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Conservation priorities for two ungulate species in

the subfamily Caprinae in Oman

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Conservation priorities for two ungulate species in the subfamily Caprinae in Oman

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Acknowledgment

Abstract

In this study, molecular genetic data of Arabian tahr and Nubian ibex alongside census data on Arabian tahr's abundance were analyzed. By combining these data, they complement each other to fully understand conservation management. To achieve this, we sampled wild Arabian tahr and Nubian ibex from Oman. The phylogenetic study was based on complete mitochondrial genomes of Arabian tahr (S0011) and Nubian ibex (SN02) together with available mitochondrion sequences in the caprinae tree on GenBank. Bioinformatically, PSMC (Pairwise Sequentially Markovian Coalescent) was used to infer the demographic history for both our samples. Furthermore, detection of Runs of Homozygosity (ROH) was analyzed and finally, both heterozygosity and heterozygosity ratio were examined. Census data on Arabian tahr from the northern Hajar mountains was only analyzed in this study to understand Arabian tahr occupancy outside protected areas. The phylogenetic analysis supports both Arabian tahr (S0011) and Nubian ibex (SN02) of being unique and having their own distinct lineages. The closest relatives to Nubian ibex (SN02) and Arabian tahr (S0011) are Alpine ibex (*Capra ibex*) and Aoudad/the Barbary sheep (*Ammotragus lervia*). PSMC analysis using Arabian tahr and Nubian ibex revealed that they did not go through a severe bottleneck phase. However, Arabian tahr had a small (Ne of ~1000) stable effective population size from ~1 million years ago till about ~ 20,000 years ago. Similarity, the Nubian ibex population maintained a low (Ne of ~1000) population size during the last glacial period, but was about twice as large during the last interglacial. Only 31.5% (23) of the total camera traps (73) deployed detected Arabian tahr. The summed occupancy across 73 cameras was 25.29 and this suggests that they occur in one third (34%) of the study area outside

protected areas. Furthermore, slope seemed to be used by Arabian tahr to gain access

to shade and forage rather than rugged terrain.

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Chapter 1: General Introduction

Human-wildlife interactions have always been important and can mainly be seen from three perspectives: (1) Utilitarian, in which humans benefit from wildlife by providing food, clothing and transport. (2) Affective, where humans create relationships with animals and show respect because of religious, philosophical and mystical reasons. (3) conflictive, such as attacks on humans, damage to crops, and livestock predation, which have motivated wildlife killings for centuries (Castillo-Huitrón et al., 2020). Wildlife infectious diseases can also threaten wildlife population and can drive species to extinction (Langwig, et al., 2015). Further indirect impacts on wildlife such as habitat loss and fragmentation are caused by infrastructure development. It has taken some time for the international community to realize the value of wildlife and it was only in 1992 that the intention to secure the value of biodiversity was declared at the International Convention on Biodiversity in Rio de Janeiro (Chardonnet, 2002).

Global change and loss of biodiversity are worldwide threats. The biggest threat to wildlife is habitat fragmentation and urbanization (Riley et a., 2003). However, wildlife population are also threatened by livestock diseases emerged from the growing of worldwide production and trade of farmed animals (Kuiken and Cromie, 2022). As human population increases, land and habitats are modified to meet our increased population demand of natural resources. In addition to this, the increase in energy consumption causes pollution and is driving climate change globally (Camill, 2010). This rapid pace of climate change may outpace some species ability to respond and adapt naturally (Refsnider and Janzen, 2016). Setting up protected areas is one of the efforts

to stop mass extinction and population loss of species in their natural habitats (Le Saout et al., 2013). Furthermore, wildlife conservationists face issues in understanding population size and connectivity, hybridization, evaluating of populations to adapt to environmental change. Advanced genomic technologies help conservationists to identify biodiversity hotspots to prioritize and ensure protection. By addressing these issues conservationists are provided with important information for management actions to mitigate threats to habitat loss and endangered species (Supple & Shapiro, 2018). With these threats being universal it is estimated that 1 million animals and plants are at risk of extinction in the coming few decades. Issues related to genetics are essential to the challenges wildlife population face. For example, loss of genetic diversity and inbreeding can lead to loss of population fitness but also directly reduce the populations' ability to adapt to change of conditions produced by diseases, invasive species and climate change. The ability to study genetics and genomes in wildlife populations using advanced genetic tool kits are important to mitigate and quantify threats to wildlife populations and management (Hohenlohe, Funk & Rajora, 2021).

1.1 Background

Oman lies at the eastern extreme of the Arabian Peninsula, extending from the southern border of the United Arab Emirates in the north, along the southeastern border of the Kingdom of Saudi Arabia, to the Republic of Yemen in the south. In the north of Oman, the topography is dominated by the Northern Hajar mountains. To the west in the south of the Hajar range are gravel plains stretching southwards into Al Wusta and Dhofar

Governorate. These gravel plains cover almost 80% of Oman's land surface and border the Arabian Sea. The climate of the Dhofar mountains is dominated by the southwest monsoon, which carries dense mists and some rain to the escarpment and the Salalah Plain during the summer months of July, August, and September, resulting in a belt of grass and woodland along the Dhofar mountains, with dense vegetation on the escarpment facing south to the Arabian Sea (Insall, 2011).

The Arabian tahr *(Arabitragus jayakari)* remains largely understudied, they are considered Endangered and endemic to the northern mountain range in Oman known as the Hajar mountains (Figure 1). Little is known about this mountain ungulate, which suggests it's rare. The Arabian tahr is one of the few indigenous mammals in the Arabian Peninsula and It is one of the smallest living wild goats. The Arabian tahr has a few living relatives like the Himalayan tahr *(Hemitragus jemlahicus),* which are found in the Himalayas from Kashmir to Sikkim, and the Nilgiri tahr *(Hemitragus hylocrius*), in the Nilgiri Hills of southern India (Harrison and Gallagher, 1974). Fossil evidence shows tahr species in Europe during the middle and late Pleistocene, therefore these isolated surviving species may be regarded as relics of a former widely distributed species. The Arabian tahr is the most distinctive species among its close relatives, as they are smaller, they stand about 60cm at the withers and are about 93 cm in total length. The males have a beard with short laterally flattened horns and marked blackish spinal crest and facial pattern. The fur is notably uneven and bushy in winter, forming noticeable tufts on the angles of the lower jaw and 'ruffs' on the legs. Females are smaller in length and weight and have smaller horns and less well-defined markings (Harrison and Gallagher, 1974). Moreover, the core Arabian tahr population lies within Wadi Sareen Nature Reserve and

Jabal Qahwan Nature Reserve, both in the southern part of the Hajar range (Ross et al., 2020a). A camera trap survey conducted in Hatta Conservation Area in Dubai Emirate very close to the Omani border recorded the first footage of the Arabian Tahr in that area, which is in the northern part of the Hajar range (Aguhob et al., 2018).

Over the past few years, the tahr population has declined and threats to its habitat are intensifying, in addition new potential challenges from climate change are emerging (Ross et al., 2019a). Previous studies have suggested that the Arabian tahr occupies the whole Hajar Mountain range in Oman and UAE and these past studies were based on local knowledge and animal signs. Data from 300 cameras across the 29,153 km^2 Hajar Mountains range showed a large decrease, with only 23.9% or 6979 km^2 of the mountain range occupied, where 83.6% of the cameras that captured Arabian tahr were inside Wadi Sareen Nature Reserve and Jabal Qahwan Nature Reserve and only 36.5% of cameras recorded the species outside nature reserves (Ross et al., 2019a). The Arabian tahr remains one of the world's least studied ungulates even though it is listed as Endangered and among the most vulnerable species in the Arabian Peninsula. Our poor understanding and limited information on Arabian tahr restrict our ability to protect and manage the remaining Arabian tahr populations in Wadi Sareen Nature Reserve and Jabal Qahwan Nature Reserves despite the increasing disturbance within its Hajar Mountain range from infrastructural developments and resource extraction. They also face threats from poaching, habitat loss and fragmentation, displacement and risk of disease from domestic livestock. Climate change in the Arabian Peninsula is also expected to impact Arabian Tahr. The average temperature is forecast to increase due to climate change, where extreme temperatures in the region already reach up to 50˚C in

the summer. Fundamentally, in order to conserve the Arabian Tahr it is vital to understand their habitat selection patterns so that critical habitats can be mapped, protected and managed, since it is at risk of extinction and actions need to be taken to secure the species survival (Ross et al., 2020a).

Towards the south, the central desert of Oman in Al Wusta governorate consists of a flat limestone gravel desert occupied by the endangered Arabian Oryx (*Oryx leucory)* (Insall, 2011). The gravel desert is bounded by the Huqf escarpment in Al Wusta Wildlife Reserve, consisting of large boulders and cliffs of up to 100m and these are known to be inhabited by the Nubian Ibex (Al Said et al., 2019). Further south in the Dhofar Governorate, monsoon-influenced areas consist of grasslands and woodlands on the Dhofar Mountains are known to be inhabited by the critically endangered Arabian Leopard (*Panthera pardus nimr*) and also the Nubian Ibex (Al Hikmani et al, 2015). The Dhofar governorate is the prime habitat for Nubian ibex. This habitat extends across the Dhofar Mountains to the edge of the desert in the Negd, and south to the Yemen border. The Dhofar Nubian Ibex population is the largest in Oman with numbers in the region of 600-1,100 individuals. Approximately another 100-250 Nubian ibex exist in the Huqf escarpment and Janabi Hills, in and surrounding Al Wusta Wildlife Reserve (Ross and Al Said, unpublished Data). The Nubian ibex is a large social goat that prefers living on steep terrain and cliffs. Males differ from females weighing on an average of 62.5kg whilst females average 26.5 kg. They are usually found in large groups of 20 individuals dominated by females and their young or larger groups of up to 100 individuals which include adult males (Tadesse & Kotler 2010). Males are also distinguished from females by their horn size; they develop horn annuli (rings formed during slow growth). For Nubian

Ibex this was not sufficiently noticeable to determine true age but on the other hand, horn knobs were useful in ageing immature males of Alpine Ibex (*Capra ibex)* and Walia Ibex (*Capra walie*) (Gross & Alkon 1996). The breeding season, also known as the Rut, begins by mid-September and extends into November and sometimes December. The gestation period is usually about 160 days and they give birth during March-May (Gross et at., 1995). Wild Nubian Ibex diet has not been studied in sufficient detail to know what species of plants they prefer in the desert. However, a study by Cambell (1997) in Saudi Arabia suggest that they have a diverse diet and preferred eating shrubs, forbs, dwarf shrubs, trees and vines. Interestingly, they did not eat grass and this could be due to the study being conducted in an unusual year of only 18mm of rainfall in the reserve, which made annual grasses and forbs not available as a food source (Cambell, 1997). The reason why Nubian ibex are mostly found on cliffs is to stay safe from predators. They are considered foragers and remain active most of the time, and cannot live far away from water pools (Shkedy & Saltz, 2000). Even though they are adapted to hot desert temperatures they still do need to drink almost every day. The predators they potentially face include Arabian leopards, Arabian Wolves (*Canis lupus arabs*) and striped hyenas (*Hyaena hayena*) (Levy and Bernadsky,1991). Due to limited and unpredictable rainfall in the Huquf escarpment, sparse natural resources occur where vegetation density increases in areas where rainfall occurs. This results in low densities and group sizes of Nubian ibex which results in the seasonality of breeding being poorly defined. It is suggested that a secondary season of breeding might be evolving in response to these unpredictable and harsh conditions. In terms of these sparse populations in the Huquf it is possible that they are adapting to a non-mountain hyper arid environment by a micro

evolutionary process (Massolo et al., 2007). The Nubian Ibex taxon is historically and sometimes still considered a subspecies of *Capra ibex* but it is regarded as a distinct species by Grubb (2005). They occur in Egypt east of the Nile, Sudan, Israel, western Jordan, central Saudi Arabia, central and southern Oman and in eastern and central Yemen. Its status in Sudan, northern Ethiopia and Eritrea is currently unknown. It has been extinct from Syria but is currently being reintroduced into Lebanon. The main threats to Nubian ibex are illegal and unregulated hunting in Sudan and Yemen. There are only limited prosecutions in all countries for those caught with Nubian ibex. Additionally, habitat loss and fragmentation are issues throughout its range especially in the Huqf escarpment in Oman. Increased genetic isolation is a threat due to reduced population connectivity. Furthermore, competition and disturbance of natural water resources by local herders with livestock lowers the water table in the arid areas that Nubian ibex inhabit. Since Nubian ibex populations are likely to be small and isolated, the risk of extinction is higher due disease outbreaks and drought (Grubb, 2005).
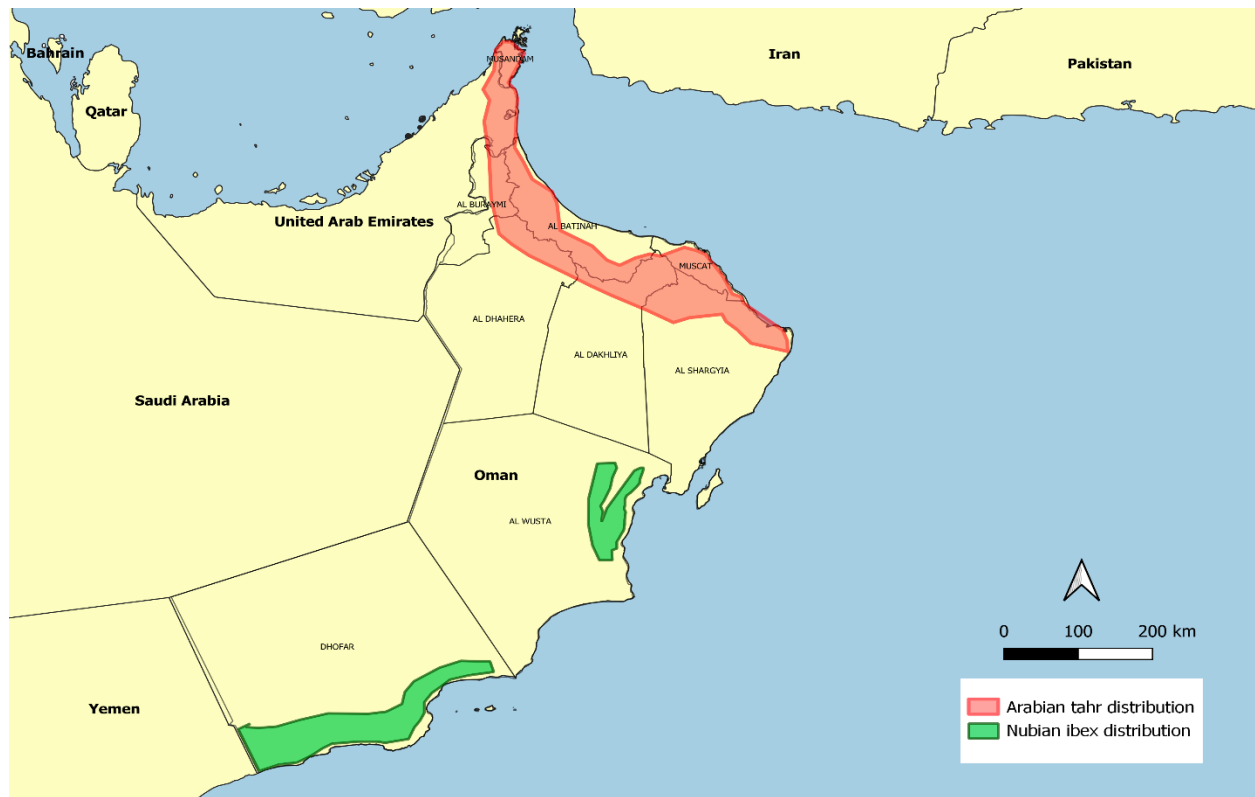
Figure 1: Shows the distribution of both Arabian tahr (red) and Nubian ibex (green) in Oman.

1.2 Combining camera trap data with genetic data

Combining two non-invasive tools such as camera trap surveys with genetic surveys help better understand the environmental factors that identify distribution, density and identity of the species of interest. Discovering their distribution and density in the study area are guided by the use of camera trap surveys. The genetic surveys on the other hand such as collecting scat samples and using Polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) method and determining rates of homozygosity and heterozygosity will also help in the identification process (Balestrieri et al., 2021). This combination of methods has been useful for instance when used to

understand habitat preferences by two closely related species that compete for territory in one habitat. Identifying habitat suitably is crucial in this case where environmental variables play a key role. Molecular genetic analyses will also provide a better understanding of their demographic history and current population size. Moreover, measures of heterozygosity and runs of homozygosity (ROH) will be used to asses and understand the amount of inbreeding in the population to provide a reference for breeding programs to sustain diversity and fitness in these species (Balestrieri et al., 2021).

Furthermore, combining camera trap data with genetic data can not only improve our understanding of their distribution and habitat usage but genetic analysis also provides information that camera traps can't like assessing genetic diversity and the risk of inbreeding, in addition to species demographic history and phylogenetic position which can reveal recent population bottlenecks and patterns of geneflow (Sollmann et al., 2013). For instance, investigating diet in a species can better our understanding of why species are distributed in a certain habitat. It is also important to understand diversity in the context of demographic history and isolation from other related taxa. This combination of the outputs gives us a better understanding of a species ecology. All of this is relevant to the effective size of local populations and the potential for connectivity among populations. These two factors directly determine genetic diversity and the risk of inbreeding depression (Sollmann et al., 2013). When wildlife population survivability and fertility are reduced, this population are known to face inbreeding depression (Charlesworth and Willis, 2009).

1.3 Aims and objectives

Due to the limited amount of research on both Arabian tahr *(Arabitragus jayakari)* and Nubian ibex *(Capra nubiaina)* in Oman, we aimed to confirm the phylogenetic positions, individual genomic diversity and demographic history of *A. jayakari* and *C. nubiaina* in the subfamily Caprinae and quantify population size and habitat use of Arabian tahr in the northern part of the Hajar mountains in Oman using occupancy. Hence, we aim to apply two non-invasive methods (camera trap data and genetic data) to better understand these species ecology and genetics.

The Arabian tahr has only recently been put into its own genus by Ropiquet and Hassanin 2005 (see chapter 2). We compare Arabian tahr with other closely related species to better resolve this lineage. This will be done using phylogenetic analysis which will allow us to infer species' relationships using molecular data. The samples collected from the wild in Oman which will have no risk of confounding with misidentification or other factors that may affect captive animals, unlike previous studies that used captive animal samples. Hence, this improves our understanding of evolutionary biology in this group of species with higher resolution and representation across the lineage.

These genetics results will be combined with the analysis of camera traps using presence/absence data of Arabian tahr outside protected areas in the northern part of the Hajar mountains in Oman. We used occupancy in the UNMARKED package available in R. The main objective was to generate models to estimate the proportion of an area occupied by Arabian tahr while accounting for imperfect detection. In addition, this will help us identify their preferred habitats and the influence of covariates (Ruggedness,

slope and elevation) on Arabian tahr's occupancy in the northern Hajar mountain range. I will compare our findings to a much broader camera trap study previously done on Arabian tahr in the Hajar mountains. Finally combining the outcomes from both the genetic analysis with the camera trap data, we hope to better understanding the ecology of Arabian tahr and Nubian ibex for population conservation.

Three hypotheses are to be tested:

1) Nubian ibex will show more genetic diversity than Arabian tahr.

2) Both Arabian tahr and Nubian ibex are phylogenetically unique in their respectful genera.

3) Arabian tahr occupancy patterns and conservation needs will be different outside compared to inside national reserves.

Chapter 2: Conservation genomics on Arabian tahr (*Arabitragus jayakari*) and Nubian ibex (*Capra nubiana*) in Oman

2.1 Introduction

2.1.1 Phylogenetic Analysis

There have been many extensive efforts made to understand the phylogeny of the Bovidae family in the past decade and the relationships within the group are still not fully resolved (Yang et al., 2013). This could be due to the use of short DNA segments or single genes which may produce incorrect or incomplete tree topologies (Nikaido et al., 1999). Using complete mitochondrial genome (mtDNA) provides a higher level of resolution to support the tree topology, unlike phylogenetic reconstruction based on a single gene or short DNA segment which may affect phylogenetic accuracy. While a whole genome phylogeny would instead be limited to available species (Yang et al., 2013). Classification of the *Capra* genus is proven to be the most complicated amongst all ungulates by different authors. This genus contains up to eleven species (Kazanskaya et al 2007).

A molecular phylogeny of the Caprinae subfamily was done by Ropiquet and Hassanin (2005) using four molecular markers: the subunit II of the cytochrome c oxidase

(CO2), the cytochrome b (Cyb), 12S rRNA gene (12S) and protein kinase C iota (PRKCI). Three of them (CO2), (Cyb), 12S rRNA gene (12S) were mitochondrial markers of *Hemitragus* and *Capra.* These mtDNA markers evolve relatively quickly and so provide good resolution. The last marker (PRKCI) was a nuclear marker and chosen because the *PRKCI* sequence of *C. hircus* (domestic goat) presents a deletion of four nucleotides (TYGA), which was not detected in two other caprinae species. This was done to determine the taxonomic status of the three types of Tahr (1) Himalayan Tahr (*Hemitragus jemlahicus*), (2) Nilgiri Tahr (*Hemitragus hylocrius*), and the (3) Arabian Tahr (*Hemitragus jayakari*). The Phylogenetic analyses were carried out on a matrix that included most extant species currently in the Caprinae lineage. The results indicated that the genus *Hemitragus* is polyphyletic, as *H. jemlahicus* is associated with *Capra* (goats), *H. hylocrius* is the sister-group of Ovis (sheep), and *H. jayakari* is allied with *Ammotragus lervia* (aoudad). Furthermore, it was proposed that a new taxonomy must be created. The genus *Hemitragus* would be restricted to the Himalayan Tahr (*Hemitragus jemlahicus)*, and two new genera would be created: *Nilgiritragus* for the Nilgiri Tahr *(Hemitragus hylocrius) and Arabitragus* for the Arabian Tahr (*Arabitragus jayakari)* (Ropiquet and Hassanin 2005).

A study by Kazanskaya et al., (2007) looked into the phylogenic positions of eight wild goats in the *Capra* genus, the Bezoar (*Capra aegagrus*), Alpine ibex (*Capra ibex*), Siberian ibex (*Capra sibirica*), Nubian ibex (*Capra nubiana*), Spanish ibex (*Capra pyrenaica*), Markhor (*Capra falconeri*), Kuban tur (*Capra caucasica*), and Dagestan tur (*Capra cylindricornis*). They used cytochrome b gene (392 bp and 1128 bp) and the mtDNA control region as their genetic markers. They constructed minimum evolution

phylogenetic trees by the maximum parsimony (MP) method using PAUP 4.10 software package. The tree produced eight branches and there was a cluster of the Western European group (*C. ibex* and *C. pyrenaica*). Highly supported clades are formed by *C. aegagrus* (Dagestan)*, C. sibirbica*, *C. nubiana*, and *C. cylindricornis*. However, weakly supported clades include clusters of *C. falconeri* and *C. caucasica*. Another interesting finding is that their data has shown that *C. sibirica* is the most ancient species and *C. nubiana* is suggested to radiate from the common stem next to it. However, morphological similarity of *C. sibirbica*, *C. ibex*, and *C. nubiana* appears to be plesiomorphic (a retained ancestral character). The phylogenetic analysis of both the cytochrome b and the control region provide identification of nearly all genetically isolated groups within the *Capra* genus. This suggests that the evolutionary history of the *Capra* genus requires analysis of nuclear DNA since they could not provide reliable determination of the species divergence despite using high resolution mtDNA genetic markers (Kazanskaya et al 2007). Moreover, another study on the evolution of the *Capra* genus using mitochondrial DNA in which they specifically used 500-bp sequence portions of the mtDNA cytochrome b gene and the mtDNA control region obtained similar results to Kazanskaya et al 2007. Interestingly, they found the greatest genetic distance was between *C. ibex* and *C. nubiana* and therefore are considered separate species (Manceau et al., 1999). They also recommended that the *Capra* phylogeny could be better resolved by longer sequences and analyzing many samples per species from throughout their geographic range (Manceau et al., 1999). Nuclear genes located on the Y-chromosome was previously analyzed from species in the *Capra* genus (Pidancier et al., 2006). Segments from the amelo- genin (AMELY) and zinc finger (ZFY) genes were used. There was some

discordance when they analyzed the phylogenetic tree of both mtDNA and Nuclear DNA, such as amplification of nuclear mtDNA copies, selection, lineage sorting of ancestral polymorphisms, or horizontal transfer of genes (i.e., introgression). Fossil evidence have also shown hybridization of wild *Capra* species in the past and they originally occurred in Central Asia and colonization of *C. sibirbica* was recent in Europe. If male *C. sibirbica* were ever to compete with male *C. aegagrus* in the mating season, *C. sibirbica* would win that competition due to its larger size (Pidancier et al., 2006).

2.1.2 Demographic History

Genomes of any organism carry evolutionary and ecological information which have shaped their current population today. The demographic history of any species can be reconstructed by using a coalescent analysis on genome sequences (Mathers, Traves & Ho, 2020). We are now able to answer various biological questions like the influence of climatic and environmental events that have affected population size and structure, timing of major events in the evolutionary history of both wildlife and humans, how human population have impacted wildlife population and the effects of domestication. It is not straightforward and simple to infer the historical demography of a species. In fact, there are many complications and challenges in extracting and obtaining historical indicators from a population. There have been various methods developed to infer the demographic history of a species based on the coalescent using site frequency spectra and approximate Bayesian computation (Mathers, Traves & Ho, 2020).

Some of these demographic methods require samples from multiple individuals in a panmictic population. However, sampling large numbers of unlinked loci spread across a single genome is a viable alternative, based on coalescent inference (Li & Durban, 2011). The Pairwise Sequentially Markovian Coalescent (PSMC) method was developed by Li & Durbin (2011) and the model uses a hidden Markov framework and identifies historical recombination events across a single diploid genome (Li & Durban, 2011). The time to the most recent common ancestor (TMRCA) is used as a reference for when PSMC infers the time for each independent DNA segment, and, based on the rate of coalescent events and the estimated TMRCA, it derives ancestral effective population size (N_e) across an ancestral time period (see Nadachowska-Brzyska et at., 2016). These reconstructions of the demographic history are used to answer many questions regarding the effect of climate change on their current population and structure, to understand the effect on the growth of populations (Mather, Traves and Ho, 2020). The benefit of using the PSMC method is that it can analyze whole-genome sequences relatively quickly and can be applied to any organism. The disadvantage is that it can't resolve recent demography (more recent than ~20Ka). Recently, a lot of genome assembly projects have been using PSMC for analysis and thus it is a common tool in the field of ecology and evolution. An apparent advantage of the PSMC method is that it gives us detailed information about the history of a species which is nearly impossible or very hard to capture from other demographic methods (Nadachowska-Brzyska et at., 2016).

2.1.3 Runs of Homozygosity

Runs of homozygosity (ROH) are the regions of the genome that are identical by descent which consists of a number of homozygous, adjacent Single Nucleotide Polymorphisms (SNPs) over a given number of Mega base (Mb). The longer the run, the closer is expected to be the most recent common ancestor (Hedrick & Garcia-Dorado, 2016). The major mechanism for increasing homozygosity is inbreeding, and the increase of inbreeding can lead to the homozygous combinations of harmful recessive genes, which eventually can lead to decreases in the fecundity and viability of offspring. This is referred to as inbreeding depression. Several factors influence the generation of ROH, such as inbreeding, natural and artificial selection, genetic drift and population bottlenecks, but inbreeding is the most important factor (typically an outcome of population bottlenecks) (Rui Xie et al., 2019). Some studies have found ROH to be associated with several diseases, especially cases related to neuropsychological diseases like schizophrenia and Alzheimer's. Some studies proved disease had connections with ROH and some did not. The evidence for these studies has been mixed and sometimes replications of these studies have found no significant associations of ROH with the same phenotypes (Samuels et al., 2016).

Threatened and endangered species usually suffer from low genetic diversity, inbreeding depression and reduced adaptability. Robinson et al., (2021) examined genome-wide diversity, ROH and demographic interference of the Critically Endangered California condor (*Gymnogyps californianus*) in comparison with the Vulnerable Andean condor (*Vultur gryphus*) and the Least Concern Turkey vulture (*Cathartes aura*). They

revealed that the genomes of all three species show evidence of historic population declines. The variation present in the California condor on the other hand is reassuring for the potential for future adaptation. Large ROH were detected which reveals recent inbreeding in the California condor, as well as spatial patterns of recombination rate showing the role of linked selection in shaping genome-wide diversity. It was unexpected for the California condor to have high genome-wide diversity since it was briefly extinct in the wild and were also historically abundant. Interestingly, the turkey vulture was less abundant historically however, they are thought to be the most abundant and wide-ranging vulture today. The California condor continues to reproduce naturally and expand its range in the wild, in addition to continue reintroducing the species to additional sites. High genetic diversity does not mean a species is protected from extinction (Robinson et al., (2021).

Therefore, using genome sequences to show genetic diversity in a species is vital for conservation, as these genomic sequence data detect species with recent population decline, which makes them vulnerable or at risk for loss of genomic diversity through inbreeding and drift. Consequently, it is important for long term sustainability of populations. ROH will be a powerful tool and will commonly be used to estimate inbreeding in wild populations. Therefore, such data should be integrated directly into conservation ranking systems such as The Red List and be used as a benchmark reference for future genomic diversity studies and research of wildlife populations (Bruniche-Olsen et al., 2018). Taking this into account, extended homozygosity regions increase the probability of homozygosity of rare deleterious variants.

2.1.4 Genome-wide heterozygosity and heterozygosity ratio

Identifying genetic diversity in a population has been vital to understand the evolutionary potential of the species and the risk of inbreeding depression. The detection of genomic runs is usually done using two approaches 1) consecutive runs or 2) sliding-window. The consecutive runs approach is a window-free method which directly scans the whole genome SNP by SNP and this was first proposed by Marras et al. (2015). The sliding-window approach also scans the genome and the characteristics of consecutive windows. It counts the number of heterozygotes in each stretch of DNA, and from this nucleotide diversity (π) is calculated (Biscarini et al., 2018). Genome-wide heterozygosity is negatively correlated with inbreeding within a population and hence heterozygosity fitness associations are also associated with inbreeding depression. Inbreeding may cause harm to population fitness, as discussed earlier. Using a large number of genetic markers to estimate heterozygosity is recommended for population assessments (Murray et al., 2013). Here I assess a single genome as representative of diversity in the population.

There have been many different measures of heterozygosity previously used. Samuels et al., (2016) defined a genome-wide measure of heterozygosity as "the ratio of the number of heterozygous SNPs divided by the number of nonreference homozygous SNPs" (the 'heterozygosity ratio'). The heterozygosity ratio method has been tested to be vital when comparing populations and individuals for disease resistance and recessive phenotypes. The main purpose of including these three metrics (ROH, Het & Het ratio) in this project is to provide a diversity of related metrics. ROH provides additional information about the genomic structure of diversity (Rui Xie et al., 2019). The het ratio

is meant to avoid some comparative issues associated with ROH or π (Samuels et al. 2016).

This chapter of my project will focus on the conservation of two ungulate species found in the Sultanate of Oman, the Arabian tahr (*Arabitragus jayakari*) and the Nubian Ibex *(Capra nubiana*) using genetic analysis we aim to confirm their phylogenetic positions, individual genomic diversity and their demographic history. The main objectives of this chapter are using phylogenetic analysis which will allow us to infer species' relationships using molecular data. By using ROH analysis in my study for Arabian tahr and Nubian ibex will give us a better understanding of the amount of inbreeding in these representative individuals and provide a reference for breeding programs to sustain diversity and fitness in these species. PSMC is the program used for demographic inferences which uses diploid genotypes from one individual to estimate demographic history.

2.2 Methods

2.2.1 Genetic samples

A total of two ear tissue samples from each species were collected from wild Arabian tahr and Nubian ibex (Table 1). Arabian tahr samples were collected from Wadi Al Sareen nature reserve and Nubian ibex samples from the Huquf escarpment in al

Wusta Wildlife Reserve both between years 2012-2018. All tissue samples from Nubian Ibex and Arabian Tahr were stored in 100% ethanol.

Table 1: Showing the samples available for this project.

Tube no.	Sample ID.	Species	Year	Location
1	S0044	Arabian Tahr	2015	Wadi As Sareen Nature Reserve
2	S0011	Arabian Tahr	2015	Wadi As Sareen Nature Reserve
3	SN01	Nubian Ibex	2020	Huquf – Al Wusta Wildlife Reserve
4	SN02	Nubian Ibex	2020	Huquf – Al Wusta Wildlife Reserve

2.2.2 DNA extraction and genome sequencing

DNA extraction was done using the Omega BIO-TEK E.N.Z.A Tissue DNA Kit Protocol (E.Z.N.A. Tissue DNA Kit, 2019) to generate our shotgun DNA libraries. DNA is quantified using the fluorescent method implemented by Qubit. A genomic DNA library

was then created for the highest quality sample from each species using the Illumina TruSeq PCR-free shotgun library kit. Sample SN02 used adapter 1 for ligation and sample S0011 used Adapter 3. Short read 2 x 125bp paired end sequencing was done on an Illumina HiSeq 2500 at DBS Genomics, Durham University. Bioinformatics tools were used to start the filtration process of our samples (S0011 & SN02) in fastq format which contains the biological sequence. The fastq files were first aligned with Cattle (*Bos taurus*) as a reference sequence using Bowtie2 software. The alignment output file in SAM format was then converted to a BAM format file using SAMtools. SAMtools is software that analyzes and manipulates alignments in SAM/BAM format. It can convert, sort and merge alignments, remove PCR duplicates, call SNPs and short indel variants. The output file allowed us to view the alignment in a text-based format (Li et al., 2009). This is then filtered using BCFtools to generate a Variant Calling File (VCF). The genome metrics such as average sequence depth and whole genome size were obtained using VCFtools and SAMtools.

2.2.3 Phylogenetics analysis

The phylogenetic study was based on complete mitochondrial genomes together with available mitochondrion sequences on GenBank to best resolve topology in the relevant portion of the tree. This included my two focus species - Arabian tahr (*Arabitragus jayakari)* and Nubian ibex (*Capra nubiana*), and an outgroup genome - Cattle (*Bos taurus*) (Table 2 & Table S1). Bcftools software was used to obtain mtDNA for my two focal species from fastq files. They were generated through an assembly against a conspecific reference, in this case *Bos taurus*, to finally generates a fasta file consisting

of ~16,000 bp. The alignment and phylogenetic tree were generated using the software MEGA 11 (Hall, 2013). Two phylogenetic trees were constructed, the maximum likelihood (ML) and neighbor joining (NJ) tree. The reason the ML was selected for phylogeny inference is to determine the tree topology, branch lengths, and parameters of the evolutionary model (Schmidt and Haeseler, 2009). On the other hand, the NJ method is an another widely used method for phylogenetic inference, which has reasonable accuracy combined with a cubic running time algorithm (Simonsen, Mailund and Pedersen, 2011). For the ML tree, 1000 bootstrap replications were applied and a Jukes-Cantor Mode model was used. For the NJ tree, 1000 bootstrap replications and Tamura-Nei-model was used for the running and construction of the tree (Newman, Duffus and Lee, 2016). We included from the Genbank database the proposed closest relatives to both Arabian tahr and Nubian ibex (based on current taxonomy, see discussion in 2.1.1). The evolution models were chosen to account for saturation and rate variation across the sequence. These mtDNA sequences were downloaded in fasta format (Table 2 and Table S1) from GenBank available at: https://www.ncbi.nlm.nih.gov/nuccore/. Table S1 available in the appendix shows the accession numbers for all the species obtained from Genbank.

Table 2: Showing the list of species in the Caprinae lineage used for the phylogeny analysis.

No.	Species	Scientific name
1	Argali	*Ovis ammon*

2	Bighorn sheep	*Ovis canadensis*
3	Sheep	*Ovis aries*
4	Siberian ibex	*Capra sibirica*
5	Alpine ibex	*Capra ibex*
6	Goat	*Capra hircus*
7	Aoudad	*Ammotragus lervia*
8	The Himalayan tahr	*Hemitragus jemlahicus*
9	The West Caucasian tur	*Capra caucasica*
10	Markhor	*Capra falconeri*
11	Wild goat	*Capra aegagrus*
12	Arabian tahr	*Arabitragus jayakari*
13	Nubian ibex	*Capra nubiana*
14	Cattle (out-group)	*Bos taurus*

2.2.4 Demographic History

PSMC is a program used for demographic inferences which uses diploid genotypes from one individual to estimate demographic history (Li & Durban, 2011).

PSMC will take the consensus fastq file and infer the history of population sizes. Once the PSMC output file is created the results are plotted using psmc-plot.pl (Sakton, 2015). The final step is bootstrapping, this can also be accomplished by PSMC software. Bootstrapping splits long chromosome sequences to shorter segments and this can be done by running 'splitfa'. When the '-b' option is applied, psmc will then randomly sample with replacement from these segments (Li, 2011). This is will allow us to visualize and analyze to what extent curves from different species overlap at certain time points (Nadachowska-Brzyska et at., 2016).

2.2.5 Detections of Runs of Homozygosity (ROH)

The software PLINK 1.9 (Purcell et al., 2007) was used to measure ROH for both Arabian tahr and Nubian ibex. PLINK uses VCF as an input file but PLINK can only analyze a limited number of variants (2147483645) and our samples had exceeded that limit. Therefore, our VCF were further filtered for depth and quality (DP >= 10 && QUAL >= 20), and some variants were removed to match the limited number of variants accepted by PLINK. Next, option - - vcf was used to create Binary PED files, which outputs a binary ped file (*.bed), (*.fam) which stores the pedigree/phenotype information and (*.bim) which contains information about the allele names (Purcell et al., 2007).

ROH was measured using the option - - homozyg, which I focused on ROH filtered at 100 kb window because when set to 1 MB runs, only one stretch of ROH for each species appeared. The inbreeding coefficient (F) is used to estimate the amount of an

individual's inbreeding in a population and for this I used F_{ROH}, which is the proportion of the genome that contains ROH at the designated threshold length (Xie et al., 2019).

$F_{ROH} = L_{ROH}/L_{AUT}$

Where L_{ROH} is the total length of ROH and L_{AUT} is the total size of the genome. This is currently the most effective method for estimating F_{ROH} (Xie et al., 2019). PLINK option - - indep slides a moving window of 5000 kb (minimum 50 SNPs) across the genome to detect long contiguous runs of homozygous genotypes. Occasionally, genotype errors or missing genotypes occur in a homozygous segment which results in an underestimation of ROH. To solve this, the program allows one heterozygous and missing calls per window (McQuillan et al., 2008).

Comparative metrics from previous studies related to our species of interest were used, which are important to better understand where the focal species lie in terms of their conservation status.

Table 3: Comparison of some parameter and metrics attained from research previously done on Ungulates.

Species	Mean (π)	Mean F_{ROH} (>100 KB)	Author
Soemmerring's gazelles *(Nanger soemmerringii)*	0.0050	-	Ibrahim et al., 2020
Dama Gazelle *(Nanger dama)*	0.0060	-	Senn et al., 2014

Dorcas gazella *(Gazella Dorcas)*	0.0020	-	Godinho et al., 2012
Caribou *(Rangifer tarandus)*	0.0019	None detected	Wootton et al., 2022
White-tailed deer *(Odocoileus virginianus)*	0.0077	0.002	Wootton et al., 2022
Mountain goat *(Oreamnos americanus)*	0.0010	0.038	Wootton et al., 2022
Alpine ibex *(Capra ibex)*	0.0004	-	Grossen et al., 2020
Iberian ibex (*Capra pyrenaica*)	0.0007	-	Grossen et al., 2020
Siberain ibex *(Capra sibirica)*	0.0022	-	Grossen et al., 2020
Bezoar *(Capra aegagrus)*	0.0019	-	Grossen et al., 2020
Domestic goat (*Capra* hircus)	0.0020	-	Grossen et al., 2020
Markhor *(Capra falconeri)*	0.0008	-	Grossen et al., 2020

2.2.6 Heterozygosity and Heterozygosity ratio

We calculated the heterozygosity ratio using the formula suggested by Samuels et al., (2016). Arabian tahr and Nubian ibex genomic data in VCF format were used to calculate both heterozygosity using a sliding window and heterozygosity ratio (Samuels et al., 2016). The heterozygote analysis was also done using VCFtools on variant call format (.vcf) files. It extracted the number of variants and nucleotide diversity (π) at each chromosome. The sliding window for detection of heterozygotes was set to 50 kb.

For the heterozygosity ratio the analysis was done using grep (Creedy, Vogler & Penlington, 2021) which is a powerful tool used on text files or similar which can search, extract, calculate and paste those values into a separate output file to view. For the heterozygosity ratio this calculated the number of heterozygous sites in an individual divided by the number of nonreference homozygous sites. Het ratio can be used to avoid some comparative issues associated with ROH or π and also has been proposed as a quality control parameter for SNP data (Samuels et al. 2016).

2.3 Results

2.3.1 DNA extraction and sequencing

After successful DNA extraction, all DNA concentrations were measured by Qubit. Only two samples (S0011 and SN02) were used for this project as they had a sufficient amount of DNA present (Table 3). Sample SN02 (Nubian ibex) resulted in 55.2 ng/ul of DNA and sample S0011 (Arabian tahr) resulted in 91.2 ng/ul of DNA. The total volume of DNA used for the fragmentation process was 80 µl for sample SN02 and 60 µl for sample S0011. Once the removal of large and small DNA fragments is completed, sample SN02 resulted in 61.4 ng/ul and sample S0011 resulted in 89 ng/ul. To prevent them from ligating to each other, a single 'A' nucleotide was added to the 3' ends of the blunt fragments. Adaptor 1 was ligated to SN02 and adaptor 3 was ligated to S0011 and finally, ligated fragments were cleaned up and Qubit resulted in 8.5 ng/ul for SN02 and 12 ng/ul for S0011. My samples were trimmed from 150bp reads down to about 125bp after the

removal of adapters. The total number of reads of Arabian tahr was 637,755,505 and had an average coverage depth of 30x with a total genome size of 2.7 GB (gigabases - refers to genome size). On the other hand, Nubian ibex had a total number of 589,697,445 reads with an average coverage depth of 28x and a genome size of 2.6 GB.

Table 4: Displays the samples that DNA was extracted from along with Qubit concentration results of post DNA extraction, post removal of fragments and post ligation.

Sample ID	Post DNA extraction (ng/ul)	Post removal of fragments (ng/ul)	Post ligation (ng/ul)
S0011	91.2	89	12
S0044	0.14	-	-
SN02	55.2	61.4	8.5
SN01	13.2	-	-

2.3.2 Phylogeny tree

The sizes of the assembled mtDNA of all species were about ~16,000 bp. Two phylogenetic trees were constructed the NJ and ML (figure 1a & b). The topology was similar for the two trees, though a deep node defining a single lineage for *H. jemlahicus* and *C. sibirica* in the NJ tree was missing from the ML tree.

The phylogenetic analysis supports the fact that our samples of Arabian tahr (S0011) and Nubian ibex (SN02) are unique and have their own distinct lineages in the caprinae sub-family tree. The bootstrap values show strong lineage support.

(a)

0.02
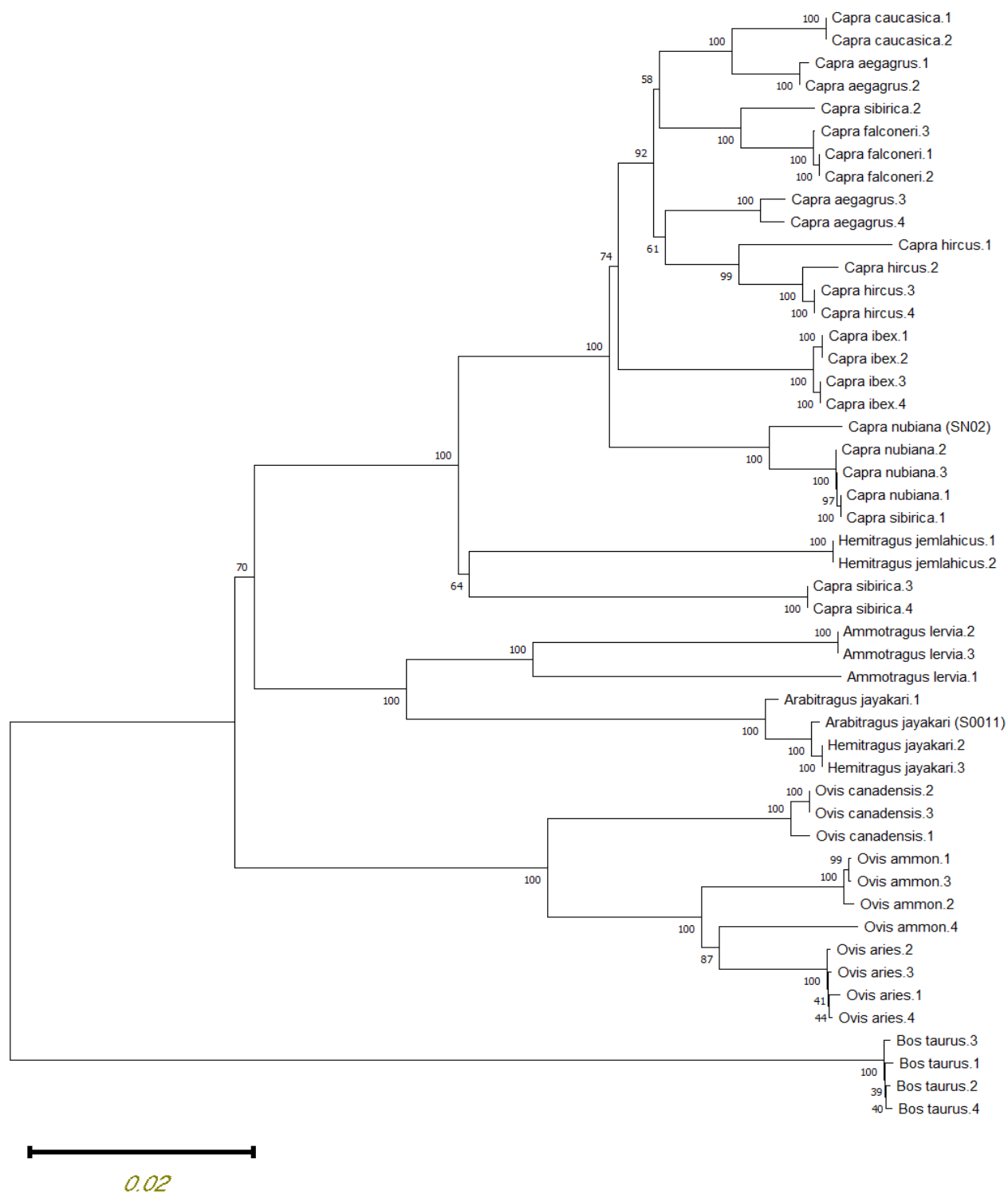
(b)
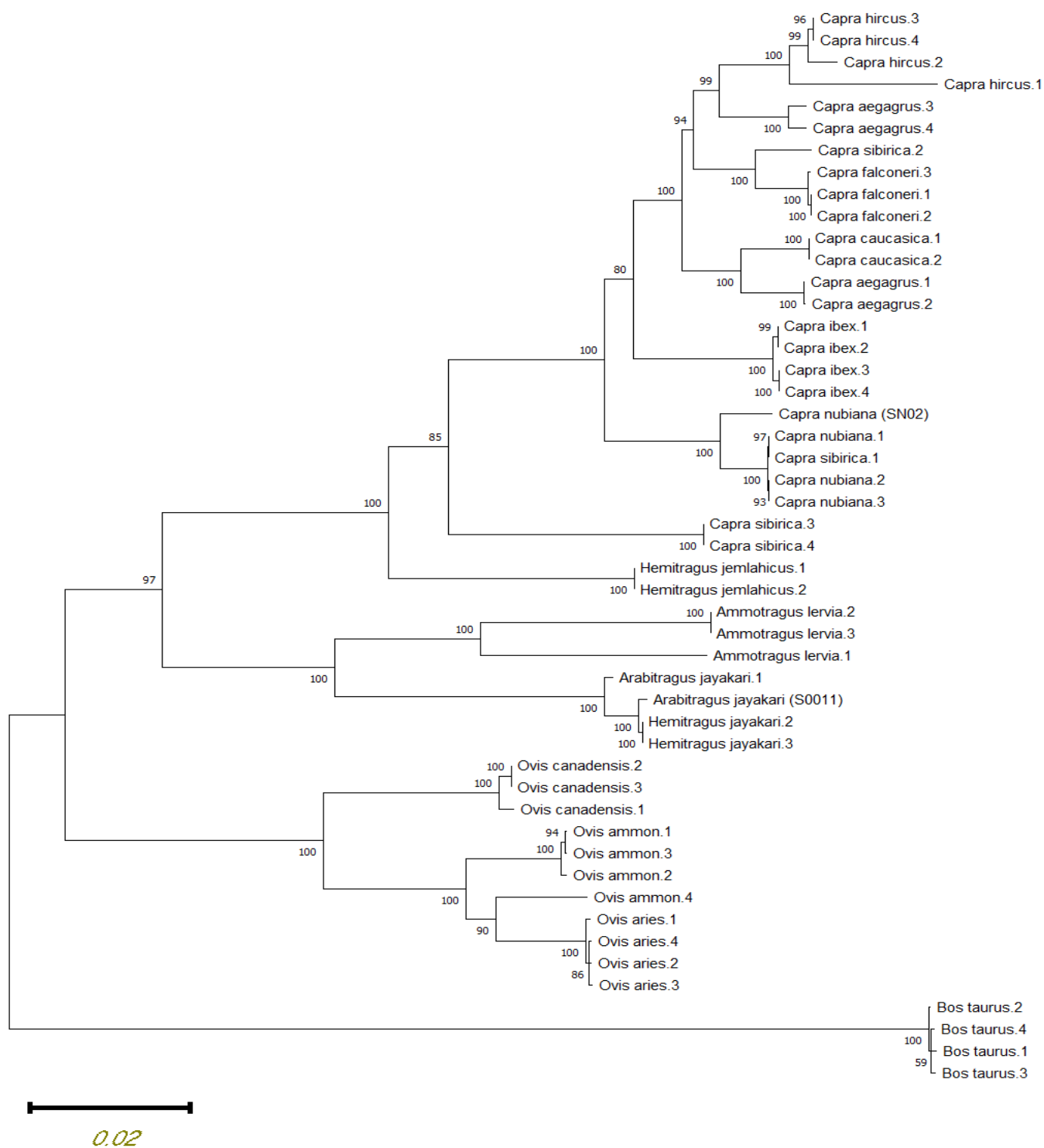
Figure 2 (a): molecular phylogenetic tree derived from complete mitochondrion DNA sequences of the sub-family caprinae using the neighbor joining (NJ) method, including bootstrap support of values from 1,000 replicates. Bos taurus samples were used as out-groups. (b): maximum likelihood (MJ) tree including bootstrap support. Bos taurus samples were used as the out-group. The values shown on the tree are branch lengths. These values indicate the estimated amount of evolutionary change that has occurred along that branch. Longer branches suggest greater evolutionary divergence.

2.3.3 Demographic History of Arabian tahr and Nubian ibex

PSMC analyses of the Arabian tahr full genome revealed a decrease in population size from at ~1 Mya and was quite stable until the present, with a slight decrease during the last glacial period (Figure 3). The Nubian ibex also revealed a decrease in effective population size from at ~1 Mya, but showed greater variation in the later Pleistocene, increasing into the last (Eemian) inter-glacial, and decreasing during the last glacial period (Figure 4). When comparing our 2 samples of Arabian tahr (S0011) and Nubian ibex (SN02) it is evident that the tahr has a smaller population size for longer period of time, though both suggest an Ne of about 1,000 at their nadir. The plots were truncated at the x-axis at 20K years ago. The recent apparent recent jump in population size in both species is likely an artifact shown in figure S2.
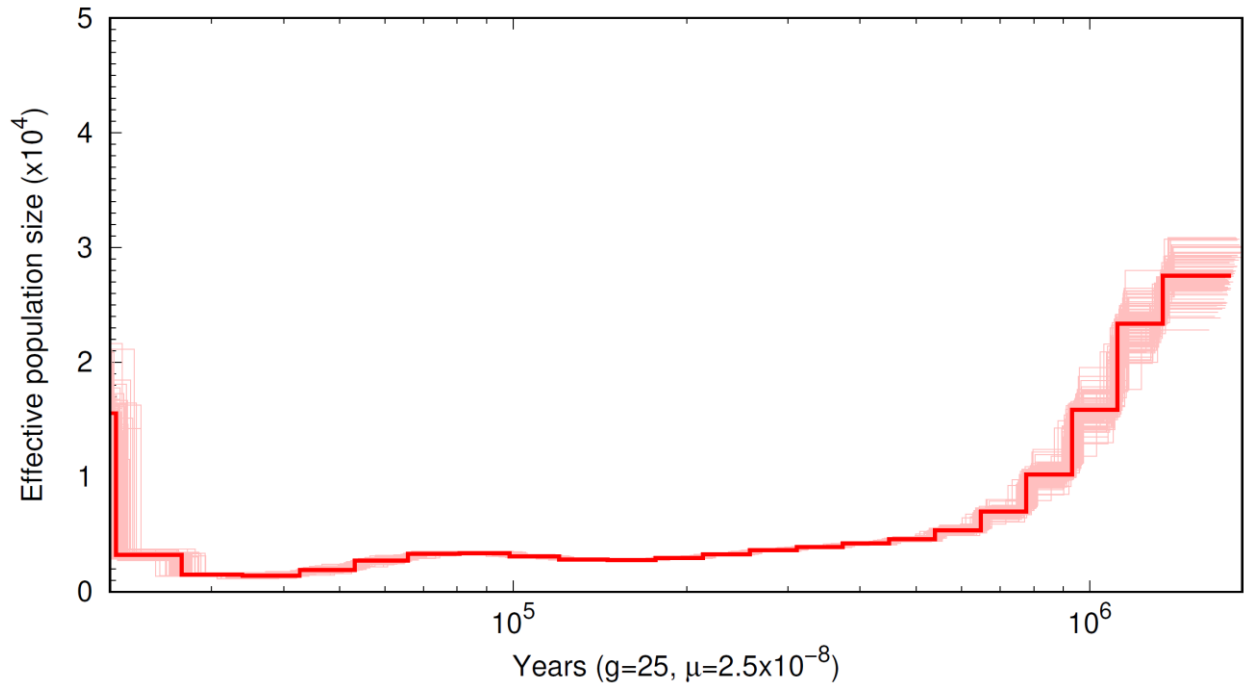
Figure 3: Pairwise Sequentially Markovian Coalescent (PSMC) model plot of the whole-genome of Arabian tahr. The Y axis represents effective population size scale and the X axis represents log time in years. The light red lines show bootstrap values. The timeline was calibrated using a generation time (g) of 25 years and a mutation rate (u) of 2.5×10^{-8} per generation (Li H & Durban, 2011; Nadachowska-Brzyska et at., 2016).
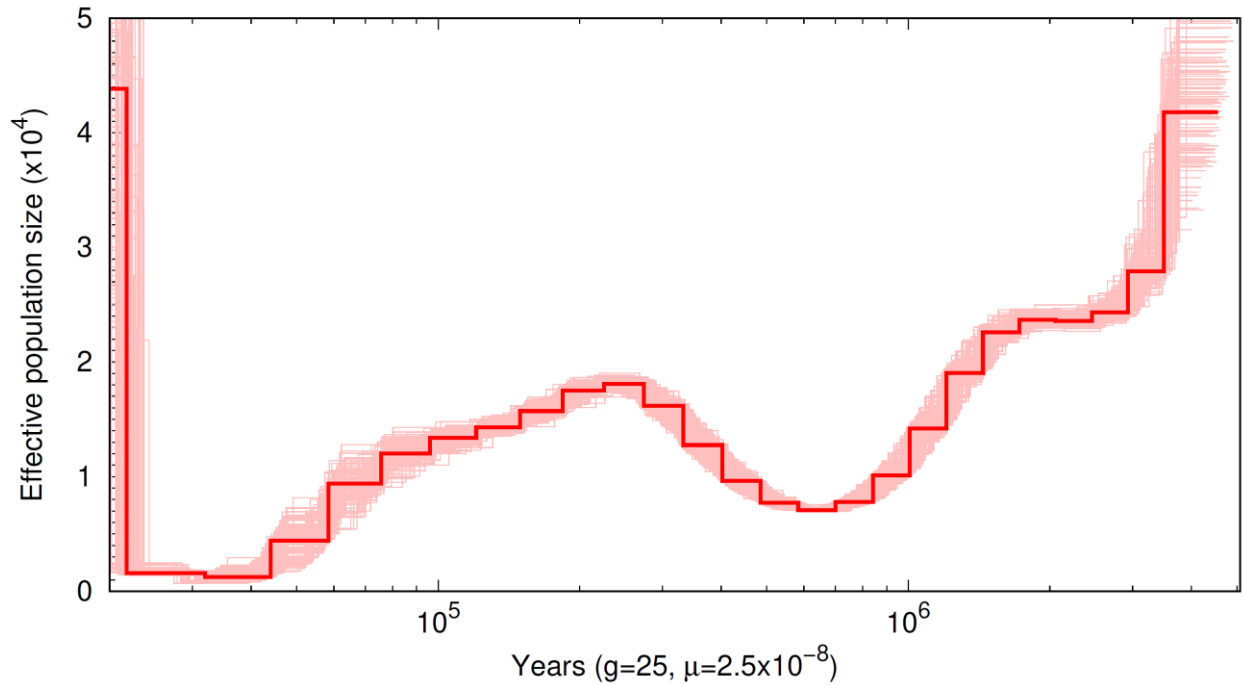
Figure 4: Demonstrates PSMC model plot of the whole-genome of Nubian ibex. The Y axis represents the effective population size scale and the X axis represents log time in years. The light red lines show bootstrap values. The timeline was calibrated using a generation time (g) of 25 years and a mutation rate (u) of 2.5x10-8 per generation (Li H & Durban, 2011; Nadachowska-Brzyska et at., 2016).

2.3.4 Runs of Homozygosity and Heterozygosity

After obtaining results from the ROH analysis for runs greater than 100kb, it is apparent that Nubian ibex has more runs of sequence that are homozygous (Figure 5) compared to the Arabian tahr shown in figure 6, though the difference is small. To discover the genome diversity of both Arabian tahr and Nubian ibex, heterozygous sites were plotted which looked within a 50KB window along the genome. Interestingly, Nubian

ibex has somewhat more heterozygous sites per window (Figure 7) compared to the Arabian tahr (Figure 8). The mean (π) for Arabian tahr and Nubian ibex was 0.0027 and 0.0032, respectively (Table 4). The inbreeding coefficient based on ROH (F_{ROH}) resulted in Arabian tahr and Nubian ibex having an inbreeding coefficient of 0.0039 (0.39%) and 0.0067 (0.67%), respectively (Table 4).

Table 5: This table illustrates the metrics and parameters obtained from ROH >100 kb and estimates of pi.

Species	Number of segments	Total length of segments (KB)	Average length of segments (KB)	Total no. of SNPs	Average density (SNP/KB)	Mean (π)	F_{ROH} (>100 KB)
Arabian tahr	80	10778.1	134.7268	5991795	0.00535	0.0027	0.0039
Nubian ibex	105	17643.5	168.0334	7103361	0.00495	0.0032	0.0067
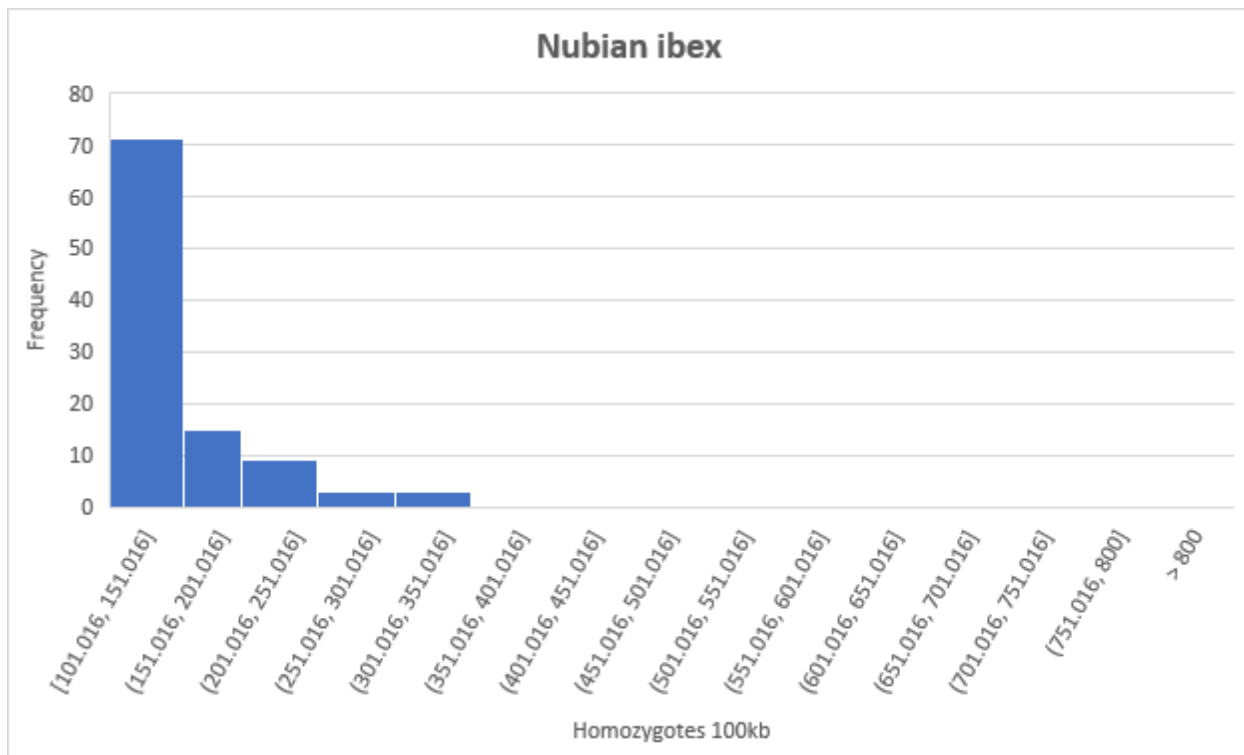
Figure 5: Histogram plot of Nubian ibex showing ROH >100kb.
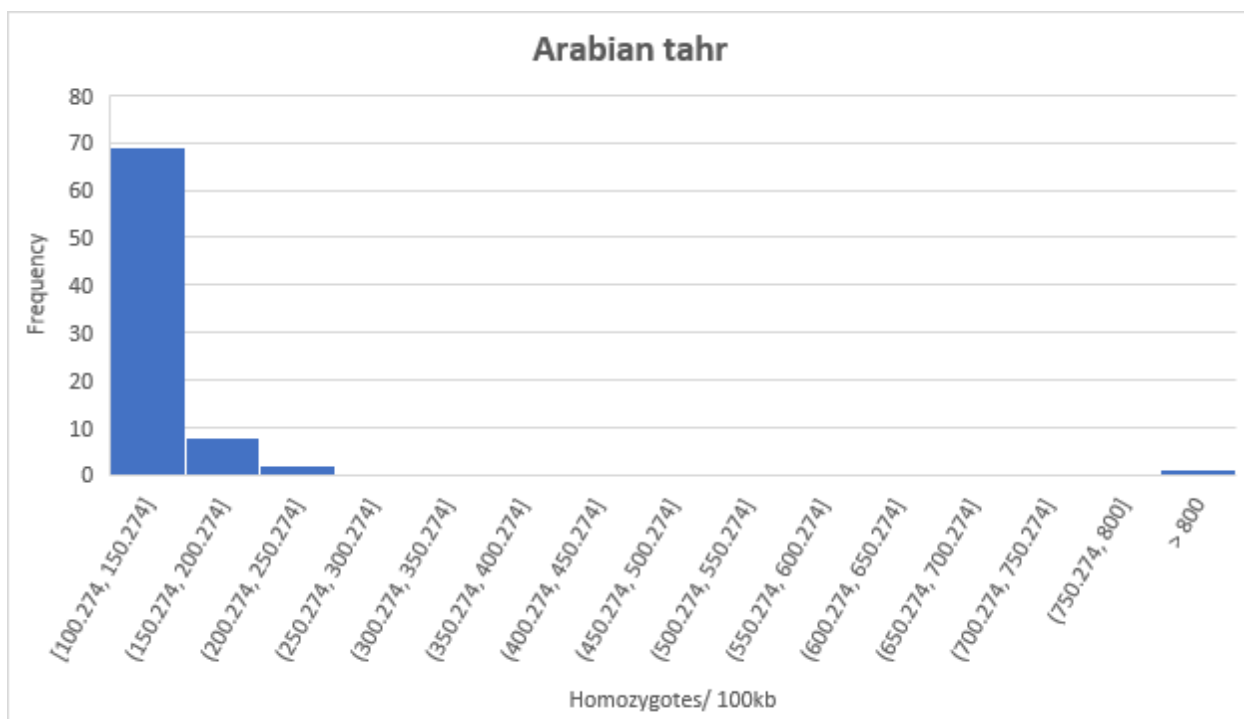
Figure 6: Histogram plot of Arabian tahr showing ROH >100kb.
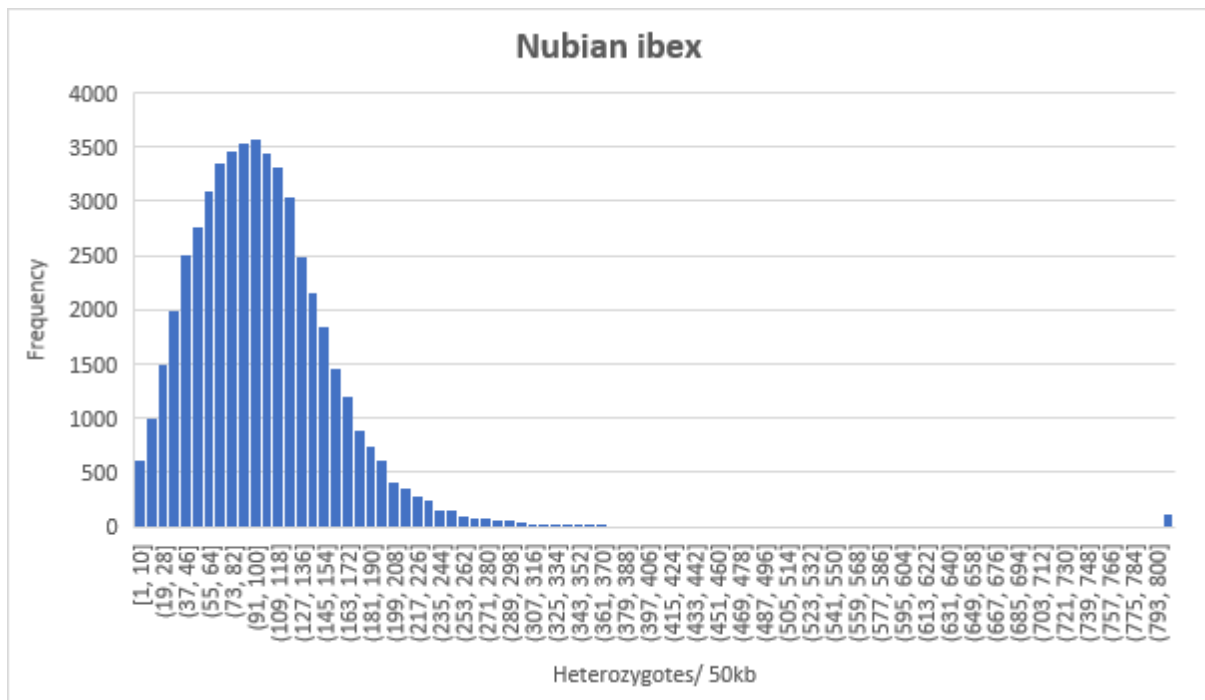
Figure 7: A histogram plot demonstrating the frequency of windows with varying levels of heterozygosity in the 50 kb sliding window for Nubian ibex.
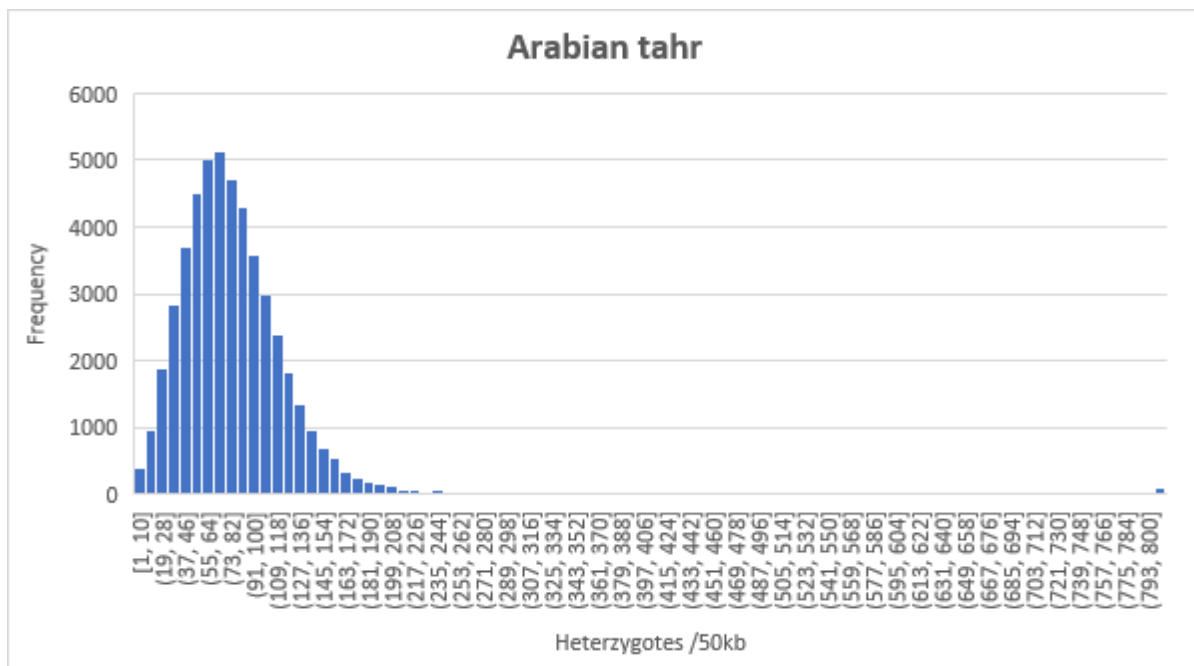
Figure 8: This histogram plot demonstrates the frequency of windows with varying levels of heterozygosity in the 50 kb sliding window for Arabian tahr.

2.3.5 Heterozygosity Ratio

We found that Arabian tahr had total heterozygosity of 4197719 and a total homozygosity of 95289137 with a hetratio of 0.0440. Nubian ibex had a total heterozygosity of 5465988 and a total homozygosity of 94159514 with a hetratio of 0.0580.

Table 6: This table shows the total heterozygosity and homozygosity of Arabian tahr and Nubian ibex including the heterozygosity ratio of both species.

No.	Sample ID	Total Het	Total Hom	Het Ratio
1	Arabian tahr	4197719	95289137	0.0440
2	Nubian ibex	5465988	94159514	0.0580

2.4 Discussion

2.4.1 Phylogenetics

We included a wild Arabian tahr (S0011) from Wadi Sareen Nature Reserve which clustered with the Aoadad (*Ammotragus lervia*) but confirmed its uniqueness in the tree in a separate lineage, grouped with the other samples of Arabian tahr (Figure 1). Ropiquet and Hassanin, 2005 used mtDNA markers which they were able to distinguish a new

taxonomy which splits the three species formally in *Hemitragus* into three monospecific genera: *Hemitragus*, which the Himalayan tahr (*Hemitragus jemlahicus*), falls under, *Arabitragus* for the Arabian tahr (*Arabitragus jayakari*) and *Nilgiritragus* for the Nilgiri tahr (*Hemitragus hylocrius)* (Ropiquet and Hassanin, 2005). Moreover, other phylogenetic studies have always shown a close relationship between *Hemitragus* (tahrs) and *Capra* (goats) and Yang et al., 2013 recently confirmed this close relationship. Using full genomic mitochondrial DNA sequences, they showed this relationship between the Arabian tahr and the Aoudad (confirmed in our study based on a larger number of individuals and species) and suggest that the genus *Hemitragus* is polyphyletic (Yang et al., 2013).

The Nubian ibex (SN02) sample was also captured from the wild and is shown to have a close relationship with alpine ibex (*Capra ibex*) (Figure 1). It is also a bit distinct from the other Nubian ibex samples in this tree. This could be due to the fact that our samples are from the wild in Oman. Interestingly, the taxonomic status of the Nubian ibex has previously been debated to be classified as a sub-species of the Alpine ibex because of the close similarity in the morphology of the horns (Schaller, 1977). Allozymes initially did not provide enough support to discard classifying Nubian ibex as a sub-species of Alpine ibex (Stüwe et al., 1992; Ranjon, Assart and Greth, 1990), but more recently allozyme and mtDNA data were used to classify the Nubian ibex as a separate species (Bibi, Vrba and Fack 2012; Hartl et al.,1990). In Figure 2, both phylogenies show the Nubian ibex to be immediately basal to the lineage that includes the alpine ibex.

Capra sibirica 1 accession no. OW568858 is shown to be paraphyletic (figure 2) occurring in a linage with *C. nubiana* 1 (accession no. OW568908), and are both from a

zoo in Paris (Jardin des Plantes MNHN) (Hassanin et al., 2009 & Daly et al., 2022).

However, the origin of the *Capra nubiana* 1 is unknown as it was given to Jardin des

Plantes MNHN and *Capra sibirica* 1 was born in the zoo. There is a high possibility that

Capra sibirica 1 is a hybrid as it was born in the zoo and mis-assigned as *C. sibirica*. This

is not an unusual event to happen in a zoo and in this case, its mother would *be C.*

nubiana. Furthermore, this is not a sequencing error as both had high coverage mtDNA

alignments (Daly et al., 2022). Our sample *Arabitragus jayakari* (S0011) was from a wild

captured animal and is in the same lineage as *Arabitragus jayakari* 1 (accession no.

MN971587) which is also a wild species from a breeding center, though its origin could

be from a different region on the Hajar mountain range. On the other hand, *Hemitragus*

jayakari 1&2 are paraphyletic to *Hemitragus jayakari* 3&4 (figure 2) and not all of their

origins are known. *Hemitragus jayakari* 2 was a captive animal from the United Arab

Emirates and the origin of *Hemitragus jayakari* 3 is not known but most probably is from

a captive animal from the same region, since both species were obtained by Hassanin et

al., 2009 and Ropiquet & Hassanin, 2005. *Capra nubiana* (SN02) was sampled from a

wild animal, and the wild samples of both *A. jayakari* (S0011) and *C. nubiana* (SN02)

show some uniqueness in the phylogeny of the *Capra* genus, supporting conservation

importance. Pidancier et al. (2006) have suggested that there was paraphyly of *C.*

aegagrus and *C. sibirica* and hybridization that might have occurred between them in the

past as, *C. sibirica* has only recently colonized Europe from Central Asia according to

fossils (more details in the introduction of this chapter). We can confirm in both trees this

connection as it was also evident in our study, as shown in figure 1a & b. The reason

these species were included in this analysis was to help confirm the phylogenetic

positions of *A. jayakari* and *C. nubiana* in Oman by selecting their closest relatives in the *Capra* genus and comparing our results to past studies. However, this study has used advanced methods in the analysis and was also able to select full mitochondrial genomes from an appropriate set of taxa for the reconstruction (details mentioned in the method section of this chapter).

The closest relatives to Nubian ibex (SN02) and Arabian tahr (S0011) are Alpine ibex (*Capra ibex*) and Aoudad/the Barbary sheep (*Ammotragus lervia*) respectively (Figure 2). it is apparent that our sample from Oman (SN02) is more distinct than the other *C. nubiana* species obtained from the Genbank. The Genbank sequences were from captive animals from a zoo in Paris (Jardin des Plantes MNHN) (Hassanin et al., 2009; Daly et al., 2022). *Capra sibirica 1* shows paraphyly (figure 2), and samples labelled *C. sibirica* and *C. nubiana* were found to be monophyletic (Figure 2). *Arabitragus jayakari* 1 accession number MN971587 is from a wild animal given to a breeding center in Oman. *Hemitragus jayakari* 2 accession number FJ207523 is from a captive animal from the United Arab Emirates. However, the origin of *Hemitragus jayakari* 3 accession NC_020621.1 is unknown (Hassanin et al., 2009 & Ropiquet & Hassanin, 2005).

2.4.2 Demography of Arabian tahr and Nubian Ibex

Our PSMC analysis suggests that Arabian tahr population did not go through a severe bottleneck phase, however they were at a small (Ne of ~1000), stable effective population size from ~1 million years ago until ~ 20,000 years ago. Similarity, the Nubian ibex population maintained a low (Ne of ~1000) population size during the last glacial

period, but was about twice as large during the last interglacial, and shows greater fluctuation over time. Apparent recent increases are likely artifacts of the method (Figure S2). This is due to the coalescent method used to generate the profile has too little information to accurately track very recent patterns, so patterns within the last 10,000 years or so can be discarded (Figure S2). One of the A PSMC study has been published on the North American mountain goat (*Oreamnos americanus*) from the subfamily Caprinae, an iconic alpine species that faces challenges from climate change, industrial development, and recreational activities. Their PSMC analysis demonstrated that there was a near 10-fold decrease in the effective population size of mountain goats at the end of the last glacial period (20,000 years ago) and the start of the Holocene, likely due to warming and loss of suitable habitat (Martchenko, Chikhi, and Shafer, 2020). A study by Yang et al., 2016 used PSMC analysis to infer demographic histories of two high-coverage samples (ZNQ24 and LOP41). Their findings were consistent which indicated historical population expansion events for Chinese sheep. The demographic trend of sheep is most similar to horse and mouflon in terms of the timing of bottlenecks and peaks when compared to other animals like wild boar, mouflon, argali and Alpine ibex. These similar trends in their demography might be attributed to the similar habitat requirements of herbivores. They observed differences in effective population sizes and the timing of contractions and expansions between sheep and two other Caprinae species (*Ovis ammon* and *Capra ibex*), This result may from smaller population size and therefore greater susceptibility to environmental change and perturbations like habitat fragmentation compared to sheep and other environmental fluctuations (Yang et al., 2016). Both Arabian tahr and Nubian ibex have similar historical demographic profiles to

Alpine ibex (*C. ibex*) and Aoudad (*A. lervia*) and may therefore be affected by similar processes.

Every population genetic method that uses Next Generation Sequencing (NGS) data is expected to have some errors in sequences, genotyping or missing data and hence PSMC results might be slightly affected. Filtration of sites with low coverage is crucial in PSMC analysis since it estimates the time to most recent common ancestor based on observed heterozygosity present in the genome sequence. There are two types of parameters that are important to consider: Mean genome-wide coverage and coverage at individual sites. The mean genome-wide coverage allows SNP calling to capture the true genotype state across the genome in order to obtain the most reliable demographic inference using PSMC analysis (Nadachowska-Brzyska et at., 2016). In next-generation sequencing, a genome may be sequenced to 30x average depth and achieve a 95% breadth of coverage of the reference genome at a minimum depth of ten reads (Sims et al., 2014). PSMC is more affected by uncertain parameter estimation than other methods that infer demographic history from NGS sequence data. This is not due to data quality but rather parameters like scaling which is used for results interpretation and/or effects of selection or specific demographic situations. For instance, sudden change in population size is something PSMC does not deal well with and may smooth them out. Other estimates like mutation rates and generation time are also important, however they do not change the shape of the PSMC but rather just move the curve along the axis (Nadachowska-Brzyska et at., 2016). Since both of the genomes reported here are around 30X and filtered as suggested, inference for their comparative assessment should be reliable. Both show a relatively low Ne during the last glacial period. The funding was

only sufficient for two genomes, but because this is a coalescent method, it reflects the broader lineage history. In future it would be very interesting to test if variation within species reflected distinct demographic histories, implying that there are relatively isolated lineages.

2.4.3 Genetic diversity

Despite Arabian tahr being critically endangered and Nubian ibex being a vulnerable species, we obtained similar results of ROH, heterozygosity and heterozygosity ratio between them. For instance, when looking at ROH for runs greater than 100kb, somewhat larger ROH runs were present in the Nubian ibex genome compared to Arabian tahr, which indicates that Nubian ibex in their current population in the Huquf escarpment in Oman may be slightly more inbred, but neither are strongly inbred. This should also mean that Nubian ibex would have lower genetic diversity than Arabian tahr. However, the mean (π) for Arabian tahr was 0.0027 and higher for Nubian ibex at 0.0032. Moreover, levels of diversity and inbreeding were compared between Nubian ibex, Arabian tahr (Table 4) and some comparative species that were >100kb (Table 5). Gathering comparative metrics from previous studies related to our species of interest is important to better understand where the focal species lie in terms of their conservation status. Table 5 shows these metrics and parameters from ungulates previously studied. The highest nucleotide diversity was from the White-tailed deer (*Odocoileus virginianus*) at 0.0077 and lowest nucleotide diversity was from Alpine ibex (*Capra ibex*) at 0.0004. The highest F_{ROH} was from Mountain goat (*Oreamnos americanus)* at 0.038 and lowest was from the White-tailed deer (*Odocoileus virginianus*)

at 0.002, though only those two studies included this metric. The inbreeding coefficient based on ROH (F_{ROH}) resulted in Arabian tahr and Nubian ibex having an inbreeding coefficient of 0.0039 (0.39%) and 0.0067 (0.67%), similar to other species in the table. A study by Wootton et al., (2022) investigated the relationship between nucleotide diversity (π), inbreeding, mutational load, and census size (NC) of Caribou (*Rangifer tarandus*), White-tailed deer (*Odocoileus virginianus*) and Mountain goat (*Oreamnos americanus*). Caribou populations are currently in the middle of a demographic bottleneck which currently reflects their low population size and nucleotide diversity. The mountain goat went through a historical bottleneck during the last glacial maximum, but fully recovered and now has a stable population. Mountain goats showed lower π nucleotide diversity compared to caribou, which suggests that the extent of their bottleneck may have been greater. This was shown to be consistent with results obtained for F_{ROH}, where mountain goats had an inbreeding coefficient of 3.8% unlike caribou which had almost no detectable ROH segments greater than 100 kb. The mountain goat also had greater F_{ROH} than white-tailed deer.

Nubian ibex is listed as a vulnerable species, yet it has very similar nucleotide diversity (π) to the Arabian tahr which is listed as critically endangered. Both have levels in the individuals measured that suggest relatively high diversity and low inbreeding. The demographic profiles indicate that the populations have been fairly small, but consistent over the years, and not at a level that will quickly lead to the loss of diversity. However, the small population size and ongoing human impact means that both species are vulnerable. This is especially true since the Nubian ibex population in the Huquf are considered to be isolated from the population in the south of Oman in the governorate of

Dhofar. The population in the Huquf are also physically smaller than animals in the Dhofar population. The southern governorate of Oman (Dhofar) is more ecologically distinct from the hyper-arid region in the central of Oman. The south of Oman encounters yearly monsoon which makes the region wetter with higher floral and faunal diversity compared to anywhere in the Arabian Peninsula (Ross and Al Said, unpublished Data). Additionally, there is a lack of rainfall, thought to average about 18mm of rainfall a year in the Huquf escarpment in central Oman (Cambell (1997). The demography over time and the genome wide heterozygosity both suggest that the Arabian tahr may be the more vulnerable of the two, though the difference is marginal. Both have a low value of the heterozygosity ratio compared to the value seen in humans (Samuels et al. 2016), however this is dependent on the reference sequence used, which is distantly related (and therefore relatively divergent) for these species (*Bos taurus*), and this lowers the value. A comparison between the two focal species in this study shows that the Arabian tahr has a lower value, consistent with the estimates of gene diversity.

To conclude, after using genetic analysis on both Arabian tahr and Nubian ibex. We were able to confirm their phylogenetic positions showing their uniqueness and having their own distinct lineages. The closest relatives to Nubian ibex (SN02) and Arabian tahr (S0011) are Alpine ibex (*Capra ibex*) and Aoudad/the Barbary sheep (*Ammotragus lervia*). Furthermore, it shows that both these species do not yet have low genetic diversity, but their populations are not large and may be decreasing.

Chapter 3: Camera trap survey of the Arabian tahr (*Arabitragus jayakari)* in the northern Hajar mountains, Oman

This chapter of my project will focus on the analysis of camera trap data of Arabian tahr (*Arabitragus jayakari*) in Oman. The camera survey was conducted in the northern Hajar mountain range, which is considered to be outside protected areas. The analysis was done using occupancy models.

3.1 Introduction

Biodiversity is rapidly declining worldwide, particularly among large vertebrates. Habitat fragmentation and degradation are the main causes of biodiversity decline (Trolliet et al., 2014). In order to be able to implement conservation and management strategies and to understand how wildlife ecology and populations respond to these modern threats, regular population updates have never been so important. Mammals, in particular can be hard to monitor, as they are often sparsely populated, nocturnal, elusive or cryptic (Hsing et al. 2022). Increasingly, camera traps are used to meet the high survey effort that this demands (Burton et al. 2015).

Camera traps are automated cameras triggered by movements and are used to collect data in photographs or video formats to identify the presence of animals in a study

area. Previously, camera traps were film cameras with a flash which was activated when infrared beams were broken by passing animals. This traditional camera trap design had some flaws and carried risk of capturing images at a low rate because of its narrow tripping field. Also, it was limited in storage data capacity, and vulnerable to environmental factors like rain, dust and sunlight. Furthermore, camera flash results in camera shyness, hence wildlife tend to avoid camera sites and thus affect observation rates. Researchers by the early 2000s developed camera traps that integrated digital and infrared systems. These newly developed camera traps have many advantages like: deployment for up to six months or more depending on the usage; ability to operate during day and night without a camera flash; robustness to weather conditions; ample data storage; and, most importantly, small size and camouflage and, hence, lower invasiveness and lower chances of stressing the wildlife (McCallum, 2012).

Moreover, gathering camera data (species detection/non-detection) are used in occupancy modelling to predict species occurrence and determine population dynamics parameters. In order to prevent recording of false absence, detection probability data are generated from these models, which has proven to be a useful inference to monitor species that are elusive and rarely observed (Trolliet et al., 2014).

3.1.1 Occupancy and detection

Occupancy is a measure that calculates the proportion of an area occupied by a species while accounting for imperfect detection; additionally, it provides insight into what aspects of the habitat favor presence over absence. It is one of the methods used for

surveying habitat preferences and distribution of a species (MacKenzie et al., 2006). A single-season occupancy model allows us to estimate both occupancy and detection by the individual or species given its presence at site. Single-season occupancy models typically assume closure, meaning that the site is either occupied or unoccupied throughout the entire period (Desrochers et al., 2021). Gathering data and knowledge of species distribution in the wild can identify the effectiveness of protected areas, helping to monitor extinction risk and the success of population recovery programs (Stewart et al., 2022). Understanding the factors that determine occurrence is crucial to guide efforts to lessen the threats to species, like: forest degradation, noise pollution, agricultural expansion and growth and wildfire (Stewart et al., 2022).

Population size estimation has become a primary objective in wildlife population monitoring programs. In some cases, however, the collection of replicated count data or capture-recapture data can be impractical and expensive, and therefore management of populations can, instead, be guided by estimating the proportion of an area occupied by a species. Estimating occupancy only requires detection and non-detection data which is less expensive to gather than capture-recapture data. Hence, occupancy models are now extensively used to estimate distribution and abundance of animals and plants. By using occupancy models, false conclusions about species habitat relationship can be prevented when a species is not detected and absent at a site, because occupancy models account for species that can be present but undetected in an area during a survey (Stauffer et al, 2021). Here, we report a large-scale assessment of Arabian tahr distribution using camera traps incorporating both presence and absence data, and accounting for

imperfect detection using occupancy modelling approaches (MacKenzie et al., 2002, 2003, 2018).

Ross et al. (2019a) also studied Arabian tahr occupancy using camera traps on the 650 km Hajar mountain range in Oman, which included protected areas like (Wadi Sareen and Jabal Qahwan) and non-protected areas. These occupancy models were fitted using PRESENCE using a two-stage logistical regression that combined 14 environmental covariates (terrain ruggedness within a 750 m radius, terrain ruggedness within a 50 m radius, altitude, designated Arabian tahr protected area, number of goats per trap-night, distance to the nearest village, distance to the nearest road, annual temperature range, water within 100 m, mean diurnal temperature range, mean incident radiation experienced, within an area of ophiolite, normalized difference vegetation index and the year the cameras were operational) at each site to understand occupancy and detection. They measured ruggedness by using the mean surface ratio within 50 m and 750 m radius buffers from camera location. Arabian tahr resulted in a naïve occupancy estimate of 0.46 across the range and a model-averaged site occupancy of 0.49 ± SE 0.29 and detection of 0.07± SE 0.07. Covariates of Arabian tahr protect areas, rugged terrain within a 750 m radius, altitude, presence of villages and goats had the highest influences on Arabian tahr occupancy. Occupancy of Arabian tahr increased in tahr protected areas and for rugged terrain. However, occupancy of Arabian tahr declined with altitude, presence of villages and goats. Hence, they concluded that Arabian tahr preferred high rugged areas with lower altitudes and stayed away from villages and goats (Ross et al., 2019a). In our study we took on a different approach in analyzing camera trap data. We used camera trap data only from outside protected areas in the northern

Hajar range, which was part of the camera trap data used in Ross et al., 2019a. We used occupancy in the UNMARKED package available in R, and also used Dredge and Nested which are functions available in MuMIn package in R which overall gives us better model selection accuracy. The focus on unprotected areas gave better resolution for that part of the range, and therefore greater conservation inference for the populations most exposed to threats.

3.1.2 Model selection

Scientists have begun to use a new approach to analyze data to understand ecology and evolution of species. The traditional approach is to use a null hypothesis method but, increasingly, this has been replaced by model selection, an approach to gathering all interferences from a set of several competing hypotheses (Johnson and Omland, 2004). This approach has some advantages over the null hypothesis approach: firstly, it is not restricted to analyzing a single model but, rather, allows competing models to be compared to one another; secondly, competing models can be ranked and weighed, providing a measure that is quantitative and can show comparative support of the models; thirdly, if models show similar support from the data, they can be model averaged to reduce the reliance on a single – potentially flawed – model for estimation and prediction (Johnson and Omland, 2004).

Dredge is a function available in the MuMIn package in R (Barton, 2014). From a global model, it will generate AIC values, delta values and weights for all potential submodels of occupancy and detection. The dredge function evaluates a set of candidate models generated by using different combinations of the terms in the global model

(Burnham and Anderson, 2002). Lower AIC values (and, correspondingly, higher model weights) indicate models that best fit the data, penalizing for the number of parameters. The delta values are the difference between the AIC values for each model and the top model (i.e., that with the lowest AIC value). Model weights, generated from a comparison of the corrected AIC values, can be interpreted as the probability of each model having generated the data observed (Mackey et at., 2020).

The "Nested" function, also in package MuMIn, is an extra filtering step taken after the use of Dredge. This function reduces overly complex models within the global model. Complex models are those models that have the same parameters as models with a lower AIC value, plus some additional parameters that confer little advantage for model fit (Richards et al., 2011).

We aim to quantify population size and habitat use of Arabian tahr in the northern part of the Hajar mountains in Oman using occupancy models.

3.2 Methods

3.2.1 Camera trap study area

Camera traps were deployed in the Hajar Mountains in Oman, an area of approximately 9492 km^2 (Figure 9). The mountain range consists of steep mountains, dry river beds and canyons. The highest point on the mountain range is on Jabal Shams at 3009 m. As elevation increases, temperature and evapotranspiration decrease. The

mean annual temperature at sea level is 29 °C but this increases to 40 °C in the summer months, 25 °C at 1070 m and 18 °C at 2000 m (Luedeling et al., 2007). The mean annual precipitation ranges from 75 mm in the lower altitudes to 400 mm in the higher altitudes of the mountains (Kwarteng, 2009). Vegetation is generally sparse across the mountain range due to the hot, arid conditions, but vegetation coverage increases in drainage lines and natural pools and with altitude, with the highest number of species found between 1000 - 1500 m (Ghazanfar, 1991).
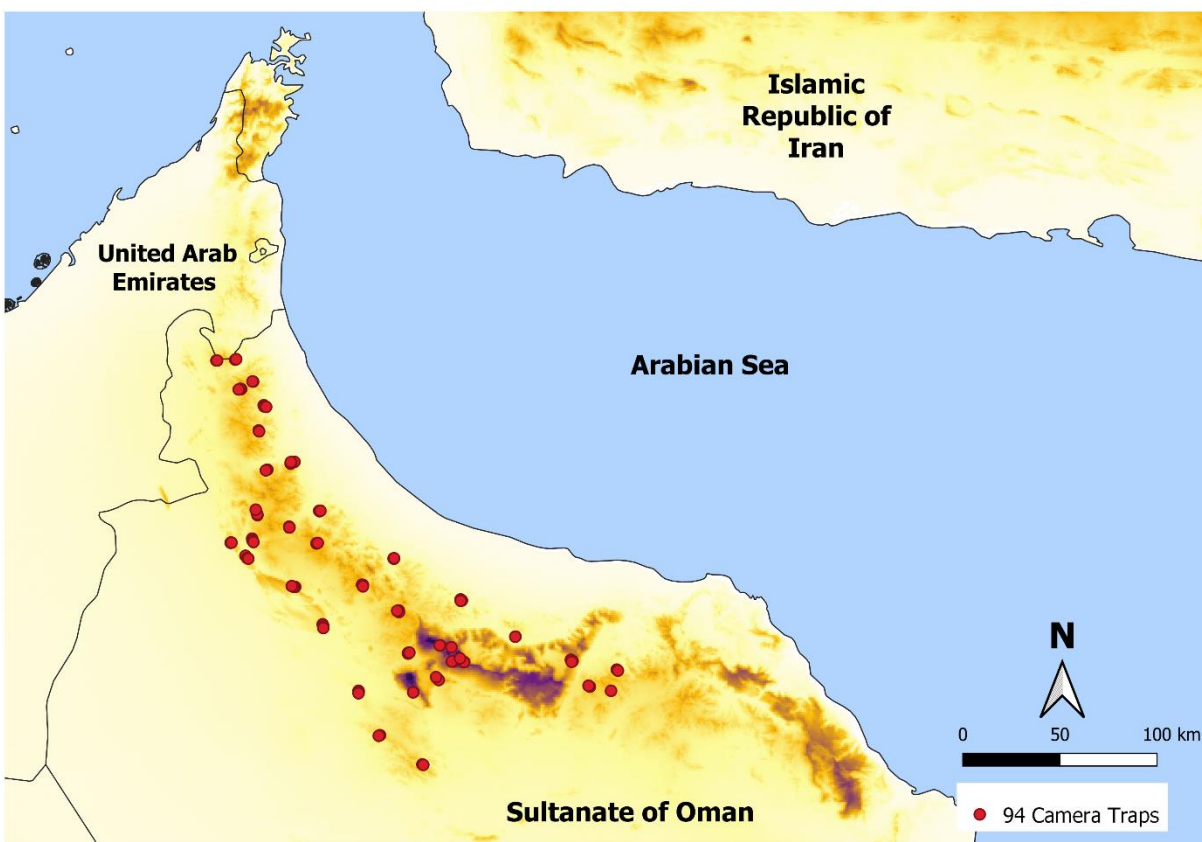
Figure (9): The locations of the camera traps (red) in the northern Hajar range in Oman. Note: A total of 43 sampling locations were separated from each other by 10-30 km. Some sampling locations had 2-3 cameras placed at least 1km apart and may appear as an

individual point. Each camera was treated as individual trap site, resulting in a total of 94 camera traps.

3.2.2 Camera trap survey

A total of 94 camera traps (Bushnell Trophy Cam HD) were deployed from October 2012 to May 2015 at sampling locations in the Northern Hajar Mountains to collect data and cast light on the drivers of occupancy underlying the spatial distribution of the northern population of Arabian tahr in the Hajar Mountains. A total of 43 sampling locations were separated by 10-30 km, in which 2-3 cameras were placed within each sampling location, but at least 1 km apart from each other (Figure 9). The altitudes of the cameras ranged from 17 m to 1957 m. Due to the rocky and difficult nature of the Hajar mountains, no distinct paths were available; therefore, cameras were placed on cliff ledges, slopes, passes and paths. The camera traps were operational for various periods of time but to avoid violation of closure assumption which can bias occupancy estimates (Kendall, 1999), only data across up to 90 days were included, with an average period of 72 days per camera trap. For each camera trap deployment, each 24-hour trapping period was used as a unique sampling occasion.

3.2.3 Environmental covariates

Three variables (elevation, slope and ruggedness) were hypothesized to have the strongest influence on Arabian Tahr occupancy based on a previous study by Ross et al., 2019a.These variables were selected for this project to compare their relative influences

on Arabian tahr occupancy using UNMARKED. All covariates were used to relate to occupancy and detection; however, only ruggedness and slope were used to relate to detection because elevation was deemed unlikely to have an effect on detectability of tahr. The three variables used were the only suitable variables to obtain using QGIS v. 3.1.6. Ruggedness values were extracted from the camera location without applying a radius buffers. GPS coordinates for each camera trap were recorded at the time of deployment and imported to a GIS database. All the variables were extracted using 30m ASTER Digital Elevation Models (DEM). Ruggedness and Slope were obtained using the QGIS Terrain Ruggedness Index option and the Slope option, respectively, followed by Point option tool to extract the values for each point/camera on the map. Elevation was obtained using the Point Sampling Tools options on QGIS. There was goat-tahr overlap in the camera trap data but we decided not to add goats/livestock as a covariate influencing tahr occupancy but instead focus on practicing obtaining covariates from GIS databases.

3.2.4 Occupancy and detection analysis

Models were fitted using the UNMARKED package in R, which provides methods to estimate occupancy and abundance of a species at a site that cannot be detected with certainty (Fiske and Chandler, 2017). Camera traps were functional for a long period of time but we only included data of 90 days to avoid seasonal influences on the analysis. Furthermore, it was assumed that the detections of species at each site were independent of one another, due to the separation of cameras by at least 1 km (MacKenzie et al.,

2006). The data used in this study were from a specified 90-day winter period in years 2012 to 2015 (and not all cameras were deployed in the same year). Therefore, the focus was not the occupancy of tahr during the winter period of a specific year but, rather, the average winter occupancy of tahr from years 2012-2015.

The Occu (which stands for occupancy) function from the UNMARKED package in R was used to fit the single season occupancy model of MacKenzie et al. (2002). The default option allows covariates of occupancy and detection, modeled using the logit link. The formula used in Unmarked is a double right-hand sided formula: (~det ~occu) where ~det is a formula for estimating detection and ~occ for estimating partially observed occupancy state (Fiske et al., 2020).

3.2.5 Model selection

After running dredge, corrected AIC values, delta values and AIC weights including all of the covariates that could have an effect on occupancy and detection are generated to estimate the performance of each model, relative to other models in the set, adjusting for the number of parameters. The models are ranked by the lowest AIC values (and correspondingly higher model weights) which indicate models that best fit the data (Mackey et at., 2020).

Running Nested will generate simpler models within more complex models and these are known to be nested. If there is a slight or no increase in fit within the additional parameters, then the complex models will have similar AIC delta values. In this case it is

not ideal to select the more complex models as the additional complexity does not improve explanatory power and is counter to the principle of parsimony. It is wise to select a model that has a delta value less than delta values of all more complex models within which it is nested (Richards, 2008). For better efficiency we used/extracted the top models which had a delta difference of <= 5.5.

After model averaging, the average model can be used to predict response values that would be expected given specific sets of predictors. Using model averaging is likely to reduce bias relative to the estimates from just the selected best model. The predictions can either be created with the full averaged coefficients or the subset-averaged coefficients (Burnham and Anderson 2002). In this study, the "full averaged coefficients" were used.

Predictions of probability of occupancy were generated for the full range of observed covariate values. Specifically, occupancy was predicted for values of ruggedness varying smoothly from its minimum to its maximum value, and both slope and elevation set to their 0.025, 0.5 and 0.975 quantiles. Fitted values were plotted against covariates using the ggplot package in R (Wickham, 2016).

3.3 Results

Only 73 cameras fit into the 90-day bracket of winter periods in 2012-2015. Across camera sites, there was an average of 77.6 trap nights and a combined effort of 5667 trap nights. The maximum number of trap nights per site/camera was 90, with a minimum of

23 days. Out of the 73 cameras, only 31.5% (23) of those cameras detected tahr. The total number of detections was 70 and the total number of non-detections was 5597. The minimum number of detections per non-zero site was 1 and the maximum detections was 10. The occupancy probability of tahr resulted in a naïve estimate of 1 which means that tahr occurs at all of the sites if we take into account that it was not seen at all sites because of imperfect occupancy. The summed occupancy across 73 cameras was 25.29 and this suggests that they occur in one third (34%) of the area. The detection probability of tahr was estimated at 0.0124 on any given day when present.

The highest ranked model shown in table 7 is model [1,] which has the lowest AIC value of (679.2) and carries the highest AIC weight of (0.356) does not include ruggedness to have an effect of Arabian tahr occupancy. However, slope has shown to have a positive effect of tahr occupancy (0.049) and elevation had a negative effect on tahr occupancy (-0.003) hence increase in elevation decreases occupancy probability. Model [2] is ranked as the second-best model and a candidate for a good model according to the AIC value (680.300) and delta difference of 1.170 to the top model and carrying a model weight of 0.199, which only has ruggedness having an effect on detection probability of tahr. The rest of the models (3 to 9) are not significant since the models have a delta value >2 and hold a combined model weight value of 0.0445. Model averaged occupancy of tahr was estimated at 0.566 and, based on the 95% confidence intervals of model-averaged coefficients, all covariates overlapped 0 which indicates uncertain direct effects on occupancy and detection (Table 8). That uncertainty notwithstanding, it may be possible to discern the most likely effects from the extent to which confidence intervals are skewed in this case. In that context, it seems that tahr

prefer lower elevations and terrain with higher slopes. Ruggedness does not seem to have any effect on the occupancy of tahr (Figure 10).

Table 7: Model selection table showing the top models ranked by Akaike Information Criterion (AIC) after the use of the function Nested which eliminated all complex model versions, retaining simpler models. Values of detection intercepts p(Int) and occupancy intercepts psi(Int) are shown. Since this model has multiple covariates, a linear predictor and a link function is used and it is usually the logistic ("logit") link. The intercept is the logit of the probability of occupancy and detection at the mean values of all the continuous covariates. Values of detection probability of ruggedness p(rug) and slope p(slp), including values of occupancy probability of elevation psi(elv), ruggedness psi(rug) and slope psi(slp). With each model showing the number of parameters (df) used to create the model, log-likelihood (logLik), (AIC) value which is a measure that calculates the likelihood of each model to have generated the data, lower values indicate models with a better fit to the data. The difference in AIC relative to the top-ranked model (delta) which is the model that is most likely to have generated the data (the one with the lowest AICc), and the Akaike weight (weight) is a transformation of delta that can be interpreted as the probability that the given model is the most likely one of the candidate models to have generated the data, and is also conditional on the candidate model set. Note: columns beginning with p and psi give the model coefficients for each of the covariates in the occupancy and detection sub-model. The missing values indicates that the covariate had no effect and therefore was not included in the given model.

Model	p(Int)	psi(Int)	p(rug)	p(slp)	psi(elv)	psi(rug)	psi(slp)	df	logLik	AICc	delta	weight
[1,]	-2.604	0.857	-0.014		-0.003		0.049	5	-334.132	679.200	0.000	0.356
[2,]	-2.638	-0.636	-0.013					3	-336.991	680.300	1.170	0.199
[3,]	-2.782	1.152		-0.019	-0.003	0.020		5	-335.409	681.700	2.550	0.099
[4,]	-2.849	1.191		-0.017	-0.003		0.043	5	-335.562	682.000	2.860	0.085
[5,]	-3.247	1.114			-0.003		0.040	4	-336.757	682.100	2.940	0.082
[6,]	-3.249	1.666			-0.002			3	-337.914	682.200	3.020	0.079
[7,]	-2.855	-0.654		-0.016				3	-338.231	682.800	3.650	0.057
[8,]	-3.265	-1.043					0.015	3	-339.124	684.600	5.440	0.024
[9,]	-3.264	-0.877					0.005	3	-339.340	685.000	5.870	0.019

Table 8: Model averaged estimates of full averaged coefficients of variables influencing occupancy and detection of Arabian tahr with 95% confidence intervals. Elevation, slope and ruggedness were set to vary against occupancy of Arabian tahr and ruggedness and slope were set to vary against detection of Arabian tahr. The estimates column represents a weighted average of the model-specific estimates of occupancy and detection which is calculated based on the AIC, usually done for model selection uncertainty. The standard

error of the regression, z-value and the Pr(>|z|) value represents the p-value associated with the z-value.

Coefficient	Estimate	Standard. Error	z-value	Pr(>|z|)	95% confidence intervals	
Occupancy (Int)	0.566	1.283	0.441	0.659	-1.948	3.081
Occupancy ~ elevation	-0.003	0.002	1.218	0.223	-0.005	0.000
Occupancy ~ slope	0.045	0.029	0.869	0.385	-0.003	0.093
Occupancy ~ ruggedness	0.020	0.007	0.283	0.777	-0.004	0.044
Detection (Int)	-2.786	0.362	7.688	<2e-16	-3.496	-2.076
Detection ~ ruggedness	-0.014	0.008	0.946	0.344	-0.026	-0.002
Detection ~ slope	-0.018	0.009	0.466	0.641	-0.039	0.004
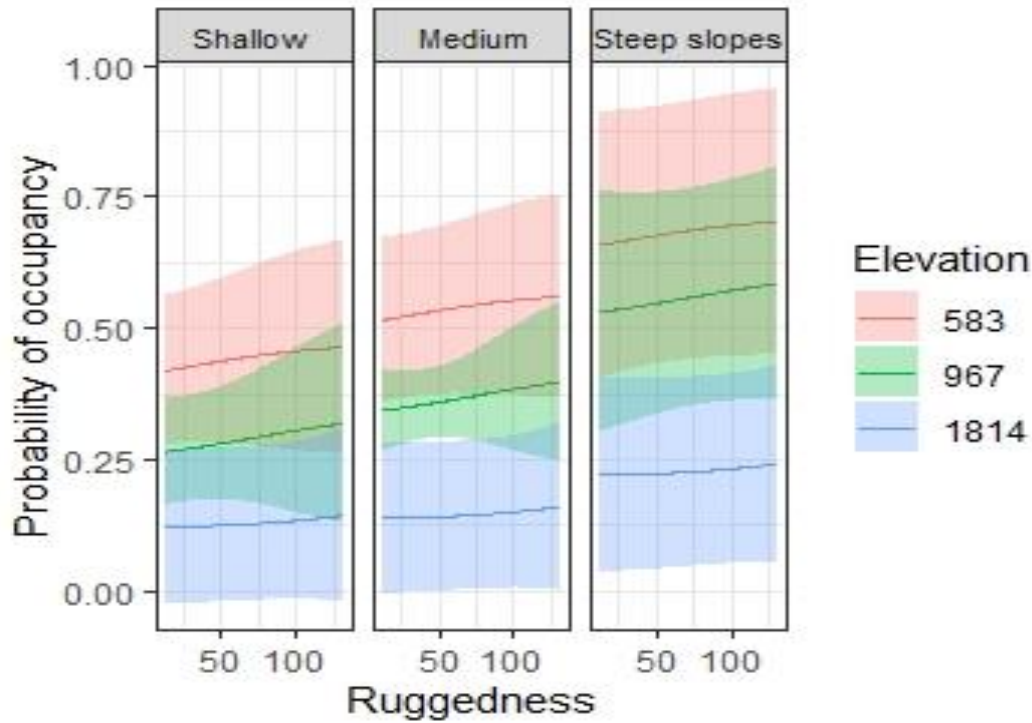
Figure 10: Estimated effects of ruggedness, elevation and slope on Arabian tahr occupancy. Shallow, medium and steep slopes correspond, respectively, to the 0.025, 0.5 and 0.975 quantiles of observed slopes in the study area.

3.4 Discussion

This study utilized a presence/absence dataset using occupancy to assess the occurrence of Arabian tahr on the northern Hajar mountain range in Oman. Environmental covariates were used to determine the influence of ruggedness, slope and elevation on tahr occupancy and detection.

The previous camera trap study by Ross et al., 2019a surveyed the whole Hajar mountain range where Arabian tahr is known to be distributed. This included both protected and non-protected areas however, more intense camera trapping was conducted inside protected areas (Wadi As Sareen and Jabal Qahwan) (figure 11). Here we instead focus on the occupancy of Arabian tahr outside protected areas by analyzing camera trap data using occupancy in the UNMARKED package available in R. In addition, we used Dredge and Nested which are functions available in MuMIn package in R, which overall gives us better model selection accuracy. In our study we found that the summed occupancy across 73 cameras was 25.29 and this suggests that they occur in about one third (35%) of the area. Compared with the earlier Arabian tahr study in the Hajars (Ross et al., 2019a) which included protected areas (Wadi Sareen & Jabal Qahwan), they detected at 139 out of 300 cameras, and the summed occupancy across 300 cameras was 46.3 (Ross et al., 2019a). Ross et al., 2019a suggests that Arabian tahr's occupancy is significantly better in protected areas and seem to help their conservation. Therefore, we suggest that the species also requires management outside protected areas.
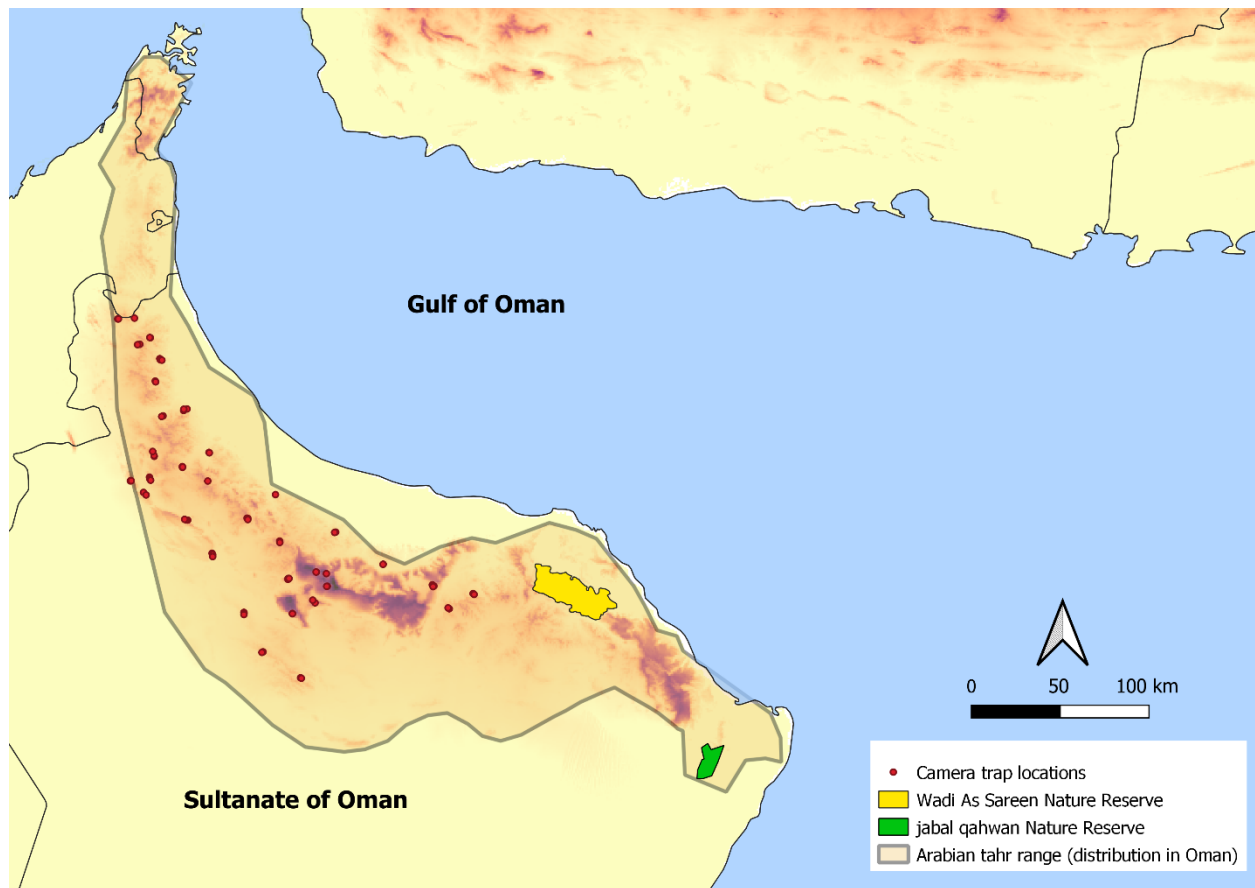
Figure 11: This map shows both Wadi Sareen Jabal Qahwan Nature Reserves in the south of Hajar mountains in Oman. Including the conducted camera trap survey.

Our results indicate that ruggedness at each camera location had no impact on tahr occupancy. However, the study by Ross et al., 2019a suggested that ruggedness had a high positive impact on tahr occupancy and model-averaged parameter estimated that ruggedness within a 750 m radius of the site (RUG750) had the greatest effect on Arabian tahr. Additionally, they suggested that areas that have high ruggedness also provide shade for tahr during the day, since Arabian tahr occur in regions that experiences higher temperatures. Therefore, finding shade is crucial for temperature regulations for the species (Ross et al., 2019a). Rugged areas also provide excellent cover from

predation and thus are known to be a robust determinant of habitat selection by ungulates, and in this case tahr occupy areas that have higher ruggedness to escape from predators (Ripple & Beschta, 2004). Elevation had a negative impact on tahr occupancy. Hence, Arabian tahr may avoid high altitudes due to colder temperatures, higher rainfall and lack of vegetation available at these conditions (Ross et al., 2019a. Finally, in our study, slope had a positive influence on Arabian tahr occupancy and distribution. However, Ross et al., (2019a) indicated that their data showed no relationship between tahr and slope.

It was expected that ruggedness would have a positive influence on Arabian tahr occupancy and that slope would have no influence on occupancy according to previous studies done on Arabian tahr occupancy in the Hajars (Ross et al., 2019a). Furthermore, predation could play an important factor in Arabian tahr's use of rugged terrain and slope as Arabian tahr are more likely to use rugged terrain to escape from predators (Ross et al., 2019a, Ripple & Beschta, 2004, Gross et al., 2002 and Hamel & Côté, 2007). However, the effect of ruggedness on Arabian tahr occupancy was not evident in our data and the reasons could be that our camera trap survey took place outside protected areas where the status of the Arabian tahr population could differ. Moreover, there was no evidence from the camera trap data showing predation of Arabian tahr in our study and this might suggest that Arabian tahr did not need to use rugged terrain to evade predation. Therefore, Arabian tahr did not use rugged terrain as its preferred terrain in our study but rather maybe used steeper slopes to get access to shade and forage in high temperatures during the day. A study by Ross et al., 2021 on resource selection using GPS on Arabian tahr in Wadi Sareen Nature Reserve suggested that Arabian tahr chose areas closer to steep slopes (>35°) equally in both summer and winter (Ross et al., 2021). Water and

vegetation availability could have influenced the use of slope on Arabian tahr occupancy, as access to vegetation and water pools could be through steep slopes. Natural water pools or plunge pools on mountains are formed when the impact of high momentum water from rainfall runs down the mountain slope which excavates a depression. Plunge pools only occur in areas where there are sharp decreases in slope of more than 4° and in well-formed in areas where the slope exceeds 15° (Lee et al., 2002). Moreover, vegetation composition in Wadi Sareen Nature Reserve is largely determined by water availability, and Arabian tahr chose wadi habitats (especially steep sided ephemeral wadis which also consist of ephemeral vegetation) during both summer and winter periods (Ross et al., 2021).

The camera traps were placed in this study outside protected areas in the north. They were at least 2.5 km away from any village or road and positioned at altitudes between 464 m and 2226 m above sea level, which was similar to Ross et al. (2019a). They deployed cameras between 1 km to 7km away from villages and positioned at altitudes between 7 m and 2768 m. This could suggest the disturbance from villages and roads are fairly low in both studies.

Arabian tahr is considered a species at risk of extinction (Ross et al., 2021). Therefore, the conservation of these species in the wild is crucial. In order to conserve Arabian tahr, identifying Arabian tahr habitat requirements for survival and adaptation is important (Ross et al., 2021). The use of GPS collars can help us help us understand tahr habitat requirements. This advanced technology sends accurate location data to our computers through satellites and discards the need to track the individuals on the ground or from the air. Thus, GPS collars are becoming more popular and have been shown to

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be a powerful tool for research. Daily activity patterns, home range and habitat use can all be determined by GPS collars which are then used for application in the management and conservation of wild species (Foley & Sillero-Zubir, 2019). Apart from a camera trap survey done on Arabian tahr, Ross et al., 2021 studied how and why Arabian tahr select their habitat. This was done by using GPS collars which were applied to Arabian tahr in the Hajar mountains in Wadi Sareen Nature Reserve. The objective was to understand how habitat may be used to provide useful information such as thermal refuge, relevant to adaptation to climate change. This was done to prioritize habitat protection for Arabian tahr. Scale, sex and season were clearly the influences that habitat selection was dependent on. But vegetation resources were not selected at the larger scales and sometimes avoided. Moreover, Arabian tahr of both sexes in both seasons selected preferred habitat with low heat load and thermal refuges, indicating the importance of thermal refuges (Ross et al., 2021). Other important factors that influenced habitat selection by Arabian tahr in the Ross et al., 2021 study using GPS collars were steep slopes, higher elevations and rugged habitats which, were selected across all scales. Although conserving wildlife under future climatic change is uncertain, understanding wildlife distribution and habitat is an important baseline for planning to preserve the resources necessary for wildlife conservation and adaptation to climatic change (Ross et al., 2021).

These differences in the covariates of slope and ruggedness on occupancy results obtained from our study compared with a similar study done by Ross et al., 2019a (see chapter 1) were initially not expected. Now after understanding Arabian tahr occupancy outside protected areas using the UMARKED package in R and other functions in MuMIn

package like Dredge and Nested for model selection. We are able to say that these results obtained certainly suit Arabian tahr occupancy outside protected areas because of possibly low predation and also suggest more research in these areas at a larger scale or longer period are required.

Chapter 4: Synthesis and conclusion

This study has uncovered new information using high resolution methods on the genetics and ecology of two ungulates in the subfamily Caprinae, the Arabian tahr (*Arabitragus jayakari*) and Nubian ibex (*Capra nubiana*). The purpose of this final chapter is to synthesize the results of each species presented in chapters 2 and 3, address the hypotheses put forward in chapter 1, and to place these into the context of the current state of the field.

4.1 Genetic diversity, phylogeny and demographic history of Arabian tahr and Nubian ibex

Here we will discuss the hypotheses mentioned in chapter 1. The first was that Nubian ibex are more genetically diverse than Arabian tahr. I also assessed their phylogenetic position using full mitochondrion genomes. According to our findings associated with nucleotide diversity, it is true that Nubian ibex is more genetically diverse than Arabian tahr, but the difference is small and the effective size of each population is likely to be similar (as they were during the last glacial maximum). Moreover, they have shown phylogenic uniqueness in the sub-family caprinae tree.

Since *Capra sibirica 1* in the phylogenetic tree is in a paraphilic position (figure 2 a & b), this suggests that the sampled individual is a hybrid (see chapter 2.4.1). It seems that *Capra sibirica 1* had poor preservation and nuclear genome was not exploited for

analysis in the study (Daly et al., 2022). In this case we recommend full genome analysis to confirm if the *Capra sibirica 1* captive individual (represented by accession no. OW568858) is indeed a hybrid.

We found that neither species have low diversity yet, but their population sizes are not large. According to the international Union for Conservation of Nature (IUCN), the Arabian population is decreasing and the estimated population is 2,202-2,324 adults based on occupancy probabilities (Ross et al., 2019b). In terms of the Nubian ibex, their population is also decreasing according to the ICUN and the estimated population size of Nubian ibex population globally is ~5,000 adults, but there is a lack of population data available especially in Sudan, Eritrea, Ethiopia and Yemen to accurately estimate its global population size (Ross et al., 2020b). In Oman, the Nubian ibex population is decreasing due to poaching and this decline is confirmed by the camera trap surveys (Ross et al., 2020b) and photographic evidence of poachers (Ross and Al-Said, unpublished data). The estimated population size in the Huquf escarpment in Al Wusta Wildlife Reserve is approximately 100-250 and in Dhofar about 600-1000 adults (Ross et al., 2020b). Estimating population size for both Arabian tahr and Nubian ibex has been found to be difficult and problematic, since these species have only few body markings and capturing them has proven to be extremely difficult. Therefore, using mark-recapture studies is challenging (Ross et al., 2019b). When comparing census data of their abundance obtained from camera trapping surveys with our genetic analysis on their demographic history, it can be said that the population estimates obtained from the ICUN have similar estimates to their population size obtained from PSMC analysis (see chapter

2, figures 2 & 3). This supports the assertion that combining genetic and abundance data is valuable for the conservation and management of these threatened species.

The phylogenetic analyses supported earlier studies, but provided a novel focus on the species closely related to these two species. Both Arabian tahr and Nubian ibex were from wild populations in Oman and showed some level of uniqueness when compared to other Arabian tahr and Nubian ibex mitochondrion data from the GenBank. This uniqueness suggests conservation importance.

4.2 Arabian tahr occupancy outside protected areas

The second hypothesis from chapter 1 states that Arabian tahr occupancy is lower outside protected areas. This statement is true. After better understanding the distribution of Arabian tahr in the northern part of the Hajar mountains, we found that the summed occupancy was 25.29. While Ross et al., 2019a obtained a summed occupancy of 46.3 both within and outside protected areas.

There are a number of reasons why tahr exist in a sparse population outside protected areas. Firstly, since goats and Arabian tahr have similar habitat preferences, domestic goats could heavily influence Arabian tahr's occurrence outside protected areas. As quoted by Ross et al., (2019a) "Any future attempts to protect or restore Arabian tahr habitat should first consider how livestock populations can be reduced or controlled". It is considered almost impossible to completely remove domestic livestock from the Hajars. Nevertheless, having a controlled plan could benefit both Arabian tahr and

domestic livestock. A possible solution to this issue is to restrict domestic goats to shallow slopes and flatter areas where they don't directly share habitats with Arabian tahr. Secondly, more suitable habitat is available inside protected areas which offer more vegetation and rainfall. Arabian tahr were first discovered in Wadi Al Sareen which is now a protected area (Harrison and Gallagher, 1975). Thirdly, poaching or illegal hunting of Arabian tahr could be one of the most important factors explaining low population densities in suitable habitat outside protected areas. Because these preferred Arabian tahr habitats are associated with steep terrain, it has been challenging to enforce their protection, especially outside protected areas. Lastly, the lack of published information, seasonal and annual studies on population estimates and status of the critically endangered species across the Hajar mountains highlights the need for more research both within and outside protected areas (Ross et al., 2019a). There are numerous ways to improve the evaluation of occupancy of species inside or outside protected areas, including the increase in survey effort. Rovero et al., (2020) suggested that there should be further research on the way that livestock may negatively impact wildlife, and that the protection of wild predators and their wild ungulate prey requires a modification of livestock grazing zones and increased law enforcement. Interestingly, in another study Oberosler et al., (2017) found little evidence for a direct impact of human disturbances on the occurrence of mammals, however they found human disturbance had an effect on detectability and the activity patterns of these mammals. The mammals in their study (those captured during their camera trap survey) were Red fox (*Vulpes vulpes*), Roe deer (*Capreolus capreolus*), Red deer (*Cervus elaphus*), Chamois (*Rupicapra rupicapra*), Brown hare (*Lepus europaeus*), Badger (*Meles meles*), Marten (*Martes sp.*), Brown bear

(*Ursus arctos*), Red squirrel (*Sciurus vulgaris*), Wolf (*Canis lupus*), Alpine marmot (*Marmota marmota*) and Least weasel (*Mustela nivalis*). When considering Rovero et al., (2020) & Oberosler et al., (2017) assessment on the impact of human disturbances and livestock on wildlife, we suggest undergoing further research on assessing whether these impacts have an influence on Arabian tahr occupancy.

we suggest that the species also requires management outside protected areas, since Ross et al., 2019a suggested that Arabian tahr's occupancy is significantly better in protected areas and seem to help their conservation. The summed occupancy across 73 cameras was 25.29 and this suggests that they only occur in about one third (35%) of the area.

4.3 Conservation efforts, management and recommendations for Arabian tahr and Nubian ibex

Based on the results obtained from the genetic analyses of both Arabian tahr and Nubian ibex, and the occupancy of Arabian tahr revealed using camera traps outside protected areas, it can be said that both species are vulnerable to environmental threats such as the loss of natural habitat and climate change. In Oman, the government has initiatives to limit the loss of biodiversity and is therefore addressing conservation issues and building knowledge and conservation capacity, particularly for endangered species such as the Arabian Leopard (*Panthera pardus nimr*) and the Arabian Tahr (Burton et al., 2013). In his Oman government funded PhD thesis on the Arabian Leopard, Al Hikamani

reports that despite its status of being highly threatened, there is a lack of scientific information for many aspects of its population and evolutionary genetics. The objective of that study was to improve the knowledge base to better develop management strategies for the future of the Arabian Leopard. It did this by generating a comprehensive mitochondrial DNA sequence database which included sequenced data from all Arabian Leopards from the Arabian Peninsula and Al Hikamani's study suggested that the Arabian Leopard is evolutionarily distinct from other leopard subspecies (Al Hikamani, 2019). A more recent study on the population genetic diversity of the Nubian Ibex also funded by the Oman government, used mitochondrial DNA of the Nubian Ibex in Oman and the UAE. Furthermore, studies on camera trap surveys and GPS collaring on both Arabian tahr and Nubian ibex have been conducted and funding by the government for conservation purposes.

Apart from the limited phylogenetic analyses of these species by Ropiquet and Hassanin (2005) and Yang et al., (2013; see chapter 2), no other phylogenetic study on the Arabian Tahr has been published to date.

Work on the Arabian tahr has shown that the protection of migration corridors, population viability analyses and periodic genetic monitoring are essential for conservation management actions for this species. One possible solution for connectivity issues is the translocation of the northern populations, which has been proven to work by Soorae, 2018. Furthermore, habitat restoration is currently an on-going project in Oman. Genetic viability must be prioritized in Oman by the implementation of functional connectivity, the restoration of habitats, and by minimizing human disturbances in Arabian tahr habitats to increase geneflow and to maintain genetic diversity (Ross et al., 2020a).

In our case neither of the focal species (Arabian tahr and Nubian ibex) have shown low genetic diversity so far.

There has been a re-introduction effort done outside of Oman. This program was set up in Sir Bani Yas Island in Abu Dhabi in the United Arab Emirates, which was not prime Arabian tahr habitat. Instead, their prime habitat in the UAE is in Wadi Wurayah in Fujairah Emirate and Jebel Hafeet in Abu Dhabi. It was reported that they introduced a total number of 4 "semi wild" Arabian tahr from 2014 to 2016 including an additional birth of Arabian tahr. The total population number of Arabian tahr was 5 but only 3 individuals survived when last recorded in 2016. One individual was hunted by striped hyaena (*Hyaena hyaena*), that were also introduced and one individual died with a fatal leg injury. For future re-introduction programs of Arabian tahr, release into their natural habitat will be essential. Also, captive animals should be re-introduced gradually, and finally the number of animals to be released should be significantly higher than during the earlier trial (Al Dhaheri et al., 2017).

Regarding future re-introduction programs for Nubian ibex, it is suggested that captive Nubian ibex are not to be used for any future reintroduction programs into the wild until more information and details on their genetic divergence (see chapter 2) becomes available. Wild Nubian ibex populations in Oman from the Huquf and Dhofar were highly distinct and not closely related to any of the evaluated captive Nubian ibex populations in both Oman and UAE. This was evident in mtDNA analysis of both cytochrome b and D-loop sequences, demonstrating a deep divergence between captive and wild populations (Al Al Ghafri et al., 2021). For soft ecology field work, it is important for managers in protected areas to assess the compatibility of biodiversity conservation with infrastructure

development and the presence of humans. Therefore, replication and expansion of camera trap data over the years for comparison is also crucial, which can benefit the assessment of habitat usage and biodiversity change over time (Oberosler et al., 2017).

Poaching still occurs in Oman, though it is considered to be against the law. However, poaching data have as not yet been retrieved/requested for analysis. This is surely an important matter to analyze. We should compare its effects on population estimates over the years to determine its direct impact alongside seasonal and annual studies on population estimates and the status of both Arabian tahr and Nubian ibex populations.

4.4 Conclusion

In conclusion, this study shed light on the conservation importance of two ungulate species in Oman. It shows that these species do not yet have low genetic diversity, but their populations are not large and may be decreasing. Census data outside protected areas have also shown lower summed occupancy of Arabian tahr than in protected areas. The main threats are likely to be poaching and the lack of effective management over domestic livestock population in wildlife habitats. Thus, this suggests that further studies on both genetics and ecology should include consideration of the effects of poaching and domestic livestock on core Arabian tahr and Nubian ibex habitats in support of the conservation of their biodiversity in Oman.

Appendix

Table S1: Showing the available mtDNA sequences of the species in the Caprinae lineage used for this analysis which were downloaded from the GeneBank.

No.	Species	Scientific name	GeneBank Accession number
1	Argali.1	*Ovis ammon*	MT768090.1
2	Argali.2	*Ovis ammon*	MT768089.1
3	Argali.3	*Ovis ammon*	MT768088.1
4	Argali.4	*Ovis ammon*	MT768087.1
5	Bighorn sheep.1	*Ovis canadensis*	MH094035.1
6	Bighorn sheep.2	*Ovis canadensis*	NC_015889.1
7	Bighorn sheep.3	*Ovis canadensis*	NC_015889.1
8	Sheep.1	*Ovis aries*	MW364895.1
9	Sheep.2	*Ovis aries*	OM869339.1
10	Sheep.3	*Ovis aries*	OM869338.1
11	Sheep.4	*Ovis aries*	OM869337.1
12	Siberian ibex.1	*Capra sibirica*	OW568858.1

13	Siberian ibex.2	*Capra sibirica*	OW568913.1
14	Siberian ibex.3	*Capra sibirica*	FJ207529.1
15	Siberian ibex.4	*Capra sibirica*	NC_020626.1
16	Alpine ibex.1	*Capra ibex*	OW568912.1
17	Alpine ibex.2	*Capra ibex*	OW568909.1
18	Alpine ibex.3	*Capra ibex*	FJ207526.1
19	Alpine ibex.4	*Capra ibex*	NC_020623.1
20	Goat.1	*Capra hircus*	MK234706.1
21	Goat.2	*Capra hircus*	OP470372.1
22	Goat.3	*Capra hircus*	MT683890.1
23	Goat.4	*Capra hircus*	MT683889.1
24	Aoudad.1	*Ammotragus lervia*	FJ207522.1
25	Aoudad.2	*Ammotragus lervia*	EF466060.1
26	Aoudad.3	*Ammotragus lervia*	NC_009510.1
27	The Himalayan tahr.1	*Hemitragus jemlahicus*	FJ207531.1
28	The Himalayan tahr.2	*Hemitragus jemlahicus*	NC_020628.1

29	The West Caucasian tur.1	*Capra caucasica*	JN632609.1
30	The West Caucasian tur.2	*Capra caucasica*	NC_020683.1
31	Markhor.1	*Capra falconeri*	OW568856.1
32	Markhor.2	*Capra falconeri*	OW568856.1
33	Markhor.3	*Capra falconeri*	NC_020622.1
34	Wild goat.1	*Capra aegagrus*	OW568859.1
35	Wild goat.1	*Capra aegagrus*	OW568857.1
36	Wild goat.1	*Capra aegagrus*	OW568852.1
37	Wild goat.1	*Capra aegagrus*	OW568916.1
38	Arabian tahr.1	*Arabitragus jayakari*	MN971587.2
39	Arabian tahr.2	*Arabitragus jayakari*	FJ207523.1
40	Arabian tahr.3	*Arabitragus jayakari*	NC_020621.1
41	Nubian ibex.1	*Capra nubiana*	OW568908.1
42	Nubian ibex.2	*Capra nubiana*	FJ207527.1
43	Nubian ibex.3	*Capra nubiana*	NC_020624.1
44	Cattle.1	*Bos taurus*	GU947019.1

45	Cattle.2	*Bos taurus*	GU947020.1
46	Cattle.3	*Bos taurus*	GU947019.1
47	Cattle.4	*Bos taurus*	GU947018.1
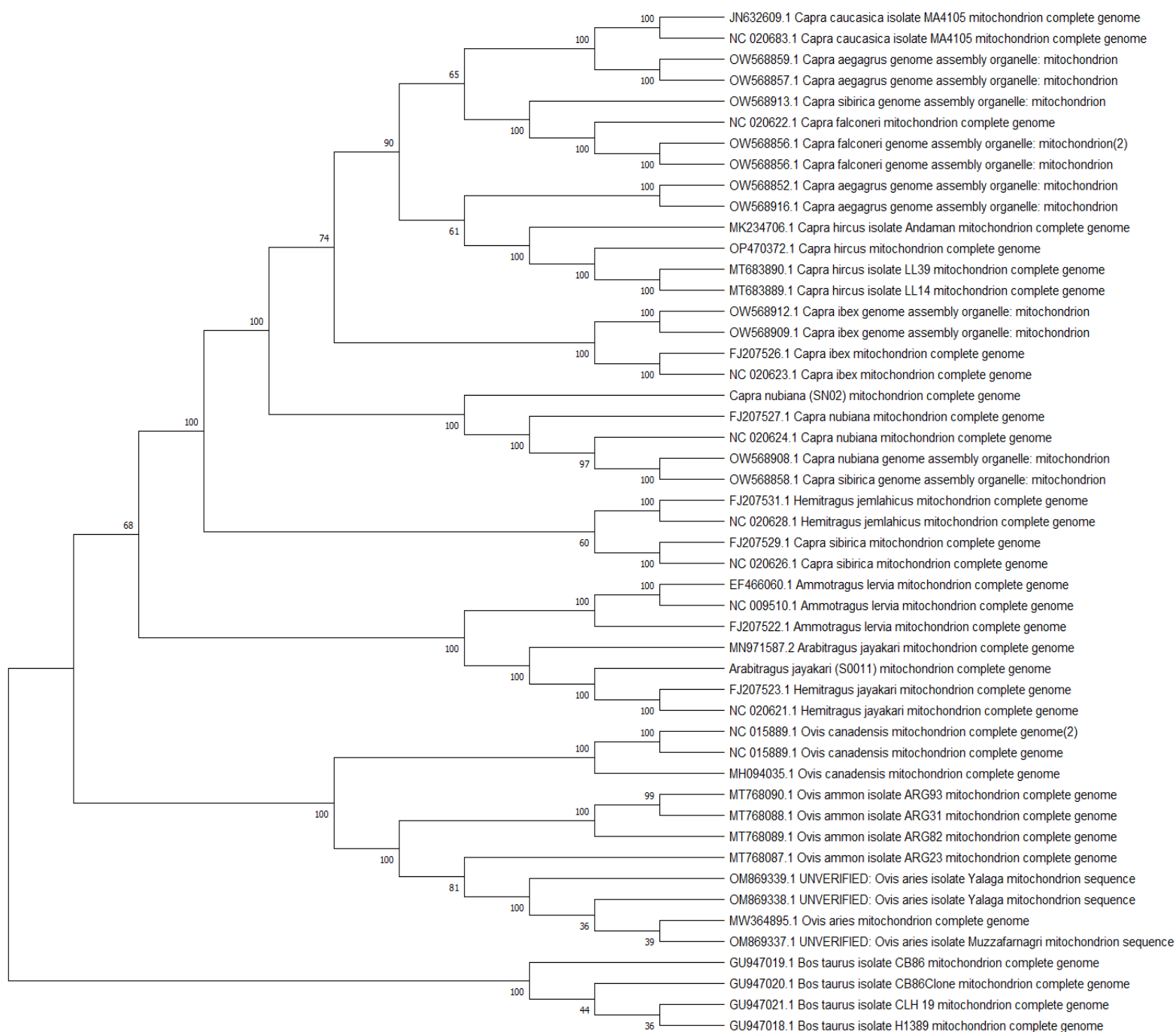
Figure S1: Shows the phylogenetic tree derived from complete mitochondrion DNA sequences of the sub-family caprinae along with the accession GeneBank no of each species. including bootstrap support of values from 1,000 replicates. The values shown on the tree are branch lengths. These values indicate the estimated amount of

evolutionary change that has occurred along that branch. Longer branches suggest greater evolutionary divergence.

Table S2: Model selection table showing the models ranked by AIC after the use of the Dredge function. Where ruggedness slope and elevation were set to vary against occupancy and ruggedness and slope set to vary on detection. Note: columns beginning with p and psi give the model coefficients for each of the covariates in the occupancy and detection sub-model. The missing values indicates that the covariate had no effect and therefore was not included in the given model.

Model	p(Int)	psi(Int)	p(rug)	p(slp)	psi(elv)	psi(rug)	psi(slp)	df	logLik	AICc	delta	weight
22	-2.604	0.857	-0.014		-0.003		0.049	5	-334.132	679.200	0.000	0.154
30	2.397	0.227	-0.020		-0.003	0.051	-0.003	6	-333.481	680.200	1.080	0.090
2	-2.638	-0.636	-0.013					3	-336.991	680.300	1.170	0.086
18	-2.527	-1.422	-0.016				0.035	4	-335.947	680.500	1.320	0.079
10	-2.419	-1.820	-0.019			0.029		4	-336.004	680.600	1.440	0.075
24	-2.602	0.748	-0.025	0.018	-0.003		0.050	6	-333.909	681.100	1.930	0.059
12	-2.462	-2.039	-0.035	0.029		0.035		5	-335.322	681.500	2.380	0.047
15	-2.782	1.152		-0.019	-0.003	0.020		5	-335.409	681.700	2.550	0.043

|												
23	-2.849	1.191		-0.017	-0.003		0.043	5	-335.562	682.000	2.860	0.037
4	-2.657	-0.627	-0.022	0.016				4	-336.749	682.100	2.930	0.036
21	-3.247	1.114			-0.003		0.040	4	-336.757	682.100	2.940	0.035
20	-2.550	-1.461	-0.027	0.020			0.037	5	-335.606	682.100	2.950	0.035
5	-3.249	1.666			-0.002			3	-337.914	682.200	3.020	0.034
13	-3.266	1.682			-0.003	0.022		4	-337.051	682.700	3.530	0.026
26	-2.468	-1.638	-0.018			0.012	0.022	5	-335.898	682.700	3.530	0.026
3	-2.855	-0.654		-0.016				3	-338.231	682.800	3.650	0.025
7	-2.900	1.866		-0.014	-0.002			4	-337.152	682.900	3.730	0.024
19	-2.808	-1.190		-0.018			0.022	4	-337.641	683.900	4.710	0.015
28	-2.464	-2.019	-0.034	0.028		0.031	0.006	6	-335.315	683.900	4.740	0.014
31	-2.745	1.120		-0.021	-0.003	0.014	0.022	6	-335.451	684.200	5.010	0.013
29	-3.267	1.413			-0.003	0.007	0.022	5	-336.771	684.400	5.280	0.011
11	-2.820	-1.019		-0.018		0.008		4	-337.952	684.500	5.330	0.011
17	-3.265	-1.043					0.015	3	-339.124	684.600	5.440	0.010
9	-3.264	-0.877				0.005		3	-339.340	685.000	5.870	0.008
27	-2.821	-1.133		-0.018		-0.009	0.037	5	-337.558	686.000	6.850	0.005
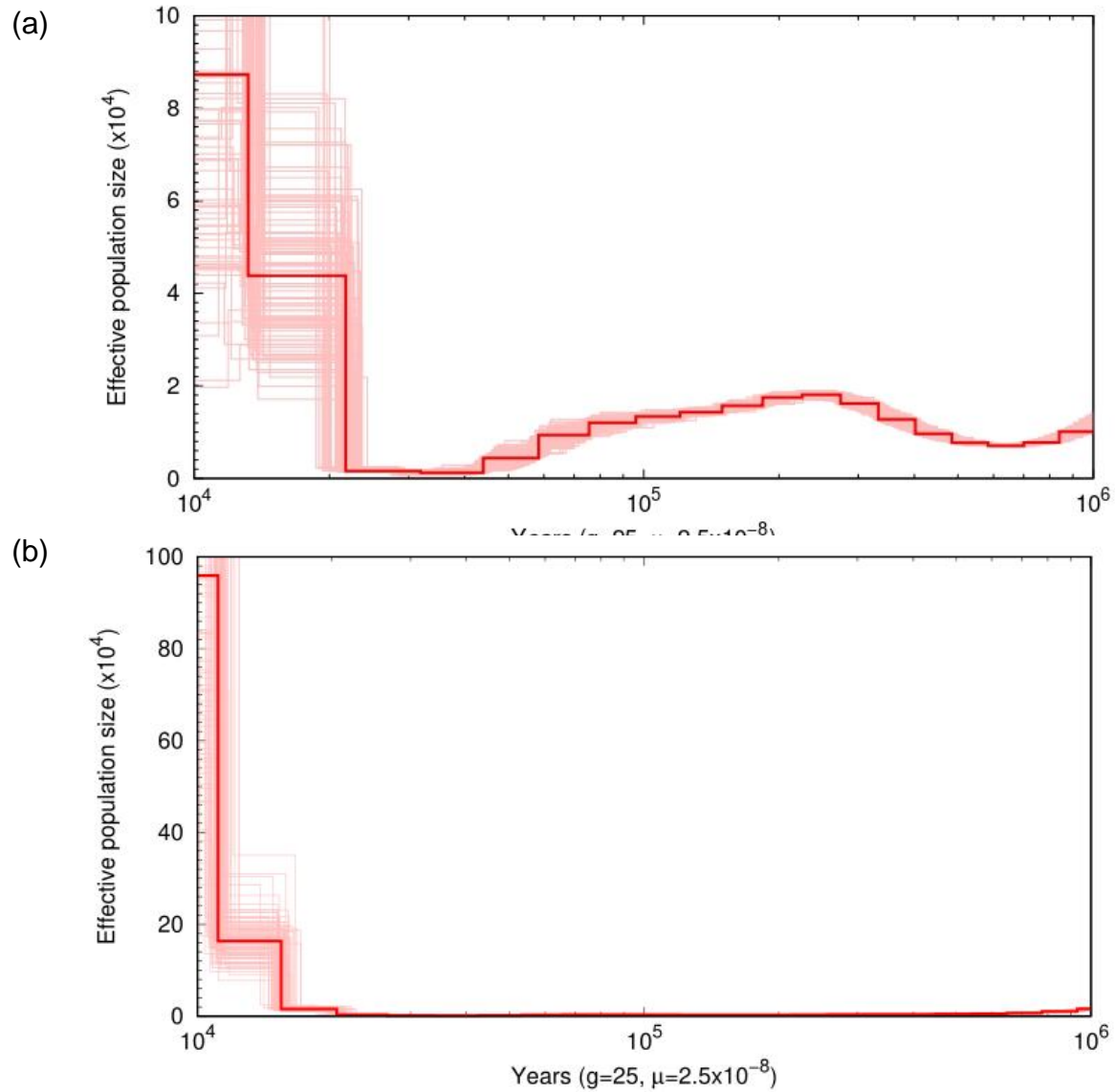
Figure S2: (a) Demonstrates PSMC model plot of whole-genome of Nubian ibex (b) PSMC model plot of whole-genome of Arabian tahr. The Y axis in both plots represent effective population size scale set to 10 K and the X axis in both plots represent time in years. Small light red bars show bootstrap values. Calibrated using a generation time (g)

of 25 years and a mutation rate (u) of 2.5x10-8 per generation. Point of inflection is shown at ~ 10,000 years ago.

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