quickly, but this might not be the case if it is reached in a higher number of generations. In this paper we analyze the likely effect of inbreeding on body size in two species of endangered gazelle in captivity by using two estimates of inbreeding: the traditional individual inbreeding coefficient (F_i) and an alternative measure of inbreeding (ΔF_i , González-Recio et al., 2007), which represents the inbreeding rate for each individual, from one generation to the next. In view of the results found by other authors (Fredrickson and Hedrick, 2002; Pertoldi et al., 2006) and the general negative effect of inbreeding depression, we would expect body size of highly inbred animals to be smaller than in little or non-inbred individuals.

Material and methods

Gazelle skeletons were from the scientific collections of the Estación Experimental de Zonas Áridas (EEZA, CSIC). All bone material in these collections comes from animals bred at "La Hoya" Experimental Field Station (EEZA-CSIC).

Since the captive Mohor and Cuvier gazelle populations were begun at the EEZA-CSIC Field Station, records have been kept of all individuals including date of birth, mother's identity, father's identity, sex and date of death. These international studbooks are available at the institute website (<http://www.eeza.csic.es/eeza/hoya.cria.aspx>). The captive population of Cuvier's gazelle is descended from 4 wild-born individuals (one male, three females; Moreno and Espeso, 2008). It is a medium-size gazelle that can weigh up to 35 kg. Females reach sexual maturity at about 8–9 months and males at 12–13. Gestation is about 5.5 months. Twins represent up to 39% of births (Moreno and Espeso, 2008). The founder population of Mohor gazelle is considered to be five individuals (one male, four females; Espeso and Barbosa, 2010). It is a large species with individuals weighing from 45 to 75 kg. Females reach sexual maturity when 9–12 months old; males at the age of 18–24 months. Single births follow 6.5 months gestation (Barbosa and Espeso, 2005).

Genealogical analyses were performed of the whole population and of the studied population using the program ENDOG v4.8

(Gutiérrez and Goyache, 2005). We have assumed the founder individuals to be unrelated to each other and not inbred. The pedigree of all the animals measured was known. The following parameters were computed:

- (i) The individual inbreeding coefficient (F_i), defined as the probability that an individual has two identical alleles by descent (Wright, 1922; Malécot, 1948). The F_i for each animal in the pedigree was calculated using the algorithm described by Meuwissen and Luo (1992).
- (ii) The number of equivalent discrete generations (t) for each individual in the pedigree. This parameter is the sum of all known ancestors of the term $(1/2)^n$, where n is the number of generations between the individual and ancestor i (Maignel et al., 1996; Gutiérrez et al., 2003).
- (iii) The individual increase in inbreeding (ΔF_i ; González-Recio et al., 2007; Gutiérrez et al., 2008), was computed for each individual in the pedigree, following the modification proposed by Gutiérrez et al. (2009) to account for the exclusion of self-fertilization, as $\Delta F_i = 1 - [t^{-1} \sqrt{1 - F_i}]$, where F_i is the inbreeding coefficient for each individual i and t the equivalent complete generations computed on the pedigree of this individual. As ΔF_i is adjusted for the depth of the known pedigree, it distinguishes between two animals with the same inbreeding coefficient but differing in the number of generations in which this inbreeding has been reached. The ΔF_i coefficient is not affected by any nonlinear increase of F_i over time and generations.

Due to cranial and postcranial functional differences, two separate analyses were performed. The cranium is presumably related to the feeding apparatus (Oïregan and Kitchener, 2005), but in polygynous species, cranial size could also be related to fighting ability and defence (from holding up different horn sizes; Geist, 1966), whereas postcranial size has been shown to reflect locomotion cost and efficiency (Steudel and Beattie, 1995).

Six metric characters on each cranium (Fig. 1), and eight postcranial characters (maximal length of limb bones: femur, tibia, metatarsus, humerus, radius and metacarpus, and length and width of scapula) were measured (Fig. 2). All cranial and postcranial measurements were made on the left side, to the nearest 0.01 mm with digital callipers and always by the same person (BI). We measured 72 Mohor gazelle and 68 Cuvier's gazelle crania, and 52 Mohor gazelle and 41 Cuvier's gazelle postcrania (Appendix I). Only gazelles over 24 months old were measured as until this age they have not yet reached adult size.

Unfortunately, individual weights have not been recorded in these captive breeding programmes, and therefore were not available to this study. Body size was estimated by principal component analysis (PCA) based on the correlation matrix of the six cranial and eight separate postcranial measurements. The first principal component (PC1) can be interpreted as a measure of body size if the measurements load strongly and evenly on PC1 (Pimentel, 1979; Rising and Somers, 1989). PC1 has been widely used as an indicator of overall body size in previous morphometric studies in many species (Wiklund, 1996; Schulte-Hostedde et al., 2004; Gür, 2010). In our study we used cranium PC1 (PC1cr) and postcranium PC1 (PC1pstr) as descriptors of overall cranium and postcranium size, respectively.

To study the relationship between body size and level of inbreeding (estimated as either F_i or ΔF_i) we used the PC1cr and PC1pstr as the independent variables in a General Linear Regression Model (GLM). As there is sexual dimorphism in both species (Barbosa and Espeso, 2005; Moreno and Espeso, 2008), sex was included in the analyses as a classification factor. As this study includes data from several decades of the two breeding pro-

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