How reliable are total counts to detect trends in population size of chamois Rupicapra rupicapra and R. pyrenaica?

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How reliable are total counts to detect trends in population size of chamois *Rupicapra rupicapra* and *R. pyrenaica*?

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Censusing wild populations and detecting trends in population size over time is an important task in the conservation and management of wildlife. We compared two methods used to monitor numbers of chamois *Rupicapra rupicapra* and *R. pyrenaica* in two contrasting populations, and explored the relationship between the sampling effort and the repeatability of the results using resampling methods. One population in the Alps had been stable at a high density for several years, whereas the other population, located in the Pyrénées, was increasing exponentially, following a reintroduction. In both sites, a long-term monitoring programme based on individually marked chamois, allowed us to estimate population size using capture-mark-recapture methods (CMR). In addition, we calculated an index of population size as the mean number of animals observed on a foot transect surveyed repeatedly. We then compared whether trends estimated by each method were consistent. In the increasing population, both the index and the CMR estimates revealed an exponential increase in population size. In the stable population, neither the index nor the CMR estimate revealed any trend in size. Consistent results between the index and the CMR suggest that the index could be used to monitor trends in population size. Resampling techniques, however, pointed out that the index is only reliable when calculated over a sufficient number of surveys per year (10 in the Pyrenees, three in the Alps) and over a sufficient number of years of monitoring (about five years).

Key words: capture-mark-recapture, census methods, chamois, Rupicapra, transect, sampling effort

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To monitor populations, managers often rely on estimates of numbers and trends in time (Harris 1986, Caughley & Sinclair 1994, Balmford et al. 2003). Population size is, however, difficult to estimate (Seber 1992). Several types of methods have been developed either to directly estimate numbers or density, or to indirectly monitor the trends in numbers through indices (Eberhardt 1978, Wilson et al. 1996). As a general pattern, methods are compromises between the quality and amount of information collected and the effort (man hours) required to obtain the information (Wilson et al. 1996, Pollock et al. 2002, Williams et al. 2002). Censuses require a careful sampling design, trained field observers, intensive field efforts, and appropriate inferential statistics (Williams et al. 2002) such as capture-mark-recapture models (Schwarz & Seber 1999) or distance sampling methods (Buckland et al. 1993). Indices (e.g. pellet counts, kilometric indices) that often require less intensive field effort, can be attractive when the monitoring is organised by local managers, but typically rely on a number of assumptions that are seldom checked (Eberhardt 1978, Pollock et al. 2002, Williams et al. 2002). As the true population size is unknown for most wild populations (but see Gonzalez-Voyer et al. 2001), the testing and calibrating of indexes and methods is a challenge. Before basing a large-scale monitoring plan on low-cost methods, managers should therefore insist on an evaluation of their reliability to detect trends (Harris 1986, Solberg & Sæther 1999). This first step in monitoring design requires preliminary pilot studies from which basic statistics on the counts or indices can be inferred, such as the coefficient of variation of the estimates, the relationship between the mean estimate and its coefficient of variation (Eberhardt 1978, Gerrodette 1991), or the relationship between the indices and the total population size (Pollock et al. 2002). From preliminary studies, at least two sets of questions can be answered:

1) Are the indices sensitive to changes in population size (Eberhardt 1978)?
2) What is the relationship between the effort spent in the field and the repeatability of the result (Harris 1986)?

One way to answer the first question is to compare a set of estimates taken simultaneously in a given population and to examine whether the trends revealed by these estimates are consistent (Gonzalez-Voyer et al. 2001, Vincent et al. 1996, Williams et al. 2002). To evaluate the second question, when counts are based on repeated sampling, a possible solution is to use resampling-based simulation (Harris 1986). Here, through the long-term monitoring of two populations of chamois, we used both approaches to test whether a simple index of population size would allow managers to monitor population trends in time, and to compare sampling effort with the reliability of the result.

The Alpine *Rupicapra rupicapra* and the Pyrenean chamois *R. pyrenaica* are small mountain ungulates found in alpine forests and meadows (Loison et al. 2003). Because they usually spend some of their time in open areas (Lovari & Cosentino 1986, Loison et al. 2003), managers have traditionally assumed that chamois populations can be easily censused. Therefore, chamois management often relies on single counts performed on a given date each year (Houssin et al. 1994). Recently, however, an increase in chamois numbers and their colonisation of forested habitats (Breitenmoser 1998, Loison et al. 2003) have raised the concern that counting with simple total counts in open areas could severely underestimate population sizes (Houssin et al. 1994). An additional problem for the interpretation of the counts is the lack of quantification of the underestimation, which may vary from year to year (Williams et al. 2002) with population density, weather or habitat. Therefore, there is an urgent need to evaluate the methods in use and to suggest reliable alternatives such as line-transect and indicators of ecological changes based on body mass or reproductive patterns (see Cederlund et al. 1998 on roe deer *Capreolus capreolus*). So, we compare temporal trends obtained by an estimate and an index of population size in two populations of chamois. Further, we evaluate by simulation: 1) the minimum number of years of monitoring necessary to detect the real temporal trend in population size, and 2) how to optimise the monitoring protocol to calculate the index of population size. We then discuss how our results can be used for a better design of monitoring protocols.

Material and methods

Study areas and populations

We studied one population of Pyrenean chamois in the French western Pyrénées (Bazès), and one population of alpine chamois in the northern French Alps ('Les Bauges'). The Bazès study area covers 400 ha and is situated in the foothills of the Pyrénées (43°03'N, 0°13'W), with an elevation ranging within 1,000-1,800 m a.s.l. About half of the surveyed area is forested. The population was founded by the introduction of 34 individuals from the Pyrenean National Park, released in 1984 and 1985. All founders were marked with coloured collars. A total of 83 different individuals were captured with snares and marked in 1990-1999, mostly during autumn and winter (October-March). More details about the study area and the captures can be found in Loison et al. (2002a).

The study area of 'Les Bauges' (45°40'N, 6°13'E) is a national game reserve that encompasses 5,170 ha and is part of a subalpine massif with a total area of 15,600 ha. Elevations are 700-2,200 m a.s.l. One half of the area is forested, with the treeline at about 1,500 m a.s.l. (Loison et al. 1999). During 1985-1999, 452 chamois were individually marked with coloured collars. Cage-traps and falling nets baited with salt were used to capture the animals, mainly from June to August. For the purpose of this study, we focused on three zones with virtually no exchange of individuals (Loison et al. 1999).

Methods

Field surveys

The monitoring of the Bazès population was based on repeated foot surveys along a 2-km path, done by the same person (i.e. Joel Appolinaire, manager of the study area) every year. The same path was used all year around and repeated 6-65 times each year during 1986-1999 (Table 1). During these surveys, all individuals seen as well as the age and sex structure of each group (kids, females, males and non-identified individuals) were recorded. In addition, all marked individuals were identified. Male and female chamois are difficult to distinguish, particularly in the spring and summer, and the protocol focused more on an accurate determination of the collar's colour than on the sex. We therefore could not analyse separately the male and female segments of the population.

In 'Les Bauges', the three zones were also covered on a fixed foot path each time (4.25 km for zone 1, 3.5 km for zone 2, and 7.5 km for zone 3), by the same person every time (i.e. Jean-Michel Jullien, manager of this study area). The survey was repeated three times during the summers of 1994-1998 (except in zone 1 in 1997, when only two surveys could be performed; data not included in the following analysis) and five times in 1999 and 2000. As in Bazès, all individuals seen were noted, classified by age and sex, and marked individuals were identified.

Table 1. Population size (N ± standard error) of Pyrenean chamois estimated using the Arnason et al. (1991) method and the index of population size (IPS ± standard deviation), according to year and season in Bazès (see text for more details). The number of censuses (censuses), the coefficient of variation of the number of animals seen (CV, in %), the total number of individuals seen (n), the number of sightings of marked individuals (m) and the number of different marked individuals seen (m') during each season are given. The estimated mean of the Poisson distribution (μ) is obtained by numerically solving the equation m/m' = $\mu/(1-\exp(-\mu))$. Goodness-of-fit tests (χ^2, df and P-values) test whether the sighting frequencies per marked individuals fit a truncated Poisson distribution with a mean of μ (see text for more details). The tests are only given when m' is > 6. P-value below 0.05 are in italics.

Year	Season	Censuses	N ± s.e.	IPS ± s.d.	CV	n	m	m'	μ	χ^2	df	P-value
1986	Autumn	9	6.6 ± 0.6	4.0 ± 3.1	77.5	36	30	6	4.793	1.031	1	0.310
1987	Autumn	8	7.6 ± 1.1	5.6 ± 5.0	89.3	45	25	5	4.793			
1990	Spring	18	22.2 ± 5.6	9.1 ± 6.0	65.9	164	16	3	5.307			
	Summer	11	21.3 ± 6.0	11.4 ± 5.5	48.2	125	13	3	4.273			
1991	Spring	12	17.6 ± 4.7	6.1 ± 4.0	65.6	73	14	4	3.381			
	Summer	9	21.3 ± 6.0	10.2 ± 6.6	64.7	92	14	4	3.381			
	Autumn	27	23.5 ± 3.4	6.6 ± 4.4	66.7	177	39	6	6.490	0.275	1	0.600
1992	Spring	26	34.7 ± 3.5	12.0 ± 9.8	81.7	311	74	9	8.220	1.513	1	0.219
	Summer	7	39.6 ± 7.5	20.0 ± 11.3	56.5	140	27	8	3.375	1.448	1	0.229
	Autumn	27	47.4 ± 4.9	12.9 ± 10.8	83.7	348	75	11	6.811	0.027	1	0.878
1993	Spring	21	64.9 ± 5.3	22.0 ± 15.3	69.5	463	116	17	6.816	1.890	1	0.169
	Summer	13	34.6 ± 5.1	8.5 ± 8.1	95.3	110	38	12	3.011	0.604	1	0.437
	Autumn	32	48.4 ± 3.0	21.7 ± 10.5	48.4	695	188	14	13.429	1.248	1	0.264
1994	Spring	16	53.8 ± 5.9	20.9 ± 15.1	72.2	334	70	12	5.816	4.120	1	*0.042*
	Summer	11	54.7 ± 13.3	9.1 ± 12.9	142.8	100	23	11	1.714	0.738	1	0.390
	Autumn	19	53.2 ± 5.9	17.4 ± 10.7	61.5	330	69	12	5.731	2.748	1	0.097
1996	Spring	18	79.9 ± 9.1	34.3 ± 20.0	58.3	617	71	10	7.094	1.641	1	0.200
	Summer	11	64.5 ± 8.3	39.9 ± 16.2	40.6	439	56	9	6.210	1.235	1	0.200
	Autumn	14	73.7 ± 7.8	40.8 ± 25.4	62.3	571	79	11	7.163	2.282	1	0.131
1997	Spring	24	133.1 ± 7.7	41.0 ± 24.8	60.5	983	231	32	7.213	30.17	4	*<0.001*
	Summer	11	109.2 ± 7.8	56.1 ± 25.1	44.7	617	155	28	5.513	0.416	2	0.812
	Autumn	16	116.2 ± 8.4	38.8 ± 25.1	64.7	620	152	29	5.213	1.601	3	0.659
1998	Spring	19	127.7 ± 7.7	35.0 ± 18.7	53.4	665	201	39	5.123	4.805	4	0.308
	Summer	6	144.6 ± 11.5	80.0 ± 19.2	24.0	480	136	40	3.271	7.333	4	0.119
	Autumn	8	157.5 ± 10.6	75.4 ± 14.8	19.6	603	178	46	3.781	5.500	4	0.240
1999	Spring	16	203.2 ± 11.7	46.4 ± 32.3	69.6	742	238	64	3.619	9.383	5	0.095
	Summer	19	189.0 ± 7.2	79.7 ± 33.0	41.4	1515	475	60	7.914	40.720	5	*<0.001*

Estimating population size and monitoring trends by capture-mark-recapture

We first calculated an estimate of the population size using the capture-mark-resighting method developed by Arnason et al. (1991). This method is an extension of the classical Petersen-Lincoln method (Seber 1992) for repeated samples with an unknown number of marked individuals alive. It was especially appropriate in our case because we did not know exactly how many marked animals were still alive, which prevented us from using other methods developed for repeated Petersen-Lincoln type of sampling (e.g. Minta & Mangel 1989). Arnason et al.'s (1991) method allows grouping of observations made during consecutive surveys. In the following, the term 'session' is used for a set of surveys grouped together for the analysis. For each session, the statistics needed to estimate the population size are the total number of individuals seen (marked plus unmarked, noted n), the total number of observations of marked individuals (noted m), and the total number of different marked individuals seen (noted m'). The main assumptions of this method are that 1) the population is closed demographically (no emigration or immigration, no death or birth) over the period during which surveys are performed, 2) sightings of individuals are independent from one survey to the next, 3) all individuals should have the same probability of being sighted, 4) marked and unmarked individuals have the same probability of being seen, and 5) all marks should be identified (Arnason et al. 1991).

At both sites, we considered surveys for periods during which mortality was unlikely. In Bazès, we grouped together transects covered during spring (April-May; birth period), summer (June-August; nursing period) and autumn (September-December; post-nursing period) and analysed a total of 28 sessions (see Table 1). In 'Les Bauges', all surveys considered occurred during summer, and 20 sessions were analysed (Table 2). At both sites, we excluded all observations of kids. The data collected included individuals for which age and/or sex could not be determined (an average of 10 and 13% of animals seen in the Bazès and 'Les Bauges' sites, respectively). We included these individuals in our counts because it is unlikely that unclassified individuals were kids, which are easy to recognise because of their smaller size and lighter coat colour. In Bazès, movement of adults into and out of the surveyed area, previously studied with radio-collared animals, was relatively rare (Levet et al. 1995), and this allowed us to also ignore movement into and out of the study area. Possible seasonal differences in home range use were dealt with through the division of the year into the three periods described above. We therefore considered that for a given year and within a given period (Bazès) or a zone ('Les Bauges'), the populations were demographically closed.

Table 2. Population size (N ± standard error) of Alpine chamois estimated using the Arnason et al. (1991) method and the index of population size (IPS ± standard deviation), according to year and zone in 'Les Bauges'. The number of censuses (censuses), the coefficient of variation of the number of animals seen (CV, in %), the total number of individuals seen (n), the number of sightings of marked individuals (m) and the number of different marked individuals seen (m') during each season are given. The estimated mean of the Poisson distribution (μ) is obtained by numerically solving the equation $m/m' = \mu/(1-\exp(-\mu))$.Goodness-of-fit tests ($\chi^2$, df and P-values) test whether the sighting frequencies per marked individuals fit a truncated Poisson distribution with a mean of μ (see text for more details). P-value below 0.05 are in italics.

Zone	Year	Censuses	N ± s.e.	IPS ± s.d.	CV	n	m	m'	μ	χ^2	df	P-value
1	1995	3	171.2 ± 51.8	55.7 ± 10.7	19.2	167	26	17	0.920	0.033	1	0.855
1	1996	3	117.2 ± 43.1	49.0 ± 13.9	28.4	147	15	9	1.126	0.085	1	0.357
1	1998	3	191.0 ± 66.4	52.0 ± 6.5	12.5	156	23	16	0.776	0.289	1	0.585
1	1999	5	197.4 ± 34.4	72.2 ± 20.2	28.0	361	47	22	1.710	3.079	1	0.079
1	2000	5	197.3 ± 38.7	79.0 ± 20.4	25.8	395	36	16	1.920	2.925	1	0.087
1	2001	5	202.7 ± 41.1	61.4 ± 19.6	31.9	307	40	21	1.464	4.515	1	*0.034*
2	1995	3	84.5 ± 24.6	23.3 ± 2.5	10.7	70	29	20	0.796	4.803	1	*0.028*
2	1996	3	73.0 ± 17.7	22.0 ± 3.0	13.6	66	36	24	0.874	0.454	1	0.500
2	1997	3	74.5 ± 15.9	28.7 ± 15.5	54.9	86	38	23	1.105	0.853	1	0.366
2	1998	3	68.4 ± 11.2	33.7 ± 5.5	16.3	101	49	26	1.339	0.527	1	0.468
2	1999	5	100.3 ± 15.9	25.6 ± 5.7	22.3	128	56	32	1.247	2.439	1	0.118
2	2000	5	116.1 ± 29.4	20.2 ± 11.1	54.9	101	37	25	0.843	0.356	1	0.551
2	2001	5	62.8 ± 6.0	27.4 ± 7.4	27.0	137	65	35	2.144	5.858	2	0.053
3	1995	3	91.6 ± 33.6	31.0 ± 7.6	24.5	93	17	11	0.944	0.851	1	0.356
3	1996	3	103.1 ± 47.1	33.7 ± 13.3	39.5	101	12	8	0.874	2.508	1	0.113
3	1997	3	96.3 ± 24.2	59.3 ± 4.2	7.1	178	23	11	2.091	0.516	1	0.472
3	1998	3	94.0 ± 26.1	35.0 ± 6.7	19.1	105	26	16	1.065	3.316	1	0.068
3	1999	5	129.1 ± 19.8	49.2 ± 8.6	17.5	246	55	25	1.856	0.801	1	0.371
3	2000	5	144.3 ± 23.6	50.4 ± 9.8	19.4	252	52	25	1.700	0.814	1	0.367
3	2001	5	120.6 ± 23.1	39.8 ± 8.8	22.1	199	40	20	1.593	1.517	1	0.218

The second assumption was that the sightings should be independent from one survey to the next. This assumption is linked with the next one, as dependent surveys would lead to some animals being seen more often than others. In the case where the data obtained from one survey would be strongly correlated to the next, one may also underestimate the variance of the population size (Arnason et al. 1991). Chamois are highly mobile and not territorial (except males in some populations; von Hardenberg et al. 2000). Given that the mean number of days between consecutive surveys was four in Bazès and nine in 'Les Bauges', chamois had the opportunity to redistribute themselves spatially over the surveyed area. The goodness-of-fit test performed for testing the third assumption (see below) would also become significant if surveys were not independent and some animals were repeatedly sighted.

The third assumption is that all animals should have the same probability of being seen. If so, the distribution of the frequency of sightings of marked animals should follow a zero-truncated Poisson distribution (a Poisson distribution for which the number of marked animals never sighted is not known). We used the goodness-of-fit test (GOF) developed by Arnason et al. (1991) to test this assumption (see Appendix 2 in Arnason et al. 1991), where the mean of the Poisson distribution (μ), and thereby the expected frequencies, are calculated based on the mean number of times each marked chamois was observed ($m/m'=\mu/(1-\exp(-\mu)$; see Tables 1 and 2). The GOF can be tested using χ^2 statistics where the number of degrees of freedom is the number of classes of sighting's frequencies minus 2 (Arnason et al. 1991). A minimum of three classes is therefore required. Although performing the test with < 5 marked individuals per class is questionable, we indicated the results of the tests for groups of surveys as long as there were at least a total of six marked individuals (see Tables 1 and 2).

The fourth assumption is difficult to test as no statistics can be drawn from unmarked animals' behaviour (Arnason et al. 1991). However, no study published so far on the behaviour or demography of ungulates marked with visual collars (Richard-Hansen 1992, Cransac et al. 1997, Loison et al. 1999, Gonzalez & Crampe 2001) has mentioned the possibility of a difference in behaviour or conspicuousness between marked and unmarked animals. Based also on our own observation, it therefore appeared reasonable to assume that marked and unmarked animals had the same behaviour and sightability.

The fifth requirement, i.e. that all marked animals should be identified, is not fulfilled in all the surveys performed at both sites. Occasionally, the observer saw that an animal had a collar without being able to identify it. This happened more frequently in 'Les Bauges' (in 12 of 18 surveys, 1-6 marked individuals were not identified) than in Bazès (two, five, and one non-identified marked animals for the spring 1997, summer 1997 and autumn 1998 surveys, respectively). Such sightings could be 1) ignored, 2) added to both m and m' (i.e. to consider these individuals as marked individuals that had never been seen during other surveys) or 3) added to m but not to m' (thereby considering that they were resightings of individuals identified during previous surveys). Since ignoring the sightings of unidentified marked individuals results in an intermediate estimate compared to the two other alternatives, and given that the number of non-identified individuals was low relative to the number of marked individual seen (see Tables 1 and 2), unidentified marked individuals were ignored both in m and m'. The freeware EAGLE (Arnason et al. 1991) was used to perform the analyses. The estimates of population size obtained using Arnason et al.'s (1991) method was denoted CMR in the following.

Monitoring trends with an index of population size

The index of population size (IPS) we used was the average number of individuals seen per foot survey, calculated over all surveys performed during a given period. We used directly this mean number without correcting for the length of the path walked as we were more interested in relative temporal changes than in comparing this index from population to population, or zone to zone within a population. A standard deviation and a coefficient of variation (CV) can be associated with this average as each path was surveyed several times (see Table 1 for Bazès and Table 2 for 'Les Bauges'). Because the relationship between CV and average estimate is important when designing a monitoring protocol (Gerrodette 1987), we explored whether the CV varied with IPS.

All analyses were performed after log-transforming the IPS and CMR estimates, because the temporal dynamics of population size is multiplicative and more easily dealt with in a linear context with log-transformed variables (Eberhardt 1978). We checked whether there was a significant trend in time of the IPS and CMR by regressing the log-transformed estimates against year, accounting for seasons or zones (respectively in the Bazès and 'Les Bauges' populations). We compared the slope estimated using IPS and CMR to test whether they indicated the same trend with time. The CMR was an estimate with a standard error, and not a true value of population size. To account for this, we performed the analyses by weighing the data points by the inverse of the CMR variance (values estimated with a small variance having therefore more weight in the analysis than points estimated with a large variance; Burnham et al. 1987). In addition, we calculated the regression slope between the log-transformed IPS and the log-transformed CMR. Indices of population sizes based on observation may show saturation (Caughley 1977) and we tested whether the slope was lower than 1 (a slope of 1 is expected if both CMR and IPS change at the same rate over time).

Number of years of monitoring and estimation of the trend in population size

Using the long-term data set from the Bazès population, we calculated the trend in time (slope of the regression of the log-transformed IPS with time) of the IPS with different time windows, from two to nine years. We considered values of IPS from 1990 to 1999 or 2000 depending on the season (see Table 1), no values being available for 1995. We then plotted the slope of the regression of the log-transformed IPS with time against the length of the time window to determine the number of years required before estimates of the slope stabilised.

Number of repetitions of each survey and variability of the result

Harris (1986) concluded that performing multiple counts each year is "the only way to achieve precision of population trend estimate within a short (<12 years) time frame". The number of times that counts should be repeated, however, must be evaluated for each study. We therefore explored how the IPS estimate varied with the number of repetitions for four season-years in Bazès and for three years (1999, 2000 and 2001) in each subpopulation of 'Les Bauges' (years when five surveys were performed). In Bazès, we chose years with a large number of repetitions and different estimated population size: spring 1990, autumn 1991, autumn 1993 and summer 1999. The total number of repetitions of the foot survey was denoted R in the following (R = 18, 27, 32 and 19 for 1990, 1991, 1993 and 1999, respectively; see Table 1).

We performed bootstrap simulation to estimate the values of IPS that would have been obtained if foot surveys had been repeated r times, r values being randomly chosen among the R possible values of number of animal seen per survey (with r < R). For each value of r, we repeated the sampling of r values among the R possible values 1,000 times. For each sampling, we estimated the mean number of animals seen over r repetitions of the foot survey (denoted IPS_r), which allowed us to obtain 1,000 values of IPS_r per value of r. We then calculated the coefficient of variation of the IPS_r over the 1,000 samples. We considered the coefficient of variation of IPS_r (denoted $CV(IPS_r)$) as a measure of the repeatability of the result. A large value of $CV(IPS_r)$ indicated that the IPS value was very variable among the 1,000 resamplings of r values while a low $CV(IPS_r)$ value indicated that the IPS value was not very dependent on the sample of r values

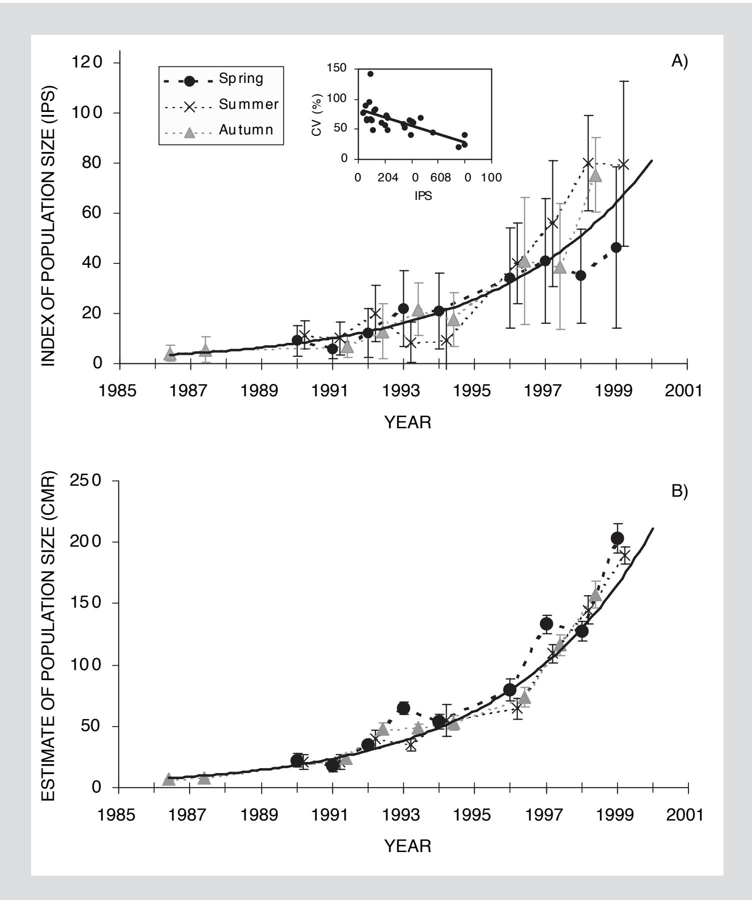

Figure 1. Index of population size (IPS; A) and estimates of population size (CMR; B), with standard errors, plotted against year in the Bazès population for spring, summer and autumn. The solid lines indicate the exponential trend of IPS or CMR with year, season being pooled together. The inserted graph in A) shows the relationship between the coefficient of variation of the IPS (in %) and the IPS value.

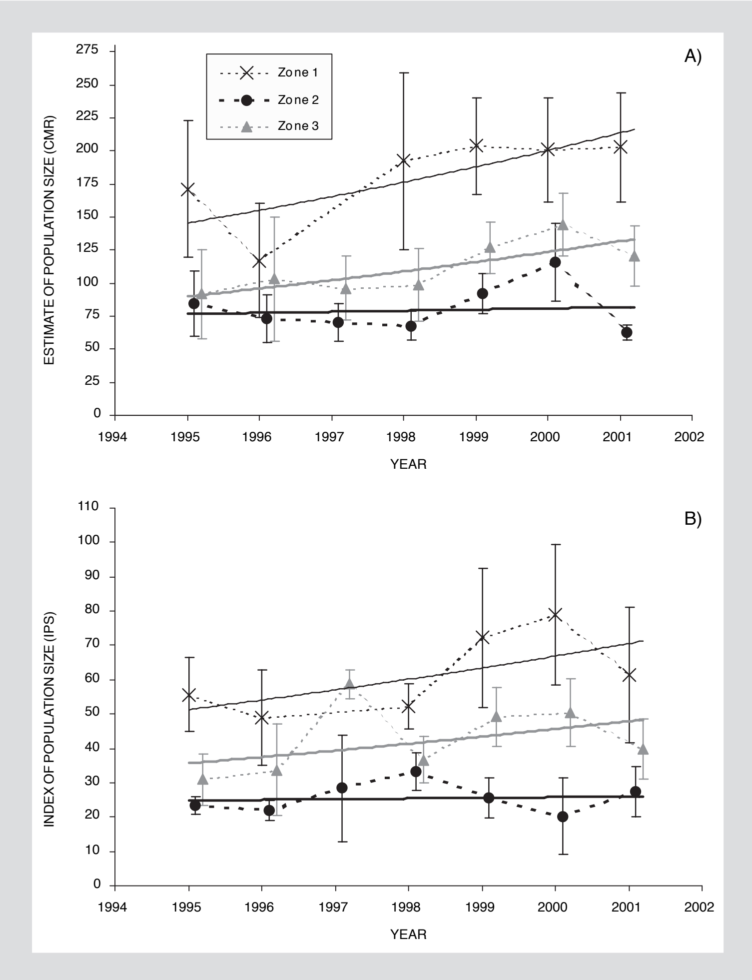

Figure 2. Index (IPS; A) and estimates of population size (CMR; B), with standard errors, plotted against year in the 'Les Bauges' population for zones 1, 2 and 3. The solid lines indicate the exponential trend of IPS or CMR with year, which are not significant in this population.

among the R possible values. CV(IPS_r) is expected to decrease with increasing r. All analyses and resamplings were performed using Splus (Venables & Ripley 1999).

Results

Comparing IPS and CMR in Bazès

We performed the GOF tests of the distribution of the number of resightings per marked individual to a truncated Poisson distribution on 23 sessions among the 28 available (see Table 1). Among the 22 GOF tests, only four revealed a poor fit (see Table 2). The possible trend through time of IPS and of CMR estimates were similar with or without these four sessions (the same significant factors and the same level of significance for the tests comparing the trend in IPS and CMR), therefore we only present results including all sessions.

The log-transformed IPS increased over time (main effect of year: $F_{1,25}$ = 138.026, P < 0.001) at the same rate whatever the season (year and season interaction: $F_{2,21}$ = 0.402, P = 0.674; main effect of season: $F_{2,23}$ = 0.632, P = 0.541; Fig. 1). The slope of the regression between log-transformed IPS and year was b = 0.229 ± 0.020. The IPS increased from about four in autumn 1986 to about 80 in summer 1999 (see Table 1). The coefficient of variation of IPS averaged 64.02% (range: 19.6-142.8%). It decreased significantly with increasing IPS (see Fig. 1A), whether including the outlier CV value of 142.8% (linear regression: slope = -0.690 ± 0.151, t = -4.560, P < 0.001) or not (linear regression: slope = -0.593 ± 0.102, t = -5.819, P < 0.001).

Analyses of the log-transformed CMR suggested the same patterns (see Fig. 1) whether the values of the CMR were weighed by the inverse of their variance or not. The weighing of the two lowest CMR estimates in 1986 and 1987 were disproportionally large as the CMR values were estimated with low standard error during these two first years (see Table 1). We therefore repeated the analysis with and without these two values. We present only the results of the weighed analyses on the whole data set, unless the results differed without the two lowest values. As for the IPS, the only significant factor was year (interaction between year and season: $F_{2,21}$ = 0.298, P = 0.745; main season effect: $F_{2,23}$ = 0.366, P = 0.697; main year effect: $F_{1,25}$ = 1518.079, P < 0.001). The slope of the regression between log-transformed CMR and year was b = 0.266 ± 0.007. It was marginally different from the slope found with IPS (Z = 1.751, P = 0.080), a trend that was, however, not confirmed when repeating the analysis without the two lowest values (b = 0.240 ± 0.017, Z = 0.663, P = 0.674). The CMR estimates increased from about seven in autumn 1986 to about 203 in spring 1999 (see Table 1). The population estimate for 1986 was quite low compared to the number of animals released on the site, which can be due to the fact

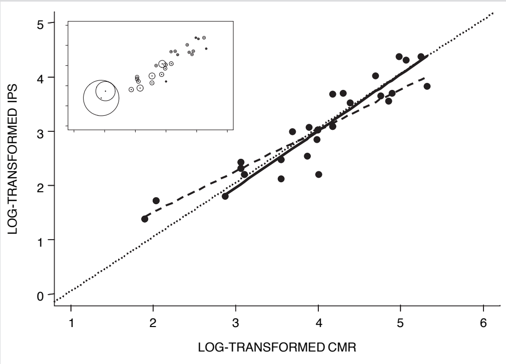

Figure 3. Index of population size (log-transformed IPS) plotted against the estimates of population size (log-transformed CMR) in the Bazès population. The dotted line corresponds to the regression line with a slope of 1. The dashed bold line is the regression estimated for the whole time series, while the solid bold line is the regression estimated without 1987 and 1988 values (see text for details). The inserted graph represents the same data points with a circle proportional to the square root of their weight in the analyses (see text for details).

that: 1) some individuals may not have settled on the study site, and 2) the GOF tests could not be performed for the first years of the study because too few of the marked chamois were seen during surveys, so estimates may be biased.

The log-transformed IPS was significantly correlated with the log-transformed CMR (weighed regression with all values: $F_{1,25} = 310.423$, $P < 0.001$; Fig. 2). The slope of the regression was $b = 0.754 \pm 0.048$, which was significantly lower than 1 ($Z = 3.243$, $P = 0.001$). Excluding the values of 1986 and 1987, however, the slope became $b = 1.045 \pm 0.085$, not significantly different from 1 ($Z = 0.703$, $P = 0.595$). The IPS amounted on average to 40.9% of the CMR estimate (range: 16.6-74.0%).

Comparing IPS and CMR in 'Les Bauges'

The GOF test revealed a significantly poor fit of the distribution of the number of resightings per marked individual to a truncated Poisson distribution for two of the 20 sessions (see Table 2). In addition, the GOF test suggested a poor fit ($0.05 < P < 0.10$) for four other sessions. However, performing the following analyses with and without these sessions lead to similar results, so we chose to present the analyses with all sessions.

The log-transformed IPS did not vary with year whatever the zone (interaction between year and zone: $F_{2,14} = 0.443$, $P = 0.651$; main effect of year: $F_{1,16} = 2.866$, $P = 0.110$; Fig. 3). The zone effect was pronounced ($F_{2,17} = 29.384$, $P < 0.001$), with a mean IPS of 61.5 individuals seen on average in zone 1, 25.8 in zone 2, and 42.6 in zone 3 (see Table 2). The CV was on average 24.7% (range: 7.1-54.9%), being similar in each zone (zone 1: 24.3%, zone 2: 28.5%, and zone 3: 21.3%). Since the IPS did not show any significant trend with time, we did not evaluate the relationship between IPS and the CV.

The results were similar with the log-transformed CMR (see Fig. 3) and whether using the weighed analyses or not. We only present the weighed analyses. No year effect appeared from the weighed ANCOVAs (interaction between zone and year: $F_{2,14} = 2.909$, $P = 0.088$; main effect of year: $F_{1,16} = 0.647$, $P = 0.088$). The weighed means for the CMR estimates were 181.6 for zone 1, 70.2 for zone 2, and 115.9 for zone 3 (main zone effect: $F_{2,17} = 23.336$, $P < 0.001$).

Whatever the zone, the log-transformed IPS was not correlated to the log-transformed CMR (weighed regression, zone 1: $F_{1,4} = 4.784$, $P = 0.094$; zone 2: $F_{1,5} = 1.077$, $P = 0.347$; zone 3: $F_{1,5} = 0.397$, $P = 0.556$). This was expected as no trends were found in IPS or CMR with time. The IPS represented on average 34.1% (range: 27.2-41.8%) of the CMR in zone 1, 33.9% (range: 17.4-49.2%) in zone 2, and 37.4% (range: 32.0-61.6%) in zone 3.

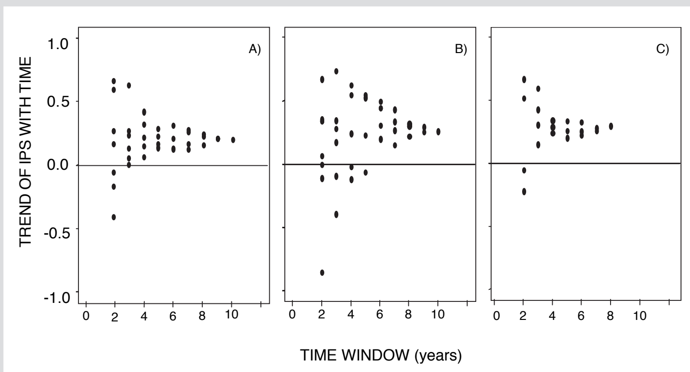

Figure 4. Trend of the index of population size (IPS) with time in the Bazès population (i.e. estimates of the slope of the regression between the log-transformed IPS and time) according to the number of consecutive years (Time window) considered for estimating this trend, based on the time series of IPS (see Table 1 for values) obtained in spring (A), in summer (B) and in autumn (C).

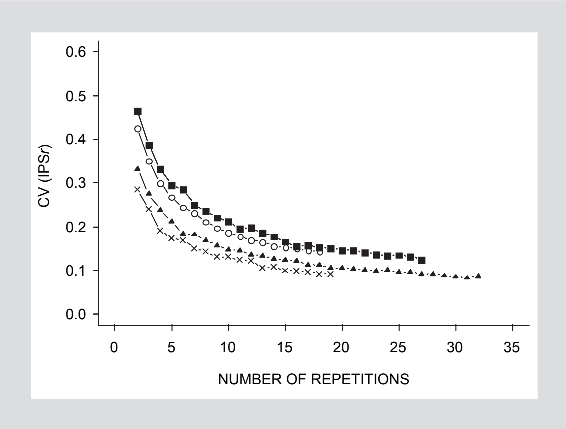

Figure 5. Relationship between the coefficient of variation of the IPS ($CV(IPS_r)$) and the number of repetitions of the foot transect in Bazès population for the season-years spring 1990 (○), autumn 1991(■), autumn 1993(▲) and summer 1999 (x).

Number of years of monitoring and estimation of the trend in population size

The estimation of the trend in population size is highly variable when this trend is estimated with only few consecutive years whatever the season (Fig. 4). In Bazès, the trend estimated with the whole time series of IPS was an exponential increase (see the preceding section). Yet, if the trend would have been assessed based on < 4 years in spring and autumn or < 6 years in the summer, the trend found could have been a decrease for some samples of consecutive IPS values (see Fig. 4). Further, when examining whether the trend (i.e. the slope of the regression between the log-transformed IPS and year) was significantly different from 0, it appeared that at least five years were necessary for always correctly concluding that the trend was positive for the spring and autumn time series whatever the sample of consecutive IPS values considered, and at least seven years for the summer time series.

Number of repetitions of each survey and variability of the result

In Bazès, the simulations for spring 1990, autumn 1991, autumn 1993 and summer 1999 all led to the obvious conclusion that the more the foot transect was repeated, the less variable was the estimate of the mean number of animals seen from one random sample to the other (Fig. 5). The number of repetitions required to reach an asymptotic coefficient of variation varied between years (e.g. four repetitions led to a 20% CV in 1999, whereas 11 would have been required in 1991). In this population, the $CV(IPS_r)$ curves indicate that 10 repetitions are advisable as a good compromise between the reliability of the result and the effort in the field.

In 'Les Bauges', the $CV(IPS_r)$ was lower than that in Bazès for the same number of repetitions (Fig. 6). The number of individuals seen did not vary in the same extent from one survey to the other, so that the $CV(IPS_r)$ estimated based on resampling was always below 20% except for 2000 in zone 2. There was no sharp decline in the variability of the results with increasing number of repetition of the transects, showing that the transects could be repeated about three times in this area.

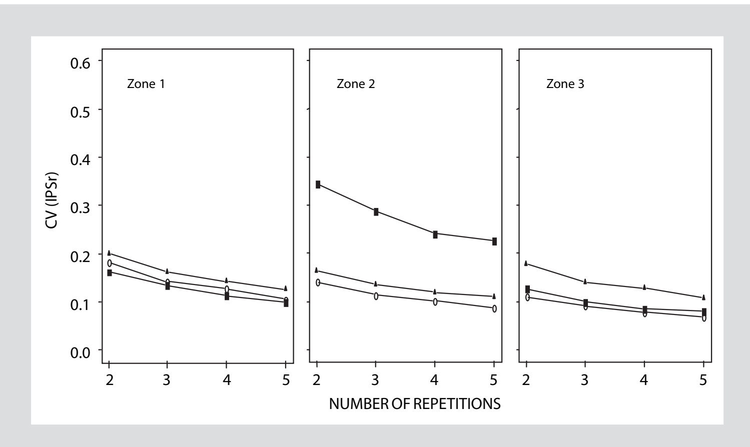

Figure 6. Relationships between the coefficient of variation of the IPS ($CV(IPS_r)$) and the number of repetitions for foot transects in the three zones of the 'Les Bauges' population in 1999 (○), 2000 (■) and 2001 (▲).

Discussion

The index and the census methods employed at the two sites suggested similar trends in numbers. Both methods indicated that the Pyrenean population was increasing exponentially and that the population in the Alps exhibited no linear trend with time whatever the subpopulation. The mean number of individuals seen along a fixed foot transect therefore appeared to be a reliable method for monitoring population trends in chamois. This conclusion held in the two populations we monitored, but should be generalised with caution to other populations for several reasons.

We did not compare the index with the true population size, but with an estimate of population size calculated using a CMR method (Arnason et al. 1991). We were therefore not in an experimental setting where the population size was precisely known (see Gonzalez-Voyer et al. 2001 for such an example). Our comparison of the trend found with IPS with the trend found with CMR therefore depends on the accuracy and precision of CMR estimates. The assumptions for the use of the CMR methods were met for the majority of years, seasons and subpopulations, so we were confident in the population size estimates, and thereby, the trend found in each population. However, the probability of detecting a trend depends on the confidence interval of the estimates (Eberhardt 1978, Gerrodette 1987, 1991, Link & Hatfield 1991). These confidence intervals were relatively low for the CMR estimates in Bazès, as the number of repetitions of the survey and the proportion of marked individuals in the population were high. The conditions were therefore favourable for the detection of the exponential increase in the population size, which led to a > 10-fold increase in numbers during the study period. On the opposite, the estimates of population size had relatively large confidence intervals at 'Les Bauges', where the number of repetitions of the surveys and the proportion of marked individuals in the population were low. Small changes in size of the three subpopulations in 'Les Bauges' could certainly have been overlooked by both methods. To evaluate the probability of detecting a given trend using the same monitoring methods in the future in both populations, power analysis such as those suggested by Gerrodette (1987) or Link & Hatfield (1991) can be performed, using the results from our analyses of already collected data.

The usefulness of indexes of population size relies on the effort spent in the field (Wilson et al. 1996, Williams et al. 2002), as gain in precision is usually obtained by an increase in sampling effort (Harris 1986). Using resampling techniques to determine how many times a survey should be repeated appears to be crucial as Harris (1986) demonstrated that the most relevant way to increase the precision of trend estimates was to increase the within-year repetition of counts. In Bazès, the trade-off between the gain in precision and the increase in field effort suggested that a minimum of 10 repetitions of the survey should be performed. It is unfortunately not possible to extrapolate this value to other populations, as the relationship between the variability of the result and the number of repetitions depends on the variance in the number of individuals seen per survey, which can vary among and within sites. For example, variability was much lower in 'Les Bauges' (see Fig. 6) than in Bazès (see Fig. 5), so that 3-5 repetitions appeared to lead to a reliable estimate of the index of population size in 'Les Bauges'. In Bazès, the variability also changed during the study (decreasing CV with increasing index of population size). Before using the index of population size proposed here as a monitoring tool, it is therefore necessary to conduct a pilot study in the field, followed by a resampling analysis, in order to determine the appropriate number of intra-annual repetitions required.

The large difference between sites in the variability of the number of individuals seen per survey may be due to several factors. Chamois in 'Les Bauges' are sedentary and have small home-range sizes (Loison 1995). In Bazès, the density of chamois was lower and movements of animals may have been more extensive than in 'Les Bauges' (Levet et al. 1995). The range of the number of individuals seen per transect in Bazès extended from one to a maximum value that depended on the population density, whereas in 'Les Bauges', it never happened that very few or very many individuals were seen. In addition, the census protocol was more standardised for the Bauges than for the Bazès study area. The grouping of transects at Bazès by season was done *a posteriori*, because transects were walked all year round in an opportunistic way when weather allowed. In contrast, the surveys in 'Les Bauges' were planned in advance and only performed when observation conditions were optimal. This decreased the number of repetitions per zone and probably also the variability of the result.

We did not observe any saturation (Caughley 1977, Vincent et al. 1991) of the IPS in the Bazès population over the range of population sizes monitored, despite an exponential increase in population size. In this population, the trend in time found with IPS and CMR was similar for a population size ranging from about 20 to about 200 individuals. Whether such a correlation between the trends found by both methods would still be found for higher values of population size remains an open question, as some individuals may move to non-surveyed area with increasing density. It is essential to continue the long-term monitoring of this population, through CMR methods, other indices of abundance and indices of ecological changes (Cederlund et al. 1998) to assess whether there will be a threshold population over which the IPS will no longer be a valid index for monitoring trends in population size.

Managers typically aim to closely track variation in population size, for example to determine yearly hunting quotas (Solberg et al. 1999). Tracking increases or decreases from one year to the next are only feasible when the extend of the variation in population size is large, because the power of detecting a trend is low when confidence intervals of estimates or coefficient of variation of counts are large (Eberhardt 1978, Gerrodette 1987). Even in a population where the growth was exponential (Bazès; Loison et al. 2002a), several years of monitoring were necessary to significantly detect the correct trend. This means that the response of management to a true increase or true decrease can only occur with delay compared to the processes acting in the population. Such unavoidable delays can inflate the variation in population size (Solberg et al. 1999). Rather than a single index of population size, a set of indicators of ecological changes should be monitored to obtain an accurate picture of demographic processes (Eberhardt & Simmons 1992, Cederlund et al. 1998). For example, monitoring the body condition and age at first reproduction may give an additional informative index to population dynamics, and can be easily obtained if the species is harvested (Hewison et al. 1995, Crampe et al. 1997, Couilloud et al. 1999, Loison et al. 2002b). Similarly, group size and home range size have been used as density indexes in several species, e.g. in ibex *Capra ibex* (Toïgo 1998), in roe deer (Vincent et al. 1995), and in axis deer *Axis axis* (Barrette 1991). We recommend a set of monitoring tools rather than reliance on only a single method that alone may not be able to detect a change in population density over a large range of population sizes.

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References

Arnason, A.N., Schwarz, C.J. & Gerrard, J.M. 1991: Estimating closed population size and number of marked animals from sighting data. - Journal of Wildlife Management 55: 716-730.

Balmford, A., Green, R.E. & Jenkins, M. 2003: Measuring the changing state of nature. - Trends in Ecology and Evolution 18: 326-330

Barrette, C. 1991: The size of axis deer fluid groups in Wilpattu National park, Sri Lanka. - Mammalia 55: 207-220.

Breitenmoser, U. 1998: Large predators in the Alps: the fall and rise of man's competitor. - Biological Conservation 83: 279-289.

Buckland, S.T., Anderson, D.R., Burnham, K.P. & Laake, J. L. 1993: Distance Sampling: Estimating Abundance of Biological Populations. - Chapman and Hall, London, 446 pp.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. 1987: Design and analysis methods for fish survival experiments based on release-recapture. - American Fisheries Society Monographs 5, Bethesda, Maryland, 437 pp.

Caughley G.C. 1977: Analysis of vertebrate populations. - Wiley and Sons, 234 pp.

Caughley, G.C. & Sinclair, A.R.E. 1994: Wildlife Ecology and Management. - Blackwell Scientific Publication, Boston, 334 pp.

Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R., Gaillard, J-M., Boisaubert, B., Ballon, P. & Duncan, P. 1998: Managing roe deer and their impact on the environment: maximising the net benefits to society. - In: Andersen, R., Duncan, P., Linnell, J.D.C. (Eds.); The European roe deer: the biology of success. Scandinavian University Press, Oslo, pp. 337-372.

Couilloud, F., Jullien, J-M. & Fraty, D. 1999: Le poids des chevreaux en automne: un bioindicateur utilisable pour suivre l'évolution d'une population de chamois (Rupicapra rupicapra). - Gibier Faune Sauvage 16: 273-287. (In French).

Crampe, J.P., Caens, J.C., Dumerc, J.L. & Pépin, D. 1997: La masse corporelle comme indicateur de la condition physique hivernale de l'isard Rupicapra pyrenaica. - Mammalia 61: 73-85. (In French).

Cransac, N., Hewison, A.J.M., Gaillard, J-M., Cugnasse, J.M. & Maublanc, M.L. 1997: Patterns of mouflon (Ovis gmelini) survival under moderate environmental conditions: effects of sex, age, and epizootics. - Canadian Journal of Zoology 75: 1867-1875.

Eberhardt, L.L. 1978: Appraising variability in population studies. - Journal of Wildlife Management 42: 207-238.

Eberhardt, L.L. & Simmons, M.A. 1992: Assessing rates of increase from trend data. - Journal of Wildlife Management 56: 603-610.

Gerrodette, T. 1987: A power analysis for detecting trends. - Ecology 68: 1364-1372.

Gerrodette, T. 1991: Models for power of detecting trends - a reply to Link and Hatfield. - Ecology 72: 1889-1892.

Gonzalez, G. & Crampe, J.P. 2001: Mortality patterns in a protected population of isards (Rupicapra pyrenaica). - Canadian Journal of Zoology 79: 2072-2079.

Gonzalez-Voyer, A., Smith, K.G. & Festa-Bianchet, M. 2001: Efficiency of aerial censuses of mountain goats. - Wildlife Society Bulletin 29: 140-144.

Harris, R.B. 1986: Reliability of trend lines obtained from variable counts. - Journal of Wildlife Management 50: 165-171.

Hewison, A.J.M., Vincent, J.P., Bideau, E., Angibault, J.M. & Putman, R. 1995: Variation in cohort mandible size as an index of roe deer (Capreolus capreolus) densities and population trends. - Journal of Zoology (London) 239: 573-581.

Houssin, H., Loison, A., Gaillard, J-M. & Jullien, J-M. 1994: Validité d'une méthode d'estimation des effectifs de chamois dans un massif des Préalpes du nord. - Gibier Faune Sauvage 11: 287-298. (In French).

Levet, M., Appolinaire, J., Catusse, M. & Thion, N. 1995: Elements démographiques, comportement spatial et dispersion d'une population d'isard (Rupicapra pyrenaica) en phase de colonisation. - Mammalia 59 :489-500. (In French).

Link, W.A. & Hatfield, J.S. 1990: Power calculations and model selection for trend analysis: a comment. - Ecology 71: 1217-1220.
Loison, A. 1995: Approches intra et inter spécifiques de la dynamique des populations. - Unpublished PhD thesis, University of Lyon, Lyon, France, 331 pp. (In French).
Loison, A., Cuyler, C., Linnell, J.D.C. & Landa, A. 2002b: Sex, age, condition and tooth wear of harvested caribou Rangifer tarandus groenlandicus in west Greenland, 1995-1998. - Wildlife Biology 7: 263-273.
Loison, A., Jullien, J-M. & Menaut, P. 1999: Subpopulation structure and dispersal in two populations of chamois (Rupicapra sp.). - Journal of Mammalogy 80: 620-632.
Loison, A., Toïgo, C., Appolinaire, J. & Michallet, J. 2002a: Demographic processes in colonizing populations of isard (Rupicapra pyrenaica) and ibex (Capra ibex). - Journal of Zoology 256: 199-205
Loison, A., Toïgo, C. & Gaillard, J-M. 2003: Large herbivore biodiversity in European mountain ecosystems: current status and challenges for the future. - In: Nagy, L., Grabherr, G., Körner, C. & Thompson, D.B.A. (Eds.); Alpine Biodiversity: Pattern, Process and Change in Europe. Springer Verlag, pp. 351-356.
Lovari, S. & Cosentino, R. 1986: Seasonal habitat selection and group size of the Abruzzo chamois (Rupicapra pyrenaica ornata). - Bolletino Zoologica 53 : 73-78.
Minta, S. & Mangel, M. 1989: A simple population estimate based on simulation for capture-recapture and capture-resight data. - Ecology 70: 1738-1751.
Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L. & Sauer, J.R. 2002: Large scale wildlife monitoring studies: statistical methods for design and analysis. - Environmetrics 13: 105-119.
Richard-Hansen, C. 1992: Associations between individually marked isards (Rupicapra pyrenaica pyrenaica): seasonal and inter-annual variations. - In: Spitz, F., Janeau, G., Gonzalez, G. & Aulagnier, S. (Eds); Ongulés-Ungulates 91. Société Francaise d'Etudes et de Protection des Mammifères-Institut de Recherche sur les Grands Mammifères, Paris, Toulouse, France, pp. 299-304.
Schwarz, C.J. & Seber, G.A.F. 1999: A review of estimating animal abundance III. - Statistical Science 14: 427-456.
Seber, G.A.F. 1992: A review of estimating animal abundance. - International Statistical Journal 60: 129-166.
Solberg, E.J. & Sæther, B-E. 1999: Hunter observations of moose Alces alces as a management tool. - Wildlife Biology 5: 107-117.
Solberg, E.J., Sæther, B-E., Strand, O. & Loison, A. 1999: Dynamics of a harvested moose (Alces alces) population in a variable environment. - Journal of Animal Ecology 68: 186-204.
Toïgo, C. 1998: La taille de groupes: un bioindicateur de l'effectif des populations de bouquetin des Alpes (Capra capra ibex)? - Mammalia 60: 463-472. (In French).
Venables, W.D. & Ripley, B.D. 1999: Modern Applied Statistics with S-PLUS. - Springer Verlag, New York, 501 pp.
Vincent, J-P., Bideau, E., Hewison, A.J.M. & Angibault, J.M. 1995: The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (Capreolus capreolus). - Journal of Zoology (London) 236: 371-382.
Vincent, J-P., Gaillard, J-M. & Bideau, E. 1991: Kilometric index as biological indicator for monitoring forest roe deer populations. - Acta Theriologica 36: 315-328.
Vincent, J-P., Hewison, A.J.M., Angibault, J.M. & Cargnelutti, B. 1996: Testing density estimators on a fallow deer population of known size. - Journal of Wildlife Management 60: 18-28.
von Hardenberg, A., Bassano, B., Peracino, A. & Lovari, S. 2000: Male alpine chamois occupy territories at hotspots before the mating season. - Ethology 106: 617-630.
Williams, B.K., Conroy, M.J. & Nichols, J.D. 2002: Analysis and management of animal population: Modeling, Estimation, and Decision Making. - Academic Press, 1040 pp.
Wilson, D.E., Cole, F.R., Nichols, J.D., Rudram, R. & Foster, M.S. 1996: Measuring and monitoring biological diversity - Standard methods for mammals. Smithsonian Institution Press, Washington, 480 pp.