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Mountain is calling – decrypting the vocal phenology of an alpine bird species using passive acoustic monitoring

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Monitoring vulnerable species inhabiting mountain environments is crucial to track population trends and prioritize conservation efforts. However, the challenging nature of these remote areas poses difficulties in implementing effective and consistent monitoring programmes. To address these challenges, we examined the potential of passive acoustic monitoring of a cryptic high mountain bird species, the Rock Ptarmigan *Lagopus muta*. For 5 months in each of two consecutive years, we deployed 38 autonomous recording units in 10 areas of the Swiss Alps where the species is monitored by a national count monitoring programme. Once the recordings were collected, we built a machine-learning algorithm to automate call recognition. We focused on studying the species' daily and seasonal calling phenology and relating these to meteorological and climatic data. Rock Ptarmigans were vocally active from March to July, with a peak of activity occurring between mid-March and late April, 1 or 2 months earlier than the second half of May when the counts of the monitoring programme take place. The calling rate peaked at dawn before dropping rapidly until sunrise. Daily vocal activity demonstrated a consistent association with weather conditions and moon phase, whereas the timing of seasonal vocal activity varied with temperature and snow conditions. We found that the peak of vocal activity occurred when the snowpack was still thick and snow cover was close to 100% but with a local peak of high temperatures. Between our two study years, the peak of vocal activity occurred 30 days later in the colder year, suggesting phenological plasticity in relation to environmental conditions. Passive acoustic monitoring has the potential to complement conventional acoustic counts of cryptic birds by highlighting periods of higher detectability of individuals, and to survey small populations that often remain undetected during single visits. Moreover, our study supports the idea that passive acoustic monitoring can provide valuable data over large spatial and temporal scales, allowing decryption of hidden ecological patterns and assisting in conservation efforts.

Keywords: autonomous recorders, *Lagopus muta*, phenology, song classifier, vocal behaviour.

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Mountain ecosystems are known for their high species richness, including a high rate of endemism (Rahbek *et al.* 2019). However, they are also particularly fragile in the face of human-induced pressures such as land use (Brambilla *et al.* 2010, Fumy & Fartmann 2021) and climate change

(Araújo *et al.* 2007, Pearce-Higgins & Grant 2009). In the European Alps, climate change is especially pronounced with air temperatures exceeding the average trend in the northern hemisphere by 1.6–2.5 times (Keiler *et al.* 2010, Foster & Rahmstorf 2011). This is leading to the onset of snowmelt advancing by 9 days per decade, to mention only one of several consequences (Klein *et al.* 2016). These regions harbour cold-adapted species highly vulnerable to climate warming (La Sorte & Jetz 2010).

Recent publications have already reported on the direct and indirect effects of rising temperatures on alpine flora and fauna, such as movements to higher elevation (Steinbauer *et al.* 2018, Hallman *et al.* 2022) and shifts in spring phenology in many taxa (Vittoz *et al.* 2013, Vitasse *et al.* 2021). In many mountain ranges, this rise in elevation results in a decrease in available habitat for many species (De Gabriel Hernando *et al.* 2021, Brambilla *et al.* 2022). In addition, phenological shifts have the potential to lead to asynchrony between periods of resource abundance and breeding efforts (Barras *et al.* 2020, Schano *et al.* 2021). Alpine birds are particularly exposed to climate change because they are physiologically and morphologically adapted to cold conditions (Lehikoinen *et al.* 2019), which also influence their distribution (Jähnig *et al.* 2020, Barras *et al.* 2021, Brambilla *et al.* 2022). This major threat to alpine species is enhanced by building activity on mountain summits for recreational purposes and the ensuing disturbances (Arlettaz *et al.* 2007, Rolando *et al.* 2007, Caprio *et al.* 2011). This contributes to the shift of their distributions to higher elevations where habitats remain undisturbed (Chamberlain *et al.* 2013, Pernollet *et al.* 2015). Consequently, Lehikoinen *et al.* (2019) reported that mountain-specialist birds had shown a decline of ~10% from 2002 to 2014 in Europe.

However, regional population trends of many of these species are poorly known (Scridel *et al.* 2018). Indeed, compared with lower-lying habitat types, alpine areas present many logistical challenges in conducting rigorous long-term monitoring (Chamberlain *et al.* 2012). Technological advances provide innovative solutions to improve or even replace conventional monitoring programmes (Bibby *et al.* 2000). Among these, passive acoustic monitoring (PAM) has proven to be a non-invasive method with a wide range of applications (Sugai *et al.* 2019). PAM requires the placement of autonomous recorders in the field to record ambient sounds and is followed by the analysis of the obtained acoustic data. It is used to survey and monitor soundscapes, but it can also be used to obtain information on the presence or absence of particular species, estimate population size or study activity patterns of a species (Browning *et al.* 2017, Sugai *et al.* 2019).

In the context of bird monitoring in mountains, where accessibility can be a challenge, PAM may provide novel and highly valuable information. This method can be used to refine, complement or possibly even replace traditional monitoring schemes that rely on visual and acoustic cues. Well-known methodological biases of conventional field monitoring, such as observer differences, modification of birds' behaviour, and changing or unfavourable weather conditions, are often aggravated in mountain environments (Mayfield 1981, Abrahams 2019, Marin-Cudraz *et al.* 2019). Combined with large topographical changes over short distances in the mountain environment, these effects can lead to high rates of inaccuracy in counting individuals, even for bird species that produce strong vocalizations. In addition, there is a lack of knowledge about the vocal phenology of most alpine birds (Chamberlain *et al.* 2012), which is crucial to maximize detectability in point count protocols, as the peak of activity and acoustic counting should be synchronized (Wilson & Bart 1985). As PAM can monitor vocal activity for weeks or even months, it is particularly suitable for gaining a better understanding of seasonal and daily rhythms of alpine species.

In this context, the Rock Ptarmigan *Lagopus muta* (hereafter referred to as Ptarmigan) is a well-suited alpine bird species to test the efficacy of PAM in remote environments (Marin-Cudraz *et al.* 2019). In central Europe, the subspecies *Lagopus muta helvetica* is typical of high mountain environments, where it lives above the tree line on peaks and screes that are difficult to access. Its plumage is cryptic in all seasons, but its vocalizations are loud and recognizable (MacDonald 1970). Revermann *et al.* (2012) showed that climate was a major factor explaining the distribution of the species in Switzerland, highlighting Ptarmigan as one of the most vulnerable species to climate change in the Alps. Indeed, Pernollet *et al.* (2015) have shown a substantial increase in the species' elevational distribution in southern and eastern Switzerland across 29 years, and Furrer

et al. ([2016](#)) identified a decrease of 13% from 1995 to 2013 in Swiss Ptarmigan populations. As a result, the Ptarmigan is classified as a near-threatened species in Switzerland (Knaus *et al.* [2021](#)).

To track Ptarmigan populations in the Swiss Alps, yearly point counts have been carried out since 1995 in approximately 40 study areas (Furrer *et al.* [2016](#)). Depending on the size and topography of the areas, surveys are performed on one or several points that remain the same across the years (Bossert [1977](#)). As surveys are logistically demanding, they are carried out once a year towards the end of May when males are supposedly displaying and calling most intensively, aiming at the highest detection probability (Marti *et al.* [2016](#)).

PAM has the potential to provide daily and systematic activity data over large temporal and spatial ranges. Such a massive increase in data is expected to lead to a more detailed description of the seasonal and daily peaks of Ptarmigan vocal activity. In this way, we aim for an improved understanding of the influence of weather and other environmental variables on vocal activity. Additionally, we intend to study the hatching phenology of Ptarmigan during our study years. We deployed autonomous recording units in the Swiss Alps and used machine learning approaches for automated acoustic detection of Ptarmigans to (1) describe the vocal activity patterns of Ptarmigan in Switzerland, more specifically daily and seasonal peak(s) of vocal activity, (2) study the environmental factors influencing vocal activity and (3) study the hatching phenology in relation to snow conditions. If applied over the long term, this method has the potential to refine the current monitoring protocol and consequently lead to more precise trend estimates of Ptarmigan populations.

METHODS

Sampling design and study areas

The research was conducted in 10 study areas in the Swiss Alps (Fig. [1](#)) at elevations ranging from 1810 to 2671 m. In each of these study areas, Ptarmigans have been counted by game wardens since 1995. The study areas were selected to include large parts of the geographical area of the Swiss Alps and to consider both marginal and comparatively large populations of the species. This meant including areas where no Ptarmigan had been recorded on the official counts since 1998 (Le Moléson FR, last casual record in 2016) as well as areas with an average of up to 16.5 males/km^2 (2011–2022, Aletsch VS).

Autonomous recordings

We used Wildlife Acoustic Song Meter Mini recorders (www.wildlifeacoustics.com) to record Ptarmigan calls from March to July in 2021 and 2022. We aimed at having all loggers running from 1 April to 15 July to encompass the start and end of calling activity with an expected activity peak at the end of May (Bossert [1995](#)). As it is known that male Ptarmigans call before sunrise (Marty & Mossoll-Torres [2012](#), Marti *et al.* [2016](#)), we programmed the devices to record continuously from 2 h before sunrise to 5 h after sunrise for a total of 7 h per day. The sample rate was 24 000 Hz, and the gain of the microphone was set at 18 dB.

Depending on the size and topography of each study area, two to six recorders were screwed to a rock (occasionally fixed to a tree or a pole) with the microphone aimed at the slopes where Ptarmigans are usually observed during the conventional counts. The aim was to survey the study area covered by the conventional counts while minimizing the overlap between the sound space covered by each recorder. In total, 38 recorders were placed in 2021 and 37 in 2022 (when one recorder could not be placed due to high risk of snow avalanches). We usually ensured a minimum distance between recorders of 1000 m considering that calls within a 500-m radius could still be detected by the recorders. However, in two cases where an acoustic obstacle intervened, we were able to place recorders within 100 m of each other, either side of a ridge, while avoiding overlap.

Automated call recognition

The automatic recognition method was developed using Python 3.9 and the OpenSoundscape open-source Python package for bioacoustics version 0.8 (Lapp *et al.* [2022](#)). Before developing our call classifier with our training data, we used BirdNET v2.2, a ready-to-use classifier for bird song recognition (Kahl *et al.* [2021](#)). The recognition results were satisfactory, but there was a large number of false positives due to the rubbing of plastic parts
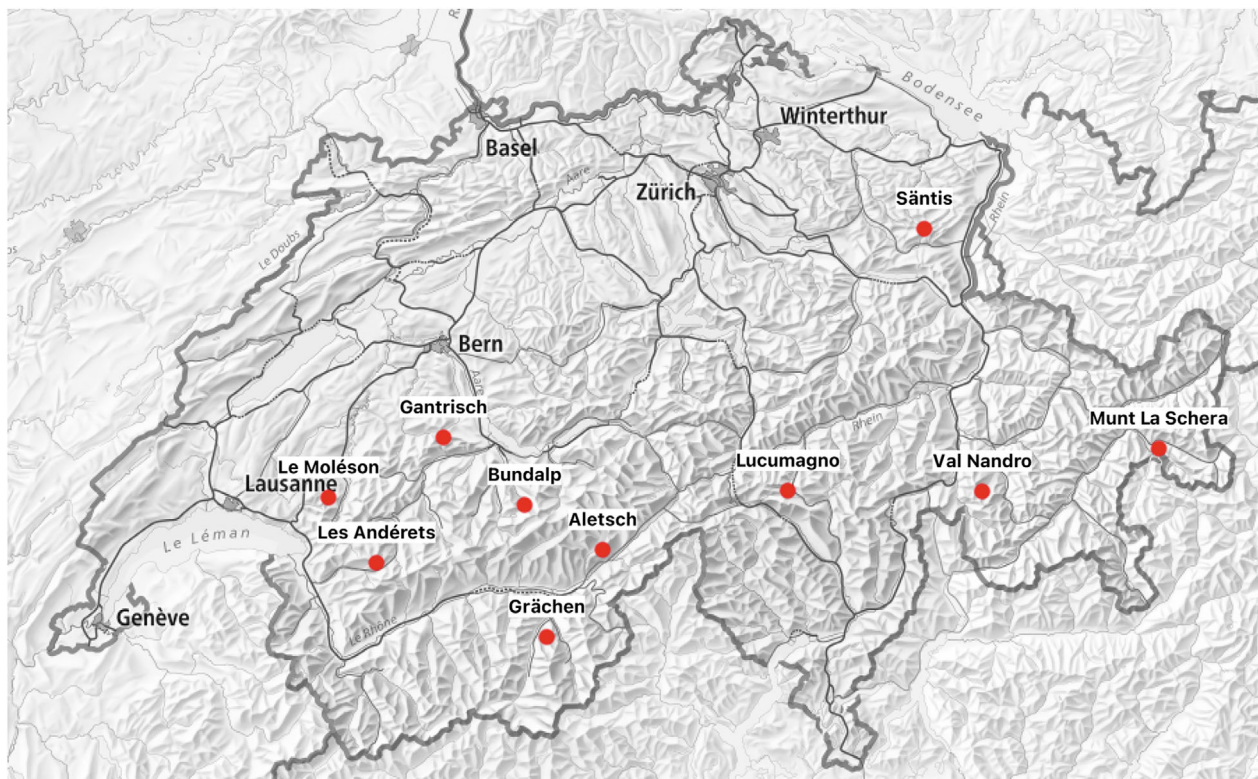
Figure 1. Map of the 10 study areas in the Swiss Alps. At each study area, two to six recorders were installed according to the size and topography of the area.

close to the microphone. The self-developed automated Ptarmigan call classifier, also available online (https://github.com/Vogelwarte/CallClassifier/tree/RPv1.0), is capable of recognizing the characteristic song of the males and identifying the rubbing of plastic parts as noise on the recordings.

The first step was to manually annotate male Ptarmigan calls on the recordings to build a training dataset. One hour randomly selected from each of the 38 different recorders was manually listened to, annotating each male call in Raven Lite 2.0.4 (K. Lisa Yang Center for Conservation Bioacoustics 2023). One second before the start of the call and 1 s after the end of the call were annotated. Each call interval longer than 3 s was then split into 3-s segments with 1.2 s of overlap between each segment. To eliminate false Ptarmigan detections as much as possible, we incorporated background noise and misidentifications as negative training into the model. The aim was to train the algorithm to recognize noises that are frequently confused with Ptarmigan calls in the recordings. To do this, we included segments of

recordings where BirdNET reported a large number of false positives (> 300) in the training. The complete training dataset, comprising about 4000 3-s files of Ptarmigan call, is available online (https://doi.org/10.5281/zenodo.8086326). We used the InceptionV3 architecture to develop the model. For model training, 80% of the training dataset was used to train the algorithm, and 20% was used to validate the model at each cycle. The standard data augmentation proposed by Open-Soundscape was used (Lapp *et al.* 2022). The model was trained for 60 cycles and took about 7 min/cycle. The inference computation time of our automated classifier was 12–15 s/h of recording, which is comparable to the performance of optimized BirdNET on the same multiprocessor server. We chose a detection window of 3 s with 2 s of overlap. After running the classifier on our recordings, we reconstructed each call longer than 3 s (thus several detections of call in a row) to have a single long call instead of several replicates. However, manual annotation of Ptarmigan calls in the study areas revealed that no more than 2.1%

of vocalizations last longer than 7 s (Fig. S1). Hence, calls longer than 7 s were split into several calls of up to 7 s. The number of classifier detections showed a correlation of 0.95 with the manual detections used as a training dataset, while the number of BirdNET detections showed a correlation of 0.91 with the manual detections in the training dataset. Pearson correlation coefficients were calculated using the 'cor' function in R ('stats' package; R Core Team 2022).

Benchmarking analysis

Each Ptarmigan detection by the call classifier is linked with a degree of confidence in identification (hereafter referred to as 'confidence score') reflecting the accuracy of the identification to species level. To evaluate the classifier's performance, we determined proportions of false positives, false negatives and true positives for each confidence score. This was achieved by manually checking 1136 detections of the classifier from a set of 38 1-h recordings from each study area. For each of these 38 files, we labelled each classifier detection as false positive or true positive. The goal of the benchmarking analysis was to find a confidence score threshold that minimized incorrect detections (false positives) and missed detections (false negatives) while keeping a maximum of correct detections (true positives). We chose a confidence score threshold at which the true-positive and false-negative curves crossed. This procedure allowed us to consider as presences all detections with a confidence score equal to or above the chosen threshold. Based on these numbers, we were then able to calculate the recall rate (proportion of correctly identified calls among all captured calling events) and the precision rate (proportion of correctly identified calls among all detections) of the classifier at this threshold, following the recommendations of Knight *et al.* (2017).

Environmental variables

Temperature (in °C), precipitation (in mm) and sun ratio (0–1) data were extracted from raster data provided by the Federal Office of Meteorology and Climatology MeteoSwiss. These rasters are modelled from interpolation of values measured at 29 national automatic weather stations. The method for temperature calculation is described by Frei (2014), that for sun ratio (ratio between sun duration during the day and maximal sun duration possible for this day) calculation by Frei *et al.* (2015) and that for precipitation by Schwarb (2000). The rasters show a resolution of 1×1 km, and their values were extracted from each daily layer at the location of each recorder using the 'raster' package in R (Hijmans 2022). Additionally, we used the package 'lunar' (Lazaridis 2022) to calculate lunar illumination, indicating the theoretical moon illumination (varying between 0 and 1, with 1 being full moon).

Snow cover (0–1) and snow depth (in cm) calculations are based on products by ExoLabs (https://exolabs-ch.gitbook.io/cosmos; Wulf *et al.* 2020). ExoLabs produces snow cover and snow depth rasters with a resolution of 20 m derived from nine optical satellites. To extract snow cover data for each recorder, we calculated the proportion of pixels assigned to high snow probability (>6 on a scale from 0 to 10) within a radius of 250 m around each recorder. Similarly, snow depth data for each recorder were calculated as the daily average snow depth over a 250-m radius around each recorder. We linearly interpolated days with missing data to fill the gaps in the datasets. On average, there were only 16 days of missing snow data (mainly in summer) out of the 184 days of our study season (1 March to 31 August).

Activity over time

To determine potential peak(s) of activity during the two seasons studied, we took calling rate as a response variable and day of the year as an explanatory variable. The variables were included in a generalized additive mixed model (GAMM; Hastie & Tibshirani 1990) using the 'gamm' function ('mgcv' package; Wood 2017). We chose this approach because we expected a non-linear relationship with calling rate over time. The calling rate was calculated as the number of Ptarmigan calls per hour and was included with a negative binomial distribution in our model. Year, location of the recorder and area were considered as random factors. The 'gamm' function uses a smoothing factor (k) that defines a larger or smaller granulometry in the activity curve. To select the best smoothing factor k, weekly point estimates were calculated with their confidence interval and 'k' was selected to best match the weekly estimates. To study vocal activity during the day, we

similarly repeated this analysis by replacing the day of the year with the number of minutes before or after dawn in a GAMM. We used an autocorrelation factor in our model, using the package 'mgcViz' (Fasiolo *et al.* 2020), to check the assumptions of our model (in particular residuals and quantile–quantile plots).

To highlight the time of vocal behaviour changes across the season, we calculated the first derivative of the GAMM curve, as described in Simpson (2018) and first applied to animal behaviour by Becciu *et al.* (2023). To do so, we used the 'derivatives' function from the 'gratia' package (Simpson 2023). The first derivative curve indicates significant rates of change when the regression line diverges from zero, highlighting positive or negative local trends of the curve. These significant rates of change were defined when both 95% confidence intervals did not overlap zero.

Activity in relation to environmental variables

To investigate which environmental variables are associated with the vocal activity of Ptarmigans, we used a generalized linear mixed model (GLMM) with calling activity, i.e. the number of calls per day, as the response variable. We used the following daily explanatory variables: temperature, precipitation (daily sum), sun ratio, lunar illumination, snow cover and snow depth. As raw temperature has a strong seasonal component, we included deviation from the mean temperature as a seventh variable. This variable is calculated as the difference between the daily raw temperature and the mean temperature values predicted by a local polynomial regression using the 'loess' function in R ('stats' package; R Core Team 2022). These predicted values use locally weighted regression to fit a smooth curve through points in a scatter plot. In other words, these values tell us how much lower or higher the temperature at point x is compared with the trend around point x. We tested the correlation between all fixed variables to avoid overfitting the data with collinear variables (Dormann *et al.* 2013). Snow cover and snow depth were highly correlated ($|cor| > 0.7$), and we excluded snow cover from the analysis because it is possible to estimate snow cover from snow depth but not the converse. Day of the year, year, and the nested factors area and location (area is each of the 10 study areas, and location is the

location of each of the 38 recorders) were included as random variables. As the response variable calling activity is a count and showed variable dispersion, we used a negative binomial distribution, which was confirmed by the 'check_distribution' function in R ('performance' package; Lüdecke *et al.* 2021). Finally, we used the 'glmmTMB' package in R (Brooks *et al.* 2017) to run the model.

To choose the most parsimonious model, all fixed and uncorrelated variables, in their quadratic and linear form, and random variables were included in the 'dredge' function ('MuMIN' package; Burnham & Anderson 2004, Bartoń 2022). This function generates GLMMs with all the combinations of predictors provided and ranks each of these models according to its Akaike information criterion (AIC). The model with the lowest AIC (and therefore the model classified as the first in the ranking) was chosen.

The assumptions of the selected model were checked using the 'check_model' function ('performance' package; Lüdecke *et al.* 2021). This function tests for overdispersion, homoscedasticity, collinearity of variables, normality of residuals and normality of random effects. The response curves were then visualized using the 'plot_model' function ('sjPLOT' package; Lüdecke 2022).

In a second step, we evaluated the relationship between lunar illumination and the onset of Ptarmigan males calling in the study areas by executing a second GLMM. We used the time of the day's first call as the response variable and lunar illumination as the explanatory variable. As for the previous GLMM, day of year, year, and the nested factors area and location were included as random variables. As onset of calling is continuous and right skewed, it was integrated in the GLMM with a γ distribution. 'glmmTMB' and 'check_model' were used to run the model and check the model's assumptions, respectively. The variables of each statistical model and their respective AIC are summarized in Table S1.

Hatching dates

To compare peaks of activity with nesting events, we obtained a dataset from an online citizen science platform (www.ornitho.ch) covering the Swiss Alps from 2000 to 2022. In addition, we obtained systematic data from the Swiss national scheme for Common Breeding Bird Monitoring

(Kéry *et al.* 2005). These data consisted of observations of Ptarmigan, including precise location, date, number of individuals and an 'atlas code' determining the type of observation (i.e. singing male, pair, nest, hatched chicks; for more information see www.ornitho.ch/index.php?m_id=41). By knowing nest building, incubation, nestling period and fledgling period (Montgomerie & Holder 2020), we could calculate an estimation of hatching date per observation based on the atlas code reported. This methodology was adapted from Schano *et al.* (2021).

We ran a linear model (LM) with hatching date as the response variable and year, elevation, mean observation day, i.e. the average date of all observations reported for each year for the whole dataset (2000–2022). We used a Gaussian distribution for the response variable and, as with the previous model, we checked the assumptions of our model with the 'check_model' function ('performance' package; Lüdecke *et al.* 2021). To relate the potential shift in hatching dates to the potential shift in the start of snowmelt in our two study years, we calculated the first day of the year on which the ground is no longer 100% covered with snow ('Snowmelt start'). We then performed a Wilcoxon test ('Wilcox.test' in the 'stats' package in R; R Core Team 2022) on the snowmelt start dates across all locations to assess whether snow started to melt at a significantly different time between 2021 and 2022. The variables of each statistical model and their respective AIC are summarized in Table S1.

RESULTS

Ptarmigan call identification

In 2021 and 2022, 66 250 h were recorded on 378 days. Ptarmigan calls were detected in all 10 study areas, even in *Le Moléson*, where no Ptarmigan had been detected during official counts since 1998 nor reported by occasional observers since 2016, and in *Les Andérets*, where no male has been registered since 2018 during conventional counts. Based on the benchmarking set of 1136 call detections from 38 single 1-h files manually checked, we were able to determine true positives, false positives and false negatives of detections by our classifier. Ptarmigan calls that could be identified with a reasonable degree of accuracy as false positives represent 25%, and true positives represent 75% with no confidence score threshold (Fig. 2). At a confidence score of 0.47, the curves of the true positives and false negatives cross each other implying a balance point between recall and precision. Therefore, only detections at 0.47 and above were selected for further analysis. These target detections > 0.47 represent 60% (716 985 call detections) of all detected calls (1 201 894 detections). At this confidence score threshold, the recall rate is 50% and the precision rate is 85%.

Daily and seasonal patterns of Ptarmigan call activity

Ptarmigan called throughout the study season, although calling activity seems to have been more intense at the beginning of the season from March to the end of April (Fig. 3). Calling activity increased and peaked at civil dawn before decreasing rapidly to reach a stable low rate 40 min after dawn (Fig. S2). The period with the highest activity of the day lasted 30–45 min.

Calling rate varied significantly along both seasons (GAMM; edf = 12.18, Ref.df = 12.18, $F = 40.42$, $P < 0.001$, Fig. 4). In 2021, calling rate was less intense and significantly increased twice during the study season, once in mid-April and once in early June (edf = 8.854, Rf.df = 8.854, $F = 7.613$, $P < 0.001$; Fig. 4a,c). The greatest peak of activity occurred from mid-March to early April for 2022 (edf = 8.164, Rf.df = 8.164, $F = 15.3$, $P < 0.001$, Fig. 4b,d). Diagnostics plots are shown in Figure S3.

Environmental variables correlating with Ptarmigan calling activity

Among the seven original environmental variables, five were retained for the final GLMM. Deviation of temperature from the mean, sun ratio, snow depth, lunar illumination and precipitation all impacted Ptarmigan call activity, measured as number of calls per day. The deviation of temperature from the mean correlated positively with calling activity (linear term: 8.956 ± 1.028, $z = 8.712$, $P < 0.001$; quadratic term: -3.293 ± 0.906, $z = -3.632$, $P < 0.001$), whereas a higher sun ratio correlated negatively with daily vocalizations (linear term: -2.394 ± 1.058 $z = -2.263$, $P = 0.023$), as did precipitation (-4.326 ± 0.993, $z = -4.355$, $P < 0.001$). Calling
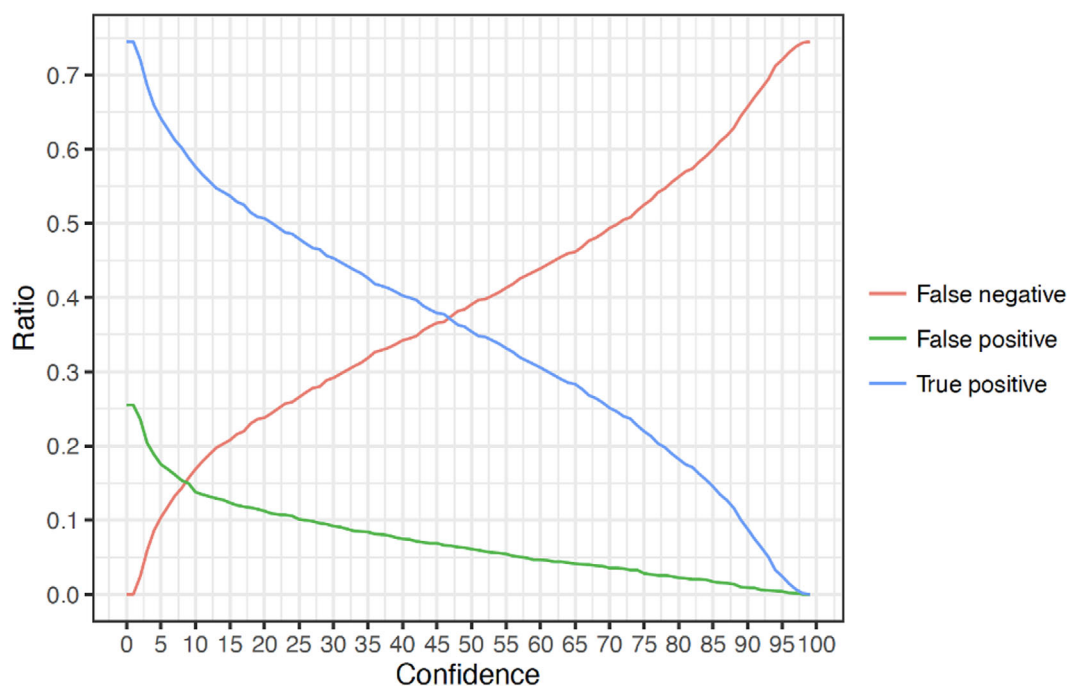
Figure 2. Benchmarking analysis. The *y*-axis 'Ratio' indicates the number of calls detected or not detected by our classifier divided by the total number of the classifier's detections without confidence score threshold. The *x*-axis 'Confidence' is the confidence score given by the classifier for each detected call.

activity showed a hump-shaped response to snow depth (linear term: 9.209 ± 1.2187, $z = 7.557$, $P < 0.001$; quadratic term: -5.239 ± 0.925, $z = -5.661$, $P < 0.001$) with an optimum around a snow depth of 100 cm. The contribution of random variables was 10.87% for area, 12.46% for location, 3.72% for day of year and 3.74% for year. Supplementary analysis examining the relationship between snow cover and snow depth reveals that the ground begins to be only partially covered with snow when the depth drops below 100 cm (Fig. S4). Maximum activity occurs when the snow depth approaches 100 cm (Fig. 5d), implying a snow cover close to 100%. Finally, lunar illumination increased the calling activity (GLMM; 3.740 ± 0.876, $z = 4.271$, $P < 0.001$; quadratic term: 2.449 ± 0.911, $z = 2.681$, $P = 0.007$). Response curves are shown in Figure 5 and regression diagnostics plots in Figure S5. Lunar illumination also had a significant effect on the onset of calling activity (GLMM; 0.207 ± 0.055, $z = 3.750$, $P < 0.001$). On average, the first daily call was detected 12 min earlier when the moon was full (illuminated fraction = 1) compared with the new moon (illuminated fraction = 0).

Regression diagnostics plots for this model are shown in Figure S6.

Hatching dates in 2021 and 2022

The average hatching date did not differ significantly between 2021 and 2022 (LM; 0.64 ± 1.136, $t = 0.320$, $P = 0.749$). However, the mean observer date, i.e. the average date of observation of Ptarmigans, showed a difference of 9 days, probably because of snow conditions. Indeed, snowmelt start showed a 69-day difference between the two years, with 2021 being the year with the latest melt (Wilcoxon test: $P < 0.001$; median day of the year in 2021 = 162; median day of the year for 2022 = 93). Mean hatching dates for 2021 and 2022 in relation to elevation are shown in Figure S7. Diagnostics plots for this model are shown in Figure S8.

DISCUSSION

In this study, we characterized the phenology of the vocal activity of Ptarmigan in the Swiss Alps in relation to environmental variables. Using 38
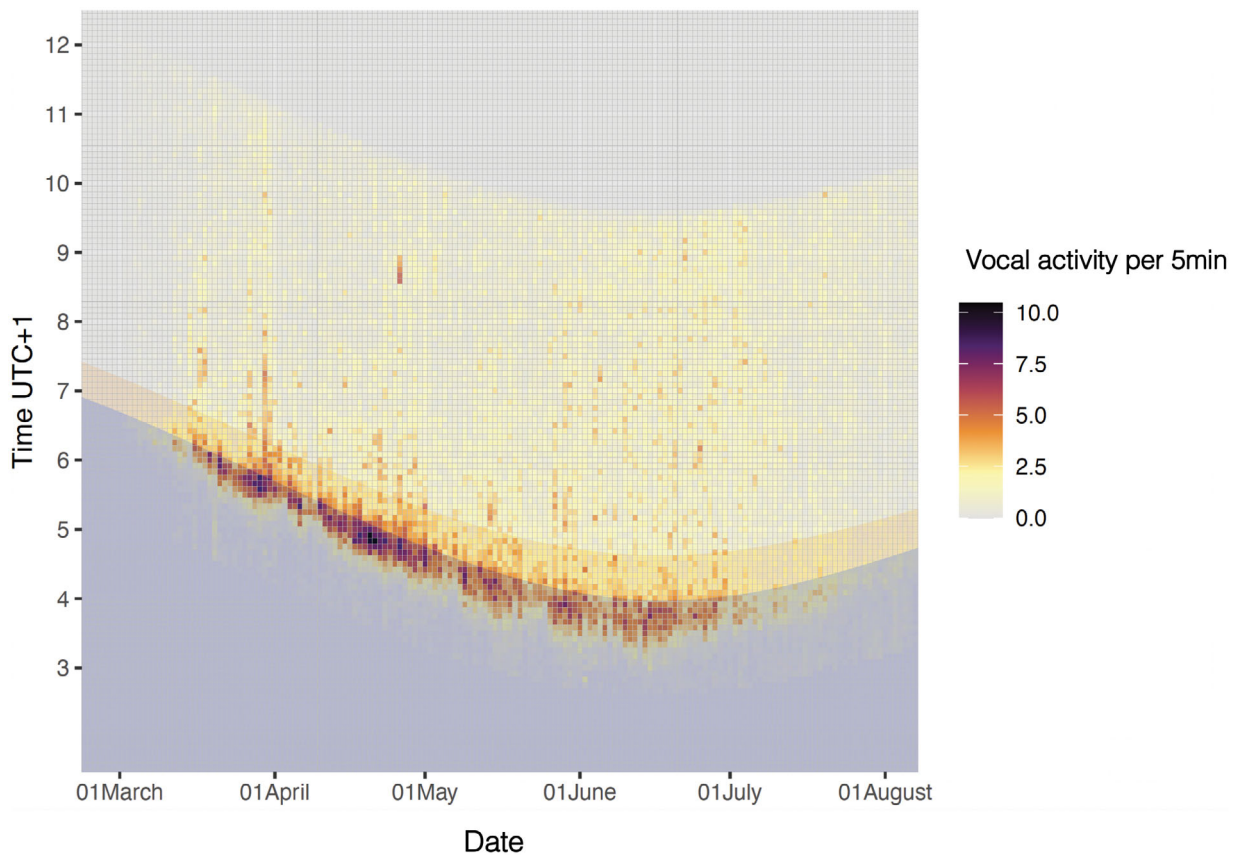
Figure 3. Number of calls detected across the two seasons. Calls were summed per 5 min and then rescaled per year and per recorder to have numbers of calls per location on the same scale. The orange area represents civil dawn to sunrise; the blue area represents night.

recorders over 2 years from March to July, we were able to study the vocal activity patterns of this elusive bird species in 10 areas in the Swiss Alps where conventional surveys are conducted each year. With 66 250 h of recordings collected and over 700 000 Ptarmigan vocalizations detected, we were able to cover a broad spatial and temporal range and highlight daily and seasonal call rhythms. We confirmed the presence of individuals in two areas where conventional counts were unable to detect Ptarmigans for the last 4–24 years. Moreover, we showed that the amount of data gathered by our study and our analytical methodology enables us to quantitatively study the vocal activity of a species over time. Finally, the application of deep learning networks for automated call recognition on our recordings demonstrated the robustness of machine learning when analysing large-scale datasets. We provide an open-source program capable of identifying the calls of

Ptarmigan males from acoustic data that can be used for further research projects on the species. PAM is a fast-evolving methodology that can be used in rare species to study vocal activity patterns, or can be applied in population surveys or phenological studies, underscoring the broader applicability of bioacoustics.

We found that a convolutional neural network for the automated recognition of Ptarmigan vocalizations on spectrograms can serve as an effective tool for extracting calling events of the species in a temporally extensive dataset. Throughout the season, we were able to extract over 700 000 reliable Ptarmigan calls from the recordings with a precision rate of 85% and a recall rate of 50% at a score confidence threshold of 0.47. Our precision rate is higher than that of other studies applying an automated classifier on grouse vocalizations. Abrahams ([2019]) found a precision rate of 0.61 for the Western
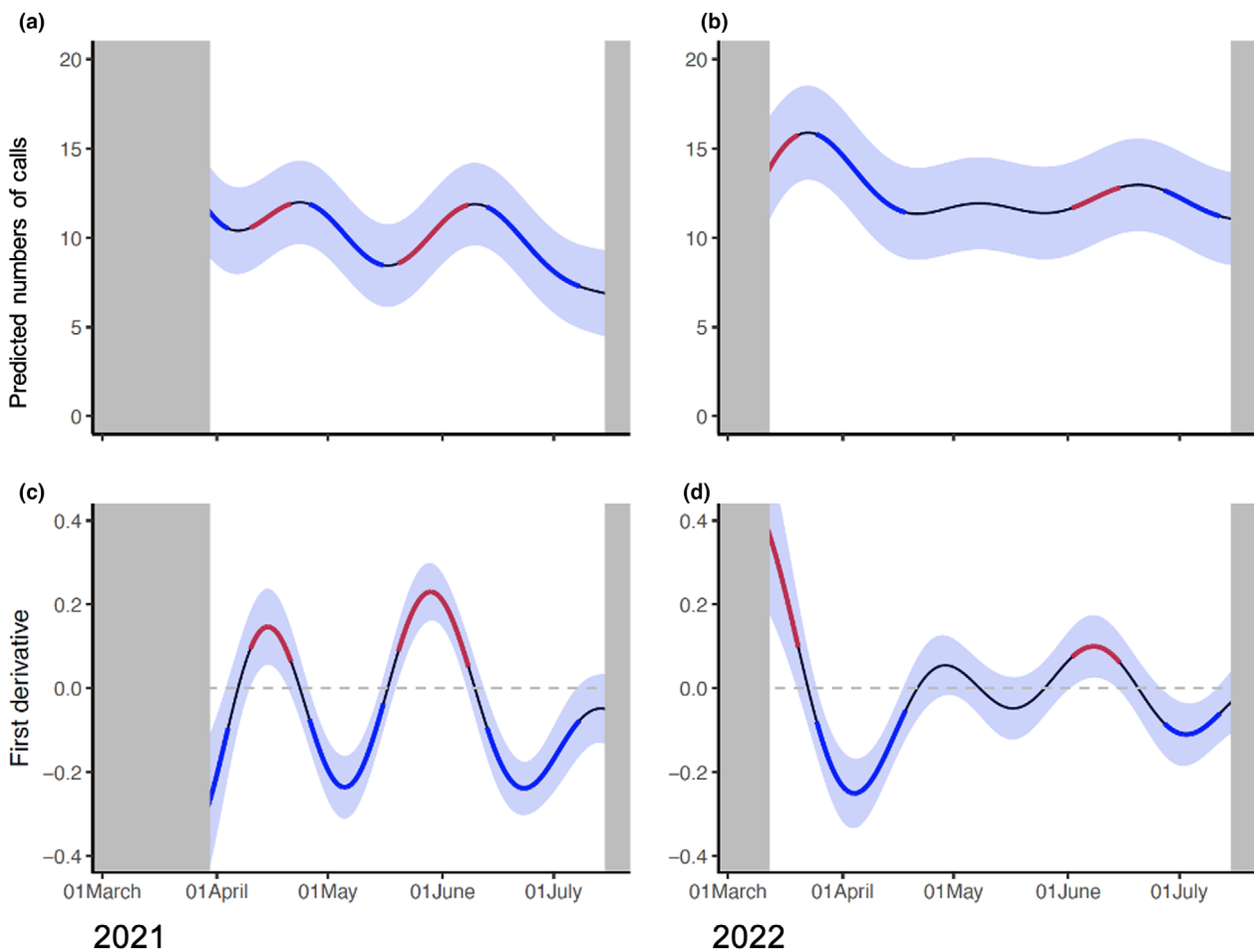
Figure 4. Generalized additive mixed models of calling rate across the season and their first derivatives. Grey areas represent the periods when < 50% of the used recorders were active. Left side panels: curves for 2021; right side panels: curves for 2022. (a, b) Non-linear regression curves of calling activity as a function of time. (c, d) First derivative curves of modelled calling activity. Coloured segments of each curve indicate significant decreases (blue) or increases (red) in calling activity at a specific time period.

Capercaillie *Tetrao urogallus*, while Lapp *et al.* (2023) calculated 0.71 for the Ruffed Grouse *Bonasa umbellus*. However, our recall rate is comparatively lower (0.81 for Western Capercaillie and 0.78 for Ruffed Grouse). The mean recall and precision rates across studies were reported as 0.60 and 0.71, respectively (Knight *et al.* 2017). To compare apart from some specific sites where background noise generated tremendous false positives, the BirdNET algorithm (version 2.2) performed well with a correlation in calling activity of 86% with our bespoke classifier. Moreover, it is now possible to train specific models of BirdNET v2.4 based on species-specific or local new data, and also incorporate local noise data.

Using these call detections as a basis for our analysis, we showed that daily peak vocal activity occurred at dawn independently of the time in the season. This can be explained by the unique conditions that occur at dawn, which lead to a particularly efficient sound propagation at this time (Henwood & Fabrick 1979, Brown & Handford 2003). Moreover, dawn suggests a peak occurrence of territorial intrusion, as observed in passerine birds (Erne & Amrhein 2008). This heightened intrusion provokes greater territorial defence and, consequently, increased vocal activity. In the case of Ptarmigans, it was widely assumed that its vocal activity begins and is strongest before sunrise (Watson 1956, Bossert 1977, Marti *et al.* 2016), but activity before dawn has
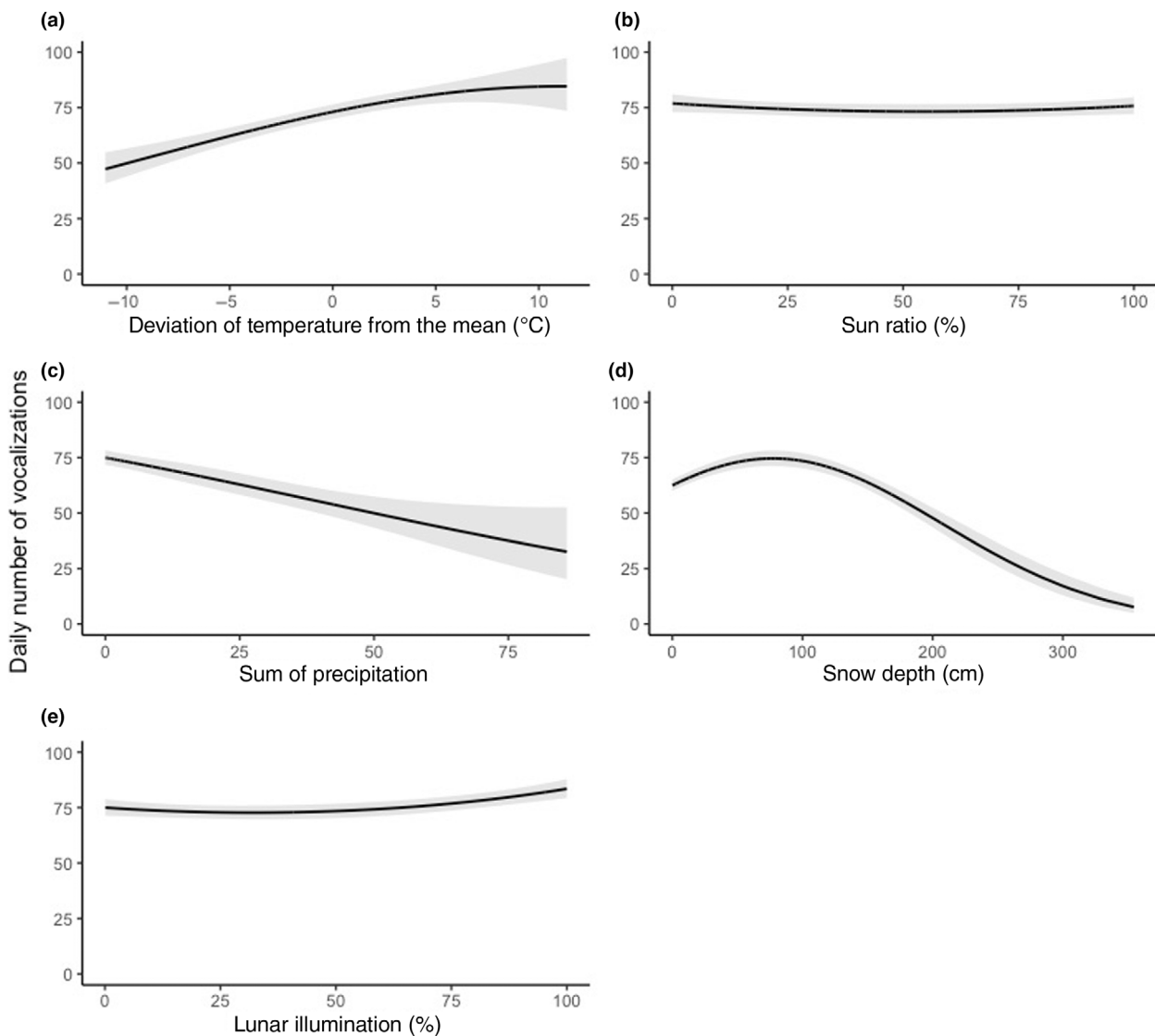
Figure 5. Response curves from generalized linear mixed models of daily number of Ptarmigan calls in relation to five environmental predictors. Grey shaded areas represent the 95% confidence intervals.

been less well documented (but see Marti *et al.* 2016). We also found that Ptarmigans started calling 12 min earlier and produced more calls when the moon was full compared with a new moon. The impact of the illuminated fraction of the moon on Ptarmigan activity has, to our knowledge, not been studied in detail. However, Marti *et al.* (2016) observed that vocalizations were given earlier on clear full moon nights in Aletsch (Switzerland, VS). Moreover, some studies have reported a significant effect of moon illumination on the onset of singing/calling activity of other

diurnal species (Bruni *et al.* 2014, York *et al.* 2014).

We demonstrated for the first time that Ptarmigan vocal activity is not constant throughout the season. We found a peak of vocal activity between mid-March and the end of April, 1–2 months earlier than documented several decades ago in field studies in the Alps (Bossert 1980, Scherini *et al.* 2003). Phenological events of many taxa among plants and animals are known to be advanced due to climate warming (Vitasse *et al.* 2021), especially pronounced in the Alps

(Keiler *et al.* 2010, Foster & Rahmstorf 2011). However, advances in song phenology comprise only about 2.5–3.8 days per decade for birds across the northern hemisphere (Strebel *et al.* 2014) and are therefore unlikely to be fully responsible for the difference of several weeks observed in our study. Additionally, the protocol for counting Ptarmigan was modified 1 year before the start of our study, with a requirement to be in the field before dawn rather than before sunrise. Our results confirm that the daily peak in vocal activity occurs at dawn and support this modification to the protocol.

This intra-annual modulation of vocal activity can exhibit significant interannual variability, as highlighted in our two study years. The earlier peak of vocal activity observed in 2022 compared with 2021 is probably attributable to climatic conditions, with the higher and delayed melting of the snow layer and lower temperatures in 2021. It has been shown that male Ptarmigans tend to arrive on their territories and defend them earlier with earlier snow melting or thinner snowpack (Bossert 1995). Novoa *et al.* (2008) showed that snow conditions played an important role in territory availability in Ptarmigans and Marin-Cudraz *et al.* (2019) found that males equipped with VHF trackers converged later to the arena in spring when snow depth was still high on their territories. Conversely, although the phenology of vocal activity seems to display a substantial interannual variability in response to climatic conditions, hatching phenology did not show a significant shift in response to contrasting environmental conditions. The difference of 69 days observed in the onset of snowmelt between the two study years is not reflected in the hatching dates dataset, potentially shedding light on this lack of plasticity.

It is expected that breeding events such as hatching would be synchronized with optimal foraging conditions (Perrins *et al.* 1970, Verboven & Visser 1998, Furrer *et al.* 2016). Indeed, the development of Ptarmigan chicks is intricately linked to the abundance of invertebrates as a high protein resource at specific times of the year (Theberge & West 1973, Savory 1989). Additionally, the physiological condition of the female Ptarmigan before laying is strongly positively related to breeding success (Moss & Watson 1984) and relies on the protein content of food plants, which in turn is influenced by the phenological stage of the plants (García-González *et al.* 2016). On top of that, in arctic–alpine habitat, these events, such as the abundance of invertebrates and the phenological stage of plants, are known to be connected to snowmelt timing (Høye & Forchhammer 2008, Jerome *et al.* 2021). Therefore, it could be expected that any temporal shift in favourable conditions for breeding should be followed by a corresponding temporal shift of breeding activity. However, in our study, the link between breeding events and environmental conditions seems imperfect, and this potential phenological mismatch could ultimately result in deteriorating breeding conditions in the face of intensifying climate warming in the Alps. Phenological mismatch has been shown for the White-tailed Ptarmigan *Lagopus leucura* in the Rocky Mountains (Wann *et al.* 2019) and suggested for another high-alpine species, the White-winged Snowfinch *Montifringilla nivalis* (Schano *et al.* 2021).

The highly adaptive nature of vocal activity phenology in relation to climatic factors suggests that conventional monitoring should be seasonally adapted each year, considering external factors. Until now, the counts took place during good weather in the second half of May. The counters were in place before sunrise, but the protocol has recently changed so that they should be on the counting area before dawn. Our results suggest that surveys for counting Ptarmigan males should be carried out between mid-March and the end of April, depending on weather and snow conditions. During this period, males are sensitive to temperature peaks. We suggest conducting the conventional count when temperatures are particularly mild compared with the local average at that time but when the snowpack is still thick, implying a snow cover of 100%. Other weather conditions, such as rain and cloud cover, can also influence the monitoring with higher activity during cloudy days but potentially lower visual detection (i.e. when flying). Finally, people conducting the monitoring should be ready to count before the start of the calls, 30 min before dawn. To validate these recommendations, conducting multiple conventional counts over several years would be necessary.

We have shown that bioacoustics have the potential to outperform humans in specific tasks and can therefore complement field studies. As we applied PAM on an elusive species in harsh environmental conditions, we offer an intriguing case study that can be adapted to any vocal species.

The combination of autonomous recorders, automated classifiers and deep statistical analysis to study vocal activity allowed us to uncover intra-annual and inter-annual trends and detect subtle changes in vocal behaviour in relation to environmental conditions. Additionally, we harnessed the power of machine learning techniques to successfully detect and classify the vocalizations within recordings. Taken together, these innovative tools enabled us to propose a new sampling period earlier in the season and ideal weather conditions to conduct the conventional count. In the context of accelerating warming of the alpine environments, the populations of this species could decline or even become locally extinct from those areas on the edges of their spatial distribution. Further investigation should prioritize these marginal populations and document their trends. This work is part of an ongoing effort to monitor Ptarmigan populations that will help to track population trends to prioritize conservation measures.

AUTHOR CONTRIBUTIONS

Amandine Serrurier: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; data curation. **Przemyslaw Zdroik:** Conceptualization; methodology; writing – review and editing; software; data curation; investigation; validation; formal analysis. **Res Isler:** Conceptualization; investigation; writing – review and editing. **Tatiana Kornienko:** Methodology; writing – review and editing; software; project administration; data curation; conceptualization. **Elisenda Peris-Morente:** Conceptualization; investigation; methodology; writing – review and editing. **Thomas Sattler:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing; project administration; supervision; formal analysis; funding acquisition; data curation; resources; writing – original draft. **Jean-Nicolas Pradervand:** Conceptualization; investigation; methodology; validation; visualization; writing – review and editing; project administration; formal analysis; supervision; funding acquisition; data curation; resources; writing – original draft.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICAL NOTE

None.

Data Availability Statement

The data that support the findings of this study are openly available in Vogelwarte repository at https://doi.org/10.5281/zenodo.8086326.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Histogram of call length of Rock Ptarmigan based on manual annotation of 907 calls in 40 h of recordings.

Figure S2. Generalized additive mixed model of calling rate during the day. Number of calls is summarized for every location.

Figure S3. Visual check of the assumptions of our negative binomial additive mixed model with number of calls/hour as response variable.

Figure S4. Relation between snow depth and snow cover. Points represent means of snow depth or snow cover around each recorder for 2021 and 2022. Lines are local regression fitting for each year.

Figure S5. Visual check of the assumptions of the negative binomial linear mixed model in our study with number of Ptarmigan calls as response variable.

Figure S6. Visual check of the assumptions of the γ linear mixed model in our study with onset of calling as response variable.

Figure S7. Mean hatching dates for Ptarmigan along the elevational gradient for 2021 (blue) and 2022 (orange). Coloured points are calculated hatching dates for both years. Shaded areas are the 95% confidence intervals. *P* values did not show a significant shift between 2021 and 2022.

Figure S8. Visual check of the assumptions of the linear model in our study with hatching date as response variable.

Table S1. Summary of the statistical models used in the study with their respective response, explanatory and random variables. AIC, Akaike information criterion for each model.