

INVITED REVIEW

Phylogeography, population genetics and conservation of the European red deer *Cervus elaphus*

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ABSTRACT

1. During the Last Glacial Maximum, European red deer *Cervus elaphus* occurred in refugia in Iberia/southern France, Italy, the Balkans and the Carpathians. Most of Europe, including large parts of the east and north-east, is now inhabited by red deer from the western lineage. The eastern lineage is largely confined to south-eastern Europe; a third lineage comprises Sardo-Corsican and Barbary red deer.

2. Sardo-Corsican, Barbary and Mesola red deer are genetically unique units. They exhibit low levels of genetic diversity and deserve particular protection, since conservation strategies should target genetic information.

3. Hybridization between sika *Cervus nippon* and red deer occurs rarely, but may lead to extensive introgression, particularly in parts of the British Isles. Further expansion of both species may lead to increased hybridization in continental Europe.

4. Although hunting has an impact on red deer gene pools, the main threat today is habitat fragmentation in human-dominated landscapes. The resulting increase in genetic drift and inbreeding reduces variability in isolated populations and may lead to inbreeding depression. To support vital meta-populations, migration corridors should be established.

Keywords: Cervidae, habitat fragmentation, hybridization, selective hunting, translocations

Mammal Review (2011), **41**, 138–150
doi: 10.1111/j.1365-2907.2010.00177.x

INTRODUCTION

The red deer *Cervus elaphus* is one of the most widespread large mammals in Europe, occurring throughout most of the continent except in northern Scandinavia, Finland and Iceland. As perhaps the most important game species, it has also been undergoing anthropogenic impacts for centuries, or even millennia. The red deer is therefore an interesting model species whose distribution and genetic structure have been shaped by both natural and human factors, resulting in a mosaic pattern of recent human-mediated demographic factors, grafted on the underlying, more ancient structuring, through natural selection and large-scale biogeographic phenomena

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(particularly the last ice age). The present review provides an overview of both aspects, by summarizing our knowledge on the systematics, phylogeography and conservation issues pertaining to red deer in the primarily cultural landscapes of Europe.

INTRASPECIFIC TAXONOMY AND PHYLOGEOGRAPHY

As well as the ongoing debate about whether western or European-type red deer (occurring in western Eurasia and North Africa), and east-Asian and American wapitis should be considered one or two species, there has been some discussion about different European subspecies. According to mtDNA data (Ludt et al. 2004), the western lineage comprises four subgroups, three of which are the target of the present review (the Middle-Eastern maral lineage is not considered): the west-European, east-European and African-Sardinian groups. These deer are often classified as seven different subspecies: British red deer *C. e. scoticus*, Norwegian red deer *C. e. atlanticus*, Swedish red deer *C. e. elaphus*, Central European red deer *C. e. hippelaphus*, Spanish red deer *C. e. hispanicus*, North-African Barbary red deer *C. e. barbarus* and Tyrrhenian red deer *C. e. corsicanus*. Carpathian red deer are sometimes also granted subspecific status as *C. e. montanus*, but in general, the subspecies category is arbitrary, and researchers should care about genetic and phylogenetic units rather than about names designated on the basis of superficial and often variable characters (Feulner et al. 2004). Although red deer on the Tyrrhenian islands (Sardinia and Corsica) and Barbary stags may derive conservation benefits from being granted subspecies status, the genetic peculiarities of the Mesola red deer from the Po delta area (see below) are veiled by taxonomy, as these deer are combined with most other European mainland red deer into *C. e. hippelaphus*.

Three studies have dealt with red deer phylogeography in Europe, as revealed by the distribution of mtDNA lineages (Ludt et al. 2004, Skog et al. 2009, Niedziałkowska et al. 2010). All of them found a western lineage (A), an eastern lineage (C) and a third lineage confined to North Africa and Sardinia (B). While the latter remains enigmatic with respect to its phylogeographic meaning, the other two hint at distinct western and eastern glacial refugia, which is in line with palaeontological findings that have identified the Iberian peninsula and southern France, and south-eastern Europe from the Balkans up to the Carpathians as refugial areas for the red deer during the Last Glacial Maximum (Sommer et al. 2008). In the Holocene, western (including the British Isles), northern and parts of central and eastern Europe were recolonized from the south-western refugium, whereas the eastern lineage remained largely confined to the east and south-east of the continent (Fig. 1). In southern Poland, Belarus and Lithuania, both lineages occur, but further east in western Russia, only the eastern one is found; however, it is difficult to disentangle natural recolonization from translocations (see Niedziałkowska et al. 2010 for a detailed discussion). Nevertheless, it is safe to say that most of Europe was recolonized from the west after the last glaciation (in contrast, the roe deer *Capreolus capreolus* seems to have recolonized large European regions from the east; Sommer et al. 2009).

The phylogenetic status of Barbary and Tyrrhenian red deer (lineage B) is not fully clear, but these two taxa are related and, at least superficially, phenotypically similar. Nuclear DNA also links the Mesola deer from the Po delta area to the Tyrrhenian red deer, and given that the only remaining autochthonous Italian red deer population

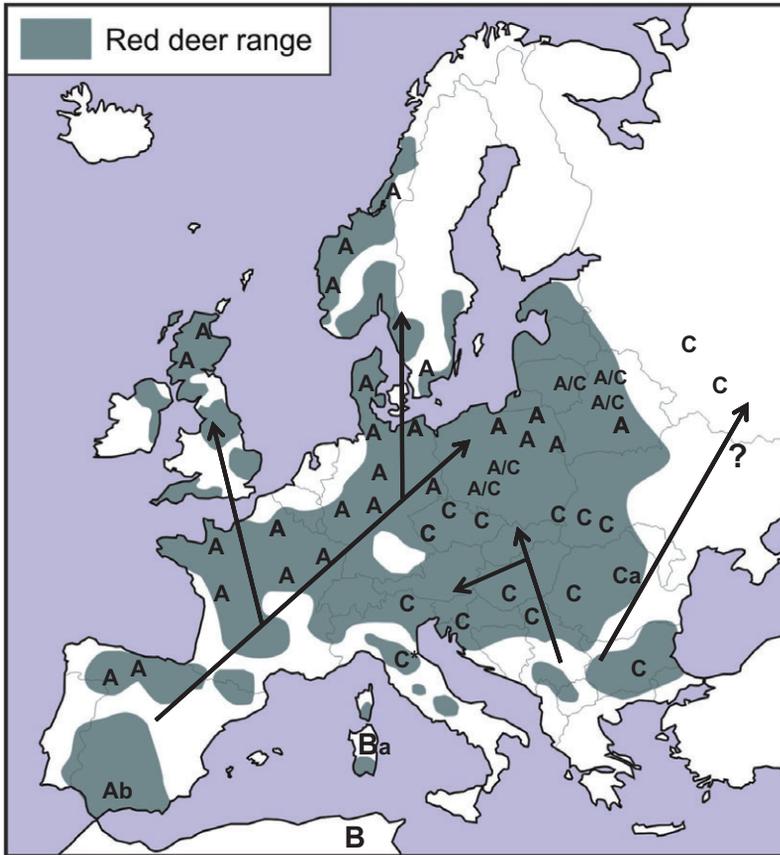


Fig. 1. Distribution of the three mtDNA lineages A, B, and C in European red deer. Current distribution range is an approximation and does not include Russia. Lower-case letters (as in Ab) indicate phylogeographic outliers found by Skog et al. (2009), A/C refers to the occurrence of the two main lineages as revealed by Niedziałkowska et al. (2010), * = Mesola red deer, the lineage of which (A or C) is not fully resolved. Black arrows denote inferred postglacial recolonization routes. Map: courtesy of M. Niedziałkowska and B. Jędrzejewska.

is in Mesola, it seems most probable (and in accordance with the fossil record) that Italian mainland red deer were introduced to Sardinia and Corsica from where, later, red deer were introduced to North Africa (Hmwe et al. 2006a, Hajji et al. 2008). This might imply rapid phenotypic evolution in Tyrrhenian and Barbary red deer, but even more rapid changes are known from fossil red deer on the island of Jersey, off the French coast (Lister 1989).

CONSERVATION ISSUES IN A COMMON SPECIES: HUMAN IMPACTS ON GENETIC STRUCTURE

In red deer, four major conservation issues exist: (i) threatened genetic lineages, and blurring of natural genetic structuring through translocations and reintroductions; (ii) local hybridization with sika *Cervus nippon*; (iii) selective hunting; and (iv) reduced effective population sizes (N_e) due to habitat fragmentation.

Genetic lineages and translocations vs. natural populations

The genetically most distinct subspecies (see above) of European red deer are *C. e. corsicanus* and *C. e. barbarus*. Both were threatened with extinction in the recent past but have recovered well after protection measures were implemented. The Barbary stag naturally occurs along the Tunisian-Algerian border (there is also an introduced population in Morocco founded with Tunisian animals) and, until recently, was considered 'Vulnerable' by the IUCN [International Union for Conservation of Nature; present status 'Lower Risk (near threatened)', Hajji et al. 2007]. After a severe bottleneck of seven animals in Tunisia in 1962, the Tunisian population now comprises about 800 (contrary to an official estimation of 2000), and although the bottleneck has left a clear signature, genetic diversity is not as low as might have been expected in light of the demographic history (Hajji et al. 2007, see Table 1 for comparative data on genetic variability in red deer). The distribution range has been expanded through reintroductions, and there is no evidence of a founder effect or of differentiation among the stocks (Hajji et al. 2007). However, Algerian red deer have not yet been studied, so their contribution to total population size and genetic diversity, and the extent of gene flow between Tunisia and Algeria, are unknown.

The Tyrrhenian red deer (IUCN status 'Endangered') has a similar history: only 100–150 animals remained in the 1970s after the extinction of the Corsican population in 1970. In the 1980s and 1990s, 13 Sardinian deer were introduced to Corsica, and the present number on Corsica is estimated to be about 250 (Kidjo et al. 2007). Population size estimates for Sardinian deer differ among authors, but at present, there may be more than 6000 (M. Apollonio, pers. comm.), and Ecological Niche Factor Analysis for Sardinia has shown that suitable habitats are available throughout the island (Puddu et al. 2009). Genetic diversity is expectedly low in *C. e. corsicanus* (Table 1), although Hmwe et al. (2006a) found eight different mtDNA haplotypes on Sardinia. A recent microsatellite study (Hajji et al. 2008) showed that the Corsican population did not suffer a decrease in genetic diversity, but was significantly differentiated ($F_{ST} = 15\%$) from the Sardinian deer in the wake of the reintroduction, a clear indication of a founder effect. Future management measures should aim at achieving genetic homogeneity and ensuring that the Corsican population represents the whole gene pool of this subspecies.

Unlike Tyrrhenian and Barbary red deer, the Mesola red deer, which harbours a unique mtDNA haplotype, is not acknowledged taxonomically but formally assigned to *C. e. hippelaphus*. It is the last autochthonous Italian red deer population (all other 'Italian' red deer were either translocated or immigrated; Zachos et al. 2009). Mesola red deer have undergone several severe bottlenecks (the estimated long-term N_e is 15; Lorenzini et al. 1998), and their level of genetic diversity is even lower than that of *C. e. corsicanus* and among the lowest found in this species (Table 1). They are of great conservation interest and have been monitored since 1982. The available demographic data have recently been used in a population viability analysis that identified catastrophes and inbreeding depression as the most important threats, and showed that splitting of this unique population while maintaining gene flow artificially through translocations (for which plans are being developed) would significantly reduce susceptibility to environmental stochasticity, and thus, extinction probability (Zachos et al. 2009). Management measures carried out from 1994 (habitat improvement, winter feeding, culling of fallow deer) have already led to an increase in reproduction and a decrease in mortality rates (Mattioli et al. 2003).

Table 1. Genetic diversity in red deer populations

Population	n	Marker	H _o (range)	H _E (range)	h	π (%)	Reference
Bulgaria (3)	13–34	AZ (43)	0.070 (0.066–0.073)	0.069 (0.065–0.073)	–	–	Hartl et al. 1993
Slovakia (2)	28–29	AZ (43)	0.037 (0.036–0.037)	0.048 (0.040–0.055)	–	–	Hartl et al. 1993
Hungary (12)	5–20	AZ (34)	0.040 (0.023–0.059)	0.036 (0.025–0.054)	–	–	Hartl et al. 1990
Achenkirch (Austria)	46	AZ (43)	0.065	0.066	–	–	Hartl et al. 1993
Eisenstadt (Austria)	21	AZ (34)	0.034	0.038	–	–	Hartl et al. 1990
Bavaria (Germany)	9	AZ (34)	0.035	–	–	–	Gyllensten et al. 1983
Vosges (France)	233	AZ (43)	0.043	0.045	–	–	Hartl et al. 1993
France (16)	12–50	AZ (7)	–	0.317 (0.215–0.391)*	–	–	Hartl et al. 2005
Mesola (Italy)	42	AZ (19)	0.023	0.029	–	–	Lorenzini et al. 1998
N Italy (3, excl. Mesola)	13–32	AZ (19)	0.024 (0.014–0.034)	0.030	–	–	Lorenzini et al. 1998
Sweden (13)	4–80	AZ (34)	0.018 (0.002–0.029)	–	–	–	Gyllensten et al. 1983
Norway (2)	15–91	AZ (34)	0.000	–	–	–	Gyllensten et al. 1983
Scotland (6)	14–41	AZ (34)	0.032 (0.026–0.036)	–	–	–	Gyllensten et al. 1983
Mesola, Italy	25	MS (20)	0.50	0.61	–	–	Zachos et al. 2009
Sardinia	28	CR	–	–	0.000	0.000	Himwe et al. 2006a
	27–29	MS (12), CR	0.48	0.66	0.872	0.473	Himwe et al. 2006a
	23	MS (8)	0.53	0.71	–	–	Hajji et al. 2008
Corsica	10	MS (8)	0.54	0.64	–	–	Hajji et al. 2008
Tunisia	19	MS (13), CR	0.46	0.78	0.529	1.266	Hajji et al. 2007
Carpathians, Romania	17	MS (8)	0.61	0.84	–	–	Hajji et al. 2008
Serbia (3)	8–33	MS (9), CR	0.57 (0.53–0.61)	0.81 (0.79–0.82)	0.020 (0.000–0.061)	0.003 (0.0–0.01)	Feulner et al. 2004
Romania (6)	8–15	MS (9), CR	0.54 (0.47–0.62)	0.88 (0.87–0.90)	0.500 (0.222–0.810)	0.644 (0.451–0.954)	Feulner et al. 2004

Haskovo, Bulgaria	7	MS (5), CR	0.74	0.85	0.667	0.986	Zachos et al. 2003
SW Spain	21	MS (8)	0.63	0.81	–	–	Hajji et al. 2008
SW Spain (17)	9–38	MS (6)	0.66 (0.58–0.74)	0.78 (0.70–0.85)	–	–	Martinez et al. 2002
L. Navas, Spain	12	CR	–	–	0.652	1.318	Zachos et al. 2003
France	14	MS (8)	0.63	0.77	–	–	Hajji et al. 2008
Vosges (France)	286	MS (14)	0.61	0.62	–	–	Frantz et al. 2008
Scotland (14)	28–67	MS (21)	0.76 (0.73–0.79)	0.78 (0.77–0.80)	–	–	Pérez-Espona et al. 2008
	25–60	CR	–	–	0.673 (0.253–0.836)	0.35 (0.01–0.57)	Pérez-Espona et al. 2009b
Scotland (6)	9–10	MS (11), CR	0.44 (0.39–0.48)	0.81 (0.78–0.84)	0.478 (0.000–0.733)	0.536 (0.000–810)	Hmwe et al. 2006b
England	10	MS (11), CR	0.50	0.76	0.356	0.729	Hmwe et al. 2006b
Ireland (4)	10–46	MS (9), CR	0.60 (0.50–0.69)	0.72 (0.55–0.85)	0.681 (0.492–0.808)	0.831 (0.157–1.639)	McDevitt et al. 2009
Grisons,	26–29	MS (18)	0.56 (0.55–0.60)	0.67 (0.65–0.68)	–	–	Kuehn et al. 2004
Switzerland (5)							
Liechtenstein	28	MS (18)	0.58	0.69	–	–	Kuehn et al. 2004
Paznaun, Austria	13	MS (18)	0.59	0.68	–	–	Kuehn et al. 2004
Vinschgau, Italy	27	MS (18)	0.51	0.67	–	–	Kuehn et al. 2004
Bavaria (Germany) and adjacent areas (11)	10–75	MS (19)	0.55 (0.50–0.61)	0.63 (0.53–0.67)	–	–	Kuehn et al. 2003
Hasselbusch, Germany**	18	MS (9), CR	0.58	0.66	0.493	0.337	Zachos et al. 2007
Denmark (14)	10–33	MS (11)	0.45 (0.32–0.57)	0.51 (0.37–0.57)	–	–	Nielsen et al. 2008
Norway (15)	15–68	MS (14)	–	0.61 (0.56–0.65)	–	–	Haanes et al. 2010a

n, sample size; AZ, allozymes, MS, microsatellite loci, CR, mitochondrial control region sequences, the number in parentheses refers to the number of loci analysed; H_o and H_e, observed and expected heterozygosity; h and π, haplotype and nucleotide diversity. If more than one population from the same region was analysed, the number of populations is given in parentheses, and diversity values are averaged over all populations. For enzyme markers, the total number of loci analysed is given (many of which may be monomorphic). Diversity analyses are based on the assumption that the loci chosen are representative of the overall genome, which may be violated in data sets based on few loci.

*Based on polymorphic loci only (therefore an order of magnitude higher than the other allozyme-based heterozygosities). **A small (n ≈ 50–60), isolated and inbred population.

As an important game species, red deer have been translocated for centuries or even millennia (Hartl et al. 2003). Interestingly, the large-scale phylogeographic pattern has not been blurred, at least as far as the mitochondrial (maternal-only) genome is concerned. While there are some exceptions to this rule (e.g. Skog et al. 2009, Niedziałkowska et al. 2010), in most cases the major problems with the identification of natural stocks come at a finer geographical scale. Feulner et al. (2004) found evidence of genetic integrity of the Carpathian red deer, notwithstanding the introduction of Austrian deer with multi-tine crowns, which took place in the 19th and early 20th centuries and left a morphological signature in the Carpathian population (Micu et al. 2009). Although the level of introgression may be low, even the Carpathian red deer are not truly natural anymore. Translocations, which are still being carried out, often illegally, can sometimes be identified with genetic tools, as was the case for a group of red deer in Luxembourg (Frantz et al. 2006). Scottish red deer have also been analysed to identify potential introductions. Pérez-Espona et al. (2009b) found evidence that the mitochondrial gene pool of deer from a region of the Scottish Highlands largely retained its naturalness, and Hmwe et al. (2006b) presented evidence that the pattern of genetic structure among Scottish red deer populations free from recorded introductions was more natural than in their overall data set. However, in most cases, it is impossible to unveil the local or even regional history of populations, and to confirm reliably that they are free from human-mediated admixture. Another methodological problem is the availability of genetic markers. While the identification of geographically large-scale units (like glacial lineages or 'subspecies') is usually based on mtDNA sequences, more recent (and local) demographic processes are most often addressed with nuclear microsatellites. Due to their high resolution power, microsatellites are suitable for the identification of even subtle genetic substructuring, but their high mutation rates and the lack of standardized data sets across Europe often make them less appropriate for studies beyond the local scale. mtDNA, on the other hand, only reveals the female side of the story and neglects the potentially frequent translocations of male deer which, due to the polygynous mating system, may have a disproportionately large impact on the genetic structure of local stocks if introduced stags are harem-holders. These methodological drawbacks may be overcome in the genomics era, but at present, our insights are limited. Y chromosome markers might uncover the male impact of translocations. Unfortunately, Y markers are not as variable as the mitochondrial genome, and are of limited applicability in intraspecific red deer studies (Barbosa and Carranza 2010), although Pérez-Espona et al. (2010), using a Y marker, were able to show that the introduction of wapiti in Scotland did not leave genetic traces in red deer in their study area.

Red deer/sika hybridization

Red deer and sika are closely related and produce fertile hybrids. Sika, native to eastern Asia, have been widely introduced in Europe and have a stronghold in the British Isles, but they are also widespread in the Czech Republic and can be found at various densities in other European countries (Apollonio et al. 2010). All European sika derive from Japanese populations, with the potential exception of some Czech sika that may be of mainland Asian origin (Goodman et al. 2001, Pitra et al. 2005, Barancekova et al. 2007). In the current management paradigm that aims at keeping populations as natural as possible, human-mediated hybridization is often viewed as

'genetic pollution'. Introgression of sika alleles into red deer populations (or vice versa, as in Austria; F. Suchentrunk, pers. comm.) has indeed been confirmed from different regions, where both species occur sympatrically, and is of interest for conservationists and game managers. A brief summary of the recent studies and reviews on this topic is presented here. Most analyses have addressed red/sika hybridization in the British Isles, where this phenomenon is more frequent than on the mainland. The evaluation of hybridization led to differing results and to some authors considering the genetic integrity of Scottish red deer to be threatened by sika introgression (Abernethy 1994). A re-analysis found more moderate hybridization, but still 40% of all individuals were introgressed in areas of sympatry (Goodman et al. 1999). The first records of red/sika hybridization (in Powerscourt Park, Wicklow, Ireland) after the introduction of sika to the British Isles in 1860 date back to the late 19th century (Pérez-Espona et al. 2009a). Hybridization has been estimated to occur once in 500–1000 mating events (Goodman et al. 1999), and is usually followed by backcrossing into the parental population. Assortative mating usually prevents hybridization between larger red and smaller sika deer, but hybridization increases phenotypic similarity between the two species, making further hybridization more likely (Senn et al. 2010b), and even low numbers of hybridization events may lead to substantial introgression at the population level (Senn et al. 2010a). When assortative mating breaks down, hybrid swarms may emerge, as is known from three areas: Wicklow in south-eastern Ireland, Cumbria in north-west England and West Loch Awe on the Kintyre Peninsula, Scotland (McDevitt et al. 2009, Pérez-Espona et al. 2009a, Senn & Pemberton 2009). Hybridization mainly occurs between red hinds and sika stags; hybrids frequently carry red deer mtDNA (Goodman et al. 1999, Senn & Pemberton 2009). Although smaller than red deer, sika stags may be successful due to their exceptional aggressiveness during the rut, and because red deer harems are dispersed over large areas with enough cover; a low number of successful sika stags may then trigger the hybridization process by simultaneously siring multiple hybrids (Pérez-Espona et al. 2009a, Senn & Pemberton 2009).

Selective hunting

Hunting, in particular if it is selective, has the potential to influence the genetic composition and fitness parameters of natural populations significantly (Milner et al. 2007). It has been shown that selective harvesting of red deer may drive adaptive responses from adult survival and growth to early and lightweight reproduction (Proaktor et al. 2007). Research in Spain has shown that different hunting practices result in different selection regimes with respect to body and antler size, which have different management implications (Torres-Porras et al. 2009). A general problem in selective hunting is that not only the desired traits are selected for, but also those linked with the traits under direct selection. Selective hunting for large and branched antlers was common practice in several European countries; both these phenotypic characteristics proved to be associated with particular genotypes at two biochemical marker loci (*Idh-2*, *Acp-2*). Homozygous carriers of certain alleles had a higher number of antler points and larger antlers. In two populations of deer in the Vosges mountains in France, directional selection of branched antlers resulted in significant allele frequency changes (Hartl et al. 1991, 1995). Homozygous and heterozygous genotypes at one of the marker loci (*Idh-2*) were found to be related to various fitness components in other red deer populations (juvenile survival, female fecun-

dity; Pemberton et al. 1988). As the genetic basis of the quantitative traits selected for is generally unknown (as is the degree of linkage with loci governing fitness components), this is a general caveat of selective harvesting regimes. The French study ultimately resulted in a change of local hunting practices in the Alsace: selective culling in favour of antler phenotypes was abandoned and replaced by hunting according to sex and age classes. Simulations by Mysterud and Bischof (2010) showed that trophy hunting does not always have detrimental evolutionary effects, although a case study on bighorn sheep *Ovis canadensis* clearly showed that trophy hunting resulted in a decline of body weight and horn size over time (Coltman et al. 2003).

Genetic drift is also relevant in the context of hunting. Hunting enclosures are often founded with a small number of individuals, without genetic exchange with other stocks. The concomitant increase in drift (Hartl et al. 1990) is potentially harmful as it may override the effects of natural selection. Martinez et al. (2002) found that hunted deer populations in Spain harboured lower levels of genetic diversity than protected ones and interpreted this as a consequence of increased genetic drift caused by the local hunting system.

Habitat fragmentation

The ever-increasing fragmentation of suitable habitat in human-dominated landscapes is probably the major present issue in red deer conservation and management. The concomitant isolation of populations leads to a decrease in N_e , which in turn results in higher levels of genetic drift and inbreeding. As a consequence, genetic variability is lost from each generation, and differentiation among formerly continuous stocks increases. A general problem in small populations – and in polygynous mammals such as red deer, N_e is *a priori* comparatively small – is that traits usually dominated by natural selection become effectively neutral, which means that their fate is governed by random drift effects. This may lead to the increase of harmful alleles, which further reduces N_e and completes the vicious circle ('mutational meltdown'). Apart from roads and settlements that cut through red deer habitat, hunting regulations often exacerbate the situation, if officially designated deer-free areas (aimed at reducing damage to forestry) in which all red deer are culled prevent migration. Fortunately, the threat posed by habitat fragmentation has been widely recognized, and as a consequence, red deer have been included in regional Red Lists to counteract the further loss of genetic variation (Zachos et al. 2007). Kuehn et al. (2003) showed that genetic structure in Bavarian red deer populations is today governed by genetic drift as a consequence of disrupted gene flow, while in the past, there was an equilibrium between drift and gene flow. Genetic structuring is expected to be more pronounced in females than in males in species with male-biased dispersal. For the red deer, this has mostly been confirmed (Frantz et al. 2008): female fine-scale structuring of <100m was found on the Isle of Rum, off Scotland (Nussey et al. 2005). Geographic distance, however, does not fully explain genetic differentiation: Pérez-Espona et al. (2008) found that landscape features such as mountains, rivers, lakes or forest patches impose differential migration costs on red deer, and significantly affect gene flow beyond simple distance. This implies that detailed habitat studies are necessary if meta-populations are to be successfully managed in cultivated landscapes. This topic has recently come into the focus of conservationists and game managers, and migration corridors and habitat connectivity are of recognized primary importance for gene flow among isolated popula-

tions. In northern Germany, a large project is being carried out combining telemetry studies on dispersal and migration behaviour with population genetic analyses, aimed at producing scientifically informed management plans and determining the need and optimal location of green bridges and/or translocations (F.E. Zachos & M. Meissner, unpublished data). This project was triggered by the fact that the remaining red deer populations are highly fragmented and that evidence of serious inbreeding depression (a fitness reduction due to mating among related individuals) is already present. Apart from generally low genetic diversity in northern Germany, one population (at Hasselbusch, Table 1) – after decades of isolation between fenced highways, roads and settlements and with a census size of only 50–60 animals – showed several cases of brachygnathia inferior (shortened lower jaw), a malformation known to be a consequence of inbreeding in many species, including humans (Zachos et al. 2007 and references therein, unpublished data). Inbreeding depression has also been confirmed for red deer on the Isle of Rum, where Slate et al. (2000) found that inbred animals showed a decrease in lifetime reproduction success. These studies highlight the importance of conservation genetics, even in a species as widely distributed and as common as the European red deer.

CONCLUSIONS AND PERSPECTIVE

The red deer is one of the most widespread, and both ecologically and economically most important, large mammal species in Europe. Its large-scale genetic structure and phylogeography, at least as assessed by mtDNA, has been uncovered: western, northern, most of central and parts of eastern Europe are inhabited by red deer from a south-western glacial refuge (Iberia/Southern France), while the Balkan/Carpathian lineage is largely confined to the south-east of the continent. A third haplogroup comprises Tyrrhenian and Barbary red deer. Equivalent studies using nuclear markers are underway. The genetic structure of red deer in the former refugial areas themselves is not yet completely clear. Although, except for in Mesola, all native Italian red deer became extinct, the patterns in Iberia and the Balkans deserve attention. For several species, it has been shown that Iberia harbours quite distinct lineages, indicative of multiple separate refugia, and a recent study has indeed confirmed this for red deer: two divergent groups were found in south-western and central-eastern Spain (J. Carranza, unpublished).

The impact that translocations have had on the phylogeographic pattern is not fully understood (particularly in those regions where red deer became extinct recently and were reintroduced subsequently), but in general, they do not seem to have blurred the overall structure. However, analyses of Croatian red deer showed that the country's two distribution regions of red deer seem to harbour exclusively western and eastern mtDNA haplotypes, respectively (J. Kosip, M. Niedziałkowska and F.E. Zachos, unpublished data). Future studies should aim to analyse the ecological consequences of such introductions, as was recently done for a Norwegian population (by Haanes et al. 2010b, who found hybrid vigour rather than detrimental effects).

Conservation efforts in red deer should also concentrate on the protection of unique genetic lineages such as Tyrrhenian, Barbary and Mesola red deer, whether or not they are acknowledged taxonomically. For the Barbary red deer, it is important, finally, to include Algerian data, and to combine conservation efforts in both countries. The Sika is present in many European countries, and in the wake of the

recent range expansions, the species might come into contact and hybridize more often than in the past. This is, for example, a matter of concern in northern Germany, where red deer are currently expanding into regions where previously only sika occurred. By far the most important issue in red deer conservation and management in large parts of Europe, however, is the direct impact of humans, mainly through habitat fragmentation and the concomitant increase in drift and inbreeding. The development of stable meta-population networks by providing corridors and habitat connectivity will be critical to the viability of populations of red deer in the future.

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Submitted 6 October 2010; returned for revision 10 November 2010; revision accepted 2 December 2010

Editor: KH