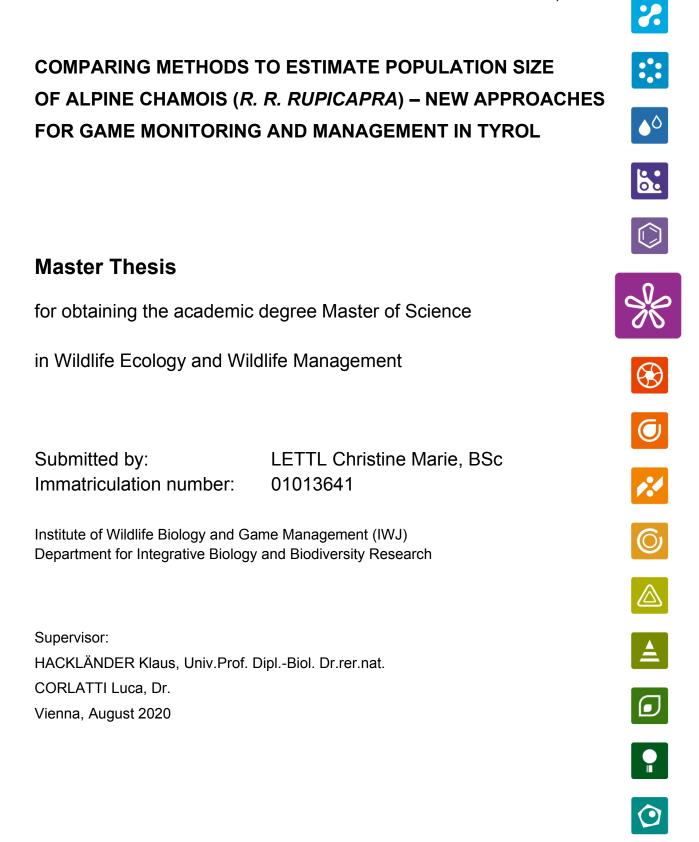


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Declaration in lieu of oath

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 acknowl-edged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

15.08.2020

Date

Signature

Abstract

Monitoring population size is a fundamental instrument for the management of hunted species as the Alpine chamois (*Rupicapra r. rupicapra*). However, population abundance is not the only point of interest for chamois management, since a biased population structure can have a long-time negative impact on the population. For future management it is important to monitor the population trend and structure and to preserve a stable population and ensure a sustainable hunting management. As monitoring of mountain dwelling ungulates can be very challenging, different monitoring approaches were tested in this study and complemented with analyses of hunting bag data. In five typical chamois habitats in Tyrol the monitoring methods were conducted using block counts, an independent double observer approach and a fecal DNA capture-mark-recapture survey. I analysed the trends of available hunting bag data, the survival probability and age-specific mortality for each sex.

Results of block counts were useful to detect minimal population size for the reference areas. Counts after the parturition period around July showed the highest amount of adult females and kids and a higher female-kids-ratio (59 %). In October female-kids-ratio was 55 %, in November it was considerably lower (37 %). The change of sex-ratio indicated a higher detectability of males during fall compared to the counts in summer. The double observer approach underlined the importance of having groups of at least two observers for conducting counts. The DNA analyses of fecal samples performed poorly and the success rate of 17 % for the individual profiles was too low for a reliable, statistical analysis. The sampling set-up for non-invasive samples in an alpine habitat should be given more attention to achieve better DNA quality and a higher success rate of DNA extraction.

The analyses of harvest data showed a slightly decreasing trend of harvested individuals and a higher female survival. Even though in chamois also males have proven to reach late age, more than twice as many females as males were found to reach the age of 15 years and older. For future management periodic block counts should be considered to detect changes in the population trends and structure and to compare these trends with the conclusions drawn with the hunting bag data.

Kurzfassung

Monitoring ist ein grundlegendes Werkzeug für das Management von jagdbarem Wild, wie der Alpengams (*Rupicapra r. rupicapra*). Bei der Alpengams ist jedoch nicht nur die Populationsentwicklung von Interesse, sondern auch die Populationsstruktur, da diese für einen stabilen Bestand ausschlaggebend ist. Für ein nachhaltiges, dem Bestand angepasstes Management ist das Monitoring dieser Daten notwendig.

Dazu wurden verschiedene Monitoringmethoden in fünf typischen Gamslebensräumen in Tirol getestet. Einerseits wurden "Block Counts", also direkte Zählungen, durchgeführt, des Weiteren eine Korrektur mittels "Independent Double Observer" sowie eine Fang-Markierung-Wiederfang Methode mittels DNA-Analysen von Losungsproben. Ergänzend dazu wurden von den verfügbaren Abgangsdaten verschiedene Trends sowie Mortalitätsdaten ermittelt.

Die Zählungen lieferten Angaben zu der minimalen Populationsgröße in den Referenzgebieten. Zählungen im Juli, nach der Setzzeit, wiesen den höchsten Anteil an Geißen und Kitzen und das höchste Geiß-Kitz-Verhältnis (59 %) auf. Im Oktober lag das Verhältnis bei 55 % und im November nur noch bei 37 %. Die Veränderung des Geschlechterverhältnisses bei den Zählungen lässt darauf schließen, dass Böcke im Herbst sichtbarer sind als im Sommer.

Die Korrektur mittels "Double Observer" zeigt, dass es wichtig ist Zählteams von zwei Beobachtern für die Zählungen zu bilden.

Die DNA-Analyse der Losungsproben wies leider eine sehr niedrige Erfolgsrate von 17 % auf, womit die Ergebnisse zu gering für eine statistische Auswertung waren. Die Probensammlung im alpinen, offenen Gelände sollte noch genauer geplant und die DNA-Zerfallsraten ermittelt werden, damit die Erfolgsrate der DNA-Analysen verbessert werden kann.

Die Jagdstatistik zeigt einen leicht abnehmenden Trend der erlegten Stücke sowie eine höhere Überlebenswahrscheinlichkeit für Geißen. Obwohl auch Böcke ein hohes Alter erreichen können (älteste Böcke im Datensatz 20 Jahre), erreichen mehr als doppelt so viele Geißen das Alter von 15 Jahren oder mehr.

Für zukünftiges Management sollten regelmäßige Zählungen durchgeführt werden, um Populationstrends und -strukturen zu ermitteln sowie mit den Ergebnissen der Analyse der Abgangsdaten verglichen bzw. ergänzt werden.

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1 Introduction

The Alpine chamois (*R. r. rupicapra*) is a mountain ungulate widely distributed on the Tyrolean Alps. Chamois hunting has a long-standing tradition in Alpine countries. In the 19th century, anthropogenic influences such as overexploitation and trophy hunting led to the decline of many populations. Following action plans to protect chamois, populations recovered since the mid-20th century. Nowadays, populations are not endangered, yet anthropogenic influence still plays an important role in chamois population dynamics; in addition to that, several diseases such as sarcoptic mange (caused by *Sarcoptes scabiei*), infective kerato-conjunctivitis (caused by *Mycoplasma conjunctivae*), and pasteurellose, together with climatic changes and interspecific competition with other alpine ungulates (as red deer and Alpine ibex) may negatively impact on wildlife dynamics, so that many hunted and also unhunted chamois populations are decreasing again (Corlatti et al., 2019; Loison et al., 1996; Meile, 2014; Pioz et al., 2008; Rughetti and Festa-Bianchet, 2012; Schweiger et al., 2015; Willisch et al., 2013).

Such a trend has been recently suggested to occur also in Tyrol, despite the abundance of suitable habitats. In Tyrol, wild ungulates are subject to yearly hunting plans, subdivided in sex and age classes. Between 2007 and 2016 on average 7.486 chamois were harvested every year. Available hunting bag data suggest a shortage of harvested individuals of class I (males \geq 8 years of age, females \geq 10 years of age). Age class II (4 – 7 years) of males on the other hand shows a strong overexploitation because of harvesting. For example, in the hunting year 2013/14¹ the hunting plan for age class I was only fulfilled up to 64 % while the harvest in age class II was exceeded by 150 %.

The yearly management plans for hunting in Tyrol are based on four pillars: the estimation of population abundance and structure, the forest condition, the prevalence of diseases and the fulfilment of hunting plans of the previous three years. Estimates of the population are based on observations conducted by local hunters. Available count data is rare and incomplete and often only a subjective estimate of the responsible hunters. This results in very vague data about chamois population size in Tyrol and poor support for management actions, e.g. change of hunting plans or management strategies. Thus, this study is part of a project to build up a new, standardised monitoring protocol for the management of chamois in the province of

¹ Duration of one hunting period (Jagdjahr) in Tyrol: 1.4. – 31.3.

Tyrol. For this purpose, the study focuses on the monitoring methods and on the analysis of hunting bag data to get information about the hunted population in the previous years.

1.1 Population abundance and structure

Assessing population size is not the only point of interest for chamois management. Since chamois reproduction rates are not as high as those of other native ungulates in Tyrol, such as roe deer (Capreolus capreolus) or red deer (Cervus elaphus), a biased population structure can have a long-lasting negative impact on population dynamics. In well structured, stable populations females generally start to reproduce at the age of four, while it normally takes longer for males to get a chance to mate successfully, at least in protected populations (6 years, cf. Corlatti et al., 2015a). The rut takes place between mid-October and mid-December (Miller and Corlatti, 2009). During this time, males experience a strong body mass loss, due to the physical stress of the rut (Garel et al. 2009; Rughetti & Festa-Bianchet 2011). Moreover, Meile and Bubenik (1979) observed that, in a population with a biased sex-age structure the rut tends to last longer. In their study old males were missing and at the same time the sexratio was shifted in favour of females. A lot of females were not successfully fertilized by December and thus still able to conceive in January or February. If the rut lasts longer, individuals may use up a lot of their energy, which they would need to survive the winter months. Lovari and Cosentino (1986) observed that mainly males of nine years and older were able to herd a group of females during the rut. If old, dominant males are missing in a population, direct conflicts between males could happen more often, because physical differences will be smaller. Also, males may spend more time and energy to secure mating with females. As a potential consequence, there could be higher an energy loss of the individuals during rut and in the following possibly a higher winter mortality of males. Therefore, information about population dynamics of the last years or decades as well as about the current population size and structure are needed to adapt future management, especially regarding hunting. Past data could be reconstructed from hunting bag data. Monitoring approaches are needed to investigate the current population trends.

BOKU, IWJ

1.2 Hunting management

Hunting is one of the main mortality factors for chamois in Tyrol. The hunting bag is registered yearly and provides long-term data of the hunted population. Harvest data can be used for multiple analyses such as harvest age and sex structure, life table, population reconstruction and change-in-ratio. For white-tailed deer (*Odocoileus virginianus*) all of these methods were not sufficient as a single monitoring instrument for precise herd management, but could be used as indicative of a population's probable position on the growth curve (Roseberry and Woolf, 1991). Bender and Spencer 1999 used harvest data for population reconstruction and identified this method as a useful and simple tool together with mark-resight data for wildlife and hunting management.

The Tirolean hunting association (Tiroler Jägerverband) has reasons to believe that chamois are decreasing and population structure is not stable, i.e. that there are less older individuals than in a natural population. Hunting regulations and hunting methods haven't changed much in the last 20 years. An analysis of hunting bag data of chamois in Tyrol, e.g. the mean survival rate of hunted chamois, therefore should be able to identify trends of the real population or respective population parameters.

1.3 Monitoring methods

In addition to the above-mentioned hunting management data, different monitoring tools can be used to support local management and to provide the basis for sustainable harvesting. In this study, different monitoring methods are tested in several reference areas and evaluated in terms of suitability and efficiency for future chamois monitoring in Tyrol. To get information about the population structure and abundance in ungulates many different methods can be found in the literature. To monitor chamois over a large area as Tyrol, methods should be noninvasive and feasible regarding costs and effort of personnel and material.

In mountain areas monitoring wild ungulates is still a challenge. Especially because different monitoring methods such as distance sampling, line transect or point counts, dung or track counts, may perform differently in different landscapes, under different field conditions and for various species (Singh and Milner-Gulland, 2011). For mountainous habitats Singh and

Milner-Gulland 2011 considered point counts and camera traps as relevant monitoring methods. Furthermore, capture-mark-resight methods are for wild ungulates in mountain areas the "golden standard" to estimate population size (Largo et al., 2008; Loison et al., 2006; Neal et al., 1993). For practical reasons, however, the most widely used methodology is direct counting, although it is known to underestimate population size (Festa-Bianchet & Apollonio 2003, Sinclair et al. 2006).

Especially in open areas with good visibility of animals, total block counts (BC) are common to assess abundance of mountain ungulate populations (Largo et al., 2008). A study of Herrero et al. (2011) in the Spanish Pyrenees determined BC as valuable tool to estimate minimum population size and to set yearly hunting quotas for chamois. Further investigations confirmed, that in study areas with good visibility, the detectability of chamois is high using BC and the underestimation bias negligible small, while line transect sampling performed poorly in the mountain environment, due to the fact that the terrain doesn't allow a random distribution of transects (Corlatti et al., 2015b).

Different factors such as meteorological conditions, season or different detectability of sexage-classes could however also bias the results of counts (Aublet et al., 2009; Corlatti et al., 2015b). A further difficulty in BC, besides the fact that it is impossible to detect every single animal even in open areas, is that also different observers may detect a different number of animals. This means detection probability can vary between observers, places and time (Nichols et al. 2000, Norvell et al. 2003). Therefore, it is important to consider this as possible source of errors and estimate the detection probability from point counts to take into account the influence of observers on counting results.

As mentioned above, capture-mark-recapture is also widely used in wildlife monitoring. Classic invasive capture-recapture methods however are often too costly and complex to be carried out sustainably in mountain ungulate populations. In a recent study, Ebert et al. (2012) discussed the use of fecal DNA to estimate the population size of wild boar in Germany and used a non-invasive population estimation approach. A similar approach for chamois could be a feasible alternative to e.g. the capture of animals or hair sampling (Croose et al., 2019) and might be useful in mountain areas, where invasive methods are very time consuming and can lead to high costs for personnel and transport.

2 Questions and hypotheses

2.1 Monitoring methods

In this study, I use different monitoring approaches in reference areas to test their suitability for future chamois monitoring and game management. Firstly, direct observations are carried out in form of block counts (BC) and a double observer (DO) approach. Additionally, a non-invasive genetic capture-mark-recapture (CMR) approach based on feces sampling will be applied for chamois in alpine habitat. This approach has never been used in chamois in Austria, and it might open up avenues for investigating chamois abundance in other, traditionally unexplored areas, e.g. forest habitats.

For this study I propose following hypotheses for the monitoring methods:

- **1.a.** BC should detect a higher minimum number of chamois when carried out more than one time per year, as if only one time in summer. Due to the natural life cycle of chamois, the habitat use and social groups are changing over the year. Females for example will settle apart from the group in June during the partition period to give birth to their kids. After some days, normally until end of June, most of the females will build larger groups again with kids and female yearlings. Males however, live mainly solitary or in small groups until the rut (Boschi and Nievergelt, 2003). As they are solitary, they are often difficult to count, because they are less prominent than larger groups of female chamois with kids. Therefore, there could also be differences in the detectability of different sex-age-classes over the year.
 - a.1. The observed sex-ratio in BC will be more balanced in fall (October and November) than in summer. The difference of the sex-ratios in reference areas is changing significantly between count dates.
 - **a.2.** In area E, BC within the small reference area will detect the same population trends as in the whole project area E.
- **1.b.** The DNA-CMR method will detect a higher populations size than BC in open alpine areas because CMR will correct for imperfect detectability. Furthermore, the proportion of males in detected individuals will be higher than with BC.

- 1.c. The detection probability in counts of wildlife populations can always be influenced by various factors, e.g. weather, wind or different interactions. Doing direct counts with different observers also includes a probability of errors in the detection rate. Hence, I hypothesise that:
 - **c.1.** Including the DO approach will correct the count of one observer significantly.
 - **c.2.** Correcting the count with the detection rate of both observers, the estimated population size will increase significantly.

2.2 Hunting management

Secondly, I will test if the hunting bag data of Tyrol can be additionally used for estimating demographic parameters.

If the population is declining and younger, as supposed by the local experts, the hunting bag data also should indicate this, as hunters try to harvest primarily old individuals. Of course there could be large differences on hunting district scale. Therefore, the by far largest hunting district of Tyrol, Landesjagd Pitztal, was chosen to compare if the large-scale results of all hunt-ing districts in Tyrol together are similar to a subunit on local scale. I gathered long-term hunting bag data from the largest hunting district in Tyrol, where only professional hunters manage the hunting.

The following hypotheses were proposed for the second part of this study:

- **2.a.** The total hunting bag is slightly decreasing over the last 15 years in Tyrol.
- **2.b.** Hunting bag shows a decrease in old individuals.
- **2.c.** Life tables of hunted chamois in Tyrol indicate an unstable population structure.
- 2.d. In the largest district (Landesjagd Pitztal) the long-term data shows the same trends as observed 2.a 2.c.

3 Material and methods

3.1 Study area

To test the monitoring methods five reference areas (point A to E) were chosen in different areas of the federal province of Tyrol, Austria. Tyrol lies in the Eastern Alps, in the northern side of the Alps. Aside from settled areas and the wider, flat valley parts, chamois occur on 75 % of the area from Tyrol which is about 10627 km². Tyrol is part of the temperate climate zone and lies in the border area between Atlantic, continental and Mediterranean climatic influence. Predominant is the inner alpine climate, which has subcontinental features. Relatively humid summers, dry autumns, snowy winters, but also strong local differences characterize the climate. Tyrol underlies the typical influence of the west wind zone in middle Europe and thus the northern border of the alps is more humid with a lot of snowfall. The climate in the inner alpine valleys is mild and less humid but with high daily temperature amplitudes.

The five reference areas were chosen in different parts of North Tyrol (Fig. 1) and lie above the treeline or in alpine meadows to ensure good visibility conditions. Two of the areas lie in the Limestone Alps (A, C) and the others in the Central Alps (B, D, E). The infectious disease mange, which can cause a temporary decrease of a population, is occurring occasionally in study site B and in study site E. Each reference area extends over 560 to 800 ha and ranges from approximately 1200 to 3100 m a.s.l. Area E is moreover part of a larger area of about 11139 ha, which was also included in block counts. Chamois are hunted in all sites following the Tyrolean-ungulate-hunting-directives. The five reference areas are:

- A. Kaiserwinkel, Kufstein
- B. Ginzling Zillertal, Schwaz
- C. Hinterriss Karwendel, Schwaz
- D. Landesjagd Pitztal, Imst
- E. Kasern-Schmirn, Innsbruck-Land

In area E-Kasern-Schmirn block counts were conducted in 2016 and continued for the next two years for a local project. The reference area E – Kasern was only a part of the local project. The whole project area E – Schmirn is about 11139 ha as shown in the map Fig. 7. Typical chamois habitat in this area is about 8890 ha according to the federal map data (JAFAT/tiris). The counts were conducted with the same methodology as in the other reference areas.

Prominent fauna in the study sites include red fox (*Vulpes vulpes*), golden eagle (*Aquila chrysaetos*) and other wild ungulates such as roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*), in several areas also Alpine ibex (*Capra ibex*), Alpine marmot (*Marmota marmota*) and barded vulture (*Gypaetus barbatus*). During the time span of the field work there was no sign of large predators of the chamois as lynx, wolf or brown bear in the study sites.

Area	Α	В	С	D	E - Kasern
m a.s.l.	1200 - 2100	1900 - 3100	1400 - 2100	2000 - 3000	1700 - 2600
Size [ha]	610	590	800	560	728
Native rocks	limestone	silicate	limestone	silicate	silicate
Exposition	SE	SW	SE(N)	SW	SWN
Grazing in summer	yes	no	yes	yes	yes
Tourism	high	none	high	medium	medium
Hiking trails	6	0	6	3	5
Biking trails	3	0	0	0	0
Forestry growing region of Austria	Nördliche Randalpen	Subkontinen- tale Innenalpen	Nördliche Randalpen	Inneralpen - kontinentale Kernzone	Subkont. In- neralpen - Westteil
Alpine ibex pre- sent	no	no	no	yes	yes

Table 1: General information about the five reference areas (A-E) of the study.

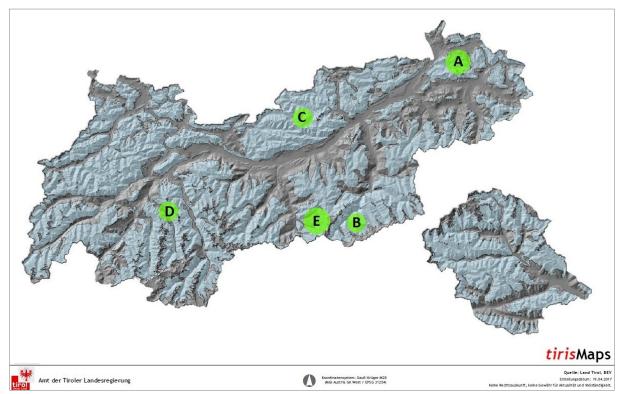


Fig. 1: Map with the rough position of the five reference areas A to E in Tyrol (green circles). Blue highlighted areas mark summer habitat of the chamois (tirisMaps 2.0).

Main economic activities are livestock farming with cattle or sheep and forest exploitation. Furthermore, touristic use is in all areas also an important economic factor. Tourism was defined as high, medium, low or none depending on the amount of hiking and biking trails in the area. High tourism was defined for areas with more than five trails, medium tourism for areas with three to five trails, low tourism for one to two trails and "none" in areas with no trails at all. Reference areas had different stages of these different economic uses, which are listed in Table 1. Only in area B no economic land use occurs.

3.2 Block counts

Block counts were carried out in each site to get information about the minimum population size and the population structure. Furthermore, the suitability and the performance of the method in the reference areas were analysed. The method was carried out as described in Miller & Corlatti (2009, pp. 141-142).

Each study site was first divided into sampling units (sectors) that covered the whole area (Fig. 2-7). In the summer months chamois show a bimodal activity pattern during daylight hours, with peaks at dawn and dusk (Hamr, 1984). Thus, the counting was done from vantage points and/or along trails in the morning, starting about half an hour after sunrise. To avoid double counts due to spatial activity of chamois, a time span of three hours was used for the BC.

Vantage points or trails for each sector within each area were chosen based on previous surveys of the area conducted in June 2015, to assure a complete coverage of the areas and to plan how many observers will be needed for each area. Each sector within each study area was sampled simultaneously by pairs of observers to reduce issues of double counts. Observers were experienced hunters, with knowledge of the area. Each observer had binoculars, spotting scopes and maps of the area. Reference areas were mapped using ArcGIS 10.4 by ESRI and geographical data by the authorities of the federal province Tyrol (Land Tirol, data.tirol.gv.at).

Date of survey, weather conditions, time of survey, estimated temperature and presence of grazing livestock were recorded in a check sheet (appendix I and II). After the counts, all observers of an area met to gather the results and exclude double counts. Three counts were conducted in each study site between late June after the parturition period, and November until the peak of rutting period. One count was carried out during summer (June – July), one

in late summer or fall (late August – October) and one at the beginning of the rutting period in November. Due to weather condition and snow coverage, counts in November were only possible in two reference areas. All counts were used to assess the minimum number of chamois present in the five reference areas, as well as the sex-age structure within the population. Observed individuals were classified after sex and age. To minimize error sources during data collection, individuals were distinguished only in sex and three age-classes: kids, yearlings and adults. If it was not possible to determine sex and age, individuals were classified as 'unknown'. For further analyses of BC results, unknown individuals were redistributed in sex-ageclasses with a weighting process. This means that unknown individuals were divided into each sex-age-class in the same proportion as the observed ratio within the known individuals. Kids were excluded from the weighting process, because it was always possible to differentiate between kids and other age classes.

In reference area E – Kasern (Fig. 6) block counts were conducted in 2016 and continued for the next two years for a local project. The area E – Kasern was only a part of the project area (Fig. 7) and represents a single hunting district, while the project area represents a number of districts (including area E-Kasern) which built a planning unit together. The counts took place every summer and every fall in the years 2016 until 2018. For every count about 60 people were needed as observers. All of them were experienced hunters with knowledge about the area. Since the counted habitat of the project area was about 15 times larger than in my other reference areas, I compared the BC results and the analysed population variables of the whole project area E with the results of the small reference area E within the project area.

Population variables

Female-kids-ratio and sex-ratio were analysed for each count in every area. To test for variations of the sex-ratio between the counts in each area a chi-square contingency table was calculated with a chi-square test and significance level was set at p = 0.05. The chi-square test requires random samples and independent observations. The sex-ratio from the first count in a reference area was calculated separately with the second count and accordingly with the third count, and also the second with the third count.

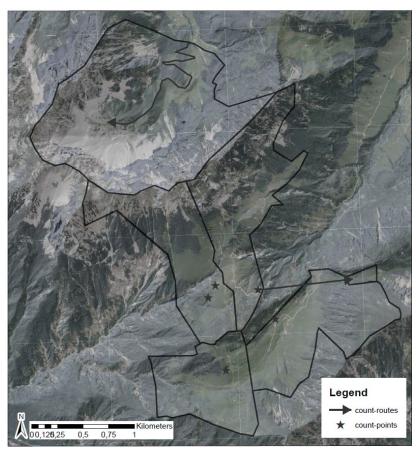


Fig. 2: The map of area A shows the sectors for the BC, the vantage points and the transect routes of each sector. The size of area A is 610 ha. Data source: Land Tirol - data.tirol.gv.at

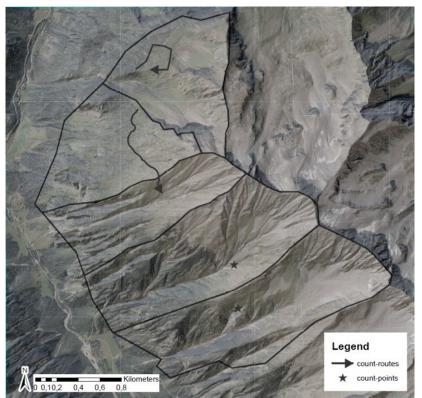


Fig. 3: The map of area B shows the sectors for the BC, the vantage points and the transect routes of each sector. The size of area B is 590 ha. Data source: Land Tirol - data.tirol.gv.at



Fig. 4: Area C has a size of 800 ha and consists of three sectors for the BC. Data source: Land Tirol - data.ti-rol.gv.at

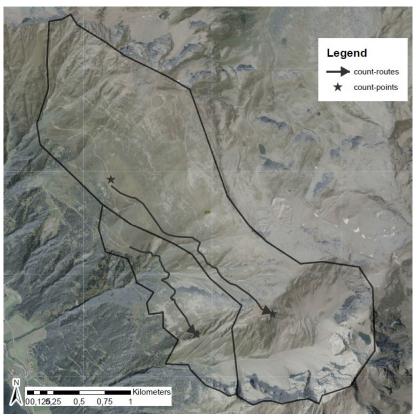


Fig. 5: Map for BC of area D (size 560 ha) with two sectors, the vantage points and the transect routes. Data source: Land Tirol - data.tirol.gv.at

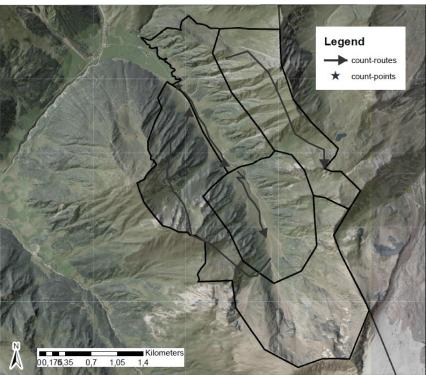


Fig. 6: Map for BC of reference area E (size 728 ha) with five sectors, the vantage points and the transect routes. Data source: Land Tirol - data.tirol.gv.at

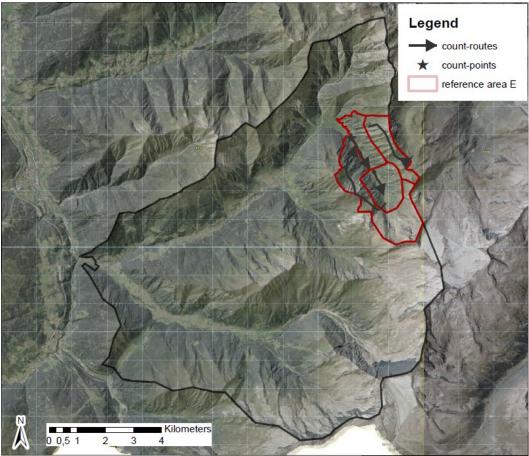


Fig. 7: Project area E - Schmirn (black): Overview of the whole project area E with the size of 11139 ha. The part within the area, where reference area E - Kasern is located, is shown in red with the count-routes and count-points. Data source: Land Tirol - data.tirol.gv.at

3.3 Double observer

Detection probability in counts of wildlife population can always be influenced by various factors, e.g. weather, wind, human or predator disturbance and other interactions as already mentioned. Doing direct counts with different observers also includes a probability of errors in the detection rate. Depending on individual experience and knowledge the detection rate can differ between observers.

In this study, I used a double-observer approach to estimate detection probability. Estimates for detection probability permit a direct estimation of population size (see formula 1), where N_i is the true abundance, C_i is the result of counts and p_i is the detection probability, *i* stands for the time and location (Nichols et al., 2000).

$$N_i = \frac{C_i}{p_i} \tag{1}$$

Basically, there are two different ways to conduct a double observer (DO) approach: the independent and the dependent DO. In this study, the independent DO approach was used. The advantage of the independent DO is the precise capture history and that observers can survey the area independently.

For this method point counts were conducted. The first observer, 'A', and the second observer, 'B', observed the same area simultaneously without interacting with each other. Each observer marked the individuals he observed for a certain area in a map and after 15 minutes the observers compared their results and marked the individuals, which were spotted from both of them. The time span of 15 minutes was chosen, because it was enough to observe the given sector. With the observation data of observer 'A' and 'B' a capture history was set up. For the capture history the observed individuals of each observer were recorded in a table consisting of counts of individuals observer 'B', but not by observer 'A' (0/1), and individuals observed by both observes (1/1). With this file a capture-mark-recapture framework was built with the Bayesian estimate using Chapman's assumptions.

3.4 Fecal DNA sampling

To test this method, area D was chosen, because this area is easier to access and the costs for genetic analysis allowed to test the method in this study only for one area.

Fecal sampling was done along transects trails, purposively chosen per the topographical characteristics of the study area. The area extends over approximately 560 ha. Hence it was possible to cover the area evenly within one day with two persons. The whole area was sampled five times, and every sampling day corresponds to one capture occasion. The sampling was done within one month and before the start of hunting season to fulfill the population closure assumption for the CMR analysis. Furthermore, a short time span should maximize the possibility to collect fresh samples. While walking along a transect trail collecting feces, the exact covered route was recorded on a map and with a GPS-device. Every time when a sample was taken, it was labelled, and the position was marked with the GPS-device. Feces was collected with 50 mL plastic tubes.

For the preservation of DNA in non-invasive samples like feces, it is important to inhibit enzymes, as nucleases, that degrade DNA. There exist different approaches to preserve samples. One possibility is the deactivation of nucleases via removal of water or another inhibition of nuclease activity via storage of samples at low temperatures (Beja-Pereira et al., 2009). In this study two samples of every chamois feces were taken, one in an empty tube for storage in the freezer and the other one was stored in a tube with silica gel. Silica gel removes water from its surroundings and allowed a storage at room temperature, while the other samples were stored in the freezer at -20 °C. I used orange silica gel with indicator function and controlled samples weekly. If the silica gel of a sample was discolored, fresh silica gel was added.

The genetic analysis was performed by the CIBIO (Centro de Investigação em Biodiversidade e Recursos Genéticos, Porto, Portugal). Tissue samples of *R. rupicapra* were used to optimize and amplify a selected set of markers to adjust the protocol for non-invasive samples in Alpine chamois.

The DNA extraction was done with E.Z.N.A commercial Kits and the species identification was based on the mitochondrial DNA fragment amplification (Cyt-b 417bp) (Palumbi, 1991). Cytochrome b (Cyt-b) is widely used to detect for species. If the species *R. rupicapra* was detected, samples were used in the next step for the individual analysis.

To achieve the individual profiles, all samples were amplified for 16 microsatellite markers (Zemanová et al., 2011), in three multiplexes, performing Pre- and Post-PCR, for the four replicates done for each multiplex.

Altogether 13 PCRs were performed per sample. With the microsatellite analysis, the individual microsatellite position on the DNA (e.g. 156 bp) of one individual will be detected. The analysis must be repeated three times to make sure of the positions of the microsatellites. When four or three results of one sample are the same (or haplotypes), it will be accepted in the analyses. The alignment was corrected manually.



Fig. 8: Two samples of every found pellet group were taken. One sample (left) was stored at -20 $^{\circ}$ C and the second one (right) with silica gel.

3.5 Hunting management

To control game management and the amount of harvested chamois the authorities register the hunting bag. Existing data gets administered by the local authorities. The data available for this study includes year, sex, age-class, the hunting district, occurrence of diseases of harvested animals and found carcasses. These data were available from 2011 until 2018 for this study and were analysed to detect trends in these seven years. The total number of yearly harvested chamois is available since 1983 in Statistik Austria. Long-term-data of exact age of harvested individuals was only recorded for the largest hunting district, "Landesjagd Pitztal", since 2000. Area D is part of the largest hunting district of Tyrol, which is administered by the federal state and called "Landesjagd Pitztal". The "Landesjagd Pitztal" is a valley of about 22.359 ha including 16.488 ha of typical chamois habitat according to the federal map data (JAFAT/tiris). It is managed by five game managers. The mountains are part of the Ötztaler Alpen. For this area it was possible to gather long term hunting bag data including the exact age of harvested chamois since 2000. Therefore, it is possible to build a life table for a longer time period and analyse the population structure based on the hunting bag data for this area and compare the results with the monitoring results of area D, which is lying in the core habitat of chamois in the "Landesjagd Pitztal". Data of all other hunting districts in Tyrol is available since 2013, because data before this year isn`t archived any more.

Data of hunting bag statistics can be useful but have several sources of bias and may not reflect the situation of a wild ungulate population, because game is not hunted randomly but following certain directives, also the number of hunters and hunting effort can influence the hunting bag (Festa-Bianchet et al., 2015; Leclerc et al., 2016; Pelletier et al., 2012). Thus, it is possible to analyse or detect and compare trends but not gather reliable information about absolute numbers of population size (Acevedo et al., 2007), unless hunting data is complemented with natural mortality (Leclerc et al., 2016). If the exact age of hunted game is known, as for chamois, it is possible to use hunting bag for indirect estimations of life table parameters (Sinclair et al., 2006). For my study I used hunting bag data, which also includes recorded natural deaths through the carcasses found by the hunters. To detect bias of the sex-agestructure in the hunting bag data due to selection of hunters I analysed natural registered deaths also separately.

As mentioned above, hunting effort should be considered as possible source of bias in bag data (Imperio et al., 2010; Ranta et al., 2008; Soininen et al., 2016; Willebrand et al., 2011). As an indication for changes of the hunting effort I analysed the number of yearly registered hunting permits.

Hunting is not underlying random conditions. Hunting directives in Tyrol are accurately defined. Only a certain percentage of individuals of the respective sex-age-classes are allowed to be harvested (see Appendix III). In practice it is not always possible to fulfill these requirements in particular because the real number of individuals in each age class is only estimated

and hunters will not always identify the actual age of a chamois while hunting, thus harvest data will not always meet all management specifications of the hunting directives.

3.5.1 Life table

Bag data was also used to build life tables to gain information how the hunted population is performing regarding the age of death. Whether a population increases, decreases or remains stable is determined by its age specific mortality and fecundity rates and the underlying distribution of ages in the population (Sinclair et al., 2006). For planning and managing the amount of the yearly permitted harvesting rate of a chamois population, it is important to have as many information about the population dynamics as possible. A life table summarizes information about the population dynamics in the past and offers the possibility to determine mortality and survival rates and possibilities. Sinclair et al. (2006) assume that the population's age distribution is in a stable form, when age-specific fecundity and survivorship-rates remain constant, even if its size may be changing.

The available data of deaths and age of death derive from hunting statistics and should be used cautiously in consideration of potential biases as already mentioned.

For the reliability of life tables developed from a sample from survival data of a population Sinclair et al. (2006) determined three assumptions of the analysis: Firstly the sample must be an unbiased representation of the age distribution in the population, controlling the usual biases from hunting data. Secondly, age specific fecundity and mortality must be stable for some generations and thirdly the population size must be stable.

To reduce the possibilities and effect of bias by selection due to hunting goals, natural deaths were also included and furthermore analysed separately. As no data is available about the age specific fecundity, I cannot detect any changes for that factor. For a large area as Tyrol however I can assume that population size and mortality were not underlying extraordinary fluctuations in the considered time period. Based on the mortality records I constructed a static vertical life table where the life expectancy (L_x) at age 'x' is calculated by the standard-ized survival probability (I_x) at age 'x' and 'x+1'.

$$L_x = \frac{l_x + l_{x+1}}{2}$$
(2)

The standardized survival probability I_x is calculated by the proportion of the number of survivors at age 'x' (N_x) to the total number of individuals alive at age 0.

$$l_x = \frac{N_x}{N_0} \tag{3}$$

Furthermore, it is possible to calculate the total number of living individuals at age 'x' (T_x) by the sum of animals expected to be alive at this age and older,

$$T_x = L_x + L_{x+1} + \dots + L_{x+n}$$
(4)

and the age specific mortality rate at age 'x' (q_x), by the proportion of deaths at age 'x' (d_x) to the survivors at age 'x' (N_x):

$$q_x = \frac{d_x}{N_x} \tag{5}$$

In relation to the standardisized survival probability I_x , T_x will lead us to the expected time yet to be lived by the surviving individuals at a certain age (e_x):

$$e_x = \frac{T_x}{l_x} \tag{6}$$

For this analysis I got hunting bag data from 2013 until 2018 with the exact registered age of hunted chamois including natural deaths.

4 Results

4.1 Block counts

In this study 12 block counts were conducted in five study areas over two years (Table 2). In area E the counts were continued in the following 2 years, so that 4 additional counts were included in the study. Each area was observed at least twice a year and additionally during rut in November, however, due to bad weather conditions it was only possible to conduct block counts in November for two areas (area C and D).

In area E – Schmirn the results from the project are shown for the smaller reference area E – Kasern and for the total area (E – Schmirn) separately.

Study area	Cour	nt 1	Coun	t 2	Count 3		
	Date	Σ ΒC	Date	ΣBC	Date	ΣBC	
A	30.06.2015	254	26.09.2015	282	-	-	
В	18.07.2015	188	29.08.2015	129	-	-	
С	02.07.2015	93	09.10.2015	09.10.2015 98 1		92	
D	22.07.2015	95	13.10.2015	79	09.11.2015	74	
E – Kasern	30.07.2016	222	22.10.2016	165	-	-	
E – Kasern	08.07.2017	211	14.10.2017	250	-	-	
E – Kasern	30.06.2018	220	06.10.2018	330	-	-	
E – Schmirn	30.07.2016	1192	22.10.2016	1157	-	-	
E – Schmirn	08.07.2017	1425	14.10.2017	1548	-	-	
E – Schmirn	30.06.2018	1422	06.10.2018	1665	-	-	

Table 2: List of block counts conducted in areas A to E and sum of counted chamois.

The results of each area are listed in Figure 9 - 11. In some cases, not all chamois could be classified after sex and age and were listed as "undefined" individuals. For further analyses of the population these undefined individuals were redistributed. The redistribution thus was done similar to the proportion of identified amount of chamois in the different sex-age-classes, except for kids-class, of a count.

The percentage of undefined individuals variated sometimes widely as shown in Table 3. The smallest amount was 0 % and the highest over 40 %. When the proportion of the undefined individuals increases, so does the potential bias of the redistribution. Especially for chamois, because males and females prefer different habitat fragments during the most time of the year and are living separately, except for the rutting time. If observers notice a larger group

of undefinable chamois, it is not likely that this is an even distributed sample of the population regarding the sex-age-classes. Moreover, the results show also in this study a higher visibility of females in summer.

Table 3: List of block counts conducted in area A to E with the sum of counted chamois, the maxima of counted kids, yearlings and adults per sex and the percentage of undefined individuals.

Study area A	ΣBC	Kids	Yearlings	Females	Males	Undef.	% undef.
Count 1	245	51	24	82	74	14	6.0
Count 2	282	53	16	78	69	66	23.4
Max. 1+2	233	53	24	82	74	-	-
Study area B	ΣBC	Kids	Yearlings	Females	Males	Undef.	% undef.
Count 1	188	56	33	56	4	39	20.7
Count 2	129	36	19	49	24	1	0.8
Max. 1+2	169	56	33	56	24	-	-
Study area C	Σ ΒΟ	Kids	Yearlings	Females	Males	Undef.	% undef.
Count 1	93	33	9	42	9	0	0.0
Count 2	98	22	16	32	6	22	22.4
Count 3	92	12	4	17	22	37	40.2
Max. 1+2	113	33	16	42	22	-	-
Study area D	ΣBC	Kids	Yearlings	Females	Males	Undef.	% undef.
Count 1	95	31	4	48	6	6	6.3
Count 2	79	14	8	38	10	8	10.1
Count 3	74	12	5	31	23	3	4.1
Max. 1+2	110	31	8	48	23	-	-
Study area	ΣBC	Kids	Yearlings	Females	Males	Undef.	% undef.
E – Kasern			rearings	remaies	Iviaic5	onder.	70 unuer.
2016-07	222	63	12	89	58	0	0.0
2016-10	165	41	6	16	11	91	55.2
Max. 1+2	222	63	12	89	58	-	-
2017-07	211	48	6	91	55	11	5.2
2017-10	250	63	22	113	50	2	0.8
Max. 1+2	253	63	22	113	55	-	-
2018-06	220	23	33	89	74	1	0.5
2018-10	330	86	44	133	65	2	0.6
Max. 1+2	337	86	44	133	74	-	-
Project area							
E – Schmirn	Σ BC	Kids	Yearlings	Females	Males	Undef.	% undef.
(total)							
2016-07	1192	243	61	509	359	20	1.7
2016-10	1157	238	56	399	154	310	26.8
Max. 1+2	1192	243	61	509	359	-	-
2017-07	1425	300	85	585	398	57	4.0
2017-10	1548	332	107	725	319	65	4.2
Max. 1+2	1562	332	107	725	398	-	-
2018-06	1422	301	150	620	350	1	0.0
2018-10	1665	380	183	697	359	46	2.8
Max. 1+2	1665	380	183	697	359	-	-

A larger amount of undefined chamois could hence hold the danger to be redistributed in favour of females and intensify the unbalanced sex-ratio in BC. Therefore, further analyses are needed, to determine limits of the redistribution of undefined individuals. In my case the highest percentage of undefined individuals occurred in a BC in area C in November during rutting time (40.2 %, see Table 3). Due to the aforesaid exception for the rutting time I still applied the redistribution for this count.

If I sum up the highest counts of the categories (kid, yearling, female, male) for each area, only in area C, D, slightly in E 2017 and E 2018 the total population size increases. Undefined individuals were excluded as a possible bias. The total counts over the year show mostly just slight variations in each area though variation in the population structure was prominent. This is also apparent in the analysis of the sex-ratio and female-kids-ratio.

Sex-ratio

To test for variations of the sex-ratio between different counts a chi-square contingency table was calculated with a chi-square calculator and significance level p = 0.05. The results in Table 4 show that there were very different trends recording the sex-ratio. The calculation of each area is recorded in appendix IV. Ten of sixteen calculations showed a dependence between sex-ratio and different counting dates.

Study area	Count months 1 / 2	Sex-ratio 1 (f/m)	Sex-ratio 2 (f/m)	p-value	Dependence of variables
A	June / Sep.	1.11	1.13	0.021	
	•			0.931	not sign.
В	July / August	14.00	2.04	0.000	sign.
С	July / Oct.	4.67	5.33	0.817	not sign.
С	July / Nov.	4.67	0.77	0.000	sign.
С	Oct. / Nov.	5.33	0.77	0.000	sign.
С	July / Oct. / Nov.	see above		0.000	sign.
D	July / Oct.	8.00	3.80	0.178	not sign.
D	July / Nov.	8.00	1.35	0.000	sign.
D	Oct. / Nov.	3.80	1.35	0.019	sign.
D	July / Oct. / Nov.	see above		0.001	sign.
E– Schmirn (2016)	July / Oct.	1.42	2.59	0.000	sign.
E– Schmirn (2017)	July / Oct.	1.47	2.27	0.000	sign.
E– Schmirn (2018)	June / Oct.	1.77	1.94	0.325	not sign.
E– Kasern (2016)	July / Oct.	1.53	1.45	0.900	not sign.
E– Kasern (2017)	July / Oct.	1.65	2.26	0.195	not sign.
E– Kasern (2018)	June / Oct.	1.20	2.05	0.015	sign.

Table 4: Results of chi-square contingency table to analyse the variation of the sex-ratio between each block count in the reference areas (p = 0.05).

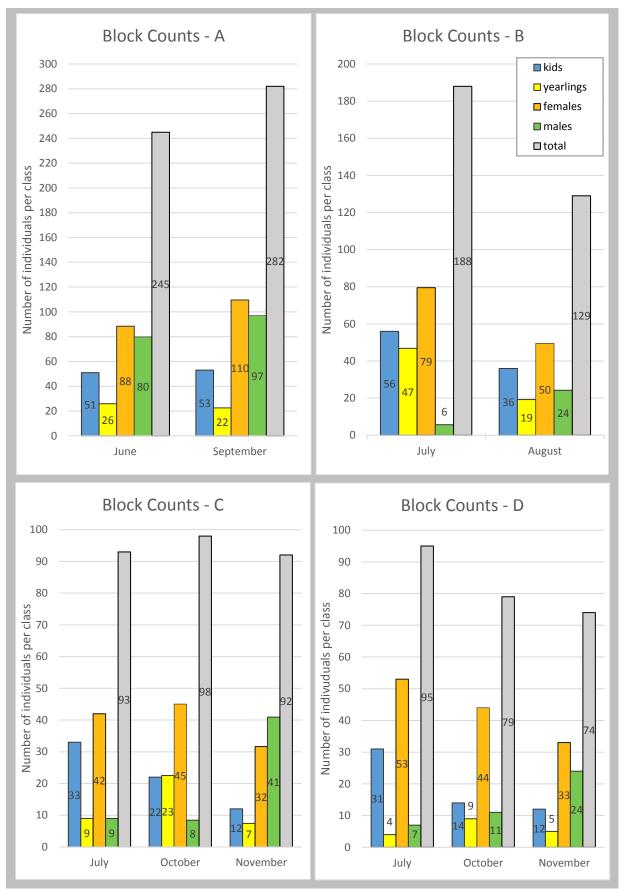


Fig. 9: Results of BC in the reference areas A - D. The blue bar shows the counted kids, the yellow male and female yearlings, the orange the females and the green the males. The total count of each sampling occasion is shown in grey.

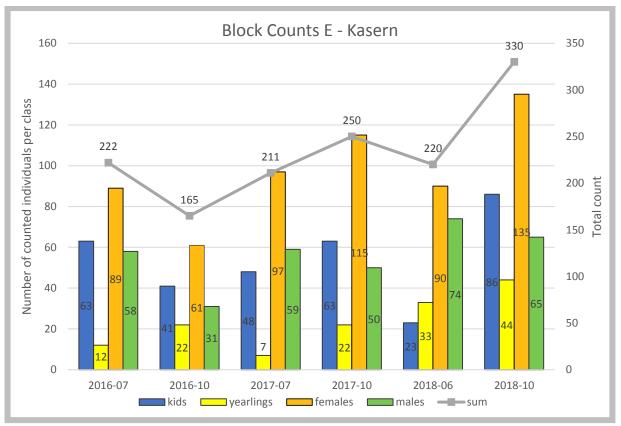


Fig. 10: Results of BC in the reference area E-Kasern. The bars show separately the counted kids (blue), male and female yearlings (yellow), females (orange) and males (green). The total count of each sampling occasion is shown with the grey line.

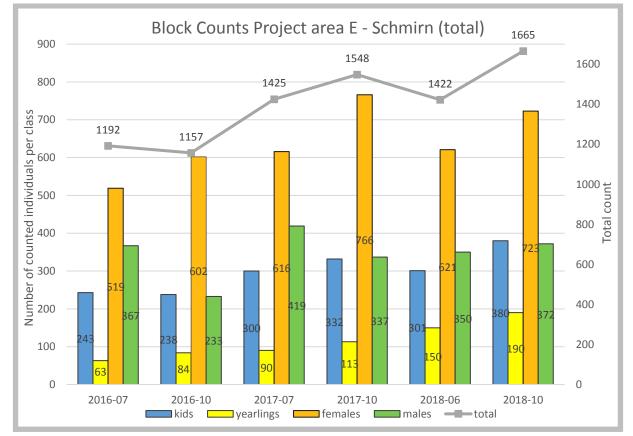


Fig. 11: Results of BC in the project area E – Schmirn. The bars show separately the counted kids (blue), male and female yearlings (yellow), females (orange) and males (green). The total count of each sampling occasion is shown with the grey line.

Female-kids-ratio

Furthermore, a comparison of the female-kids-ratio was conducted for all counts (Table 5). For the calculation of the ratio, the kids and the sum of females (except female yearlings) after the weighting process of each count were used. For the total project area E – Schmirn a separated analysis for the female-kids-ratio was done in Table 6, to take a look at the differences of the small and the large BC area. The results are interesting to compare with the other study areas, because the observed area was much larger. The tendency of the total count was however developing similar as in the smaller part of the area E – Kasern.

Table 5: Result of female-kids-ratio for each BC in reference areas A to E and mean value for the three counting seasons. Females include the weighted individuals of the undefined individuals in a count except the female yearlings.

Study area	C	Count 1		(Count 2		C		
Study area	Females	Kids	Ratio	Females	Kids	Ratio	Females	Kids	Ratio
Α	88	51	0.58	110	53	0.48	-	-	-
В	79	56	0.71	50	36	0.72	-	-	-
С	42	33	0.79	45	22	0.49	32	12	0.38
D	53	31	0.58	44	14	0.32	33	12	0.36
E (2016)	89	63	0,71	61	41	0,67	-	-	-
E (2017)	97	48	0,49	115	63	0,55	-	-	-
E (2018)	90	23	0,26	135	86	0,64	-	-	-
Mean value			0,59			0,55			0.37

Table 6: Female-kids-ratio of BC in the project area E – Schmirn (total) in the years 2016, 2017 and 2018.

Year		Count 1			Count 2	
rear	Females	Kids	Ratio	Females	Kids	Ratio
2016	519	243	0.47	602	238	0.40
2017	616	300	0.49	766	332	0.43
2018	621	301	0.48	723	380	0.53
Mean value			0.48			0.45

4.2 Double observer

Results of the double observer method are showing a very good detection rate of 84 % for both observers (Table 7). Correction with the CMR – Chapman estimator yields a minimal population size of 83 individuals instead of the counted 82 individuals. Using the Bayesian estimate the corrected count was about 84 (83.7 \pm 0.9). Hence, with the correction of the independent double observer approach the detection rate of two observers together was 98.6 % of the corrected count.

Table 7: Results of the DO method in area C with counted individuals of observer A and B in sector 1 to 4, the total count and the correction with CMR – Chapman estimator. The total population size observed by observer A and B was 82 individuals. With the correction using the CMR – Chapman estimator a minimum population size of 83 individuals was computed and by using the Bayesian estimate 84 individuals (83.7 ± 0.9).

Independent double observer		Sector 1		Sector 2		Sector 3		or 4	Population	
Observer	А	В	А	В	А	В	Α	В	size total	
Total individuals observed	21	24	13	13	9	7	30	36	82	
Individuals observed from A+B	21		13		7		29		70	
CMR - Chapman estimator	24		13		9		37.2		83.2	
Bayesian estimate (N≈)	24 ±	0.5	13.1 ± 0.3		9.6 ± 1.2		37.6 ± 0.9		83.7 ± 0.9	

4.3 Fecal DNA sampling

5/E

Fecal sampling was conducted in July 2016 in area D. There were five sampling occasions in an interval of three to seven days, depending on the weather situation. When it was stormy, foggy or the risk of an upcoming thunderstorm forecasted, sampling wasn't possible in this alpine area.

able 8. List of the five sampling occasions of fecal sampling with date, sampling size and dominant weather condition.			
Sampling occasion	Date	Sample size	Weather / Mean Temp.
1/A	7.7.2016	24	Sunshine / 23°C
2 / B	11.7.2016	44	Sunshine / 21°C
3 / C	18.7.2016	23	Changeable and Humid / 24°C
4 / D	21.7.2016	30	Rain / 17°C

28.7.2016

Table 8: List of the five sampling occasions of fecal sampling with date, sampling size and dominant weather condition.

I tracked the route of every sampling occasion as well as each position where a sample was taken. Altogether I took 153 fecal samples (see Table 9). The DNA analyses was conducted

32

Clouded / 18°C

with the samples stored at -20°C. For 137 samples the species analysis could be done, this equals a success rate of 89 %. 129 of the samples were from chamois, *R. r. rupicapra*, 7 of sheep, *Ovis aries*, and 1 of red deer, *Cervus elaphus*. A total of 22 complete individual profiles were obtained (17 % success rate) and 12 different individuals identified (Table 10). Sex was determined and missing data loci were amplified individually for each marker. Of the identified individuals five were males and seven females. Altogether the total number of identified samples was unfortunately too small for a CMR estimation for population abundance.



Fig. 12: A view in the sampling area shows the difficulty and steepness of the area (during sampling on July 18th, 2016).

Table 9: Result of the species analysis from the 153 fecal DNA samples.

Species	Samples
R. rupicapra	129
Ovis aries	7
Cervus elaphus	1
No amplification	16
Total	153

Table 10: Captured individuals of each DNA sampling occasion.
Individuals were named alphabetically from A to L.

		Samp	oling occ	asion	_
	1	2	3	4	5
	А	С		D	F
	В			Е	G
	I			I	Н
lals				J	Н
Captured individuals				К	I
indi				К	J
ed i				L	
otur				L	
Cap				L	
				L	
				L	
				L	
Total	3	1	0	6	5

4.4 Hunting management

The yearly issued hunting permits were only fluctuating very slightly in the last 20 years (Fig. 13). For the years 2001 and 2002 there was no data available. In 2015 the issued licences decreased about 1.000 hunting permits, however at this time the yearly fee was nearly doubled. This was the only price change in the observed time span.

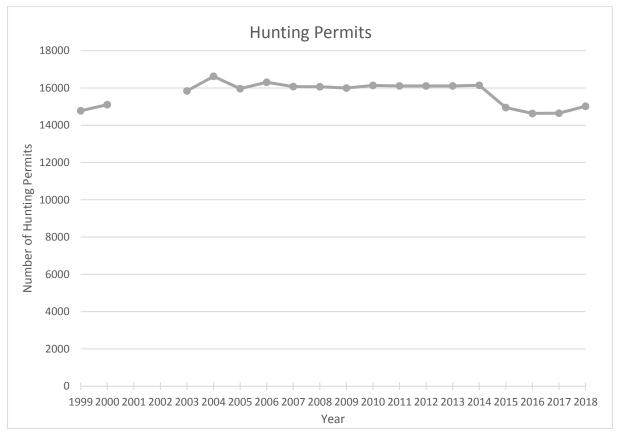


Fig. 13: Number of yearly hunting permits in Tyrol from 1999 – 2018. There was no data available from 2001 and 2002.

Hunting bag data of chamois from the years 1983 until 2016 show a slight decrease of overall amount of harvested chamois in Tyrol, especially since 2004 (Fig. 14). More detailed data was available since 2011. In this period the number of harvested chamois was permanently below 8000 individuals. Recorded natural deaths fluctuated between 1281 at the maximum and 434 individuals minimum (Fig. 15). The amount of harvested chamois in different sex and age classes show that there are mostly less adult males than females in the hunting bag. In some years young males (2-3 years old) were harvested more than males of eight years and older. The sum of yearly harvested males and females since 2011 is mostly balanced at 1:1.02 males to females (Fig. 16 and 17).

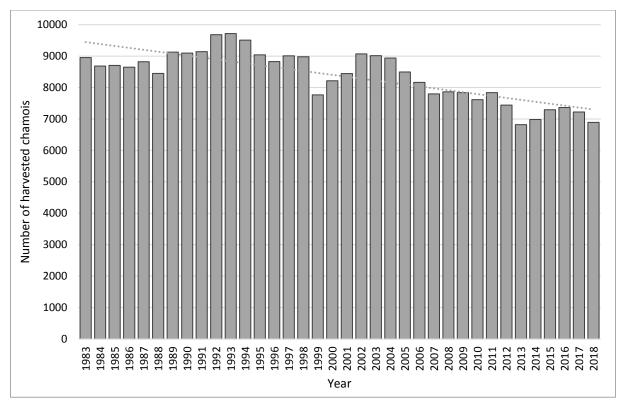


Fig. 14: Number of yearly hunted chamois in Tyrol from 1983 – 2018.

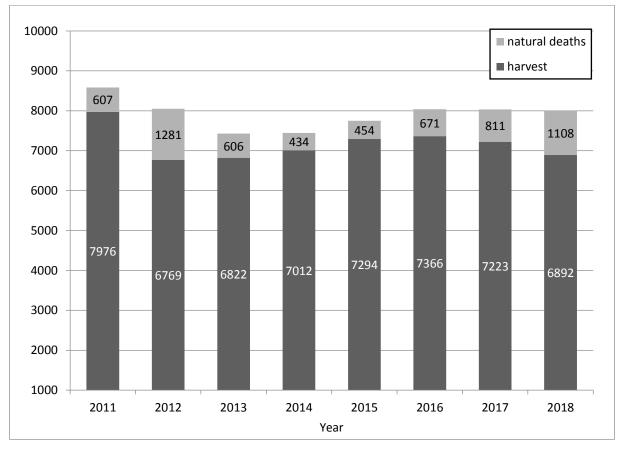


Fig. 15: Hunting bag data of chamois in Tyrol showing the actual hunted individuals (harvest) and the registered carcasses (natural deaths).

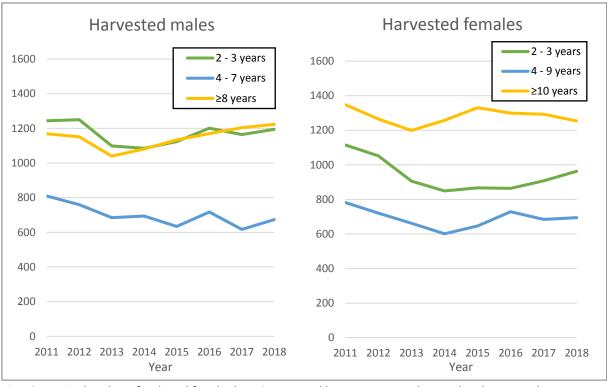


Fig. 16: Hunting bag data of male and female chamois separated between sex-age-classes. Blue shows age class III, orange age class II and grey age class I. Data also includes registered carcasses.

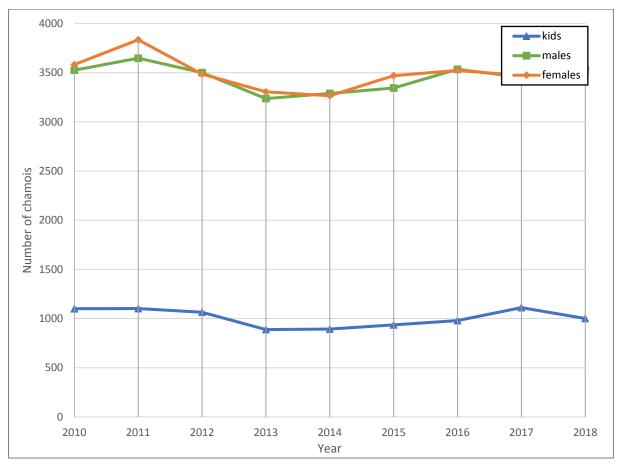


Fig. 17: Hunting bag data (including registered carcasses) from 2011 – 2018 of females, males and kids.

Natural deaths of males (2011-2018)

Natural deaths of females (2011-2018)

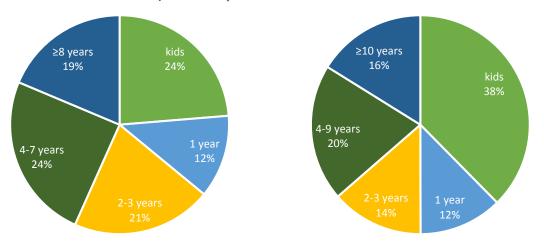


Fig. 18: Proportion of registered carcasses from 2011 – 2018 for males and females in the different age classes.

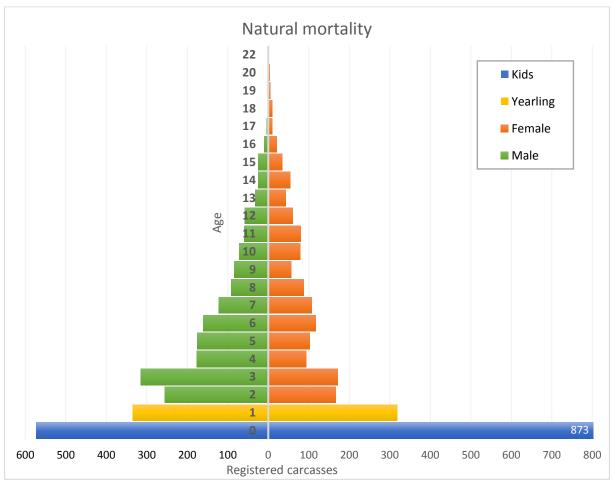


Fig. 19: Number of registered carcasses of female and male chamois of each age from 2013 – 2018.

In a second step I separately compared the number of found carcasses in each age class (Fig. 18) and for every age (Fig. 19) separately for each sex. From 1.4.2011 until 31.3.2018 5970

natural deaths were registered (males=3022, females=2948). The total number of registered natural deaths is 6 - 16 % of the yearly hunting bag. Comparing the distribution of deaths in the different sex-age-classes to the hunting bag there are obviously differences. The amount of kids is much higher, also the percentage of middle-aged individuals (age class II). The number of male carcasses is higher than the number of female carcasses. Found kids and yearlings are more often females. Between the age of three and nine more males are found than females. Between the age of 15 and older only 40 males were found, but 85 females. The oldest found carcasses were a 22-year-old female and a 20-year-old male. Altogether, the yearly amount of registered carcasses is fluctuating strongly, depending on climate conditions, natural disasters and diseases which are the common factors for natural deaths in a landscape with barely any predators.

Analysis of changes of the mean age, maximum age and total number of harvested chamois in age class I showed no specific trend since 2013, where data of exact age is available (tab. 11). Mean age of harvested males in age class I was from 2013 until 2018 always about 10 years. Mean age of harvested females in age class I was about 13 years.

Veer	Females	Females Age Class I (≥10 years)			age Class I (≥	8 years)
Year	Mean age	Max. age	Nº registered	Mean age	Max. age	Nº registered
2013	12,68	22	1199	10,03	19	1040
2014	12,89	21	1258	10,11	18	1081
2015	12,88	22	1331	10,19	19	1134
2016	12,95	23	1299	10,31	20	1170
2017	13,07	21	1293	10,32	20	1204
2018	12,86	22	1254	10,3	20	1223

Table 11: Mean age, maximal age and total number of registered carcasses and hunted chamois in age class I from 2013 – 2018.

4.4.1 Life table

One main goal of hunters is to select for old and for weak individuals. This should also favour a compensatory mortality effect rather than additional mortality. Under these circumstances the found age specific mortality rate (l_x) can tell us, how old chamois most likely get in hunted populations of Tyrol. This can give important information for the management of this species, because for a long-living species as the Alpine chamois age is an important factor for stable populations. Since there are some references of a slightly higher life expectancy of females than of males (Bocci et al., 2010; Corlatti et al., 2012a; Schröder, 1971), the life tables were built separately for each sex (Appendix V).

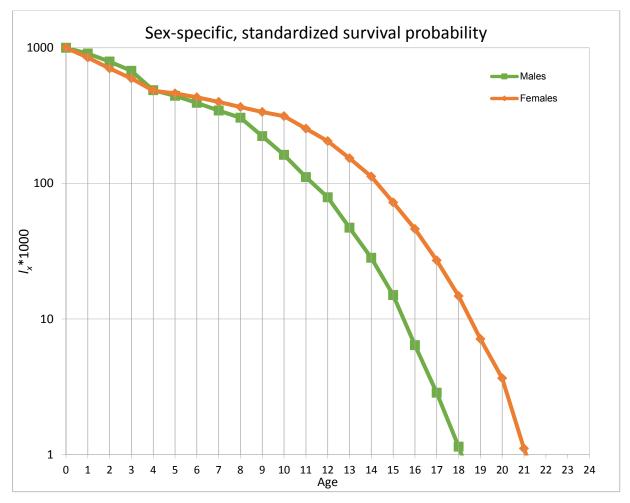


Fig. 20: Sex-specific, standardized survival probability (I_x) for male (green) and female (orange) chamois in Tyrol.

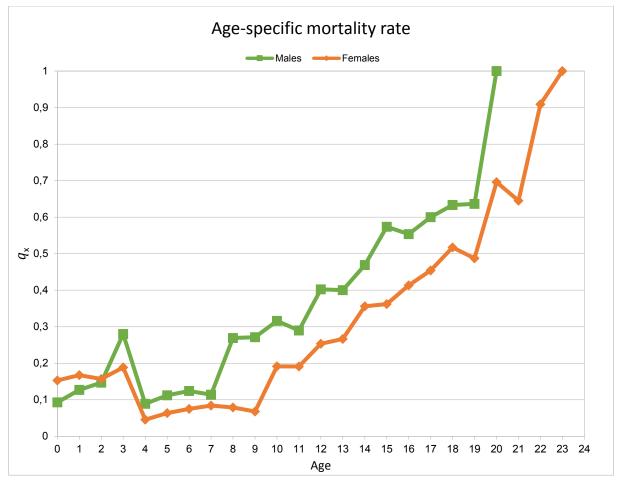


Fig. 21: Age-specific mortality rate (q_x) for male (green) and female (orange) chamois in Tyrol.

4.4.2 Hunting bag analyses "Landesjagd Pitztal"

A separate analysis was done for the largest hunting district "Landesjagd Pitztal", where study site D is located. Firstly, the BC were conducted in study area D. The results of the different classes are listed below in Fig. 21. Due to the rough classification it is only possible to compare the percentage of kids, yearlings, adult females and adult males. Secondly the hunting bag data from 2000 until 2018 was analysed and used to build a life table (see Appendix V). The hunting bag data showed in general a decreasing tendency as the hunting bag data of Tyrol (Fig. 22). The mean age of harvested males in age class I was fluctuating between nine

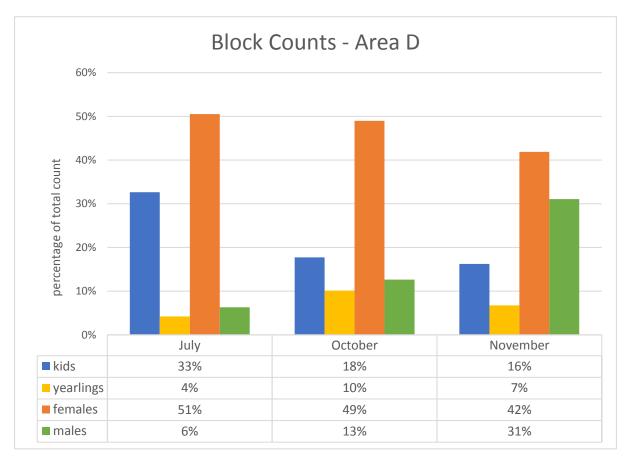


Fig. 22: BC results of area D with the percentage of each sex-age-class of the count.

D	Individuals	Kids	Yearlings	Females	Males
Count 1	95	31	4	48	6
Count 2	79	14	8	38	10
Count 3	74	12	5	31	23
Sum Max.	110	31	8	48	23
	100 %	28.2 %	7.3 %	43.6 %	20.9 %

Table 12: Results of BC in area D and maximal number of counted individuals per class.

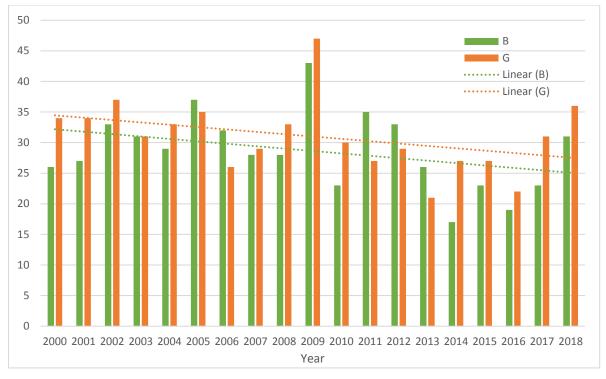


Fig. 23: Number of harvested males (green) and females (orange) in area D from 2000 – 2015 (kids were excluded). The mean sex ratio is 1:1.1 M:F. This is slightly under the by the hunting directives recommended 1:1.2.

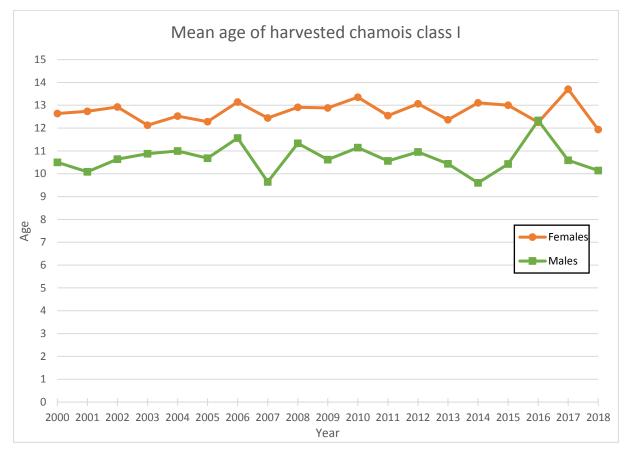


Fig. 24: Mean age of harvested chamois from 2000 - 2018 in the hunting district "Landesjagd Pitztal". The analysis was done separately for males age class I, ≥ 8 years (green) and females age class I, ≥ 10 years (orange).

		Female	es		Males	
Year	Mean age	Max. age	Mean age class I (≥10 years)	Mean age	Max. age	Mean age class I (≥8 years)
2000	6.17	19	12.64	5.50	14	10.50
2001	7.02	16	12.73	5.62	14	10.08
2002	6.23	18	12.93	5.53	17	10.64
2003	6.49	16	12.13	7.24	15	10.88
2004	7.74	17	12.53	6.32	14	11.00
2005	6.50	14	12.28	6.86	15	10.68
2006	7.45	18	13.14	7.03	15	11.56
2007	7.37	16	12.44	6.25	13	9.64
2008	7.82	17	12.91	8.47	16	11.33
2009	9.32	17	12.88	7.27	15	10.62
2010	8.87	16	13.35	8.52	14	11.14
2011	5.76	16	12.55	5.70	14	10.56
2012	9.06	18	13.06	8.19	15	10.95
2013	6.96	16	12.36	7.86	16	10.44
2014	9.70	20	13.11	6.26	13	9.60
2015	9.29	19	13.00	6.07	15	10.43
2016	7.72	16	12.25	7.52	16	12.33
2017	7.90	18	13.71	6.15	15	10.59
2018	6.13	15	11.93	6.19	14	10.14
Sum.	7.47	20	12.76	6.72	17	10.70

Table 13: Maximum age and mean age of yearly harvested chamois (including natural deaths) in "Landesjagd Pitztal" from 2000 to 2018 for each sex and in the third column only for the bag of age class I.

and 12 years and of females between 12 and 14 years. Also, the mean age of all harvested females (7.47 years) was higher than for males (6.72 years).

With the available hunting bag data, sex-age structure was rebuilt for the years 2000 and 2001 with the life table. In 2000 13 % of carcasses were kids, 10 % yearlings, 43 % adult females and 34 % adult males. In 2001 there were 13 % kids, 11 % yearlings, 39 % adult females and 37 % adult males. The BC were conducted in 2015 with at the maximum 28 % kids, 7 % yearlings, 44 % females and 21 % males. Compared to the life table results, in BC fewer adult males and yearlings were observed. This fits to the assumption, that females and kids could be overrepresented in block counts. However, a direct comparison is not yet possible, because to rebuild the chamois population of 2015 with the life table, data of 15 years is needed.

The sex-specific, standardised survival probability shows higher survival probabilities for males until the age of five and then for females. The higher the age, the higher was the difference between the sex-specific survival probability for males and females. Females showed a longer lifespan, the oldest female individual was 20 years old and the oldest male individual 17 years.

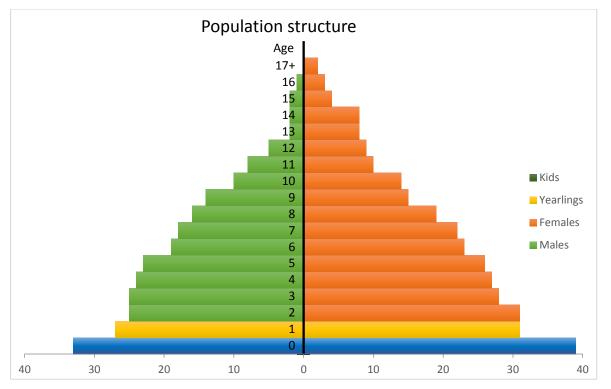


Fig. 25: Population structure rebuilt with the hunting bag data of "Landesjagd Pitztal" for the birthyear 2000.

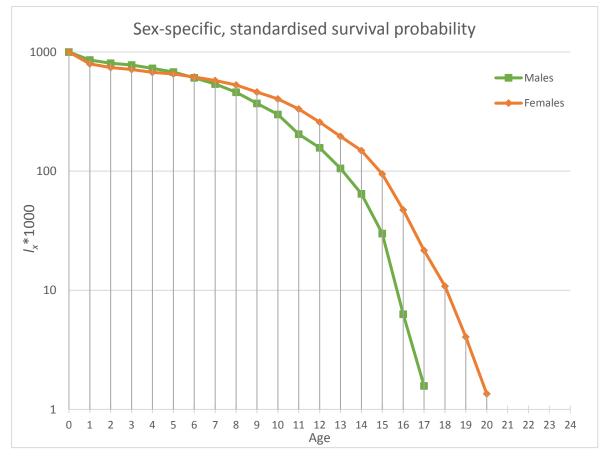


Fig. 26: Sex-specific, standardized survival probability (l_x) of female (orange) and male (green) chamois in the "Landesjagd Pitztal" built with hunting data from 2000 – 2018.

5 Discussion

The monitoring of a large population of mountain dwelling ungulates such as the Alpine chamois in Tyrol is challenging. Monitoring should be feasible in all areas of Tyrol at low costs and detect reliable population trends. Loison et al. (2006) recommended a set of monitoring tools to reliably and fatly detect changes in population abundance. Hence in this study, the mix of monitoring methods and the analyses of hunting statistics were compared and evaluated.

5.1 Block counts

BC were useful to detect the minimal population size. Furthermore, the repetition of counts within a year were important to obtain additional information about the population structure. Counts after the parturition period around July showed in every study area the highest amount of adult females and kids of observed individuals and a higher female-kids-ratio (59%). In October female-kids-ratio was 55%, but in November the ratio was considerably lower (37%). This decrease of observed kids can on the one hand be caused by the mortality of kids in the first four months of their lives when they are potential prey of golden eagles, foxes or lynx or other natural causes (hunting doesn't play a great role in this time, because only ill kids or kids of diseased females will be taken by hunters). On the other hand, it is known that females often leave their kids behind or hidden during the mating time (Zeiler, 2012). Therefore, the decrease could also partly be influenced by this behavior and kids may be less likely to be observed.

Because of the high mortality of kids, yearlings are a better indicator for the effective birth rate. If BC are repeated every year it is possible to estimate kid mortality. The amount of yearlings was mostly the highest during October counts, for this observation I couldn't find any correlation in the common literature.

The change of sex-ratio indicated a higher detectability of males during October and November compared to the counts in June or July. Thus, I can conclude that visibility of males is significantly higher in fall than in summer. This would also match with what we know about the annual life cycle of male chamois. In summer males tend to use habitats in lower altitudes with higher vegetation and adult males live mostly solitary or in small groups (Hamr, 1984; Lovari and Cosentino, 1986). This can lead to a lower visibility and underestimation of males

during summer, because they are less noticeable than large groups of females with kids and they can use higher vegetation as a cover. For future management counts should thus be conducted in summer and in fall, to detect the birth rate in summer and a minimal number of males in fall. Furthermore, a larger counting area including all different parts of the chamois habitat of one population could reduce this bias (see 5.1.1).

The highest number of males was counted in the two reference areas C and D in November, when the rutting time had already started. However, it is not always possible to access the rutting sites during this time of the year in Tyrol.

5.1.1 Block counts and size of reference area

Even though the reference area E – Kasern (728 ha) was just a small part of the whole project area E – Schmirn (11139 ha), the trend of the total counted chamois showed the same development. Analyses of the population structure, as female-kids-ratio and sex-ratio however reveal very different results. The BC results in each class in the smaller areas varied a lot between the counts, assumingly due to the given habitat, environmental influences and the life cycle of chamois. Alpine chamois have certain preferences during the year for their habitat also depending on the sex-age-class of the individuals (Boschi and Nievergelt, 2003; Lovari and Cosentino, 1986). Even different temperature and weather conditions can influence the results in a smaller area.

Thus, one reference area could be preferred at certain times and from different groups of chamois. The larger the size of an observed area, the more habitat structures are included, and BC can represent a less biased sample of the population.

The sex-ratio in the whole project area E – Schmirn for example was sometimes in summer less distorted towards females than in October. The total number of counted males was higher in July than in October in 2016 and 2017. The female-kids ratio was in average 0.48 in June/July and 0.45 in October. Thus, I can conclude that larger areas are useful to reduce the already mentioned bias in population structure of BC. Of course, the personnel needed for such counts is very high. In Tyrol local hunters voluntarily participated the counting events, otherwise it wouldn't have been possible to conduct the BC in such a large area.

With the results of BC in project area E we can also see, that in the small part of E – Kasern the same population trends occurred as in the whole area E – Schmirn. For this reason, it is possible to conclude, that for the observation of the population trend also the small reference areas can give us a good estimation. Moreover, if the sex-ratio and effective growth of a population is known, it is likely to detect the population trends by observing only females (and kids), because females mostly represented the largest part of observed individuals. Including yearly count data of kids and yearlings the population growth could be estimated.

Altogether I can conclude that, hypothesis 1.a. can be accepted, although BC in the small study area provided not sufficient data to evaluate population structures and are rather in danger to represent a distorted sample of the whole population and therefore should not be the only basis for a monitoring for the hunting plan. For a sustainable hunting plan the whole population or at least a large part of a mountain massif should be monitored, as in project area E, and data about growth rates and sex-ratio should be gathered.

5.2 Double observer

The detection rate of two observers was at first unexpectedly high (98.6 %) compared to the estimated abundance with the DO correction. However, observer groups in the study areas only included experienced persons, and every group had at least one experienced, local hunter who also had good knowledge about the chamois habitat. Furthermore, the observation sectors were small and open with a good sight. A single observer however only had a detection rate of about 84 % of the estimated population. Thus, I can accept hypothesis 1.c.1 that two observers show significant better detection rates than one observer. Two observers however performed very good in the open areas, so that the estimated minimal population was detected by about 99 % and hypothesis 1.c.2. will be rejected.

This study still demonstrates that, conducting direct counts with different observers always includes a probability of errors in the detection rate. Depending on individual experience and knowledge the detection rate can differ between observers. Therefore, it is important to consider this as possible source of errors and estimate the detection probabilities to minimize the influence of different observers on counting results. Furthermore, I can show with this results

that in open areas with two experienced observers detection rate is very high and that direct counts are a valuable monitoring instrument to detect trends in population size.

5.3 Fecal DNA sampling

The DNA analyses of the fecal samples performed poorly and the success rate of 17 % for the individual profiles was too low for a reliable statistical analysis. For this reason, I'm not able to answer hypothesis 1.b. in this study. Such low success rates occur when DNA quality and quantity is low. Due to the per se low content of genetic material DNA-analyses of non-invasive samples are always more challenging than invasive samples as tissue or blood. Thus, environmental influences or storing have an intense impact on the results. DNA is for example very sensible to UV-light or humid and warm conditions. In a recent study, Agetsuma-Yanagihara et al. 2017 showed for example the degradation process of DNA in samples of deer feces. The study showed that, for efficient genetic analyses samples of deer feces in warm temperate zones should not be older than three days in periods without rainfall and from under the cover of trees. By now there aren't any studies for chamois feces in alpine regions however, the study area lies relatively high above sea level (about 2.000 meters) hence UV-light for example is much stronger and there are no trees or higher vegetation for a sufficient cover of feces. I suspect that the degradation rate during July, when weather was mostly warm and humid with temperatures over 25°C, could be even higher. Also due to the humid weather conditions it was probably not always clear how fresh a pellet group in the open alpine meadows was.

Furthermore, the transport way could be a weakness. The transport from the study area to the storage place took over an hour until samples were in the freezer. The samples stored with silica gel were controlled weekly and if the indicator was chancing the color, I added some additional silica gel for the removal of water content. In august samples were sent to the CIBIO in Porto. The transport took about one to two days, during this time samples were not cooled continually at -18°C. For further studies observations of the defecation rate of chamois and sampling strategies for fecal sampling would be helpful. As mentioned by Ebert et al. (2012), more studies with the focus on the sampling techniques are needed that allow a better representation of the sampled population.

5.4 Hunting management

The development of hunting bag data showed a decreasing trend in the last 15 to 20 years in Tyrol, as expected in hypothesis 2.a. A more detailed look would be possible with a higher data quality. The essential data for population structure analyses exists only since 2013. These data as exact age, cause of death and date of death are however essential for further analyses.

As recommended by Roseberry and Woolf 1991 most analyses of harvest data were done separately for males and females because hunting pressure and goals are differently for each sex. Males for example are easier to hunt during rutting time. Females with kids are mostly spared or shot together with the kid. Youngs are often subjectively selected after their condition or poor trophy quality.

The second assumption (2.b.), that hunting bag data shows a decrease of old individuals couldn't be met by the data of the last six years. The observed time span showed no significant shift of the mean age or maximum age of harvested individuals in age class I. Even the number of the in the hunting bag registered individuals of age class I showed no clear trend. This is however a very short time span to detect a change in the population. Long term data would be needed to confirm or reject this hypothesis. Thus, I recommend for future management to improve the gathering and archiving of hunting bag data including the exact age of chamois and the result of the assessment commission.

What we can see in the analysis of harvested chamois in the different age classes is that, males and females are hunted differently in the age of two to three years. While significantly more class I females are hunted than 2- to 3-year-old females, in case of the males the number of hunted individuals in these two groups are at the same level. If the hunting pressure on young males is higher, we can also expect that there are less old males than females. This result is also indicated by the analysis of survival probability.

The analysis of the hunting bag data shows us in this study a difference between male and female sex-specific survival probabilities. While survival probability of males decreases between the age of three and four, then tends to be stable until eight years and starts decreasing again, female survival probability is lower in the beginning but from the age of four starts to be higher than for males. This trend enhances with age. The decline of survival probability for females intensifies at the age of ten. This covers with the hunting directives, where males

should be spared between the age of four and seven and mainly harvested when they are eight years and older and females when they are ten and older. To stabilize male survival probably a change of the age limit for harvesting could be helpful and a more careful use of young males (2-3 years). Altogether I accept hypothesis 2.c. for male chamois, as less old males are found than females and by now studies of senescence conclude that there is just a slight difference of natural senescence between male and female chamois (Bocci et al., 2010; Corlatti et al., 2012b).

The data of carcasses confirmed that males can reach a high age. The oldest registered carcass of a male individual was 20 years old and the oldest female 22 years. In total however more old females were found than males.

Natural deaths showed a higher mortality of males. The most registered carcasses were kids, the second most yearlings as expected. Sinclair et al. (2006) report an underestimation of the first age class in picked-up samples in spring. In Tyrol however hunters have to pick up carcasses during the whole year, therefore maybe this bias isn't as strong as in the referred study. Natural deaths may give a good overview of natural survival probability because they are indiscriminate samples, however the recorded number of registered natural deaths is only about 0.6 - 2 % of the estimated population (as indicated by local hunters) and thus rather low for reliable analysis. Furthermore, hunters also actively select for weak and sick individuals while hunting, so hunting also could have a compensatory mortality effect, when e.g. seriously ill animals are shot and not left to die. Moreover, in serious cases hunters are allowed to end the life of perishing or suffering game all over the year.

The survival probability was analysed separately for the largest hunting area of Tyrol, where hunting is only done by professionals or under the guidance of the professional hunters. Between the age of three and 15 the survival probability of males was significantly higher. This indicates that hunting in large planning units and under the guidance of professionals could lead to a better population structure especially regarding the males. Further investigations of large hunting districts with professional hunting are needed to confirm this trend and answer hypothesis 2.d.

5.5 Conclusions for future management

Altogether block counts are a very useful tool to gather information about the chamois population. The double observer approach was important to estimate source of bias by observers. For future management it is essential for reliable counts to build groups of two observers with at least one local expert to achieve a high detection probability. In Tyrol local hunters participated the counts voluntarily, therefore counts were a free service as in citizen science projects.

The DNA CMR in this case turned out to be very complex and more expensive, especially for larger areas, compared to the BC. It seems that collecting feces in July was not a suitable time, because it was hot, humid and there is a high UV-index in open areas. All these factors fasten DNA degradation.

Hunting bag data provided supplementary information about the population. However, a good knowledge about the local hunting regulations is essential for the interpretation of these data. The combination of monitoring methods and hunting bag is widely discussed and studies also confirm the usefulness of complementing population data with hunting bag (Soininen et al., 2016). Especially for hunting management plans of chamois a profound monitoring is needed to preserve stable populations and population structure. Hence periodical BC, a constant analysis of the population structure and the hunting bag statistic are recommended for future management in Tyrol. Thereby it should be considered to build counting areas for each mountain massif to count a closed population and to minimize the risk of double counts. Further investigations of long-term monitoring and hunting bag data would be interesting and could improve hunting management.

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7 Appendix

Appendix I: Scheme of a data sheet for the BC

Beobachtungspunkt: Zähltraganet: Zähltraganet: Zähltraganet: Zähltraganet: Zähltraganet: Victor in terminet: Victor in terminet: Zähltraganet: Victor in terminet: Victor in terminet: Victor in terminet: Victor in terminet: Victor in terminet: Zähltraganet: Victor in terminet: Victor in terminet: Zähltragenet: Victor in terminet: Victor in terminet: Zähltragenet:
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Appendix II: Data sheet for complementary information, as meteorological data, observing persons and external circumstances for BC.

Appendix III

Relevant points from the Tyrolean hunting management manifest for chamois for the determination of hunting-management-index.

5. Bestandsaufbau:

Idealer Altersklassenaufbau des Winterstandes:

	BÖCKE		GEIßEN	
Klasse III	Bockkitze	7 %	Geißkitze	8 %
	Jahrlinge	5 %	Jahrlinge	6 %
	2- und 3-jährige	9 %	2- und 3-jährige	10 %
Klasse II	4- bis 7-jährige	14 %	4- bis 9-jährige	21 %
Klasse I	8-jährig und älter	10 %	10-jährig und älter	10 %
Summe		45 %		55%

6. Abschussrichtlinien:

Abschussplanung:

Je Geschlecht der Stückzahl der Planungsgrundlage:

Kitze:	10 % der Planungsgrundlage in dieser Klasse
Jahrlinge:	10 % der Planungsgrundlage in dieser Klasse
restliche Klasse III:	5 % der Planungsgrundlage in dieser Klasse
Klasse II:	5 % der Planungsgrundlage in dieser Klasse (Hegeabschüsse)
Klasse I:	30-35 % der Planungsgrundlage in dieser Klasse

In Berücksichtigung der natürlichen Mortalität in allen Altersklassen darf der **jährliche Abschuss je nach Habitat 10-12 % des Bestandes nicht überschreiten.** Die Prozentsätze "je Geschlecht von der Stückzahl der Planungsgrundlage" sind aus diesem Grund unter Berücksichtigung des idealen Altersklassenaufbaus ggf. nach unten oder oben zu korrigieren.

Unterschreitet der Bockabschuss der Klasse I wiederholt die Abschussvorgabe ist der Gesamtabschuss von Böcken zu kürzen.

Je Geschlecht sollen nach dem Abschuss die einzelnen Klassen wie folgt vertreten sein:

45 % Klasse III und Kitze 55 % Klasse II und I

Sollte bei einer notwendigen Reduzierung oder einem notwendigen Aufbau des Gamsbestandes eine Erhöhung bzw. Senkung des Abschusses notwendig werden, so sind die Prozentsätze insbesondere in der Klasse III entsprechend anzuheben bzw. abzusenken!

Appendix IV – Chi-square contingency tables

A - KAISERTAL

	female	male	Marginal Row Totals
Count 1	82 (82.38) [0]	74 (73.62) [0]	156
Count 2	78 (77.62) [0]	69 (69.38) [0]	147
Marginal Column Totals	160	143	303 (Grand Total)
The chi-square statistic is 0	.0075. The <i>p</i> -value is	.930964. Not significant	at <i>p</i> < .05.

B - ZILLERTAL - GINZLING

	Female	Male	Marginal Row Totals
Count 1	56 (47.37) [1.57]	4 (12.63) [5.9]	60
Count 2	49 (57.63) [1.29]	24 (15.37) [4.85]	73
Marginal Column Totals	105	28	133 (Grand Total)
The chi-square statistic is 13	.6118. The <i>p</i> -value is .0	00225. This result is signi	ficant at <i>p</i> < .05.

C - HINTERRISS

	Female	Male	Marginal Row Totals			
Count 1	42 (42.4) [0]	9 (8.6) [0.02]	51			
Count 2	32 (31.6) [0.01]	6 (6.4) [0.03]	38			
Marginal Column Totals	al Column Totals 74 15 89 (Grand Total)					
The chi-square statistic is 0.0536. The <i>p</i> -value is .816882. This result is <i>not</i> significant at $p < .05$.						

	Female	Male d			
Count 1	42 (33.43) [2.2]	9 (17.57) [4.18]	51		
Count 3	17 (25.57) [2.87]	22 (13.43) [5.46]	39		
Marginal Column Totals	59	31	90 (Grand Total)		
The chi-square statistic is 14.7063. The p-value is .000126. This result is significant at $p < .05$.					

Count 232 (24.18) [2.53]6 (13.82) [4.42]38Count 317 (24.82) [2.46]22 (14.18) [4.31]39		Female	Male	Marginal Row Totals	
Count 3 17 (24.82) [2.46] 22 (14.18) [4.31] 39	Count 2	32 (24.18) [2.53]	6 (13.82) [4.42]	38	
	Count 3	17 (24.82) [2.46]	22 (14.18) [4.31]	39	
Marginal Column Totals 49 28 77 (Grand Total)	Marginal Column Totals	49	28	77 (Grand Total)	

The chi-square statistic is 13.724. The p-value is .000212. This result is significant at p < .05.

	Females	Male	Row Totals		
Count 1	42 (36.26) [0.91]	9 (14.74) [2.24]	51		
Count 2	32 (27.02) [0.92]	6 (10.98) [2.26]	38		
Count 3	17 (27.73) [4.15]	22 (11.27) [10.21]	39		
Column Totals9137128 (Grand Total)					
The chi-square statistic is 20.6834. The <i>p</i> -value is .000032. The result is significant at $p < .05$.					

D – PITZTAL

	Female	Male	Marginal Row Totals		
Count 1	48 (45.53) [0.13]	6 (8.47) [0.72]	54		
Count 2	38 (40.47) [0.15]	10 (7.53) [0.81]	48		
Marginal Column Totals	86	16	102 (Grand Total)		
The chi-square statistic is 1.8161. The <i>p</i> -value is .177774. This result is <i>not</i> significant at $p < .05$.					

	Female	Male				
Count 1	48 (39.5) [1.83]	6 (14.5) [4.98]	54			
Count 3	31 (39.5) [1.83]	23 (14.5) [4.98]	54			
Marginal Column Totals	79	29	108 (Grand Total)			
The chi-square statistic is 13,6237. The p-value is 000223. This result is significant at $n < 0.5$						

The chi-square statistic is 13.6237. The p-value is .000223. This result is significant at p < .05.

	Female	Male	
Count 2	38 (32.47) [0.94]	10 (15.53) [1.97]	48
Count 3	31 (36.53) [0.84]	23 (17.47) [1.75]	54
Marginal Column To- tals	69	33	102 (Grand Total)

The chi-square statistic is 5.4974. The *p*-value is .019044. This result is significant at p < .05.

	Female	Male	Row Totals		
Count 1	48 (40.50) [1.39]	6 (13.50) [4.17]	54		
Count 2	38 (36.00) [0.11]	10 (12.00) [0.33]	48		
Count 3	31 (40.50) [2.23]	23 (13.50) [6.69]	54		
Column Totals 117 39 156 (Grand Tot					
The chi-square statistic is 14.9136. The <i>p</i> -value is .000578. The result is significant at $p < .05$.					

E - SCHMIRN

	Female	Male	Marginal Row Totals		
Count 1	509 (554.64) [3.76]	359 (313.36) [6.65]	868		
Count 2	399 (353.36) [5.89]	154 (199.64) [10.43]	553		
Marginal Column Totals	908	513	1421 (Grand Total)		
The chi-square statistic is 26.7321. The <i>p</i> -value is < 0.00001 . Significant at $p < .05$.					

E – KASERN

	female	male	Marginal Row Totals		
Count 1	89 (88.71) [0]	58 (58.29) [0]	147		
Count 2	16 (16.29) [0.01]	11 (10.71) [0.01]	27		
Marginal Column Totals	105	69	174 (Grand Total)		
The chi-square statistic is 0.0157. The p-value is .900164. Not significant at $p < .05$.					

Appendix V

Life table:

			qx= age	sx = age	l(x) =				
			specific	specific	stand.	14			
age	n°carcas-	n°survi-	mortality	survival	survival	l(x) x		_	
(m)	ses(dx)	vals(Nx)	rate	rate	prob.	1000	Lx	Tx	ex
0	91	635	0,050	0,950	1,000	1000,000	0,928	7,197	7,197
1	32	544	0,031	0,969	0,857	856,693	0,831	6,269	7,317
2	17	512	0,063	0,938	0,806	806,299	0,793	5,437	6,743
3	32	495	0,063	0,937	0,780	779,528	0,754	4,644	5,958
4	31	463	0,099	0,901	0,729	729,134	0,705	3,890	5,335
5	46	432	0,106	0,894	0,680	680,315	0,644	3,185	4,682
6	44	386	0,114	0,886	0,608	607,874	0,573	2,541	4,180
7	50	342	0,146	0,854	0,539	538,583	0,499	1,968	3,654
8	57	292	0,195	0,805	0,460	459,843	0,415	1,469	3,193
9	45	235	0,191	0,809	0,370	370,079	0,335	1,054	2,847
10	60	190	0,316	0,684	0,299	299,213	0,252	0,719	2,403
11	30	130	0,231	0,769	0,205	204,724	0,181	0,467	2,281
12	33	100	0,330	0,670	0,157	157,480	0,131	0,286	1,815
13	26	67	0,388	0,612	0,106	105,512	0,085	0,154	1,463
14	22	41	0,537	0,463	0,065	64,567	0,047	0,069	1,073
15	15	19	0,789	0,211	0,030	29,921	0,018	0,022	0,737
16	3	4	0,750	0,250	0,006	6,299	0,004	0,004	0,625
17	1	1	1,000	0,000	0,002	1,575			

			qx= age	sx = age	l(x) = stan. sur-				
age	n°carcas-	n°survi-	specific mortality	specific survival	vival	l(x) x			
-			rate	rate		1000	Lx	Тх	01
(f)	ses(dx)	vals(Nx)			prob.				ex
0	151	740	0,204	0,796	1,000	1000,000	0,898	7,785	7,785
1	40	589	0,068	0,932	0,796	795,946	0,769	6,887	8,653
2	21	549	0,038	0,962	0,742	741,892	0,728	6,118	8,247
3	28	528	0,053	0,947	0,714	713,514	0,695	5,391	7,555
4	16	500	0,032	0,968	0,676	675,676	0,665	4,696	6,950
5	27	484	0,056	0,944	0,654	654,054	0,636	4,031	6,163
6	30	457	0,066	0,934	0,618	617,568	0,597	3,395	5,498
7	36	427	0,084	0,916	0,577	577,027	0,553	2,798	4,849
8	49	391	0,125	0,875	0,528	528,378	0,495	2,245	4,249
9	43	342	0,126	0,874	0,462	462,162	0,433	1,750	3,787
10	53	299	0,177	0,823	0,404	404,054	0,368	1,317	3,259
11	55	246	0,224	0,776	0,332	332,432	0,295	0,949	2,854
12	46	191	0,241	0,759	0,258	258,108	0,227	0,653	2,531
13	35	145	0,241	0,759	0,196	195,946	0,172	0,426	2,176
14	40	110	0,364	0,636	0,149	148,649	0,122	0,254	1,709
15	35	70	0,500	0,500	0,095	94,595	0,071	0,132	1,400
16	19	35	0,543	0,457	0,047	47,297	0,034	0,061	1,300
17	8	16	0,500	0,500	0,022	21,622	0,016	0,027	1,250
18	5	8	0,625	0,375	0,011	10,811	0,007	0,011	1,000
19	2	3	0,667	0,333	0,004	4,054	0,003	0,003	0,833
20	1	1	1,000	0,000	0,001	1,351	0,001	0,001	0,500
20	0	1	1,000	0,000	0,001	0,000	0,001	0,001	0,500
21	0	0		0,000	0,000	0,000		0,000	