

Variable decline of Alpine Rock Ptarmigan (*Lagopus muta helvetica*) in Switzerland between regions and sites

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Abstract Alpine species adapted to mountain climate are particularly vulnerable to environmental changes and have recently come under multiple environmental pressures, such as climate change associated with habitat loss (e.g. upward shift of the treeline) and unfavourable weather, as well as increasing human recreation activities. A prime example is the Alpine Rock Ptarmigan (*Lagopus muta helvetica*), a subspecies restricted to the Alps. We analysed counts of territorial males from 40 sites in the Swiss Alps since 1995 with state-space models including various environmental variables. Over the 18 study years, population growth rate (as deduced from territorial males) was negative overall (−13 %), but varied greatly between different regions of the Swiss Alps (from −50 to +6 %) and between sites, with some declining drastically and others doing well. Overall and within regions, growth rates showed little evidence for synchrony between local study sites. We did not find an overall factor which explained variation in population growth rates, except for a

curvilinear effect of July temperature. It thus seems that various factors act locally to different degrees, such as upward shift of the treeline, unfavourable weather, and perhaps local increase in winter and/or summer tourism and unsustainable hunting. Together with a predicted shrinkage of the distribution area in the future due to global warming, the observed decrease of this isolated subspecies is of conservation concern. A better understanding of the different causes of decline and possibly different management strategies will be essential for the conservation of Alpine Rock Ptarmigan in Switzerland.

Keywords Alpine Rock Ptarmigan · Grouse · Population growth · Synchrony · Alpine habitat

Zusammenfassung

Regional unterschiedliche Abnahme des Alpenschneehuhns (*Lagopus muta helvetica*) in der Schweiz

Alpine Arten, die an das spezielle Klima der Gebirge angepasst sind, sind besonders empfindlich auf Umweltveränderungen, wie Klimawandel und die damit einhergehenden Habitatveränderungen (z.B. Höhersteigen der Baumgrenze), widriges Wetter und zunehmende Freizeitaktivitäten. Ein gutes Beispiel dafür ist das Alpenschneehuhn (*Lagopus muta helvetica*), eine Unterart, die auf die Alpen beschränkt ist. Wir werteten die Zählungen von territorialen Hähnen aus 40 Zählflächen in den Schweizer Alpen seit 1995 mit Zustandsraummodellen (state-space-models) unter Berücksichtigung verschiedener Umweltvariablen aus. Über die 18 Untersuchungsjahre war die Populationswachstumsrate (gemessen an den territorialen Hähnen) über alle Zählgebiete negativ (−13 %),

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variierte aber stark zwischen Regionen (von -50% bis $+6\%$) und Zählgebieten. In manchen Zählgebieten nahm der Bestand stark ab, während er in anderen eher zunahm. Über alle Zählgebiete, aber auch innerhalb der Regionen ergaben sich kaum Hinweise auf Synchronie in den Populationswachstumsraten der Zählgebiete. Wir fanden keinen Umweltfaktor, der die Variation in der Populationswachstumsrate erklärte, mit Ausnahme eines kurvilinearen Effekts der mittleren Juli-Temperatur. Es scheint somit, dass verschiedene Umweltfaktoren auf lokaler Ebene in unterschiedlicher Stärke auf die Bestandsentwicklung wirken, wie z.B. das Höhersteigen der Baumgrenze, widriges Wetter und lokal vielleicht auch die Zunahme des Winter- und Sommertourismus und nicht nachhaltige Jagd. Der hier beobachtete Rückgang des Alpenschneehuhns zusammen mit dem aufgrund der Klimaerwärmung vorausgesagten Schrumpfen des Verbreitungsgebietes ist beunruhigend. Es ist deshalb wichtig, die verschiedenen Gründe für den Bestandsrückgang besser zu verstehen und daraus verschiedene Managementstrategien für die Erhaltung des Alpenschneehuhns in der Schweiz zu entwickeln.

Introduction

Many species living in alpine habitats above the treeline, especially sedentary species, are well adapted to the extreme climatic conditions of mountains (Martin 2001). However, alpine species are particularly vulnerable to environmental changes (Chamberlain et al. 2013). A prime example is the Alpine Rock Ptarmigan (*Lagopus muta helvetica*), a subspecies of a circumpolar arctic species which occurs as a glacial relict in the Alps.

In high mountain areas, the rise in temperature associated with global warming has been particularly high (Beniston et al. 1997). As a result, alpine species are considered to move their ranges upward in elevation which will lead to considerable restrictions of their ranges (Chamberlain et al. 2013; Pernellet et al. 2015). For the Alpine Rock Ptarmigan an upward shift in certain parts of the Alps has been observed over the last 20 years (Pernellet et al. 2015). On the basis of rising temperatures during the breeding season, it was predicted that the distribution area in Switzerland will potentially decrease by up to two-thirds until the year 2070 if the temperature increases by $4\text{ }^{\circ}\text{C}$ (Revermann et al. 2012).

Negative population trends for Alpine Rock Ptarmigan have been found in Switzerland (Keller et al. 2010), Italy (Brichetti and Fracasso 2004; Peronace et al. 2012) and France (Haute-Savoie; Novoa et al. 2014), and the subspecies is classified as vulnerable in Italy (Peronace et al. 2012) and as near-threatened in Switzerland (Keller et al.

2010). However, as trends in population counts varied greatly among the studied populations in Switzerland, it remained unclear whether the negative population trend occurred range-wide or in certain areas only. It was also unclear what factors potentially affected the negative trend.

The first aim of this study was to analyse the country-wide population trend and to investigate whether synchrony in local population fluctuations (cf. Paradis et al. 2000) exists on a national or regional level. Synchronous population fluctuations are often an indication of a common impacting factor that operates over large spatial scales.

A second aim was to investigate which factors may influence the population trends. We specifically selected environmental factors which, in earlier studies, were suspected to influence the distribution, population size or population dynamics of the Alpine Rock Ptarmigan. One potential factor is summer temperature per se, because the thermoregulatory ability of animals is adapted to the climate of their environment (Speakman and Król 2010) and inhabitants of arctic or alpine areas may face physiological problems in warm ambient temperatures. Another factor for the potential habitat loss is the upward shift of the treeline (the limit of single trees higher than 2–3 m; Körner 2012) due to rising temperatures (Gehrig-Fasel et al. 2007; Harsch et al. 2009; Pernellet et al. 2015); the upper treeline is determined by a mean air temperature of greater than $6.4\text{ }^{\circ}\text{C}$ during at least 3 months of the year (Körner 2012). Associated with global warming, the amount and seasonal occurrence of precipitation and snow depths have altered (Terzago et al. 2013). In Rock Ptarmigan an early snowmelt in spring and a dry summer positively affect breeding success and thus population dynamics (Novoa et al. 2008; Imperio et al. 2013). In arctic and some high altitude ptarmigan populations, warm winters reduce population growth rates of the White-tailed Ptarmigan (*Lagopus leucurus*) (Wang et al. 2002; but see Wann et al. 2014). Although winter temperature did not seem to affect Rock Ptarmigan populations in the Alps until the 1970s (Bossert 1980), this may be the case now.

Derived from these findings, we considered the following factors in our study: July temperature and elevation (representing summer climate), distance to forest (representing the risk of habitat shrinkage due to an upward shifting treeline), summer precipitation and date of snowmelt (representing factors affecting breeding success), and winter temperature (representing winter climate). In this study we could not take into account the effects of human recreational activities in summer and winter (e.g. mountain biking, off-piste skiing; e.g. Thiel et al. 2008) which are increasing in the Alps and could locally affect the distribution and population size of the Alpine Rock Ptarmigan, and the effects of hunting (the species is hunted in most of

its range in Switzerland). The intensities of tourism and hunting have not been recorded systematically.

Methods

Study species and area

The Alpine Rock Ptarmigan is a relatively small species of grouse Tetraonidae with an adult body mass of 385–520 g (autumn weights; Brenot et al. 2005). In Switzerland it lives in the higher subalpine and alpine zone between 1700 and 3100 m above sea level (Schmid et al. 1998; Pernellet et al. 2015). While the global population is estimated to number over 8 million individuals (Rich et al. 2004), the alpine population, assigned to the subspecies *helvetica*, is relatively small with about 20,000–30,000 breeding pairs (BirdLife International 2004). Alpine Rock Ptarmigan are territorial during the breeding season and occur in pairs. The onset of breeding seems to be influenced by the time of spring snowmelt (Bossert 1980). In Switzerland the peak of courtship generally takes place from mid to late May. Chicks hatch in July. During autumn and winter birds often occur in flocks (Glutz von Blotzheim et al. 1973). During

courtship, territorial males regularly produce their characteristic calls, particularly in the early morning before sunrise, which can be heard up to 1000 m in good weather conditions (Bossert 1977).

For monitoring Alpine Rock Ptarmigan in Switzerland, 32 sites known to harbour ptarmigan were established within a project of the Swiss Federal Office for the Environment under the leadership of AB and RI and 15 sites by the Fish and Game Department of the canton of Grisons in the Grisons under the leadership of HJ. The sites varied in size from 65 to 500 ha and covered all of the Alpine Rock Ptarmigan distribution area in Switzerland with the exception of the Bernese Alps and marginal areas (Appendix S1). The starting year of monitoring varied among sites between 1995 and 2006 and counts were normally done annually. We used counts up to 2012. In seven sites counts could not be done each year because of logistic reasons and difficult access and were eventually given up. Hence in this study we included counts of the 40 sites presented in Fig. 1 (see also Appendix S1) which were grouped into five regions: Central Alps ($n = 6$), Eastern Alps ($n = 7$), Grisons ($n = 15$), Ticino ($n = 5$), Western Alps ($n = 7$). Most of these regions represented cantonal management units and also conformed, with a few exceptions, to biogeographical regions.

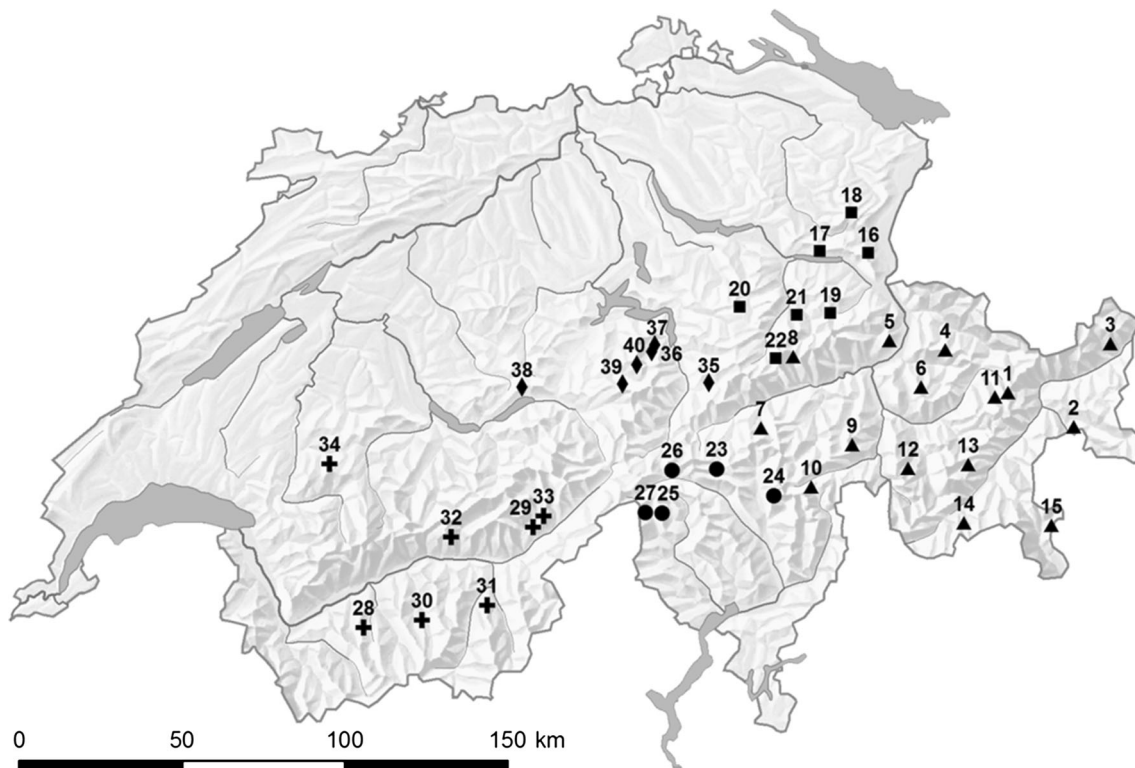


Fig. 1 Map of Switzerland showing the 40 Alpine Rock Ptarmigan sites of this study, grouped in five regions: *diamonds* Central Alps, *squares* Eastern Alps, *triangles* Grisons, *circles* Ticino, *plus signs* Western Alps. Elevation model © swisstopo

Population counts

Counts were done according to written instructions and a checklist by previously trained (field courses) local game wardens and assistants (mostly volunteer ornithologists, birdwatchers and hunters) between mid and late May, in the Grisons mainly in the first half of June, when weather conditions were favourable. Each site was counted once annually. In a few cases access was difficult, particularly when snow cover was above average, and counts were conducted on more than one day. In 65 of 765 cases (8.5 %) counts could not be conducted as a result of adverse weather conditions or prolonged snow cover.

Observers arrived at previously defined exposed locations (e.g. ridges, summits, rock prominences) with good audibility before dawn (at the end of May prior to 04:30). Being on-site early was important because cocks in areas with low population density may only vocalize at the beginning of the activity period. To cover the whole site, more than one observer was generally needed to record cocks simultaneously from several observation points. Each observer localized Alpine Rock Ptarmigan cocks within a defined perimeter (generally 1–3 observers per km², depending on topography) and marked the approximate location of the cock on a map. Counts lasted about 2 h. Afterwards observers tried to find further cocks by walking through the site. Observations of the same individual by more than one observer were eliminated by comparing location and time of calling. These field methods remained the same across years. For our analyses we used the annual number of recorded males per site as a measure of population size.

Environmental variables

We compiled the environmental variables listed in Table 1 which are assumed to potentially affect Alpine Rock

Ptarmigan populations (see “Introduction”). The mean elevation of ptarmigan observations (one value per site) and its square were taken from the field maps of the years 1998 and 2009 (an early and a late year) using Arc-Map 10.0 (ESRI, Environmental Systems Research Institute, Redlands, CA, USA).

To measure the proximity of the ptarmigan occurrence to the treeline (and thus the risk of being affected by an upward moving treeline), the shortest distances between all locations of Alpine Rock Ptarmigan and the nearest forest edge, as indicated on the Swiss topographical maps (1:25,000), were measured for the years 1998 and 2009 using ArcMap 10.0 and averaged (one value per site). The two site-specific variables “elevation” and “distance to forest” were correlated ($r = 0.37$, $p = 0.02$).

We used the four weather variables mean temperature and precipitation in July, the period of chick rearing (Marti and Bossert 1985), mean temperature during winter (mean of December, January, February and March) and date of snowmelt of the current year to explain the population growth rate from the current to the following year. Temperature and precipitation data were taken from the meteorological station closest to the study site (MeteoSwiss, Federal Office of Meteorology and Climatology, <http://www.meteoschweiz.admin.ch>). We calculated the difference between the mean monthly temperatures of the focal year and the long-term average monthly temperature (years 1961–1990, given by MeteoSwiss). These measures focus on the annual variability of temperature and eliminate differences in absolute temperature between meteorological stations. Furthermore, the total amount of precipitation in July was included in the model for each year (using differences to the long-term mean gave very similar results).

Snow conditions were accounted for by quantifying the inter-annual variability of the melt-out dates. For alpine terrain, an average snow depth of 10 cm represents a

Table 1 Values, specifications and measurement units of parameters used as explanatory variables to model population growth rate

Parameter	Description	Specification	Measurement unit
Elevation	Mean elevation	Elevation of the ptarmigan locations (mean of 1998 and 2009)	Metres above sea level (m)
Distance to forest	Mean distance to nearest forest	Distances measured from ptarmigan locations in 1998 and 2009	Metres (m)
July temperature	Deviance of monthly temperature in July from long-term mean	Yearly data taken from nearest weather station of the year before ($t - 1$)	Degree Celsius (°C)
Winter temperature	Mean deviance of monthly temperature in December, January, February and March from long-term monthly means	Yearly data taken from nearest weather station	Degree Celsius (°C)
Precipitation	Sum of monthly precipitation in July	Yearly data taken from nearest weather station of the year before ($t - 1$)	Millimetres (mm)
Snowmelt	Date in spring when snow cover was reduced to 25 % of the surface area	Date taken of the year before ($t - 1$)	Day of year (day)

remaining snow cover fraction of approximately 25 % (Helbig et al. 2015). This is why for this study the melt-out date was defined as the first occurrence of a snow depth below 10 cm after reaching the maximum winter snow height. Snow data for each of the study sites was gathered from a gridded data set at 1-km spatial and daily temporal resolution (Jörg-Hess et al. 2014) by averaging all grid cells that overlapped the respective site area. The snow data set used was originally derived from data of over 200 snow monitoring sites in the Swiss Alps. In particular, it was shown to be consistent with independent satellite observations of the snow cover fraction (Hüsler et al. 2014).

Statistical analyses

The count data from the 40 sites over up to 18 years were analysed with state-space models (de Valpine and Hastings 2002; Dennis et al. 2006) using the Bayesian framework (Kéry and Schaub 2012). State-space models consist of a set of linked models, namely a model for the state process, a model for the observation process and a model for the initial state. The state process describes the dynamics of the state (in our case population size) over time with a first-order Markovian model and the observation model links the observations (counts) with the state. The model thus allows one to get rid of random sampling errors (counting errors), which is important for an accurate description of the population dynamics (Kéry and Schaub 2012). While classical state-space models analyse a single time-series (de Valpine and Hastings 2002; Dennis et al. 2006), we extended the model such that time-series from several sites are analysed jointly. For the three main purposes (estimation of region-specific population trends, assessing synchrony, assessing the impact of explanatory variables) the process models differed slightly, but the observation model and the model for the initial states were always the same. We now describe the different models in turn.

The process models always assume stochastic exponential population growth. We have not considered density dependence because its relevance for the mostly declining populations is expected to be small and its estimation is difficult and imprecise with the kind of data we have (Knape 2008). Thus, the size of population g in year $t + 1$ ($N_{g,t+1}$) is given by

$$\log(N_{g,t+1}) = \log(N_{g,t}) + r_{g,t}$$

where $r_{g,t}$ is the growth rate of population g from year t to $t + 1$. For the different aims we applied different models on $r_{g,t}$. Because the population growth rate is the logarithm of the ratio of two successive population sizes, the different sizes of the monitored sites has no impact on the results.

To assess population synchrony we followed the approach outlined by Grosbois et al. (2009). We decomposed $r_{g,t}$ into a mean population-specific growth rate (\bar{r}_g , trend), a component that is the same in all populations (γ_t), and a residual ($\varepsilon_{g,t}$): $r_{g,t} = \bar{r}_g + \gamma_t + \varepsilon_{g,t}$. Both temporal components are assumed to be serially independent and normally distributed random effects, whose variances indicate the temporal variability of growth rates that are common across populations (σ_{temp}^2) and the temporal variability that is population specific (σ_{res}^2), thus $\gamma_t \sim \text{Normal}(0, \sigma_{temp}^2)$ and $\varepsilon_{g,t} \sim \text{Normal}(0, \sigma_{res}^2)$. Population synchrony can then be quantified by the intra-class correlation of the population growth rates ($(\sigma_{temp}^2 / (\sigma_{temp}^2 + \sigma_{res}^2))$). An intra-class correlation close to one indicates strong synchrony while a value close to zero indicates lack of synchrony. This model assesses the synchrony of all studied populations, but it may well be that synchrony only operates over smaller spatial scales, thus regionally. Therefore we fitted a similar model in which synchrony is estimated for each of the five regions separately and independently of each other.

To assess the impact of the explanatory variables, we applied the following linear model to $r_{g,t}$:

$$r_{g,t} = \bar{r}_g + \sum_i \alpha_i X_{i,g,t} + \varepsilon_{g,t}$$

$$\varepsilon_{g,t} \sim \text{Normal}(0, \sigma_{res_g}^2)$$

where \bar{r}_g is the mean growth rate of population g (trend), $X_{i,g,t}$ are the explanatory variables as defined in Table 1 (including some first-order interactions), α_i is the regression coefficient of explanatory variable i , and $\varepsilon_{g,t}$ are the residuals that are assumed to be serially independent and stemming from the normal distribution with population-specific variance $\sigma_{res_g}^2$. This variance reflects the variability in the growth rates that is not explained by the explanatory variables and is a component of environmental stochasticity. In order to evaluate whether the explanatory variables had an effect on population growth, we computed the probability that the regression coefficients (α_i) were larger than zero.

Finally, we estimated population trends within the five regions in order to assess whether they were contrasting. For this purpose we used the model as above, but without explanatory variables and regarded the population-specific mean growth rates as random effects that are clustered within the five regions. Thus, $r_{g,t} = \bar{r}_g + \varepsilon_{g,t}$, $\varepsilon_{g,t} \sim \text{Normal}(0, \sigma_{res_g}^2)$ and $\bar{r}_g \sim \text{Normal}(\mu_v, \sigma_{reg}^2)$, where μ_v are the region-specific growth rates and σ_{reg}^2 is the variability of the growth rates among populations.

To define the initial state (population size in the year when the monitoring started (f)) we used in all models the same

Table 2 Posterior means and credible intervals of the region-specific population growth rates of Alpine Rock Ptarmigan

Region	Posterior mean	95 % Credible interval	% Change across total study period	$P (r < 0)$
Grisons ($n = 15$)	-0.007	-0.041, 0.022	-11.25 %	0.671
Eastern Alps ($n = 7$)	0.003	-0.035, 0.040	6.00 %	0.407
Ticino ($n = 5$)	-0.011	-0.042, 0.023	-17.63 %	0.771
Western Alps ($n = 7$)	-0.041	-0.099, 0.013	-50.10 %	0.928
Central Alps ($n = 6$)	-0.011	-0.076, 0.049	-16.40 %	0.612
Overall ($n = 40$)	-0.008	-0.025, 0.008	-12.86 %	0.831

The estimated proportional total change in population size during the 18 study years and the probability that the growth rate is negative (population declining) are also shown. The overall mean across all 40 populations is given at the bottom

prior distribution, that is $\log(N_{g,t[g]}) \sim \text{Uniform}(-5, 5)$. This prior imposes an upper limit of the initial population size of about 150 which is sufficiently wide (maximum initial count was 19). Finally, for the observation process we used the log-normal distribution, thus

$$\log(y_{g,t}) \sim \text{Normal}\left(\log(N_{g,t}), \sigma_{obs_g}^2\right)$$

where $y_{g,t}$ are the counts and $\sigma_{obs_g}^2$ are the population-specific residual variance (observation error). Note that this observation model assumes that the counts were correct on average and adjusted for random variation of counting errors. If detection had been consistently imperfect (i.e. detection probability $p < 1$), it is not possible to estimate true population size (N) with these models, but just a population index given by $N * p$ (Kéry and Schaub 2012). Yet, since we were interested in the change of population sizes rather than in their absolute values, this limitation does not pose a serious problem for our inference.

We implemented the models in the Bayesian framework. Inference is therefore based on the posterior distributions which are obtained from the likelihood and the specified prior distributions. Since we had no prior knowledge about the growth of these populations, we have specified vague priors (a list of the priors is given in Appendix S3). We used JAGS (Plummer 2003) to fit the models (for the code see Appendix S4) that was run from R via package jagsUI (Kellner 2014). JAGS performs Markov chain Monte Carlo (MCMC) simulations to get samples from the posterior distributions, which were then summarized for inference. A total of 200,000 samples were simulated from the posteriors, but the first 100,000 were discarded to get rid of initial conditions. For memory reasons we only retained every 100th sample and used three chains with dispersed initial values to check the convergence of the simulations. Convergence was satisfactory (in all cases the Brooks–Gelman–Rubin criterion was $\hat{R} < 1.2$; Brooks and Gelman 1998). We assessed the probability that effects were different from zero by the proportion of MCMC samples that were positive (Kéry and Schaub 2012).

Results

Overall and region-specific population trends

Over all 40 sites, mean population growth rate of Alpine Rock Ptarmigan was negative with a mean change in population size of -13 % over the 18 study years (Table 2; for counts and estimated population sizes see Appendix S2). The mean population growth rate differed quite remarkably between regions (Table 2). In the Eastern Alps, populations increased slightly on average, while in the other four regions mean population growth rate was negative, most strongly in the Western Alps.

Assessment of synchrony in population fluctuations

Little evidence for synchrony of fluctuations in population size among sites was found. The intra-class correlation among all studied Alpine Rock Ptarmigan sites was low, indicating that the populations fluctuated asynchronously (Table 3). Within the geographical regions, population synchrony was highest in Ticino and lowest in the Eastern Alps (Table 3). However, generally the synchrony between populations was relatively low in all five regions, indicating that factors acting on a local scale affected the population growth rates.

Impact of environmental variables

In the most general model predicting yearly population growth rate, we included the variables “July temperature” and “rainfall” in July of the year before, squared values of “July temperature” and interactions between “July temperature” and “rainfall”, “winter temperature” as well as the variables “snowmelt”, “elevation” and its square, and “distance to forest”. The growth rates of Alpine Rock Ptarmigan populations were affected by the variation between years in July temperature (quadratic effect), while the other variables were unlikely to be of importance, as evidenced by the low probability that their regression coefficients were different from zero (Table 4). We also computed models including “July

Table 3 Synchrony of Alpine Rock Ptarmigan population growth for all study sites and within each region separately

Area	ICC	95 % CRI
Overall		
Switzerland	0.1300	0.0045, 0.3487
Within regions		
Central Alps	0.0832	0.0001, 0.3754
Eastern Alps	0.1085	0.0001, 0.5603
Grisons	0.1813	0.0003, 0.7929
Ticino	0.2371	0.0006, 0.8297
Western Alps	0.1642	0.0003, 0.5991

ICC intra-class correlation, CRI 95 % credible intervals

temperature” and “July temperature squared” plus only one other focal variable, but the regression coefficients of all these focal variables were also not different from zero. In a reduced model including only “July temperature” and “July temperature squared”, both affected population growth rate (Table 4). On the basis of the estimates of this reduced model, we predicted population growth rate for the observed range of temperature deviations in July. Population growth rate increased with increasing July temperature the year before, reached a maximum at a July temperature deviation of 1.74 °C (CRI 0.17–5.61 °C), and declined with higher temperatures (Fig. 2).

Discussion

On the basis of the number of displaying cocks, we showed that overall population growth rate of Alpine Rock Ptarmigan sampled in 40 Swiss sites was negative over the

18 study years and was dependent on July temperature. However, the population growth rates varied greatly between different regions. Overall and within regions, growth rates showed little evidence for synchrony of fluctuations in population size between local study sites.

Overall and region-specific mean trends and assessment of synchrony in population fluctuations

From the 40 monitored sites and on the basis of the number of displaying cocks, we found a negative overall population trend of the Alpine Rock Ptarmigan in Switzerland with a decline of –13 % over the 18 years of our study. This is in line with findings in the Italian (Brichetti and Fracasso 2004; Peronace et al. 2012; Imperio et al. 2013) and French Alps (Haute-Savoie; Novoa et al. 2014).

However, population trends in Switzerland varied greatly between different regions. While populations in the Eastern Alps showed a slightly positive growth rate, all other regions revealed negative rates. Of particular concern is the trend in the Western Alps where monitored populations have been reduced by half during the study period. Moreover, the study sites were not selected to cover the entire distribution area of the species. In particular, small populations and populations at low density were not monitored or could not be used for our analysis. This is particularly true for populations at the northern (pre-Alps) and southern (Ticino) edge of the distribution area in Switzerland where the Alpine Rock Ptarmigan disappeared from certain areas (N. Zbinden and T. Sattler, personal communication; see also Novoa et al. 2014 and Desmet 2014 for France).

Table 4 Effect of various environmental variables on Alpine Rock Ptarmigan population growth rate

Parameter	Posterior mean	95 % CRI	<i>P</i> ($\alpha > 0$)
General model			
Elevation	–0.009	–10.610, 10.572	0.511
Elevation ²	–0.357	–62.295, 62.046	0.498
Distance to forest	0.103	–10.530, 10.627	0.507
July temperature	0.063	0.014, 0.114	0.994
July temperature ²	–0.015	–0.031, –0.001	0.019
Winter temperature	–0.009	–0.052, 0.036	0.345
Precipitation	–0.003	–0.062, 0.054	0.473
July temperature × precipitation	–0.015	–0.039, 0.010	0.116
July temperature ² × precipitation	0.006	–0.004, 0.016	0.870
Snow melt	0.001	–0.065, 0.070	0.510
Reduced model			
July temperature	0.041	0.007, 0.076	0.991
July temperature ²	–0.011	–0.022, –0.001	0.021

Given are the posterior means, 95 % credible intervals of the slope parameters (CRI) and the probability that posterior means of the slope parameters are larger than zero for the general model including all parameters and interactions and for the reduced model with only the two important parameters

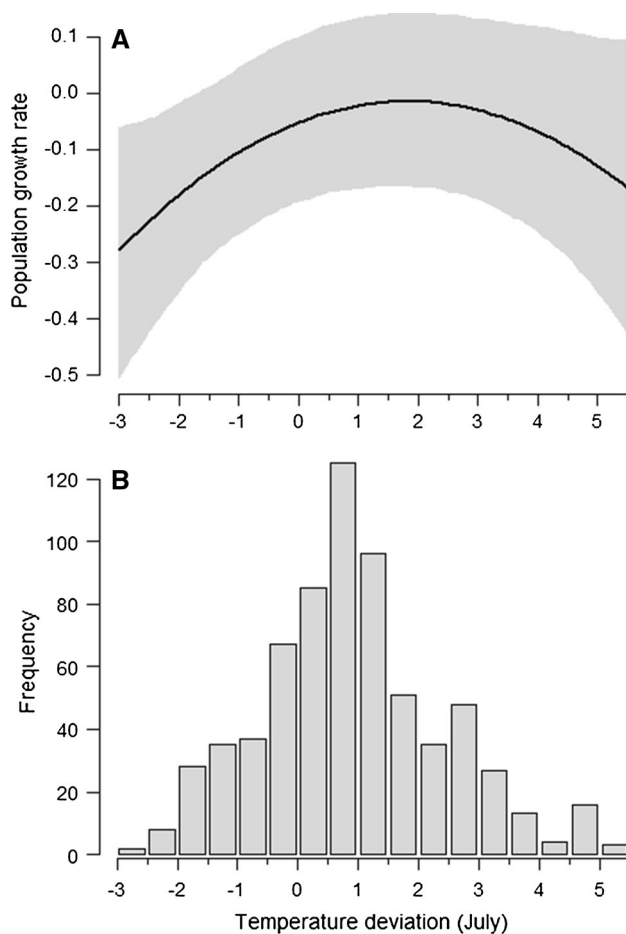


Fig. 2 **a** Predicted population growth rate (mean \pm 95 % CRI) of Alpine Rock Ptarmigan with respect to the observed range of temperature deviations in July based on the model that contained only temperature as explanatory variable (Table 4). The model was parameterised in such a way that a mean growth rate across all populations was calculated. **b** Histogram of the temperature deviations in July as recorded during the study period in the populations

Hence it appears that in Switzerland the Alpine Rock Ptarmigan overall is in decline, but that this decline is apparent in particular regions and areas only, especially at the edge of the distribution. Monitoring of this species, therefore, should also include these marginal areas.

Among Swiss Rock Ptarmigan sites the level of synchrony in fluctuations of population size was generally low. We would actually expect some degree of synchrony in population fluctuations because deviations in July temperatures covary strongly between study sites (correlation coefficients are greater than 0.66, mostly greater than 0.9, between weather stations, $n = 18$ years and 20 weather stations) and deviations in July temperatures affected population changes. However, because the effect of the deviation in July temperature was not linear but quadratic, this may have concealed a direct synchrony among populations due to temperature. The low regional synchrony in

population fluctuations rather indicates that factors acting on a small, local scale affect population growth rate more strongly and override synchronizing factors, as found in other studies (Engen et al. 2005). Such local factors could be the high local variability in topography, habitat heterogeneity, local weather events or human disturbance.

Impact of environmental variables

Among the environmental variables examined, only temperature deviation in July affected population growth rate of Alpine Rock Ptarmigan significantly. The relationship was curvilinear with an optimum at $+1.74$ °C above the long-term mean. Hence, both cool and hot July temperatures negatively affected populations. Cold July weather is normally combined with rain and snowfall and known to reduce breeding success drastically, because chicks during their first 2 weeks are not yet able to thermoregulate and in bad weather they can starve when being brooded by the female or become chilled to death when trying to forage (Marti and Bossert 1985; Wilson and Martin 2008). Why very hot summer temperatures affect population size negatively is less clear. Alpine Rock Ptarmigan have been observed panting and cooling in water or snow during hot sunny days in the Alps (Glutz von Blotzheim et al. 1973; AB personal observation) and the White-tailed Ptarmigan started panting at 21 °C (Johnson 1968). Hence, chicks and adults may stop foraging on hot summer days (AB observed a hen panting in the shade which did not forage with her 3-week-old chicks) with possible consequences for survival, but systematic evidence for such a mechanism is lacking. However it seems that the distribution of the Alpine Rock Ptarmigan is indeed limited to areas with a mean July temperature below 10–12 °C (Revermann et al. 2012) and birds prefer relatively cool places in the shade during hot summer days at the microhabitat scale (Visinoni et al. 2015).

July temperature deviations measured during the 18 study years (1995–2012) at the meteorological stations nearest to the study sites varied from -2.9 to $+5.2$ °C. They were on average $+0.94$ °C above the long-term mean (1961–1990), but did not show a trend over the 18 study years (Spearman rank correlation: $r = 0.055$, $P = 0.829$, $n = 18$). Hence, the deviation of July temperatures during the study years from the long-term mean ($+0.94$ °C) was not far from the predicted optimum of $+1.74$ °C. A substantial further increase in July temperatures would therefore not be beneficial for the Alpine Rock Ptarmigan; increases of 3.7 – 4.1 °C are predicted between the reference period 1980–2009 and 2085 in summer (July–August), depending on region for the A1B greenhouse gas emission scenario (CH 2011).

We did not find an influence of precipitation in July on population fluctuations of Swiss Alpine Rock Ptarmigan. Rainfall and snowfall during the chick rearing period (especially the first 2 weeks after hatching) negatively affects chick survival (Novoa et al. 2008; Kobayashi and Nakamura 2013). It may be that a possible direct effect of rain on population fluctuations of ptarmigan is concealed by the curvilinear effect of summer temperature (precipitation in July is usually correlated with low temperatures in the Alps) or that there was no carry-over effect of low breeding success due to rain on the numbers of territorial males in the next spring.

An early spring snowmelt allows early and successful breeding of Alpine Rock Ptarmigan in the French Pyrenees (Novoa et al. 2008) and a higher population growth rate in the Italian Alps (Imperio et al. 2013). However, we did not find an effect of the time of spring snowmelt on population fluctuations in our study. It may be that an early snowmelt, although enhancing breeding success, affects population size the next year in a more complex way than accounted for by the model used here (e.g. by affecting the number of territorial males in the current year, although this was not statistically significant either), or that other factors (e.g. human-induced, see below) overrode the effect of snowmelt.

We did not find an influence of winter temperature on population fluctuations of Swiss Alpine Rock Ptarmigan which was to be expected from earlier findings (Bossert 1980). The elevation at which Alpine Rock Ptarmigan were found did not seem to influence population fluctuations. Moreover, no influence of the distance to the nearest forest on population trend was found during our study, although tree cover just below the treeline and the treeline itself have increased in the Swiss Alps (Gehrig-Fasel et al. 2007). At least in one study site (site 29), arolla pines (*Pinus cembra*) colonized the lowest part during the study period and ptarmigan disappeared from this part of the site (CM personal observation).

It was impossible to statistically deal with a whole range of potential human disturbance factors (recreational activities in winter and summer, hunting, military practice), and with the potential influence of predation, because such data were not collected systematically in a standardized manner or were lacking. Locally, however, human disturbance factors may well have caused declines in population size.

Conclusions

Our study reveals that in Switzerland the mean population growth rate of Alpine Rock Ptarmigan was negative. However, there was a large variation in population trends between regions and sites, with some declining drastically and others doing well. Apart from the influence of July

temperature, we did not find an overall factor which may cause the declines observed. As supported by the absence of synchrony in population variation, it seems that various factors act locally to different degrees. Depending on local exposition and weather, hot summer temperatures may cause a decline in population size at some sites (see Fig. 2). Depending on local proximity to forest, the upward shift of the treeline and reforestation just below the upper treeline may cause declines at other sites. These two consequences of global warming may eventually shrink the area of suitable habitat drastically, as predicted by Revermann et al. (2012). At some sites, population declines may be caused by a local increase in winter or summer tourism, by unsustainable hunting quotas or by other factors.

The finding that different reasons may be responsible for declines in different areas calls for careful considerations of the possible causes and possibly different strategies of conservation. However, our understanding of the reasons for the decline of the Alpine Rock Ptarmigan is quite incomplete. We advocate a more complete monitoring of breeding populations which should be representative of the whole area and also include marginal populations. The suspected effects of hot summers on ptarmigan populations remain to be studied in detail (effect on breeding success, survival or habitat use). It also remains unclear how much of the ptarmigan area is affected by winter and summer leisure activities of humans and how sustainable hunting quotas can be determined.

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