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

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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-max *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 *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

Table 1. Characteristics of the ibex populations studied with details on counts performed in each population (A), data used to analyse reproductive success of females in each population (B), and data used to analyse female survival in each population (C).

A: Park	Population	Counting season	Years	Reintroduction
Ecrins	Valbonnais	Summer	1999-2005	1989 & 1990
	Champsaur	Winter	1999-2005	1994 & 1995
Mercantour	Nord-Ouest	Fall	1987-1996	1987-1994
	St-Ours	Fall	1998-2004	1995
Vanoise	Maurienne	Summer	1986-2003	-
	Prariond-Sassière	Summer	1985-2003	-

B: Populations	Years	Years of monitoring of individual females	Number of females	Female age
Ecrins				
Valbonnais	1989-2002	3-14	14	3-19
Champsaur	1995-2005	2-11	16	2-18
Mercantour:				
Nord-Ouest	1987-2005	1-11	22	2-18
St-Ours	1995-2005	1-11	11	2-13
Vanoise				
Maurienne	1997-2005	2-9	44	2-19
Prariond-Sassière	1998-2006	1-7	22	2-17

C: Populations	Period of monitoring	Number of marked females	Age at first capture Minimum	Age at first capture Maximum
Ecrins				
Valbonnais	1989-2005	15	1 year	8 years
Champsaur	1995-2005	16	2 years	8 years
Mercantour				
Nord-Ouest	1987-2005	27	1 year	12 years
St-Ours	1995-2005	11	1 year	10 years
Vanoise				
Maurienne	1981-2004	67	0 year	17 years
Prariond-Sassière	1987-2004	28	0 year	12 years

(France), ground counts consistently underestimated population size by 20-60% (Toïgo 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 km^2 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°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.

Mercantour National Park
The Mercantour National Park, located in the southern Alps on the Italian border, covers 2,150 km^2 at elevations within 490-3,143 m a.s.l. The Nord-Ouest population (44°18'N, 6°43'E) originates from reintroductions of 27 females and 22 males marked with coloured ear tags during

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 km^2 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-Sassière (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-Sassière).

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-Sassière.

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-Sassière (all χ^2 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;

Pradel 1993). The probability of seeing an individual in state 1 is 1 and the probability of seeing an individual in state 2 is 0. The multi-state model then estimated the probability of transition from state 1 to state 2, from state 2 to state 1, and the survival rates. The CMR data covered the period 1989-2005 in Valbonnais, 1995-2005 in Champsaur, 1987-2005 in Nord-Ouest, 1995-2005 in St-Ours, 1981-2004 in Maurienne, and 1987-2004 in Prariond-Sassière.

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 fit a generalised linear mixed model (glmmML 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 using demographic models

For each population, we built a Leslie matrix (Leslie 1945), which is a deterministic, age-structured and female-based model, commonly used for management of ungulate populations (Eberhardt 1991, Gaillard & Yoccoz 2003). We used the estimates of survival and reproductive success in terms of female offspring only for each age class and for each population. Because very few females were marked at one year of age, yearling survival could not be estimated from field data. As a recent analysis of the Belledonne population showed that ibex yearling survival is close to 1 (Toïgo et al. 2007), we assigned a value of 0.95 to yearling survival.

In the absence of estimates of kid survival to one year for the two populations in the Mercantour National Park, we used values from the other ibex populations for which we had both kid survival and fecundity. We thus considered values of kid survival varying from 0.66 to 1. Following Caswell (2001), we calculated λ as the largest positive eigenvalue of the Leslie matrix that includes the average estimates of age-specific demographic parameters.

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, λ1, was estimated as the slope of the regression of the log-transformed annual counts on year. Second, the intrinsic rate of population increase (λ2) 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:

$$\lambda 2 = \sum (Ni+1\ldots+Nj)/\sum (Ni\ldots+Nj\text{-}1)$$
(1).

Third, the intrinsic rate of population increase (λ3) was the mean of the ratio of counts in year $t+1$ to counts in year t:

$$\lambda 3 = \sum (Ni+1/Ni)/t \qquad (2).$$

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 λ_t. Lastly, the intrinsic rate of population increase (λ4) was estimated as the tth root of the ratio of Nt on N0:

$$\lambda 4 = t\sqrt{\frac{Nt}{N0}} \qquad (3).$$

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. Adult female survival estimated for different age classes in the six ibex populations in the three French national parks.

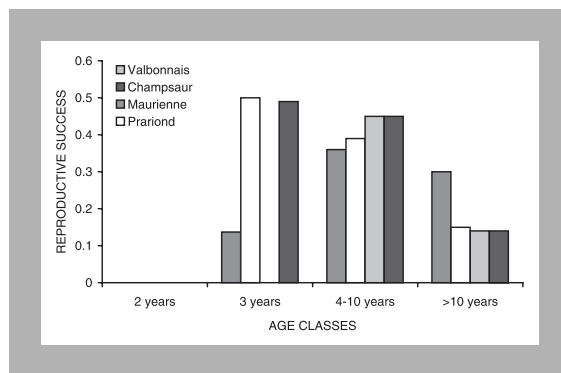| Park and populations	Age class		
	2-7 years $\pm$ s.e.	8-12 years $\pm$ s.e.	>13 years $\pm$ s.e.
Ecrins			
Champsaur	0.92 ± 0.034	0.97 ± 0.023	0.86 ± 0.104
Valbonnais	0.89 ± 0.044	0.83 ± 0.057	0.81 ± 0.11
Mercantour			
Nord-Ouest	0.92 ± 0.042	0.95 ± 0.031	0.77 ± 0.058
St-Ours	0.97 ± 0.025	0.78 ± 0.080	0 ± 0
Vanoise			
Maurienne	0.97 ± 0.013	0.93 ± 0.026	0.69 ± 0.059
Prariond-Sassière	0.91 ± 0.046	0.91 ± 0.044	0.76 ± 0.11

Figure 1. Female reproductive success estimated for the four different age classes in the four ibex populations in the Ecrins (Valbonnais and Champsaur) and Vanoise (Maurienne and Prariond-Sassière).

ulation size. For Champsaur, ground counts data were available for both December and January, so we checked the concordance between time series using regression analysis.

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 to 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 λ from counts (λ1, λ2, λ3, λ4 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.

Park and populations	λ 1; 95% CI	λ 2	λ 3; 95% CI	λ 3c	λ 4	Leslie
Mercantour						
Nord-Ouest	1.457 (1.354-1.568)	1.312	1.519 (1.082-1.956)	1.299	1.464	1.07 1.13 1.15
St-Ours	1.240 (1.218-1.263)	1.292	1.243 (1.176-1.312)	1.227	1.241	1.10 1.17 1.19
Ecrins						
Champsaur	1.232 (1.081-1.404)	1.194	1.284 (0.777-1.791)	1.060	1.169	1.073
Valbonnais	1.085 (0.992-1.186)	1.059	1.111 (0.789-1.434)	0.900	1.049	1.019
Vanoise						
Maurienne	1.047 (1.038-1.057)	1.048	1.049 (1.016-1.081)	1.049*	1.036	1.052
Prariond-Sassière	1.055 (1.038-1.072)	1.051	1.047 (0.971-1.123)	1.047*	1.049	1.032
before 1990	1.063 (0.994-1.138)	1.078	1.119 (0.968-1.269)	1.119*	1.059	-
after 1990	1.013 (0.999-1.027)	1.014	1.011 (0.928-1.094)	1.011*	1.010	1.032

λ estimating from counts: $\lambda 1 = \exp(r)$ with r being the slope of $\ln(Nt) = f(t)$; $\lambda 2 = \Sigma(Ni+1 \ldots + Nj)/\Sigma(Ni \ldots + Nj-1)$; $\lambda 3 = \Sigma(Ni+1/Ni)/t$ and $\lambda t = Nt+1/Nt$; λ3c: λ3 corrected; $\lambda 4 = t^{th}$ root of Nt/N0; * indicates the populations in which no corrections had to be performed.

Table 4. Estimates of recruitment (proportion of females that produced a kid that survived until April), productivity (kids born per adult female) and kid survival (Sj) in the four ibex populations in the two French national parks.

Park and populations	Recruitment	Productivity	Sj
Ecrins			
Valbonnais	0.402	0.728	0.552
Champsaur	0.496	0.535	0.926
Vanoise			
Maurienne	0.365	0.559	0.654
Prariond	0.344	0.500	0.688

Figure 2. Changes of the Prariond-Sassière ibex population during 1985-2003.

Estimating population growth rate using demographic models

The Leslie matrix estimate of λ 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 λ 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 λ obtained from demographic models and from censuses

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

In Vanoise, the yearly $\lambda 3_t$ 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, $\lambda 3_t$ ranged within 0.59-2.42 in Champsaur,
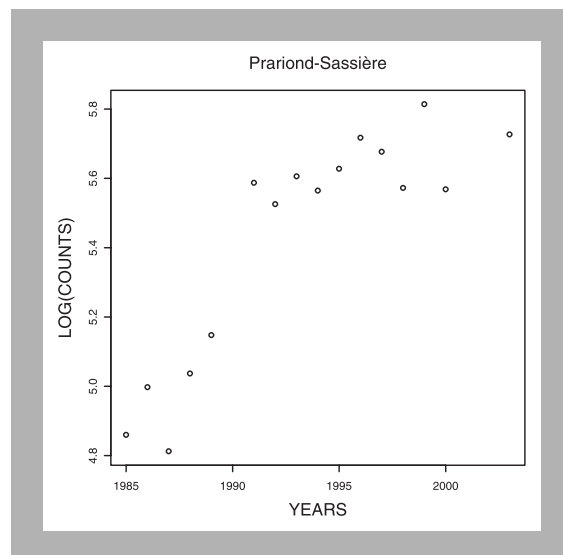
and within 0.74-1.72 in Valbonnais. In Mercantour, for the population of Nord-Ouest and St-Ours, $\lambda 3_t$ ranged within 0.99-3.25 and within 1.11-1.46, respectively. The highest estimates of $\lambda 3_t$ for both populations of Ecrins and Mercantour were >1.35, which is the λ-maximum of ibex. Empirical studies of colonising populations suggest that monotocous ungulates can reach a maximum λ 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 re-introduction. Therefore, a threshold λ of 1.35 can be confidently assumed as an upper limit of maximum λ for ibex.

In the Ecrins, the high values of $\lambda 3_t$ 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 $\lambda 3_t$ was closer to λ estimated from demographic models ($\lambda 3 = 1.06$ for Champsaur and $\lambda 3 = 0.90$ for Valbonnais).

In Mercantour, high values of $\lambda 3_t$ corresponded to years of ibex reintroductions. When we took reintroductions in the estimation of $\lambda 3_t$ 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 λ from demographic models, irrespective of the value of kid survival considered, because of overestimates of some $\lambda 3_t$ (>1.35) that have to be removed from
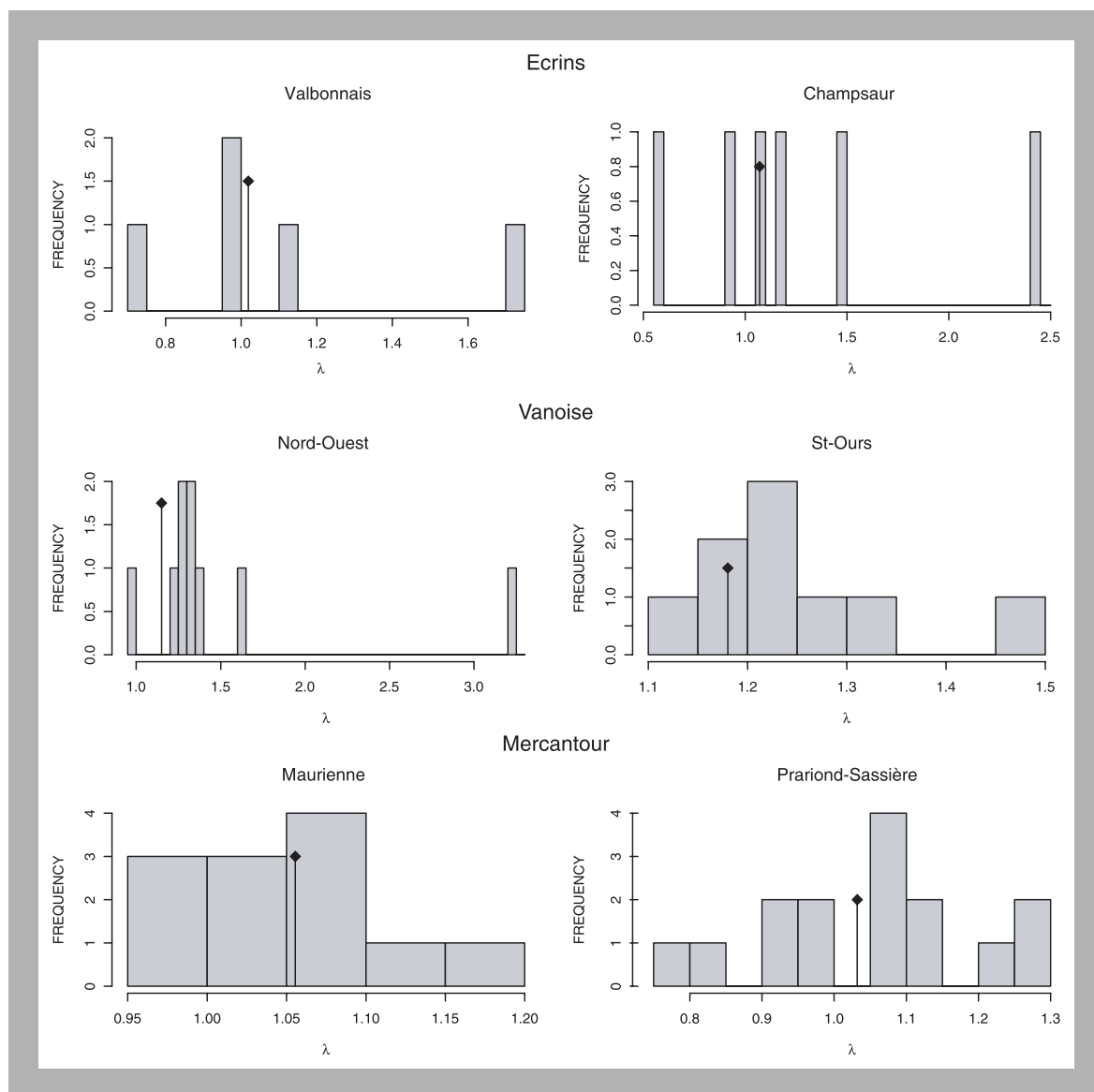
Figure 3. Distribution of $\lambda 3_t$ estimated from annual counts of ibex in the six populations in the three national parks with the value of λ estimated from demographic models indicated by ◆.

count data. In Nord-Ouest, the values of λ estimated from the demographic model did not fall within the distribution of $\lambda 3_t$ 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 λ than λ obtained from demographic models (see Table 3), but the distribution of $\lambda 3_t$ included no doubtful values (see Fig. 3). When considering the two demographic periods, $\lambda 3$ before 1990 was 1.12 and after 1990, $\lambda 3$ (1.01) was lower than the value of λ estimated from the demographic model and outside the distribution of $\lambda 3_t$ estimated from annual counts after 1990. Also, as expected, in this population we found a significant negative autocorrelation of $\lambda 3_t$ (GM test: $P < 0.001$; Table 5).

The two time series of ibex counts in Champsaur provided similar estimates of $\lambda 1$ (1.19 vs 1.21 in December and January, respectively) and were highly correlated (slope of 0.87 ± 0.22, $R^2 = 0.73$, $P = 0.0073$).

Table 5. Yearly estimates of $\lambda 3_t$ in the Prariond-Sassière population of Alpine ibex.

Years	$\lambda 3_t$
1985	1.147
1986	0.831
1987	1.252
1988	1.117
1989-1991	1.246
1991	0.940
1992	1.084
1993	0.960
1994	1.065
1995	1.094
1996	0.961
1997	0.901
1998	1.274
1999	0.782
2000-2003	1.054

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), $\lambda 1$ and $\lambda 3$ perform better when the population is censused at regular intervals and in count series with no outliers. On the other hand, $\lambda 2$ and $\lambda 4$ are less sensitive to missing counts and to large errors in some years. The similarities of λ 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 λ 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. $\lambda > \lambda$ maximum) are removed from analyses. The removal of years with severe undercount will require removal of two consecutive values of λ (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 λ 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 λ only in the stabilising period. In those conditions, the demographic model can only lead to a slightly lower estimate of λ than the time series of counts.

Inaccurate counting and autocorrelation

In Prariond-Sassière, we found no obvious outlier ($\lambda > 1.35$) in the distribution of λ_t, but a negative autocorrelation was evident. Inaccurate counts can account for such autocorrelation. Let us consider a population with a growth rate of λa between the first two years of the study period, and a growth of λb 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 $\lambda a'$ would be lower than the true growth rate. If in the third year, the population size is estimated accurately, the growth rate of $\lambda b'$ would be larger than the true one, λb. 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 λ, all values of λ higher than this maximum can be considered outliers. Conversely, low values of λ would not inevitably be considered outliers. At Champsaur, calculations of λ 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 λ 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,

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.

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