Burger et al. /Journal of Camelid Science 2026, 19:10-25
http://www.isocard.info/journal_camelid

Wild camel (*Camelus ferus*) conservation genomics: Twenty^{+} years of genetic research

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Submitted: September 19, 2025; **Accepted:** February 19, 2026; **Published:** June 15, 2026

Abstract

The integration of genomic data in the monitoring of wild populations plays an important role for the development of conservation and management strategies. Conservation genetic studies have been essential to investigate the genetic and ecological status-quo of wild camels in their natural habitat. First described by Nikolaj Przewalski in 1878, wild camels were once distributed throughout the desert areas of Central Asia. Today, they have become restricted to four separated desert areas of China (the Gashun Gobi, Lop Nur, Taklamakan) and Mongolia (Great Gobi A Strictly Protected Area) with an estimated population size between 400 and 1100 individuals. The species status of the wild two-humped camel has long been under debate. Morphological resemblances with its domestic congener led to the assumption that wild camels were merely descendants of domestic animals that returned to the wild. Notably, the International Commission of Nomenclature (2003) ascribed the first available specific name based on a wild population "*Camelus ferus*" to the wild camel. An important step for the conservation of the wild camel was the confirmation of its legal species status and its long-term divergence from the domestic Bactrian camel around 1.1 [0.58–1.8] million years ago. Through genome-wide analysis, we detected introgression of domestic camel genes in the Mongolian wild camel genomes. In this review article, we give an overview about the achievements of over more than 20 years in wild camel genomic research. Particularly, we emphasize that wild two-humped camels are an evolutionary significant species, which are threatened by hybridization with domestic two-humped camels. We reflect that parts of the genome in wild camels show a reduced amount of diversity when compared to Bactrian camels, including genes involved in immune response and shy behaviour. Ongoing genetic monitoring efforts aim to support the conservation of these Critically Endangered (IUCN) animals.

Keywords: Introgression, Immune response gene diversity, Positive selection

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1. Introduction

With the development of next generation sequencing, the inclusion of genomic data into conservation and management decisions for wild populations has become feasible. In the conservation and management of small, domesticated populations as well as in natural wild populations, we are confronted with parallel challenges: (i) a small effective population size (Ne) accompanied by evolutionary forces like genetic drift or natural selection, (ii) inbreeding along with a high risk of inbreeding depression, and (iii) the potential benefits and costs of genetic admixture (hybridization) with a more distant gene pool (Kristensen et al. 2015). Genomic tools developed for genomic selection to increase genetic gain in livestock, as well as for understanding the genetic architecture of production traits, can be used to identify genomic regions associated with adaptation to different environmental variables, and as such, maximize the adaptive potential of local natural populations and evolutionary significant units (ESUs; Funk et al. 2012). There are many extant wild species that are either (closely) related to a domestic species (e.g., wild camel, Przewalski's horse, Khulan), or are their direct ancestors (e.g., guanaco, vicuña, wolf, Mouflon, ibex, wild boar). High-density single nucleotide polymorphism (SNP) arrays or whole (reference) genomes developed for a domestic species, such as the ones established for camel (Fitak et al. 2020, Lado et al. 2020), or for horse (Gaunitz et al. 2018) and dog (Gopalakrishnan et al. 2017), can offer much information about the evolutionary history of the wild ancestral species, which often is endangered or even at the edge of extinction.

Mobilizing resources and efforts for the genomic monitoring and conservation of the wild ancestors of our livestock is also an investment in the domestic breeds, as preserving (ancestral) genetic variation is important for the evolutionary potential of a species (Groeneveld et al. 2010). In this review based on 55 papers, we unroll the progress of genomic research in the Critically Endangered wild camel (*Camelus ferus*).

2. The wild camel (*Camelus ferus*)

2.1 Species status of the wild camel

Modern camels belong to the order of Artiodactyla (even-toed ungulates), suborder Tylopoda, and the family of Camelidae consisting of the tribes Camelini (Old World camels) and Lamini (New World camels), which diverged 16.3 [9.4-25.3] million years ago (mya) (Wu et al. 2014). Within Old World camels, three species are recognized today: the domesticated one-humped *Camelus dromedarius* and two-humped *Camelus bactrianus*, and the only remaining wild species, the two-humped *Camelus ferus*. While one- and two-humped camels diverged around 4.4 [1.9-7.2] mya (Wu et al. 2014), the split between the ancestors of wild and domestic Bactrian camels is more recent and was estimated at 1.1 [0.6-1.8] mya (Mohandesan et al. 2017, Ji et al. 2009).

In 1874, the Russian explorer Nikolaj Przewalski identified wild two-humped camels for the first time as being different from domestic Bactrian camels in terms of smaller pointier humps and flatter skulls. Although wild camels might have been distributed throughout Central Asia, it is difficult to reconstruct their original distribution, as remains from archaeological sites, rock art and historical writings are rare (Peters and von den

Driesch 1997). Today, their range is restricted to three small areas in China – the Taklamakan desert, Gashun Gobi desert and the Arjin Mountains at the Lop Nor (Lei et al. 2012) – and one in Mongolia – the Great Gobi A Strictly Protected Area (SPA) (Kaczensky et al. 2014, Yadamsuren et al. 2019). These four locations are now the last refuges for wild camels, which are listed as Critically Endangered by the International Union for Conservation of Nature (IUCN 2020). Current estimates of the remaining animals range between 400 and 1100 individuals (Yadamsuren et al. 2012, Yadamsuren et al. 2019, Lei et al. 2012).

The species status of the wild two-humped camel has long been under debate. Morphological resemblances with its domestic congener led to the assumption that wild camels were merely descendants of domestic animals that returned to the wild (Peters and von den Driesch 1997). The International Commission of Nomenclature (2003) designated "*Camelus ferus*" to the wild camel, because it was the initial name given to the wild population by Przewalski in 1874 (Gentry et al. 2004). The name for the wild camel in Mongolia is хавтгай (khavtgai), translating to 'flat head'. In China, the animal is called 野骆驼 (ye luo tuo), which means 'wild camel' (Jemmett et al. 2023). Genetic and genomic studies (Ji et al. 2009, Silbermayr et al. 2010, Jirimutu et al. 2012, Mohandesan et al. 2017a, Yi et al. 2017) confirmed the wild camel as a separate species, *Camelus ferus*, which has never been domesticated.

2.2 Genomic research in the wild camel

The earliest molecular genetic studies used mitochondrial DNA (mtDNA) to understand the evolutionary relationship between the wild and domestic two-humped camel (Jianlin et al. 1999; Jianlin et al. 2004; Ji et al. 2009; Silbermayr et al. 2010) and between Bactrian camels and dromedaries (Kadwell et al. 2001). MtDNA and microsatellites have been (and still are) employed to investigate genetic diversity, population structure, and hybridization in national and international studies (e.g., Chuluunbat et al. 2014, Silbermayr and Burger 2012).

With the advancement of next generation sequencing techniques, the first de novo assemblies of the wild camel (Jirimutu et al. 2012), domestic Bactrian camels (Burger and Palmieri 2014; Wu et al. 2014) and dromedaries (Wu et al. 2014, Fitak et al. 2015) were presented, however, in rather fragmented form and only on scaffold-level. High-quality chromosome-level reference genome assemblies now are finally available (Lado et al. 2020; Ming et al. 2020a; Elbers et al. 2019). The chromosome-level assembly of the wild camel genome is based on high-coverage long-read sequencing and chromatin interaction mapping. With a contig N50 of 5.37 Mb and a scaffold N50 of 76.03 Mb, this assembly represents the most contiguous wild camel genome to date (Ming et al. 2020a). The first large-scale genome-wide population studies were published about the origin and migration of Bactrian camels (Ming et al. 2020b), and post-domestication migration routes of worldwide dromedaries (Lado et al. 2020). With the genomic tools available now, it is possible to identify the genomic basis for desirable production traits but also for the evolutionary significant physiological adaptations in camels.

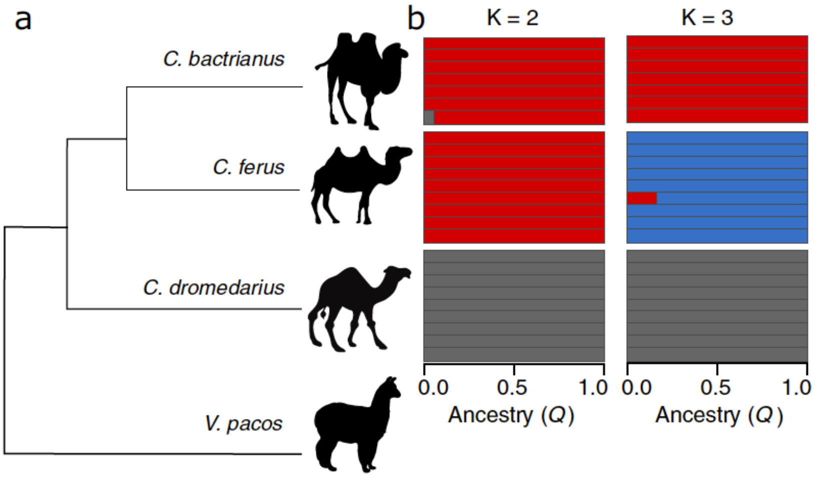


Figure 1. (a) Phylogenetic relationship among Old World camels using alpaca as an outgroup. (b) Each horizontal bar corresponds with the ancestry proportion of one individual in either two or three population clusters. Introgression from domestic camel genes in a wild camel genome is visible. Source: Fitak et al. (2020), open access under the Creative Commons Attribution 4.0 International License.

2.3 *Immune genomic research in the wild camel*

The diversity in immune response (IR) genes is a key parameter for the adaptability and resilience of a species to environmental challenges and emerging pathogens. Hence, a better understanding of IR genomic diversity will support conservation and sustainable management of wild two-humped camels in the Mongolian Great Gobi, Chinese Taklimakan and Lop Nur deserts. When we compared nucleotide diversity among domestic and wild two-humped camel species, wild camels had a lower mean nucleotide diversity in IR genes, except for the major histocompatibility complex (MHC) class I and II genes, and for nonsynonymous SNPs in adaptive IR genes (Fig. 2). In general, the domestic Bactrian camel had a higher mean nucleotide diversity compared to the wild camel (Lado et al. 2020). Wild camels have experienced a strong population decline over the last decades that has led to the current status of Critically Endangered (IUCN). This reduction in effective population size could be a possible explanation for the described lower genome-wide diversity in wild camels. With the number of individuals decreasing, loss of genetic diversity is unfortunately real. Large parts of the immune genome of *Camelus ferus* have been characterized by Ming et al. (2020a) and Lado et al. 2020), including the major histocompatibility complex (MHC), which is located on the long arm of chromosome 20 (Plasil *et al.* 2016) and has a similar structure (MHC class II – III – I) like in other mammals (Plasil *et al.* 2019a, Plasil *et al.* 2019b, Futas *et al.* 2019).

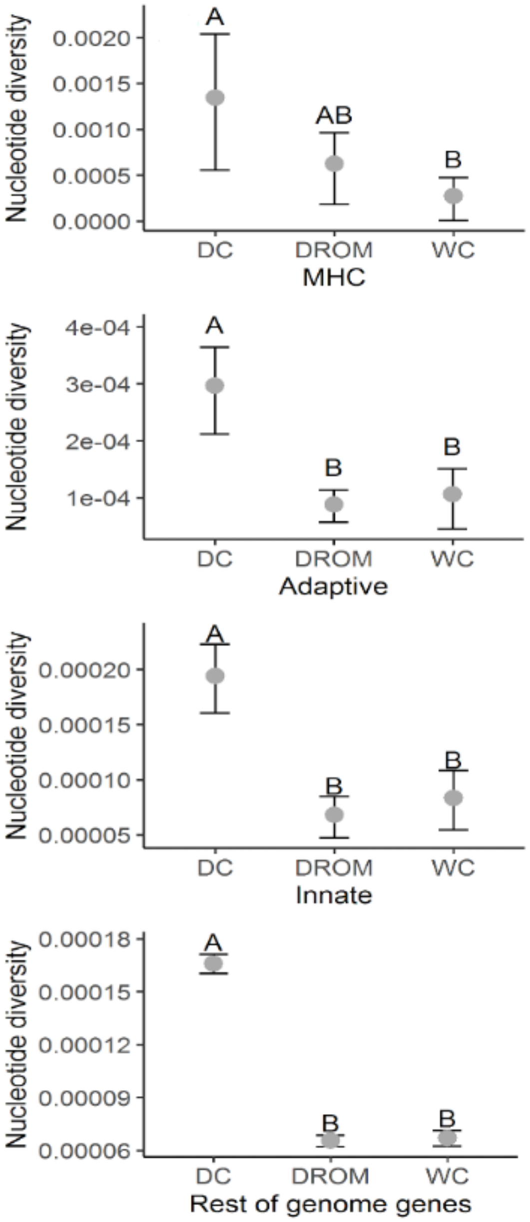


Figure 2. Nucleotide diversity (means with 95 % bootstrap confidence intervals) based on non-synonymous and synonymous SNPs and indels in MHC class I and II genes (top panel), innate (second panel), adaptive (third panel) immune response genes, and the rest of genome genes (bottom panel) for: DROM (*C. dromedarius*), DC (*C. bactrianus*), and WC (*C. ferus).* Source: Supplementary figure 3. In: Lado et al. (2020), open access under the Creative Commons Attribution 4.0 International License.

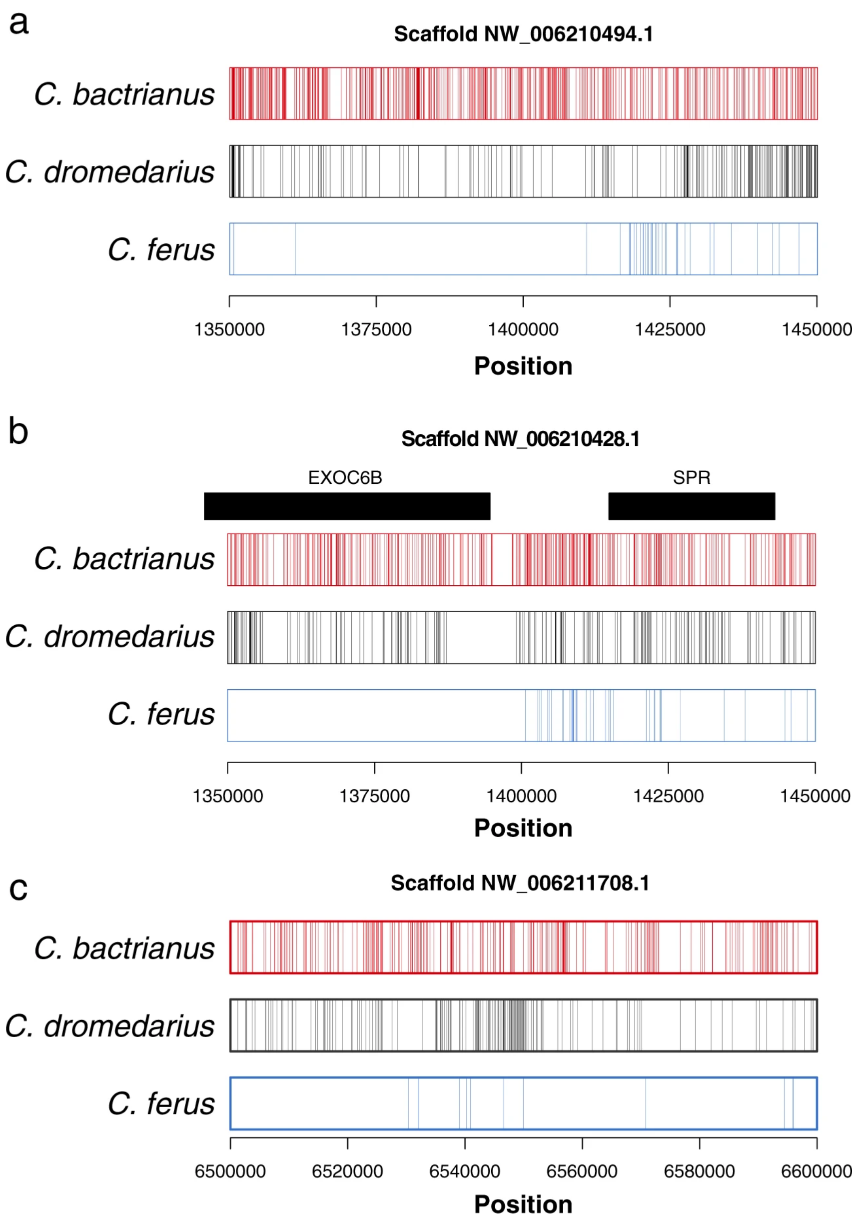
Camelids are the only mammals that produce heavy-chain homodimeric immunoglobulins (IGs) without a light chain and with the antigen-binding fragment reduced to a single heavy-chain variable domain, in addition to the conventional antibodies (Ciccarese et al. 2019, Arbabi-Ghahroudi 2017, Muyldermans et al. 2009). The unique features of these nanobodies make them useful in biotechnology and for clinical applications, e.g., in active targeting cancer therapy, which applies camelid nanobodies for the specific delivery of an active drug (Jovčevska and Muyldermans 2020), and for developing a treatment for COVID-19 (Wrapp et al. 2020).

The genomic organization of immunoglobulin heavy-chain locus was similar between the wild camel and alpaca, and genes encoding for conventional and heavy-chain antibodies were intermixed (Ming et al. 2020a). Furthermore, camel T-cell receptors (TR) and their genes are quite unique in terms of their structure and function, as somatic hypermutations in the TR gamma (TRG) and delta (TRD) loci increase their repertoire diversity (Antonacci et al. 2020, Ciccarese et al. 2019). The organizations of two immunoglobulin light-chain loci and four T-cell receptor loci were also fully deciphered using the wild camel genome assembly. Additionally, the complete classical MHC region was resolved into a single contig (Ming et al. 2020a).

2.4 Signals of positive selection in wild camels

Three specific regions in the wild camel genome showed signals of positive selection (i.e., negative measure of Tajima's $D \leq -2$) when compared to the domestic Bactrian camel. One of the regions contained two protein-coding genes, *SPR* and *EXOC6B* (Fig. 3), which might be related to timid or aggressive behaviour in wild camels. A region containing both these genes has been described as differentiating between tame and aggressive silver foxes. In humans, deficiencies in SPR cause dystonia – uncontrollable muscular contractions, psychomotor retardation, and progressive neurologic deterioration. The gene *EXOC6B* is part of the exocyst complex, which is critical for cellular trafficking, and mutations *in EXOC6B* have been associated with intellectual disability, language delay, hyperactivity, ear malformations, and craniofacial abnormalities in humans (Fitak et al. 2020).

In wild and domestic camels, it was furthermore shown that they have a higher number of copies of *CYP2J* and *CYP2E* genes than cattle, horses and humans. The activity of *CYP2J2* is regulated by a high-salt diet and its suppression can lead to high blood pressure. Camels are known to be able to take in a large amount of salt apparently without developing hypertension, perhaps because they have more copies of *CYP2J* genes (Jirimutu et al. 2012).


a
Scaffold NW_006210494.1
C. bactrianus
C. dromedarius
C. ferus
1350000
1375000
1400000
1425000
1450000
Position
b
Scaffold NW_006210428.1
EXOC6B
SPR
C. bactrianus
C. dromedarius
C. ferus
1350000
1375000
1400000
1425000
1450000
Position
c
Scaffold NW_006211708.1
C. bactrianus
C. dromedarius
C. ferus
6500000
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6540000
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Position

Figure 3. Regions of positive selection in the wild camel genome. The three 100-kb windows in *Camelus ferus* (a–c) were found to contain evidence of positive selection. The location of variants within each species are shown as vertical lines and overlapping genes as black bars. While in the domesticates species the three regions show high variation, they are almost fixed in the wild camel. Source: Fitak et al. (2020), open access under the Creative Commons Attribution 4.0 International License.

3. Conservation and genetic monitoring of wild camels

3.1 Introgression and hybridization between wild and domestic camels

Natural hybridization between two taxa is an important driver of evolution, mainly in plants, but also in animal species (Baack and Rieseberg 2007). In livestock, anthropogenic hybridization between different populations, breeds, or species aims at creating a heterosis or hybrid vigour effect, i.e., an increase in body mass, fertility and production traits in the first (F1) generation (Birchler et al. 2006). Consecutive interbreeding of F1/F2 hybrids usually results in a reduction or loss of fertility and other traits due to genetic incompatibilities and outbreeding depression (Allendorf and Luikart 2007).

In Old World camels, the practice of crossbreeding between dromedaries and Bactrian camels began in Roman times (Çakırlar and Berthon 2014) and was associated with the transport of goods along the Silk Road. This practice intended to produce animals with the robustness of the Bactrian camel, the endurance of dromedary, and the ability to tolerate sharply contrasting climatic conditions (Wilson 1984). Today, hybridization facilitates improved milk and wool yield in hybrid Tulu or Nar camels from Middle Eastern and Central Asian countries, with elaborate schemes of backcrossing with either parental species (Faye and Konuspayeva 2012). In western regions of Turkey, a relished sport is camel wrestling, where prized male Tulus compete against each other in heavily regulated fights (Çakırlar and Berthon 2014).

While hybridization refers to the interbreeding of individuals from two populations, breeds, or species with different heritable traits, introgression is the permanent incorporation of genes from one population to another, i.e., the introduction of "alien" genes into a new, reproductively integrated population (Rieseberg and Wendel 1993). Favourable among domestic breeds to increase production traits, introgression between domestic animals and their wild progenitors poses a threat to the wild, often-endangered species. There are multiple examples in the wild, as it has been shown in wolves and dogs (Pilot et al. 2018; Anderson et al. 2009), the European wildcat (Beaumont et al. 2001), and bison and cattle (Halbert and Derr 2006). The Critically Endangered (IUCN) wild camels in Mongolia and China are threatened by hybridization with domestic Bactrian camels, which are kept in large numbers close to the protected areas. In some cases, hybridization of domestic females with wild bulls is initiated to enhance the fitness of domestic camels (Yadamsuren et al. 2012). Continuous introgression can lead to intrinsic (genetic incompatibility) or extrinsic (reduced fitness due to loss of local adaptation) outbreeding depression and ultimately to a "hybrid swarm" or the complete extinction of the wild population (Allendorf and Luikart 2007).

Introgression of domestic Bactrian camel genes into wild camels has been demonstrated in mitochondrial (Silbermayr et al. 2010) and nuclear DNA (Jemmet 2025, Fitak et al. 2020, Silbermary and Burger 2012) as shown in Figures 1 and 4. Among 204 potentially pure wild camels investigated, the amount of detected hybrids was 28.3% using a threshold of 5% of domestic camel ancestry (Jemmett, 2025). Unexpectedly, there was introgression observed also in the Y-chromosome, as one wild camel clustered into the domestic Bactrian camels' haplogroup (Felkel et al. 2019). The observation of a domestic paternal lineage within the wild camel population is concerning in view of the importance to conserve the genetic integrity of these Critically Endangered species in their natural habitat.

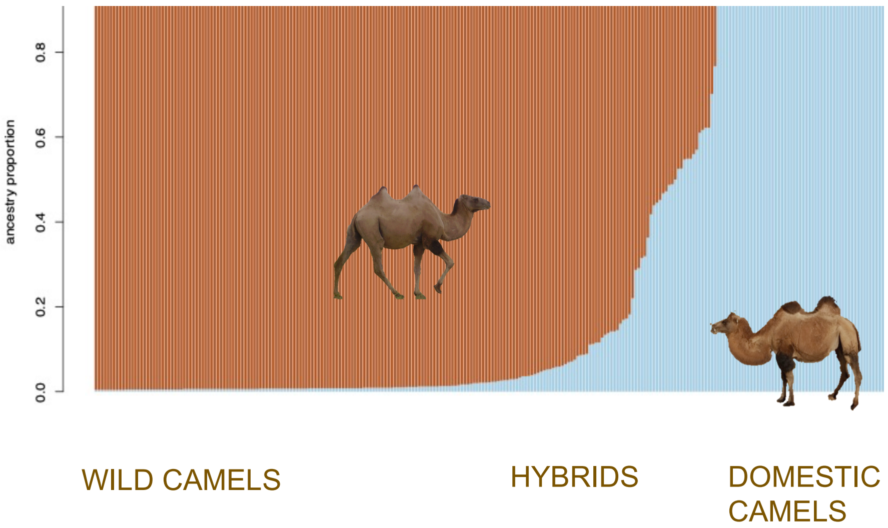

Figure 4. Admixture plot displaying the ancestry proportions for each individual camel (single bars) based on 16 microsatellite loci. Wild camel ancestry is depicted in the brown colour, while the domestic Bactrian camel genetic background is shown in blue. Hybrid camels collected in the Great Gobi A Strictly Protected Area show mixed ancestry. Source data to create this figure originated from Jemmett (2025).

3.2 Monitoring of genetic diversity and hybridization in wild camels

Biodiversity worldwide is in alarming decline. About 31,000 species, equivalent to 27% of all assessed organisms, are threatened with extinction, and many more are near threatened or vulnerable (IUCN 2020). Genetic diversity, and species diversity, is fundamental for stable, functional and adaptive ecosystems, which provide vital services such as natural products, air and water filtration, water storage, habitat creation and carbon sequestration. The resilience of an ecosystem will depend on the conservation of its constituent species' diversity, which enables combined adaptive responses to a changing climate and/ or land use. Likewise, livestock diversity is at risk with 17% (1,458) of the worldwide farm animal breeds currently being exposed to extinction, while the risk status of 58% is even not known due to missing data on the structure and size of their populations (Pilling and Rischkowsky 2007).

In Old World camels, we observe both phenomena: (i) the threat of extinction for the last remaining wild camels, *Camelus ferus* and (ii) the need to preserve genetic diversity in the two domestic species *Camelus bactrianus* and *Camelus dromedarius*, which provide vital products for thousands of people in marginal agro-economic zones. The conservation status of wild camels in Mongolia and China has been Critically Endangered on the IUCN Red List of Threatened Species since 2002 (IUCN 2024). The Zoological Society of London identified wild camels as one of the top ten focal species within the EDGE (Evolutionarily Distinct and Globally Endangered) program, which prioritizes conservation of species at the edge of extinction (www.edgeofexistence.org). The major threats to the survival of wild camels are habitat loss, desertification and grazing competition with domestic Bactrian camels, illegal hunting and poaching, wolf predation and hybridization (Yadamsuren et al. 2019; Lei et al. 2012).

Wild camels have been protected in the Mongolian Great Gobi A Strictly Protected Area since 1982, managed by the Mongolian Ministry of Agriculture with the support of the Wild Camel Protection Foundation (www.wildcamels.com) and in the Lop Nur Wild Camel National Nature Reserve in China established in 2000. Hybridization monitoring assays have been developed for (i) mtDNA (Silbermayr et al. 2010), (ii) Y-chromosome (Felkel et al. 2019), and nuclear microsatellites (Jemmett 2025).

Working in conservation with limited resources, there is always the question, what should be conserved (Allendorf and Luikart 2007). Different national and international bodies (e.g.., IUCN) endeavour to define conservation and prioritization strategies. While some argue for conserving the products of evolution (e.g., monophyletic species), others advocate saving the process of evolution per se, i.e., the dynamics underlying biodiversity at all levels (Templeton 2002) with regard to functional ecosystem services (Luck et al. 2003).

The EDGE (Evolutionary Distinct and Globally Endangered) of Existence program of the Zoological Society of London (ZSL) prioritizes conservation of threatened species by scoring every species in a particular taxonomic group according to the amount of unique evolutionary history (based on phylogeny) and its conservation status (based on the IUCN Red List of Threatened Species (IUCN 2020)). There are currently over 585 EDGE mammal species (around 10% of all species), and the top 100 represent the most unique species for which conservation action is of utmost importance (https://www.edgeofexistence.org/download-edge-lists/; accessed on 31.07.2025). The wild camel (*Camelus ferus*) is listed in the 28th place among mammals due to its monophyletic position within the Camelidae evolutionary tree, as we have shown (Mohandesan et al. 2017, Silbermayr et al. 2010, Jirimutu et al. 2012) and its conservation status is shown as Critically Endangered (IUCN 2024). As such, wild camels are the only surviving wild species within the genus Camelus. Besides their evolutionary significance, wild camels are an important umbrella species, because parts of their natural range lie in the unique ecosystem of the Mongolian Great Gobi A Strictly Protected Area, which has been included in the UNESCO Biosphere Reserve System since 1992. Under the umbrella of wild camels, several other large mammals and flora listed in the Mongolian Red Book are being protected as well, including snow leopard, Khulan, Goitered Gazelle, Aragali sheep, Ibex, and the endemic Gobi Brown bear (Yadamsuren et al. 2019, ZSL and IUCN National Red List Working Group 2022).

Conservation monitoring started in 2006 (Silbermayr et al. 2010, Silbermayr and Burger 2012, and continues combining genetic and ecological methods (Jemmett 2025, Felkel et al. 2019). There are on-going efforts from the Wild Camel Protection Foundation (WCPF) together with the Zoological Society of London, Prague Zoo, Knowsley Safari Park, Universities of Cardiff and Kent, and Vetmeduni Vienna for the *in situ* conservation of wild camels in the Great Gobi A SPA and the Lop Nor, and for effective support of a wild camel captive breeding herd outside of the protected areas. At the moment, the full genomes of wild camels from the WCPF wild camel breeding centre and from the Great Gobi A SPA are sequenced to investigate (immune) genomic diversity, genetic load and hybridization with domestic Bactrian camels.

References

Allendorf, F.W., Hohenlohe, P.A., Luikart, G.: Genomics and the future of conservation genetics. Nature Reviews Genetics 11, 697-709 (2010).

Anderson, T.M., vonHoldt, B.M., Candille, S.I., Musiani, M., Greco, C., Stahler, D.R., Smith, D.W., Padhukasahasram, B., Randi, E., Leonard, J.A., Bustamante, C.D., Ostrander, E.A., Tang, H., Wayne, R.K., Barsh, G.S.: Molecular and Evolutionary History of Melanism in North American Gray Wolves. Science 323, 1339-1343 (2009).

Antonacci, R., Linguiti, G., Burger, P.A., Castelli, V., Pala, A., Fitak, R., Massari, S., Ciccarese, S.: Comprehensive genomic analysis of the dromedary T cell receptor gamma (TRG) locus and identification of a functional TRGC5 cassette. Developmental & Comparative Immunology 106, 103614 (2020).

Arbabi-Ghahroudi, M.: Camelid Single-Domain Antibodies: Historical Perspective and Future Outlook. Frontiers in Immunology 8 (2017).

Baack, E.J., Rieseberg, L.H.: A genomic view of introgression and hybrid speciation. Current

Opinion in Genetics & Development 17, 513-518 (2007).

Beaumont, M., Barratt, E.M., Gottelli, D., Kitchener, A.C., Daniels, M.J., Pritchard, J.K., Bruford, M.W.: Genetic diversity and introgression in the Scottish wildcat. Molecular Ecology 10, 319-336 (2001).

Birchler, J.A., Yao, H., Chudalayandi, S.: Unraveling the genetic basis of hybrid vigor. Proceedings of the National Academy of Sciences of the United States of America 103, 12957-12958 (2006).

Burger, P.A., Palmieri, N.: Estimating the Population Mutation Rate from a de novo Assembled Bactrian Camel Genome and Cross-Species Comparison with Dromedary ESTs. Journal of Heredity 105, 839-846 (2014).

Çakırlar, C., Berthon, R.: Caravans, camel wrestling and cowrie shells: Towards a social zooarchaeology of camel hybridization in Anatolia and adjacent regions. Anthropozoologica 49, 237-252 (2014).

Ciccarese, S., Burger, P.A., Ciani, E., Castelli, V., Linguiti, G., Plasil, M., Massari, S., Horin, P., Antonacci, R.: The Camel Adaptive Immune Receptors Repertoire as a Singular Example of Structural and Functional Genomics. Frontiers in Genetics 10, 997 (2019).

Chuluunbat, B., Charruau, P., Silbermayr, K., Khorloojav, T., Burger, P.A. Genetic diversity and population structure of Mongolian domestic Bactrian camels (Camelus bactrianus). Animal Genetics 45, 550-558 (2014).

Elbers, J.P., Rogers, M.F., Perelman, P.L., Proskuryakova, A.A., Serdyukova, N.A., Johnson, W.E., Horin, P., Corander, J., Murphy, D., Burger, P.A.: Improving Illumina assemblies with Hi-C and long reads: An example with the North African dromedary. Molecular Ecology Resources 19, 1015-1026 (2019).

Faye, B., Konuspayeva, G.: The encounter between Bactrian and dromedary camels in Central Asia. In: Knoll, E.M., Burger, P.A. (eds) Camels in Asia and North Africa. Interdisciplinary perspectives on their significance in past and present. Austrian Academy of Sciences, Vienna, pp 29-36 (2012).

Felkel, S. Wallner, B. Chuluunbat, B. Yadamsuren, A. Faye, B. Brem, G., Walzer, C., Burger, P.A.: A First Y-Chromosomal Haplotype Network to Investigate Male-Driven Population Dynamics in Domestic and Wild Bactrian Camels. Frontiers in Genetics 10, 423 (2019).

Fitak, R.R., Mohandesan, E., Corander, J., Yadamsuren, A., Chuluunbat, B., Abdelhadi, O., Raziq, A., Nagy, P., Walzer, C., Faye, B., Burger, P.A.: Genomic signatures of domestication in Old World camels. Communications Biology 3, 316 (2020).

Funk, W.C., McKay, J.K., Hohenlohe, P.A., Allendorf, F.W.: Harnessing genomics for delineating conservation units. Trends in Ecology & Evolution 27: 489-496 (2012).

Futas, J., Oppelt, J., Jelinek, A., Elbers, J.P., Wijacki, J., Knoll, A., Burger, P.A., Horin, P.: Natural Killer Cell Receptor Genes in Camels: Another Mammalian Model. Frontiers in Genetics 10, 620 (2019).

Gaunitz, C., Fages, A., Hanghøj, K., Albrechtsen, A., Khan, N., Schubert, M., Seguin-Orlando, A., Owens, I.J., Felkel, S., Bignon-Lau, O., de Barros Damgaard, P., Mittnik, A., Mohaseb, A.F., Davoudi, H., Alquraishi, S., Alfarhan, A.H., Al-Rasheid, K.A.S., Crubézy, E., Benecke, N., Olsen, S., Brown, D., Anthony, D., Massy, K., Pitulko, V., Kasparov, A., Brem, G., Hofreiter, M., Mukhtarova, G., Baimukhanov, N., Lõugas, L., Onar, V., Stockhammer, P.W., Krause, J., Boldgiv, B., Undrakhbold, S., Erdenebaatar, D., Lepetz, S., Mashkour, M., Ludwig, A., Wallner, B., Merz, V., Merz, I., Zaibert, V., Willerslev, E., Librado, P., Outram, A.K., Orlando, L.: Ancient genomes revisit the ancestry of domestic and Przewalski's horses. Science 360: 111-114 (2018).

Gentry, A., Clutton-Brock, J., Groves, C.P.: The naming of wild animal species and their domestic derivatives. Journal of Archaeological Science 31, 645-651 (2004).

Gopalakrishnan, S., Samaniego Castruita, J.A., Sinding, M.-H.S., Kuderna, L.F.K., Räikkönen, J., Petersen, B., Sicheritz-Ponten, T., Larson, G., Orlando, L., Marques-Bonet, T., Hansen, A.J., Dalén, L., Gilbert, M.T.P.: The wolf reference genome sequence (Canis lupus lupus) and its implications for Canis spp. population genomics. BMC Genomics 18: 495 (2017).

Groeneveld, L.F., Lenstra, J.A., Eding, H., Toro, M.A., Scherf, B., Pilling, D., Negrini, R., Finlay, E.K., Jianlin, H., Groeneveld, E., Weigend, S., The, G.C.: Genetic diversity in farm animals – a review. Animal Genetics 41: 6-31 (2010).

Halbert, N.D., Derr, J.N.: A Comprehensive Evaluation of Cattle Introgression into US Federal Bison Herds. Journal of Heredity 9, 1-12 (2006).

Jemmet, A.: Conservation genetics and population surveys of the critically endangered wild camel Camelus ferus in Mongolia. – PhD thesis. Kent Academic Repository - University of Kent (2025).

Jemmett, A. M., Groombridge, J. J., Hare, J., Yadamsuren, A., Burger, P. A., Ewen, J. G.: What's in a name? Common name misuse potentially confounds the conservation of the wild camel Camelus ferus. Oryx, 57, 175-179 (2023).

Ji, R., Cui, P., Ding, F., Geng, J., Gao, H., Zhang, H., Yu, J., Hu, S., Meng, H.: Monophyletic origin of domestic bactrian camel (Camelus bactrianus) and its evolutionary relationship with the extant wild camel (Camelus bactrianus ferus). Animal Genetics 40, 377-382 (2009).

Jianlin, H., Jiexia, Q., Zhenming, M., Yaping, Z., Wen, W.: Rapid Communication: Three Unique Restriction Fragment Length Polymorphisms of EcoRI, PvuII, and ScaI Digested Mitochondrial DNA of Bactrian Camels (Camelus bactrianus ferus) in China. Journal of Animal Science 77, 2315-2316 (1999).

Jianlin, H., Ochieng, J.W., Lkhagva, B., Hanotte, O.: Genetic diversity and relationship of domestic Bactrian camels (Camelus bactrianus) in China and Mongolia. Journal of Camel Practice and Research 11, 97-99 (2004).

Jirimutu, Wang, Z., Ding, G., Chen, G., Sun, Y., Sun, Z., Zhang, H., Wang, L., Hasi, S., Zhang, Y., Li, J., Shi, Y., Xu, Z., He, C., Yu, S., Li, S., Zhang, W., Batmunkh, M., Ts, B., Narenbatu, Unierhu, Bat-Ireedui, S., Gao, H., Baysgalan, B., Li, Q., Jia, Z., Turigenbayila, Subudenggerile, Narenmanduhu, Wang, Z., Wang, J., Pan, L., Chen, Y., Ganerdene, Y., Dabxilt, Erdemt, Altansha, Altansukh, Liu, T., Cao, M., Aruuntsever, Bayart, Hosblig, He, F., Zha-ti, A., Zheng, G., Qiu, F., Sun, Z., Zhao, L., Zhao, W., Liu, B., Li, C., Chen, Y., Tang, X., Guo, C., Liu, W., Ming, L., Temuulen, Cui, A., Li, Y., Gao, J., Li, J., Wurentaodi, Niu, S., Sun, T., Zhai, Z., Zhang, M., Chen, C., Baldan, T., Bayaer, T., Li, Y., Meng, H., The Bactrian Camels Genome Consortium: Genome sequences of wild and domestic bactrian camels. Nature Communications 3, 1202 (2012).

Jovčevska, I., Muyldermans, S. The Therapeutic Potential of Nanobodies. BioDrugs 34, 11-26 (2020).

Kadwell, M., Fernandez, M., Stanley, H.F., Baldi, R., Wheeler, J.C., Rosadio, R., Bruford, M.W.: Genetic analysis reveals the wild ancestors of the llama and the alpaca. Proceedings of the Royal Society of London B 268, 2575-2584 (2001).

Kristensen, T.N., Hoffmann, A.A., Pertoldi, C., Stronen, A.V.: What can livestock breeders learn from conservation genetics and vice versa?Frontiers in Genetics 6: 38 (2015).

Lado, S., Elbers, J.P., Doskocil, A., Scaglione, D., Trucchi, E., Banabazi, M.H., Almathen, F., Saitou, N., Ciani, E., Burger, P.A.: Genome-wide diversity and global migration patterns in dromedaries follow ancient caravan routes. Communications Biology 3, 387 (2020).

Lado, S., Elbers, J. P., Rogers, M. F., Melo-Ferreira, J., Yadamsuren, A., Corander, J., Horin, P., & Burger, P. A.: Nucleotide diversity of functionally different groups of immune response genes in Old World camels based on newly annotated and reference-guided assemblies. BMC genomics 21, 606 (2020).

Lei, Y., Hare, J., Guoying, Y., Yun, C.: The status of the wild camel in China. In: Knoll, E.M., Burger, P.A. (eds) Camels in Asia and North Africa. Interdisciplinary perspectives on their significance in past and present. Austrian Academy of Sciences, Vienna, p55-60 (2012).

Luck, G.W., Daily, G.C., Ehrlich, P.R.: Population diversity and ecosystem services. Trends in Ecology & Evolution 18, 331-336 (2003).

Ming, L., Wang, Z., Yi, L., Batmunkh, M., Liu, T., Siren, D., He, J., Juramt, N., Jambl, T., Li, Y., Jirimutu: Chromosome-level assembly of wild Bactrian camel genome reveals organization of immune gene loci. Molecular ecology resources, 20, 3 (2020a).

Ming, L., Yuan, L.Y., Yi, L., Ding, G.H., Hasi, S.R., Chen, G.L., Jambl, T., Hedayat-Evright, N., Batmunkh, M., Badmaevna, G.K., Gan-Erdene, T., Ts, B., Zhang, W.B., Zulipikaer, A., Hosblig, Erdemt, Natyrov, A., Mamay, P., Narenbatu, Meng, G., Narangerel, C., Khongorzul, O., He, J., Hai, L., Lin, W.L., Sirendalai, Sarentuya, Aiyisi, Li, Y.X., Wang, Z., Jirimutu.: Whole-genome sequencing of 128 camels across Asia reveals origin and migration of domestic Bactrian camels. Communications Biology 3, 1 (2020b).

Mohandesan, E., Fitak, R.R., Corander, J., Yadamsuren, A., Chuluunbat, B., Abdelhadi, O., Raziq, A., Nagy, P., Stalder, G., Walzer, C., Faye, B., Burger, P. A.: Mitogenome Sequencing in the Genus Camelus Reveals Evidence for Purifying Selection and Long-term Divergence between Wild and Domestic Bactrian Camels. Scientific Reports 7, 9970 (2017).

Muyldermans, S., Baral, T.N., Retarnozzo, V.C., De Baetselier, P., De Genst, E., Kinne, J., Leonhardt, H., Magez, S., Nguyen, V.K., Revets, H., Rothbauer, U., Stijemans, B., Tillib, S., Wernery, U., Wyns, L., Hassanzadeh-Ghassabeh, G., Saerens, D.: Camelid immunoglobulins and nanobody technology. Veterinary Immunology and Immunopathology 128, 178-183 (2009).

Peters, J., von den Driesch, A.: The two-humped camel (Camelus bactrianus): new light on its distribution, management and medical treatment in the past. Journal of Zoology 242: 651-679 (1997).

Pilot, M., Greco, C., vonHoldt, B.M., Randi, E., Jedrzejewski, W., Sidorovich, V.E., Konopiński, M.K., Ostrander, E.A., Wayne, R.K.: Widespread, long-term admixture between grey wolves and domestic dogs across Eurasia and its implications for the conservation status of hybrids. Evolutionary Applications 11, 662-680 (2018).

Pilling, D., Rischkowsky, B.: The State of the World’s Animal Genetic Resources for Food and Agriculture – in brief. FAO, Rome, pp 39 (2007).

Plasil, M., Mohandesan, E., Fitak, R.R., Musilova, P., Kubickova, S., Burger, P.A., Horin, P.: The major histocompatibility complex in Old World camelids and low polymorphism of its class II genes. BMC Genomics 17, 1-17 (2016).

Plasil, M., Wijkmark, S., Elbers, J.P., Oppelt, J., Burger, P., Horin, P.: The major histocompatibility complex of Old World camelids: Class I and class I-related genes. HLA Immune Response Genetics 93, 203-215 (2019a).

Plasil, M., Wijkmark, S., Elbers, J.P., Oppelt, J., Burger, P.A., Horin, P.: The Major Histocompatibility Complex of Old World Camels – A Synopsis. Cells 8, 1200 (2019b).

Rieseberg, L.H., Wendel, J.F.: Introgression and its consequences in plants. In: Harrison, R.G. (ed) Hybrid Zones and the Evolutionary Process. Oxford Universiy Press, Oxford, UK, pp 70-109 (1993).

Silbermayr, K., Burger, P.A.: Hybridization: A Threat to the Genetic Distinctiveness of the Last Wild Old World Camel Species. In: Knoll, E.M., Burger, P.A. (eds) Camels in Asia and North Africa. Interdisciplinary perspectives on their significance in past and present. Austrian Academy of Sciences, Vienna, pp 69-76 (2012).

Silbermayr, K., Orozco-terWengel, P. Charruau, P., Enkhbileg, D., Walzer, C., Vogl, C., Schwarzenberger, F., Kaczensky, P., Burger, P. A.: Animal Genetics 41, 315-318 (2010).

Templeton, A.R.: The Speke's Gazelle Breeding Program as an Illustration of the Importance of Multilocus Genetic Diversity in Conservation Biology: Response to Kalinowski et al. Conservation Biology 16, 1151-1155 (2002).

Wilkins, A.S.: Revisiting two hypotheses on the "domestication syndrome" in light of genomic data. Vavilov Journal of Genetics and Breeding 21, 435-442 (2017).

Wu, H., Guang, X., Al-Fageeh, M.B., Cao, J., Pan, S., Zhou, H., Zhang, L., Abutarboush, M.H., Xing, Y., Xie, Z., Alshanqeeti, A.S., Zhang, Y., Yao, Q., Al-Shomrani, B.M., Zhang, D., Li, J., Manee, M.M., Yang, Z., Yang, L., Liu, Y., Zhang, J., Altammami, M.A., Wang, S., Yu, L., Zhang, W., Liu, S., Ba, L., Liu, C., Yang, X., Meng, F., Wang, S., Li, L., Li, E., Li, X., Wu, K., Zhang, S., Wang, J., Yin, Y., Yang, H., Al-Swailem, A.M., Wang, J.: Camelid genomes reveal evolution and adaptation to desert environments. Nature Communications 5: 5188 (2014).

Wrapp, D., De Vlieger, D., Corbett, K.S., Torres, G.M., Wang, N., Van Breedam, W., Roose, K., van Schie, L., VIB-CMB COVID-19 Response Team, Hoffmann, M., Pöhlmann, S., Graham, B.S., Callewaert, N., Schepens, B., Saelens, X., McLellan, J.S.: Structural Basis for Potent Neutralization of Betacoronaviruses by Single-Domain Camelid Antibodies. Cell 181, 1004-1015.e15 (2020).

Yadamsuren, A., Daria, O., Liu, S.: The Seasonal Distribution of Wild Camels (Camelus ferus) in Relation to Changes of the Environmental Conditions in Mongolia. Open Journal of Ecology 9, 293-314 (2019).

Yi, L., Ai, Y., Ming, L., Hai, L., He, J., Guo, F.-C., Qiao, X.-Y., Ji, R.: Molecular diversity and phylogenetic analysis of domestic and wild Bactrian camel populations based on the mitochondrial ATP8 and ATP6 genes. Livestock Science 199, 95-100 (2017)

ZSL and IUCN National Red List Working Group: National Red List Database. Version 2022-x. https://www.nationalredlist.org. Accessed on 10.07.2025. (2022).