ESTIMATION OF CHAMOIS ABUNDANCE IN THE SWISS NATIONAL PARK

MASTER THESIS

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Abstract

The estimation of wildlife population abundance is a complex and important issue, the key stone for a proper wildlife management. So far it has been assumed that chamois population can be easily surveyed by means of focal counts from vantage points, since this species can be often observed in open areas. However, the recent increase in chamois density and the subsequent colonization of forested areas have raised some concerns about the reliability of focal counts, which could lead to severe bias in the estimate of population size. In my thesis I investigated the size of a chamois population living in the Swiss National Park through the use of focal counts and capture-mark-resight (CMR). Between 1997 and 2008, focal counts have been carried four times per year (January, April, August, November) from vantage point by the experienced personnel of the Park; during the same time span, 125 chamois (44 males, 81 females) have been captured and individually marked with ear tags and/or collars, and their resightings occurred ever since. I compared the outcome of focal counts with the estimates obtained with CMR models, built with three different software (MARK, NOREMARK and CAPTURE). Despite CMR models are traditionally (and successfully) used for estimating abundance, in this research all three software gave erroneous results. Specifically, MARK and NOREMARK overestimated population size, with no significant difference between them, while CAPTURE showed a remarkable underestimation. Such a strong bias is likely due to the insufficient accuracy as far as the fulfilment of some basic CMR assumptions is concerned. The assumption of closed population might have been violated during the survey sessions, while non-consistent survey strategy and low proportion of marked individuals might have directly biased the final estimates of population abundance. Nevertheless, defined minimum number of resightings, distribution of vantage points, usage of a proper marking method, fulfillment of all CMR assumptions, right choose of software and estimator for data set analysis are obligatory for the proper CMR study. The capture heterogeneity is another important issue, which should be taken in consideration, especially during the marking of individuals. Moreover, the use of Minimum Number Alive (MNA) to estimate "marks at risk" should be avoided.

Keywords: chamois, focal counts, capture-mark-resight, population abundance

Zusammenfassung

Die Schätzung von Wildtierpopulationsdichten ist ein komplexer, jedoch wichtiger Bestandteil eines vernünftigen Wildtiermanagements. Gämse (*Rupicapra rupicapra* L.) halten sich vorwiegend in frei ersichtlichem Gelände oberhalb der Baumgrenze auf. Aus diesem Grund wurde bislang angenommen, dass deren Populationsgrößen auf zufriedenstellende Weise durch Zählungen von fixen Beobachtungspunkten aus erfasst werden können. Der derzeitige Anstieg der alpinen Gamspopulationen und die damit verbundene Ausdehnung der von Gamswild besiedelten Fläche auf die darunter liegenden Waldgebiete lässt jedoch Zweifel an der Verlässlichkeit dieser Ermittlungen aufkommen.
Meine Masterarbeit basiert auf der Untersuchung einer Gamspopulation im Schweizerischen Nationalpark durch Zählung (focal counts) und der „Capture-Mark-Resight" Methode (CMR). Von 1997 bis 2008 wurden durch das erfahrene Nationalparkpersonal vier Zählungen pro Jahr (Januar, April, August, November) von stets den gleichen Beobachtungspunkten aus durchgeführt. Während dieser Zeit wurden insgesamt 125 Tiere (44 Böcke, 81 Geißen) gefangen, durch Ohrmarken und/oder Halsbänder markiert und bei späteren Beobachtungen individuell registriert. Die Ergebnisse der Zählungen wurden mit Schätzungen von CMR-Modellen verglichen, die mit drei verschiedenen Softwareprogrammen (MARK, NOREMARK und CAPTURE) berechnet wurden. Obwohl CMR-Modelle häufig (und erfolgreich) zum Abschätzen von Populationsgrößen herangezogen werden, konnte in dieser Studie mit keinem der drei Programme zufriedenstellende Ergebnisse erzielt werden. Während MARK und NOREMARK, ohne signifikanten Unterschied zueinander, die Populationsgrößen deutlich überschätzten, waren die mit CAPTURE berechneten Werte zu klein. Diese großen Abweichungen sind mit hoher Wahrscheinlichkeit auf die mangelnde Genauigkeit der Grundannahmen des CMR zurückzuführen. Möglicherweise wurde zu den verschiedenen Beobachtungszeitpunkten die Annahme einer geschlossenen Population nicht beruecksichtigt. Die endgueltigen Ergebnisse koennten durch eine uneinheitliche Beobachtungsstrategie, einem zu geringen Anteil markierter Individuen und heterogene Fänge verzerrt sein. Darüber hinaus sollte bei weiteren Studien die „Minimum Number

Alive“ Methode (MNA) zur Abschätzung der potentiell gefährdeten markierten Individuen („marks at risk“) vermieden werden.

Kennwörter: Gemse (*Rupicapra rupicapra* L.), focal counts, Capture-Mark-Resight, Populationsgröße

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Introduction

The estimation of wildlife population abundance is a complex and important issue, as the knowledge of population number is the key stone for a proper wildlife management. Several methods have been developed either to directly estimate population size or density, or to indirectly monitor their numerical trend through indices (see Loison *et al.* 2006). For many ungulates, management often relies on single focal counts performed on a given date each year (e.g. chamois, Houssin *et al.* 1994).

The Alpine chamois (*Rupicapra rupicapra rupicapra* Linnaeus 1758) is found in the European Alps at altitudes ranging between 450 m and 2,500 m a.s.l. (Sägesser & Krapp 1986). Since this species can be found in open, steep and rocky terrains, so far it has been assumed that chamois populations can be easily surveyed (Lovari and Cosentino 1986). However, the recent increase in chamois density and the subsequent colonization of forested areas (Breitenmoser 1998, Loison *et al.* 2002) have raised some concerns about the reliability of focal counts, which could lead to severe underestimates of the population size (Houssin *et al.* 1994).

In fact, although focal counts appear sustainable in the long term, they find limitations in habitat environmental features, animal detectability and in the ability of the participants to recognize individuals. According to Toïgo 1998 (see also Largo *et al.* 2008), for the Alpine ibex (*Capra ibex*) populations of Belledonne (France), focal counts consistently underestimated population number up to 20-60%. Therefore the use of an alternative estimate methodology, such as capture-mark-recapture (CMR), is recommended whenever possible. Thanks to its statistical robustness, CMR is nowadays considered to be one of the most effective methodologies for estimating animal abundance. For large herbivores, in particular, the recapture session has often been substituted by simple resightings, which makes CMR-models cheaper and less disruptive both to the animals and to the environment (Fattorini *et al.* 2007).

In my study I wanted to test if the focal counts are reliable method for the estimation of chamois abundance. Therefore, the focal counts, as the reliable method, are presented in the null hypothesis, while in the alternative hypothesis focal counts are disputable method. To confirm any of the hypotheses, I compared the annual numerical estimates of chamois population living in the Swiss National Park, through both focal counts and

CMR models. Two types of focal counts estimates have been taken in consideration, the monthly-periodical and the annual one. On such a way I could check if the former provided a sufficiently reliable method for the numerical estimation of populations**.** If the focal counts show no significantly different final estimates than the CMR estimates, the first hypothesis will be confirmed. If there is significant difference between the final estimates, the alternative hypothesis will be approbated. Moreover, I will calculate the intrinsic population growth rate for both methods in order to analyze if they show similar trends. The presence of a constant parallelism between the trends will confirm the reliability of focal counts, even if there is underestimation of abundance.

In recent years the literature describing methods for estimating animal abundance continues to grow (Schwarz and Seber 1999). Plenty of software are used for data analyses, where ESTIMATE, CAPTURE, BROWNIE, MULT, SURVIV, SURGE, MARK, EAGLE, JOLLY, RELEASE, POPAN, NOREMARK are just some of them. Such variety gives advantage to the ecologists to implement their method in different program (Rotella *et al.* 2004), while at the same time they have important task to choose the right program (McClintock et al. 2006). In my research I choose three different software (MARK, NOREMARK and CAPTURE) to analyse CMR data, in order to test the performance of each one of them. Each of this software is commonly used by researchers (White 1996, McDonald and Amstrup 2001, Pollock 2002, Pollock *et al.* 2002, Fattorini *et al.* 2007, Barker 2008,). The primary software used for estimating the population abundance is MARK, software which also deals with the survival rates and capture probability, but I also used NOREMARK, as the software which was developed for estimating population number of demographically and geographically closed but free-ranging populations, and CAPTURE which is mostly used for Mark-Recapture data. With each of them I analyzed the data for the annual estimation, except in NOREMARK thanks to which I also analyzed the data for monthly-periodical estimation.

Since all three software are reliable, I expect that the final estimates obtained with each one of them will not be significantly different. This statement is present as distinct null hypothesis. If the final estimates appear to be significantly different, it will confirm the distinct alternative hypothesis, that each software will show different results.

Study site

The Swiss National Park (SNP) covers 172.4 km² and it is located in Grison Canton, Switzerland (46°40'10.74"N, 10°9'15.15"E). According to the International Union for Conservation of Nature (IUCN), the Park belongs to the category I nature reserve. Because human impact is minimized, the Park is close to pristine nature and its main purposes lie in the conservation of natural processes and the promotion of scientific research. Forests cover 28% of the SNP area, out of which conifers account for 99.5% (http://www.nationalpark.ch/snp.html).

The data collection has been carried out in the region of Il Fuorn, which extends over 5,026 ha covered by 29.4 % of forest, 21.2% of alpine meadows and 49.4% of rocks and scree. The climate is dry continental (Campell and Filli 2006). Vegetation is subalpine to subnival, and it occupies less than 20% of area above timberline (2,250 m a.s.l). Il Fuorn is mostly covered with Mountain pine (*Pinus mugo*), European larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) woodlands, small stands of mountain pine shrub and pastures with diverse nutrient values (Meyer and Filli 2006).

Methods

Data collection

Data of chamois abundance were collected through focal counts and CMR.

Focal counts

Usually, for estimating chamois population abundance, focal counts are carried out once per year. Nevertheless, according to Corlatti (2008), the detectability of individuals of different age and sex classes varies across the year, due to the seasonality of chamois behaviour. This, as a consequence, can lead to severe bias in the estimation of abundance. For this reason, in the SNP focal counts are performed four times a year (January, April, August, November), a fact that can help to reduce the seasonality problem.

To properly carry out focal counts, the area of Il Fuorn has been divided into sub-sectors, where two observers carried out observations from vantage points. As for the CMR (see below), the observers were equipped with 8.5 x 42 binoculars and telescopes with a 60x magnification. The number, sex- and age-class, group size, location, and time of observation of each individual chamois were recorded.

CMR

Between 1994 and 2008, 125 chamois individuals were captured, marked and released (44 males and 81 females). The age of the marked individuals (estimated through the counting of horn notches) was between 0 and 15 for males and between 0 and 17 for females. Individuals were captured with trap boxes and snares, from December to May, and marked with individually recognizable ear tags and/or collars.

To avoid bias in surveys, resightings were performed throughout the year from vantage points, which allowed the observers to monitor the whole study site. The data set of resighting events contained the following information for each re-sighted individual: animal identity, sex, age at observation, date and time of observation, number of cubs (if present) and group size (consisting of unmarked individuals). No marked animals remained unidentified during resightings.

Data analyses

Focal counts

I collected historical data from focal counts for the period 1997 and 2008 and classified them into the following groups: number of males and females >1 year old, kids (<1 year of age) and animals whose sex remained undetermined (Table 1).

To calculate the total number of individuals per each year, I summed the maximum number of individuals observed per sex-class in the different months. Some issues might arise due to the presence of unidentified individuals; to assign unknown individuals (U) to sex-classes (males and females), I used the following algorithms:

$$M = \frac{m}{m+f} * U + m$$

$$F = \frac{f}{m+f} * U + f$$

where the total number of males (M) and females (F) as well as the counted number of males (m) and females (f). Finally, I excluded kids from the estimation of population abundance, because the mortality rate in this group is typically highly variable due to the unpredictable Alpine climate (Loison *et al.* 1999).

Table 1. Historical data from focal counts, for the period 1997 and 2008, Il Fuorn, Swiss National Park.

Year	Month	Total	Unknown	Males	Females	Kids
1997	May	214	26	70	118	0
	August	173	0	69	65	39
	November	368	19	102	177	70
1998	January	134	9	41	72	12
	May	237	16	91	127	0
	August	219	1	62	93	63
	November	346	8	97	150	91
1999	January	339	11	68	178	82
	May	234	4	63	117	0
1999	August	220	8	72	101	39
	November	144	3	51	64	26
2000	January	306	2	37	182	55
	May	204	19	62	113	0
	August	164	5	48	57	44
	November	162	0	29	84	44
2001	January	121	0	32	63	23
	May	173	1	68	75	0
	August	293	9	71	122	48
	November	296	0	91	133	60
2002	January	319	2	81	155	64
	May	225	11	82	81	7
	August	263	7	48	120	64
	November	319	0	91	138	74
2003	Jan	107	4	28	47	23
	April	200	23	50	105	14
	August	147	0	49	58	30
	November	216	0	49	104	61
2004	January	162	6	29	76	44
	April	185	0	63	79	34
	August	226	0	61	93	56
	November	300	0	71	137	80
2005	January	280	2	70	132	61
	April	267	0	61	154	43
	August	240	0	73	92	59
	November	392	6	92	179	87
2006	January	259	1	47	138	61
	April	205	1	48	122	26
	August	177	0	66	67	38
	November	239	4	58	115	53
2007	January	287	5	67	150	55
	April	241	8	42	144	19
	November	378	22	70	177	109
2008	January	164	3	27	90	44
	May	186	46	47	96	0
	August	249	9	54	126	60

CMR

For the analyses of CMR data, I first checked the fulfilment of several assumptions, typical for almost all capture-recapture/resight models: all marks must be permanent, all individuals must have equal chances to be seen, marking must not affect individual survival rate and all animals must have an equal chance of dying or emigrating (Beagon 1978). I also assumed that the population was closed within years, demographically and geographically. For this task, I found a period within each year when the population might not be susceptible to severe losses or gains, i.e. from July to November. Based on the previous knowledge on the chamois biology and observations carried out by the gamekeepers of the SNP, death of individuals over this period was unlikely to occur; the birth season, also, occurred before the considered time span.

Since the survey period was long (1994-2008), I used the principle of Minimum Number Alive (MNA) to define the number of marked individuals ("marks at risk") in population. The number of marked individuals was estimated according to the last date of the resighting of each individual. Individuals were considered alive in population from the date of capture until the date of the last observation. Following this procedure I estimated the minimum number of marked individuals present in the population during each year.

After defining the number of marked animals for each period, I analyzed the data retrieved from CMR by means of different software: MARK, CAPTURE and NOREMARK. For the annual estimations, all resightings were grouped in five sessions. Each session consisted of monthly resighting data, pooled together so to have five sessions over the time span July-November. The choice of the monthly duration for each session is justified by the time needed to carry out resightings all over the entire study site.

The CMR estimates obtained from each software were compared in STATGRAPHICS PLUS for detecting eventual statistical differences. For that purpose several statistical tests were used: t-test to compare the means, F-test to compare the standard deviations and Kolmogorov-Smirnov test to compare the distributions. I used the same software - STATGRAPHICS PLUS, to compare monthly-periodical estimation obtained with NOREMARK and focal counts, running the F-test to compare the standard deviations, Mann-Whitney W test to compare the medians and Kolmogorov-Smirnov test to compare the distributions. Below I provide detailed information regarding the analysis of data by means of different software.

- *MARK*

The data set was transformed to contiguous series of specific dummy variables (encounter history). For each year I analyzed five sessions, therefore for each marked individual the encounter history consisted of five variables. If the marked individual was seen during the session, the dummy variable would be 1 and if it was not seen the dummy variable would be 0. For each session I calculated the number of unmarked individuals that were seen. In MARK I chose the option Mark-Resight, sub-option Logit-Normal. For each year the easy robust design times was set on one primary occasion and five secondary occasions within the primary one, for an overall of five encounter occasions per year. When I inserted the data set for a particular year, I created models in the Parameter Index Matrix (PIM), by changing recapture/resighting rates. When I ran the models I used in Setup numerical estimation default options and identity design matrix. I looked for the most suitable model by comparing AICc values in Results browser. Except the annual estimations, I also analyzed the whole data set, through four models that I defined in PIM, by changing resighting rates and individual heterogeneity.

- *CAPTURE*

The input data of resightings were transformed in the encounter history format. The task read matrix was based on five capturing occasions which were equivalent to five resighting sessions. I defined the format for data analyses: '(0x,a3,1x,5f1.0)' because each individual was identified with three-digit numbers and for each year I defined the number of marked individuals in the population. The program ran the analyses trough all standard models.

- *NOREMARK*

I carried out two types of analyses: the estimate of annual population size, (with the same data which I used in CAPTURE and MARK) and the monthly estimation of the population size. Because focal counts were performed four times per year (January, April/May, August and November), I also had to estimate the number of individuals for the period when the population was not closed. The bias in these calculations was likely reduced, because kids were not included in the population's estimation and the number of marks at risk was constant throughout the whole year. In both cases I used Bowden's Model estimator, since it is appropriate for dealing with individual heterogeneity in sighting probabilities, sampling with replacement and unidentified marked individuals (White and Shank 2001, McClintock and White 2007). The input data consisted of the number of marked individuals (which I defined for each calculation), and the sum of the unmarked animals which were seen with marked individuals. According to the observers of the SNP, all marked individuals have been identified during resightings, therefore this column was skipped. Alpha level for confidence interval construction was set at 0.5.

Growth rate estimation

To estimate the population growth, I used four different methods, four intrinsic rates of population increase: λ1, λ2, λ3 and λ4, developed by Lebreton and Millier (1982). Each intrinsic rate has been calculated differently. The first intrinsic rate λ1 was calculated as the slope of the regression of the log-transformed annual estimates in a year. The second intrinsic rate of population increase λ2 was calculated as the ratio between the sum of the estimates from the second to the last year of and the sum of the estimates from the first to the penultimate year:

$$\lambda 2 = \frac{\Sigma(Ni + 1 + \ldots + Nj)}{\Sigma(Ni + \ldots + Nj - 1)}$$

The third intrinsic rate of population increase λ3 was calculated as the mean of the ratio of estimate in year t+1 to estimate in year t:

$$\lambda 3 = \Sigma\left(\frac{Ni + 1}{Ni}\right) / t$$

If the range of λ3 goes beyond the upper limit of chamois population growth, corrected values of λ3 have to be calculated. The last intrinsic rate of population growth λ4 was calculated as the t^{th} root of the ratio between Nt and N0:

$$\lambda 4 = \sqrt{\frac{Nt}{N0}}$$

where Nt is the abundance in the last year and N0 is the abundance in the first year.

The choice to use different values of lambda appears justified by their different performances: λ1 and λ3 perform better when the population census is regular and without outliers in count series, while λ2 and λ4 are less sensitive to irregular counts and errors in some years (Lebreton and Millier 1982).

Results

Focal counts

According to the results of focal counts, the population of chamois in Il Fuorn appears to be decreasing. The difference within the sex classes was tested with the t-test, to compare the means, and it is significant ($t = -8.75914$; $P = 1.26929 \times 10^{-8}$; $df = 22$). The estimate of chamois abundance is presented in table 2:

Table 2. Focal counts estimates per sex class in Il Fuorn, Swiss National Park, between 1997 and 2008.

Year	Males	Females	Total
1997	109	189	298
1998	100	155	255
1999	75	186	261
2000	69	184	253
2001	91	133	224
2002	91	156	247
2003	57	121	178
2004	71	137	208
2005	94	183	277
2006	66	139	205
2007	76	193	269
2008	62	132	194

The results of the annual estimates are shown in Figure 1:

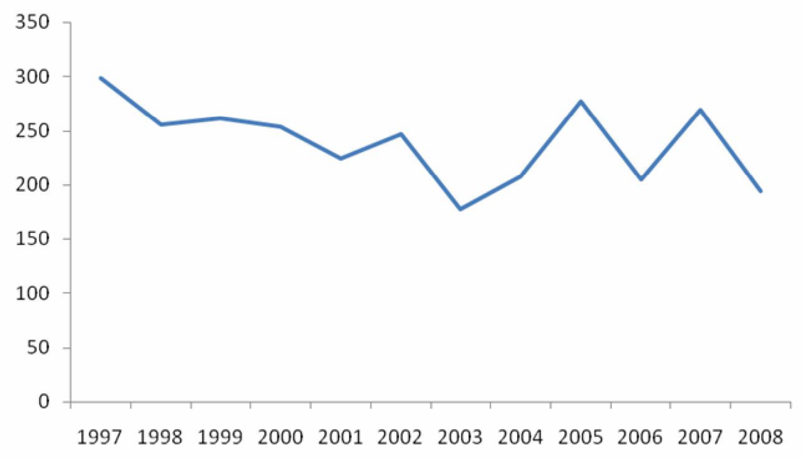

Figure 1. Focal counts estimates in Il Fuorn, Swiss National Park, between 1997 and 2008.

Up to 2002 the population decreased quite regularly, while in 2003 there was a drop in chamois number. After 2003, large variations occurred in the demographic trend from year to year.

CMR

MARK

The analysis of the data set in MARK did not result in a uniform series. Instead, the variations between years were not acceptable from the biological point of view, due to the distinct differences among annual estimates. I ran several models to obtain a demographic trend of the population – the analysis of the annual estimates and the analysis of the whole data set. In total I ran seven models, three for annual estimates and four for the analysis of the whole data set. When estimating the annual abundance, each model gave the same result. Eventually, I estimated the animal abundance for each year and made a demographic trend of the population (Fig. 2).

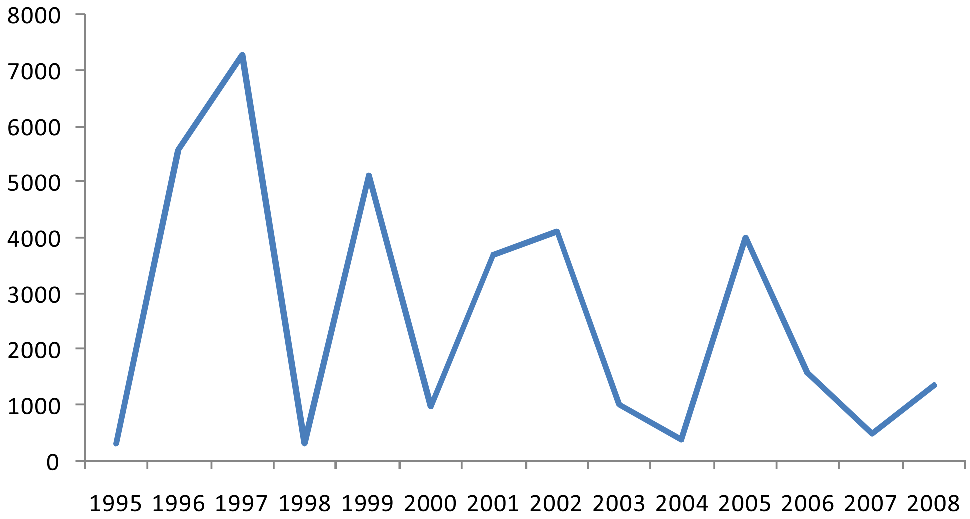

Figure 2. MARK estimates of population abundance in Il Fuorn, Swiss National Park, between 1995 and 2008.

The estimates in this model range from 336 to 7,289 individuals. Due to biological characteristics of chamois, the result appears erroneous. The analysis of the whole data set gave results that varied among models, and they were different from the annual estimates. For the model with a constant recapture probability and the individual heterogeneity, I obtained the estimates given in Fig.3.

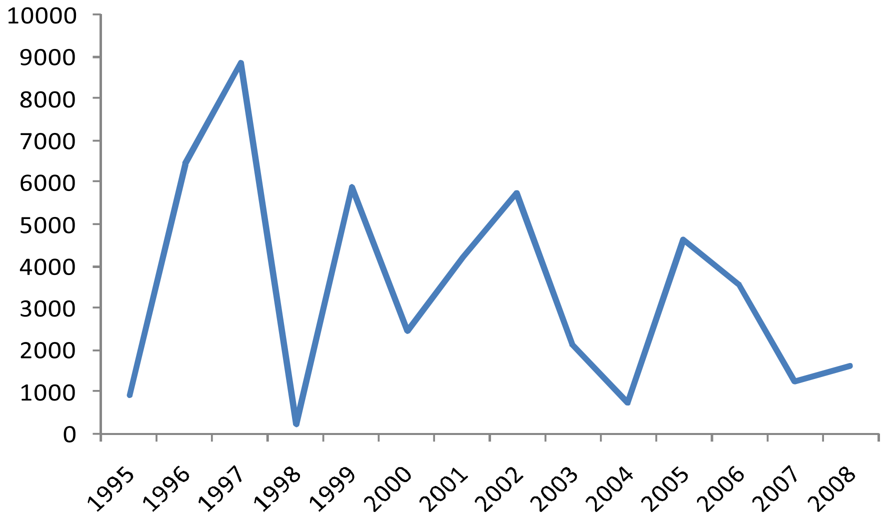

Figure 3. MARK estimate of population abundance in Il Fuorn, Swiss National Park, between 1995 and 2008, Model: Analyses of the whole data set, constant recapture probability and individual heterogeneity.

For the model with variable recapture probability and constant individual heterogeneity, the estimate of population abundance is shown in Fig. 4.

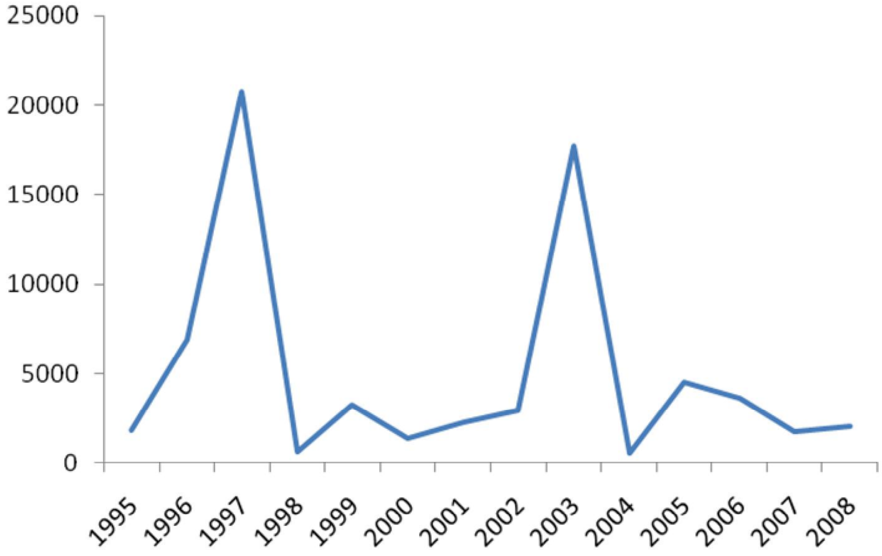

Figure 4. MARK estimate of population abundance in Il Fuorn, Swiss National Park, between 1995 and 2008, Model: Analysis of the whole data set, variable recapture and constant individual heterogeneity.

The third model is based on constant recapture probability and variable individual heterogeneity (Fig. 5).

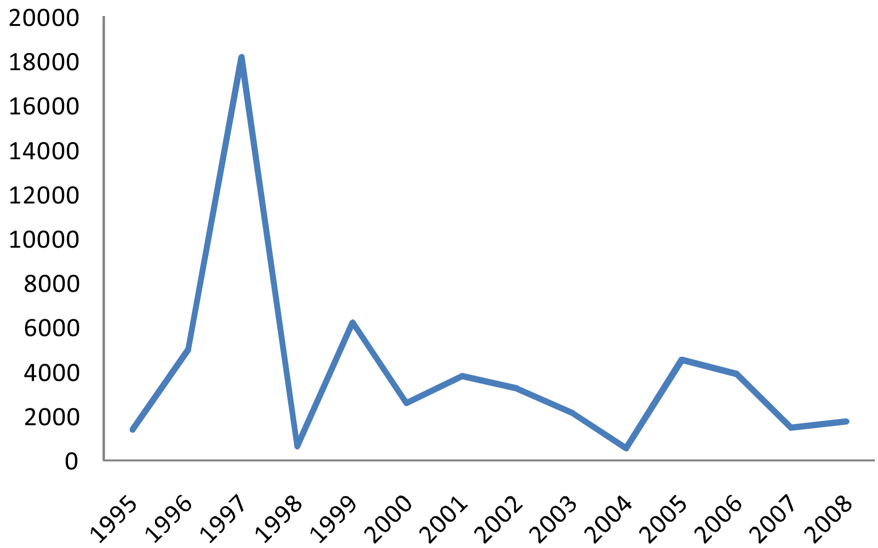

Figure 5. MARK estimate of population abundance in Il Fuorn, Swiss National Park, between 1995 and 2008, Model: Analysis of the whole data set, constant recapture and variable individual heterogeneity.

The fourth model was based on variable recapture probability and individual heterogeneity (Fig. 6).

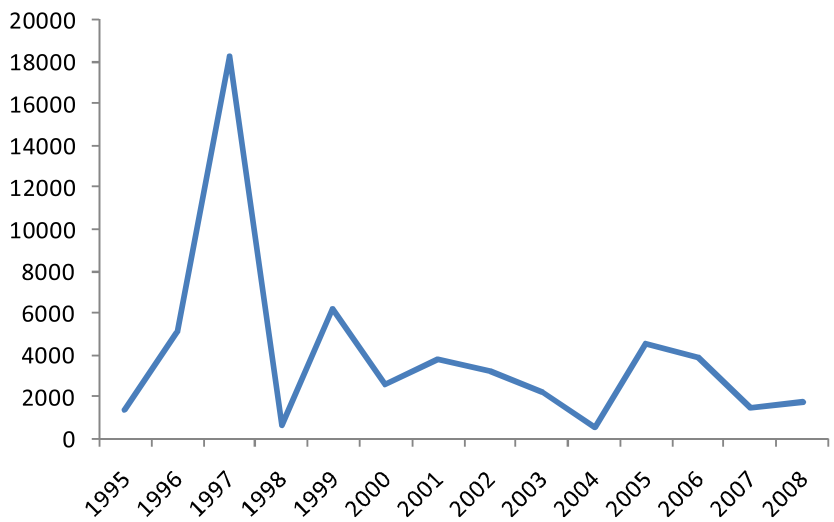

Figure 6. MARK estimate of population abundance in Il Fuorn, Swiss National Park, between 1995 and 2008, Model: Analysis of the whole data set, variable recapture probability and individual heterogeneity.

All four analyses of the whole data-set in MARK showed different results. Only the model of constant recapture probability and individual heterogeneity showed results similar to the annual estimates. The other three models have similar trend lines, although the model of variable recapture and constant individual heterogeneity showed higher deviation in 2003, which is not present in the other two models. Each analysis shows highest estimates in 1997, followed by a significant decrease, and lowest estimates in 1998. Nevertheless, all estimates can be rejected because of the big variations which do not fit the biological growth rate of chamois populations.

CAPTURE

This software calculated a maximum population number of approximately 70 individuals in 2002, which is significantly lower than the estimates obtained in other software (Fig. 7). The variation in the estimates obtained with this software ranges from 0 to 70 individuals. Despite such variations are less than in MARK, they still do not seem realistic from the biological point of view.

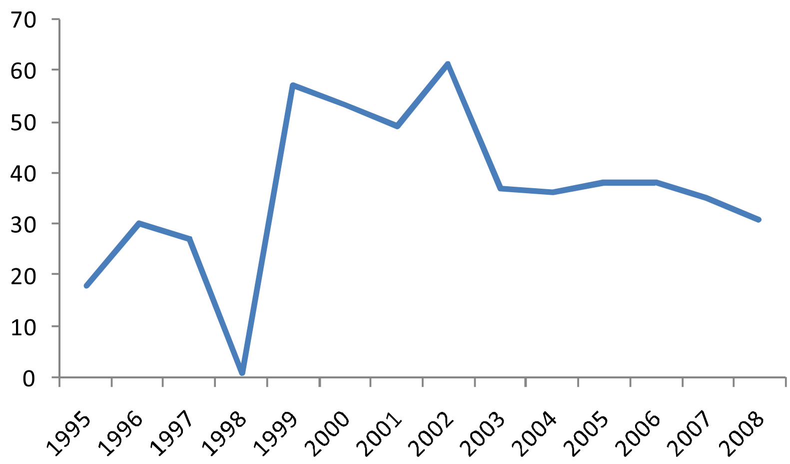

Figure 7. CAPTURE estimate of population abundance in Il Fuorn, Swiss National Park, between 1995 and 2008

NOREMARK

The results of annual estimates are similar to the estimates from MARK. Again, the highest estimation occurs in 1997, while the lowest one in 1998. The rest of variations are lower, but still in range of several thousand individuals, which make them not coherent to the biology of the study species. The demographic trend of the annual estimates is shown in Fig. 8:

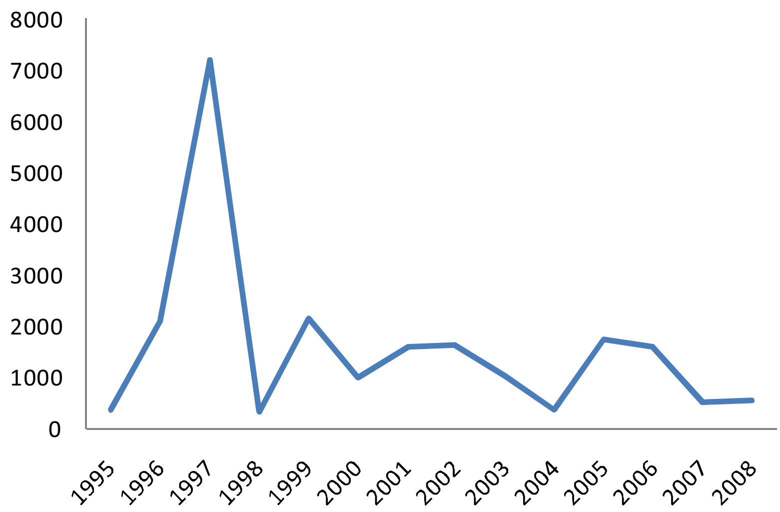

Figure 8. NOREMARK estimates of annual counts in Il Fuorn, Swiss National Park, between 1995 and 2008.

Beside the estimate of the annual abundance, I calculated the population size within each month. The results are shown in Fig. 9.

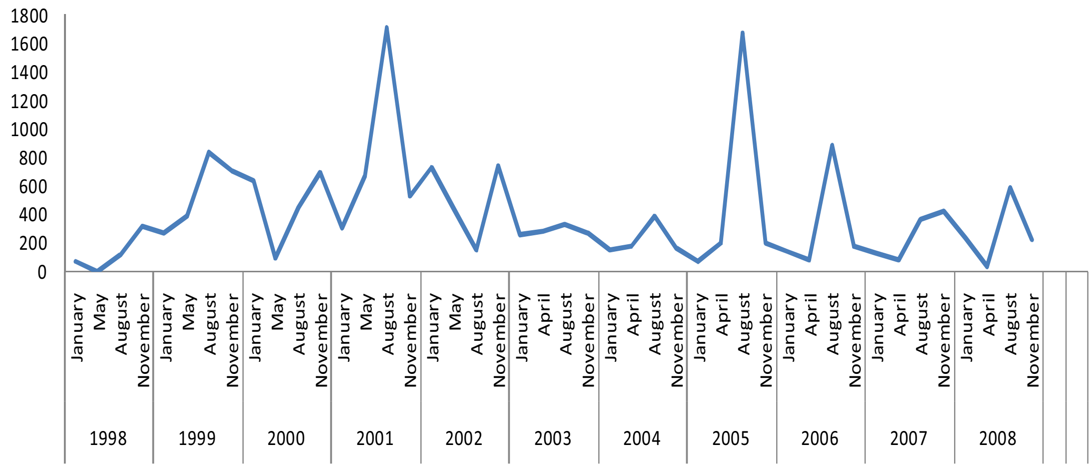

Figure 9. NOREMARK estimates of monthly counts in Il Fuorn, Swiss National Park, between 1995 and 2008.

The only similarity with other estimates is that the lowest population number is calculated for year 1998.

Comparison of results from resightings

In each software the estimates of annual abundance were biased (i.e. see the big variations over years). Nevertheless, it is characteristic for each result, that the lowest population number is calculated in 1998. The results these analyses are in table 3. The bias in the estimates might have occurred either during the analyses or during the data collection. To check if the fault occurred during the analysis, I planned to compare the estimates from all three software to look for a possible difference. Since the CAPTURE estimates showed big underestimation, I excluded them from comparison, because it was obvious that they were significantly different from the other two. I compared two other estimates, of MARK and NOREMARK, to test if there was a difference between them. (table 4).

Table 3. MARK, NOREMARK and CAPTURE estimates of population abundance in Il Fuorn, Swiss national Park, between 1994 and 2008.

Year	MARK	NOREMARK	CAPTURE
1995	336	335	18
1996	5,589	2,104	30
1997	7,289	7,179	27
1998	321	315	-
1999	5,145	2,124	57
2000	998	976	53
2001	3,701	1,566	49
2002	4,126	1,609	61
2003	1,032	1,004	37
2004	391	354	36
2005	4,018	1,724	38
2006	1,590	1,586	38
2007	512	510	35
2008	1,362	530	31

I used the Kolmogorov-Smirnov test to compare the distributions (K-S statistic = 0.945; P = 0.336), the t-test to compare the means (t = - 1.335; P = 0.193; df = 26) as well as the F-test to compare standard deviations, (F = 0.564; P = 0.315; df: n1-1=13 and n2-1=13), and did not detect any significant difference between the estimates in MARK and NOREMARK.

Table 4. Statistical analysis and comparison of MARK and NOREMARK estimates of chamois population in Il Fuorn, Swiss National Park, between 1995 and 2008.

	Estimates in NOREMARK	**Estimates in MARK**
Count	14	14
Average	1,564	2,600
Median	1,285	1,476
Mode	-	-
Geometric mean	1057	1583
Variance	3.04117×10^6	5.38915×10^6
Standard deviation	1743.89	2321.45
Standard error	466.08	620.44
Minimum	315	321
Maximum	7,179	7,289
Range	6,864	6,967
Lower quartile	510	513
Upper quartile	1,724	4,126
Interquartile range	1214.0	3613.0
Skewness	2.86	0.71
Stnd. skewness	4.37	1.09
Kurtosis	9.43	-0.77
Stnd. kurtosis	7.20	-0.59
Coeff. of variation	111.45%	89.26%
Sum	21906.0	36412.0

Focal counts vs CMR

The bias occurred during the estimation made the CMR not suitable for the calculation of lambda values.

As far as the focal counts are concerned, in Table 9 I report the results of the calculation of intrinsic population growth rates. Since λ_3 perform better with no outliers (Lebreton and Millier 1982) I checked its range. The yearly λ_3 estimated from annual counts ranged from 0.7-1.3. According to Gaillard *et al.* 2000, monotocous ungulates can reach a maximum of 1.25-1.35, while Loison *et al.* 2002 estimated 1.3 as the highest productivity value of ibex species in Belledonne. Adopting a parsimony approach, I excluded the highest value of λ_3, since it might not be coherent with the growth rate of the study population. By excluding the highest value, the mean of λ_{3c} is closer to other population growth rate's values. The range of λ_3 is presented in Fig. 10:

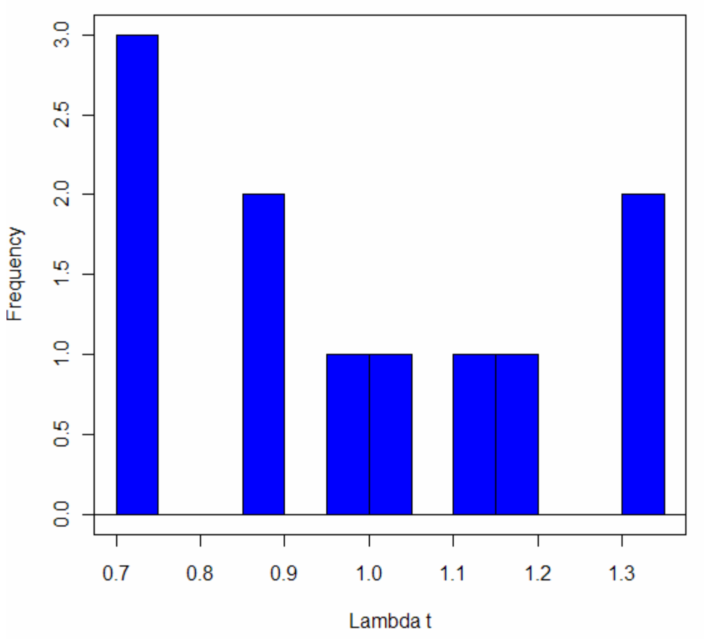

Figure 10. Range of λ_3 intrinsic population growth rate, for focal counts estimates in Il Fuorn, Swiss National Park.

Table 5. Intrinsic rates of population growth for focal counts estimates from Il Fuorn, Swiss National Park, between 1997 and 2008.

Intrinsic rate	Focal counts
λ_1	0.979
λ_2	0.961
λ_3	0.985
λ_{3C}	0.950
λ_4	0.965

From the calculated intrinsic rates of population growth, the population appears to be decreasing slowly with a mean rate of ca. 3-4 % each year.

To check whether monthly estimates could be more reliable than annual estimates, in Fig 11. I present the trend lines of the monthly estimates from NOREMARK and from the focal counts.

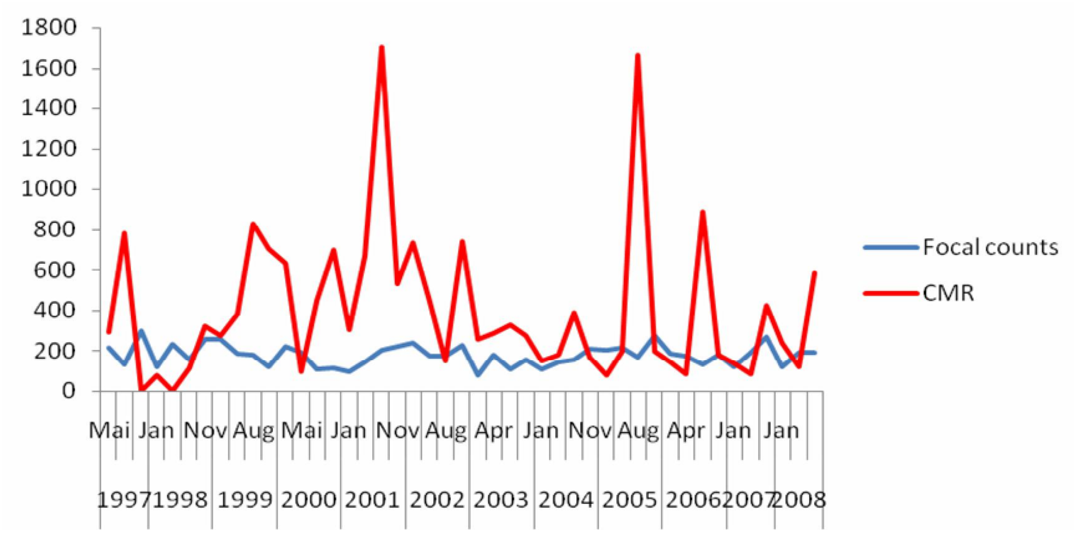

Figure 11. Comparison of the focal counts and NOREMARK (CMR) monthly estimates of the chamois population in Il Fuorn, Swiss National Park, between 1997 and 2008.

To test if this two results can be compared I ran in STATGRAPHICS PLUS the Kolmogorov-Smirnov test for the comparison of distributions (K-S statistic = 2.42441; P = 0.00002), the Mann-Whitney W test to compare medians (W = 1390.0; P = 0.00235) and F-test to compare standard deviations, (F = 0.0198; P = 0.0; df: n1-1=44 and n2-1=44). The results show significant differences between focal counts and CMR estimates both in terms of absolute values and range of variation.

Discussion

The CMR approach has been used successfully for estimating wildlife populations (e.g. Hein and Andelt 1995, McCullough *et al.* 2000, Focardi *et al*. 2002, Gould *et al.* 2005), including ungulates (Bartmann *et al.* 1987, Neal *et al.* 1993, Bowden and Kufeld 1995, Loison *et al.* 2003, McClintock *et al.* 2006). The CMR estimates in my research, however, appeared erroneous, making focal counts the only useful estimate of population abundance. According to such results, the chamois population in Il Fuorn is slightly decreasing. To get a deeper understanding of the reasons why CMR estimates proved to be unreliable and to check for the mismatches, I went through all the steps of my analysis.

The data set was analyzed in three programs, out of which two results showed no significant statistical difference (MARK and NOREMARK), whilst the third one showed remarkable underestimates (CAPTURE). The bias in CAPTURE was likely due to the intrinsic characteristics of the software, which successfully analyzes recapture data, but it's not suitable for resightings. Since two different software obtained similar results, I presume that the cause of the wrong estimates lies in the violation of certain assumptions: several authors (Gould and Fuller 1995, Focardi *et al*. 2002, Barker 2008) claimed the assumptions violation to be one of the main causes for biased CMR estimates. I took into consideration some key-points that may strongly influence the outcome of mark-resight models and checked whether they have been fulfilled or not:

Mark-lost: the potential bias caused with mark lost was avoided through the use of Minimum Number Alive (MNA) principle. This principle is justified by Hanley and Barnard (1999), since the MNA assumptions are minimal compared to the statistical estimators. Nevertheless, according to Pocock *et al.* 2004, the MNA is subject to negative bias, despite it has been commonly used for assessing the population size by means of CMR models. Studies using MNA as an index of population size tend to overestimate abundance during the middle of the study relative to the beginning and the end (Pocock *et al.* 2004). To get some further insight into the subject, I propose the numerical trend of marks in the population -estimated trough the MNA- over time (Fig. 12).

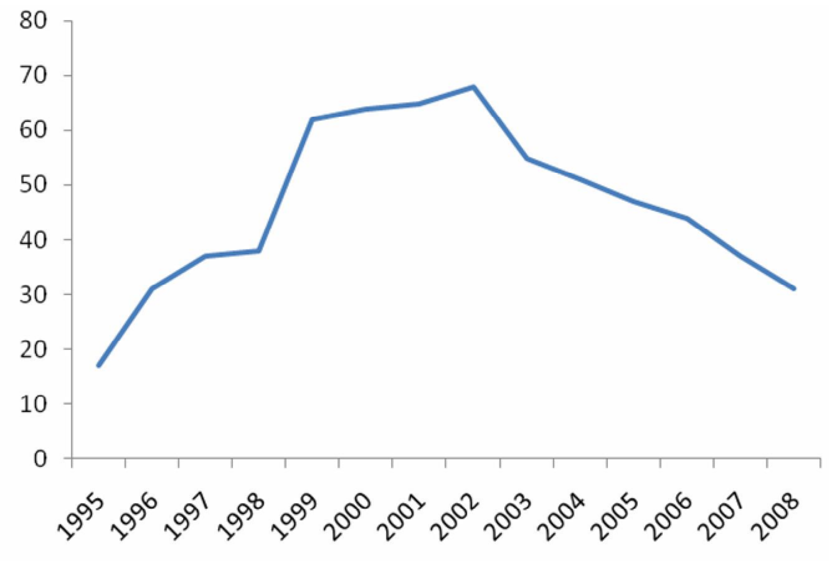

Figure 12. Annual estimates of marked individuals within the chamois population in Il Fuorn, Swiss National Park, between 1995 and 2008.

The trend line shows that the highest number of marked animals was actually estimated in the middle of the considered time-span, a result that is in line with Pocock *et al.* (2004). I therefore speculate that the adoption of MNA might indeed have been a major cause for the bias observed in the final estimates.

Marking: the trapping itself may bias the estimate of the resightings (Seber 1970, Burnham and Overton 1979, Seber 1982, Minta and Mangel 1989, Nicholas 1992, Bowden and Kufeld 1995, White 1996, Schwarz and Seber 1999, Hebeisen *et al.* 2008), because handling animals can trigger different individual behavior. Since the marking of individuals has been conducted before the analyzed survey sessions, I assumed that the resightings have not been affected.

Behavior of the marked/unmarked individuals: the individual probability of being resighted is independent of marked or unmarked status (Gardner and Mangel 1996), while Nussberger and Ingold (2006) found no significant difference in the behavior of marked and non-marked individuals. Therefore I assumed that there is no difference between marked or unmarked individuals in their behavior.

Closed population: the population was considered close during the survey period, because death was less likely to occur, while the birth period has already been finished. The length of the counting sessions was defined, which satisfied the assumption for a closed population (Hebeisen *et al.* 2008). According to the employees in the SNP, migrations were not present. Nevertheless, it was possible that the closure of the population was violated and that during this period some individuals might have died, migrated. In that case, the assumptions of closure were violated, which would directly affect the final estimates of the population abundance.

Proportion of marked individuals: according to Bartmann *et al.* (1987) and Barker (2008), a large proportion of animals (>45%) in small populations should be marked before reliable estimates and confidence intervals could be obtained. According to Hein and Andelt (1995), the population must have at least 20% of marked individuals, so that numerous surveys will give precise results. As far as the low proportion of marked animals might cause poor precision (Hebeisen *et al.* 2008), I calculated the yearly proportion of the marked individuals in the population, using the results of focal counts as the true population size (since they represent the minimum number of individuals present in the study site). The result is presented in figure 13.

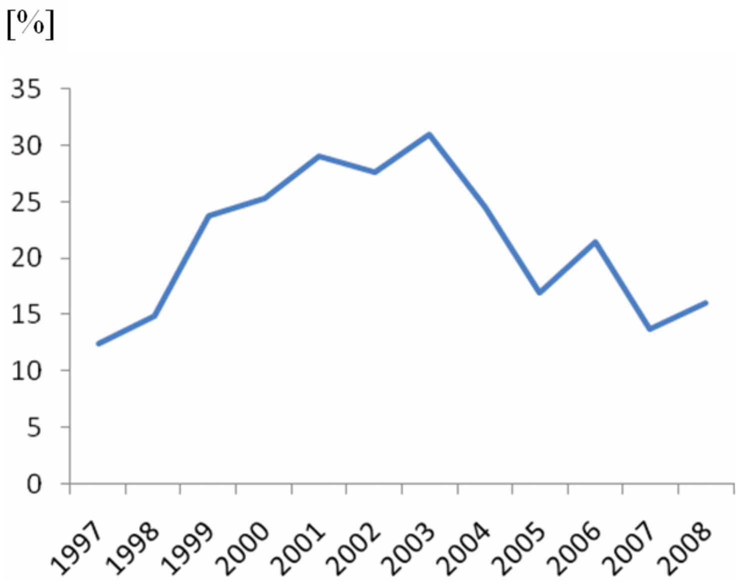

Figure 13. Proportion of the marked individuals within the chamois population in Il Fuorn, Swiss National Park, between 1997-2008.

According to the results from figure 13., for five years, the proportion is under 20%, while the highest value is around 30%. Overall, the ratio of the marked individuals within the chamois population is low, which affected the final estimates.

Survey strategy: another condition which can influence CMR estimates is the trapping/survey strategy (Gardner and Mangel 1996, Lettink and Armstrong 2003). Each trapping occasion or survey must cover the entire study area and search effort should be consistent over the area. In many studies (e.g. Casagrande and Beissinger 1997, Focardi *et al*. 2002, Fattorini *et al*. 2007, Hebeisen *et al.* 2008,), regular resightings have been carried out with a standard procedure. In the Swiss National Park the whole study site of Il Fuorn was visually covered from several vantage points. Analyzing the frequency of the resightings I noticed big variations over time, which probably had some impact on the final estimates. The biggest variation was between 1997, when almost 500 surveys were done, and 1998, when less than 50 surveys were conducted. Figure 14 illustrates the qualitative correlation between resight frequencies and final estimations.

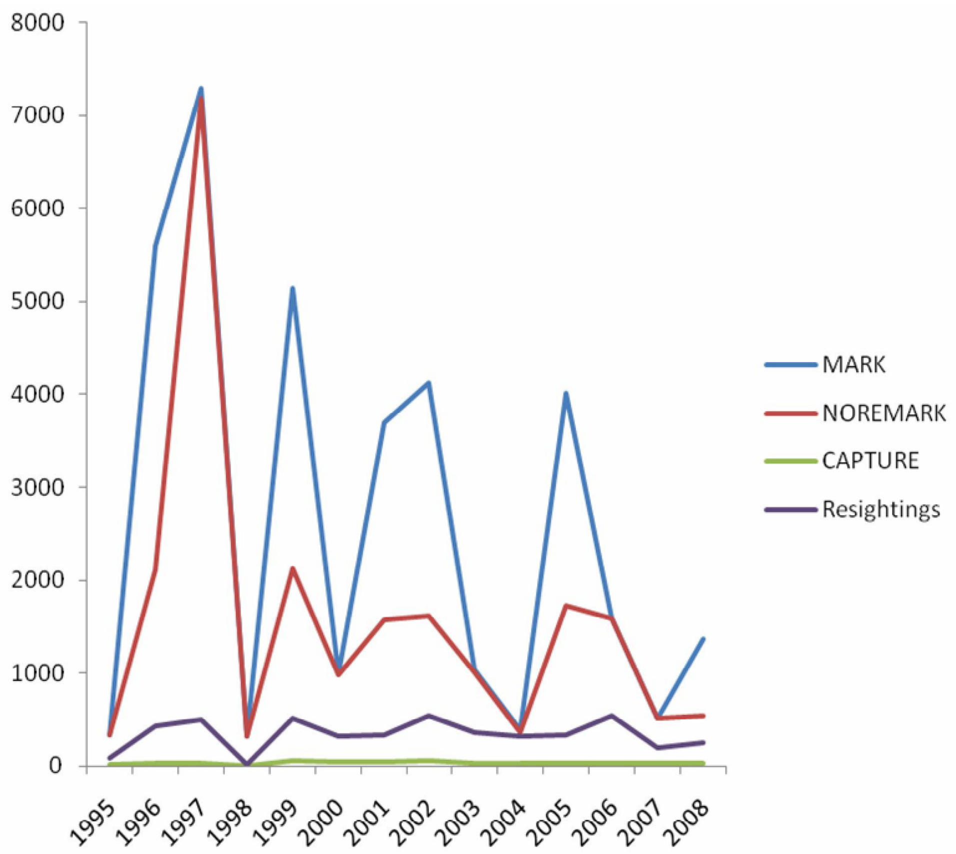

Figure 14. Comparison of MARK, NOREMARK and CAPTURE estimates with the trend line of resighting frequency within Il Fuorn, Swiss National Park, between 1995 and 2008.

The trend lines for all programs follow the trend line of resight frequency. This suggests a strong influence of the number of resightings per year on the estimate of the population abundance.

Capture heterogeneity is another important factor which can lower the precision of the estimation (Neal *et al.* 1993, Prévot-Julliard *et al.* 1998). Following Focardi *et al.* (2002), a main problem in sampling wildlife populations is the spatial variability of the "capture" probability. If marks are unevenly distributed among the groups, no mark-resighting procedure seems to be reliable (Fattorini *et al*. 2007). For my data set, I analyzed the number of resightings per sex classes. In total 44 males and 81 females were marked, with the ratio 1:1.8 for females. Out of 4,476 resightings which were conducted, 815 times marked males were spotted and 3,661 times the females. Therefore the ratio between males–females' resightings is 1:4.5, much higher difference than between marked individuals. This difference can be explained with male-biased dispersal (Greenwood 1980, Loison *et al.* 2008), since the males tend to move farther away from females (Levet *et al.* 1995). According to several authors (Loison 1995, Bonenfant *et al.* 2007, Loison *et al.* 2008) sexual segregation of chamois is present at population level, because adult males are not often seen within the groups of females. Therefore, it is more difficult to survey males than the females. The frequent resights of marked females directly influence the final estimates of population abundance, trough the higher number of unmarked individuals. Since chamois appear to be frequently involved in fusion-fission events (Pépin and Gerard 2008), the groups are not fixed in size and composition, which cause more difficulties in capture heterogeneity. For NOREMARK, I used Bowden's estimator, which many authors found appropriate (Neal *et al* 1993, Bowden and Kufeld 1995, White and Shank 2001, Kaminski *et al.* 2005, Hebeisen *et al.* 2008, Morley and van Aarde 2007, McClintock *et al.* 2008), but for dealing with individual heterogeneity, McClintock *et al.* 2006 propose the usage of the beta-binomial estimator (BBE) as a reliable alternative to Bowden's.

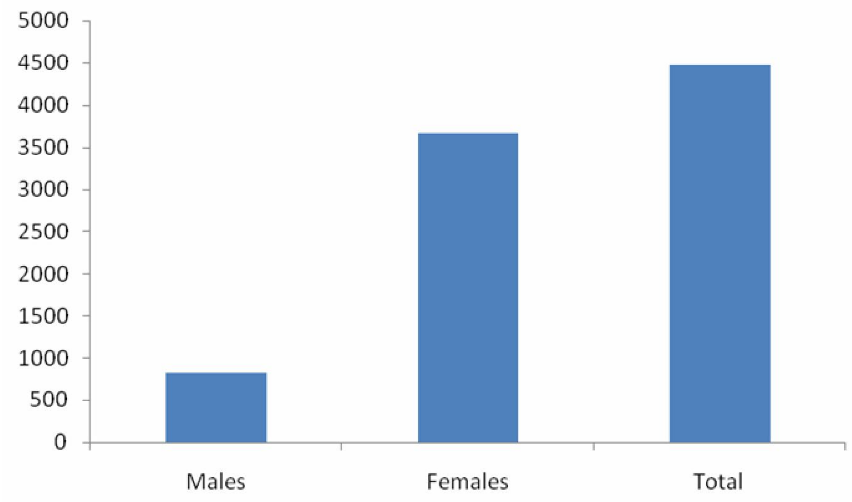

Figure 15. The number of resightings per sex class of chamois population in Il Fuorn, Swiss National Park, between 1995 and 2008.

Conclusion

Since I could not estimate the chamois abundance from the CMR data set, it was not possible to test the reliability of the focal counts. Therefore any of the hypotheses could not be neither rejected nor accepted. Nevertheless, the distinct hypotheses were partly confirmed. Since there was no significant difference between MARK and NOREMARK estimates, the null hypothesis was partly validated. The distinct alternative hypothesis was also partly confirmed, due to underestimated CAPTURE results. According to these results software appropriate for mark-resight data analyses showed similar results, while the software designed for mark-recapture data failed. Therefore it can be concluded that for proper CMR data analysis it is important to choose right software, which will be in accordance with the Capture-Mark-Recapture/Resight study.

Approximately 9,000 resightings have been conducted from 1994 to 2008, a great overall effort. During these resightings all marked individuals have been identified, meaning that the marking system used in the SNP is suitable for the chamois resightings. The right distribution of vantage points allowed the observers to monitor the whole study site, excluding possible bias.

Nevertheless, the data set appears to be erroneous, since the non-consistent survey strategy appears to be one of the main factors affecting CMR estimates, making their trend lines not acceptable from the biological point of view. According to the results of this research, it would be important for the future to define a clear survey strategy, i.e. with regular resighting sessions. Except the regular resightings, it is important to define the minimum recommended number of observations (Casagrande and Beissinger 1997). According to the same authors, the total number of sightings during each survey period, which in this case consists out of five sessions for the period July-November, should be twice higher than the estimated population size. Nevertheless, the number of sightings in the SNP was adequate, but not regularly distributed. Beside the number and the frequency of the resightings, it is also recommended to define time of a day, according to chamois behavior, when the resightings would be carried. Since the chamois is active during the daylight (Valchev *et al.* 2006), it is recommended to conduct observations from the morning until the afternoon.

Other factors such as low proportion of the marked individuals in the population, capture heterogeneity within sex classes, and usage of the MNA principle also have influenced the final estimation. The number of marked individuals should be increased up to 40-45% (Barker 2008), trying to be as much homogeneous as possible with regards to the sex classes. The principle of Minimum Number Alive should not be used for estimating “marks at risk”, since it causes the greatest bias at the beginning and the end of the study. Instead, some other estimator should be used. However, choosing an appropriate estimator is an important and difficult task, which should be based on variations present in sighting probabilities (McClintock *et al.* 2006). According to several authors (e.g.Casagrande and Beissinger 1997, Loison *et al.* 2006), the methodology developed by Arnason *et al.* (1991) is suitable for a closed population with an unknown number of “marks at risk”, which I would also recommend. Nevertheless, despite the direct influence of these factors on final CMR estimates, their impact can not be tested, due to bias caused with the non-consistent survey strategy.

The data analysis would not be possible, without the fulfillment of CMR assumptions. The main assumption is that the population was considered close, demographically and geographically, during the survey period. According to the gamekeepers’ experience, the period from July to November was suitable, since the assumption of demographical closure was meet. Nevertheless, there is always possibility that a death of an individual occurred. The geographical closure during the considered time span may be also violated, due to migrations of the individuals, since the region of Il Fuorn is difficult to monitor. Probably the migrations were at low level, but it can still affect the final estimates. Therefore, the knowledge about migration corridors and intensity is crucial for usage of the CMR methods, due to possible bias.

Concerning the effort which was put in this research, the proportion of financial input, amount of collected information and the precision of final estimates, it can be concluded that necessary preparations as defined: goals, survey strategy, minimum number of resightings, proportion of marked individuals, usage of a proper marking method, distribution of vantage points, fulfillment of all CMR assumptions, right proportion of “marks at risk” individuals within the sex classes due to capture heterogeneity, right choose of software and estimator for data set analysis are obligatory for the proper CMR study. Nevertheless, it seems that the resightings of an individuals marked with radio collars would be more effective, since it would be easier to estimate "marks at risk" and there would be more precise data concerning migrations of the individuals.

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