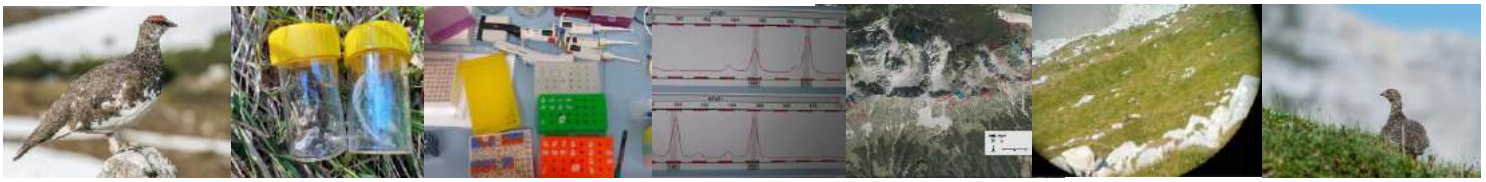
universität innsbruck

Territoriality, mobility, and population structure of an Eastern Alpine rock ptarmigan (*Lagopus muta helvetica*) population

Nina Feistmantl, BSc



Masterarbeit

zur Erlangung des akademischen Grades „Master of Science“

am Institut für Ökologie

der Leopold-Franzens-Universität Innsbruck

Betreuer: Mag. Dr. PD, Assoc. Prof. Florian M. Steiner

Innsbruck, am 11.01.2021

Territoriality, mobility, and population structure of an Eastern Alpine rock ptarmigan (*Lagopus muta helvetica*) population

Nina Feistmantl[1], Anselm Fried[1], Stephanie Vallant[1], Marlene Haider[1], Reinhard Lentner[1,2], Birgit C. Schlick-Steiner[1], Florian M. Steiner[1]

[1]Department of Ecology, University of Innsbruck, Innsbruck,
[2]Department of Environmental Protection, Provincial Government of Tyrol, Innsbruck, Austria

Key Words

grouse, non-invasive sampling, microsatellites, population genetics, conservation

Abstract

The rock ptarmigan *Lagopus muta* is confronted with several threats, which increases the importance of monitoring programs. Its biology and behaviour enables us to explore it with non-invasive methods. We collected feathers and faeces during one growing season in an Eastern Alpine area. From these, we extracted DNA and did an individual identification using 10 microsatellite markers. We estimated the population size and compared the molecular results with those from a classic method where singing cocks were counted, to determine territories. We examined the flexibility of territories and the mobility of the birds. Additionally, we did population genetics. We found 70 Individuals in the investigated area, with more males than females. The molecular data were highly compatible with the data from the classic method, which indicates that both might be well suitable methods to investigate territories. They showed overlapping as well as rather separate territories. We found a tendency that hens move farther than cocks but the difference was not significant. Population genetics showed that the investigated individuals belong to one connected population. There were no signs of inbreeding. The methods used here may provide the opportunity to conduct intense monitoring programs without creating negative impacts on the birds.

Danksagung

An dieser Stelle möchte ich meinem gesamten Team meinen besonderen Dank aussprechen. Ihr wart das beste Team, das ich mir vorstellen kann, ohne euch wäre all das heute NICHT hier zu lesen. Vielen Dank für eure Unterstützung!

Angefangen bei meinen BetreuerInnen Florian Steiner, Birgit Schlick-Steiner und Reinhard Lentner, die immer ein offenes Ohr für mich hatten und mir mit außerordentlich wertvollen Ratschlägen zur Seite gestanden sind. Über meinen Teamkollegen Anselm Fried, der mit mir die Feldarbeit auf die Beine gestellt und diese zu einer wahren Freude gemacht hat, und meine Teamkolleginnen Ramona Steixner und Teresa Zeni, die mir die vielen Stunden im Labor versüßt haben und mich auch im weiteren Verfahren immer unterstützt haben. Bis hin zu meinen Leitlichtern Stephanie Vallant und Marlene Haider, die mich in all die anfallenden Arbeiten eingeschult haben und mir und meinen Fragen Tag und Nacht mit guter Laune zur Verfügung gestanden sind. Danke an Albuin Neuner, der uns die Feldarbeit ermöglicht hat. Weiters gilt mein besonderer Dank unserem Kartierteam bestehend aus Reinhard Lentner, Gregor Schartner, Felix Lassacher, Alois Masoner, Ramona Steixner und Teresa Zeni und den technischen AssistentInnen Philipp Andesner, Elisabeth Zangerl und Florian Reischer. Danke auch an Molinia Landmann für die Hilfe mit R. Auch der Stadt Innsbruck und der Universität Innsbruck, die diese Arbeit erst finanziell möglich gemacht haben, möchte ich danken. Und mein spezielles und privates Dankeschön geht an meine wunderbaren Eltern für die besondere Unterstützung!

Danke

Acknowledgments

Here I want to give my special thanks to my supervisors Florian Steiner, Birgit Schlick-Steiner and Reinhard Lentner who always supported me and gave me an open ear as well as invaluable advices. Also I am grateful for my marvellous team. Anselm Fried also did his master thesis within this project and we worked together very closely. Beside our enjoyable collaboration he also helped me with things not belonging to his work such as handling GIS and so on. For helping us in the field I want to thank Reinhard Lentner, Gregor Schartner, Felix Lassacher, Alois Masoner, Ramona Steixner and Teresa Zeni. For making the field work possible thanks to Albuin Neuner who is working at the forestry office of Innsbruck. Ramona Steixner and Teresa Zeni are also thanked for sharing our lab work. For their theses they also needed to extract DNA out of grouse feces and feathers and we did this together which was much more fun than doing it alone. For showing us how, I want to thank Stephanie Vallant as well as for helping us with the allele calling and supporting us with all problems we had throughout our theses. Another person who always supported us was Marlene Haider whom I also want to thank. Also I would like to thank the technical assistants, Philipp Andesner, Elisabeth Zangerl and Florian Reischer. Another thanks goes to Molinia Landman for helping me with R. The project was only possible thanks to the university and the city of Innsbruck.

Introduction

The rock ptarmigan is an arcto-alpine grouse species that lives beyond the treeline (Glutz von Blotzheim 1973; Storch 2007). *Lagopus muta helvetica* is the subspecies that evolved in the Alps. In the IUCN Red List of Threatened Species, it is classified as of least concern, but with a tendency of decreasing populations in some areas (IUCN 2016) – it is confronted with various threats, such as human activities and climate change (Revermann et al. 2012; Imperio et al. 2013). Mountain areas and their inhabitants are particularly affected by climate change (Martin 2001; IPCC 2015, 2015) and therefore are in particular need of intense monitoring programs. Investigating the rock ptarmigan could probably reveal trends representative also of how other alpine species react to climate change.

The rock ptarmigan's biology and behaviour facilitate exploring it with non-invasive methods. Firstly, rock ptarmigan change their plumage three to four times in the course of a year, and because its diet is poor in nutrients, it produces a lot of droppings (Glutz von Blotzheim 1973; Bauer 2012). On these grounds, collecting feathers and faeces, followed by the extraction of the DNA from both allows an individual identification and population-genetic analyses. Secondly, in the breeding season (from May to June-July), males and females form pairs. During this time, the cocks sing to defend their territories, where the pairs stay together until the chicks hatch (Glutz von Blotzheim 1973). This system stands in contrast to other grouse species like black grouse (*Tetrao tetrix*), capercaillie (*Tetrao urogallus*), where several males display on lekking places (Lentner et al. 2018). Based on the rock ptarmigan's territorial behaviour and the assumption that territories are stable indeed, the classic method to determine territories by counting calling cocks (and recording other territorial behaviours) has been implemented (Südbeck 2005; Marti et al. 2016).

However, the stability of territories has not been clarified entirely. For example, Glutz von Blotzheim (1973) and Bossert (1995) described territory boundaries as non-overlapping and remaining stable over years, whereas Favaron et al. (2006) found an overlap in home ranges, even during one breeding season by radio-tracking. Thus, determining territory boundaries via counting calling cocks might be prone to over- and/or underestimates. Other drawbacks of counting cocks are that tracking the birds in parts of the year when the cocks do not sing is not possible and that addressing questions that require the identification of individual birds is not possible.

Here, we used a molecular approach based on microsatellites to identify individuals in one population in the year 2019. **Research Question (1) Population size:** We estimated the population size. **Research Question (2) Territories:** We compared the molecular results with those from the classic method. The analyses of the classic method were conducted by (Fried 2020). Additionally, we used the genetic data to identify a potential flexibility of territories, that is, whether additional males are tolerated within a particular territory and/or if neighbouring territories overlap. **Research Question (3) Mobility:** We measured how far rock ptarmigans move during and after the breeding season and if hens and cocks differ in their mobility. **Research Question (4) Population genetics:** We aimed to identify whether the population is structured according to geographically separated parts of the research area and to evaluate the extent of inbreeding.

Material and Methods

Field Work

Study area and study sites

The study area is located in the northern mountains of the city Innsbruck (Tyrol, Austria) in the eastern part of the European Alps. It extends from 1910 m to 2459 m above sea level (Table 1). The habitat is dominated by alpine grassland interspersed with big rocks and steep cliff sides. Within this area, six study sites were analysed (Figure 1) based on habitat suitability and excluding parts steeper than 40°. Sites 5 and 6 can be seen as geographically rather separate from the rest of the study area because of the shape of the mountain.

Sampling faeces and feathers

For the collection of samples, loops of 100 m were walked within the study sites and the ground intensively searched for faeces and feathers. If for topographic reasons using the optimal track was not possible or if a structure especially suitable for rock ptarmigan was spotted, deviating from the loop was allowed. Faeces and feathers were collected and stored at -22 °C directly after the fieldtrip. For every sample found, the GPS coordinates were recorded. Faeces and/or feathers found less than 50 m from each other were considered to belong to the same sample. We did six rounds of sampling from June to October 2019 (Table 2). (In this assignment the rounds will be labelled with roman letters (I - VI)). Since breeding season of rock ptarmigan is approximately from May to June-July (Glutz von Blotzheim 1973), here the Rounds I-III were treated as during breeding season. Round IV-VI represent the time after breeding season.

Counting calling cocks

Additionally, the classic method to determine territories, by counting the singing cocks and reporting other territorial behaviour, was applied (Fried 2020). This was done by sitting in the study sites before sunrise and listening quietly for 30 minutes. If there were no calls heard by then, a recorded call was played with a speaker, followed by five minutes of waiting. The recorded call had the following sequence: four seconds of singing, 11 seconds break, four seconds of singing, 20 seconds brake, and another four seconds of singing. The recording can be found in the supplementary information. If there was no answer, the recorded call was played again followed by 10 minutes of waiting. All acoustically and visually noticed rock ptarmigans were protocolled (with the exact time to avoid double counts by more than one person), paying particular attention to simultaneous singing cocks. All other behaviours that indicate territoriality, for example females and males walking together or fighting males, were also noted. This method was used in Rounds I-III as well as in Round VI.

Laboratory Work

DNA Extraction

For DNA extraction from faeces, the DNA Stool Mini kit (Qiagen, Hilden, Germany) was used, following the protocol of the manufacturer. Therefor the top layer of the half frozen faecal pellets were scraped off and put into 950 µl preheated ASL InhibitEX (included in DNA Stool Mini kit) buffer. If the pellet was too dry to scrap off the top layer properly, a little piece was cut off and pestled in the InhibitEX buffer. 25 µl proteinase K and 600 µl AL buffer were added. Then the mixture was incubated over night at 56 °C and 550 RPM (rounds per minute) in a thermomixer. After incubation was completed, the samples were centrifuged at 1300 RPM for one minute. The supernatant was mixed with 95-100% ethanol by vortexing every sample for 15 seconds. After this, the samples were transferred onto a silica membrane and centrifuged at 1300 RPM for one minute. This was followed by two washing steps, first with AW1 buffer at 1300 RPM for 1 minute, and second with AW2 buffer at 15000 RPM for 3 minutes. To dry the membrane there was another centrifuge step in a new tube at 15000 RPM for 5 minutes. To elute the DNA from the membrane, it was incubated twice with 40 µl

ATE buffer for 5 minutes and subsequently centrifuged at 1300 RPM for one minute. The DNA extracts were then stored at - 22 °C until further use.
For the DNA extraction from feathers the Qiagen DNA Micro Kit was used. The procedure was the same as just described with the following modifications. The end part of the feather was cut and put unto 500 µl hair buffer (Hellmann et al. 2001). Subsequently, 50 µl proteinase K and 20 µl Dithiothreitol (1 M) buffer were added. After the incubation step over night, the samples were mixed with 500 µl AL buffer and incubated at 56 °C for 5 minutes. Thereafter, 500 µl ethanol (96%) were added and again incubated for 5 minutes at room temperature. The next steps were the same as in the extraction from faeces, except that in the two elution steps only 20 µl ATE buffer were used.

Microsatellite PCR and Allele calling
Microsatellites by Vallant et al. (2018) were used (Table 3). The concentration of the primers was 20 nM. In MPX 1 and MPX 2 0.08 µl primer per sample (forward and reverse) was mixed with 2,36 µl water per sample. In MPX 3 0,08 µl of all primers except TtZa were mixed with 2,125 µl water. The TtZa forward and reverse primers were aded 0,0375 µl to MPX 3. For the master mix 5 µl Quiagen Taq PCR mastermix was combined with 0.6 µl BSA and 0.4 µl $MgCl_2$ (25mM). The PCR reaction was conducted with 10 µl reaction volume, 6 µl master mix, 3 µl primer MPX, and 1 µl sample. The PCR program was the same as used by Vallant et al. (2018). After heating at 95 °C for 15 minutes there were 37 cycles of denaturation at 94 °C for 30 seconds, annealing at 56 °C for 2 minutes and extension at 72 °C for 30 seconds. This was followed by a heating step at 72 °C for 45 minutes. Afterwards, the PCR products were stored at 4 °C. The capillary electrophoreses was carried out by the company CRC Sequening Facility in Chicago (USA) by using an Applied Biosystem 3130 machine. The allele calling was conducted with GeneMarker 3.0.1. (SoftGenetics). Here we noticed that the two markers TTT1 and TTT2 did not produce clear alleles in rock ptarmigan. Therefore, we decided to go on by only considering the 10 remaining markers (plus the two sex markers (designed by Harald Niederstätter, Medical University of Innsbruck)) for all further analyses. After allele calling, the PCR was repeated for all samples where less than 10 markers showed successful alleles.

Data analyses
Individual Identification
For the identification of individuals only samples without missing values for any of the 10 microsatellites were used (no missing values) using the R (version 3.6.3, R Core Team, 2020) package allele match by Galpern et al. (2012). We tolerated a maximum number of 5 mismatching alleles. The unique genotypes were adjusted by hand.

Sex determination
Two microsatellites located on the sex chromosomes were used in sexing individuals; locus TtZa is located on the Z chromosome, locus TtWa on the W chromosome. Individuals with an allele in both loci were classified as hens, individuals without an allele for locus TtWa as cocks. If there were more than two samples of one individual with alleles for TtZa and TtWa (hinting at a hen) and only one sample with an allele for TtZa (hinting at a cock) the Individual was classified as a hen. This was based on the assumption that allele dropouts are possible. If there were individuals with only one sample indicating a hen and one indicating a cock, the sex of the individual was classified as unclear. The same was done with individuals for which more samples indicated a cock and some (two and more) indicated a hen, as well as if the alleles were not analysable at all.

Research Question (1) Population size

Number of individuals

All individuals were counted, once for all rounds and once only for the first three rounds (during breeding season). The same was done for females and males separately. Additionally, it was counted how many individuals were found more than once and are represented by more than one sample (following called multiply found) and how many individuals were only found once (following called singly found). This individuals were numbered consecutively to give them individual names (Individual 1, Individual 2 …). In some parts of this manuscript we talk about Cock 8 Cock 9 etc. here Individual 8 and Individual 9 are meant. The cocks and hens are not separately numbered.

Research Question (2) Territories

Estimation of territories based on the classic method

Data were taken from (Fried 2020) who calculated the number of cocks based on the protocols that were filled out in the field while counting calling cocks. With this number (and position), the number of territories was estimated.

Maps & Spatial analyses

For the special analyses and for the construction of maps the program ArcGIS 10.7.1 was used. For every multiply found individual, all samples and the corresponding sampling rounds as well as the sex (where available) were visualised in an individual map. The singly found individuals are shown together within one map.

To estimate territory flexibility the individuals that showed up in the same study sites during breeding season (in the first three rounds), were combined and shown within one map (separately for cocks and hens). Because of the assumption that birds that live within a territory produce a lot of faeces and feathers, only individuals of which more than one sample was found in the first three rounds were considered in these maps.

Research Question (3) Mobility

To find out about possible movements of rock ptarmigan, the distances between samples were measured in ArcGIS 10.7.1. For each individual, the distance between the samples farthest apart where measured. This was done separately across all six rounds (maximal distance in Round I-III) and across the last three rounds (maximal distance in Round IV-VI).

These three distances were compared between male and female birds to investigate if there were differences in mobility between sexes. The maximal distance across the first three rounds and maximal distance across the last three rounds were compared with each other to get a hint if distances are less in breeding season and expanded after breeding season.

The statistics to prove if the differences are significant were carried out in Excel (version 15.0.5249.1001) and with SPSS Statistics Version 24. Following confirmation that the values were Gaussian variables, Student's t-test was used to test for differences between sexes and between the first and the last three rounds (alpha 0.05).

Research Question (4) Population genetics

The population-genetic analyses were conducted with GenAlEx v6.5 (Peakall and Smouse 2012). All genetic analyses were calculated twice, once using all individuals (all = multiply found and singly found), and once using only the multiply found individuals. The data was tested for Hardy Weinberg Equilibrium. The microsatellites were tested for linkage using Genepop on the Web 4.7 (Raymond and Rousset 1995; Rousset 2008). The values were Bonferroni corrected. To get information about the population structure, an unbiased approach was carried out by using STRUCTURE v2.3. (Pritchard et al. 2000). Here, the following settings were used: K=10, 5 million burn in, 20 million Markov-Chain-Monte-Carlo chains, and 10 replicates. To identify the number of clusters K best suiting the data, the approach described by Evanno et al. (2005) and pophelper v 2.3.0 (Francis 2017) was applied.

Results

Research Question (1) Population size

Number of individuals, females and males, overall and over time

We analysed 601 samples (560 faeces and 41 feathers), 253 of which were genotyped successfully in all 10 microsatellites. This is a success rate of approximately 42.1%. The individual-identification program suggested 77 unique genotypes. After an adjustment by hand, we ended up with 70 individuals (supplementary table 1). 37 individuals were found more than once and were represented by more than one genotype (sample) (multiply found). 31 individuals have only been found once (singly found). Two individuals (the individuals 20 and 25) are also represented by more than one sample, but these samples have been found less than 50 m apart from each other and therefore have only one GPS point (per individual). In this work they count as multiply found for the genetic analyses, but as singly found in all other sectors.
Of the 70 individuals, 38 were cocks and 24 were hens. For eight individuals, the sex microsatellites showed inconsistent results. Therefore, it was not possible to define a clearer sex here. Figure 2 shows the sex ratio found within the population. An overview of individual numbers can be found in Table 4.

Research Question (2) Territories

Estimation of territories based on the classic method

The absolute number of territories based on the classic method was estimated at 13 territories for the whole study area (Figure 3) (Fried 2020). On average, this would equal five territories per 100 hectare.

Territory numbers, molecular data vs classic method

The classic method suggests 13 territories in the investigated area (Figure 3). The molecular data (Table 4) represented 29 males and 17 females overall and 19 males and 12 females multiply found in the breeding season (Round I-III).

Territory flexibility

The places where and time when the individuals were found are shown in individual maps for every multiply found individual (Supplementary Figure 1 - 39) and in one map for the singly found individuals (Supplementary Figure 40). Twelve cocks and five hens were found more than once within the first three rounds. In Site 1, all cocks and hens were only found once in the first three rounds. Thus, it was not possible to interpret if any cock had its territory in Site 1 (no map). In the Sites 2, 3, and 4, seven cocks and three hens were found more than once during the first three rounds. Figure 4 shows where the samples of these cocks were found. Cock 13 was found several times in Site 4 and only one time in Site 3. In Site 4 no other cock was found in the close surrounding of Cock 13. Individuals 12, 16, and 18 were also not found surrounded very closely by other cocks. Cock 8, 9, and 10 were all found in the Sites 2 and 3 with only little distance to each other. Figure 5 shows the hens that were found in the shown study Site within the first three rounds. Hen 17 was found in Site 4 with no neighbouring findings. The hens 5 and 6 were found in Site 2 close to each other. In the Sites 5 and 6, five cocks (Figure 6) and two hens (Figure 7) were found during breeding season.

Research Question (3) Mobility

To investigate possible movements of rock ptarmigan, the distances between samples were measured. The measurements of the three maximal distances (absolute, in Round I-III, and in Round IV-VI) for males and females are shown in Table 5. In the comparison of maximal distances between the sexes, it turned out that females cover longer distances than males. This runs through all values of descriptive statistics (Figure 8). The difference is not statistically significant (Student's t test, $p = 0.282$). The differences between the maximal distances in Round I-III and Round IV-VI are very variable. A clear trend is not visible.

Research Question (4) Population genetics

Microsatellites

The microsatellites are not linked. The microsatellites TTT1 and TTT2 did not produce clear alleles. They were not used in the further analyses. The other 10 microsatellites and the sex microsatellites did show analysable alleles.

Population genetics

The pairwise Fst values (Table 6 and Table 7) were overall very low (much closer to 0=panmixture than to 1=no gene flow). The Fis value was only calculated for the 39 multiply found Individuals, to avoid errors coming from allelic drop outs. It showed no signs of inbreeding (Fis value =0.059 (P value =0.021)).

STRUCTURE

The STRUCTURE analyses for the multiply found individuals (Figure 9) and for all individuals (all = multiply found and singly found) (Figure 10) did not show a division in two populations (P1 Sites 1-4; P2 Sites 5&6). The most likely K was 3 and 5 for multiply found and all individuals, respectively.

Discussion

Research Question (1) Population size

Since sampling took place six times in every study site via walking loops of 100 m, it is likely that a high percentage of individuals occurring in the area were found. We do not assume that many birds were missed, even though we cannot preclude this entirely. Because only the samples that showed clear alleles in all 10 microsatellites were used (success rate 42.1%), many samples could not be interpreted. This might be due to DNA quality. Bergan et al. (2016) showed that DNA in faecal samples of rock ptarmigan does not stay stable over a long time even if it is found on snow. Our samples were mostly not found on snow but on bare ground exposed to weather conditions and decomposing. This might have decreased the percentage of detected of all individuals occurring in the area, but it also means that it is legitimate to trust the allocation of a faeces to the particular round it was found in.

Sex ratio

In an ideal population without any pressures some could expect a more or less even number of males and females. Here, we found overall more males than females (Figure 2). This pattern has also been found by other authors, for example Watson (1965), who recorded 58.5% males in a rock ptarmigan population in Scotland or Sakuria and Tsuruta (1972) who found a 2:1 ratio males to females in Japan. This could probably be due to a biological and evolutionary aspect. Males sing on prominent spots and have to present themselves to attract females and defend their territories, whereas females are more likely to hide, especially when they lead chicks (Glutz von Blotzheim 1973). Under the assumption that males are more at the risk of predation, it is imaginable that more male individuals are born. In a population with less predation pressure, there would then be more cocks than hens. But it is also possible that the different results come from a methodological bias. On the one hand, this could be a sampling bias. While singing and defending their territories, cocks are sitting on prominent spots in the landscape such as big stones or ledges. Spots like this are eye-catching and therefore, it is possible that the search was more intense there. Therefore, it might be easier to find faeces and feathers from males than from females. The fact that here 12 cocks but only five hens were found more than once in the first three rounds supports this notion. Also, hens do not produce a lot of faeces while they sit on the eggs. In this time, they leave their nests only about once a day to defecate. Therefore, it is likely that we missed some hens in this period, but this should be balanced more or less through the sampling in the other rounds. On the other hand, the bias could

be a result from the microsatellites. It is possible that errors occur in the amplification of the sex markers, which could lead to wrong sex determinations. In grouse the sex chromosomes are Z W (heterozygote) for females and Z Z (homozygote) for males. If the allele on the W chromosome drops out the individual would wrongly be shown as male. In multiply found individuals, this was corrected for, but in singly found individuals no correction was possible. This could lead to wrongly inferred males. Caizergues et al. (2003) describes the detection of differences in sex ratio as difficult because of the higher migration rate of females.

Research Question (2) Territories

Comparison of territories, molecular data vs classic method

The classic method suggests 13 territories in the investigated study sites (Figure 3). The molecular data (Table 4) represented 38 males and 24 females in the whole sampling period and 29 males and 17 females during the breeding season (Round I-III). Prima facie this looks like a quite big difference, which would indicate that the classic method leads to strong underestimations. Under the assumption that rock ptarmigans stay more or less in their territories during the breeding season, it is likely that individuals, only found in the Rounds IV-VI, are either offspring or have their territories outside the study sites and came in after the territories dissolved. This would mean they have no influence on the territoriality within the study site. Therefore, it makes sense to only compare the individuals that were found in Round I-III (breeding season) (29 males and 17 females) with the territories found by the classical method. By living in their territories over the whole breeding season rock ptarmigan produce a lot of faeces and feathers in the relevant area (Glutz von Blotzheim 1973). For this reason it is likely that individuals that have their territories within the investigated area would be found more than once. Thus, we decided to compare only the multiply found individuals in Round I-III with the number of 13 territories. Here, the numbers are 19 cocks and 12 hens. Consequently, the difference is much lower. One argument for the 6 additionally found cocks in the molecular data might be young unpaired cocks. Rock ptarmigan cocks become procreative already after one year but are not yet able to defend their own territories (Glutz von Blotzheim 1973). In an experiment in Scotland, males were removed from a rock ptarmigan population. After a very short time, nearly all of them were replaced by other males (Jenkins and Watson 1970). This indicates that there is a pressure on territory defending cocks, coming from unpaired males that are around.
By comparing the spots where cock samples were found during breeding season in Figure 4 and the estimated territories based on the classic method in Figure 3, it stands out that the general patterns match quite well with each other. Cocks could be assigned to territories as follows: Cocks 8, 9, and 10 could belong to Territories 3, 4, or 5 (one territory each). Cock 12 would match with territory 5 and 6 (could also be 7), but considering that territory 5 might already be inhabited by Cock 8, 9, or 10 it is more likely that Cock 12 inhabits Territory 6. Supposing this is the case, it is likely that Cock 16 belongs to territory 7. It would also be possible that it is the other way round, Cock 12 in territory 7 and Cock 16 in territory 6. Then Cock 13 would match with territory 8. Cock 18's territory might be in 9 and 10. We did investigate the area between the sites 4 and 5. It is imaginable that Cock 18 has its territory in this zone and the territories 9 and 10 are only the edges of this territory. Under this assumption the Territories 9 and 10 might probably be combined to one territory. The fact that the classic method in the sites 4 and 5 was applied on different days (Table *2*), dose at least not contradict that. Doing so that would reduce the number of territories resulting out of the classic method from 13 to 12 which matches with the 12 hens found by the molecular data. The molecular method found 7 cocks in this area and the classic method estimated 8 territories. Under the supposition that 9 and 10 is one single territory the two methods have very similar results, but even by leaving the territories 9 and 10 separate the results match quite well.
With both methods, strict territory boundaries are difficult to clarify, but the detailed numbers and the general spatial pattern are very similar. This leads to the assumption that the classic method seems to be well suitable to estimate territories without big errors caused by over- or underestimations.

Territory flexibility

One research question was how strict or flexible territories are, if additional males are tolerated within a particular territory or if territories can overlap. The examples in the Sites 2-4 (Figure 4) give a hint that there might be both. Cock 13 was mainly found in one area with no other cocks found in his close surrounding. In this case, it looks like Cock 13 has a strict territory, not tolerating other males within it, as it is described in Glutz von Blotzheim (1973). In contrast to this, Cocks 8, 9, and 10 occur together in the same area. This suggests that these three cocks might share their territories or at least tolerate each other. This matches with the results of Favaron et al. (2006) who found an overlap in home ranges. In the Sites 5 and 6 (Figure 6) the picture is not so clear. The Cocks 27, 29, 31, and 33 appear relatively close to each other as well as that they also seem to have spaces where only one of them occurs. Cock 37 was found alone, in distance from the others.

One of the reasons why some territories overlap and some do not might be food availability. Peer (2005) describes the availability of nutritious food as a possible reason for the territoriality and the monogamy of rock ptarmigan. She found a higher density of territories in areas with protein-rich food plants. In our study area, we found the most territories in Site 2, which is highly frequented by tourists brought up by cable car. Possibly the rock ptarmigans use the things that the tourists leave behind as a food source, which is available all over the year, rich in nutrient and easy to get. If they do not use the humans waste directly, it could probably also be that it brings nutrients into the system, which might change the plant community, and which thereby could become a better food source for the birds. If there is enough food anyway it might be possible to share territories and tolerate others (like the cocks 8 9 and 10 seem to do), even if the area is small. The place where Cock 13 has his territory is much more separated and only marginally visited by humans. Thus, there is not much input from outside, and he has to deal with the limited natural food sources, which might make it necessary to defend his territory more strictly. Territoriality seems to be a cost-benefit question. (These are only speculations.)

It is also mentionable that the density of territories with 11.5 territories / 100 ha in Site 2 is extraordinarily high for alpine areas (Fried 2020). The yet reported maxima are 7 to 10 cocks / 100 ha (Peer 2005; Nopp-Mayr and Zohmann 2008; Marti et al. 2016) Thus, it could also be that this is really an exceptional case, and that the patterns we see here are not conferrable to other areas.

Research Question (3) Mobility

Rock ptarmigans are good flyers, with flights up to 3-4 km reported (Glutz von Blotzheim 1973). Here, we could not find samples of the same individual that were that far apart but our recorded maximal distances are of the same order of magnitude (Table 5). Our data show slight differences in mobility between sexes. There seems to be a trend that hens move further than cocks, but this difference is not statistically significant. The lack of significance could, in theory, be due to sample size, but because of the considerably high p value of 0,282 and the large standard deviation in the data, it may be more likely that the non-significant difference is just coincidence. Nevertheless, literature shows that dispersal is mainly based on females, in rock ptarmigan (Gardarsson 1988; Novoa et al. 2005) as well as in closely related species like the willow ptarmigan *Lagopus lagopus* (Hörnell-Willebrand et al. 2014), and other grouse species (Greenwood 1980; Clarke et al. 1997; Caizergues and Ellison 2002). If our data would be true despite the missing significance it would not dissent, but underpin this pattern.

The comparison of the maximal distances between Round I-III and Round IV-VI showed no clear trend. The values are very variable among individuals. Based on this, we cannot make a clear statement about less movement in the breeding season and expanded movement after it. Even though some individuals show a pattern like this, such as Individual 17 (Supplementary Figure 17), others behave very differently. Some stay in their territory even after the breeding season (e.g. the individuals 5 & 6 (Supplementary Figure 5 and 6)), whereas others travel around and are found within different areas in breeding season and after. The variable values might also be explained by food availability. Flying longer distances might be necessary if there is not enough food within their

own territory even if it is breeding season. Examples where this might have been the case could be Individual 3 (Supplementary Figure 3) and 19 (Supplementary Figure 19). Here, we want to mention that, with this method, it was not possible to investigate a bigger area due to the steepness of the landscape. Therefore, we do not want to overinterpret these data. To get more information, tracking methods could be used additionally to the molecular approach.

Research Question (4) Population genetics

Microsatellites

Since the ten microsatellites used were not linked and showed clear evaluable alleles, we suggest that they are suitable for genetic analyses in rock ptarmigan. Due to numerous allele drop outs during the analyses, we would recommend to repeat every sample at least twice or even more often. By not repeating samples that seem to work straight away, one might get false homozygote samples. This would be especially a problem for population genetic analyses, since many values, like F-Stat values are based on homo- and heterozygosity. Here 39 out of 70 individuals were genotyped more than once and 31 individuals were genotyped only once. We cannot exclude that this effect has, at least in some parts, an influence on our data. For individual identification, this might be more or less negligible.

Population structure

The STRUCTURE diagram does not show a clear clustering in separated populations. The clusters that STRUCTURE suggests cannot be assigned to the spatial patterns of where the samples were found. This gives a hint that the investigated rock ptarmigan have gene flow with each other and seem to belong to one single population. This assumption is also supported by the missing signs of inbreeding and the continuously low pairwise F_{st} values that do not show any pattern of separation or isolation. Thinking about the movements found in the literature (Glutz von Blotzheim 1973; Caizergues and Ellison 2002; Bauer 2012), as well as our observed maximal distances, this is actually not surprising. If individuals commonly move over a broad part of the investigated area in short time, it is easy to imagine that there is no boundary of gene flow. The high percentage of singly found individuals (44.3%), could give a hint that the population is larger and extends much wider than the investigated area.

Acknowledgments

This project was only possible thanks to the University and the City of Innsbruck. We thank Albuin Neuner, who is working at the forestry office of Innsbruck, for making the sampling in the field possible. For helping us in the field we want to thank Alois Masoner, Felix Lassacher and Gregor Schartner. Ramona Steixner and Teresa Zeni are thanked for the help in the field as well as for the collaboration in the laboratory. Thanks Molinia Landman for methodological support. Another big Thankyou goes to the technical assistants, Philipp Andesner, Elisabeth Zangerl and Florian Reischer.

References

Bauer, H.-G. (Editor) (2012). Das Kompendium der Vögel Mitteleuropas: Alles über Biologie, Gefährdung und Schutz, 1st edition. AULA-Verlag, Wiebelsheim, Hunsrück.

Bergan, F., M. Sæbø, and H. Parker (2016). Evaluation of in-field stability of mitochondrial and nuclear DNA in snow sampled fecal pellets from Rock ptarmigan (*Lagopus muta*). Oecologia Montana 25:1–14.

Bossert (1995). Bestandsentwicklung und Habitatnutzung des Alpenschneehuhns *Lagopus mutus* im Aletschgebiet (Schweizer Alpen)., Ornitologische Beobachtungen.

Caizergues, A., A. Bernard-Laurent, J.-F. Brenot, L. Ellison, and J. Y. Rasplus (2003). Population genetic structure of rock ptarmigan *Lagopus mutus* in Northern and Western Europe. Molecular ecology 12:2267–2274.

Caizergues, A., S. Dubois, A. Loiseau, G. Mondor, and J.-Y. Rasplus (2001). Isolation and characterization of microsatellite loci in black grouse (*Tetrao tetrix*). Molecular Ecology Notes 1:36–38.

Caizergues, A., and L. N. Ellison (2002). Natal dispersal and its consequences in black grouse *Tetrao tetrix.* Ibis 144:478–487.

Clarke, A. L., B.-E. Sæther, and E. Røskaft (1997). Sex biases in avian dispersal: a reappraisal. Oikos 429–438.

Evanno, G., S. Regnaut, and J. Goudet (2005). Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular ecology 14:2611–2620.

Favaron, M., G. C. Scherini, D. Preatoni, G. Tosi, and L. A. Wauters (2006). Spacing behaviour and habitat use of rock ptarmigan (*Lagopus mutus*) at low density in the Italian Alps. Journal of Ornithology 147:618–628.

Francis, R. M. (2017). pophelper: an R package and web app to analyse and visualize population structure. Molecular Ecology Resources 17:27–32.

Fried, A. (2020). Das Alpenschneehuhn (*Lagopus muta helvetica*) an der Innsbrucker Nordkette: Revierdichte, Habitatwahl und Bedeutung als Schirmart für alpine Singvogelarten. not published yet.

Galpern, P., M. Manseau, P. Hettinga, K. Smith, and P. Wilson (2012). Allelematch: an R package for identifying unique multilocus genotypes where genotyping error and missing data may be present. Molecular Ecology Resources 12:771–778.

Gardarsson, A. (1988). Cyclic population changes and some related events in Rock Ptarmigan in Iceland. Adaptive strategies and population ecology of northern grouse 1:300–329.

Glutz von Blotzheim (1973). Handbuch der Vögel Mitteleuropas: Vol 5. Akademische Verlagsgesellschaft, Frankfurt am Main.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162. Animal Behaviour, 28(4), 1140-1162.

Hellmann, A., U. Rohleder, H. Schmitter, and M. Wittig (2001). STR typing of human telogen hairs--a new approach. International journal of legal medicine 114:269–273.

Hörnell-Willebrand, M., T. Willebrand, and A. A. Smith (2014). Seasonal movements and dispersal patterns: Implications for recruitment and management of willow ptarmigan (*Lagopus lagopus*). The Journal of Wildlife Management 78:194–201. The Journal of Wildlife Management, 78(2), 194-201.

Imperio, S., R. Bionda, R. Viterbi, and A. Provenzale (2013). Climate change and human disturbance can lead to local extinction of Alpine rock ptarmigan: new insight from the western Italian Alps. PloS one 8:e81598.

IPCC (2015). Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

IUCN (2016). *Lagopus muta* (errata version published in 2017). The IUCN Red List of Threatened Species: e.T22679464A113623562. BirdLife International (BirdLife International). https://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T22679464A89358137.en Downloaded on 08 September 2020.

Jacob, G., R. Debrunner, F. Gugerli, B. Schmid, and K. Bollmann (2010). Field surveys of capercaillie (*Tetrao urogallus*) in the Swiss Alps underestimated local abundance of the species as revealed by genetic analyses of non-invasive samples. Conservation Genetics 11:33–44.

Jenkins, D., and A. Watson (1970). Population control in red grouse and rock ptarmigan in Scotland.

Lentner, R., A. Masoner, and F. Lehne (2018). Sind Zählungen an Balzplätzen von Auer-und Birkhühnern noch zeitgemäß. Ergebnisse aus dem Raufußhühner-Monitoring Tirol. Der Ornithologische Beobachter 115:215–238.

Marti, C., A. Bossert, and H.-R. Pauli (2016). Bestand und Verbreitung von Birkhuhn *Tetrao tetrix* und Alpenschneehuhn *Lagopus muta* im Aletschgebiet von 1970 bis 2015, Der Ornithologische Beobachter.

Martin, K. (2001). Wildlife in Alpine and Sub-alpine Habitats. Wildlife – Habitat Relationships in Oregon and Washington 285–310.

Nopp-Mayr, U., and M. Zohmann (2008). Spring densities and calling activities of Rock Ptarmigan (*Lagopus muta helvetica*) in the Austrian Alps. Journal of Ornithology 149:135–139.

Novoa, C., L. Ellison, J. F. Desmet, A. Miquet, J. Sentilles, and F. Sarrazin (2005). Lagopède alpin: Démographie et impact des activités humaines. ONCFS.

Peakall, R., and P. E. Smouse (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research--an update. Bioinformatics (Oxford, England) 28:2537–2539.

Peer (2005). Habitatmerkmale von Brutrevieren des Alpenschneehuhns (*Lagopus mutus*) im Kühtai, Tirol. Ergatta 48 34–44.

Piertney, S. B., and J. Höglund (2001). Polymorphic microsatellite DNA markers in black grouse (*Tetrao tetrix*). Molecular Ecology Notes 1:303–304.

Pritchard, J. K., M. Stephens, and P. Donnelly (2000). Inference of population structure using multilocus genotype data. Genetics 155:945–959. https://www.genetics.org/content/155/2/945.

Raymond, and Rousset (1995). GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Heredity 248–249.

Revermann, R., H. Schmid, N. Zbinden, R. Spaar, and B. Schröder (2012). Habitat at the mountain tops: how long can Rock Ptarmigan (*Lagopus muta helvetica*) survive rapid climate change in the Swiss Alps? A multi-scale approach. Journal of Ornithology 153:891–905.

Rousset (2008). genepop'007: a complete re-implementation of the genepop software for Windows and Linux. Molecular Ecology Resources 103–106.

Sakuria, N., and S. Tsuruta (1972). Population studies of the Japanese Ptarmigan (*Lagopus mutus japonicus* Clark) in the Murode area, Tateyama, Japan, Alps, from 1967 to 1969.

Segelbacher, G., R. J. Paxton, G. Steinbrück, P. Trontelj, and I. Storch (2000). Characterization of microsatellites in capercaillie *Tetrao urogallus* (AVES). Molecular ecology 9:1934–1935.

Storch, I. (2007). Grouse: Status survey and conservation action plan 2006-2010. IUCN; World Pheasant Assoc, Gland, Switzerland, Fordingbridge, UK.

Südbeck, P. (Editor) (2005). Methodenstandards zur Erfassung der Brutvögel Deutschlands, Radolfzell.

Vallant, S., H. Niederstätter, B. Berger, R. Lentner, and W. Parson (2018). Increased DNA typing success for feces and feathers of capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*). Ecology and evolution 8:3941–3951.

Watson, A. (1965). A population study of ptarmigan (*Lagopus mutus*) in Scotland. The Journal of Animal Ecology 135–172.

Figures and Tables

Figure 1: Aerial picture of the mountains north of the city Innsbruck (Tyrol, Austria) with the study sites where faeces and feathers of rock ptarmigan were collected from June to October 2019 in red.

Table 1: Size and elevation of the investigated study sites shown in Figure 1.

Site	Size [ha]	Elevation	[m above	sea level]
		minimal	maximal	average
1	14.72	2120	2370	2254
2	7.12	2183	2333	2273
3	10.04	2117	2312	2205
4	50.72	1910	2281	2076
5	78.13	1918	2165	2050
6	70.87	2011	2459	2193

Table 2: Dates, on which the collection of rock ptarmigan faeces and feathers took place. The field sampling was conducted in 2019, in the six study sites at the northern mountains of the city Innsbruck (Tyrol, Austria) shown in Figure 1.

	Round I	Round II	Round III	Round IV	Round V	Round VI
Site 1	19 June	4 July	11 July	4 August	4 September	18 October
Site 2	19 June	4 July	11 July	4 August	4 September	18 October
Site 3	19 June	4 July	10 July	4 August	4 September	18 October
Site 4	19 June	4 July	12 July	5 August	4 September	18 October
Site 5	25 June	5 July	16 July	9 August	13 September	14 October
Site 6	25 June	5 July	16 July	9 August	13 September	14 October

Table 3: To identify rock ptarmigan individuals, DNA was extracted out of the collected faeces and feathers and a PCR reaction was conducted. Here the sequences of the forward and reverse primers in the three multiplexes (MPX) used in this assignment are shown.

MPX	Locus	Forward primer (5´- 3´)	Reverse Primer (5´- 3´)	Reference
1	sTuT2	FAM-TCTCCAAACTAGATATGGAAACCAG	CAAAGCTGTGTTTCATTAGTTGAAG	(Jacob et al. 2010)
	mTuT1	GGTCTACATTTGGCTCTGACC	HEX-GCACAGGAACAGCAATAGATGG	(Segelbacher et al. 2000; Jacob et al. 2010)
	BG18	NED-CGCCATAACTTAACTTGCACTTTC	CTTCCTGATACAAAGATGCCTACAA	(Piertney and Höglund 2001)
	sTuT3	GCCTCAACTAATCACCCCTTTATC	ATTO565-GAGGGATTTATGCATGCTGCTAG	(Jacob et al. 2010)
2	BG15	FAM-GAATAAATATGTTTGCTAGGGCTTAC	GATCTTACATTTTTCATTGTGGACTTC	(Piertney and Höglund 2001)
	sTuD6	HEX-AGCCTTTTACTGCACTACTTGC	GGTGTGTGGGAAATGAGGAC	(Jacob et al. 2010)
	sTuT4	TAM-TGGGAGCATCTCCCAGAGTC	ACAAACAAGGCAGCAGCATG	(Jacob et al. 2010)
	sTuD1	ATTTO565-ATTTGCCAGGAAACTTGCTC	CCTTTGCCTCCTTATGAAATCC	(Jacob et al. 2010)
3	TTT2	GTGAATGGATGGATGTATGAA	FAM-AGTCTGTCAATGAACTTCTTGG	(Caizergues et al. 2001)
	BG19	HEX-CAAGGCGCAACATTAAGATTC	TGTATTTTGGAAACTCTGTGTGC	(Piertney and Höglund 2001)
	BG20	TAM-AAGCACTTACAATGGTGAGGAC	TATGTTTTCCTTTTCAGTGGTATG	(Piertney and Höglund 2001)
	TTT1	ATTO565-TGCAGTCCAGCCTTATTTCA	TCAGTGCTTCACTAACCTCTT	(Caizergues et al. 2001)
	TtWa	ATTO565-TTTGATGGTAGTAGCGAAGAAGC	CCAAAAGAATTGAGGGCAAG	unpublished
	TtZa	ATTO565-TGTTCATCCCGAACTTAC	GACCATGTCCACTTGGCTTT	unpublished

Table 4: An overview of rock ptarmigan individual numbers overall and over time, based on the molecular data.

	Individuals	Males	Females	Sex unclear
Absolute Number	70	38	24	8
Amount in %	100	54	34	12
Multiply found	37	21	13	3
Singly found	33	17	11	5
Absolute Number in round I-III	50	29	17	4
Multiply found in round I-III	35	19	12	2
Singly found in round I-III	15	10	5	2

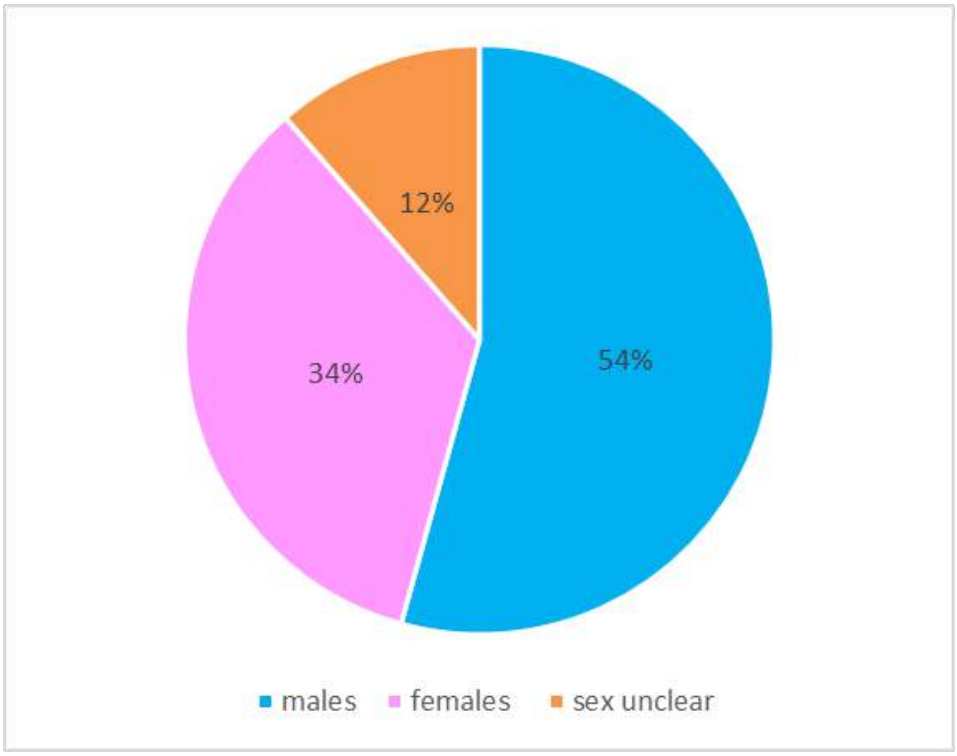


Figure 2: Percentage of the males and females found and of individuals of which sex was unclear.

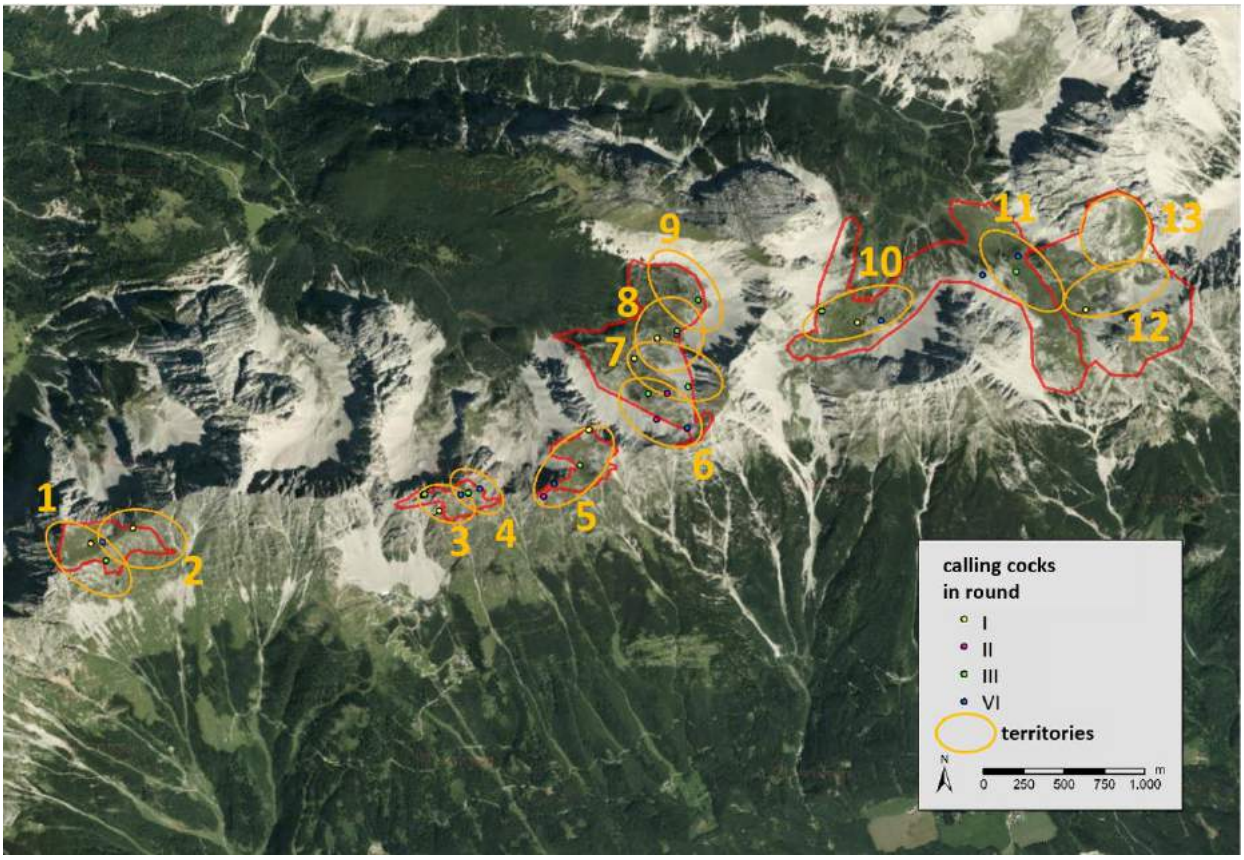


Figure 3: Estimated territories based on the classic method by listening to calling cocks (Fried 2020).

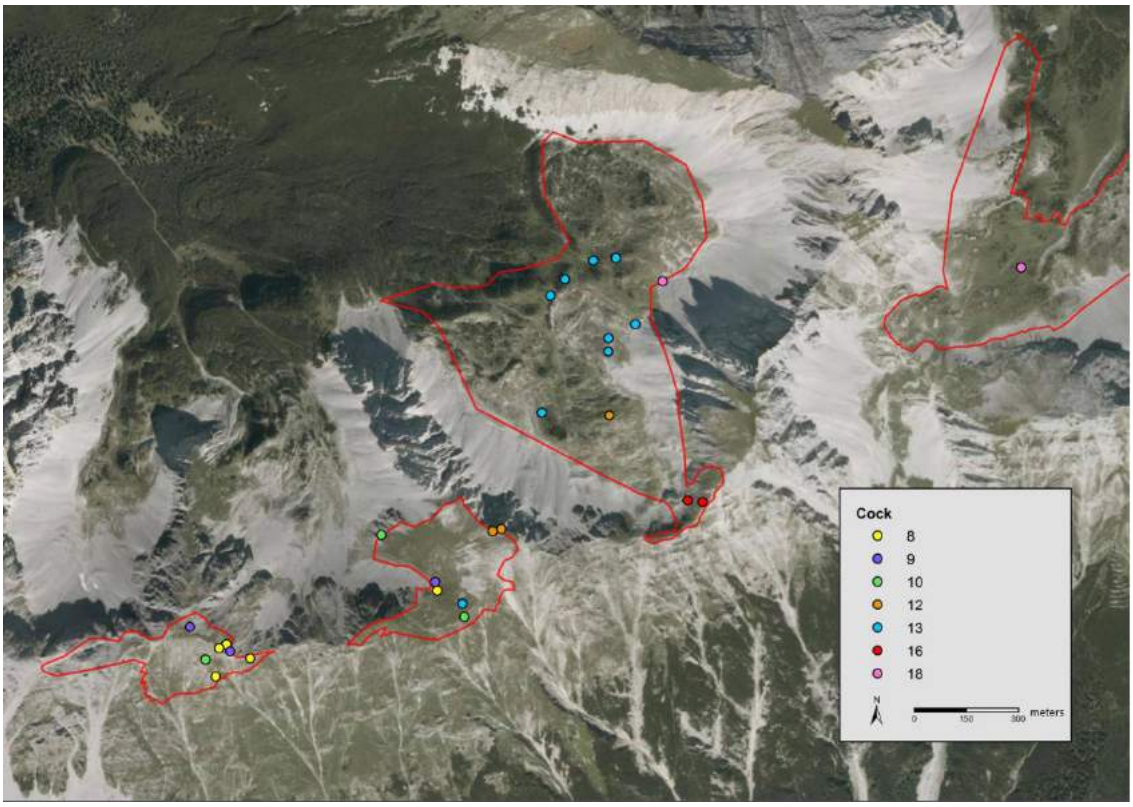


Figure 4: Cocks found more than once while breeding season (Round I-III) in the study Sites 2-4 based on the molecular method.

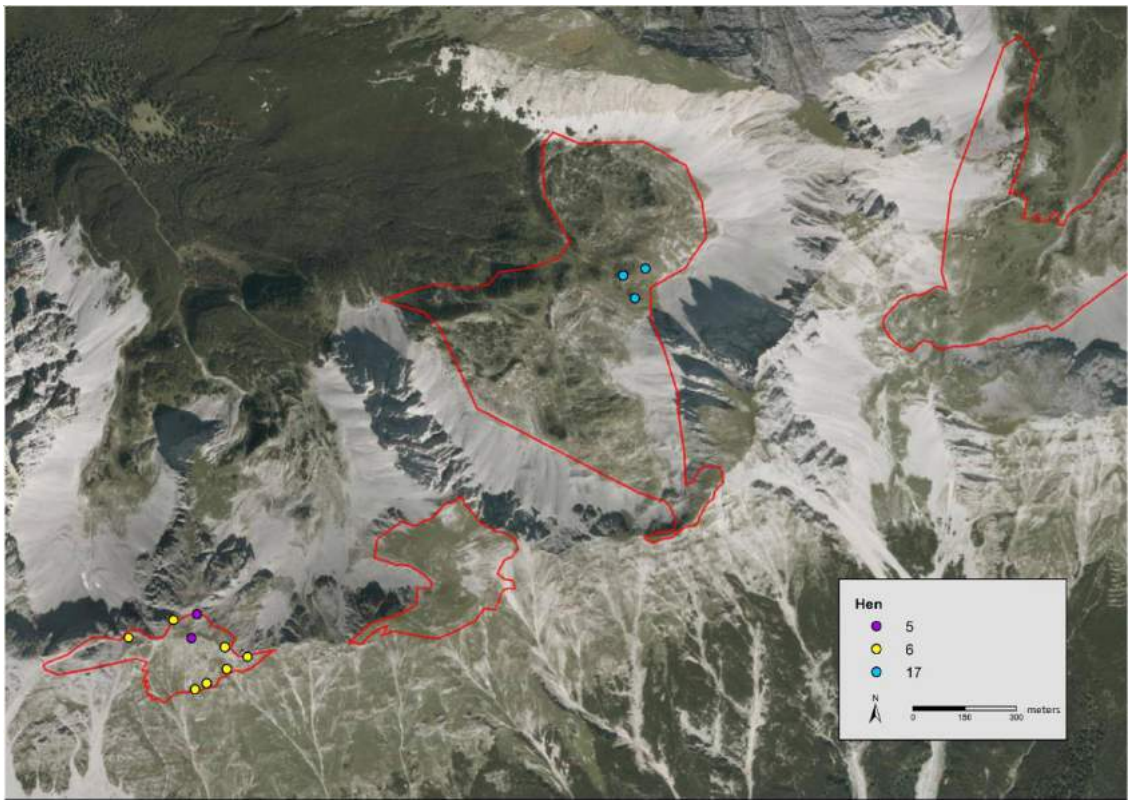


Figure 5: Hens found more than once while breeding season (Round I-III) in the study Sites 2-4 based on the molecular method.

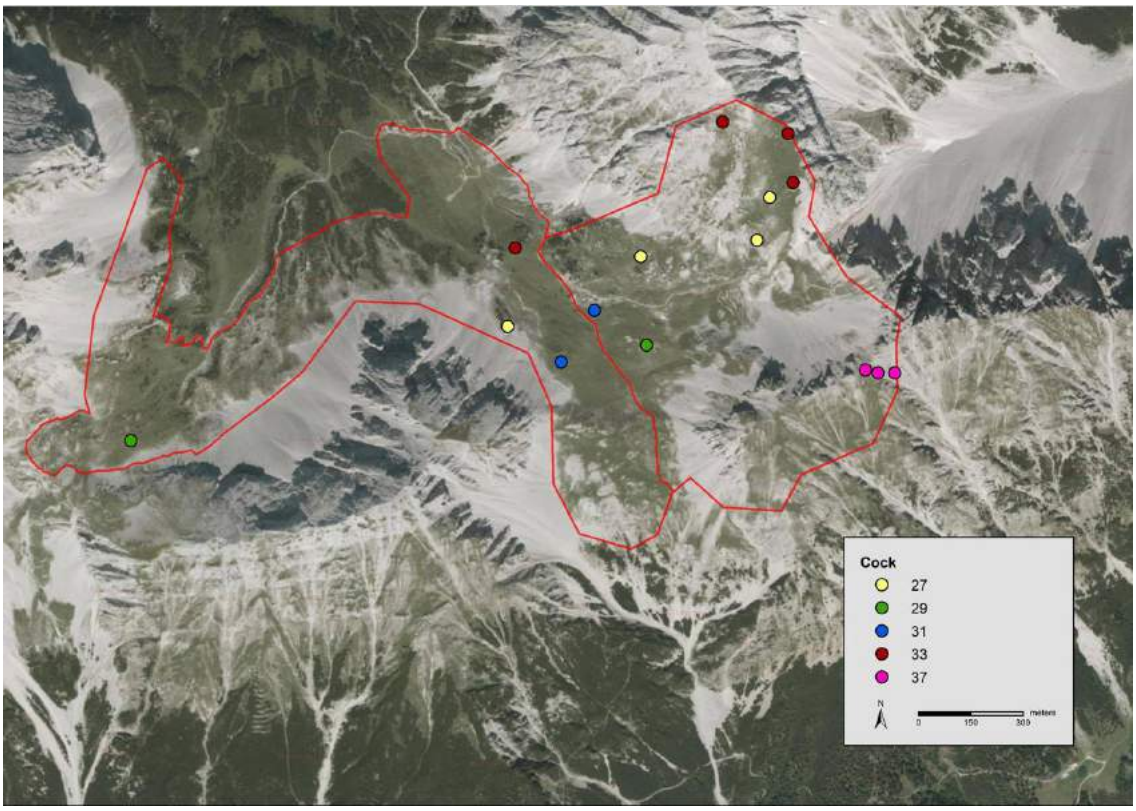


Figure 6: Cocks found more than once while breeding season (Round I-III) in the study Sites 5 & 6 based on the molecular method.

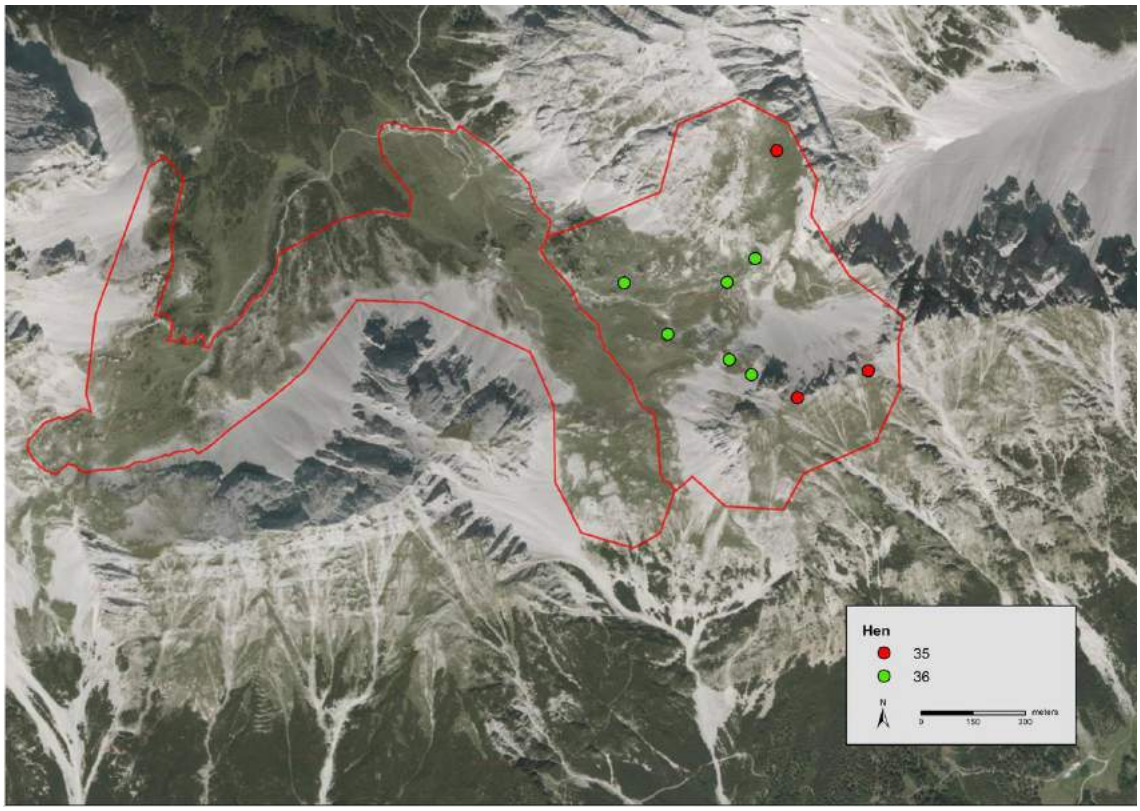


Figure 7: Hens found more than once while breeding season (Round I-III) in the study Sites 5 & 6 based on the molecular method.

Table 5: The maximal distances measured between the samples of the correspondent Individual. Once over the whole sampling time, once within breeding season (Round I-III) and once after Breeding season (Round IV-VI).

individual	sex	distance max [m]	distance max round I-III [m]	distance max round IV-VI [m]
29	male	1930	1506	900
13	male	1635	1090	1364
12	male	1523	473	1523
10	male	1222	623	849
18	male	1035	1035	-
9	male	1027	723	376
27	male	942	838	895
33	male	851	697	433
30	male	770	-	770
8	male	685	685	-
22	male	501	-	501
24	male	444	-	-
31	male	357	176	-
21	male	226	-	-
2	male	221	-	-
15	male	170	-	-
39	male	155	-	-
37	male	82	82	-
16	male	43	-	-
19	female	2850	2658	2835
3	female	2275	2275	322
17	female	1748	97	1522
23	female	1173	-	-
34	female	1062	-	1062
32	female	995	-	979
38	female	812	-	812
35	female	715	710	-
36	female	597	450	135
5	female	352	71	352
6	female	349	348	-
26	female	215	-	215
7	female	95	-	-

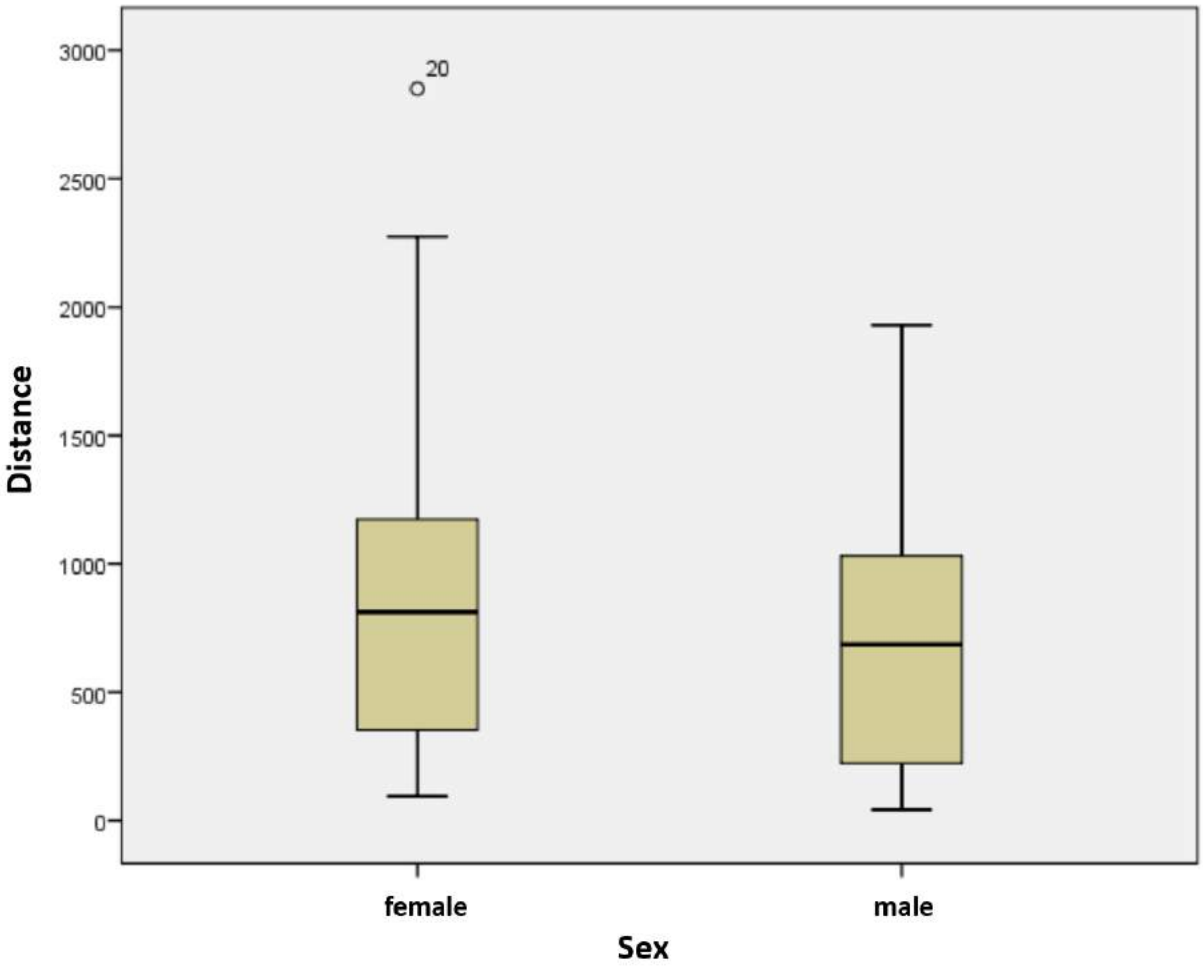


Figure 8: Boxplot diagram of the measured maximal distances in female and male individuals.

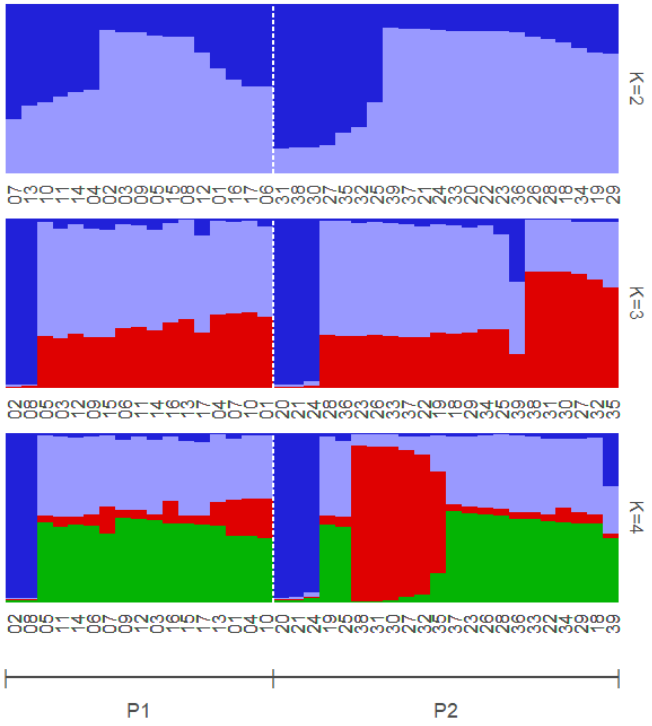


Figure 9: STRUCTURE plot of the 39 multiple found individuals. The suggested most likely K is 3. P1 is accorded to the samples found in the investigated sites 1-4 and P2 includes the samples found in the sites 5 and 6. The numbers underneath the plots represent the individual numbers.

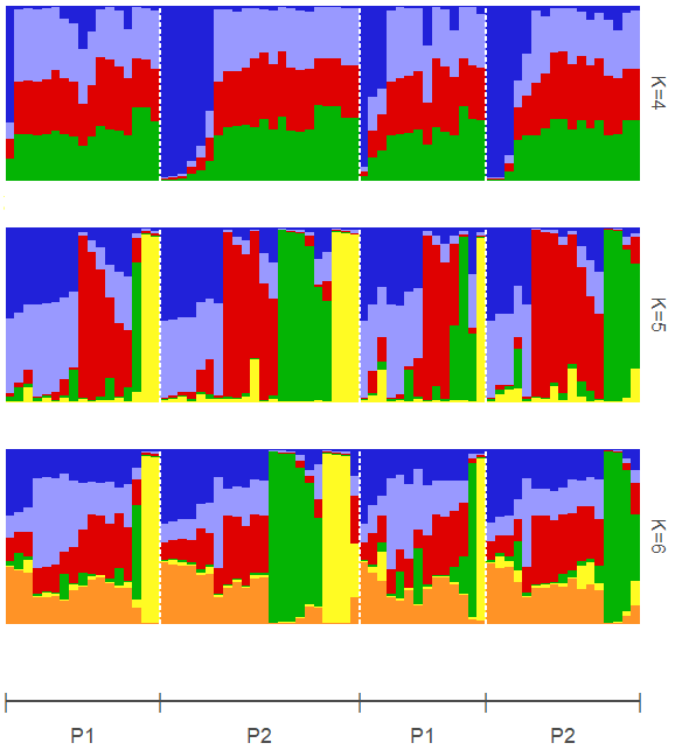


Figure 10: STRUCTURE plot of the all 70 individuals. The multiply found individuals are shown on the left side and the singly found individuals are shown on the right side. P1 is accorded to the samples found in the investigated Sites 1-4 and P2 includes the samples found in the Sites 5 and 6. The suggested most likely K is 5.

Table 6: Parewise Fst-values between the particlar investigated sites for the 39 multiply found individuals.

Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	
0.000						**Site 1**
0.053	0.000					**Site 2**
0.082	0.057	0.000				**Site 3**
0.065	0.058	0.057	0.000			**Site 4**
0.045	0.033	0.045	0.041	0.000		**Site 5**
0.076	0.054	0.070	0.065	0.030	0.000	**Site 6**

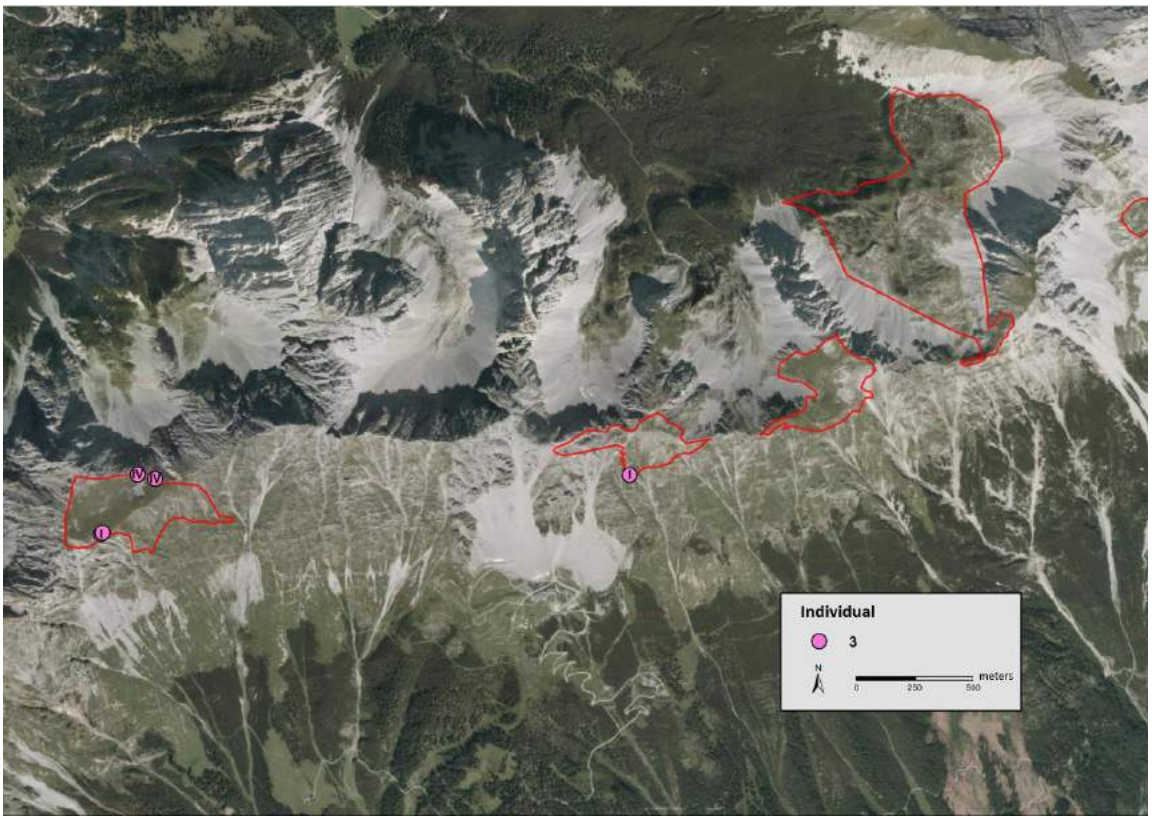
Table 7: Pairwise Fst-values between the particlar investigated sites for all 70 individuals.

Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	
0.000						**Site 1**
0.034	0.000					**Site 2**
0.046	0.041	0.000				**Site 3**
0.037	0.034	0.052	0.000			**Site 4**
0.039	0.033	0.045	0.029	0.000		**Site 5**
0.035	0.026	0.046	0.021	0.015	0.000	**Site 6**

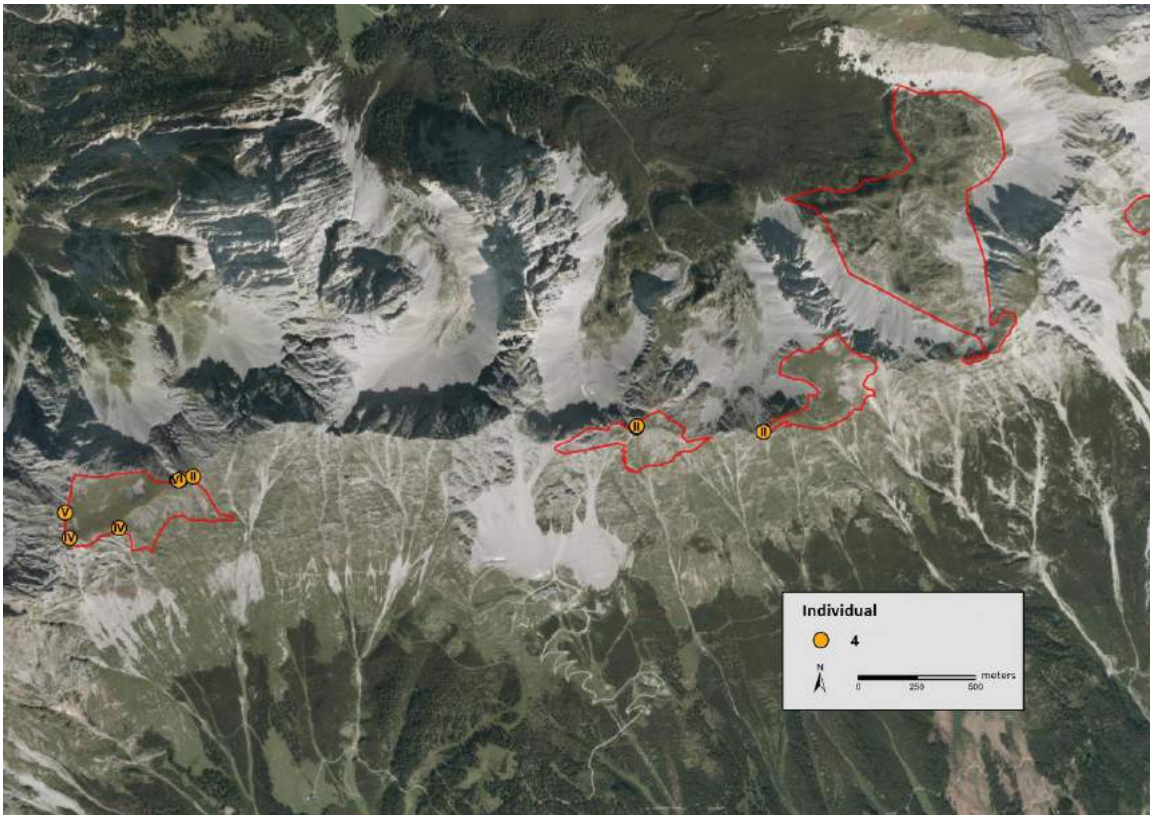
Supplement

Supplementary Figure 1: The spots where Individual 1 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this individual is a cock.

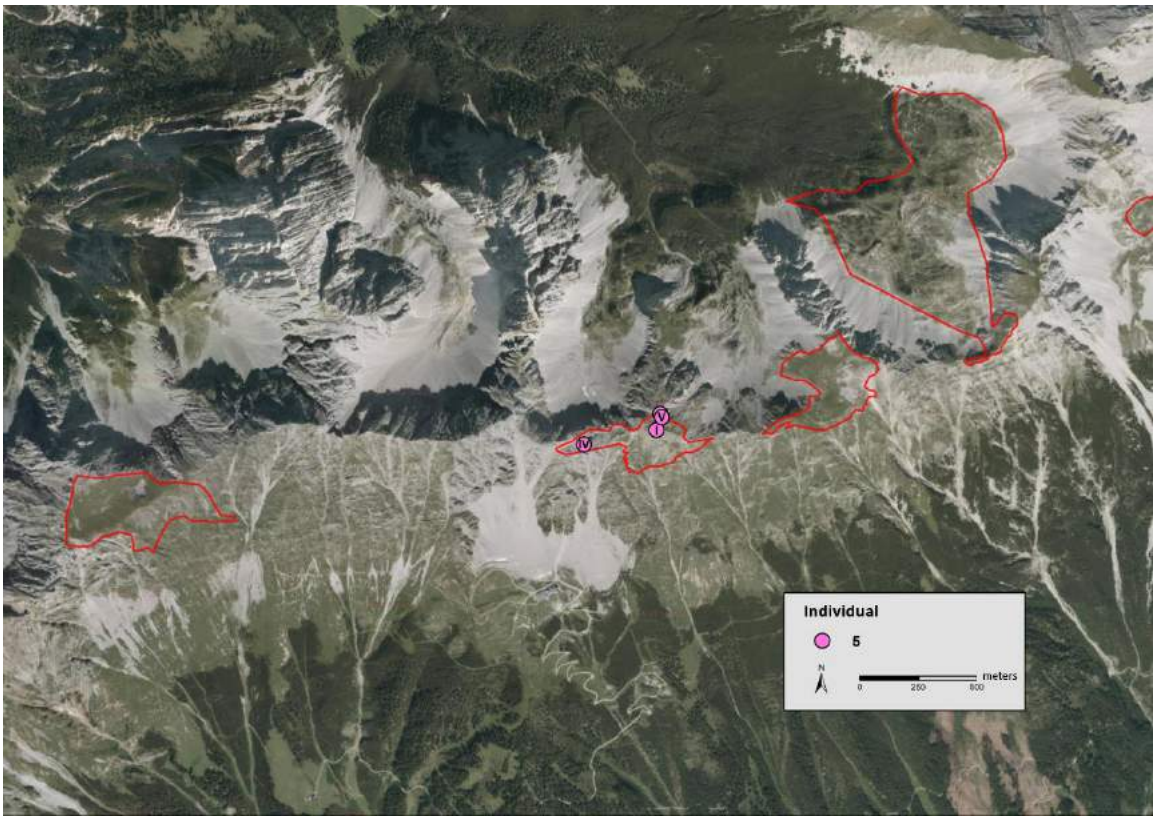
Supplementary Figure 2: The spots where Individual 2 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this individual is a cock.



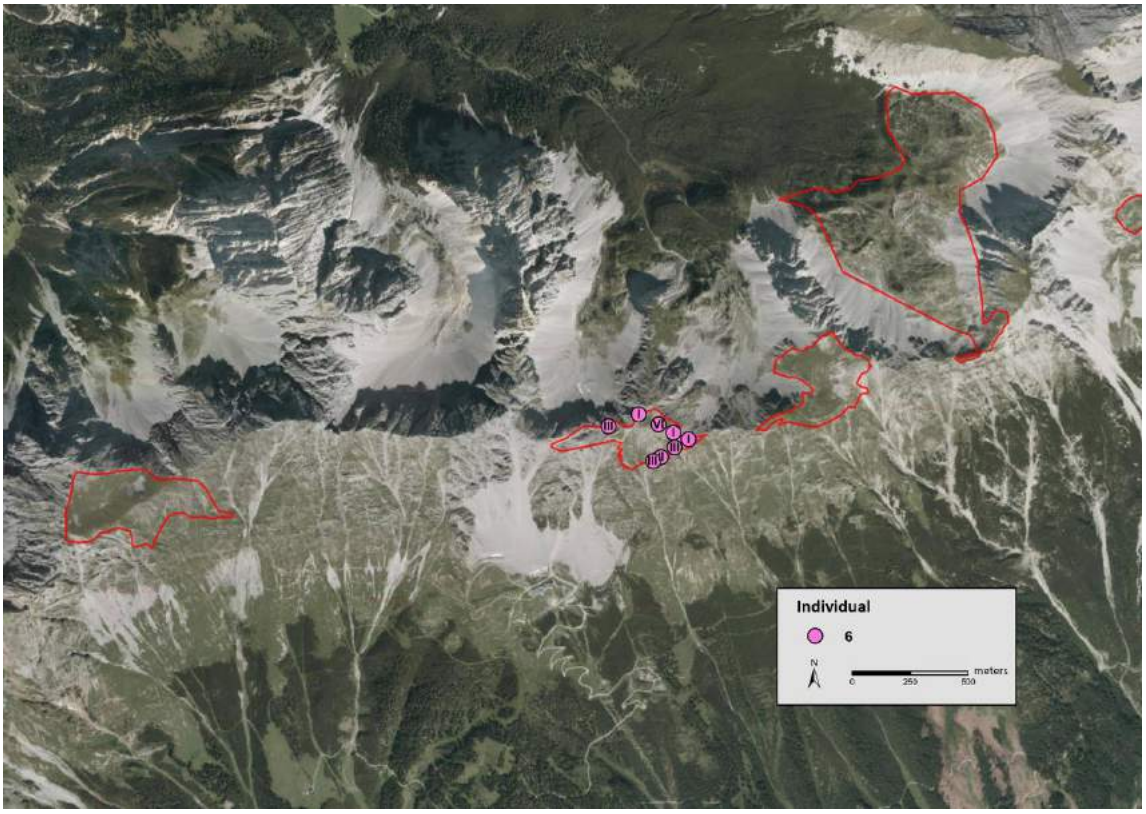
Supplementary Figure 3: The spots where Individual 3 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



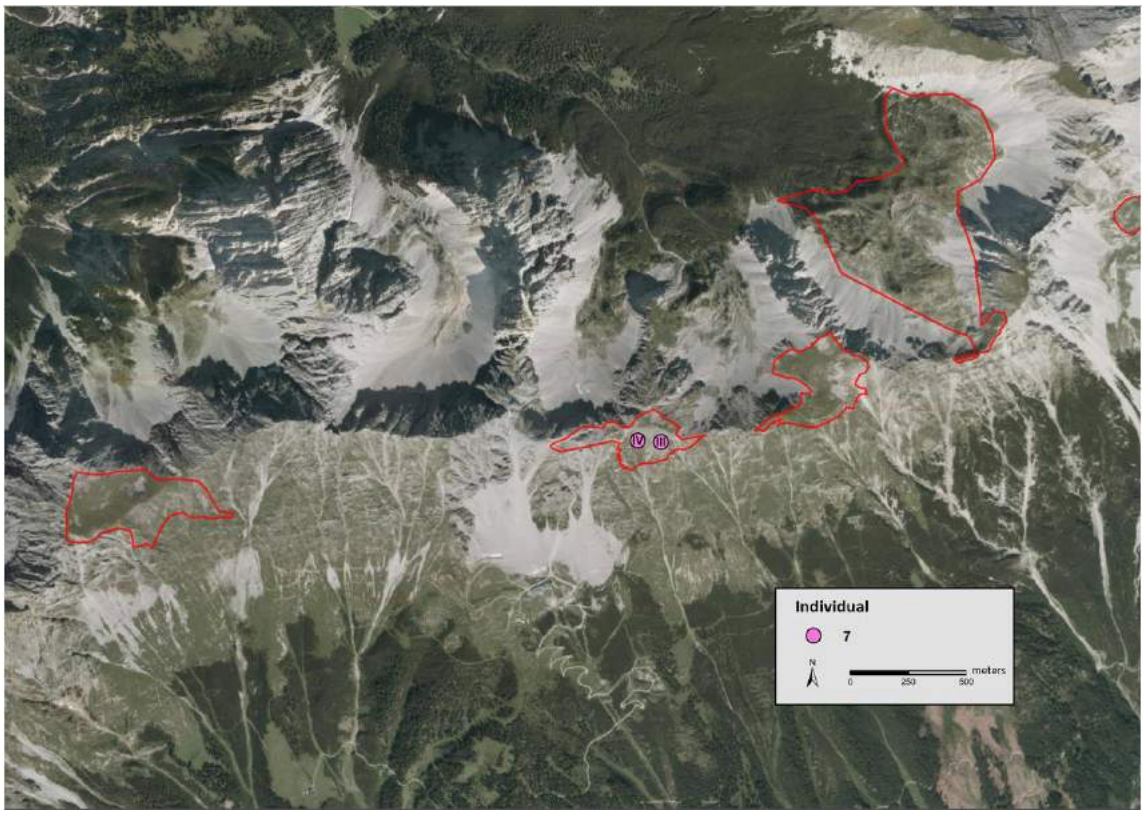
Supplementary Figure 4: The spots where Individual 4 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Orange means the sex of this individual is not known.



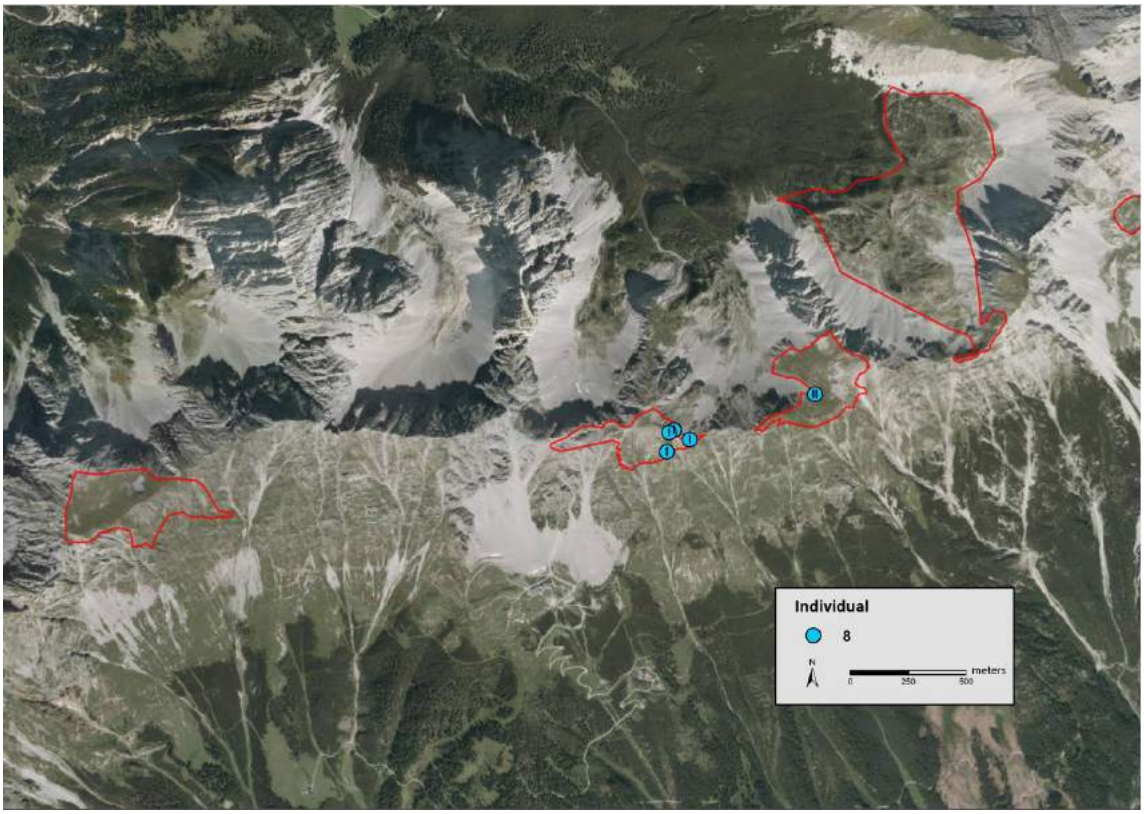
Supplementary Figure 5: The spots where Individual 5 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



Supplementary Figure 6: The spots where Individual 6 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.

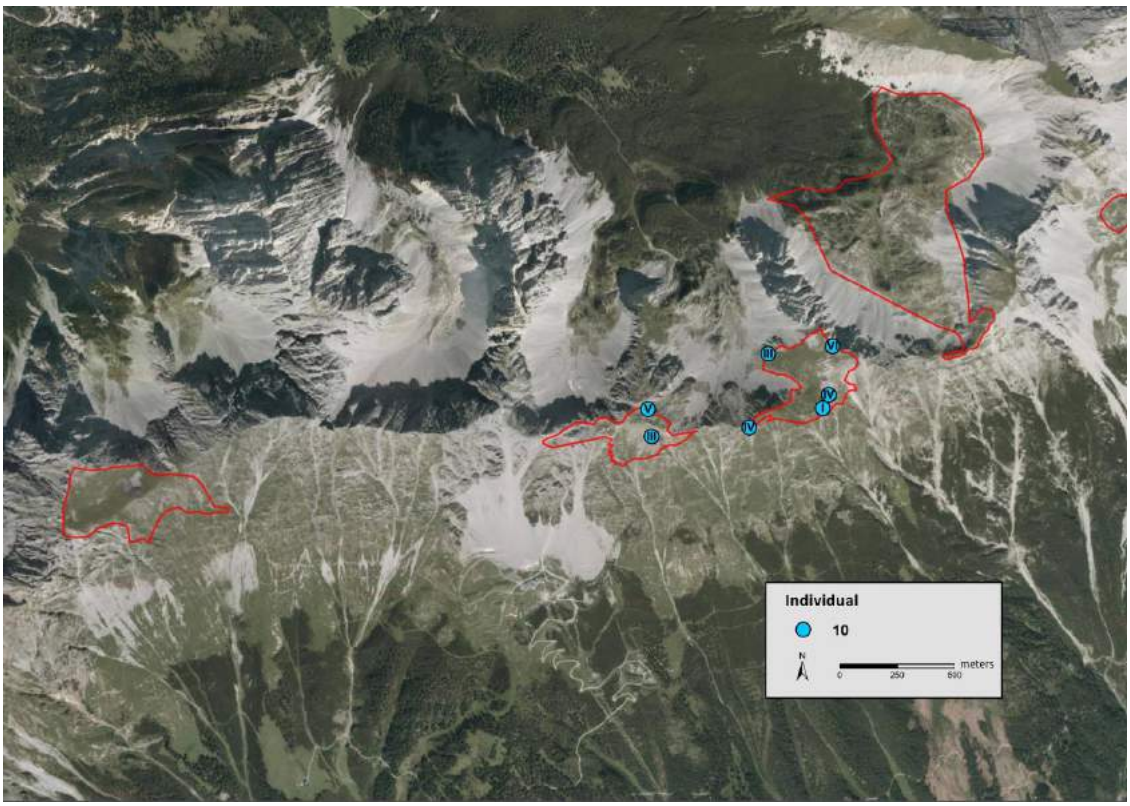


Supplementary Figure 7: The spots where Individual 7 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



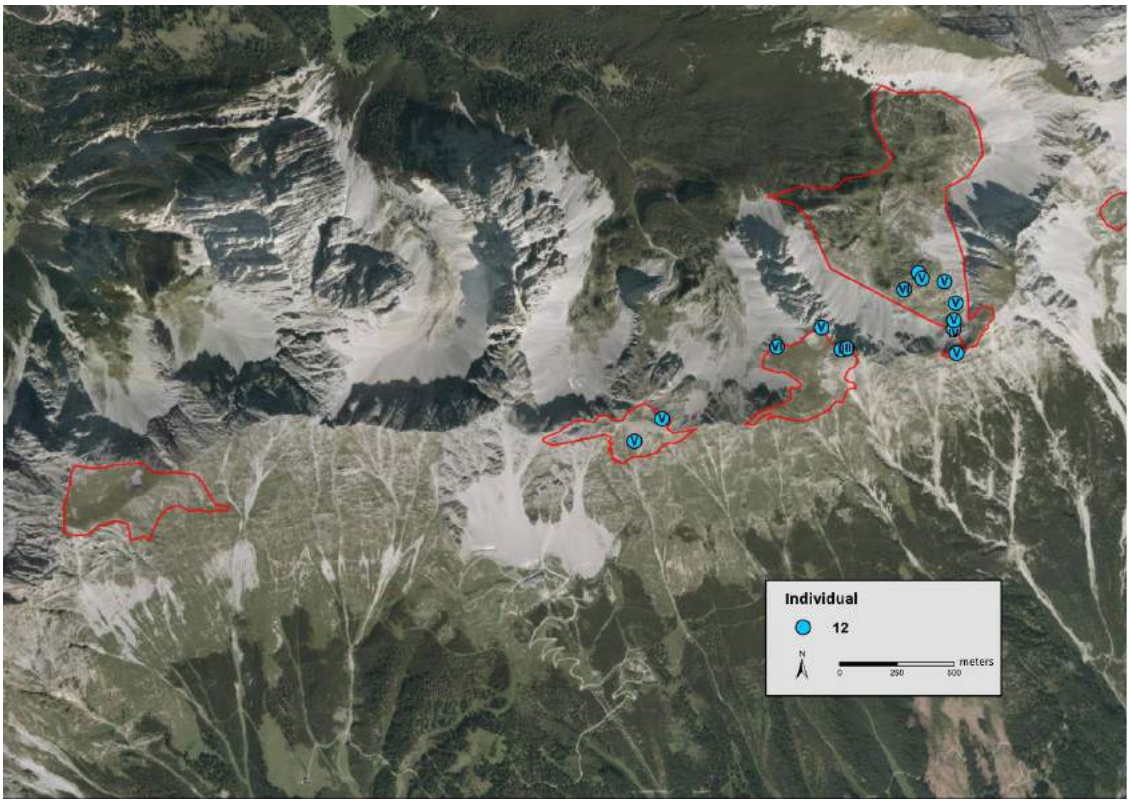
Supplementary Figure 8: The spots where Individual 8 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.

Supplementary Figure 9: The spots where Individual 9 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this individual is a cock.

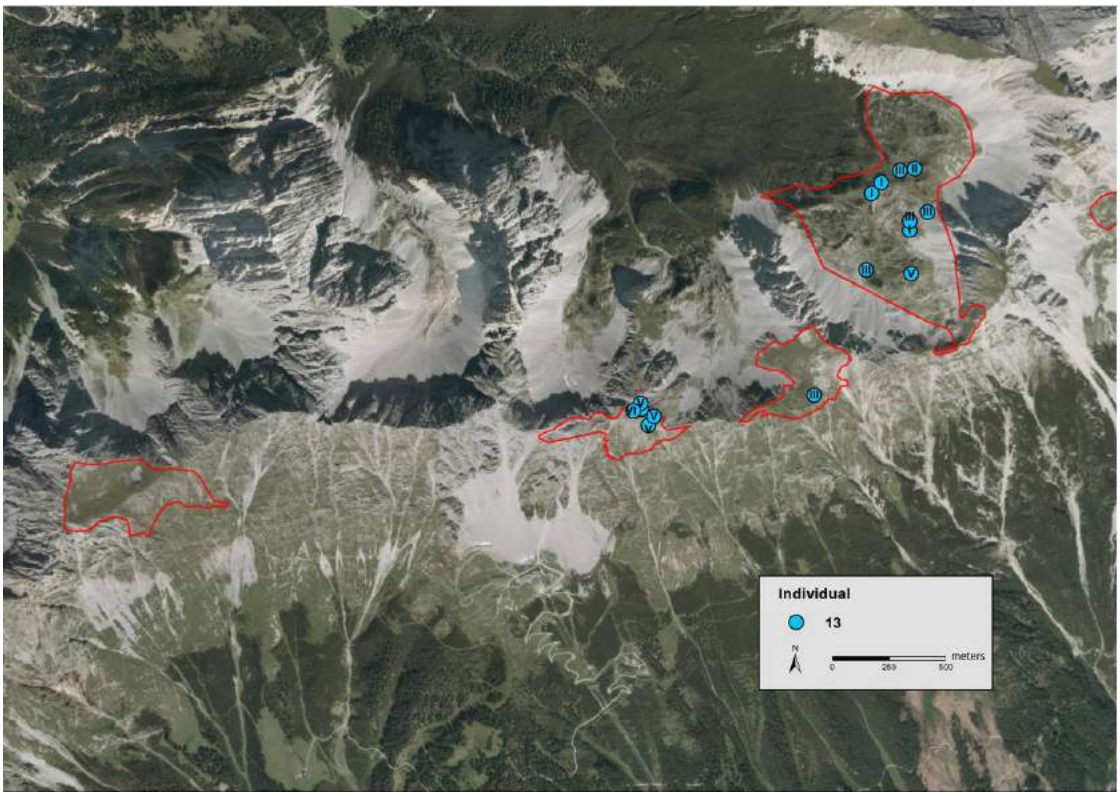


Supplementary Figure 10: The spots where Individual 10 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this individual is a cock.

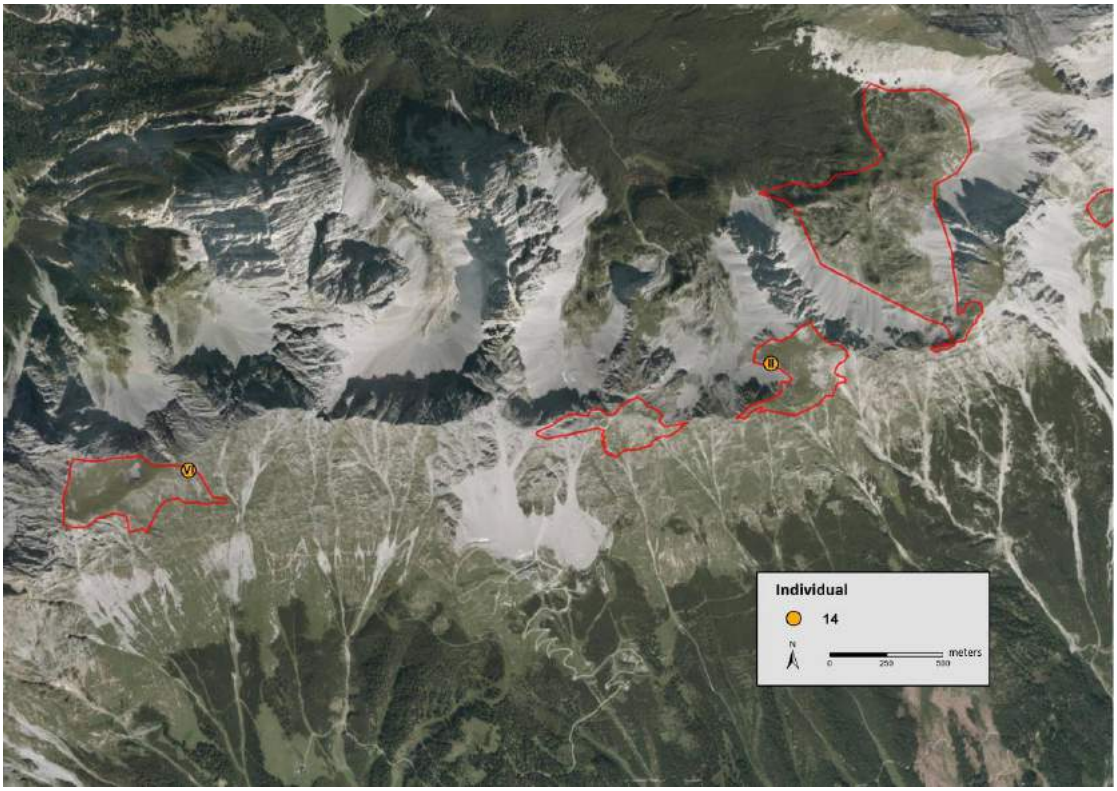
Supplementary Figure 11: The spots where Individual 11 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



Supplementary Figure 12: The spots where Individual 12 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



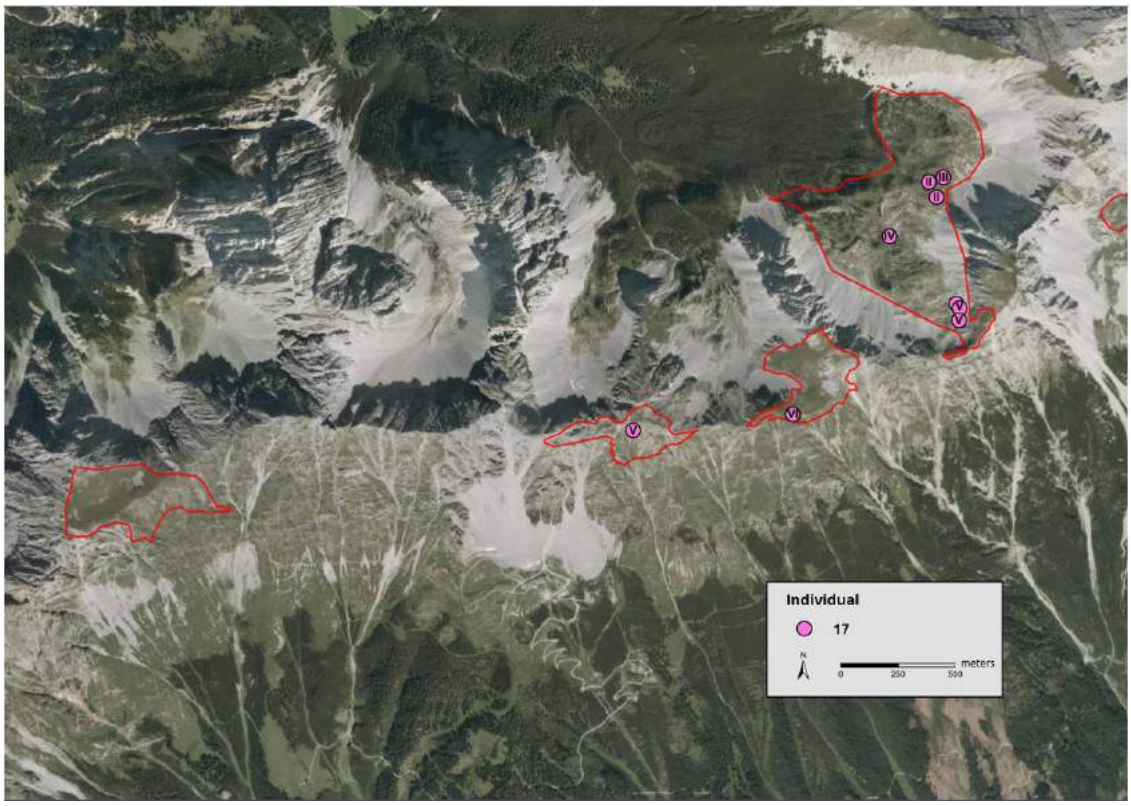
Supplementary Figure 1311: The spots where Individual 13 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



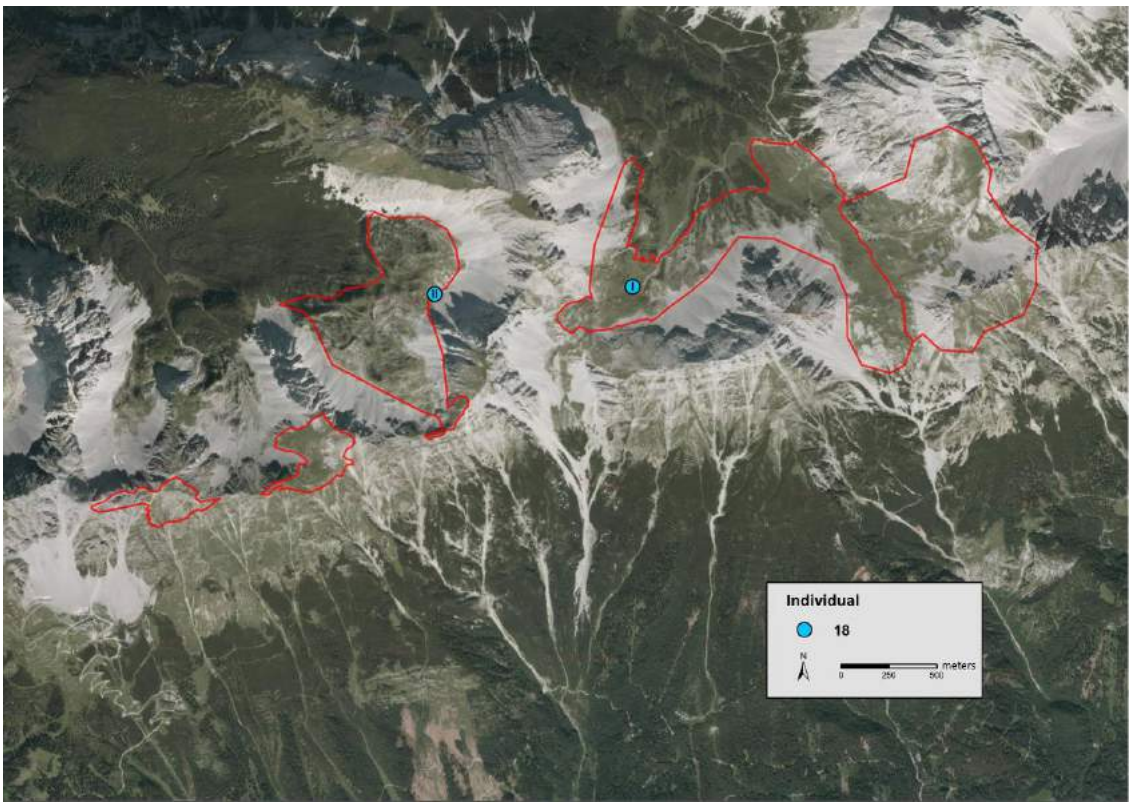
Supplementary Figure 14: The spots where Individual 14 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Orange means the sex of this individual is not known.

Supplementary Figure 15: The spots where Individual 15 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.

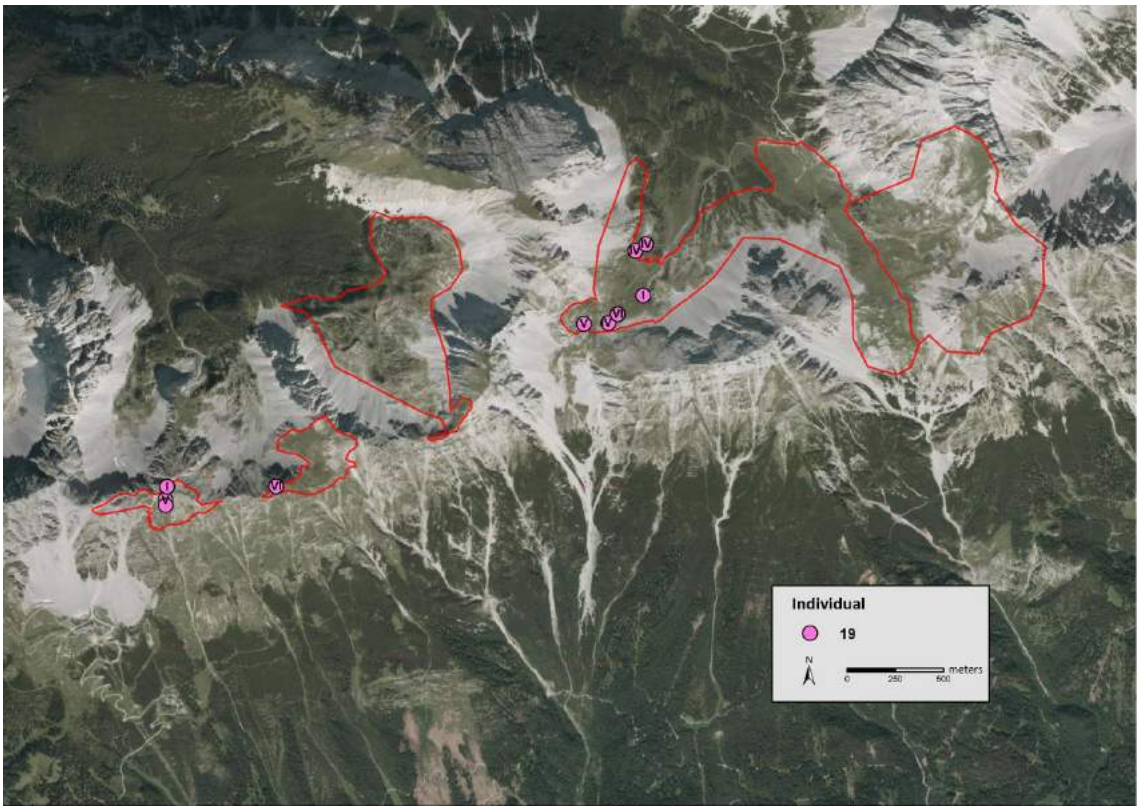
Supplementary Figure 16: The spots where Individual 16 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



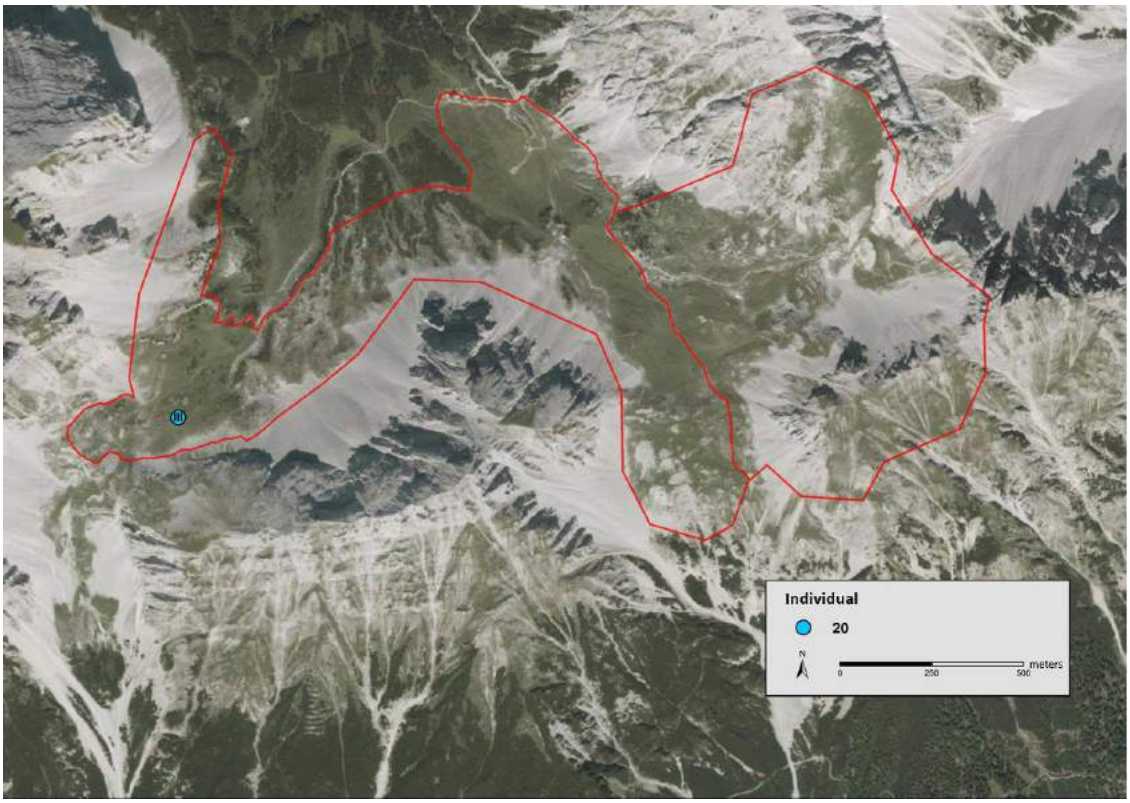
Supplementary Figure 17: The spots where Individual 17 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



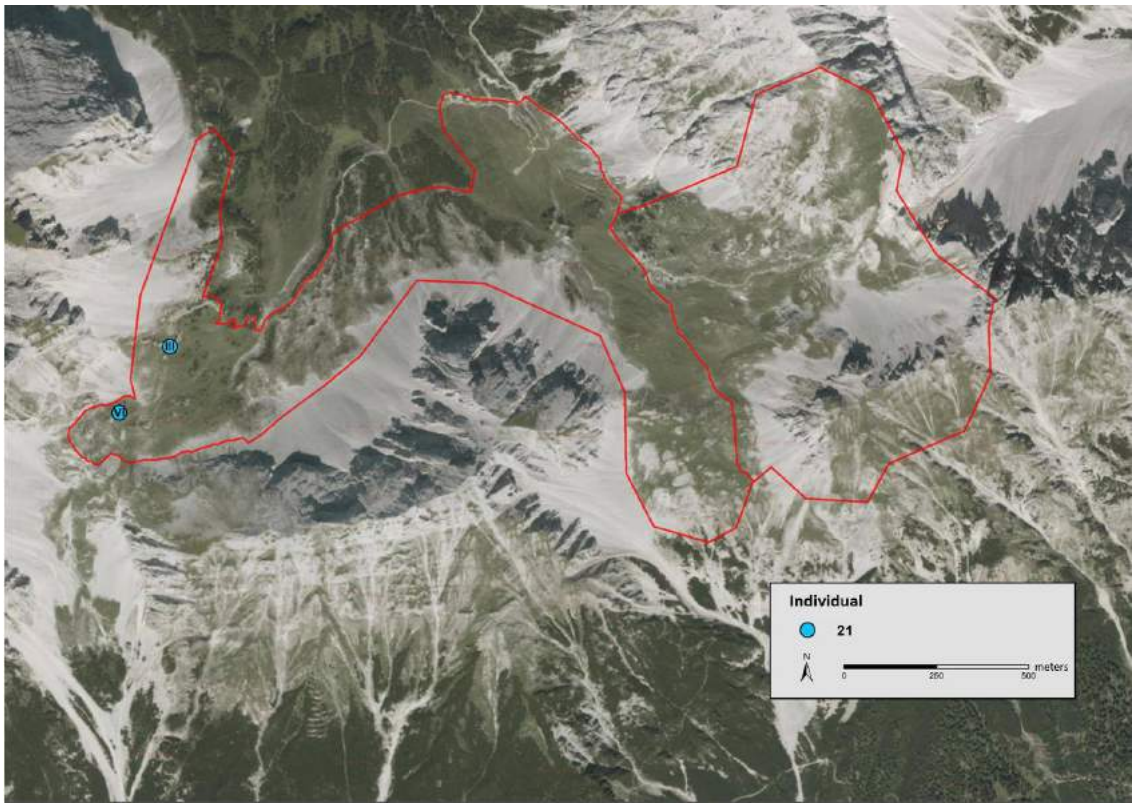
Supplementary Figure 1812: The spots where Individual 18 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



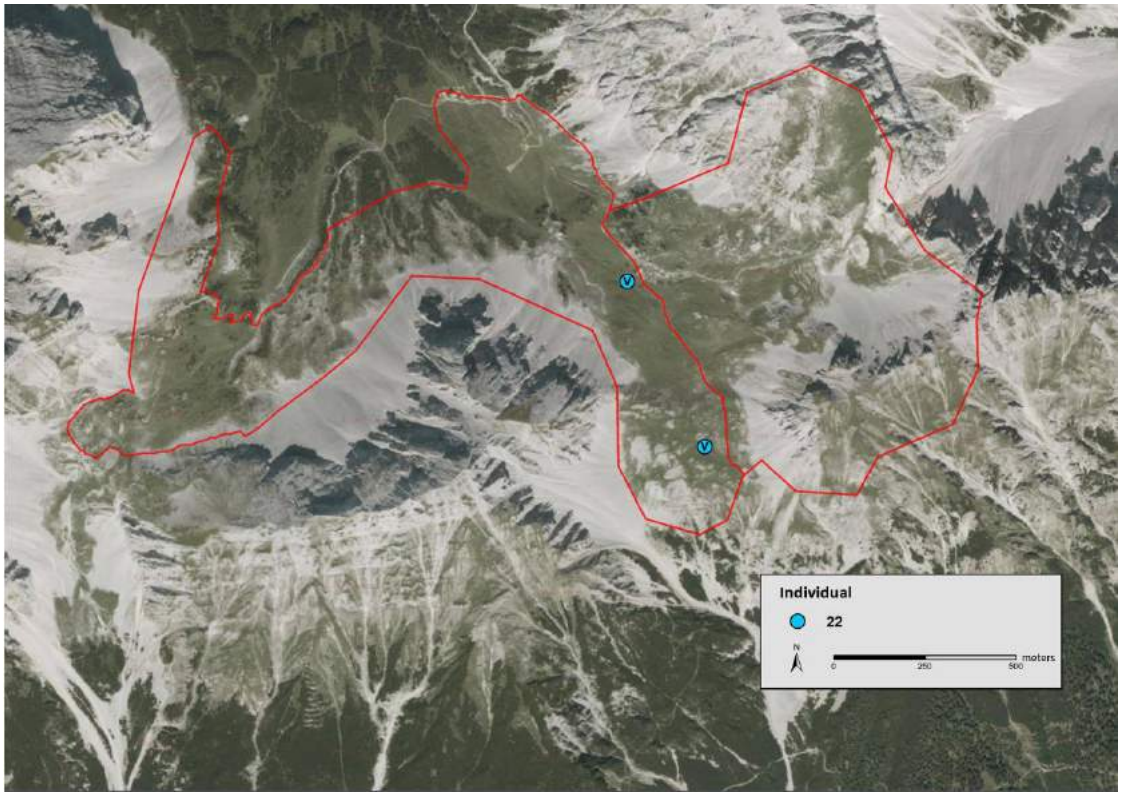
Supplementary Figure 19: The spots where Individual 19 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



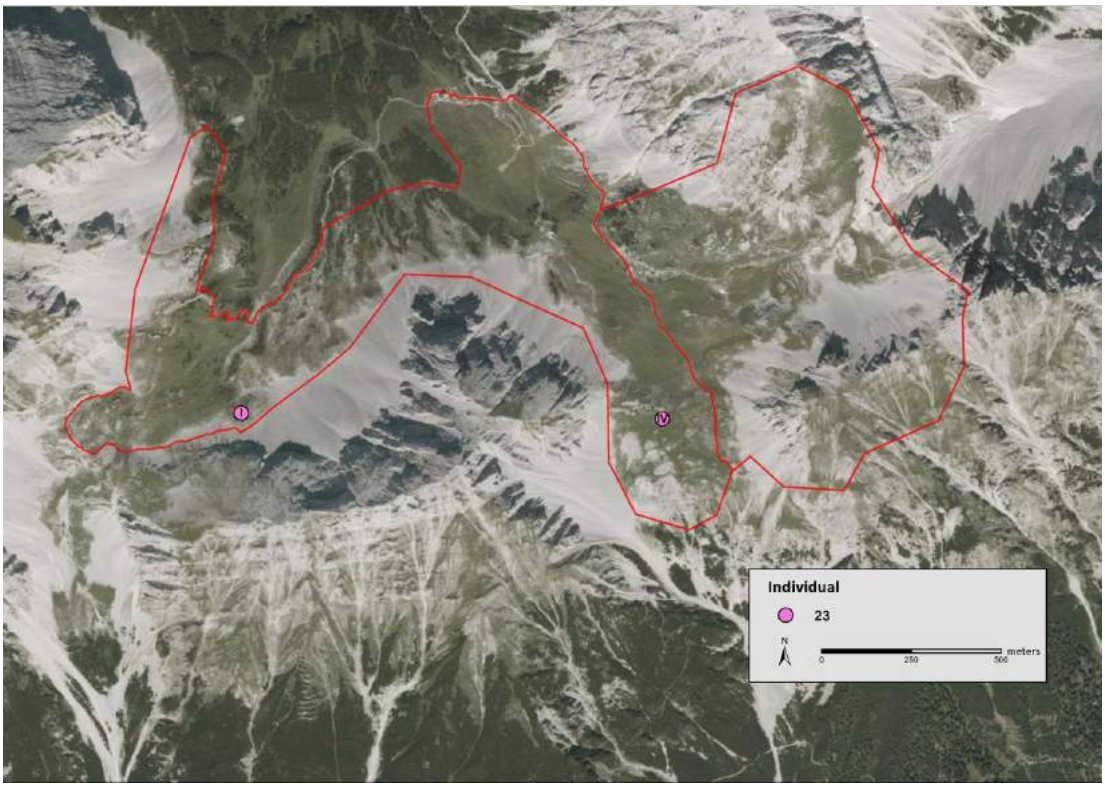
Supplementary Figure 20: The spots where Individual 20 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



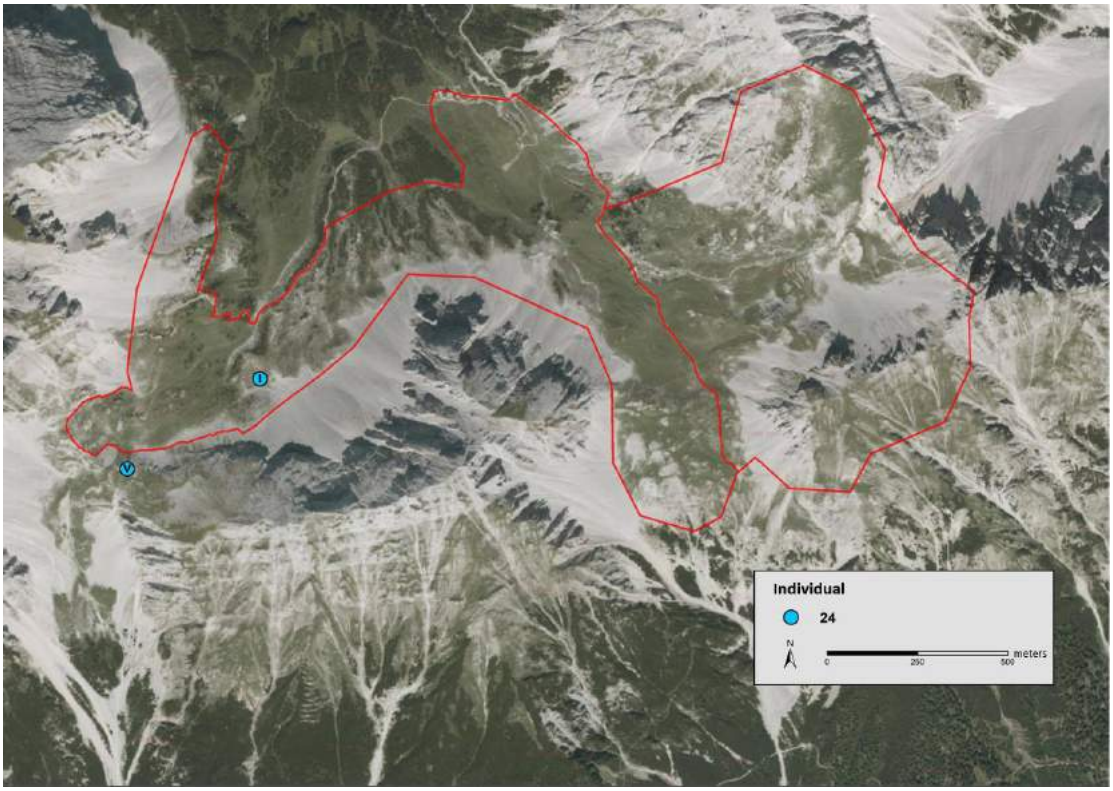
Supplementary Figure 21: The spots where Individual 21 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



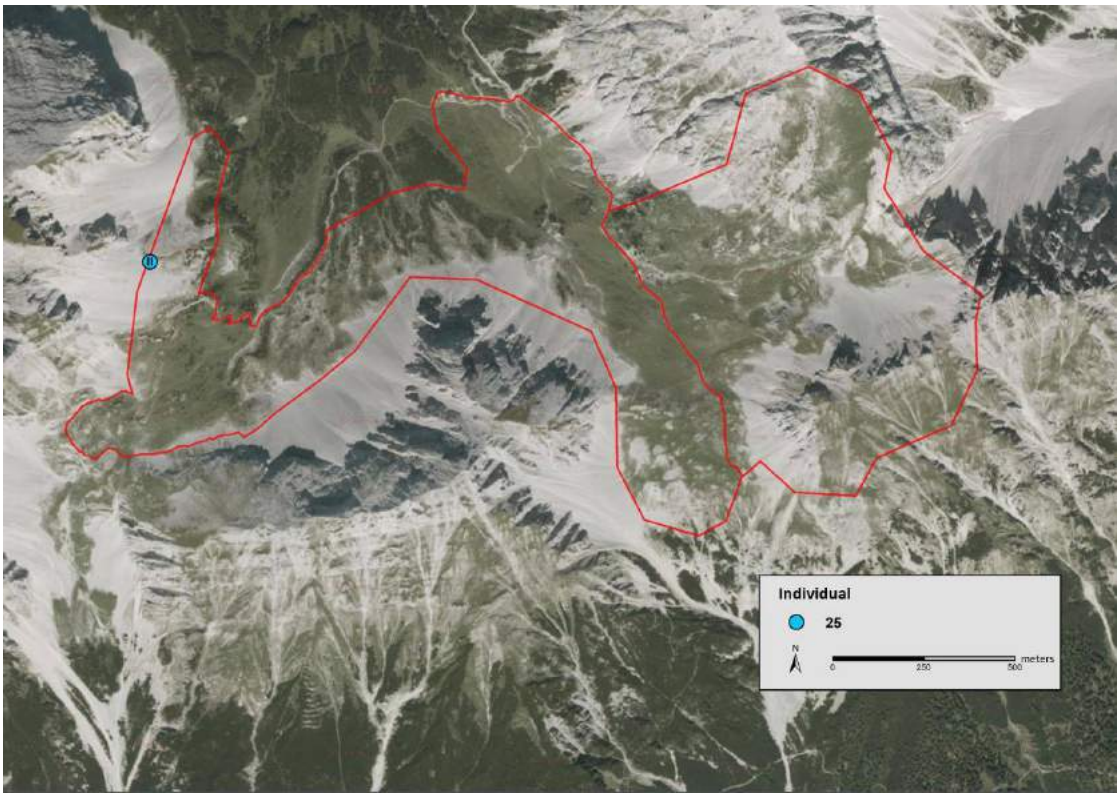
Supplementary Figure 22: The spots where Individual 22 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



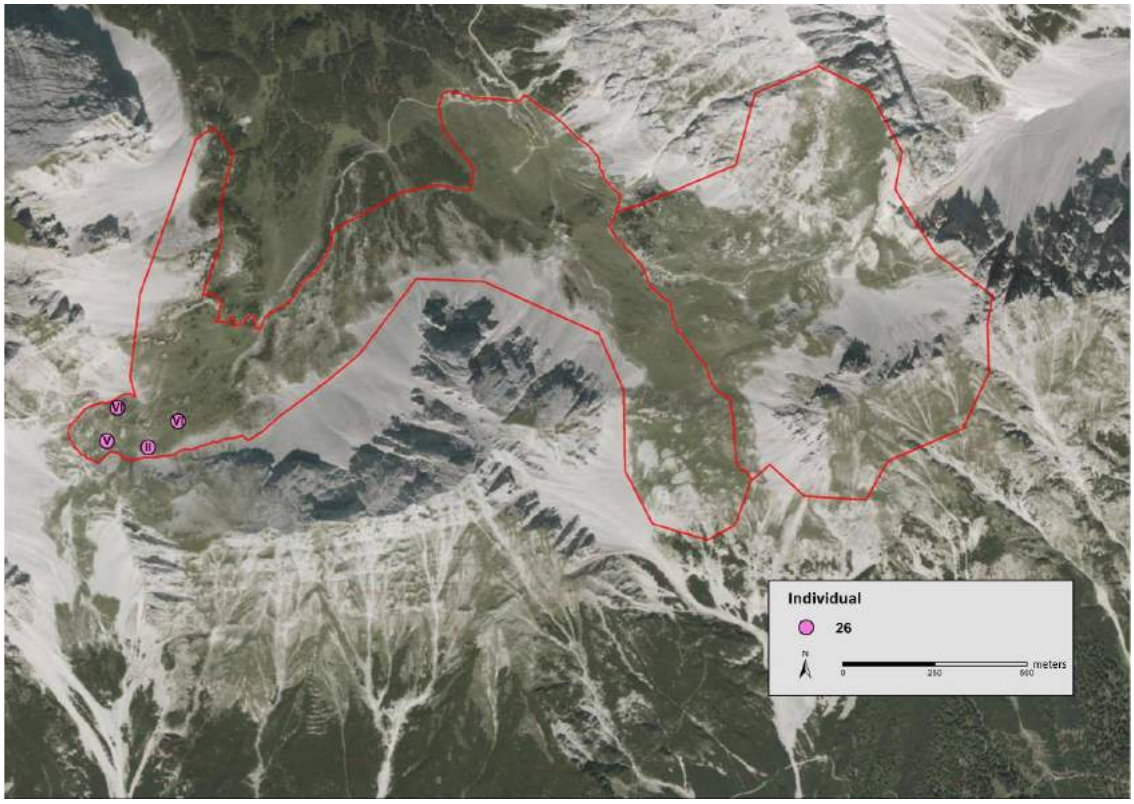
Supplementary Figure 23: The spots where Individual 23 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



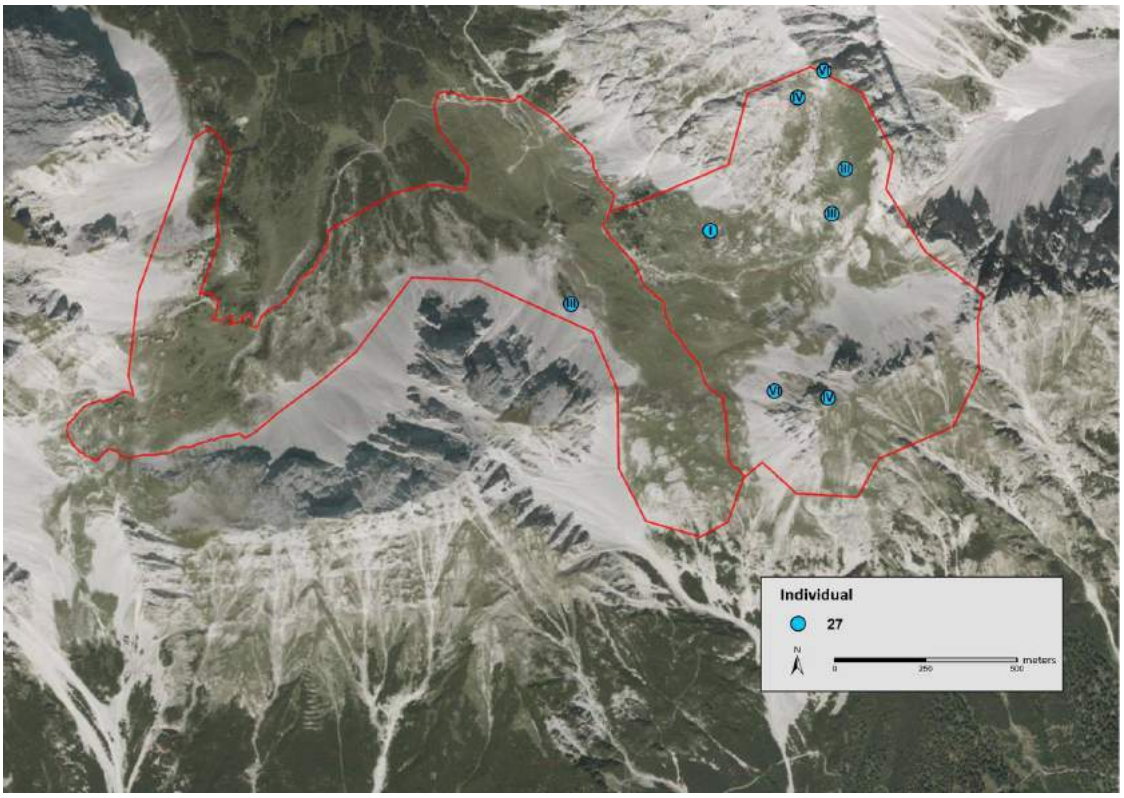
Supplementary Figure 24: The spots where Individual 24 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



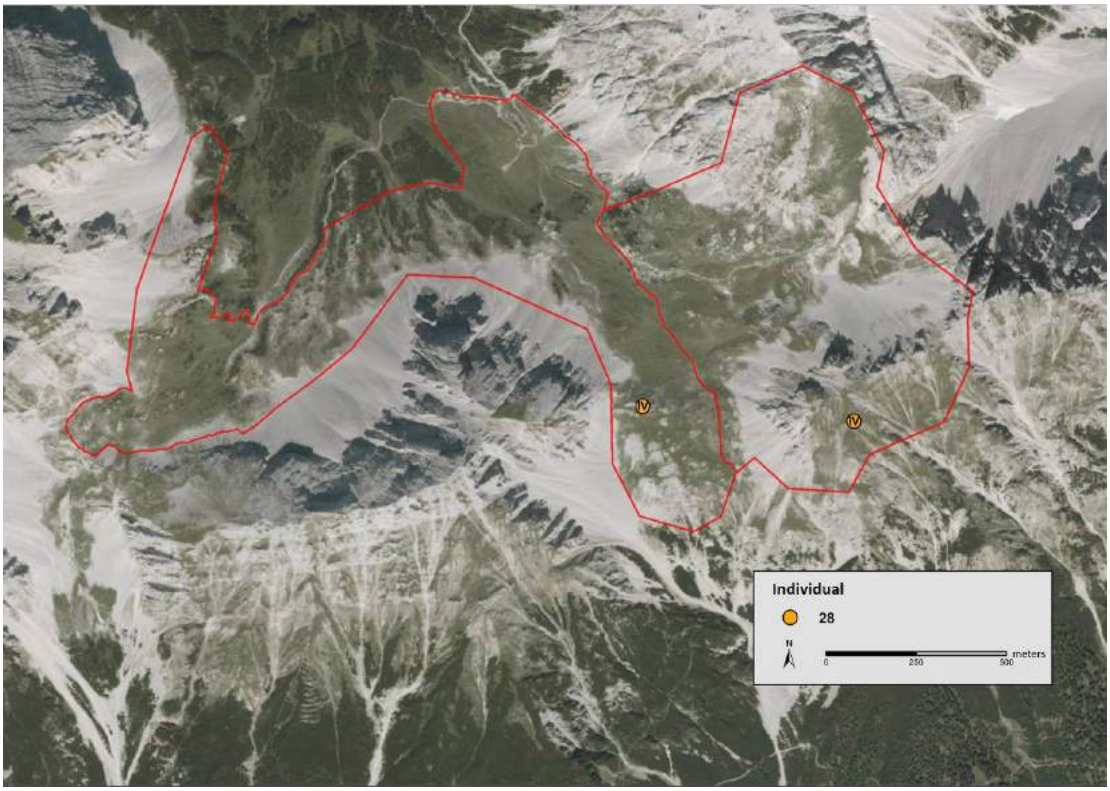
Supplementary Figure 25: The spots where Individual 25 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



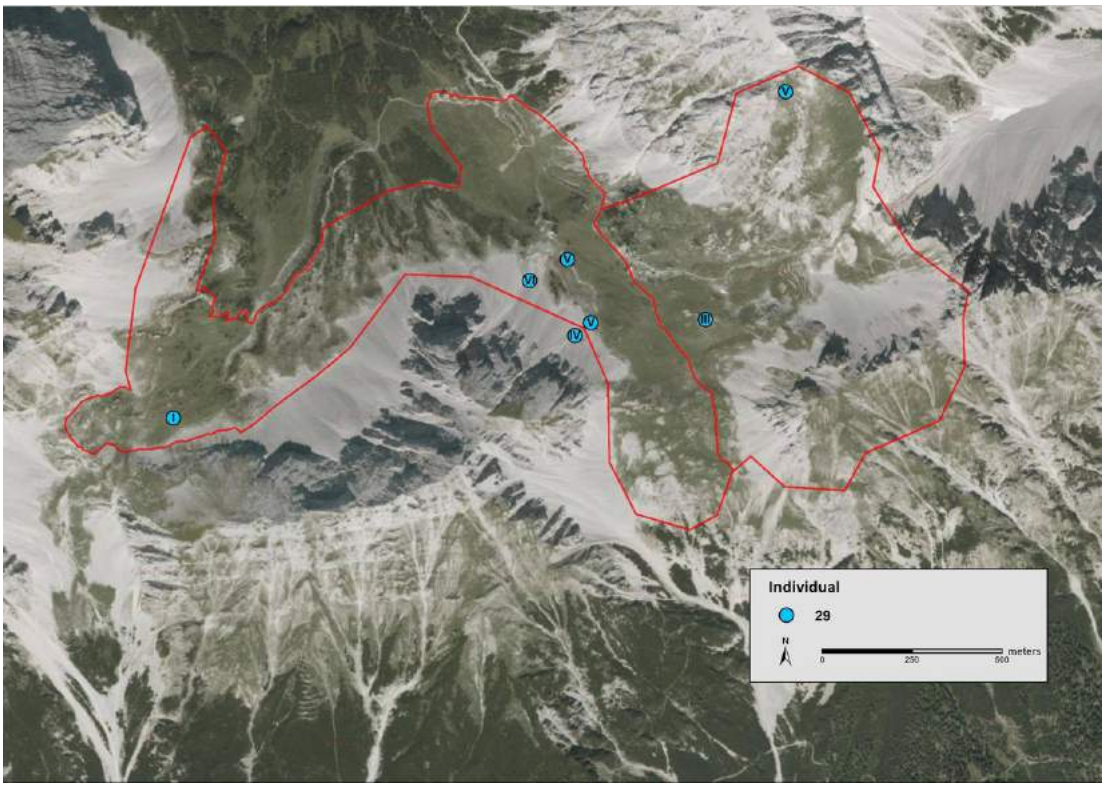
Supplementary Figure 26: The spots where Individual 26 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



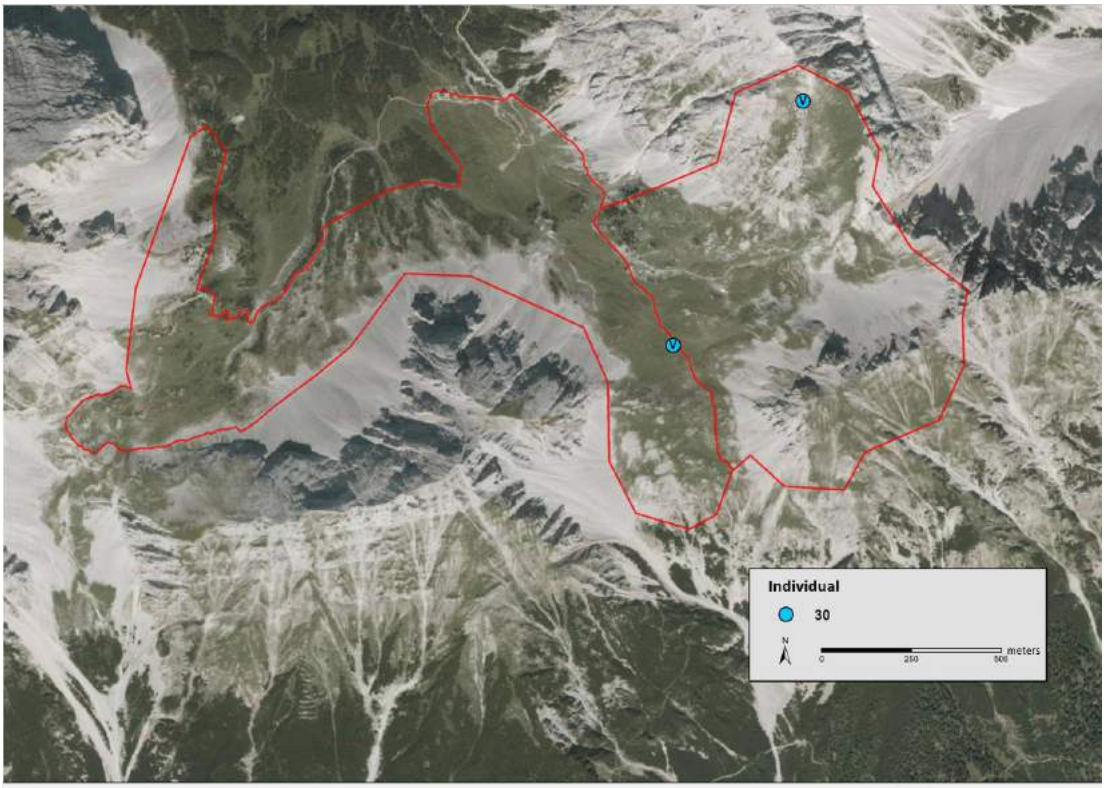
Supplementary Figure 27: The spots where Individual 27 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



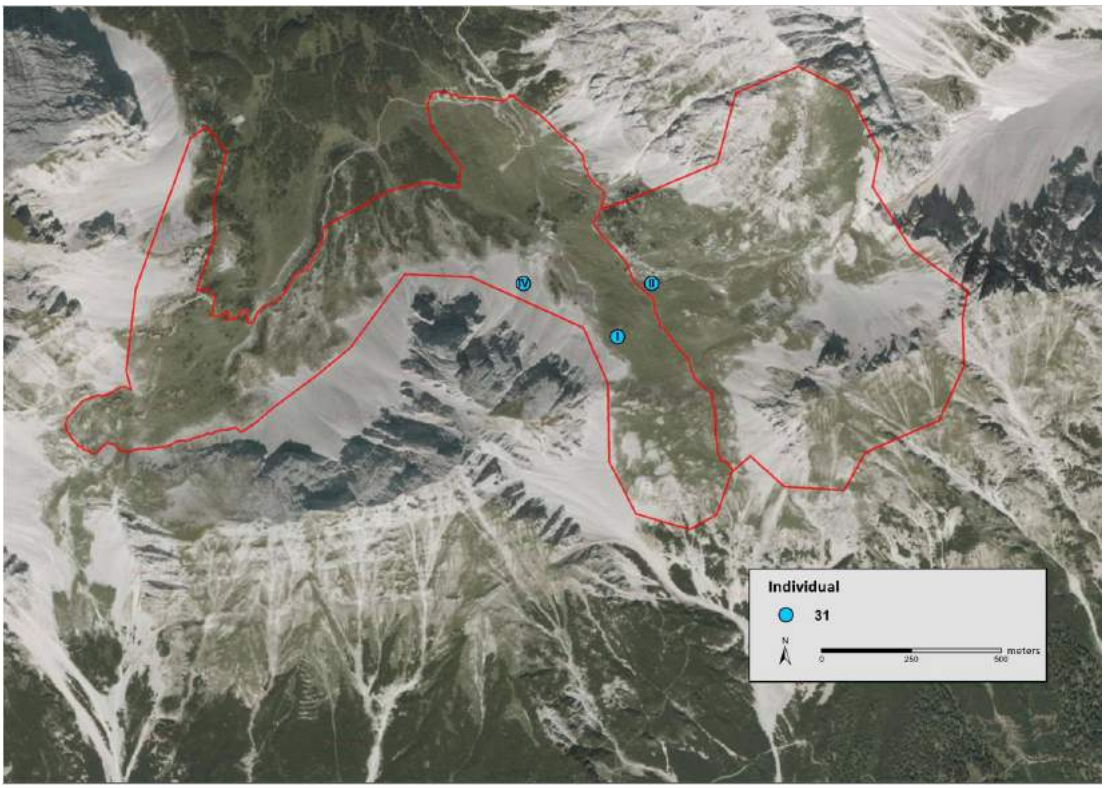
Supplementary Figure 28: The spots where Individual 28 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Orange means the sex of this individual is not known.



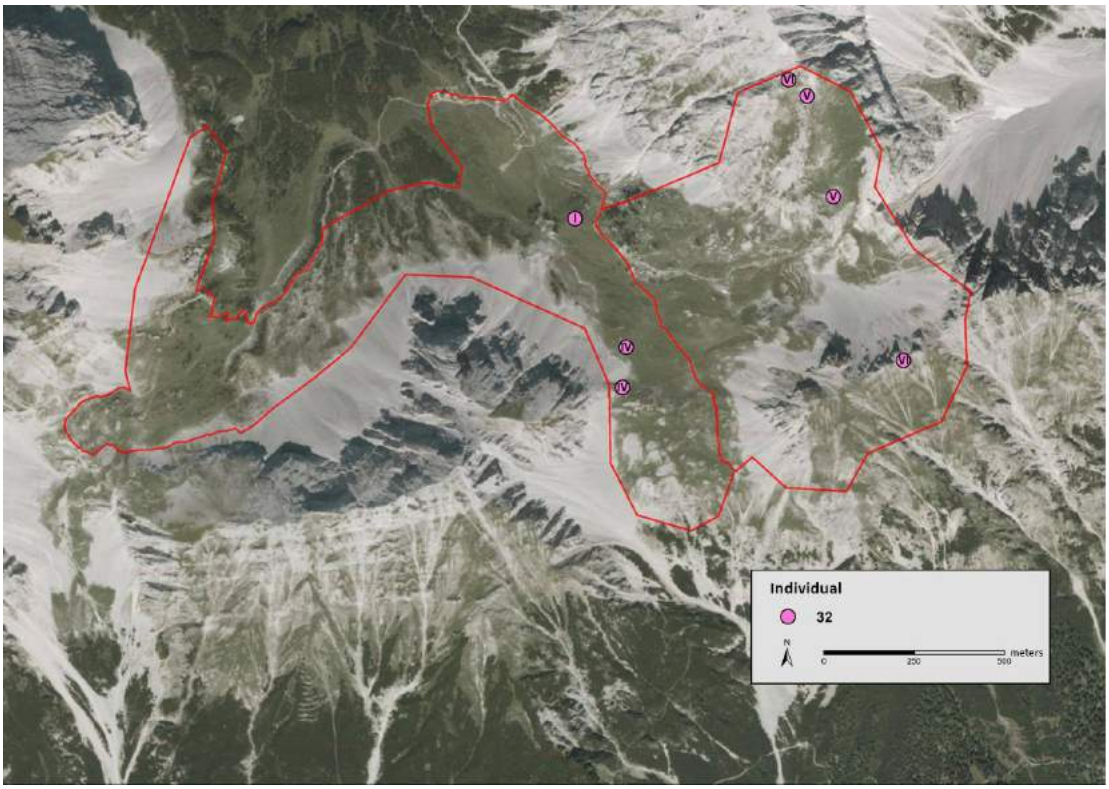
Supplementary Figure 29: The spots where Individual 29 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



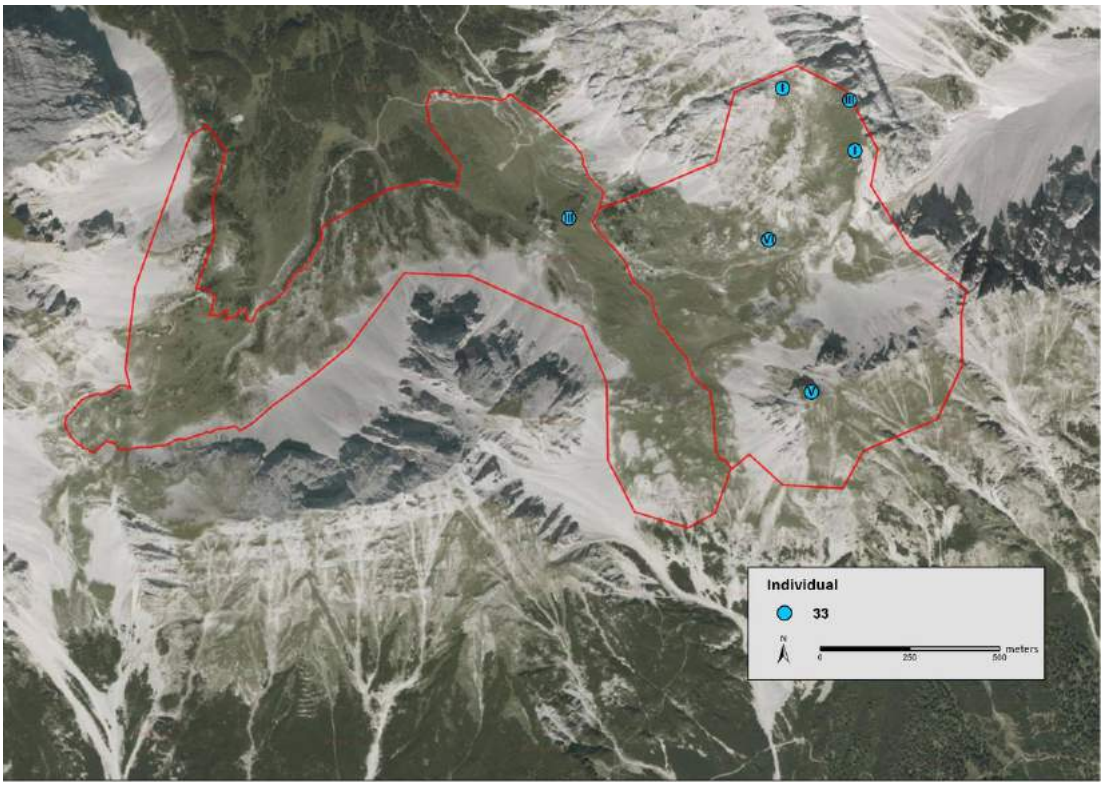
Supplementary Figure 30: The spots where Individual 30 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



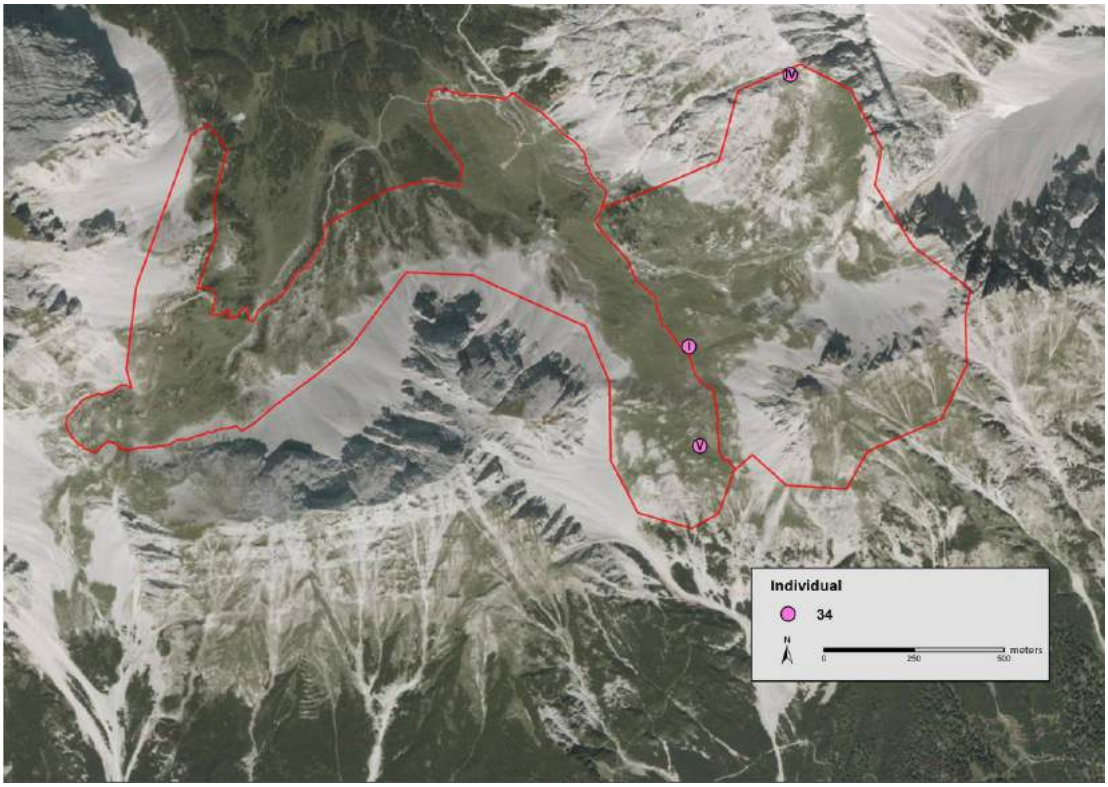
Supplementary Figure 31: The spots where Individual 31 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



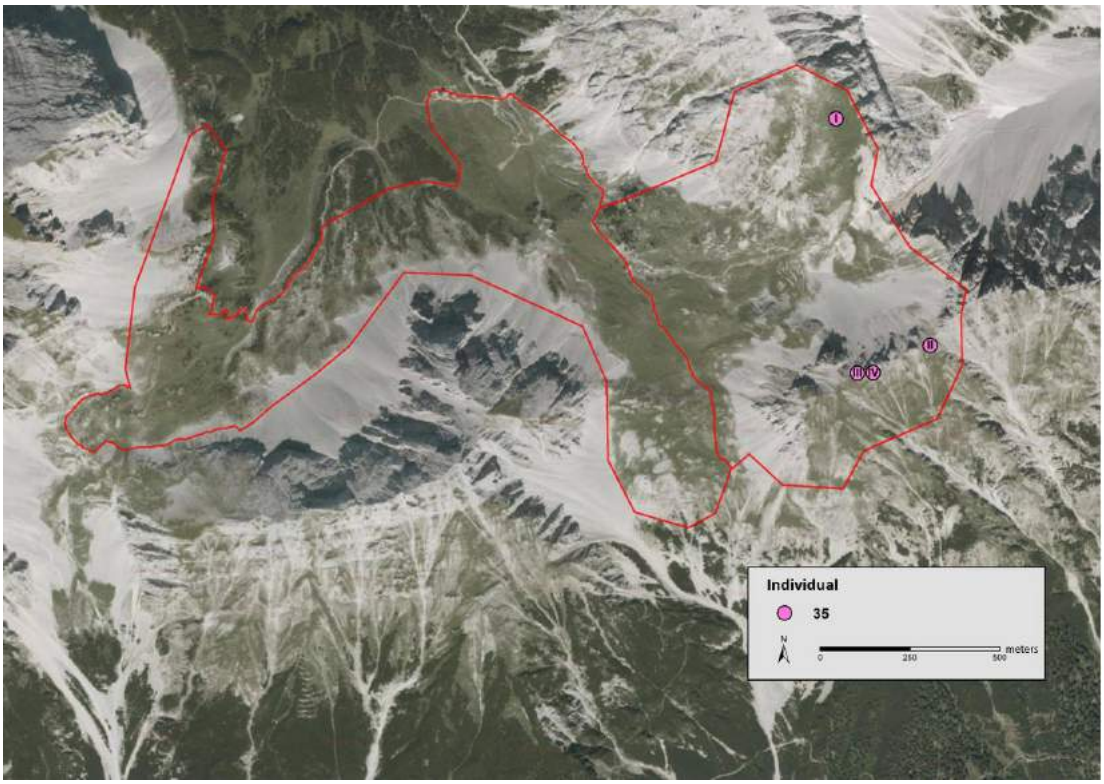
Supplementary Figure 32: The spots where Individual 32 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



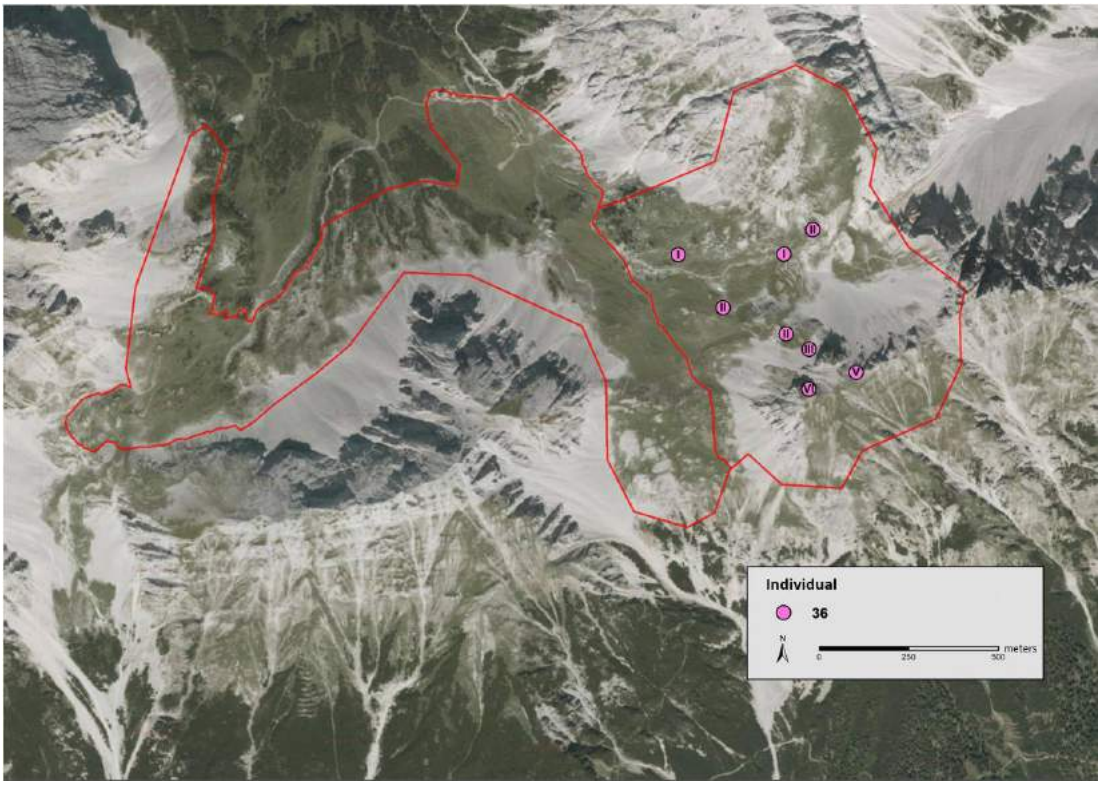
Supplementary Figure 33: The spots where Individual 33 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



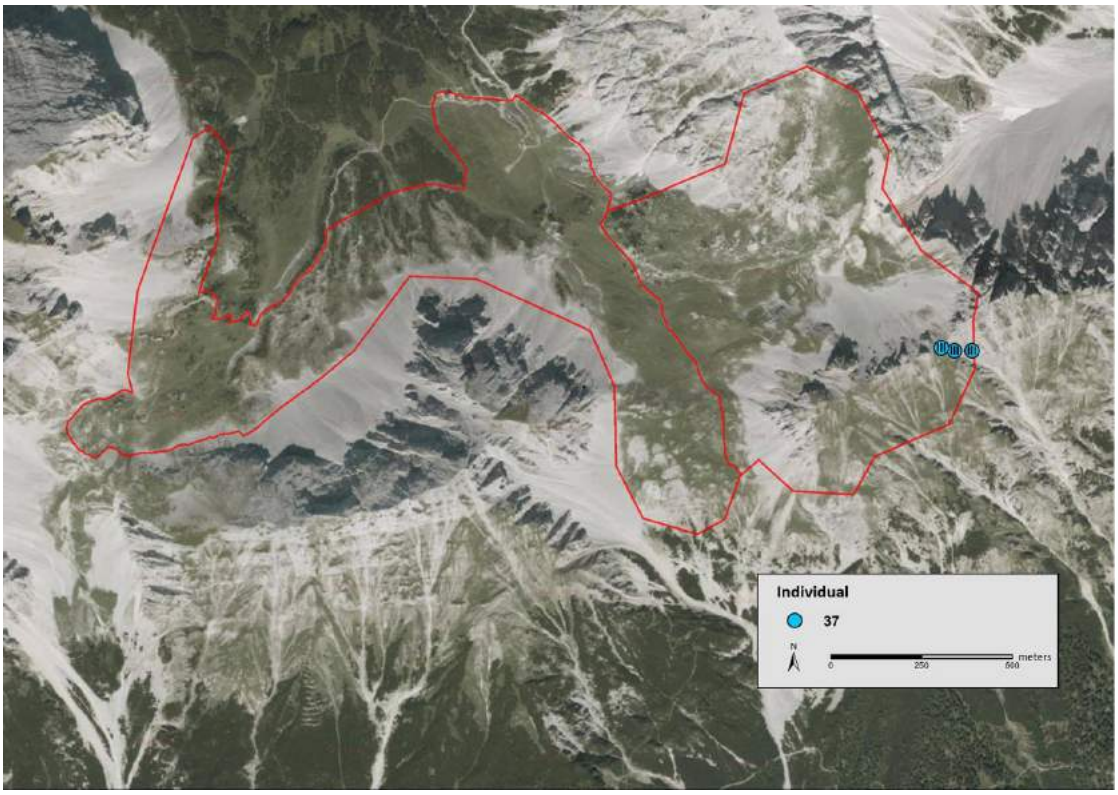
Supplementary Figure 34: The spots where Individual 34 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



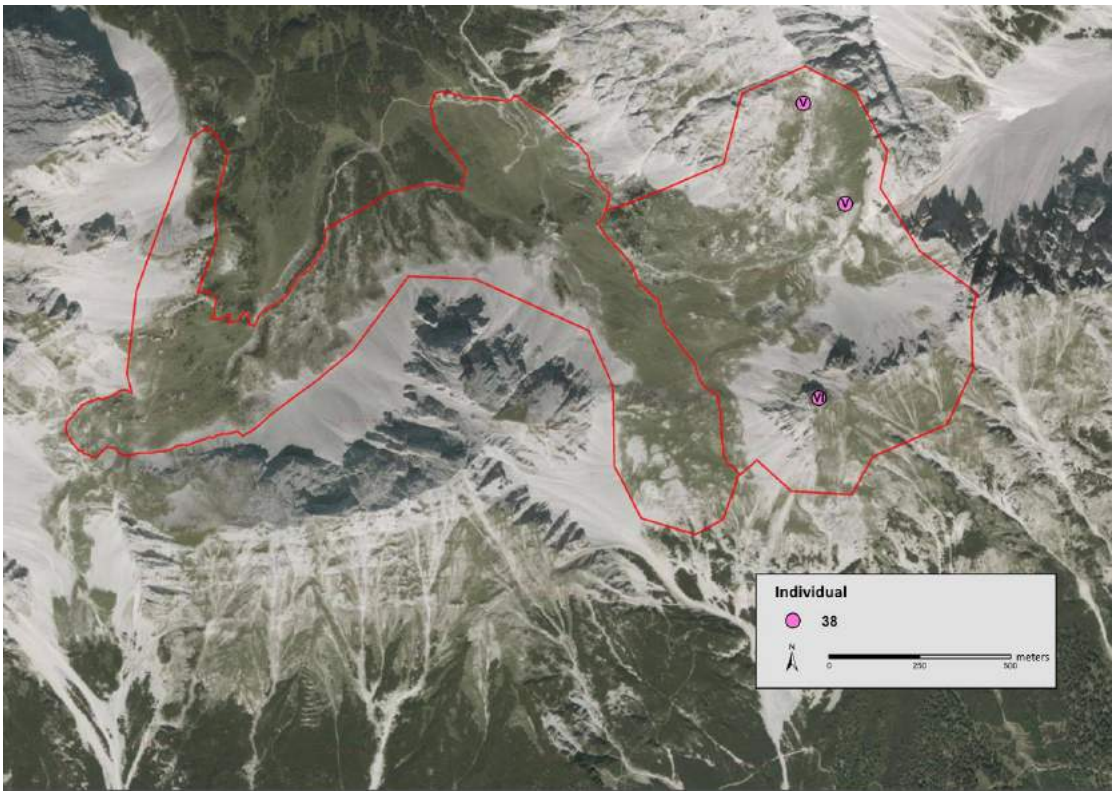
Supplementary Figure 35: The spots where Individual 35 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



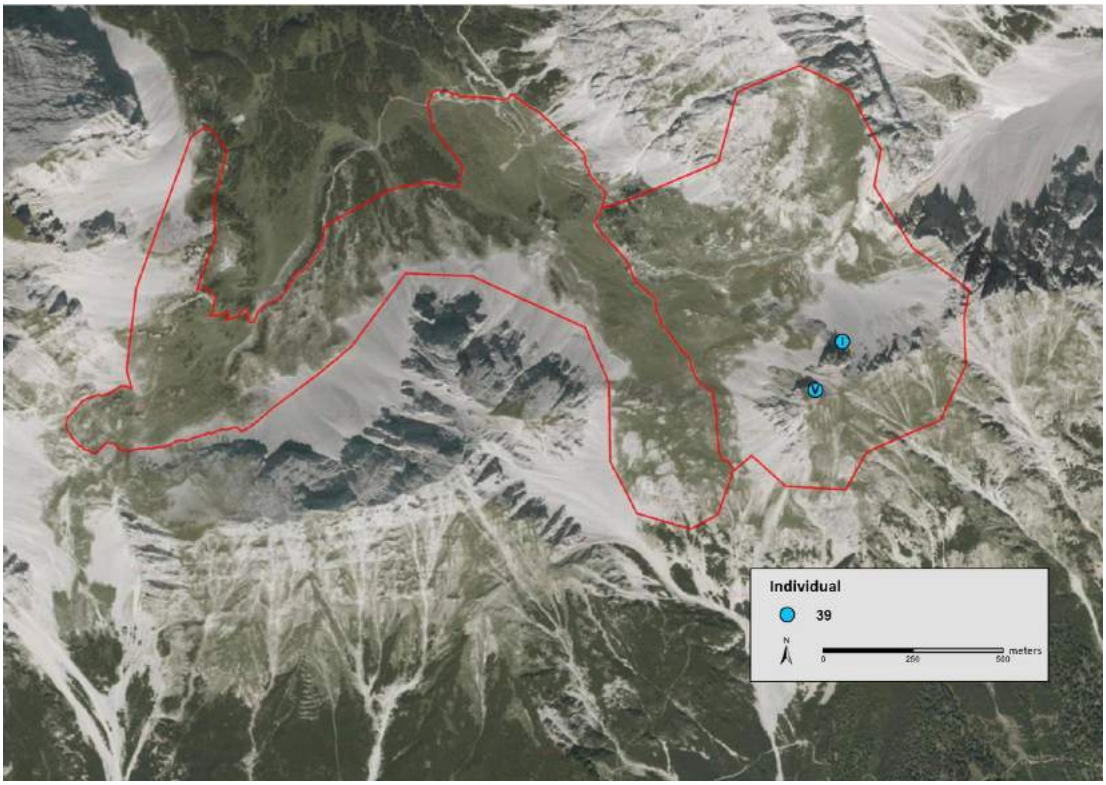
Supplementary Figure 36: The spots where Individual 36 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



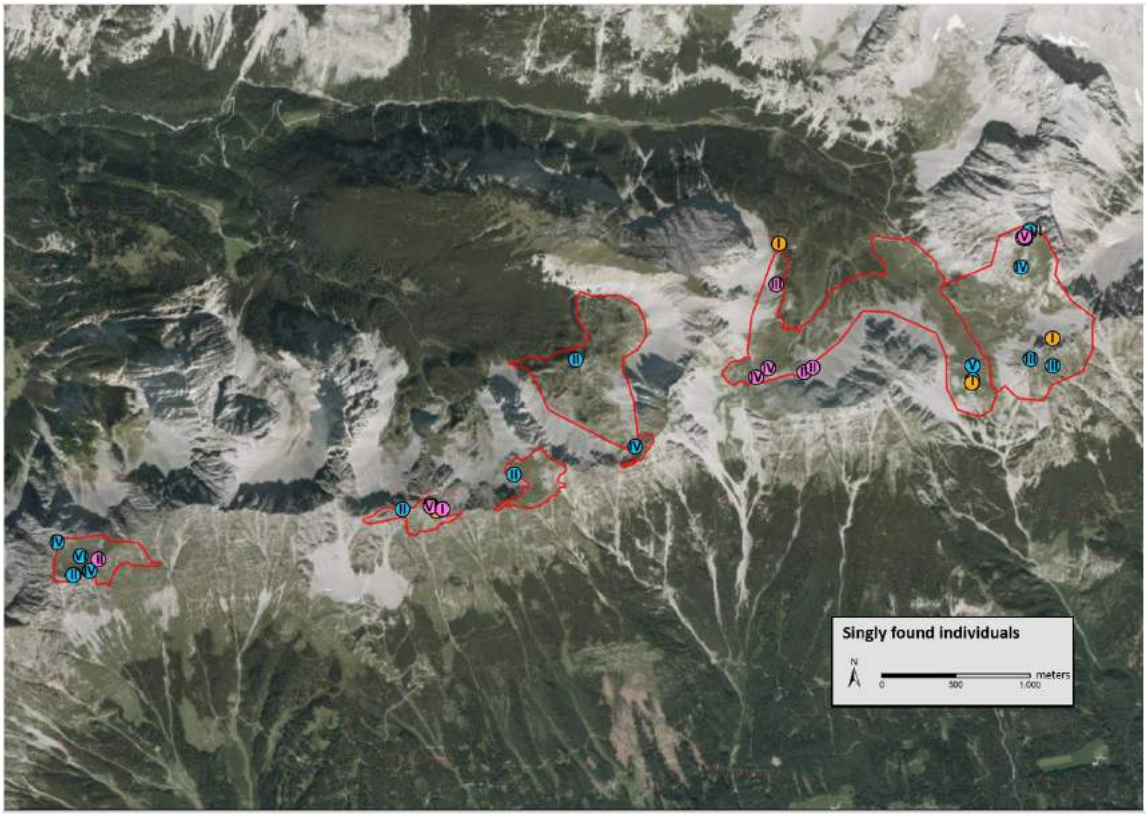
Supplementary Figure 37: The spots where Individual 37 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



Supplementary Figure 38: The spots where Individual 38 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Pink means that this individual is a hen.



Supplementary Figure 39: The spots where Individual 39 was found. The roman letters indicate in which round the samples were found. The colour stands for the sex. Light blue means this Individual is a cock.



Supplementary Figure 4013: Every point on this map represents one singly found individual. The roman letters indicate in which round the individuals were found. The colour stands for the sex, light blue for cocks, pink for hens and orange for individuals where the sex is not known.

Supplementary Table 1: Individuals with their related genotypes as well as the related samples, study site and round they were found in. The orange colour marks the differing alleles. In the sex column M stands for (ZZ) males, F for (ZW) females and NA for missing value.

Individual	Sample	Site	Round	Sex	sTuT2		mTuT1		BG18		sTuT3		BG15		sTuD6		sTuT4		sTuD1		BG19		BG20	
I_1	IRS006B	1	II	M	149	149	133	137	156	156	100	104	140	140	155	155	134	134	162	166	156	164	119	127
I_1	IRS006C	1	II	M	149	149	133	137	156	156	100	104	140	140	155	155	134	134	162	166	156	164	119	127
I_1	INF083A	1	V	M	149	149	133	137	156	160	104	104	140	140	155	169	134	134	166	166	156	164	119	119
I_1	INF083B	1	V	M	149	149	133	137	156	156	100	104	140	140	155	155	134	134	162	166	156	164	119	127
I_2	IGS033	1	III	M	124	144	133	133	148	148	100	104	152	160	161	161	122	142	162	162	164	172	127	127
I_2	IAF078C	1	IV	M	124	144	133	133	148	148	100	104	152	152	161	161	122	142	162	170	164	172	127	127
I_3	IAF008	1	I	F	137	145	133	133	148	156	104	108	152	156	155	163	134	134	160	166	172	172	127	127
I_3	INF024	2	I	M	137	145	133	133	148	148	104	108	152	156	155	155	134	134	160	166	172	172	127	127
I_3	IAF075	1	IV	F	137	145	133	133	148	156	104	108	152	156	155	163	134	134	160	166	172	172	127	127
I_3	IAF076	1	IV	F	137	145	133	133	148	156	104	108	152	156	155	163	134	134	160	166	172	172	127	127
I_3	IAF081A	1	IV	F	137	145	133	133	148	156	104	108	152	156	155	163	134	134	160	166	172	172	127	127
I_3	IAF081B	1	IV	F	137	145	133	133	148	156	104	108	152	156	155	163	134	134	160	166	172	172	127	127
I_4	IAF002	1	I	M	132	156	133	133	152	152	100	108	152	152	155	167	134	138	162	162	168	172	131	131
I_4	IRS009	1	II	M	132	156	133	133	152	152	100	108	152	152	155	155	134	138	162	164	172	172	131	131
I_4	IAF019B	2	II	F	132	156	133	133	152	152	100	108	148	152	155	155	134	138	162	162	172	172	131	131
I_4	INF039	3	II	M	132	156	133	133	152	152	100	108	152	152	155	167	134	138	162	164	168	172	131	131
I_4	IAF054	2	III	F	132	156	133	133	152	152	100	108	152	152	155	167	134	138	162	162	172	172	131	131
I_4	IAF074	1	IV	M	132	156	133	133	152	152	100	108	152	152	155	167	134	138	162	164	168	172	131	131
I_4	IAF080A	1	IV	NA	132	132	133	133	152	152	100	100	152	152	155	155	138	138	162	164	172	172	131	131
I_4	IAF082	1	IV	M	132	156	133	133	152	152	100	108	152	152	155	155	134	138	162	164	168	172	131	131
I_4	INF082B	1	V	M	132	156	133	133	152	152	100	108	152	152	155	167	134	138	162	164	172	172	131	131
I_5	IAF021B	2	II	F	124	145	133	133	156	164	88	100	152	152	155	159	134	142	166	166	168	168	127	127
I_5	ITZ001	2	IV	F	124	145	133	133	156	164	88	100	152	152	155	159	134	142	166	166	168	168	127	127
I_5	IRS125E	2	V	F	124	145	133	133	156	164	88	100	152	152	155	159	134	142	166	166	168	168	127	131
I_5	INF021	2	I	F	124	145	133	133	156	164	88	100	152	152	155	159	134	142	166	166	168	168	127	127
I_5	IRS125E	2	V	F	124	145	133	133	156	164	88	100	152	152	155	159	134	142	166	166	168	168	127	127
I_6	INF004B	2	I	F	144	149	163	163	148	160	88	96	148	156	159	159	134	134	162	162	156	156	127	127
I_6	IAF27A	2	II	M	144	144	163	163	148	160	96	96	148	156	159	159	134	134	162	162	156	156	127	127
I_6	IAF048B	2	III	F	144	149	163	163	148	148	88	96	148	156	159	159	134	134	162	172	156	156	127	127
I_6	IAF049A	2	III	F	144	149	163	163	148	160	88	96	148	156	159	159	134	134	162	162	156	156	127	127
I_6	IAF051A	2	III	F	144	149	163	163	148	160	88	96	148	156	159	159	134	134	162	162	156	156	127	127
I_6	IAF051B	2	III	F	144	149	163	163	148	160	88	96	148	148	159	159	134	134	162	162	156	156	127	127
I_6	IRL107	2	VI	F	144	149	163	163	148	160	88	96	148	156	159	159	134	134	162	162	156	156	127	127
I_6	INF008A	2	I	F	144	149	163	163	148	160	88	96	148	148	159	159	134	134	162	162	156	156	127	127
I_6	INF016B	2	I	F	144	149	163	163	148	160	88	96	148	156	159	159	134	134	162	162	156	156	127	127
I_7	IAF053B	2	III	F	141	144	133	133	156	156	100	108	152	156	155	159	130	134	162	166	156	168	127	135
I_7	INF066A	2	IV	F	141	144	133	133	156	156	100	108	152	156	155	159	130	134	162	166	156	168	127	135
I_7	INF066E	2	IV	F	141	144	133	133	156	156	100	108	152	156	155	159	130	134	162	166	156	156	127	135
I_8	INF002	2	I	M	144	148	133	133	148	148	100	112	148	152	161	161	122	142	162	162	172	172	119	119
I_8	INF003B	2	I	M	144	144	133	133	148	148	100	112	148	152	161	173	122	122	162	162	172	172	119	119
I_8	INF014A	2	I	M	148	148	133	133	148	148	112	112	152	152	161	161	122	142	162	162	172	172	119	119
I_8	INF017	2	I	M	144	148	133	133	148	148	100	112	148	152	161	161	122	142	162	162	172	172	119	127
I_8	INF038	3	II	M	144	148	133	133	148	148	100	112	148	152	161	161	122	142	162	170	172	172	119	127
I_9	INF010	2	I	M	124	132	133	167	156	156	100	100	148	152	159	161	142	142	166	166	168	180	127	127
I_9	INF015	2	I	M	124	132	133	167	156	156	100	100	148	152	159	161	142	142	166	166	180	180	127	127
I_9	IAF045	3	III	NA	124	132	133	167	156	156	100	100	148	152	159	161	142	142	166	166	168	168	127	127
I_9	ITZ002A	2	IV	M	124	132	133	167	156	156	100	100	148	152	159	159	142	142	166	166	168	180	127	127
I_9	ITZ002B	2	IV	M	124	132	133	167	156	156	100	100	148	152	159	161	142	142	162	166	168	180	127	127
I_9	IRL112	2	VI	M	124	132	133	133	156	156	100	100	148	152	159	161	142	142	166	166	168	180	127	131
I_10	IAF053A	2	III	M	128	128	133	133	152	156	96	100	152	152	155	155	142	142	164	166	156	156	127	131
I_10	IAF044	3	III	M	128	156	133	133	152	156	96	100	152	152	155	159	142	142	164	166	156	156	127	131
I_10	INF059	3	IV	M	128	156	133	133	152	156	96	100	152	152	159	159	142	142	164	164	156	156	131	131
I_10	INF062	3	IV	M	128	128	133	133	152	156	96	100	152	152	155	155	142	142	164	166	156	156	127	127
I_10	IRL005A	3	I	M	128	128	133	133	152	156	96	100	152	152	155	159	138	142	164	164	156	156	127	131
I_10	IRS125B	2	V	M	128	156	133	133	152	156	96	100	152	152	155	159	138	142	164	166	156	156	127	131
I_10	IAF128	3	VI	M	128	156	133	133	152	156	96	100	152	152	155	159	138	142	164	166	156	156	127	131
I_10	IRS125C	2	V	M	128	156	133	133	152	156	96	100	152	152	155	159	138	142	164	166	156	156	127	131
I_10	IRS125D	2	V	M	128	156	133	133	152	156	96	100	152	152	155	159	142	142	166	166	156	156	127	131

I_11	INF034	3	II	M	144	144	133	133	148	152	92	96	152	160	155	155	134	139	162	166	156	168	131	135
I_11	IAM031	4	II	M	144	144	133	133	148	152	92	92	160	160	155	155	134	139	166	166	156	168	131	135
I_12	INF035	3	II	M	137	141	133	133	148	152	96	108	152	156	155	155	139	139	162	162	168	176	127	127
I_12	IAM030A	4	II	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	170	168	176	127	127
I_12	IAF038A	3	III	M	137	141	133	133	148	152	96	96	152	156	155	155	139	142	162	162	168	176	127	127
I_12	IAF038B	3	III	M	137	137	133	133	152	152	108	108	152	156	155	155	139	139	162	162	176	176	127	127
I_12	IAF084	4	IV	M	137	141	133	133	148	148	96	108	152	156	155	155	142	142	162	170	168	176	127	127
I_12	IRS118A	2	V	M	137	141	133	133	148	152	96	108	152	152	155	155	139	139	162	170	168	168	127	127
I_12	IRS123J	2	V	M	137	141	133	133	148	152	108	108	152	156	155	155	139	142	162	162	176	176	127	127
I_12	IAF103	3	V	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	IAF101	4	V	M	137	141	133	133	148	148	96	96	156	156	155	155	139	139	162	162	168	176	127	127
I_12	ITZ011C	4	V	M	137	141	133	133	148	148	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	ITZ012A	4	V	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	ITZ012B	4	V	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	ITZ013A	4	V	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	ITZ013B	4	V	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	ITZ014A	4	V	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	IAF123	3	VI	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	176	176	127	127
I_12	INF107C	4	VI	M	137	141	133	133	148	152	96	108	152	152	155	155	139	142	162	162	168	176	127	127
I_12	IGS040B	4	III	M	137	141	133	133	152	152	96	108	152	156	155	155	139	139	162	162	168	168	127	131
I_12	IRS123F	2	V	M	137	141	133	133	148	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_12	ITZ012C	4	V	M	137	141	133	133	152	152	96	96	152	156	155	155	142	142	162	162	176	176	127	127
I_12	ITZ012D	4	V	M	137	141	133	133	152	152	96	108	152	156	155	155	139	142	162	162	168	176	127	127
I_13	ILA001	4	I	M	148	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	ILA002A	4	I	M	140	148	159	159	160	160	96	96	156	156	155	155	134	139	166	166	160	168	131	135
I_13	IGS006	4	I	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IAM024A	4	II	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IAF042	3	III	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IGS036	4	III	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IGS038A	4	III	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IGS038B	4	III	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IAF057	4	III	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IAF059	4	III	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IRS123B	2	V	M	140	140	137	159	156	160	100	100	148	156	155	155	134	139	166	166	160	168	131	131
I_13	IRS123C	2	V	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	131
I_13	IRS124A	2	V	M	140	140	137	159	160	160	96	96	148	148	155	155	134	139	166	166	160	168	131	135
I_13	IRS125A	2	V	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	131
I_13	ITZ011B	4	V	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IRL108	2	VI	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IAM024B	4	II	M	140	148	137	159	156	160	96	100	156	156	155	155	139	139	158	166	168	168	131	135
I_13	IRS120C	2	V	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_13	IRS124B	2	V	M	140	148	137	159	156	160	96	100	148	156	155	155	134	139	166	166	160	168	131	135
I_14	INF037B	3	II	F	144	144	133	133	156	160	88	96	148	152	159	163	134	139	162	162	168	172	127	135
I_14	IRS137	1	VI	M	144	148	133	133	156	156	96	96	152	152	159	163	134	139	162	162	168	168	127	135
I_15	IAM020	4	II	M	149	149	133	151	148	156	96	100	148	152	155	157	138	142	166	166	160	164	127	135
I_15	IAF100B	4	V	M	149	149	133	151	148	156	96	100	148	152	155	157	138	142	166	166	160	164	127	135
I_16	IGS001	4	I	M	124	144	133	133	156	160	100	108	156	156	165	177	134	142	164	164	156	172	119	127
I_16	IGS010	4	I	M	124	144	133	133	156	160	100	108	156	156	165	177	134	142	164	164	156	172	119	127
I_17	IAM025	4	II	F	144	148	133	133	160	160	96	108	152	156	161	163	134	139	162	172	164	172	127	135
I_17	IAM026	4	II	F	144	148	133	133	160	160	96	108	152	156	161	163	134	139	162	172	164	172	127	135
I_17	IAM036	4	II	F	144	148	133	133	160	160	108	108	152	156	161	163	134	139	162	172	164	172	127	135
I_17	IAF058	4	III	F	144	148	133	133	160	160	96	108	152	156	161	163	134	139	162	172	164	172	127	135
I_17	IAF089	4	IV	F	144	148	133	133	160	160	96	108	152	156	161	163	134	139	162	162	164	172	127	135
I_17	IRS119B	2	V	F	144	144	133	133	160	160	96	96	152	156	161	163	134	139	162	162	164	172	127	135
I_17	IRS119C	2	V	F	144	148	133	133	160	160	96	96	152	156	161	163	134	139	162	172	164	172	127	135
I_17	ITZ013C	4	V	F	144	148	133	133	160	160	96	108	152	156	161	161	139	139	162	162	164	172	127	135
I_17	IAF129	4	VI	F	144	144	133	133	160	160	96	108	152	156	161	163	134	139	162	162	164	172	127	135
I_17	ITZ014C	4	V	F	144	148	133	133	160	160	96	108	152	156	161	163	134	139	162	172	164	172	127	135
I_17	IAF131	3	VI	F	144	148	133	133	160	160	96	108	152	156	161	163	134	139	162	172	164	172	127	135
I_18	IAF014	5	I	M	132	144	137	151	148	152	100	108	152	152	155	159	138	138	166	166	164	168	127	127
I_18	IAM027	4	II	M	132	144	137	151	148	152	100	108	152	152	155	159	138	138	166	166	164	168	127	127

I_19	INF008C	2	I	NA	132	145	133	133	148	148	96	108	148	156	155	157	134	134	162	166	164	168	127	127
I_19	IAF015	5	I	F	132	145	133	133	148	156	108	108	148	156	155	157	142	142	162	166	164	168	127	127
I_19	INF066B	2	IV	F	132	145	133	133	148	156	96	108	148	156	155	157	134	134	162	166	164	168	127	127
I_19	INF069D	5	IV	F	132	145	133	133	148	156	96	108	148	156	155	157	134	134	162	166	164	168	127	127
I_19	INF075	5	IV	F	132	145	133	133	148	148	96	108	148	156	155	157	134	134	162	162	164	168	127	127
I_19	IRS119A	2	V	F	132	145	133	133	148	156	96	108	148	156	155	157	134	134	162	166	164	168	127	127
I_19	IRS127C	5	V	F	132	145	133	133	148	148	96	108	148	156	155	157	142	142	162	162	164	164	127	127
I_19	IRL101B	3	VI	F	132	145	133	133	148	156	96	108	148	156	155	157	134	134	162	166	164	168	127	127
I_19	IRL101A	3	VI	M	132	145	133	133	148	156	96	108	148	156	155	157	134	134	162	166	164	164	127	127
I_19	INF104C	5	VI	F	132	145	133	133	148	156	96	108	148	156	155	157	134	134	162	166	164	168	127	127
I_19	INF072	5	IV	F	132	145	133	133	148	156	96	108	148	156	155	157	134	134	166	166	164	168	127	127
I_20	INF058A	5	III	M	144	149	133	133	148	148	100	100	148	152	161	161	138	138	162	166	164	164	119	119
I_20	INF058B	5	III	M	144	149	133	133	148	148	100	100	148	152	161	161	122	138	162	166	164	164	127	127
I_20	INF058C	5	III	M	144	149	133	133	148	148	100	112	148	152	161	161	122	138	162	166	164	164	119	127
I_20	INF058D	5	III	M	144	149	133	133	148	148	100	112	148	152	161	161	122	138	162	166	164	164	119	127
I_21	INF053B	5	III	M	144	149	133	133	148	148	112	112	148	152	161	161	122	122	160	170	164	164	119	127
I_21	INF101C	5	VI	M	144	149	133	133	148	148	100	112	148	152	161	163	122	122	170	170	164	164	119	119
I_22	INF090C	5	V	M	149	149	133	133	152	164	92	100	156	156	165	173	134	134	166	166	164	164	127	135
I_22	INF096A	5	V	M	149	149	133	133	152	164	92	100	156	156	165	165	134	142	166	166	164	164	127	127
I_23	IAF016	5	I	F	124	149	141	141	152	152	104	108	144	144	161	165	134	134	166	166	168	168	127	127
I_23	IRS101C	5	IV	F	124	149	133	133	152	156	104	108	144	152	161	165	134	134	166	166	168	168	127	127
I_24	INF032	5	I	M	124	149	133	133	148	148	104	104	152	152	161	173	122	142	162	166	164	164	127	135
I_24	IRS129A	5	V	M	124	149	133	133	148	148	104	104	152	152	161	173	122	142	162	166	164	164	127	135
I_25	INF040B	5	II	M	148	148	133	133	148	160	96	96	152	152	155	161	139	139	162	166	172	172	135	135
I_25	INF040C	5	II	M	148	148	133	133	148	160	96	108	152	160	155	161	134	139	162	166	168	172	135	135
I_26	INF043	5	II	F	124	128	133	133	156	164	100	108	152	160	155	155	134	134	156	162	160	172	119	127
I_26	IRS127A	5	V	F	124	128	133	133	156	164	100	108	152	160	155	155	134	134	162	162	160	172	119	127
I_26	INF101A	5	VI	F	124	128	133	133	156	164	100	108	152	160	155	155	134	134	156	162	160	172	119	119
I_26	INF104A	5	VI	F	124	128	133	133	156	164	100	108	152	160	155	155	134	134	156	162	160	172	119	127
I_26	INF104B	5	VI	F	124	128	133	133	156	164	100	108	152	160	155	155	134	134	156	162	160	172	119	127
I_27	IAM011	6	I	M	141	141	137	137	152	160	100	104	148	156	161	161	130	134	164	166	156	168	131	131
I_27	IAF071	5	III	M	141	141	137	137	152	160	100	104	148	156	161	161	130	134	164	166	156	168	131	131
I_27	IAF060	6	III	M	141	141	137	137	152	152	100	104	156	156	161	161	130	130	164	166	156	168	131	139
I_27	IAF063	6	III	M	141	141	137	137	152	160	100	104	148	156	161	161	130	134	164	166	156	168	131	131
I_27	IAF095A	6	IV	M	141	141	137	137	152	160	100	104	148	156	161	161	130	134	164	166	156	168	131	131
I_27	IAF095B	6	IV	M	141	141	137	137	152	152	100	104	148	156	161	161	130	134	164	166	156	168	131	131
I_27	IAF120B	6	VI	M	141	141	137	137	152	160	104	104	156	156	161	161	130	134	164	164	156	168	131	131
I_27	IGS049	6	VI	M	141	145	137	137	152	160	100	104	156	156	161	161	130	134	164	164	156	168	131	131
I_27	ILA101	6	IV	M	141	141	137	137	152	160	100	104	148	156	161	161	130	134	164	166	156	168	131	131
I_28	IRS107	5	IV	M	132	144	163	163	152	156	88	96	160	160	165	175	139	142	160	166	160	172	127	131
I_28	IAF091	6	IV	F	132	144	163	163	156	156	88	96	152	160	165	175	139	142	160	166	160	172	127	131
I_29	IAF013	5	I	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	IAM055	6	III	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	IRS109	5	IV	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	166	166	156	168	127	127
I_29	INF089A	5	V	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	INF089B	5	V	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	INF091B	5	V	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	IGS043A	6	V	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	ITZ020A	5	VI	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	ITZ020B	5	VI	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	IGS043B	6	V	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_29	ITZ120C	5	VI	M	145	149	133	133	148	168	96	100	148	156	157	161	134	134	162	166	156	168	127	127
I_30	INF092	5	V	M	141	141	133	137	156	160	100	108	148	152	155	157	134	142	164	166	156	156	119	131
I_30	IGS042E	6	V	M	141	141	133	137	156	160	100	108	148	152	155	157	134	142	164	166	156	156	119	131
I_31	INF028A	5	I	M	141	141	137	137	160	160	100	108	148	148	155	157	134	142	162	162	156	164	135	135
I_31	INF028B	5	I	M	141	141	137	137	160	164	108	108	148	148	157	157	134	134	162	162	156	164	131	135
I_31	ILA017	6	II	M	141	141	137	137	160	160	100	108	148	148	155	157	134	142	162	162	156	164	131	131
I_31	IRS114	5	IV	M	141	141	137	137	160	160	100	108	148	148	155	157	134	142	162	162	156	164	131	131

I_32	INF029B	5	I	F	156	156	133	133	152	156	108	108	152	160	157	157	142	142	162	166	156	164	119	131
I_32	IRS111	5	IV	F	156	156	133	133	152	156	108	108	152	160	157	157	142	142	162	166	156	164	119	131
I_32	IGS042F	6	V	F	156	156	133	133	152	156	108	108	152	160	157	157	142	142	162	166	156	164	119	131
I_32	IGS044B	6	V	F	156	156	133	133	152	156	108	108	152	160	157	157	142	142	162	166	156	164	119	131
I_32	IAF119A	6	VI	F	156	156	133	133	152	156	108	108	152	160	157	157	142	142	162	166	156	164	119	131
I_32	IGS045B	6	VI	F	156	156	133	133	152	156	108	108	152	160	157	157	142	142	162	166	156	164	119	131
I_32	IRS108	5	IV	F	156	156	133	133	152	156	104	108	152	160	157	157	142	142	162	166	156	164	119	131
I_33	IAM007B	6	I	M	149	149	133	133	152	164	92	108	152	156	157	173	138	142	166	166	160	160	123	123
I_33	IAM008	6	I	M	149	149	133	133	152	164	92	108	152	156	157	173	138	142	166	166	160	164	123	135
I_33	IAF072	5	III	M	149	149	133	133	152	164	92	108	152	156	157	173	142	142	166	166	160	164	123	135
I_33	IAF065	6	III	M	149	149	133	133	152	164	96	108	156	156	173	173	142	142	166	166	160	160	123	135
I_33	IAF108B	6	V	M	149	149	133	133	152	152	92	108	156	156	157	173	142	142	166	166	160	160	123	123
I_33	IAF122	6	VI	M	149	149	133	133	152	164	92	108	152	156	157	173	138	142	166	166	160	164	123	135
I_34	IGS110	6	I	F	149	156	133	133	152	164	100	108	152	152	167	169	134	138	162	162	164	172	127	131
I_34	INF096D	5	V	F	149	156	133	133	152	164	100	108	152	152	167	169	134	138	162	162	164	172	127	131
I_34	ILA100	6	IV	F	149	156	133	133	152	164	100	108	152	152	169	169	134	138	162	162	164	172	127	131
I_35	IAM005A	6	I	F	137	148	137	137	156	160	88	100	148	156	161	165	134	134	162	166	156	164	131	135
I_35	ILA011	6	II	F	137	148	137	137	156	160	88	100	148	156	161	165	134	134	162	166	156	164	131	135
I_35	IAM048	6	III	F	137	148	137	137	156	160	88	100	148	156	161	165	134	134	162	166	156	164	131	135
I_35	IAF094B	6	IV	F	137	148	137	137	156	160	88	100	148	156	161	165	134	134	162	166	156	164	131	135
I_36	IAM001	6	I	F	137	137	133	133	156	156	92	100	152	156	155	155	134	142	166	166	172	172	119	123
I_36	IGS020	6	I	F	137	137	133	133	156	164	92	100	152	156	155	159	134	142	166	166	172	172	119	123
I_36	ILA015	6	II	F	137	137	133	133	156	164	92	100	152	156	155	155	134	142	166	166	172	172	119	123
I_36	ILA016	6	II	F	137	137	133	133	156	164	92	100	152	156	155	155	134	142	166	166	172	172	119	123
I_36	IGS025	6	II	M	137	137	133	133	156	164	92	100	156	156	155	155	134	134	166	166	172	172	119	119
I_36	IAM052	6	III	F	137	137	133	133	156	164	92	100	152	156	155	155	134	142	160	166	172	172	119	123
I_36	IAF107	6	V	F	137	137	133	133	156	164	92	100	152	156	155	159	134	142	166	166	172	172	119	123
I_36	IGS048A	6	VI	F	137	137	133	133	156	164	92	100	152	156	155	159	134	142	166	166	172	172	119	123
I_36	IGS048C	6	VI	F	137	137	133	133	156	164	92	100	152	156	155	155	134	142	166	166	172	172	119	123
I_37	IAM043	6	III	NA	137	137	133	163	172	172	100	104	140	148	173	173	130	130	166	166	160	172	127	127
I_37	IAM045	6	III	M	124	137	133	163	160	172	100	104	140	148	173	175	130	130	166	166	160	172	127	127
I_37	IAM044	6	III	M	124	137	133	163	160	172	100	104	140	148	175	175	130	130	166	166	160	160	127	127
I_38	IGS042C	6	V	F	141	141	137	137	156	160	100	108	148	160	157	161	134	134	166	166	156	156	131	131
I_38	IGS042D	6	V	F	141	156	137	137	156	160	100	108	148	160	157	161	134	142	166	166	156	156	131	131
I_38	IGS044C	6	V	F	141	156	137	137	156	160	100	108	148	160	157	161	134	142	166	166	156	156	131	131
I_38	IGS048B	6	VI	F	141	156	137	137	160	160	100	108	148	160	157	161	134	142	166	166	156	156	131	131
I_39	IGS015	6	I	M	124	152	133	133	148	164	104	104	148	152	161	175	130	142	166	166	172	180	119	127
I_39	IAF108A	6	V	M	124	124	133	133	148	148	104	104	152	152	161	175	142	142	166	166	180	180	119	127
I_40	IRS001B	1	II	F	149	149	133	133	148	164	104	112	148	152	161	173	122	138	162	166	164	172	119	135
I_41	IRS003A	1	II	M	132	144	133	167	144	168	88	108	148	148	155	157	134	134	162	162	168	176	127	135
I_42	IGS031	1	III	M	132	137	133	133	152	168	108	108	152	160	161	161	142	142	166	166	164	164	119	135
I_43	IAF078B	1	IV	M	124	132	133	137	156	156	108	108	140	140	155	155	130	130	162	162	172	172	131	131
I_44	IAF080B	1	IV	M	132	149	133	133	152	164	92	104	152	156	159	159	138	142	166	166	160	160	135	135
I_45	IRS135B	1	VI	M	124	132	133	133	152	156	100	108	152	152	161	167	138	147	162	162	168	172	127	131
I_46	INF014B	2	I	F	141	148	133	133	156	156	104	108	140	148	157	157	142	142	166	166	156	164	131	131
I_47	IAF28B	2	II	M	148	148	133	133	152	160	92	92	152	160	163	163	134	139	166	172	156	164	135	135
I_48	ITZ004A	2	IV	NA	124	124	133	133	168	168	88	88	152	152	155	155	142	142	166	166	168	168	127	127
I_49	ITZ005	2	IV	NA	137	137	133	151	148	152	96	96	152	156	173	173	147	147	162	172	168	168	127	131
I_50	IRL105	2	VI	F	132	152	137	137	148	156	88	100	152	160	157	157	130	134	162	162	160	176	127	127
I_51	INF037A	3	II	M	144	144	133	151	156	156	100	108	152	152	155	155	139	142	160	166	172	172	127	127

I_52	IAM022	4	II	M	148	148	137	137	156	156	100	100	148	148	155	155	146	146	166	166	160	168	135	135
I_53	IAF083	4	IV	M	140	148	133	137	152	152	100	104	148	156	155	157	139	139	162	166	160	168	131	135
I_54	IAF009	5	I	NA	149	149	133	133	144	160	104	108	148	152	155	155	122	134	166	166	160	160	131	131
I_55	INF027	5	I	M	124	144	133	163	156	168	100	104	140	144	161	175	130	134	162	166	160	172	127	135
I_56	INF046B	5	II	F	124	149	133	133	160	160	100	104	140	140	161	173	134	134	166	166	164	164	131	139
I_57	INF047A	5	II	F	137	137	137	137	148	148	88	100	148	152	161	165	134	142	162	166	156	160	127	135
I_58	INF051	5	III	F	124	132	133	133	148	152	100	100	148	152	157	175	134	134	164	166	156	172	127	135
I_59	INF068C	5	IV	F	145	145	133	133	148	156	108	108	148	156	157	157	134	142	162	162	168	168	127	131
I_60	INF069B	5	IV	F	128	141	133	133	164	164	96	108	156	156	155	159	122	122	162	166	160	164	119	135
I_61	IRS103A	5	IV	NA	124	124	133	163	148	148	100	100	140	140	155	175	134	134	166	166	172	172	127	127
I_62	INF095	5	V	M	132	156	133	133	156	156	92	100	152	156	155	159	142	142	162	166	160	160	123	131
I_63	IGS016	6	I	NA	124	152	133	137	148	164	96	100	148	152	161	173	130	142	166	166	156	180	127	127
I_64	IAM042	6	III	M	149	149	133	133	168	168	100	104	148	148	161	161	134	134	162	166	156	168	127	127
I_65	IAM050	6	III	M	141	148	133	151	148	156	96	108	152	156	155	155	134	134	162	162	168	172	135	135
I_66	ILA103	6	IV	M	141	141	137	137	160	160	100	100	148	148	155	161	134	134	164	166	156	156	131	131
I_67	IGS042A	6	V	F	149	149	133	133	152	164	100	108	148	156	157	159	134	142	162	162	164	164	127	135
I_68	IGS042G	6	V	F	124	149	133	137	152	156	100	108	160	160	155	157	134	142	162	166	156	164	119	131
I_69	IGS042B	6	V	F	141	156	137	137	156	160	100	108	148	160	155	157	134	142	162	162	156	164	119	131
I_70	IAF120C	6	VI	M	137	144	133	133	156	156	108	108	144	152	177	177	142	142	166	166	172	172	127	135

universität
innsbruck

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt durch meine eigenhändige Unterschrift, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe. Alle Stellen, die wörtlich oder inhaltlich den angegebenen Quellen entnommen wurden, sind als solche kenntlich gemacht.

Die vorliegende Arbeit wurde bisher in gleicher oder ähnlicher Form noch nicht als Magister-/Master-/Diplomarbeit/Dissertation eingereicht.

Datum	Unterschrift