UNIVERSIDADE DE LISBOA

Faculdade de Medicina Veterinária

UPDATE ON DEMOGRAPHIC AND GENETIC PARAMETERS OF A CAPTIVE POPULATION OF THREATENED SAHARAWI DORCAS GAZELLE (*Gazella dorcas neglecta*)

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DISSERTAÇÃO DE MESTRADO INTEGRADO EM MEDICINA VETERINÁRIA

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Para a minha Família, que fundou os alicerces sobre os quais hoje me torno veterinário.

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Abstract

Update on demographic and genetic parameters of a captive population of threatened Saharawi dorcas gazelle (*Gazella dorcas neglecta*)

Between 1970 and 1975, 72 (36♂.36♀) Saharawi dorcas gazelles (*Gazella dorcas neglecta*) arrived in *Finca Experimental la Hoya*, Almería, southeast Spain. They were the founding individuals of a captive breeding programme, now managed as an European Endangered species Programme, currently with 236 (104.132) living individuals distributed among 12 institutions.

Previous demographic and genetic assessment of this population was published in 2002 (Abáigar, 2002). An updated analysis was commended, ultimately motivated by the recent establishment of *in situ* reintroductions in Senegal. Besides the inclusion of the last 14 years of studbook data, this is the first thorough study to use the software programmes Population Modelling, ENDOG and SplitsTree4 for this taxon.

The census history shows an overall increasing population, consistent with the incorporation of more institutions in the programme, although a tendency towards a stationary population is observed since 2010. Such tendency is corroborated by the current demographic parameters of annual growth rate (1.058), instantaneous rate of change (0.056) and net reproductive rate (1.283).

Age-specific life table parameters show higher mortality rate, fecundity rate and reproductive value in males in almost all age-classes in contrast with higher survival rate and life expectancy in females.

Sex and age structure of the global living population is close to pyramidal shape, as would occur in demographically stable populations.

Plotting of annual gene diversity and mean inbreeding coefficient shows a positive impact of the incorporation of eight wild-caught individuals in the programme in the 90s. Current genetic parameters are the result of proper reproductive management of threatened species, and are in accordance with standardised targets when planning cooperative metapopulation breeding.

Key-words: gazelles, captive breeding, reintroduction, studbook, metapopulation

Resumo

Atualização dos parâmetros demográficos e genéticos de uma população em cativeiro de gazela dorcas Saharawi (*Gazella dorcas neglecta*)

Entre 1970 e 1975, 72 (36♂.36♀) gazelas dorcas Saharawi (*Gazella dorcas neglecta*) foram transportadas até à *Finca Experimental la Hoya*, Almería, no sudeste de Espanha. A partir destes indivíduos desenvolveu-se um programa de cria em cativeiro, hoje em dia inserido no âmbito de um *European Endangered species Programme*, atualmente com 236 (104.132) animais distribuídos por 12 instituições.

A mais recente avaliação de cariz demográfico e genético desta população foi publicada em 2002 (Abáigar, 2002). Foi, assim, recomendada a realização de um novo estudo, em parte motivado pelo recente programa de reintrodução *in situ* levado a cabo no Senegal. Para além da inclusão dos últimos 14 anos de registos do *studbook*, este é o primeiro estudo completo em que se usaram os *software* informáticos Population Modelling, ENDOG e SplitsTree4 nesta subespécie.

O censo histórico mostra uma população globalmente crescente, consistente com a gradual incorporação de mais instituições no programa de cria, apesar de, desde 2010, ser notória uma tendência para a estabilização. Esta tendência é corroborada pelos parâmetros atuais de taxa anual de crescimento (1,058), taxa intrínseca de crescimento (0,056) e taxa reprodutiva líquida (1,283).

As tabelas de vida mostram taxa de mortalidade, taxa de fecundidade e valor reprodutivo mais elevados em machos em praticamente todas as classes etárias, contrastando com taxa de sobrevivência e esperança média de vida superiores em fêmeas.

A estrutura de género e idade da população viva aproxima-se a uma forma piramidal, própria de populações demograficamente estáveis.

Os gráficos de variação de diversidade genética e de coeficiente de consanguinidade médio ao longo dos anos mostram que a incorporação de oito indivíduos não relacionados, na década de 1990, teve um impacte benéfico em ambos. Os parâmetros genéticos atuais são o resultado de um maneio reprodutivo correcto de uma espécie ameaçada e estão em concordância com os objectivos traçados aquando do planeamento de reprodução conjunta de metapopulações.

Palavras-chave: gazelas, cria em cativeiro, reintrodução, *studbook*, metapopulações

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List of Abbreviations, Acronyms and Symbols

% - Percentage
λ – Annual growth rate
AIZA – *Asociación Ibérica de Zoos y Acuarios*
CBP – Captive Breeding Programme
CITES – Convention on International Trade in Endangered Species
CSIC – *Consejo Superior de Investigaciones Científicas*
EAZA – European Association of Zoos and Aquaria
EEP – European Endangered species Programme
EEZA – *Estación Experimental de Zonas Áridas*
EN – Endangered
ESU – Evolutionary Significant Unit
EX – Extinct
e.g. – *exempli gratia*
F – Inbreeding coefficient
FELH – *Finca Experimental la Hoya*
GD – Gene diversity
GSMP – Global Species Management Plan
G.d. – *Gazella dorcas* (taxon: species)
ISIS – International Species Information System
IUCN – International Union for Conservation of Nature
i.e. – *id est*
LTF – Lost to follow-up
L*x* – Age-specific survivorship
M*x* – Age-specific fecundity rate
N – Number of individuals
N_e – Effective population size
PMx – Population Modelling
P*x* – Age-specific survival rate
QPA – Quick Population Assessment
Q*x* – Age-specific mortality rate
r – Instantaneous/intrinsic rate of change
R_0 – Net reproductive rate
RFFN – *Réserve de Faune du Ferlo-Nord*
RSFG – *Réserve Spéciale de Faune de Guembeul*
SAD – Stable Age Distribution
SPARKS - Single Population Animal Records Keeping Software
Spp. – species
SSC – Species Survival Comission
STD – Studbook
STD# - Studbook number
TAG – Taxon Advisory Group
VU – Vulnerable
vs. – *versus*
WAZA – World Association of Zoos and Aquariums

CHAPTER I – TRAINING PERIOD ACTIVITIES

The final year of the Integrated Masters in Veterinary Medicine, University of Lisbon, includes the possibility of doing an internship abroad, under the programme ERASMUS +. The candidate's traineeship took place in *Estación Experimental de Zonas Áridas* (EEZA) – *Consejo Superior de Investigaciones Científicas* (CSIC) –, in Almería, from 28th September 2015 to 12th February 2016. It was supervised by Professor Teresa Abáigar Ancín (EEZA-CSIC) and co-supervised by Professor Dr Luís Telo da Gama (Faculty of Veterinary Medicine, University of Lisbon).

The EEZA, located in the University of Almería campus, is a Spanish governmental institution dedicated to the study of ecology and sustainable environment exploitation, comprising five main research groups. The main purpose of the group for Conservation of Endangered Species is to improve the conservation status of three species of gazelles native to northern Africa, Mhorr gazelle (*Nanger dama mhorr*), Cuvier's gazelle (*Gazella cuvieri*) and Saharawi dorcas gazelle (*Gazella dorcas neglecta*), through captive breeding in *Finca Experimental la Hoya* (FELH) and, more recently, to coordinate *in situ* reintroduction programmes.

The majority of the traineeship period was spent in EEZA, where most bibliographic research and analyses of studbook database were carried out. Throughout November, veterinarian Gerardo Espeso kindly let the candidate join the FELH capture team for a vaccination campaign for Q fever and clostridiosis infections (Figure 1). All gazelles were physically captured with nets and besides vaccination (Coxevac® and Basquin Plus®) and deworming (Virbamec®), the need for hoof trimming and eventual wound disinfection was assessed.

During the stay in EEZA, there was an opportunity to present preliminary results of this study on the XII *Maratón Científico* (http://www.eeza.csic.es/es/mediateca.aspx), which were then made available to the Antelope and Giraffe Taxon Advisory Group as complement of the 2015 Quick Population Assessment for *G.d.neglecta*.

Figure 1 – Vaccination of male Saharawi dorcas gazelle, FELH. (Original photo: Gerardo Espeso).

CHAPTER II – INTRODUCTION

In the two decades from 1962 to 1982, large numbers of non-domestic ruminants were imported from their natural habitat, ultimately becoming founding individuals of current self-sustaining captive populations (Thomas, Barnes, Crotty & Jones, 1986). This was the case of the three species of gazelles whose main breeding centre is FELH, southeast Spain.

Progress in cooperative management of *ex situ* populations soon led to the conclusion that both demographic and genetic recommendations are relevant guidelines for threatened species' conservation (Foose, 1980; Leus, Traylor-Holzer & Lacy, 2011). The study of such parameters requires access to the studbook database, in this case supervised by the European Endangered species Programme (EEP) coordinator, Teresa Abáigar.

The captive population of Saharawi dorcas gazelle (*Gazella dorcas neglecta*, Lavauden 1926) has been closely managed for over 45 years (Cano, 1988; Abáigar, 2002) and *in situ* reintroduction programmes have been possible (Abáigar & Cano, 2007; López & Abáigar, 2013). This taxon represents an example of success in antelopes' captive breeding and its characterisation could therefore serve as reference to other programmes.

Because the previous publication addressing demographic and genetic management of this population dates back to 2002 (Abáigar, 2002), the opportunity to include the last 14 years of record keeping and to use for the first time other software programmes in addition to SPARKS arose.

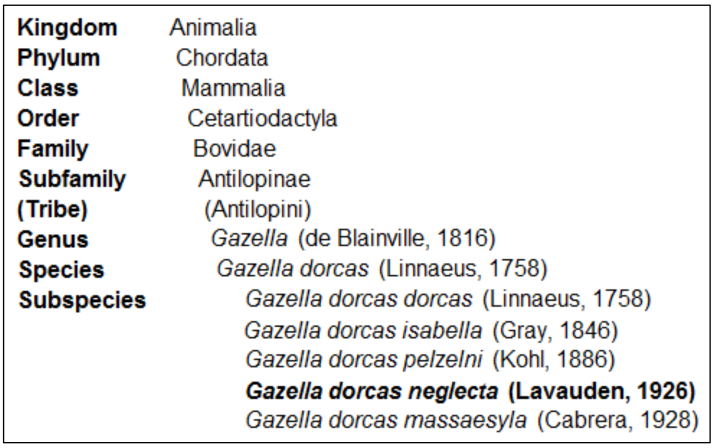
CHAPTER III – LITERATURE REVIEW

1. Taxonomy

Gazella dorcas spp. (Linnaeus, 1758) is a polytypical species within the tribe Antilopini, sub-family Antilopinae (East, 1999; Lafontaine, Beudels, Devillers-Terschuren, Beudels & Devillers, 2005; Groves & Leslie Jr., 2005). The taxonomy of the subspecies of Dorcas gazelles has been reviewed by several authors, and distinct classifications have been published on the basis of historical geographic distribution and phenotypic variation (see Groves, 1968; Alados, 1987; Yom-Tov, Mendelssohn & Groves, 1995). Two of the first known reports claimed the existence of 11 and 13 subspecies, respectively, each placing *G.d.neglecta* in different taxonomic positions (Alados, 1987).

The adopted nomenclature for the International Studbook is *G.d.neglecta*, based on the latest and more thorough taxonomic review by Alados (1987) which consisted in a cladistic analysis of cranial dimensions of Dorcas gazelles' subspecies and *Gazella gazella arabica*, from different regions in northern Africa and the Arabian Peninsula. A shorter review of five subspecies (Figure 2) was proposed based on probable common ancestry and geographical delimitations, with relevant changes such as *G.d.littoralis* being included in *G.d.isabella* and *G.d.osiris* being included in *G.d.dorcas* (Alados, 1987).

Figure 2 – Taxonomic classification of Dorcas gazelles, proposed by Alados (1987). (Adapted from López & Abáigar, 2013).



Kingdom	Animalia
Phylum	Chordata
Class	Mammalia
Order	Cetartiodactyla
Family	Bovidae
Subfamily	Antilopinae
(Tribe)	(Antilopini)
Genus	*Gazella* (de Blainville, 1816)
Species	*Gazella dorcas* (Linnaeus, 1758)
Subspecies	*Gazella dorcas dorcas* (Linnaeus, 1758) *Gazella dorcas isabella* (Gray, 1846) *Gazella dorcas pelzelni* (Kohl, 1886) ***Gazella dorcas neglecta* (Lavauden, 1926)** *Gazella dorcas massaesyla* (Cabrera, 1928)

Despite Alados's clarification of previous reviews, possible isolation of Dorcas' subspecies does not seem entirely documented and is still currently under discussion (Lafontaine et al., 2005; López & Abáigar, 2013). Not only morphological characteristics are not enough to fully clarify this issue, but also the wide range of the species' distribution, the confirmed gene transfer between populations and the fact that most populations have been extirpated from their natural range still raises questions (Lerp, Wronski, Pfenninger & Plath, 2011; Godinho et al., 2012).

Inconsistencies between subspecies' classifications based on morphological vs. genetic parameters have been reported in other gazelle species (Rebholz & Harley, 1999; Wronski et al., 2010; Kurihara & Kawada, 2013), and Dorcas gazelles are no exception. Elucidation of the subspecies taxon problem is relevant when it comes to prioritising captive breeding strategies for conservation purposes, since taxonomic uniqueness is one of the criteria for selection of candidates for establishment of a captive breeding programme (CBP) (Seal, 1986).

Genetic-based approaches became progressively relevant in this field of research and attempts for disambiguation have been proven useful, not only in mammals but also in other vertebrates (Johns & Avise, 1998). Successful analysis of genetic markers, namely mitochondrial cytochrome *b* gene and control region, in samples covering the entire presumed distribution range of Dorcas gazelles, have confirmed little intraspecific genetic structure and support the idea that *Gazella dorcas* spp. can be regarded as one evolutionary significant unit (ESU) (Lerp et al., 2011).

Likewise, a more recent approach by Godinho et al. (2012) testing for mitochondrial cytochrome *b* gene and microsatellite markers in samples from wild, semi-wild and captive populations in northwestern Sahara strongly suggests that a vast part of the Dorcas gazelle populations in this region are genetically very homogeneous. No unequivocal support for the distinction of *G.d.dorcas* and *G.d.neglecta* was reported, advocating that all animals south of the Atlas Mountains should be included in a single subspecies taxon. This had already been suggested by Lafontaine et al. (2005).

In conclusion, no evidence for any clear-cut geographic pattern of genetic structure was found, thus shedding doubt on the validity of the previously proposed subspecies (Lerp et al., 2011).

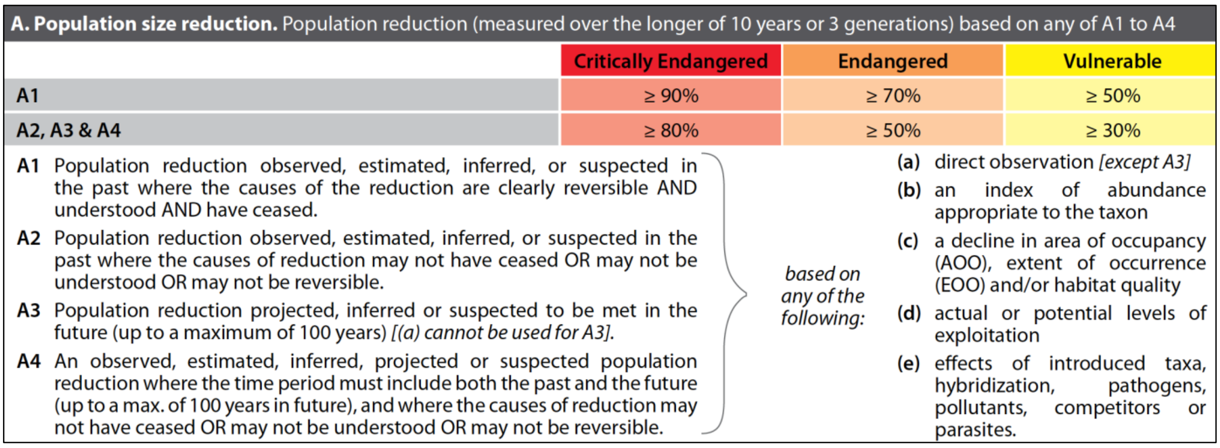
Progress in non-invasive sampling for identification of North African ungulates (see Silva et al., 2014) and ongoing broader molecular studies addressing this issue are expected to put forward more accurate classifications. Moreover, as stated by Godinho et al. (2012), dependence of future action plans also rely on the results of molecular studies, which will invariably lead to more publications attempting to provide useful recommendations regarding species' conservation.

Regardless of future perceptions, the conservation value of the population described in this study remains unalterable since, to the best of our knowledge, this is the only captive population of *Gazella dorcas* spp. whose geographic origin of founding individuals is known and that has been managed under an *ex situ* programme.

2. Wild populations’ status and areas of distribution

In the most recent global International Union for Conservation of Nature (IUCN) Red List assessment, *Gazella dorcas* spp. was classified as Vulnerable (VU) A2cd, according to the 2001 Red List categories and criteria, version 3.1 (IUCN, 2008; IUCN, 2012). As shown in Figure 3, the VU A2 category includes species facing a high risk of extinction in the wild, with an observed, estimated, inferred or suspected population size reduction of ≥30% over the last three generations (IUCN, 2012). Letters *c* and *d* express the causes for population decline (IUCN, 2012).

Figure 3 – Criteria A for evaluation of taxa belonging to an IUCN Red List threatened category (Adapted from IUCN, 2012).



A. Population size reduction. Population reduction (measured over the longer of 10 years or 3 generations) based on any of A1 to A4

	Critically Endangered	Endangered	Vulnerable
A1	≥ 90%	≥ 70%	≥ 50%
A2, A3 & A4	≥ 80%	≥ 50%	≥ 30%

A1 Population reduction observed, estimated, inferred, or suspected in the past where the causes of the reduction are clearly reversible AND understood AND have ceased.

A2 Population reduction observed, estimated, inferred, or suspected in the past where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.

A3 Population reduction projected, inferred or suspected to be met in the future (up to a maximum of 100 years) *[(a) cannot be used for A3]*.

A4 An observed, estimated, inferred, projected or suspected population reduction where the time period must include both the past and the future (up to a max. of 100 years in future), and where the causes of reduction may not have ceased OR may not be understood OR may not be reversible.

based on any of the following:

(a) direct observation *[except A3]*

(b) an index of abundance appropriate to the taxon

(c) a decline in area of occupancy (AOO), extent of occurrence (EOO) and/or habitat quality

(d) actual or potential levels of exploitation

(e) effects of introduced taxa, hybridization, pathogens, pollutants, competitors or parasites.

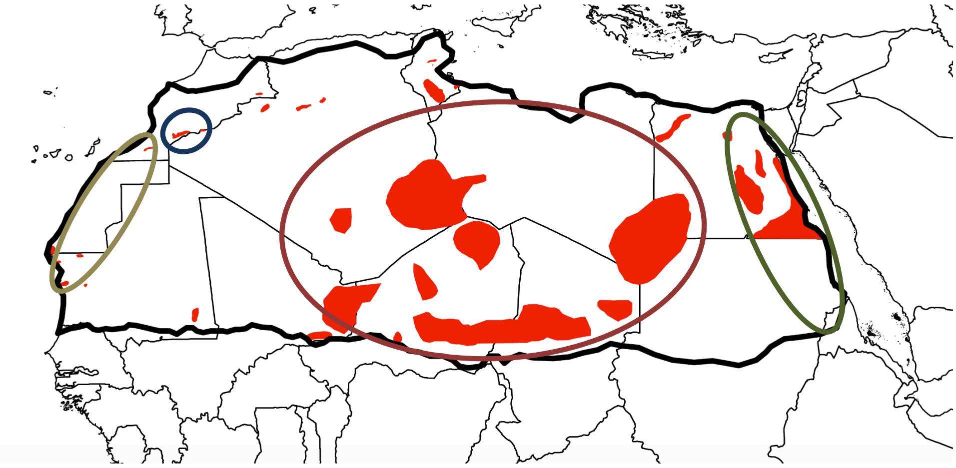
Although the Red List categories and criteria were designed for global taxon assessments, national, regional or local classifications can be proposed (Mallon & Kingswood, 2001; IUCN, 2012). An example is the Mediterranean assessment by Jdeidi, Masseti, Nader, de Smet & Cuzin (2010), which classified Dorcas gazelles as regionally Endangered (EN), mostly due to recent decline of over 50% in circum-mediterranean countries. Thorough descriptions of national historical population tendencies and *in situ* conservation strategies were compiled by East (1999) and Lafontaine et al. (2005). Severe situations occur in Senegal, where it was described as extinct (EX) in the wild in the mid-1970s (East, 1999), and in Nigeria, where it is now also possibly EX.

Concerning the subspecies *neglecta*, a 90/100 captivity programme was recommended, after suggestion of EN classification based on Mace & Lande criteria (Abáigar, 2002). In this case, the goal is to maintain 90% of gene diversity (GD) of the source population in the next 100 years (Ballou & Foose, 1996; Lacy, 2013).

Dorcas gazelles are also subject to the Convention of International Trade in Endangered Species and the Convention on Migratory Species, appendix III and I respectively (López & Abáigar, 2013).

First reports on Dorcas gazelles' distribution date back to late 19th and beginning of 20th centuries. Although often not penetrating to the interior of hyper-arid deserts and upper elevations of the central-Saharan massifs (East, 1999; Lafontaine et al., 2005), it is the most widely distributed antelope species in North Africa (Mallon & Kingswood, 2001) and the only which extends its range to the western region of the Middle East (East, 1999). The southern border of its distribution is the Sahel region (East, 1999). They were said to persist throughout most its historical distribution range, but population fragmentation is now more evident and an 86% range loss was estimated in a recent assessment of large Saharan vertebrates (Durant et al., 2014). Figure 4 shows the historical range (prior to 19th century) and resident range (where Dorcas gazelles are known to occur within the last 10 years), as well as a delimitation of subspecies' distribution (East, 1999; Mallon & Kingswood, 2001; Durant et al., 2014).

Figure 4 – Historical and resident range of Dorcas gazelles. (Adapted from East, 1999; Mallon & Kingswood, 2001; Durant et al., 2014).



Legend: black line – historical range; brown line – *G.d.neglecta*; blue line – *G.d.massaesyla*; red line – *G.d.dorcas*; green line – *G.d.isabella* & *G.d.pelzelni* / shaded red: resident range.

Areas of subspecies' distribution should be considered rough approximates, as it may be impossible to completely establish the boundaries between subspecies, especially *G.d.pelzelni* and *G.d.isabella* (East, 1999). Attempts to define clear borders must be regarded with caution, as it should be reminded that no statistically significant support was found for any geographic structure within the distribution range of Dorcas gazelles (Lerp, Wronski, Butynski & Plath, 2013).

Information on available surveys led to an estimated population of 35 to 40 thousand Dorcas gazelles in sub-Saharan countries, with the largest numbers in Niger and Chad (East, 1999). This number, when added to broader surveys from North Africa and the Middle East, and assuming densities of 0.2/km^2 and 0.02/km^2 in areas where their presence is known and not known, respectively, indicates a likely total population size within the tens of thousands, including protected areas, where less than 25% of Dorcas gazelles live (East, 1999; Mallon & Kingswood, 2001).

Despite potentially at risk due to inadequate representation in conservation areas, Dorcas gazelles are the only species of antelopes still listed as widespread within the region, meaning their survival is not under immediate threat (Mallon & Kingswood, 2001). Nonetheless, the above estimates are not updated and a decrease is anticipated due to continued threats.

3. Establishment of the *ex situ* captive breeding programme

Captive breeding, or captive propagation, of threatened species as a mean of attempting extinction prevention and creating stock for possible reintroductions in wild environments has been referred to as crucial to their survival (Frankel & Soulé, 1981; Ballou & Ralls, 1982; Seal, 1986), and has received increasing attention by conservationists (Chesser, Smith & Brisbin, 1980; Frankel & Soulé, 1981; Schonewald-Cox, Chambers, Macbryde & Thomas, 1983).

3.1. Incorporation of the first individuals

The idea of starting an *ex situ* CBP for Saharawi dorcas gazelle was first conceived by Professor José Antonio Valverde (Cano, 1988), a spanish naturalist and biologist, whose areas of research included, among others, the study of the biogeography and taxonomy of iberian and north african vertebrates (Herrera, 2003). His studies in the territory of Western Sahara, of spanish occupancy until 1975 (Hamoudi, 2012), led him to conclude that taking no action to preserve some of the local non-domestic ungulate species would most likely result in the extinction of both wild and captive remnant populations. At that time, in the late 60s, the main concern species was the Mhorr gazelle (*Nanger dama mhorr*) (Cano, 1988), which had already been declared extinct in the wild.

The location chosen for the *ex situ* CBP was the FELH, founded in the 50s by the CSIC, initially as a research site for flora acclimatisation (EEZA, 2013a). After two decades of work on agriculture related subjects, institutional changes led to a reduction in activity in this field and the opportunity to house the CBP emerged (EEZA, 2013a).

Valverde's relationship with the military and to spanish Major Estalayo, who kept a group of Mhorr and Saharawi dorcas gazelles in *Río de Oro* (Walther, 1989; López & Abáigar, 2013), made it possible to translocate a total of 28 gazelles from October 1970 to October 1971: October 1970 – 1.1 *G.d.neglecta*; January 1971 – 6.11 *G.d.neglecta* + 1.6 *N.d.mhorr*; October 1971 – 0.2 *N.d.mhorr* (Cano, 1988). Until 1975, more imports occurred, including the incorporation of the Cuvier's gazelle (*Gazella cuvieri*) and Saharan barbary sheep (*Ammotragus lervia sahariensis*), or *Arrui*, in Spanish, and the increasing number and available area of enclosures at FELH allowed an increase to a total of 260 animals by 31st December 1986 (Cano, 1988).

Antonio Cano and his daughter, Mar Cano, were responsible for the implementation of the CBP for the four species. The main focus of FELH is their continuous captive breeding and management of dispersion among collaborating institutions, which involves keeping records, under the form of studbooks, and genetic resources bank for all species (EEZA, 2013a). After assuring the establishment of each species, the goal was to reach a population size and gene diversity likely to assure their future viability when reintroduction eventually takes place (Abáigar & Cano, 2007; EEZA, 2013a).

3.2. Establishment of groups in captivity

Captive populations are subject to the human-influenced establishment of groups of individuals, which forcely take in consideration the target species' social structure and the planned reproductive management.

Cassinello (2005) describes the four types of groups currently established in all three species of gazelles kept at FELH, classified as follows:

- all-male groups: single males, with no mating experience, usually made up of no more than five individuals;
- reproductive groups: females and infants together with one adult male in reproductive age;
- isolated males: often males who have been kept in reproductive groups tend to be aggressive if kept with other single or reproductively non-experienced males, so they are separated to prevent fatal accidents;
- all-female groups with infants: formerly reproductive groups from which the adult male has been removed.

The first study on the social organization of *G.d.neglecta* in non-captive conditions shows these categories accurately simulate what would happen in wild populations, despite annual variation in the proportion of each group (Abáigar et al., 2016).

In captive conditions, groups' size and constitution are established depending mostly on enclosure dimensions and management goals. A number of expected and unexpected situations, such as traumatisms or the report of an infectious disease, may require translocation of individuals.

Regarding the normal dynamics of reproductive and all-female with infants groups, females are kept in the same group as they were born and young males are removed when they reach juvenile status, at approximately 6 months of age, to prevent them from mating with females in breeding-age (Alados, Escós & Emlen, 1995). As for males, their physical isolation is the only reproductive control method used in FELH, and their rotation naturally depends on whether they are selected for breeding.

3.3. Founding population

The number of founding individuals is one of the factors with direct repercussions in the development of the population (Mace, 1986). Estimating the number of individuals required to retain the desired proportion of genetic variation would demand assessing its distribution in the wild source population, because only a limited fraction will reach the captive gene pool (Nei, 1973; Mace, 1986). However, when molecular studies are not performed and only phenotype is evaluated, as it was the case for many vertebrate species, including these three species of gazelles, as many individuals as possible should be used, increasing the range of genetic variation in the captive population (Thomas, Barnes, Crotty & Jones, 1986; Mace, 1986).

After establishment of the breeding population, the potential for future generations highly depends on its early management (Mace, 1986). Deleterious effects are likely to arise in the presence of few founding individuals, due to the increased rate of loss of GD and as a consequence of inbreeding (Cassinello, 2005).

In gazelle conservation programmes, different strategies have been followed, often depending on the ability to establish a founding population of adequate size. As an example, a quantitative description of the *G.d.neglecta* and *G.cuvieri* founding populations is provided, as they represent two contrasting situations. Table 1 summarises previous reports for both species and includes information on the number of founding individuals ($N_{f.i.}$), correspondent number and proportion that produced descendants (B_{males} and $B_{females}$), total population size (N) and mean inbreeding (F). Data for N and F for both species are as of 31st December 2007, as no updated records on *G.cuvieri* were found.

Table 1 – Founding individuals, proportion producing descendants, total population size and mean inbreeding for Dorcas and Cuvier's captive populations.

Species	$N_{f.i.}$ (m.f)	B_{males}	$B_{females}$	N	F	References
G.d.neglecta	37.37	5 (14%)	26 (70%)	162	0.0607	Cano, 1988; Abáigar, 2002; Ballou et al., 2011
G.cuvieri	2.2	1 (50%)	2 (100%)	260	0.192*	Escós, 1992; Cassinello, 2005; Moreno & Espeso, 2008

* F for Cuvier's gazelle is reported only for the EEP population (captive North American population excluded)

The conservation nucleus of *G.d.neglecta* was established with 72 individuals (36.36), imported between 1970 and 1975 (Alados et al., 1995). However, in the Single Population Animal Records Keeping Software (SPARKS) records, 74 (37.37) are registered as wild-born in Western Sahara. Assuming the SPARKS prefix *Sahar-* is correct for both extra individuals, this means they were offspring born to two females that were pregnant at the time of import. Despite being born in FELH, for the purpose of this study they were also considered founding individuals, following the approach by Abáigar (2002).

One of the pregnant females was identified as STD#31, who gave birth to male STD#32. As there is no other *Sahar*- with known mother, presumably due to lack of record, it was not possible to determine the other pregnant female.

Founding individuals were imported as follows: 1970 (1.1), 1971 (6.11), 1973 (1.0), and 1975 (29.25). Eight additional founders were subsequently incorporated from two private owners, in 1993 (2.2) from Fuerteventura and in 1996 (1.3) from Nueva Llanes, but are not part of the initial founding population (López & Abáigar, 2013). Their incorporation was possible due to previous common origin of individuals (Abáigar, 2002; López & Abáigar, 2013), and influenced mean F and GD for the global population, as discussed later.

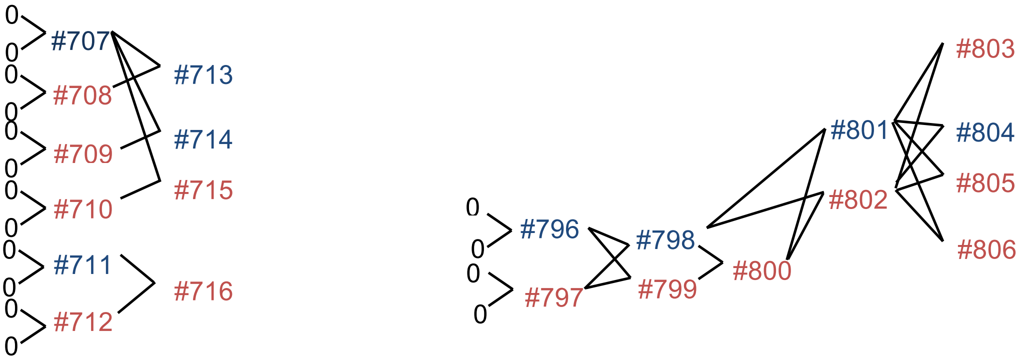
As for the conservation nucleus of *G. cuvieri*, the founding individuals were brought in 1975 from a captive population in the Oued Draa Valley, ex-spanish Sahara, by Dr Valverde (Escós, 1992). They arrived in FELH on 7th May (1.2) and 14th November (1.0) (Cano, 1988). Later on, in 1987, a female from Morocco was incorporated from a private farm as an additional founder, even though it was not strictly part of the founding population (Cano, 1988; Escós, 1992).

A first consideration in respect to both species may be put forward: the number of males who produced descendancy is likely to be underestimated. This is because, in the early years, more than one male in reproductive age was kept in the same enclosure with several females (Cano, 1988; Escós, 1992; Moreno & Espeso, 2008), and fatherhood could not always be established with certainty. In the case of Saharawi dorcas gazelle, the unknown sires of the first individuals born in FELH were designated as *UNK* in the STD. If their correct identity was known, the number of mating males would possibly be higher. As for Cuvier's gazelle, the parenthood of the 20 calves born between 1975 and 1977 was attributed to only one of the males (STD#1), assuming a worst case scenario (Escós, 1992; Moreno & Espeso, 2008), although it is likely that both founding males contributed to reproduction (Escós, 1992). In what concerns females, 70 and 100% of *G.d.neglecta* and *G.cuvieri* respectively, produced offspring, in line with the recommendation that all females reaching sexual maturity should be encouraged to breed (Ballou & Ralls, 1982).

Another relevant aspect of studbook creation and establishment of CBP, transversal to all species, including these two, is that, unless their relationship is known, wild-caught founding individuals are assumed to be unrelated (Ballou & Ralls, 1982). Because in most cases they are caught in the same or in nearby regions, this supposition might be questioned, as there is possibility of some relationship amongst them. When they come from previous captive conditions, which was the case for all species of gazelles in FELH and, for example, for the herd of Dorcas gazelle in the National Zoological Park, Washington (Ralls, Brugger & Glick, 1980), this premise may even be less accurate.

As for the eight *G.d.neglecta* subsequently incorporated in the programme, STD#713 to STD#716 and STD#803 to STD#806 (Abáigar, 2002; López & Abáigar, 2013), they were not unrelated and, assuming a worst case scenario and according to the owners' records of previous matings, the pedigree was completed (Figure 5) by creating 13 hypothetical ancestors, which should be a more rigorous approach. The inclusion of these eight animals in the programme was beneficial when it came to increasing the number of founders and avoiding the proliferation of small reproductive nuclei hardly viable at mid-range (Abáigar, 2002). Individuals STD#707 to STD#712 and STD#796 to STD#802 (n=13) are, for this reason, hypothetical or *phantom* animals, with *wild* parentage.

Figure 5 – Hypothetical pedigree for the eight individuals (3.5) later incorporated in the CBP, from Fuerteventura (left) and Nueva Llanes (right)



Legend: blue – males; red – females; 0 – *wild* parentage

Captive populations have done reasonably well, in terms of annual census of population size (N), when both sufficient founding individuals and adequate species-specific husbandry are present (Thomas et al., 1986). In fact, specifically in ungulates, even when only small founding populations and associated small gene pool are available, they have still done well in captivity (Thomas et al., 1986). The population of Cuvier's gazelle at FELH, descending from only 1 male and 2 females, is another example of success with small founding populations (Cano, 1988; Escós, 1992; Moreno & Espeso, 2008), as shown in Table 1.

Indirectly related to the number of founding individuals is the correspondent proportion producing surviving offspring, which should be as high as possible, attending to the available carrying capacity (Mace, 1986), in order to maximise genetic propagation of wild genes. In this context, *as high as possible* means as close to the actual proportion producing offspring regardless of their survival. This proportion, non-regarding survival of young, was higher is females for both species (Table 1), nevertheless representing very distinct numbers (26 $B_{females}$ in *G.d.neglecta* and 2 $B_{females}$ in *G.cuvieri*). An example where all offspring of founding individuals survived is the Scimitar-horned oryx (*Oryx dammah*) captive population studied by Mace (1986).

3.4. European Endangered species Programme

Nevertheless, the outcome of captive establishment of ungulates doesn't only concern the number of founding individuals. As demonstrated by a broad survey of 49 zoological collections (Thomas et al., 1986), co-operation amongst zoos, pattern of dispersion throughout collections and access to new wild specimens are also pointed as determinants of the success or failure of the programmes.

In 2002, the European Association of Zoos and Aquaria (EAZA) established the EEP for *G.d.neglecta* (López & Abáigar, 2013), currently with 236 living individuals throughout 12 collaborating institutions, presented later. The ultimate goal of an EEP is to reinforce wild populations to the point that their size allows long-term survival and evolution by natural selection (Seal, 1986). As captive stocks increase, reintroductions become increasingly feasible and *in situ* action plans are designed (Bertram, 1986), which was possible for Saharawi dorcas gazelle through cooperation between the Senegalese and Spanish governments (Abáigar & Cano, 2007; López & Abáigar, 2013).

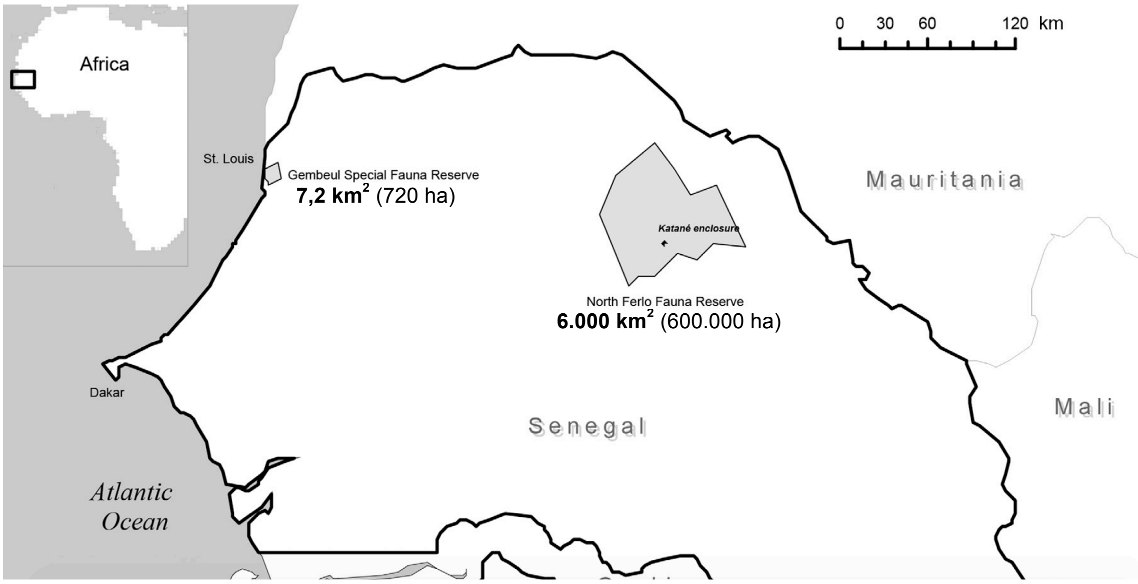
4. Establishment of the *in situ* reintroduction programme

Significant experience in ungulates' reintroduction derives from translocations of native game species, such translocations having been described, in general, as more successful than those of threatened species (Griffith, Scott, Carpenter & Reed, 1989).

4.1. Description of reintroduction locations

In 2002, a study on the viability of reintroducing Saharawi dorcas gazelles was initiated (Abáigar & Cano, 2007) and efforts on both source and destination sites began. The destination were two reserves in Senegal, the *Réserve de Faune du Ferlo Nord* (RFFN) and the *Réserve Spéciale de Faune de Guembeul* (RSFG) (Figure 6), founded in 1972 and 1983, respectively, where the Environment Ministry of the Senegalese government had already been working on the recovery of the Mhorr gazelle and the Scimitar-horned oryx (WAZA, 2016a). RSFG would serve as acclimatisation site (WAZA, 2016a; Abáigar et al., 2016) and as reproductive and genetic stock for RFFN, where the fenced area of *Katané* (4,4km^2; 440ha) would become the final destination of the reintroduction programme prior to eventual release in the wild. In *Katané*, gazelles would range in semi-wild conditions, without food supplementation nor supervision or management (López & Abáigar, 2013; Abáigar et al., 2016).

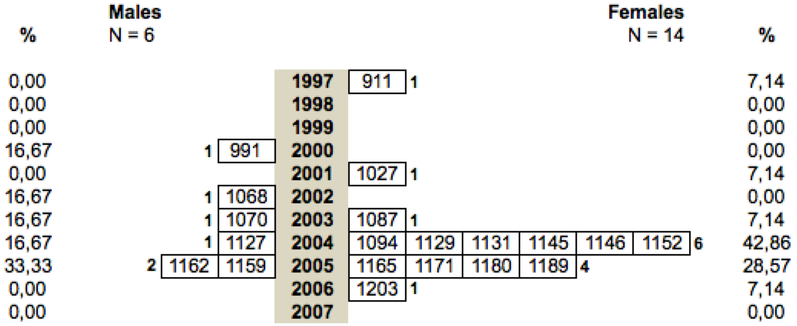
Figure 6 – Size and location of RSFG and RFFN, in Senegal. (Adapted from Abáigar et al., 2016).



4.2. Reintroduction founding group

Of the 174 captive individuals available in all institutions in 2007, 20 (6.14) were chosen for reintroduction in RSFG. The age distribution of the founding group to be translocated must be considered (Foose, 1980), and, for this case, is presented in Figure 7. Animals are ordered from top to bottom according to their year of birth (centre column) and are identified by STD#. Percentage of individuals in each age class is also presented on both sides.

Figure 7 – Sex and age distribution of the RSFG founding group.



%	Males N = 6		Females N = 14	%
0,00		**1997**	911 1	7,14
0,00		**1998**		0,00
0,00		**1999**		0,00
16,67	1 991	**2000**		0,00
0,00		**2001**	1027 1	7,14
16,67	1 1068	**2002**		0,00
16,67	1 1070	**2003**	1087 1	7,14
16,67	1 1127	**2004**	1094 1129 1131 1145 1146 1152 6	42,86
33,33	2 1162 1159	**2005**	1165 1171 1180 1189 4	28,57
0,00		**2006**	1203 1	7,14
0,00		**2007**		0,00

Preference was given to females in age classes 2-3 and 3-4 and to males covering a wide range of adult age classes. More explanations about populations' sex and age distribution are presented in Chapter V (Materials and Methods). Of the 20 individuals transferred, STD#1027, STD#1068 and STD#1180 are still alive in RSFG.

According to Mace (1986), choosing individuals from different subpopulations would increase the chance of preserving genetic variation in the reintroduced population, because each would have lost a different set of alleles (Foose, 1980). It is therefore relevant, from a genetic perspective, to mention that four other institutions apart from FELH contributed with animals to the programme, namely *Zoo Aquarium Madrid*, *Nueva Llanes*, *Tabernas* OASYS and Marwell Wildlife.

One month before the planned date for translocation, the seven individuals from outside FELH were brought in for sanitary exams and request for translocation permits to the Convention of International Trade of Endangered Species (CITES) (Abáigar & Cano, 2007). Two breeding groups were constituted, on the basis of assuring the maximum founder representation on the expected offspring (Abáigar & Cano, 2007).

On 10th April 2007, individuals were moved to RSFG, where the same groups previously established were maintained: two breeding groups (1.6 and 1.8) and one male group (4.0) (Abáigar & Cano, 2007; López & Abáigar, 2013). Males chosen to start breeding were STD#1068, which effectively bred with females STD#1165, 1131, 1094, 1027 and 1171, and STD#1127, which effectively bred with females STD#1145, 1152, 1189, 1129.

The first birth occurred on the 21st September 2007 and, after two years, another 33 births were registered, with a consequent increase of the population size to almost its double. The last phase of the programme – reintroduction in semi-wild conditions and genetic reinforcement of RSFG – could then start (López & Abáigar, 2013).

On 29th March 2009, 23 (9.14) gazelles, three of which founding individuals of the RSFG population (STD#991, STD#1087 and STD#1131), were finally moved to *Katané* enclosure (WAZA, 2016a; Abáigar et al., 2016), where cohabitation with other endogenous species, such as the african wild boar (*Phacochoerus africanus*), jackal (*Canis aureus*) and other reintroduced Sahelo-Saharan antelopes, is possible (López & Abáigar, 2013).

This reintroduction programme was partly funded by the *Asociación Ibérica de Zoos y Acuarios* (AIZA) and is recognised as *branding-project* by the World Association of Zoos and Aquaria (WAZA) (EEZA, 2013b). Adaptation from captive to natural-living conditions is now evident, after four years of seasonal monitoring of the reintroduced population (Abáigar et al., 2016).

As for Mhorr and Cuvier's gazelles, they have also been reintroduced in other protected areas, in Morocco and Tunisia (EEZA, 2013b).

CHAPTER IV – AIMS OF THE STUDY

The purpose of this study is to characterise, from a demographic and genetic perspective, the captive EEP population of Saharawi dorcas gazelle, using the updated STD data and pedigree analyses software.

This work is expected to provide useful information applicable to other captive populations and, more importantly, the parameters obtained could serve as guidance to what would occur in free ranging populations, which is relevant especially when reintroduction programmes are in progress or in a study phase. A detailed pedigree analysis might be useful in determining which measures can be put to practice in the population as a whole and eventually in each CBP member institution, in order to delay as much as possible the continuous increase in inbreeding, one of the main concerns in captive populations' genetic management.

The outcome of this updated analysis, namely life history parameters, demographic variation and relatedness of subpopulations, is one of the fundamental factors to be considered when assessing populations' viability and probability of extinction under natural conditions, which would ideally be performed after interpretation of this dissertation.

Because this work has a strong didactic component for the author, in Chapter VI (Results and Discussion) each parameter is followed by theoretical background and discussion, in an attempt to put in better context the results obtained. For the same reason, formulas needed to calculate each software output are also presented.

5. Studbook description

As mentioned before, the *ex situ* CBP for Saharawi dorcas gazelle began in 1970. The programme led to the creation of an International Studbook in 1990 (López & Abáigar, 2013) and, since then, five updates have been published by the keeper and EEP coordinator (Abáigar, 2014). At the time, the existence of a STD was regarded as criterion of the degree of concern felt for a species (Bertram, 1986), and projections on the need for STDs covering progressively more species were put forward (Seal, 1986). The updated International Studbook used for this study can be accessed at www.eeza.csic.es/es/programadecria.aspx.

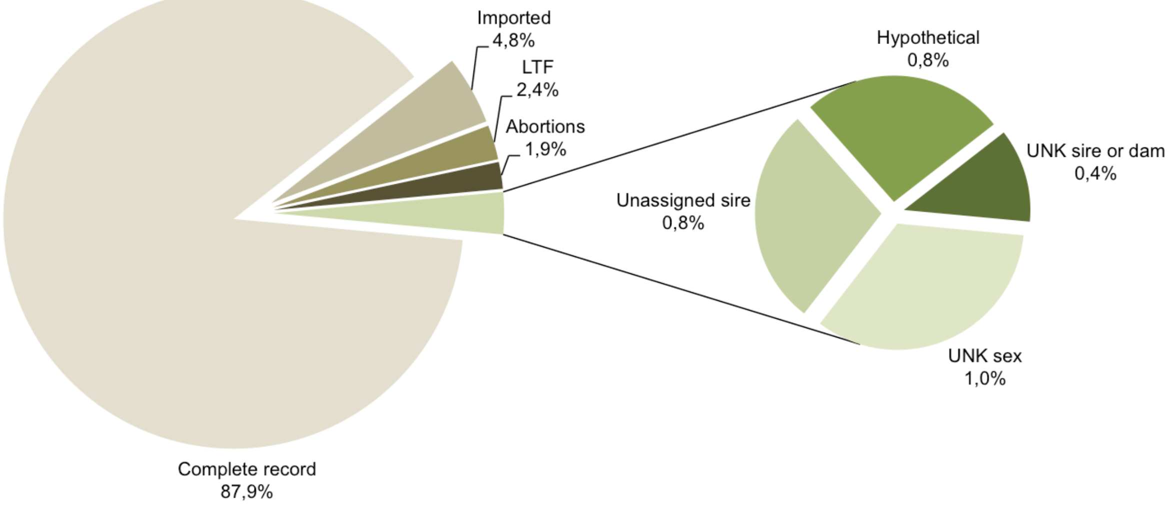
The currently used STD database software is SPARKS version 1.6, distributed by the International Species Information System (ISIS). Each registered individual has information on STD identification number (STD#), gender, parentage, date & place of birth and death, translocations and birth type – wild vs. captive, as outlined by Scobie, Lackey, Porter & Princeé (2005). Such information is essential for both demographic and genetic analyses of the taxon of concern (Foose, 1980; Seal, 1986).

An overview of the record integrity in the studbook is presented in Graph 1, considering the available information for each individual. There are records on 1693 animals, each included in one of the categories described as follows:

- complete record (n=1488): parentage and date of birth and death, if not alive, is available;
- imported (n=82): no certain birth date available;
- lost to follow up (LTF) (n=41): no death date available, due to lack of record keeping or because they were sent to *Katané* enclosure;
- abortions (n=32): late abortions started being recorded in 2011, as well as stillbirths, by request from ISIS. Until then, these were not notified to the STD keeper and no entry was created on SPARKS. Despite the fact that discrimination of both concepts is not consensual, unlike stillbirths, abortions were not considered for any of the parameters studied;
- UNK sex (n=17): individuals that died within the first month after birth, whose gender was not registered;
- unassigned sire (n=14): uncertainty due to breeding groups having more than one male, in the first years of the CBP;
- hypothetical (n=13): *phantom* individuals created to complete the STD (see establishment of *ex situ* CBP);
- UNK sire or dam (n=6): due to lack of record keeping (no individuals in this condition were used for reproduction).

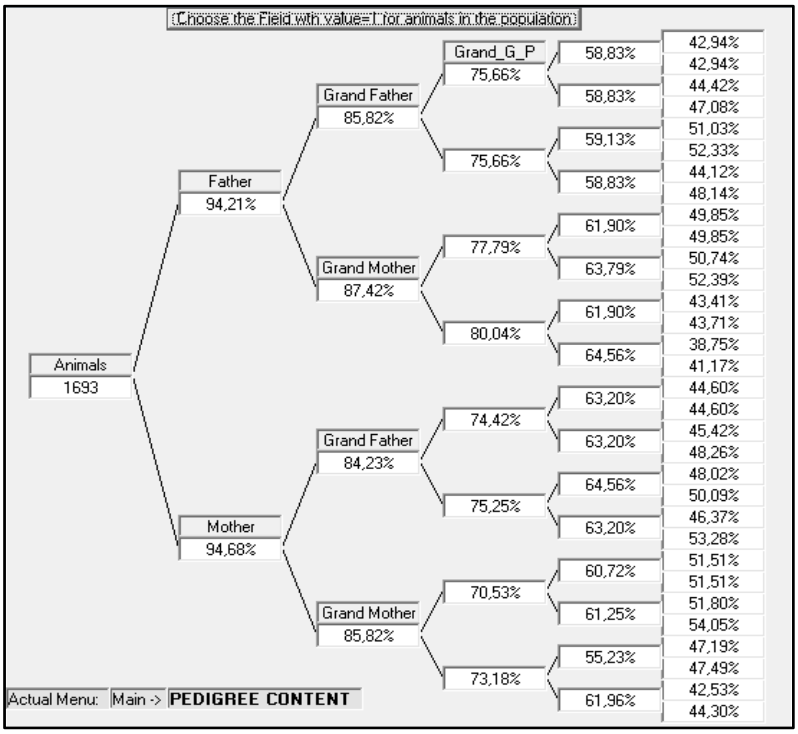
All individuals lacking relevant information for each parameter were excluded from the calculations in question.

Graph 1 – Record integrity (where a complete record corresponds to an individual with known parents and known date of birth and death, except if alive).



ENDOG software provides a complementary perspective (Figure 8), aimed at the known pedigree content to the 5th parental generation (Gutiérrez, Goyache & Cervantes, 2010).

Figure 8 – Known pedigree content (with percentage of animals with different ancestors known).



6. Software packages for data registration and analyses

Computerised record keeping systems and software programmes equipped with mathematical algorithms allow extensive data analysis and optimisation of demographic health and retention of GD (Leus et al., 2011). For the purpose of managing zoological collections, a number of software packages are available and in constant update (Leus et al., 2011). Some of the most commonly used include SPARKS (Scobie et al., 2005), PopLink (Faust, Bergstrom, Thompson & Bier, 2012), ZooRisk (Earnhardt, Bergstrom, Lin, Faust, Schloss & Thompson, 2008) and PMx (Ballou, Lacy & Pollak, 2010).

A brief description of the software programmes used for this dissertation is provided, as well as the results obtained with each one and correspondent input files and settings.

6.1. Microsoft Excel

An Excel file containing all the STD records until 31st December 2014 was exported from an Access file, and was the most relevant tool to get familiarised with the data. Records for each individual included: STD#, gender, STD name (initials of the place of birth), sire, dam, place & date of birth and death, cause of death, current location if alive and individual inbreeding coefficient (F_i) computed from pedigree information. Age in days, months and years was added. An Excel file containing all translocations was also available, with date of translocation and correspondent place of origin and destination.

Various preliminary analyses were carried out in Excel, to assess STD completeness, distribution of living population, sex and age pyramids, annual records of births and deaths and global population census. Even though the presented age-specific life table parameters were obtained with PMx software, traits such as mortality rates, survival rates and life expectancy were also calculated in Excel for the purpose of practice and to confirm identical results by the two approaches.

Questions regarding missing or conflicting data were discussed with the STD keeper and, when possible, resolved.

6.2. SPARKS version 1.6

In 2011, ISIS maintained a library of active SPARKS datasets for 156 taxa (WAZA, 2016b), one of which being Saharawi dorcas gazelle. SPARKS is not only a software for record keeping, as shown, but also allows the user to conduct demographic and genetic analyses and to export the database to other programmes (Scobie et al., 2005).

For the purpose of this study, the data from SPARKS was exported as a specific Excel file (*.Exchange*), which served as input file for PMx.

Of great relevance in SPARKS is the STD data and user defining fields' validation report, which quickly provides a list of data inconsistencies, such as conflicts with IDs, location of birth and/or death and missing information (Scobie et al., 2005). This list is one of the information currently provided by EAZA to the EEP coordinator in the annual Quick Population Assessment, so there is awareness of inappropriate information that might affect the reliability of pedigree information. Again, the detected inconsistencies were discussed and, if possible, amended.

The SPARKS User Manual (Scobie et al., 2005) provides guidance to dealing with uncertain or unknown information likely to affect the STD completeness, which should be interpreted accordingly to the output calculations desired (Scobie et al., 2005). An example of uncertain data is the approximate birth date attributed to imported wild-caught individuals, which, by request from each Taxon Advisory Group, should be included in all databases, including for *G.d.neglecta*.

6.3. PMx version 1.0

The software package Population Modelling (PMx) is an update of the previous PM2000 (Pollak, Lacy & Ballou, 2002) and is currently distributed among population managers (Leus et al., 2011). It was developed by Jonathan Ballou, Robert Lacy and John Pollak, in collaboration with several international organisations, including the Chicago Zoological Society, EAZA, ISIS and IUCN/SSC Conservation Breeding Specialist Group (Traylor-Holzer, 2011). The input file *.Exchange*, in Excel format, originated from SPARKS, was used to run PMx. Approximate estimates of birth and/or death dates were excluded from the *.Exchange* file before running it in PMx, so as to not induce error in age-specific life table parameters. Also, in the PMx individuals' selection screen, abortions (n=32) were excluded from both demographic and genetic analyses, leaving a total of 1661 individuals to be included. Subpopulations were defined according to present location, for computing of their genetic relationships.

Age-specific life table parameters and genetic analyses, with reference to the living population, where obtained with PMx. Settings for both demographic and genetic calculations are presented later.

6.4. ENDOG version 4.8

ENDOG (Gutiérrez & Goyache, 2005) is a software for demographic and genetic analyses of pedigree information that allows monitoring of changes in genetic variability and population structure (Gutiérrez et al., 2010). It is written in Fortran77 and is based on mathematical and statistical procedures developed by different authors (Gutiérrez et al., 2010).

The following assumptions were made when creating the Excel file that would serve as input for ENDOG:

- abortions were not excluded;
- random gender was attributed to individuals with UNK gender (as none reproduced, their gender is not relevant for genetic purposes);
- a reference population of animals born in 2014 (n=45) was created.

After running the programme, the following information on each individual is computed: individual inbreeding, average relatedness coefficient, number of full generations traced, equivalent complete generations, offspring size and increase in inbreeding.

Pedigree content, founders of reference population, generation intervals and effective population size (N_e) were obtained from ENDOG.

6.5. SplitsTree4 version 4.14.3

SplitsTree4 (Huson & Bryant, 2006) provides evolutionary analyses of pedigrees through the construction of trees and phylogenetic networks (Huson & Bryant, 2016). The Fst distance matrix between subpopulations computed by PMx (Table 14) was copied into a *.txt* format file, and then used by SplitsTree4.to build a Neighbor-Network, which translates distances between subpopulations and reflects the occurrence of translocations since the beginning of the CBP.

7. Description of current captive population

The assumed end date for the analysis was 31st December 2014, as the complete records for 2015 were not yet available by the time of beginning of the study. This is referred to as *current* date throughout the dissertation.

7.1. Collaborating institutions

The distribution of the 236 (104.136) Saharawi dorcas gazelles is shown in Table 2. Institutions are named according to the EAZA annual report 2013/14 (EAZA, 2015).

Table 2 – Distribution of living population in collaborating institutions.

	Males	**Females**	**Total**
Finca Experimental la Hoya, CSIC (Spain)	46	64	110
Réserve Spéciale de Faune de Guembeul (Senegal) *	13	18	31
Parc Zoologic de Barcelona (Spain)	7	17	24
Zoobotanico de Jerez (Spain)	12	8	20
Zoo Aquarium Madrid (Spain)	5	6	11
Wilhelma Zoologisch-Botanischer Garten Stuttgart (Germany)	3	7	10
Marwell Wildlife (England)	5	4	9
Zamosc Zoological Park (Poland)	3	4	7
Centro de Recuperación de Fauna Salvaje Nueva de Llanes (Spain) *	2	4	6
Chessington World of Adventures (England)	4	0	4
Parque Temático del Desierto de Tabernas OASYS (Spain)	3	0	3
Bioparc Doué-la-Fontaine (France)	1	0	1
Total	**104**	**132**	**236**

* non-EAZA members

Collaborating institutions play different roles in the CBP, such that, e.g. FELH stands out as the main breeding centre, holding 46.6% of the living population. In 2011, it represented 46.8% of the population (Abáigar, 2012), which indicates consistency over the past three years in maintaining this proportion. Since 2002, the goal has been to maintain an approximate population of 100 individuals in FELH (Abáigar, 2002). Although this is only one institution, from a metapopulation perspective, it should in fact be regarded as multiple breeding groups, because families are kept isolated with rotation of breeding animals, mostly males. This would correspond, in other CBP where no main breeding centres exist, to several institutions exchanging breeding stock.

Chessington World of Adventures, *Tabernas* OASYS and *Bioparc Doué la Fontaine* have male groups only and therefore can only contribute indirectly to the species reproduction, through exchange of males. If local reproduction becomes desirable, transferring females would be required, as no assisted reproduction methods are used.

Réserve Spéciale de Faune de Guembeul is, as explained above, the source subpopulation for reintroduction in *Katané* enclosure in Senegal. Animals living in *Katané* enclosure are not considered is this table because they are kept in semi-wild conditions and are not monitored on a daily basis (Abáigar et al., 2016). For the purpose of this study, if an animal living in *Katané* has no death date, it is regarded as lost to follow up and considered *dead* both in PMx and ENDOG software.

7.2. Breeding status

A description of the overall population breeding status is presented in Table 3.

Table 3 – Breeding status of the living population.

	Males	Females	Total
Total	104	132	236
Pre reproductive (Mx=0)	13	15	28
Breeding age (Mx>0)	91	115	206
Post reproductive (Mx=0)	0	2	2
Proven breeder	27	79	106
Of breeding age	27	77	104
Contracepted	0	0	0
Sterilised	0	0	0
Fertile	104	132	236

Pre-reproductive and post-reproductive ages were set at 11 months and 14 years, respectively, according to the recorded ages at first and last reproduction. The fecundity rates (M*x*) provide information on the age of first, last and maximum reproduction (Traylor-Holzer, 2011). Of the 91 males and 115 females of breeding age, only 27 (29.7%) and 77 (67%) are proven breeders, respectively, meaning they have bred at least once, regardless whether their offspring are still alive. These values give an idea of which fraction of the living population has actually contributed to passing their genes, which affects the effective population size (N_e), a key concept that will be further discussed in Chapter VI (Results and Discussion). There are no contracepted or sterilised individuals, and therefore all are presumed capable of breeding.

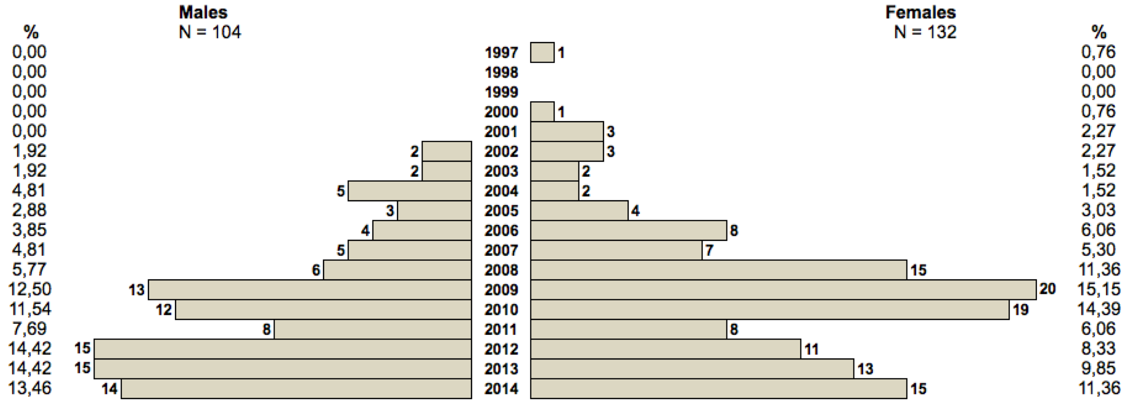
For the status of any captive breeding stock to be considered satisfactory, it clearly needs a large enough population, breeding at a sufficient rate to sustain itself (Bertram, 1986). The importance of maintaining large effective breeding populations has been recognised as necessary to avoid the undesirable effects of inbreeding and genetic drift (Flesness, 1977; Chesser, 1980; Falconer & Mackay, 1996).

7.3. Sex and age distribution

Information on age distribution is defined as the number of individuals in each age class at a given time (Foose, 1980), and is presented in Figure 9, for the global living population. As previously remarked, animals are placed according to their year of birth and there is information on number and percentage in each age class.

It may suggest about growth and gender-specific life expectancy (Krebs, 1985). Populations with increasing census typically have a large predominance of young individuals (Krebs, 1985) and, in demographically stable populations, each age class has an equal or greater number of individuals than the immediately older age class (Foose, 1980), hence their pyramidal-shape.

Figure 9 – Sex and age distribution of living population.



Although these findings are not accurately verified for the captive population studied, an approximate tendency is observed. In males, the three younger age classes have 42.3% of the individuals, but age classes 0-1, 3-4, 4-5 and 11-12 do not meet the criterion of having more animals than the older age class, whereas in females the two most abundant age classes are 4-5 and 5-6, and there is an increase of 118,8% from age class 3-4 to 4-5.

Regarding gender-specific life expectancy, not only are there five females older than the oldest male, but also the oldest female is five years older, suggesting a greater longevity in females. Nevertheless, calculations of life table parameters are required to confirm this. Finally, the existence of past population bottlenecks can also be subject of analysis through historical sex and age pyramids, since a significant reduction in birth rate or an increase in first-year mortality have an impact on its shape, which will persist and move upwards as years go by.

The mathematical concept of stable age distribution (SAD) refers to a population in which the proportion of individuals in each age class is pyramidal and remains constant, according to demographic parameters discussed later (Foose, 1980).

When age distribution is close to a SAD, demographic fluctuations are small and thus have less influence on GD, and the rates of change predicted by demographic parameters, such as net reproductive rate (R_0) and annual growth rate (λ), are expected to be more regular (Foose, 1980; Seal, 1986). Past extinctions of species within institutions seem related to distortion of age structure, which should therefore be avoided as a management option (Foose, 1980; Ballou & Foose, 1996).

The proportion of individuals in each age class in a hypothetical SAD (Cx) can be calculated by using $Cx = \frac{\lambda - xlx}{\sum \lambda - xlx}$, where $_x lx$ is the age-specific survivorship of the age class in question (Foose, 1980).

These numbers should serve as guidance for comparison with those in the actual distribution, as persisting deviations will cause the short-term population growth rate to vary from the deterministic life table expected growth rate (Foose, 1980; Traylor-Holzer, 2011).

One example of cause for distortion of age distribution is the sudden reproduction control when maximum capacity is reached, with the resulting ageing of the population and diminished breeding capacity when reproduction is again desired (Foose, 1980).

Particularly in species with long life-spans, more specific pyramids can be built, such as for proven breeders or non-breeders considering various reproductive ages, in order to assess whether mature individuals are equally contributing to the species' reproductive success, which may be a major factor for differences between total census and effective population size (N and N_e, respectively) (Seal, 1986).

An analysis restricted to institutions keeping 20 or more individuals was performed (Annex 1) and average male and female ages were calculated (Table 4).

Table 4 – Average age (years) and corresponding standard error, in institutions with more than 20 individuals.

Institution	Ave. age males (y)	Ave. age females (y)
Global population	4.35 ± 0.31	5.16 ± 0.30
FELH	4.68 ± 0.52	5.73 ± 0.47
Réserve Spéciale de Faune de Guembeul	2.92 ± 0.89	3.83 ± 0.89
Parc Zoologic Barcelona	4.12 ± 0.21	5.24 ± 0.60
Zoobotanico Jerez de la Frontera	2.85 ± 0.56	4.54 ± 1.55

Average age in females is higher in both global population and individual subpopulations, consonantly with the higher survivorship in females, as shown later.

8. Global captive population demography

8.1. Births

Only captive births were considered, as there is no data available on the age of imported founding individuals and hypothetical birth dates are only approximations, not used when sample size is sufficiently large. A total of 1567 captive births were registered (Table 5).

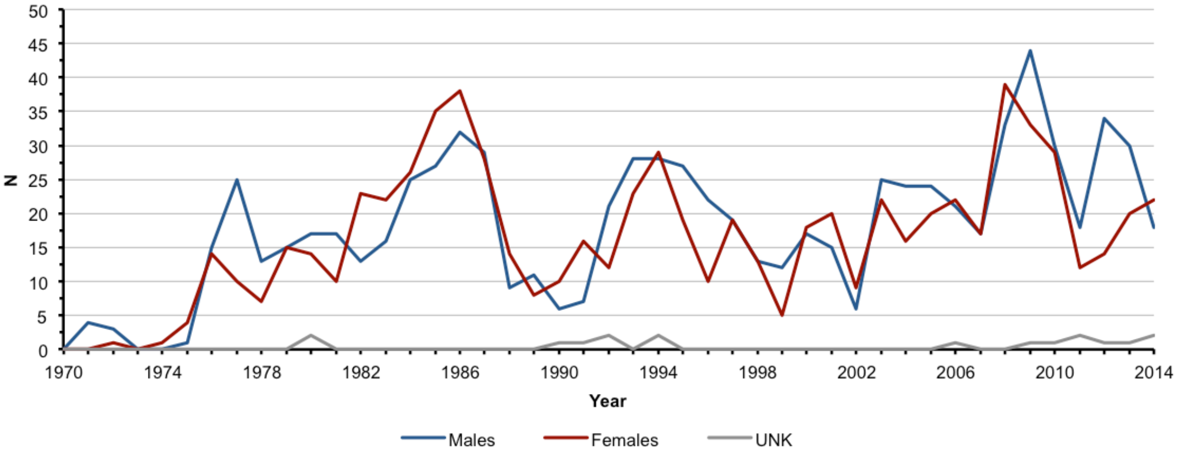
Table 5 – Total number (N) of male, female and UNK gender births since the establishment of the CBP, by institution.

	Males	**Females**	**UNK**	**Total**	
	N	N	N	N	%
FELH	515	443	7	965	61.6
Madrid	66	76	0	142	9.1
Barcelona	59	71	6	136	8.7
Jerez	49	32	1	82	5.2
RSFG	34	34	2	70	4.5
Marwell	28	21	0	49	3.1
Benisa*	14	12	0	26	1.7
Hannover*	13	12	0	25	1.6
Nueva Lla.*	11	11	0	22	1.4
Elche*	4	13	0	17	1.1
Santillana*	7	6	0	13	0.8
Stuttgart	5	6	0	11	0.7
Zamoscz	4	2	0	6	0.4
OASYS*	2	0	1	3	0.2

Zoo-Aquarium Madrid and *Parc Zoologic Barcelona* stand out as the second and third most contributing institutions when considering number of captive births, because they have been in the CBP the longest (after FELH) and produced offspring throughout the period analysed, with exception of a total of six and three years, respectively. Institutions marked with "*" are no longer members of the CBP, meaning that their contribution will inevitably decrease. Institutions not represented in Table 5 only received males and no reproduction occurred, therefore no births have been recorded.

The number of births, by gender and year of birth, is shown in Graph 2.

Graph 2 – Birth records, by gender and year of birth.



An average of 34.8 ± 0.49 births/year was recorded, and 2009 was the year with the highest number of births, with 78 registrations (44.33.1). As previously noted, since 2002 the number of births was annually programmed to maintain a population of about 100 individuals in FELH (Abáigar, 2002).

The interpretation of birth records by year is indissociable from that of the species carrying capacity (Seal, 1986), which varies depending on the number of collaborating institutions and their correspondent housing capacity. A proposed analysis of the birth distribution in six time periods is presented, considering FELH as reference for the global population and bearing in mind a previous interpretation by Abáigar (2002):

- 1970 to 1986: no reproductive restrictions implemented, resulting in a progressively increasing number of annual births and reaching the maximum carrying capacity in 1986/87;
- 1987 to 1991: drastic reduction in the number of births achieved through reproductive management, mainly isolation of males;
- 1992 to 1995: increase of birth rate to enhance the representation of founder lines from Fuerteventura and Nueva Llanes;
- 1996 to 2004: consecutive and proportional fluctuations in the number of births, with a consequent stabilisation of population size seen in the census graph;
- 2005 to 2009: great increase in birth rate, as four new institutions joined the CBP and the strategy for the *in situ* reintroduction programme was designed;
- 2010 to 2014: breeding recommendations that are overall expected to result in a number of births balancing the likely number of deaths.

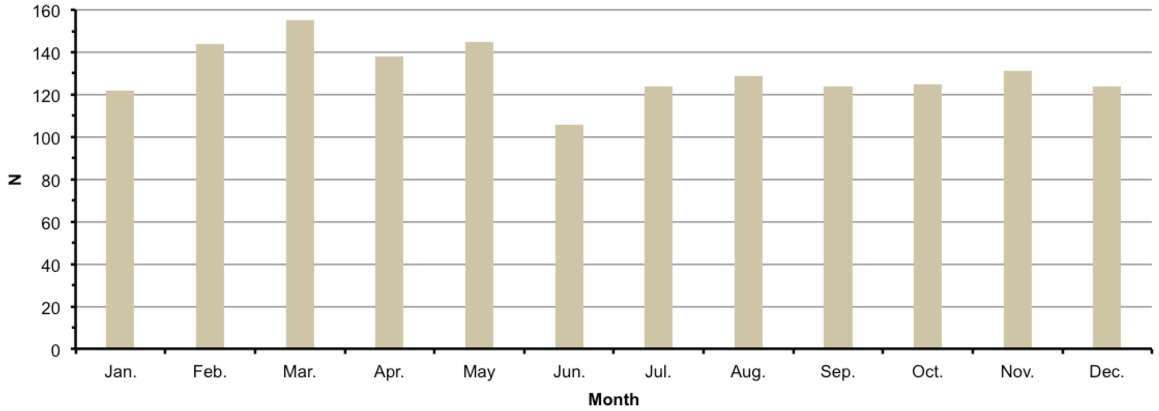
A table with age at sexual maturity, gestation period and average age at first birth of the three species of gazelles, according to previous studies, was compiled by Cassinello (2005).

The gestation period of *G.d.neglecta*, assessed in previous works, is, on average, five months and 20 days (Alados, 1984; Cassinello, 2005). This duration was not investigated in our work due to absence of information on date of mating. In our analysis, all births were single, as had also been previously described (Alados, 1984).

The only gazelle species in FELH which gives birth to two calves is the Cuvier's gazelle (38,7% of births) (Escós, 1992). A direct relationship between sexual maturity and allometry has been reported (Cassinello, 2005), where the smaller *G.d.neglecta* reaches sexual maturity earlier, in agreement with observations in other mammals (Peters, 1983).

The distribution of the total number of births by month is shown in Graph 3, which indicates a uniform distribution throughout the year.

Graph 3 – Total birth distribution since the beginning of the CBP, by month.



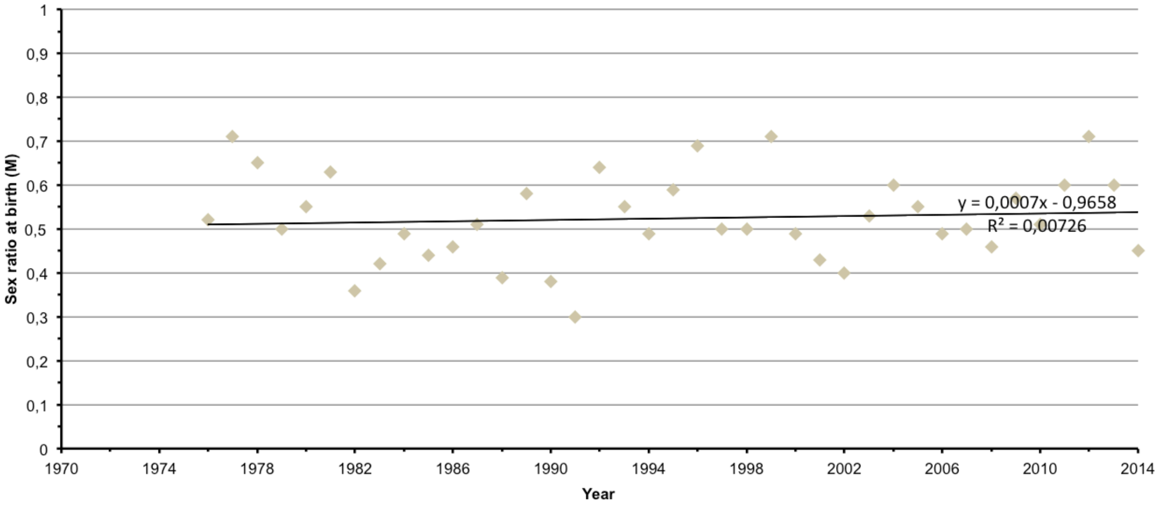
Accordingly to what had previously been concluded by Alados (1984), no statistically significant seasonal birth variation was observed (P>0.05; Chi-square = 14.25; df = 11), strongly supporting the idea that, when kept in captivity, the species is fertile throughout the entire year.

As opposed to what happens in free ranging populations, feed availability is not a limiting factor in captivity and it has been shown that, in the presence of the male, females give birth twice a year, with an average of 186,4 days between births, due to their fertile heat 6 to 36 days post-partum (Loggers, 1991; Alados, 1984).

In their natural habitat and in semi-wild conditions, females give birth only once a year, most likely during the rainy season (Abáigar et al., 2016). In contrast, there are other free ranging ungulates species, including other species of gazelles, whose reproductive cycle is described as non-seasonal (see Alados, 1984).

Sex ratio at birth, in relation to males, by year of birth is shown in Graph 4, indicating that the birth of males is close to 0,5, as expected and accordingly to previous analysis (Abáigar, 2002; Cassinello, 2005).

Graph 4 – Sex ratio at birth in relation to males.



8.2. Deaths

The total number of animals dead by institution throughout the period analysed is shown in Table 6. Again, hypothetical individuals were excluded, as well as lost to follow-up, leaving a total of 1368 records to be included.

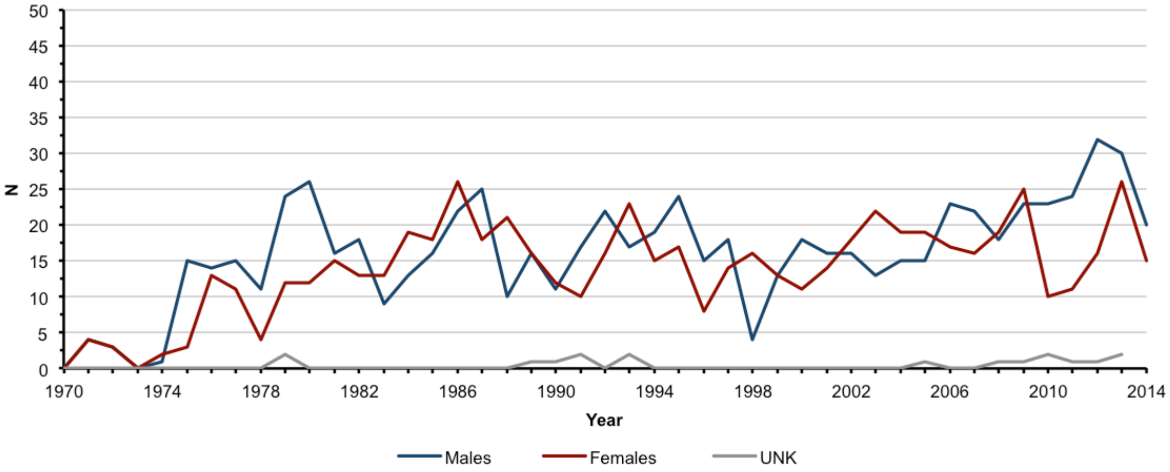
Table 6 – Total number (N) of male, female and UNK gender deaths since the establishment of the CBP, by institution.

	Males	Females	UNK	Total	
	N	N	N	N	%
FELH	471	364	7	842	61.5
Madrid	61	71	0	132	9.6
Barcelona	51	59	6	116	8.5
Jerez	37	28	1	66	4.8
RSFG	19	21	2	42	3.1
Marwell	11	15	0	26	1.9
Nueva Lla.*	10	13	0	23	1.7
Elche*	5	17	0	22	1.6
Santillana	7	13	0	20	1.5
OASYS*	8	10	1	19	1.4
Benisa*	9	3	0	12	0.9
Hannover*	4	5	0	9	0.7
Doué	8	0	0	8	0.6
UECK*	7	0	0	7	0.5
Katané	5	2	0	7	0.5
Stuttgart	5	1	0	6	0.4
Zamoscz	2	2	0	4	0.3
RNSELWO*	3	0	0	3	0.2
Chessington	2	0	0	2	0.1
Icona/Almeria*	1	1	0	2	0.1

As in Table 5, institutions marked with "*" are no longer members of the CBP, meaning their contribution percentage will inevitably decrease. As expected, the six institutions with the most deaths are the same with the most births, in the same order.

The number of dead animals by gender and year for the period analysed is presented in Graph 5.

Graph 5 – Death records, by gender and year of death.

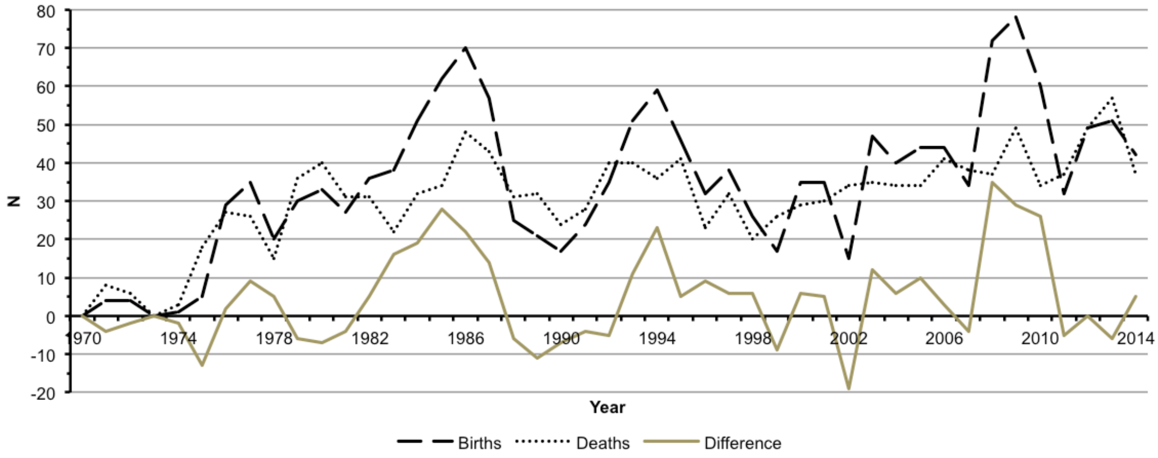


Contrary to births, deaths are not annually planned, but attempting a prediction is relevant for demographic management. An average of 30.4 ± 0.34 deaths/year was recorded, and 2013 was the year with the highest number of deaths, with 57 registrations (30.26.1).

8.3. Difference between births & deaths

The total number of births and deaths (Graph 6) show an overall similar variation pattern. A positive and negative *difference* line corresponds to periods of increasing and decreasing population census, respectively. There are globally more years of positive difference, as would correspond to a growing population, which can be confirmed in the census graph (Graph 8).

Graph 6 – Total number of births, deaths and corresponding difference, by year.



8.4. Translocations and metapopulation management

A translocation has been defined as an intentional release of animals to the wild, whichever the motivation (Griffith, Scott, Carpenter & Reed, 1989). In this work, transfers between captive institutions are also called *translocations*. The need to move animals from one institution to another for breeding purposes, the joining of a new institution and the context of the *in situ* reintroduction programme were the most common reasons for translocations. The first would be genetically equivalent to the dispersal occurring in natural populations (Chesser et al., 1980), although artificially controlled, and aims at controlling inbreeding.

Avoiding the persistence of isolated captive populations is the great motor for translocations (Cassinello, 2005), and there was an historical tendency to use regular translocations as a way of virtually suppressing spatial distance and create a metapopulation, managed as a whole (Margan et al., 1998). This management option was questioned and the outcome proposal was that a reduced rate of translocations, to the point that none occurred for several generations, would not only minimise costs and reduce risk of disease spreading, but also and most importantly have genetic advantages (Chesser et al., 1980; Margan et al., 1998; Woodworth, Montgomery, Briscoe & Frankham, 2002).

Although small populations experience more genetic drift (Frankham, 2010), this is a random phenomenon and subpopulations retain genetic composition differently, with a resulting metapopulation with higher genetic diversity if compared to a single large population with the same N (Leus et al., 2011). In fact, population fragmentation is presented as one of the strategies to reduce the dependency of a species to the conditions of captivity, which tends to happen more quickly in larger populations (Margan et al., 1998; Leus et al., 2011). Besides, a relatively high number of subpopulations is more likely to assure maintenance of some of the rarer alleles within some of the subdivisions (Chesser et al., 1980).

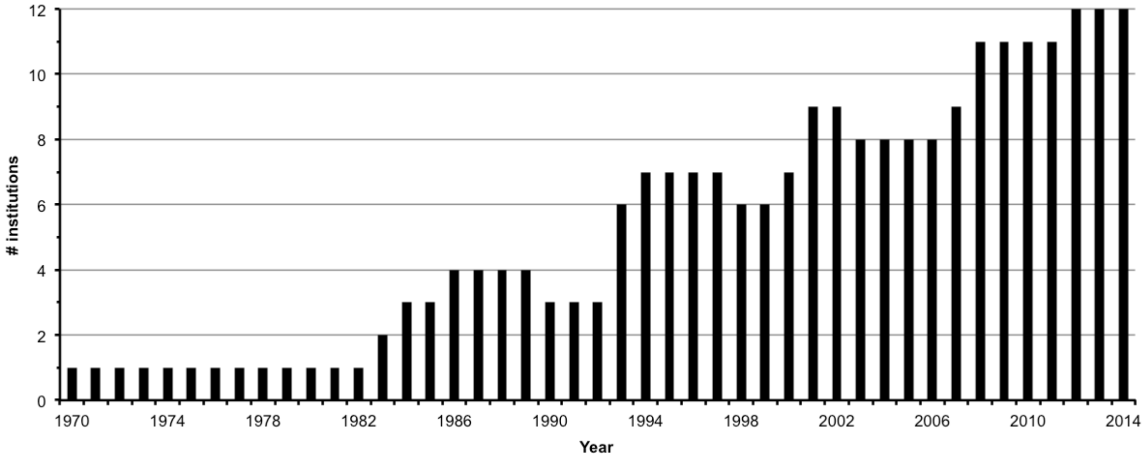
A metapopulation approach is effective in maintaining GD, provided no subpopulation goes extinct and the rate of translocations is not too frequent (Leus et al., 2011). The purpose of the creation of the Global Species Management Plan (GSMP) by the World Association of Zoos and Aquariums (WAZA) is the standardisation and reorganisation of regional programmes into global programmes, in an attempt to increase chances of meeting long-term genetic objectives (Leus et al., 2011).

Regarding the joining of new institutions, they often begin by transfer of males only, and females afterwards if breeding is attempted after a period of habituation. Abáigar (2002) presents the rate of translocation, or difference between entries and exits, for FELH, calculated in two different ways: entries including imports and births & exits including exports and deaths vs. entries including imports & exits including exports. In both cases, rate of translocation was calculated by using $Rate\ of\ translocation = \frac{n\ entries - n\ exits}{total\ N} \text{x}\ 100$ (see Abáigar, 2002).

A table with all translocations between institutions since the beginning of the CBP is presented in Annex 2. In total, 360 translocations were registered. Of the 24 different institutions, ten only received animals and two (*Fuerteventura* and Western Sahara) only provided animals. *Réserve Spéciale de Faune de Guembeul* was included only as receiver simply because translocations to *Katané* enclosure were not considered in the table.

The variation in the number of institutions since the beginning of the CBP was also plotted (Graph 7), excluding four institutions receiving animals from FELH (*Aviación Española*, *Zoo Extremadura Almendralejo*, *Icona Almería* and *Sparks Tenerife*) that were actually never part of the programme, since the total of 11 individuals (7.4) donated to them were not followed post-translocation.

Graph 7 – Number of member institutions since the beginning of the CBP.



The number of participating institutions has varied since the beginning of the CBP, and there are presently five more if compared to 2000. This shows a recent effort in increasing the housing capacity for the population while avoiding the proliferation of small reproductive nuclei (Abáigar, 2002) and allowing a higher N, both affecting positively some of the parameters discussed later. The number of institutions is highly correlated with the concept of carrying capacity and, interestingly, the higher the growth rate of a population, the more each change in the available carrying capacity affects the population's viability (Li & Jiang, 2002).

9. Demographic and Genetic analysis

Demographic and genetic management have been studied and put to practice in species kept in zoological collections mostly since the second half of the 20th century (Foose, 1977; Flesness, 2003; Frankham, 2010). The ultimate objective of demographic management is stability, and inherent resilience to demographic decline and potential to recover if facing unexpected high mortality (Foose, 1980). Maintenance of genetic variability would be the correspondent major goal of genetic management (Foose, 1980).

Characterising the life-history parameters of each taxa is essential because significant variation between age classes may occur (Leus et al., 2011) and it represents a way of establishing baseline approximations of what could happen in free-ranging populations (Foose, 1980).

Adaptation to captivity and metapopulation management should be addressed in threatened species management and are indissociable from thorough analysis of such parameters (Leus et al., 2011).

9.1. Demography

Demographic management is relevant in assuring a SAD and the necessary control of captive population size (Foose, 1980). Interpretation of demographic performances may suggest husbandry improvements in case populations are not corresponding to expectations, by pointing age-specific probable causes (Foose, 1980).

The longer the captive history of the population, the shorter the gap between expected and observed parameters, making results statistically more valid (Foose, 1980). Also, dealing with means over time absorbs some of the fluctuations observed in specific years, since it is expected that these show some variation over time, even under stable and optimum population conditions (Foose, 1980).

Foose (1980) proposes four aims of demographic management:

- establishment of a population that possesses the potential for growth and hence self-sustainment;
- expansion of the population to a predetermined carrying capacity as quickly as is consistent with genetic management;
- stabilisation of the population at the given capacity, with a sex and age composition which will achieve an agreed objective;
- production of surplus for dispersal outside zoos, especially for reintroduction into the wild.

It is reasonable to say that all the above targets were accomplished throughout the different phases of the CBP, suggesting that correct management options have been adopted, with the outcome of a successfully self-sustaining population already in condition of supplying reintroductions without jeopardizing the population as a whole.

Some demographic parameters greatly influence tendencies of genetic variability, meaning that these are therefore indissociable and must not be regarded separately (Gutiérrez & Goyache, 2005).

9.1.1. Demography overview

Table 7 summarises the key demographic statistics for the population studied. The species is characterised by an early sexual maturity, producing their first offspring before completing one year of age. On the other hand, males and females are able to remain in the captive herd for as long as 17 and 20 years, respectively, even though their longevity at birth is only 4,5 and 7 years, as discussed later. This is largely due to the very high offspring mortality up to 30 days of age, 23% in males and 20% in females.

Table 7 – Demography overview.

Summary statistics	Ave. males and females	Males	Females
Oldest alive (years)	-	12.4 (STD#1061)	18 (STD#891)
Oldest recorded (years)	-	16.9	20
Mean longevity (years)	3.24	2.35	4.12
Mean age of parents (years)	4.88	4.86	4.90
Earliest reproduction (months)	-	11	11
30-day mortality	-	0.23	0.20
Annual growth rate (λ)	1.058	1.054	1.062
Instantaneous rate of change (r)	0.056	0.052	0.060
Net reproductive rate (R_0)	1.283	1.266	1.300
Mean generation time (T) (years)	4.5	4.5	4.4

Annual growth rate (λ) corresponds to the proportional change in population size from one year to the next, based on life table calculations (Traylor-Holzer, 2011), and can be calculated by using $\lambda = R0^{1/generation}$, where *generation* is the mean generation time (Foose, 1980). A λ of 1.058 indicates an annual population increase of 5.8%.

The instantaneous or intrinsic rate of change (r) is positive if population is increasing and negative if population is decreasing (Traylor-Holzer, 2011) and can be calculated by using $\lambda = e^r$, where *e* is the base of natural logarithms (≈ 2,71828), or, alternatively, by using $r = ln\lambda$ (Foose, 1980).

Net reproductive rate (R_0) is the potential change in total number expected per generation, or the average total number of offspring of the same sex that an individual will produce in its lifespan (Foose, 1980; Traylor-Holzer, 2011). It can be calculated by using $R0 = \sum lx \text{ x } mx$ i.e. the sum of the product of survivorship and fecundity for each age class, in other words, the probability that an animal will survive to a given age multiplied by the average number of offspring it should produce in that age class (Foose, 1980). Again, like for λ, R_0 must be greater than 1 for increasing populations and R_0 smaller than 1 for declining populations.

In summary, λ, r and R_0 are indicators of the population's capacity for change under constant schedule of survivorships and fecundities (Foose, 1980). They are related to the point that, with a given set of survivorships and fecundities, there are three possible scenarios:

- λ & R_0 < 1 and r < 0 → population will decrease to extinction;
- λ & R_0 = 1 and r = 0 → population will remain constant (*zero population growth*);
- λ & R_0 > 1 and r > 0 → population will increase, indicating demographic viability.

Concerning the third scenario, experienced by the study population, management for reducing survivorship and/or fecundity is therefore eventually necessary, as no population can grow indefinitely (Foose, 1980). Regular rates of change predicted by λ, r and R_0 will not occur until or unless there is a SAD (Foose, 1980).

Mean age of parents corresponds to the mean age when breeders produce offspring (Gutiérrez et al., 2010), while mean generation time (T) is the average age at production of offspring that become parents (Traylor-Holzer, 2011). The latter can be calculated by using $T = \frac{lnR0}{ln\lambda}$ (Foose, 1980) and is also the average interval between reproduction in one generation to reproduction in the next (Traylor-Holzer, 2011). Expected loss of genetic variation over time in one particular population is greater with increasing time in captivity and with smaller population size, increasing the number of rarer genotypes (Mace, 1986).

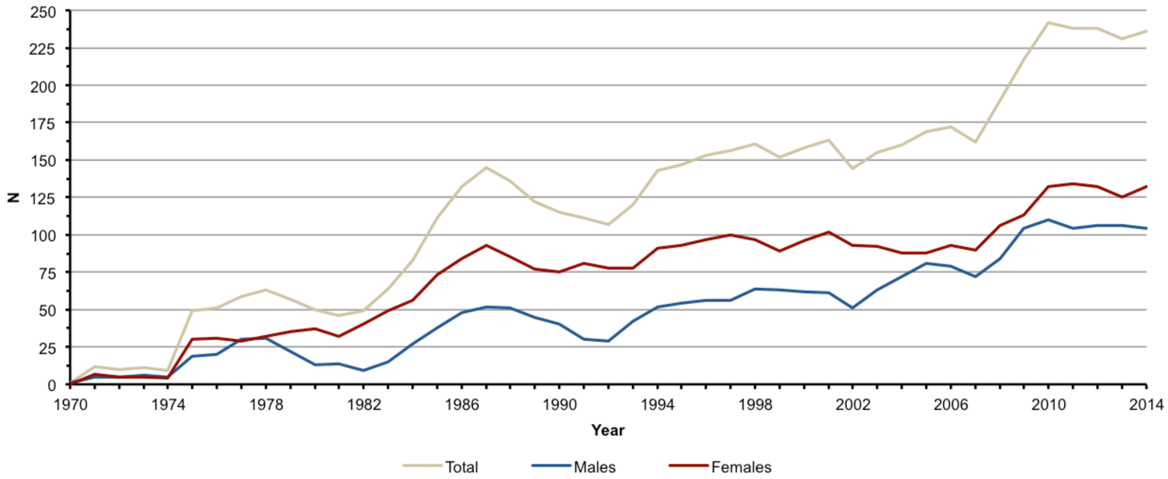
Therefore, extending generation time and minimising time in captivity are ways of delaying the loss of genetic variation (Mace, 1986, Ballou & Foose, 1996). The first can be accomplished by shifting mean age of reproduction to later in life, which may, however, turn out a treacherous strategy if mating is at random (Ballou & Foose, 1996), as the risk of matings among closely related individuals increase.

Before the carrying capacity is fully reached, survivorships and reproduction must be adjusted to a *zero population growth* scenario, where λ = 1, $R_0 = 1$ and r = 0, which ultimately corresponds to a stable population (Foose, 1980). These values characterise *stationary* populations, often seen in natural populations, where on average births are sufficient so that each animal produces a replacement for itself in the next generation, achieving equal family sizes (Foose, 1980). Restriction of reproduction and removal of animals are ways of reducing fertilities and survivorships, respectively, and the combination of both may also be used (Foose, 1980). Restriction of reproduction has drawbacks and removal of animals of certain age classes is probably a safer management option (Foose, 1980).

9.1.2. Population census

The population census (Graph 8) represents the total number of individuals at the end of each year (31st December). Overall, there is an increasing population size over time. A maximum population size of 242 (110.132) was registered in 2010. Yearly variations in population size (N) are determined by balance between births and deaths, described earlier, and the same considerations regarding time frames can be made when interpreting annual census.

Graph 8 – Global population census.

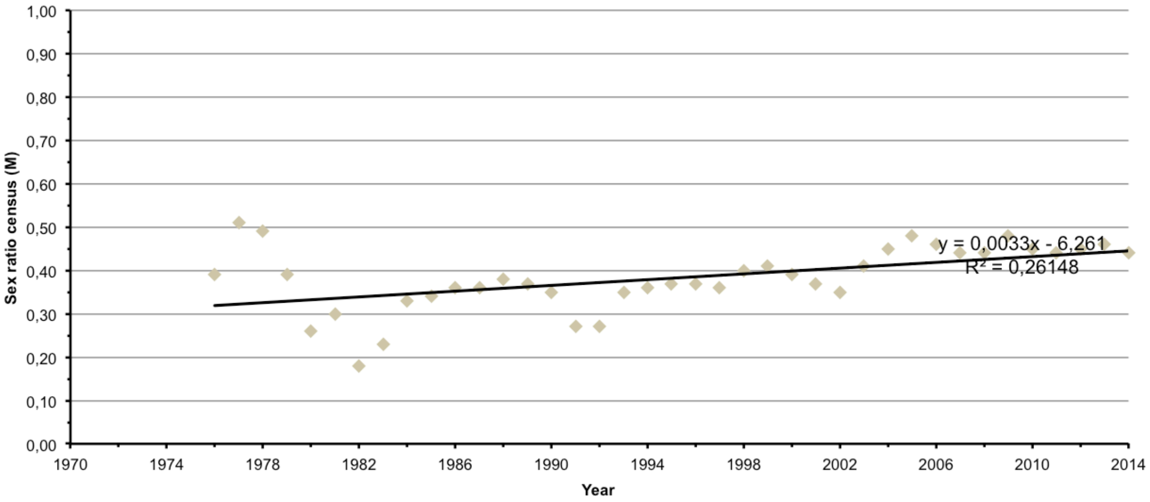


The effective management of genetic variability, discussed later, can be readily attained if efforts for quickly increasing N since the very beginning of the CBP are acknowledged (Foose, 1980; Chesser et al., 1980; Ballou & Ralls, 1982). This did not happen during the first five years of the programme, and even after the imports in 1975 there was difficulty in quickly securing a higher N. Only after 1981 a growing tendency was observed, interestingly not long before the first institutions besides FELH joined the CBP.

From 1978 onwards, the total number of living males was always less than the number of females, which explains the female biased census sex ratio (<0.5) (Graph 9), different from the sex ratio at birth previously shown (Graph 4). The reason for this is that age-specific mortality rate is higher in males, with exception of one age class.

As previously mentioned, determining the species carrying capacity is essential (Seal, 1986). This, together with establishing a programme length and allowable rates of loss of GD, will influence the minimum N that must be achieved and later maintained (Seal, 1986).

Graph 9 – Sex ratio at census in relation to males.



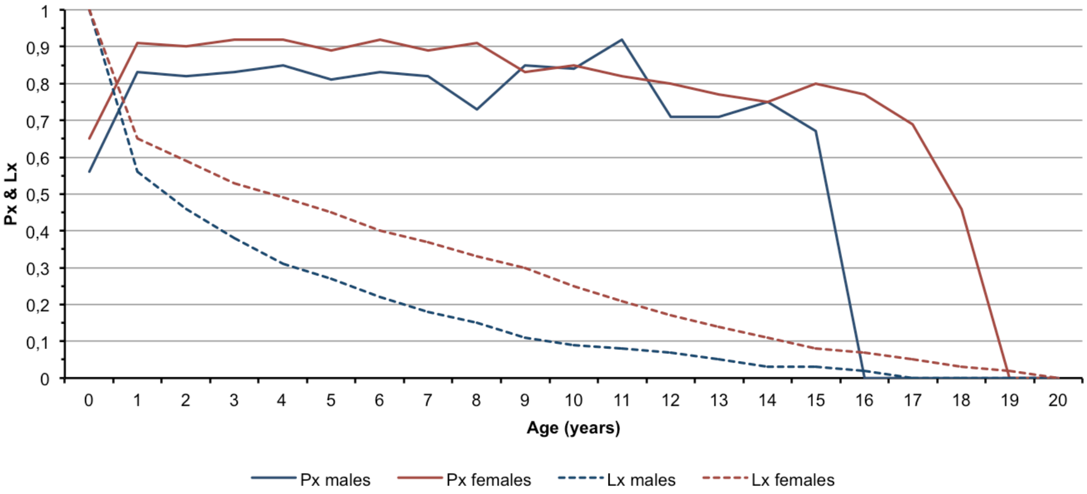
9.1.3. Life tables

All life table parameters are age and gender specific, and age classes were defined as years in PMx demography settings. For this section, only individuals with known date of birth and death were subject to analysis, such that N=1290 out of 1693, where the difference between the two figures corresponds to founding animals, *phantom* individuals, abortions and currently living individuals. Other defined settings included: continuous birth flow; UNK gender as 0.5 male; and each birth contributing to the fecundity of both parents.

9.1.3.1. Survival rate (P*x*) and Survivorship (L*x*)

These concepts are often described and expressed together (Foose, 1980). Survival rate (P*x*) corresponds to the probability that an animal in age class *x* will survive to age class *x* + 1 (Foose, 1980; Traylor-Holzer, 2011). Survivorship (L*x*), on the other hand, is a cumulative measure of the probability that an animal will survive from birth to the beginning of a specific age class *x* (Foose, 1980; Traylor-Holzer, 2011), therefore survivorship curves start in 1.
Age-specific P*x* and L*x* curves are plotted in Graph 10.

Graph 10 – Age-specific P*x* and L*x* curves, by gender.



P*x* in males is always lower than in females, with the exception of age classes 9-10 and 11-12. From age class 0-1 to 1-2, it increases from 56% to 83% and from 65% to 91% in males and females, respectively, which is related to a consistently higher first year mortality in both genders. In the following six age classes, age-specific P*x* is quite constant. A great decline is observed from age 14 in males and 16 in females, as they approach their maximum life span. These are typical P*x* and L*x* curves, seen in many other species (Foose, 1980).
A possible interpretation of the L*x* curves can be found in Table 8, where survivorship up to standard percentages is presented.

Table 8 – Age, in years, at which L*x* reaches 0.5, 0.25, 0.1, 0.05 and 0.01.

Summary statistics	Ave. males and females	Males	Females
50% live to	2.7	1.6	3.7
25% live to	7.7	5.3	10.0
10% live to	11.9	9.4	14.3
5% live to	15.0	13.0	17.0
1% live to	17.9	16.4	19.4

9.1.3.2. Mortality rate (Q*x*)

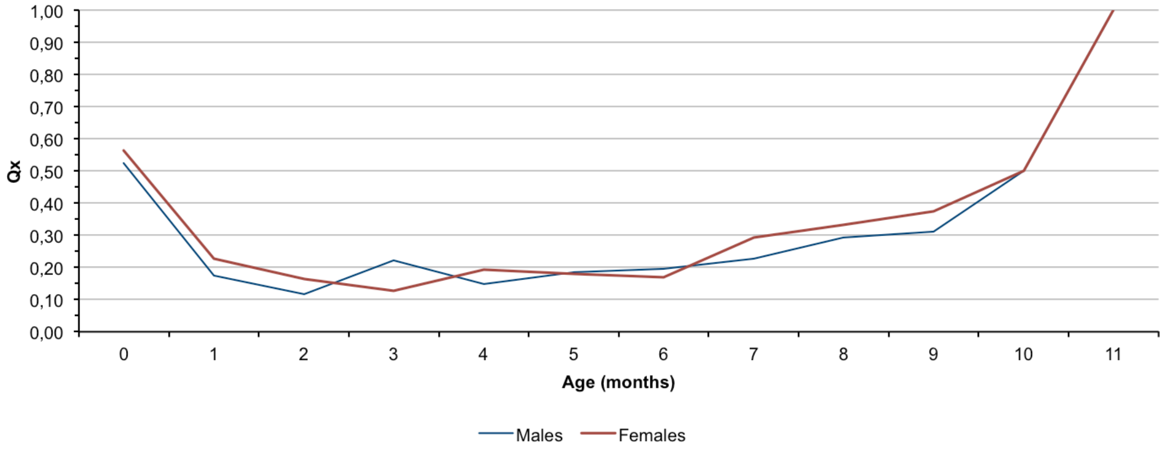
Defined as the probability of dying in age class *x* (Foose, 1980; Traylor-Holzer, 2011). Mathematically, it represents the complement to 1 of survival rate (P*x* = 1 – Q*x*) (Foose, 1980), and is calculated by using $Qx = \frac{n\ of\ deaths\ per\ age\ class}{n\ individuals\ at\ risk\ for\ Qx}$, bearing in mind that individuals at risk are accounted accordingly to whether they survived or not through the whole age class considered (Faust, Bier, Schowe & Gazlay, 2012). Age-specific mortality rates were calculated for the global population (Graph 11), ignoring whether animals had been translocated.

Graph 11 – Age-specific Q*x* curves, by gender (n=1290).

Mortality was consistently higher in males, with exception of age class 11-12. During the first year of life, M*x* is 44% in males and 35% in females, but decreases to less than half by the second year of life. These values represent, for both genders, the highest M*x* in their entire life span.

For a better understanding of first-year mortality, male and female month-specific mortality during the first year of age is also presented (Graph 12). Population size is shorter (n=620) because it only includes animals dying during the first year of life. Both graphs are complementary, such that a possible conclusion is that e.g. of the 44% of males dying in the first year of life (Graph 11), those who survive the first two months have a 12% chance of dying in month 2-3 (Graph 12).

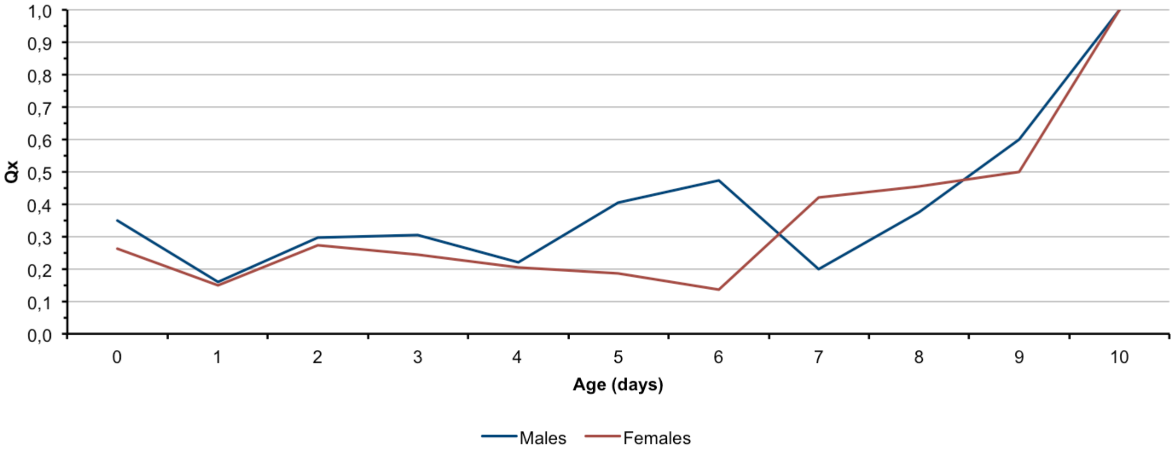
Graph 12 – Age-specific Q*x* during the first year of life, by gender (n=620).



Of the males and females who died in the first year of life, over 50% die during the first month (Graph 12). The fact that weaning generally takes place during month 3 to 4 of age (López & Abáigar, 2013) might explain the increase in 10% in Q*x* of males from age classes 2-3 to 3-4. Females also experience some degree of increase, despite only in the following age class. Age classes of 6 to 9 months are particularly sensitive when in comes to the animals' reactivity to physical capture, a phenomenon directly related to the slight continued increase in Q*x* in both males and females due to capture incidents.

The same analysis of mortality in a shorter period of time was conducted for animals dead in the first 10 days after birth – *perinatal* mortality (Graph 13). Again, only animals dead in this period are considered.

Graph 13 – Age-specific perinatal Q*x*, by gender (n=263).

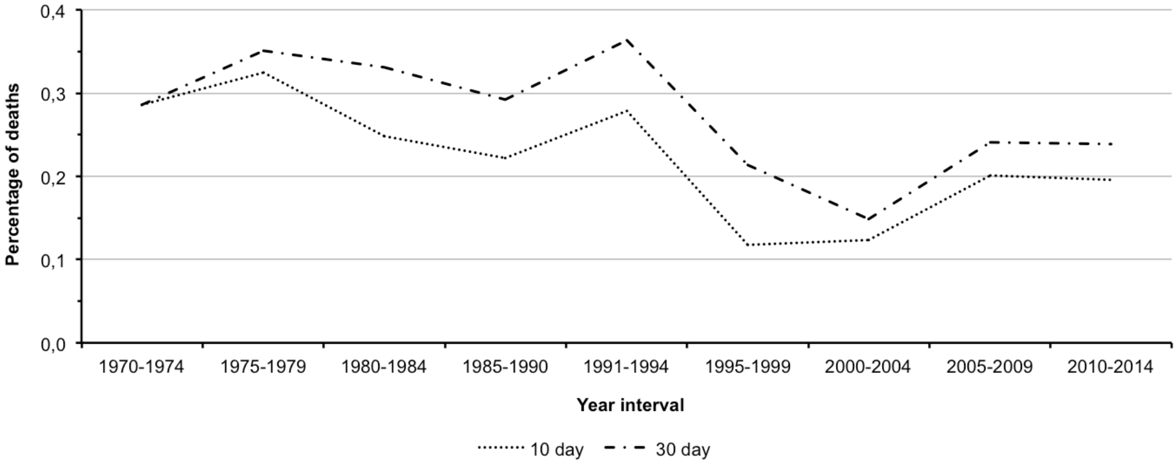


Age classes 5-6 and 6-7 days seem particularly problematic for males, with the highest levels of mortality reaching 47%. The abandon of calves has been reported in this population as one of the major causes of perinatal mortality (López & Abáigar, 2013), and it is more common with primiparous mothers or when the calf lacks vigour (López & Abáigar, 2013). In the three species of gazelles kept at FELH, birth weight is correlated with perinatal mortality (Alados & Escós, 1991), although this was not addressed in this study.

Graphs 12 and 13 were plotted using the same formula as for Graph 11, but individuals *at risk* were defined as individuals alive at beginning of age class *x*, as described by Deevey (1947). Therefore, for the first age classes, individuals *at risk* correspond to the total number of males and females dead in the whole interval considered for the graph in question (n presented for each case).

Instead of plotting age-specific Q*x*, another option is studying the percentage of deaths occurring at 10 and 30 days, with respect to the total number of deaths (Graph 14). Rather than plotting annual records, 9 different time-periods of 4 years each were defined, and average percentage of deaths calculated. Deaths at 30 days include perinatal deaths plus deaths between day 11 and 30.

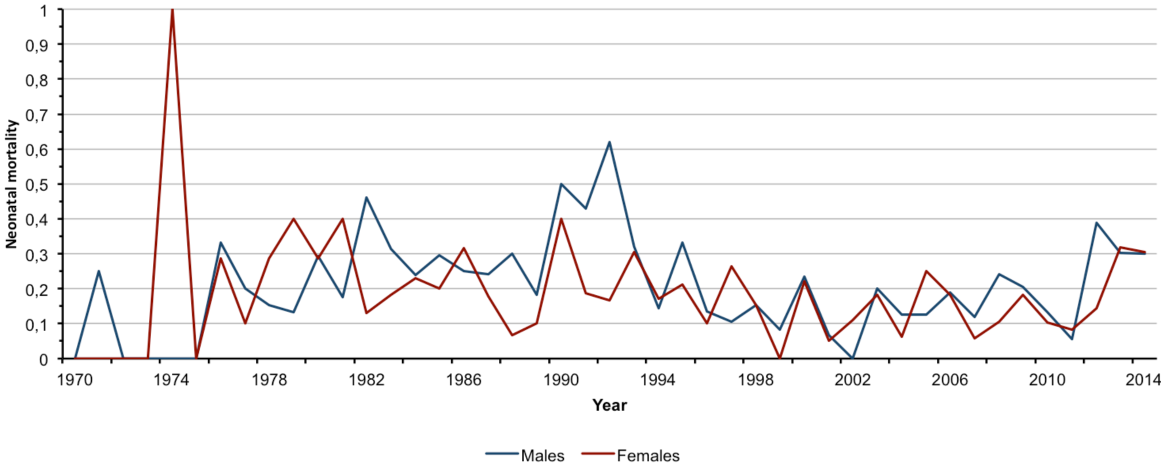
Graph 14 – Percentage of deaths occurring at 10 and 30 days after birth.



There is an indication of general improvement in husbandry practices of neonates from 1994 onwards. From previous programmes rearing ungulates in captive conditions, there are reports of management changes in the early 70s, which included intramuscular injection of long-acting penicillin, disinfection of remnant portions of the umbilical cord with iodine solution and supplementation of diet with selenium and vitamin E (Ralls, Brugger & Glick, 1980; Ballou & Ralls, 1982). In the case of our study population, selenium and vitamin E are preventively given to neonates, as well as complex B vitamins in case of debility, as appetite stimulator (López & Abáigar, 2013).

Annual 30-day mortality, calculated by using $30 - day\ mortality = \frac{n\ of\ deaths\ from\ day\ 0\ to\ 30}{n\ individuals\ at\ risk}$, is also shown (Graph 15). Even though there is an apparent cyclic tendency with years of less mortality followed by years of greater mortality, a general decrease after 1994 is again observed. Despite the current value of 30% for both genders, the balanced value since the beginning of the CBP is 23% in males and 20% females, as previously observed in Table 7.

Graph 15 – Annual 30-day mortality since the beginning of the CBP.



Age-specific Q*x* by institution in FELH, *Zoo Aquarium Madrid*, *Parc Zoologic Barcelona*, *Jerez de la Frontera* and *Guembeul* were also obtained (Annex 3), since there is a possibility of contrasting values due to distinct location and related implications, although these were not addressed in this study. Only individuals born and dead in the same institution were included, so as to exclude the variable of being subjected to dissimilar origin and destiny conditions.

It is apparent that life expectancies differ between institutions, which had been previously suggested by Abáigar (2002). Interestingly, the same was not verified for Mhorr gazelles in a previous study by Cassinello (2005). Bearing in mind great differences in sample sizes, the main causes for such discrepancy between institutions should be further investigated. A plausible hypothesis is that division in smaller subpopulations under exhibit conditions may play a relevant role in antelopes' longevity.

Management practices between institutions are under constant standardisation, and husbandry guidelines for Saharawi dorcas gazelles have been published (see López & Abáigar, 2013), hopefully reducing the environmental effects of the various institutions. Data on longevity in semi-wild conditions is now being collected (Abáigar et al., 2016) and will help clarifying this issue and, more importantly, making more approximate estimates of what the actual longevity of free-ranging animals would be, a much more relevant aspect.

Of the 1290 deaths in individuals of known age, 387 (30%) were of unknown causes, whether because neither *in vivo* diagnosis nor *post-mortem* necropsy was performed. Previous studies on causes of death in captive gazelles (Ralls et al., 1980; Cassinello, 2005; Anderson, Garder & Stedman, 2016) generally define subcategories within major categories, covering all possible causes. In the case of our study population, although cause of death is noted on the Excel database, no in-depth analysis was conducted because this information lacks validation, as not all causes described match at least one of the consensual terminologies proposed in previous studies (Ralls et al., 1980; Cassinello, 2005).

An interesting assessment was performed by veterinarian Miguel Quevedo, with deaths from 1993 to 2007 in *Zoobotanico de Jerez*. The causes of death of a total of 45 gazelles were fit into one of the following categories – trauma; gastrointestinal disorder; respiratory disorder; tumor; septicemia; perinatal death and natural death (ageing) – after proper determination of cause of death, including *post-mortem* and isolation of infectious agents, when necessary. The list of individuals and correspondent causes of death analysed has been reported by López & Abáigar (2013). Traumatisms and perinatal death were the two most common causes of death, in both males and females, even though, in males, traumatisms more than doubled perinatal deaths.

The most recent retrospective study was validated through histopathology and includes, besides Dorcas gazelles, seven other species of gazelles kept in captive conditions in the US, from 1996 to 2014 (Anderson et al., 2016). Even if no definitive conclusion could be formulated for Dorcas gazelles due to small sample size, results show consistency with those of Quevedo i.e., trauma was the most common cause of mortality in all gazelle species, ages and gender, followed by bronchopneumonia and maternal neglect (Anderson et al., 2016).

A common concern among keepers is the *juvenile* mortality – death until 6 months of age (Ralls et al., 1980) –, reported as frequent across gazelle species in captivity (Anderson et al., 2016), and its possible association with individual inbreeding (F_i). Ballou & Ralls (1982) showed that juvenile mortality was higher in inbred young ($P<0.05$), and unlikely attributed to differences between mothers (captive vs. wild caught, primiparous vs. multiparous) or environmental conditions (time of birth, population density and management). The only dam factor influencing higher mortality rate in inbred young was actually their own F_i (Ballou et Ralls, 1982).

9.1.3.3. Fecundity rate (M*x*) and Reproductive value (V*x*)

Age-specific fecundity (M*x*) is defined as the number of same-sex young produced on average by an individual in age class *x* (Traylor-Holzer, 2011). For each offspring born, each parent is attributed 0.5 of the birth. Fecundity rates, calculated by using $Mx = \frac{n\ of\ births\ attributed\ to\ parents\ in\ age\ class\ x}{n\ individuals\ at\ risk\ for\ reproduction\ in\ age\ class\ x}$ (Faust et al., 2012), provide information on age at first, last and maximum reproduction (Traylor-Holzer, 2011), as previously mentioned.

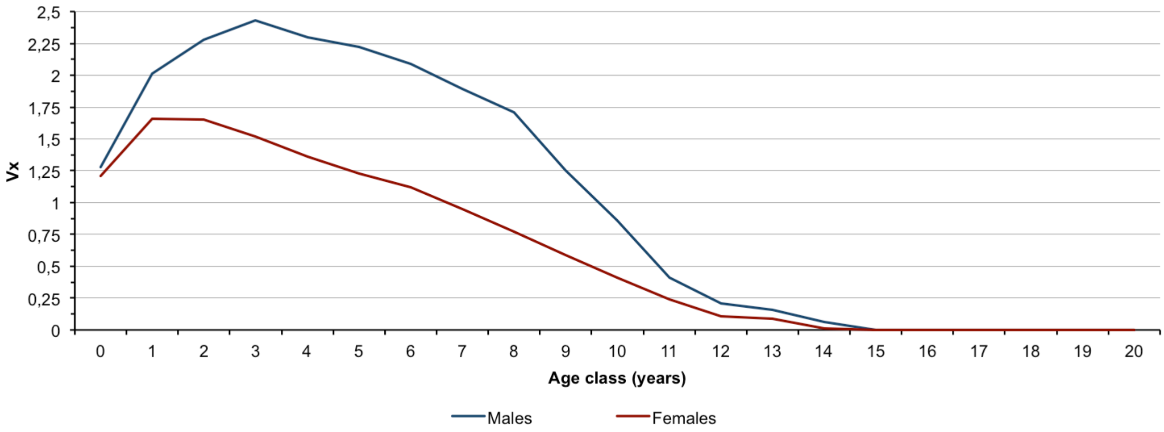
Age-specific M*x*, by gender, is presented in Graph 16.

Graph 16 – Age-specific M*x*, by gender.

Reproduction in some age classes is favored due to reproduction management, which justifies the observed variations, mostly in males, already noted by Abáigar (2002).

A related concept, reproductive value (V*x*), is the expected number of offspring produced in this year and in future years by an animal in age class *x* (Traylor-Holzer, 2011), and measures the number of offspring contributing to the next generation expected on average from an animal in age class *x* (Foose, 1980).

Graph 17 – Age-specific V*x*, by gender.



The plotted curves for V*x* (Graph 17) correspond to a typical increase from birth to a maximum in the major reproductive ages, before progressively declining (Foose, 1980). Because many new-borns do not reach sexual maturity, V*x* of those who do is expected to increase in the first year of age.

Maximising V*x* is a way of providing the population with resistance to demographic decline and potential for recovery after unexpected high mortality in certain age classes (Foose, 1980). However, because this strategy may not produce the largest N_e possible, shifting to maximisation of N_e should be attempted when the population is in its stationary phase (Foose, 1980).

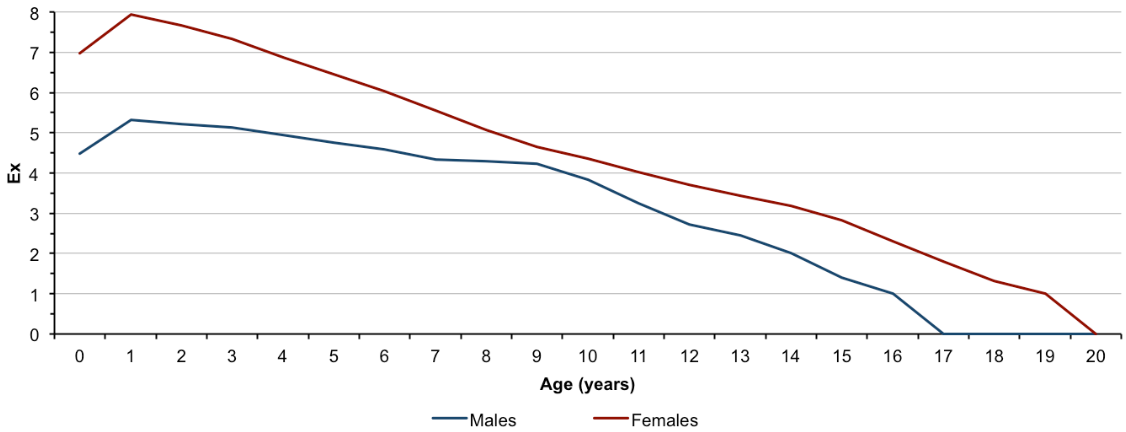
In the eventual necessity of removal of surplus animals, V*x* curves should be examined to define which age classes should be susceptible of intervention (Foose, 1980).

9.1.3.4. Life expectancy (E*x*)

Life expectancy (E*x*) is the average number of additional years an individual in age class *x* can expect to live (Traylor-Holzer, 2011), also referred to as *longevity* (Cassinello, 2005), and calculated by using $Ex = \frac{n\ individuals\ beyond\ age\ class\ x}{n\ individuals\ alive\ at\ beginning\ of\ age\ class\ x}$ (Deevey, 1947).

Age-specific E*x*, by gender, is plotted in Graph 17.

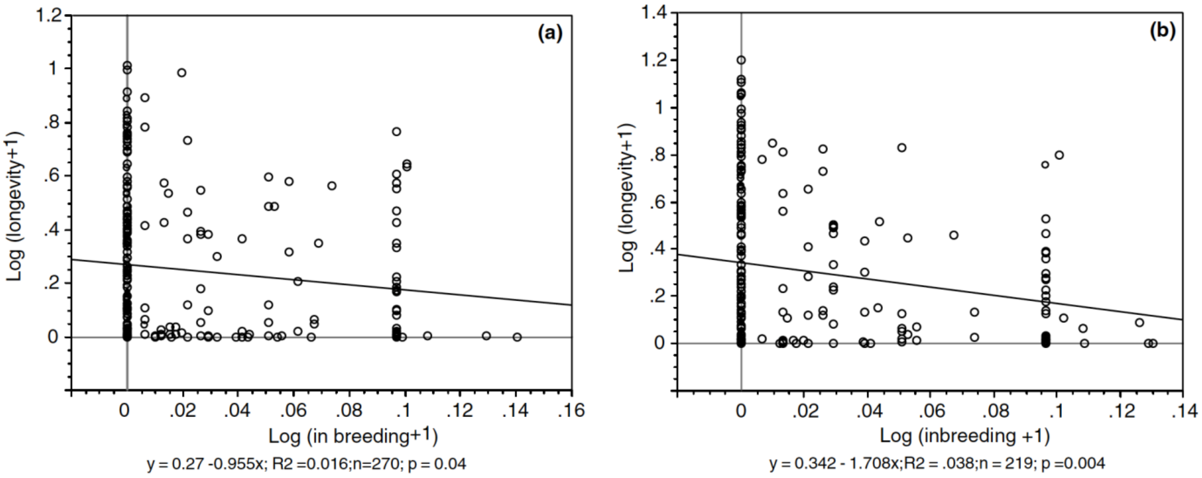
Graph 18 – Age-specific E*x*, by gender.



Although males and females may live up to 17 and 20 years in captivity, respectively, E*x* from birth is 4.5 and 7 years. Such discrepancy is explained by the previously presented age-specific L*x* and Q*x*, mostly in the first age classes, such that animals that survive through the first year have a greater E*x*. Females exhibit a higher longevity than males, which was also verified by Cassinello (2005) and Anderson et al. (2016) for the other species of gazelles, and which is expected in polygynous mammals.

Previous studies have reported a positive correlation between birth weight and longevity in females (Alados & Escós, 1991) and negative correlation between F_i and longevity in both genders, although only statistically significant in females (Cassinello, 2005) (Graph 19).

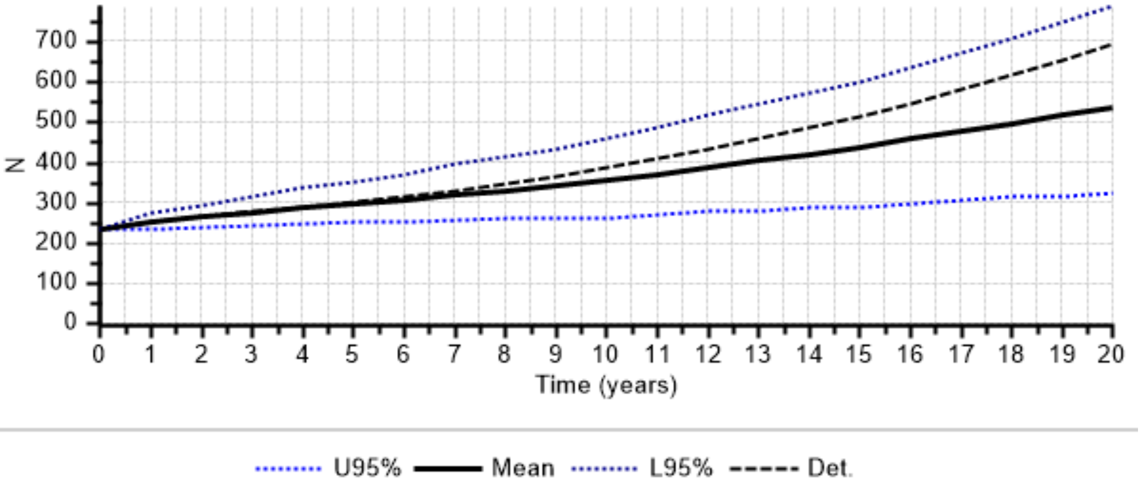
Graph 19 – Relationship between F and longevity (log-transformed) for *G.d.neglecta* males (a) and females (b). Regression equation (y), sample size (n) and probability (p) are shown below each graph. (Adapted from Cassinello, 2005).



9.1.4. Population size projections

PMx includes the possibility of running projections of population size, based on age structure and age-specific survivorships and fecundities (Leslie, 1945; Foose, 1980; Traylor-Holzer, 2011). Settings for projections were defined as follows: 500 iterations for simulation; 95% confidence interval; births treated as 0.5 male; 1.6 as the maximum number of females bred per male (ratio male/female M*x* = 1,58).

Graph 20 – Stochastic and deterministic projections for 20-year time frame.



The resulting stochastic projections (Graph 20, *Mean*) have a typical graphical representation of captive populations with potential to increase rapidly and beyond their carrying capacity (Foose, 1980). There is therefore need to maintain contained growth, whether by adjusting fecundities or by selectively culling individuals according to the age structure. The first is the management option of first choice in our study population.

A deterministic projection, based on average achieved survivorship and fecundity rates over time across individuals (Traylor-Holzer, 2011), is also presented (Graph 20, *Det.*). Because it does not incorporate individual variations, stochastic projections tend to be more reliable as years go by, especially in small populations where effects of stochasticity play a more important role.

A summary of the stochastic projections is presented in Table 9 and gender specific deterministic N in 5, 10 and 20 years in Table 10.

Table 9 – Stochastic projections summary.

Projections summary
P[extinction in 20 years] = 0
P[decline next year] = 0.04
P[increase next year] = 0.95
Overall stochastic λ = 1.016<>1.041<>1.062
Stochastic λ next year = 0.987<>1.068<>1.157

Table 10 – Deterministic projections of N in 5, 10 and 20 years.

	Total	Males	Females
N 5 years	303.1	123.9	179.2
N 10 years	384.9	153.4	231.5
N 20 years	691.2	274.3	416.9

9.2. Genetics

Although in a different context, the genetics of animal domestication are well understood (Mace, 1986). From a conservation perspective, continuous reproduction alongside with maintenance of approximate natural levels of genetic variability are the main genetic goals of captive breeding of threatened species (Chesser et al., 1980; Seal, 1986), notably because future reintroductions into the wild are desirable (Chesser et al., 1980; Mace, 1986; Frankham, 2010). Ballou & Foose (1996) propose that long-term conservation of such species be achieved through maintenance of viable populations and preservation of gene diversity (GD).

The minimisation of generations in captivity, or increase in T, and population fragmentation are management options to minimise the increase in F and maintain genetic adaptation to captivity (Margan et al., 1998; Frankham, 2010; Leus et al. 2011).

Increasing homozygosity due to drift and F in small, closed populations should be avoided (Ballou & Ralls, 1982) otherwise it is likely that they remain dependent on intensive management (Chesser, 1980). Mutation alone is ineffective in restoring genetic variability, because of its low frequency (Chesser, 1980). Selection of breeding individuals according to their genetic variability and kinship reduces the presence individuals homozygous for deleterious effects (Foose, 1980; Foose & Ballou, 1988).

In the specific case of Saharawi dorcas gazelle, the following four strategies are outlined as having had much influence in the resulting current genetic parameters (Abáigar, 2002): pairing favouring lower F_i of resulting offspring; incorporation of eight new founders in the programme; increasing of effective population size (N_e) and balancing founders' representation.

It is consensual that efficient genetic management can increase the number of taxa to be propagated for conservation purposes (Seal, 1986). Furthermore, genetic parameters have significant influence on the individuals' ability to cope with environmental variation and therefore on extinction risk (Mace, 1986; Frankham, 2010).

9.2.1. Genetics overview

An overview of the genetic parameters for the global population is presented in Table 11, and each is presented subsequently.

Table 11 – Genetics overview, with reference to the living population.

Parameter	Current values
Founders	24
Living animals	236
- percent ancestry known	100%
- percent ancestry certain	100%
GD (based on kinship matrix)	0.9134
FGE (based on kinship matrix)	5.78
Mean inbreeding	0.0631
Mean kinship	0.0866
Mean N_e	48.71
Current N_e	80.49
N_e/N	0.3411

9.2.2. Founders

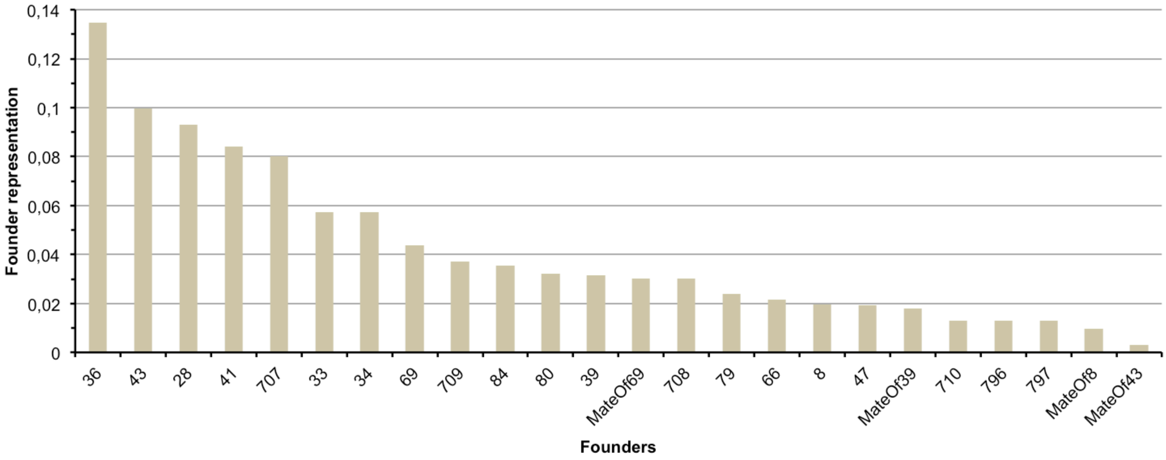
The software PMx describes the genetic contribution of each founder in five variables (Traylor-Holzer, 2011) – representation; contribution; allele retention; potential retention and number of descendants in the living population –, based on the autossomal Mendelian inheritance premise (Ballou & Foose, 1996). Annex 4 shows each of these values for all founders.

There are 24 founders in the current population, the same as identified by Abáigar (2002) since no additional founders have been introduced in the population and no loss of existing founders' contribution has occurred meanwhile. Founders reported as *mate of STD#* are males who bred during the period when there was no father attributed to each birth, which are reported as UNK in the Excel database, as previously mentioned. Of the 24 founders, there are ten who have representation in all 236 living individuals.

The general recommendation regarding management of founder contributions is that, in case there are living founders in the population, they should be given preference in breeding over non-founders with similar or larger mean kinships (Traylor-Holzer, 2011).

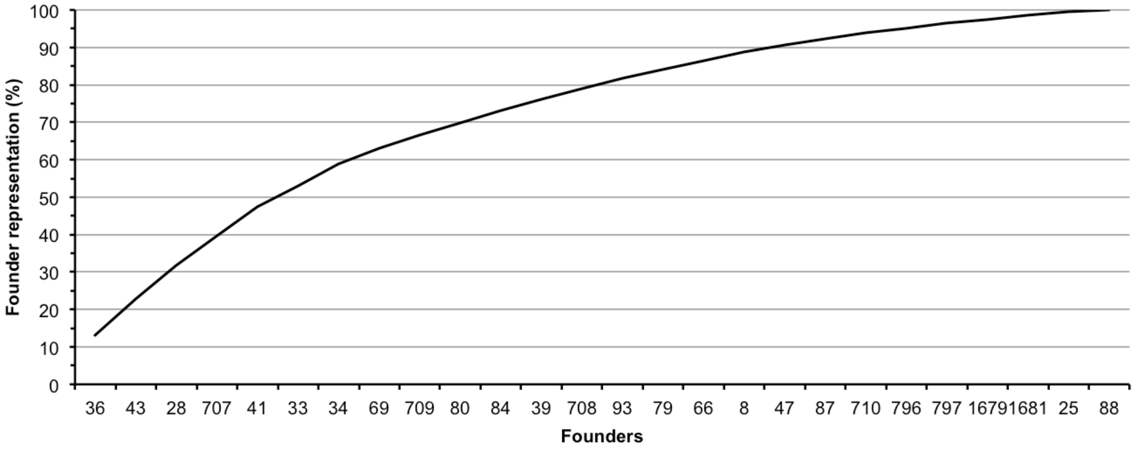
Graph 21 plots the representation of each founder in the current population, in other words, the proportion of genes in the current population that derive from each founder (Traylor-Holzer, 2011).

Graph 21 – Founder representation in the living population.



The ENDOG software was used to plot founder representation in an alternative way (Graph 22), but based on somewhat different assumptions. While PMx computes contributions to the current living population, ENDOG assumes a reference population, which in this case was defined as the group of animals born in 2014 (n=45).

Graph 22 – Cumulative founder representation in reference population born in 2014 (n=45).



This approach indicates the existence of 26 founders, of which 5 contribute with nearly 50% of the gene pool of the reference population. Values of such magnitude have been published for other species (Seal, 1986), together with the underlying hypothesis that much of the original GD is either lost or poorly represented in such cases (Mace, 1986; Seal, 1986). Founders 25, 87, 88, 93, 1679 and 1681 are considered *phantom* in ENDOG software because their ancestry could not be traced back to the original founder. Instead of creating individuals *mate of STD#*, ENDOG classifies as founders the offspring of the mating in question, so that a correspondence between both interpretations can be made by conferring the studbook records. Founders 93, 87, 25 and 88 correspond to founders *mate of 69*, *39, 8* and *43* respectively, in PMx. The other two founders, 1679 and 1681, have no correspondence in PMx.

In both graphs, it is clear that representation is not equally distributed among founders. Balancing this representation is one of the criteria when it comes to making breeding recommendations (Mace, 1986), and the main reason presented for such disparity in the study population is that some founders died leaving few descendents (Abáigar, 2002).

Founder contributions in most captive populations are often biased due to breeding of only a small proportion of the founding individuals in the early years (Ballou & Foose, 1996).

Pedigree bottlenecks occur when the genetic contribution of a founder passes through only few individuals (Ballou & Foose, 1996). Individuals carrying genes from overrepresented founders are not as genetically valuable as those carrying genes from underrepresented founders (Ballou & Foose, 1996).

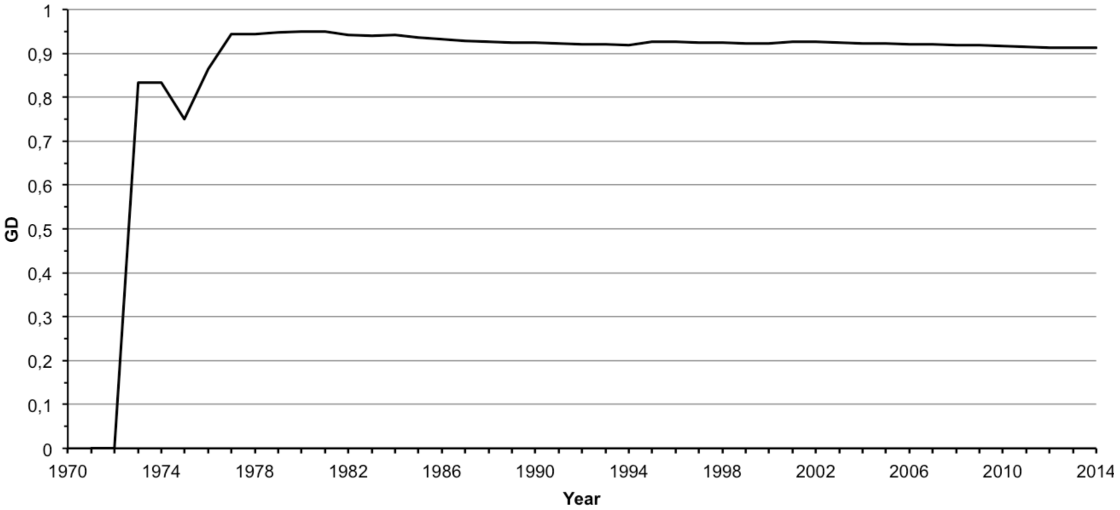
The column *my descendants* in PMx (not displayed in the annex), shows the first 25 descendants of each founder, which is useful in identifying descendants of underrepresented founders (Traylor-Holzer, 2011).

9.2.3. Gene diversity

Gene diversity (GD) is the probability that two alleles from the same locus sampled at random from the population are not identical by descent from a common ancestor, or, in other words, the heterozygosity of founder alleles expected in progeny produced by random mating (Traylor-Holzer, 2011).

Mean annual values of gene diversity based on kinship matrix are plotted in Graph 23.

Graph 23 – Mean annual values of gene diversity.



The GD in the founder stock should be preserved as much as possible in the resulting captive population (Flesness, 1977; Ballou & Foose, 1996), through aiming at achieving an equal founder representation in the living population at all times (Seal, 1986), as discussed above.

In a closed population, allelic diversity and heterozygosity, which are elements of GD, are both lost over time through changes in number and frequency of alleles, known as genetic *drift*, when offspring are unrepresentative of the parents' generation (Ballou & Foose, 1996). This process is partly function of size and structure of the population (Flesness, 1977) and genetic pedigree bottlenecks and founder effects are essentially extreme cases of genetic drift (Ballou & Foose, 1996).

Current GD for the global population is 0.9134, based on kinship matrix (Table 11). This value is still within the generally outlined goal of 90/100 for CBP. The observed increase from 1975 (0.75) to 1981 (0.9491), resulted from an important incorporation of founding individuals in the programme in July and November of 1975. Since then, another increase, although very discrete, was due to the incorporation of the eight individuals from *Fuerteventura* and *Nueva Llanes* in the 90s.

Differences in allele and genotype frequencies between populations determine genetic divergence among them, and can be measured through Fst and analogue distances, genetic distances (e.g. Nei's) or sequence divergence.

Developments on molecular genetics and non-invasive sampling have made it possible to define and compare patterns of GD in mtDNA and microsatellite loci of FELH's population relatively to six other populations of Dorcas gazelles throughout north-western Africa (Godinho et al., 2012). The values of haplotype and nucleotide diversities of FELH's population were not only the highest, but also similar to the only wild population sampled, in Safia, south of Morroco (Godinho et al., 2012). This is in agreement with the origin of the founding individuals imported from 1970 to 1975 and elucidates the success in hampering decrease in GD (Godinho et al., 2012).

The related concept of genetic variability, seen as plasticity of genetic characteristics due to occurrence of polymorphisms (alternative forms of alleles) within a population (Chesser, 1980), is often assessed by allelic diversity (Chesser et al., 1980).

Finding a balance between selecting for a high degree of polymorphism and simultaneously minimising effects of inbreeding in each subpopulation is crucial, and can be attained by optimisation of both effective population size (N_e) and rate of translocations among managed populations (Chesser, 1980).

The initial allele frequency and the N_e determine the loss or fixation of alleles (Mace, 1986; Chesser et al., 1980), such that a small N_e is related to higher rate of loss of heterozygosity (Chesser et al., 1980), as described later.

9.2.4. Effective population size

The genetically effective population size (N_e) is an approximation of the proportion of animals contributing to the next generation (Seal, 1986). In other words, it is defined as the number of breeding individuals that would lead to the current increase in F if they contributed equally to the next generation (Gama, 2002; Gutiérrez et al., 2010).

The effective population size is a broader concept than the census population size, because it is determined by sex and age structure of the breeding population (Foose, 1980; Seal, 1986), as well as by variance in family size (Foose, 1980; Chesser et al., 1980; Seal, 1986), which results from the unbalanced contribution of breeders to the next generation. Its value has implications on the loss and fixation of alleles (Mace, 1986).

A slightly different definition is advanced by Traylor-Holzer (2011), who defines N_e as the size of a randomly mating population of constant size, with sex ratio 1:1 and a Poisson distribution of family sizes that would result in the same mean F or same change in gene frequencies (genetic drift) as that observed in the actual population. This further assumes that the population is in random mating with no migration, no mutation, no selection and non-overlapping generations, in which case $N_e = N$ (Mace, 1986).

Interpreting the ratio N_e/N, usually in the interval 0.2-0.4 (Mace, 1986), is often more useful for management purposes than simply looking at N_e (Foose, 1980; Leus et al., 2011), because it relates the N to its capability of preserving GD (Leus et al., 2011).

Maximising the number of breeding animals, while equalising their sex ratio, and lowering variance in family size both increase the N_e/N ratio (Flesness, 1977; Chesser et al., 1980; Foose, 1980; Frankham, 2010), the second described as having more impact (Mace, 1986; Seal, 1986). Variations in family sizes of the breeding populations occur when there is lack of production of offspring by many individuals of one gender or whose offspring doesn't get the chance to be selected and breed (Seal, 1986). This is a premise for wastage of GD and available housing area of the species in question (Seal, 1986).

A number of descriptions for computing N_e are described (Gama, 2002; Harmon & Braude, 2010; Gutiérrez et al., 2010), and two were used in this work, based on PMx and ENDOG software:

- PMx

Current N_e, 80.49, was calculated based on numbers of proven breeders (27.79) (Table 3), as $Ne = \frac{4NmNf}{Nm+Nf}$.(Frankel & Soulé, 1981). Mean N_e since the beginning of the CBP is 48.71, a much lower value.

- ENDOG

The computation of N_e is useful in describing GD and for predictive purposes (Gutiérrez et al., 2010) and ENDOG provides alternative values of N_e besides the computation as $Ne = \frac{1}{2\Delta F}$, based on increase in inbreeding per generation (Gutiérrez et al., 2010).

An alternative approach, followed by Piccoli et al. (2014) and not dependent on the whole reference population mating policy but on the matings carried out throughout the pedigree of each individual (Gutiérrez et al., 2010), is termed *realised* N_e and uses the same formula but through addressing the individual rate of inbreeding (ΔF_i), calculated by using $\Delta Fi = 1 - (1 - Fi)^{1/(ni-1)}$, where n_i is the equivalent number of complete generations known (Gutiérrez et al., 2010).

ENDOG estimate of *realised* N_e and associated parameters are presented in Table 12.

Table 12 – Estimate of N_e and associated parameters.

ENDOG	
Mean average relatedness	0.1149
Mean equivalent generations	4.35
Increase in inbreeding by equivalent generations	0.88%
Realised N_e	56.74

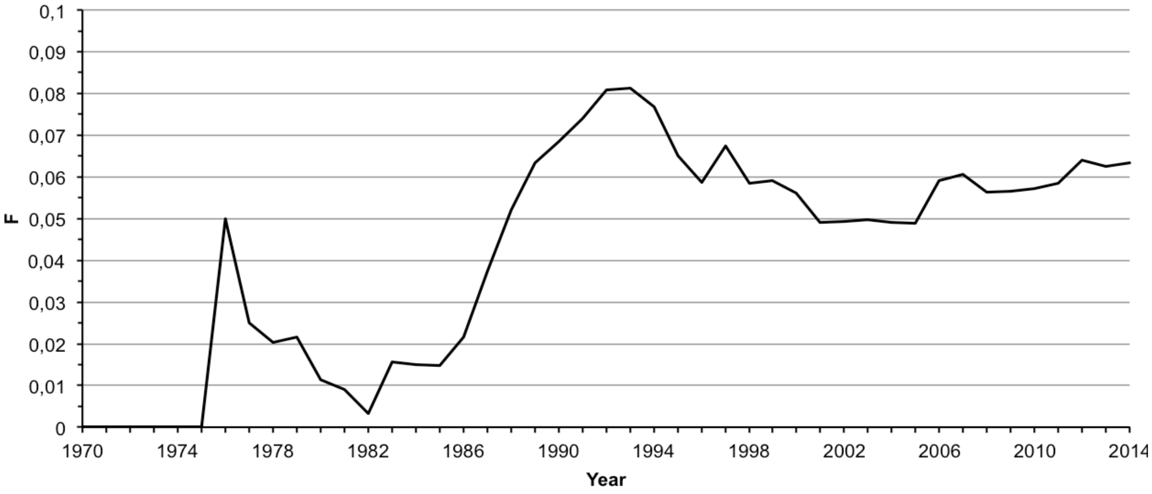
9.2.5. Inbreeding coefficient

The concept of inbreeding can be presented in a straightforward manner as the mating between related individuals, that is, individuals who share common ancestor(s) (Gama, 2002). The inbreeding coefficient is the probability of an individual receiving the same allele from each parent (Ballou & Foose, 1996) or, in other words, that two alleles at a genetic locus are identical by descent from an ancestor common to both parents (Gutiérrez et al., 2010; Traylor-Holzer, 2011).

The rate of inbreeding thus depends on the distribution of alleles in the parental generation and on the mating policy being at random or not (Traylor-Holzer, 2011).

Together with loss of GD, inbreeding compromises viability of wild populations (Frankham, 2010), whether in terms of vigour, fertility and/or offspring survivorship (Ballou & Ralls, 1982; Cassinello, 2005). These parameters typically present higher heterosis values and low heritability, in contrast to genes with additive action, with higher heritability (Gama, 2002).

Graph 24 – Evolution of mean inbreeding by year of birth.



The average of the inbreeding coefficients of the living population, known as mean inbreeding (Graph 24), corresponds to the proportional decrease in observed heterozygosity relative to the expected heterozygosity of the founder population (Gama, 2002; Traylor-Holzer, 2011).

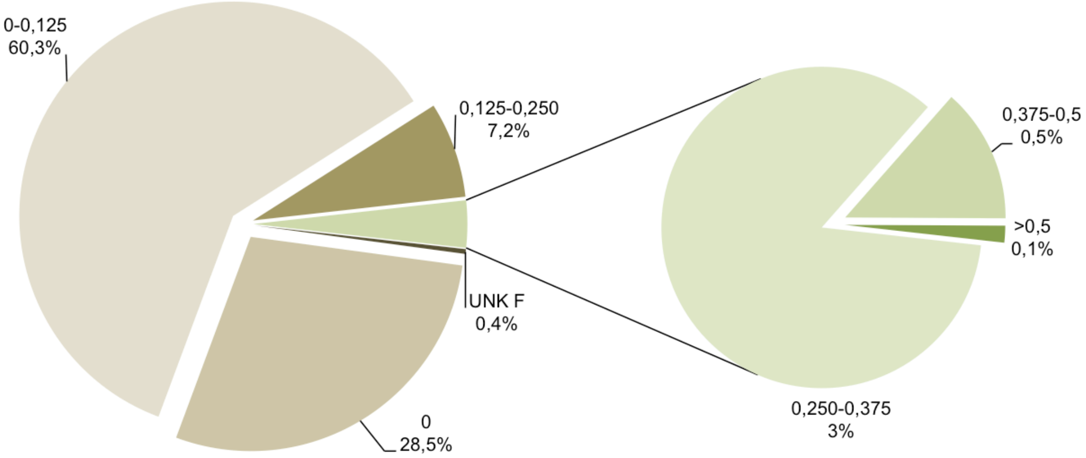
Three previous works have addressed inbreeding in captive populations of Dorcas gazelles based solely on pedigree records (Ballou & Ralls, 1982; Alados et al., 1995; Cassinello, 2005), and helped clarifying risks of inbreeding. The analysis conducted here is complementary.

Of the three species kept at FELH, Saharawi dorcas gazelle has the lowest mean inbreeding coefficient, followed by Mhorr and Cuvier's gazelles (Cassinello, 2005), which is in agreement with the different number of founding individuals imported.

Current mean inbreeding is 0.0631 (6.31%). Significant decreases in mean inbreeding, after 1975 and 1994, correspond to the referred incorporations of wild-caught individuals in the CBP mentioned above. Similar associations had also been noted by Ralls et al. (1980) in the population of the National Zoological Park, Washington.

Distribution of individual inbreeding values (F_i) is presented in Graph 25.

Graph 25 – F_i values.



Individual inbreeding values were calculated by using $Fi = \sum[(\frac{1}{2})^{n+1}(1 + Fc)]$, where *n* is the number of steps in a path relating one parent to a common ancestor and back to the other parent and *Fc* is the inbreeding coefficient of the common ancestor (Ralls et al, 1980).

Like in Cassinello's (2005) study, founding individuals as well as hypothetical and individuals later incorporated in the CBP are included in this analysis, and all have F_i=0 in pedigree records, which, as mentioned, is possibly an error inducing premise. Parentage of individuals with F_i=0 are unrelated.

It was not possible to calculate inbreeding coefficients for six individuals, whose ancestry is unknown. Of the 1661 records corresponding to animals born alive, the most significant proportion (60.3%; n=1002) had F_i values greater than 0 and smaller or equal to 0.125 (Graph 25).

Ballou & Ralls (1982) documented father-daughter matings as responsible for inbreeding in many of the inbred captive Dorcas gazelles and as occasionally verified in wild populations of ungulates. Equivalently, high-inbred individuals in our target population result mostly from parent-offspring matings (6.56% of total matings), followed by half-siblings (3.48%) and full siblings (0.71%) matings. No data on wild populations has been collected so far, but monitoring in semi-wild conditions is progressing (Abáigar, 2016).

Despite documented cases of successful inbred populations, their past reproductive history must be taken into account and they are, nonetheless, more prompt to extinction due inbreeding depression (Ballou & Ralls, 1982). Inbreeding depression, as a result of increase of homozygous genotypes (Ralls et al., 1980; Gama, 2002), remarkably shape the outcome of population viability analysis, including its extinction prognosis (O'Grady et al., 2006). Inbreeding depression has concerned authors in the past, who have relied in STD records for its comprehension (Ralls et al., 1980). The inverse concept, heterosis, is result of the increase in heterozygosity (Gama, 2002).

The general recommendation for captive populations is that inbreeding rates should not exceed 1 to 3% per generation, otherwise fixation of deleterious genes will overwhelm selection (Ballou & Ralls, 1982). In the study population, this value is lower than 1% (Table 12).

The larger the number of individuals in each subpopulation and the interval between pulses of translations (*outbreeding*), the shorter the rate of increase in inbreeding depression (Chesser et al., 1980).

ENDOG provides information on the increase of inbreeding (ΔF) for each generation, as shown before, and then uses ΔF to calculate N_e (Gutiérrez et al., 2010).

9.2.5. Kinship matrix

The kinship matrix is essentially a cross table with all living individuals, where the kinship value between any pair of individuals is displayed (Traylor-Holzer, 2011). This value is equal to the inbreeding coefficient of any offspring that would be produced by mating of that pair and must therefore be taken into account when defining breeding groups.

Mean kinship of a population, in this case 0.0866 (Table 11), predicts loss of gene diversity expected in the subsequent generation if all animals were to mate randomly and all were to produce the numbers of offspring expected for animals of their age. The fact that this value is higher than the mean inbreeding (Table 11) evidences efforts in avoiding mating of related individuals.

9.2.6. Relationship between subpopulations

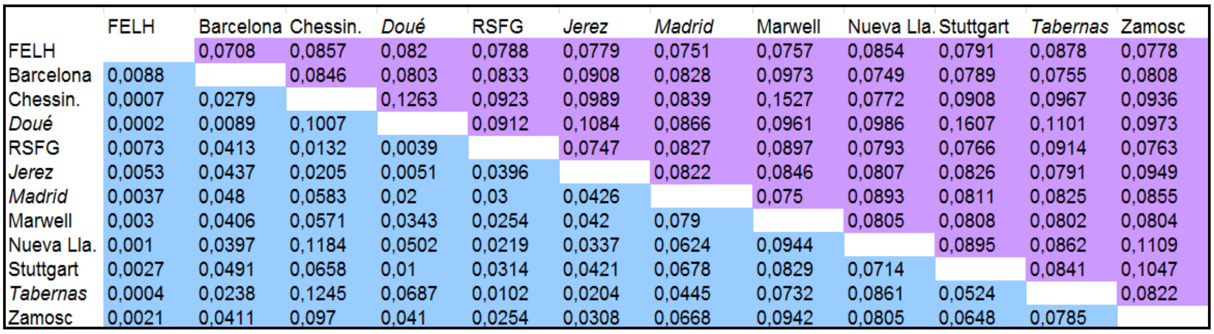
Mean GD and mean F for each subpopulation and for the global population are presented in Table 13.

Table 13 – Size, mean GD and mean F for each subpopulation.

Subpopulation	**N**	**GD**	**Mean F**
FELH	110	0.9056	0.0609
RSFG	31	0.8545	0.0667
Parc Zoo Barc	24	0.8237	0.0574
Jerez	20	0.845	0.0568
Madrid	11	0.8085	0.0624
Stuttgart	10	0.7942	0.0833
Marwell	9	0.7583	0.0662
Zamoscz	7	0.7609	0.0646
Nueva Llanes	6	0.7489	0.095
Chessington	4	0.6584	0.066
Tabernas	3	0.7742	0.0497
Doué	1	0.4682	0.0636
Global Pop.	236	0.9134	0.0631

There is an association between size and mean GD of distinct subpopulations, however not translated in differences in mean F, which show little variation (between 0.0497 and 0.0833). The genetic distances between subpopulations, computed by PMx, are presented in Table 14, in two alternative ways.

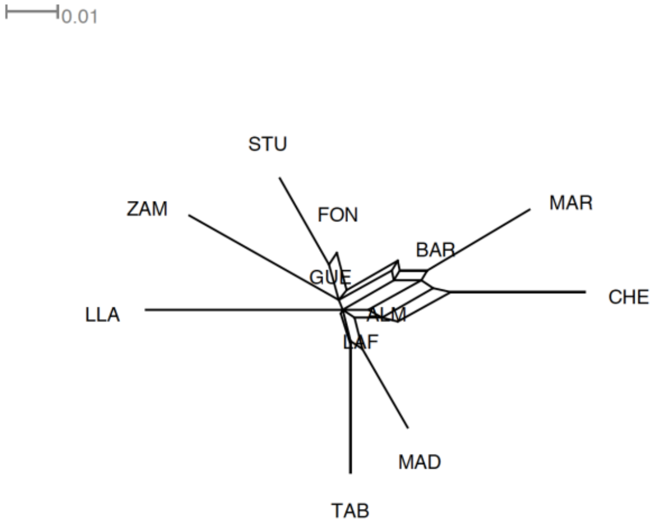
Table 14 – Fst (blue) and MKb (pink) distances between subpopulations.



	FELH	Barcelona	Chessin.	*Doué*	RSFG	*Jerez*	*Madrid*	Marwell	Nueva Lla.	Stuttgart	*Tabernas*	Zamosc
FELH		0,0708	0,0857	0,082	0,0788	0,0779	0,0751	0,0757	0,0854	0,0791	0,0878	0,0778
Barcelona	0,0088		0,0846	0,0803	0,0833	0,0908	0,0828	0,0973	0,0749	0,0789	0,0755	0,0808
Chessin.	0,0007	0,0279		0,1263	0,0923	0,0989	0,0839	0,1527	0,0772	0,0908	0,0967	0,0936
Doué	0,0002	0,0089	0,1007		0,0912	0,1084	0,0866	0,0961	0,0986	0,1607	0,1101	0,0973
RSFG	0,0073	0,0413	0,0132	0,0039		0,0747	0,0827	0,0897	0,0793	0,0766	0,0914	0,0763
Jerez	0,0053	0,0437	0,0205	0,0051	0,0396		0,0822	0,0846	0,0807	0,0826	0,0791	0,0949
Madrid	0,0037	0,048	0,0583	0,02	0,03	0,0426		0,075	0,0893	0,0811	0,0825	0,0855
Marwell	0,003	0,0406	0,0571	0,0343	0,0254	0,042	0,079		0,0805	0,0808	0,0802	0,0804
Nueva Lla.	0,001	0,0397	0,1184	0,0502	0,0219	0,0337	0,0624	0,0944		0,0895	0,0862	0,1109
Stuttgart	0,0027	0,0491	0,0658	0,01	0,0314	0,0421	0,0678	0,0829	0,0714		0,0841	0,1047
Tabernas	0,0004	0,0238	0,1245	0,0687	0,0102	0,0204	0,0445	0,0732	0,0861	0,0524		0,0822
Zamosc	0,0021	0,0411	0,097	0,041	0,0254	0,0308	0,0668	0,0942	0,0805	0,0648	0,0785	

The Fst distances between subpopulations were used to create a Neighbor-Network tree (Figure 10), which is the ultimate result of all translocations.

Figure 10 – Neighbor-Network tree built on Fst distances.



FELH (represented as ALM in the figure) was involved in the most number of translocations, having sent 65 males and 74 females and received 29 males and 21 females. As the major source of animals to other institutions, it stands at the centre of the network tree as related to all other subpopulations.

CHAPTER VII – CONCLUSION

This work summarises relevant aspects to take into account when implementing and supervising species' conservation. The results obtained emphasize the success of the EEP for Saharawi dorcas gazelle and their perception is useful in understanding cooperative management.

The standard programme phases of implementation, exponential growth and stabilisation were clearly identified in the census graph. In what concerns captive breeding, demographic and genetic goals have been achieved by fragmentation of subpopulations under a metapopulation scenario; adequate planning of number of births; rotation of males in accordance to their past breeding history; and implementation of suitable husbandry measures. The good adaptation to captive environments, the relatively short gestation period, the current duration of the CBP and the existence of a main breeding centre with capacity for over 100 individuals have largely contributed to the prosperity of the programme.

Study limitations included the bias of interpreting only STD records; the lack of crossing information of institution-specific mortality rates with correspondent husbandry practices; the need for clearer information on causes of death to allow a broader study; need for careful interpretation of results, given the use of different analysis software which rely on distinct assumptions. Mention must be made of the time available to perform this work, which constrained further analyses.

Now that there is an updated analysis of the captive population, the next challenge would be to apply these parameters to free-ranging simulations. A Population and Habitat Viability Analysis for this taxa is now of great applicability, especially to assess which factors might be more determinant in semi-wild conditions, an intermediate phase until the ideal and ultimate complete release is implemented. This, together with the already published and upcoming molecular genetic studies, will without doubt provide solid arguments for proper future management decisions.

Finally, it should be reminded that record keeping and continuous analyses of captive populations are far from ending after reintroduction projects take place. Besides from being essential for identifying possible data inconsistencies, as long as supplementation of wild environments with captive-born individuals is needed, in-depth analyses will always remain as a support for assuring the long-term viability of reintroductions.

Preliminary results of this study were presented on the *XII Maratón Científico* (http://www.eeza.csic.es/es/mediateca.aspx) in February 2016, in *Estación Experimental de Zonas Áridas*, and a poster was submitted and accepted for the V FAUNA International Conference in November 2016, in the Faculty of Veterinary Medicine, University of Lisbon (Annex 5).

CHAPTER VIII – REFERENCES

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Annex 1 – Sex and age distribution in institutions with 20 or more individuals.

Finca Experimental la Hoya

%		Males N = 46		Females N = 64		%
0,00			**1997**	891	1	1,56
0,00			**1998**			0,00
0,00			**1999**			0,00
0,00			**2000**	983	1	1,56
0,00			**2001**	1037 1051	2	3,13
2,17	1	1061	**2002**	1054	1	1,56
4,35	2	1092 1091	**2003**	1074 1084	2	3,13
6,52	3	1153 1148 1133	**2004**	1124	1	1,56
4,35	2	1176 1167	**2005**			0,00
2,17	1	1206	**2006**	1202 1205 1207 1213 1219	5	7,81
4,35	2	1272 1251	**2007**	1244 1245 1246 1248 1250	5	7,81
4,35	2	1303 1289	**2008**	1274 1283 1286 1287 1302 1307 1311 1312	8	12,50
15,22	7	1394 1392 1390 1369 1368 1361 1350	**2009**	1351 1362 1367 1371 1373 1374 1383 1385 1387 1389 1391 1395 1397	13	20,31
10,87	5	1451 1449 1448 1441 1432	**2010**	1398 1429 1430 1431 1433 1434 1446	7	10,94
4,35	2	1497 1491	**2011**			0,00
10,87	5	1556 1543 1541 1540 1539	**2012**	1538 1544 1546 1548 1550 1551 1558	7	10,94
15,22	7	1621 1620 1618 1615 1602 1601 1592	**2013**	1559 1596 1598 1614 1616 1619	6	9,38
15,22	7	1683 1674 1663 1661 1658 1651 1639	**2014**	1656 1657 1662 1680 1684	5	7,81

Réserve Spéciale de Faune de Guembeul

%		Males N = 13		Females N = 18		%
0,00			**2001**	1027	1	5,56
7,69	1	1068	**2002**			0,00
0,00			**2003**	1136	1	5,56
0,00			**2004**	1180	1	5,56
0,00			**2005**			0,00
0,00			**2006**			0,00
0,00			**2007**			0,00
0,00			**2008**	1321	1	5,56
0,00			**2009**	1428	1	5,56
23,08	3	1487 1455 1450	**2010**	1456	1	5,56
7,69	1	1501	**2011**	1489 1490 1505	3	16,67
7,69	1	1571	**2012**	1533 1574	2	11,11
23,08	3	1629 1627 1624	**2013**	1626	1	5,56
30,77	4	1670 1669 1668 1665	**2014**	1664 1666 1667 1671 1672 1673	6	33,33

Parc Zoologic de Barcelona

%		Males N = 7		Females N = 17		%
0,00			**2002**	1063	1	5,88
0,00			**2003**			0,00
0,00			**2004**			0,00
0,00			**2005**			0,00
0,00			**2006**			0,00
0,00			**2007**	1275	1	5,88
0,00			**2008**	1327 1329 1330	3	17,65
14,29	1	1412	**2009**	1406 1407 1411	3	17,65
57,14	4	1483 1481 1478 1464	**2010**	1474 1476 1477 1479 1480 1482	6	35,29
28,57	2	1517 1512	**2011**	1510 1516	2	11,76
0,00			**2012**			0,00
0,00			**2013**			0,00
0,00			**2014**	1686	1	5,88

Zoobotanico Jerez de la Frontera

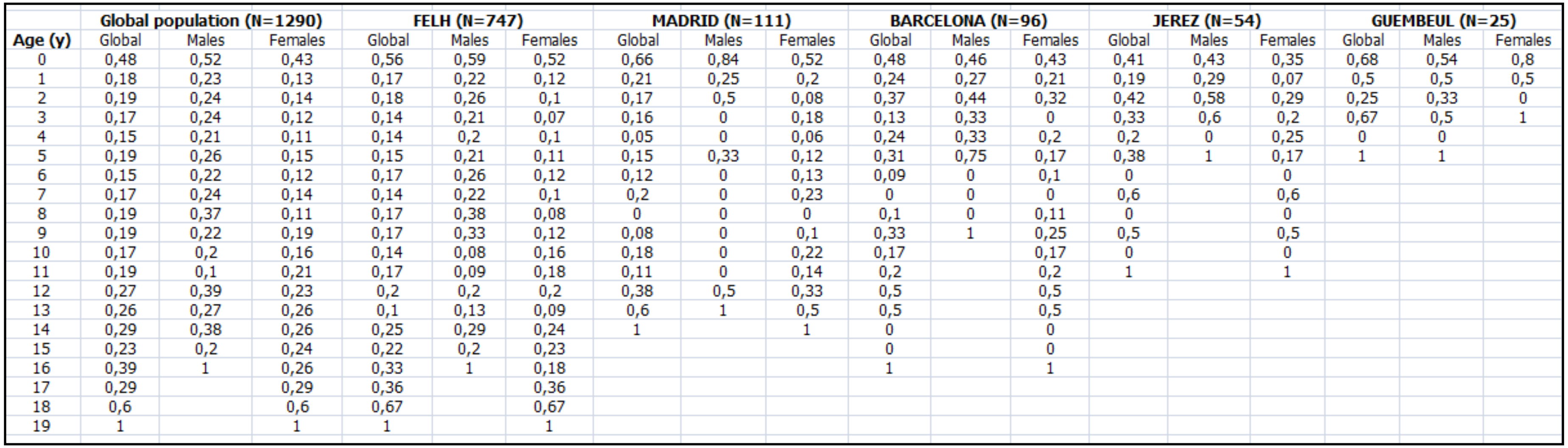
%		Males N = 12		Females N = 8		%
0,00			**2002**	1064	1	12,50
0,00			**2003**			0,00
0,00			**2004**			0,00
0,00			**2005**	1183	1	12,50
0,00			**2006**			0,00
8,33	1	1243	**2007**			0,00
0,00			**2008**	1278	1	12,50
8,33	1	1382	**2009**			0,00
0,00			**2010**			0,00
25,00	3	1520 1519 1514	**2011**			0,00
33,33	4	1581 1580 1579 1578	**2012**	1576	1	12,50
8,33	1	1610	**2013**	1608 1609 1647	3	37,50
16,67	2	1690 1688	**2014**	1689	1	12,50

Annex 2 – Translocations since the beginning of the CBP.

	TO	Alm.	Aviación Esp.	Benisa	Doué	Chessington	Elche	FELH	RSFG	Hannover	Icona Alme.	Jerez	Marwell	Nueva Lla.	Barcelona	Santillana	Selwo	Tenerife	Stuttgart	Tabernas	Ueck.	Zamoscz	Madrid
FROM																							
Benisa								1 0						2 0	2 0	0 4							
Doué												1 0			2 0								
FELH		2 2	2 1	5 3			1 4		10 19	1 0	1 1	8 4	3 7	3 4	4 10	0 4		2 0	1 2	15 4			7 9
Fuerteve.								2 2															
Hannover					2 0			1 0						0 2	4 0				5 1	0 4		0 4	1 0
Jerez								0 3												2 0	7 0	1 0	1 0
Marwell					3 0	6 0		2 5		0 3													5 0
Nueva Lla.								5 3								1 0							1 0
Barcelona					3 0			6 3		2 0		1 0	1 0	1 0			1 0			0 2			
Santillana								0 1						1 0									
Stuttgart					2 0					1 1													
Tabernas								5 0							2 0								2 0
W. Sahara								37 37															
Madrid				3 0	2 0			7 4				0 3			2 0		2 0			1 0			
TOTAL		**4** Alm.	**3** Aviación Esp.	**11** Benisa	**12** Doué	**6** Chessington	**5** Elche	**124** FELH	**29** RSFG	**8** Hannover	**2** Icona Alme.	**17** Jerez	**11** Marwell	**13** Nueva Lla.	**26** Barcelona	**9** Santillana	**3** Selwo	**2** Tenerife	**9** Stuttgart	**28** Tabernas	**7** Ueck.	**5** Zamoscz	**26** Madrid

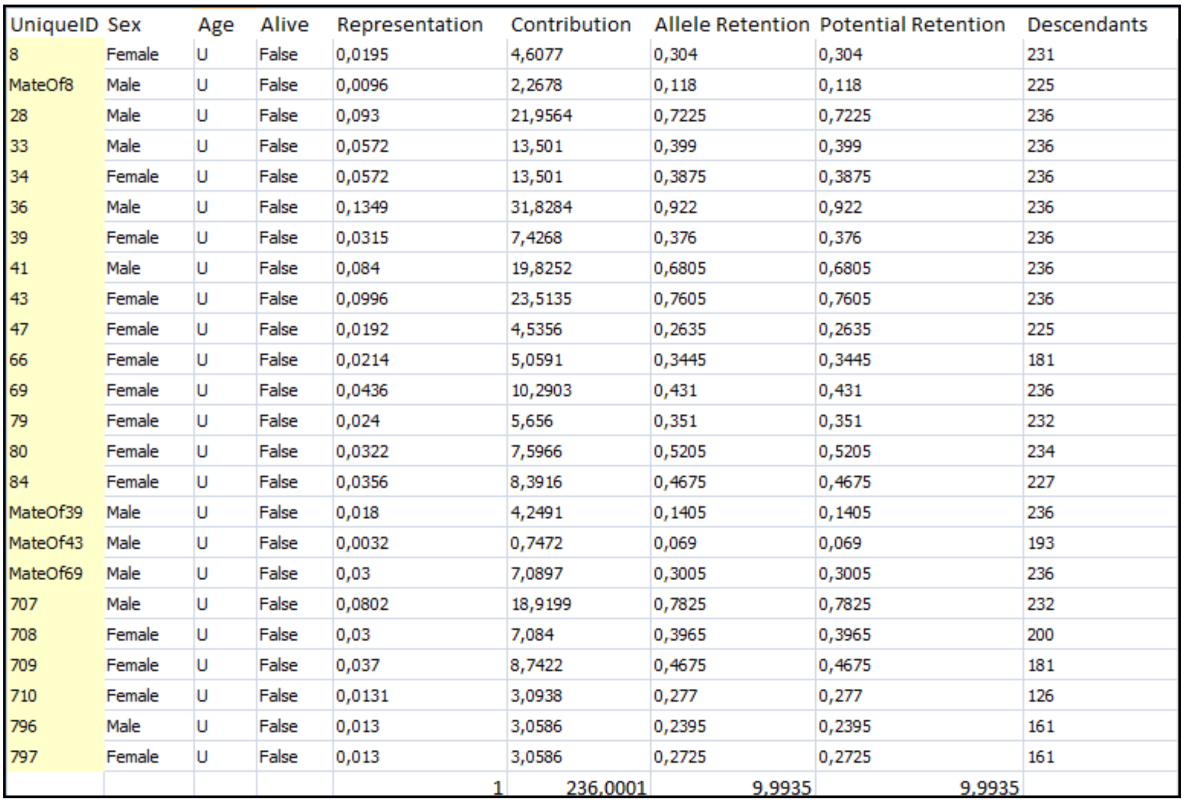
The upper cell refer to males and the lower cell refer to females.

Annex 3 – Age-specific Q*x* by institution.



	Global population (N=1290)			FELH (N=747)			MADRID (N=111)			BARCELONA (N=96)			JEREZ (N=54)			GUEMBEUL (N=25)		
Age (y)	Global	Males	Females	Global	Males	Females	Global	Males	Females	Global	Males	Females	Global	Males	Females	Global	Males	Females
0	0,48	0,52	0,43	0,56	0,59	0,52	0,66	0,84	0,52	0,48	0,46	0,43	0,41	0,43	0,35	0,68	0,54	0,8
1	0,18	0,23	0,13	0,17	0,22	0,12	0,21	0,25	0,2	0,24	0,27	0,21	0,19	0,29	0,07	0,5	0,5	0,5
2	0,19	0,24	0,14	0,18	0,26	0,1	0,17	0,5	0,08	0,37	0,44	0,32	0,42	0,58	0,29	0,25	0,33	0
3	0,17	0,24	0,12	0,14	0,21	0,07	0,16	0	0,18	0,13	0,33	0	0,33	0,6	0,2	0,67	0,5	1
4	0,15	0,21	0,11	0,14	0,2	0,1	0,05	0	0,06	0,24	0,33	0,2	0,2	0	0,25	0	0	
5	0,19	0,26	0,15	0,15	0,21	0,11	0,15	0,33	0,12	0,31	0,75	0,17	0,38	1	0,17	1	1	
6	0,15	0,22	0,12	0,17	0,26	0,12	0,12	0	0,13	0,09	0	0,1	0		0			
7	0,17	0,24	0,14	0,14	0,22	0,1	0,2	0	0,23	0	0	0	0,6		0,6			
8	0,19	0,37	0,11	0,17	0,38	0,08	0	0	0	0,1	0	0,11	0		0			
9	0,19	0,22	0,19	0,17	0,33	0,12	0,08	0	0,1	0,33	1	0,25	0,5		0,5			
10	0,17	0,2	0,16	0,14	0,08	0,16	0,18	0	0,22	0,17		0,17	0		0			
11	0,19	0,1	0,21	0,17	0,09	0,18	0,11	0	0,14	0,2		0,2	1		1			
12	0,27	0,39	0,23	0,2	0,2	0,2	0,38	0,5	0,33	0,5		0,5						
13	0,26	0,27	0,26	0,1	0,13	0,09	0,6	1	0,5	0,5		0,5						
14	0,29	0,38	0,26	0,25	0,29	0,24	1		1	0		0						
15	0,23	0,2	0,24	0,22	0,2	0,23				0		0						
16	0,39	1	0,26	0,33	1	0,18				1		1						
17	0,29		0,29	0,36		0,36												
18	0,6		0,6	0,67		0,67												
19	1		1	1		1												

Annex 4 – Variables of genetic contribution for each founder.



UniqueID	Sex	Age	Alive	Representation	Contribution	Allele Retention	Potential Retention	Descendants
8	Female	U	False	0,0195	4,6077	0,304	0,304	231
MateOf8	Male	U	False	0,0096	2,2678	0,118	0,118	225
28	Male	U	False	0,093	21,9564	0,7225	0,7225	236
33	Male	U	False	0,0572	13,501	0,399	0,399	236
34	Female	U	False	0,0572	13,501	0,3875	0,3875	236
36	Male	U	False	0,1349	31,8284	0,922	0,922	236
39	Female	U	False	0,0315	7,4268	0,376	0,376	236
41	Male	U	False	0,084	19,8252	0,6805	0,6805	236
43	Female	U	False	0,0996	23,5135	0,7605	0,7605	236
47	Female	U	False	0,0192	4,5356	0,2635	0,2635	225
66	Female	U	False	0,0214	5,0591	0,3445	0,3445	181
69	Female	U	False	0,0436	10,2903	0,431	0,431	236
79	Female	U	False	0,024	5,656	0,351	0,351	232
80	Female	U	False	0,0322	7,5966	0,5205	0,5205	234
84	Female	U	False	0,0356	8,3916	0,4675	0,4675	227
MateOf39	Male	U	False	0,018	4,2491	0,1405	0,1405	236
MateOf43	Male	U	False	0,0032	0,7472	0,069	0,069	193
MateOf69	Male	U	False	0,03	7,0897	0,3005	0,3005	236
707	Male	U	False	0,0802	18,9199	0,7825	0,7825	232
708	Female	U	False	0,03	7,084	0,3965	0,3965	200
709	Female	U	False	0,037	8,7422	0,4675	0,4675	181
710	Female	U	False	0,0131	3,0938	0,277	0,277	126
796	Male	U	False	0,013	3,0586	0,2395	0,2395	161
797	Female	U	False	0,013	3,0586	0,2725	0,2725	161
				1	236,0001	9,9935	9,9935	

Annex 5 – Poster presented on the V FAUNA International Conference (11-13th November 2016).

Update on demographic and genetic parameters of a captive population of threatened Saharawi dorcas gazelle (*Gazella dorcas neglecta*)

FAUNA
V INTERNATIONAL CONFERENCE

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INTRODUCTION

Between 1970 and 1975, 72 (36♂.36♀) Saharawi dorcas gazelles arrived in *Finca Experimental la Hoya*, Almería. They were the founding individuals of a captive breeding programme, now managed as an European Endangered species Programme, currently with 236 (104♂.132♀) living individuals distributed among 12 institutions. The previous assessment of this population was published in 2002 and an updated analysis until the 31st december 2014 was commended, ultimately motivated by the recent establishment of *in situ* reintroductions in Senegal.

AIMS OF THE STUDY

The purpose of this study is to characterise, from a demographic and genetic perspective, the captive EEP population, using the updated studbook data and recommended pedigree analyses software. The presented results should be considered when assessing the populations' viability and probability of extinction under natural conditions.

MATERIALS AND METHODS

The updated International Studbook used for this study can be accessed at www.eeza.csic.es/es/programadecria.aspx. The currently used STD database software is SPARKS version 1.6, distributed by the International Species Information System (ISIS). Of the 1693 registered individuals, nearly 88% have a complete record, which includes information on STD identification number, gender, parentage, date & place of birth and death, translocations and birth type. The results were obtained using the software packages PMx v1.0, ENDOG v4.8 and SplitsTree4 v4.14.3.

RESULTS AND DISCUSSION

Sex and age distribution of the current population (**Figure 1**) is close to a pyramidal shape, as would correspond to a stable age distribution. The increasing population census (**Figure 2**) is the result of adequate annual birth planning and growing number of collaborating institutions joining the CBP.

Figure 1 – Sex and age distribution of living population.

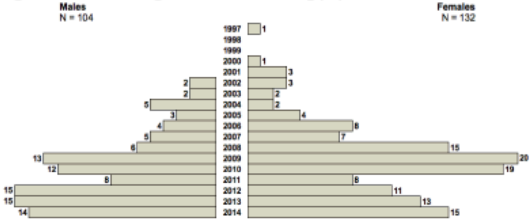

Figure 2 – Global population census.

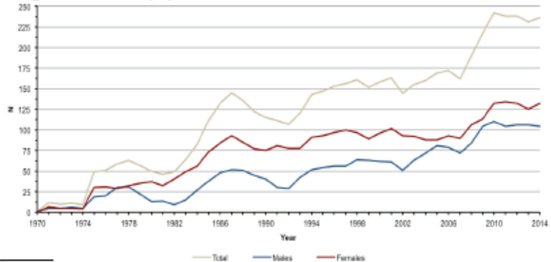

Figure 3 – Demography overview.

Summary statistics	Ave. males and females	Males	Females
Oldest alive (years)	-	12,4 (STD#1061)	18 (STD#891)
Oldest recorded (years)	-	16,9	20
Mean longevity (years)	3,24	2,35	4,12
Mean age of parents (years)	4,88	4,86	4,90
Earliest reproduction (months)	-	11	11
30-day mortality	-	0,23	0,20
Annual growth rate (λ)	1,058	1,054	1,062
Instantaneous rate of change (r)	0,056	0,052	0,060
Net reproductive rate (R_0)	1,283	1,266	1,300
Mean generation time (T) (years)	4,5	4,5	4,4

The most relevant demographic parameters are presented in **Figure 3**. Although males and females may live up to 17 and 20 years of age, mean longevity is 2,35 and 4,12 years, respectively. Such discrepancy is explained by a first year mortality of 44% in males and 35% in females.

Decreases in mean inbreeding (**Figure 4**) are coincident with the incorporation of wild-caught individuals in the population. The current gene diversity based on kinship matrix is 0,91, the N_e/N ratio is 0,34 and there are 24 founders with representation in the living population.

Figure 4 – Evolution of mean inbreeding, by year of birth.

CONCLUSION

In what concerns captive breeding, proposed goals have been achieved by fragmentation of subpopulations under a **metapopulation scenario**; adequate **planning** of number of births; **rotation of males** in accordance to their past breeding history; and implementation of suitable **husbandry** measures.

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