



University of Natural Resources  
and Life Sciences, Vienna

# Evaluation of chamois (*Rupicapra rupicapra*) home ranges on the basis of two methods in the Swiss National Park

## Master Thesis

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**Declaration in lieu of oath**

**I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.**

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## Abstract

During 16 years (2004 – 2019), the spatial behaviour of a total of 22 male and 43 female chamois (*Rupicapra rupicapra*) were surveyed using GPS transmitters in the Swiss National Park. This resulted in 70'525 individual localizations across the two study areas Il Fuorn (41'841) and Val Trupchun (28'684), from which the home range sizes during the summer, rutting, and winter seasons were calculated. Home ranges were calculated and compared using two methods: kernel density estimation and continuous time movement modelling. Overall, when home ranges were small, results from the two methods had a high degree of agreement. However, with increased space requirements of chamois, the outputs of the two estimators tend to differ more and more. As a result, median estimates of home range sizes differed significantly between the two methods during the rut, but not during the other two seasons. Furthermore, the variation within and between seasons was large and there were also sex-specific differences. Regardless of study area, median home range sizes (95% kernel density estimation) for males were largest during the rut (333 ha), followed by summer (103 ha), and were smallest in winter (61 ha). For females, on the other hand, the median space requirement was greatest during summer (525 ha) and decreased continuously during the rut (155 ha) and winter (120 ha). At Il Fuorn, the home range sizes of the two sexes differed significantly between all three seasons examined. In comparison, significant differences between the sexes in the Val Trupchun could only be found during the rut. When comparing the home range sizes of the same sex at the same time of the year between the two study areas no significant differences could be found. Furthermore, forest chamois generally had a smaller space requirement than ridge chamois. Nevertheless, with the exception of males during the rut (262 ha and 1391 ha respectively) and females during the summer (172 ha and 792 ha respectively), forest and ridge chamois did not differ significantly in terms of their home range sizes during the seasons examined.

**Keywords:** forest chamois, ridge chamois, home range size, kernel density estimation, continuous time movement modelling

## Zusammenfassung

Während 16 Jahren (2004 – 2019) wurde das räumliche Verhalten von insgesamt 22 männlichen und 43 weiblichen Gämsen (*Rupicapra rupicapra*) anhand von GPS-Sendern im Schweizerischen Nationalpark erfasst. Dadurch konnten 70'525 individuelle Lokationen für die beiden Untersuchungsgebiete Il Fuorn (41'841) und Val Trupchun (28'684) erhoben und auf deren Grundlage die Streifgebietsgrössen für den Sommer, der Brunft und den Winter berechnet werden. Zusätzlich zur räumlichen Analyse wurden die beiden Berechnungsmethoden „kernel density estimation“ und das „continuous time movement modelling“ miteinander verglichen. Insgesamt konnte eine hohe Übereinstimmung bezüglich der Resultate bei kleineren Streifgebietsgrössen festgestellt werden. Nahm der Raumanspruch der Gämsen jedoch zu, zeigte sich tendenziell eine immer grösser werdende Abweichung der Ergebnisse zwischen den beiden Methoden. Infolgedessen unterschieden sich die berechneten mittleren Streifgebietsgrössen der beiden Methoden während der Brunft signifikant, jedoch nicht während den beiden anderen Jahreszeiten. Abgesehen vom Methodenvergleich, war die Variation innerhalb und zwischen den einzelnen Jahreszeiten gross und es haben sich geschlechtsspezifische Unterschiede abgezeichnet. Unabhängig vom Untersuchungsgebiet, resultierten die grössten, mittleren Streifgebietsgrössen (95% kernel density estimation) für männliche Gämsen während der Brunft (333 ha), gefolgt vom Sommer (103 ha) und Winter (61 ha). Bei den weiblichen Gämsen hingegen, war der Raumanspruch während des Sommers am grössten (525 ha) und nahm während der Brunft (155 ha) und des Winters (120 ha) kontinuierlich ab. Im Untersuchungsgebiet Il Fuorn unterschieden sich die Streifgebietsgrössen der beiden Geschlechter während allen untersuchten Jahreszeiten signifikant. Im Gegensatz dazu konnte in der Val Trupchun ein signifikanter Unterschied nur während der Brunft festgestellt werden. Der Vergleich der Streifgebietsgrössen des gleichen Geschlechts zur gleichen Jahreszeit ergab, dass zwischen den beiden Untersuchungsgebieten keine Unterschiede bestehen. Ausserdem hat sich gezeigt, dass Waldgämsen einen grundsätzlich kleineren Raumbedarf als Gratgämsen hatten. Mit Ausnahme der Männchen während der Brunft (262 ha bzw. 1391 ha) und Weibchen während des Sommers (172 ha bzw. 792 ha) unterschieden sich Wald- und Gratgämsen jedoch nicht signifikant bezüglich ihrer Streifgebietsgrössen während den untersuchten Jahreszeiten.

**Schlagworte:** Waldgämsen, Gratgämsen, Streifgebietsgrösse, kernel density estimation, continuous time movement modelling

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# 1 Introduction

## 1.1 Home range concept and influencing factors

Fundamental knowledge of the ecology of a species is crucial when it comes to implementing sustainable management and/or conservation measures. The home range (HR) size, describing spatial behaviour, and thus where an animal can be found over time, is an essential part of it. According to Burt (1943, p 351), the term HR is defined as follows: "That area traversed by an individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range". To what extent this definition corresponds to the actual HR size and what is meant by it, is a controversial issue (Powell and Mitchell 2012). Nonetheless, HR sizes among animals differ both between different species and among individuals of the same species (Powell and Mitchell 2012). The cause of interspecific variations is largely attributed to body-size-dependent metabolic requirements (Carbone et al. 2005; Lindstedt et al. 1986). In a review by Ofstad et al. (2016), differences regarding habitat, diet, sex and mating systems are also mentioned as possible causes in ungulates, whereas a separate meta-analysis showed that only the habitat (after accounting for metabolic requirements) had a significant influence on variation in HR size. Therefore, intraspecific differences in HR sizes of cervids (moose, mule deer, roe deer, white-tailed deer and red deer) are influenced both by intrinsic and extrinsic factors, as compiled by van Beest et al. (2011). This study also highlighted the important role played by the temporal scale in estimating HRs. For example, climatic factors mainly influenced the HR size of moose at a daily and biweekly scale, whereas there was no effect on a monthly scale.

In addition to biotic and abiotic factors, the method used to calculate the HR size can furthermore have a major impact on the results (Gregory 2016). Overall, there are a number of possible estimators for calculating the HR size of an animal as accurately as possible (Kernohan et al. 2001). As Downs and Horner (2008) described, the most commonly used estimators include the minimum convex polygon method (MCP; Mohr 1947; Hayne 1949) or the kernel density estimator method (KDE; Gregory 2016; Worton 1989). Additionally, there are parametric methods like the developed ellipses of Jenrich and Turner (1969) or the Dunn estimator of Dunn and Gipson (1977) and non-parametric methods like the grid method (Siniff and Tester 1965), harmonic mean method (Dixon and Chapman 1980), Fourier analysis (Anderson 1982), cluster method (Kenward 1987), Dirichlet tessellation method (Wray et al. 1992) and the low convex hull method (LoCoH; Getz et al. 2007). The MCP method is easy to calculate and reflects the HR size based on the smallest polygon to contain all the point locations (Downs and Horner 2008; Noonan et al. 2019). However, this makes the method sensitive to sample size, does not provide any further information on the use of the HR and sometimes contains large areas that are not used at all (Worton 1987, 1989). The latter can be avoided



with the KDE method by placing a kernel (a probability density) over each individual location and thus determining the utilization distribution (UD; Downs and Horner 2008; Seaman and Powell 1996; Worton 1989). When calculating the UD, the width of the kernel (bandwidth or smoothing parameter) is crucial, overly large bandwidths will oversmooth the point pattern, whereas if the bandwidth is too small, HR sizes will be underestimated (Kernohan et al. 2001; Seaman and Powell 1996). However, based on the UD, the HR size (often the 95% volume contour) can then be calculated. Compared to the MCP method, the KDE method is a nonparametric estimator, in which the location data are assumed to be independent and identically distributed (IID). In other words, methods such as the KDE were developed on the basis of less than 100 VHF (very high frequency) locations and it was assumed that there was no correlation of the data in space or time (Walter et al. 2015). As a result of the enormous progress in technology, movement studies are now almost exclusively carried out using GPS (global positioning system) devices (Kays et al. 2015). Therefore a much larger amount of data can be recorded per time unit, which often leads to an increase of autocorrelation (Walter et al. 2015). Fleming et al. (2015, p 1182) even wrote: “Autocorrelation is the rule, not the exception, in animal movement data”. Consequently, the basic assumption of the KDE method is violated, which can result in grossly underestimated HR sizes (Fleming et al. 2015). One possible solution is the continuous-time movement modelling (ctmm) package introduced by Calabrese et al. (2016). Various continuous-time stochastic process (CTSP) models are used, which take the autocorrelation of the data into account. Based on the best model, adapted with variogram analysis (Fleming et al. 2014a) and non-Markovian maximum likelihood estimation (Fleming et al. 2014b), the accurate HR size can finally be determined with the autocorrelated kernel density estimation (Fleming et al. 2015).

## 1.2 The chamois and its home range sizes

The alpine chamois (*Rupicapra rupicapra*) is the most common ungulate species in the higher regions of the Alps (Giacometti et al. 1997). Due to its high numbers and extensive distribution, the chamois is also an important game species. Its habitat requirements include access to rocky outcrops as refuge areas from predators during all seasons, and availability of high quality forage such as forbs during summer (e.g. Baumann and Struch 2000). On the other hand, high forage biomass is less important than for larger mixed feeders such as red deer (e.g. Schweiger et al. 2015). Chamois typically spend the summer above the treeline on alpine meadows at high altitudes and the winter in more protected forests at lower altitudes. However, some populations remain in open areas year-round, whereas others spend the entire year within the forest (e.g. Baumann and Struch 2000). Individuals representing these two ‘ecotypes’ – termed ‘ridge chamois’ and ‘forest chamois’, respectively - may even occur within the same valley (Bögel et al. 2001).

Chamois HR sizes can vary between 12.3 ha and 749 ha (e.g. Nesti et al. 2010; Unterthiner et al. 2012; Table 1). The large variation can be explained by (i) only one sex being examined (e.g. Clarke

and Henderson 1984; Hamr 1984, 1985; Pachlatko and Nievergelt 1985; Hardenberg et al. 2000; Campell 2003; Lovari et al. 2006), (ii) differences in temporal scale (e.g. Baumann and Struch 2000; Nesti et al. 2010; Unterthiner et al. 2012), (iii) the use of different estimators (e.g. Clarke and Henderson 1984; Pachlatko and Nievergelt 1985; Lovari et al. 2006), or (iv) visual observations vs. GPS data (e.g. Pachlatko and Nievergelt 1985). Nonetheless, larger and more variable HR sizes have been detected during the warm compared to the cold period (Hamr 1985; Lovari et al. 2006; Nesti et al. 2010), most likely due both to snow cover limiting movement, and to lower forage availability requiring energy saving behaviour during winter (Hardenberg et al. 2000; Brivio et al. 2016). Conversely, energy intake needs to be maximised during summer, leading to an increase in activity during the warm season (Brivio et al. 2016). This increase in activity can be all the more pronounced in females if there are additional costs for lactation (Hamel and Côté 2008). On the other hand, adult male HR sizes depend on their mating strategy (i.e. territorial vs. migratory; Lovari et al. 2006; Nesti et al. 2010; Unterthiner et al. 2012). Especially during the summer and the rut, migrating males have a far greater spatial requirement than territorial males (Lovari et al. 2006).

In the study area, the Swiss National Park (SNP), the number of chamois is between 1000 and 1500, corresponding to a density of 5.81 – 8.72 individuals/100ha (Filli 1995). In the long term, population numbers have been remarkably constant. In contrast to the red deer (*Cervus elaphus*) and the Alpine ibex (*Capra ibex*), which were absent at the time the SNP was founded in 1914, the chamois has always been present in the park (Campell 2003). Furthermore, there are chamois which can be found mainly in and outside of the forest and in addition, inhabit areas that vary greatly in terms of food availability and red deer density. While the Val Trupchun mainly has calcareous bedrock leading to a higher food availability, this is less pronounced in the dolomite-shaped area Il Fuorn (Anderwald et al. 2016). As a result, summer densities of red deer reach up to 29 individuals per km<sup>2</sup> in the Val Trupchun whereas lower densities with 11 red deer per km<sup>2</sup> can be found at Il Fuorn (Filli and Suter 2006; Anderwald et al. 2016). So far, Boschi and Nievergelt (2003), Campell (2003) as well as Filli and Campell (2006) have examined the different space requirements of chamois in the SNP. However, since the studies mentioned differ considerably in the methodology used (season, sex, study area, estimator), there are still gaps in knowledge about the HR sizes of chamois in the nature reserve. Moreover, in the last two decades, data collection has increasingly been based on GPS data, which means that previously used methods as MCP (Filli and Campell 2006) or KDE (Boschi and Nievergelt 2003; Campell 2003) may no longer be suitable due to autocorrelation.

**Table 1: Literature overview and results on home range size in chamois. The abbreviations MCP and KDE in the column home range estimator correspond to the minimum convex polygon or the kernel density estimation method. If several HR estimators and temporal scales were used in one study, the highlighted corresponds to the specified HR size.**

Study area	Sample size (n)	Age	Temporal scale	Home range estimator	Home range size [ha]	Fixes (n)	Duration (months)	Reference
Maritime Alps Regional Park (Italy)	21 (12 ♂; 9 ♀)	adult	bimonthly	50% & <b>95% fixed KDE</b>	12.3 resident ♂ 19.1 migrant ♂ 56.3 ♀	ca. 7'000	24	Unterthiner et al. 2012
Gran Paradiso National Park (Italy)	29 (23 ♂; 6 ♀)	adult	<b>warm period</b>	50% & <b>95% KDE</b>	49 resident ♂ 749 migrant ♂ 711 ♀	7'902	35	Nesti et al. 2010
			<b>cold period</b>		32 resident ♂ 45 migrant ♂ 36 ♀			
Gran Paradiso National Park (Italy)	21 ♂	adult	bimonthly, warm & cold period, <b>annual</b>	50% & <b>95% KDE</b> <b>95% &amp; 100% MCP</b>	69.6 141.8	ca. 10'000	22	Lovari et al. 2006
Gran Paradiso National Park (Italy)	6 ♂	adult	bimonthly & <b>annual</b>	<b>95% &amp; 100% MCP</b>	14.1 – 193.6	1192	24	Hardenberg et al. 2000
Northern Tyrol (Austria)	28 ♂	juvenile, subadult & adult	seasonal	100% MCP	< 200 (all seasons)	ca. 700	49	Hamr 1984
Northern Tyrol (Austria)	27 ♀	juvenile, subadult & adult	seasonal	own 4 ha grid method	74 (summer-fall) 60 (winter)	ca. 500	24	Hamr 1985
Aletschwald (Switzerland)	7 ♀	juvenile & adult	seasonal (only summer)	own grid method	71	-	4	Pachlatko and Nievergelt 1985
Northern edge of the Alps (Switzerland)	19 (5 ♂; 14 ♀)	subadult & adult	annual	25%, 50%, 75%, <b>95%</b> & 100% <b>adaptive KDE</b>	183 ♀ 168 ♂	3438	12	Baumann and Struch 2000
Biosphere reserve Berchtesgaden (Germany)	11 (7 ♂; 4 ♀)	subadult & adult	seasonal	?% KDE	<b>ridge chamois:</b> 400 (summer and winter); 250 (spring) <b>forest chamois:</b> 300 (all seasons)	4911	48	Bögel et al. 2001
Southern Alps (New Zealand)	14 ♀	subadult & adult	annual	own contour method	341	-	36	Clarke and Henderson 1984

### 1.3 Research questions and hypotheses

Overall, there are a number of factors that can influence the HR size of chamois. Accordingly, the methodology used often differs greatly among existing studies, which means that the resulting HR sizes are not easily comparable (Campbell 2003). For this reason, and to expand the basic ecological knowledge of the species, the HR size of the chamois in the SNP should be examined using a consistent methodology. The following questions (Q) and hypotheses (H) shall be developed and checked within the framework of this master thesis:

**Q1:** Do the calculated HR sizes differ significantly ( $\alpha = 0.05$ ) between the two methods (KDE and ctmm)?

**H1:** They differ significantly due to the autocorrelation of the data.

**Q2:** Do the HR sizes of adult female and male chamois differ significantly ( $\alpha = 0.05$ ) in the Val Trupchun during different seasons (summer, rutting and winter)?

**H2:** A significant difference only occurs during the summer due to the higher energy costs and habitat selection in female chamois.

**Q3:** Do the HR sizes of adult female and male chamois differ significantly ( $\alpha = 0.05$ ) in the Il Fuorn area during different seasons (summer, rutting and winter)?

**H3:** A significant difference only occurs during the summer due to the higher energy costs and habitat selection in female chamois.

**Q4:** Do the HR sizes for the same sex differ significantly ( $\alpha = 0.05$ ) between the two areas?

**H4:** There are no significant differences due to similar habitat conditions.

**Q5:** Are there significant ( $\alpha = 0.05$ ) differences in the HR sizes between forest and ridge chamois in the Il Fuorn area?

**H5:** Due to different habitat conditions there is a significant difference.

## 2 Material and Methods

### 2.1 Study area

The study was carried out in two sub-areas of the SNP (17'200 ha) which is located in the eastern part of Switzerland (Figure 1). As an IUCN Category 1a Protected Area (=Wilderness), all hunting activities are prohibited and visitors are restricted to designated hiking trails. The central location in the middle of the Alps and altitudes from approximately 1400 to 3200 m above sea level result in a continental climate (Haller 2002). Annual rainfall is low with approximately 850 mm in the montane and approximately 1000 mm in the subalpine and alpine zones (Haller et al. 2013). Accordingly, lower snow depths are recorded in the region compared to the rest of the canton of Grison, with an average maximum of 90 cm at the weather station Buffalora (1970 m.a.s.l.), located just outside the park boundary (Haller et al. 2013). Few episodes of fog or mist, relatively low humidity, intense solar radiation, and large diurnal and seasonal temperature fluctuations are characteristic for the area (Landolt 1992; Zoller 1995). Forest and forest-like vegetation covers an area of 4800 ha and the tree line runs between 2150 and 2250 above sea level (Zoller 1995). In addition to 3450 ha of subalpine and alpine grassland, rocks, rubble, gravel alluvions and water form further components of the habitat in the SNP.

The two sub-areas in which chamois were GPS-collared were Val Trupchun (2060 ha) and Il Fuorn (3689 ha; Figure 1), which differ in their habitat characteristics. Val Trupchun is dominated by calcareous bedrock, comparatively nutrient-rich alpine pastures above the treeline, and forest communities consisting of European larch (*Larix decidua*), Swiss stone pine (*Pinus cembra*) and Norway spruce (*Picea abies*) at lower elevations (Zoller 1995; Haller 2002). The limestone and marl form good conditions for the formation of productive alpine turf, which is used by a high density of ungulates: 29 red deer, 9 chamois and 18 alpine ibex per km<sup>2</sup> inhabit the area during the summer (Filli and Suter 2006; Anderwald et al. 2016). At Il Fuorn, patches of both nutrient-rich and nutrient-poor pastures are found at higher altitudes but vegetation quality (measured by NDVI) declines more rapidly with increasing elevation than in Val Trupchun (Anderwald et al. 2016). The forests at Il Fuorn mainly consist of dwarf mountain pine (*Pinus mugo*) with occasional stands of European larch and Swiss stone pine (Zoller 1995). Furthermore, small areas of dwarf mountain pine shrub are characteristic at the upper woodland edge. With approximately 11 red deer, 13 chamois and 1 Alpine ibex per km<sup>2</sup> this area also supports a large number of ungulates (Filli and Suter 2006; Anderwald et al. 2016). The golden eagle (*Aquila chrysaetos*) and red fox (*Vulpes vulpes*) are currently the main natural predators of chamois in the study area, although the grey wolf (*Canis lupus*) is slowly returning.

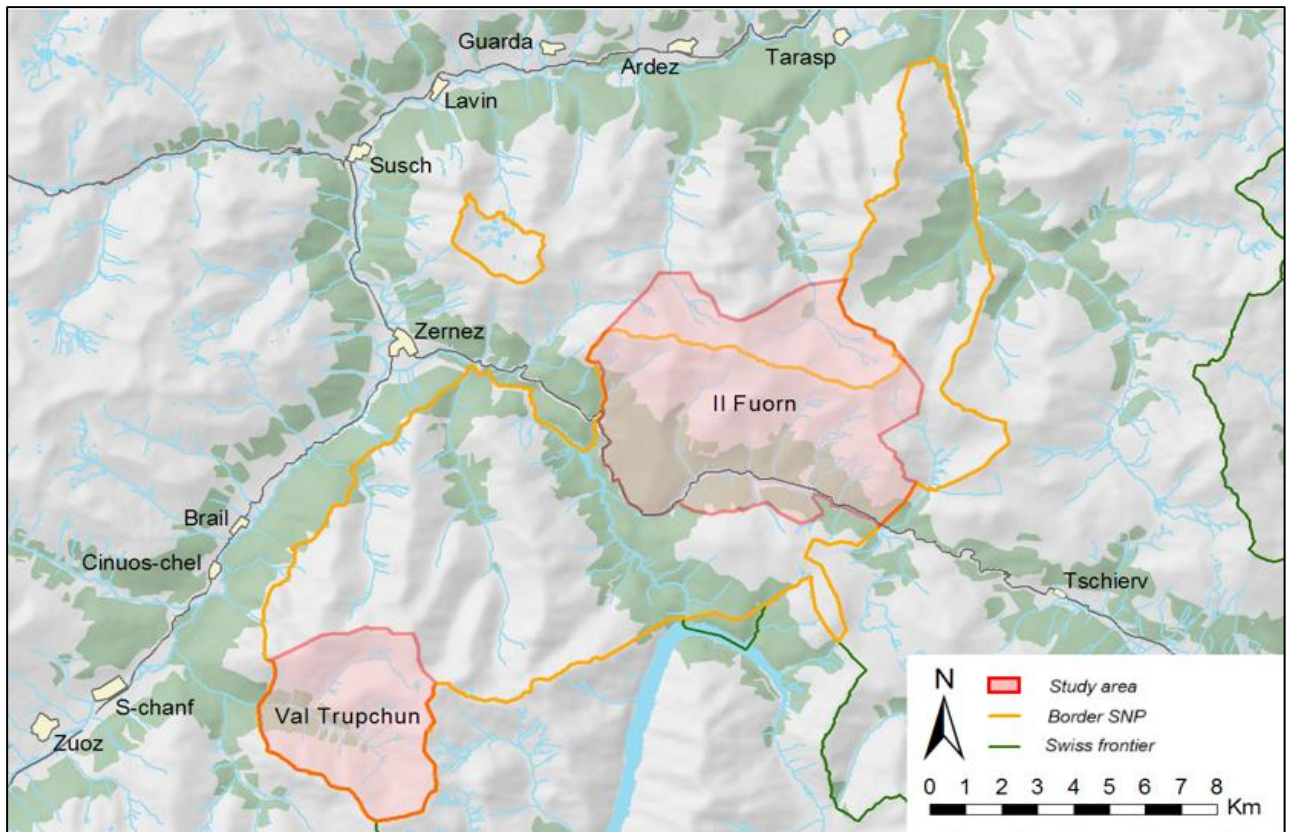


Figure 1: The two study areas Il Fuorn (3689 ha) and Val Trupchun (2060 ha) within the Swiss National Park (© Schweizerischer Nationalpark).

## 2.2 GPS-collaring

A total of 65 adult chamois ( $\sigma = 22$ ;  $\text{♀} = 43$ ) have been equipped with GPS PLUS collars (VECTRONIC Aerospace GmbH, Berlin, Germany) since 2004: 45 individuals ( $\sigma = 18$ ;  $\text{♀} = 27$ ) in the Il Fuorn area and 20 individuals in Val Trupchun ( $\sigma = 4$ ;  $\text{♀} = 16$ ). In addition to the transmitters, coloured ear tags with an individual number were attached for visual detection in the field. The park rangers darted and tranquilised the chamois with xylazine (Provet AG, Lyssach, Switzerland) and ketamine (Dr. E. Graeub AG, Bern, Switzerland; 0.3-0.8 ml Hellabrunner mixture) using three different approaches: (I) stalking and darting in the field (used at Il Fuorn and in Val Trupchun); (II) darting during the night from a vehicle (Il Fuorn only); (III) catching in a gate trap and subsequent anaesthesia (Val Trupchun only). The darting was carried out at a maximum of 30 meters, the total handling time was within 45 minutes and chamois were released after injection of the antagonist (0.3-0.8 ml of atipamezol, VIRBAC Schweiz AG, Opfikon, Switzerland). All capture, handling and tagging was conducted under the permit from the Canton of Grisons (no. 2011-07) and the Swiss Federal Office for the Environment FOEN (no. J 074-0727). Depending on the GPS collar, the data were collected in two different ways: (I) by using satellite communication, which sent the data independently via Iridium or Globalstar; (II) by using a VHF (30-300 MHz) or UHF (300-3000 MHz) Handheld Terminal (VECTRONIC Aerospace GmbH, Berlin, Germany) with a Yagi antenna Y-4FL (148-150 MHz),

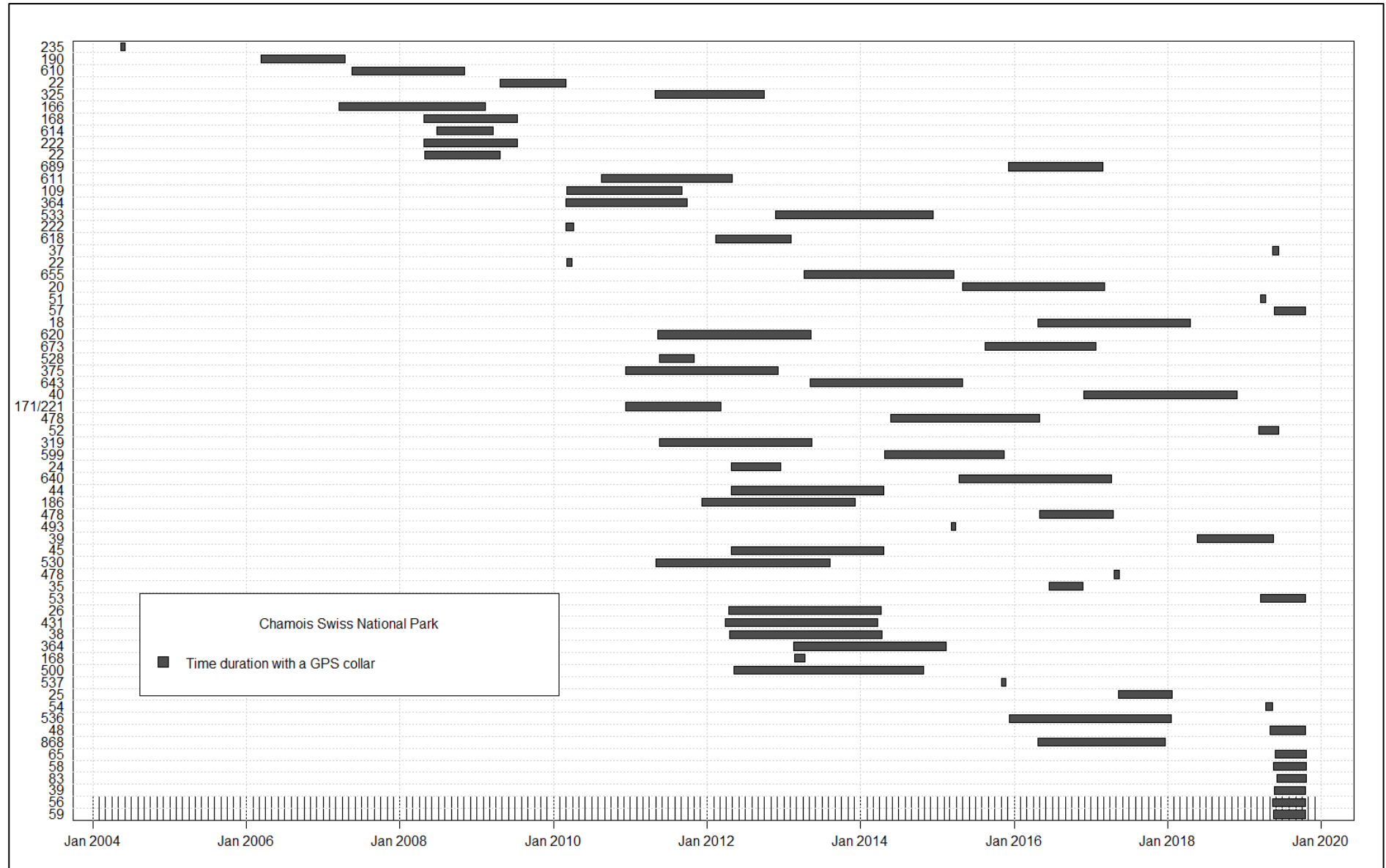
which enabled the data to be downloaded within range of the GPS transmitter. Just before the battery was empty, the GPS collars were removed from the chamois using a drop-off mechanism.

### 2.3 Data processing and estimation of home range size

In preparation for the calculation of HR sizes and the method comparison I filtered the data set according to several criteria. On the one hand, I divided the chamois data into seasons, which were defined as follows: summer (June, July and August), rutting (November and December) and winter (January, February and March). Only seasons in which localizations were available for all associated months were selected for the calculation of the HR sizes. In order to maximize the battery life of the GPS collars, different intervals (5, 10, 30, 60, 120, 180, 240, 360, 480 and 1440 min.) between the localizations had been used throughout the investigation period. In order to make the results comparable at a later point in time, I used a subset of all data with a constant interval of 240 minutes. For 50% of the chamois, data were available for more than one year. As a result, there are twice the number of data per season for these individuals. In these cases, I included both seasons to increase the sample size, but as independent events. To exclude any possible behavioural effects from capture, I did not include data within the first three days after anaesthesia took place (White and Garrott 2012). The final data set contained 64 individuals ( $\sigma = 25$ ;  $\phi = 39$ ) out of the total of 65 collared chamois, 25 ( $\sigma = 5$ ;  $\phi = 20$ ) of them for the Val Trupchun and 39 ( $\sigma = 20$ ;  $\phi = 19$ ) for Il Fuorn (Figure 2). For 19 individuals (Il Fuorn = 9; Val Trupchun = 10) more than one year of data was available.

The HR size of the chamois was calculated using two different methods. The first is the kernel density estimation (KDE; Worton 1989), which I determined using the `adehabitatHR` package (Calenge 2006) in R version 3.5.1 (R Core Team 2018). To set the bandwidth, I chose the reference smoothing parameter ( $h_{ref}$ ), which is defined as  $h = \sigma \times n^{-1/6}$  where  $\sigma = 0.5 \times (\sigma_x + \sigma_y)$  (Calenge 2006).  $\sigma_x$  and  $\sigma_y$  correspond to the standard deviations of the x and y coordinates of the relocations. Based on the bandwidth, I was able to calculate the utilization distribution (UD) and derive the HR (95% volume isopleth). The second method is the continuous time movement modelling package (`ctmm`; Calabrese et al. 2016). This method also offers the possibility of a web application (`ctmmweb`; <https://ctmm.shinyapps.io/ctmmweb/>) for the evaluation, which I used in this work. Following Calabrese et al. (2016) I proceeded as follows: (I) data import and identification of errors using scatterplots; (II) plot variograms and periodograms to judge the suitability of different models; (III) adjust suitable models via maximum likelihood and compare them with the Akaike information criterion (AIC; Akaike 1974); (IV) selection of the best model and calculation of the 95% HR with the corresponding 95% confidence intervals via autocorrelated kernel density estimation (AKDE). Finally, for both methods I exported the calculated HRs as polygon shapefiles for further visualisation.

Figure 2: Overview of the individual time duration that chamois in the Swiss National Park were equipped with a GPS collar.





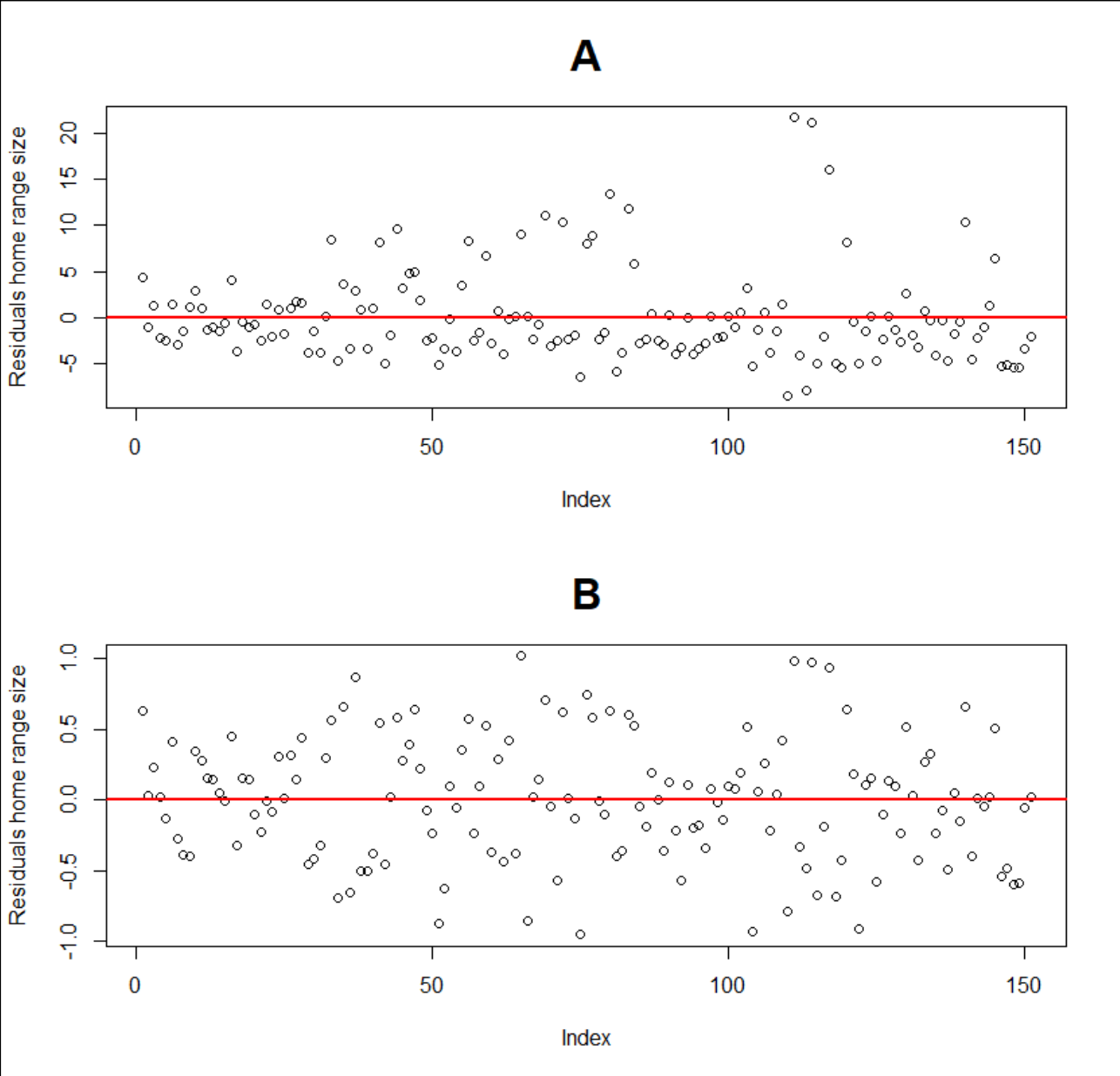
## 2.4 Method comparison: ctmm vs. KDE

In order to check the extent to which the two methods coincide with regard to their results, I first plotted the estimated HR sizes of the ctmm method against those of the KDE method and applied the Spearman's rank correlation coefficient ( $r_s$ ). In a further step, I created a more detailed boxplot with the HR sizes of both methods divided according to summer, rut and winter. To test H1, I then used the Wilcoxon-Test to evaluate possible significant differences. The test was chosen due to the non-normally distributed data (Shapiro-Wilk-Test:  $p$ -value < 0.05 for each season). To counter an alpha error accumulation, I adjusted the resulting  $p$ -values with the help of the Bonferroni-Holm correction (Holm 1979). In a final step, I displayed the exported shapefiles from the HR analysis (95% KDE and 95% ctmm) based on a true colour image produced from ESA remote sensing data (Sentinel 2) using ArcGIS 10.4.1 for a visual comparison of the two methods.

## 2.5 Ecological questions

As with the method comparison, in a first step I created boxplots to get an overview of how the seasonal HR sizes of chamois vary depending on the sex, study area and forest. For the analysis, I only used the 95% KDE. This is because from a biological point of view it is not necessary to include both methods, and the 95% ctmm tended to sometimes overestimate the HR size (see results). Based on the independent samples and the non-normally distributed HR size (Shapiro-Wilk-Test:  $p$ -value < 0.05 for each season), I used the Mann-Whitney U-Test to test H2 – H4 and thus identify any significant differences. The resulting  $p$ -values were again adjusted according to Holm (1979). To test H5, I first had to determine which chamois were mainly found in and outside of the forest. For this purpose I overlaid the localizations with the topographic landscape model (TLM; © swisstopo) of Switzerland using the geographic information system ArcGIS (version 10.4.1). If at least 60% of locations were recorded in the forest during all seasons examined, I classified an individual as a forest chamois. The following categories were defined as forest: (I) brushwood; (II) open forest and (III) closed forest. Of the 39 chamois in the Il Fuorn area, 14 were classified as forest chamois ( $\text{♂} = 10$ ;  $\text{♀} = 4$ ) and 25 as ridge chamois ( $\text{♂} = 10$ ;  $\text{♀} = 15$ ). The influence of the variable forest could not be checked for the study area Val Trupchun due to insufficient data. However, in a last step I again applied the Mann-Whitney U-Test and adjusted the resulting  $p$ -values according to Holm (1979). In addition, to determine the overall influence of the area (Il Fuorn vs. Val Trupchun), sex (female vs. male), year (2004 – 2019), season (summer, rut and winter) and forest (forest vs. ridge chamois) on the HR size of chamois, I used both a conditional inference tree (ctree; Hothorn et al. 2006) and linear mixed-effects models (LMMs; Bates et al. 2015). For both, the HR size was chosen as the dependant variable and the area, sex, year, season and forest as independent variables. I chose the LMM's as an additional approach in order to include the chamois ID as a random factor

and thus exclude a stronger weighting of individuals with double data volume. For the residuals to show homogeneous variances and to be normally distributed, I logarithmized the response variable “HR size” (Figure 3 and Figure 4). To determine the most suitable model, I used the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Moreover, I assessed the relative importance of each parameter by calculating predictor weights taking all candidate models into account (Burnham and Anderson 2002). Model selection was carried out using the AICmodavg package to calculate AICc (Mazerolle 2019). All analyses were carried out using R version 3.5.1. (R Core Team 2018) or ArcGIS (ESRI 2015).



**Figure 3: Residual variance of the response variable „home range size“ in the linear mixed-effects models before (A) and after (B) the logarithmic transformation. The red line corresponds to the reference line and the index reflects the individual data points (N = 152) of the linear mixed-effects models.**

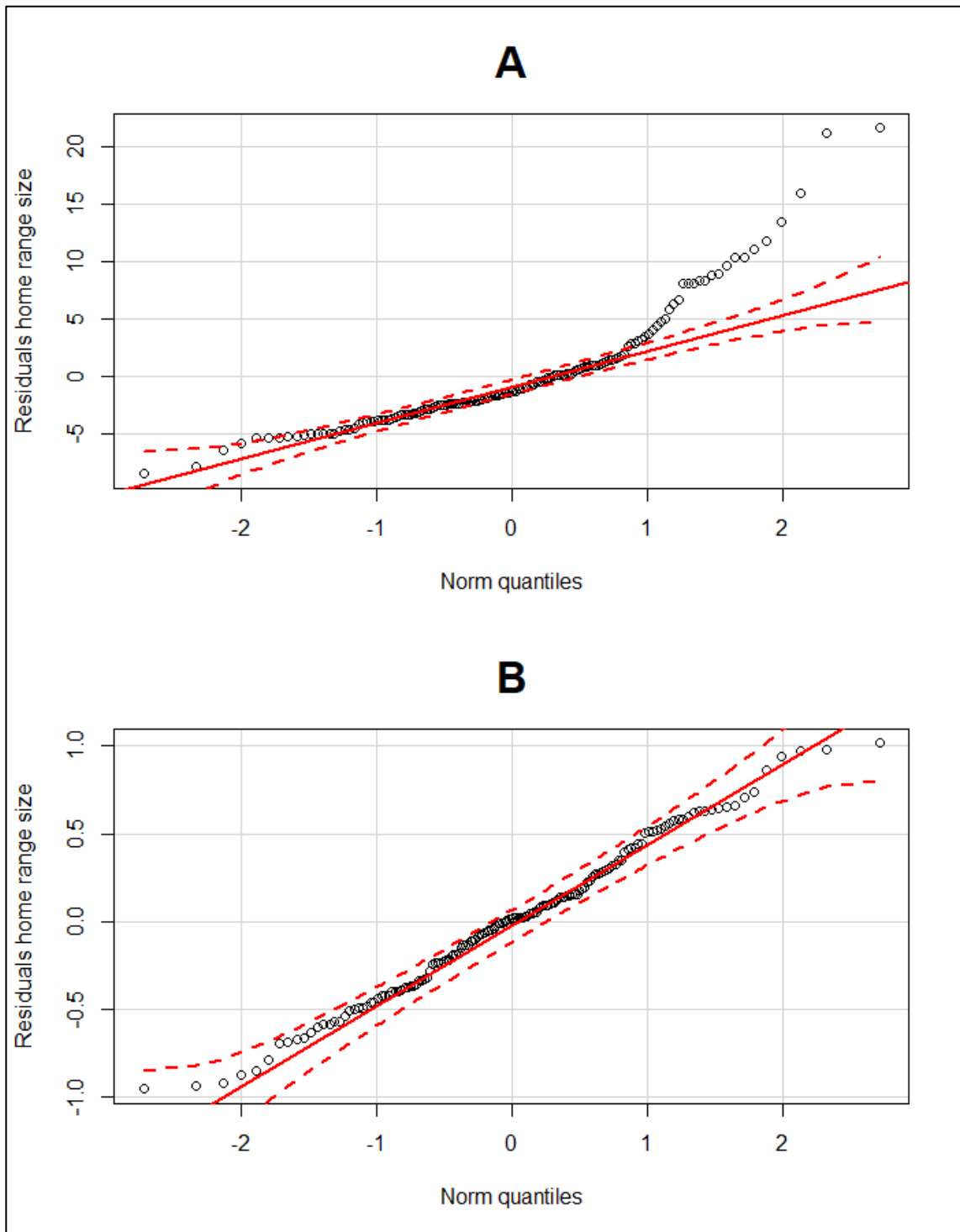


Figure 4: Q-Q plots of the residuals of the response variable „home range size“ in the linear mixed-effects models before (A) and after (B) the logarithmic transformation. The solid red line corresponds to the reference line for a normal distribution and the dashed red lines to the corresponding 95% confidence interval.

### 3 Results

A total of 70'525 chamois locations from the study areas Il Fuorn ( $\sigma = 19'550$ ;  $\phi = 22'291$ ) and Val Trupchun ( $\sigma = 6'672$ ;  $\phi = 22'012$ ) were included in the analysis. Within the data set for the study area Il Fuorn, 15'982 ( $\sigma = 9'716$ ;  $\phi = 6'266$ ) locations corresponded to forest chamois and 25'859 ( $\sigma = 8'586$ ;  $\phi = 17'273$ ) locations to ridge chamois. Overall, the sample size of chamois monitored ( $n$ ) for the individual seasons was 62 for the summer, 47 during the rut and 42 during the winter.

#### 3.1 Method comparison

The two methods (95% KDE vs. 95% ctm) correlated strongly with each other ( $r_s = 0.978$ ; Figure 6). Nevertheless, there was a clear tendency towards larger ctm values as soon as a certain HR size was reached (approx. 2000 ha). This was also reflected in the medians of the calculated seasonal HR sizes, with a significant difference during the rut (Wilcoxon-Test:  $V = 848.5$ ,  $p$ -value  $< 0.001$ ), but no difference during summer (Wilcoxon-Test:  $V = 1086$ ,  $p$ -value = 0.419) or winter (Wilcoxon-Test:  $V = 426.5$ ,  $p$ -value = 0.830; Appendix A1). A good visual comparison is shown, for example, by a male chamois in the Val Trupchun (Figure 5). When the locations were further apart (e.g. during the rut), the distance to the calculated HR border were clearly higher than seen in the summer or winter where locations were more closely spaced. An additional difference in the calculation of the HR sizes can be seen where a large-scale change of location has taken place (Appendix B1 & B2). While the KDE method delimited the two locations, the ctm method included the entire area and used it to calculate the corresponding HR size. However, this did not always happen, which can be seen from the rut locations for the male forest chamois ID 10173 (Appendix B2).

#### 3.2 Home range sizes and influencing factors

Overall, the resulting median HR sizes (95% KDE) had a wide range, varying between 12 ha and 1391 ha (Table 2). The smallest HR sizes were seen in both sexes (with the exception of males in the Val Trupchun) during the winter (Figure 7 & 8). Conversely, there was a sex-specific difference, with HR sizes of female chamois that peaked during the summer and those of male chamois during the rut. Accordingly, both season (statistic  $\chi^2 = 19.95$ ,  $p$ -value  $< 0.001$ ) and sex (statistic  $\chi^2 = 9.95$ ,  $p$ -value = 0.008) had a significant influence on the space requirements of chamois as revealed by the conditional inference tree (Figure 11). Overall, however, HR sizes did not differ significantly between the rut and summer (estimate = 0.120, SE = 0.090,  $p$ -value = 0.189) but only between the rut and winter (estimate = -0.362, SE = 0.099,  $p$ -value  $< 0.001$ ; Table 3 and Figure 11). Interestingly, there was no significant difference between sexes in the linear mixed-effects model (estimate = -0.203, SE = 0.110,  $p$ -value = 0.072) as in the conditional inference tree (Table 3 and Figure 11). Nonetheless, there was a tendency towards larger HR sizes for females compared to male chamois.

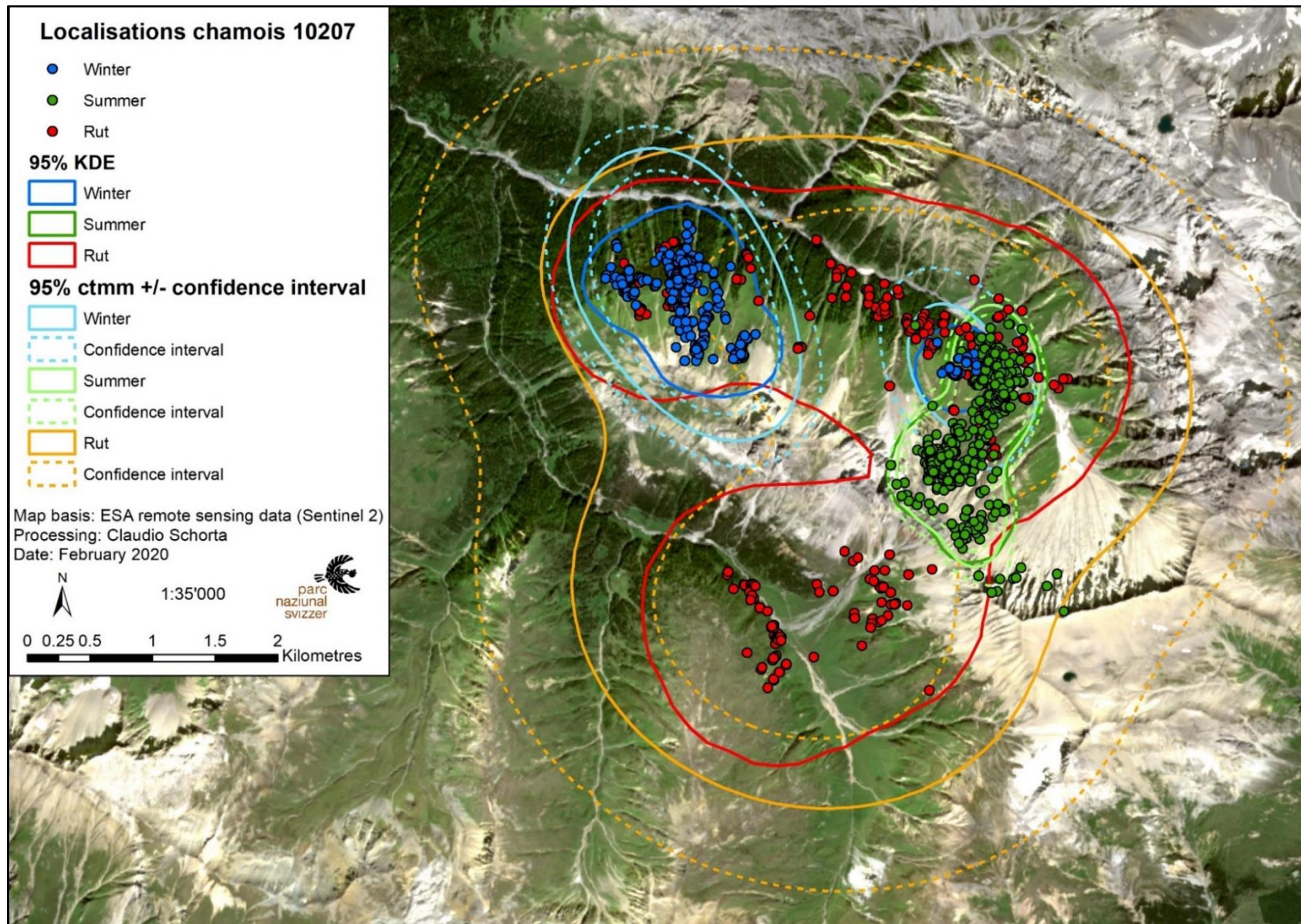


Figure 5: Estimated 95% KDE and 95% ctm home range sizes for a male chamois (ID 10207) during summer (green), rut (red) and winter (blue) located in the Val Trupchun. The dashed lines correspond to the 95% confidence interval for the ctm method.

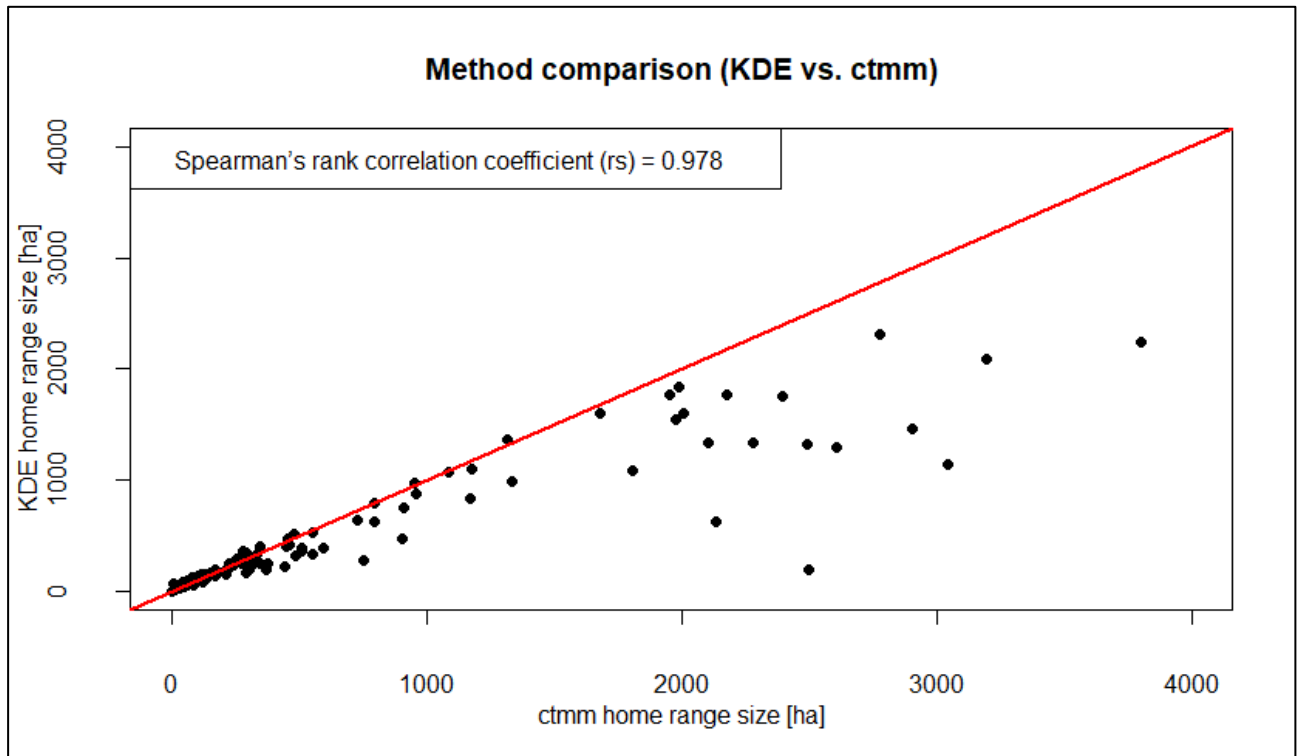


Figure 6: Correlation between the two methods kernel density estimation (KDE) and continuous time movement modelling (ctmm).

### 3.2.1 Space requirements in the study area Val Trupchun

The evaluations regarding HR sizes of chamois in the Val Trupchun have shown that the females and males differed significantly during the rut (Mann-Whitney U-Test:  $W = 9$ ,  $p$ -value = 0.029; Figure 7). With 249 ha, the space requirements by the males were almost twice as large as that of the females (131 ha) and furthermore showed a greater variation (Table 2). During the summer there was a large variation among females, whereas the HR sizes did not differ significantly from those of the males (Mann-Whitney U-Test:  $W = 71$ ,  $p$ -value = 0.057; Figure 7). Moreover, there were also no differences in space requirements during winter, with 112 ha for female chamois and 175 ha for male chamois (Mann-Whitney U-Test:  $W = 35$ ,  $p$ -value = 0.849; Figure 7).

### 3.2.2 Space requirements in the study area Il Fuorn

The HR sizes of both sexes differed significantly during summer (Mann-Whitney U-Test:  $W = 328$ ,  $p$ -value < 0.001), rut (Mann-Whitney U-Test:  $W = 42$ ,  $p$ -value = 0.020) and winter at Il Fuorn (Mann-Whitney U-Test:  $W = 125$ ,  $p$ -value = 0.001; Figure 8). Females had the largest HR sizes during summer (521 ha), whereas for males the largest HR were seen during the rut (435 ha; Table 2). In contrast, during winter females had larger space requirements (136 ha) than males (38 ha; Table 2).

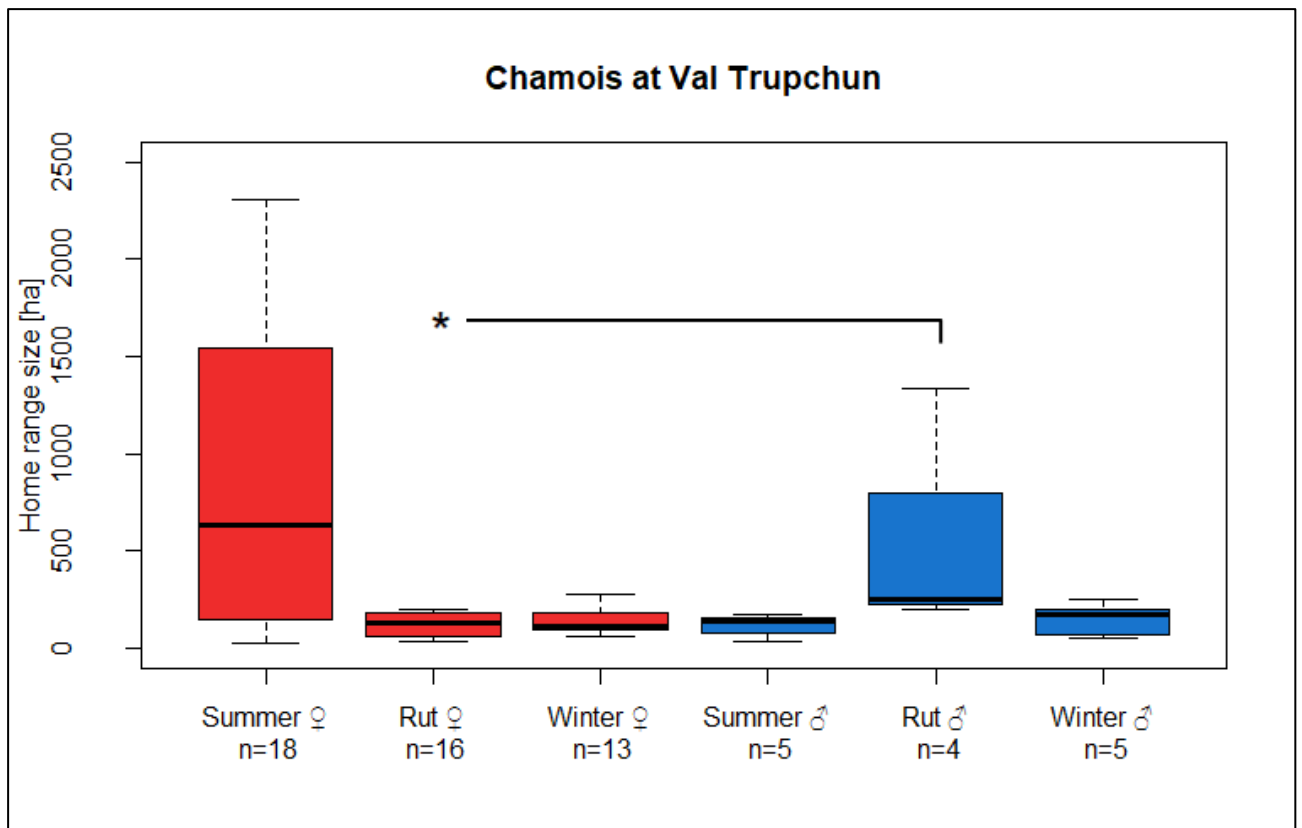


Figure 7: Comparison of female chamois (red) and male chamois (blue) during the summer, rut and winter at Val Trupchun (Mann-Whitney U-Test with  $\alpha = 0.05$ ; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

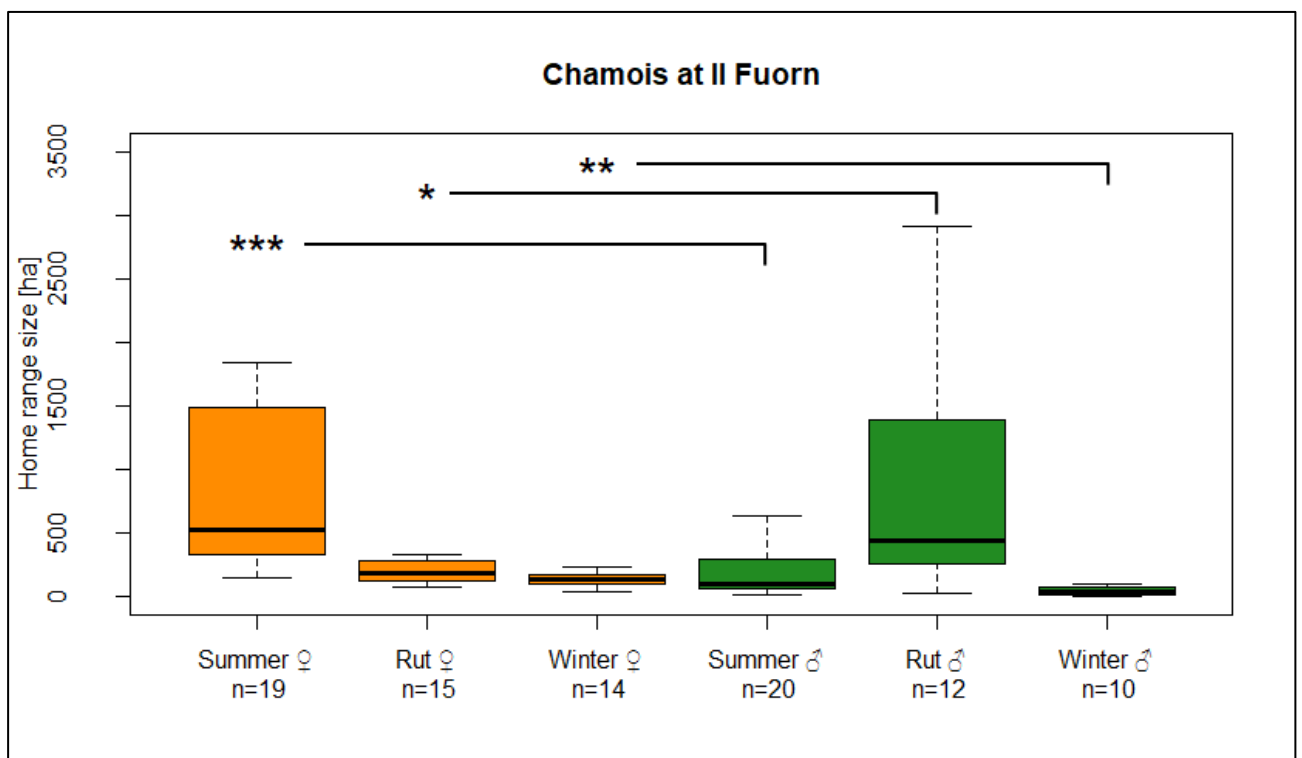


Figure 8: Comparison of female chamois (orange) and male chamois (green) during the summer, rut and winter at Il Fuorn (Mann-Whitney U-Test with  $\alpha = 0.05$ ; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

**Table 2: Overview of medians, the corresponding sample sizes (n) and the average number of localisations ( $\pm$  standard deviation) of the calculated 95% home range size, divided according to sex, calculation method, season (S = summer, R = rut, W = winter), location (FUO = Il Fuorn; TRU = Val Trupchun), forest chamois and ridge chamois.**

	♀						♂					
	95% ctm (ha)			95% KDE (ha)			95% ctm (ha)			95% KDE (ha)		
	S	R	W	S	R	W	S	R	W	S	R	W
<b>FUO</b>	<b>483</b> (n = 19) 516 $\pm$ 46	<b>172</b> (n = 15) 339 $\pm$ 30	<b>131</b> (n = 14) 523 $\pm$ 18	<b>521</b> (n = 19) 516 $\pm$ 46	<b>188</b> (n = 15) 339 $\pm$ 30	<b>136</b> (n = 14) 523 $\pm$ 18	<b>83</b> (n = 20) 521 $\pm$ 39	<b>711</b> (n = 12) 325 $\pm$ 38	<b>12</b> (n = 10) 518 $\pm$ 17	<b>97</b> (n = 20) 521 $\pm$ 39	<b>435</b> (n = 12) 325 $\pm$ 38	<b>38</b> (n = 10) 518 $\pm$ 17
<b>TRU</b>	<b>733</b> (n = 18) 532 $\pm$ 38	<b>133</b> (n = 16) 346 $\pm$ 31	<b>94</b> (n = 13) 526 $\pm$ 32	<b>636</b> (n = 18) 532 $\pm$ 38	<b>131</b> (n = 16) 346 $\pm$ 31	<b>112</b> (n = 13) 526 $\pm$ 32	<b>127</b> (n = 5) 552 $\pm$ 0	<b>1226</b> (n = 4) 340 $\pm$ 26	<b>296</b> (n = 5) 507 $\pm$ 44	<b>137</b> (n = 5) 552 $\pm$ 0	<b>249</b> (n = 4) 340 $\pm$ 26	<b>175</b> (n = 5) 507 $\pm$ 44
<b>FUO + TRU</b>	<b>552</b> (n = 37) 524 $\pm$ 43	<b>151</b> (n = 31) 343 $\pm$ 31	<b>116</b> (n = 27) 525 $\pm$ 26	<b>525</b> (n = 37) 524 $\pm$ 43	<b>155</b> (n = 31) 343 $\pm$ 31	<b>120</b> (n = 27) 525 $\pm$ 26	<b>87</b> (n = 25) 527 $\pm$ 37	<b>711</b> (n = 16) 329 $\pm$ 36	<b>51</b> (n = 15) 515 $\pm$ 29	<b>103</b> (n = 25) 527 $\pm$ 37	<b>333</b> (n = 16) 329 $\pm$ 36	<b>61</b> (n = 15) 515 $\pm$ 29
<b>Forest chamois (only FUO area)</b>	<b>150</b> (n = 4) 517 $\pm$ 43	<b>151</b> (n = 3) 358 $\pm$ 12	<b>96</b> (n = 3) 526 $\pm$ 20	<b>172</b> (n = 4) 517 $\pm$ 43	<b>170</b> (n = 3) 358 $\pm$ 12	<b>116</b> (n = 3) 526 $\pm$ 20	<b>115</b> (n = 10) 535 $\pm$ 19	<b>250</b> (n = 6) 328 $\pm$ 32	<b>11</b> (n = 7) 515 $\pm$ 16	<b>123</b> (n = 10) 535 $\pm$ 19	<b>262</b> (n = 6) 328 $\pm$ 32	<b>12</b> (n = 7) 515 $\pm$ 16
<b>Ridge chamois (only FUO area)</b>	<b>793</b> (n = 15) 516 $\pm$ 47	<b>275</b> (n = 12) 335 $\pm$ 31	<b>133</b> (n = 11) 522 $\pm$ 17	<b>792</b> (n = 15) 516 $\pm$ 47	<b>217</b> (n = 12) 335 $\pm$ 31	<b>152</b> (n = 11) 522 $\pm$ 17	<b>71</b> (n = 10) 508 $\pm$ 48	<b>2755</b> (n = 6) 322 $\pm$ 44	<b>51</b> (n = 3) 526 $\pm$ 15	<b>85</b> (n = 10) 508 $\pm$ 48	<b>1391</b> (n = 6) 322 $\pm$ 44	<b>72</b> (n = 3) 526 $\pm$ 15



### 3.2.3 Val Trupchun vs. Il Fuorn

A comparison between the two study areas Il Fuorn and Val Trupchun revealed that HR sizes for neither female nor male chamois differed significantly between the two areas during the same season ( $p$ -values  $> 0.05$ ; Appendix A2 & A3). That the variable area had no significant influence on the space requirements of chamois was also confirmed by the conditional inference tree and the linear mixed-effects models (Figure 11 and Table 3). In the former, the variable area was not included at all and in the latter it was only included in the fourth ( $\Delta\text{AICc} = 3.99$ ,  $\text{AICc}$  weight = 0.06) and in lower-ranking models (Figure 11, Table 3 and Appendix A4). The only notable difference between the two areas is that the females showed a greater variation in summer HR sizes in the Val Trupchun and the males in HR sizes during the rut at Il Fuorn (Appendix A2 & A3).

### 3.2.4 Forest chamois vs. ridge chamois

Overall, the two highest-ranked linear mixed-effects models ( $\Delta\text{AICc} < 2$ ; model 1: estimate = -0.383, SE = 0.090,  $p$ -value = 0.189) and the conditional inference tree (statistic  $\chi^2 = 9.24$ ,  $p$ -value = 0.012) revealed, that forest chamois had significantly smaller HR sizes than ridge chamois (Figure 11 and Table 3). In more detail, the space requirements of male forest chamois turned out to significantly smaller during the rut (Mann-Whitney U-Test:  $W = 1$ ,  $p$ -value = 0.004) but not during summer (Mann-Whitney U-Test:  $W = 46$ ,  $p$ -value = 0.796) and winter (Mann-Whitney U-Test:  $W = 2$ ,  $p$ -value = 0.067) compared to male ridge chamois (Figure 9). Conversely, female forest chamois had significantly smaller HR sizes during summer (Mann-Whitney U-Test:  $W = 8$ ,  $p$ -value = 0.031) but not during the rut (Mann-Whitney U-Test:  $W = 10.5$ ,  $p$ -value = 0.312) and winter (Mann-Whitney U-Test:  $W = 14$ ,  $p$ -value = 0.769) compared to female ridge chamois (Figure 10). In total, however, space requirements of female ridge chamois during the summer and male ridge chamois during the rut varied greatly with interquartiles between 300 – 1800 ha and 500 – 3000 ha (Figure 9 & 10).

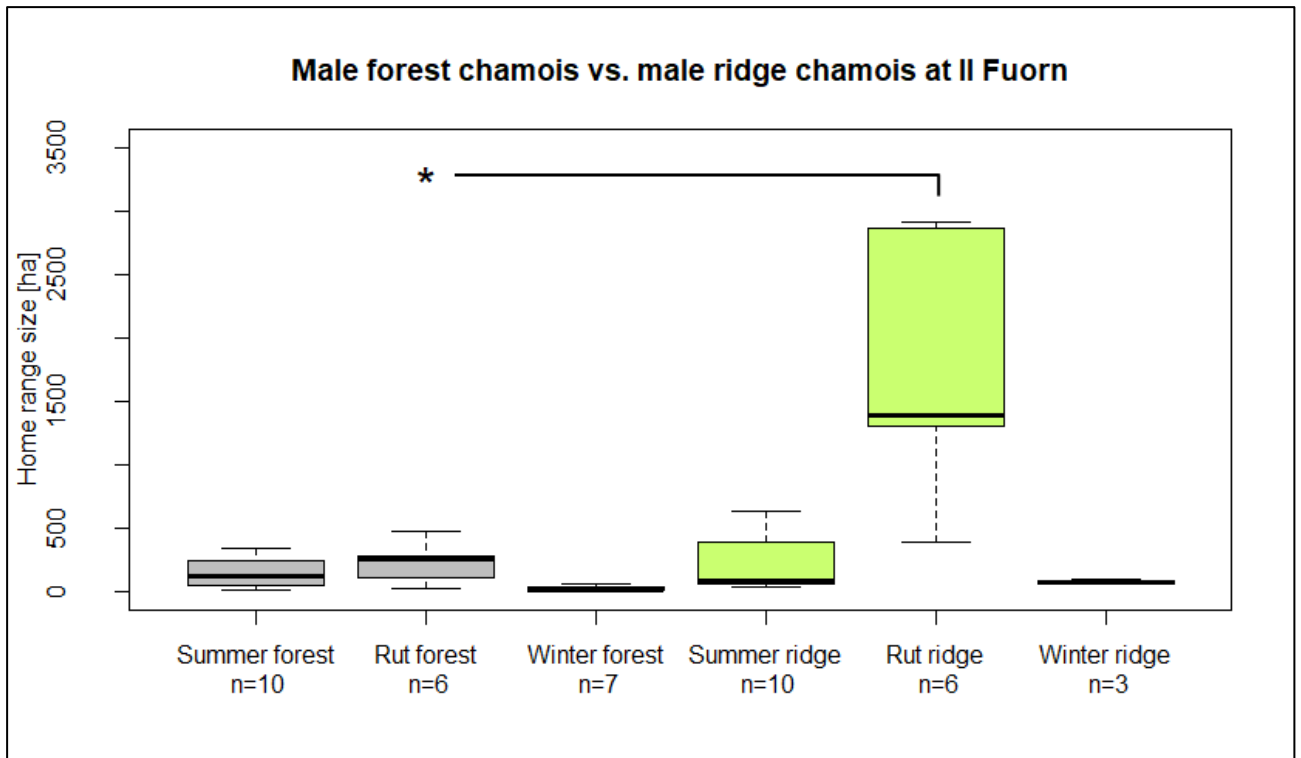


Figure 9: Comparison of male forest chamois (grey) and male ridge chamois (light green) during the summer, rut and winter at Il Fuorn (Mann-Whitney U-Test with  $\alpha = 0.05$ ; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

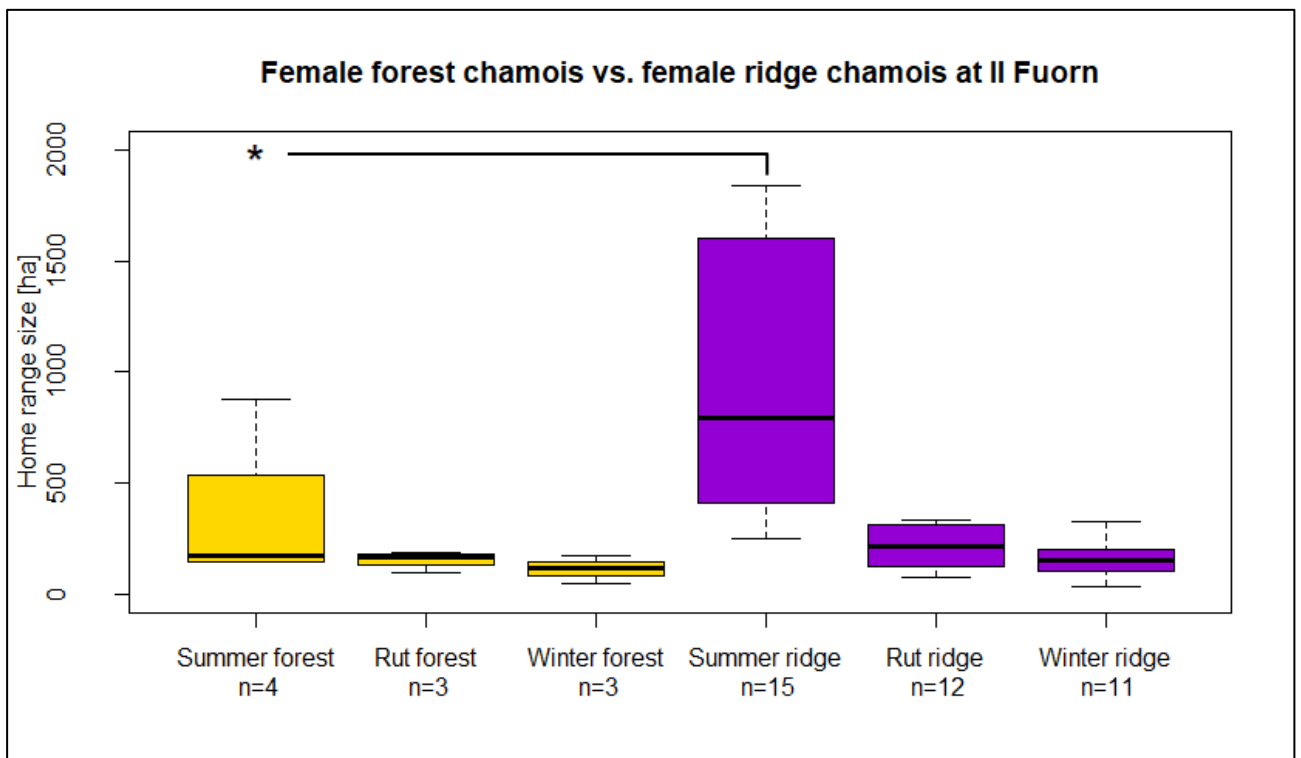


Figure 10: Comparison of female forest chamois (yellow) and female ridge chamois (violet) during the summer, rut and winter at Il Fuorn (Mann-Whitney U-Test with  $\alpha = 0.05$ ; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

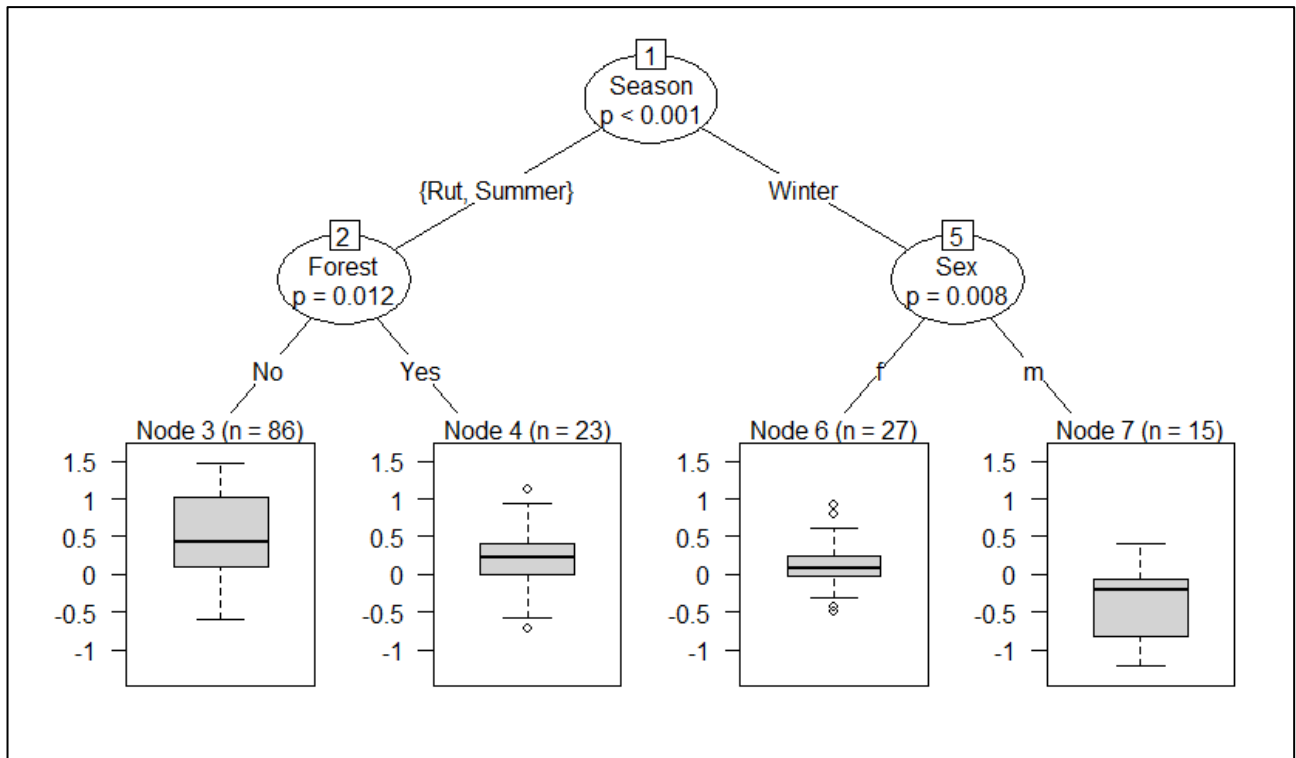


Figure 11: Conditional inference tree on the influence of the factors sex, area, forest, year and season on the home range size ( $\alpha = 0.05$ ).

Table 3: AICc-based ranking of candidate linear mixed-effects models explaining variation in home range size. Only the five highest-ranked models are shown and X indicates that the variable was included in the model. Specifications are given for the two most suitable models ( $\Delta\text{AICc} < 2$ ;  $\alpha = 0.05$ ).

Model		Area	Forest	Sex	Season	Year	Chamois ID	$\Delta\text{AICc}$	AICc weight
Home range size	1		X		X		X	0.00	0.45
	2		X	X	X		X	1.40	0.22
	3			X	X		X	2.54	0.13
	4	X	X		X		X	3.99	0.06
	5				X		X	4.26	0.05
		<b>Estimate</b>	<b>Std. error</b>	<b>t-value</b>	<b>p-value</b>				
<b>Model 1</b>									
(Intercept)		0.418	0.080	5.282	<0.001				
Forest (vs. no forest)		-0.383	0.119	-3.211	0.002				
Season summer (vs. rutting season)		0.120	0.090	1.322	0.189				
Season winter (vs. rutting season)		-0.362	0.099	-3.668	<0.001				
<b>Model 2</b>									
(Intercept)		0.473	0.085	5.598	<0.001				
Forest (vs. no forest)		-0.312	0.125	-2.491	0.016				
Male chamois (vs. female chamois)		-0.203	0.110	-1.847	0.072				
Season summer (vs. rutting season)		0.127	0.089	1.421	0.158				
Season winter (vs. rutting season)		-0.362	0.097	-3.710	<0.001				

## 4 Discussion

Overall, the present study was able to demonstrate that the calculation method, seasons (summer, rut and winter), sex and habitat characteristics (forest vs. no forest) can all have an important influence on the HR size of chamois. In summary, the evaluations have shown that the two methods (ctmm vs. KDE) only differed significantly during the rut (Appendix A1). Moreover, significant differences in HR sizes for female and male chamois occurred across all seasons examined within the study area Il Fuorn and during the rut at the study area Val Trupchun (Figure 7 & 8). In addition, no differences between the study areas were found when comparing the same sexes between areas (Appendix A2 & A3). Finally, space requirements of forest chamois and ridge chamois at Il Fuorn differed significantly in females during summer and in males during the rut (Figure 9 & 10).

### 4.1 Ctm vs. KDE

An essential part of the calculation of HR sizes with the ctm method includes the visual diagnostics of the data by means of variograms (Calabrese et al. 2016). This makes it possible to check whether the structure of the data has autocorrelation (Morato et al. 2016). The visual inspection using the plotted semi variance as a function of time has shown that there is also a spatial and/or velocity (time) autocorrelation for the data used in this work. This finding was confirmed on the basis of the AIC model selection, which highlighted either the Ornstein-Uhlenbeck (OU) or the Ornstein-Uhlenbeck Foraging (OUF) model as the most suitable approach. The spatial autocorrelation is taken into account in both models and the velocity autocorrelation is additionally included in the OUF (Calabrese et al. 2016). The comparison of the resulting HR sizes with those of the KDE method revealed that there was a significant difference during the rut, but not during the summer and winter (Appendix A1). However, since the median space requirement during the rut was similar as in summer and significantly larger than in winter, a possible difference due to the autocorrelation of the data does not seem likely, as for example reported by Fleming et al. (2015). So there has to be another reason why the ctm method tended to overestimate the HR size during the rut (e.g. Appendix B2). A possible explanation could be the basic prerequisite for the ctm method that the semi variance of the variogram should approach an asymptote with increasing time interval that is proportional to HR size (Calabrese et al. 2016). In other words, if the individual did not cross the entire HR size within the examined period, no asymptote is shown and the data is therefore not suitable for such an analysis. According to Calabrese et al. (2016), this is the case if the recording period is too short or the individual migrates and there is a relocation. As shown in this work, this applied to male chamois, who migrated during the rut (Appendix B2). As a result, the model contained a great deal of uncertainty about the actual space requirement, which probably led to overestimated HR sizes and confidence intervals. Overall however, there was a high degree of agreement between the KDE and ctm methods examined (Figure 6). There are also other methods too, such as LoCoH (Getz et al. 2007) or

MCP (Mohr 1947; Hayne 1949) which in turn would have probably provided different results, better or less well adapted to the actual HR sizes. But since nowadays GPS data is used almost exclusively due to the advancement of technology (Kays et al. 2015), non-autocorrelated data is the exception (Fleming et al. 2015). Accordingly, methods that assume independent and identically distributed data (IID), including geometric methods such as LoCoH and MCP, are known to deliver HR sizes that are overall too small (Noonan et al. 2019). However, both older and newer methods benefit from either increasing the sampling frequency or by extending the sampling duration (Noonan et al. 2019). Regardless of which methods are used in the future, the procedure should be standardized as much as possible and the methods and data used should be described in detail (Gregory 2016). This allows future studies to be compared with one another and the methods to be improved.

## 4.2 Space requirements of chamois within the SNP

Season, sex and habitat type all had a major influence on HR sizes of chamois in the SNP (Table 3 and Figure 11). On the other hand, there were no differences between the two study areas, and the space requirements were relatively constant over the course of the study period. Compared to other studies to date, the resulting HR sizes are relatively large (Table 1 and Table 2). However, it should be kept in mind that none of the studies listed used exactly the same methodology (HR estimator, temporal scale, sample size, data acquisition) and therefore a direct comparison would not be appropriate.

### 4.2.1 Sex-specific seasonal home ranges sizes

Due to the alpine location, it is not surprising that the seasons examined (summer, rut and winter) had a crucial influence on the space requirements of chamois. Both climatic conditions and availability of food are subject to pronounced seasonal changes (Brivio et al. 2016). During winter, there is usually a food shortage which is associated with reduced temperatures and snow. Alpine landscapes are also highly heterogeneous in terms of climatic conditions and food availability during spring and summer (Pettorelli et al. 2005). As a result, mountain-dwelling species are subject to pronounced seasonal changes and therefore have to make compromises (trade-offs) in order to meet all of their needs. If such compromises lead to a change in the spatial distribution, this can also be seen from the individual HR sizes.

As the present work shows, both sexes had significantly smaller HR sizes in winter compared to the rut (Table 3 and Figure 11). This finding is consistent with studies by Hamr (1985) and Nesti et al. (2010), who also found a larger space requirement during the warm compared to the cold season (Table 1). From an energetic point of view, a reduction in the area used is advantageous because movements in deep snow cost a lot of energy (Boldt 2003). However, in the Val Trupchun the winter

HRs between female and male chamois were not significantly different (Figure 7). In the Il Fuorn study area, on the other hand, there was a significant difference with larger HR sizes for female chamois (Figure 8). A possible explanation could be that the females stay at higher altitudes even during the cold season, as reported by Nesti (2004). Due to the deeper snow, the already scarce food resources are even more difficult to access, which means that food has to be searched for more extensively and the space requirement increases. Another reason for the larger HRs in females could be due to the fact that proportionally more forest chamois were present among the males at Il Fuorn (Table 2). As the analyses have shown, forest chamois had significantly smaller HR sizes than ridge chamois (Table 3).

Unlike during winter, the HR sizes of chamois did not differ significantly in summer compared to the rut, when data were combined for both sexes (Table 3 and Figure 11). However, if the data was divided according to sex there were clear differences. The median summer HRs of female chamois (Il Fuorn = 521 ha, Val Trupchun = 636 ha) were up to five times larger than for males in both study areas (Il Furon = 97 ha, Val Trupchun = 137 ha; Table 2). Basically, it can be assumed that the larger space requirements of female chamois resulted due to the higher energy demands during summer compared to the males (Unterthiner et al. 2012). In the case of mountain goats in Canada, Hamel and Côté (2008) demonstrated that lactating females increased the time spent foraging at the expense of time spent laying down. Another important aspect that could contribute to the larger space requirement of female chamois is based on the fact that they live in groups (Ingold et al. 1998; Ruckstuhl and Ingold 1998, 1999; in Nesti et al. 2010). Due to the higher number of individuals, it is expected that a larger amount of food resources is required, which could lead to an increase in HR size (Nesti et al. 2010). As a result, a significant difference between the sexes again resulted for the study area Il Fuorn (Figure 8). A possible explanation for the non-significant differences in the Val Trupchun is described by Anderwald et al. (2016). As a consequence of interspecific competition with red deer, chamois move to steeper slopes which also have a lower productivity than available on average. As a result, males are also forced to use larger HRs which probably narrows the difference to the females.

During the rut, the opposite pattern of the summer results was found with around two and a half times larger HR sizes for males (Il Fuorn = 435 ha, Val Trupchun = 249 ha) compared to females (Il Fuorn = 188 ha, Val Trupchun = 131 ha; Table 2). However, the significantly larger HRs of male chamois must be put into perspective. This is because the present work does not consider the two different mating strategies of males: migratory or resident (Lovari et al. 2006; Nesti et al. 2010; Unterthiner et al. 2012). HR sizes of resident males (median < 100 ha) do not differ significantly between seasons and the shift in altitudinal movements is small. The migrating males in turn follow the females to higher altitudes, which results in significantly larger HRs compared to the residents (Lovari

et al. 2006). The authors attribute one possible explanation for the different behaviour to the reproductive success during the rut. If there is no snow, female chamois remain at higher altitudes searching for food and the migrating males have higher mating success. Conversely, the territorial males are more successful when there are snowy conditions that cause the females to move to lower elevations (Hardenberg et al. 2000). Furthermore, the larger rutting HRs of non-territorial migrating males compared to the females may be explained by the fact that these have to move around to find mating partners as well as to compete with other opponents.

#### 4.2.2 Forest chamois vs. ridge chamois

Of a total of 39 chamois in the study area Il Fuorn, 14 were classified as forest chamois and 25 as ridge chamois. Overall, forest chamois had significantly smaller HR sizes compared to ridge chamois, and seasonal space requirements varied between 12 and 1391 ha within habitat types (Table 2 and Table 3). Similar HR sizes have also been found in forest and ridge chamois in the Berchtesgaden biosphere reserve (100 – 800 ha), with the seasons spring, summer and winter being examined (Bögel et al. 2001). While forest chamois have a space requirement of 12 – 262 ha within seasons, this varies much more for ridge chamois with 72 – 1391 ha (Table 2). Accordingly, there is a less pronounced seasonal change in the habitat quality for the forest chamois, which was also found by Bögel et al. (2001). However, the seasonal and sex-specific analysis showed that the large space requirement of the ridge chamois compared to the forest chamois was significantly influenced by the females in summer and by the males during the rut (Figure 9 and Figure 10). The female ridge chamois used areas at the upper edge of the forest, alpine pastures, rocks and even switched to the north-exposed mountain side. An obvious reason for visiting higher locations is the higher quality of the vegetation, which contains more minerals and proteins than lower areas during summer (Johnston et al. 1968; Shank 1985). However, this is also likely to result in a higher heterogeneity of the habitat, which could lead to a larger HR size to cover all needs. This effect could also be enhanced by living together in groups. In contrast to the females, there is a clear cause for the significant difference between the male forest chamois and the male ridge chamois during the rut. As mentioned above, there are two different tactics in males during the rut. On the one hand there are the resident male chamois, which can be classified as forest chamois by their small HR sizes in lower forested areas. On the other hand, there are the migrating male chamois, which are mostly found above the tree line and furthermore have larger HR sizes and can therefore be classified as ridge chamois. Overall, the findings offer an insight into the complex differences between forest and ridge chamois in the SNP. Whether a life for chamois in or outside of the forest brings a greater advantage in the SNP, could only be guessed. For more precise statements, factors such as the body constitution and condition of the chamois should also be considered. For example, Baumann and Struch (2000)

were able to determine that forest chamois were larger compared to ridge chamois, tended to have more kidney fat and were heavier on average in late summer.

### 4.3 Conclusion

Overall, the present work offers an insight into the HR sizes of chamois in the Swiss National Park. As a result, existing knowledge about the spatial requirements of the species within the nature reserve (Boschi and Nievergelt 2003; Filli and Campell 2006) could be partially checked and supplemented. In addition, it could be demonstrated that both habitat selection and the calculation method can have a significant impact on the resulting HR size.

In summary, the comparison of the two methods for calculating the HR sizes showed that the kernel density estimation and the continuous time movement modelling differed significantly only during the rut. It cannot be conclusively assessed in this work whether the autocorrelation of the data alone led to this result. Consequently, the first hypothesis (H1) cannot be confirmed or rejected. Moreover, space requirements of both sexes varied considerably over the course of the year. Significant differences between males and females during the summer, rut and winter occurred at the study area Il Fuorn and only during the rut in the study area Val Trupchun. Accordingly, the second hypotheses (H2) can be confirmed and the third hypothesis (H3) cannot be confirmed. On the other hand, the fourth hypothesis (H4) can be confirmed, since the HR size did not differ significantly between the two study areas. And at least, also the fifth hypothesis (H5) can be confirmed, since forest chamois had significantly smaller HR sizes overall and even males during rut and females during summer.



## 5 References

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## Appendix A: Additional boxplots and model overview of the data analysis regarding the median home range sizes of the chamois in the Swiss National Park

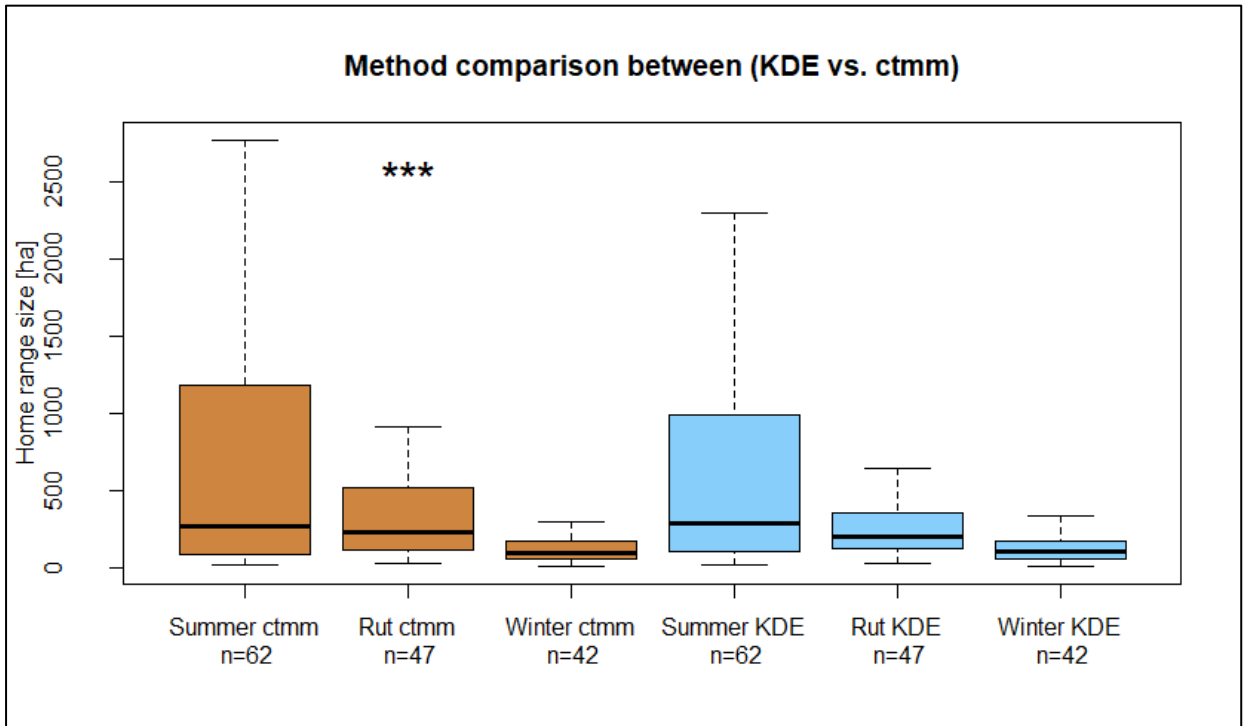


Figure A1: Comparison of the calculated home range sizes during summer, rut and winter between the two methods kernel density estimation (KDE; light blue) and continuous time movement modelling (ctmm; brown; Wilcoxon-Test with  $\alpha = 0.05$ ; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

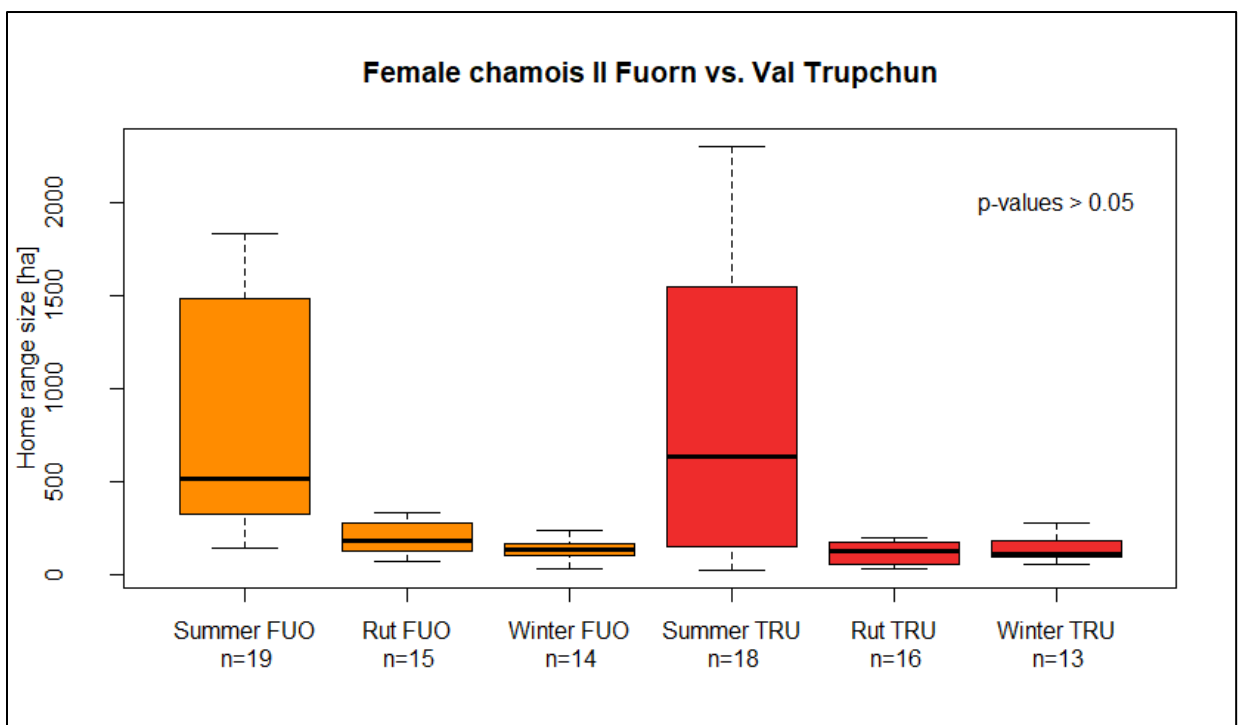
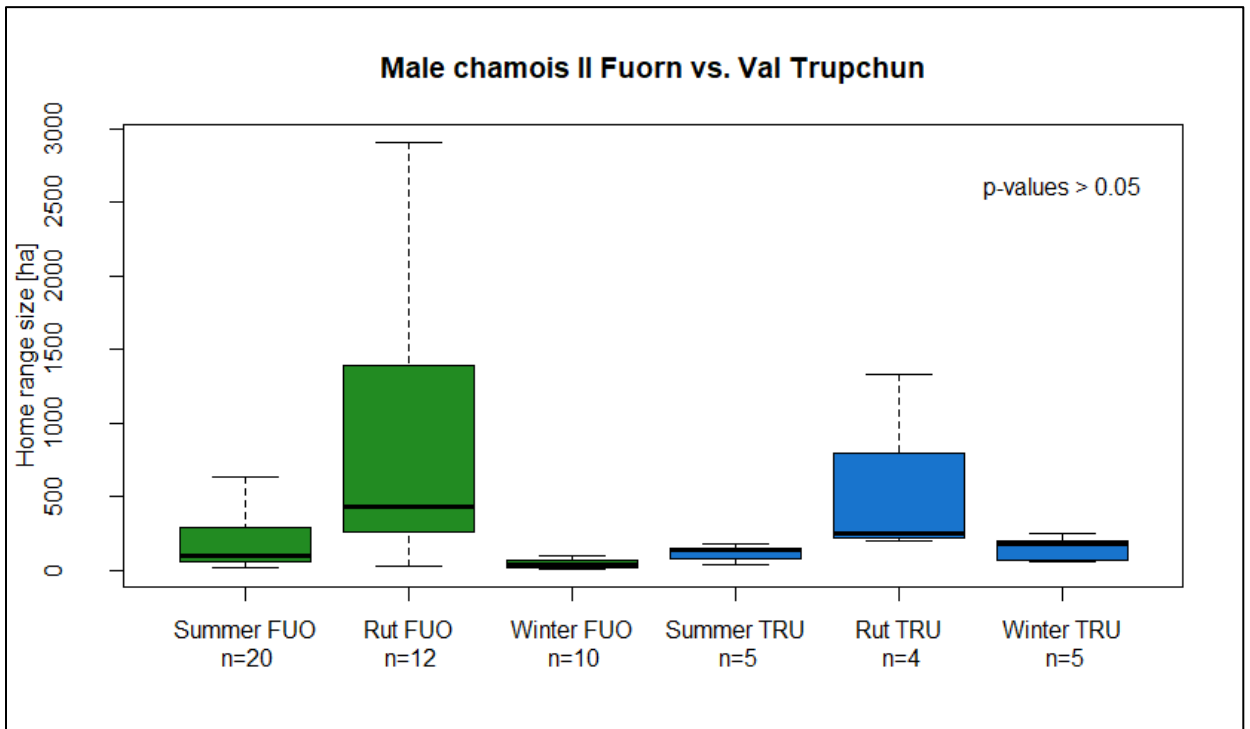


Figure A2: Comparison of female chamois between II Fuorn (orange) and Val Trupchun (red) during the summer, rut and winter (Mann-Whitney U-Test with  $\alpha = 0.05$ ; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).



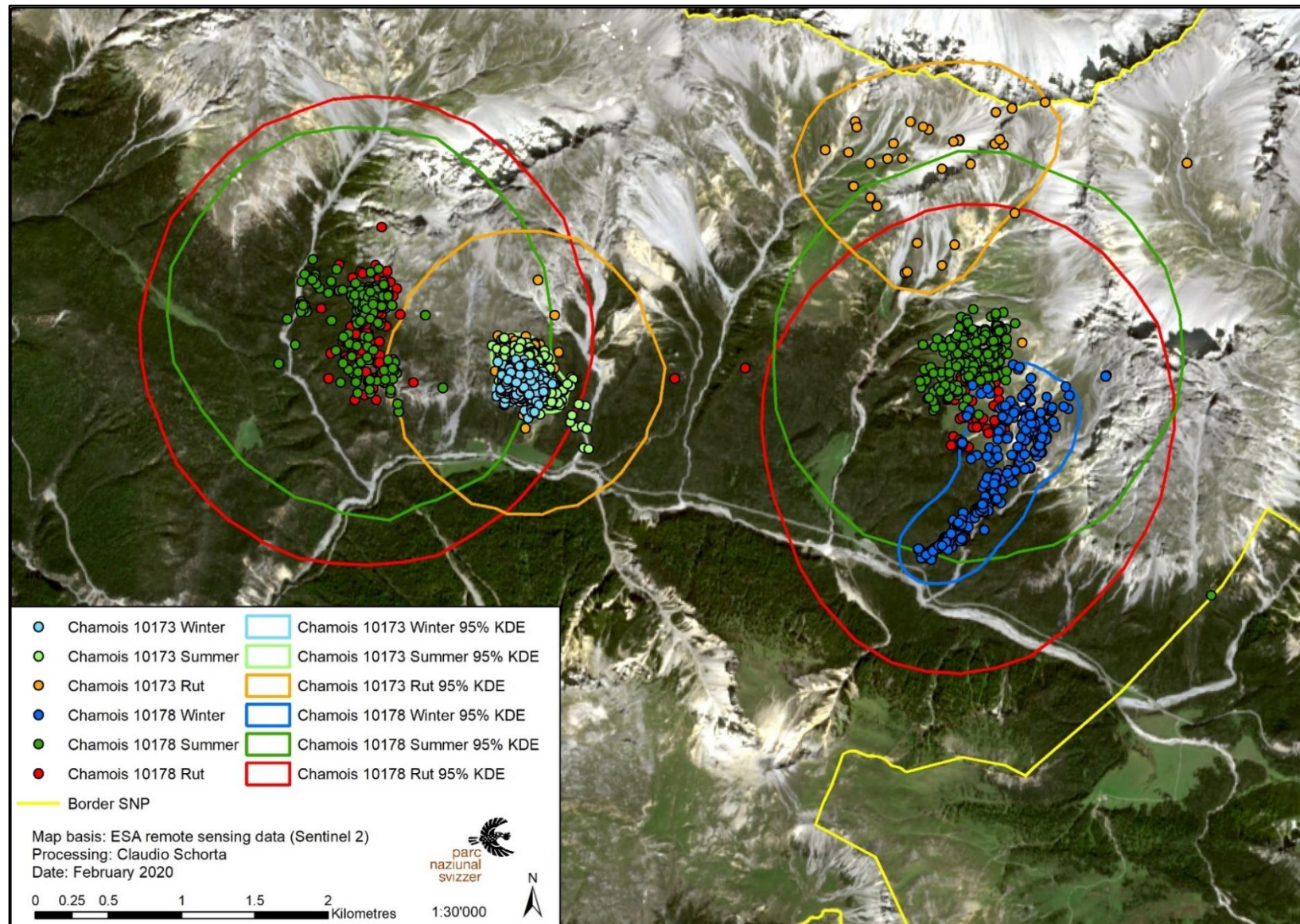


**Figure A3: Comparison of male chamois between II Fuorn (green) and Val Trupchun (blue) during the summer, rut and winter (Mann-Whitney U-Test with  $\alpha = 0.05$ ; \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).**

**Table A4: Overview of the AICc-based ranking of all candidate linear mixed-effects models explaining variation in home range size. X indicates that the variable was included in the corresponding model.**

	Model	Area	Forest	Sex	Season	Year	Chamois ID	$\Delta$ AICc	AICc weight
Home range size	1		X		X		X	0.00	0.45
	2		X	X	X		X	1.40	0.22
	3			X	X		X	2.54	0.13
	4	X	X		X		X	3.99	0.06
	5				X		X	4.26	0.05
	6	X	X	X	X		X	4.95	0.04
	7		X		X	X	X	6.55	0.02
	8	X		X	X		X	7.19	0.01
	9	X			X		X	8.64	0.01
	10		X	X	X	X	X	8.80	0.01
	11			X	X	X	X	10.59	0.00
	12	X	X		X	X	X	10.71	0.00
	13				X	X	X	11.63	0.00
	14	X	X	X	X	X	X	12.57	0.00
	15		X				X	14.77	0.00
	16	X			X	X	X	15.94	0.00
	17		X	X			X	17.19	0.00
	18	X	X				X	17.95	0.00
	19			X			X	19.13	0.00
	20						X	19.71	0.00
	21	X	X	X			X	19.93	0.00
	22		X			X	X	20.53	0.00
	23	X		X			X	23.59	0.00
	24		X	X		X	X	23.73	0.00
	25	X	X			X	X	23.97	0.00
	26	X					X	24.15	0.00
	27					X	X	26.39	0.00
	28			X		X	X	26.58	0.00
	29	X	X	X		X	X	26.81	0.00
	30	X				X	X	30.77	0.00
	31	X		X		X	X	31.11	0.00

**Appendix B: Additional GIS maps for the visual comparison of the resulting seasonal median home range sizes between the ctm and KDE method**



**Figure B1: Estimated 95% KDE home range sizes for a male forest chamois (ID 10173) and a male ridge chamois (ID 10178) during summer, rut and winter located at Il Fuorn.**

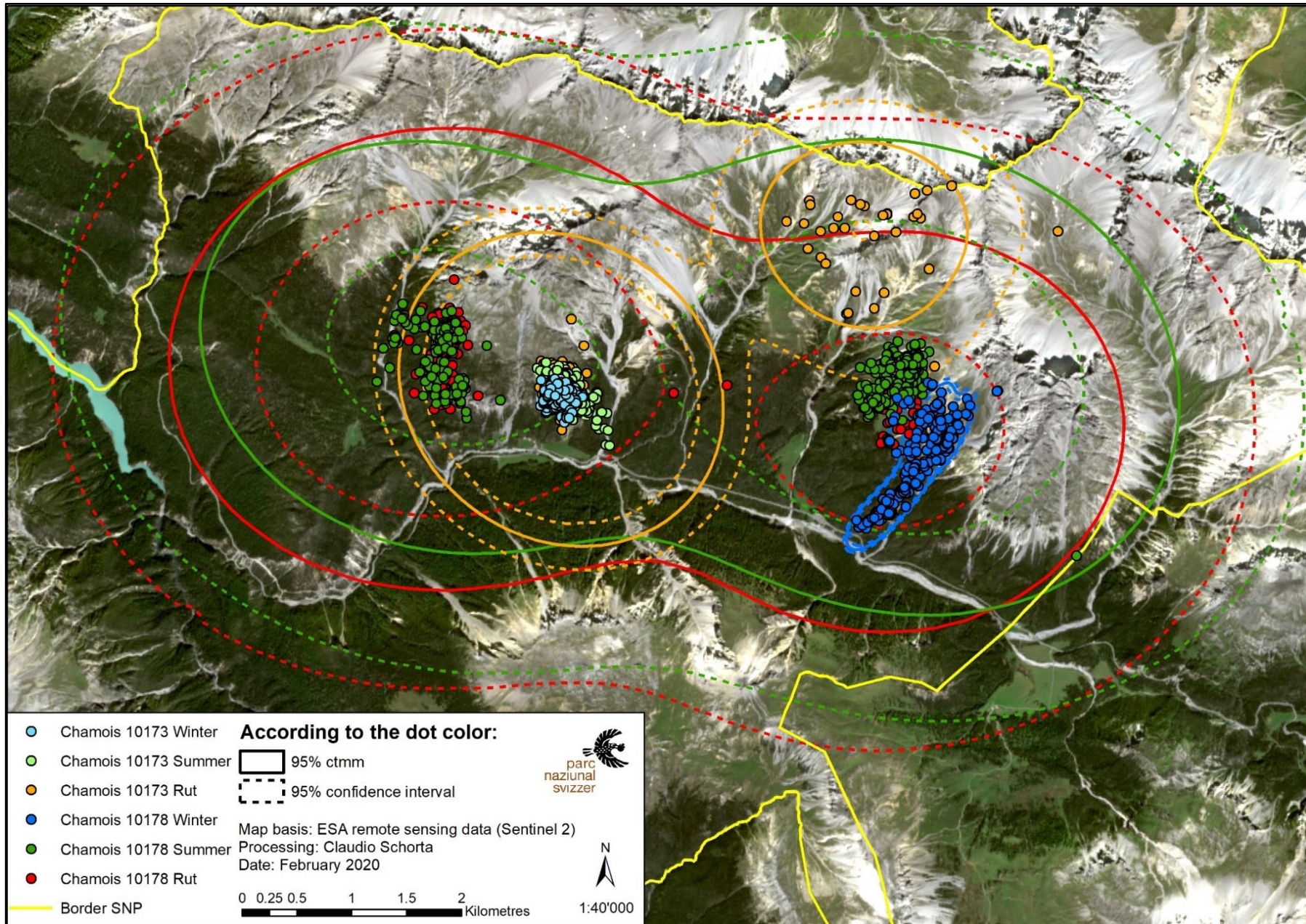


Figure B2: Estimated 95% ctmm home range sizes for a male forest chamois (ID 10173) and a male ridge chamois (ID 10178) during summer, rut and winter located at Il Fuorn. The dashed lines correspond to the 95% confidence interval for the ctmm method.

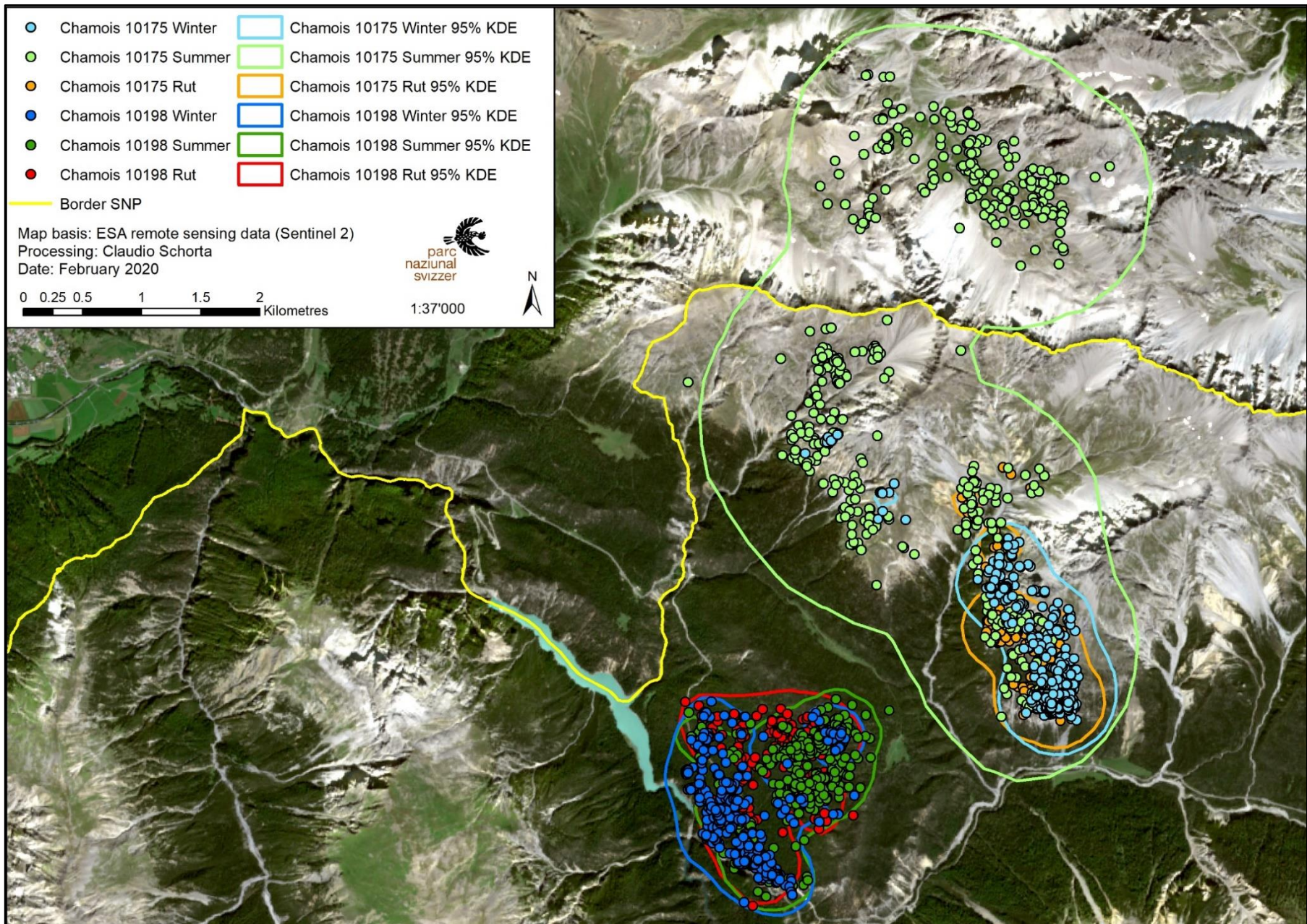


Figure B3: Estimated 95% KDE home range sizes for a female forest chamois (ID 10198) and a female ridge chamois (ID 10175) during summer, rut and winter located at Il Fuorn.

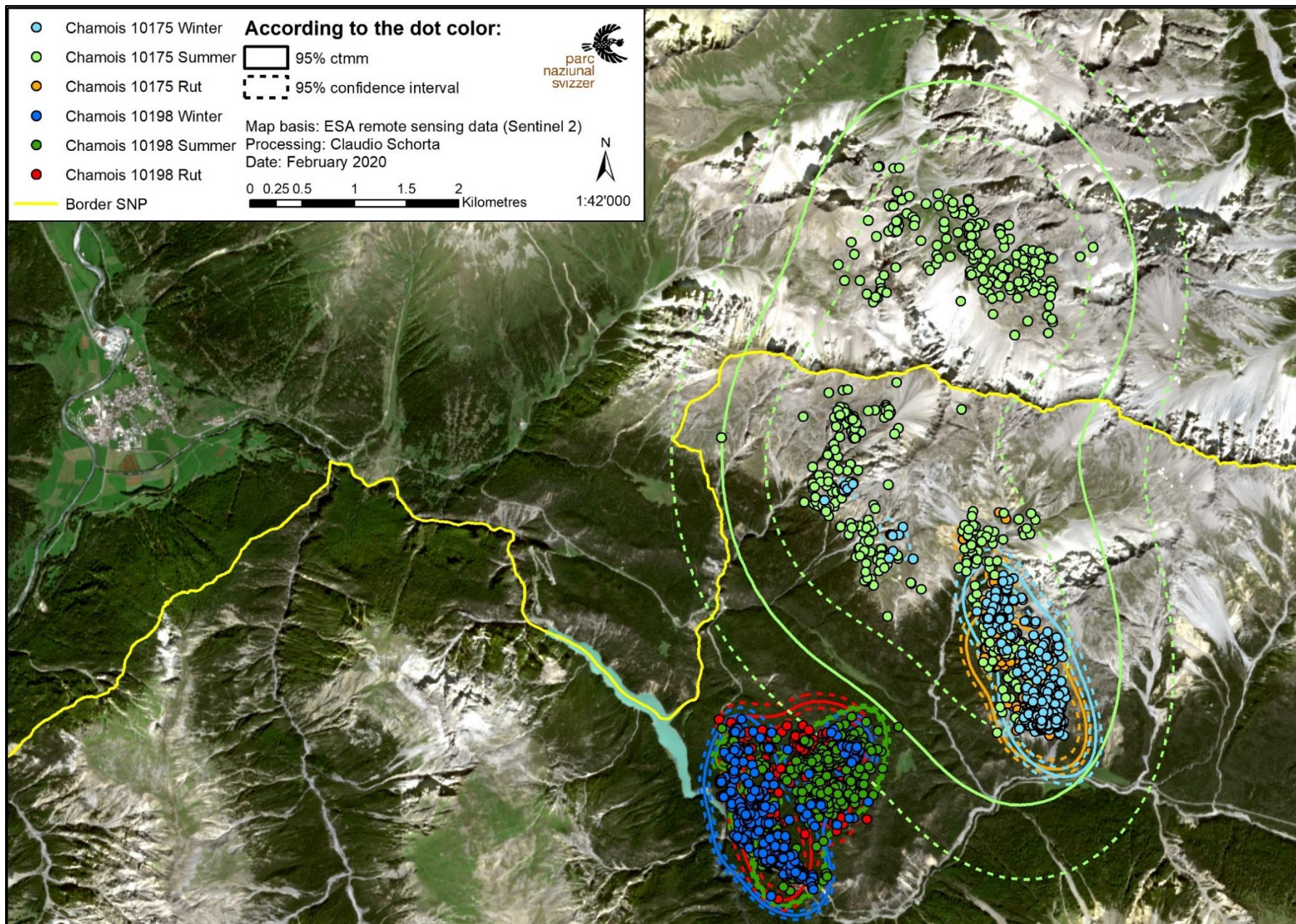


Figure B4: Estimated 95% ctmm home range sizes for a female forest chamois (ID 10198) and a female ridge chamois (ID 10175) during summer, rut and winter located at Il Fuorn. The dashed lines correspond to the 95% confidence interval for the ctmm method.