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Life on the edge: common slow pace of life but contrasted trajectories of alpine rock ptarmigan populations at their southern margin

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Investigating how and why the life history and demographic traits of a species vary across its range is fundamental to understand its evolution and population ecology and then develop sustainable management recommendations. At the margins of a species' distribution range, populations are expected to exhibit a slower pace of life than in core areas, making them less able to withstand pressures that impact survival. To explore these questions, we estimated age and sex-dependent seasonal survival probabilities using 305 radio-tagged birds monitored over a 18-year period in two alpine rock ptarmigan populations at the southern limit of their distribution, one in the Alps and one in the Pyrenees. We also estimated fecundity of both populations and then conducted sensitivity analysis as well as population viability analyses using deterministic and stochastic population models. Annual survival probability was high in both populations (0.65 for adults and 0.60 for juveniles), but reproductive success was much lower in the Alps (0.55 chicks per hen in the Alps vs 1.19 in the Pyrenees). The results showed that adult survival was the most sensitive demographic parameter. While population in the Pyrenees was stable (λ=1.01; 0.87–1.16), the other in the Alps appeared to be strongly declining (λ=0.81; 0.72–0.91) and this difference was clearly driven by differences of fecundity. While our findings confirm that our peripheral populations are associated with a slower pace of life, they present the particularity to be situated both at the edge and at high altitude. A more systematic study of peripheral population at higher latitude or on island may provide new insight on inter-pop variations of pace of life that would be useful for manager of these cold-adapted species. Key-words: Life history traits, demography, matrix model, telemetry, population viability analysis, age-class survival, fecundity.

Investigating how and why demographic traits of a species vary across its range is fundamental to understand life history evolution and population ecology (Holt and Keitt 2005). The limits of a species' distribution provide natural laboratories to explore these questions (Kawecki 2008, Nadeau and Urban 2019). Because marginal populations occupy less favorable habitat, their demographic characteristics may vary from those located at the core of the species' distribution (Holt and Keitt 2000). Populations at margins are often more fragmented resulting in lower and more variable density than populations in core habitats (Channell and Lomolino 2000, but see Sagarin et al. 2006). Consequently, they tend to be more prone to local extinctions due to environmental fluctuations and demographic stochasticity (Channell and Lomolino 2000, Hampe and Petit 2005, Angert 2006, Munilla et al. 2007, Kawecki 2008). Peripheral populations may use a strategy characterized by a longer lifespan and reduced annual productivity allowing spreading the reproductive effort over several years to lower the risk associated with harsh years (Stearns 1976, Gillespie 1977, Bennett and Owens 2002). Hence, marginal populations are expected to exhibit a slower pace of life than core populations (Hampe and Petit 2005).

Because life history strategies may differ across a species distribution, their populations' growth rate are also expected to varyingly be sensitive to changes in the demographic rates

(Saether et al. 2008). Understanding the variation in demographic rates that impact the growth rate may inform management plans. In exploited species, differences in life history strategies among populations can result in a potential risk of unsustainable hunting in peripheral populations if harvest management regulations are based on knowledge acquired from core populations, which have a different life history strategy. Populations with this fast life history pattern are indeed more sensitive to variation in fecundity than adult survival (Bennett and Owens 2002). In contrast, populations with a slow life history, such as peripheral populations, are expected to be more sensitive to changes in adult survival (Oli and Dobson 2003).

Arctic and alpine ptarmigan, *Lagopus* sp., are relevant subjects for studying demographic strategies and harvest tolerance along the core–periphery gradient (Ellison 1991, Sandercock et al. 2005b, Boakes et al. 2018) driven both by latitude and elevation (Balasubramaniam and Rotenberry 2016). They have large populations and wide distributions across Eurasia and North America. The peripheral populations occur in mountaintop refugia or in islands (McCarty 2001, Bech et al. 2009), and many are known to be declining. Ptarmigan at the southern extent appear to have declined earlier than in core populations (Storch 2000). While habitat loss and degradation seem to be the main causes, interactions with other threats, such as disturbance by human activity or climate change, remain poorly understood (Storch 2007).

Grouse are game birds and monitoring their populations has a long tradition in many parts of Europe and North America (Rogers 1963, Gates et al. 1968). Studies providing demographic parameters on arctic and alpine grouse in their core range are widespread, especially for cyclic northern populations: e.g. in Scotland (Watson et al. 1998), Norway (Unander et al. 2016), Iceland (Magnússon et al. 2004, Nielsen 2011), Alaska (Theberge and Bendell 1980) and Canada (Cotter 1999). In contrast, smaller mountain populations at the southern edge of the European range have been the subject of only few demographic studies (however see Caizergues 1997, Montadert and Leonard 2003, Novoa et al. 2008, Kobayashi and Nakamura 2013). This paucity of research stems from the fact that these are low density populations living at high altitudes, making field work particularly arduous (Imperio et al. 2013).

The rock ptarmigan *Lagopus muta* is a small-bodied grouse (male mass 448–880 g; female mass 406–700 g) occurring over a wide latitudinal range (Del Hoyo et al. 1994). While its distribution is continuous over large areas of North America and Russia (Supplementary material Appendix 1), rock ptarmigan is also present in several alpine areas in North America and in the southern mountains of Europe and Japan. Most populations inhabit subarctic or arctic lands above 60°N, where they exhibit major cyclic fluctuations caused by a well-studied combination of biotic factors and climatic variation (Watson et al. 1998, Moss and Watson 2001, Nielsen 2011). Spring population density in core areas is variable but generally high: e.g. 7–34 males per km^2 at some locations in Iceland (Gardarsson 1988) and 3–5 pairs per km^2 in Svalbard (Henden et al. 2017). A recent review of populations from seven arctic countries also indicated a mean density of males in spring around 4.3 per km^2, with high variations among the monitoring sites (range = [0.4, 17.1], Fuglei et al. 2019). Populations of the southern mountains of Europe tend to have medium to low density, varying from 1.5 to 6.7 per km^2 in the Austrian Alps (Nopp-Mayr and Zohmann 2008) and from 1.1 to 4.8 in northern French Alps, Italy and Switzerland (Desmet 1988a, Morscheidt 1994, Imperio et al. 2013).

A recent comparison of inter-population rock ptarmigan vital rates suggests a continuum from a relatively fast to a relatively slow pace of life along a latitudinal gradient (Unander et al. 2016). The same pattern has been documented in comparisons of closely related species of ptarmigan across biomes, with peripheral alpine populations exhibiting slower life history strategies (Sandercock et al. 2005a, b, Wilson and Martin 2011).

In our study, we aimed to test the hypothesis that peripheral populations of rock ptarmigan exhibit a slower pace of life than core populations. To do this, we estimated age and sex-dependent survival and fecundity parameters of two alpine rock ptarmigan populations at the southern edge of their distribution (one in the Alps and one in the Pyrenees), and then compared these estimations with recent results from core populations (Unander et al. 2016). We expected these two peripheral populations to exhibit higher survival and lower fecundity compared to northern core populations. In addition, we developed deterministic and stochastic population models to obtain insights on population trajectories and population growth rate sensitivity to demographic parameters.

Material and methods

Study areas

The study was conducted in the Pyrenees and Alps mountain ranges in France, located approximately 520 km apart (Fig. 1). We studied two subspecies of rock ptarmigan *Lagopus m. helvetica*, and *L. m. pyrenaica*, the first one living in the Alps and the second one in the Pyrenees. Our study areas in the northern Alps was the Haut Giffre massif (HG, 20 000 ha) and in the Pyrenees the Canigou Massif (CM, 27 000 ha). Additional data was also collected on adjacent massifs approximately 10–25 km from the study sites (Fig. 1). In both locations, rock ptarmigan occupy alpine habitats between 1850 and 2900 m a.s.l., dominated by ericaceous shrubs mixed with other dwarf alpine plants. However, the substrate and climate differ markedly between the two locations. The HG study area is a limestone plateau with abundant crevasses and small cliffs and is one of the wettest regions in the French Alps (mean annual precipitation 1666 mm at 700 m a.s.l.; Desmet 1988b). The CM study area is a succession of eroded plateaus and U-shaped valleys with large extents of gneiss scree and a relatively dry climate (850 mm at 1550 m a.s.l.), where woodlands of mountain pine *Pinus uncinata* occur at the lowest elevations of rock ptarmigan habitat. Hunting of rock ptarmigan was permitted during autumn from late September to mid-November in the department of Haute-Savoie (including HG) but was a minimal cause of death (annual hunting

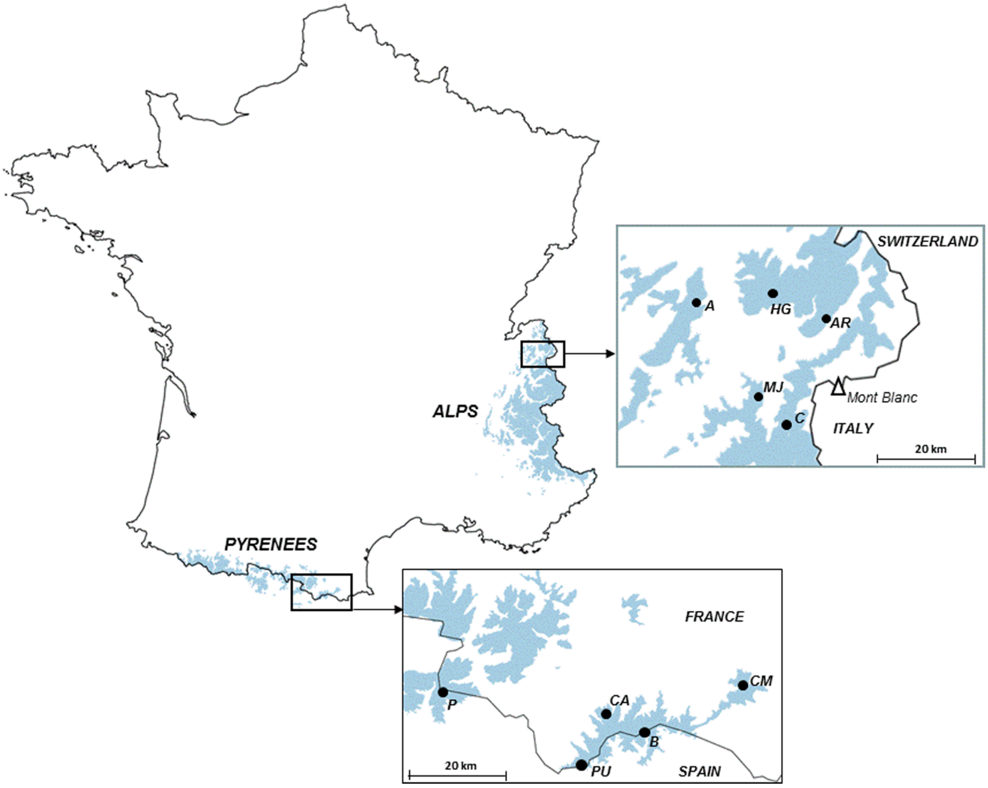

Figure 1. Maps of the two French mountain range where rock ptarmigan birds were captured, radioequipped and monitored to estimate survival and reproductive parameters, from 1999 to 2007. Light blue surfaces correspond to the potential rock ptarmigan distribution. Black dots represent capture sites within the study areas (northern Alps: A = Aravis, HG = Haut Giffre, AR = Aiguilles Rouges, MJ = Mont Joly, C = Contamines-Montjoie; eastern Pyrenees: P = Puigpedrós, PU = Puigmal, CA = Cambre d'Ase, B = Bastiments, CM = Canigou massif).

bag varying from 0 to 17 birds during the study period). On the contrary it was prohibited at CM and surrounding areas. During the study period, cattle and sheep grazing were moderate at the two locations, with stocking rates of around 0.05–0.10 animal unit month/ha (Novoa et al. 2011). Both areas are visited by a large number of hikers in July–August. The HG site includes a popular ski resort (Flaine-Grand Massif), which covers one-third of the study area, while CM is only sparsely frequented in winter. At both sites, the potential predators of adult rock ptarmigan are the golden eagle *Aquila chrysaëtos*, goshawk *Accipiter gentilis*, peregrine falcon *Falco peregrinus*, Eurasian eagle-owl *Bubo bubo*, red fox *Vulpes vulpes*, pine marten *Martes martes*, stone marten *Martes foina* and stoat *Mustela erminea*. Potential nest predators are mainly the red fox, pine marten, stone marten, stoat, occasionally the alpine marmot *Marmota marmota*, northern raven *Corvus corax* and red-billed chough *Pyrrhocorax pyrrhocorax*.

Data collection

From 1999 to 2017, 305 rock ptarmigan were captured and fitted with 7–8.5-g necklace radio-transmitters (Holohil system, <3% of body mass) with an expected lifespan of 1–3 years. Each bird was weighted (before marking) and its age was determined by the amount of black pigment on the second and third outermost wing primaries (Weeden and Watson 1967, Ellison and Léonard 1996). Females were classified as juveniles (0–7 months), yearlings (8–20 months) if the ninth wing primary (P9) had darker pigmentation than the eighth (P8), and as adults (>20 months) if P9 had the same or lighter pigmentation than P8. We considered chicks to be fully grown at the age of 4–5 weeks. We defined juveniles as young birds independent of parental care and less than 8 months old: thus birds moved from one age class to the next on 31 March (i.e. at the onset of the spring molt). Capture effort was comparable between the two areas (Supplementary material Appendix 2), and the most effective capture method was to lure brood-rearing females toward a net with a tape-recorded chick distress call (Brenot et al. 2002). The sample of radio-tagged individuals was female-biased (105 adult females versus 18 adult males at HG, and 68 females versus 6 males at CM). Juveniles (30 at HG and 78 at CM) were caught in the autumn (mostly September) by driving the brood toward a barrage of nets. In addition, several birds (13 adult females and 18 adult males at HG and 6 adult males at CM) were captured outside the rearing period using a net gun. Some previously equipped adult females were physically recaptured, either during reproduction (in order to change their transmitter – 35 birds) or during autumn (in order to change their transmitter – 3 birds, or in order to capture their chicks – 13 birds).

Birds were located at least once per month from the ground using a portable receiver (Yaesu, Custom Electronics or ICOM ICR20) and a handheld Yagi antenna. Location monitoring intensity varied throughout the year, with a maximum of effort during reproduction and autumn dispersal (Supplementary material Appendix 3). Nests for the majority of birds were located using binoculars, from a distance of approximatively five meters during incubation. Nests were not found for 18% of birds in the Alps, however it was unknown if nests were initiated or not based on our monitoring effort. Clutch size was rarely known. Brood size was recorded from hatching to the end of reproduction using both transmitter monitoring and counts with pointing dog at the end of August (Novoa et al. 2011). We considered that a female had a successful clutch when at least one egg hatched, and had successfully reared a brood when at least one chick fledged in late August.

Transmitter failure was characterized by a sudden ceasing of the signal, whereas the mortality sensor that activated after 12 h of immobility. Aerial surveys by fixed-wing aircraft were conducted one month after transmitter signal was lost. Nearly all birds whose transmitter stopped working prematurely have been observed using color banding, confirming the distinction between transmitter failure and mortality. We considered the date of bird death to be the median between the last 'alive' and the first 'dead' signal (CM: median 8.5 days; HG: 13.5 days, with the difference due to challenging access during winter). Dead birds were discovered and they were examined to determine the cause of mortality.

Data analysis

Survival analysis

We estimated monthly survival using multi-state capture–mark–recapture (CMR) models (Lebreton and Pradel 2002). The data consisted of monthly individual encounter histories from the date of capture to the date of death or radio failure. We applied right censoring on individuals whose transmitters stopped working, thus detection probability was always equal to 1. We grouped encounter occasions by season, according to the species' annual life cycle: [Apr–Aug] = breeding season, [Sep–Oct] = autumn dispersal and [Nov–Mar] = winter. We considered that the breeding season starts in April at the molting period, which also corresponds to pair formation (Scherini et al. 2003). The autumn period starts in September when family groups break up and juveniles begin to disperse (Favaron et al. 2006).

Individuals could be in nine mutually exclusive states (Fig. 2, Supplementary material Appendix 4). These states combined information on a bird's age class (juvenile: J, yearling: Y or adult: A and AR) and whether they were recently equipped or not (1: less than one month, 2+ two months or over). Female adults that were physically recaptured a second or third time were coded AR. The two last possible states were 'newly dead' (ND) and 'dead' (D) in order to model the detection probability of dead individuals (Lebreton et al. 1999). Hence, the nine states are J1, Y1, A1, J2, Y2, A2, AR, ND and D. At first capture, birds could be in one of the three following states: J1, Y1 or A1. The transition from one state to another from month t to $t+1$ was modeled through three successive steps: survival (φ), physical recapture (r) and ageing (a). The step of recapture here refers to radio-equipped birds that were physically recaptured a second or a third time. In our dataset, it included only adult females that were recaptured in order to mark their brood. Ageing refers to the transition from one age class to another, thus (a) was equal to 1 at occasions corresponding to the March–April transition (no captures from December to March) and 0 for other transitions.

Numerous studies conducted on radio-tagged grouse (Caizergues and Ellison 1998, Blomberg et al. 2018) have highlighted the potential for negative impacts of capturing, handling and marking on survival (Cotter and Gratto 1995) and/or reproduction (Erikstad 1979), while others have found no effect (Thirgood 1995, Hagen et al. 2006). Gen-

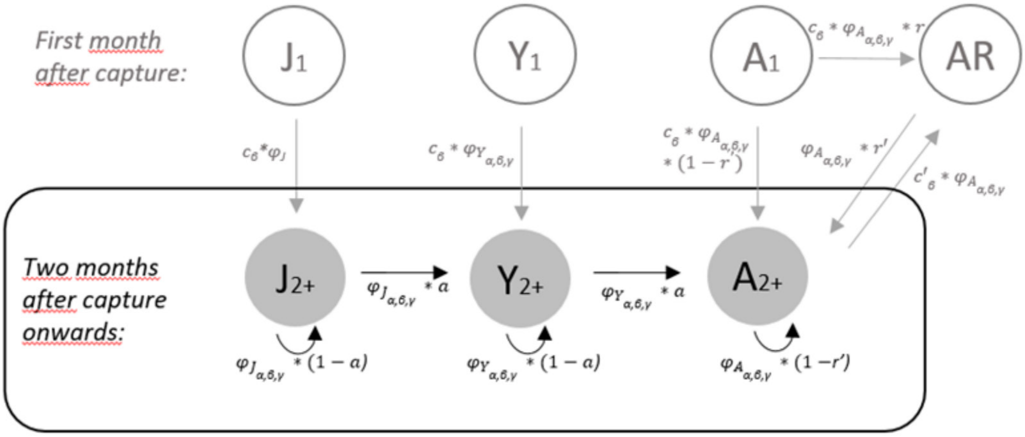

Figure 2. The complete post-breeding lifecycle used as base model (before model selection) in the survival analysis of radio-equipped rock ptarmigan in northern Alps and eastern Pyrenees from 1999 to 2007. We defined nine states combining information on the age class of the bird (juvenile: J, yearling: Y or adult: A and AR) and whether they were recently radio-equipped (1: less than one month ago, 2+ two months or more). The states AR represented female adults that were physically recaptured a second or third time. The last two possible states were 'newly dead' (ND) and 'dead' (D). A bird entered at state J1, Y1 or A1. The transition from one state to another from month t to $t+1$ was modeled through three successive steps: survival (φ), physical recapture (r and r') and ageing (a). Ageing was the transition from one age class to the next, thus (a) was equal to 1 at occasions corresponding to the transition March–April and 0 for other transitions (no capture from December to March). We tested several effects on survival probabilities: α season, β sex, γ site and finally coefficients c and c' that model capture effects.

erally, short-term effects on survival are right censored and individuals that died 2–4 weeks after release are excluded from the analysis (Caizergues 1997, Kaler et al. 2010). Thus, potentially inflating the survival as some birds may have died from natural causes. In our study, we modeled survival using 'time since release' as a temporal covariate. We applied an additive effect of first capture and physical recapture on survival to deal with the fact that captures occurred unevenly across months and seasons (A1 captures: 1.3% winter, 95.3% breeding period, 3.1% autumn; Y1 captures: 94.7% breeding period, 5.3% autumn; J1 captures: 97.2% autumn, 2.8% breeding period; R1 recaptures: 68.6% breeding period, 31.4% autumn). Consequently, the impact of capture on juvenile survival was extrapolated from the effect on yearlings and adults.

Model selection and parameter estimations were carried out using the E-SURGE program (2.1.4) (Choquet et al. 2009) and based on Akaike's information criterion for small samples (AICc) (Burnham and Anderson 2002). We adopted a sequential backward selection procedure from a general model that included effects, as well as all interactions between effects, of 1) age and season on state at first capture, 2) state (A or AR) on physical recapture probability, 3) age, sex, season and site on natural survival rate, and lastly, 4) season and sex of the capture effect on survival following capture/recapture. We first simplified the effects on initial states, then on physical recapture probability, and finally on monthly survival. We progressively simplified the monthly survival estimation, first we tried to remove site effect, then age, then sex by season and finally season, always starting with interactions, this order being based on expert knowlegde regarding the most important factors.

Analysis of breeding parameters

We estimated apparent nest success (the proportion of initiated nests that successfully hatched) using data from females that had been monitored since the beginning of the breeding season in March ($n = 164$). We fitted generalized linear mixed models (GLMM), assuming binomial error with year and individual identity as random effects using the lme4 package. We tested for potential effects of age and site on both nest success and the proportion of hens with chicks at the end of August (hens with a successful nest and then at least one chick that survived through the rearing period). Next, we looked for potential effects of age (yearling versus adult) and site on the number of chicks per hen, but only for females with at least one chick in late August ($n = 154$). We fitted a GLMMs assuming truncated Poisson error with year as a random effect and the number of hens as an offset using the glmmTMB package (Brooks et al. 2017) in R ver. 3.4.4 (<www.r-project.org>). All reproductive parameters model selections were done using ANODEV.

Matrix population model and population viability analysis

To build the matrix population model, we used estimates from the best model obtained on survival and reproduction above. Hence, because, neither survival nor reproduction varied significantly between yearlings and adults we grouped them, ending up with only two age classes: juveniles and yearling-adults (below referred to as adults). We built a two-age-class post-breeding female-based matrix model to estimate the population growth rate at each site (Caswell 2006). Variation in the size and age structure of a population from time t to $t+1$ was computed from:

$$n_{t+1} = A \times n_t$$

where n was a vector describing the age structure of the population and A was the population projection matrix below:

$$A : \begin{bmatrix} sj \times bp \times Nbc \times \frac{1}{2} & sa \times bp \times Nbc \times \frac{1}{2} \\ sj & sa \end{bmatrix}$$

where sa was the yearly survival of adults and yearlings and sj the yearly survival of juveniles (from September to August); bp was the proportion of hens with chicks at the end of August and $Nbc \times 1/2$ was the number of juvenile females per brood assuming a balanced sex ratio at fledging.

Following the model selection performed using E-SURGE, we coded the best model for the survival analysis in Bayesian using JAGS (4.2.0 Plummer 2015). We derived annual survival (sj and sa) from the product of monthly survival. Fecundity (f) was defined as the product of $bp \times Nbc \times 1/2$. We modeled the proportion of hens with chicks (bp) using a binomial distribution, and brood size (Nbc) using a zero-truncated Poisson distribution. We then jointly coded likelihoods for survival and fecundity estimations along with the matrix model. We used Markov chain Monte Carlo (MCMC) methods to obtain the posterior distributions of the parameters of interest, with vague prior distributions for all the parameters to reflect little prior knowledge. We ran three chains of 100 000 iterations with 50 000 burn-in iterations and a thinning of 9. We checked for convergence by visualizing the mixing of chains and using the Brooks–Rubin–Gelman diagnostic (Brooks and Gelman 1998). We first ran a deterministic model using constant values for sj, sa, bp and Nbc over the years, retrieving parameter estimations from each iteration of the MCMC chain. The deterministic model allowed us to estimate, for both sites, population growth rates (the dominant eigenvalue), reproductive values, stable-age distributions, generation times and elasticities, using the popbio package (Stubben and Milligan 2007) in R (<www.r-project.org>). We also looked at elasticities of lambda to the lower-level parameters (sa, sj, bp and Nbc), keeping in mind that these elasticities do not sum to unity and thus cannot directly be interpreted as absolute contributions to lambda (Caswell 2006).

In a second step, we introduced environmental stochasticity in the model by allowing the matrix A to be drawn each year from the posterior distributions of each demographic parameter. Such a modeling approach intentionally mixed environmental stochasticity and sampling variance. We simulated 1000 population trajectories over 40 years and then calculated extinction risk and the median time to extinction (Morris and Doak 2004). We fixed the initial number of females in a population to 100, which we assumed corresponds to the minimum size of the study population based on the number of territories. We applied an initial age ratio

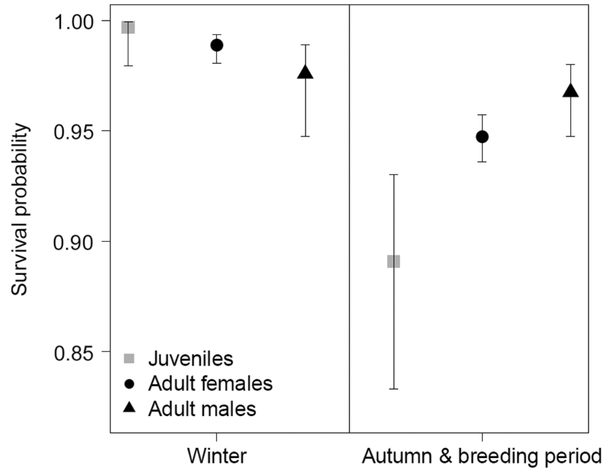

Figure 3. Seasonal monthly survival rates (95% CI) of 305 radio-equipped rock ptarmigans (juveniles n = 108, adult females n = 173, adult males n = 24), estimated from the multi-event model, from 1999 to 2017 at both study sites (survival was comparable in the northern Alps and in the eastern Pyrenees). Presented survivals take into account correction for short-term capture effect.

of 75% adults and 25% juveniles, based on observations during the study period of July–August. Because we lack proper information to deal with it, we did not include density dependence in our models. Our study design allowed us to take into account emigration, since the location of birds was known and no bird left the study area. However, we had no information about immigration.

Results

Survival analysis

The best model from the selection procedure included the effects of age and season on initial state and of age, sex and season on survival probability (Supplementary material Appendix 4). The best model did not include any site effect; however, survival during the first month after release was different from base survival. We did not find any impact of site or sex on the capture effect.

Monthly survival probability was similar between yearlings and adults (hereafter, adult survival). Moreover, the best model included similar monthly survival probability for the breeding period and autumn for both juveniles and adults. However, compared to these two seasons, monthly survival probability in winter was about 2% higher for adults and 10% higher for juveniles (Fig. 3). During winter, juveniles survival was higher than adults (+2% per month, adult female = 0.99, IC 0.98-0.99; adult male = 0.98, IC 0.95–0.99; juvenile = 1.00, IC 0.98–1.00). In contrast, juvenile monthly survival probability was 11.46% lower than that of adults during the breeding period and autumn (juvenile = 0.89, CI 0.83–0.93; adult female = 0.95, CI 0.46–0.96; adult male = 0.97, IC 0.95–0.98).

Despite the relatively low number of adult males sampled, we found marginal effects of sex on adult monthly survival probability, which varied between seasons. Adult male monthly survival probability was slightly higher than that of females during the breeding period and autumn (female = 0.95, 95% CI 0.94–0.96; male = 0.97, 95% CI 0.95–0.98), but lower during winter (female = 0.99, 95% CI 0.98–0.99; male = 0.98, 95% CI 0.95–0.99). Derived annual survival probability for adult and yearling males was on average 11% higher than annual survival probability for adult and yearling females, however, the 95% CI overlapped. Monthly survival probability in the month following initial capture, as well as following physical recapture in the breeding period, was 9% lower compared to the monthly survival probability one month after the capture and later (beta capture = −3.99, 95% CI 4.30–3.69; beta recapture = −3.09, 95%CI −3.91 to −2.27). However, monthly survival immediately after physical recapture in autumn was equal to one because all birds survived (n = 16).

Analysis of breeding parameters

We found no significant effect of age on nest success (Supplementary material Appendix 6, β = −0.09, SE = 0.43, zvalue = −0.20, p = 0.84; Yearlings: mean = 0.56, SE = 0.01; Adults: mean = 0.58, SE = 0.01). We found a marginally significant effect of site, as nest success was 22% lower at HG than at CM (β = −0.56, SE = 0.33, zvalue = −1.73, p = 0.08, HG: mean = 0.51, SE = 0.002; CM: mean = 0.65, SE = 0.002). The proportion of hens with chicks at the end of August did not differ according to age (β = −0.02, SE = 0.46, zvalue = −0.05, p = 0.96; HG: mean = 0.30, SE = 0.02; CM: mean = 0.29, SE = 0.01), but differed between sites, with almost twice as much at CM than at HG (Table 1, β = 0.88, SE = 0.35, zvalue = 2.50, p = 0.01). The brood size of hens with chicks at the end of August did not vary with age (β = −0.003, SE = 0.13, zvalue = −0.02, p = 0.98; HG: mean = 2.76, SE = 0.03; CM: mean = 2.81, SE = 0.03), but was almost twice as high at CM than at HG (Table 1, β = 0.20, SE = 0.10, zvalue = 1.96, p = 0.05). Our models converged and had minimal overdispersion (~1.1) in the truncated Poisson.

Table 1. Median rates of demographic parameters (derived quantities from posterior densities) with credibility intervals (CI) from the deterministic demographic models for the two sites (CM Canigou massif and HG Haut Giffre).

Parameter	CM median (95% CI)	HG median (95% CI)
φYAy adult female yearly survival	0.65 (0.59–0.70)	
φJy juvenile yearly survival	0.60 (0.51–0.67)	
bp Proportion of hens with chicks in late August	0.39 (0.29–0.51, n = 74)	0.22 (0.14–0.31, n = 90)
Nbc Number of chicks per brood in late August	3.06 (2.67–3.49, n = 78)	2.49 (2.13–2.9, n = 76)

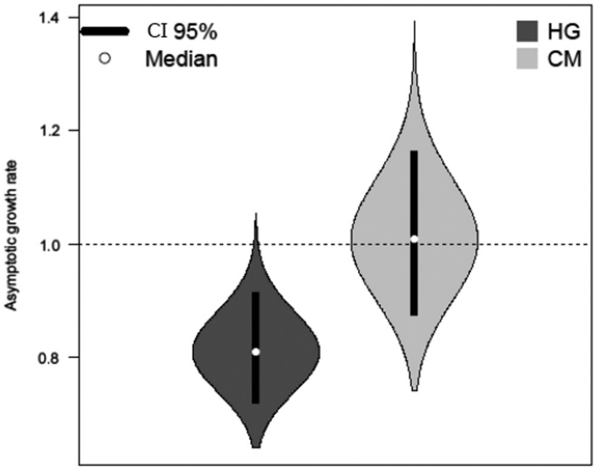

Figure 4. Asymptotic population growth rates from 1999 to 2017 of rock ptarmigan populations at Haut Giffre (HG, dark grey) and Canigou Massif (CM, light grey) obtained with the deterministic model that combined both the models of survival and reproduction. The outer shape represents the posterior distribution of parameters. The inner black line represents the 95% credibility interval. The central white dot represents the median value.

Matrix population model and population viability analysis

Deterministic model

Our demographic models revealed contrasting population dynamics between the two sites, where λ at CM indicated stable population (median = 1.01; 95% CI = 0.87–1.16, Fig. 4, Table 2). Alternatively, λ at HG suggested a declining population (median = 0.81; 95% CI = 0.72–0.91). Generation time was about 11% higher at HG than at CM (4.94 and 4.41 respectively, Table 2). Adults were the dominant age class at both sites, but the stable age structure differed with nearly twice the proportion of juveniles at CM (39%) versus HG (20%). The elasticity of λ to the lower-level parameters indicated that changes in adult survival were affecting λ (Table 2). Adult survival elasticity accounted for ~66% of λ variations at HG, but ~50% at CM.

Stochastic model

After modeling 1000 population trajectories, estimates indicated that the risk of extinction after 40 years was null at CM, whereas it was 100% at HG (Fig. 5). With an initial population size of 100 females, the median time to extinction at HG was 23 years. The median stochastic λ resulting from the 1000 trajectories was comparable to the asymptotic λ obtained with deterministic models: 0.811 (SD = 0.007) at HG and 1.01 (SD = 0.01) at CM.

Table 2. Median rates of parameters (derived quantities from posterior densities) with credibility intervals (CI) from the deterministic demographic models for the two sites (CM Canigou massif and HG Haut Giffre).

Parameter	CM median (95% CI)	HG median (95% CI)
λ Asymptotic growth rate	1.01 (0.87–1.16)	0.81 (0.72–0.91)
Gt Generation time	4.41 (4.16–4.72)	4.94 (0.46–5.65)
E φYA Elasticity adult survival	0.65 (0.57–0.72)	0.80 (0.73–0.87)
E φJ Elasticity juvenile survival	0.35 (0.28–0.43)	0.20 (0.13–0.27)
E f Elasticity fecundity	0.35 (0.28–0.43)	0.20 (0.13–0.27)

Discussion

Based on the monitoring of more than 300 individuals over 18 years from two alpine rock ptarmigan populations at the southern margin of the species' European distribution, our results indicated high annual survival at both sites compared to estimates for core populations. As expected, the opposite pattern was found for fecundity where mean brood size was low at both sites compared to what is known in arctic populations. Consistent with our hypothesis, the pace of life was thus slower in southern peripheral populations than in the northern core populations. Thus, peripheral populations were more sensitive to changes in adult survival than those in the core. These patterns were manifested in contrasting estimates of λ for our two study populations.

Short-term impact of radio-tagging on survival

Radio-tagging estimation of survival relies on the assumption that transmitters do not influence demographic rates (Pollock et al. 1989, Hagen et al. 2006). Previous studies on grouse species have observed negative impacts of this marking method on survival and/or reproduction (Erikstad 1979, Caizergues and Ellison 1998). We developed an innovative modeling method to test a potential short-term capture effect on survival directly by modeling its effect on survival. We also explored the hypothesis that the impact of capture/physical recapture on survival would be noticeable over several months by using a more complex model based on 17 states (Supplementary material Appendix 5). This analysis showed that only the first month after the recapture present a different survival probability. Survival probability immediately after breeding season capture was on average 9–10% lower than survival probability not following capture. The magnitude of this negative impact is quite low compared to that highlighted in a previous study on rock ptarmigan in Canada (Cotter and Gratto 1995), where they found that radio-equipped adult males had a survival rate about 20–38% lower than leg-banded birds during the month of June. We estimated the impact of capture on survival by comparing survival immediately after the first capture with the survival of birds during the whole season and of the years after. However, in our study first captures were biased towards brood-rearing females, which are known to have lower survival than non-brood hens. Thus, our study design may overestimate the impact of capture on survival. Females recaptured during the breeding period that were handled in order to change their transmitter had similar mortality rates to that following initial capture. The 16 females recaptured during autumn survived the first month after release, however, only three were fitted with new transmitters, the remainder were only lured to catch their chicks. We cannot conclude whether this higher survival in autumn is related to body condition or reduced stress related to brooding older chicks.

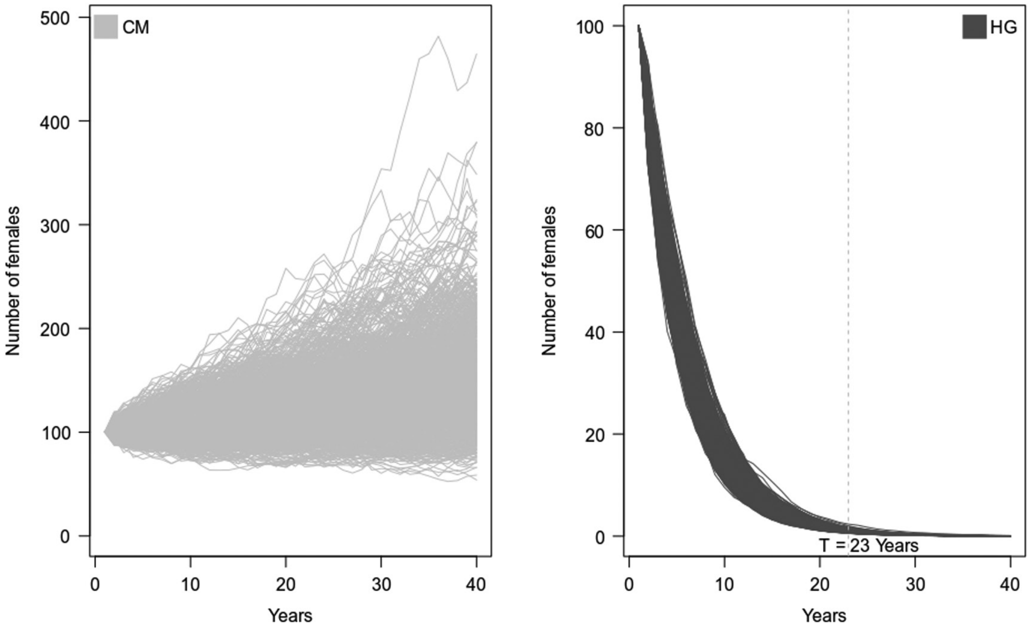

Figure 5. Population trajectories predicted for the next 40 years by the stochastic model for the Canigou massif (CM, left) and Haut Giffre (HG, right), that combined both the models of survival and reproduction, with an initial population of 100 females. Parameter values were derived each year from the posterior distributions. 'T = 23' corresponds to the median extinction rate at HG.

Contrasting population trajectories

Our findings suggested that the population at CM was stable, and the one at HG was declining. The asymptotic λ obtained at CM (λ = 1.01) was consistent with annual spring counts of males and late summer counts of adults and young, which indicated a slight decline (<1% per year) from 2000 to 2009 (<www.observatoire-galliformes-montagne.com>). Spring counts at HG indicated a decline (4% per year) (Calenge 2011, Novoa et al. 2014), but our estimates indicated a 19% annual decline. We speculate that asymmetrical dispersion may explain this difference between the estimated λ and observations from counts. Source–sink dynamics seem a common feature of grouse populations in anthropogenic, fragmented landscapes (Kirol et al. 2015). Previous studies on white-tailed ptarmigan have shown the importance of external recruitment on the persistence of small populations (Martin et al. 2000).

We did not find measurable difference in survival between our two sites. Alternatively, we detected strong differences in breeding success that explained the contrasting trajectories of our populations. We found a 30% lower nest success, and productivity (i.e. chicks per hen and brood size) two times lower at HG than at CM. These results indicated that breeding failure was much higher at HG and throughout the reproductive period. We speculate that a succession of years with an unfavorable climate, especially due to rainfall during the chick-rearing period in the Alps lead to this low reproductive success. Additionally, bird body condition in the Alps was poor compared to the Pyrenees (Novoa et al. 2008, Kobayashi and Nakamura 2013). Breeding failure could related to a divergence in predator community related to the large ski resort in HG that may foster generalist predators (Watson and Moss 2004).

Sex, age and seasonal-dependent variations of survival probabilities

Our results showing variation in survival between sexes and seasons are consistent with those of other studies. Monthly survival was higher in winter compared to autumn or breeding period. This seasonal pattern of survival is consistent to what has been observed in Norway for the willow ptarmigan (Sandercock et al. 2011). Mountain populations' natural mortality was highest during autumn movements and nesting due to predation by gyrfalcons *Falco rusticolus*, while lower for coastal populations with wintering falcons (Brøseth et al. 2012). We suspect a comparable pattern in our mountain populations with a decrease in the occurrence of mammalian predators and raptors during winter. We also found that adult male monthly survival was marginally higher than females during autumn and the breeding period, but the opposite occurred in winter. Generally, females are more exposed to predation during reproduction (from June to August), and males are more vulnerable during territorial defense (from March to June, Hannon et al. 2003).

Slow pace of life in peripheral populations of rock ptarmigan

As expected, our annual survival estimates were high (female = 0.65) compared to previous estimates for northern populations of rock ptarmigan (range = 0.40–0.65, Unander et al. 2016). However, we found the opposite pattern for fecundity: mean brood size in late August turned out to be low at both sites (2.5 at HG and 3.0 at CM) in comparison with arctic populations (from 5.5 to 7.1 in Svalbard; Steen and Unander, 1985). Our results support the hypothesis that these southern populations exhibit survivor strategies of the 'slow–fast continuum' within this species (Unander et al. 2016). With higher survival and reduced annual fecundity, the generation times estimated at both sites (Alps = 4.94 years, Pyrenees = 4.41 years) were about 43% higher than those reported for rock ptarmigan in Canada (2.61 years; Wilson and Martin 2012). In addition, adults were the dominant age class at both sites (60–80%) in contrast to northern populations (70–83% of young; Magnússon et al. 2004, Novoa et al. 2008). Demographic strategies based on a longer lifespan allow reproductive efforts to distributed over time, lessening the consequences of the occasional year of reproductive failure (Stearns 1976, Gillespie 1977, Bennett and Owens 2002). The populations we studied are inevitably more sensitive than northern populations to changes in survival compared to changes in reproduction. The slow demography of our study populations make them less able to tolerate disproportional mortality to adults (i.e. excessive predation or harvesting rates) compared to populations from core areas (Lebreton 2005, Péron 2013, Okamoto 2018).

Conclusion

We confirmed our hypothesis indicating that peripheral population was associated with a slower pace of life compared to core populations. Nevertheless, our two populations were unique because they were situated at their distributional limits and at high altitude. The importance of interactive effects across elevation and latitude on life history-traits for precocial birds in temperate regions cannot be ignored (Balasubramaniam and Rotenberry 2016). Indeed, latitude determines the altitude at which preferred ptarmigan habitats occur (Unander et al. 2016, Balasubramaniam and Rotenberry 2016). Arctic and alpine habitats are both characterized by short breeding seasons, cold temperatures, limited food availability and potentially high predation rates. However, day length and breeding prospect duration differs drastically during the breeding period along the latitudinal gradient (Sandercock et al. 2005b). Therefore, the disentangling of the respective influence of latitude versus position at the periphery or core was not totally possible in our study.

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Supplementary material (available online as Appendix wlb-00628 at <www.wildlifebiology/appendix/wlb-00628>). Appendix 1–6.