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Authors: Martínková, Natália, Zemanová, Barbora, Kranz, Andreas, Giménez, Mabel D., and Hájková, Petra

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Chamois introductions to Central Europe and New Zealand

Natália MARTÍNKOVÁ^{1,2*}, Barbora ZEMANOVÁ¹, Andreas KRANZ³, Mabel D. GIMÉNEZ⁴ and Petra HÁJKOVÁ¹

¹ Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Květná 8, 603 65 Brno, Czech Republic; e-mail: martinkova@ivb.cz, barca_zemanova@centrum.cz, hajkova@ivb.cz

² Institute of Biostatistics and Analyses, Masaryk University, Kamenice 3, 625 00 Brno, Czech Republic

³ ALKA Kranz, Am Waldgrund 25, 8044 Graz, Austria; e-mail: andreas.kranz@aon.at

⁴ Facultad de Ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, Posadas, Argentina; e-mail: mdg205@yahoo.com.ar

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Abstract. Chamois (*Rupicapra rupicapra*) introductions were popular at the beginning of the 20th century when first animals were shipped from Austria to the Czech Republic and New Zealand. The historical record of the Czech introduction indicates Neuberg Müzzsteg Game Reserve in Eastern Alps, Styria, Austria as the main area of origin of founders. First animals for the New Zealand population are thought to have originated from Ebensee, Upper Austria, Austria and later more animals came from the Müzzsteg region. We sequenced mitochondrial control region of chamois from the introduced populations and their putative source areas, and we applied median-joining networks and Bayesian inference analysis to distinguish the regions of origin of female founders. We found the Müzzsteg region as the most likely source population for introductions to the Czech Republic and New Zealand, supplemented with close association with sequences from Ebensee in populations from the Czech Republic. Genetic diversity present in the Czech Republic was further relocated to the introduced populations in Slovakia in the 1960's.

Key words: Alpine chamois, animal translocations, introduction, invasive species, *Rupicapra rupicapra*

Introduction

Game management practices included extensive trade and exchange of wildlife in the past. Northern chamois (*Rupicapra rupicapra*) were intensely affected as they are desired trophy animals. The species indigenous distribution contains mountain ranges in southwestern Asia, southeastern Europe, the Carpathians, Chartreuse massif and Alps. However, introductions, primarily motivated with additional hunting opportunities, expanded the distribution range to include also mountains in the Czech Republic, New Zealand and Argentina (Corlatti et al. 2011).

The long-distance introductions of chamois (*R. r. rupicapra*) began with introductions to New Zealand and the Czech Republic. In 1907, Austrian emperor Franz Joseph I gifted eight animals, two males and six females to New Zealand (Christie 1964). The origin of

these animals is not clear, and it is assumed they came from Müzzsteg, Ebensee or Tyrolean Alps in Austria (Fig. 1, 2; Schasching 1995, Forsyth & Clarke 2001). The main reason for the discrepancy is the ambiguity of the historical records. The Emperor ordered capture of animals from the Neuberg Müzzsteg Game Reserve, Styria, Austria. The travel documents state that the chamois were kept in quarantine in the Schönbrunn zoo, Vienna, Austria prior to shipment to New Zealand and they travelled through Tyrol, Austria. Further addition to the quagmire of the historical record of chamois introductions is that the veterinary certificate of health issued for the journey states that the chamois originated and were shipped from Ebensee, Upper Austria, Austria (Fig. 2; Schasching 1995, Sauper 2008). At a later date, two additional females were caught in the Neuberg Müzzsteg Game Reserve

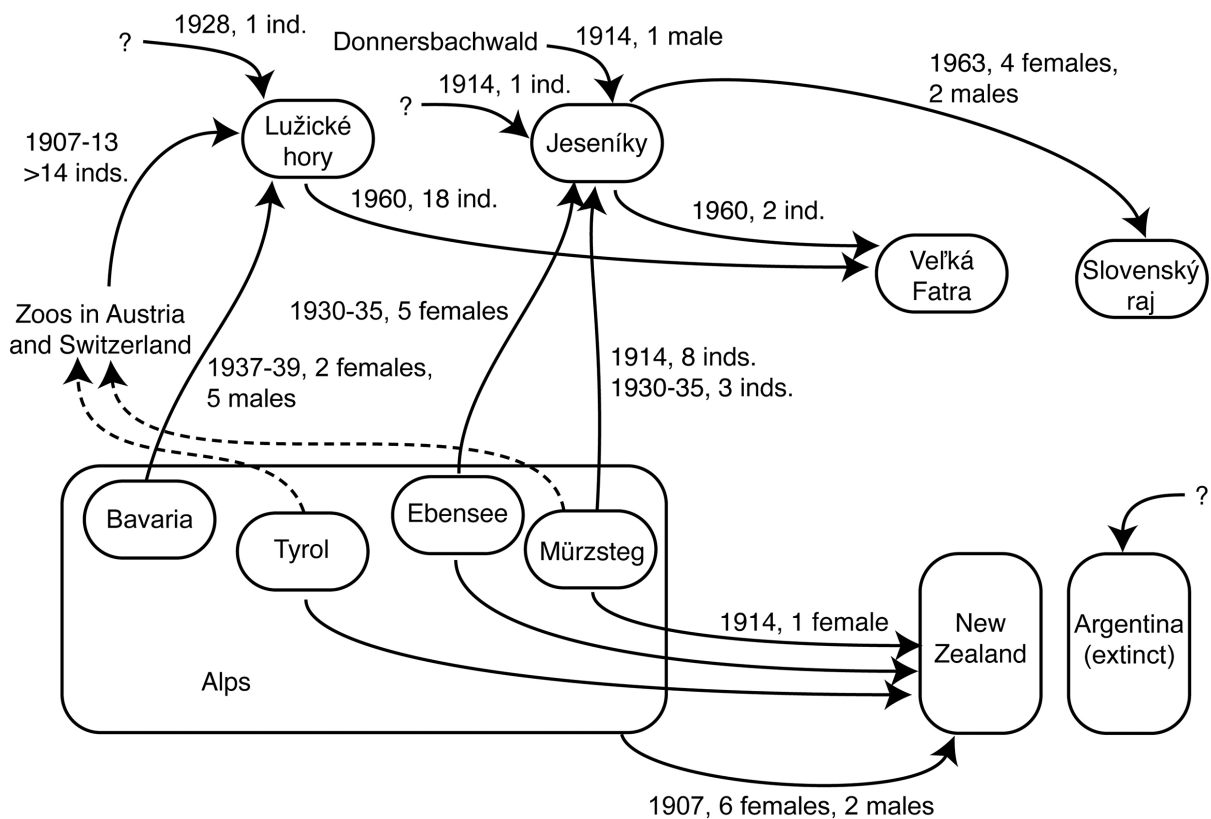


Fig. 1. Scheme of assumed introductions of Alpine chamois (*R. rupicapra rupicapra*) to Central Europe and New Zealand according to the historical record. See text for details and references.

(Christie 1964, Mlčoušek 2000), but only one was released in New Zealand in 1914 (Sauper 2008). The New Zealand population nowadays exceeds 18000 individuals, making it the largest introduced chamois population by about two orders of magnitude (Forsyth 2005, Crestanello et al. 2009).

Mlčoušek (2000) demonstrates in detail that the chamois shipped to New Zealand in 1914 were caught in the trapping device in Mürtzsteg that was built to capture animals intended for introduction to Jeseníky Mts. in the Czech Republic. In total, eight individuals from Mürtzsteg, one male from Donnersbachwald, Styria, Austria and one of unknown origin were transported to Jeseníky in 1913-14 (Mlčoušek 2000). The second introduction included three individuals from a site near Mürtzsteg and five females from Ebensee transported between 1930 and 1935 (Mlčoušek 2000).

Introduction to Lužické hory Mts. in the Czech Republic contained at least 14 animals that were bought from game traders and zoos in Austria and Switzerland between 1907 and 1913 (Briedermann & Štill 1976). They possibly originated from Mürtzsteg or Tyrolean Alps with another animal of unknown origin imported around 1928 (Jelínek 1987). According

to Briedermann & Štill (1976), additional seven individuals, including two females, from Bavarian Alps were released between 1937 and 1939 in the adjacent German part of Lužické hory.

The two Czech chamois populations were subsequently used to populate introductions to Slovakia; namely, to Velká Fatra in 1960 – two individuals from Jeseníky and 18 from Lužické hory, and to Slovenský raj in 1963 – four females and two males from Jeseníky (Fig. 1; Hell & Chovancová 1995). The Tatra and Low Tatra Mts. in Slovakia host populations of a different subspecies *R. rupicapra tatrica* (Blahout 1972).

Genetic signature mapping the chain of introductions was ambiguous in a previous study (Crestanello et al. 2009). The sequences from the Czech and Slovak introduced populations were most closely related to those from Italian Eastern Alps, but the putative regions of origin in Austria were not sampled previously.

Chamois introduction to Argentina is more enigmatic (Mitchell-Jones et al. 1999, Aulagnier et al. 2008, Corlatti et al. 2011). The only specific reference known to us lists Asia as the region of origin of chamois introduced to Argentina (Chebez 1999). Chamois are most likely absent from Argentinean fauna today (Mabel Giménez, pers. comm.).

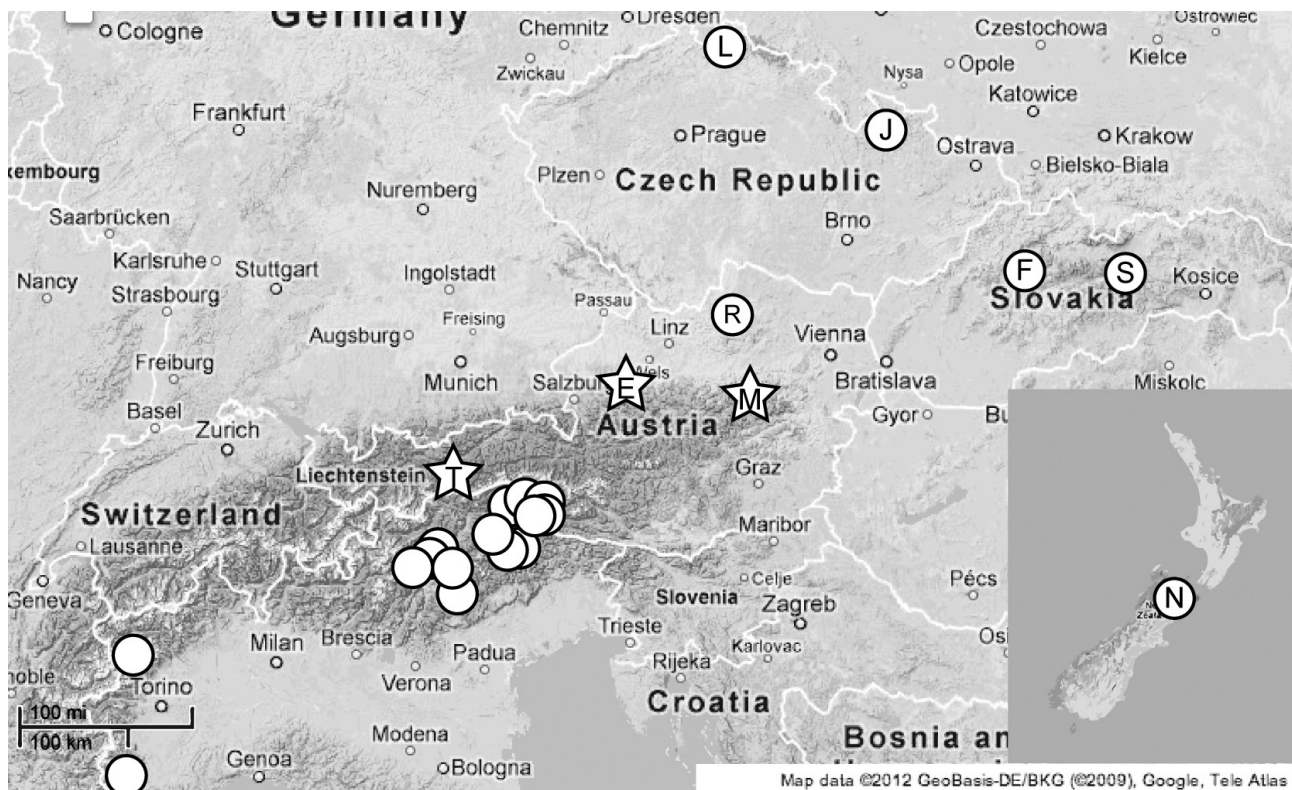


Fig. 2. Sampling localities of *R. rupicapra rupicapra* for mitochondrial sequences of the CR. Open circles – previously available data; symbols embedded with letters – data from this study. L – Lužické hory, Czech Republic; J – Jeseníky, Czech Republic; F – Veľká Fatra, Slovakia; S – Slovenský raj, Slovakia; T – Tyrolean Alps, Austria, Italy; E – Ebensee, Austria; R – Traunstein, Austria; M – Mürzsteg, Austria; N – Kaikoura Mts., New Zealand. Stars represent assumed localities of origin of New Zealand chamois according to Schasching (1995).

We expect that the common origin of several founders of New Zealand and Central European chamois populations is genetically traceable using genetic diversity of the mitochondrial control region (CR) sequences. CR is a marker extensively used for phylogeographic research of chamois, enabling us to utilise previous data from other Alpine regions in our study. Based on phylogenetic relationships between sequences, we investigated the genetic signature of the introductions in comparison to the historical record, and we assessed matrilineal gene-flow between populations.

Material and Methods

We sequenced mitochondrial CR in two individuals from Kaikoura Mountain Range, North Canterbury, New Zealand, nine individuals from Veľká Fatra, Slovakia, six from Lužické hory Mts., three from Jeseníky Mts. in the Czech Republic and 28 individuals from assumed source areas for introductions in Eastern Alps, Austria and Italy (Fig. 2). DNA was isolated from alcohol-stored tissue samples using the DNeasy Blood & Tissue Kit (Qiagen Inc., Hilden,

Germany) following the manufacturer's protocols. CR was amplified using primers MF (Mannen et al. 2001) and Hphe (Douzery & Randi 1997). The polymerase chain reaction consisted of 1x Buffer, 100 µM dNTPs, 3 mM MgCl₂, 25 µM of each primer, 1 U Platinum *Taq* (Invitrogen, Carlsbad, CA, USA) and approximately 20 ng of template DNA. The cycling conditions consisted of initial denaturation at 95 °C for 5 min, followed by 40 cycles of 94 °C for 30 s, 60 °C for 1 min and 72 °C for 1 min, with a final extension of 72 °C for 5 min. PCR products were purified using PCR Purification Kit (Qiagen) and commercially sequenced on ABI 3730XL sequencers with Big Dye Terminator sequencing chemistry (Applied Biosystems, Foster City, CA, USA). The sequences assembled in Aligner 3.7 (CodonCode Corp., Dedham, MA, USA) contained also partial sequence of the *mt-cyb* gene, tRNA-Thr and tRNA-Pro at the 3' end, and they were submitted to EMBL-bank with accession numbers: HE795486-HE795533. Additional Alpine chamois (*R. rupicapra rupicapra*) sequences longer than 1 kb were obtained from GenBank (Appendix; Crestanello et al. 2009) and

Table 1. Sample size and genetic diversity of target populations of Alpine chamois.

Population	No. of samples	No. of haplotypes	Haplotype diversity (\pm SD)	Nucleotide diversity (\pm SD)
Lužické hory	8	4	0.64 ± 0.184	0.001 ± 0.001
Jeseníky	11	5	0.76 ± 0.107	0.014 ± 0.008
Velká Fatra	15	4	0.70 ± 0.074	0.017 ± 0.009
Slovenský raj	5	1	0	0
New Zealand	5	3	0.80 ± 0.164	0.026 ± 0.016
Mürzsteg	13	4	0.62 ± 0.136	0.007 ± 0.004
Ebensee	2	2	1.00 ± 0.500	0.030 ± 0.030
Tyrol	9	6	0.89 ± 0.091	0.008 ± 0.005

aligned in Geneious 5.5 (Drummond et al. 2009). In total, the target regions were represented in the final dataset by 2-15 sequences (Table 1) and 187 sequences were from other regions in Alps. Haplotypes were identified from nucleotide substitutions in Collapse 1.2 (Posada 2006) with gaps ignored in haplotype designation. To optimize haplotype finding, the sequences were ordered according to descending length of the sequence. Haplotypes were checked against GenBank using BLAST search (Zhang et al. 2000) to validate that they represent the nominate

Alpine chamois subspecies. Genetic diversity in populations was calculated in Arlequin 3 (Excoffier et al. 2005). Median-joining (MJ) networks were constructed in Network 4.2 (Bandelt et al. 1999) using equal transition/transversion ratio. The hypotheses of alternative origin of the New Zealand chamois were tested by comparing marginal likelihoods of the Markov chains Monte Carlo (MCMC) runs from Bayesian phylogeny inference (Ronquist & Huelsenbeck 2003) rooted with two *R. pyrenaica* sequences and constrained tree topology using Bayes

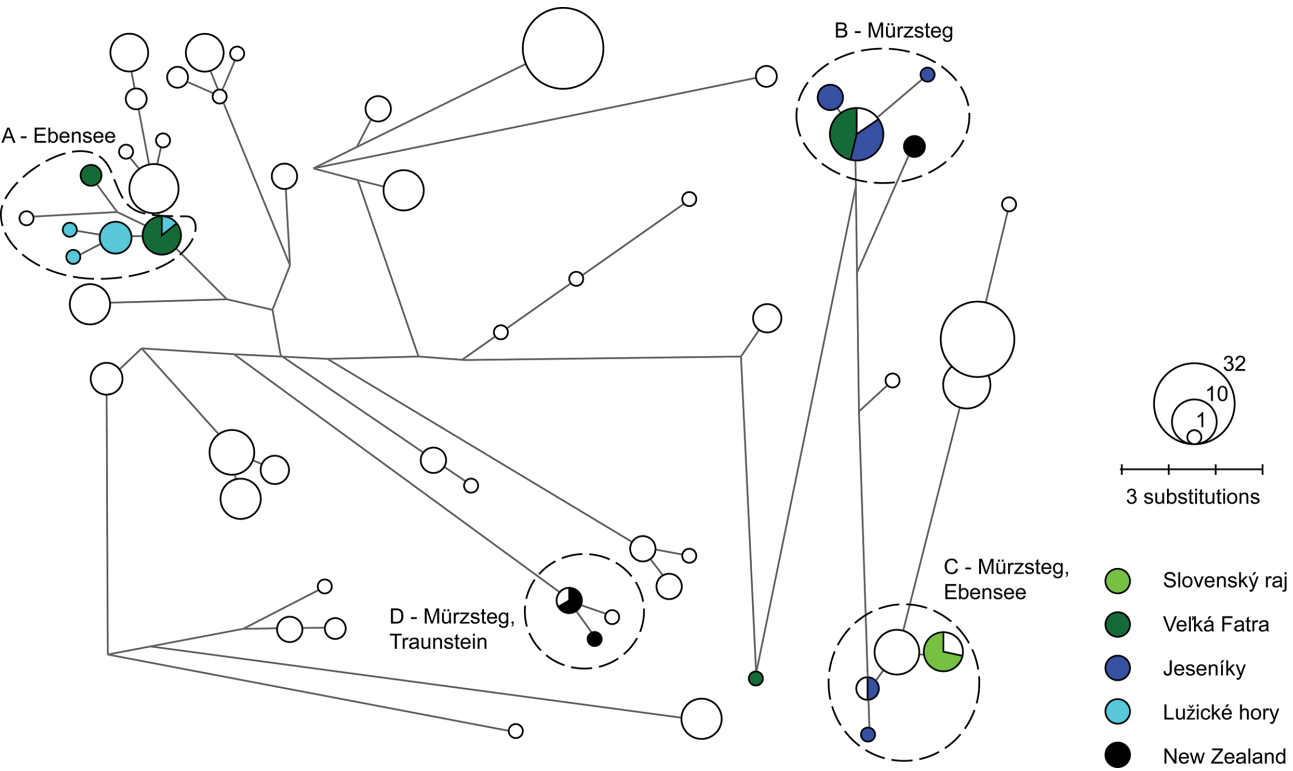


Fig. 3. Median-joining network of mitochondrial CR sequences (1012 bp, positions with gaps ignored) of *R. rupicapra rupicapra*. Branch lengths measured between node centroids are proportional to number of substitutions along a given branch, and circle size is proportional to haplotype frequency. Dark blue – Jeseníky; light blue – Lužické hory; dark green – Velká Fatra; light green – Slovenský raj; black – Kaikoura Mts.; white – Alps. Localities in Alps that belong to identified groups are listed.

Table 2. Mean likelihood of Bayesian inference trees with topology constraints representing alternative scenarios of origin of New Zealand chamois. Marginal likelihoods were compared with Bayes factors. a/n – available.

Scenario	–lnL	Bayes factor
Unconstrained	3061.34	n/a
Groups A-D	3060.23	1.2
Mürzsteg	3070.89	–2.6
Ebensee	3119.83	–23.8
Northern Tyrol	3094.62	–14.5
Southern Tyrol	3110.78	–20.5

factors in Tracer 1.5 (Rambaut & Drummond 2007). Bayes factor > 20 was considered as good support for detecting differences in optimality criteria between tested scenarios.

Results and Discussion

All new CR sequences represented *R. rupicapra rupicapra*. The ingroup alignment was 1012 base-pairs (bp) long and contained 252 Alpine chamois CR sequences; the outgroup contained two Pyrenean chamois sequences. They represented 57 haplotypes distinguished by 92 sites with substitutions. Our data showed that the chains of chamois introductions from Austria to New Zealand and the Czech Republic followed by introductions to Slovakia were genetically traceable. Individuals from introduced populations from the Czech Republic, Slovakia and New Zealand formed four groups in the MJ network separated by at least 12 substitutions (Fig. 3). Chamois from Central European introduced populations were found in groups A, B and C, and the chamois from New Zealand belonged to groups B and D. One sequence from Velká Fatra was found outside of these groups and it was not closely related to any other sample.

Group A contained sequences from Lužické hory, Velká Fatra and Ebensee. The Ebensee sequence differed from the sequences from the introduced populations by 3 bp, but a haplotype from Val di Fiemme e Fassa and Primiero in Italian Eastern Alps differed by 1 bp from them. Together with the ungrouped sequence from Velká Fatra (population founded mostly of animals from Lužické hory), this might indicate diverse origin of animals that were bought from game traders and zoos for the introduction to Lužické hory Mts.

The sequences from the Mürzsteg region were included in three groups – B, C and D. Group B included sequences from two individuals from the Mürzsteg area and sequences from Jeseníky and Velká

Fatra. Interestingly, chamois from the Velká Fatra population shared haplotypes with animals from both known source populations. In group A, Velká Fatra sequences were identical to those from the Lužické hory population and in group B to the Jeseníky population. Although only two individuals from Jeseníky were brought to Velká Fatra, in contrast to 18 individuals from Lužické hory (Hell & Chovancová 1995), matrilineal descendants from both lineages were similarly represented in our sample (Fig. 3).

Sequences that belonged to group C were found in Jeseníky, Slovenský raj and in Mürzsteg and Ebensee areas in Eastern Alps. A single haplotype was identified in the Slovenský raj samples, although genetic diversity of nuclear markers of this population is more variable (Zemanová et al. 2011). This haplotype was also found in Mürzsteg, whereas no direct introduction from Alps occurred in Slovenský raj (Hell & Chovancová 1995). The population was established from animals from Jeseníky, but we did not find carriers of this haplotype in the known source population; they were 2 bp different from the haplotype from Slovenský raj. This is possibly due to extinction of the haplotype in Jeseníky.

Group D included sequences from New Zealand, Mürzsteg and Traunstein, Lower Austria, Austria (Fig. 3). No sequence from the Czech and Slovak populations was found in this group. Two sequences from New Zealand were included in group B, where they were separated by six substitutions from the Mürzsteg haplotype. This suggests confirmation of the origin of the New Zealand chamois from Mürzsteg, which we further tested using Bayesian phylogenetics. The mean log-likelihood of the unconstrained phylogeny was –3061.34 (Table 2). Constraining the tree topology to represent monophyletic lineages of alternative introduction scenarios for New Zealand female chamois produced poorer trees. Comparison of the marginal likelihoods of the MCMC runs showed that the absolute values of Bayes factors were the lowest between the unconstrained phylogeny and the phylogeny with constrained monophyly of sequences from Mürzsteg, indicating least difference between phylogenies (Table 2). Introductions to New Zealand from Tyrol and Ebensee regions indicated by the travel documents issued prior to shipment of the animals (Schasching 1995, Sauper 2008) were not confirmed in our study. In fact, we rejected the hypotheses that the matrilineal lineages from New Zealand analysed in this study originated in Ebensee or South Tyrol. The Bayes factors signified that the trees with topology constraints for monophyly of these scenarios were

considerably worse than the unconstrained trees. North Tyrolean origin is also unlikely although the difference in marginal likelihoods was less pronounced. However, our sample sizes were small and common haplotypes might have been omitted because of the sampling bias.

The putative origin of the Czech populations from both Ebensee and Mürtzsteg was confirmed. The two sequences from Ebensee samples analysed here were included in groups A (the only white haplotype) and C (haplotype shared between Alps and Jeseníky; Fig. 3). We found that constraining tree topology with monophyletic groups A-D (as per Fig. 3) slightly improved the mean likelihood of the posterior sampled trees indicating diverse origin of the introduced populations. This is reflected also in haplotype and nucleotide diversity of the introduced populations that markedly varied among populations (Table 1).

We conclude that introductions of chamois from Eastern Alps favoured at the beginning of the 20th century by the last Austrian emperor left their genetic legacy across the globe. The Mürtzsteg region is the

most likely origin of the female lineages for populations now inhabiting Czech Republic, Slovakia and New Zealand, whereas the Czech and Slovak populations are also closely associated with chamois from Ebensee.

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Appendix. Accession numbers of sequences from introduced chamois populations published previously by Crestanello et al. (2009).

Acc. no.	Region
GQ291411	Velká Fatra
GQ291467	Velká Fatra
GQ291468	Velká Fatra
GQ291469	Velká Fatra
GQ291472	Velká Fatra
GQ291558	Velká Fatra
GQ291403	Slovenský raj
GQ291404	Slovenský raj
GQ291405	Slovenský raj
GQ291406	Slovenský raj
GQ291407	Slovenský raj
GQ291408	Jeseníky
GQ291409	Jeseníky
GQ291410	Jeseníky
GQ291412	Jeseníky
GQ291413	Jeseníky
GQ291414	Jeseníky
GQ291415	Jeseníky
GQ291416	Jeseníky
GQ291470	Lužické hory
GQ291471	Lužické hory
GQ291500	New Zealand
GQ291501	New Zealand
GQ291502	New Zealand