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## **Contrasted impacts of weather conditions in species sensitive to both survival and fecundity: A montane bird case study**

Coline Canonne<sup>1,2</sup>, Ariane Bernard-Laurent<sup>3</sup>, Guillaume Souchay<sup>4</sup>, Charlotte Perrot<sup>2</sup>, Aurélien Besnard<sup>1</sup>

1 CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, 1919 route de Mende, Montpellier, France

2 DRAS OFB, French Biodiversity Agency, F147 av de Lodève Juvignac, France

3 DRAS OFB, French Biodiversity Agency, Micropolis, F-05000 Gap, France

4 DRAS OFB, French Biodiversity Agency, 8 Bd Albert Einstein, F-44300 Nantes, France

Corresponding Author: Coline Canonne. E-mail: [coline.canonne@gmail.com](mailto:coline.canonne@gmail.com)

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## Abstract

There is growing evidence that the Earth's climate is undergoing profound changes that are affecting biodiversity worldwide. This gives rise to the pressing need to develop robust predictions on how species will respond in order to inform conservation strategies and allow managers to adapt mitigation measures accordingly. While predictions have begun to emerge on how species at the extremes of the so-called slow-fast continuum might respond to climate change, empirical studies for species for which all demographic traits contribute relatively equally to population dynamics are lacking. Yet, climate change is expected to strongly affect them throughout their entire lifecycle. We built a 21-year integrated population model to characterize the population dynamics of the rock partridge (*Alectoris graeca*) in France, and tested the influence of nine weather covariates on demographic parameters. As predicted both annual survival and breeding success were affected by weather covariates. Thick snow cover during winter was associated with low survival and small brood size the following breeding season. Brood size was higher with intermediate winter temperatures and snowmelt timing, positively correlated to breeding period temperature, but negatively correlated to temperature during the coldest fortnight and precipitation during the breeding period. Survival was positively correlated to winter temperature, but negatively to breeding period precipitation. Large-scale indices indicated that cold and wet winters were associated with small brood size the following breeding season but with high survival. Expected changes of weather conditions due to climate change are likely to impact demographic traits of the rock partridge both positively and negatively depending on the traits and on the affected weather variables. Future population dynamics will thus depend on the magnitude of these different impacts. Our study illustrates the difficulty to make strong predictions about how species with a population dynamic influenced by both survival and fecundity will respond to climate change.

Key words: climate change, fecundity, IPM, montane birds, rock partridge, survival, weather conditions

## **Introduction**

There is growing evidence that the Earth's climate is undergoing profound changes, and these are expected to amplify in the next century (Pachauri et al. 2015). In its latest report, the IPCC (Intergovernmental Panel on Climate Change) offered recent details on how the different drivers of climate change may interact, i.e. how rising of temperatures and modifications of the water cycle lead to either more droughts or floods and a reduction of the snow cover (IPCC, Sixth Assessment Report, Konapala et al. 2020). Climate change is already known to be affecting biodiversity worldwide (Vitasse et al. 2021). It is considered a major cause of changes in species distribution and abundances (Parmesan and Yohe 2003), phenology (Visser et al. 2004), and physiology (Fuller et al. 2010) and, in turn, in community composition and ecosystem functioning (Mokany et al. 2015). There is thus a pressing demand to develop robust predictions on how species will respond to climate change to refine species conservation status, inform conservation strategy, and allow managers to adapt mitigation measures accordingly (Bachman et al. 2019). Yet identifying the underlying mechanisms through which climate change affects species is far from straightforward as there are numerous and interacting potential drivers (Douhard et al. 2018).

To guide conservation efforts, it is important to disentangle how strongly each demographic trait contributes to the population dynamics of a species and to what extent these parameters might buffer changing environmental conditions throughout the year (Hindle et al. 2019).

Traditionally, life-history strategies have been ranked along an axis of variation from slow to fast life histories, referred to as the slow-fast continuum (Stearns 1992). Slow species are characterized by long lifespan, late age at first reproduction, and low fecundity, while fast species are characterized by the opposite strategy. The position of a species along this

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continuum will then determine populations growth rate sensitivity to variation of the different demographic traits. In long-lived species, such as large mammals and seabirds, population growth rates are mostly sensitive to changes in adult survival, whereas, in short-lived species, population growth rates are more sensitive to changes in fecundity or juvenile survival (Saether and Bakke 2000). Hereafter, we will refer to as “intermediate”, species at the center of the slow-fast continuum, that are characterized by a growth rate that may be equally impacted by changes of survival and fecundity (Stearns 1992). Environmental fluctuations increase variation in vital rates and usually decrease the long-term growth rate of populations. The demographic buffering hypothesis posits that the vital rates contributing most to the population growth rate are expected to be buffered against stochastic variation and thus present low variance (Hilde et al. 2020). Hence, the demographic strategy of a species will determine what demographic parameter will most likely be buffered. Adult survival is predicted to be buffered in slow-living species in contrast to recruitment, which is expected to be more variable, while in fast-living species fecundity or early survival would be expected to be buffered (Saether and Bakke 2000). Many studies on long-lived species confirm these predictions, demonstrating a strong influence of weather conditions on the survival and recruitment of young age classes. Regarding short-lived species, annual changes in the survival of passerine birds, for example, have been correlated to periods of low temperature or long periods of drought (Robinson et al. 2007).

When weather variations become too extreme, as is most likely to be the case with climate change, species may no longer be able to buffer the impacts on demographic rates, leading to population collapse (Hilde et al. 2020). Recent studies on long-lived seabirds in UK waters implicate the role of climate change on population decline in the last two decades via two main processes: through the reduction of both adult survival and breeding success due to changes in food supply, and through direct mortality from extreme weather such as strong

winds and high rainfall (Mitchell et al. 2020). In short-lived passerines, numerous studies have illustrated how phenological shifts due to climate change induce mismatches between chicks' needs and resource peaks, with profound consequences on fecundity and population growth rates (Visser et al. 2004), despite the fact that fecundity is predicted to be the most buffered against environmental variation in these species. While the influence of climate change on the population dynamics of species at the two extremes of the slow-fast continuum has been well documented, allowing robust predictions of population trajectories (White et al. 2018), there is still a lack of knowledge about the relationship between demographic rates and weather conditions for species with intermediate demography. The fact that all the demographic parameters of these species are likely to be affected by weather variation in a more balanced way than for species at edges of the slow-fast continuum makes predicting their fate in response to climate change very challenging.

In this study our goal was to test these predictions by providing a case study of a species with an intermediate demography and shed light on the influence of weather variation on both its survival and fecundity. We investigated the demography of the rock partridge (*Alectoris graeca saxatilis*) in the French Alps. In a recent review on generation time of birds the expected generation time of the rock partridge predicted from closed species and life history traits was 2.15 (Bird et al. 2020). Based on this value, the rock partridge population growth is expected to be equally influenced by survival and fecundity (see fig 5.2 in Lebreton and Clobert 1991). The study area is located at high elevations at the species cold-edge range limit of this this medium-sized Galliform (Srinivasan and Wilcove 2021). Montane ecosystems are characterized by strong spatial and interannual variation in climatic conditions at a relatively small scale, resulting in different topoclimates within narrow elevation gradients (Beniston 2006). Models predict that climate change is occurring faster in mountains than in plains, and these changes are expected to have a particularly strong impact on mountainous ecosystems

(Beniston, 2006; IPCC, 2021). This makes the rock partridge a good candidate to disentangle the relative influence of weather variation on the different vital rates of a species with intermediate demography and assess the potential long-term impacts of climate change on its viability. To explore this question, we built an integrated population model (IPM) (Besbeas et al., 2003; Schaub and Kéry, 2021) using data from different sources (radio-tracking, counts of singing males, counts with pointing dogs) collected over 21 years (2000–2020). This type of model provides a flexible framework that allows demographic rates to be broken down over the entire lifecycle while taking into consideration potential carry-over effects so that the relative contribution of different weather variables on both survival and reproduction can be explored (Zipkin and Saunders, 2018).

Based on previous studies conducted on related species, we made hypothesis on how weather conditions might impact the rock partridge demographic parameters (Table 1):

1) Winter temperatures and snowcover hypothesis

Regarding winter weather, we expected that during harsh winters, movements for food prospection would result in thermoregulation costs, altering birds' state of health and reserve storage and in turn leading to low winter survival (Didillon 1993). For birds that survived very snowy winters, we can expect lower reproductive output the following season due to poor body condition of breeders (Thompson and Fritzel 1988).

2) Snow melting and vegetation phenology hypothesis

We expected a long vegetative season to positively influence birds' body condition and overall survival, given the longer period to accumulate resources and frequent attempts of double brooding (Bernard-Laurent et al. 2017). Many studies have shown the importance of snowmelt timing on the development of vegetation phenology and the nutritive value of food resources for reproductive hens as well as for chicks (Novoa et al. 2016, Canonne et al. 2021).

3) Breeding period temperatures and precipitations hypothesis

During the breeding period, we expected a positive effect of warm temperatures and low precipitation on nest success and chick survival, as hatchlings are nidifugous and cannot thermoregulate during the first two weeks of life (Cattadori and Hudson 2000).

## **Material and methods**

### **Study species**

The rock partridge is an alpine Galliform suspected to be declining in most of its range from the French Alps to Bulgaria (Griffin 2011) and has recently been classified as Near Threatened by the IUCN (BirdLife International, 2021). This decline is most likely due to habitat loss and fragmentation resulting from the abandonment of agropastoral activities, hybridization with related species, and predation pressure and/or parasitism (Rippa et al. 2011). The habitat structure of our study area in the French Alps remained relatively constant during the study period (2000–2020), as major changes associated with the abandonment of agropastoral activities occurred mostly before the 1980s (Fischer et al. 2008). During the breeding season, the species is mainly found on shrublands and rocky meadows of sunny slopes between 1400 and 2500 m. Pair bonds form when winter flocks break up in March, then females lay eggs in April–June (average clutch size 10.2 eggs, range 7–15). Females may lay a second clutch, one of which is raised by the male and the other by the female. The proportion of double-nesting with males incubating varies between years (from 33% to 88%, Bernard-Laurent et al. 2017). Chicks are nidifugous and grow rapidly, they reach adult size after two months. During winter, some birds temporarily move upwards during heavy snowfall to reach elevations where the snow is swept away by the wind, while others descend to a lower altitude in the valleys (Bernard-Laurent et al. 2017). The rock partridge diet consists of a mix of herbaceous plants, flowers, seeds, berries and insects during the post-hatching season, while during the winter the diet consists exclusively of leaves of herbaceous plants (Didillon 1993).



## Data collection

Point counts of singing males were conducted by the French Mountain Galliformes Observatory (OGM) using call playback during the period in which pairs are territorial (Apr–Jun). Censuses were carried out in the first four hours after dawn on days without strong wind and/or rain (Bernard-Laurent and Laurent 1984). We considered maximum counts on 10 legacy sites that had been surveyed since 2000 and had few missing values (Appendix S1). Counts of both adult and juvenile birds using pointing dogs were conducted by the OGM in August each year during the study period to establish a fledging/adult ratio that we used as a proxy of brood size (mean number of chicks per successful adult at the end of August). The absence of dimorphism did not allow distinction between sexes. We selected 16 legacy sites available from 2000 onwards and with few missing values (Appendix S1). We completed this dataset with opportunistic observations of adults with broods in the Dévoluy massif from 2011 to 2020 (see below). Both spring and summer legacy sites were selected based on several subjective criteria that depended on the sites. Some sites have been selected because they were easily accessible and occupied by a high number of birds, others only because they were close to observers' domiciles, and finally some sites were selected because hunters felt that a local population was decreasing so they wanted to monitor the trend. Because the selection criteria were multiple, we hypothesized that their distribution on a large geographical area was to some extent representative of the whole population fluctuations (Fournier et al. 2019). While a bias in the median values cannot be excluded, the response to the weather covariates should not be affected.

From 2011 to 2020, a total of 212 rock partridges were captured in the Dévoluy massif (44°41'N, 5°56'E, 149 sq km; Bernard-Laurent et al., 2017 and Appendix S1&S2). Birds were fitted with 9–14-g necklace radio transmitters (Holohil system Ltd., <3% of body mass, expected lifespan of 18–36 months) and tracked until their death or the failure of the tag

(Bernard-Laurent et al. 2017). Our sample was male-biased (104 adult males, 61 adult females, 28 juvenile males and 19 juvenile females). Birds were weighed and aged based on the moult of outer wing primaries (Bernard-Laurent et al. 2017). For birds older than eight months, sex was determined by the presence or absence of spurs on the tarsus, while for young birds we used DNA sexing from feathers (Appendix S2). Throughout the year, birds were located two to three times per month by approaching the bird on the ground, using a portable receiver (ICOM R20 or AOR AR-8200MK3). Monitoring during the breeding season was more intensive, with visits four to five times per week from a spot at a long distance. This intensive monitoring allowed us to get information about clutch size, hatching date and the fate of chicks until September, when it became impossible to distinguish juveniles from adults in flight. No bird was lost during the monitoring and all of the devices were found when the mortality signal occurred, hence we had no permanent emigration.

Environmental covariates were selected to represent both local and large-scale weather variations experienced by the rock partridge over its annual cycle. The choice of covariates was made on an a priori hypothesis of the potential impact on survival and fecundity, based on results from studies on other Galliformes or on the effects of weather variation on vegetation and fauna (Table 1). Covariates measured during winter (Dec, Jan, Feb, Mar) were expected to directly influence overwinter survival in a given year, and to indirectly influence subsequent breeding success through carry-over effects. Covariates measured during the breeding season (May, Jun, Jul, Aug) were expected to directly influence breeding success the same year, and to indirectly influence breeding success through carry-over effects the following year. All variables were scaled prior to analysis. When we suspected a potential non-linear response or optimal value, we tested for both a linear and a quadratic effect. Local weather indices were based on meteorological conditions estimated by SAFRAN (Système d'Analyse Fournissant des Renseignements Atmosphériques à la Neige), a mesoscale

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atmospheric analysis system for surface variables using ground data observations from Météo France (Durand et al. 1993). We calculated a mean value per site, weighted by the proportion each 8-km grid cell overlapped study site areas. We extracted snowmelt dates from the Moderate Resolution Imaging Spectroradiometer (MODIS), defining the date of snowmelt as the end of the period of continuous snow cover. Date\_100 corresponded to total snowmelt at the counting sites (100% of pixels of the site with bare ground), and Date\_50 to 50% bare ground (Novoa et al. 2016, Canonne et al. 2021). Covariates built from SAFRAN and MODIS data were calculated for the Dévoluy area (Appendix S1) for the survival analysis (as all birds were caught in this area), and on the summer counting sites for the analysis of fecundity. To explore the impact of large-scale weather conditions, we collected both winter (Dec–Feb) and summer (Jun–Aug) North Atlantic Oscillation indexes (Hurrell et al., 2003), which summarize weather variations in a single index encompassing both precipitation and temperature (Stenseth et al. 2003). Finally, as hunting of this species of rock partridge is allowed, though very limited (depending on the year, hunting bags ranged from 55 to 407 birds at the national scale during the study period), we tested for an influence of the number of harvested birds on annual survival.

## **Statistical analyses**

### ***Population model***

We developed an integrated population model (IPM) to jointly analyse different datasets in a single framework (Besbeas et al. 2003, Schaub and Kéry 2021). The core of the IPM was a two-age-class pre-breeding female-based matrix model that linked age-specific population size at the end of May with demographic rate using a Binomial distribution (Fig 1, for a complete description of the model refer to Appendix S3). We defined birds independent of parental care and less than 8 months old as juvenile: thus, birds moved from one age class to the next at the end of March (onset of breeding territory).

### ***Population growth rate estimation using spring counts of males***

We analysed population trends with log-normal regressions (de Valpine and Hastings 2002). As our populations were expected to be mainly declining and to occur at low densities (Bernard-Laurent et al. 2017), we assumed stochastic exponential population growth and chose not to consider density dependence. The link between site-specific temporal variation in the number of counted males in spring and our matrix population model was done through the network's mean annual growth rate  $\bar{r}_t$ , with  $\sigma^2_{proc}$  reflecting site variability in the population growth rate around the network's mean annual growth rate (Fig 1).

### ***Survival estimation using radio-tracking data***

Monthly survival was estimated using multi-state capture–mark–recapture (CMR) models (Lebreton and Pradel 2002), following the approach described in Canonne et al. (2020) to explicitly model extra mortality associated with capture during the first month after release (Blomberg et al. 2018). We built monthly individual encounter histories from the date of capture to the date of death or radio failure, applied right censoring on individuals whose transmitters stopped working, and fixed detection probability to 1 as we used telemetry data. In our IPM (Fig 1), we included a random effect of year on monthly survival probability to capture interannual variation in survival probability ( $\sigma^2_{ms}$ ). We derived annual survival ( $ys_{ad}$  and  $ys_j$ ) from the product of adult and juvenile monthly survival ( $ms_{ad}$  and  $ms_j$  respectively).

### ***Fecundity estimation using radio-tracking data and summer counts with pointing dogs***

We broke down reproductive success into three steps. First, we used two successive Bernoulli distributions, to first model the probability of laying at least one clutch ( $bp1$ ), and then the probability of laying one or two clutches ( $bp2$ ) for individuals that laid at least one (i.e. double nesting: one incubated by the female and one by the male), using reproductive data from the 31 pairs for which both the male and the female were equipped and radio-tracked.

Second, using data from radio-tracked individuals ( $N=74$ ), we used a Bernoulli distribution to estimate the probability that an initiated clutch succeeded, i.e. that at least one chick survived until August ( $ns$ ). Third, we used data from radio-tracked individuals, summer counts and opportunistic observations to estimate the number of chicks per successful bird (i.e. birds with at least one chick, hereafter brood size  $bs$ ) using a normal distribution, to cope with overdispersion issues (Schaub and Kéry 2021). Brood size was estimated from data collected on several sites, hence we included random effects of both year ( $\sigma^2_{\text{year}}$ ) and site ( $\sigma^2_{\text{site}}$ ), with  $\sigma^2_{\text{res}}$  the variance of the residual variation. Yet, because sites were not the same than the ones used to estimate growth rate nor survival, we only used the mean brood size and the temporal variation in the matrix part of the IPM. Lastly,  $N_{\text{♀},c,t}$  the number of female chicks per hen at the end of August in year  $t$  was modelled using a Poisson distribution in the IPM.

***Generation time, growth rate elasticities, identification of population drivers and covariates influence***

We computed the generation time of our rock partridge populations, defined as “the average age of parents of the current cohort” using the formula from Schaub & Kéry (2021). We calculated growth rate elasticities to assess how much a small change in a demographic rate or in the population structure would affect the population growth rate the next year (Schaub and Kéry 2021). We then computed changes of the population growth rates between successive years and the contributions of the changes in demographic rates and of population structure (Schaub & Kéry 2021). We broke down the observed temporal variability of the realized population growth rate into the contribution from temporal variability and the covariability of the demographic rate and of population structure using a transient life table response experiment (LTRE) (Koons et al., 2016). The influence of explanatory variables on interannual variation in survival was tested as an additive effect of age on monthly survival. As for the influence on brood size ( $bs_t$ ), we tested the covariates effects while considering

both random effects of year (time) and site (loc). Because the study length was relatively short (21 years), we chose to include only one covariate at a time (see covariate correlations in Appendix S4 & S5), fitting as many IPMs as covariates. We computed the probability (hereafter,  $p$ ) that regression coefficients of explanatory covariates were below zero and examined the size of the effect (Kéry and Schaub 2012). For quadratic polynomials, the probabilities associated to both coefficients are reported below as  $pX$  and  $pX2$ . While we considered that an effect was strong when this probability was below 0.10 or above 0.90, and weak when included in the 0.1-0.2 or 0.8-0.9 ranges, we were mostly interested in comparing effect size.

### ***Joint likelihood and model fitting***

We implemented the IPM in the Bayesian context using the R (R Core Team 2018) package “rjags” (Plummer et al. 2019). We specified relatively vague priors for all parameters (Schaub and Kéry, 2021). All models ran three chains of 250,000 iterations with a thinning of 15, discarding 100,000 iterations as a burn-in. We checked that convergence was satisfactory by visualizing the mixing of chains and using the Brooks–Rubin–Gelman diagnostic (Brooks and Gelman 1998). We performed GOFs separately for each model component, all models converged and results did not show any strong lack of fit (Besbeas and Morgan 2014, Schaub & Kéry 2021; details and results in Appendix S6). Estimates are presented using posterior means and associated 95% credible intervals (CRI).

## **Results**

### **Population trend, survival and breeding success**

The posterior estimates of the median annual population growth rate in the network of sites showed strong interannual variation ( $\sigma_{proc} = 0.32$ , CRI 0.29–0.36; Appendix S7), but there was no general increasing or decreasing trend in population size over the study period (realized mean growth rate = 0.99, CRI 0.98–1.01). Monthly survival probability was on

average quite similar between age classes ( $\overline{ms_j} = 0.92$ , CRI 0.88–0.95;  $\overline{ms_{ad}} = 0.93$ ; CRI 0.92–0.95), resulting in a slight difference of about 10% in mean annual survival probability ( $\overline{s_j} = 0.39$ , CRI 0.27–0.52;  $\overline{s_{ad}} = 0.43$ , CRI 0.36–0.51). Survival probability varied greatly between years (Fig 2;  $\sigma_{ms} = 0.24$ , CRI 0.15–0.42). Results also showed a strong short-term effect of capture on survival probability: monthly survival probability during the first month after capture was about 9.68% (CRI 4.30–6.13%) lower, compared to the monthly survival probability estimated in other cases for the corresponding month. Almost all hens attempted reproduction and laid at least one clutch ( $bp1 = 0.88$ , CRI 0.77–0.96); about half also laid a second clutch ( $bp2 = 0.56$ , CRI 0.37–0.74). Half of all initiated clutches succeeded: that is, at least one chick survived until August ( $ns = 0.51$  CRI, 0.42–0.60). The mean number of chicks per successful bird at the end of August ( $bs$ ) was 4.47 (CRI 3.60–5.44). Hence, the mean number of female chicks per hen at the end of August ( $N_{\text{♀},c,t}^{\text{♀}}$ ) derived from these parameters was 1.56 (CRI 0.80–2.73). Brood size was quite heterogenous between sites ( $\sigma_{site} = 1.30$ , CRI 0.87–2.43), but also varied greatly between years (Fig 2;  $\sigma_{year} = 1.07$ , CRI 0.68–1.86).

### Generation time and elasticities

The estimated generation time of our populations was  $GT = 1.72$  [1.54-1.96]. The population growth rate was relatively equally sensitive to all demographic parameters, with a slightly higher sensitivity to changes in brood size and sub-adult annual survival probability compared to other demographic parameters (Appendix S8). Results from the retrospective analyses showed that variation in all three demographic rates contributed to the variation in population growth rates, while the population structure ( $n_j$  and  $n_{ad}$ ) had a negligible contribution ( $\overline{s_j} = 0.03$ , CRI 0.01–0.05;  $\overline{s_{ad}} = 0.02$ , CRI 0.01–0.03;  $N_{\text{♀},c,t}^{\text{♀}} = 0.02$ , CRI 0.01–0.04;  $n_j$  &  $n_{ad} < 0.01$ ). The annual contribution of demographic parameters to the annual growth rate was unevenly distributed, with growth rate more influenced by survival probability in some years, while in others it was more influenced by fecundity (Fig 2).

## **Influence of environmental covariates**

### ***Survival probability (Fig 3A & Appendix S9)***

Our results did not find any significant impact of the number of harvested birds on our estimates of mean survival probability for the population ( $p=0.56$ , Fig 3A & Appendix S9). Regarding winter conditions, results showed a strong negative correlation between survival probability and snow height ( $p<0.01$ ). For every additional 10 cm of snow, annual survival probability decreased about 0.05 (Fig 3A). We found a positive relationship between survival probability and mean temperature during winter, with a 0.02 increase in annual survival probability for each additional degree ( $p=0.81$ , Fig 3A). Results suggested a weak correlation between mean temperature during the coldest fortnight and survival probability ( $p=0.20$ , Fig 3A). We also found a weak negative correlation between winter NAO and survival ( $p=0.17$ ), suggesting that survival probability was higher when winters were both cold and wet. Late snowmelt dates (Date\_50) were associated with higher survival ( $p=0.92$ ), with an increase of about 0.02 for every 10-day delay in snowmelt (Fig 3A). The complete snowmelt date did not seem to have any influence on survival probability ( $p=0.50$ , Fig 3A). Regarding breeding period, results demonstrated a strong negative correlation between precipitation and survival probability ( $p=0.03$ ), with a decrease of 0.07 of annual survival probability for every additional 100 mm of rain. Our results did not suggest any influence of breeding period temperature or summer NAO on survival probability (respectively  $p=0.50$  and  $p=0.28$ , Fig 3A).

### ***Brood size (Fig 3B & Appendix S10)***

While thin snow cover did not seem to have a strong influence on brood size, the latter decreased steeply for snow cover higher than 1 m ( $pX=0.57$ ,  $pX^2=0.01$ , Fig 3B & Appendix S10). Brood size was high for intermediate winter mean temperatures ( $pX=0.45$ ,  $pX^2=0.02$ ), yet the effect size was small and the CRI large (Fig 3B). The temperature during the coldest



fortnight was strongly negatively correlated with brood size, with a decrease of about 0.18 chicks per hen at the end of August for every additional degree ( $p=0.04$ , Fig 3B). The positive correlation we found between winter NAO and brood size suggests that cold and wet winter conditions were associated with smaller brood size, while drier winters may have had a positive influence ( $p=0.88$ , Fig 3B). Brood size was highest for intermediate snowmelt dates of around mid-April (Date\_50,  $pX=0.16$ ,  $pX^2<0.01$ ), while years with a late vegetation phenology were associated with a smaller brood size than years with early vegetation phenology (Fig 3B). We did not find any significant relationship between brood size and the date in spring of snow-free ground ( $p=0.44$ , Fig 3B). Brood size was negatively correlated to breeding period precipitation ( $p=0.06$ ), with a decrease of about 0.35 for every additional 100 mm of rain (Fig 3B). Likewise, the results found a positive relationship between breeding period temperature and brood size, with an increase of about 0.20 chicks for every additional degree ( $p=0.91$ , Fig 3B). This negative correlation between cold and wet summers and brood size was confirmed by the negative correlation we found between brood size and summer NAO ( $p=0.08$ , Fig 3B).

## **Discussion**

Our findings showed that all vital rates relatively equally contributed to the annual population growth rate of the rock partridge over the study period (2000–2020). Our results also showed a significant effect of all the tested weather covariates on demographic parameters, illustrating that the rock partridge demography is impacted by environmental conditions all along its life cycle. We also show that the same weather conditions could result in either negative or positive impacts depending on demographic traits, highlighting the difficulty of making strong predictions about the influence of climate change on the rock partridge population trajectory.

The estimated generation time is lower than the value predicted from closely related species and life history traits, but remains nevertheless in the range corresponding to intermediate species. This difference is most likely due to an underestimation of survival in our study. Our model showed a rather strong effect of capture and wearing of a transmitter on survival during the first month after release. Such effects have been reported for other Galliformes species, mainly in the fortnight following capture: sage-grouse (Gibson et al. 2013), black grouse (Baines et al. 2007) and rock ptarmigan (Canonne et al. 2020). Survival after the first month of capture remained lower than expected. While we lack any information to rely on to decide between the various hypotheses, we may expect a prolonged negative impact of transmitters or rather peculiar conditions in the area, notably higher predation rates. As expected for an intermediate species, all vital rates contributed relatively equally to the observed population growth rates. Some years population growth rates were driven mostly by survival, others mostly by fecundity, and about half of the years equally by both. This highlights the need to consider all life stages when studying the potential impact of climate change in species with intermediate demography.

As densities were quite low, we did not include density dependence in our model. Yet, previous work showed that density dependence can have strong influence on buffering capacity. Indeed, when populations are close to their carrying capacity, the life cycle generally slows down and the elasticity of survival increases while those of breeding parameters decreases (Hilde et al. 2020). The relative influence of the different covariates may then be modified, but unfortunately, we lack any information to make predictions about the extent of such a phenomenon in our studied population.

Several weather covariates, in either winter or summer, were correlated to both survival and fecundity. As the rock partridge in the Alps is situated at the cold-edge of its range and does not share the morphological and physiological adaptations to cold weather of other alpine

Galliformes (Bernard-Laurent 1991), we expected both demographic rates to be negatively impacted by very harsh winter conditions: that is, low temperatures associated with large amounts of snow (Srinivasan and Wilcove 2021). In line with this hypothesis, we found that thick snow cover was associated with low annual survival as well as low fecundity during the following breeding season. Mean winter temperatures were also positively correlated with annual survival. Similar results have been found for several species of montane ungulates and Galliformes known to be constrained by snow, notably for foraging (Chirichella et al. 2021, Rosenblatt et al. 2021). Thick snow cover may limit access to underlying herbaceous resources and can hinder movement, thus altering birds' body condition. This can either result in death during the winter or in a carry-over effect to the following reproduction period for birds that survive, as they must initiate reproduction with lower protein reserves.

However, at a larger scale, the winter NAO index suggested the opposite pattern, with survival probability higher in years characterized by rather cold and wet winters. This highlights the probable importance of the interaction between temperature and precipitation, which can have major consequences on food availability and thus body condition. Notably, the formation of an ice layer at the base of the snowpack with increasing temperatures can limit access to the herbaceous plants underneath or alter their nutritive quality (Domine et al. 2018).

Regarding fecundity, the optimum mean winter temperature for this trait was around  $-1^{\circ}\text{C}$ , yet we found a negative correlation with the temperature during the coldest fortnight. At a larger scale, the winter NAO index suggested that brood size was smaller following cold and wet winters. Hence, our prediction that harsh winters would have consequences on the body condition of surviving individuals leading to poor reproductive output the following season was only partially supported; it is difficult to make general conclusions as there were contrasting responses between different covariates. The pattern observed with the winter

NAO index and the temperature during the coldest fortnight may be the result of the counter-selection of lower-quality individuals during harsh winters, leaving only high-quality individuals with good reproductive output the following season. However, the weak correlation between mean annual survival and fecundity in the results does not seem to support this hypothesis ( $r= 0.16$ , Appendix S8). An alternative possibility is that a period of frost is needed for the proper development of some alpine plants used as resources by the rock partridge (Beniston 2006). A more mechanistic understanding of the relationship between the winter covariates we used would be needed in order to disentangle their effects on brood size (Jonas et al. 2008). Brood size was higher in years with an intermediate snowmelt date (around mid-April), while survival was higher in years with a late vegetative season. In mountain ecosystems, winter weather conditions determine the length of the snow-free season, as well as the state of soil and plants at the start of the vegetative season (Jonas et al. 2008). This then defines the favourable period for resource availability and, in turn, reproduction. While a longer reproductive season may increase the possibility of double laying (Bernard-Laurent et al. 2017), thus spreading the amount of energy allocated for reproduction over time, our results suggest that an intermediate vegetative season phenology leads to higher brood sizes, possibly due to better synchronization of chick rearing with the period of maximum food supply (Visser et al. 2004). The positive correlation we found between survival probability and snowmelt date is yet more surprising, as a long vegetative season should result in higher protein storage. This pattern may also point to an energetic trade-off, with lower reproductive investment in a given year leading to higher annual survival, yet the absence of correlation between mean annual survival and fecundity does not seem to support this hypothesis (Appendix S8). Regarding breeding period conditions, as predicted, our results showed a negative influence of summer precipitation on survival and fecundity and a positive influence of warm temperature on fecundity. The direct impact of

precipitation associated with low temperature on chick thermoregulation has been well described for nidifugous bird species, and notably Galliformes (Schekkerman 2008, Novoa et al. 2016). However, the influence of these parameters on vegetation growth and the timing and quantity of insect emergence is less clear (Beniston 2006). Vegetation growth determines not only the quantity and quality of resources, but also provides sufficient cover for both chicks and adults. Thus, a potential positive influence of precipitation leading to enhanced vegetation growth may to some extent counterbalance its negative impact on bird survival. This strong signal of various weather conditions on the interannual variation in both demographic traits suggests that climate change is likely to have a major impact on rock partridge population demography. While snow height remained relatively stable over the study period (Appendix S11), it has significantly decreased since the 1970s, and climatic models predict that it will decline at a faster rate in the years to come (IPCC, 2021). In addition, increased temperatures during both the breeding period and winter are already observable at the site and are expected to intensify (IPCC, 2021 & Appendix S11). As the study site is located at the cold-edge distribution range of the rock partridge, an increase in winter bird survival and breeding success associated with lower metabolic costs of thermoregulation might be expected (Srinivasan and Wilcove 2021). Our results suggest that the rock partridge may respond positively to the ongoing reduction of the snowpack, at least to some extent. Nevertheless, the contrasting influence of both breeding period and winter temperatures we found makes it difficult to predict how the species will respond to increasing temperatures. Regarding snowmelt timing, while no advance was observed at our study site (Appendix S11), climatic models predict earlier spring phenology and longer breeding seasons in the years to come (IPCC, 2021). Our results suggest that this phenology change may reduce both survival and fecundity. Lastly, while we found a strong negative impact of breeding period precipitation on both survival and fecundity, predictions based on this result

remain challenging as climatic models point towards heterogenous and small-scale changes in precipitation.

In this study we found contrasting responses of survival and fecundity to variation in weather conditions, highlighting the difficulty of making any general predictions about the population trajectory for intermediate species in future climate change scenarios. Species' demographic strategy on the fast–slow continuum determines what demographic parameter is most likely to be buffered: adult survival is predicted to be buffered in slow-living species in contrast to recruitment, which is expected to be more variable, while in fast-living species fecundity or early survival would be expected to be buffered (Saether and Bakke 2000). Yet for species with an intermediate demographic strategy, the relative magnitude of these different impacts will be decisive, as these species are expected to show contrasting responses to different climatic conditions. Unfortunately, it remains challenging to quantify the magnitude of the influence of different climatic conditions and their potential interactions with other components of the ecosystem. It is also unclear to what extent the relationships found in our study can be extrapolated outside the current range of weather condition values. Further studies would be valuable to explore these questions.

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Table 1: Environmental conditions potential effect on survival and brood size of the rock partridge in the French Alps (2000-2020). Studies on similar species: RP=rock ptarmigan, BG=black grouse, HG=hazel grouse, RLP=red-legged partridge, RG=red grouse, RFG=ruffed grouse, GP=grey partridge, NB=northern bobwhite. Breeding period (BP) was defined from May to August, and winter (W) from December to March.

	Annual survival	Brood size	Overall expected influence	Proxy	References
Snowmelt timing	Strongly influences spring phenology, affecting adults' body condition (health and energy storage, notably proteins), through influence on vegetation growth (height and density of herbaceous plants, quality of flowers and seeds) and emergence of insects (quantity and timing).	Adults' condition will influence chick quality at birth and adults' ability to rear the chicks. Long breeding seasons may favour double-nesting possibilities, but unpredictability can cause mismatches between insect phenology (peaks of resources used by chicks) and brood rearing timing.	-	Julian day with snow cover on 50% of area; Julian day of snow-free ground	Moss et al. 1975 (RG), Swenson et al. 1994 (HG), Bernard-Laurent et al. 2017, Nadal et al. 2021 (RLP)
Snow height	Thermoregulation costs that can limit time for foraging and escaping predation. Snow on the ground can also limit food accessibility (herbaceous plants), and increase exposure to predation.	A thick snowpack may take longer to melt and delay spring phenology and can also affect adults' body condition (thermoregulation costs, predation exposure, food accessibility), hence chicks' birth quality and rearing.	-	Mean snow height (cm)	Panek 1990, Bernard-Laurent 1991, Didillon 1993, Mihajlov et al. 2018, Rosenblatt et al. 2021 (NB)
W T°	Metabolic costs of	Chicks' quality and rearing	-	Mean T° (°C)	Thompson and Fritzel 1988



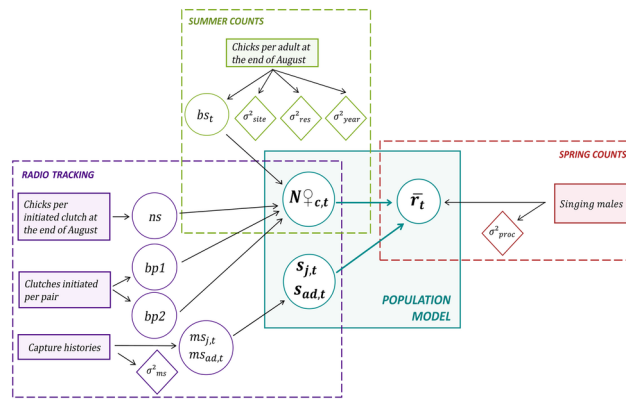
	<p>thermoregulation and movement (food prospection and predator avoidance). Influence on birds' energy storage through effects on vegetation. T° can favour freezing and limit the development and access to herbaceous plants, influence vernalization and spring phenology.</p>	<p>depend on adults' body condition. Influence on energy storage of adults for reproduction that is affected by food availability and quality.</p>		<p>Mean T° (°C) the coldest fortnight</p>	<p>(RFG), Mihajlov et al. 2018</p>
BP T°	<p>Influences vegetation growth (height and density of herbaceous plants, quality of flowers and seeds), and the timing and quantity of insects, which are used as resources by adults (vegetation is used for both food and cover). Potential carry-over effect on birds' energy storage and thus on over-winter survival.</p>	<p>T° induces metabolic costs for chicks (low thermoregulation during the first two weeks) and influences vegetation growth (height and density of herbaceous plants, quality of flowers and seeds), and the timing and quantity of insects (chicks and adult resources).</p>	+	<p>Mean T° (°C)</p>	<p>Watson et al. 1998 (RP), Cattadori and Hudson 2000, Rotelli 2006, Giordano et al. 2013</p>

Precipitation	Influences vegetation growth (height and density of herbaceous plants, quality and timing of flowers and seeds), so affects resource availability and quality for adult birds. Potential carry-over effect during the rest of the year through birds' condition (health state and energy storage).	Metabolic cost for chicks (low thermoregulation) and influence on vegetation growth (height and density of herbaceous plants, quality and timing of flowers and seeds) and resource availability and quality.	-	Sum of monthly precipitation during BP (mm)	Cattadori et al. 1999, Lusk et al. 2002 (NB), Novoa et al. 2008, 2016 (RP), Giordano et al. 2013, Canonne et al. 2021(BG)
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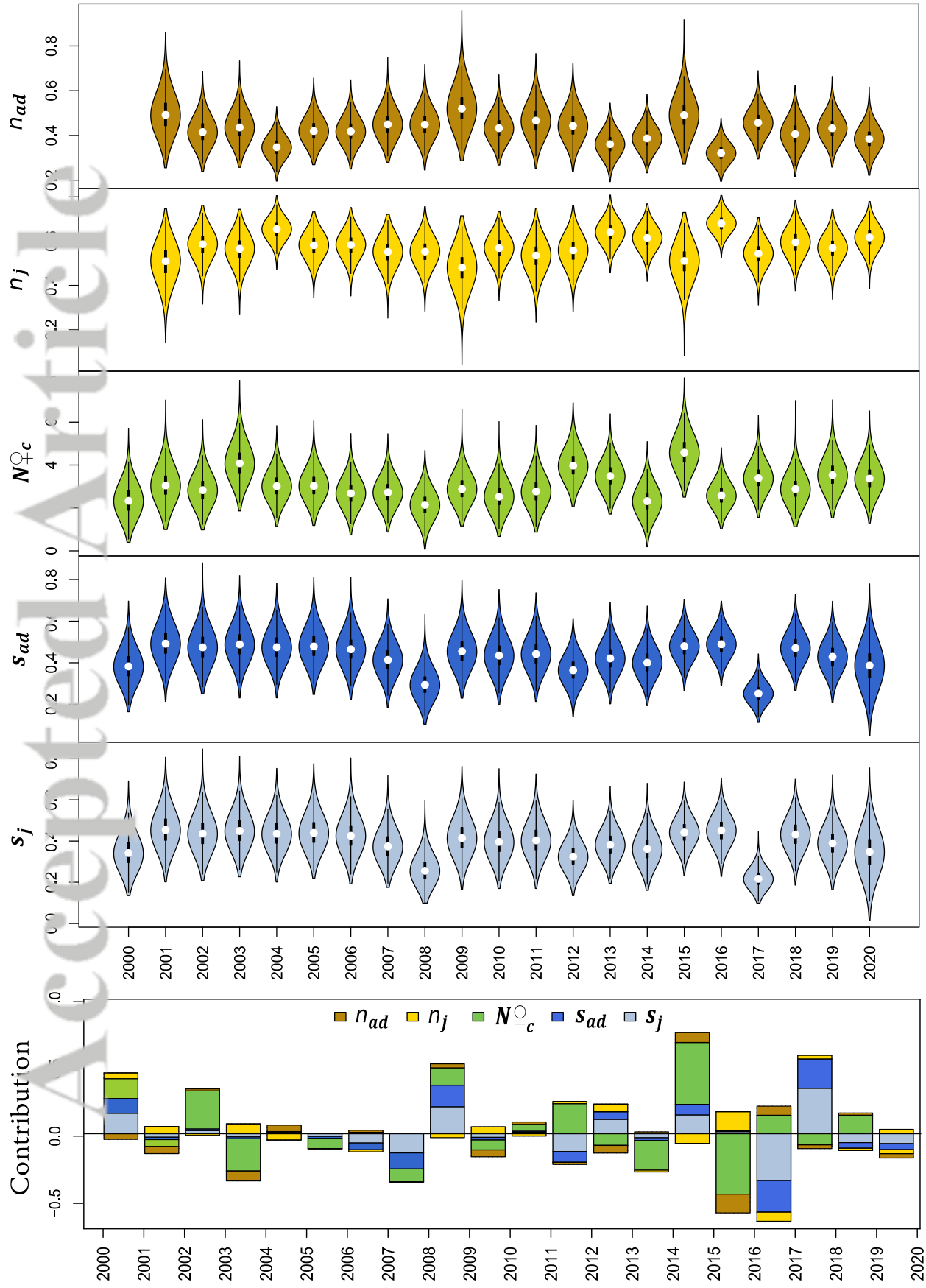
**Figure 1:** Simplified diagram of the IPM for the rock partridge as a directed acyclic graph (DAG) with nodes representing observed or unobserved quantities in the model. Observed data is symbolized as squares, estimated quantities as circles or diamonds (the latter represent variances of random effects) and arrows show dependencies between the nodes. Large dashed boxes represent the three different datasets, while the aqua box corresponds to the three main parameters used in the matrix population model. See the article for more information on notation.

**Figure 2:** Posterior distribution (mean  $\pm$  50 & 95% CRI) of annual demographic rates estimated by the IPM for the rock partridge in the French Alps for the period 2000–2020, along with annual contributions of the demographic rates and population structure to the variation in population growth rates estimated by the LTRE (lower panel).  $s_j$ = sub-adult annual survival,  $s_{ad}$ = adult annual survival,  $N_{\text{♀}c}$ = number of chicks per hen at the end of August,  $n_j$  = proportion of sub-adults,  $n_{ad}$  = proportion of adults.

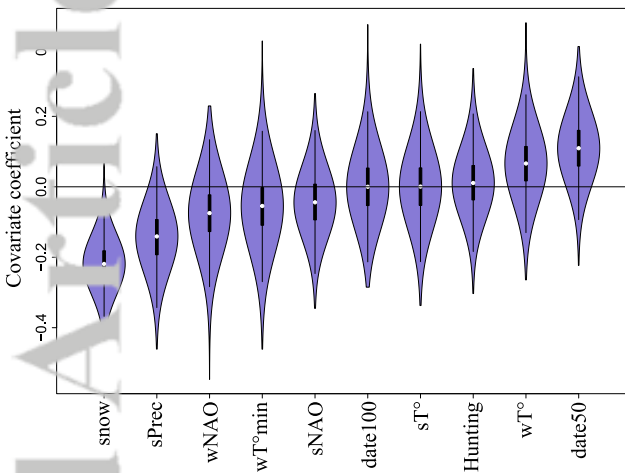
**Figure 3:** Regression coefficients (mean  $\pm$  50 & 95% CRI) of covariate effects on interannual variation of (A) monthly survival and (B) brood size, estimated by the IPM for the rock partridge in the French Alps. Both alpha and beta coefficients were represented for covariates for which the best model was a quadratic relation. Hunting = number of harvested birds the previous autumn, date50 = Julian date in spring when snow cover was reduced to half of the surface area, date100 = Julian date of snow-free ground in spring, snow = mean snow height during the winter (Dec–Mar), sNAO= summer North Atlantic Oscillation index (Jun–Aug), sT°= breeding period mean temperature (May–Aug), wNAO= winter North Atlantic Oscillation index (Dec–Feb), wT°= winter mean temperature (Dec–Mar), wT°min= temperature during the coldest fortnight of the winter, sPrec= breeding period sum of precipitation (May–Aug).



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### A Monthly survival $ms$



### B Brood size $bs$

