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Can ground counts reliably monitor ibex *Capra ibex* populations?

Emilie Largo, Jean-Michel Gaillard, Marco Festa-Bianchet, Carole Toïgo, Bruno Bassano, Hervé Cortot, Gilles Farny, Benoît Lequette, Dominique Gauthier & Jean-Pierre Martinot


Although ground counts are often used to monitor ungulate populations, several studies show that counts of ungulates have low precision and often underestimate population size. We assessed the reliability of ibex *Capra ibex* counts as performed in French national parks, by analysing up to 23 years of annual censuses of six ibex populations for which a subset of animals were individually marked. We compared the population growth rate obtained from census data (estimated by use of four different methods) with the growth rate calculated from a demographic model including parameters estimated from capture-mark-recapture methods. The correlations between count-based estimates and growth rate obtained from demographic models were adequate to suggest that ground counts can monitor trends in population size of ibex, provided that the occasional undercounts are identified. Substantial undercounts in some years led to biologically impossible values of yearly population growth ($\lambda > 1.35$) and, in the longest time series available, to marked autocorrelations in counts. Managers should replicate counts within the same year to check for underestimated counts. To reduce errors, population biologists analysing time series of ungulate counts should check the plausibility of annual growth rates estimated from two consecutive counts.

Key words: *Capra ibex*, capture-mark-recapture, census, demography, density estimate, ibex, monitoring, population growth, ungulate

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Most populations of large herbivores are subject to conservation plans or intensive management (Caughley & Sinclair 1994) that require an estimate of population size. Numerical monitoring is important to understand how populations respond to environmental variation and to different management actions (Yoccoz et al. 2001). However, the true population size is unknown for most wild populations and is often difficult to estimate (Gaillard et al. 2003). To monitor populations, managers often rely on sample counts (Balmford et al. 2003, Caughley & Sinclair 1994) because complete censuses are rarely feasible (Link & Sauer 1997).

Different methods can estimate either population size or density directly, or various indices correlated with trends in numbers (Eberhardt 1978). There is an obvious correlation between data quality and quantity and censusing effort (Pollock et al. 2002). Most attempts to assess temporal trends of population size over time adopted one of two approaches (but see Morellet et al. 2007 for a possible alternative): 1) time series analyses of counts that are usually yearly estimates of population size, and 2) demographic models based on yearly estimates of demographic parameters from long-term monitoring of individually recognisable animals using capture-mark-recapture (CMR) methods (Gaillard et al. 2003). Because the costs of CMR monitoring are prohibitive, counts of animals or indices of animal presence are usually the only way to monitor changes in population size (Link & Sauer 1997).

Regardless of whether populations are monitored through time series or demographic models, the key parameter to estimate is the population growth rate measured either as the Malthusian growth rate r or as its antilog, the natural rate of increase λ, (Gaillard et al. 2008). The maximum population growth rate \( r_{\text{max}} \) \textit{sensu Caughley 1977}) is a species-specific trait that varies with life history strategy (Stearns 1976) and only occurs when resources are abundant and the population is increasing at its maximum possible rate. Depending on environmental conditions, the population growth rate varies widely and, hence, can be considered an indicator of the well-being of the population (Morellet et al. 2007). Therefore, changes in the intrinsic rate of increase play a critical role in management decision (Loison et al. 2002).

While several methods can estimate population growth rate from time series of population counts (Lebreton & Millier 1982), the usual procedure involves regressing log-transformed yearly population counts on time: the slope of the regression provides a direct measure of λ (Gaillard et al. 2003). For 20 years, French national parks have adopted this method and conducted ungulate counts at regular intervals to follow changes in population size. As direct counts of animals rather than counts of presence indices have been performed in these areas, we will focus on direct counts in the following. Although counts appear reasonably reliable to monitor expanding ungulate populations, for well established populations at intermediate or high densities most counts underestimate population size (Gaillard et al. 2003, Morellet et al. 2007). Therefore, it is necessary to evaluate our ability to assess population trends from counts.

Unlike most other European ungulates, ibex \textit{Capra ibex} usually live in open mountainous areas above the treeline. Because ibex are thought to be highly visible, managers have assumed that ibex numbers can be accurately estimated from ground counts (Hirzel 2001, Sæther et al. 2007). Managers often rely exclusively on a single yearly ground count to assess ibex population status (Girard 2000). Although it has been argued that estimates based on ibex ground counts are accurate and precise (Sæther et al. 2007), in the population of Belledonne...
(France), ground counts consistently underestimated population size by 20-60% (Toı¨go 1998, Gaillard et al. 2003).

In this paper, we explore the reliability of ground counts to estimate population size in six different populations of Alpine ibex. Because marked individuals were monitored in all of these populations, reliable estimates of age-specific demographic parameters were also available. Thus, the observed λ calculated from time series of counts was compared to the expected λ calculated from projection matrices based on estimates of demographic parameters.

**Material and methods**

**Populations and study areas**

**Ecrins National Park**
The Ecrins National Park, established in 1973 on the western slope of the Alps, covers 2,700 km² at elevations within 800-4,102 m a.s.l. We studied two populations of ibex in this park (Table 1). The Valbonnais population (44°54’N, 5°54’E) in Nord-Ouest was founded by reintroductions in April 1989 and April 1990 of 15 females and 24 males individually marked with coloured ear tags. The population was estimated at 70 individuals in July 2005 by ground counts. The Champsaur population (44°54’N, 6°13’E) in the southwestern part of the massif of the Ecrins was founded by reintroductions in September 1994 and April 1995 of 16 females and 14 males individually marked with coloured ear tags. Ground counts in 2006 led to an estimate of 172 ibex.

**Mercantour National Park**
The Mercantour National Park, located in the southern Alps on the Italian border, covers 2,150 km² at elevations within 490-3,143 m a.s.l. We studied two populations of ibex in this park (Table 1). The Nord-Ouest population (44°40’N, 6°13’E) in the southwestern part of the massif of the Ecrins was founded by reintroductions in September 1994 and April 1995 of 16 females and 14 males individually marked with coloured ear tags. Ground counts in 2006 led to an estimate of 172 ibex.
1987-1994 (see Table 1). Based on ground counts, the population was estimated at 540 individuals in 2005, when it was supplemented with 10 females from the Belledonne Massif, marked with coloured ear tags. The St-Ours population (44°30'N, 6°47'E) was founded by two reintroductions in 1995 of 11 females and 17 males, marked with coloured ear tags, and its size was estimated by ground counts at about 156 individuals in 2005 (see Table 1). In this population, two ibex were also reintroduced in 1998 and one marked individual was released in 1997, 2002 and 2003.

**Vanoise National Park**

Situated between the valleys of Maurienne and Tarentaise, this park covers 2,000 km² with elevations ranging within 1,280-3,855 m a.s.l. The Maurienne population (45°20'N, 6°45'E) originated from two groups of immigrants from the Italian Gran Paradiso National Park and was estimated at about 600 individuals (see Table 1). During 1981-2004, 67 females and 48 males were captured, ear-tagged and released. The population of Prariond-Sassiè re (45°29'N, 6°59'E) originated from immigration from the Gran Paradiso National Park (see Table 1). It was estimated from ground counts at 320 ibex in 2003. From 1979 (males) and 1987 (females) to 2004, 28 females and 65 males were captured, ear-tagged and released. There were no translocations to the Vanoise populations, and all marked ibex were captured and released within each population. Captures occurred throughout the study period usually during April-July (in 1981, 1984, 1986-1988, 1990-1992 and 1997-2004 in Maurienne, and in 1988, 1996-1999, 2002-2004 in Prariond-Sassiè re).

**Methods**

**Counts**

Each year, ground counts were conducted to assess population size. Within a park, all counts were conducted in the same month, although the timing of counts varied among parks. Each park was divided into sectors and observers, including the wardens responsible for each sector, counted ibex using binoculars and telescopes, either along foot transects or from vantage points. During these surveys, the total number of ibex seen was recorded, as well as group size, location and age and sex classes (kids, female yearlings, male yearlings, females ≥ 2 years, males aged 2-3 years, 4-8 years and ≥ 8 years for the populations of Vanoise and Ecrins, and males aged 2-5 years and ≥ 5 years for the Mercantour populations). Counts covered the period 1999-2005 in Valbonnais and Champsaur, 1998-2004 in St-Ours, 1987-1996 in the Nord-Ouest population 1986-2003 in Maurienne, and 1985-2003 in Prariond-Sassiè re.

**Captures**

Ibex were captured using teleanaesthesia, leg-hold snares and cage traps, all methods approved by French legislation. Each ibex was marked with a unique combination of coloured ear tags. Resightings of marked ibex were obtained during ground searches throughout the entire year.

**Estimating survival rates of ibex females using CMR models**

We assumed that the availability of males did not limit female reproduction, and used female-based models to estimate population growth rates (Caswell 2001). Fecundity was measured as the number of females produced per female (for a yearly maximum of 0.5, assuming an even sex ratio at birth). We used CMR models (Lebreton et al. 1992) to estimate female survival rates for different age classes (2-7 years old, 8-12 years old and > 13 years old), known to differ in survival from studies of other populations (Toïgo et al. 2007), using the software M-SURGE (Choquet et al. 2004). We checked for the goodness-of-fit of the Cormack-Jolly-Seber model (CJS model with time-dependent survival and resighting probabilities) using the software U-CARE (Choquet et al. 2003). The CJS model fitted the data well for females of Valbonnais, St-Ours and Prariond-Sassiè re (all χ² close to 0, and P-values close to 1). However, the CJS model did not fit the data for females of the Champsaur, Nord-Ouest and Maurienne where we detected a positive trap-dependence (Z = -2.069, P = 0.0385 for Champsaur, Z = -3.612, P = 0.0003 for Nord-Ouest and Z = -4.942, P < 0.0001 for Maurienne), so that an individual seen in a given year had a higher chance of being seen the following year than an individual that was not seen. These results likely arose because a few marked ibex that used the periphery of each census area were seen less frequently than ibex using the core of the area. To account for trap-dependence, we considered that resighting probability followed a two-state model with state 1 (seen in a given year) and state 2 (not seen in a given year;

**Estimating reproductive success**

Marked females were systematically observed by park wardens to assess whether they gave birth each summer and whether their kids survived to the following April. From these observations, we measured reproductive success as the probability of each female raising a kid to one year of age. We then estimated reproductive success for four age classes (2-year-olds, 3-year-olds, 4-10-year-olds and >10 years old). Our measure of reproductive success was thus a product of fecundity and kid survival. As females were observed in consecutive years, we obtained repeated measures of reproductive success for each female. We therefore fitted a generalised linear mixed model (glmmlR package implemented in the software R), to account for pseudo-replication (sensu Hurlbert 1984). As we performed separate analyses for each population, the only random effect was female identity. For both populations of the Mercantour National Park, we knew whether or not each female gave birth in a given year, but did not have information on kid survival. The reproductive data covered the period 1995-2005 in Champsaur, 1989-2002 in Valbonnais, 1987-2005 in Nord-Ouest, 1995-2005 in St-Ours, 1997-2005 in Maurienne, and 1998-2006 in Prariond-Sassière.

**Estimating population growth rate from annual counts**

Initially, for each population, we plotted log-transformed annual counts against time to see if they showed different demographic trends, first expanding then stabilising. In this case, all estimates of λ were calculated for each period determined on the graph.

For each population, growth rate was estimated from the time series of annual counts using four different methods (Lebreton & Millier 1982). First, the intrinsic rate of population increase, \( \lambda_1 \), was estimated as the slope of the regression of the log-transformed annual counts on year. Second, the intrinsic rate of population increase (\( \lambda_2 \)) was estimated as the ratio between the sum of the counts from the second to the last year of census and the sum of the counts from the first to the penultimate census:

\[
\lambda_2 = \frac{\sum (N_t + 1) \ldots + N_j)}{\sum (N_i \ldots + N_j - 1)}
\]

Third, the intrinsic rate of population increase (\( \lambda_3 \)) was the mean of the ratio of counts in year \( t + 1 \) to counts in year \( t \):

\[
\lambda_3 = \frac{\sum (N_t + 1/N_t)}{t}
\]

When the estimates of population growth rate obtained from demographic models and ground counts differed, we looked at the times series of counts of each population in more details by plotting the distribution of annual λs. Lastly, the intrinsic rate of population increase (\( \lambda_4 \)) was estimated as the \( t^{th} \) root of the ratio of \( N_t \) on \( N_0 \):

\[
\lambda_4 = t \sqrt[N_t]{N_0}
\]

In the Prariond-Sassière population, for which a long time series was available, we also tested for negative autocorrelation, which is expected to occur with underestimation or overestimation of pop-
Table 2. Estimate of \( \lambda \) from counts (\( \lambda_1, \lambda_2, \lambda_3, \lambda_4 \) and their 95% Confidence Interval (CI); see text for further explanations) or demographic models (Leslie matrix) from CMR estimates based on marked individuals in the six ibex populations in the three French national parks. Kid survival was unavailable for the Nord-Ouest and St-Ours populations. To calculate the reproductive success in these two populations, we thus used three different scenarios (with kid survival of 0.66, 0.92 and 1, respectively, and expressed from the left to the right under the heading Leslie) based on kid survival observed in other populations.

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<thead>
<tr>
<th>Park and populations</th>
<th>( \lambda_1 ); 95% CI</th>
<th>( \lambda_2 )</th>
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<tr>
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<td></td>
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<tr>
<td>Nord-Ouest</td>
<td>1.457 (1.354-1.568)</td>
<td>1.312</td>
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<td>before 1990</td>
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\( \lambda \) estimating from counts: \( \lambda_1 = \exp(r) \) with \( r \) being the slope of \( \ln(N_t) - \ln(N_0) \); \( \lambda_2 = \frac{(\sum(N_i + 1 \ldots + N_j) \sum(N_i \ldots + N_j - 1))}{S(N_i \ldots + N_j)} \); \( \lambda_3 = \frac{\Sigma(N_i + 1/N_i)}{1} \) and \( \lambda_4 = N_t + 1/N_t \); \( \lambda_3c: \lambda_3 \) corrected; \( \lambda_4 = 1^{th} \) root of \( N_t/N_0 \); * indicates the populations in which no corrections had to be performed.

Results

Female survival

The yearly survival rate of ibex females aged 2-7 years ranged within 0.89-0.97 (Table 2) and for females 8-12 years of age, it ranged within 0.78-0.97. Survival then decreased from 13 years of age onwards, with no female > 13 years at St-Ours, and ranging within 0.69-0.86 in the other populations.

Reproductive success

In the Ecrins and Vanoise Parks, no 2-year-old female raised a kid in one year of age (Fig. 1). No 2-year-old or 3-year-old female raised a kid in Champsaur. In Maurienne and Champsaur, the reproductive success of ibex females peaked between four and 10 years of age and then decreased. In Prariond-Sassière and Valbonnais, the reproductive success of females peaked at three years of age and then decreased, although the decrease was greater after 10 years.

In Mercantour National Park, a few females produced kids at 2 years of age (0.17 for Nord-Ouest and 0.24 for St-Ours). Fecundity first increased with age (Nord-Ouest: 0.68 at three years and 0.70 between four and 10 years; St-Ours: 0.66 and 0.77, respectively). It then decreased for females > 10 years in the Nord-Ouest population (0.49), but remained high for the population of St-Ours (0.89).

Table 3. Estimate of \( \lambda \) from counts (\( \lambda_1, \lambda_2, \lambda_3, \lambda_4 \) and their 95% Confidence Interval (CI); see text for further explanations) or demographic models (Leslie matrix) from CMR estimates based on marked individuals in the six ibex populations in the three French national parks. Kid survival was unavailable for the Nord-Ouest and St-Ours populations. To calculate the reproductive success in these two populations, we thus used three different scenarios (with kid survival of 0.66, 0.92 and 1, respectively, and expressed from the left to the right under the heading Leslie) based on kid survival observed in other populations.

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Estimating population growth rate using demographic models

The Leslie matrix estimate of \( \lambda \) was 1.052 in Maurienne and 1.032 in Prariond-Sassière (Table 3). In Ecrins National Park, the estimates were 1.073 in Champsaur and 1.019 in Valbonnais (see Table 3).

In the Mercantour National Park, we used three different values of kid survival to one year (0.66, 0.92 and 1; Table 4). Estimates of \( \lambda \) ranged within 1.07-1.15 for Nord-Ouest, and within 1.10-1.18 for St-Ours (see Table 3), depending on the value of kid survival.

Estimating population growth rate from annual counts

All populations had stable demographic trends over the monitoring periods, except for Prariond-Sassière in which the demographic trends increased before 1990 and seemed to stabilise after 1990 (Fig. 2), despite that neither counting method or area covered changed before and after 1990. In all populations, the growth rates obtained from the four methods were remarkably similar.

Comparing estimates of \( \lambda \) obtained from demographic models and from censuses

Except for the population of Maurienne and after 1990 in Prariond-Sassière, \( \lambda \) estimated from demographic models were lower than \( \lambda \) estimated from annual counts (see Table 3). We first plotted annual \( \lambda_3 \) obtained from annual counts to assess whether \( \lambda \) obtained from the demographic model belonged to the observed distribution of \( \lambda_3 \) obtained from counts.

In Vanoise, the yearly \( \lambda_3 \) estimated from annual counts ranged within 0.97-1.15 in Maurienne and within 0.78-1.27 in Prariond-Sassière (Fig. 3). In the Ecrins, \( \lambda_3 \) ranged within 0.59-2.42 in Champsaur, and within 0.74-1.72 in Valbonnais. In Mercantour, for the population of Nord-Ouest and St-Ours, \( \lambda_3 \) ranged within 0.99-3.25 and within 1.11-1.46, respectively. The highest estimates of \( \lambda_3 \) for both populations of Ecrins and Mercantour were >1.35, which is the \( \lambda \)-maximum of ibex. Empirical studies of colonising populations suggest that monotocous ungulates can reach a maximum \( \lambda \) of 1.25-1.35 (Gaillard et al. 2000). Loison et al. (2002) reported a value of 1.30 in the highly productive population of ibex at Belledone in the years following its reintroduction. Therefore, a threshold \( \lambda \) of 1.35 can be confidently assumed as an upper limit of maximum \( \lambda \) for ibex.

In the Ecrins, the high values of \( \lambda_3 \) corresponded to 2001 and 2002 in Champsaur, and to 2003 in Valbonnais. If these years were removed (reducing by two the number of \( \lambda_3 \) that can be calculated), the mean of \( \lambda_3 \) was closer to \( \lambda \) estimated from demographic models (\( \lambda_3 = 1.06 \) for Champsaur and \( \lambda_3 = 0.90 \) for Valbonnais).

In Mercantour, high values of \( \lambda_3 \) corresponded to years of ibex reintroductions. When we took reintroductions in the estimation of \( \lambda_3 \) into account, the mean (\( \lambda_3 \) in Table 3) was 1.29 for Nord-Ouest and 1.22 in St-Ours, so that the estimate of \( \lambda_3 \) from counts remained higher than the estimate of \( \lambda \) from demographic models, irrespective of the value of kid survival considered, because of overestimates of some \( \lambda_3 \) (>1.35) that have to be removed from...
count data. In Nord-Ouest, the values of \( \lambda \) estimated from the demographic model did not fall within the distribution of \( \lambda \) estimated from annual counts.

As mentioned above, for the population of Prariond-Sassière, over the entire study period count data led to a slightly higher \( \lambda \) than \( \lambda \) obtained from demographic models (see Table 3), but the distribution of \( \lambda \), included no doubtful values (see Fig. 3). When considering the two demographic periods, \( \lambda \) before 1990 was 1.12 and after 1990, \( \lambda \) (1.01) was lower than the value of \( \lambda \) estimated from the demographic model and outside the distribution of \( \lambda \) estimated from annual counts after 1990. Also, as expected, in this population we found a significant negative autocorrelation of \( \lambda \) (GM test: \( P < 0.001 \); Table 5).

The two time series of ibex counts in Champsaur provided similar estimates of \( \lambda \) (1.19 vs 1.21 in December and January, respectively) and were highly correlated (slope of 0.87 ± 0.22, \( R^2 = 0.73 \), \( P = 0.0073 \)).

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Figure 3. Distribution of \( \lambda \) estimated from annual counts of ibex in the six populations in the three national parks with the value of \( \lambda \) estimated from demographic models indicated by ◆.
Discussion

Our results suggest that ground counts can, under some circumstances, provide satisfactory estimates of ibex population trends, as expected from the characteristics that make this species suitable for ground counts: large body size, open habitat and gregariousness. In all populations, the average growth rates calculated with different methods were very similar. According to Lebreton & Millier (1982), \( l_1 \) and \( l_3 \) perform better when the population is censused at regular intervals and in count series with no outliers. On the other hand, \( l_2 \) and \( l_4 \) are less sensitive to missing counts and to large errors in some years. The similarities of \( l \) estimates obtained in the present analyses reflect the regular intervals between counts (about one year) and suggest that the quality of the counts was rather constant. Year-to-year population growth, however, was overestimated in some years, as \( l \) was greater than biologically possible for this species. High values are generally the result when the population is substantially underestimated in a given year, leading to the impression of a major increase the following year. These errors can be avoided if unrealistically high estimates of population growth (i.e. \( l > l_\text{maximum} \)) are removed from analyses. The removal of years with severe undercount will require removal of two consecutive values of \( l \) (the overestimated value and the value of the year before). To avoid undercounts, replicated yearly counts should be planned.

For the Maurienne population, we did not detect any apparent problems in count data as the results obtained from both methods were similar: the population is currently increasing by about 3-5% a year. In Prariond-Sassière, over the entire study period, we found a weak overestimation of \( \lambda \) from time series of counts compared to demographic models. This result is not surprising as the population first increased then stabilised, but the demographic model estimated \( \lambda \) only in the stabilising period. In those conditions, the demographic model can only lead to a slightly lower estimate of \( \lambda \) than the time series of counts.

Inaccurate counting and autocorrelation

In Prariond-Sassière, we found no obvious outlier (\( l > 1.35 \)) in the distribution of \( l_t \), but a negative autocorrelation was evident. Inaccurate counts can account for such autocorrelation. Let us consider a population with a growth rate of \( l_a \) between the first two years of the study period, and a growth of \( l_b \) between the next two years. Assume that in the first year the count was accurate, but in the second year, it underestimated population size. The estimated growth rate of \( l'_a \) would be lower than the true growth rate. If in the third year, the population size is estimated accurately, the growth rate of \( l'_b \) would be larger than the true one, \( l_b \). Such patterns occur in population counts of ibex in this area, because in some years, for unknown reasons, several ibex were missed during counts.

Another major problem with counts data is the asymmetry in retrospective detection of erroneous values. Because each species has a maximum \( l \), all values of \( l \) higher than this maximum can be considered outliers. Conversely, low values of \( l \) would not inevitably be considered outliers. At Champsaun, calculations of \( l \) in 2001 and 2004 suggested that the population decreased by half in successive December counts but not in January counts. The January counts allowed us to detect the error in December counts, highlighting the need for replicating counts.

Unaccounted factors

Our demographic models calculated \( \lambda \) from a Leslie matrix based on mean estimates of demographic parameters. The matrix accounts for age variation, but life history variation also originates from many other factors such as density dependence (Fowler 1987), environmental variation and sex ratios that were not taken into account. Moreover, the matrix was based on marked individuals that were not necessarily representative of the entire population.

<table>
<thead>
<tr>
<th>Years</th>
<th>( l_{3t} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1985</td>
<td>1.147</td>
</tr>
<tr>
<td>1986</td>
<td>0.831</td>
</tr>
<tr>
<td>1987</td>
<td>1.252</td>
</tr>
<tr>
<td>1988</td>
<td>1.117</td>
</tr>
<tr>
<td>1989-1991</td>
<td>1.246</td>
</tr>
<tr>
<td>1991</td>
<td>0.940</td>
</tr>
<tr>
<td>1992</td>
<td>1.084</td>
</tr>
<tr>
<td>1993</td>
<td>0.960</td>
</tr>
<tr>
<td>1994</td>
<td>1.065</td>
</tr>
<tr>
<td>1995</td>
<td>1.094</td>
</tr>
<tr>
<td>1996</td>
<td>0.961</td>
</tr>
<tr>
<td>1997</td>
<td>0.901</td>
</tr>
<tr>
<td>1998</td>
<td>1.274</td>
</tr>
<tr>
<td>1999</td>
<td>0.782</td>
</tr>
<tr>
<td>2000-2003</td>
<td>1.054</td>
</tr>
</tbody>
</table>

Table 5. Yearly estimates of \( l_{3t} \) in the Prariond-Sassière population of Alpine ibex.
especially when only the translocated animals were marked. The demographic performance of reintroduced individuals may be different from the population average, especially if the age structure of the marked sample was different from that of the total population.

Differences in age structure among marked and unmarked ibex were likely in Champsaur and Valbonnais, where the sample of monitored marked ibex aged over time as no new animals were marked. In Prariond-Sassière, where native individuals were marked continuously, the results mostly supported our expectation that ground counts would underestimate population size. Continuous and unbiased marking of individuals over time is required to ensure that the sample of marked animals is representative of the population.

**Conclusion**

Currently, annual counts are the tool most often used to monitor ibex populations (Jacobson et al. 2004, Sæther et al. 2002, 2007). Our analyses suggest that ground counts provide acceptable estimates of population trends, after checking for outliers. Such a precaution has not been taken in previous ibex studies based on counts, so that those analyses are likely to have been biased by some annual population growth much higher than biologically possible for ibex. As illustrated by the occurrence of marked underestimates in some years without a possibility to identify a factor causing them, annual counts of ibex cannot be used to estimate population size in a given year. Instead, a time series of counts carefully checked for outliers is needed to provide information useful for management. We suggest that replicate counts within the same year would provide more reliable information on population size and trends by offering a way to detect anomalies in counts as well illustrated by the case study of Champsaur. Given the time and cost of ground counts, replicated counts may require a reduction in sampling intensity.

**References**


