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# Chick survival and hunting are important drivers for the dynamics of two Alpine black grouse *Lyrurus tetrix* populations

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Alpine black grouse populations are generally declining, but the underlying demographic drivers are largely unknown. We studied the dynamics of two adjacent black grouse populations over a 20 years period in the Italian Alps that differ in hunting pressure to identify the main demographic process affecting these populations and to study the impact of hunting on males. We collected radio-tracking data and conducted population surveys in spring to count displaying cocks and in late summer to determine the breeding success by means of pointing dogs. These different data sets were jointly analysed using a seasonal integrated population model to estimate population sizes and various demographic rates. The two populations fluctuated in size and the number of males from one population increased after hunting intensity was reduced. The main demographic rates did not differ between the populations. Adult survival was relatively low and productivity was high, so the life history shows the feature of a fast turnover species. In both populations, the variability of survival from hatching to the age of five weeks (chick survival) contributed more to the variation of the population growth rates than the variability of survival in later life-history stages, and the former was positively affected by ambient temperatures in July, favouring chick survival. The adult sex ratio of the population where males hunting occurred was shifted towards females, but it evened over time with the reduction of hunting pressure. The adult sex ratio in the population without hunting and the chick sex ratios in both populations were even, suggesting that hunting acted as a mostly additive source of mortality.

Keywords: breeding success, effect of hunting, integrated population model, *Lyrurus tetrix*, sex ratio, stage-structured population size, survival

Black grouse *Lyrurus tetrix* populations in western and central Europe have been declining during the 20th century and particularly since the 1970s (Bergmann and Klaus 1994, Storch 2000). In the Alps, the black grouse is a typical inhabitant of timberline ecosystems, and its decline and range contraction is largely associated with habitat loss, degradation and fragmentation as a consequence of the abandonment of traditional forms of agriculture (Laiolo et al. 2004), disturbance through various outdoor activities (Arlettaz et al. 2007, Patthey et al. 2008, Bartaletti 2011, Vanat 2020), parasite infestation (Belleau 2013) and mortality due to collision with cables of the ski facilities (Meile 1980, Miquet 1990, Buffet and Dumont-Dayot 2013). Black grouse are also hunted in most countries of the Alps (the only exception being Germany), and a study from Switzerland has shown that hunting can have an impact on black grouse population structure (Zbinden et al. 2018).

Black grouse population dynamics are typically characterized by strong temporal variation of breeding success (Moss 1986, Zbinden and Salvioni 2004) and by large-scale population synchrony in some areas (Lindström et al. 1996, Baines et al. 2007), but not in others (Cattadori et al. 2000, Canonne et al. 2021). Detailed radio-tracking studies have provided insights into different components of productivity (Marjakangas and Törmälä 1997, Caizergues and Ellison 2000, Warren and Baines 2002, Bowker et al. 2007) and in the survival of both adults and juveniles (Angelstam 1984, Willebrand 1992, Caizergues and Ellison 1997, Baines et al. 2007, Bowker et al. 2007, Pekkola et al. 2014). The interplay between demography and resulting population dynamics has, however, only rarely been investigated. In these studies, the variation of productivity has been identified to be the principal process inducing variation in population size (Baines et al. 2007, Jahren et al. 2016).

In Italy, the black grouse is classified as endangered on the national Red List (Gustin et al. 2019). Moreover, it is included in Appendix I of the Birds Directive

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(2009/147/EC) and thus plays an important role in conservation policy, and also in Appendix III of the Bern Convention, as a species whose exploitation shall be regulated in order to keep its populations out of danger. The black grouse is an important game species in the Italian Alps, being hunted in fall by means of pointing dogs. While in the past no limits on the hunting bag were set, since the middle of the 1990s, hunting is allowed only on the basis of the results of counts carried out in spring and in summer, which allows setting quotas.

Here, we study the dynamics of two adjacent populations of black grouse in the Italian Alps over a period of 20 years that differ from each other by hunting management. We monitored black grouse populations both in spring by counting displaying males and in late summer by means of pointing dogs in order to determine the breeding success. The former survey has the disadvantage that it includes the males only, while the latter method typically does not include all individuals due to imperfect detection and incomplete coverage. An advantage of the summer counts is that adults and chicks can be counted and thus breeding success and its components can be assessed. We also captured, radio-collared and tracked individuals from these two populations. These different data sets are informative about relevant demographic rates and about population sizes. We developed an integrated population model (Besbeas et al. 2002, Schaub and Kéry 2021) with a seasonal resolution to jointly analyse these different data sets. We estimate age- and sex-specific seasonal survival probabilities, different components of productivity and age- and sex-structured population sizes.

The goals of the study are three-fold. First, we aim to provide estimates of demographic rates and of mortality causes of the poorly studied Alpine black grouse. Second, we study the potential impact of a change in a demographic rate on the population growth rate and identify the main demographic drivers of the two populations. Following findings from other studies, we expect that black grouse is particularly sensitive to changes in breeding success, and because breeding success is supposed to be strongly variable between years, it should also be a main driver for the two populations. Third, we aim to assess the impact of hunting on population dynamics. The two study populations offer similar habitat for black grouse but differ in hunting management; hunting was performed in one population with decreasing intensity over time while in the other population hunting was banned during the complete study period. Hunting was conducted in fall by means of pointing dogs and was restricted to males. If hunting affects black grouse populations, we expect 1) a female-biased sex ratio in the hunted population, 2) a decline of the sex bias over time in the hunted population due to decreasing hunting intensity and 3) lower male survival in the hunted than in the non-hunted population.

## Material and methods

### Study areas

The study was carried out in the western Italian Alps (region Piemont) between 1997 and 2016. We worked in two areas, the Alpe Devero (46°19′N, 8°16′E, size: 1620 ha) and the Alpe Veglia (46°16′N, 8°9′E, size: 830 ha), which are about 5 km apart from each other and divided by high mountains that largely isolate the two black grouse populations. Both of them belong to areas of special conservation and protection (SAC/SPA IT11140016 Alpi Veglia and Devero – Monte Giove) and mostly lie within the Veglia-Devero Natural Park (IUCN category 5). Both study areas are characterized by gentle slopes with a prevalent exposure to north–west, dominated by scattered subalpine larch *Larix decidua* forests in a belt between 1700 and 2200 m a.s.l. with abundant shrubby vegetation of different species (*Rhododendron ferrugineum*, *Vaccinium myrtillus*, *V. vitis-idea*, *V. uliginosum*, *Juniperus communis*, *Calluna vulgaris*, *Arctostaphylos uva-ursi*, *Empetrum nigrum*). Interspersed pastures are dominated by the grasses *Nardus stricta* and *Calamagrostis* spp. Potential black grouse predators include golden eagle *Aquila crysaetos*, goshawk *Accipiter gentilis*, eagle owl *Bubo bubo*, raven *Corvus corax*, red fox *Vulpes vulpes*, badger *Meles meles*, stone marten *Martes foina,* pine marten *M. martes* and stoat *Mustela erminea*.

Black grouse hunting was allowed in a part of the Alpe Devero study site (on 600 ha, corresponding to about 40% of the total area) until 2011. Hunting occurred in fall, was restricted to males, and from 1997 to 2011, a total of 147 males were shot (9.8 per year on average). From 2012 onwards, hunting was banned in some years, and in others strong bag limits were applied. An average of 1.8 cocks per year was hunted in this period, hence hunting pressure declined over time at the Alpe Devero. At the Alpe Veglia, hunting was completely banned since 1973.

While electric lines are present in both areas, there is, in addition, a small ski resort with a chair lift and two ski lifts at the Alpe Devero.

### Data sampling

Three different data sets have been collected in both study areas. First, displaying cocks were counted every spring (1997–2016; average date 15 May) on the complete study areas (comprising cocks on leks as well as solitary displaying cocks). Displaying cocks typically use open areas above the timberline, often covered by snow in spring and are therefore visible and audible from long distances. We assume there is no systematic bias due to imperfect detection or incomplete coverage, but there may be some random counting errors.

Second, the populations were surveyed every year in late summer (1997–2016; average date 22 August) by means of pointing dogs. At that time of the year, chicks are at least five weeks old, able to fly, but still together with their mothers. Flushed individuals were sexed, aged (chick or adult) and counted. It was not possible to cover the entire study area, but there was a focus on the most suitable areas to work with the pointing dogs (i.e. avoidance of too rough terrain). The areas covered by the summer surveys were about 610 ha at the Alpe Devero and 460 ha at the Alpe Veglia. Therefore, it is likely that not all individuals have been counted, because some might have been present in areas that were not searched and some individuals might have escaped detection even if they were present in the searched area.



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Third, between 1998 and 2006, we captured and radio collared 159 black grouse using two capture methods. We used three-pocket mist-nets on leks in spring and 2 × 2 m hand-nets in August to catch grouse that were detected by pointing dogs. The birds captured in spring were aged as yearlings (about ten months old) or adults (more than 22 months old) on the basis of primary feather pigmentation (Helminen 1963). Birds captured in summer were aged as juveniles (about five weeks old) and adults (more than 13 months old). A neck-lace tag equipped with an activity sensor (RI-2DM Holohil Systems Ltd., Ontario, Canada) was fitted on all captured birds. For juveniles, the tag weighed 10 g and had an expected lifespan of 12 months. For yearlings and adults, we use a larger tag (15 grams) with an expected lifespan of 24 months. Birds that died or disappeared within 15 days after capture were excluded from the analysis reducing our sample size to 143 individuals (Supporting information).

Tagged birds were tracked from the ground with a portable receiver and a four-element hand-held Yagi antenna. In case the signal was lost, the search was done by airplane. Locations were obtained by homing-in and by triangulation, according to season and purpose. We also recorded whether the tracked individual was alive or dead. The date of eventual death was estimated as the mean of the last day the individual was alive and the day when it was found dead (Caizergues and Ellison 1997). The mortality causes of these dead individuals were determined by the examination of their remnants. All tagged individuals were located several times a week from spring to autumn. At the Alpe Veglia, the location frequency decreased during winter because of the danger of avalanches, while at the Alpe Devero, multiple locations within a week were possible also during winters. By following tagged females, we also found nests. All nests were inspected after hatching or failing to hatch to record the numbers of hatched and unhatched eggs and of dead chicks. Females with broods were located daily from hatching until the end of August. The number of chicks was counted when chicks were about five weeks old and before brood break up by means of pointing dogs.

## Statistical analyses

### *Population model*

We developed an integrated population model (IPM) to jointly analyse the different data (Besbeas et al. 2002, Schaub and Abadi 2011, Kéry and Schaub 2012, Schaub and Kéry 2021). The data from both populations were included in the same model, offering the possibility to define common parameters. Since the populations were surveyed in spring and in late summer, we have developed a seasonal model that describes the dynamics from 15 May to 31 August in year $t$ and the dynamics from 31 August in year $t$ to 15 May in year $t+1$. The core of the IPM is a demographic population model that links stage-specific population sizes with demographic rates (Schaub and Kéry 2021). In the following, we first develop the population model, then describe the likelihoods separately for the different data sets and finally the joint likelihood which forms the IPM.

The seasonal population model comprised two survey periods: the spring survey was composed of individuals that were nearly one year old ('yearlings') and of individuals that were older than one year ('adults'), and the late summer survey was composed of individuals that were just four to five weeks old ('juveniles') and of individuals that were at least one year old ('adults'). We denote the population size in spring by $S$, the population size in late summer by $A$ and we use superscript $x$ indicating the sex (with levels $m$ (male) and $f$ (female)) and a further superscript $p$ indicating the population (with levels $d$ (Devero) and $v$ (Veglia)). According to the life cycle graph of black grouse (Supporting information), the age and sex-specific population sizes for each population in spring of year $t+1$ are given by the population size in late summer of year $t$ and survival:

$$S_{y,t+1}^{x,p} \sim \text{Binomial}\left(\sqrt{\phi_{j,2,t}^{x,p}}\left(\phi_{j,3,t}^{x,p}\right)^2\left(\phi_{j,4,t}^{x,p}\right)^5\phi_{a,1,t+1}^{x,p}, A_{j,t}^{x,p}\right)$$

$$S_{a,t+1}^{x,p} \sim \text{Binomial}\left(\sqrt{\phi_{a,2,t}^{x,p}}\left(\phi_{a,3,t}^{x,p}\right)^2\left(\phi_{a,4,t}^{x,p}\right)^5\phi_{a,1,t+1}^{x,p}, A_{a,t}^{x,p}\right)$$

The monthly survival probabilities ($\phi$) have subscripts that refer to the age ($j$: juvenile; $a$: at least one year old), season (1: spring, defined as the period between 15 April and 14 June; 2: summer, 15 June to 14 September; 3: autumn, 15 September to 14 November; 4: winter, 15 November to 14 April; Supporting information) and to the calendar year ($t$). The superscripts $x$ and $p$ refer to sex and population, respectively, as explained above. The applied power functions accounted for the different durations of the seasonal periods. We used binomial distributions to explicitly include demographic stochasticity.

The sex and age-specific sizes of population $p$ in late summer of year $t$ are given by spring population size in year $t$, survival and components of productivity:

$$A_{j,t}^{*,p} \sim \text{Poisson}\left(\left(S_{y,t}^{f,p}+S_{a,t}^{f,p}\right)\phi_{a,1,t}^{f,p}\tau_t^p\xi^p\psi^p\kappa_t^p\omega_t^p\right)$$

$$A_{j,t}^{m,p} \sim \text{Binomial}\left(0.5, A_{j,t}^{*,p}\right)$$

$$A_{j,t}^{f,p} = A_{j,t}^{*,p} - A_{j,t}^{m,p}$$

$$A_{a,t}^{m,p} \sim \text{Binomial}\left(\phi_{a,1,t}^{m,p}\left(\phi_{a,2,t}^{m,p}\right)^{2.5}, S_{y,t}^{m,p}+S_{a,t}^{m,p}\right)$$

$$A_{a,t}^{f,p} \sim \text{Binomial}\left(\phi_{a,1,t}^{f,p}\left(\phi_{a,2,t}^{f,p}\right)^{2.5}, S_{y,t}^{f,p}+S_{a,t}^{f,p}\right)$$

The components of productivity are the probability that a female initiates a clutch (breeding propensity, $\tau$), the clutch size ($\xi$), the probability that a nest was successful (clutch was not predated, $\psi$), the hatching success of eggs from nests that did not fail ($\kappa$) and the survival probability of the chicks from hatching until 31 August ($\omega$; chicks are then about five weeks old). Broods found during the summer survey for which all chicks could be sexed revealed 50.9% male chicks at the Alpe Devero (n = 547 chicks from 157 broods) and 52.4% at the Alpe Veglia (n = 471 chicks from 148 broods). These sex ratios did not significantly differ from 50% (binomial tests; Alpe Devero: $p = 0.73$; Alpe Veglia: $p = 0.31$). We, therefore, assumed an even sex ratio of the chicks when they



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are five weeks old and use the binomial distribution to allocate a sex to the chicks. The Poisson and the binomial distributions were used to include demographic stochasticity.

### *Population survey data*

Next, we describe the likelihoods of the models for the different data sets. We start with the population survey data, which were modelled with a state–space model. The state-transition model is given by the above-defined seasonal population model. We used different observation models for the two surveys. The spring counts of the males ( ${}^{S}C_t^p$ ) covered the complete area and were supposed to be unbiased and we, therefore, modelled observation errors with Poisson distributions as:

$${}^{S}C_t^p \sim \text{Poisson}\left(S_{y,t}^{m,p} + S_{a,t}^{m,p}\right)$$

The late summer counts ( ${}^{A}C_t^{x,p}$ ) distinguished between male and female adults but only covered a fraction of each study area and therefore not all individuals were included on average. This justified the usage of the binomial distribution whose rate parameters, the detection probabilities, were estimated. These detection probabilities ( $p_t^p$ ) were allowed to vary temporally and to differ between populations but were the same for both sexes. They not only accounted for imperfect detection but also for not covering the complete sampling area. Thus, the late summer counts were modelled as:

$${}^{A}C_t^{x,p} \sim \text{Binomial}\left(p_t^p, A_{a,t}^{x,p}\right)$$

### *Radio-tracking data to estimate survival*

The tracking data **y** were summarized in monthly capture histories, that is, in each monthly period $t$ which lasted from day 15 of a month to day 14 of the next month, and it was noted whether a tracked individual $i$ was alive ($y_{i,t}=1$) or dead ($y_{i,t}=0$). A possible observation was also the failure of the radio transmitter, in which case the capture history was censored after the occasion when the individual was recorded to be alive for the last time. Since tracking was very intense and occurred usually at intervals shorter than one month, the reencounter probability was assumed to be 1, and thus a known fate model could be used (Devineau et al. 2014). Given the data **y**, the following model was used:

$$y_{i,t} \sim \text{Bernoulli}\left(\phi_{i,t}\, y_{i,t-1}\right)$$

where $t$ runs for each individual $i$ from the occasion of marking until the occasion of censoring or the occasion of observed death. $\phi_{i,t}$ is the survival probability of individual $i$ between occasions $t$ to $t+1$. We applied linear models to impose the desired age structure, sex-dependence and temporal seasonal pattern on the monthly survival probabilities.

Based on the estimated monthly survival probabilities, we calculated annual survival probabilities. Juvenile annual survival covered the time span from brood breaking up (that we assumed to happen on 31 August) until the next reproduction season (15 May), thus 8.5 months. Adult annual survival covered the complete year.

### *Radio-tracking data to estimate components of productivity*

We modelled different components of productivity, namely the probability to lay a clutch (breeding propensity, $\tau$), clutch size ($\xi$), the probability that a nest was not predated during incubation (nest success, $\psi$), the probability that an egg of a non-predated nest hatches (hatching success, $\kappa$) and the survival probability of a chick until 31 August ($\omega$). The product of these five components is breeding success ($\rho$), that is, the number of five-week-old chicks that a female that is alive on 31 August produced annually. The estimation of these components was based on radio-tracking data of mature females and on population survey in late summer by means of pointing dogs.

During the breeding period in the years between 1998 and 2008, we tracked a total of 24 females (16 yearlings, 8 adults) to record productivity. Eight females were tracked in more than one breeding season (range: 2–5) resulting in a total of 40 possible nesting attempts. For each possible nesting attempt, it was recorded whether the females initiated a clutch, and if so, the size of the clutch and the number of chicks it produced. If a female attempted to renest after the failure of the first clutch, only the outcome of the renesting attempt was included in the analysis ($n=3$, but all of these renesting attempts also failed). To model the probability to initiate a clutch, we used the Bernoulli distribution as:

$$D_i \sim \text{Bernoulli}\left(\tau_t^p\right)$$

where $D_i$ is a binary variable indicating for each possible nesting attempt $i$ whether a clutch was laid and $\tau_t^p$ is breeding propensity in year $t$ and population $p$.

Not all females reproduced every year, and in three failed broods we could not record clutch size. For each of the remaining 33 nesting attempts $j$, we recorded clutch size ($E_j$) and the number of chicks ($H_j$) at hatching. We modelled clutch size using a normal distribution rather than a Poisson distribution, because the Poisson appeared to be overdispersed. We formulated;

$$E_j \sim \text{Normal}\left(\xi^p, \sigma_\xi^2\right)$$

where $\xi^p$ is the estimated average clutch size in population $p$ and $\sigma_\xi^2$ is the residual variation. Note that clutch size was assumed to be constant over time to reduce the number of parameters to be estimated. The number of chicks at hatching was modelled with a zero-inflated binomial distribution as:

$$H_j \sim \text{Binomial}\left(z_j \kappa_t^p, E_j\right)$$

$$z_j \sim \text{Bernoulli}\left(\psi^p\right)$$



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where $z_j$ is a latent binary variable indicating whether or not clutch $j$ failed, $\psi^p$ is the population-specific probability that a nest was successful (i.e. was not predated), and $\kappa_t^p$ is the estimated hatching success. Note that clutch failure was modelled only with a population but not with a temporal effect, while hatching success was allowed to differ among years $t$ and between populations $p$.

During the late summer surveys in each year $t$ and in each population $p$, the total number of flushed hens ($R_t^p$) and the total number of flushed juveniles ($J_t^p$) were counted. Breeding success per female in year $t$ in population $p$ ($\rho_t^p$) was modelled using the Poisson distribution as:

$$J_t^p \sim \text{Poisson}\left(R_t^p \rho_t^p\right)$$

Breeding success is defined as the number of five-week-old chicks per adult female alive on 31 August. Under the assumption that the death of a reproducing female between the time of clutch initiation and 31 August causes a complete failure of her reproductive attempt, breeding success also includes an element of female survival. This is slightly inconsistent with the way how we model reproduction in the population equations that is unconditional on female survival until 31 August. Yet, as we estimate chick survival as a latent parameter without direct data, this inconsistency is likely to be soaked up by this parameter (Schaub and Kéry 2021). Hence chick survival as reported here is conditional on female survival; unconditional chick survival is expected to be slightly higher.

Most of the demographic rates were specified with temporal (year) random effects that were different in the two populations. Thus, a demographic parameter θ was generally modelled as $f\left(\theta_t^p\right) \sim \text{Normal}\left(f\left(\bar{\theta}^p\right), \sigma^2_{\theta(p)}\right)$, where $\bar{\theta}^p$ and $\sigma^2_{\theta(p)}$ are the population-specific means and temporal variances of θ, respectively, and $f$ is the link function (logit for probabilities, log for numbers). Due to data sparseness, clutch size and the nest success were assumed to be constant over time but could differ between populations. The seasonal survival probabilities were also allowed to vary among years, but it was assumed that the temporal variability was the same across seasons, sexes and populations but differed between age classes ($\text{logit}\left(\phi_{j,s,t}^{x,p}\right) \sim \text{Normal}\left(\text{logit}\left(\bar{\phi}_{j,s}^{x,p}\right), \sigma^2_{\phi(j)}\right)$ and $\text{logit}\left(\phi_{a,s,t}^{x,p}\right) \sim \text{Normal}\left(\text{logit}\left(\bar{\phi}_{a,s}^{x,p}\right), \sigma^2_{\phi(a)}\right)$). The detection probabilities during the late summer counts were also modelled with random year effects that differed between populations ($\text{logit}\left(p_t^p\right) \sim \text{Normal}\left(\text{logit}\left(\bar{p}^p\right), \sigma^2_{p(p)}\right)$). Finally, chick survival was modelled as a linear function of the mean daily temperature in the period 15–19 July. This period is known to be a sensitive one for chick survival (Zbinden and Salvioni 2004), and we expected to find a positive relationship. We assumed that the slope parameter (η) describing the relationship between chick survival and temperature ($T$) to be the same in both populations, but we also included temporal random effects that were independent between populations. Hence we used the following model: $\text{logit}\left(\omega_t^p\right) \sim \text{Normal}\left(\text{logit}\left(\bar{\omega}^p\right) + \eta T_t, \sigma^2_\omega\right)$. The temperature measurements originated from the weather station Codelago (1869 m a.s.l.) that is close to both study populations.

### *Joint likelihood and model fitting*

The complete IPM is formed by the product of the different likelihoods explained above. The survey data sets provide information about all the demographic rates, while the radio-tracking data are informative only about specific parameters. The joint analysis of the data results in more precise and consistent parameter estimates and also allowed the estimation of chick survival, which is not estimable from the survey data alone. The joint likelihood of the IPM was analysed using Bayesian methods (Schaub and Kéry 2021). We specified vague prior distributions for the estimated parameters (Supporting information). The model was fit using MCMC methods with JAGS (Plummer 2003) that was run from R (<www.r-project.org>) via package jagsUI (Kellner 2019). Code for the model including the specified priors is available at Zenodo (<https://doi.org/10.5281/zenodo.5211226>)/. We let the MCMC chains run for 500 000 iterations, removed the first 250 000, thinned the remaining samples by a rate of 100 and used three chains to evaluate convergence. This resulted in 7500 samples from the posterior distributions. Convergence was assessed with the R-hat values (Brooks and Gelman 1998) and by visual inspection of the MCMC chains. To evaluate the fit of the model we computed posterior predictive checks (Gelman et al. 1996) for the different model parts (Besbeas and Morgan 2014, Schaub and Kéry 2021).

### *Growth rate elasticities and identification of population drivers*

We first assessed to what extent a small change in a demographic rate or in the population structure would affect the population growth rate in the next year (prospective perturbation analysis). In order to compare these perturbations, we calculated growth rate elasticities, which express relative changes (Koons et al. 2016, 2017). We then decomposed the observed temporal variability of the realized population growth rate (obtained from the spring population sizes) into contribution from the temporal variability and covariability of the demographic rates and of population structure by using a transient life-table response experiment (retrospective population analysis, Koons et al. 2016, 2017). This allowed assessing how much each demographic process, as well as population structure, has contributed to the observed population dynamics. Both prospective and retrospective perturbation analyses were performed separately for each population and all calculations were closely followed Koons et al. (2017) and Schaub and Kéry (2021) (Supporting information for R code).

## Results

The parameters of the IPM converged, and the posterior predictive checks did not indicate lack of fit (Supporting information). The output of the IPM is rich with many parameters, and in the following, we present the biologically relevant ones. Estimates of nuisance parameters are shown in the Supporting information.

The sizes of both populations fluctuated over the twenty years (Fig. 1). Spring population sizes were with the exception of one year not different between males and females



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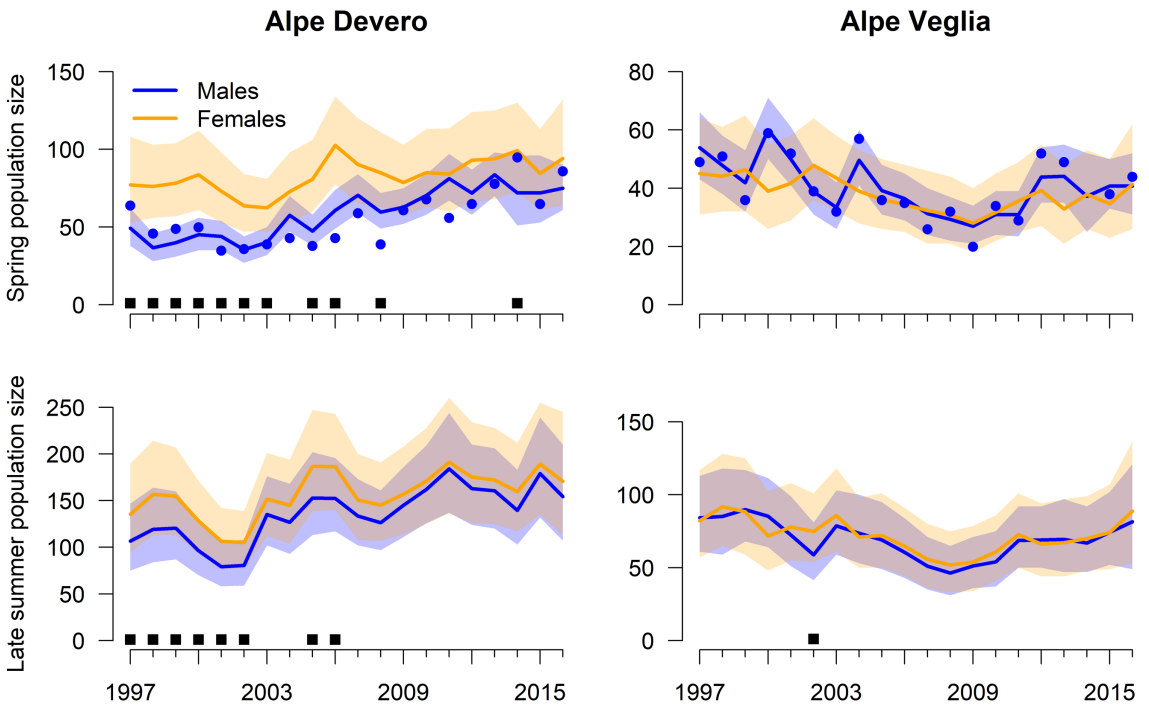



Figure 1. Estimated population sizes in spring and late summer of male and female black grouse at the Alpe Devero and at the Alpe Veglia. The lines show the posterior means, and the areas are the 95% credible intervals. Note that the estimates include individuals of all age classes. The small blue dots show the male counts in spring. The black squares indicate years in which the probability that the number of females was larger than that of males was >0.95.

at the Alpe Veglia, while females significantly outnumbered males by up to 2.1 times at the Alpe Devero in most years of the first half of the time series, but the sex ratio evened when hunting was banned. Summer population sizes were about 2 times larger than spring population sizes and at the Alpe Devero females outnumbered males again at the beginning of the time series but only up to 1.3 times (Fig. 1). The mean population density in spring was 3.6 (SD: 1.02) males and 5.1 (SD: 1.03) females per 100 ha at the Alpe Devero, and 4.9 (SD: 1.19) males and 4.6 (SD: 1.07) females per 100 ha at the Alpe Veglia (Supporting information).

The number of males increased at the Alpe Devero on average by 2.4% annually, while at the Alpe Veglia the numbers declined by 1.6% (Table 1). Female population sizes increased at the Alpe Devero by 1.1% and declined at the Alpe Veglia slightly by 0.5% annually. The total population sizes (males and females together) finally increased at the Alpe Devero on average by 1.6% annually, while the population at the Alpe Veglia declined on average by 1.0%. The population trends of females did not differ between the two populations, while the trend was larger for males and the complete population size at the Alpe Devero compared to the Alpe Veglia (Table 1).

Table 1. Posterior means (across the 20 years) and associated 95% credible intervals (CRI) of demographic parameters and of the geometric population growth rates of black grouse from the two study populations. Given are also the probabilities that the parameters from the population at the Alpe Devero were larger than those from the Alpe Veglia (p (D>V)).

| | Alpe Devero | | Alpe Veglia | | |
|---|---|---|---|---|---|
| Parameter | Mean | CRI | Mean | CRI | p (D>V) |
| Breeding propensity (τ) | 0.92 | 0.79, 0.99 | 0.78 | 0.57, 0.94 | 0.91 |
| Clutch size (ξ) | 5.97 | 5.35, 6.59 | 6.51 | 5.70, 7.29 | 0.13 |
| Nest success (ψ) | 0.91 | 0.78, 0.99 | 0.73 | 0.53, 0.92 | 0.95 |
| Hatching success (κ) | 0.94 | 0.88, 0.98 | 0.94 | 0.86, 0.98 | 0.49 |
| Chick survival (ω) | 0.50 | 0.39, 0.65 | 0.68 | 0.45, 0.93 | 0.09 |
| Breeding success (ρ) | 2.35 | 2.02, 2.68 | 2.27 | 2.00, 2.57 | 0.63 |
| Annual survival juvenile males ( $s_j^m$ ) | 0.38 | 0.25, 0.53 | 0.51 | 0.27, 0.76 | 0.18 |
| Annual survival adult males ( $s_a^m$ ) | 0.45 | 0.31, 0.59 | 0.50 | 0.34, 0.67 | 0.32 |
| Annual survival juvenile females ( $s_j^f$ ) | 0.44 | 0.31, 0.56 | 0.42 | 0.27, 0.57 | 0.59 |
| Annual survival adult females ( $s_a^f$ ) | 0.55 | 0.45, 0.64 | 0.57 | 0.46, 0.69 | 0.38 |
| Mean population growth rate (complete population) | 1.016 | 0.999, 1.034 | 0.990 | 0.972, 1.008 | 0.98 |
| Mean population growth rate (females) | 1.011 | 0.986, 1.037 | 0.995 | 0.969, 1.022 | 0.80 |
| Mean population growth rate (males) | 1.024 | 1.006, 1.041 | 0.984 | 0.966, 1.002 | 1.00 |



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### Patterns of survival and mortality causes

The monthly survival probabilities tended to be lower in juveniles than in adults, but differences were small and the uncertainty was considerable (Fig. 2). The posterior means differed most between age classes in summer, when the individuals were younger. Survival did not show strong seasonal patterns, and they were not consistent among sexes and populations.

Annual survival was slightly lower in juveniles than in adults (Table 1). Female adult survival tended to be higher than male adult survival, and the probability that this difference was real was 0.88 at the Alpe Devero and 0.73 at the Alpe Veglia. Furthermore, male survival tended to be lower at the Alpe Devero than at the Alpe Veglia in both age classes, while differences in female survival between populations were smaller and not consistent between age classes. Yet, due to large uncertainties, the probabilities that survival differed between populations were rather low (Table 1).

Of the 143 tracked individuals, 107 were found dead, and the mortality cause could be determined. The vast majority of the individuals died due to predation (n = 96, 89.7%). The remaining mortality fatalities were due to the collision with cables (n = 4, 3.7%) and due to hunting (n = 7, 6.6%). Hunting only occurred in tracked males at the Alpe Devero (n = 45), thus the proportion of hunting induced mortality was 0.16. Yet, only 45% of all radio-tracked males were ever-present in the area on which hunting took place. If the calculation of the proportion of hunting mortality is restricted to those individuals that were actually exposed to hunting, the proportion of hunting-induced mortality is 0.35. The predator could be identified as avian (n = 27, 28.1% [goshawk, golden eagle, eagle owl]) or as mammalian (n = 29, 30.2 [only red foxes]), for the other cases the predator was unknown (n = 40, 41.7%). Females were more often taken by an avian predator (n = 14, corresponding to 49% of female predation mortality), than males (n = 13, 19%). By contrast, females were less often predated by mammals (n = 6, 21%) than males (n = 23, 34%).

### Components of breeding success

Breeding propensity and hatching success did not show important annual fluctuations, while chick survival varied strongly from year to year and was fairly synchronous in the two populations (Fig. 3). Consequently, the resulting breeding success (number of chicks by 31 August per female) also fluctuated strongly over time and the temporal patterns were synchronous between the two populations.

The average breeding propensity and nest success probabilities tended to be larger at the Alpe Devero compared to the Alpe Veglia, while chick survival and clutch size tended to be higher at the Alpe Veglia than at the Alpe Devero. The hatching success was very similar in both populations and the resulting average breeding success did not differ between them (Table 1).

Chick survival was positively affected by temperature in July (Fig. 4, effect on logit survival per 1°C: 0.094 [95% CRI: 0.003, 0.196]), and the probability that the effect was positive is 0.98.

### Growth rate elasticities and population drivers

Growth rate elasticities indicate how much the population growth rate would change relatively in the next year, if a demographic rate or population structure changes (Caswell 2000). They show that both populations were particularly sensitive to changes in components of productivity (Fig. 5) and the sensitivity was the same for all of these components. Furthermore, the population growth rate was more sensitive to changes in juvenile than to changes in adult survival and slightly more sensitive to changes in female than to male survival. Finally, changes in population structure have a less strong impact on population growth than changes in demographic rates. An increase in the proportion of females would positively affect population growth, while a negative effect of population growth would result from an increase in the proportion of males.

The retrospective analyses show how much the temporal variation of the demographic rates and of population structure have actually contributed to the temporal variation of

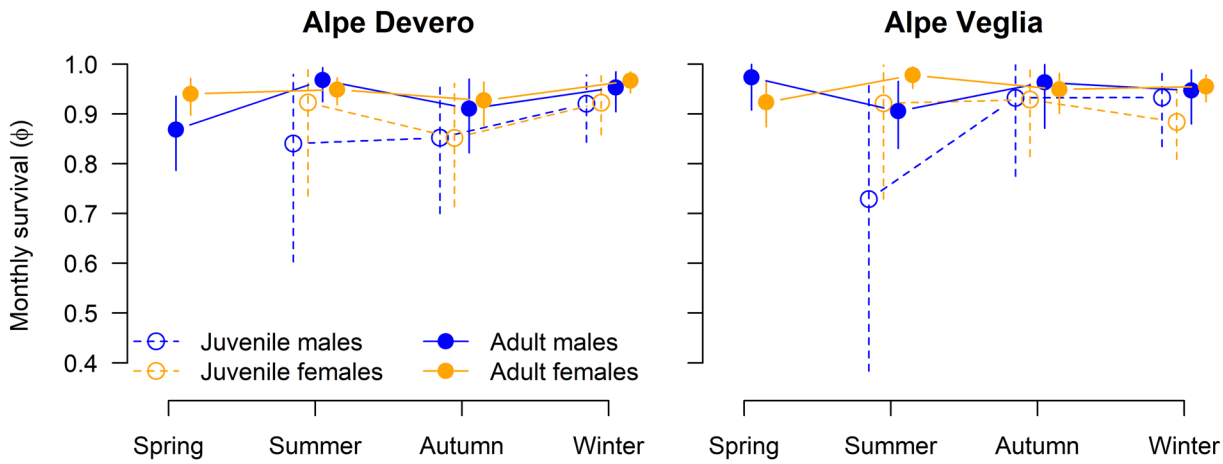



Figure 2. Monthly survival probabilities of black grouse from the two study populations in different seasons by age and sex. The dots show the posterior means, and the vertical lines are the 95% credible intervals.



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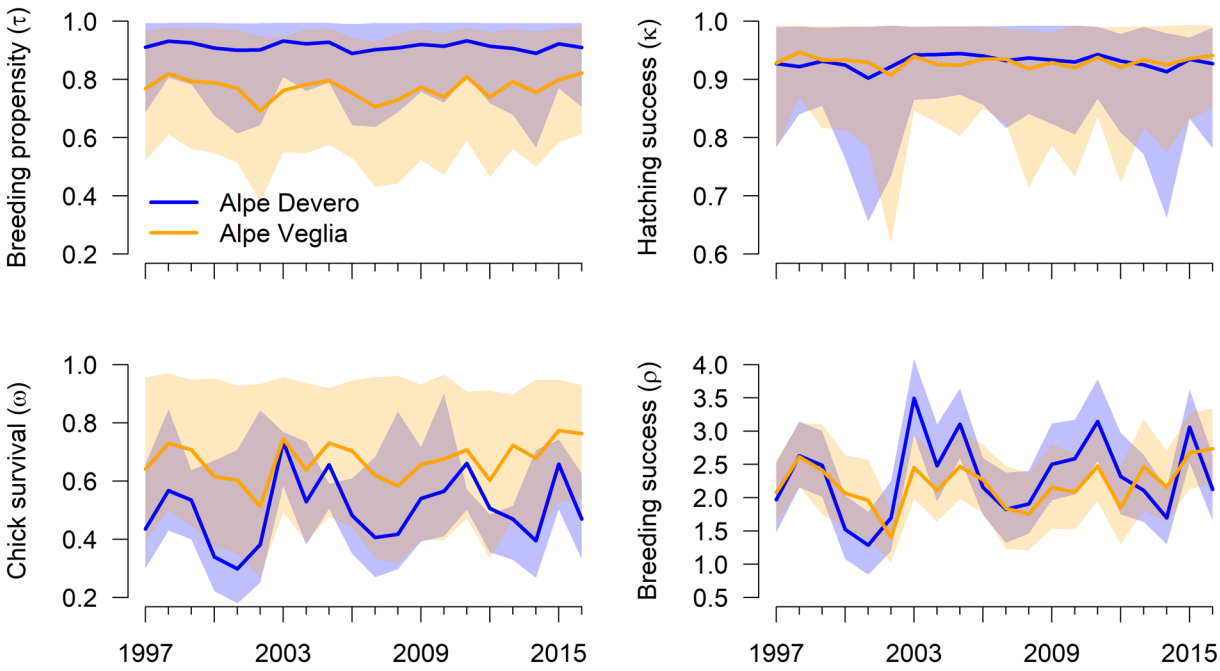



Figure 3. Temporal variability of different components of breeding success (breeding propensity τ, probability to initiate a clutch; hatching success κ, probability that an egg hatches given that the clutch was successful; chick survival ω, probability for a chick to reach the age of about five weeks) and of breeding success (ρ, number of about five weeks old chicks per adult female) of black grouse in the two populations. The lines show posterior means, the areas are the 95% credible intervals.

the population growth rate and hence to the population dynamics during the study period (Caswell 2000). The transient LTRE revealed that in both populations the variation in the demographic rates contributed more to the variation of the population growth rates than the variation in population structure (Fig. 5). The variation in chick survival to which the temperature in the hatching period of the chicks (middle of July) contributes was by far the most important component followed by the variation in annual juvenile survival. The variations of adult survival and of the other components of productivity have contributed less to the observed dynamics.

## Discussion

The dynamics of the two studied Alpine black grouse populations shared many similarities. Both populations were particularly sensitive to changes in components of productivity and were driven by temporal fluctuations of chick survival.

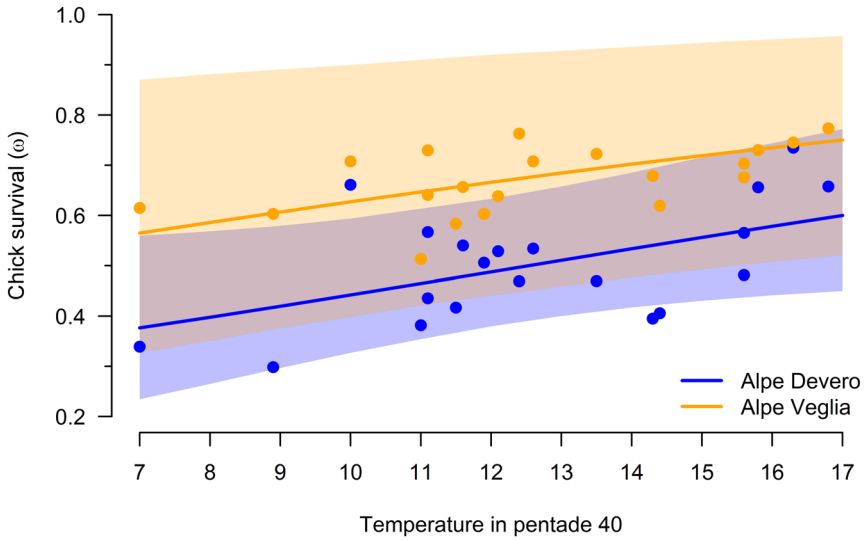



Figure 4. Relationship between the annual average daily temperature from 15 to 19 July (pentade 40) and the annual chick survival probability (ω) in the two black grouse populations. The lines and the areas show posterior means and the 95% credible intervals of the predictions, the dots are the estimates for single years.



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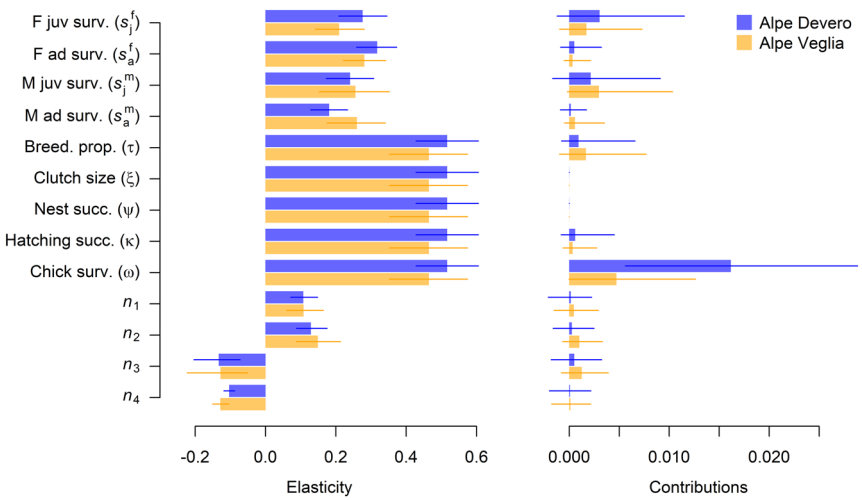



Figure 5. Growth rate elasticities (left) and c ontributions of the temporal variability of demographic rates and of stage-specific proportion of abundance on the past variation of realized spring population growth rates for the black grouse populations at the Alpe Devero and Alpe Veglia between 1997 and 2016 (right). The bars show the posterior means and the vertical lines indicate the 95% credible intervals. Stage-specific proportion of abundance: $n_1$ = yearling females, $n_2$ = adult females, $n_3$ = yearling males, $n_4$ = adult males.

The survival probabilities other than chick survival did not show extensive temporal fluctuations, and they did not strongly contribute to the temporal variation of the growth rates of both populations. The mean demographic parameters were similar in both populations, but the hunted population developed a female-biased sex ratio.

We performed a population dynamical study on black grouse by simultaneously studying demographic rates and the resulting population trajectories, which allowed the identification of the potential and realized demographic drivers of the studied populations. Most other population studies on black grouse focused either on single demographic processes (Caizergues and Ellison 1997, 2000, Warren and Baines 2002) or included all main processes but did not use a proper population model for inference (Baines et al. 2007). Hence, our approach seems more complete than previous ones.

## Comparison of demographic rates from other populations

The estimates of annual adult survival as found in our study (0.45–0.50 for males and 0.55–0.57 for females) compare well with estimates from other studies (Sweden: 0.56, Angelstam 1984; Wales: 0.44 (both sexes combined) Bowker et al. 2007; Finland: 0.53–0.69, Pekkola et al. 2014; French Alps: 0.68, Caizergues and Ellison 1997; England: 0.72, Warren and Baines 2002) but are slightly in the lower range of the reported values. Our estimates of seasonal survival did not show a consistent pattern across age classes or sexes. Some black grouse studies identified spring as a period of high mortality (Angelstam 1984, Caizergues and Ellison 1997, Pekkola et al. 2014), but we have not found such a pattern. Although we tracked many individuals intensively and used an integrated population model to estimate parameters, the survival estimates were still subject to high uncertainty, which might have obscured possibly existing temporal and spatial patterns of seasonal and annual survival as well as their possible correlations with the population growth rates.

The breeding success of about 2.3 chicks per female in both populations was higher than in most other studies (e.g. Wales: 1.0, Bowker et al. 2007; French Alps: 1.4, Caizergues and Ellison 2000; Sweden: 1.7, Willebrand 1992) but in the range of those found in northern Britain (1.7–2.7 chicks per female) (Baines 1991). An important component to explain the difference in breeding success between our and other studies is the much higher nest success in our populations (between 0.7 and 0.9). In the French Alps, the nest success of adults was only 0.5, in yearlings 0.64 (Caizergues and Ellison 1997), similarly to findings from central Sweden (0.52 and 0.54 for yearlings and adults, respectively) (Willebrand 1992). By contrast, the nest success of Finnish black grouse yearlings and adults were 0.88 and 0.79, respectively (Marjakangas and Törmälä 1997), and thus similar to the estimates from our study areas.

Although we have not explicitly distinguished female ages in our models of breeding success, our tracking data by which most estimates of the components of breeding success are directly informed, included yearling as well as adult individuals (Supporting information), whose data are very similar in all components. Therefore, we think it is unlikely that in our studied populations there is such a strong age-related pattern.

## Main driver of the population

We found a strong positive association between the realized annual population growth rates and survival of chicks during the first five weeks after hatching suggesting that chick survival was an important driver of population fluctuations. The variability of chick survival was partially due to the temperature in July. At this time, the plumage of the chicks is not yet fully developed such that they are not able to thermoregulate without being heated by the female (Marti and Bossert 1985). The sensitivity of chicks in black grouse and other tetronids to weather has been reported repeatedly (Hissa et al. 1983, Zbinden and Salvioni 2004, Baines et al. 2007). Although the weather is usually synchronized over



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large spatial areas, the complicated mountainous surface can result in effects that differ at small spatial scales and hence in only weak population synchrony (Cattadori et al. 2000, Canonne et al. 2021). This differs from black grouse populations from Scandinavia that may cycle and exhibit large-scale synchrony (Lindström et al. 1996). Changes in summer temperature as predicted by climate change (Easterling et al. 1997) may, therefore, have profound consequences for black grouse population dynamics. Chick survival is a component of breeding success, and the decline of breeding success has been suggested to be the main demographic mechanism also for the long-term decline in black grouse populations in Europe (Jahren et al. 2016)

Black grouse populations were equally sensitive to changes in other components of productivity than chick survival, but in our populations, these other components did not contribute much to the temporal variability of the population growth rate. This can be explained by their much lower temporal variability compared to chick survival. However, due to the relatively low sample size, we were not able to estimate the temporal variability in all these components, and for those where it was possible, the variability might have been underestimated. Because breeding propensity, clutch size, nest and hatching success are expected to be less strongly impacted by weather than chick survival, we expect stronger temporal variability in chick survival than in the other components and thus we think that chick survival is generally an important driver of black grouse population dynamics. However, future studies will have to show how much variable other components of productivity are to more properly assess their impact on black grouse population dynamics.

Given the rather low survival and high breeding success, black grouse at our study sites have the life history characteristics of a 'fast turnover' species (Sæther and Bakke 2000), whose dynamics is more sensitive to changes in recruitment than to changes in adult survival and thus is expected to show strong population fluctuations. This view agrees with the findings from many other black grouse populations (Jahren et al. 2016) but differs from another Alpine population that was supposed to be a rather long-lived species (slow turnover, Caizergues and Ellison 1997). We can only speculate about the reason for these differences; presumably, life history can flexibly be adapted to environmental conditions.

## Effect of hunting

Hunting was intense and restricted to males (about 10 cocks per year, corresponding to a total of 147 cocks during the study period), occurred only on a part of the Alpe Devero study area (600 ha), and was banned in 2012 and from 2014 onwards so that four of the last five years of the time series were not affected by hunting. We predicted a female-biased sex ratio of the hunted Devero population that should even over time and higher male mortality, if hunting had an effect. Two of these predications are supported by the data.

The main environmental difference between the two adjacent studied populations is that male hunting was allowed in one population only. Hence, we can consider the population dynamics at the Alpe Veglia to be more natural, while that at the Alpe Devero is potentially impacted by hunting. The sex ratio of chicks in both populations was even. The survival of grouse at the Alpe Veglia did not differ between sexes and hence the resulting sex ratio of mature grouse was even. An even sex ratio of mature individuals has been reported also from other black grouse populations without hunting (Ellison and Magnani 1985, Marti et al. 2016). Male hunting at the Alpe Devero tended to result in lower survival of males compared to females and to males from the Alpe Veglia (Table 1), although the uncertainty in all estimates of survival was large so that probability that the observed differences of the means were real remained moderate. Nevertheless, these moderate differences resulted in a female-biased sex ratio of mature grouse. As the hunting pressure declined over time, the sex ratio of mature grouse tended to become more even. These results clearly show that male hunting had an effect on the population structure of the black grouse population at the Alpe Devero, which supports similar findings on a hunted black grouse population in Switzerland (Zbinden et al. 2018).

The vast majority of mortality causes was natural in both populations, but 16% of the males at the Alpe Devero were hunted. If we assume hunting mortality to be additive to natural mortality, we can calculate natural male survival at the Alpe Devero as $1 - (1 - 0.45) \times (1 - 0.16) = 0.54$ for adults and $1 - (1 - 0.38) \times (1 - 0.16) = 0.48$ for juveniles. These values are remarkably close to the survival estimates of males from the Alpe Veglia and suggest that hunting mortality was mostly additive to natural mortality.

An important question is whether a biased-sex ratio in a species with a lek mating system where one male can mate with several females has a negative effect on the population dynamics. First of all, the size of leks increases with population size (Chamberlain et al. 2012, Nelli et al. 2016, Zbinden et al. 2018), for which we also have evidence. A total of 13 large leks with at least 10 displaying cocks were counted at the Alpe Veglia during the 20 years, while only 8 at the Alpe Devero, 5 of them since 2012 when hunting intensity was very low. Hence, large leks were more common when no hunting occurred in our study and also in Switzerland (Zbinden et al. 2018). Larger leks are generally attended by more females resulting in more copulations and increasing mating success of males (Alatalo et al. 1992). At larger leks, females have increased chances to mate with the fittest male, which may increase genetic diversity (Svobodová et al. 2011). All these findings suggest that an even sex ratio of mature grouse is beneficial.

Although black grouse hunting has a long tradition in the Italian Alps, it needs to be reconsidered, as other factors already jeopardize the species. Our data show how even a low to moderate hunting intensity can turn into a high impact at a local scale. This happens because hunters tend to concentrate their activities in black grouse habitats of high quality and easy accessibility. We suggest that black grouse male hunting, when allowed, is to be based on management practices that ensure sustainable harvest also at local scales.

## Impact of radio tags

Radio tagging on galliformes may negatively affect their survival (Bro et al. 1999, Buner and Schaub 2008, Homberger et al. 2021). As negative effects are expected to occur immediately after tagging, we have excluded individuals that



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disappeared within two weeks after tagging. In this way, we hope to have measured survival that is as natural as possible. From the 16 excluded birds, 11 were predated (all of them were juveniles tagged in August), one collided with a cable and in the remaining four individuals, the radio tag failed to work properly. Although we are not sure whether the deaths of the 12 grouse that died within two weeks post tagging were due to the radio tag, we advocate the use of radio tags in grouse studies is balanced carefully between the expected knowledge gain and potential detrimental effects.

## Conclusions

Black grouse have lost parts of their habitats at the timberline in the Alps in the last decades, both due to natural and human causes. The natural vegetation succession after the abandonment of traditional farming has transformed the original heterogeneous habitat mosaic, consisting of patches of grassland and shrubland interspersed with scattered coniferous trees, to more homogenous habitats of the same type that are less suitable for rearing chicks (Bergmann and Klaus 1994, Signorell et al. 2010). High-quality habitat for chicks is of prime importance for black grouse populations as they are driven in the first place by breeding success. In addition, the tourist industry, especially the construction of ski resorts, has degraded and fragmented large areas along and over the timberline (Patthey et al. 2008). A negative effect of climate change is also to be expected on Alpine black grouse populations (Zurell et al. 2012, Brambilla et al. 2017). Finally, black grouse hunting alters population structure and potentially affects populations negatively.

In order to prevent a further decline of black grouse populations in the Alps, improvements at all levels should be achieved. Existing habitat should be maintained and restored, and disturbance through human activities should be reduced as much as possible (Arlettaz et al. 2007). Hunting should be allowed only when it is sustainable and scientifically sound population monitoring is implemented for judging sustainability and for setting hunting bags.

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*Permit* – The permission to handle the studied animals was issued by Istituto Nazionale per la Fauna Selvatica (National Wildlife Institute), Italy.

### Author contributions

LR and RB collected the data and designed the study. MS analysed the data. MS and LR wrote the paper. All authors commented on drafts of the manuscript.

### Data availability statement

Data are available from vogelwarte.ch Open Repository and Archive: <https://doi.org/10.5281/zenodo.5211226> (Rotelli et al. 2021).

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