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Item Type	Article
Authors	Panaccio, Matteo;Brambilla, Alice;Bassano, Bruno;Smith, Tessa;von Hardenberg, Achaz
Citation	Panaccio, M., Brambilla, A., Bassano, B., Smith, T. E., & von Hardenberg, A. (2024). Monitoring wildlife population trends with sample counts: A case study on the Alpine ibex ( <i>Capra ibex</i> ). <i>Wildlife Biology: A journal for wildlife science</i> , (1), article-number e01162. <a href="https://doi.org/10.1002/wlb3.01162">https://doi.org/10.1002/wlb3.01162</a>
DOI	<a href="https://doi.org/10.1002/wlb3.01162">10.1002/wlb3.01162</a>
Publisher	Wiley Open Access
Journal	Wildlife Biology: A journal for wildlife science
Rights	Licence for VoR version of this article: <a href="http://creativecommons.org/licenses/by/3.0/">http://creativecommons.org/licenses/by/3.0/</a>
Download date	2026-05-21 16:42:54
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Link to Item	<a href="http://hdl.handle.net/10034/628252">http://hdl.handle.net/10034/628252</a>

## Research article

### Monitoring wildlife population trends with sample counts: a case study on the Alpine ibex (*Capra ibex*)

Matteo Panaccio<sup>1,2</sup>, Alice Brambilla<sup>2,3</sup>, Bruno Bassano<sup>2</sup>, Tessa Smith<sup>1</sup> and Achaz von Hardenberg<sup>1</sup>

<sup>1</sup>Department of Biological Sciences, University of Chester, Chester, UK

<sup>2</sup>Alpine Wildlife Research Centre, Gran Paradiso National Park, Valsavarenche (AO), Italy

<sup>3</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

Correspondence: Matteo Panaccio ([panaccio.matteo@gmail.com](mailto:panaccio.matteo@gmail.com))

#### Wildlife Biology

2023: e01162

doi: [10.1002/wlb3.01162](https://doi.org/10.1002/wlb3.01162)

Subject Editor: Luca Corlatti

Editor-in-Chief: Ilse Storch

Accepted 2 October 2023



Monitoring population dynamics is of fundamental importance in conservation but assessing trends in abundance can be costly, especially in large and rough areas. Obtaining trend estimations from counts performed in only a portion of the total area (sample counts) can be a cost-effective method to improve the monitoring and conservation of species difficult to count.

We tested the effectiveness of sample counts in monitoring population trends of wild animals, using as a model population the Alpine ibex *Capra ibex* in the Gran Paradiso National Park (Italy), both with computer simulations and using historical count data collected over the last 65 years. Despite sample counts failed to correctly estimate the true population abundance, sampling half of the target area could reliably monitor the trend of the target population. In case of strong changes in abundance, an even lower proportion of the total area could be sufficient to identify the direction of the population trend. However, when there is a high yearly trend variability, the required number of samples increases and even counting in the entire area can be ineffective to detect population trends. The effect of other parameters, such as which portion of the area is sampled and detectability, was lower, but these should be tested case by case.

Sample counts could therefore constitute a viable alternative to assess population trends, allowing for important, cost-effective improvements in the monitoring of wild animals of conservation interest.

Keywords: Alpine ibex, mountain ungulates, population dynamics, power analysis, sample counts, wildlife monitoring

#### Introduction

Monitoring population dynamics is a key goal for conservationists, as it allows to investigate the effects of ecological variability on wildlife populations (Jacobson et al. 2004, Jonas et al. 2008, Mignatti et al. 2012), to quantify the efficacy of management interventions (Hinkson and Richter 2016, Saunders et al. 2018) and to evaluate



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the conservation status of a species (Vors and Boyce 2009, Brambilla et al. 2020a). For instance, the assessment of population trends is used in the IUCN framework to evaluate the risk of extinction of a species, which under criterion A (IUCN 2022) is considered threatened if it suffered a population decline of 30% or more over the last 10 years or three generations.

Trends in abundance are primarily estimated through multiple counts over time (Magurran et al. 2010), but this process implicates several challenges and can be subject to different sources of errors (Yoccoz et al. 2001). However, the true long-term population trends are often hidden by short-term random fluctuations, due to demographic stochasticity and environmental year-to-year variability (McCain et al. 2016). Surveys too limited in time can therefore fail to identify the direction and magnitude of a population trend (Wauchope et al. 2019). Moreover, population dynamics can also vary across sites, with different subpopulations exhibiting different trends (Urquhart 2012). If this variability is not considered, biases in determining the real population trend can easily arise (Palmer 1993, Weiser et al. 2019, Fournier et al. 2019). Finally, imperfect detection during counts (Kellner and Swihart 2014, Lahoz-Monfort et al. 2014) can influence the ability to detect population trends (Kéry et al. 2009, Ficetola et al. 2018, Wood et al. 2019).

The design of population monitoring programs should try to minimize the above-mentioned potential biases, but also reduce survey costs in order to make long term monitoring financially sustainable (Caughlan and Oakley 2001, White 2019). Power analysis is the tool generally used to quantify the minimum sampling effort required to correctly detect the true population trend (Gerrodette 1987, Taylor and Gerrodette 1993, Thomas 1997, Vallecillo et al. 2021). In a power analysis, multiple replicates of the data are built, either with simulations or subsets of real measures, and the statistical power is estimated as the proportion of replicates in which a statistical model fitted to the data can detect the change in population size over time (Steidl and Thomas 2001). Many authors have used power analyses to estimate the minimum number of years required in a monitoring project to detect a significant trend (Luymes and Chow-Fraser 2019, Wauchope et al. 2019), showing that a minimum of 5–35 years is needed depending on the species (Reynolds et al. 2011, White 2019). However, fewer studies considered the use of censuses conducted only in a sample of the target area (defined here as sample counts) in monitoring population trends and estimated the proportion of sites of the total area required to detect trends with similar power to total counts. Sample counts have been described as imprecise (Stoddard et al. 1998, Yoccoz et al. 2001), as it has been shown for instance that a limited number of sites generally enables detection of only strong declines in the population (Sewell et al. 2012, Wagner et al. 2022), unless the species is particularly abundant and easy to detect (Ficetola et al. 2018). The efficacy of a particular sampling design, such as sample counts, in detecting population dynamics is closely intertwined with the study system (Weiser et al. 2019, White

2019). Therefore, the analysis of monitoring trends by sampling only a portion of the target area should be examined on a system-by-system basis.

Monitoring certain taxa such as mountain ungulates, can present several technical constraints due to difficult terrain, climatic conditions, remote habitats and required logistics (Singh and Milner-Gulland 2011). Mountain ungulates are usually counted with helicopter censuses (Gonzalez-Voyer et al. 2001, Rice et al. 2009) or ground counts (Jacobson et al. 2004, Largo et al. 2008, Suryawanshi et al. 2012), but both these methods require substantial financial and human efforts, especially in large areas and rough terrain conditions. Reducing the effort in terms of time or number of surveyed sectors, while maintaining enough power to detect trends, is therefore of critical importance in monitoring species living in remote areas (Lindenmayer and Likens 2010).

In some cases, the survey effort can be reduced by sampling the population less often (interval sampling), for instance every three or five years as suggested by some authors (Urquhart et al. 1998, Reynolds et al. 2011, Singh and Milner-Gulland 2011). However, interval sampling has proved to be less effective than sampling every year in detecting the magnitude of a trend (Wauchope et al. 2019) and could therefore not be adequate if the goal is to analyze the drivers of population dynamics in a long-term monitoring project or for endangered species for which declines must be detected quickly in order to provide appropriate conservation strategies. Consequently, surveying only a sample of the target area every year could be the only viable and cost-effective alternative. To the best of our knowledge, a complete assessment of the statistical power of sample counts for monitoring has not been performed before.

In this study, we investigated the reliability of sample counts in estimating population trends, using the Alpine ibex *Capra ibex* population of Gran Paradiso National Park (GPNP, North-West Italian Alps) as an example. For this population an exceptionally long-term series of 65 years of count data, collected with block counts over the whole territory of the park, is available (Jacobson et al. 2004, Mignatti et al. 2012). Using parameters derived from this case study, we simulated populations under various scenarios of abundance trends over 10 and 20 years and calculated the power of population models based on sample counts in detecting the true trend. We also estimated the minimum proportion of sectors (count areas in which GPNP is divided) needed to correctly detect the population trend of Alpine ibex population in the whole area from which the samples are drawn. Moreover, we explored the effect of different strategies for selecting which sectors to monitor: 1) random selection each year; 2) random selection in the first year, then the same sectors are surveyed each of the following years and 3) biased selection towards the sectors with the highest abundance. We also included different magnitudes of both trend variability between years and sectors and variability of detection probability, a phenomenon that heavily affects the species and possibly leads to severe underestimates of abundance (Gaillard et al. 2003, Morellet et al. 2007, Largo et al. 2008).

Finally, we tested the predictions obtained with simulations analyzing the real count data collected in GPNP over the last 65 years and comparing trends estimated from the entire area with trend estimations that would have been obtained from sample counts.

## Material and methods

### Study species and area

The Alpine ibex is a mountain ungulate endemic to the European Alps, where it lives mostly in alpine meadows and rocky cliffs between 1600 and 3200 m a.s.l. (Brambilla et al. 2020b). The species recovered from near extinction during the last century (Biebach and Keller 2009) and due to reintroduction programs, is now present again on the entire Alpine arc with a population of around 55 000 individuals (Brambilla et al. 2020a). However, low genetic variability (Biebach and Keller 2010) and climate change (Brivio et al. 2019) may constitute a severe threat for the species in the future.

The number of counted Alpine ibex in Gran Paradiso National Park ranged from ~ 2600 to ~ 5000 individuals over the last 65 years, with a fluctuating population dynamic, showing a recent strong decline after a population peak in the 1990's (Jacobson et al. 2004, Mignatti et al. 2012). Alpine ibex abundance in GPNP has been estimated with annual

total counts performed by expert park rangers every year since 1956 over the whole territory of GPNP (a total area of 720 km<sup>2</sup>). The counts have been performed with a standardized protocol since 1956, i.e. over the same established routes and vantage points and in the same period of the year (beginning of September). During the total counts, the entire park area is divided into 38 sectors (or surveillance areas) that range from 5.24 to 37.21 km<sup>2</sup> each. Alpine ibex of both sexes show a rather high site fidelity (Parrini et al. 2003, Grignolio et al. 2004), and are assumed to remain in the same sector during the summer season.

### Power analysis on simulated trends

We simulated populations of Alpine ibex in GPNP, with a given total abundance (A) randomly distributed among the 38 sectors of the park. In each simulation, A was drawn from a Poisson distribution under three different abundance scenarios, with expected values of A of 2500, 3500 or 5000 individuals (Table 1), thus a low, medium and high abundance (based on the historical count data for Alpine ibex in GPNP, Mignatti et al. 2012). The probability for an individual to be assigned to a specific sector was given by the average Alpine ibex density of the sector (i.e. the mean number of individuals observed in that area during actual total counts in GPNP conducted between 2000 and 2021). Therefore, the simulated ibex distribution was not dependent only on the extent of the sectors (as it would occur

Table 1. Parameters used in the simulations and their values.

Abbreviation	Parameter	n of possible values	Values	Meaning
A	Abundance	3	2500, 3500, 5000	Low, medium or high population size in GPNP
r	Overall yearly trend over 10 years	1	1	Stable population in 10 years
		5	1.01, 1.018, 1.027, 1.034, 1.041	10, 20, 30, 40 or 50% total population increase in 10 years
		5	0.989, 0.978, 0.965, 0.95, 0.933	-10, -20, -30, -40 or -50% total population increase in 10 years
	Overall yearly trend over 20 years	1	1	Stable population in 20 years
		5	1.005, 1.009, 1.013, 1.017, 1.0250.995, 0.989, 0.982, 0.975	10, 20, 30, 40 or 50% total population increase in 20 years
		5	0.966	10, 20, 30, 40 or 50% total population increase in 20 years
cv <sub>y</sub>	Coefficient of variation of the trend between years	4	0.05, 0.1, 0.15, 0.2	Low, medium and high variability
cv <sub>s</sub>	Coefficient of variation of the trend between sectors	4	0.05, 0.1, 0.15, 0.2	Low, medium and high variability
p	Detection probability	3	0.4, 0.6, 0.8	Low, medium and high detectability
cv <sub>d</sub>	Coefficient of variation for detection probability	3	0.1, 0.3, 0.5	Low, medium or high variability
Selection	Sector-selection (method to select the survey sectors)	3	'random each'	Sectors are selected randomly each year
			'random first'	Sectors are selected randomly the first year
			'best'	Only the sectors with the highest abundance are selected
n	Number of sectors used for the trend estimation	38	1-38	

assuming a constant density across the target area), but was determined by unknown multiple factors that in the real counts affect the presence of animals and their density in each sector.

For each random population we simulated a growth of the population with a yearly overall abundance trend ( $r$ ) over a 10 or 20-year period, either with a decrease or increase in population size. The different values of  $r$  that were used are reported in [Table 1](#) and correspond to a total change of 10, 20, 30, 40 and 50% in 10 or in 20 years. As many Alpine ibex populations currently exhibit a stable population ([Brambilla et al. 2020b](#)), we also included in the analysis a stable yearly trend ( $r = 1$ ).

We simulated different scenarios of year-to-year and sector-to-sector variability in the overall trend  $r$ , assigning a random trend,  $T_{y,s}$ , to each  $y$ -th year and  $s$ -th sector, sampled around the value of  $r$  with a specified coefficient of variation ( $cv_y$  for the year and  $cv_s$  for the sector). Further details about the mathematical formulation of the simulations are provided in Supporting information.

We simulated different scenarios of variability in the overall trend by assigning four different possible values (0.05, 0.1, 0.15 and 0.2) to the coefficient of variation between years ( $cv_y$ ) and sectors ( $cv_s$ ). A coefficient of variation of around 0.05 between years and of 0.05–0.10 between sectors was indeed historically found in GPNP over the last 65 years ([Brambilla and Bassano unpubl.](#)). We also included higher variability to potentially extend the results to other species.

Simulated counts were run on the random-built population in only  $n$  out of the 38 total sectors and population growth rates were estimated from the total number of individuals counted in the sample sectors and compared to the real assigned growth rate  $r$ .

We further accounted for differences in detectability of animals in our simulations by varying detection probability in each repetition (i.e. between years and among sectors). The coefficient of variation of the detectability from one survey to the other (thus either between a sector and another in the same year or for the same sector across different years) was either 0.1 (low variation, thus most surveys have a similar detectability), 0.3 (medium variation, detectability is different between each survey) and 0.5 (high variation, detectability is very different between the surveys) around an estimated detection probability for Alpine ibex ranging from 0.4 to 0.8 ([Gaillard et al. 2003](#)). Such values of detectability and its coefficient of variation were also observed in our study population with Capture–Mark–Resight ([Schwarz and Seber 1999](#)) and double observer ([Suryawanshi et al. 2012](#)) data in one of the 38 sectors of the Park ([Panaccio and Brambilla unpubl.](#)). Further details about the simulations are provided in the Supporting information.

The  $n$  survey sectors were selected as: 1)  $n$  sectors selected at random the first year and then sampled each following year; 2)  $n$  randomly selected sectors where the random selection was repeated each year; 3) a biased selection with only the  $n$  initial sectors with the highest number of individuals detected in the first year of monitoring.

We estimated the growth rate in each simulation with a generalized linear model (GLM) with a Poisson data distribution ([O’Hara and Kotze 2010](#)).

We ran the simulation 500 times for each of the 787 968 combinations of our seven parameters: assigned overall trend ( $r$ ), method to select the survey sectors, total population size ( $A$ ),  $cv$  between areas ( $cv_a$ ),  $cv$  between years ( $cv_y$ ),  $cv$  for detectability between sectors ( $cv_d$ ), and the number of sectors in which the surveys were conducted ( $n$ ). Over the total of 393 984 000 simulations, statistical power was calculated as the proportion of simulations in which a significant trend was estimated and matched the assigned direction ([Weiser et al. 2019](#)), with a threshold of 0.8 (80%). A statistical power of 0.8 (i.e. an 80% probability of detecting the effect of interest) is conventionally considered sufficient to conclude that the sampling design can detect the true population trend ([Cohen 1992](#)).

We also evaluated the performance of sample counts in correctly detecting the magnitude of the trend with an error lower than 5 and 2% (i.e.  $|r_{\text{estimated}} - r| < 0.05$  or  $0.02$ ). Similar tolerance levels were used by [Wauchope et al. \(2019\)](#) in simulations to estimate the required length of a time series of counts.

All population and counts simulations, together with the growth rates estimation, were performed in R ver. 4.1.3 ([www.r-project.org](http://www.r-project.org)) and the full script is provided in Supporting information.

We utilized linear models (LMs) to determine the relevant parameters influencing the statistical power of the sample counts to correctly detect the assigned population trend. For this we modeled statistical power depending on combinations of the parameters used in the simulations ([Table 1](#)). We built models using all possible combinations of these parameters and selected the best predictive model as the one with the lowest AIC value ([Akaike 1974](#)).

## Power analysis on real ibex trends in GPNP

We randomly sampled 112 000 total time intervals each of a specified length (5, 10, 15 or 20 years) from the original dataset of Alpine ibex counts in GPNP and estimated the population trend with a GLM for the Poisson distribution. If a trend was detected (with  $p < 0.05$ ) in the target interval using the full number of sectors (complete trend), we randomly selected  $n$  sectors (with  $1 < n < 38$ ) and again estimated the trend using only the sum of the individuals counted in the  $n$  sectors (sample trend). We compared the two trends and, following [Wauchope et al. \(2019\)](#), classified the sample trend as matching or opposing the complete trend, missed (sample counts that did not detect the complete trend) or false trends (sample counts that erroneously detected a stable complete trend). As for our simulations, we considered the sample trend correct in magnitude if the difference with the complete trend was of 0.02 or lower (2% error each year). The procedure was repeated 1000 times for each possible number of sampled sectors (1–38) and we assessed the statistical power as the proportion of samples in which the sample trend matched the complete trend, in terms of direction (increase or decrease in the population) or magnitude, with

a threshold power of 0.8 (80%). All the analyses were performed in R, ver. 4.1.3 ([www.r-project.org](http://www.r-project.org)) with the code provided in Supporting information.

## Results

### Power analysis on simulated data

In this section we report the outcomes obtained for a simulated decrease in population size over time, as increasing and decreasing trends showed very similar results. The results for the case of simulated population increases are presented in Supporting information.

Sample counts were able to correctly identify the direction of a population trend if it was as strong as  $-40\%$  or more over 10 or 20 years (Fig. 1), or for a change in abundance of  $-30\%$  if the yearly trend variability was 0.1 or lower. If the population showed a change in abundance of  $-20\%$  in 10 or 20 years, sample counts were able to detect the trend only under low trend variability ( $cv_y = 0.05$ ) and at least 15 sampled sectors. Under a 10% overall trend sample counts never reached a sufficient statistical power in identifying the direction of the population trend, even sampling the entire area. When the direction of the trend was detected, its magnitude was also correctly identified with an error lower than 5% on the yearly trend. However, sample counts were never able to reach a sufficient statistical power in estimating the 10-year trend with an annual error lower than 2%, even when sampling the entire area. Conversely, on a time span of 20 years, trends of  $-30\%$  or higher were detected within the 2% error in at least 80% of the cases if the yearly trend variability was 0.05 (Fig. 2). With a higher annual variability in trends, the correct magnitude over 20 years was never detected with sufficient power. A number of sectors between 15 and 20 (out of

38 total) was sufficient to estimate correctly both the direction and the magnitude of the trend, corresponding to 23.4–60% of the total GPNP area (as the extent of the sectors is highly variable). However, while estimating actual abundance instead of the population trend, sample counts in 15–20 sectors were biased and produced a mean error of around +16% compared to total counts.

The model selection for the effect of all the parameters on the statistical power of the sample counts allowed us to choose a single best predictive model (Table 2). The strongest effects in the model were the number of sectors surveyed and the strength of the overall assigned trend (Table 3). In particular a higher number of surveyed sectors increased the statistical power of the analysis, while a lower decline over time decreased the proportion of sample counts that correctly detected the population trend. The abundance trend variability between years had also a strong effect on the statistical power, with statistical power decreasing as the variability increases. Other parameters, such as variability between sectors and variability of detection probability, also influenced the outcome with a lower inverse effect on statistical power, increasing the number of sectors needed to be sampled. For example, with  $cv_y = 0.05$  and  $r = 0.982$ , the number of sectors required to quantify the 20-years trend passed from 12 (32% of total sectors) with a low  $cv_s$  to 22 (58% of the total) for a high  $cv_s$  and from 13 (34% of total sectors) with a low  $cv_d$  to 19 (50% of sectors) with a high  $cv_d$  (Supporting information). Population size and detection probability did not have any effect in the models. All the graphs for the effect of the parameters are provided in Supporting information.

When selecting the sectors to be sampled, choosing those with the highest ibex abundance in the first year of the monitoring resulted in a slightly higher statistical power, while a random selection in the first year only or in each year decreased the reliability of the analysis (Table 3), lowering

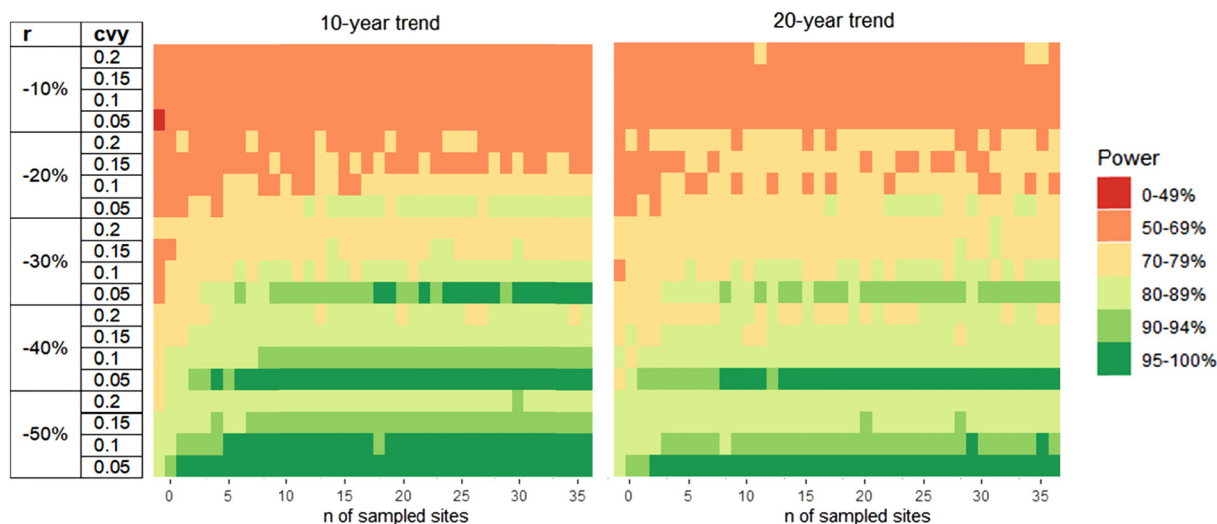


Figure 1. Statistical power of sample counts in correctly detecting the direction of the real population trend over 10 years (left) and 20 years (right).  $r$  is the total population decline over the time period and  $cv_y$  is the yearly coefficient of variation in the trend. Statistical power is averaged between all the combinations of the other parameters.

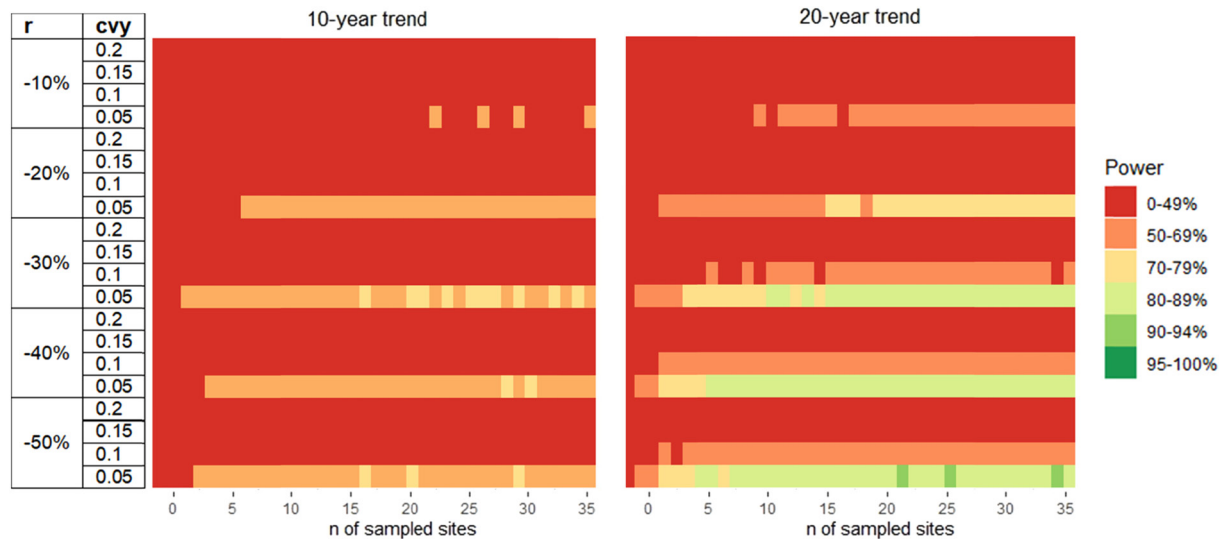


Figure 2. Statistical power of sample counts in correctly detecting the magnitude (with an yearly error lower than 2%) of the real population trend over 10 years (left) and 20 years (right).  $r$  is the total population decline over the time period and  $cv_y$  is the yearly coefficient of variation in the trend. Statistical power is averaged between all the combinations of the other parameters.

the average statistical power by 1.7 and 2.6%, respectively, for the 10-year trend and by 0.9 and 1.2% for the 20-year trend. This difference was relevant in terms of the number of sectors to be sampled to reach the 80% power threshold, as for instance, with  $cv_y=0.05$  and  $r=0.978$  the correct magnitude of a 20-year trend was detected with the 11 most abundant sectors (20% of the sectors), with 16 sectors (42% of the total) selected at random in the first year or with 20 sectors (53% of total sectors) selected at random each year (Supporting information). However, if abundance was estimated instead of the population trend, choosing the sectors with the highest ibex abundance in the first year produced an overestimation of population size, that was 41.7% higher on average than with a random sector selection.

To monitor the population trend of Alpine ibex in GPNP (yearly variability of 0.05 and sector variability of 0.05–0.10), sampling 15–20 sectors was in general sufficient (Fig. 3): the direction of the trend was detected in at least 80% of the cases for trends equal to –20% both in 10 and 20 years (Fig. 3a–b). The direction of trends of –30% or more was correctly estimated even when sampling less than five sectors, while a

trend of –10% was never detected even performing counts in all sectors. For a period of 20 years, surveying 10 sectors was sufficient to correctly detect the magnitude of a trend of –30% or more, while lower trends were not correctly quantified even sampling the entire area (Fig. 3d). However, the magnitude of a 10-year trend was impossible to detect with an error within 2% and the desired threshold of statistical power of 80% whatever the real trend was (Fig. 3c).

The proportion of opposite (i.e. in the wrong direction) and non-significant trends estimated with weak counts was low but not increased for weak trends (Fig. 4). Counting animals in half of the sectors led, in the simulations, to 2.6% of non-significant and 1.2% of opposite trends estimated when the population was declining by 30% in 10 years ( $r=0.965$ ), while with the same yearly trend over 20 years ( $r=0.966$ ), the population trend was always estimated in the right direction and in 90% of the cases with the correct magnitude. Monitoring low changes in abundance, such as a 10% decline in 10 or 20 years, led in 34.4% (in 10 years) and 36.4% (in 20 years) of the cases to estimating incorrectly the direction of the population trend.

Table 2. Model selection for the effect of simulation parameters on the statistical power of sample counts in detecting the true population trend. The best model is highlighted with bold characters.

Response	Models	df	AIC	$\Delta$ AIC
Power 10-years decreasing trend	<b><math>\sim r + n + cv_y + cv_d + cv_s + \text{selection}</math></b>	9	–83178.6	0
	$\sim r + n + cv_y + cv_d + \text{selection}$	8	–83155.7	22.9
	$\sim r + n + cv_y + cv_s + \text{selection}$	8	–82995.1	183.5
	$\sim r + n + cv_y + \text{selection}$	7	–82972.4	206.2
	$\sim r + n + cv_y + cv_d + cv_s$	7	–82105.0	1073.5
	Power 20-years decreasing trend	<b><math>\sim r + n + cv_y + cv_d + cv_s + \text{selection}</math></b>	9	–90655.7
$\sim r + n + cv_y + cv_s + \text{selection}$		8	–90624.5	31.2
$\sim r + n + cv_y + cv_d + \text{selection}$		8	–90590.7	65.0
$\sim r + n + cv_y + \text{selection}$		7	–90559.6	96.1
$\sim r + n + cv_y + cv_d + cv_s$		7	–90318.4	337.3

Table 3. Summary of the best models for the effect of simulation parameters on the statistical power. All variables were standardized.

Model	Parameter	Estimate	SE	p-value
10 years trend (decrease)	Intercept	0.793	<0.001	p < 0.001
	r	-0.113	<0.001	p < 0.001
	n	0.034	<0.001	p < 0.001
	cv <sub>y</sub>	-0.037	<0.001	p < 0.001
	cv <sub>d</sub>	-0.004	<0.001	p < 0.001
	cv <sub>s</sub>	-0.002	<0.001	p < 0.001
	Selection random each	-0.026	<0.001	p < 0.001
	Selection random first	-0.016	<0.001	p < 0.001
20 years trend (decrease)	Intercept	0.786	<0.001	p < 0.001
	r	-0.094	<0.001	p < 0.001
	n	0.018	<0.001	p < 0.001
	cv <sub>y</sub>	-0.028	<0.001	p < 0.001
	cv <sub>d</sub>	-0.002	<0.001	p < 0.001
	cv <sub>s</sub>	-0.002	<0.001	p < 0.001
	Selection random each	-0.012	<0.001	p < 0.001
	Selection random first	-0.009	<0.001	p < 0.001

Under the case of a stable population ( $r=1$ ), both sample counts and complete counts detected false trends, with 20% (with a yearly trend variability of 0.05) to 70% (with a variability of 0.2) of false trends (decreases or increases) detected on a 10-years interval, and 10–60% of false trends on the 20 years period. The number of sectors surveyed did not substantially change the results of the trend estimation in the case of a stable trend: with more than 10 sectors sampled, the results were similar to those obtained with a complete count (Fig. 5).

### Power analysis on real ibex total counts in GPNP

If the complete trend observed in the ibex count data in GPNP was significant (86.9% of the time intervals), sample counts were able to correctly detect its direction with a sufficient statistical power (Fig. 6a) using a number of sectors between 5 (for a 20-year trend) and 28 (for a 5-year trend), corresponding to 13–74% of the sectors and 5–88% of the total surface. To correctly measure the magnitude of the trend, a higher number of sectors was required (Fig. 6b). The complete trend was detected with an error lower than 2% and in at least 80% of the cases if 10 (for a 20-years trend) to 33 (for a 5-years trend) sectors were surveyed, corresponding to 26–87% of the sectors and 14–95% of the total surface. To detect a trend over 10 years, 15 sectors (39% of the sectors) were needed to correctly assess the direction of the trend and 22 sectors (58% of the total) to also detect its magnitude, while for a 20-year trend 10 sectors were sufficient to accurately quantify the trend. Sampling more sectors reduced the number of false, missed and opposing trends (Fig. 7). Indeed, counting in the full area compared to half of sectors led to false trends declining from 14 to 6%, missed trends from 10 to 3% and opposing trends from 5 to 0%.

### Discussion

Our results show that sample counts can be adequate to monitor population trends of a mountain ungulate in a large area. Sampling half of the total area allowed us to correctly identify

medium to strong population trends. In addition, in most of the cases in which sample counts were not able to estimate the population trend, also complete counts failed in detecting the direction or magnitude of the trend, as for example under low or null population trends. The retrospective power analysis confirmed our results, as the trends historically estimated with complete counts would have been inferred equally well, with a sufficient statistical power, using sample counts with only half of the sectors monitored. Given that the results obtained with sample counts are very similar to those obtained with a complete count, we suggest that sample counts (in particular: monitoring half of the target area) can be used as a viable alternative when monitoring trends, hence allowing for important, cost-effective improvements in the monitoring of wild species of conservation interest. Time and budget constraints can indeed disincentivize wildlife managers from implementing monitoring programs (McDonald-Madden et al. 2010), while potentially reducing the survey effort could lead to undertake monitoring projects that are otherwise impossible to perform.

Reducing the costs of monitoring by using sample counts, could be of critical importance to allow more conservation and management authorities to perform yearly counts. Assessing population trends in wild species is indeed essential, especially in the current scenario of environmental changes (Giorgi 2006, Gobiet et al. 2014, Rogora et al. 2018). In the case of the Alpine ibex, for example, the lack of data made it impossible to draw reliable conclusions about the population trends in some areas (Brambilla et al. 2020a) while correctly monitoring population trends is essential as the species may be sensitive to future declines (Toïgo et al. 2020) because of low recolonization rates, low genetic diversity and high inbreeding levels (Biebach and Keller 2009, Brambilla et al. 2015, 2020b) and heat-sensitivity (Aublet et al. 2008, Mason et al. 2017, Semenzato et al. 2021).

Sample counts could therefore be an important tool to initiate an assessment of population trends in areas where logistic or human resources are too scarce to survey the entire population. Moreover, sample counts can also be considered

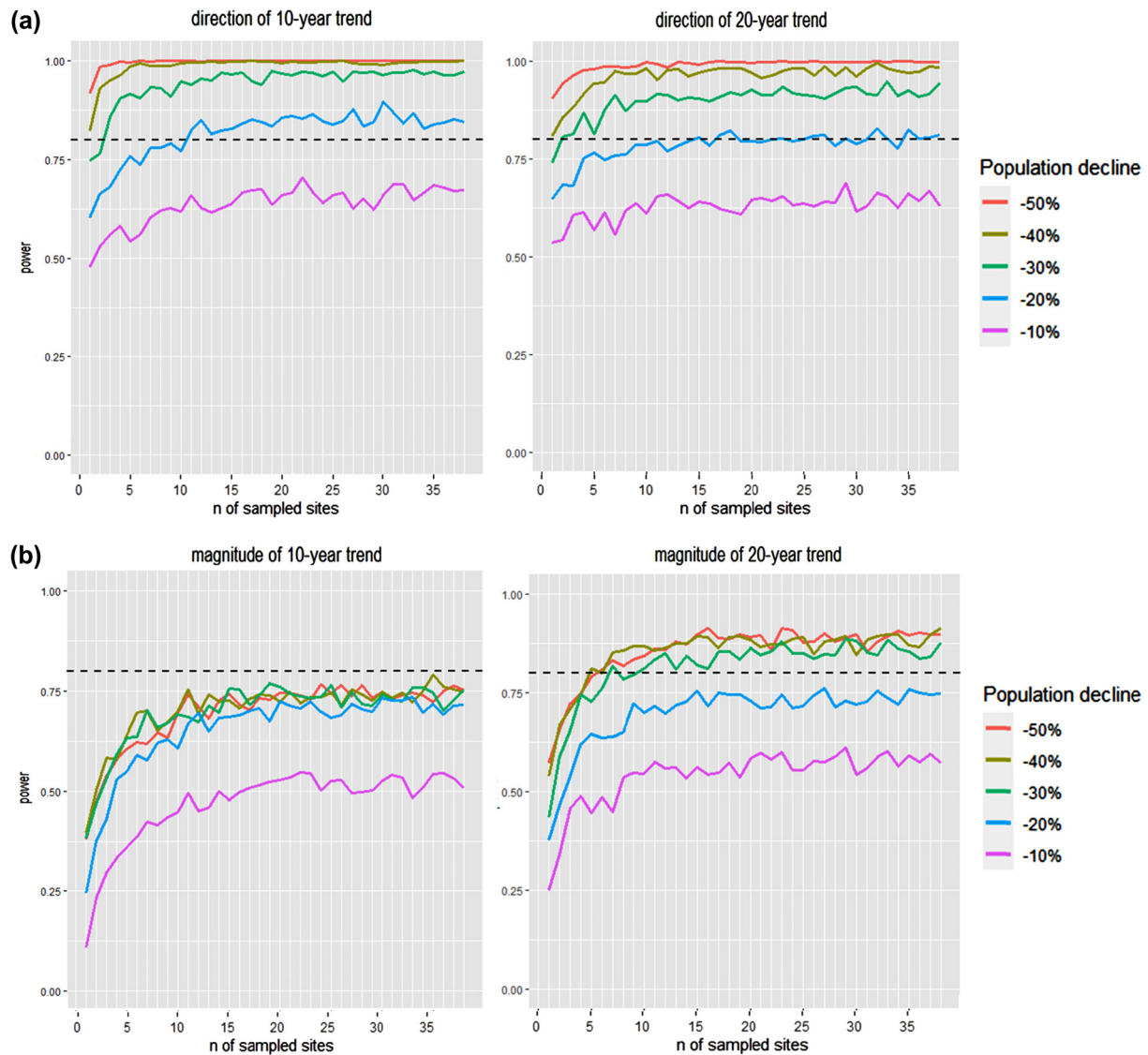


Figure 3. Statistical power for sample counts in detecting the direction (Fig. 3a) and magnitude (Fig. 3b) of the population trend for a 10 years trend (on the left) and 20 years (on the right). The hashed line represents the threshold for statistical power (0.8). Trend variability between years and sectors is the one measured for ibex in GPNP ( $cv_y=0.05$ ,  $cv_s=0.10$ ) and statistical power is averaged between all the combinations of the other parameters.

by conservationists and managers, that already perform monitoring projects, as an alternative to maintain historical series of population trends even in case of possible reduction of logistic or human resources available for monitoring.

Finally, sample counts can also be useful to perform a quick and highly cost-effective preliminary monitoring in new areas to collect information on the status of a population in the short term, as we showed that the direction of a strong trend over 10 years can be detected even with very few sectors sampled (less than 5 out of 38). For instance, the method can be useful to track strong decrease in population size linked to epidemic outbreaks, common in mountain ungulates as the Alpine ibex (Giacometti et al. 2002, Garnier et al. 2016, Pérez et al. 2021), or to identify a strong response after management actions such as reintroductions (Giacometti 1991, Stüwe and Nievergelt 1991, Brambilla et al. 2020a).

When using sample counts, the monitoring costs can be further reduced by performing counts only in the sectors with the highest abundance (likely easier to sample). However, as the method of sector selection had a weak effect on statistical power of trend estimations, also selecting sectors based on other criteria (as accessibility) could lead to a reliable analysis. This result is in contrast with Fournier et al. (2019) who claimed that counting in the sites with the highest abundance leads to detections of false trends (Fournier et al. 2019). However, as also pointed out by Fournier and colleagues, not every real population exhibits this bias. The advantage of selecting the most abundant sectors however disappears if abundance is estimated instead of the population trend, with a considerable overestimation compared to a random sector selection.

We also showed that neither sample counts nor complete counts could reliably monitor the magnitude of short-term

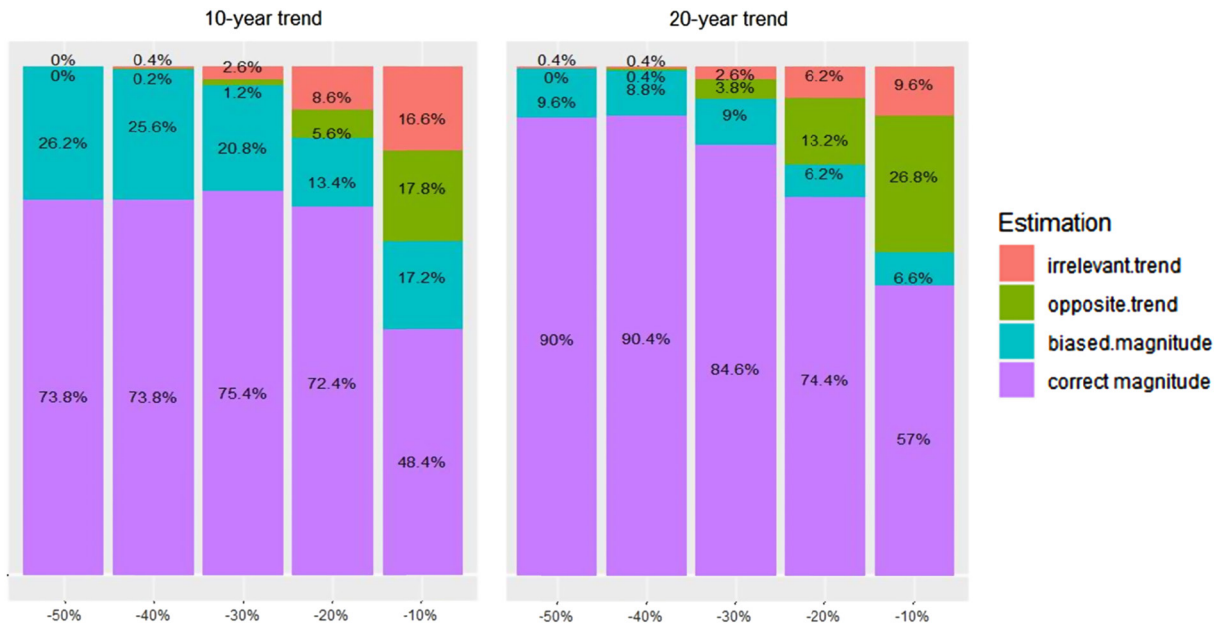


Figure 4. Proportion of correct and erroneous trends detected surveying half of the sectors in 10 years (left) and 20 years (right) in the simulated populations of Alpine ibex in GPNP ( $cv_y = 0.05$  and  $cv_s = 0.1$ ). The correct magnitude correspond to the simulations in which yearly trend is estimated with less than 2% error, the biased magnitude to all the other cases in which the direction of the trend is correctly estimated but with an error higher than 2% yearly. Irrelevant trend correspond to the cases in which sample counts erroneously estimate a trend that is non-significant ( $p > 0.05$ ) and irrelevant trend are the simulations in which a trend in the opposite direction (increase of the population) is detected. The first bar on the left of each graph is a decrease of 50% over the time period, the rightmost a decrease of 10%.

trends and that for such an analysis at least 15 or 20 years of count data are needed. This result is consistent with several other studies pointing out that more than 10 years are required to draw reliable conclusions on population trends (Gerber et al. 1999, Hatch 2003, White 2019). In the case of stable trends, complete counts (as well as sample counts) were likely to detect false declines or increases in the population also over 20 years of monitoring. Long-term wildlife monitoring projects are indeed of critical importance for

conservation (Nichols and Williams 2006, Magurran et al. 2010, Giron-Nava et al. 2017), but series of yearly counts are lacking for most mountain ungulates (Singh and Milner-Gulland 2011, Brambilla et al. 2020a, Nuttall et al. 2022). Therefore, we recommend that stakeholders plan long-term monitoring projects to correctly evaluate population trends at a local and global scale. Sample counts can constitute a viable method to reduce the required census effort for such projects.

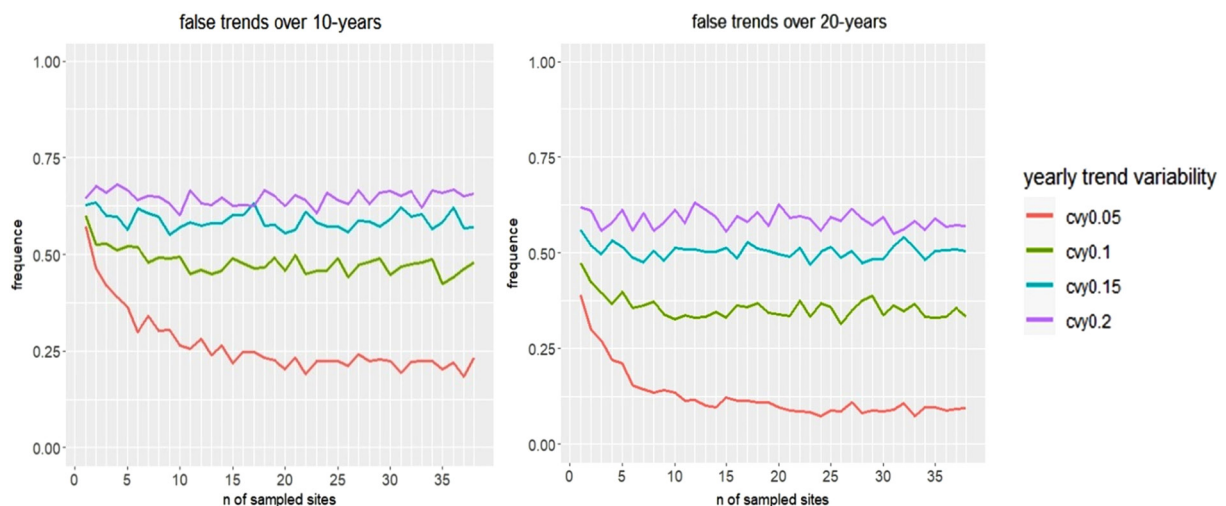


Figure 5. Proportion of false trends detected by sample counts over 10 years (left) or 20 years (right) on a stable population, depending on the yearly trend variability. False trends are classified as those in which sample counts estimated an yearly trend higher than  $\pm 2\%$  compared to the real trend.

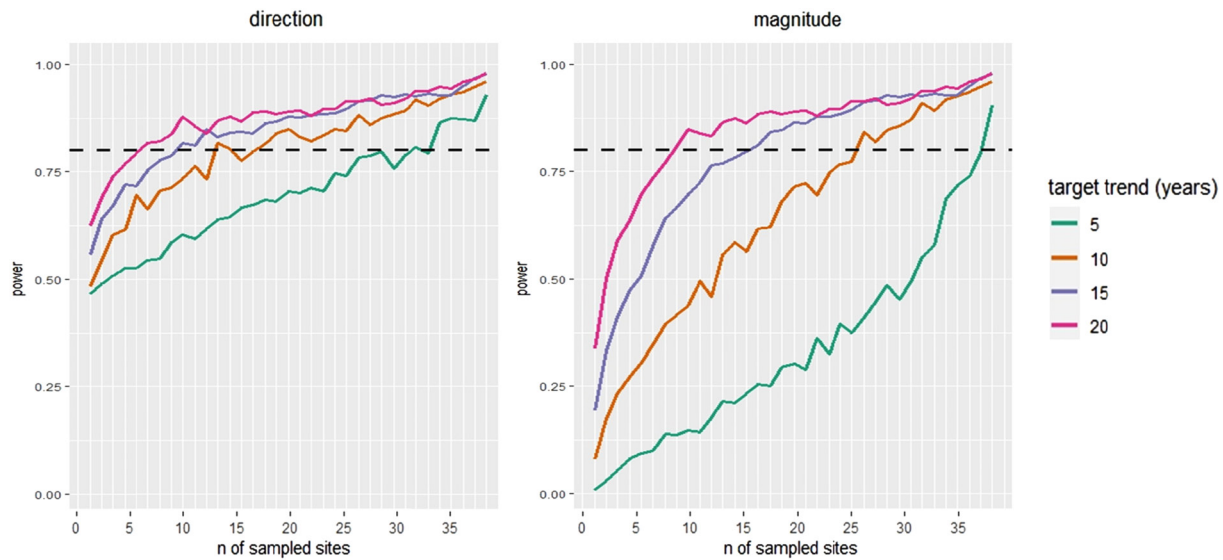


Figure 6. Statistical power for sample trends in detecting the direction (left) and the magnitude (right) of a significant complete trend in total count data in GPNP over the last 65 years.

However, the use of reduced sampling is not always advisable and, if there are sufficient resources, sampling the entire area may still be preferable than using sample counts. Complete counts would allow for less biased abundance estimates, as shown in our results and as pointed out by Sutherland (2006). An accurate estimate of population size is important for instance to measure carrying capacity (Holzgang 1997, Terry Bowyer et al. 2014) or for management purposes such as monitoring the success of reintroductions (Peracino and Bassano 1990) and hunting (Carvalho et al. 2018). In

addition, sample counts should be avoided if overlooking or erroneously detecting trends could have a massive impact for conservation, such as for assessments of extinction risks in the IUCN red list framework (Rueda-Cediel et al. 2018). In such cases, complete counts are always advisable as sampling all sectors reduced the occurrence of errors in trend detection that, even if at a low frequency, were present with sample counts. Therefore, conservation authorities must weigh up the costs and benefits of using sample counts, using them to reliably detect population trends at a lower cost or performing complete counts to measure abundance with higher financial effort but also reduced errors in the estimation of trends and abundance.

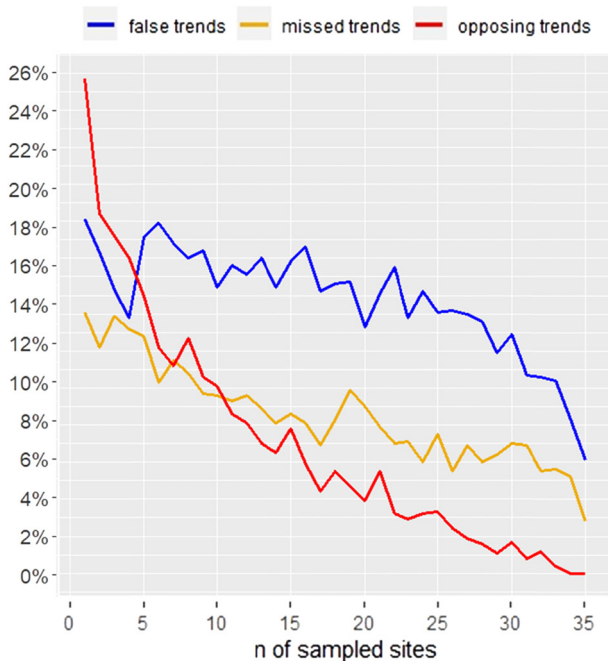


Figure 7. Percentage of false, missed and opposing trends in the retrospective power analysis given the number of sectors sampled.

While our analysis was conducted using the Alpine ibex as a study system, our results could be potentially extended to other species of mountain ungulates. Indeed, our results show that the strongest constraint for accurate trend estimations is the variability between years, for which Alpine ibex in GPNP showed a coefficient of variation around 0.05 in the last 65 years. Keith et al. (2015) found that, among nine species of terrestrial mammals for which population trend was estimated counting the total number of individuals in a specified area, the mean variability between years was 0.052, and *Saiga tatarica*, the only ungulate species in the study, showed a yearly variation of 0.058. Therefore, sample counts would likely have been efficient for estimating the trend also in those species and other with similar trend variability over time. Under an high yearly trend variability, estimating the population dynamics could be subject to severe errors even with complete counts and especially for weak trends, as also pointed out by other studies (Rhodes and Jonzén 2011, Wilson et al. 2011, Rueda-Cediel et al. 2015). Furthermore, in our simulations sampling half of the sectors allowed to achieve a sufficient statistical power even with high variability among sectors ( $cv_s$ ) or regarding detection probability ( $cv_d$ ). A

large number of species is likely to exhibit a trend variability between sectors in the range we used in our simulations (i.e. 0.05–0.20): Weiser et al. (2019) reported a sector-specific variation between 0.05 and 0.1 in many species of different taxa. Additionally, the wide range of  $cv_d$  we used in the simulations (0.1–0.5) suggests that our results can be expanded to many study areas with high spatial variation in detectability.

However, our results are not guaranteed to apply to all other mountain ungulate species (Caprinae group) and populations. Indeed, for many Caprinae population parameters such as trend variability are unknown (Shackleton 1997), and some of those species also inhabit areas with different environmental conditions compared to our study area (Khattak et al. 2022). In particular, block counts (and thus also sample counts, as were tested here) could not be used in areas with reduced visibility, such as those with high vegetation cover, in which performing visual counts is challenging.

In our results, detectability had a significant effect on the statistical power of sample counts, but only in terms of its variability rather than its absolute value. Such results contrast with other studies which showed that low detectability critically influenced the ability to detect a trend (Newson et al. 2013, Ficetola et al. 2018, Sanz-Pérez et al. 2020). However, some of these studies included the possibility of sites with very few animals and a detectability ( $p$ ) close to zero (e.g. abundance of 7.5 per site and  $p=0.05$  in Ficetola et al. 2018), analyzing the situation in which no animals were detected in most of the sites. This condition could have been the primary cause of biased trend estimates in such studies. In contrast, in the Alpine ibex population of our study, individuals were much more abundant per sector. Other studies mentioned above showed that detectability was also variable across sites (Sanz-Pérez et al. 2020), and this variability could have been the cause of biased trend estimates rather than the value of detectability itself. The variability of detection probability, indeed, is still an important factor that can influence the reliability of sample counts, as under a highly variable detectability more sectors have to be sampled. To reduce the variability in detection probability between sectors and years, wildlife managers could plan counts that are standardized over time, as it occurs in GPNP where the same routes and count periods have been consistently used since 1956. Moreover, the use of multiple counts in the same year, already experimented in the Alpine ibex (Bison et al. 2019), could be a suitable method to minimize the environmental or biological causes of variation of detection probability.

Finally we showed that, under weak and null trends or high trend variability, even complete counts are not able to correctly monitor a wild population. Indeed, block counts (either if performed in a sample of the sectors or in the complete area) are widely believed to underestimate population size (Loison et al. 2006, Corlatti et al. 2015). In such cases, other estimation methods could be therefore more advisable, such as Capture-Mark-Resight (Schwarz and Seber 1999), Distance Sampling (Buckland et al. 2001), Double Observer (Suryawanshi et al. 2012), indicators of ecological changes (Morellet et al. 2007) or also simple repeated counts in the

same year (Bison et al. 2019). These techniques require a higher field or data analysis effort and should therefore be preferred when the precision of the analysis is fundamental or when trend parameters (e.g. under weak or null trends) prevent the use of block counts, while sample counts could be selected if reducing the survey effort is a primary concern.

## Management recommendations

In this study we showed that sample counts, i.e. counting the population in only a portion of the total target area, are an effective tool to draw reliable conclusions about population trends while reducing the monitoring costs.

Given our results, we suggest wildlife managers and conservationists to consider the use of sample counts in their monitoring projects, under some specific recommendations.

Sample counts could potentially be used in the Alpine ibex, as tested in this study, but also in other species of ungulates and terrestrial mammals living in open environments and that can be easily recorded by visual counts. In particular, sample counts could be used to: 1) reliably monitor trends of wild animal populations with a lower effort; 2) continue long-term monitoring projects if economic resources decrease; 3) detect strong changes in the populations, also in the short-term, with a minimum cost. However, sample counts are not indicated if the target is to estimate abundance or if a very high accuracy in quantifying the trend is required.

To correctly plan a monitoring based on sample counts, managers should be aware that the reliability of the method depends on several population parameters, including trend variability between years and sectors. However, the following generalization can be made to effectively apply sample counts: 1) monitoring half of the total area is sufficient to quantify medium-strong trends, but the proportion of sectors required could also be lower if the population exhibit similar dynamics and detectability over the years and between the sectors. Information on whether the population is strongly declining or increasing could be obtained even with about 15% of the sectors only; 2) the selection of the sectors to sample can follow different criteria (e.g. randomly, those with higher abundance or easier to reach etc.) with no effect on the reliability of the estimates; 3) counts in the selected sectors can be performed with block counts or other census methods (such as Mark-Resight, Double Observer etc.); 4) long-term monitoring is strongly advisable to reliably estimate trends, as only long-term surveys allow to detect also weak trends and to reduce the negative effects of trend variability. For the Alpine ibex this means at least 15–20 years of sampling, but this may differ between species. Strong trends can be detected, but not correctly quantified, also over a shorter period (10 years for Alpine ibex).

Finally, before using sample counts, stakeholders and conservationists should consider to preliminary evaluate, in their given study region and population, the magnitude of the various parameters that proved to influence the reliability of the method (Results and Discussion for a more detailed explanation). In particular, counting animals in all the sectors during

a first year would allow to estimate the variability (coefficient of variation, Supporting information) of the trend between different sites/sectors and the variability of detectability, while repeating such counts over multiple years would provide an assessment of annual fluctuations. Such information could then legitimize the use of sample counts if the parameters prove to be within the intervals analyzed in this study, or could allow to understand the direction of potential biases.

*Acknowledgements* – We are grateful to all the Park wardens of the Gran Paradiso National Park who have consistently collected census data over the last 65 years and provided fundamental support to all research activities on Alpine ibex in the Park.

*Funding* – MP was financially supported by a Sustainable Futures studentship by the Univ. of Chester sponsored with a matched funding by the Gran Paradiso National Park (grant reference: BIO20/10).

### Author contributions

**Matteo Panaccio:** Conceptualization (equal); Formal analysis (lead); Methodology (equal); Writing – original draft (lead). **Alice Brambilla:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (equal). **Bruno Bassano:** Conceptualization (supporting); Supervision (supporting); Writing – review and editing (supporting). **Tessa Smith:** Supervision (supporting); Writing – review and editing (supporting). **Achaz von Hardenberg:** Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Supervision (lead); Writing – review and editing (equal).

### Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1002/wlb3.01162>.

### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cfxpnvxj> (Panaccio et al. 2023).

### Supporting information

The Supporting information associated with this article is available with the online version.

### References

- Akaike, H. 1974. A new look at the statistical model identification. – IEEE Trans. Autom. Control 19: 716–723.
- Aublet, J. F., Festa-Bianchet, M., Bergero, D. and Bassano, B. 2008. Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. – Oecologia 159: 237–247.
- Biebach, I. and Keller, L. F. 2009. A strong genetic footprint of the re-introduction history of Alpine ibex (*Capra ibex* ibex). – Mol. Ecol. 18: 5046–5058.
- Biebach, I. and Keller, L. F. 2010. Inbreeding in reintroduced populations: the effects of early reintroduction history and contemporary processes. – Conserv. Genet. 11: 527–538.
- Bison, M., Bonnot, N., Garel, M., Toigo, C. and Pellerin, M. 2019. Prestations de service pour la mise en place d'indicateurs de changement écologique pour la suivi du bouquetin des Alpes (*Capra ibex*) à l'échelle de l'arc alpin. – ALCOTRA LEMED IBEX Report.
- Brambilla, A., Biebach, I., Bassano, B., Bogliani, G. and von Hardenberg, A. 2015. Direct and indirect causal effects of heterozygosity on fitness-related traits in Alpine ibex. – Proc. R. Soc. B. 282: 20141873.
- Brambilla, A., Bassano, B., Biebach, I., Bollmann, K., Keller, L., Toigo, C. and von Hardenberg, A. 2020a. Alpine ibex Linnaeus, 1758. – In: Hackländer, K. and Zachos, F. E. (eds), Handbook of the mammals of Europe. Springer, pp. 1–27.
- Brambilla, A., von Hardenberg, A., Nelli, L. and Bassano, B. 2020b. Distribution, status, and recent population dynamics of Alpine ibex *Capra ibex* in Europe. – Mamm. Rev. 50: 267–277.
- Brivio, F., Zurmühl, M., Grignolio, S., von Hardenberg, J., Apollonio, M. and Ciuti, S. 2019. Forecasting the response to global warming in a heat-sensitive species. – Sci. Rep. 9: 3048.
- Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Oxford, T. L. 2001. Introduction to distance sampling. – Oxford Univ. Press.
- Carvalho, J., Fandos, P., Festa-Bianchet, M., Büntgen, U., Fonseca, C. and Serrano, E. 2018. Sustainable trophy hunting of Iberian ibex. – Galemys 30: 1–4.
- Caughlan, L. and Oakley, K. L. 2001. Cost considerations for long-term ecological monitoring. – Ecol. Indic. 1: 123–134.
- Cohen, J. 1992. A power primer. – Psychol. Bull. 112: 155–159.
- Corlatti, L., Fattorini, L. and Nelli, L. 2015. The use of block counts, mark-resight and distance sampling to estimate population size of a mountain-dwelling ungulate. – Popul. Ecol. 57: 409–419.
- Ficetola, G. F., Romano, A., Salvidio, S. and Sindaco, R. 2018. Optimizing monitoring schemes to detect trends in abundance over broad scales. – Anim. Conserv. 21: 221–231.
- Fournier, A. M. V., White, E. R. and Heard, S. B. 2019. Sector-selection bias and apparent population declines in long-term studies. – Conserv. Biol. 33: 1370–1379.
- Gaillard, J. M., Loison, A. and Toigo, C. 2003. Variation in life history traits and realistic population models for wildlife management: the case of ungulates. – In: Festa-Bianchet, M. and Apollonio, M. (eds), Animal behavior and wildlife conservation. Island Press, pp. 115–132.
- Garnier, A., Gaillard, J. M., Gauthier, D. and Besnard, A. 2016. What shapes fitness costs of reproduction in long-lived iteroparous species? A case study on the Alpine ibex. – Ecology 97: 205–214.
- Gerber, L. R., DeMaster, D. P. and Kareiva, P. M. 1999. Gray whales and the value of monitoring data in implementing the US Endangered Species Act. – Conserv. Biol. 13: 1215–1219.
- Gerrodette, T. 1987. A power analysis for detecting trends. – Ecology 68: 1364–1372.
- Giacometti, M. 1991. Beitrag zur Ansiedlungsdynamik und aktuellen Verbreitung des Alpensteinbockes (*Capra i. ibex* L.) im Alpenraum. – Z. Jagdwissenschaft 37: 157–173.
- Giacometti, M., Janovsky, M., Belloy, L. and Frey, J. 2002. Infectious keratoconjunctivitis of ibex, chamois and other Caprinae. – Rev. Sci. Tech. (Int. Off. Epizootics) 21: 335–345.

- Giorgi, F. 2006. Climate change hot-spots. – *Geophys. Res. Lett.* 33: 8707.
- Giron-Nava, A., James, C. C., Johnson, A. F., Dannecker, D., Kolody, B., Lee, A., Nagarkar, M., Pao, G. M., Ye, H., Johns, D. G. and Sugihara, G. 2017. Quantitative argument for long-term ecological monitoring. – *Mar. Ecol. Prog. Ser.* 572: 269–274.
- Gobiet, A., Kotlarski, S., Beniston, M., Heinrich, G., Rajczak, J. and Stoffel, M. 2014. 21st century climate change in the European Alps – a review. – *Sci. Total Environ.* 493: 1138–1151.
- Gonzalez-Voyer, A., Festa-Bianchet, M. and Smith, K. G. 2001. Efficiency of aerial surveys of mountain goats. – *Bulletin* 29: 140–144.
- Grignolio, S., Rossi, I., Bassano, B., Parrini, F. and Apollonio, M. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. – *Ethol. Ecol. Evol.* 16: 255–264.
- Hatch, S. A. 2003. Statistical power for detecting trends with applications to seabird monitoring. – *Biol. Conserv.* 111: 317–329.
- Hinkson, K. M. and Richter, S. C. 2016. Temporal trends in genetic data and effective population size support efficacy of management practices in critically endangered dusky gopher frogs (*Lithobates sevosus*). – *Ecol. Evol.* 6: 2667–2678.
- Holzgang, O. 1997. Herbivore-carrying capacity of grasslands in the Swiss National Park. – PhD thesis, ETH, Switzerland.
- IUCN 2022. IUCN red list categories and criteria, ver. 15.1. – <https://www.iucnredlist.org>, accessed 2 Feb 2023.
- Jacobson, A. R., Provenzale, A., von Hardenberg, A., Bassano, B. and Festa-Bianchet, M. 2004. Climate forcing and density dependence in a mountain ungulate population. – *Ecology* 85: 1598–1610.
- Jonas, T., Geiger, F. and Jenny, H. 2008. Mortality pattern of the Alpine chamois: the influence of snow–meteorological factors. – *Ann. Glaciol.* 49: 56–62.
- Keith, D., Akçakaya, H. R., Butchart, S. H. M., Collen, B., Dulvy, N. K., Holmes, E. E., Hutchings, J. A., Keinath, D., Schwartz, M. K., Shelton, A. O. and Waples, R. S. 2015. Temporal correlations in population trends: conservation implications from time-series analysis of diverse animal taxa. – *Biol. Conserv.* 192: 247–257.
- Kellner, K. F. and Swihart, R. K. 2014. Accounting for imperfect detection in ecology: a quantitative review. – *PLoS One* 9: e111436.
- Kéry, M., Dorazio, R. M., Soldaat, L., Van Strien, A., Zuurwijk, A. and Royle, J. A. 2009. Trend estimation in populations with imperfect detection. – *J. Appl. Ecol.* 46: 1163–1172.
- Khattak, R. H., Teng, L., Ahmad, S., Bari, F., Rehman, E. U., Shah, A. A. and Liu, Z. 2022. In pursuit of new spaces for threatened mammals: assessing habitat suitability for Kashmir Markhor (*Capra falconeri cashmeriensis*) in the HinduKush range. – *Sustainability* 14: 1544.
- Lahoz-Monfort, J. J., Guillera-Aroita, G. and Wintle, B. A. 2014. Imperfect detection impacts the performance of species distribution models. – *Global Ecol. Biogeogr.* 23: 504–515.
- Largo, E., Gaillard, J. M., Festa-Bianchet, M., Toigo, C., Bassano, B., Cortot, H., Farny, G., Lequette, B., Gauthier, D. and Martinot, J. P. 2008. Can ground counts reliably monitor ibex *Capra ibex* populations? – *Wildl. Biol.* 14: 489–499.
- Lindenmayer, D. B. and Likens, G. E. 2010. The science and application of ecological monitoring. – *Biol. Conserv.* 143: 1317–1328.
- Loison, A., Appolinaire, J., Jullien, J. and Dubray, D. 2006. How reliable are total counts to detect trends in population size of chamois *Rupicapra rupicapra* and *R. pyrenaica*? – *Wildl. Biol.* 12: 77–88.
- Luymes, N. and Chow-Fraser, P. 2019. Optimizations for time and effort in long-term monitoring: a case study using a multidecadal terrestrial salamander monitoring program. – *Environ. Monit. Assess.* 191: 597.
- Magurran, A. E., Baillie, S. R., Buckland, S. T., Dick, J. M. P., Elston, D. A., Scott, E. M., Smith, R. I., Somerfield, P. J. and Watt, A. D. 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. – *Trends Ecol. Evol.* 25: 574–582.
- Mason, T. H. E., Brivio, F., Stephens, P. A., Apollonio, M. and Grignolio, S. 2017. The behavioral trade-off between thermoregulation and foraging in a heat-sensitive species. – *Behav. Ecol.* 28: 908–918.
- McCain, C., Szweczyk, T. and Bracy Knight, K. 2016. Population variability complicates the accurate detection of climate change responses. – *Global Change Biol.* 22: 2081–2093.
- McDonald-Madden, E., Baxter, P. W. J., Fuller, R. A., Martin, T. G., Game, E. T., Montambault, J. and Possingham, H. P. 2010. Monitoring does not always count. – *Trends Ecol. Evol.* 25: 547–550.
- Mignatti, A., Casagrandi, R., Provenzale, A., von Hardenberg, A. and Gatto, M. 2012. Sex- and age-structured models for Alpine ibex *Capra ibex* population dynamics. – *Wildl. Biol.* 18: 318–332.
- Morellet, N., Gaillard, J. M., Hewison, A. J. M., Ballon, P., Boscardin, Y., Duncan, P., Klein, F. and Maillard, D. 2007. Indicators of ecological change: new tools for managing populations of large herbivores. – *J. Appl. Ecol.* 44: 634–643.
- Newson, S. E., Massimino, D., Johnston, A., Baillie, S. R. and Pearce-Higgins, J. W. 2013. Should we account for detectability in population trends? – *Bird Study* 60: 384–390.
- Nichols, J. D. and Williams, B. K. 2006. Monitoring for conservation. – *Trends Ecol. Evol.* 21: 668–673.
- Nuttall, M. N., Griffin, O., Fewster, R. M., McGowan, P. J. K., Abernethy, K., O’Kelly, H., Nut, M., Sot, V. and Bunnefeld, N. 2022. Long-term monitoring of wildlife populations for protected area management in southeast Asia. – *Conserv. Sci. Pract.* 4: e614.
- O’Hara, R. B. and Kotze, D. J. 2010. Do not log-transform count data. – *Methods Ecol. Evol.* 1: 118–122.
- Palmer, M. W. 1993. Potential biases in sector and species selection for ecological monitoring. – *Environ. Monit. Assess.* 26: 277–282.
- Panaccio, M., Brambilla, A., Bassano, B., Smith, T. and von Hardenberg, A. 2023. Data from: Monitoring wildlife population trends with sample counts: a case study on the Alpine ibex (*Capra ibex*). – Dryad Digital Repository, <https://doi.org/10.5061/dryad.cfxpvnxcj>.
- Parrini, F., Grignolio, S., Luccarini, S., Bassano, B. and Apollonio, M. 2003. Spatial behaviour of adult male Alpine ibex *Capra ibex* in the Gran Paradiso National Park, Italy. – *Acta Theriol.* 48: 411–423.
- Peracino, V. and Bassano, B. 1990. Metodologie di cattura di ungulati nel Parco Nazionale del Gran Paradiso. – *Praxis Vet.* 11: 25–26.
- Pérez, J. M., Granados, J. E., Espinosa, J., Ráez-Bravo, A., López-Olvera, J. R., Rossi, L., Meneguz, P. G., Angelone, S., Fandos, P. and Soriguer, R. C. 2021. Biology and management of sar-

- coptic mange in wild Caprinae populations. – *Mamm. Rev.* 51: 82–94.
- Reynolds, J. H., Thompson, W. L. and Russell, B. 2011. Planning for success: identifying effective and efficient survey designs for monitoring. – *Biol. Conserv.* 144: 1278–1284.
- Rhodes, J. R. and Jonzén, N. 2011. Monitoring temporal trends in spatially structured populations: how should sampling effort be allocated between space and time? – *Ecography* 34: 1040–1048.
- Rice, C. G., Jenkins, K. J. and Chang, W. 2009. A sightability model for mountain goats. – *J. Wildl. Manage.* 73: 468–478.
- Rogora, M. et al. 2018. Assessment of climate change effects on mountain ecosystems through a cross-sector analysis in the Alps and Apennines. – *Sci. Total Environ.* 624: 1429–1442.
- Rueda-Cediel, P., Anderson, K. E., Regan, T. J., Franklin, J. and Regan, H. M. 2015. Combined influences of model choice, data quality, and data quantity when estimating population trends. – *PLoS One* 10: e0132255.
- Rueda-Cediel, P., Anderson, K. E., Regan, T. J. and Regan, H. M. 2018. Effects of uncertainty and variability on population declines and IUCN red list classifications. – *Conserv. Biol.* 32: 916–925.
- Sanz-Pérez, A., Sollmann, R., Sardà-Palomera, F., Bota, G. and Giralt, D. 2020. The role of detectability on bird population trend estimates in an open farmland landscape. – *Biodivers. Conserv.* 29: 1747–1765.
- Saunders, S. P., Cuthbert, F. J. and Zipkin, E. F. 2018. Evaluating population viability and efficacy of conservation management using integrated population models. – *J. Appl. Ecol.* 55: 1380–1392.
- Schwarz, C. J. and Seber, G. A. F. 1999. Estimating animal abundance: review III. – *Stat. Sci.* 14: 427–456.
- Semenzato, P., Cagnacci, F., Ossi, F., Eccel, E., Morellet, N., Hewison, A. J. M., Sturaro, E. and Ramanzin, M. 2021. Behavioural heat-stress compensation in a cold-adapted ungulate: forage-mediated responses to warming Alpine summers. – *Ecol. Lett.* 24: 1556–1568.
- Sewell, D., Guillera-Aroita, G., Griffiths, R. A. and Beebee, T. J. C. 2012. When is a species declining? Optimizing survey effort to detect population changes in reptiles. – *PLoS One* 7: e43387.
- Shackleton, D. M. 1997. Wild sheep and goats and their relatives: status survey and conservation action plan. – IUCN/SSC Caprinae Specialist Group, IUCN.
- Singh, N. J. and Milner-Gulland, E. J. 2011. Monitoring ungulates in central Asia: current constraints and future potential. – *Oryx* 45: 38–49.
- Steidl, R. J. and Thomas, L. 2001. Power analysis and experimental design. – *Des. Anal. Ecol. Exp.* 2: 415.
- Stoddard, J. L., Driscoll, C. T., Kahl, J. S. and Kellogg, J. H. 1998. Can sector-specific trends be extrapolated to a region? An acidification example for the northeast. – *Ecol. Appl.* 8: 288–299.
- Stüwe, M. and Nievergelt, B. 1991. Recovery of alpine ibex from near extinction: the result of effective protection, captive breeding, and reintroductions. – *Appl. Anim. Behav. Sci.* 29: 379–387.
- Suryawanshi, K. R., Bhatnagar, Y. V. and Mishra, C. 2012. Standardizing the double-observer survey method for estimating mountain ungulate prey of the endangered snow leopard. – *Oecologia* 169: 581–590.
- Sutherland, W. J. 2006. *Ecological census techniques: a handbook*. – Cambridge Univ. Press.
- Taylor, B. L. and Gerrodette, T. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. – *Conserv. Biol.* 7: 489–500.
- Terry Bowyer, R., Bleich, V. C., Stewart, K. M., Whiting, J. C. and Monteith, K. L. 2014. Density dependence in ungulates: a review of causes, and concepts with some clarifications. – *Calif. Fish Game* 100: 550–572.
- Thomas, L. 1997. Retrospective power analysis. – *Conserv. Biol.* 11: 276–280.
- Toïgo, C., Brambilla, A., Grignolio, S. and Pedrotti, L. 2020. *Capra ibex*. – The IUCN red List of threatened species e. T42397A161916377.
- Urquhart, N. S. 2012. The role of monitoring design in detecting trend in long-term ecological monitoring studies. – In: Gitzen, R. A., Millsbaugh J. J., Cooper A. B. and Licht, D. S.(eds), *Design and analysis of long-term ecological monitoring studies*. Cambridge Univ. Press, pp. 151–173.
- Urquhart, N. S., Paulsen, S. G. and Larsen, D. P. 1998. Monitoring for policy-relevant regional trends over time. – *Ecol. Appl.* 8: 246–257.
- Vallecillo, D., Gauthier-Clerc, M., Guillemain, M., Vittecoq, M., Vandewalle, P., Roche, B. and Champagnon, J. 2021. Reliability of animal counts and implications for the interpretation of trends. – *Ecol. Evol.* 11: 2249–2260.
- Vors, L. S. and Boyce, M. S. 2009. Global declines of caribou and reindeer. – *Global Change Biol.* 15: 2626–2633.
- Wagner, T., McLaughlin, P., Smalling, K., Breitmeyer, S., Gordon, S. and Noe, G. B. 2022. The statistical power to detect regional temporal trends in riverine contaminants in the Chesapeake Bay Watershed, USA. – *Sci. Total Environ.* 812: 152435.
- Wauchope, H. S., Amano, T., Sutherland, W. J. and Johnston, A. 2019. When can we trust population trends? A method for quantifying the effects of sampling interval and duration. – *Methods Ecol. Evol.* 10: 2067–2078.
- Weiser, E. L., Diffendorfer, J. E., López-Hoffman, L., Semmens, D. and Thogmartin, W. E. 2019. Consequences of ignoring spatial variation in population trend when conducting a power analysis. – *Ecography* 42: 836–844.
- White, E. R. 2019. Minimum time required to detect population trends: the need for long-term monitoring programs. – *BioScience* 69: 40–46.
- Wilson, H. B., Kendall, B. E. and Possingham, H. P. 2011. Variability in population abundance and the classification of extinction risk. – *Conserv. Biol.* 25: 747–757.
- Wood, C. M., Popescu, V. D., Klinck, H., Keane, J. J., Gutiérrez, R. J., Sawyer, S. C. and Peery, M. Z. 2019. Detecting small changes in populations at landscape scales: a bioacoustic sector-occupancy framework. – *Ecol. Indic.* 98: 492–507.
- Yoccoz, N. G., Nichols, J. D. and Boulinier, T. 2001. Monitoring of biological diversity in space and time. – *Trends Ecol. Evol.* 16: 446–453.