# Effects of physical environmental variables on the behaviour of mountain woodland songbirds

Inauguraldissertation

zur

Erlangung der Würde eines Doktors der Philosophie vorgelegt der Philosophisch-Naturwissenschaftlichen Fakultät der Universität Basel von

Julia Paterno

Basel, 2025

Originaldokument gespeichert auf dem Dokumentenserver der Universität Basel edoc.unibas.ch

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät auf Antrag von

Erstbetreuer: Prof. Dr. Valentin Amrhein Zusätzliche Erstbetreuerin: Dr. phil. Pia Anderwald Zweitbetreuer: Prof. Dr. Walter Salzburger Externe Expertin: Priv.-Doz. Dr.rer.nat. Sabine Hille

> Basel, den 15. Oktober 2024 Prof. Dr. Marcel Mayor Dekan



Effects of physical environmental variables on the behaviour of mountain woodland songbirds

Julia Paterno 2024

Piz Linard at dawn, SNP / Hans Lozza

# Contents

Acknowledgements / Dank	7
Abstract / Zusammenfassung	13
Introduction	17
Chapter 1 Start of dawn singing as related to physical environmental variables in an alpine environment	35
Chapter 2 An exercise in conducting small studies: Road construction noise and start of dawn singing in mountain woodland songbirds	51
Chapter 3 Effects of habitat and road noise on singing activity of coal tits in subalpine woodland	77
Chapter 4 Songbirds at higher elevations fledge at harsher environmental conditions	99
General discussion	121
Curriculum vitae	130



Eurasian chaffinch (Fringilla coelebs), SNP / Hans Lozza

## Acknowledgements

This thesis and the studies presented herein would not have been possible without the help of many people to whom I am greatly indebted. During this project I was financially supported by the Zigerli Hegi Foundation, the Swiss National Park, the Swiss Ornithological Institute and the Nukahiva Foundation.

First, my sincere thanks goes to my supervisor Valentin Amrhein for his unconditional support, his quick and constructive responses and several enriching (philosophical) conversations. Furthermore, I am greatly indebted to Fränzi Korner-Nievergelt, for inspiring conversations, great ideas and statistical support. I thank Walter Salzburger from the University of Basel for his support as co-supervisor and Sabine Hille from the University of Natural Resources and Life Sciences Vienna for her work as an external expert.

I am greatly indebted to the Team of the Swiss National Park. Many thanks go to Pia Anderwald, who laid the foundation for this project, and supported me from the beginning. Further, I would like to thank Ruedi Haller for his support and his magnificent ideas. Thanks go to Sonja Wipf and Flurin Filli for their support during the project. Nahuel Ozan and Sven Buchmann supported me with R-coding – thank you for your support. Special thanks go to Flavio Cahenzli, for his unconditional support in every situation. Further, I am very grateful to Andrea Rossi, for her support at work and for always being a friend. I would also like to thank Seraina Campell Andri, Sam Cruickshank, Christian Rossi, Ursi Sterrer, Fabienne Koenig and all team members and interns that helped with field work and supported me during this project. I am also grateful to Samuel Wiesmann, Tamara Estermann, Jan Schweizer, Stefan Triebs and Christine Roesch for their work-related support and several inspiring conversations after work. I would like to thank Hans Lozza for his support during this project and for providing beautiful photographs, and a thank you also goes to Fadri Wehrli, Flurin Filli and Steivan Luzi for impressing photographs. Thanks to Thomas Rempfler and Raphael von Büren, who started their PhD during my time at the SNP. I would also like to thank Kathrin Lüscher, Stania Bunte, Nicole Kunz, Lilian Conrad and Erna Romeril for administrative support whenever needed. A thank you also goes to Marcus Willms and Enzo Roncoletta for IT support. Further, I would like to thank Stefanie Gubler for her work and support for Chapter 4. Thanks also go to the park wardens Fadri Bott, Andri Cuonz, Curdin Eichholzer, Claudio Irniger, Domenic Godly, Steivan Luzi, Reto Strimer and Not Armon Willy for their support and expertise during this project.

I am grateful to the Museo cantonale di storia natural (Ticino) for lending us their SM4 sound loggers in 2020. Further, I would like to thank Gilberto Pasinelli from the Swiss Ornithological Institute for his support during this project. A thank you also goes to Rafael da Silva from the Tiefbauamt Graubünden, for information on construction works. Mathis Müller and Christian Rixen supported me, especially in the beginning, with the analysis of mysterious sounds. Thanks also go to Jeannine Fluri, Yann Rime and Lilla Lovász from my research group at the University of Basel. Further, I would like to thank Nadja Bernhard for her unconditional support, inspiring days in the field and always being a friend.

A big thanks goes to my friends and close colleagues for inspiring discussions and activities to dispel my thoughts. I especially thank Marie-Louise Seidel, Nina Brunner, Anja Dünser, Rebecca Bolter and Suzana Blažević for always supporting me.

Last but not least, I am indebted to my family and their unconditional support during my whole life. I would like to thank Elisabeth, Hugo, Sabine and Hansi for their ongoing support and unconditional love. Special thanks go to Sarah for joining my life in the last 33 years. Further, I would also like to thank Wolfi for interesting discussions and his support. In the end, there is only one person left: Thank you Andi, for your unconditional support, your patience and your magnificent, inspiring ideas!

"Maybe they do it because it's fun."

## Dank

Die vorliegende Arbeit und die darin enthaltenen Studien wären nicht möglich gewesen ohne die Unterstützung von vielen vielen Personen, welchen ich zu tiefem Dank verpflichtet bin. Während des Projekts wurde ich finanziell von der Zigerli Hegi Stiftung, dem Schweizerischen Nationalpark, der Schweizerischen Vogelwarte und der Nukahiva Stiftung unterstützt.

Mein aufrichtiger Dank gilt zunächst meinem Betreuer Valentin Amrhein für seine unvoreingenommene Unterstützung, seine raschen und konstruktiven Rückmeldungen und viele bereichernde (philosophische) Gespräche. Darüber hinaus bin ich Fränzi Korner-Nievergelt zu tiefem Dank verpflichtet, für viele inspirierende Gespräche, grossartige Ideen und ihre fachlich fundierte Unterstützung. Ich danke Walter Salzburger von der Universität Basel für seine Unterstützung als Co-Betreuer und Sabine Hille von der Universität für Bodenkultur Wien für ihre Arbeit als externe Expertin.

Dem Team des Schweizerischen Nationalparks bin ich zu grossem Dank verpflichtet. Ein grosser Dank geht an Pia Anderwald, welche den Grundstein für dieses Projekt gelegt und mich von Beginn an unterstützt hat. Weiter möchte ich mich bei Ruedi Haller für seine Unterstützung und seine grossartigen Ideen bedanken. Danken möchte ich auch Sonja Wipf und Flurin Filli für ihre Unterstützung während des Projekts. Nahuel Ozan und Sven Buchmann unterstützen mich beim R-Coding - vielen Dank für eure Unterstützung. Ein besonderer Dank geht an Flavio Cahenzli, für seine unvoreingenommene Unterstützung in allen Lebenslagen. Weiter bin ich Andrea Rossi sehr dankbar für ihre Unterstützung bei der Arbeit und ihre Freundschaft. Ich möchte mich auch bei Seraina Campell Andri, Sam Cruickshank, Christian Rossi, Ursi Sterrer, Fabienne Koenig und allen Teammitgliedern und Praktikant/innen bedanken, welche mir bei der Feldarbeit geholfen und mich während des Projekts unterstützt haben. Ich danke auch Samuel Wiesmann, Tamara Estermann, Jan Schweizer, Stefan Triebs und Christine Roesch für ihre Unterstützung bei der Arbeit und viele, bereichernde, erheiternde Momente nach der Arbeit. Ich möchte Hans Lozza für die Unterstützung während des Projekts und das Bereitstellen der schönen Fotos danken, und ein Dankeschön geht auch an Fadri Wehrli, Flurin Filli und Steivan Luzi für die beeindruckenden Fotos. Danke an Thomas Rempfler und Raphael von Büren, welche während meiner Zeit am SNP ihre Dissertation begonnen haben. Ich möchte mich auch bei Kathrin Lüscher, Stania Bunte, Nicole Kunz, Lilian Conrad und Erna Romeril für die administrative Unterstützung bedanken, wann immer ich sie benötigte. Ein Dank geht auch

an Marcus Willms und Enzo Roncoletta für den IT Support. Ferner möchte ich Stefanie Gubler für ihre Arbeit und ihre Unterstützung bei Kapitel 4 danken. Ein Dank geht auch an Fadri Bott, Andri Cuonz, Curdin Eichholzer, Claudio Irniger, Domenic Godly, Steivan Luzi, Reto Strimer und Not Armon Willy für ihre Unterstützung und ihre fachliche Expertise während des Projekts.

Ich danke dem Museo cantonale di storia natural (Tessin), dass sie uns im Jahr 2020 ihre SM4-Soundlogger zur Verfügung gestellt haben. Weiter danke ich Gilberto Pasinelli von der Schweizerischen Vogelwarte für seine Unterstützung während des Projekts. Ein Dank geht auch an Rafael da Silva vom Tiefbauamt Graubünden für die Bereitstellung von organisatorischen Details. Mathis Müller und Christian Rixen unterstützten mich, vor allem zu Beginn, mit ihrem Fachwissen. Ein Dank geht auch an Jeannine Fluri, Yann Rime und Lilla Lovász aus meiner Forschungsgruppe an der Universität Basel. Weiter möchte ich mich bei Nadja Bernhard für ihre unvoreingenommene Unterstützung, inspirierende Tage im Feld und ihre Freundschaft bedanken.

Ein grosser Dank geht an meine Freunde für inspirierende Diskussionen und viele besondere Momente. Mein besonderer Dank gilt Marie-Louise Seidel, Nina Brunner, Anja Dünser, Rebecca Bolter und Suzana Blažević dafür, dass sie mich immer unterstützt haben.

Zu guter Letzt, bin ich meiner Familie zu tiefem Dank verpflichtet. Ich möchte Elisabeth, Hugo, Sabine und Hansi für ihre Unterstützung und ihre bedingungslose Liebe danken. Mein besonderer Dank gilt Sarah, welche mich seit 33 Jahren begleitet. Ausserdem möchte ich Wolfi für interessante Diskussionen und seine Unterstützung danken. Am Ende bleibt nur noch eine Person: Danke Andi für deine bedingungslose Unterstützung, deine Geduld und deine grossartigen, inspirierenden Ideen!

# Abstract

Background: The behaviour of songbirds depends on several physical

environmental factors that may change with increasing elevation. For example, temperature decreases and the vegetation period is shorter at higher elevations. Birds may need to adapt to changes in environmental conditions by changing their breeding or singing behaviour. This thesis aims to contribute to understand the effects of physical environmental variables on the behaviour of mountain woodland songbirds.

Location: Switzerland, Swiss National Park

Methods: To investigate the singing behaviour of mountain woodland

songbirds (Alpine tit, coal tit, Eurasian chaffinch, song thrush, mistle thrush and ring ouzel) we used passive acoustic monitoring and observations in the field. We also used citizen science data to examine changes in breeding phenology along an elevational gradient.

Results and main conclusions: We observed species-specific differences

in the singing behaviour according to the investigated variables, and found only small differences in the timing of breeding between higher and lower elevations independent of climatic conditions. The effect of anthropogenic noise seemed to be context- but not species-specific, since all investigated songbird species changed their singing behaviour in noisier areas and during nosier times. Physical environmental variables, like moon phase, temperature, cloud cover or aspect, had consistent but small effects on all investigated songbird species. The effects of elevation and date, in contrast, were more species-specific. Further, alpine songbirds seem to have evolved adaptations to cope with harsher environmental conditions at higher elevations, since the investigated species were only raised with a relatively small delay at higher compared to lower elevations.

Keywords: willow tit, automated recording, Audiomoth, SM4, breeding

phenology, dawn chorus

# Zusammenfassung

Hintergrund: Das Verhalten von Singvögeln hängt von verschiedenen

physikalischen Umweltfaktoren ab, die sich mit zunehmender Höhe ändern können. In höheren Lagen ist beispielsweise die Temperatur niedriger und die Vegetationsperiode kürzer. Vögel müssen sich möglicherweise durch ein verändertes Brut- oder Gesangsverhalten an die geänderten Umweltbedingungen anpassen. Die vorliegende Studie untersucht den Einfluss von physikalischen Umweltbedingungen auf das Verhalten von Bergwaldvögeln.

Ort: Schweiz, Schweizerischer Nationalpark

Methoden: Um das Gesangsverhalten von Singvögeln der Bergwälder

(Alpenmeise, Tannenmeise, Buchfink, Singdrossel, Misteldrossel und Ringdrossel) zu untersuchen, setzten wir automatisierte Aufnahmegeräte ein und führten Beobachtungen im Feld durch. Mit Hilfe von Citizen Science Daten untersuchten wir Veränderungen in der Brutphänologie entlang eines Höhengradienten.

Resultate und Fazit: Wir beobachteten artspezifische Unterschiede im

Gesangsverhalten in Abhängigkeit der untersuchten Variablen. Weiters fanden wir nur geringe Unterschiede im Zeitpunkt des Brütens zwischen höheren und niedrigeren Lagen. Die Auswirkungen von menschlichem Lärm scheinen kontext-, jedoch nicht artspezifisch zu sein: Alle untersuchten Singvogelarten veränderten ihr Gesangsverhalten während Zeiten mit erhöhtem Lärmpegel und in lauteren Gebieten. Physikalische wie Mondlicht, Umweltvariablen Temperatur, Bewölkung oder Hangausrichtung hatten konsistente, aber geringe Auswirkungen auf die untersuchten Singvogelarten. Die Auswirkungen der Höhenlage und des Datums dagegen waren eher artspezifisch. Ausserdem scheinen alpine Singvögel Anpassungen entwickelt zu haben, um mit den härteren Umweltbedingungen in höheren Lagen zurechtzukommen, da die untersuchten Arten nur mit relativ geringer Verzögerung in höheren Lagen zu brüten begannen verglichen mit niedrigeren Lagen.

## Introduction

- 1. Context and general introduction
  - 1.1. Context of the thesis

N atural habitats are increasingly affected by anthropogenic activities,

and anthropogenic noise is no longer restricted to urban areas. For example, the European Environmental Agency (2020) estimated that in Europe, nearly 20 % of "Nature 2000" sites were located in areas characterised by increased levels of anthropogenic noise. Furthermore, more than 40 million people living outside of urban areas are exposed to noise levels > 55 dB, and more than 70% of these people (31.1 million people) are exposed to increased levels of road noise (European Environmental Agency, 2020). Road noise is the most dominant source of anthropogenic noise and several previous studies found negative effects on humans and animals (i.e., Benfield et al., 2020; Jin et al., 2024; Kunc & Schmidt, 2019, 2020). Songbirds can be particularly affected, since acoustic communication can be impaired: Reproductive success can be reduced (i.e., Gross et al., 2010; Habib et al., 2007; Halfwerk et al., 2011; Holm & Laursen, 2011), predator-prey interactions altered (McIntyre et al., 2014) and warning or mating calls can be masked (i.e., Francis et al., 2011; Rheindt, 2003; Slabbekoorn & Peet, 2003).

Previous studies investigated the effects of anthropogenic noise on songbirds in different habitats. Most focused on road noise in urban areas and in wood- or grasslands. Common species like the great tit (*Parus major*) or the European blackbird (*Turdus merula*) are relatively well studied in this respect (i.e., Pohl et al., 2009, 2012; Ripmeester et al., 2010; Sierro et al., 2017; Templeton et al., 2016). Investigations in otherwise undisturbed areas such as mountain woodlands are largely lacking so far, as are studies dealing with the effects of noise pollution due to construction works.

In order to investigate the effects of anthropogenic noise in a near-natural area, we conducted our studies in the Swiss National Park (SNP). The SNP represents a completely protected area (IUCN category la i.e., "wilderness"), and since a cantonal road (Ofenpass road) runs through the SNP, it is a suitable study site to investigate effects of anthropogenic noise on the behaviour of songbirds in a highly undisturbed, alpine area.

Previous studies on songbird behaviour observed increased singing activity during early breeding stages (Brown, 1963; Bruni & Foote, 2014; Holmes & Dirks, 1978; Welling et al., 1995), and decreased singing activity later during the breeding season (i.e., Erne & Amrhein, 2008; Hyman, 2005).

As the breeding season may be shortened at higher elevations, the timing of breeding in birds may be changed at higher compared to lower elevations. We therefore investigated differences in the timing of breeding at higher and lower elevations, to account for differences in singing activity due to differences in breeding stage.



## 1.2. Origin of the thesis

In 2018, Pia Anderwald started a project to investigate the soundscapes of the SNP. She selected ten suitable sites to investigate changes in species richness, diversity and composition of songbirds. Two years later, I started my PhD partly based on the previously selected sites. I conducted a study on the start of dawn singing at 70 sites (differently affected by road noise) along an elevational gradient (Chapter 1) and included research on the effects of construction noise on singing behaviour during dawn (Chapter 2). Furthermore, I investigated the effects of road noise on the singing activity of coal tits (Chapter 3), and since singing behaviour is closely related to the breeding stage (i.e., Brown, 1963; Bruni et al., 2014; Hegelbach & Spaar, 2000b; Holmes & Dirks, 1978; Merilä & Sorjonen, 1994; Naguib et al., 2016; Slagsvold, 1977; Welling et al., 1995), I also investigated changes in breeding phenology along an elevational gradient (Chapter 4).

### 1.3. How to measure noise in a noisy environment?

When investigating the effects of road noise on singing behaviour of birds, it is necessary to quantify the amount of road noise. Therefore, I tested different methods: First I measured the ambient noise level with a noise level metre (Extech SL 510 Sound Level Meter), but since it was not possible to distinguish between anthrophonic, geophonic and biophonic sounds I discarded this method. Then, I classified sites using subjectively experienced

road noise levels. I used four noise categories: non-audible, audible, disturbing and extreme. This method worked well and is described further in Chapter 1. Additionally, I investigated changes in road noise level over time, and for this purpose, I placed nine automated acoustic recorders (sound loggers) along the Ofenpass road. I then measured noise levels by RMS SPL (Root Mean Square Sound Pressure Level, unit: decibels relative to full scale, dBFS). This method also worked well; for further explanations see Chapter 3.

#### 1.4. How to investigate singing behaviour of birds in a noisy environment?

When investigating the singing behaviour of birds in noisy environments, the observer must be aware of possible masking effects of background noise. An increased level of background noise means that an observer may hear less. Thus, an apparent observed reduction in singing behaviour could lead to wrong conclusions (i.e., there might be no difference in singing behaviour, but the observer might have heard fewer song phrases). Therefore, in this thesis I focused on singing behaviour in noise-polluted areas, but concentrated on noise-reduced times (i.e., dawn chorus during morning when there is low traffic) or noise-reduced areas (see Chapter 3) for data analysis.

#### 1.5. How to investigate songbird behaviour?

Several previous studies used point-count data (i.e., Bayne et al., 2008; Polak et al., 2013; Wiącek et al., 2019) or passive acoustic monitoring (i.e., Bahía et al., 2024; Cretois et al., 2024; Sánchez et al., 2022) to investigate the effects of anthropogenic noise on songbirds. Automated acoustic recorders are a common tool in bird ecology (i.e., Bardeli et al., 2010; Hagens et al., 2018; S. B. Holmes et al., 2014; Sethi et al., 2022; Shonfield & Bayne, 2017) with several advantages: Data can be collected with minimal disturbance in the study area and one can collect data at several sites at the same time without



observer bias. Since data are analysed in the office, there may be only one observer, also leading to a reduction in observer bias. Furthermore, one can listen to the same section of an audio file several times and thus may be able to obtain different information compared to observers in the field. In contrast, an observer in the field is able to distinguish between individuals and is able to determine the position of a bird. This information can only be collected with a high amount of additional effort (triangulation; i.e., Gayk & Mennill, 2020) when using automated acoustic recorders. Depending on the study question, I decided to use point-count data or passive acoustic monitoring for data collection.

## 1.6. Types of sound loggers

In Chapters 1 and 3, I used two different types of sound loggers for data collection: The SM4 song meter (Wildlife Acoustics) and the Audiomoth (Open Acoustic Devices, 2020; Table 1, Figure 1). For the investigation of dawn singing behaviour I used 112 Audiomoths (Chapter 1), and to investigate differences in singing activity of coal tits (Chapter 3) I used twelve SM4 song meters, a bigger, stereo-recording, but more expensive alternative to the Audiomoth (Table 1).

	SM4	Audiomoth
Microphone	Stereo	Mono
Recordings	16-bit PCM .wav files or compressed .w4v files uncompressed .WAV files	
	H 218 mm	H 58 mm
Measures	W 186 mm	W 48 mm
	D 78 mm	D 15 mm
Powered by	4 D-cell Alkaline or NiHM Batteries	3 AA Batteries

Table 1 Specification of two common acoustic recording devices.



Figure 1 Deployment of sound loggers. A) JP prepares the deployment material: SM4 song metre, Audiomoth, a noise level metre (from left to right) and a strip. B) Last check if everything is working and the schedule is correct (SM4 song metre). C) JP deploys the Audiomoth. Picture source: SNP / Hans Lozza.

### 1.7. Species detection with sound loggers

Prior to data collection I investigated differences in the detection distance and detection probability of bird vocalizations depending on the type of sound logger (SM4, Audiomoth).

### 1.7.1. Detection distance

I tested and compared detection distance in woodland and open grassland for SM4 and Audiomoth. For this purpose, I created a sound file with 12 frequencies between 1 – 12 kHz (most songbirds produce frequencies between 0.2 kHz and 10 KHz; Mikula et al., 2021) with the packages tuner (Ligges et al., 2018), audio (Urbanek, 2020) and seewave (Sueur et al., 2008) in R (R Core Team, 2020). In the sound file a frequency was played for 1.5 seconds and then the next higher frequency followed.

To determine the detection distance I played the sound in the field (woodland and grassland without elevations) with a Samsung Galaxy A32 (noise level of speaker set to maximum) at distances between 0 - 80 m. Afterwards I analysed the recordings of the SM4 and the Audiomoth with the programme Raven (Center for Conservation Bioacoustics, 2019).

The SM4 detected all frequencies above 1 kHz at all tested distances (0 – 80 m) independent of habitat. The Audiomoth performed well in grassland and at distances of up to 70 m in woodland, but failed to detect frequencies between 1 – 2 kHz and 10 – 12 kHz in the woodland at a distance of 80 m (Table 2). The two devices thus performed similarly at intermediate frequencies in both habitats up to a distance of 70 m.

Table 2 Detection distances of SM4 song meter and Audiomoth in grassland and woodland.

Habitat	Distance	SM4	Audiomoth
Grassland	0 – 80 m	1 – 12 kHz	1 – 12 kHz
Woodland	0 – 70 m	1 – 12 kHz	1 – 12 kHz
Woodland	80 m	1 – 12 kHz	3 – 10 kHz

### 1.7.2. Detection probability

In 2020 I also investigated the detection probability of SM4 (at this time, we did not have the Audiomoth). For this purpose, I deployed an SM4 on a tree at about 2 m height and set to record continuously. Then I walked around in the area and noted for each vocalizing bird the time, position, type of vocalization and bird species on a map. Back in the office, I compared the recordings and the manually collected data and noted whether a manually collected vocalization of a bird was detected by the SM4 or not. I conducted this approach at four sites within the SNP with similar results.

I found different detection probabilities depending on the species and the type of vocalization and a reduced detection probability in areas with rough terrain surface. This means that the SM4 detected vocalizations of birds less often when there was an elevation in the landscape compared to areas without elevations (i.e., flat landscapes) and that some vocalizations were easily detected near the SM4, while others were not detected (Figure 2).



Figure 2 Detection distances and detection probabilities of different species in the Swiss National Park (SNP). The map in the lower right-hand corner shows the location of the study site within the SNP. For a detailed map of the location of the SNP see Figure 4. ALPTI = Alpine tit; CRESTI = Crested tit, *Lophophanes cristatus*; COATI = Coal tit, *Periparus ater*, CHAFF = Eurasian chaffinch; TREEC = Eurasian treecreeper, *Certhia familiaris*; NUTCR = Spotted nutcracker, *Nucifraga caryocatactes*; GRSWO = Great spotted woodpecker, *Dendrocopos major*; CROSS = Red crossbill, *Loxia curvirostra*; LESWH = Lesser whitethroat, *Curruca curruca*. © SNP, 2024 / 08, map: swisstopo, Julia Paterno.

#### 1.8. How to analyse large amounts of data?

In total we collected more than 33 000 hours of acoustic recordings for data analysis in Chapters 1 and 3. To analyse this data, we considered the use of automated intelligence.

Several authors have been working on different solutions to analyse data by automated intelligence (i.e., Akçay et al., 2020; Kahl et al., 2021; Marcoň et al., 2021). For example, Kahl et al. (2021) developed the application BirdNET, which can be used to determine bird species based on vocalizations of birds (K. Lisa Yang Center for Conservation Bioacoustics, 2024).

In order to investigate whether BirdNET could be a suitable tool for our analysis, I tested two different settings. First, I compared the start of dawn singing extracted by BirdNET Version 1.4 with manually extracted start of dawn singing for six common woodland songbird species (Eurasian chaffinch; Alpine tit; coal tit; mistle thrush, *Turdus viscivorus*; song thrush, *Turdus philomelos*; European robin, *Erithacus rubecula*). BirdNET provided reliable results for the detection of bird species, but there seemed to be a lack of sensitivity. Even when sensitivity was set to maximum, BirdNET detected species much later compared to the manual detection.

In a next step, I compared the number of coal tit song phrases detected by BirdNET Version 2.4 with the manually counted number of coal tit song phrases. Here I observed that BirdNET produced a low number of false positives, but several false negatives. A previously published study observed large species-specific differences in the number of true positives (Singer et al., 2024) and developed a method to better distinguish between falsepositive and false-negative detections by including contextual information in the analysis (Singer et al., 2024). Future work on our data could be conducted with this new method that may lead to higher precision. However, at the time when we conducted our data analysis, BirdNET was an insufficient tool for our purpose.

Since data analysis with automated intelligence was not possible, I decided to conduct data analysis manually. Thus, I used the program Raven (Center for Conservation Bioacoustics, 2019) to visualize and analyse the recordings (Figure 3). Species determination of individual vocalizations was possible, as individual sound patterns have evolved for each species (i.e., Seddon, 2005; H. Slabbekoorn, 2004; Van Buskirk, 1997).



Figure 3 Spectrogram of the dawn chorus in the Swiss National Park (Mingèr, 19 May 2019), with some species highlighted by white cubes and labelled with name and picture. 1: dunnock *Prunella modularis*, 2: Eurasian treepcreeper, 3: black grouse *Lyrurus tetrix*, 4: crested tit, 5: Alpine tit, 6: coal tit, 7: mistle thrush; picture source: 1: fotocommunity.de, 2, 4 – 6: SNP / Hans Lozza, 3: SNP / Steivan Luzi.

#### 1.9. Study area

#### 1.9.1. Switzerland

Data collection for all studies were conducted in the mountain woodlands of Switzerland. The climate in Switzerland is strongly influenced by the Alps and its proximity to the Atlantic Ocean. Four seasons can clearly be distinguished with maximum temperatures in July / August and minimum temperatures in January / February (MeteoSwiss, 2024). The annual mean temperature in the Swiss lowlands is 8 – 12 °C; in the Alps the temperature

decreases by an average of  $0.65^{\circ}$ C per 100 m increase in elevation (ISO 2533:1975) and in the highest areas the average temperatures are below freezing (Federal Office of Meteorology and Climatology MeteoSwiss, 2024). The amount of precipitation strongly depends on the location: For example, the highest amount of annual precipitation was observed in the Alps (incl. Alpine foothills, south side of the Alps, western peaks of Jura), with an annual total of 2000 mm of precipitation (Federal Office of Meteorology and Climatology MeteoSwiss, 2024). In contrast, in the inner-Alpine valleys precipitation is much lower, for example, in the Engadin the average annual precipitation is 700 – 1000 mm (Federal Office of Meteorology and Climatology MeteoSwiss, 2024). From 1200 – 1500 m a.s.l. precipitation predominantly falls as snow, and the snow cover between 1200 – 1800 m lasts from approximately October to April (Federal Office of Meteorology and Climatology MeteoSwiss, 2024). Three of the four studies were conducted in the SNP (Chapter 1, 2 and 3).



Figure 4 Left: Map of Switzerland with the Swiss National Park (SNP) located in the canton of Grisons. Right: Zoomed in, map of the SNP. Maps: Swisstopo, 2024.

#### 1.9.2. Swiss National Park



The SNP is situated in eastern Switzerland (Figure 4) and covers an area of about 170 km<sup>2</sup> at elevations between 1400 m (Clemgia/Scuol) and 3174 m (Piz Pisoc). As an IUCN la protected area (i.e., "wilderness") the SNP is characterised by minimal human disturbance: There are no management measures such as logging or hunting, visitors must stay on trails and are not allowed to stay overnight.

About 30% of the area is covered by coniferous woodlands, with two subspecies of the mountain pine (*Pinus mugo / Pinus mugo spp. uncinata*), cembra pine (*Pinus cembra*) and

European larch (*Larix decidua*) representing the main tree species (Haller et al., 2013).

The climate is characterised by inner-Alpine dryness with minimum temperatures of about -15.8 °C (long-term minimum) to maximum temperatures up to +22.8 °C (long-term maximum; Haller et al., 2013). The mean annual precipitation is about 800 mm (Haller et al., 2013), and the mean snow melt-out date in the area is at the beginning of May (end of March – beginning of June; Meteo Station Buffalora, source: MeteoSwiss).



## 2. Outline of the thesis



In Chapter 1, we investigated changes in the start of dawn singing of six common woodland songbirds related to different physical environmental variables.



Chapter 2 describes the effects of an additional type of anthropogenic noise: construction noise.



In Chapter 3, we concentrated on changes in singing activity of coal tits due to anthropogenic noise.



In Chapter 4, we focused on differences in breeding phenology depending on elevation.

#### References

- Akçay, H. G., Kabasakal, B., Aksu, D., Demir, N., Öz, M., & Erdoğan, A. (2020). Automated bird counting with deep learning for regional bird distribution mapping. *Animals*, 10, 1– 24. https://doi.org/10.3390/ani10071207
- Bahía, R., Lambertucci, S. A., & Speziale, K. L. (2024). Anthropogenic city noise affects the vocalizations of key forest birds. *Biodiversity and Conservation*, 33, 2405–2421. https://doi.org/10.1007/s10531-024-02862-5
- Bardeli, R., Wolff, D., Kurth, F., Koch, M., Tauchert, K. H., & Frommolt, K. H. (2010). Detecting bird sounds in a complex acoustic environment and application to bioacoustic monitoring. *Pattern Recognition Letters*, 31, 1524–1534. https://doi.org/10.1016/j.patrec.2009.09.014
- Bayne, E. M., Habib, L., & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, 22, 1186–1193. https://doi.org/10.1111/j.1523-1739.2008.00973.x
- Benfield, J. A., Rainbolt, G. A. N., Troup, L. J., & Bell, P. A. (2020). Anthropogenic noise source and intensity effects on mood and relaxation in simulated park environments. *Frontiers in Psychology*, 11, 1–8. https://doi.org/10.3389/fpsyg.2020.570694
- Brown, R. G. B. (1963). The behaviour of the willow warbler phylloscopus trochilus in continuous daylight. *Ibis*, 105, 63–75. https://doi.org/10.1111/j.1474-919X.1963.tb02475.x
- Bruni, A., & Foote, J. R. (2014). Dawn singing of eastern phoebes varies with breeding stage and brood number. *Wilson Journal of Ornithology*, 126, 500–507. https://doi.org/10.1676/13-175.1
- Bruni, A., Mennill, D. J., & Foote, J. R. (2014). Dawn chorus start time variation in a temperate bird community: Relationships with seasonality, weather, and ambient light. *Journal of Ornithology*, 155, 877–890. https://doi.org/10.1007/s10336-014-1071-7
- Center for Conservation Bioacoustics. (2019). Raven Lite: Interactive Sound Analysis Software (2.0.1). The Cornell Lab of Ornithology. http://www.birds.cornell.edu/raven
- Cretois, B., Bick, I. A., Balantic, C., Gelderblom, F. B., Pávon-Jordán, D., Wiel, J., Sethi, S. S., Betchkal, D. H., Banet, B., Rosten, C. M., & Reinen, T. A. (2024). Snowmobile noise alters bird vocalization patterns during winter and pre-breeding season. *Journal of Applied Ecology*, 61, 340–350. https://doi.org/10.1111/1365-2664.14564
- Erne, N., & Amrhein, V. (2008). Long-term influence of simulated territorial intrusions on dawn and dusk singing in the winter wren: Spring versus autumn. *Journal of Ornithology*, 149, 479–486. https://doi.org/10.1007/s10336-008-0288-8
- European Environmental Agency. (2020). Environmental noise in Europe 2020. In *Publications Office of the European Union*.
- Federal Office of Meteorology and Climatology MeteoSwiss. (2024). MeteoSwiss. https://www.meteoswiss.admin.ch/climate/the-climate-of-switzerland.html
- Francis, C. D., Ortega, C. P., & Cruz, A. (2011). Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2025–2031. https://doi.org/10.1098/rspb.2010.1847
- Gayk, Z. G., & Mennill, D. J. (2020). Pinpointing the position of flying songbirds with a wireless microphone

array: three-dimensional triangulation of warblers on the wing. *Bioacoustics*, 29, 375–386. https://doi.org/10.1080/09524622.209.1609376

Gross, K., Pasinelli, G., & Kunc, H. P. (2010). Behavioral plasticity allows short-term

adjustment to a novel environment. *American Naturalist*, 176, 456–464. https://doi.org/10.1086/655428

- Habib, L., Bayne, E. M., & Boutin, S. (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds Seiurus aurocapilla. *Journal of Applied Ecology*, 44, 176– 184. https://doi.org/10.1111/j.1365-2664.2006.01234.x
- Hagens, S. V., Rendall, A. R., & Whisson, D. A. (2018). Passive acoustic surveys for predicting species' distributions: Optimising detection probability. *PLoS ONE*, 13, 1–17. https://doi.org/10.1371/journal.pone.0199396
- Halfwerk, W., Holleman, L. J. M., Lessells, C. M., & Slabbekoorn, H. (2011). Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, 48, 210–219. https://doi.org/10.1111/j.1365-2664.2010.01914.x
- Haller, H., Eisenhut, A., & Haller, R. (2013). Atlas des Schweizerischen Nationalparks. Die ersten 100 Jahre. *Nationalpark Forschung Schweiz* 99/1, Haupt Verlag Bern.
- Hegelbach, J., & Spaar, R. (2000). Saisonaler Verlauf der Gesangsaktivitfit der Singdrossel (Turdus philomelos), mit Anmerkungen zum nachbrutzeitlichen Gesangsschub. *Journal für Ornithologie*, 434, 425–434.
- Holm, T. E., & Laursen, K. (2011). Car traffic along hedgerows affects breeding success of great tits *Parus major. Bird Study*, 58, 512–515. https://doi.org/10.1080/00063657.2011.596186
- Holmes, S. B., McIlwrick, K. A., & Venier, L. A. (2014). Using automated sound recording and analysis to detect bird species-at-risk in southwestern Ontario woodlands. *Wildlife Society Bulletin*, 38, 591–598. https://doi.org/10.1002/wsb.421
- Holmes, W. G., & Dirks, S. J. (1978). Daily Song patterns in golden-crowned sparrows at 62°N latitude. *The Condor*, 80, 92–94. https://doi.org/10.1016/j.anbehav.2013.10.013
- Hyman, J. (2005). Seasonal variation in response to neighbors and strangers by a territorial songbird. *Ethology*, 111, 951–961. https://doi.org/10.1111/j.1439-0310.2005.01104.x
- Jin, T., Kosheleva, A., Castro, E., Qiu, X., James, P., & Schwartz, J. (2024). Long-term noise exposures and cardiovascular diseases mortality: A study in 5 U.S. states. *Environmental Research*, 245, 118092. https://doi.org/10.1016/j.envres.2023.118092
- K. Lisa Yang Center for Conservation Bioacoustics. (2024). BirdNET-Analyzer. https://github.com/kahst/BirdNET-Analyzer
- Kahl, S., Wood, C. M., Eibl, M., & Klinck, H. (2021). BirdNET: A deep learning solution for avian diversity monitoring. *Ecological Informatics*, 61, 101236. https://doi.org/10.1016/j.ecoinf.2021.101236
- Kunc, H. P., & Schmidt, R. (2019). The effects of anthropogenic noise on animals: A metaanalysis. *Biology Letters*, 15. https://doi.org/10.1098/rsbl.2019.0649
- Kunc, H. P., & Schmidt, R. (2020). Species sensitivities to a global pollutant: A meta-analysis on acoustic signals in response to anthropogenic noise. *Global Change Biology*, 27, 1– 14. https://doi.org/10.1111/gcb.15428
- Ligges, U., Krey, S., Mersmann, O., & Schnackenberg, S. (2018). {tuneR}: Analysis of Music and Speech. https://cran.r-project.org/package=tuneR
- Marcoň, P., Janoušek, J., Pokorný, J., Novotný, J., Hutová, E. V., Širůčková, A., Čáp, M., Lázničková, J., Kadlec, R., Raichl, P., Dohnal, P., Steinbauer, M., & Gescheidtová, E. (2021). A system using artificial intelligence to detect and scare bird flocks in the protection of ripening fruit. *Sensors*, 21. https://doi.org/10.3390/s21124244
- McIntyre, E., Leonard, M. L., & Horn, A. G. (2014). Ambient noise and parental communication of predation risk in tree swallows, Tachycineta bicolor. *Animal Behaviour*, 87, 85–89.https://doi.org/10.1016/j.anbehav.2013.10.013

- Merilä, J., & Sorjonen, J. (1994). Seasonal and diurnal patterns of singing and song-flight activity in bluethroats (Luscinia svecica). *The Auk*, 111, 556–562.
- Mikula, P., Valcu, M., Brumm, H., Bulla, M., Forstmeier, W., Petrusková, T., Kempenaers, B., & Albrecht, T. (2021). A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. *Ecology Letters*, 24, 477–486. https://doi.org/10.1111/ele.13662
- Naguib, M., Van Rooij, E. P., Snijders, L., & Van Oers, K. (2016). To sing or not to sing: seasonal changes in singing vary with personality in wild great tits. *Behavioral Ecology*, 27, 932–938. https://doi.org/10.1093/beheco/arv235
- Open Acoustic Devices. (2020). Audiomoth.

https://www.openacousticdevices.info/audiomoth

- Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M., & Langemann, U. (2012). Great tits in urban noise benefit from high frequencies in song detection and discrimination. *Animal Behaviour*, 83, 711–721. https://doi.org/10.1016/j.anbehav.2011.12.019
- Pohl, N. U., Slabbekoorn, H., Klump, G. M., & Langemann, U. (2009). Effects of signal features and environmental noise on signal detection in the great tit, Parus major. *Animal Behaviour*, 78, 1293–1300. https://doi.org/10.1016/j.anbehav.2009.09.005
- Polak, M., Wiącek, J., Kucharczyk, M., & Orzechowski, R. (2013). The effect of road traffic on a breeding community of woodland birds. *European Journal of Forest Research*, 132, 931–941. https://doi.org/10.1007/s10342-013-0732-z
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/
- Rheindt, F. E. (2003). The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? *Journal für Ornithologie*, 144, 295–306. https://doi.org/10.1046/j.1439-0361.2003.03004.x
- Ripmeester, E. A. P., Kok, J. S., van Rijssel, J. C., & Slabbekoorn, H. (2010). Habitat-related birdsong divergence: A multi-level study on the influence of territory density and ambient noise in European blackbirds. *Behavioral Ecology and Sociobiology*, 64, 409– 418. https://doi.org/10.1007/s00265-009-0857-8
- Sánchez, N. V., Sandoval, L., Hedley, R. W., St. Clair, C. C., & Bayne, E. M. (2022). Relative importance for Lincoln's sparrow (*Melospiza lincolnil*) occupancy of vegetation type versus noise caused by industrial development. *Frontiers in Ecology and Evolution*, 10, 1–15. https://doi.org/10.3389/fevo.2022.810087
- Seddon, N. (2005). Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution*, 59, 200–215. https://doi.org/10.1111/j.0014-3820.2005.tb00906.x
- Sethi, S. S., Ewers, R. M., Jones, N. S., Sleutel, J., Shabrani, A., Zulkifli, N., & Picinali, L. (2022). Soundscapes predict species occurrence in tropical forests. *Oikos*, 3, 1–8. https://doi.org/10.1111/oik.08525
- Shonfield, J., & Bayne, E. M. (2017). Autonomous recording units in avian ecological research: current use and future applications. *Avian Conservation and Ecology*, 12. https://doi.org/10.5751/ace-00974-120114
- Sierro, J., Schloesing, E., Pavón, I., & Gil, D. (2017). European blackbirds exposed to aircraft noise advance their chorus, modify their song and spend more time singing. *Frontiers in Ecology and Evolution*, 5, 1–13. https://doi.org/10.3389/fevo.2017.00068
- Singer, D., Hagge, J., Kamp, J., Hondong, H., & Schuldt, A. (2024). Aggregated time-series features boost species-specific differentiation of true and false positives in passive acoustic monitoring of bird assemblages. *Remote Sensing in Ecology and*

Conservation, 10, 1-14. https://doi.org/10.1002/rse2.385

- Slabbekoorn, H. (2004). Singing in the wild: the ecology of birdsong. In: *Nature's Music: The Science of Birdsong* (P. Marler & H. Slabbekoorn, eds), 178–205. Elsevier, San Diego.
- Slabbekoorn, Hans, & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature*, 424, 267. https://doi.org/10.1038/424267a
- Slagsvold, T. (1977). Bird Song Activity in Relation to Breeding Cycle, Spring Weather, and Environmental Phenology. *Ornis Scandinavica*, 8, 197. https://doi.org/10.2307/3676105
- Sueur, J., Aubin, T., & Simonis, C. (2008). seewave: a free modular tool for sound analysis and synthesis. *Bioacoustics*, *18*, 213–226.
- Templeton, C. N., Zollinger, S. A., & Brumm, H. (2016). Traffic noise drowns out great tit alarm calls. *Current Biology*, 26, R1173–R1174. https://doi.org/10.1016/j.cub.2016.09.058
- Urbanek, S. (2020). audio: Audio Interface for R. R Package Version 0.1-7. https://cran.rproject.org/package=audio
- Van Buskirk, J. (1997). Independent evolution of song structure and note structure in American wood warblers. *Proceedings of the Royal Society B: Biological Sciences*, 264, 755–761. https://doi.org/10.1098/rspb.1997.0107
- Welling, P., Koivula, K., & Lahti, K. (1995). The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. *Journal of Avian Biology*, *26*, 241. https://doi.org/10.2307/3677325
- Wiącek, J., Polak, M., Filipiuk, M., & Kucharczyk, M. (2019). Does railway noise affect forest birds during the winter? European Journal of Forest Research, 138, 907–915. https://doi.org/10.1007/s10342-019-01212-3

# CHAPTER 1

This chapter is published as

Paterno J, Korner-Nievergelt F, Anderwald P, Amrhein V (2024). Start of dawn singing as related to physical environmental variables in an alpine environment. *Journal of Ornithology* 165, p. 533 – 544.

Ofenpass at dawn, SNP / Hans Lozza

Journal of Ornithology (2024) 165:533–544 https://doi.org/10.1007/s10336-023-02134-z

**ORIGINAL ARTICLE** 



## Start of dawn singing as related to physical environmental variables in an alpine environment

Julia Paterno<sup>1,2</sup> · Fränzi Korner-Nievergelt<sup>3</sup> · Pia Anderwald<sup>2</sup> · Valentin Amrhein<sup>1</sup>

Received: 14 September 2023 / Revised: 14 November 2023 / Accepted: 23 November 2023 / Published online: 23 December 2023 © The Author(s) 2023

#### Abstract

Birds often have a peak of singing activity at dawn, and the timing of dawn song is species-specific. However, the start of singing at dawn may also depend on environmental factors. We investigated the effects of different environmental variables on the start of dawn singing in six common songbird species in the woodlands of the Swiss National Park. Moon phase, aspect, temperature and road noise had the most consistent effects across species: dawn singing started earlier after brighter and warmer nights, on more east-exposed slopes, and in areas with more road noise. On average, birds started to sing 2.8 min earlier in areas with high road noise level compared to areas without road noise, and 4.7 min earlier in east-exposed slopes compared to west-exposed slopes. Further, birds started to sing on average 5.0 min earlier after full moon compared to new moon nights, 1.2 min earlier after warmer compared to colder nights, and 2.5 min earlier at the end compared to the beginning of the study period, whilst Song Thrushes started to sing 9.0 min earlier. Our findings are in line with the results of previous studies on the effects of road noise, nocturnal light, and partly on temperature. Our study shows that variation in environmental variables may influence the start of dawn singing in different ways, and that anthropogenic factors like road noise can affect bird behaviour even in a highly protected area.

Keywords Diurnal activity pattern · AudioMoth · Mistle thrush · European robin · Coal tit · Eurasian chaffinch

#### Zusammenfassung

## Beginn des Morgenchors von Singvögeln in Zusammenhang mit physikalischen Umweltvariablen in einer alpinen Umgebung.

Die Gesangsaktivität von Vögeln erreicht in der Morgendämmerung ihren Höhepunkt, wobei der Zeitpunkt des Morgenchors artspezifisch ist. Der Beginn des Morgenchors kann jedoch auch von verschiedenen Umweltfaktoren abhängen. In der vorliegenden Studie untersuchten wir die Auswirkungen solcher Umweltvariablen auf den Beginn des Morgenchors bei sechs häufigen Singvogelarten in den Wäldern des Schweizerischen Nationalparks. Mondphase, Hangausrichtung, Temperatur und Straßenlärm hatten die konsistentesten Auswirkungen auf alle Arten: Der Gesang in der Morgendämmerung begann früher nach helleren und wärmeren Nächten sowie an stärker ost-exponierten Hängen und in Gebieten mit mehr Straßenlärm. Im Durchschnitt begannen die Vögel in Gebieten mit hohem Straßenlärmpegel 2,8 min früher zu singen als in Gebieten ohne Straßenlärm, und 4,7 min früher an ost-exponierten im Vergleich zu west-exponierten Hängen. Außerdem begannen die Vögel im Durchschnitt nach Vollmondnächten 5,0 min früher zu singen als nach Neumondnächten, 1,2 min früher nach

Communicated by T. S. Osiejuk.

Julia Paterno julia.paterno@nationalpark.ch

<sup>1</sup> Department of Environmental Sciences, University of Basel, 4051 Basel, Switzerland

- <sup>2</sup> Department of Research and Monitoring, Swiss National Park, 7530 Zernez, Switzerland
- <sup>3</sup> oikostat GmbH, 6218 Ettiswil, Switzerland

Description Springer

#### 534

wärmeren im Vergleich zu kälteren Nächten und 2,5 min früher auf 2200 m als auf 1500 m ü.d.M. Die Auswirkungen des Datums waren eher artspezifisch: Alpenmeisen begannen am Ende des Untersuchungszeitraums im Durchschnitt 4,9 min später zu singen als zu Beginn, während Singdrosseln 9,0 min früher zu singen begannen. Unsere Ergebnisse stehen im Einklang mit den Resultaten früherer Studien über die Auswirkungen von Straßenlärm, nächtlichem Licht und teilweise auch der Temperatur. Unsere Studie zeigt, dass unterschiedliche Umweltvariablen den Beginn des Morgenchors von Singvögeln auf unterschiedliche Weise beeinflussen können und dass anthropogene Faktoren wie Straßenlärm das Verhalten der Vögel selbst in einem streng geschützten Gebiet beeinflussen können.

#### Introduction

Dawn singing of songbirds serves as mate attraction, territory defence, or mate guarding (Gil and Llusia 2020; Staicer et al. 1996). Further, Henwood and Fabrick (1979) suggested that more consistent conditions (less wind or convection) in the morning than later during day would favour a peak of singing activity at dawn because songs would travel further. Staicer et al. (1996) proposed social dynamics to be one of the main drivers for singing at dawn, since dawn singing and social activity seem to be strongly related (e.g. Amrhein et al. 2004; Otter et al. 1997; Poesel et al. 2006; Welling et al. 1995, 1997). However, the importance of different functions of dawn singing may vary amongst bird species.

The start of dawn singing is also highly species-specific (Berg et al. 2006; Thomas et al. 2002). Whilst European Robins (Erithacus rubecula), Common Blackbirds (Turdus merula) and Song Thrushes (Turdus philomelos) usually start singing earlier relative to sunrise, Eurasian Chaffinches (Fringilla coelebs) and Eurasian Blue Tits (Cvanistes caeruleus) start singing later (Catchpole and Slater 2008). The species-specific eye size, and thus increased sensitivity to light (Berg et al. 2006; Chen et al. 2015; Thomas et al. 2002), as well as the stage of the breeding cycle are correlated with the start of dawn singing; for example, Bruni et al. (2014) observed an earlier start of singing at the beginning of the breeding season in four of six bird species. On the other hand, Puswal et al. (2020) found temperature to be a stronger predictor for start of dawn singing than date. They observed no clear change in start of dawn singing according to date, but three of four bird species started singing later after warmer nights (Puswal et al. 2020). In contrast, Naguib et al. (2019) observed a later start of dawn singing after colder nights in Great Tits (Parus major). Singing early after cold nights may be costly and therefore reveal quality and condition of males. Ward and Slater (2005), for example, observed up to 80% higher thermoregulatory costs when birds sang in cold, windy environments. Also Strain and Mumme (1988) found a positive correlation between song rate and ambient temperature.

Here, we investigated the start of dawn singing relative to sunrise of six common songbird species along an alpine elevational gradient in the Swiss National Park. We accounted for factors that may influence the start of dawn singing, such as time of year (Erne and Amrhein 2008) and

D Springer

moon phase (Nakamura-Garcia and Ríos-Chelén, 2022; Pérez-Granados and López-Iborra 2020; Zhao et al. 2016). Since anthropogenic noise can also affect the timing of bird song (Dominoni et al. 2016) and generally influence singing behaviour (e.g. Colino-Rabanal et al. 2016; Francis et al. 2011a, b; Gross et al. 2010), we further compared start of singing relative to sunrise at plots that differed in road noise levels during the morning.

In mountainous regions, factors such as light intensity and temperature also change with elevation and aspect, and thus elevation and aspect might both influence the start of dawn singing. Moreover, the onset of breeding may change along elevational gradients, thus leading to differences in start of dawn singing, as several species start singing earlier at dawn at the beginning of the breeding season (Bruni et al. 2014; Bruni and Foote 2014; Keast 1994). Since birds are sensitive to light intensity and anthropogenic noise, we a) expected birds to start singing earlier relative to sunrise in noisier territories and when there is more light at night due to a fuller moon. Depending on the onset of breeding, we b) expected an earlier start of singing relative to sunrise at the beginning of the season and in higher compared to lower regions (because we expected higher light intensities earlier in the morning at higher elevations). Since an early start of dawn singing is considered costly, we c) expected birds to start singing earlier relative to sunrise after warmer nights and in more east-exposed terrain, i.e. on slopes that were exposed to the rising sun.

#### Methods

The study was conducted along the Ofenpass road and nearby hiking trails of the Swiss National Park (SNP) in eastern Switzerland in spring and early summer 2021 and 2022. The SNP is the oldest national park in the Alps and central Europe. The study area extended over 100 km<sup>2</sup>, with 80 km<sup>2</sup> located within the SNP (Fig. 1). As an IUCN 1a protected area (i.e. "wilderness"), the SNP has minimal human disturbance, and there are no management measures such as hunting or logging. Visitors must stay on trails and are not allowed to bring dogs into the park or to stay overnight.

A cantonal road runs through the SNP. This "Ofenpass road" is an important transport route between the Engadine and South Tyrol (Fig. 1). From Zernez to Süsom Givè, it is
### Chapter 1

535



Fig.1 Location of the study sites. The dark grey area shows the woodlands in the study area, and the grey lined area shows the Swiss National Park. Locations of sound loggers are indicated by black squares (data from 1 year) and white cubes (data from 2 years). Let-

21.6 km long; its orientation is from southeast to northwest, and elevations range from 1473 (Zernez) to 2149 m a.s.l. (Süsom Givè).

The main habitat type along the road is coniferous forest, with Swiss and Dwarf Mountain Pine (*Pinus mugo/Pinus mugo* spp. *uncinata*), Cembra Pine (*Pinus cembra*) and European Larch (*Larix decidua*) representing the main tree species. There are also Scots Pine (*Pinus sylvestris*) and Norway Spruce (*Picea abies*; Haller et al. 2013).

The climate is characterised by inner-Alpine dryness with high temperature differences between summer and winter. Average annual precipitation is about 800 mm (Haller et al. 2013). The total sum of precipitation during the two study periods (Table 1) was 67.0 and 96.3 mm, respectively. The minimum temperature was -0.6 °C (in 2021) and the ters indicate road noise levels (N non-audible, A audible, D disturbing, E extreme; x no data available). The location of the study area within Switzerland is shown in the upper right corner, with the border of the Swiss National Park marked in black

maximum 23.3 °C (in 2021; Table 1). Snow melt-out date in the area lies between the end of March and the beginning of June, with a mean snow melt-out date at the beginning of May. Snow melt-out and weather data are from a nearby weather station at Buffalora and were obtained from MeteoSwiss, the Swiss Federal Office of Meteorology and Climatology.

### Acoustic recordings

We deployed a total of 133 AudioMoth sound loggers (Open Acoustic Devices 2023, Table 1) to record bird songs between 3.00 and 8.00 a.m. local summertime (UTC + 2). AudioMoths were placed on tree trunks at a height of 1.60-1.80 m along hiking trails and the Ofenpass road,

Table 1	Dates of deployment of	sound loggers and	weather data dur	ing the two study periods
	b dieb of deprojiment of	ooune regere une		ing the the biddy periods

Year	Earliest deployment	Latest removal	Total number of sound loggers	Number of sound log- gers used for analysis	Minimum tem- perature [°C]	Maximum tem- perature [°C]	Precipita- tion sum [mm]
2021	02.06.2021	05.07.2021	63	43	-0.6	23.3	67.0
2022	06.05.2022	17.06.2022	70	69	-1.9	21.6	96.3

Deringer

representing an elevational gradient from 1500 to 2200 m (Fig. 1). All sites were located in woodland. Deployment positions of AudioMoths were planned with ArcGIS Version 10.7.1 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, US), taking into consideration terrain surface and accessibility of sites. We deployed nine AudioMoths per 100-m segment of elevation in 2021, and 10 AudioMoths per 100-m segment in 2022. To reduce spatial dependence, we placed them at least 400 m in linear distance from each other. In the field, we selected locations in woodland at maximum direct distance to creeks or rivers to reduce ambient noise, and within a radius of 20 m of the planned coordinates. To avoid edge effects, we placed the AudioMoths at least 20 m away from the forest edge and directed the microphones away from a road or hiking trail. We deployed the AudioMoths at the beginning of June 2021 and May 2022, respectively, and collected them by 5th of July 2021 and 17th of June 2022 (Table 1). Gain was set to medium, and sample rate was 48 kHz.

Each sound logger site was also equipped with a temperature logger; we used iButtons (Moritz Fuchs Elektronik 2022) in 2021 and TMS thermologgers (TOMST 2023) in 2022. We placed the iButtons into plastic balloons and fixed them on a tree at a height of about 2 m, recording temperature every 10 min with an accuracy of 0.5 °C. TMS thermologgers were installed into the ground (with the reading probe above ground level), recording temperatures at three different levels. For analysis, we used aboveground temperature measured at about 25 cm above the surface. We set TMS thermologgers to record temperature every 15 min with an accuracy of 0.5 °C.

In 2021, we measured ambient noise at all locations using a noise level metre (Sound Level Meter SL 510), with the aim to quantify road noise from the Ofenpass road. Since it was not possible to distinguish between biophonic, geophonic and anthrophonic sounds using the noise level metre, we discarded this method and used a different approach in 2022: to quantify road noise, we classified sites using subjectively experienced road noise levels during the morning (8.00–12.00 a.m. local summertime, UTC+2; classification performed by J.P.). We used four different noise categories: N (non-audible): no road noise audible; A (audible): road noise audible at a moderate volume; D (disturbing): road noise disturbing; E (extreme): difficult to follow a human conversation because of the road noise (Fig. 1).

In 2021, 14 of 63 sites were retrospectively determined to be too noisy to reliably detect bird songs due to nearby creeks or rivers. These sites were excluded from subsequent analysis, as were six sites where the temperature logger failed. We used the remaining 43 sites for further analyses on data from five mornings without wind or rain in early June (3, 4, 5, 9 and 11 June 2021). There are more data available that could be used for future work. Here we

D Springer

concentrated on a subset of all potentially suitable data since the analysis of song start was done manually and thus was very time-consuming.

In 2022, one logger failed, and we thus used 69 of 70 sites for analysis. We increased the recording period to 6 weeks from the beginning of May until mid-June. We analysed data from 1 day per week (Monday–Sunday) by selecting days without wind or rain in the morning (12, 18, 24 May, 1 and 6 June 2022).

### **Data extraction and analysis**

We analysed the recordings acoustically and visually using the programme Raven (Center for Conservation Bioacoustics 2019). A trained person (J.P.) scanned the audio files and noted the start of singing of the six most common songbird species: Song Thrush, Mistle Thrush (Turdus viscivorus), European Robin, Eurasian Chaffinch, Coal Tit (Periparus ater) and Alpine Tit (Poecile montanus montanus). In Switzerland, there are two forms of Poecile montanus, the Willow Tit (Poecile montanus rhenanus/salicarius) and the Alpine Tit. Both species have distinct songs and occupy different ecological niches (Glutz von Blotzheim and Bauer 1993). The present study refers to the Alpine Tit. All audio files were scanned until all of the species had started to sing, or at maximum until sunrise. Identification of individual birds from the recordings was not possible; thus, we describe our results as referring to observations, not to individuals.

We calculated sunrise for Zernez with the package suncalc (Thieurmel and Elmarhraoui 2022) in the software R (R Core Team 2020), in which we also conducted statistical analyses. For preparing data, we used the packages dplyr (Wickham et al. 2021) and lubridate (Grolemund and Wickham 2011).

### **Environmental variables**

We extracted elevation and aspect using a  $2 \times 2$  m digital elevation model (swissALTI3D) in ArcGIS. For further analysis, we used northing and easting, calculated as cos(aspect) and sin(aspect), respectively. To investigate effects of average nocturnal temperatures on song start, we used data from the 6 h before the approximate start of dawn singing (i.e. 0.00-06.00 a.m., UTC+2). Mean nocturnal temperature was strongly correlated with temperature at sunrise (Pearson's r=0.96, CI 0.95-0.97); we thus included only nocturnal temperature into the model (see Naguib et al. 2019). Furthermore, we calculated the visible area of the moon using the package oce (Kelley and Richards 2020). Effects of artificial light on dawn singing were unlikely due to the near-natural character of the area and thus the absence of anthropogenic light sources. Journal of Ornithology (2024) 165:533-544

### Model fitting

For fitting Bayesian linear mixed models, we used the package rstanarm (Goodrich et al. 2020). The response variable was minutes relative to sunrise. We used nine environmental variables as predictors (for a correlation matrix of the variables used for the Model, see S1). Road noise was used as a categorical variable, with the four noise categories described above. Year, as well as day of the year, was also included as fixed-effects predictors. By including the year into the model, we also accounted for the different heights above ground at which temperature measurements were taken in the two study years. We think this was justifiable because the variance of the measured temperatures was similar for iButtons (2 m above ground) and TMS thermologgers (25 cm above ground), indicating that the temperature changes recorded by the two devices within a given year were comparable. Locations of AudioMoths and date of recording were included as random effects, to account for repeated measures within site and date. Using the locations of AudioMoths as a random effect also accounted for spatial autocorrelation. In addition, species was used as a random effect, and all predictor effects were modelled by species (random slopes), to obtain species-specific coefficients for each predictor. Numeric predictor variables were z-transformed (mean = 0 and SD = 1) prior to model fitting.

We assessed convergence of Markov chains by visual inspection of the history plots, Rhat values, and the number of effective samples that were above 7500 for all parameters. We used posterior predictive model checking and standard residual plots to assess model fit. Posterior predictive model checking was done visually based on histograms and overlaid densities. In addition, mean, standard deviation, minimum and maximum were compared between replicated data from the model and the data (Gabry 2018). To check whether using locations of Audio-Moths as a random effect sufficiently accounted for spatial

Table 2Average $(\pm SD)$ startof dawn singing in minutes		Song Thrush	European Robin	Mistle Thrush	Coal Tit	Alpine Tit	Eurasian Chaffinch
before sunrise for the six most common songbird species in woodlands of the Swiss National Park	Start of 2021 2022 Total	dawn singing $-52.5 \pm 8.6$ $-50.1 \pm 9.5$ $-50.7 \pm 9.3$ of observation	$-52.9 \pm 7.9$ $-49.2 \pm 8.9$ $-50.2 \pm 8.8$	$-50.3 \pm 7.5$ $-46.0 \pm 9.8$ $-47.1 \pm 9.4$	$-31.3 \pm 7.9$ $-35.7 \pm 8.5$ $-34.6 \pm 8.6$	$-27.0 \pm 7.3$ $-30.8 \pm 9.5$ $-29.9 \pm 9.1$	$-22.6 \pm 8.2$ $-19.6 \pm 8.8$ $-20.4 \pm 8.7$
	2021 2022 Total	99 295 394	93 252 345	76 219 295	129 371 500	103 338 441	113 292 405

Table 3 Parameter estimates and 95% Bayesian compatibility intervals (CI; Amrhein and Greenland 2022) for the environmental variables over all species

	Standardised coefficients Mean [95% CI] in minutes	Standard deviation of the predictor variable	Unstandardized coefficients Mean [95% CI] in minutes	Unit of the predictor vari- able
Intercept: road noise non- audible, 2021	-38.5 [-45.9; -31.1]			
Northing	+0.3[-1.6;+2.2]			
Easting	-1.5[-2.9;-0.1]			
Road noise audible	-2.2[-4.6;+0.1]			
Road noise disturbing	-2.5 [-5.0; 0.0]			
Road noise extreme	-2.9[-5.3; -0.4]			
Year 2022	+2.4[-1.3;+6.0]			
Night temperature	-0.2[-1.1;+0.8]	2.11 °C	-0.1 [-0.5; +0.4]	1 °C
Elevation	-0.7[-2.2;+0.7]	195 m	-0.4[-1.1;+0.4]	100 m
Visible area of the moon	-1.7 [-3.4; -0.1]	0.33%	-0.5[-1.0; 0.0]	10%
Date	-0.4 [ $-2.5$ ; $+1.8$ ]	10.1 days	0.0[-0.3;+0.2]	1 day

Standardised coefficients measure by how many minutes the start of dawn singing changed when the predictor variables changed by one standard deviation. Unstandardized coefficients measure by how many minutes the start of dawn singing changed when the predictor variables changed by 1 unit

🖄 Springer

### Journal of Ornithology (2024) 165:533-544

autocorrelation, we displayed the residuals on a map and could not find any conspicuous spatial pattern.

### Results

Over both study years and all days and locations, the earliest singers at dawn, on average, were Song Thrushes, European Robins, and Mistle Thrushes (Table 2). Coal tits, Alpine Tits and Eurasian Chaffinches started singing about 20 min later, with Eurasian Chaffinches being the last.

Amongst the investigated environmental variables (Table 3) and accounting for all other variables, the visible

area of the moon had the strongest apparent effect on start of dawn singing. All species started to sing earlier after nights with fuller moon (Fig. 2a and Table 4). We found the largest effect sizes in Coal Tits and Alpine Tits, with an average start of dawn singing that was 7.0 and 6.4 min earlier relative to sunrise after nights with full moon compared to nights with new moon, and the smallest effect size in Mistle Thrushes (3.3 min).

Birds also differed in their start of dawn singing in relation to aspect. Overall, birds started singing 4.7 min earlier on east-exposed slopes compared to west-exposed slopes (Table 4 and Fig. 3g), and aspect seemed to play a larger



Fig. 2 Start of dawn singing relative to sunrise in relation to environmental parameters. Black lines are overall regression lines, grey areas are 95% Bayesian compatibility areas (Amrhein and Greenland 2022)

based on the linear mixed model. Coloured lines show the regression lines for the different species. The dotted line represents sunrise

Springer

538

### Journal of Ornithology (2024) 165:533-544

role in thrushes and Eurasian Chaffinches than in the two tit species (Table 4).

Road noise had the third-largest effect size, showing an overall 2.8 min earlier start of dawn singing relative to sunrise at extreme versus non-audible road noise; again, this pattern was found in all six species, with Eurasian Chaffinches showing the strongest response (4.8 min earlier start; Table 4 and Fig. 4). European Robins and Alpine Tits seemed least affected, starting to sing 1.5 and 1.9 min earlier relative to sunrise with extreme road noise.

Elevation had a similar effect size as road noise (Table 4); overall, birds started singing 2.5 min earlier relative to sunrise at higher compared to lower elevations, with Alpine Tits showing the strongest response (7.2 min earlier start of dawn singing at 2200 compared to 1500 m, Fig. 2b and Table 4). Again, European Robins seemed least affected, with a song start 0.4 min earlier relative to sunrise at higher elevation.

Furthermore, birds started singing earlier after warmer nights (1.2 min at 12 °C compared to 0 °C, Fig. 2c and Table 4), with Eurasian Chaffinches and Alpine Tits showing the strongest response (2.9 and 2.6 min earlier start of dawn singing relative to sunrise, respectively).

Two of the six species started singing later relative to sunrise as the season progressed (Fig. 2d and Table 4), whilst four species started earlier, with Song Thrushes showing the largest effect size (9.0 min earlier start of dawn singing relative to sunrise at the end compared to the beginning of the season).

Visible and

-7.0[-11.5;

-6.4 [-11.0;

-2.61

-2.0]

+0.6]

-0.11

-3.9 [-8.6

-5.0 [-10.1;

Coal Tit

Alpine Tit

finch

Overall

Eurasian Chaf-

c

Eastin

-2.8 [-6.6;

-1.6 [-5.9;

-5.0 [-9.6;

-4.7 [-9.0;

+1.2]

+2.71

-0.51

-0.41

### Discussion

We found small but consistent effects of moon light, aspect, temperature and road noise on start of dawn singing relative to sunrise for all six investigated species. The effects of elevation and date were more species-specific.

Nights with fuller moon were associated with an earlier start of dawn singing relative to sunrise for all species. This is in line with results of previous studies (Pérez-Granados and López-Iborra 2020; York et al. 2014; Zhao et al. 2016); for example, York et al. (2014) showed that White-browed Sparrow Weavers (Plocepasser mahali) started to sing 10 min earlier relative to nautical twilight after nights with full moon compared to new moon. Artificial light at night seems to have similar, but stronger effects. For example, Da Silva et al. (2014) investigated the start of dawn singing relative to sunrise of four different species depending on artificial light at night. They found that European Robins started singing on average 37 min earlier after experimentally illuminated mornings. In their study, Da Silva et al. (2014) simulated a brightness of 4 lx, comparable to light intensities in big cities at night. Light intensity in nights with a full moon, however, is less than 0.3 lx (Kyba et al. 2017). Those differences in light intensities may explain the large differences in effect sizes between our study and the study of Da Silva et al. (2014). Other studies found that birds started singing earlier at dawn in brighter compared to darker territories (e.g. Kempenaers et al. 2010; Miller 2006), and Raap et al. (2015) showed that birds left their nest boxes earlier

NT 1 ...

-0.6[-5.7:

-2.6 [-8.1;

-2.9 [-8.5;

-1.2 [-6.7;

+4.71

+2.91

+2.7]

+4.51

	the moon 100 vs. 0%	E vs. W	N vs. S	Extreme vs. non-audible	2200 vs. 1500 m	ture 12 vs. 0 °C	day 162 vs. 132
Song Thrush	-4.9 [-9.4;	-6.6 [-10.8;	-2.4 [-6.5;	-2.7 [-5.6;	-1.7 [-5.3;	-0.2 [-5.5;	-9.0 [-14.0;
	-0.4]	-2.5]	+1.6]	+0.2]	+1.9]	+5.4]	-4.0]
European Robin	-4.6 [-9.3; 0.0]	-7.3 [-11.6; -2.9]	+2.2 [-2.3; +6.8]	-1.5 [-4.5; +1.8]	-0.4 [-4.1; +3.5]	-0.9 [-6.5; +4.8]	-1.1 [-6.0; +3.9]
Mistle Thrush	-3.3 [-8.0;	-5.0 [-9.4;	-0.2 [-4.7;	-2.6 [-5.7;	-2.4 [-6.1;	+0.3 [-5.2;	-1.2 [-6.2;
	+1.4]	-0.4]	+4.4]	+0.5]	+1.3]	+6.2]	+3.9]

Deadaraia

-3.6[-6.4;

-1.9 [-4.8;

-4.8 [-8.1;

-2.8 [-5.6;

-0.81

+1.1]

-1.6]

0.0]

E1 ...

-1.9 [-5.2;

-7.2 [-10.9;

+1.51

-3.51

-1.3 [-5.1;

-2.5 [-7.2;

+2.6]

+2.21

Table 4 Differences and 95% CI in start of dawn singing in minutes relative to sunrise, in relation to different environmental variables

Manthing

+0.6[-3.2]

-3.5 [-7.6;

+8.3 [+3.8;

+0.8[-4.8;

+4.31

+0.51

+12.8]

+6.31

Comparisons are made between the two extreme values of the predictors to make effect sizes comparable between numeric variables and the categorical predictor road noise. Variables are ordered from largest to smallest overall sizes of estimates

### Springer

+0.9[-3.7]:

+4.9[+0.2;

+5.71

+9.8]

+3.6]

+5.31

-1.5 [-6.4;

-1.1 [-7.6;



Fig. 3 Start of dawn singing in relation to aspect of a location. Black circles represent the time before sunrise in minutes (0 is sunrise and -60 is 1 h before sunrise). Coloured lines are estimates for the different species based on the GLMM. The symbol of the sun shows the angle of sunrise

Journal of Ornithology (2024) 165:533-544



Fig. 3 (continued)

after nights with artificial light treatment compared to nights with the control (dark) treatment. As expected in our study, all species started singing earlier relative to sunrise after nights with fuller moon. Besides moon phase, weather may also affect brightness at night. In our study, we did not take into account the amount of cloud cover, because we could not retrospectively determine the local cloud cover. Future studies may investigate differences in effects between full moon nights with higher and lower cloud cover.

Furthermore, all six species started singing earliest relative to sunrise in east-exposed areas, when accounting for temperature. East-exposed territories probably have more light in the morning (because east is the direction of sunrise). Especially in Song Thrushes and European Robins, start of dawn singing was related to aspect; the relation was a bit smaller in Mistle Thrushes and Eurasian Chaffinches, but they still showed a difference of 5 min between east and west-exposed areas. Interestingly, differences between south- and north-exposed areas were more species-specific.

As expected, all species in our study started singing slightly earlier relative to sunrise at higher elevations when accounting for temperature, date, and the other investigated variables, which might be due to higher light intensities earlier in the morning at higher elevations.

Previous studies have shown an earlier start of singing at dawn during early stages of the breeding season (Brown 1963; Bruni et al. 2014; Holmes and Dirks 1978; Welling et al. 1995). For example, Bruni et al. (2014) found that four of the six investigated North American bird species started singing earlier at dawn relative to nautical twilight at the beginning compared to the end of the breeding season (study period of 108 days). Some of the species they investigated showed only weak variation in start of dawn

singing, whereas others had differences of up to 20 min over the course of the season (Bruni et al. 2014). In contrast, Nolan (1978) found Prairie Warblers (Dendroica discolor) to start singing earlier with ongoing breeding season until late in the season, when they started singing later again. In our study, we found for four of the six species that date had a surprisingly small effect: the start of dawn singing relative to sunrise differed by less than 1.5 min between two dates that were a month apart. We found stronger and opposing effects of date in two species: Alpine Tits started singing about 5 min later relative to sunrise at the end of our field season (mid of June), whilst Song Thrushes started singing 9 min earlier. Whilst both species usually start their first brood at about the same time, only Song Thrushes have a second brood (Glutz von Blotzheim 1988; Glutz von Blotzheim and Bauer 1993). Thus, Song Thrushes may need to continue singing early with advancing season. Hegelbach and Spaar (2000) found two seasonal peaks of singing activity for Song Thrushes: whilst the first peak was correlated with the arrival of the birds and the onset of breeding, the second peak was at the end of the breeding season, i.e. it was not directly associated with breeding. In our study, birds may also have continued singing until the end of the breed-

ing season.

We found a small but relatively consistent effect of temperature: all but one species started to sing slightly earlier relative to sunrise at locations where nocturnal temperatures were higher. This is in line with several previous studies, in which Eurasian Blackbirds, Great Tits and Cerulean Warblers (Setophaga cerulea) started dawn singing earlier after warmer nocturnal temperatures (MacDonald and Islam 2019; Naguib et al. 2019; Nordt and Klenke 2013). Nevertheless, there are also studies showing the opposite effect, with birds starting to sing later at dawn relative to sunrise or civil twilight with warmer temperatures (Da Silva et al. 2014; Puswal et al. 2020; Stuart et al. 2019). Da Silva et al. (2014), for example, found a delay of about 1 min per °C temperature increase for the start of dawn singing relative to sunrise for Song Thrushes. Puswal et al. (2020) also detected a later start of dawn singing relative to sunrise with warmer temperatures 1 h before sunrise, but only for three of the four investigated species, with the fourth species starting to sing earlier. Bruni et al. (2014) found that two of their four investigated species started to sing later relative to nautical twilight, whereas the other two species started to sing earlier when temperature was higher. Those results indicate that correlations of the start of dawn singing with temperature are species- or context-specific (or. of course, that differences amongst studies in the size and direction of effects are due to sampling variation; e.g. Berner and Amrhein 2022). Nevertheless, it has been suggested that early singing at colder temperatures may be costly due to increased energy loss (but see Gil and Llusia 2020; Staicer

Deringer



Fig. 4 Start of dawn singing relative to sunrise in relation to road noise level, in minutes before sunrise. Boxplots are based on the GLMM. The dotted line represents sunrise

et al. 1996). For example, Thomas and Cuthill (2002) found that European Robins lost more body mass during cold than warm nights, which supports predictions from stochastic dynamic programming models of daily singing and foraging routines in birds that are based on weather variables or trade-offs between time spent singing and foraging (Houston and McNamara 1987; Hutchinson et al. 1993; Hutchinson and McNamara 2000). Another explanation for an earlier start of dawn singing with higher temperatures might be that arthropod prey activity increases with temperature (Avery and Krebs 1984). Therefore, birds may start feeding earlier, and, before that, start singing earlier with higher temperatures in the morning.

In addition to the natural predictors discussed above, the start of dawn singing relative to sunrise also correlated with the level of road noise: accounting for all other variables, all species started singing earlier relative to sunrise at sites with higher perceived levels of road noise. The effect was strongest in Eurasian Chaffinches and Coal Tits, which are species with a relatively late start of dawn singing relative to sunrise. A proximate explanation for an earlier start of dawn singing at noisier locations could be that birds simply wake up earlier when there is more traffic noise in the morning. Nevertheless, several previous studies showed that birds changed their singing behaviour not only during noisy times, but also in noisy areas (e.g. Bayne et al. 2008; Bergen and Abs 1997; McClure et al. 2013; Polak et al. 2013). Road noise can mask mating and warning calls (Francis et al. 2011b; Rheindt 2003; Slabbekoorn and Peet 2003)

Description Springer

and is associated with reduced reproductive success (Gross et al. 2010; Habib et al. 2007; Halfwerk et al. 2011; Holm and Laursen 2011). Thus, birds might try to avoid being masked at noisy locations by starting to sing earlier, or they may even avoid noisy locations; for example, Polak et al. (2013) showed that species richness and diversity of woodland songbirds decreased with increasing proximity to roads. McClure et al. (2013) found similar results in their study on migratory birds: bird abundance was 28% higher in silent compared to noisy periods. Thus, territories near roads may be less suitable, and therefore species richness and diversity may be smaller at noisy locations, such as along the Ofenpass road, which could be investigated in the future.

Our observations from the current study are in line with previous results on the effects of nocturnal light and road noise, and partly with previous results on temperature. The examined physical environmental variables affected the start of dawn singing relative to sunrise in different ways. We found moon phase, aspect, temperature and road noise to have the most consistent effects, whereas effects of elevation and time of year were more species-specific.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-023-02134-z.

Acknowledgements This project was funded by the Zigerli Hegi Foundation, the Swiss National Park, the Swiss Ornithological Institute and the Nukahiva Foundation. For analysis, we used services provided by MeteoSwiss (the Swiss Federal Office of Meteorology and Climatology). We thank Seraina Campell Andri, Ursi Sterrer, Sam Cruickshank, Saskia Aeschbach, Franz Hagmann, Nadline Kjelsberg, Fabienne

### 542

### Journal of Ornithology (2024) 165:533-544

König and Erwan Zimmermann for help in the field, and Sven Buchmann for support with coding. We thank Franz Bairlein, Tomasz S. Osiejuk, David Spector and an anonymous reviewer for helping us to improve the manuscript.

Funding Open access funding provided by University of Basel.

### Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval We did not conduct experiments with animals, thus no animal trial permit was required. Access to our study area was granted by the Swiss National Park after project approval by its Research Commission.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

### References

- Amrhein V, Greenland S (2022) Discuss practical importance of results based on interval estimates and *p*-value functions, not only on point estimates and null *p*-values. J Inf Technol 37:316–320. https://doi.org/10.1177/02683962221105904
- Amrhein V, Kunc HP, Naguib M (2004) Non-territorial nightingales prospect territories during the dawn chorus. Proc R Soc B Biol Sci 271: S167–S169. https://doi.org/10.1098/rsbl.2003.0133
- Avery MI, Krebs JR (1984) Temperature and foraging success of Great Tits Parus major hunting for spiders. Ibis 126:33–38. https://doi. org/10.1111/j.1474-919X.1984.tb03661.x
- Bayne EM, Habib L, Boutin S (2008) Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. Conserv Biol 22:1186–1193. https://doi.org/10. 1111/j.1523-1739.2008.00973.x
- Berg KS, Brumfield RT, Apanius V (2006) Phylogenetic and ecological determinants of the neotropical dawn chorus. Proc R Soc B Biol Sci 273:999–1005. https://doi.org/10.1098/rspb.2005.3410
- Bergen F, Abs M (1997) Verhaltensökologische Studie zur Gesangsaktivität von Blaumeise (*Parus caeruleus*), Kohlmeise (*Parus major*) und Buchfink (*Fringilla coelebs*) in einer Großstadt. J Ornithol 138:451–467. https://doi.org/10.1007/bf01651380
- Berner D, Amrhein V (2022) Why and how we should join the shift from significance testing to estimation. J Evol Biol 35:777–787. https://doi.org/10.1111/jeb.14009
- Brown RGB (1963) The behaviour of the Willow Warbler Phylloscopus trochilus in continuous daylight. Ibis 105:63–75. https://doi.org/ 10.1111/j.1474-919X.1963.tb02475.x
- Bruni A, Foote JR (2014) Dawn singing of Eastern Phoebes varies with breeding stage and brood number. Wilson J Ornithol 126:500– 507. https://doi.org/10.1676/13-175.1

- Bruni A, Mennill DJ, Foote JR (2014) Dawn chorus start time variation in a temperate bird community: relationships with seasonality, weather, and ambient light. J Ornithol 155:877–890. https://doi. org/10.1007/s10336-014-1071-7
- Center for Conservation Bioacoustics (2019) Raven Lite: interactive sound analysis software (2.0.1). The Cornell Lab of Ornithology. http://www.birds.cornell.edu/raven
- Colino-Rabanal VJ, Mendes S, Peris SJ, Pescador M (2016) Does the song of the Wren *Troglodytes troglodytes* change with different environmental sounds? Acta Ornithol 51:13–22. https://doi.org/ 10.3161/00016454AO2016.51.1.002
- Da Silva A, Samplonius JM, Schlicht E, Valcu M, Kempenaers B (2014) Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. Behav Ecol 25:1037–1047. https://doi.org/10.1093/ beheco/aru103
- Dominoni DM, Greif S, Nemeth E, Brumm H (2016) Airport noise predicts song timing of European birds. Ecol Evol 6:6151–6159. https://doi.org/10.1002/ece3.2357
- Erne N, Amrhein V (2008) Long-term influence of simulated territorial intrusions on dawn and dusk singing in the Winter Wren: spring versus autumn. J Ornithol 149:479–486. https://doi.org/10.1007/ s10336-008-0288-8
- Francis CD, Ortega CP, Cruz A (2011a) Noise pollution filters bird communities based on vocal frequency. PLoS ONE 6:e27052. https://doi.org/10.1371/journal.pone.0027052
- Francis CD, Ortega CP, Cruz A (2011b) Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. Proc R Soc B Biol Sci 278:2025–2031. https://doi.org/10.1098/rspb.2010.1847
- Gabry J (2018) shinystan: interactive visual and numerical diagnostics and posterior analysis for Bayesian models. R Package Version 2.5.0. https://cran.r-project.org/package=shinystan
- Gil D, Llusia D (2020) The bird dawn chorus revisited. In: Aubin T, Mathevon N (eds) Coding strategies in vertebrate acoustic communication. Animal signals and communication, vol 7. Springer, Cham. https://doi.org/10.1007/978-3-030-39200-0\_3
- Glutz von Blotzheim U, Bauer KM (1993) Passeriformes (4. Teil) Muscicapidae—Paridae. In: Handbuch der Vögel Mitteleuropas, vol 13. Springer, Leipzig
- Glutz von Blotzheim U (1988) II Passeriformes (2. Teil) Turdidae. In: Handbuch der Vögel Mitteleuropas, vol 11. Akademische Verlagsgesellschaft, Leipzig, p. 1226
- Goodrich B, Gabry J, Ali I, Brilleman S (2020) rstanarm: Bayesian applied regression modeling via Stan. R Package Version 2.21.1. https://mc-stan.org/rstanarm
- Grolemund G, Wickham H (2011) Dates and times made easy with lubridate. J Stat Softw 40:1-25
- Gross K, Pasinelli G, Kunc HP (2010) Behavioral plasticity allows short-term adjustment to a novel environment. Am Nat 176:456– 464. https://doi.org/10.1086/655428
- Habib L, Bayne EM, Boutin S (2007) Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. J Appl Ecol 44:176–184. https://doi.org/10.1111/j.1365-2664.2006.01234.x
- Halfwerk W, Holleman LJM, Lessells CM, Slabbekoorn H (2011) Negative impact of traffic noise on avian reproductive success. J Appl Ecol 48:210–219. https://doi.org/10.1111/j.1365-2664. 2010.01914.x
- Haller H, Eisenhut A, Haller R (2013) Atlas des Schweizerischen Nationalparks. Die ersten 100 Jahre. Nationalpark Forschung Schweiz 99/1, Haupt Verlag Bern
- Hegelbach J, Spaar R (2000) Saisonaler Verlauf der Gesangsaktivität der Singdrossel (*Turdus philomelos*), mit Anmerkungen zum nachbrutzeitlichen Gesangsschub. J Ornithol 141:425–434

Springer

Journal of Ornithology (2024) 165:533-544

- Henwood K, Fabrick A (1979) A quantitative analysis of the dawn chorus: temporal selection for communicatory optimization. Am Nat 114:260–274. https://doi.org/10.1086/283473
- Holm TE, Laursen K (2011) Car traffic along hedgerows affects breeding success of Great Tits *Parus major*. Bird Study 58:512–515. https://doi.org/10.1080/00063657.2011.596186
- Holmes WG, Dirks SJ (1978) Daily song patterns in Golden-Crowned Sparrows at 62°N latitude. Condor 80:92–94. https://doi.org/10. 2307/1367794
- Houston AI, McNamara JM (1987) Singing to attract a mate: a stochastic dynamic game. J Theor Biol 129:57–68. https://doi.org/ 10.1016/S0022-5193(87)80203-5
- Hutchinson JMC, McNamara JM (2000) Ways to test stochastic dynamic programming models empirically. Anim Behav 59:665– 676. https://doi.org/10.1006/anbe.1999.1362
- Hutchinson JMC, McNamara JM, Cuthill IC (1993) Song, sexual selection, starvation and strategic handicaps. Anim Behav 45:1153–1177
- Keast A (1994) The dawn chorus in a eucalypt forest bird community, seasonal shifts in timing and contribution of individual species. Corella 18:133–140
- Kelley D, Richards C (2020) oce: analysis of oceanographic data. R Package Version 1.2–0. https://cran.r-project.org/package=oce
- Kempenaers B, Borgström P, Loës P, Schlicht E, Valcu M (2010) Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. Curr Biol 20:1735–1739. https://doi. org/10.1016/j.cub.2010.08.028
- Kyba CCM, Mohar A, Posch T (2017) How bright is moonlight? Astron Geophys 58:1.31-1.32. https://doi.org/10.1093/astrogeo/ atx025
- MacDonald GJ, Islam K (2019) Do social factors explain seasonal variation in dawn song characteristics of paired male Cerulean Warblers (*Setophaga cerulea*)? Bioacoustics 30:1–16. https://doi. org/10.1080/09524622.2019.1682671
- McClure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR (2013) An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proc R Soc B Biol Sci. 280:20132290. https://doi.org/10.1098/rspb.2013.2290
- Miller MW (2006) Apparent effects of light pollution on singing behavior of American Robins. Condor 108:130–139. https://doi.org/10. 1650/0010-5422(2006)108[0130:AEOLPO]2.0.CO;2
- Moritz Fuchs Elektronik (2022) iButton. https://www.mfe24.com/de/ shop/4/. Accessed 13 Sept 2022
- Naguib M, Diehl J, van Oers K, Snijders L (2019) Repeatability of signalling traits in the avian dawn chorus. Front Zool 16:16–27. https://doi.org/10.1186/s12983-019-0328-7
- Nakamura-Garcia MT, Ríos-Chelén AA (2022) More than noise: light, moon phase, and singing behavior in a passerine. Urban Ecosyst 25:291–303. https://doi.org/10.1007/s11252-021-01142-2
- Nolan V (1978) The ecology and behavior of the Prairie Warbler Dendroica discolor. Ornithol Monogr 26:1–595
- Nordt A, Klenke R (2013) Sleepless in town—drivers of the temporal shift in dawn song in urban European Blackbirds. PLoS ONE 8:e71476. https://doi.org/10.1371/journal.pone.0071476
- Open Acoustic Devices (2023) Audiomoth. https://www.openacoust icdevices.info/audiomoth. Accessed 13 Feb 2023
- Otter K, Chruszcz B, Ratcliffe L (1997) Honest advertisement and song output during the dawn chorus of Black-capped Chickadees. Behav Ecol 8:167–173. https://doi.org/10.1093/beheco/8.2.167
- Pérez-Granados C, López-Iborra GM (2020) Dupont's Lark males start to sing earlier but reduce song rate on full moon dawns. J Ornithol 161:421–428. https://doi.org/10.1007/s10336-019-01731-1
- Poesel A, Kunc HP, Foerster K, Johnsen A, Kempenaers B (2006) Early birds are sexy: male age, dawn song and extrapair paternity in Blue Tits, *Cyanistes* (formerly *Parus*) *caeruleus*. Anim Behav 72:531–538. https://doi.org/10.1016/j.anbehav.2005.10.022

- Polak M, Wiącek J, Kucharczyk M, Orzechowski R (2013) The effect of road traffic on a breeding community of woodland birds. Eur J for Res 132:931–941. https://doi.org/10.1007/s10342-013-0732-z
- Puswal SM, Jinjun M, Liu F (2020) Effects of temperature and season on birds' dawn singing behavior in a forest of eastern China. J Ornithol 162:447–459. https://doi.org/10.1007/ s10336-020-01848-8
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.
- Raap T, Pinxten R, Eens M (2015) Light pollution disrupts sleep in free-living animals. Sci Rep 5:13557. https://doi.org/10.1038/ srep13557
- Rheindt FE (2003) The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? J Ornithol 144:295–306. https://doi.org/10.1007/BF02465629
- Slabbekoorn H, Peet M (2003) Birds sing at a higher pitch in urban noise. Nature 424:267. https://doi.org/10.1038/424267a
- Staicer CA, Spector DA, Horn AG (1996) Chapter 24. The dawn chorus and other diel patterns in acoustic signaling. In: Kroodsma DE, Miller EH (eds) Ecology and evolution of acoustic communication in birds. Cornell University Press, Ithaca, pp 426–453. https://doi. org/10.7591/9781501736957-033
- Strain JG, Mumme RL (1988) Effects of food supplementation, song playback, and temperature on vocal territorial behavior of Carolina Wrens. Auk 105:11–16. https://doi.org/10.1093/auk/105.1.11
- Stuart CJ, Grabarczyk EE, Vonhof MJ, Gill SA (2019) Social factors, not anthropogenic noise or artificial light, influence onset of dawn singing in a common songbird. Auk 136:ukz045. https://doi.org/ 10.1093/auk/ukz045
- Thieurmel B, Elmarhraoui A (2022) suncalc: compute sun position, sunlight phases, moon position and lunar phase. R Package Version 0.5.1. https://cran.r-project.org/package=suncalc
- Thomas RJ, Cuthill IC (2002) Body mass regulation and the daily singing routines of European Robins. Anim Behav 63:285–295. https://doi.org/10.1006/anbe.2001.1926
- Thomas RJ, Székely T, Cuthill IC, Harper DGC, Newson SE, Frayling TD, Wallis PD (2002) Eye size in birds and the timing of song at dawn. Proc R Soc B Biol Sci 269:831–837. https://doi.org/10. 1098/rspb.2001.1941
- TOMST (2023) TMS-4. https://tomst.com/web/en/systems/tms-4/. Accessed 28 Mar 2023
- Ward S, Slater PJB (2005) Raised thermoregulatory costs at exposed song posts increase the energetic cost of singing for Willow Warblers *Phylloscopus trochilus*. J Avian Biol 36:280–286. https:// doi.org/10.1111/j.0908-8857.2005.03379.x
- Welling P, Koivula K, Lahti K (1995) The dawn chorus is linked with female fertility in the Willow Tit *Parus montanus*. J Avian Biol 26:241–246. https://doi.org/10.2307/3677325
- Welling P, Koivula K, Orell M (1997) Dawn chorus and female behaviour in the Willow Tit *Parus montanus*. Ibis 139:1–3. https://doi. org/10.1111/j.1474-919x.1997.tb04497.x
- Wickham H, François R, Henry L, Müller K (2021) dplyr: a grammar of data manipulation. R Package Version 1.0.3. https://cran.r-proje ct.org/package=dplyr
- York JE, Young AJ, Radford AN (2014) Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase. Biol Lett. 10:20130970. https://doi.org/10.1098/rsbl.2013.0970
- Zhao T, Lin J, Zhang X, Wan D, Yin J (2016) The primary study of the relationship between environmental factors and dawn song in Varied Tits. In: ACM international conference proceeding series, pp 75–80. https://doi.org/10.1145/3022702.3022721

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

D Springer

## CHAPTER 2

This chapter is submitted as

Paterno J, Korner-Nievergelt F, Anderwald P, Amrhein V (2024). An exercise in conducting small studies: Road construction noise and start of dawn singing in mountain woodland songbirds. *In revision: peerJ* 

Construction site at the Ofenpassroad, SNP / Flurin Filli

### An exercise in conducting small studies: Road construction noise and start of dawn singing in mountain woodland songbirds

Julia Paterno<sup>1,2</sup>, Fränzi Korner-Nievergelt<sup>1,3</sup>, Pia Anderwald<sup>2</sup> and Valentin Amrhein<sup>1,3</sup>

### Abstract

Anthropogenic noise can negatively affect communication of birds. For example, road construction sites are a common source of noise, and construction noise often differs from normal road noise. Previous studies found changes in start of dawn singing due to increased levels of anthropogenic noise or environmental variables like moon phase, date, or cloud cover. In the present study, we investigated how the start of dawn singing of six common songbird species was related to several environmental variables in mountain woodlands of the Swiss National Park. Our study also illustrates how seemingly small changes in data sets can turn conclusions of small studies upside down. When conducting analyses on two slightly different data sets using either manually collected data on temperature as measured in the field or temperature data from a weather station in 4 km distance, we found that not only the strength, but also the direction of the effects of cloud cover, date, and anthropogenic noise differed between the two analyses. We thus warn against drawing strong inferences from single analyses, particularly in small studies, even if some of the results may turn out "statistically significant". In both analyses, however, temperature had the most consistent effect: all six investigated songbird species started dawn singing earlier on mornings with warmer temperatures, which is in line with previous studies on the effects of temperature on bird song; depending on the analysis, the overall average was a 6 or 9 minutes earlier starting time.

Keywords: dawn chorus, temporal shift, breeding stage, timing, weather, animal behaviour

Julia Paterno julia.paterno(at)nationalpark.ch

<sup>1</sup> Department of Environmental Sciences, University of Basel, 4051 Basel, Switzerland

<sup>2</sup> Department of Research and Monitoring, Swiss National Park, 7530 Zernez, Switzerland

<sup>3</sup> Swiss Ornithological Institute, 6204 Sempach, Switzerland

### Introduction

Anthropogenic noise is no longer restricted to urban areas but also affects near-natural areas with increasing intensity. For example, in Europe, nearly 20% of "Nature 2000" areas are located within regions characterised by increased levels of anthropogenic noise (European Environmental Agency, 2020). Among the sources of anthropogenic noise in Europe, road noise is the most dominant and is one of the top environmental risks to human health (European Environmental Agency, 2020). Previous studies found negative effects of anthropogenic noise on humans and animals (e.g., Benfield et al., 2020; Jin et al., 2024; Kunc & Schmidt, 2019, 2020). Because acoustic communication can be impaired, in particular songbirds are affected: Warning or mating calls can be masked (e.g., Francis et al., 2011; Rheindt, 2003; Slabbekoorn & Peet, 2003), predator-prey interactions altered (McIntyre et al., 2014), and reproductive success reduced (Gross et al., 2010; Habib et al., 2007; Halfwerk et al., 2011; Holm & Laursen, 2011).

An additional disturbance factor along roads is that construction sites may be even noisier, or emit a different quality of noise, than the general traffic. Noise disturbance from construction work can be more erratic than traffic noise, and construction works are normally limited to workdays and conducted mostly during the day. Furthermore, emitted frequencies of construction noise differ depending on the type of construction work: For example, demolition-stage machineries generate a constant sound energy with frequencies between 0.5 and 2 kHz (Lee et al., 2015), whereas machines like bulldozers generate noise with higher energy levels and frequencies between 4 and 5 kHz (Lee et al., 2015). The peak frequency of normal road noise, in contrast, is about 1 kHz (Yang et al., 2020; songbirds produce songs with mean peak frequencies between 0.2 - 10 kHz, but most passerine species produce songs at ~4 kHz (Mikula et al. 2021)). The occurrence of different sound types (i.e., the timing of noise emissions), but also the frequencies and amplitudes of noise during construction works depend on the work that is conducted, thus birds may not be able to predict the timing of the disturbance in advance compared to disturbance due to road noise (i.e., birds may know that there is a peak in road traffic in the early morning and may be able to adapt).

Noise from construction sites therefore has different characteristics compared to road noise, and birds may react differently depending on the type of noise. Previous studies showed varying results when investigating the effects of construction noise versus road noise on songbirds. For example, a long-term study in Texas found no clear differences in territory placement, reproductive success, and territory density of golden-cheeked warblers (Setophaga chrysoparia) between sites disturbed either by road noise or by construction noise compared to an undisturbed control site (Lackey et al., 2011, 2012; Long et al., 2016, 2017). In contrast, Yrjölä et al. (2018) found a population decrease of about 9% in common forest birds during a construction period of 10 years; however, other factors such as habitat changes made it difficult to deduce the cause of the population decline (Yrjölä et al., 2018). Other studies compared species abundance (Hostetler et al., 2005) and species densities (Pearce-Higgins et al., 2012), and found no clear differences between pre- and post-construction periods. To our knowledge, however, there are so far no published studies on the effects of noise from road construction sites on dawn singing behaviour of birds. Dawn singing of songbirds serves in territory defence, mate attraction or mate guarding (Gil & Llusia, 2020; Staicer et al., 1996), and social dynamics seem to be one of the main drivers for singing at dawn Staicer et al. (1996). Differences in the timing of song start at dawn may lead to changes in social behaviour: For example, Poesel et al. (2006) observed a larger number of mating partners and a higher probability to gain extrapair paternity in males that started to sing six minutes earlier at dawn.

Here, we studied possible effects of a road construction site on dawn singing of mountain woodland songbirds. We used a before vs. after and control vs. treatment design (e.g., Morrison et al., 2008; Stewart-Oaten et al., 1986) and investigated the timing of song start at dawn before and during construction works (i.e., on mornings after days with construction works) at a construction site and a site with normal traffic (control site). Most songbirds have a peak of singing activity at dawn during the breeding season (Bruni et al., 2014; Pérez-Granados et al., 2018), and dawn singing mostly serves

territory defence, mate attraction, or mate guarding (Gil & Llusia, 2020). We compared the start of dawn singing before and during construction noise (i.e., on mornings after days with construction works) while accounting for other environmental variables that may affect start of dawn singing: date (i.e., Bruni et al. 2014, Erne and Amrhein 2008, Paterno et al. 2024), temperature (Naguib et al. 2019, Puswal et al. 2020), and cloud cover (Bruni et al. 2014, Da Silva et al. 2014, Nordt & Klenke 2013, Zhao et al. 2016). Previous studies observed that birds avoided singing during noisy times and shifted their singing activity to times when the noise level was lower (Dominoni et al., 2016; Gil et al., 2015; Paterno et al., 2024).

We thus expected an earlier start of dawn singing due to road construction noise, similar to the change that previous studies observed due to normal road noise, but stronger.

Our study also offers a case showing how conclusions from small studies can easily change depending on seemingly small changes in data sets: Interpretation and reporting of our data took an unexpected turn when, after the journal invited us to submit a revision, we decided to include data on three more observation days that we had so far excluded due to missing data on temperature and cloud cover. To be able to include the three observation days, we used data from a weather station at a distance of 4 km from the study sites, rather than our own weather data collected by hand in the field. After this change in the data set, the conclusions we could have drawn with respect to our main study question about the effects of construction noise were turned upside down. Since temperature data obtained in the field and from the weather station were quite comparable (Figure A1), this seemed to be a good example showing that even if results are partly "statistically significant", small changes in a data collection protocol can lead to completely different conclusions regarding the main study question.

We thus present our result section in two different versions, highlighting the changes after inclusion of additional data, and discuss how an open and honest presentation of the research process could transform our view of scientific results.

### Materials & Methods

### Study area

Data were collected during 20 days between mid-April and mid-May 2021 in the Swiss National Park (SNP), at a site along the "Ofenpass road" with construction works and at a nearby control site along the same road, but without construction works. Both sites were surveyed in parallel and in two time periods: before and during construction works started in the surveyed area (thus, each of the two sites also served as their own control; before vs. during and control vs. treatment design; Morrison et al., 2008; Stewart-Oaten et al., 1986).

The Ofenpass road is an important transition route between the Engadin and South Tyrol and has a length of 21.6 km between Zernez, the village at the start of the pass, and the top of the pass (Süsom Givè). It leads right through the SNP, which is a strictly protected nature conservation area (IUCN category Ia; access to our study area was granted by the Swiss National Park after project approval by its Research Commission, field study approval number: CH-7228). The main habitat type along the Ofenpass road is mountain woodland, with the two subspecies of Dwarf Mountain Pine (Pinus mugo / Pinus mugo spp. uncinata) as the main tree species. The climate is alpine, with marked temperature differences between the seasons. Mean annual precipitation for the area is about 800 mm (Haller et al., 2013). The sum of precipitation over all analysis days was 11.4 mm and temperatures ranged from -10.4 to +11.1 °C (data from nearby weather station Buffalora; source MeteoSwiss) on the days used for analysis II, respectively. The mean snow melt-out date in the area is at the beginning of May.

### Study sites

The Ofenpass road is a two-lane road with a speed limit of 80 km / h; it has a mean traffic volume of 1561 cars per day (mean of average daily traffic 2012 – 2022; Tiefbauamt Graubünden, 2024) leading

to noise emissions of about 90 dB (measured about 1 m from the road with a noise level metre; Sound Level Meter SL 510). The Ofenpass road was built between 1870 and 1872 (Puorger, 1955) and since then, there have been regular renovations of the road.

For data collection, we selected a construction site aimed at widening the road, generating medium to high noise pollution (estimated maximum noise emission at the construction site: 100 - 110 dB). Construction works started in May 2021, and traffic was regulated by a traffic light during construction works; one lane of the road was always open to traffic.

Working hours of construction works were 7 am - 12 pm and 1 pm - 5 pm from Monday to Friday (Rafael da Silva, pers. communication); thus daily construction works started after we finished our observations. Our control site at the same Ofenpass road was about 500 m (linear distance) from the construction site (total length of the construction site was 1140 m; Figure 1). The control site had a similar normal road noise level (the same numbers of cars passing by), and it was at a similar elevation (~ 1800 m), slope (~ 10 °), and exposition (north-west). The main difference was that due to the topography and the distance to the construction site, there was no construction noise audible at the control site.



Figure 1 (A) shows the location of the Swiss National Park within Switzerland. (B) gives an overview of the study area with yellow (construction site) and orange (control site) areas indicating the two study sites, and yellow and orange dots indicating the position of the observer. (C) shows the construction site at an early stage and (D) and (E) show the habitat at the construction and control site.

### Data collection

We visited the sites daily in alternating order, starting at the construction site on 21 April 2021 and ending at the control site on 20 May 2021 (Table 1). We visited the control site on all days of the week and the construction site only on working days. Construction works started on 3 May 2021 at the construction site, two weeks after we started data collection, and continued beyond data collection. We thus selected the period of data collection in such a way that we were able to compare both the control site and the construction site during two weeks before construction works started, and during two weeks of construction works. Thus, we had 5 days of data collection per period (before / during construction works) and site (Table 1).

The observer (JP) went to the observation site at least 1 hour before sunrise, i.e., before the first birds started to sing, and sat in complete silence at a central point of the construction or control site

(Figure 1), noting the position and the time of each singing bird until sunrise (data are available in the Supplementary material). When two or more individuals of the same species were simultaneously singing, the number of individuals was identified based on their singing position in their territories, and for each territory the time of the first song was noted. Therefore, multiple observations of the same species per day and site were possible. We also noted temperature as measured in the field and cloud cover at the beginning of each observation (i.e., once per day). Due to technical problems, we have no data on local temperature at the study sites for 4 and 13 May and no cloud data for 24 April, and those three days were excluded from the first analysis (analysis I, Table 1). In the second analysis (analysis II), we added data for those three dates: According to a forecast based on data from historical station observations and historical remote observations (Visual Crossing Corporation, 2024) for the study site, the 24 April was a sunny day with 0 % cloud cover and we thus included this day in the analysis with 0 % cloud cover (Table 1). To be able to include the two days with missing temperature data in the analysis, we replaced all manually recorded temperature data with temperature data of a weather station at Buffalora in 4 km distance from the study sites; data were obtained from MeteoSwiss, the Swiss Federal Office of Meteorology and Climatology. The temperature curve over the whole study period was similar when using manually collected data and data from the weather station (Table 1, Figure A1).

We thus used data from three more days in analysis II compared to the analysis with the manually collected temperature and cloud data (analysis I), in which we used data from 17 days. We visually checked for outliers on the three additionally included days but did not find any suspicious pattern.

			analy	ysis I	ana	lysis II	
	site	date	temperature [°C]	cloud cover [%]	temperature [°C]	cloud cover [%]	comments
	construction site	21.04.2021	-5	40	-8	40	
s	control site	22.04.2021	-2	100	-2.6	100	
/ork	construction site	23.04.2021	-1.5	0	-7.5	0	
v nc	control site	24.04.2021	-5	NA	-8.7	0	
ucti	construction site	25.04.2021	-1	40	-3.1	40	
nstr	control site	26.04.2021	-1.5	70	-0.6	70	
e co	construction site	27.04.2021	1	100	0.3	100	
efor	control site	28.04.2021	2	100	0.9	100	
þ(	construction site	29.04.2021	4	100	1.9	100	light drizzle
	control site	30.04.2021	1.5	100	1.1	100	fog and light drizzle
	construction site	03.05.2021	-3.5	20	-7	20	
S	control site	04.05.2021	NA	0	-5	0	
vork	construction site	05.05.2021	1.5	60	2.1	60	
v no	control site	06.05.2021	-3.5	40	-4.9	40	
ucti	construction site	07.05.2021	2	40	1.9	40	
nstr	control site	10.05.2021	6	100	4.3	100	
b CO	construction site	13.05.2021	NA	90	1.2	90	
liring	control site	14.05.2021	1	90	-2.6	90	
ιp	construction site	18.05.2021	0.5	30	1.1	30	light snow fall
	control site	20.05.2021	0	100	-0.8	100	light snow fall

Table 1 Dates of observations and weather data for analyses I and II during the study period.

### Statistical analysis

We included the six songbird species for which we had at least five observations (start of dawn singing of an individual) per site and period (i.e., a minimum of 20 observations in total; Table 2). We used the package dplyr (Wickham et al., 2021) in R (R Core Team, 2020) to prepare the data, and the package ggplot2 (Wickham, 2016) for visualization. To fit Bayesian linear mixed models, we used the

package rstanarm (Goodrich et al., 2020). The response variable was minutes relative to sunrise, and we used date, temperature, and cloud cover as predictor variables (z-transformed prior to model fitting). We included site (construction site, control site), period (before, during construction works) and a two-way interaction of site and period as fixed effects predictors, and species as a random effect. We modelled all predictor effects (but not site) by species (random slopes), to obtain species-specific coefficients for the predictors.

We assessed convergence of Markov chains by visual inspection of Rhat values (analysis I and II: mean = 1.0, max = 1.0), history plots, and the number of effective samples that were above 6000 (analysis I: mean = 15652, min = 6694; analysis II: mean = 16799, min = 6317; the higher the value, the lower the Monte Carlo Error). To assess model fit, we used standard residual plots and posterior predictive model checking (visually based on overlaid densities and histograms). Furthermore, we compared mean, standard deviation, minimum and maximum between the data and replicated data from the model (Gabry, 2018).

In the following we present the result section in two different versions, highlighting the differences in the results arising when using the two slightly different data sets. The results of analysis I are presented on the left page and the results of analysis II are presented on the right page.

### **Results from analysis I**

We detected at total of 13 songbird species for which we noted the start of dawn singing. Eurasian chaffinch (*Fringilla coelebs*) and coal tit (*Periparus ater*) were the most abundant species (Table 2). The earliest singers at dawn were ring ouzel (*Turdus torquatus*), mistle thrush (*Turdus viscivorus*), European robin (*Erithacus rubecula*), and song thrush (*Turdus philomelos*). Coal tit, dunnock (*Prunella modularis*), Eurasian blackbird (*Turdus merula*), Eurasian wren (Troglodytes troglodytes), Eurasian treecreeper (*Certhia familiaris*), and crested tit (*Lophophanes cristatus*) started to sing about half an hour before sunrise, while Alpine tit (*Parus montanus montanus*), lesser whitethroat (*Curruca curruca*), and Eurasian chaffinch started to sing about 15 - 20 minutes before sunrise (Table 2). Within the woodlands of the SNP there are a total of 58 songbird species breeding (unpublished data) and from personal observations we know that the songbird species listed in Table 2 represent some of the most common songbird species of the SNP.

Table 2 Average  $\pm$  SD start of dawn singing in minutes before sunrise for common songbird species along a control / construction site before and during construction works in the woodlands of the Swiss National Park. Numbers of observations are given in brackets, and species are ordered by overall start time of dawn singing. Species with less than five observations per cell were excluded from further analysis.

	before construction works 21. April – 30. April		during constru 3. May – 2	iction works 20. May		included
species	construction site	control site	construction site	control site	overall	in analysis
ring ouzel	$-43.8 \pm 9.6 \ (11)$	$-46.3 \pm 6.0$ (7)	$-46.3 \pm 4.1 \ (13)$	$-43.2 \pm 3.5 \; (5)$	$-45.1 \pm 6.5 \; (36)$	yes
mistle thrush	$-41.2 \pm 5.5$ (5)	-52.1 ± 5.6 (12)	-38.6 ± 9.4 (11)	-43.5 ± 5.1 (10)	$-44.5 \pm 8.6 \ (38)$	yes
European robin	$-38.8 \pm 8.9$ (5)	$-45.1 \pm 10.6 \ (9)$	-32.7 ± 13.2 (6)	$-44.8 \pm 4.6$ (8)	$\textbf{-41.2} \pm 10.4 \ \textbf{(28)}$	yes
coal tit	$-26.3 \pm 6.4 \ (15)$	$-28.8 \pm 7.8$ (11)	-30.7 ± 10.4 (21)	-31.3 ± 3.4 (16)	$-29.5 \pm 7.8 \ (63)$	yes
Alpine tit	$-17.7 \pm 8.5 (11)$	$-17.0 \pm 10.0 \ (8)$	$-25.9 \pm 9.6 \ (15)$	$-24.4 \pm 6.7$ (8)	$-21.8 \pm 9.5 \; (42)$	yes
Eurasian chaffinch	$-17.1 \pm 5.0 (13)$	$-15.2 \pm 7.1$ (16)	-17.2 ± 5.6 (18)	$-19.5 \pm 4.6 \ (19)$	$-17.4 \pm 5.7$ (66)	yes
song thrush	$-37.9 \pm 4.9$ (8)	$-40.4 \pm 3.1$ (4)	$-39.1 \pm 9.4 \ (19)$	-42.4 ± 4.8 (13)	$-40.0 \pm 7.1 \; (44)$	no
dunnock	$-20.5 \pm 9.8$ (7)	$-41.9 \pm 9.5 \ (9)$	-15.6 ± 18.2 (3)	-36.7 ± 9.1 (8)	$-31.9 \pm 14.3 \ (27)$	no
common blackbird	-37.1 ± 4.1 (2)	(0)	-18.0 (1)	(0)	-30.7 ± 11.3 (3)	no
Eurasian wren	-29.5 ± 5.1 (7)	-29.2 ± 3.6 (2)	-24.1 ± 8.0 (9)	$-29.3 \pm 7.8$ (5)	-27.3 ± 7 (23)	no
Eurasian treecreeper	-21.5 ± 4.2 (3)	$-33.6 \pm 3.2$ (7)	$-15 \pm 5.4$ (2)	$-26.7 \pm 7.0$ (3)	-27.3 ± 8.1 (15)	no
crested tit	$-18.0 \pm 10.1$ (5)	-27.3 ± 8.9 (8)	-20.3 ± 15.6 (3)	-33 ± 14.5 (4)	-25.1 ± 11.9 (20)	no
lesser whitethroat	(0)	(0)	(0)	-21.3 ± 27.4 (2)	-21.3 ± 27.4 (2)	no

In the following, we present results on the six songbird species for which we had at least five observations per cell in Table 2 and thus at least 20 observations overall. At the construction site, all but one of the six species started dawn singing earlier during construction works compared to the period before construction works started; only European robins started dawn singing at about the same time during and before construction works started. On average, the bird species started to sing about 2 minutes earlier (Table 3, Figure 2). At the control site, in contrast, the species started to sing on average about 3 minutes later during the time of construction works compared to the time before construction works started in the area (there were no construction works at the control site itself). Thus, species started to sing on average about 5 minutes earlier relative to sunrise at the construction site during construction works than one would expect from the change (before vs. during construction works) in song start at the control site.

Analysis I

### **Results from analysis II**

We detected at total of 13 songbird species for which we noted the start of dawn singing. Eurasian chaffinch (*Fringilla coelebs*) and coal tit (*Periparus ater*) were the most abundant species (Table 2). The earliest singers at dawn were ring ouzel (*Turdus torquatus*), mistle thrush (*Turdus viscivorus*), European robin (*Erithacus rubecula*), and song thrush (*Turdus philomelos*). Coal tit, Eurasian blackbird (*Turdus merula*), dunnock (*Prunella modularis*), Eurasian wren (*Troglodytes troglodytes*) and Eurasian treecreeper (*Certhia familiaris*) started to sing about half an hour before sunrise, while crested tit (*Lophophanes cristatus*), Alpine tit (*Parus montanus montanus*), lesser whitethroat (*Curruca curruca*), and Eurasian chaffinch started to sing about 15 - 20 minutes before sunrise (Table 2). Within the woodlands of the SNP there are a total of 58 songbird species breeding (unpublished data) and from personal observations we know that the songbird species listed in Table 2 represent some of the most common songbird species of the SNP.

Table 2 Average  $\pm$  SD start of dawn singing in minutes before sunrise for common songbird species along a control / construction site before and during construction works in the woodlands of the Swiss National Park. Numbers of observations are given in brackets, and species are ordered by overall start time of dawn singing. Species with less than five observations per cell were excluded from further analysis.

	before constru 21. April –	ction works 30. April	during constru 3. May –	uction works 20. May		included
species	construction site	control site	construction site	control site	overall	analysis
ring ouzel	-41.0 ± 13.2 (12)	$-46.3 \pm 6$ (7)	$-46.3 \pm 4.1 \ (13)$	-43.2 ± 3.5 (5)	$-44.2 \pm 8.5$ (37)	yes
mistle thrush	$-36.0 \pm 14.4$ (7)	-52.1 ± 5.6 (12)	-38.6 ± 9.4 (11)	$-43.5 \pm 5.1 \; (10)$	$-43.4 \pm 10.4$ (40)	yes
European robin	$-38.8 \pm 8.9$ (5)	-45.1 ± 10.6 (9)	-32.7 ± 13.2 (6)	$-44.8 \pm 4.6$ (8)	$-41.2 \pm 10.4$ (28)	yes
coal tit	$-22.2 \pm 10.4$ (20)	-28.8 ± 7.8 (11)	$-30.7 \pm 10.4 \ (21)$	$-31.3 \pm 3.4$ (16)	$-28.0 \pm 9.5 \ (68)$	yes
Alpine tit	-16.1 ± 9.7 (12)	$-17.0 \pm 10.0$ (8)	$-25.9 \pm 9.6 \ (15)$	$-24.4 \pm 6.7$ (8)	-21.3 ± 10 (43)	yes
Eurasian chaffinch	-8.7 ± 14.5 (19)	$-14.3 \pm 7.9 (17)$	$-17.2 \pm 5.6 (18)$	$-19.5 \pm 4.6 \ (19)$	$-14.9 \pm 9.8$ (73)	yes
song thrush	$-35.8 \pm 4.7$ (15)	-40.4 ± 3.1 (4)	$-39.1 \pm 9.4$ (19)	$-42.4 \pm 4.8 (13)$	-39.1 ± 7.1 (51)	no
common blackbird	-37.1 ± 4.1 (2)	(0)	-18.1 (1)	(0)	-30.7 ± 11.3 (3)	no
dunnock	$-18.2 \pm 8.9$ (10)	$-41.9 \pm 9.5$ (9)	$-15.6 \pm 18.2$ (3)	-36.7 ± 9.1 (8)	$-30.0 \pm 14.8$ (30)	no
Eurasian wren	-29.5 ± 5.1 (7)	-29.2 ± 3.6 (2)	-24.1 ± 8.0 (9)	-29.3 ± 7.8 (5)	$-27.3 \pm 7.0$ (23)	no
Eurasian treecreeper	-21.4 ± 3.4 (4)	-33.6 ± 3.2 (7)	$-15.0 \pm 5.4$ (2)	-26.7 ± 7 (3)	-27.0 ± 7.9 (16)	no
crested tit	-17.1 ± 9.3 (6)	-27.3 ± 8.9 (8)	$-15.0 \pm 16.5$ (4)	-33.0 ± 14.5 (4)	$-23.3 \pm 12.8$ (22)	no
lesser whitethroat	(0)	(0)	(0)	$-21.3 \pm 27.4$ (2)	-21.3 ± 27.4 (2)	no

In the following, we present results on the six songbird species for which we had at least five observations per cell in Table 2 and thus at least 20 observations overall. We observed a similar or later start of dawn singing for all of the six species at the construction site during construction works (i.e., after days with construction works) compared to the period before construction works started; only Alpine tits started dawn singing a bit later during and before construction works started. On average, the bird species started dawn singing at about the same time (Table 3, Figure 2). At the control site, in contrast, the species started dawn singing on average about 1 minute earlier during the time of construction works compared to the time before construction works started in the area (there were no construction works at the control site itself). Thus, species started to sing on average about 1 minute later relative to sunrise at the construction site during construction works than one would expect from the change (before vs. during construction works) in song start at the control site (Table 3, Figure 2).

Analysis II

The effect was most pronounced in mistle thrushes that started to sing 4.8 minutes later at the control site during construction works compared to the time period before construction works started. At the construction site, mistle thrushes started to sing on average 1.5 minutes earlier during construction works compared to the time period before construction works started; thus, mistle thrushes started to sing 6.2 minutes earlier at the construction site during construction works than one would expect from the change in song start at the control site (before vs. during construction works; Table 3). Ring ouzel, coal tit, Alpine tit and Eurasian chaffinch started to sing about 4 - 7 minutes earlier than expected from the change in song start at the control site (before vs. during construction works), and the effect was smallest in European robins that started dawn singing 1.8 minutes earlier. In traditional testing language, effects would have been called "statistically significant" in two of the six investigated species (coal tit and Alpine tit), because the 95% compatibility intervals did not overlap zero (Table 3).

Of the investigated variables, temperature had the strongest overall effect on the start of dawn singing of the six songbird species (Table 3, Table 4).

Birds started to sing on average 6 minutes earlier on warmer than on colder mornings (+6 vs. -5 °C, Table 3, Figure 3C), whereas the effect of date on song start at dawn was more species-specific (Table 3, Figure 3A). On warmer compared to colder mornings, ring ouzels started to sing 14.1 minutes earlier, mistle thrushes and European robins about 5 - 6 minutes earlier, and Alpine tits, Eurasian chaffinches and coal tits about 2 - 4 minutes earlier (Table 3, Figure 3C).

We observed an earlier song start for mistle thrushes (1.1 minutes) with advancing season (Table 3, Figure 3A). Alpine tits and coal tits delayed their song start by about 7 - 8 minutes and Eurasian chaffinches by about 5 minutes at the end compared to the beginning of the breeding season (Table 3, Figure 3A).

Cloud cover had the smallest overall effect: on average, the six species started to sing at about the same time relative to sunrise on days with 100% cloud cover compared to days with a clear sky (Table 3, Figure 3B). Nevertheless, the effect of cloud cover was also species-specific: for example, mistle thrushes and European robins started to sing about 4 minutes earlier on days with 100% cloud cover compared to days with a clear sky (Table 3, Figure 3B); in contrast, coal tits, Alpine tits, Eurasian chaffinches and ring ouzels started their dawn song 1 - 4 minutes later (Table 3, Figure 3B).



Figure 2 Start of dawn singing relative to sunrise of six common woodland songbird species in the Swiss National Park at a construction site and a control site before (light grey shading) and during (dark grey shading) construction works. Boxplots are based on the GLMM.

Colour code:	control	construction	before	during

Analysis I

All species but mistle thrushes started to sing 1 - 3 minutes earlier at the control site during construction works compared to the time period before construction works started; mistle thrushes started dawn singing about 1 minute earlier at the control site during construction works compared to the time period before construction works started. At the construction site, mistle thrushes and European robins started to sing about 2 minutes later, and Eurasian chaffinches at about the same time during construction works compared to the time period before construction works started dawn singing about 0.4 - 0.5 minutes earlier and Alpine tits 3.7 minutes earlier at the construction works started. Thus, birds started to sing up to about 3 minutes later at the construction site during construction works; Table 3). In traditional testing language, none of the effects would have been called "statistically significant", because in all six investigated species the 95% compatibility intervals overlapped zero (Table 3).

Birds started to sing on average 9 minutes earlier on warmer than on colder mornings (+6 vs. -5 °C; Table 3, Figure 3C). Ring ouzels started to sing 13.1 minutes earlier, Alpine tits, coal tits and mistle thrushes about 10 minutes earlier, and Eurasian chaffinches and European robin 7 – 8 minutes earlier on warmer compared to colder mornings (Table 3, Figure 3C).

We observed an earlier song start for mistle thrushes (6.9 minutes), European robins (5.0 minutes), ring ouzels (1.0 minutes) and Eurasian chaffinches (0.5 minutes) with advancing season (Table 3, Figure 3A). Coal tits and Alpine tits delayed their song start by about 2 minutes at the end compared to the beginning of the breeding season (Table 3, Figure 3A). Figure 3A).

After temperature, cloud cover had the second-largest effect: on average, the six species started to sing about 4 minutes later on days with 100% cloud cover compared to days with a clear sky (Table 3, Figure 3B). All but one species started to sing later on days with 100% cloud cover compared to days with a clear sky; only European robins started to sing at about the same time relative to sunrise on days with 100% cloud cover compared to days with a clear sky (Table 3, Figure 3B).





Colour code	control	construction	before	during
Colour coue.	control	construction	belole	uuring

# Analysis II

Table 3 Differences and 95% compatibility intervals (CI; Amrhein & Greenland, 2022) of start of dawn singing in minutes in relation to different physical environmental variables. \*interaction period [before, during] x site [control, construction site]

						effect of
	date	cloud cover	temperature	control site	construction site	construction
species	140 vs. 111	100% vs. 0%	+6 vs5 °C	during vs. before	during vs. before	noise*
mistle	+1.11 [-10.69;	-3.62 [-13.79;	-6.19 [-17.09;	+4.75 [-2.11;	-1.47 [-9.42;	-6.22 [-14.61;
thrush	+14.68]	+5.74]	+5.20]	+12.59]	+6.14]	+0.96]
ring	-3.34 [-13.87;	+1.41 [-6.87;	-14.09 [-28.33; -	+2.91 [-4.10;	-1.38 [-8.06;	-4.35 [-11.22;
ouzel	+7.61]	+10.67]	2.63]	+10.08]	+5.28]	+2.56]
European	-0.61 [-12.23;	-3.74 [-14.79;	-5.28 [-17.40;	+1.92 [-5.31;	+0.20 [-8.01;	-1.79 [-8.95;
robin	+13.47]	+5.51]	+8.74]	+8.26]	+9.02]	+7.16]
anal tit	-7.34 [-16.50;	+3.62 [-2.90;	-1.73 [-9.88;	+3.02 [-2.59;	-2.56 [-8.16;	-5.60 [-11.16; -
coartit	+1.08]	+10.46]	+7.28]	+8.90]	+3.07]	0.21]
A lucius tit	-7.81 [-19.19;	+2.23 [-5.95;	-3.97 [-13.89;	+0.91 [-6.24;	-5.75 [-12.41;	-6.53 [-13.11; -
Alpine th	+2.71]	+9.94]	+6.04]	+7.10]	+0.58]	0.20]
Eurasian	-4.96 [-14.84;	+1.49 [-6.08;	-3.49 [-12.67;	+2.22 [-3.78;	-1.59 [-7.80;	-3.79 [-9.62;
chaffinch	+5.27]	+8.99]	+5.57]	+8.09]	+4.76]	+2.29]
N	-3.81 [-13.03;	+0.27 [-7.71;	-5.71 [-15.73;	+2.62 [-2.87;	-2.09 [-8.11;	-4.72 [-10.30;
overall	+6.17]	+7.86]	+4.34]	+8.02]	+4.09]	+0.97]



Analysis I

Figure 3 Start of dawn singing in minutes before sunrise of six common woodland songbird species in relation to date, cloud cover, and temperature. Overall regression lines are in black, and individual regression lines for the six species are in colour, with coloured areas indicating 95% CI.

Table 4 Parameter estimates and 95% CI for the investigated physical environmental variables over all six species. The standardised coefficients show the change in start of dawn song (in minutes) when predictor variables change by one standard deviation. The unstandardized coefficients show the change in start of dawn singing (in minutes) when the predictor variables change by one unit.

ring ouzel

European robin

Alpine tit

Eurasian chaffinch

	Standardised coefficients, mean [95% CI] number of species	SD of the predictor variable	Unstandardized coefficients, mean [95% CI] number of species	Unit of the predictor variable
Intercept: control site; period before construction works	-35.70 [-44.22; -27.25]			
Date	-1.00 [-3.57; +1.69]	7.93 days	-0.13 [-0.45; +0.21]	1 day
Temperature	-1.30 [-3.70; +1.02]	2.59 °C	-0.50 [-1.43; +0.39]	1 °C
Cloud cover	+0.10 [-2.61; +2.66]	33.84%	+0.03 [-0.77; +0.79]	10%
Timing during	+2.60 [-2.87; +8.02]			
Control site	+4.10 [-0.05; +8.39]			
Interaction: Period during construction works : construction site	-4.70 [-10.30; +0.97]			

Table 3 Differences and 95% compatibility intervals (CI; Amrhein & Greenland, 2022) of start of dawn singing in minutes in relation to different physical environmental variables. \*interaction period [before, during] x site [control, construction site]

						effect of
	date	cloud cover	temperature	control site	construction site	construction
species	140 vs. 111	100% vs. 0%	+6 vs5 °C	during vs. before	during vs. before	noise*
mistle	+6.87 [-5.03;	+1.51 [-7.96;+	-9.14 [-19.37;	+1.07 [-5.65;	+1.85 [-6.22;	+0.66 [-7.23;
thrush	+21.04]	9.92]	+1.84]	+8.69]	+9.52]	+7.89]
ring	+1.00 [-10.16;	+4.47 [-3.50;	-13.13 [-24.79; -	-0.50 [-7.26;	-0.45 [-7.36;	+0.05 [-6.92;
ouzel	+12.12]	+13.11]	3.31]	+6.61]	+6.70]	+6.95]
European	+4.96 [-6.88;	-0.11 [-11.11;	-6.45 [-16.95;	-0.99 [-7.85;	+2.36 [-6.13;	+3.28 [-4.29;
robin	+19.32]	+8.37]	+8.54]	+5.53]	+11.11]	+11.68]
agal tit	-1.63 [-11.27;	+8.48 [+2.33;	-9.48 [-17.91; -	-1.15 [-6.68;	-0.35 [-6.48;	+0.82 [-5.00;
coartit	+7.34]	+15.47]	1.46]	+4.62]	+5.85]	+6.58]
A la inc dit	-1.52 [-12.74;+	+4.56 [-3.28;	-9.99 [-19.40; -	-3.31 [-10.53;	-3.74 [-11.08;	-0.36 [-7.05;
Alpine tit	9.14]	+11.82]	0.65]	+2.95]	+3.14]	+6.24]
Eurasian	+0.51 [-9.83;	+5.24 [-1.63;	-8.80 [-17.63;	-2.41 [-8.47;	+0.12 [-6.50;	+2.51 [-3.23;
chaffinch	+11.21]	+11.85]	+0.17]	+3.38]	+6.77]	+8.60]
	+1.70 [-7.84;	+4.05 [-3.60;	-9.47 [-17.94; -	-1.24 [-6.54;	-0.09 [-6.39;	+1.15 [-4.46;+
overall	+11.99]	+11.03]	0.76]	+4.17]	+6.36]	6.81]



Figure 3 Start of dawn singing in minutes before sunrise of six common woodland songbird species in relation to date, cloud cover, and temperature. Overall regression lines are in black, and individual regression lines for the six species are in colour, with coloured areas indicating 95% CI.

mistle thrush ring ouzel European robin -2 Ó 2 4 6

coal tit

Alpine tit

Eurasian chaffinch

Table 4 Parameter estimates and 95% CI for the investigated physical environmental variables over all six species. The standardised coefficients show the change in start of dawn song (in minutes) when predictor variables change by one standard deviation. The unstandardized coefficients show the change in start of dawn singing (in minutes) when the predictor variables change by one unit.

	Standardised coefficients, mean [95% CI] number of species	SD of the predictor variable	Unstandardized coefficients, mean [95% CI] number of species	Unit of the predictor variable
Intercept: control site; period before construction works	-34.30 [-42.99; -25.69]			
Date	+0.50 [-2.15; +3.30]	7.97 days	+0.18 [-0.27; +0.41]	1 day
Temperature	-2.70 [-5.04; -0.21]	3.65 °C	+0.33 [-1.38; -0.06]	1 °C
Cloud cover	+1.50 [-1.34; +4.11]	37.26%	+0.38 [-0.36; +1.10]	10%
Timing during	-1.20 [-6.54; +4.17]			
Control site	+3.30 [-0.68; +7.29]			
Interaction: Period during construction works : construction site	+1.20 [-4.46; +6.81]			

Analysis II

63

### Discussion

Along the Ofenpass road in the Swiss National Park (SNP), we expected birds to start singing earlier at dawn due to road construction noise, on colder mornings with clearer sky, and later in the season. We found that changes in start of dawn singing related to anthropogenic noise differed strongly between the two analyses; overall, however, the intervals obtained from both analyses indicate that there is a relatively low probability that birds start singing more than 10 minutes earlier or more than 7 minutes later due to construction noise.

When including more analysis days (analysis II), birds tended to start singing later at dawn at the construction site during construction works than could be expected from the change (before vs. during construction works) in start of dawn singing at the control site with normal road noise. In contrast, when including less analysis days (analysis I), birds tended to start singing earlier at dawn at the construction site during construction works than could be expected from the change (before vs. during construction works) in start of dawn singing at the control site with normal road noise. Even though differences in start of dawn singing between control and construction site were "statistically significant" in two out of six investigated species (Table 3), inclusion of three more days completely reversed the direction of effect. We would like to use this case to warn about drawing strong inferences based on "statistically significant" results, particularly those obtained from small studies. The overreliance on "statistically significant" results from single analyses and single studies is a general problem in many branches of science (reviewed, e.g., in Amrhein et al., 2017); we hope that more journals will allow authors to publish several analyses on the same data (Amrhein et al., 2019), even if results from those analyses may be contradicting, hindering communication of a straightforward storyline in the published paper. In the following, we nonetheless provide a more general discussion of effects of road noise and construction noise.

Previous studies found an earlier start of dawn singing due to increased levels of anthropogenic noise: For example, two studies conducted in the vicinity of major European airports found that birds started dawn singing earlier near airports than in silent control areas (Dominoni et al., 2016; Gil et al., 2015). Both studies concluded that birds may have shifted their start of dawn singing to aviod the noisy times later during the day (Dominoni et al., 2016; Gil et al., 2015). Arroyo-Solís et al. (2013) found similar results when investigating changes in the start of dawn singing depending on noise levels in the city of Seville, Spain, which were experimentally enhanced beyond normal noise levels in the area. In their study, five of six bird species started singing earlier on days with extra noise exposure compared to days with normal city noise (Arroyo-Solís et al., 2013). The Spotless starling (Sturnus unicolor) showed the largest shift and started dawn singing about 20 minutes earlier on days with extra noise exposure (Arroyo-Solís et al., 2013).

In comparsion with those previous studies from urban areas, we found relatively small effects of road noise on start of dawn singing in our earlier study conducted along the Ofenpass road in the Swiss National Park (Paterno et al., 2024): Eurasian chaffinches started to sing up to 5 minutes earlier in areas disturbed by road noise compared to areas completely undisturbed by road noise (in that study, we used a subjective classification of experienced road noise levels at multiple sites throughout the SNP). Despite the relatively small effect sizes, our ealier results (Paterno et al., 2024) showed that songbirds can be affected by road noise also in near-natural areas. Further, birds may not only change their singing behaviour during noisy times or in noisy areas (e.g., Bayne et al., 2008; Bergen & Abs, 1997; McClure et al., 2013; Polak et al., 2013), but may even completely avoid the noisy areas (e.g., McClure et al., 2013; Polak et al., 2013).

Only few independent studies investigated the effects of construction works on birds. In a series of studies in Texas, the territory placement, territory density, breeding success, and song characteristics of golden-cheeked warblers were compared near a construction site, a traffic noise site, and an undisturbed control site (Lackey, 2010; Lackey et al., 2011, 2012; Long et al., 2016, 2017). The studies were conducted along two Highways (1000 – 3000 vehicles and 16200 vehicles per day, respectivley), and the authors investigated three different time periods: pre-construction phase, construction phase, and

post-construction phase (Lackey, 2010; Lackey et al., 2011, 2012; Long et al., 2016, 2017). Lackey et al. (2011) found similar densities of golden-cheeked warbler territories in all three study areas during construction works (construction site = 0.31 territories / ha, traffic noise site = 0.36 territories / ha, control area = 0.33 territories / ha). At the same study site, however, Long et al. (2016) found a 1.3 to 1.8 times greater mean territory density (e.g., territories / ha) in the control site compared to the construction site and the traffic noise sites. They also found a 1.5 to 1.7 greater mean territory density (e.g., territories / ha) in the post-construction compared to the pre-construction phase. Furthermore, Long et al. (2017) found an increase in territory density of about 25% at the construction site and about 14% in the control area after construction works ended, while at the traffic noise site, there was a decrease in territory density of about 3% after construction works ended. Lackey et al. (2011) and Long et al. (2016, 2017) concluded that the observed differences in territory density and breeding success were small: For example, Long et al. (2017) found a decrease in breeding success of 5 - 10% at the construction and the traffic noise site compared to an increase of 5% in the control area in the postconstruction compared to the construction phase. The changes in territory density and breeding success that Lackey et al. (2011) and Long et al. (2016, 2017) observed may be due to normal between-year variation rather than an effect of construction works (e.g., Davies & Cooke, 1983; Marciniak et al., 2007). Lackey et al. (2011) and Long et al. (2016, 2017) stated that there were only small increases in noise emissions during the construction works that probably did not have negative effects on territory density, pairing success, or fledging success of golden-cheeked warblers.

Some previous studies (e.g., Bermúdez-Cuamatzin et al., 2011; Gross et al., 2010; Mendes et al., 2011; Villain et al., 2016) described an increase in the maximum lower frequencies of birdsong due to road noise, while Long et al. (2016, 2017) found no increase in the minimum frequency in goldencheeked warblers due to construction or traffic noise. Long et al. (2016, 2017) argued that traffic and construction noise are characterized by low frequencies and that warblers typically sing at higher frequencies, and concluded that construction and traffic noise were unlikely to mask the song of goldencheeked warblers. Long et al. (2016, 2017) suggested that there may have been no need for the birds in their study to change their singing behaviour due to construction or traffic noise. Thus, the behavioural responses of birds when exposed to construction or traffic noise and therefore also the suitability of territories near roads or construction sites likely depend on the investigated species (e.g., Clark & Karr, 1979; Ferris, 1979; Reijnen & Foppen, 2006). In the above described observational studies, and also in our own study, it is possible that not only noise emissions, but also other factors related to construction works affected the start of dawn singing, for example dust or visual disturbance. Further, if the effect of date differs between construction and control site (normal road noise), we may find an effect of construction noise, where in reality no such effect exists. Since construction works only started at 7 am and we conducted our data collection earlier in the day (e.g., start of dawn singing) we also have to be aware that birds may not need to adapt to the increased noise levels later during day by an earlier start of singing at dawn. Instead, birds may use different strategies to cope with the increased noise levels during day, like an increased minimum frequency (Bermúdez-Cuamatzin et al., 2011; Francis et al., 2011b; Goodwin & Podos, 2013; Hanna et al., 2011; Hu & Cardoso, 2010), a higher song volume (Brumm, 2004; Nemeth & Brumm, 2010) or a change in the duration of songs (Francis et al., 2011a).

The overall effect was highest in the variable temperature: In both analyses, i.e., using our own temperature data or the data from the nearby weather station, we found that warmer temperatures during the morning led to an earlier song start relative to sunrise in all six species, when accounting for date and the other investigated variables. Previous studies conducted in Europe found similar results, with birds starting to sing earlier after warmer compared to colder nights (Naguib et al., 2019; Nordt & Klenke, 2013; Paterno et al., 2024). In contrast, Da Silva et al. (2014) found a small delay in start of dawn singing for song thrushes, and no clear effects for the other investigated species. However, the temperature differences experienced by the birds in their study were quite small (Da Silva et al., 2014), which could explain the small changes in start of dawn singing.

Singing early at dawn may be costly due to increased energy loss at low temperatures in the morning (but see Gil & Llusia, 2020; Staicer et al., 1996). For example, Thomas & Cuthill (2002) found a positive correlation between overnight temperature and overnight loss of body mass of European robins, supporting predictions made by stochastic dynamic programming models that traded-off time spent foraging with time spentsinging under different weather conditions (Houston & McNamara, 1987; Hutchinson et al., 1993; Hutchinson & McNamara, 2000). Another explanation for the earlier start of dawn singing with increasing temperatures may be related to an increase in arthropod prey activity with warmer temperatures (Avery & Krebs, 1984). Birds may advance their start of feeding with higher temperatures in the morning, and therefore also advance their start of singing to be able to deliver the same amount of song at dawn.

We found varying effects of date among the six investigated species and depending on the analysis. When using our own temperature data including fewer analysis days (analysis I), five of six songbird species started their dawn song earlier 29 days later into the season, and when including temperature data from the weather station and more analysis days (analysis II), two of six songbird species started their dawn song earlier 29 days later into the season. For Alpine tit, coal tit and mistle thrush, we observed the same direction in effects in both analyses. For ring ouzel, European robin and Eurasian chaffinch, in contrast, the direction of effects changed from an earlier start of dawn singing (analysis with fewer days) to a later start of dawn singing (analysis with more days) depending on the number of analysis days. Similarly to the effect of anthropogenic noise, both analyses showed comparably wide compatibility intervals.

Several previous studies found a correlation between early breeding stages and early start of dawn singing for songbirds (Brown, 1963; Bruni & Foote, 2014; Holmes & Dirks, 1978; Welling et al., 1995). In our study, mistle thrushes may have stopped singing early at dawn after nest building at the end of April / beginning of May (Glutz von Blotzheim, 1988). Coal tits and Alpine tits usually start breeding at the beginning of May (Glutz von Blotzheim & Bauer, 1993) and thus somewhat later than mistle thrushes, and therefore may have continued singing earlier at dawn until breeding started. In our earlier study (Paterno et al., 2024), Alpine tits started dawn singing about 5 minutes later between two dates that were about a month apart, but that study was conducted later in the year, i.e., from mid-May until mid-June. Alpine tits therefore may have been at a later breeding stage and may have stopped singing early at dawn (Paterno et al., 2024).

Previous studies also found a delay in start of dawn singing on overcast mornings compared to mornings with a clear sky (Bruni et al., 2014; Da Silva et al., 2014; Nordt & Klenke, 2013; Zhao et al., 2016). This is in line with the model predictions of Hutchinson (2002) suggesting that cloud cover influences the start of dawn singing. In our study, cloud cover at dawn seemed to affect the six investigated species in different ways, when accounting for temperature and the other investigated variables and depending on the number of analysis days: When including less analysis days (analysis I), four of six songbird species started dawn singing about 1 - 4 minutes later on mornings with 100% cloud cover compared to mornings with a clear sky; mistle thrushes and European robins started dawn singing later on mornings with 100% cloud cover compared to mornings later on mornings with 100% cloud cover compared to mornings with a clear sky, only European robins started dawn singing at about the same time on mornings with 100% cloud cover compared to mornings with a clear sky.

### Conclusions

Construction noise starting at 7 am in addition to normal road noise may have a smaller effect on the start of dawn singing than temperature. In both analyses, all six investigated songbird species started to sing earlier relative to sunrise on mornings with warmer temperatures, which is in line with previous studies. The direction of estimated effects of cloud cover, date, and anthropogenic noise differed between the two analyses on slightly different data sets. As a result, the conclusions that we could draw partly changed. We thus warn against drawing strong conclusions from single studies, especially if using small sample sizes, even if some of the results may turn out "statistically significant". More generally,

we suggest that fitting alternative models, and then reporting all results, should be the norm in scientific reporting (Amrhein et al., 2019).

### Acknowledgements

The Tiefbauamt Graubünden supported us with details on construction works along the Ofenpass road. Further, we used services provided by MeteoSwiss, the Swiss Federal Office of Meteorology and Climatology for analysis.

### References

- Amrhein, V., & Greenland, S. (2022). Discuss practical importance of results based on interval estimates and p-value functions, not only on point estimates and null p-values. *Journal of Information Technology*, 37, 316–320. https://doi.org/10.1177/02683962221105904
- Amrhein, V., Greenland, S., & McShane, B. (2019). Retire statistical significance. Nature, 567, 305– 307. https://doi.org/doi: https://doi.org/10.1038/d41586-019-00857-9
- Amrhein, V., Korner-Nievergelt, F., & Roth, T. (2017). The earth is flat (p > 0:05): Significance thresholds and the crisis of unreplicable research. *PeerJ*, 7, 1–40. https://doi.org/10.7717/peerj.3544
- Arroyo-Solís, A., Castillo, J. M., Figueroa, E., López-Sánchez, J. L., & Slabbekoorn, H. (2013). Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. *Journal of Avian Biology*, 44, 288–296. https://doi.org/10.1111/j.1600-048X.2012.05796.x
- Avery, M. I., & Krebs, J. R. (1984). Temperature and foraging success of Great Tits *Parus major* hunting for spiders. *Ibis*, 126, 33–38. https://doi.org/10.1111/j.1474-919X.1984.tb03661.x
- Bayne, E. M., Habib, L., & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energysector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, 22, 1186– 1193. https://doi.org/10.1111/j.1523-1739.2008.00973.x
- Benfield, J. A., Rainbolt, G. A. N., Troup, L. J., & Bell, P. A. (2020). Anthropogenic noise source and intensity effects on mood and relaxation in simulated Park environments. *Frontiers in Psychology*, 11, 1–8. https://doi.org/10.3389/fpsyg.2020.570694
- Bergen, F., & Abs, M. (1997). Etho-ecological study of the singing activity of the Blue Tit (*Parus caeruleus*), Great Tit (*Parus major*) and Chaffinch (*Fringilla coelebs*). Journal für Ornithologie, 138, 451–467. https://doi.org/10.1007/bf01651380
- Bermúdez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D., & Garcia, C. M. (2011). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, 7, 36–38. https://doi.org/10.1098/rsbl.2010.0437
- Brown, R. G. B. (1963). The behaviour of the Willow warbler *Phylloscopus trochilus* in continuous daylight. *Ibis*, 105, 63–75. https://doi.org/10.1111/j.1474-919X.1963.tb02475.x
- Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, 73, 434–440. https://doi.org/10.1111/j.0021-8790.2004.00814.x
- Bruni, A., & Foote, J. R. (2014). Dawn singing of Eastern phoebes varies with breeding stage and brood number. *Wilson Journal of Ornithology*, 126, 500–507. https://doi.org/10.1676/13-175.1
- Bruni, A., Mennill, D. J., & Foote, J. R. (2014). Dawn chorus start time variation in a temperate bird community: Relationships with seasonality, weather, and ambient light. *Journal of Ornithology*, 155, 877–890. https://doi.org/10.1007/s10336-014-1071-7
- Clark, W. D., & Karr, J. R. (1979). Effects of highways on Red-winged blackbird and Horned lark populations. *The Wilson Bulletin*, 91, 143–145. http://www.jstor.org/stable/4161183
- Da Silva, A., Samplonius, J. M., Schlicht, E., Valcu, M., & Kempenaers, B. (2014). Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. *Behavioral Ecology*, 25, 1037–1047. https://doi.org/10.1093/beheco/aru103
- Davies, C. J., & Cooke, F. (1983). Annual nesting productivity in Snow geese: Prairie droughts and Arctic springs. *Journal of Wildlife Management*, 47, 291–296.

- Dominoni, D. M., Greif, S., Nemeth, E., & Brumm, H. (2016). Airport noise predicts song timing of European birds. *Ecology and Evolution*, 6, 6151–6159. https://doi.org/10.1002/ece3.2357
- Erne, N. & Amrhein, V. (2008). Long-term influence of simulated territorial intrusions on dawn and dusk singing in the Winter Wren: Spring versus autumn. Journal of Ornithology, 149, 479–486. https://doi.org/10.1007/s10336-008-0288-8
- European Environmental Agency. (2020). Environmental noise in Europe 2020. *Publications Office*. https://data.europa.eu/doi/10.2800/686249
- Ferris, C. R. (1979). Effects of Interstate 95 on breeding birds in northern Maine. Journal of Wildlife Management, 43, 421–427.
- Francis, C. D., Ortega, C. P., & Cruz, A. (2011). Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2025–2031. https://doi.org/10.1098/rspb.2010.1847
- Francis, C. D., Ortega, C. P., & Cruz, A. (2011a). Different behavioural responses to anthropogenic noise by two closely related passerine birds. *Biology Letters*, 7, 850–852. https://doi.org/10.1098/rsb1.2011.0359
- Gabry, J. (2018). shinystan: Interactive visual and numerical diagnostics and posterior analysis for Bayesian models. *R Package Version 2.5.0*. https://cran.r-project.org/package=shinystan
- Gil, D., & Llusia, D. (2020). The bird dawn chorus revisited. In: Aubin T, Mathevon N (eds) Coding strategies in vertebrate acoustic communication. Animal signals and communication, Vol 7. Springer, Cham. https://doi.org/10.1007/978-3-030-39200-0\_3
- Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E., & Macías Garcia, C. (2015). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behavioral Ecology*, 26, 435–443. https://doi.org/10.1093/beheco/aru207
- Glutz von Blotzheim, U. (1988). I Passeriformes (2. Teil) Turdidae (Vol 11). Akademische Verlagsgesellschaft.
- Glutz von Blotzheim, U. (1997). II: Passeriformes (5.Teil) Fringillidae (Vol 14). Akademische Verlagsgesellschaft.
- Glutz von Blotzheim, U., & Bauer, K. M. (1993). I: Passeriformes (4. Teil) Muscicapidae Paridae. In Handbuch der Vögel Mitteleuropas (Vol 13). Akademische Verlagsgesellschaft.
- Goodrich, B., Gabry, J., I, A., & S, B. (2020). rstanarm: Bayesian applied regression modeling via Stan. *R Package Version 2.21.1*. https://mc-stan.org/rstanarm
- Goodwin, S. E., & Podos, J. (2013). Shift of song frequencies in response to masking tones. Animal Behaviour, 85, 435–440. https://doi.org/10.1016/j.anbehav.2012.12.003
- Gross, K., Pasinelli, G., & Kunc, H. P. (2010). Behavioral plasticity allows short-term adjustment to a novel environment. *American Naturalist*, 176, 456–464. https://doi.org/10.1086/655428
- Habib, L., Bayne, E. M., & Boutin, S. (2007). Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *Journal of Applied Ecology*, 44, 176–184. https://doi.org/10.1111/j.1365-2664.2006.01234.x
- Halfwerk, W., Holleman, L. J. M., Lessells, C. M., & Slabbekoorn, H. (2011). Negative impact of traffic noise on avian reproductive success. *Journal of Applied Ecology*, 48, 210–219. https://doi.org/10.1111/j.1365-2664.2010.01914.x
- Haller, H., Eisenhut, A., & Haller, R. (2013). Atlas des Schweizerischen Nationalparks. Die ersten 100 Jahre. Nationalpark Forschung Schweiz 99/1, Haupt Verlag Bern.
- Hanna, D., Blouin-Demers, G., Wilson, D. R., & Mennill, D. J. (2011). Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). *Journal of Experimental Biology*, 214, 3549–3556. https://doi.org/10.1242/jeb.060194
- Holm, T. E., & Laursen, K. (2011). Car traffic along hedgerows affects breeding success of Great tits Parus major. Bird Study, 58, 512–515. https://doi.org/10.1080/00063657.2011.596186
- Holmes, W. G., & Dirks, S. J. (1978). Daily song patterns in Golden-crowned sparrows at 62°N latitude. *The Condor*, 80, 92–94.

- Hostetler, M., Duncan, S., & Paul, J. (2005). Post-construction effects of an urban development on migrating, resident, and wintering birds. *Southeastern Naturalist*, 4, 421–434. https://doi.org/10.1656/1528-7092(2005)004[0421:PEOAUD]2.0.CO;2
- Houston, A. I., & McNamara, J. M. (1987). Singing to attract a mate: a stochastic dynamic game. Journal of Theoretical Biology, 129, 57–68. https://doi.org/10.1016/S0022-5193(87)80203-5
- Hu, Y., & Cardoso, G. C. (2010). Which birds adjust the frequency of vocalizations in urban noise? Animal Behaviour, 79, 863–867. https://doi.org/10.1016/j.anbehav.2009.12.036
- Hutchinson, J. M. C. (2002). Two explanations of the dawn chorus compared: How monotonically changing light levels favour a short break from singing. *Animal Behaviour*, 64, 527–539. https://doi.org/10.1006/anbe.2002.3091
- Hutchinson, J. M. C., & McNamara, J. M. (2000). Ways to test stochastic dynamic programming models empirically. *Animal Behaviour*, 59, 665–676. https://doi.org/10.1006/anbe.1999.1362
- Hutchinson, J. M. C., McNamara, J. M., & Cuthill, I. C. (1993). Song, sexual selection, starvation and strategic handicaps. *Animal Behaviour*, 45, 1153–1177.
- Jin, T., Kosheleva, A., Castro, E., Qiu, X., James, P., & Schwartz, J. (2024). Long-term noise exposures and cardiovascular diseases mortality: A study in 5 U.S. states. *Environmental Research*, 245, 118092. https://doi.org/10.1016/j.envres.2023.118092
- Kunc, H. P., & Schmidt, R. (2019). The effects of anthropogenic noise on animals: A meta-analysis. *Biology Letters*, 15, 20190649. https://doi.org/10.1098/rsbl.2019.0649
- Kunc, H. P., & Schmidt, R. (2020). Species sensitivities to a global pollutant: A meta-analysis on acoustic signals in response to anthropogenic noise. *Global Change Biology*, 27, 675–688.
- Lackey, M. A. (2010). Avian response to road construction noise with emphasis on the endagered Golden-cheeked warbler. PhD Thesis, Texas A&M University, College Station, Texas, USA.
- Lackey, M. A., Morrison, M. L., Loman, Z. G., Collier, B. A., Wilkins, R. N., Lackey, M. A., Morrison, M. L., Loman, Z. G., Collier, B. A., & Wilkins, R. N. (2012). Chapter 8: Experimental determination of the response of Golden-cheeked warblers (*Setophaga chrysoparia*) to road construction noise - Determinación Experimental de la Respuesta de Setophaga chrysoparia al Ruido de la Construcción de Carreteras Publishe. *Ornithological Monographs*, 74, 91–100. https://doi.org/10.1525/om.2012.74.1.91
- Lackey, M. A., Morrison, M. L., Loman, Z. G., Fisher, N., Farrell, S. L., Collier, B. A., & Wilkins, R. N. (2011). Effects of road construction noise on the endangered golden-cheeked warbler. *Wildlife Society Bulletin*, 35, 15–19. https://doi.org/10.1002/wsb.6
- Lee, S. C., Hong, J. Y., & Jeon, J. Y. (2015). Effects of acoustic characteristics of combined construction noise on annoyance. *Building and Environment*, 92, 657–667. https://doi.org/10.1016/j.buildenv.2015.05.037
- Long, A. M., Colón, M. R., Bosman, J. L., Mcfarland, T. M., Locatelli, A. J., Stewart, L. R., Mathewson, H. A., Newnam, J. C., & Morrison, M. L. (2017). Effects of road construction noise on goldencheeked warblers: An update. *Wildlife Society Bulletin*, 41, 240–248. https://doi.org/10.1002/wsb.777
- Long, A. M., Colón, M. R., Bosman, J. L., Robinson, D. H., Pruett, H. L., McFarland, T. M., Mathewson, H. A., Szewczak, J. M., Newnam, J. C., & Morrison, M. L. (2016). A before–after control–impact assessment to understand the potential impacts of highway construction noise and activity on an endangered songbird. *Ecology and Evolution*, 7, 379–389. https://doi.org/10.1002/ece3.2608
- Marciniak, B., Nadolski, J., Nowakowska, M., Loga, B., & Bańbura, J. (2007). Habitat and annual variation in arthropod abundance affects Blue tit *Cyanistes caeruleus* reproduction. *Acta Ornithologica*, 42, 53–62. https://doi.org/10.3161/068.042.0113
- McClure, C. J. W., Ware, H. E., Carlisle, J., Kaltenecker, G., & Barber, J. R. (2013). An experimental investigation into the effects of traffic noise on distributions of birds: Avoiding the phantom road. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20132290.

https://doi.org/10.1098/rspb.2013.2290

- McIntyre, E., Leonard, M. L., & Horn, A. G. (2014). Ambient noise and parental communication of predation risk in tree swallows, *Tachycineta bicolor. Animal Behaviour*, 87, 85–89. https://doi.org/10.1016/j.anbehav.2013.10.013
- Mendes, S., Colino-Rabanal, V. J., & Peris, S. J. (2011). Bird song variations along an urban gradient: The case of the European blackbird (*Turdus merula*). *Landscape and Urban Planning*, 99, 51– 57. https://doi.org/10.1016/j.landurbplan.2010.08.013
- Mikula, P., Valcu M., Brumm H., Bulla M., Forstmeier W., Petruskova T., Kempenaers B., Albrech T. (2021). A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. *Ecology Letters* 24, 477–486. https://doi.org/10.1111/ele.13662
- Morrison, M. L., Block, W. M., Strickland, M. D., Collier, B. A., & Peterson, M. J. (2008). Wildlife Study Design (2nd ed.). Springer.
- Naguib, M., Diehl, J., Van Oers, K., & Snijders, L. (2019). Repeatability of signalling traits in the avian dawn chorus. *Frontiers in Zoology*, 16, 1–12. https://doi.org/10.1186/s12983-019-0328-7
- Nemeth, E., & Brumm, H. (2010). Birds and anthropogenic noise: Are urban songs adaptive? American Naturalist, 176, 465–475. https://doi.org/10.1086/656275
- Nordt, A., & Klenke, R. (2013). Sleepless in town Drivers of the temporal shift in dawn song in urban European blackbirds. *PLoS ONE*, 8, 1–10. https://doi.org/10.1371/journal.pone.0071476
- Paterno, J., Korner-Nievergelt, F., Anderwald, P., & Amrhein, V. (2024). Start of dawn singing as related to physical environmental variables in an alpine environment. *Journal of Ornithology*, 165, 533–544. https://doi.org/10.1007/s10336-023-02134-z
- Pearce-Higgins, J. W., Stephen, L., Douse, A., & Langston, R. H. W. (2012). Greater impacts of wind farms on bird populations during construction than subsequent operation: results of a multi-site and multi-species analysis. *Journal of Applied Ecology*, 49, 386–394. https://doi.org/doi: 10.1111/j.1365-2664.2012.02110.x
- Pérez-Granados, C., Osiejuk, T. S., & López-Iborra, G. M. (2018). Dawn chorus interpretation differs when using songs or calls: The Dupont's lark *Chersophilus duponti* case. *PeerJ*, 6, 1–17. https://doi.org/10.7717/peerj.5241
- Polak, M., Wiącek, J., Kucharczyk, M., & Orzechowski, R. (2013). The effect of road traffic on a breeding community of woodland birds. *European Journal of Forest Research*, 132, 931–941. https://doi.org/10.1007/s10342-013-0732-z
- Puorger B. (1955). Ofenpass (Pass dal Fuorn). Generaldirektion der Post-, Telegraphen- und Telephonverwaltung (ed.)
- Puswal, S. M., Jinjun, M., & Liu, F. (2020). Effects of temperature and season on birds' dawn singing behavior in a forest of eastern China. *Journal of Ornithology*, 162, 447–459. https://doi.org/10.1007/s10336-020-01848-8
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.
- Reijnen, R., & Foppen, R. (2006). Impact of road traffic on breeding bird populations. In J. Davenport,
  & J. L. Davenport (Eds.), The ecology of transportation: managing mobility for the environment (pp. 255-274). (Environmental Pollution; No. 10). Springer.
- Rheindt, F. E. (2003). The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? *Journal für Ornithologie*, 144, 295–306. https://doi.org/10.1046/j.1439-0361.2003.03004.x
- Slabbekoorn, H., & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature*, 424, 267. https://doi.org/10.1038/424267a
- Staicer, C. A., Spector, D. A., & Horn, A. G. (1996). 24. The dawn chorus and other diel patterns in acoustic signaling. In D. E. Kroodsma & E. H. Miller (Eds.), Ecology and Evolution of Acoustic Communication in Birds (pp. 426–453). Cornell University Press.

https://doi.org/https://doi.org/10.7591/9781501736957-033

- Stewart-Oaten, A. (1986). The before–after/control-impact-pairs design-for environmental impact. Prepared for Marine Review Committee, Inc., Encinitas, CA.
- Strain J.G., Mumme R.L. (1988). Effects of food supplementation, song playback, and temperature on vocal territorial behavior of Carolina Wrens. *Auk* 105,11–16. https://doi.org/10.1093/auk/105.1.11
- Thomas, R. J., & Cuthill, I. C. (2002). Body mass regulation and the daily singing routines of European robins. *Animal Behaviour*, 63, 285–295. https://doi.org/10.1006/anbe.2001.1926
- Tiefbauamt Graubünden (2024) Verkehsfrequenzen. https://www.gr.ch/DE/institutionen/verwaltung/diem/tba/Strassennetz/Seiten/Verkehrsfrequenze n.aspx Accessed 26 Feb 2024
- Villain, A. S., Fernandez, M. S. A., Bouchut, C., Soula, H. A., & Vignal, C. (2016). Songbird mates change their call structure and intrapair communication at the nest in response to environmental noise. *Animal Behaviour*, 116, 113–129. https://doi.org/10.1016/j.anbehav.2016.03.009
- Visual Crossing Corporation (2024). Visual Crossing Weather (2021). [data service]. Retrieved from https://www.visualcrossing.com/
- Ward S., Slater P.J.B. (2005). Raised thermoregulatory costs at exposed song posts increase the energetic cost of singing for Willow Warblers *Phylloscopus trochilus*. *Journal of Avian Biology* 36, 280–286. https://doi.org/10.1111/j.0908-8857.2005.03379.x
- Welling, P., Koivula, K., & Lahti, K. (1995). The dawn chorus is linked with female fertility in the Willow tit *Parus montanus*. *Journal of Avian Biology*, 26, 241. https://doi.org/10.2307/3677325
- Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org
- Wickham, H., François, R., Henry, L., & Müller, K. (2021). dplyr: A Grammar of Data Manipulation. *R Package Version 1.0.3*. https://cran.r-project.org/package=dplyr
- Yang, W., Cai, M., & Luo, P. (2020). The calculation of road traffic noise spectrum based on the noise spectral characteristics of single vehicles. *Applied Acoustics*, 160, 107128. https://doi.org/10.1016/j.apacoust.2019.107128
- Yrjölä, R. A., Tanskanen, A., Sarvanne, H., Vickholm, J., & Lehikoinen, A. (2018). Can common forest bird species tolerate disturbances in neighbouring areas? A case study of the Vuosaari Harbour construction in southern Finland. *Ornis Fennica*, 95, 49–60. https://doi.org/10.51812/of.133929
- Zhao, T., Lin, J., Zhang, X., Wan, D., & Yin, J. (2016). The primary study of the relationship between environmental factors and dawn song in varied tits. In *Proceedings of the 3<sup>rd</sup> International Conference on Biomedical and Bioinformatics Engineering (ICBBE '16)*. Association for Computing Machinery, New York, NY, USA, 75–80. https://doi.org/10.1145/3022702.3022721



Figure A1 Comparison of manually collected temperature data and temperature data from a nearby weather station (Buffalora; source MeteoSwiss).


Figure S2 Distributions of test statistics of analysis I (manually collected temperature data). The observed data are indicated by the dark blue line and the observed data by the light blue area. A: mean, B: sd, C: min, D: max.



**Supplementary Material** 

Figure S3 Distribution of observed data (dark blue line) vs. replication (light blue lines) based on the model in analysis II (temperature data from a weather station in 4 km distance).



Figure S4 Distributions of test statistics of analysis II (temperature data from a weather station in 4 km distance). The observed data are indicated by the dark blue line and the observed data by the light blue area. A: mean, B: sd, C: min, D: max.

73

# CHAPTER 3

This chapter is submitted as

Paterno J, Korner-Nievergelt F, Anderwald P, Amrhein V (2024). Effects of habitat and road noise on singing activity of coal tits in subalpine woodland. *In submission: Animal Behaviour* 

Coal tit, SNP / Fadri Wehrli

#### Effects of habitat and road noise on singing activity of coal tits in subalpine woodland

Julia Paterno<sup>1,2</sup>, Fränzi Korner-Nievergelt<sup>1,3</sup>, Valentin Amrhein<sup>1, 3</sup> and Pia Anderwald<sup>2</sup>

#### Abstract

Road noise can negatively affect the communication of birds, which in response may apply strategies to mitigate increased levels of road noise, for example by singing louder, changing song frequencies, or adjusting the timing or amount of singing. We investigated the effects of road noise on singing activity of coal tits (Periparus ater) breeding in the woodlands of the Swiss National Park. To this end, we recorded singing activity at 12 site in varying distances to the road over four years. Because other environmental variables may also affect singing activity, we accounted for forest type, time of day, date, and temperature in the analyses of song activity. We observed the strongest effects due to road noise and habitat: During the day, coal tits produced up to 18% more song phrases near the road compared to further away from the road, and up to 17% more song phrases at sites in mountain pine forests compared to sites in mixed forests. Interestingly, in the morning and evening, when there was much less road noise, coal tits produced up to 8% more (morning) and 20% less (evening) song phrases near the road compared to further away. The effects of date and temperature were smaller: Coal tits produced 4% more song phrases at the beginning of May compared to the beginning of June, and 8 - 10% more song phrases during times with moderate temperatures (+3.0 °C to +12.0 °C) compared to colder (-5.5 to +3.0 °C) or warmer temperatures (+12.0 to +34.0 °C). Our findings are in line with previous results on the effects of forest type, date, temperature, time of day, and road noise. Our study shows that road noise may affect the singing behaviour of coal tits even in a highly protected area.

**Keywords:** acoustic recording, anthropogenic noise, habitat, sound logger, songbirds, singing intensity, weather, season

Julia Paterno julia.paterno(at)nationalpark.ch

<sup>1</sup> Department of Environmental Sciences, University of Basel, 4051 Basel, Switzerland

<sup>2</sup> Department of Research and Monitoring, Swiss National Park, 7530 Zernez, Switzerland

<sup>3</sup> Swiss Ornithological Institute, 6204 Sempach, Switzerland

#### Introduction

Road noise is one of the most dominant sources of anthropogenic noise (European Environmental Agency, 2020) and previous studies found negative effects on humans and animals (i.e., Benfield et al., 2020; Jin et al., 2024; Kunc & Schmidt, 2019). Especially communication of birds may be affected by anthropogenic noise (e.g., Rheindt, 2003; Slabbekoorn & Peet, 2003), since mating and warning calls can be masked (Francis et al., 2011b; McIntyre et al., 2014; Rheindt, 2003; Slabbekoorn & Peet, 2003). Previous studies found reduced anti-predator behaviour of birds when exposed to alarm calls in a noisy environment (Damsky & Gall, 2016; Grade & Sieving, 2016; McIntyre et al., 2014; Templeton et al., 2016). For example, McIntyre et al. (2014) found that tree swallow nestlings (Tachycineta bicolor) failed to crouch in the nest and continued begging when exposed to parental alarm calls and white noise at the same time; the authors concluded that increased noise levels may lead to increased predation risk in tree swallows.

However, birds may use strategies to cope with increased noise levels: For example, several bird species were found to increase the minimum frequency of their songs (i.e., Bermúdez-Cuamatzin et al., 2011; Francis et al., 2011b; Goodwin & Podos, 2013; Hanna et al., 2011; Hu & Cardoso, 2010; LaZerte et al., 2017; Parris & Schneider, 2009); low frequency songs and calls seem to be particularly strongly affected by anthropogenic noise (Hu & Cardoso, 2010; Parris & Schneider, 2009; Warrington et al., 2018). Hu & Cardoso (2010) found an increased average minimum frequency of songs or calls in urban birds compared to that of nonurban conspecifics. They also observed a stronger increase of minimum frequency due to anthropogenic noise for species with intermediate minimum frequencies (1 – 1.5 kHz) compared to species with higher or lower minimum frequencies. Hu & Cardoso (2010) then assumed that species with high-frequency songs may be less affected by urban noise and therefore may not need to adjust their minimum frequency of vocalisations. Species with low frequency songs or calls, in contrast, may not be able to overcome masking noise even at an increased minimum frequency, and thus Hu & Cardoso (2010) assumed that low-frequency species may use other adaptations to cope with increased levels of urban noise.

Nemeth & Brumm (2010) investigated whether an increase in minimum frequency led to better communication in great tits (Parus major; i.e., increased communication distance), but observed only marginal improvement. They further observed much larger effects of increased vocal amplitude adjustments. Thus, with increased song amplitude, the communication distance in great tits increased strongly (Nemeth & Brumm, 2010). Brumm (2004) found a similar effect in Berlin, where he observed that nightingales (Luscinia megarhynchos) sang about 14 dB louder in the noisiest territory compared to the most silent territory. An increase in song duration may also be an adaptation of birds to increased noise levels. For example, Francis et al. (2011a) found a change in frequency and duration of songs of plumbeous vireos (Vireo plumbeus) and grey vireos (Vireo vicinior) with increasing noise levels. The two closely related bird species reacted in different ways: the plumbeous vireo produced shorter songs with higher minimum frequencies and the grey vireo produced longer songs with higher maximum frequencies. Francis et al. (2011a) thus assumed that the two bird species might use different strategies to cope with increased noise levels. Some species may use a combination of different strategies as reaction to increased levels of noise: For example, Hamao et al. (2011) investigated differences in singing behaviour of great tits occupying parks with varying noise levels in Tokyo (18.8 dB difference between loudest and most silent park). They observed that great tits produced longer songs with higher minimum frequencies and a larger number of song phrases in noisier parks (Hamao et al., 2011).

In reaction to increased noise levels, birds may as well change their singing activity at certain times of the day; for example, Bermúdez-Cuamatzin et al. (2020) observed generally lower singing activity for urban great tits compared to rural great tits but an earlier start of singing at dawn. Thus, urban great tits produced more songs during more silent periods of the day compared to rural great tits (Bermúdez-Cuamatzin et al., 2020). Other studies also observed a shift in the timing of dawn singing due to anthropogenic noise (Dominoni et al., 2016; Paterno et al., 2024). For example, in our previous study (Paterno et al., 2024) conducted in the Swiss National Park, all six investigated song bird species started

dawn singing earlier in noisier compared to more silent areas. We observed the largest shifts in Eurasian chaffinches (Fringilla coelebs, -4.8 min) and coal tits (Periparus ater, -3.6 min), two relatively late-rising species (Paterno et al., 2024).

In the present study, we focused on singing activity in the coal tit, the most common songbird species in mountain and subalpine coniferous forests in Switzerland (Mattes et al., 2005). Male coal tits use about six different song types (Bauer et al., 2012) with 2-5 elements of different frequencies per phrase (Glutz von Blotzheim & Bauer, 1993). We counted the number of phrases per minute and used that measurement as singing activity. The single phrases (Figure 1) are easy to distinguish and well audible in the sound files.

We investigated the singing activity of coal tits in the mountainous woodlands of the Swiss National Park and accounted for five environmental factors that may influence singing activity, such as time of day (see Gil & Llusia, 2020), time of year (Bruni et al., 2014; Erne & Amrhein, 2008; Paterno et al., 2024) and temperature (Naguib et al., 2019; Paterno et al., 2024; Puswal et al., 2020). Because habitat type can also affect singing behaviour of birds (Lindenmayer et al., 2004), we further compared plots that differed in tree species composition. Since several previous studies found that songs and calls of birds can be masked by anthropogenic noise (i.e., Francis et al., 2011b; Rheindt, 2003; Slabbekoorn & Peet, 2003), we expected coal tits to increase their singing activity near the road during the day in order to compensate for reduced communication during this noisy time.



Figure 1 Spectrogram of coal tit song. The red cube shows a single phrase of the song.

#### Methods

#### Study area

The study was conducted in the woodlands of the Swiss National Park (SNP), in the eastern part of Switzerland (Figure 2), between mid-May and mid-June over a period of four years (2017 – 2020). The SNP is a strictly protected IUCN 1a area (, i.e. wilderness) encompassing 170 km2, with 28% of its area covered by woodland. The main tree species are two subspecies of the mountain pine (Pinus mugo / Pinus mugo spp. uncinata), cembra pine (Pinus cembra), and European larch (Larix decidua); there are also some Scots pine (Pinus sylvestris) and Norway spruce (Picea abies; Haller et al., 2013).

Since there are no management measures like clearance or hunting in the SNP, the area is highly undisturbed without human interference apart from 100 km of hiking trails. Nevertheless, a cantonal road runs through the SNP, with a mean daily traffic volume of 1561 cars per day (mean of average daily traffic between 2012 – 2022, Tiefbauamt Graubünden, 2024), representing an important transit route between the Engadin and South Tyrol.

The area is characterised by an alpine climate with marked temperature differences between summer and winter. Annual precipitation is about 800 mm (Haller et al., 2013), whereas the sum of precipitation during analysis days was between 0.0 mm and 10.1 mm (Table 1) and temperatures reached from -6.3  $^{\circ}$ C to +21.5  $^{\circ}$ C (Table 1).

Year	Earliest / latest deployment	Earliest / latest removal	Analysis days	Minimum temperature during analysis period [°C]	Maximum temperature during analysis period [°C]	Precipitation sum during analysis period [mm]	Study sites (see Figure 2)
2017	24 May / 24 May	28 June / 28 June	25 May 28 May 02 June	+0.2	+21.5	0.6	S3
2018	19 April / 08 May	04 July / 17 July	09 May 22 May 26 May 05 June	-1.5	+18.8	6.7	S1 / S2 / S4 / S5 / S6 / S7 / S8 / S9 / S10 / S12
2019	24 April / 02 May	19 July / 26 July	10 May 22 May 27 May 05 June	-1.1	+19.4	10.1	S1 / S2 / S4 / S5 / S6 / S7 / S8 / S9 / S10 / S12
2020	24 April / 19 May	13 July / 22 July	07 May 22 May 27 May 03 June	-6.3	+16.9	0.0	S1 / S2 / S4 / S5 / S6 / S7 / S8 / S9 / S10 / S11 / S12

Table 1 Mounting dates of data loggers, recording days selected for data analysis, and weather during analysed days (data from nearby weather station Buffalora; MeteoSwiss, 2021).

#### Ethical note

To investigate the singing activity of wild coal tits, we used acoustic recording devices (sound loggers) at twelve study sites. This allowed us to study the singing behaviour of coal tits in the wild with minimal human disturbance. Battery change of the data loggers was required after about six weeks, and at the end of the study period we removed the sound loggers from the area, thus human disturbance was reduced to a minimum. We obtained approval to conduct the study in the highly protected area by the Research Commission of the Swiss National Park (approval number: CH-7228).

#### Study sites and acoustic recordings

We used sound loggers (Wildlife Acoustics SM4 Song Meters) to record the soundscapes at 12 sites in the SNP (Table 2, Figure 2). In the four years of the study (2017 - 2020), we installed the sound loggers from mid-April / beginning of May until mid-July, depending on accessibility of the sites (Table 1, Figure 2). Locations were selected to avoid noise from rivers or from too much wind, and sites near the road were selected at such a distance that birds could be affected by road noise but analysis of audio files was still possible without too much background noise from the road. The two study sites nearest to the road (S1, S2) were at a distance of 170 m to it; woodland started about 10 m from the road. At one of the selected sites (S3), data collection started in 2017, whereas at the other sites, data collection started in 2018 (S1, S2, S4, S5, S6, S7, S8, S9, S10, S12) and 2020 (S11), respectively (Table 2).

The sound loggers recorded for 10 minutes every 30 minutes, thus we obtained 20 minutes of recordings per hour. In total, the loggers recorded for 12 296 hours (= 1537 days). All recordings were in stereo, with a sampling rate of 24 kHz and a gain of 16 dB. Preamp was set to 26 dB and the filter was disabled. We used a strap to mount the sound loggers on a tree about 2 m above the ground. We noted the coordinates, the orientation of the sound logger, and the deployment height. We equipped each sound logger site with a USB-502 PLUS or an EL-USB-2 temperature and humidity logger (temperature logger) and set the temperature loggers to record every 30 minutes, with an accuracy of 0.5°C for temperature, 2% for relative humidity, and 1.1°C for the dew point. We placed the temperature logger in a post 1 m above ground beneath the sound logger.

Data extraction from the recordings was done manually, and we therefore analysed only a subset of the data. We selected 3 - 4 days per site and year that had no wind or rain during the morning (Table 1); since there is always some wind or rain in the afternoon in this area, we were not able to select days that were completely without wind or rain.

In 2018, there was no data collection at site S9 between 23 and 30 May due to battery failure, and in 2020, the SD-card of the logger at site S10 broke and we were not able to recover its data for this year.



Figure 2 Locations of the sound logger sites (singing activity: white cubes; road noise: green dots) in the Swiss National Park (SNP). The grey lined area is within the SNP, and woodlands are shown in dark grey. For a description of the sites, see Table 2. The location of the study area within Switzerland is shown in the lower left corner, with the SNP shown in grey (map:  $\mathbb{C}$  swisstopo, SNP).

Table 2 Description of the 12 logger sites in the Swiss National Park; for the locations of the sites, see Figure 2. The column "Tree species composition" shows the proportion of the different tree species per site.

	Linear distance to	Elevation	Exposition	Slope	Tree cover	_	Tree species	Year of data
Site	road [m]	[m a.s.l.]	[°]	[°]	[%]	Forest type	composition	collection
<b>S</b> 1	169	1986	186	15	60 - 90	mountain pine		2018 / 2019 / 2020
S2	170	1920	194	4	60 - 90	mountain pine		2018 / 2019 / 2020
S3	229	1911	195	6	60 - 90	mountain pine		2017
S4	243	1864	189	15	40 - 60	mixed forest		2018 / 2019 / 2020
S5	354	1939	194	12	40 - 60	mixed forest		2018 / 2019 / 2020
S6	555	1827	192	3	10 - 40	mixed forest		2018 / 2019 / 2020
S7	726	1760	192	9	60 - 90	mixed forest		2018 / 2019 / 2020
S8	1050	2034	180	22	40 - 60	mountain pine		2018 / 2019 / 2020
S9	1079	2118	194	9	10 - 40	mixed forest		2018 / 2019 / 2020
S10	1247	2123	196	9	60 - 90	mountain pine		2018 / 2019 / 2020
S11	2790	1939	203	24	90 - 100	mixed forest		2020
S12	6128	2114	191	13	60 - 90	mixed forest		2018 / 2019 / 2020
							mountain	

Colour code:	mountain Pine <i>Pinus mugo</i> spp. uncinata	European larch <i>Larix</i> decidua				mountain pine Pinus mugo spp. mugo	other deciduous tree species
-----------------	---	---	--	--	--	---	------------------------------------

#### Data extraction and analysis

To investigate singing activity of coal tits, we analysed a total of 4480 sound files using the program Raven (Center for Conservation Bioacoustics, 2019). A trained person (JP) analysed the first minute of each 10-minute recording between 5.00 am to 10.00 pm local summertime (UTC + 2.00) and counted the number of coal tit song phrases.

Since from the recordings it was not possible to distinguish between the song of a focal male coal tit and songs of distant neighbours, we counted all occurring coal tit song phrases. In the following, we thus compare the total amount of singing at different sites rather than the amount of singing of single males. From personal observations in the field (unpublished data) we know that there are usually 1 - 3 individuals that can be heard singing at the same time from one particular location in the study area.

For further analysis, we excluded evening recordings made after 8.30 pm because there were hardly any coal tits singing (two observations of a singing coal tit at 8.30 pm in the whole dataset, and no observations between 9.00 and 10.00 pm).

We used a 4 x 4 m digital elevation model (swissALTI3D) in ArcGIS Version 10.7.1 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, US) to extract elevation and aspect, and we calculated the nearest distance to roads. Further, we extracted the tree species composition and tree cover from the dataset "HABITALP" (Lotz, 2006) in ArcGIS. To investigate effects of temperature, we used the data from the temperature loggers.

#### Road noise

In 2023, we deployed nine AudioMoths (Open Acoustic Devices, 2024) sound loggers along the Ofenpass road to record road noise (Figure 2). We attached AudioMoths to tree trunks at a height of about 2 m and at a maximum distance of 14 m from the road, depending on the availability of trees. We selected suitable sites in the field based on accessibility (Figure 2). AudioMoths collected data at 48 kHz and medium gain from mid-May until the end of September 2023 and recorded for 1 minute every 15 minutes (96 recordings per day). In total, we obtained 2889 hours of recordings (=173 307 recordings) from AudioMoth sound loggers between April and September.

To extract the noise level, we calculated root mean square sound pressure level (RMS SPL; Henn et al., 2005) in dBFS with the command line utility "SoX" (SOX, 2024) using the packages dplyr (Wickham et al., 2021) and tidyverse (Wickham et al., 2019) in R (R Core Team, 2020). RMS SPL is a measure of noise level and is calculated from the frequency-weighted microphone signal (Henn et al., 2008). Previous studies used RMS SPL values to measure the amplitude of bird vocalizations (i.e, Grabarczyk & Gill, 2020; Mizuguchi et al., 2024) or anthropogenic noise (i.e., Higgs & Humphrey, 2020; Leone & Warren, 2024). We summarized (i.e., averaged) the noise level over all sites per 30 min. Thus, we obtained two RMS SPL values per hour and were able to correlate the mean calculated noise level (RMS SPL) with the singing activity of coal tits (Figure 4). The noise level recorded in 2023 was similar (pers. obs.) as during data collection (2017 - 2020); in 2020 there was the COVID-19 lockdown (Hornberg et al., 2021), but our data collection only started after the lockdown.

#### Model fitting

We used R (R Core Team, 2020) for data preparation (package dplyr; Wickham et al., 2021), statistical analysis (package brms; Bürkner, 2017) and visualization (package ggplot2; Wickham, 2016). We used a Bayesian zero-inflated negative binomial model to analyse the number of coal tit song phrases per minute. As explanatory variables, we used six environmental variables (for the correlation matrix, see Table S1): elevation, distance to the nearest road, date, and a smooth function of temperature. All numeric variables were z-transformed (mean = 0, SD = 1) prior to model fitting, whereas time (i.e., the hour) and forest type were included as categorical variables, and logger site and year as random factors. Further, we included an interaction of distance to the nearest road and time of day, thus assuming that road noise affected singing activity at different times of the day differently near the road than further

away. We also considered to include aspect into the model, but since there was only low variation in the exposition of the sites (mostly plain terrain), we did not include aspect in the model.

To assess convergence of Markov chains, we inspected Rhat values and history plots visually, and we checked the number of effective sample size that were above 5000 for all parameters. We assessed model fit using standard residual plots and posterior predictive model checking. For posterior predictive model checking, we inspected histograms and overlaid densities visually and compared the mean, standard deviation, minimum and maximum between raw data and replicated data from the model (Gabry, 2018). Furthermore, we displayed the residuals on a map to check whether using locations of loggers as random effect accounted adequately for spatial autocorrelation, and we found no conspicuous spatial patterns.

#### Results

Over all sites, dates and times, we found the highest singing activity at dawn: Between 5.00 and 5.30 am coal tits produced on average 5.8 [95% CI: 5.1; 6.5] song phrases per minute (Figure 3, Table 3). A second, albeit smaller peak of singing activity occurred at dusk (5.30 pm to 6.00 pm), when coal tits produced on average 4.7 [4.4; 5.0] song phrases per minute (Figure 3, Table 3). During the day (6.00 am to 5.30 pm), coal tits produced on average 3.9 [3.2; 4.5] song phrases per minute and thus showed a decreased singing activity (Figure 3, Table 3).

Among the investigated variables (Table 3) and accounting for all other parameters, distance to road in combination with time of day had the strongest apparent effect on song output. In the following, we compare the singing activity of coal tits near the road (0.2 km from the road) and further away from the road (1 km from the road). We used those two distances since we expected areas that were at a distance of more than 1 km from the road not to be affected by road noise, and since the nearest study site was 0.17 km from the road, we defined 0.2 km as "near the road".

During the day (6.00 am to 5.30 pm), coal tits produced up to 18% more song phrases near the road (0.2 km from the road) compared to further away from the road (1 km from the road). In the evening (6.30 pm to 7.00 pm) coal tits sang up to 20% fewer song phrases near the road compared to further away from the road, and in the morning (5.00 am to 5.30 am) up to 8 % more song phrases near the road compared to further away from the road (Figure 4, Table 3). Thus, we found higher singing activity of coal tits near the road than further away in the morning and during the day, but not in the evening. When investigating the effects of distance to the road independently of the time of day (i.e., accounting for time of the day and the other investigated variables), we found only small effect sizes: Coal tits produced 2% more song phrases near the road compared to further away from the road compared to further away from the road compared to further away from the road compared to further away for the road independently of the time of day (i.e., accounting for time of the day and the other investigated variables), we found only small effect sizes: Coal tits produced 2% more song phrases near the road compared to further away from the road (Figure 5A, Table 3).

We further observed a different singing behaviour depending on forest type: Coal tits produced 17% more song phrases at sites in mountain pine forests compared to sites in mixed forests, when accounting for all other investigated variables including distance to the road (Figure 5, Table 3).

The advancing season also led to a change in singing behaviour of coal tits, but to a smaller extent than, e.g., habitat: coal tits produced 4% more song phrases at the beginning of May compared to the beginning of June (Figure 5B, Table 3).

Furthermore, during times with moderate temperatures between +3.0 °C and +12.0 °C, coal tits produced about 8% more song phrases compared to colder temperatures (-5.5 to +3.0 °C), and about 10% more song phrases than during warmer temperatures (+12.0 to +34.0 °C; Figure 5D, Table 3).



Figure 3 Number of song phrases of coal tits (n = 12 study sites) per minute in relation to time of day. Green dots show the estimates and 95% Bayesian compatibility intervals based on the zero-inflated negative binomial model. Grey dots show the number of coal tit song phrases per minute (raw data) for all sites, days and times.

Table 3 Parameter estimates and 95% Bayesian compatibility intervals (CI; Amrhein & Greenland, 2022) for the investigated variables based on the zero-inflated negative binomial model

Intercept: Time 05:00, Forest	Standardised coefficients Mean [95% CI] in number of coal tit song phrases per minute +2 87 [+2 67: +3 07]	Standard deviation of the predictor variable	Unstandardized coefficients Mean [95% CI] in number of coal tit song phrases per minute	Unit of the predictor variable
type mixed forest	+0.55 [+0.48; +0.62]			
	0.04 [ 2.02; +2.52]			
s(Temperature)	-0.04 [-2.93; +2.55]			
Distance to road	-0.04 [-0.16; +0.09]	1.7 km	-0.02 [-0.09; +0.16]	1 km
Date	-0.04 [-0.07; +0.00]	9.6 days	-0.04 [-0.07; +0.00]	10 days
Forest type mountain pine	-0.19 [-0.34; -0.04]			
Time 05:30	-0.26 [-0.41; -0.10]			
Time 06:00	-0.46 [-0.64; -0.28]			
Time 06:30	-0.51 [-0.69; -0.32]			
Time 07:00	-0.48 [-0.68; -0.29]			
Time 07:30	-0.44 [-0.64; -0.24]			
Time 08:00	-0.47 [-0.67; -0.27]			
Time 08:30	-0.54 [-0.75; -0.34]			
Time 09:00	-0.53 [-0.75; -0.31]			
Time 09:30	-0.50 [-0.74; -0.27]			
Time 10:00	-0.69 [-0.93; -0.45]			
Time 10:30	-0.38 [-0.61; -0.15]			
Time 11:00	-0.41 [-0.64; -0.18]			
Time 11:30	-0.50 [-0.74; -0.27]			
Time 12:00	-0.57 [-0.81; -0.33]			
Time 12:30	-0.54 [-0.81; -0.28]			

Time 13:00	-0.38 [-0.63; -0.12]
Time 13:30	-0.43 [-0.69; -0.17]
Time 14:00	-0.61 [-0.88; -0.33]
Time 14:30	-0.57 [-0.85; -0.29]
Time 15:00	-0.44 [-0.70; -0.18]
Time 15:30	-0.70 [-0.97; -0.42]
Time 16:00	-0.43 [-0.69; -0.17]
Time 16:30	-0.64 [-0.93; -0.36]
Time 17:00	-0.75 [-1.03; -0.48]
Time 17:30	-0.26 [-0.55; +0.03]
Time 18:00	-0.40 [-0.68; -0.11]
Time 18:30	-0.67 [-1.01; -0.34]
Time 19:00	-0.92 [-1.34; -0.51]
Time 19:30	-0.52 [-0.79; -0.25]
Time 20:00	-0.77 [-1.19; -0.35]
Distance to road : Time 05:30	-0.12 [-0.27; +0.03]
Distance to road : Time 06:00	+0.00 [-0.18; +0.18]
Distance to road : Time 06:30	+0.06 [-0.13;+ 0.25]
Distance to road : Time 07:00	-0.03 [-0.20; +0.15]
Distance to road : Time 07:30	+0.03 [-0.19; +0.25]
Distance to road : Time 08:00	-0.09 [-0.27; +0.08]
Distance to road : Time 08:30	+0.02 [-0.15; +0.18]
Distance to road : Time 09:00	-0.07 [-0.25; +0.10]
Distance to road : Time 09:30	+0.00 [-0.17; +0.18]
Distance to road : Time 10:00	-0.26 [-0.53; +0.01]
Distance to road : Time 10:30	-0.05 [-0.24; 0.14]
Distance to road : Time 11:00	-0.05 [-0.26; 0.16]
Distance to road : Time 11:30	-0.03 [-0.22; 0.15]
Distance to road : Time 12:00	-0.09 [-0.29; 0.11]
Distance to road : Time 12:30	-0.37 [-0.66; -0.08]
Distance to road : Time 13:00	-0.02 [-0.22; 0.19]
Distance to road : Time 13:30	0.18 [-0.06; 0.42]
Distance to road : Time 14:00	0.17 [-0.05; 0.39]
Distance to road : Time 14:30	-0.33 [-0.69; 0.01]
Distance to road : Time 15:00	0.04 [-0.19; 0.27]
Distance to road : Time 15:30	-0.14 [-0.39; 0.11]
Distance to road : Time 16:00	-0.06 [-0.33; 0.21]
Distance to road : Time 16:30	-0.08 [-0.33; 0.19]
Distance to road : Time 17:00	-0.13 [-0.39; 0.13]
Distance to road : Time 17:30	0.25 [-0.05; 0.58]
Distance to road : Time 18:00	0.02 [-0.19; 0.23]
Distance to road : Time 18:30	0.06 [-0.17; 0.29]
Distance to road : Time 19:00	0.33 [0.05; 0.62]
Distance to road : Time 19:30	-0.03 [-0.31; 0.25]
Distance to road : Time 20:00	0.16 [-0.23; 0.56]



Figure 4 Mean difference in number of coal tit song phrases (n = 12 study sites) per minute and 95% CI (Amrhein & Greenland, 2022) between sites at 0.2 km distance (near the road) compared to 1.0 km distance (further away) from the road (left y-axis). The yellow area indicates times when coal tits produced more song phrases per minute near the road compared to further away, and the blue-green area indicates times when coal tits produced more song phrases per minute further away from the road than nearer to it. The red line shows the mean noise level. Estimates and 95% CI are based on the zero-inflated negative binomial model and the mean noise level (right y-axis; 0 = loudest value, mean RMS SPL= root mean square sound pressure level; Henn et al., 2005).



Figure 5 Number of coal tit song phrases (n = 12 study sites) per minute in relation to physical environmental parameters. Green lines are regression lines for 04:00, grey areas are 95% Bayesian compatibility intervals based on the zero-inflated negative binomial model. Black dots show the number of coal tit song phrases per minute (raw data) for all sites, days and times.



Figure 6 Number of coal tit song phrases (n = 12 study sites) per minute in relation to two forest types. Green dots show the estimates and 95% Bayesian compatibility intervals based on the zero-inflated negative binomial model. Grey dots show the number of coal tit song phrases per minute (raw data) for all sites, days and times.

#### Discussion

We found higher singing activity of coal tits near the road than further away in the morning and during the day, but not in the evening. Further, coal tits produced more song phrases in mountain pine forests compared to mixed forests, and we observed small changes in singing activity due to date and temperature.

Coal tits produced more song phrases per minute at times and in areas with increased road noise levels (i.e., near the road, in the morning and during the day) compared to times and areas without road noise. This is in line with the results of some previous studies on birds; for example, Hamao et al. (2011) and Barrero et al. (2021) observed higher calling rates (little bustard male (Tetrax tetrax); Barrero et al., 2021) and song phrases (great tit; Hamao et al., 2011) at sites with increased noise levels (increase of 14 - 18 dB). Further, great tits produced songs of longer durations at sites with increased noise levels (65.1 vs. 46.3 dB; Hamao et al., 2011), but little bustard males produced shorter calls when the prevailing noise level prior to the calls was louder (63.7 vs. 49.5 dB; Barrero et al., 2021). Birds may adapt their songs and calls in such a way that masking (Francis et al., 2011b; McIntyre et al., 2014; Rheindt, 2003; Slabbekoorn & Peet, 2003) is reduced. But birds may react differently depending on whether they are habituated to noise or not (LaZerte et al., 2017). For example, LaZerte et al. (2017) observed different reactions to increased noise levels for mountain chickadees (Poecile gambeli) probably depending on previous experiences the birds had with noise: Mountain chickadees in areas with high local ambient noise levels produced relatively more songs when exposed to additional experimental noise, and mountain chickadees in areas with low local ambient noise levels produced relatively more calls when exposed to experimental noise (LaZerte et al., 2017). LaZerte et al. (2017) concluded that the responses of mountain chickadees to anthropogenic noise may differ depending on the experiences the birds had with anthropogenic noise: Birds that are habituated to high noise levels may increase the number of song phrases to avoid masking, whereas birds that are not habituated to noise may react to a novelty (increased noise level) by increased alarm (i.e., increased calling rate; LaZerte et al., 2017). In contrast to these results, Potvin et al. (2014) observed a decrease in singing activity for silvereyes (Zosterops lateralis) in urban compared to rural areas ( $\sim 66$  vs.  $\sim 34$  dB). Silvereyes produced 0.03 syllables less per second per decibel increase in noise level; Potvin et al. (2014) predicted 0.75 syllables per second less at the noisiest site compared to the most silent site. Furthermore, zebra finches (Taeniopygia guttata) stopped singing at levels of background noise above  $\sim$ 80 dB (Cynx et al., 1998) and the two birds of a pair called more rapidly and less often during relief and visit duets (in zebra finches, different duet types are used depending on the context of the encounter: relief duet = incubation duties, visit duets = other nesting activites; Villain et al., 2016). When exposed to noise playback at the nest, zebra finches produced louder calls with higher-frequency and less broadband calls (Villain et al., 2016). Several previous studies observed an increase in amplitude (i.e., Brumm, 2004; Cynx et al., 1998; Lowry et al., 2012; Templeton et al., 2016) or duration of vocalizations (i.e., Díaz et al., 2011; Lengagne et al., 1999; Potash, 1972; Ríos-Chelén et al., 2013; Sierro et al., 2017); according to these studies, noise seems to have negative consequences for birds. Goto et al. (2023), however, observed a different reaction of birds to increased noise levels: they played bursts of white noise of different amplitudes (60, 65, 70, 75, and 80 dB) to 34 male outbred domesticated canary birds (Serinus canaria) and investigated changes in singing behaviour during times with increased noise levels. In their study, canary birds started singing preferentially during noise bursts; white noise, therefore, seemed to trigger singing in canary birds (Goto et al., 2023). In our study, coal tits may also have been triggered by increased levels of anthropogenic noise, since they produced an increased number of song phrases near the road during the day – the noisiest time of the day.

Furthermore, coal tits produced more song phrases in mountain pine forests compared to mixed forests. A proximate explanation for this increased singing activity would be that coal tit density is higher in mountain pine forests compared to mixed forests within the SNP. Coal tits usually occupy spruce forests, but also other coniferous forests like pine forests (Bauer et al., 2012). Mixed forests may be less suitable habitats for coal tits, and the consequence may be a smaller number of individuals producing a lower overall number of song phrases in mixed compared to mountain pine forest.

Further, higher population densities may also lead to a changed communication behaviour, the size and direction of such changes may be species- or context-specific: In a literature review about changes in vocal behaviour due to higher densities, Sánchez & Mennill (2024) observed positive and negative changes in vocal behaviour. From 19 investigated studies, 13 studies examined changes in song rate (or singing rate, syllable rate, number of phrases in a song) due to an increased number of conspecific neighbours (Sánchez & Mennill, 2024). Seven of these 13 studies observed a positive effect, i.e., a higher song rate with a larger number of conspecific neighbours; three studies observed a negative effect, and for three studies, Sánchez & Mennill (2024) stated that they found no change in song rate. In the present study, we did not take into account the number of singing coal tits, since it was not possible to determine the number of singing males from the audio files. Future studies may investigate density dependent changes in vocal behaviour of coal tits.

Another possible explanation for the increased singing activity in mountain pine forests compared to mixed forests could be a tight correlation between singing and foraging (Glutz von Blotzheim & Bauer, 1993; Goller, 1987): Food availability for coal tits may be higher in mountain pine compared to mixed forests, since coal tits are well adapted to coniferous forests (Bauer et al., 2012; Glutz von Blotzheim & Bauer, 1993). Thus, coal tits may find more food in mountain pine forests than in mixed forests and therefore may also show increased singing activity in this habitat.

As expected, coal tits produced more song phrases at average temperatures, when more food may be available. Previous studies observed a positive correlation between song output and ambient temperature (Garson & Hunter, 1979; Liao et al., 2018; Strain & Mumme, 1988; Thomas, 1999). For example, Thomas (1999) demonstrated higher song output at dawn, but not at dusk, in European robins (Erithacus rubecula) with warmer temperatures (dawn: -3 °C vs. +3.5 °C, dusk: -5 °C vs. +2.5 °C). When investigating the effects of larger temperature ranges, previous studies found similar results: Garson & Hunter (1979) observed an increase in duration of great tit song bouts per hour and number of wren (Troglodytes troglodytes) songs per hour with warmer overnight temperatures (-4 to +12 °C), and Strain & Mumme (1988) observed that Carolina wrens (Thryothorulsu dovicianuisn) produced more songs per hour at +18 °C compared to -10 °C. In our study, we observed a hump-shaped distribution in singing activity depending on temperature: Singing activity was highest at mean temperatures, but lower at the extremes (low and high temperatures, -5.5 °C to +34 °C). We thus investigated a relatively wide temperature range, and average temperatures in our study are similar to the "high" temperatures of the studies mentioned above. Our results are in line with previous studies, but add more information on the singing behaviour at high temperatures (e.g., lower singing activity at higher temperatures = +34 °C).

Several previous studies also found a correlation between the breeding cycle and singing activity, with a decrease in singing activity after clutch initiation (i.e., Hegelbach & Spaar, 2000; Merilä & Sorjonen, 1994; Naguib et al., 2016; Slagsvold, 1977). This correlation may be species-specific; for example, Amrhein et al. (2008) observed a decrease in singing activity after clutch initiation in blue tits (Cyanistes caeruleus), but not in great tits. Great tits continued singing at high levels after clutch initiation, and Amrhein et al. (2008) assumed that this was due to ecological differences between the two species (i.e., different reproductive strategies). In the present study, we found a small decrease in singing activity for coal tits between two dates that were a month apart (i.e., beginning of May vs. beginning of June). In an earlier study (Paterno et al., 2024), we investigated changes in the singing behaviour of six woodland songbird species at dawn due to date and observed that coal tits started dawn singing about 1 minute later at the beginning of June compared to the beginning of May (similar time period as in the present study). Thus, our present results emphasize that, like in the earlier study, coal tits decrease singing behaviour later in the season (i.e., after clutch initiation).

#### Conclusions

Our observations are in line with previous results on the effects of forest type, temperature, date and time of the day and partly with previous results on road noise. We found increased singing activity near the road, during noisy time periods, earlier in the season, at mean temperatures, and in mountain pine compared to mixed forests. From a discussion about possible ecological consequences, we have deliberately refrained in this paper, as we can only speculate based on our data.

#### Acknowledgements

This project was funded by the Zigerli Hegi Foundation, the Swiss National Park, the Swiss Ornithological Institute, and the Nukahiva Foundation. For analysis, we used services provided by MeteoSwiss (the Swiss Federal Office of Meteorology and Climatology).

#### Ethics declaration

There was no animal trial permit required, since we did not conduct experiments with animals. Access to the study area was granted by the Swiss National Park after project approval by its Research Commission.

#### References

- Amrhein, V., & Greenland, S. (2022). Discuss practical importance of results based on interval estimates and p-value functions, not only on point estimates and null p-values. *Journal of Information Technology*, 37, 316–320. https://doi.org/10.1177/02683962221105904
- Amrhein, V., Johannessen, L. E., Kristiansen, L., & Slagsvold, T. (2008). Reproductive strategy and singing activity: Blue tit and great tit compared. *Behavioral Ecology and Sociobiology*, 62, 1633– 1641. https://doi.org/10.1007/s00265-008-0592-6
- Barrero, A., Llusia, D., Traba, J., Iglesias-Merchan, C., & Morales, M. B. (2021). Vocal response to traffic noise in a non-passerine bird: The little bustard *Tetrax tetrax*. Ardeola, 68, 143–162. https://doi.org/10.13157/arla.68.1.2021.ra8
- Bauer, H.-G., Bezzel, E., & Fiedler, W. (2012). Das Kompendium der Vögel Mitteleuropas (2nd ed.). AULA-Verlag Wiesbaden.
- Benfield, J. A., Rainbolt, G. A. N., Troup, L. J., & Bell, P. A. (2020). Anthropogenic noise source and intensity effects on mood and relaxation in simulated park environments. *Frontiers in Psychology*, 11, 1–8. https://doi.org/10.3389/fpsyg.2020.570694

- Bermúdez-Cuamatzin, E., Delamore, Z., Verbeek, L., Kremer, C., & Slabbekoorn, H. (2020). variation in diurnal patterns of singing activity between urban and rural great tits. *Frontiers in Ecology and Evolution*, 8, 1–15. https://doi.org/10.3389/fevo.2020.00246
- Bermúdez-Cuamatzin, E., Ríos-Chelén, A. A., Gil, D., & Garcia, C. M. (2011). Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. *Biology Letters*, 7, 36–38. https://doi.org/10.1098/rsbl.2010.0437
- Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, 73, 434–440. https://doi.org/10.1111/j.0021-8790.2004.00814.x
- Bruni, A., Mennill, D. J., & Foote, J. R. (2014). Dawn chorus start time variation in a temperate bird community: Relationships with seasonality, weather, and ambient light. *Journal of Ornithology*, 155, 877–890. https://doi.org/10.1007/s10336-014-1071-7
- Bürkner, P.-C. (2017). brms: An R package for bayesian multilevel models using stan. Journal of Statistical Softwar, 80, 1–28.
- Center for Conservation Bioacoustics. (2019). *Raven Lite: Interactive sound analysis software* (2.0.1). The Cornell Lab of Ornithology. http://www.birds.cornell.edu/raven
- Cynx, J., Lewis, R., Tavel, B., & Tse, H. (1998). Amplitude regulation of vocalizations in noise by a songbird, Taeniopygia guttata. *Animal Behaviour*, 56, 107–113. https://doi.org/10.1006/anbe.1998.0746
- Damsky, J., & Gall, M. D. (2016). Anthropogenic noise reduces approach of black-capped chickadee (*Poecile atricapillus*) and tufted titmouse (*Baeolophus bicolor*) to tufted titmouse mobbing calls. *Condor*, 119, 26–33. https://doi.org/10.1650/CONDOR-16-146.1
- Díaz, M., Parra, A., & Gallardo, C. (2011). Serins respond to anthropogenic noise by increasing vocal activity. *Behavioral Ecology*, 22, 332–336. https://doi.org/10.1093/beheco/arq210
- Dominoni, D. M., Greif, S., Nemeth, E., & Brumm, H. (2016). Airport noise predicts song timing of European birds. *Ecology and Evolution*, 6, 6151–6159. https://doi.org/10.1002/ece3.2357
- Erne, N., & Amrhein, V. (2008). Long-term influence of simulated territorial intrusions on dawn and dusk singing in the winter wren: Spring versus autumn. *Journal of Ornithology*, 149, 479–486. https://doi.org/10.1007/s10336-008-0288-8
- European Environmental Agency. (2020). Environmental noise in Europe 2020. In *Publications Office* of the European Union.
- Francis, C. D., Ortega, C. P., & Cruz, A. (2011a). Different behavioural responses to anthropogenic noise by two closely related passerine birds. *Biology Letters*, 7, 850–852. https://doi.org/10.1098/rsbl.2011.0359
- Francis, C. D., Ortega, C. P., & Cruz, A. (2011b). Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2025–2031. https://doi.org/10.1098/rspb.2010.1847
- Gabry, J. (2018). shinystan: Interactive visual and numerical diagnostics and posterior analysis for bayesian models. *R Package Version 2.5.0*. https://cran.r-project.org/package=shinystan
- Garson, P. J., & Hunter, M. L. (1979). Effects of temperature and time of year on the singing behaviour of wrens *Troglodytes troglodytes* and great tits *Parus major*. *Ibis*, 121, 481–487.
- Gil, D., & Llusia, D. (2020). The bird dawn chorus revisited. In: Aubin T, Mathevon N (eds) Coding strategies in vertebrate acoustic communication. *Animal signals and communication*, Vol 7. Springer, Cham. https://doi.org/10.1007/978-3-030-39200-0\_3
- Glutz von Blotzheim, U., & Bauer, K. M. (1993). I: Passeriformes (4. Teil) Muscicapidae Paridae. In Handbuch der Vögel Mitteleuropas (Vol 13). Akademische Verlagsgesellschaft.
- Goller, F. (1987). Der Gesang der Tannenmeise (Parus ater): Beschreibung und kommunikative Funktion. Journal of Ornithology, 128, 291–310. https://doi.org/10.1007/BF01640299
- Goodwin, S. E., & Podos, J. (2013). Shift of song frequencies in response to masking tones. Animal Behaviour, 85, 435–440. https://doi.org/10.1016/j.anbehav.2012.12.003
- Goto, H., de Framond, L., Leitner, S., & Brumm, H. (2023). Bursts of white noise trigger song in

domestic canaries. *Journal of Ornithology*, 164, 835-844. https://doi.org/10.1007/s10336-023-02070-y

- Grabarczyk, E. E., & Gill, S. A. (2020). Anthropogenic noise masking diminishes house wren (*Troglodytes aedon*) song transmission in urban natural areas. *Bioacoustics*, 29, 518–532. https://doi.org/10.1080/09524622.2019.1621209
- Grade, A. M., & Sieving, K. E. (2016). When the birds go unheard: Highway noise disrupts information transfer between bird species. *Biology Letters*, 12, 7–10. https://doi.org/10.1098/rsbl.2016.0113
- Haller, H., Eisenhut, A., & Haller, R. (2013). Atlas des Schweizerischen Nationalparks. Die ersten 100 Jahre. Nationalpark Forschung Schweiz 99/1, Haupt Verlag Bern.
- Hamao, S., Watanabe, M., & Mori, Y. (2011). Urban noise and male density affect songs in the great tit *Parus major*. *Ethology Ecology and Evolution*, 23, 111–119. https://doi.org/10.1080/03949370.2011.554881
- Hanna, D., Blouin-Demers, G., Wilson, D. R., & Mennill, D. J. (2011). Anthropogenic noise affects song structure in red-winged blackbirds (*Agelaius phoeniceus*). *Journal of Experimental Biology*, 214, 3549–3556. https://doi.org/10.1242/jeb.060194
- Hegelbach, J., & Spaar, R. (2000). Saisonaler Verlauf der Gesangsaktivität der Singdrossel (*Turdus philomelos*), mit Anmerkungen zum nachbrutzeitlichen Gesangsschub. *Journal für Ornithologie*, 434, 425–434.
- Henn, H., Sinambari, G. R., & Fallen, M. (2008). Ingenieurakustik: Physikalische Grundlagen und Anwendungsbeispiele. *Springer-Verlag*, 4th ed.
- Higgs, D. M., & Humphrey, S. R. (2020). Passive acoustic monitoring shows no effect of anthropogenic noise on acoustic communication in the invasive round goby (*Neogobius melanostomus*). *Freshwater Biology*, 65, 66–74. https://doi.org/10.1111/fwb.13392
- Hornberg, J., Haselhoff, T., Lawrence, B. T., Fischer, J. L., Ahmed, S., Gruehn, D., & Moebus, S. (2021). Impact of the covid-19 lockdown measures on noise levels in urban areas—a pre/during comparison of long-term sound pressure measurements in the ruhr area, germany. *International Journal of Environmental Research and Public Health*, 18. https://doi.org/10.3390/ijerph18094653
- Hu, Y., & Cardoso, G. C. (2010). Which birds adjust the frequency of vocalizations in urban noise? Animal Behaviour, 79, 863–867. https://doi.org/10.1016/j.anbehav.2009.12.036
- Jin, T., Kosheleva, A., Castro, E., Qiu, X., James, P., & Schwartz, J. (2024). Long-term noise exposures and cardiovascular diseases mortality: A study in 5 U.S. states. *Environmental Research*, 245, 118092. https://doi.org/10.1016/j.envres.2023.118092
- Kunc, H. P., & Schmidt, R. (2019). The effects of anthropogenic noise on animals: A meta-analysis. *Biology Letters*, 15. https://doi.org/10.1098/rsbl.2019.0649
- LaZerte, S. E., Otter, K. A., & Slabbekoorn, H. (2017). Mountain chickadees adjust songs, calls and chorus composition with increasing ambient and experimental anthropogenic noise. Urban Ecosystems, 20, 989–1000. https://doi.org/10.1007/s11252-017-0652-7
- Lengagne, T., Aubin, T., Lauga, J., & Jouventin, P. (1999). How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proceedings of the Royal Society B: Biological Sciences*, 266, 1623–1628. https://doi.org/10.1098/rspb.1999.0824
- Leone, M. T., & Warren, J. D. (2024). Vessels and aircraft are chronic sources of anthropogenic noise in coastal marine and terrestrial soundscapes on Long Island, New York. *Environmental Pollution*, 355, 124208. https://doi.org/10.1016/j.envpol.2024.124208
- Liao, C. C., Shieh, B. Sen, & Chen, C. C. (2018). Air temperature influenced the vocal activity of birds in a subtropical forest in southern Taiwan. *Taiwan Journal of Forest Science*, 33, 291–304.
- Lindenmayer, D. B., Cunningham, R. B., & Lindenmayer, B. D. (2004). Sound recording of bird vocalisations in forests. II. Longitudinal profiles in vocal activity. *Wildlife Research*, 31, 209– 217. https://doi.org/10.1071/WR02063

- Lotz, A. (2006). *Alpine Habitat Diversity HABITALP Project Report 2002 2006*. EU Community Initiative INTERREG III B Alpine Space Programme. Nationalpark Berchtesgaden. 196 pp
- Lowry, H., Lill, A., & Wong, B. B. M. (2012). How noisy does a noisy miner have to be? Amplitude adjustments of alarm calls in an avian urban "adapter." *PLoS ONE*, 7, 1–5. https://doi.org/10.1371/journal.pone.0029960
- Mattes, H., Maurizio, R., & Bürkli, W. (2005). Die Vogelwelt im Oberengadin, Bergell und Puschlav: Ein Naturführer zur Avifauna in einem inneralpinen Gebiet. Schweizerische Vogelwarte Sempach.
- McIntyre, E., Leonard, M. L., & Horn, A. G. (2014). Ambient noise and parental communication of predation risk in tree swallows, *Tachycineta bicolor*. *Animal Behaviour*, 87, 85–89. https://doi.org/10.1016/j.anbehav.2013.10.013
- Merilä, J., & Sorjonen, J. (1994). Seasonal and diurnal patterns of singing and song-flight activity in bluethroats (*Luscinia svecica*). *The Auk*, *111*, 556–562.
- MeteoSwiss. (2021). IDAweb. Data protal for teaching and research. *Bundesamt Für Meteorologie und Klimatologie MeteoSchweiz*, Zürich, Switzerland. http://meteoschweiz.admin.ch/home/service-und-publikationen/ beratung-und-service/datenportal-fuer-lehre-und-forschung.html
- Mizuguchi, D., Sánchez-Valpuesta, M., Kim, Y., dos Santos, E. B., Kang, H. J., Mori, C., Wada, K., & Kojima, S. (2024). Daily singing of adult songbirds functions to maintain song performance independently of auditory feedback and age. *Communications Biology*, 7. https://doi.org/10.1038/s42003-024-06311-5
- Naguib, M., Diehl, J., Van Oers, K., & Snijders, L. (2019). Repeatability of signalling traits in the avian dawn chorus. *Frontiers in Zoology*, 16, 1–12. https://doi.org/10.1186/s12983-019-0328-7
- Naguib, M., Van Rooij, E. P., Snijders, L., & Van Oers, K. (2016). To sing or not to sing: seasonal changes in singing vary with personality in wild great tits. *Behavioral Ecology*, 27, 932–938. https://doi.org/10.1093/beheco/arv235
- Nemeth, E., & Brumm, H. (2010). Birds and anthropogenic noise: Are urban songs adaptive? American Naturalist, 176, 465–475. https://doi.org/10.1086/656275
- Open Acoustic Devices. (2024). Audiomoth. https://www.openacousticdevices.info/audiomoth
- Parris, K. M., & Schneider, A. (2009). Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecology and Society*, 14. https://doi.org/10.5751/ES-02761-140129
- Paterno, J., Korner-Nievergelt, F., Anderwald, P., & Amrhein, V. (2024). Start of dawn singing as related to physical environmental variables in an alpine environment. *Journal of Ornithology*, 0123456789. https://doi.org/10.1007/s10336-023-02134-z
- Potash, L. M. (1972). Noise-induced changes in calls of the Japanese quail. *Psychonomic Science*, 26, 252–254. https://doi.org/10.3758/BF03328608
- Potvin, D. A., Mulder, R. A., & Parris, K. M. (2014). Silvereyes decrease acoustic frequency but increase efficacy of alarm calls in urban noise. *Animal Behaviour*, 98, 27–33. https://doi.org/10.1016/j.anbehav.2014.09.026
- Puswal, S. M., Jinjun, M., & Liu, F. (2020). Effects of temperature and season on birds' dawn singing behavior in a forest of eastern China. *Journal of Ornithology*, 162, 447–459. https://doi.org/10.1007/s10336-020-01848-8
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/.
- Rheindt, F. E. (2003). The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? *Journal Fur Ornithologie*, 144, 295–306. https://doi.org/10.1046/j.1439-0361.2003.03004.x
- Ríos-Chelén, A. A., Quirós-Guerrero, E., Gil, D., & Macías Garcia, C. (2013). Dealing with urban noise: Vermilion flycatchers sing longer songs in noisier territories. *Behavioral Ecology and Sociobiology*, 67, 145–152. https://doi.org/10.1007/s00265-012-1434-0
- Sierro, J., Schloesing, E., Pavón, I., & Gil, D. (2017). European blackbirds exposed to aircraft noise

advance their chorus, modify their song and spend more time singing. *Frontiers in Ecology and Evolution*, 5, 1–13. https://doi.org/10.3389/fevo.2017.00068

- Slabbekoorn, H., & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature*, 424, 267. https://doi.org/10.1038/424267a
- Slagsvold, T. (1977). Bird song activity in relation to breeding cycle, spring weather, and environmental phenology. Ornis Scandinavica, 8, 197. https://doi.org/10.2307/3676105
- SOX. (2024). Sox: Sound Exchange. SourceForge. https://sox.sourceforge.net/
- Staicer, C. A., Spector, D. A., & Horn, A. G. (1996). 24. The dawn chorus and other diel patterns in acoustic signaling. In D. E. Kroodsma & E. H. Miller (Eds.), *Ecology and Evolution of Acoustic Communication in Birds* (pp. 426–453). Cornell University Press. https://doi.org/https://doi.org/10.7591/9781501736957-033
- Strain, J. G., & Mumme, R. L. (1988). Effects of food supplementation, song playback, and temperature on vocal territorial behavior of carolina wrens. *The Auk*, 105, 11–16. https://doi.org/10.1093/auk/105.1.11
- Templeton, C. N., Zollinger, S. A., & Brumm, H. (2016). Traffic noise drowns out great tit alarm calls. *Current Biology*, 26, R1173–R1174. https://doi.org/10.1016/j.cub.2016.09.058
- Thomas, R. J. (1999). Two tests of a stochastic dynamic programming model of daily singing routines in birds. *Animal Behaviour*, 57, 277–284. https://doi.org/10.1006/anbe.1998.0956
- Tiefbauamt Graubünden (2024) Verkehrsfrequenzen. https://www.gr.ch/DE/institutionen/verwaltung/diem/tba/Strassennetz/Seiten/Verkehrsfrequenze n.aspx accessed 26 Feb 2024
- Villain, A. S., Fernandez, M. S. A., Bouchut, C., Soula, H. A., & Vignal, C. (2016). Songbird mates change their call structure and intrapair communication at the nest in response to environmental noise. *Animal Behaviour*, 116, 113–129. https://doi.org/10.1016/j.anbehav.2016.03.009
- Warrington, M. H., Curry, C. M., Antze, B., & Koper, N. (2018). Noise from four types of extractive energy infrastructure affects song features of savannah sparrows. *The Condor*, 120, 1–15. https://doi.org/10.1650/condor-17-69.1
- Wickham, H. (2016). ggplot2: Elegant graphics for data analysis. Springer-Verlag New York. https://ggplot2.tidyverse.org
- Wickham, H., Averick, M., Bryan, J., Chang, W., D'Agostino McGowan, L., Franccois, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Milton Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., ... Yutani, H. (2019). Welcome to the {tidyverse}. Journal of Open Source Software, 4, 1686. https://doi.org/10.21105/joss.01686
- Wickham, H., François, R., Henry, L., & Müller, K. (2021). dplyr: A grammar of data manipulation. *R Package Version 1.0.3*. https://cran.r-project.org/package=dplyr

### **Supplementary Material**

Time	Mean [95% Cl]	Time	Mean [95% CI]	Time	Mean [95% CI]
05:00	+1.5 [+9.0; -7.7]	10:30	+4.1 [+13.3; -7.3]	16:00	+4.9 [+17.1; -11.5]
05:30	+7.8 [+14.6; -0.3]	11:00	+4.2 [+14.1; -8.2]	16:30	+5.6 [+17.2; -9.8]
06:00	+1.4 [+10.3; -9.5]	11:30	+3.2 [+12.2; -7.9]	17:00	+8.1 [+19.3; -6.2]
06:30	-2.0 [+7.9; -14.5]	12:00	+6.1 [+15.2; -5.1]	17:30	-14.4 [+3.7; -43.0]
07:00	+2.9 [+11.5; -7.7]	12:30	+18.4 [+28.5; +5.5]	18:00	+0.3 [+10.9; -13.5]
07:30	-0.1 [+11.0; -14.2]	13:00	+2.3 [+12.2; -9.8]	18:30	-2.2 [+9.4; -17.1]
08:00	+6.4 [+14.5; -3.4]	13:30	-9.3 [+4.7; -28.5]	19:00	-20.0 [-1.8; -46.2]
08:30	+0.3 [+8.9; -9.9]	14:00	-8.6 [+4.0; -25.1]	19:30	+3.2 [+16.4; -14.7]
09:00	+5.4 [+13.7; -4.8]	14:30	+16.9 [+29.2; +0.1]	20:00	-7.8 [+12.7; -40.9]
09:30	+1.3 [+9.9; -9.5]	15:00	-0.6 [+10.8; -15.5]		
10:00	+13.9 [+24.4; +0.7]	15:30	+8.7 [+19.4; -4.9]		

Table S1: Mean difference in number of coal tit song phrases per minute and 95% CI (Amrhein & Greenland, 2022) between sites at 0.2 km distance compared to 1.0 km distance from the road.

# CHAPTER 4

This chapter is published as

Paterno J, Korner-Nievergelt F, Gubler S, Anderwald P, Amrhein V (2024). Alpine songbirds at higher elevations are only raised with a slight delay and therefore under harsher environmental conditions. *Ecology and Evolution* 14, p. 1 – 20.

Zernez, SNP / Hans Lozza

DOI: 10.1002/ece3.70049

## Ecology and Evolution WILEY

#### RESEARCH ARTICLE

## Alpine songbirds at higher elevations are only raised with a slight delay and therefore under harsher environmental conditions

Julia Paterno<sup>1,2</sup> | Fränzi Korner-Nievergelt<sup>1,3</sup> | Stefanie Gubler<sup>4</sup> | Pia Anderwald<sup>2</sup> | Valentin Amrhein<sup>1,3</sup> |

<sup>1</sup>Department of Environmental Sciences, University of Basel, Basel, Switzerland <sup>2</sup>Department of Research and Monitoring, Swiss National Park, Zernez, Switzerland <sup>3</sup>Swiss Ornithological Institute, Sempach, Switzerland

<sup>4</sup>Swiss Academy of Sciences SCNAT, Bern, Switzerland

Correspondence Julia Paterno, Department of Environmental Sciences, University of Basel, Basel, Switzerland. Email: julia.paterno@nationalpark.ch

#### Abstract

The breeding phenology of birds is often timed to coincide with a peak in food availability. However, the shortening of the vegetation period with increasing elevation may force bird species at high elevations to breed earlier in relation to optimal environmental conditions due to time constraints. We investigated differences in fledging dates in five Alpine woodland songbird species along an elevational gradient from 1500 to 2200 m in Switzerland. We estimated fledging dates from a nationwide citizen science bird monitoring dataset and used the date when the proportion of observations of 'fledged young' reached 50% among all observations indicating breeding behaviour. This measure had the advantage that we could estimate average timing of the broods across a wide geographic range and over many years without the need to search for individual nests. We then compared differences in timing of the broods with climatic conditions and larch budburst across different elevational bands. The daily mean air temperature of 10-15°C was reached 34-38 days later at 2200 m compared to 1500 m, which is a similar delay as found in previous reports on snow meltout date. The average delay in larch budburst was 19.2 days at 2200 m compared to 1500 m. In comparison, the average timing of the birds' broods was only 5.4 days later in coal tits and 0.5 days later in Alpine tits at 2200 compared to 1500 m (the two species for which we had the narrowest interval estimates). Also, the estimated delay at higher elevations in the broods of song thrushes, mistle thrushes and Eurasian chaffinches was relatively small. Rather than postponing breeding dates to better environmental conditions later in the season that would match the earlier conditions at low elevation, songbirds breeding at higher elevations may thus have evolved adaptations to cope with the harsher conditions.

#### KEYWORDS

Atlas code, breeding stage, detectability, passerine, plant phenology, willow tit

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Author(s). Ecology and Evolution published by John Wiley & Sons Ltd.

www.ecolevol.org 1 of 20

### 2 of 20 WILEY\_Ecology and Evolution

#### 1 | INTRODUCTION

Physical environmental factors such as temperature or snow meltout change with increasing elevation. In the Swiss Alps, for example, temperature decreases by an average of 0.65°C per 100m increase in elevation (ISO 2533:1975), and mean snow melt-out date is delayed by about 40 days at an elevational difference of 700m (1500 vs 2200m asl; Schano et al., 2021). Due to later snow melt-out dates, harsher climatic conditions and resulting differences in food availability, the breeding season of birds is usually shorter at higher compared to lower elevations (Dillon & Conway, 2015; Labarbera & Lacey, 2018; Yeh & Price, 2004), and thus breeding at higher elevations is under time pressure (Illán et al., 2012; Stier et al., 2014 for butterflies).

At lower elevations, the timing of breeding in birds is often correlated with the peak of insect abundance in spring (Daan et al., 1989; Hinks et al., 2015; Lack, 1950; Visser & Both, 2005), and this peak is usually correlated with spring temperatures (Thackeray et al., 2016; Visser & Holleman, 2001; Vitasse et al., 2021). Accordingly, birds may fine-tune their phenology to that of lower trophic levels; for example, in a lowland population of great tits (Parus major), there was a strong correlation between oak budburst (as a proxy for plant phenology) and the peak in caterpillar abundance, and oak phenology close to the nest was related to the timing of egg-laying and hatching of the young (Hinks et al., 2015). The (possibly indirect) relationship between bird breeding phenology and spring temperatures was investigated by Verhagen et al. (2020) who found that great tits started breeding earlier when exposed to warmer compared to colder temperatures in climate-controlled aviaries. Similarly, Saracco et al. (2018) found a difference of 11-14 days in mean capture dates of the young of 25 North American bird species between the warmest and coldest spring in their study.

Cold temperatures and late snow melt-out date can thus delay the timing of breeding in birds (e.g. Pereyra, 2011; Smith & Andersen, 2014: Williams, 2012). Accordingly, previous studies found a delayed breeding phenology of songbirds at higher compared to lower elevations (Table 1). For example, Perfito et al. (2004) investigated changes in the testis volume of adult male song sparrows (Melospiza melodia morphna) and found a delay in testis growth of 1-2 months between coastal (0-10 m) and montane (280-1220 m) habitats. Further, Johnson et al. (2018) found that tree swallows (Tachycineta bicolor) began egg-laving 10 days later at 2482 m (+41 m. SD) compared to 1359 m (±99 m), and Gil-Delgado et al. (1992) found a delay of 7 days in the mean egg-laying date for blue tits (Cyanistes caeruleus) at 900-1000 m compared to 500-750 m. Most of the studies on elevational differences in the timing of breeding investigated the start of egg-laying of single populations by observing nests in the field (Table 1). While birds at higher elevations generally breed later, it is unclear whether this delay in reproduction allows them to experience the same optimal environmental and ecological conditions as birds that breed earlier at low elevations.

Several previous studies also investigated national or international datasets and used data from bird nest record cards to

deduce the start of breeding (Bairlein et al., 1980; Dunn et al., 2000; Gibbs, 2007). For example, Bairlein et al. (1980) investigated elevational differences in the start of egg-laying of four Sylvia species, using more than 2000 nest record cards from Germany, Finland, France and the Canary Islands; they found a delay in egg-laying date of 5-9 days between the highest and lowest elevational belt (<250 m and >500m) depending on the species. The interpretation of the delay is difficult, since Bairlein et al. (1980) investigated three elevational belts (including 250-500m) and it is unclear where the elevational gradient ended. Another study also used data from nest record cards: Gibbs (2007) found a delay in breeding of Australian Magpies (Gymnorhina tibicen) of 2.7-3.9 days per 100 m increase in elevation. depending on the dataset used. Gibbs (2007) investigated data from different databases like the Australian Nest Record Scheme (NRS). the Garden Bird Survey of the Canberra Ornithologists (GBS), the Atlas of Australian Birds and the NSW Bird Atlas to estimate hatching and fledging dates of Australian Magpies. The NRS and the GBS represented suitable sources for their study because detailed breeding data were available. In contrast, only little information on the timing of breeding was available in the Atlas of Australian Birds and the NSW Bird Atlas (Gibbs, 2007). Thus, nationwide datasets can be used to investigate the timing of breeding in birds, but suitability of a dataset depends on how information on the timing of the brood is recorded.

Several nationwide or continent-wide citizen science breeding bird monitoring schemes are primarily used to gain information on population trends and ranges (e.g. Keller et al., 2020; Knaus et al., 2018). Because such nationwide bird monitoring schemes may not involve systematic nest searches, the resulting data often may not be suitable to directly deduce egg-laying or fledging dates. However, there may be sufficient information to estimate the timing of the broods if the observed bird behaviour is recorded in a standardised way such as using international breeding codes (e.g. Keller et al., 2020).

In this study, we used data from the Swiss monitoring of common breeding birds (Knaus et al., 2018) and opportunistic observations from the online database ornitho.ch (Ornitho, 2023; data obtained from the Swiss Ornithological Institute; Figure 1, Tables 2 and 3) to investigate the breeding phenology of five woodland songbird species all over Switzerland along an elevational gradient from 1500 to 2200m. We estimated the dates when the fledged young were reported in 50% of the observations that indicated a brood, which means that no nest searches and thus no disturbance at the nests were necessary. We also compared climatic conditions and larch budburst between 1500 and 2200m. Since previous studies found strong correlations between plant phenology and food availability (e.g. Hinks et al., 2015), we used larch budburst as a proxy for food availability. The European larch (Larix decidua) is a suitable species to investigate plant phenology in our study because the main distributional area of the European larch is between 1500 and 2000m (up to 2250m; Brändli, 1998), and measurement of larch budburst is a common proxy for plant phenology at higher elevations (Brügger & Vasella, 2003). We expected a later rise of spring temperatures, later

#### PATERNO ET AL

snow melt-out dates and a delay in larch budburst at higher elevations; accordingly, we expected later observations of fledged young birds at 2200 m compared to 1500 m.

#### 2 | MATERIALS AND METHODS

All data used in this study were collected throughout the mountainous regions of Switzerland. Larch budburst data were collected across the same elevations and in close proximity to the breeding phenology observations, but not at the exact locations of the breeding bird observations (Figure 1). Data on temperature covered the elevational range between 1500 m and 2200 m of the whole country (i.e. a similar region as for bird and larch budburst observations). The elevational range for data on temperature and breeding phenology was the same (1500–2200m); for larch budburst, we used a slightly lower elevational range because data were only available up to 1933 m (i.e. there were no Swiss Phenology stations of MeteoSwiss above 1933m), and we predicted larch budburst for the higher elevations (see below for further explanation).

#### 2.1 | Temperature and larch budburst

To compare the timing of the warm-up between 1500 m and 2200 m. we used the dates when the mean daily temperature exceeded thresholds between -5 and +15°C (mean daily temperatures above 15°C are rarely reached at 2200 m), in steps of 1°C, at 1500 m and 2200 m throughout Switzerland. This analysis was based on the daily mean air temperature grid at 2 × 2 km resolution of Switzerland, that is, on the TabsD dataset for the years 1991-2022 by MeteoSwiss (Frei, 2013). For each year and temperature threshold, the first day of the year (in the following called exceedance day) on which the respective temperature threshold was exceeded in spring or early summer was determined. Each exceedance day was calculated using a stepwise procedure for each temperature threshold separately. First, we calculated the exceedance day for a particular threshold at each of the grid cells of the countrywide dataset for each year separately. We then determined the median exceedance day on each of the two elevational bands separately. The elevational bands are defined as all grid cells within +100m around 1500 m and 2200m. respectively. We calculated the difference of the exceedance days between the two elevational bands for each year, and our final result was the median difference in exceedance days of all years between 1991 and 2022 per temperature threshold. To investigate differences in plant phenology, we calculated differences in larch budburst between 1500 m and 2200 m using data from MeteoSwiss. Data were available from 2013 to 2022 from 41 sites (Swiss Phenology Network) distributed over Switzerland between 1000 and 1933m (Figures 1 and 2). For those sites, we extracted the date when 50% of the young tufts of needles of a single tree or tree stand began to loosen up and spread (= larch budburst, Brügger & Vasella, 2003). We used the R base package (R Core Team, 2020) to build a linear

model on the date of larch budburst as predicted by the two continuous variables elevation and year, and used the regression line of best fit to predict the expected difference in number of days of average larch budburst between 1500 m and 2200m, since data were only available up to 1933m.

#### 2.2 | Estimation of the timing of the broods

We analysed data on five common woodland bird species that breed across a large elevational range in Switzerland: song thrush (*Turdus philomelos*), mistle thrush (*Turdus viscivorus*), Eurasian chaffinch (*Fringilla coelebs*), coal tit (*Periparus ater*) and Alpine (*Poecile montanus montanus*) or willow tit (*Poecile montanus rhenanus*/salicarius; Table 3). In Switzerland, both *Poecile montanus* forms exist, occupying different ecological niches. The Alpine tit can be found in higher regions, especially in the Alps, whereas the willow tit is more frequent in the lowlands (Glutz von Blotzheim & Bauer, 1993; Knaus et al., 2018). We summarised all observations as Alpine tits because morphological differentiation between the two forms in the field is difficult, and because the elevational range considered in this study starts at the upper range of the willow tit distribution and covers the main distribution of the Alpine tit (Knaus et al., 2018).

For estimation of the timing of the brood (as defined below), we used data from the Swiss monitoring of common breeding birds (Knaus et al., 2018), which is part of the Swiss Biodiversity Monitoring program (BDM Coordination Office, 2014; data obtained from the Swiss Ornithological Institute; Figure 1, Tables 2 and 3). We additionally used opportunistic observations from the online database ornitho.ch (Ornitho, 2023; data obtained from the Swiss Ornithological Institute; Figure 1, Tables 2 and 3) that were collected between 2013 and 2022 (before 2013, there were not enough data available). Both datasets are mostly collected by volunteer naturalists and thus are from nationwide citizen science projects.

The combined dataset included records on species, date, coordinates, elevation and the 'Atlas code' providing descriptions of bird behaviour and specifying whether a brood is either possible, likely or certain; the Atlas codes used in Switzerland (Knaus et al., 2018; Swiss Ornithological Institute, 2019) are based on the international Atlas codes (Keller et al., 2020). In the online database ornitho.ch. the Atlas codes are required for entries of all breeding birds in Switzerland during the breeding season (Ornitho, 2023). We selected observations that indicated a brood and that allowed to distinguish between early and late stages of the brood (Tables 2 and S1). For each breeding observation, we thus assigned one of the two developmental stages 'early; certainly or likely not fledged' and 'late; certainly fledged' and then calculated the proportion of broods with certainly fledged young among all observed broods at a given elevation. We included the observation 'adults with food for their young' in the early stage even though in the investigated species adults continue feeding their young for a few days up to 2-3 weeks after fledging (Figure A1; Glutz von Blotzheim, 1988, 1997; Glutz von Blotzheim & Bauer, 1993). Eurasian chaffinch

4 of 20 WIL	EY_Ecology	and Evolution							PATERNO ET AL.
TABLE 1 List of	different stu	dies investigating tir	ning of breeding	g along elev	ational grad	lients.			
							Low elevation		
Species	Region	References	Observation	Low elevation	High elevation	Elevational difference	N	SD	SE
Alpine tit Parus montanus montanus	Switzerland	Paterno et al.	Citizen science data observations	1500	2200	700			
Carrion Crow Corvus corone	UK	Driver (2005)	Nest search	75	646	571	61		
Coal Tit Periparus	Germany	Zang (1980)	Nest boxes	450	920	470			
ater	France	Bison et al (2020)	Nest boxes	1324	1874	550	60 nest boxes		
		Clouet (2005)	Nest boxes	1325	1900	575	Nest boxes were occupied from 0 to 30%		
	Switzerland	Paterno et al.	Citizen science data observations	1500	2200	700			
Common Whitethroat Curruca communis	Germany	Bairlein et al. (1980)	Nest record cards	<250	>500		47		
Eurasian Blackcap Sylvia atricapilla	Germany	Bairlein et al. (1980)	Nest record cards	<250	>500		224		
Eurasian Blue Tit Cyanistes caeruleus	Spain	Gil-Delgado et al. (1992)	Nest boxes	625	950	325	25	7.25	
	Germany	Zang (1980, 1982)	Nest boxes	120	540	420			
	France	Brändli (1998)	Nest boxes	532	1181	649	353	7	
Eurasian chaffinch Fringilla coelebs	Switzerland	Paterno et al.	Citizen science data observations	1500	2200	700			

102

European Pied Flycatcher Ficedula hypoleuca

Germany Zang (1980)

Nest boxes

100 900 800

.Е ү		Open		-							
				Fledging			ite	Egg-laying da			High elevation
Comments	Delay in days/100 m	Difference in days high versus low	High elevation	Low elevation	Delay in days/100 m	Difference in days high versus low	High elevation	Low elevation	SE	SD	N
	0.19	+1.1 [-19.8; +15.9]	170.9 [153.3; 182.3]	169.7 [164.2; 175.3]							
					1.58	+9	22 April-24 April	13 April-15 April			17
A total quanti of 10%-45% of nest boxes were occupied in different years and elevations					1.68 1.5						50 nest boxes
No information on the number of nest boxes low elevation					First=1.91 Mean=1.74	+10	First=30 April Mean=15 May	First=19 April Mean=5 May			37 nest boxes Nest boxes were occupied in max 55%
	1.48	+10.5 [-2.2; +20.6]	173.4 [161.8; 183.2]	163.2 [157.9;169.0]							
Three elevational belts: <250, 250-500 and >500m. Unclear at which elevatii the gradient ends						+9	26 May	17 May			38
Three elevational belts: <250, 250-500 and >500m. Unclear at which elevati the gradient ends	Incubation and nestling period increase with increasing elevation					+6	20 May	14 May			129
					2.15 Overall 5.24	+7	13 May	6 May		8.43	83
					Birds that are older than 1 year 5.37 1-year-old birds 4.17						
					First=0 Mean=1.69	+11	First=27 March Mean=24 April	First=27 March Mean=13 April		15	74
	2.80	+19.6	193 [156.3; 241.3]	174.8 [166.2; 182.8]							

(Continues)

6 of 20   WILI	EY-Ecology	and Evolution							PATERNO ET AL.
TABLE 1 (Contin	nued)								
							Low elevation		
Species	Region	References	Observation	Low elevation	High elevation	Elevational difference	N	SD	SE
Garden Warbler Sylvia borin	Germany	Bairlein et al. (1980)	Nest record cards	<250	>500		126		
Great Tit Parus major	Germany	Zang (1980, 1982)	Nest boxes	100	900	800			
	Austria	Schöll and Hille (2014)	Nest boxes	544	789	245	35		
Grey Wagtail Motacilla cinerea	UK	Ormerod & Tyler (1987)	Nest search	75	370	295			
Grey-backed Shrike Lanius tephronotus	Tibet	Lu et al. (2010)	Nest search						
House Wren Troglodytes aedon	California	Levin et al. (2023)	Nest boxes	480	2164	1684	83 nest boxes		4-6.5
Lesser Whitethroat Curruca curruca	Germany	Bairlein et al. (1980)	Nest record cards	<500	>500		31		
Marsh Tit Poecile palustris	Germany	Zang (1980)	Nest boxes	120	540	420			
Mistle thrush Turdus viscivorus	Switzerland	Paterno et al.	Citizen science data observations	1500	2200	700			
Mountain Bluebird Sialia currucoides	Wyoming	Johnson et al. (2006)	Nest boxes	1482	2504	1022	2004: 30+33, 2005: 18 nest boxes		
Northern Raven Corvus corax	France, Corsica	Delestrade (2002)	Nest search	20	1500	1480			
Oregon Juncos Juncus hyemalis oregonus	Canada	Bears (1999)	Nest search	1021	1985	964	72		
Pacific Wren Troglodytes pacificus	Canada	Ogden et al. (2012)	Nest search	200	1010	810	40		
Red-billed Chough Pyrrhocorax pyrrhocorax	Spain	Blanco et al. (1998)	Nest search	330	1300	970	33	6.8	
Red-faced Warbler Cardellina rubrifrons	Arizona	Dillon and Conway (2015)	Nest search	1964	2711	747			
Rock Sparrow Petronia	Italy	Tavecchia et al. (2002)	Nest boxes	1570	1780	210	79		
Russet Sparrow Passer cinnamomeus former rutilans	China	Yang et al (2012)	Nest boxes	200	1500	1300	24	15	

	ligh elevation			Egg-laying date					Fledging				
N	SD	SE	Low elevation	High elevation	Difference in days high versus low	Delay in days/100m	Low	High elevation	Difference in days high versus low	Delay in days/100 m	Comments		
221			22 May	31 May	+9					Incubation and nestling period increase with increasing elevation	Three elevational belts: <250, 250-500 and >500m. Unclear at which elevation the gradient ends		
21			13 Apr	20 Apr	+7	Overall 2.19 Birds that are older than 1 year 2.13 1-year-old birds 2.45 2.86							
						First-egg dates ~13 days/100 m					The number o observations i unclear, since additional data were used for this particular analysis		
						Later							
73 nest boxes		28	1 April-9 June	20 May-11 June	+26	1.54	6 June	30 June		1.54	No informatio about how many nest boxes were occupied		
51			17 May	22 May	+5								
						1.97							
							188.0 [-134.6; 479.4]	187.6 [172.7; 214.4]	+32.8 [-295.7; +329.4]	4.69			
2004: 68, 2005: 112 nest boxes			26 Apr	10 May	+14	1.37					No informatio about how many nest boxes were occupied		
						Later							
45			17 April–5 August	27 May-15 June	-6	First=4.15							
6			ca. 21 April	ca. 31 May	+40	4.93							
60	10.9		24 March	04 Apr	+11	1.13							
						1.82							
65			22 June	27 June	+5	2.38							
57	19		9 May	7 June	+29	2.23							

(Continues)

## 8 of 20 WILEY\_Ecology and Evolution

TABLE 1 (Continued)

							Low elevation		
Species	Region	References	Observation	Low elevation	High elevation	Elevational difference	N	SD	SE
Small Ground Finch Geospiza fuliginosa	Galapagos Archipelago	Kleindorfer (2007)	Nest search	50	500	450	90		
Song Sparrow Melospiza melodia	Washington State	Perfito et al. (2004)	Mist nets	5	750	745	11		
Song Thrush Turdus philomelos	Switzerland	Paterno et al.	Citizen science data observations	1500	2200	700			
Thorn-tailed Rayadito Aphrastura spinicauda	Chile	Altamirano et al. (2015)	Nest boxes direct observations camera traps	368	952	584	High and low together=103		
Tree Swallow Tachycineta bicolor	Wyoming	Johnson et al. (2018)	Nest boxes	1359	2482	1123	80		

Whinchat Saxicola rubetra	Switzerland France	Müller et al. (2005) Fontanilles (2022)	Nest search Nest search	1160 440	1600 1468	440 1028	12 10	
White-bellied Redstart Luscinia phaenicuroides	Tibet	Lu et al. (2010)	Nest search	1325	4325	3000	38	4
White-throated Dipper Cinclus cinclus	Scotland	Logie (1998)	Nest search	106.08+- 64.80	305.75+- 97.56	200	305	

fledglings are relatively independent after about 1 week, but occasional feeding by adults can occur up to 3 weeks after fledging (Glutz von Blotzheim, 1997); and Alpine tits become independent about 5–6 days after fledging, with occasional feeding events up to 2weeks after fledging (Glutz von Blotzheim & Bauer, 1993). Because feeding frequency decreases after fledging (e.g. mistle thrush chicks are fed up to six times more often during the nestling period than after fledging; Glutz von Blotzheim, 1988), we assume that a record 'adults with food for their young' refers to the nestling period (early breeding stage) in the majority of the cases. However, a substantial portion of the Atlas code 16 observations may actually include fledged broods, because observers are instructed to record the highest Atlas code when more than one behaviour is observed. Therefore, 'adults with food for their young' (Atlas code 16) instead of 'freshly fledged young' (Atlas code 13) is usually recorded in cases when adults with food and fledged young are observed simultaneously.

As an alternative to estimating the dates when the fledged young were reported in 50% of the observations that indicated a brood from a combination of different Atlas codes, we could have used only the dates of observations of 'recently fledged birds' (Atlas code 13) to calculate average dates of fledging; in this case, however, results would have been strongly influenced by observer effort: Early in the season, there are probably fewer observers present at higher elevations, and thus average fledging dates at higher elevations would have been biased towards a later date simply because there are fewer early observations available.

#### 2.3 | Statistical analysis of timing of the broods

We used R version 4.0.3 (R Core Team, 2020) and the package birdring (Korner-Nievergelt & Robinson, 2019) to prepare the data. We used a separate binomial generalized linear model (GLM) to estimate

PATERNO ET AL.					Ecology and Evolution			_EY 9 of 20			
High elevation			Egg-laying date				Fledging				
N	SD	SE	Low elevation	High elevation	Difference in days high versus low	Delay in days/100m	Low elevation	High elevation	Difference in days high versus low	Delay in days/100 m	Comments
63			27 February	2 February	-25	-5.56					
10			April	May/June							
							168.7 [119.7; 215.3]	169.6 [163.2; 175.3]	+1.8 [-47.2; +49.5]	0.26	
High and low together = 103			7 October	12 November	+36	6.16	13 November	19 December	+36	6.16	
140			31 May	10 June	+10	0.89					In total, 28 females were sampled in bott years and not all data were obtained for each female and clutch in each year, so sample sizes vary for different analyses
44			29 May	3 June	+5	1.31	1 July	5 July	+4	1.14	
30							24 June-5 July	22 June-16 July	+13	0.58	
18		4	9 June	19 June	+10	0.33	2 July	21 July	+19	0.63	Fledging dates at low elevation ranged from 7 May to 9 August and at high elevation from 31 May to 9 August
103			8-10 March	17-19 March	+9	4.5					

the proportion of young birds observed as fledged in relation to the two continuous variables date (day of year) and elevation for each year. To do so, we assigned to each observation whether young were certainly fledged or not (a binary response variable y; Table 2). We then used elevation, date and a categorical variable 'year' as predictors. We included a two-way interaction of elevation and date. To account for among-year differences in the onset of spring, we included a random year effect  $d_{year}$  (i.e. the difference between the timing of the brood in a given year and the average timing from all years) on the predictor variable 'date' (day of year). Thus, we assumed that the strength of the increase of the proportion of independent young birds (p) with increasing date as well as its elevational gradient is equal across years, but we allowed the average timing of the broods to vary among years according to a normal distribution:

 $y_i \sim \text{Bernoulli}(p_i)$ 

# $\begin{aligned} \mathsf{logit}(p_i) &= \beta_0 + \beta_1 \mathsf{elevation}_i + \beta_2 \Big( \mathsf{date}_i + d_{\mathsf{year}[i]} \Big) \\ &+ \beta_3 \Big( \mathsf{date}_i + d_{\mathsf{year}[i]} \Big) \mathsf{elevation}_i \end{aligned}$

#### $d_{year} \sim Normal(0, \sigma)$

We thus used a logit-link function and assumed a Bernoulli distribution. We also assumed a sigmoid increase of the proportion of certainly fledged young birds among the observed broods over the breeding season, and we allowed for a gradual change in slope with elevation, that is, we allowed for steeper increase in the certainly fledged young as would be expected when breeding season is shorter at higher elevations. Elevation and day of the year were z-transformed. We fitted the model in Stan (http://mc-stan.org, Carpenter et al., 2017) via the interface rstan (Stan Development Team, 2023) using Hamiltonian Monte Carlo (Betancourt, 2013).

### 10 of 20 WILEY\_Ecology and Evolution

The model code is available in Data **S1**. We simulated four chains of length 2000 and used the second half of each, that is, we used a total 4000 draws to describe the posterior distributions of the model parameters. We thus present the difference in the number of days of the date when 50% of the broods were certainly fledged between elevations as well as the 2.5% and 97.5% quantiles as lower and upper limits of the 95% Bayesian compatibility intervals (Amrhein



FIGURE 1 Map of Switzerland, with yellow dots indicating bird observations used for this study, and blue marks indicating the 41 Swiss Phenology stations of MeteoSwiss that were used to calculate the date of larch budburst at different elevations.

& Greenland, 2022). We present the results for the three elevations low=1650m, medium=1850m and high=2050m, to show the change in proportion of certainly fledged young birds as the season progresses.

#### 3 | RESULTS

#### 3.1 | Temperature and larch budburst

In spring, temperature thresholds below 0°C were exceeded at about the same time at 1500 m and 2200m. With increasing temperature (0–7°C), the difference in exceedance days between 1500 m and 2200m increased, and daily mean air temperatures of 10– 15°C were reached, on average, 34–38 days later at 2200 m compared to 1500m (Figures 3 and S1). However, these differences in the exceedance days between the two elevational bands 2200 m and 1500m showed a high interannual variability. For temperature thresholds between 10°C and 15°C, the difference ranged between 5 days and approximately 70 days in individual years. A clear trend indicating a smaller or larger difference in the exceedance day between the two elevations was not evident; thus, we found no indication that climate change was accelerating warming more rapidly at

TABLE 2 Atlas codes describing observations of a brood in birds (Schweizerische Vogelwarte Sempach, 2019), the developmental stage associated with the specific Atlas code, category in relation to fledging, assigned response category for the analyses (Bernoulli model) and the number of observations per Atlas code.

Atlas	code	Developmental stage Category		Value of response variable	Number of observations
9	Female adult with breeding spot	Incubation or nestlings	Certainly before fledging	0	4
15	Adult carrying faecal sac from the nest	Nestlings	Certainly before fledging	0	5
16	Adult with food for nestlings	Nestlings (or freshly fledged)	Likely before fledging, but after fledging possible	0	853
18	Nest with breeding adult	Incubation or nestlings	Certainly before fledging	0	72
19	Nest with eggs or nestlings	Incubation or nestlings	Certainly before fledging	0	26
13	Recently fledged birds	Fledged	Certainly after fledging	1	1020

Year	Coal tit	Alpine/willow tit	Eurasian chaffinch	Song thrush	Mistle thrush
2013	38	30	11	11	50
2014	114	54	23	16	48
2015	147	44	36	21	59
2016	97	30	54	59	91
2017	52	11	12	5	33
2018	51	20	24	14	35
2019	57	12	22	20	45
2020	52	18	28	21	58
2021	73	13	30	8	43
2022	65	26	24	17	58
Total	764	258	264	192	520

TABLE 3 Number of observations per species and year.
#### PATERNO ET AL.

one elevation versus the other. For example, the difference in the exceedance days increased by 5 days per decade for a temperature threshold of  $10^{\circ}$ C, by 0 days per decade for a  $11^{\circ}$ C and decreased by -3 days per decade for a temperature threshold of  $12^{\circ}$ C (Figure 3).

Between 2013 and 2022, larch budburst in Switzerland started on average 19.2 days later at 2200 m compared to 1500m. Larch budburst, therefore, was delayed by 2.74 days per 100m increase in elevation (Table 4).

# 3.2 | Dates when 50% of the broods are certainly fledged

Overall, we found strong variation from year to year in the dates when young broods certainly fledged (as opposed to 'certainly or likely not fledged') in 50% of observations (Figures 4a-8a, Table 5), with Eurasian chaffinches showing the least variation (Figure 6a, Table 5). However, we found that the date when broods were

#### 

certainly fledged in 50% of observations was relatively similar between high and low elevation in most species. In the following, we compare the date when broods were certainly fledged in 50% of observations at three elevations (low=1650, medium=1850 and high=2050; see also Figures 4–8b, Table 6) in an average year. Due to increased uncertainty in the estimates at high elevation, a comparison between high and low elevation was not possible for all species, so in some cases, we used the medium elevation for comparison with the low elevation.

For coal tits (Figure 4a, Table 5), the date when broods were certainly fledged in 50% of observations was 5.4 days later (1.48 days/100 m) at high compared to low elevation (Figure 4b, Table 6). For Alpine tits (Figure 5a, Table 5), the date when broods certainly fledged in 50% of observations was 0.53 days later (0.19 days/100 m) at high compared to low elevation (Figure 5b, Table 6). For Eurasian chaffinches (Figure 6a, Table 5), we found a delay of 4.5 days (2.86 days/100 m) in the date when broods were certainly fledged in 50% of observations at medium compared to



FIGURE 2 Coloured solid lines show the dates when the broods of coal tit, Alpine tit and song thrush became certainly fledged in 50% of observations in an average year (in this plot, we used only the species and elevations for which estimates had sufficient precision). Dotted lines show the date of mean snow melt-out, based on data from Schano et al. (2021); the date when a temperature threshold of 14°C was exceeded (Figure 3); and larch budburst, defined as the date when 50% of the young of three other songbird species fledged based on data from the literature (Altamirano et al., 2015; Fontanilles, 2022; Levin et al., 2023; Müller et al., 2005, see also Table 1).

### 12 of 20 WILEY\_Ecology and Evolution

low elevation, and the difference between high and medium elevation was similar (6.7 days) but had higher uncertainty, as shown by wider compatibility intervals (Figure 6b, Table 6). The date when song thrush broods were certainly fledged in 50% of observations was about the same at high compared to medium elevation (Figure 7a,b, Tables 5 and 6, 0.29 days/100 m). Nevertheless, we found later 'certainly fledged' observations at high compared to medium and low elevation (grey empty points in Figure 7c). The difference between the dates of the first 'certainly fledged' observations between the three elevations was smaller for mistle thrushes (5.06 days/100 m) than for song thrushes (grey points in Figures 7c and 8c). Song and mistle thrushes often have more than one brood per season, leading to high uncertainty in our estimates at all elevations especially for the mistle thrush (Figure 8b, Table 6). Additionally, there was a lack of observations of 'certainly fledged' broods for mistle thrushes at the end of the season at low elevations, when we still found observations of 'certainly or likely not fledged' broods (see grev points in Figure 8c); thus, it seems like mistle and song thrushes became 'certainly fledged' later at lower compared to higher elevations.



FIGURE 3 Difference in the number of days that a certain temperature threshold was reached at 2200 m compared to 1500 m. Data are based on the dataset TabsD (years 1991–2020) by MeteoSwiss (Frei, 2013). Red data points show the change in number of days per decade over the last 30 years.

# 3.3 | Comparison of environmental variables and fledging dates

The delay in snow melt-out date across elevations (5.7 days/100m; Schano et al., 2021) was similar to the delay in temperature exceedance days at 14°C (4.9–5.4 days/100m; Figure 2). However, the delay in larch budburst timing across elevations was smaller (2.7 days/100m), and the delay in dates when 50% of the broods were certainly fledged was even smaller (coal tits: 1.48 days/100m, Alpine tits: 0.19 days/100m, song thrushes: 0.29 days/100m; Figure 2).

#### 4 | DISCUSSION

We found a similar delay in temperature threshold exceedance (daily mean air temperature 10-15°C) at higher elevations (a delay of 34-38 days at 2200 m compared to 1500m, i.e. 4.9-5.4 days/100m) as Schano et al. (2021) found for the mean snow melt-out date (about 40 days delay at 2200 m compared to 1500m, i.e. 5.7 days/100m). The timing of larch budburst was delayed by an average of 2.7 days/100 m increase in elevation; thus, the delay was slightly shorter than in temperature and snow melt-out.

Despite the harsher conditions at higher elevations earlier in the season, birds were raised with a relatively small delay at higher elevations: The mean delay in the time when broods were certainly fledged in 50% of observations was 1.48 days/100m in coal tits and 0.06 days/100m in Alpine tits, the two species for which we had the clearest results (the narrowest compatibility intervals). Therefore, the investigated songbird species were likely raised under harsher environmental conditions at higher elevations.

Previous studies reported similar elevational differences when investigating fledging dates (Table 1, Figure 2). For example, Müller et al. (2005) found an average delay in fledging date of 1.14 days/100 m for whinchats (*Saxicola rubetra*) in Switzerland, and Fontanilles (2022) found a delay of 0.58 days/100 m in the French Pyrenees. Lu et al. (2010) found a delay in fledging dates of 0.63 days/100 m for white-bellied redstarts (*Hodgsonius phaenicuroides*) in Tibet, and Levin et al. (2023) a delay of 1.54 days/100 m for house wrens (*Troglodytes aedon*) in California. Altamirano et al. (2015) found the largest elevational effect, with a delay in fledging dates of 6.16 days/100 m for thorn-tailed rayaditos (*Aphrastura spinicauda*) in an Andean temperate forest in Chile. Apart from this latter study, it therefore seems not unusual that there is only a slight delay in fledging dates at higher elevations.

TABLE 4 Parameter estimates and 95% CI for larch budburst in relation to elevation and year.

	Standardised coefficients mean [95% CI] in days	Standard deviation of the predictor variable	Unstandardized coefficients mean [95% Cl] in days	Unit of the predictor variable
Intercept	$+904.48 \pm 430.10$			
Elevation	$+0.03\pm0.00$	243 m	$+0.01\pm0.00$	100 m
Year	$-0.41 \pm 0.21$	2.9 days	$-0.14 \pm 0.07$	1 day



FIGURE 4 Coal tit. Grey dots are all observed broods (empty = certainly or likely not fledged, full = certainly fledged; for our definition of those stages, see main text). Lines in (a) show the dates when the broods were certainly fledged in 50% of observations from a given year (for a more straightforward comparison, the uncertainty in our estimates is depicted in the plots (b)). The horizontal grey dashed lines show the average elevations used in (b). Plots in (b) show the modelled proportions of observations from broods certainly or likely not fledged at 1650 m, 1850 m and 2050 m in an average year; dotted lines are 95% Bayesian compatibility intervals. Red dots show the dates when the broods became certainly fledged in 50% of observations of a brood in an average year; red lines are 95% Bayesian compatibility intervals. Plots in (c) show the proportions and 95% Bayesian compatibility intervals of certainly fledged observations, based on raw data, over 20-day bins summarized for three elevational bets (1500–1733, 1734–1967 and 1968–2200 m). Note that what matters are the relative differences in dates among elevations. Estimates and 95% Bayesian compatibility intervals to plots in (a) and (b) are in Tables 5 and 6.

However, elevational gradients in gonadal development may differ from those in fledging dates. In Canada, Bears (2007) found a delay of more than 30 days in breeding readiness (defined as the average date when the functional gonads had developed) of male darkeyed juncos (*Junco hyemalis*) at 2000 m compared to 1000m. This delay in breeding readiness reversed when birds were kept under controlled environmental conditions (constant temperature and photoperiod, unlimited food supply). Birds captured at 2000m and brought to the laboratory were 4–8 days earlier ready to breed compared to birds captured at 1000m (Bears, 2007). Thus, dark-eyed junco males captured at high elevation were ready to breed earlier compared to birds captured at low elevations when exposed to the same conditions (Bears, 2007) and males at high elevations initiated breeding at lower temperatures than their conspecifics at lower elevations. Our results may be explained by a similar mechanism as the one described by Bears (2007). If birds at high elevation initiated breeding at lower temperatures than their conspecifics at low elevations, the elevational gradient in the timing of the broods is steeper compared to the elevational gradient of the temperature threshold exceedance.

The bird species investigated in our study did not seem to adapt to the harsher environmental conditions at higher elevations by raising their brood later at a time when conditions were milder. Rather, such species may have evolved other adaptations to cope with the harsher conditions at higher elevations (Martin et al., 2023). For example, previous studies found morphological adaptations, where birds at higher elevations were smaller but had longer wings, tails or feathers (Bears, 1999, 2007; Lu et al., 2009; Sander & Chamberlain, 2020).

Further, birds living at higher elevations probably have evolved adaptations to cope with increased energy requirements, for example,

## Hand Free WILEY-Ecology and Evolution

PATERNO ET AL

TABLE 5 Estimates to Figures 3-7a. Estimates and 95% Bayesian compatibility intervals (CI; Amrhein & Greenland, 2022) in number of days, in relation to species and year for the mean elevation (1743m).

Year	Coal tit	Alpine / willow tit	Eurasian chaffinch	Song thrush	Mistle thrush
2013	-1.04 [-1.85; -0.38]	-0.04 [-0.55; +0.44]	+0.01 [-0.77; +0.93]	+0.08 [-0.62; +0.92]	-0.98 [-4.10; +0.57]
2014	+0.24 [-0.23; +0.76]	+0.15 [-0.21; +0.68]	-0.13 [-1.26; +0.36]	+0.18 [-0.34; +1.15]	+0.67 [-0.75; +3.05]
2015	+0.35 [-0.09; +0.84]	+0.32 [-0.07; +1.00]	-0.07 [-0.97; +0.46]	-0.02 [-0.70; +0.70]	+0.37 [-1.14; +2.67]
2016	-0.19 [-0.70; +0.34]	-0.09 [-0.64; +0.35]	-0.18 [-1.13; +0.25]	-0.20 [-0.94; +0.26]	-1.15 [-3.71; +0.32]
2017	+0.11 [-0.44; +0.69]	-0.13 [-0.95; +0.33]	+0.01 [-0.83; +0.82]	-0.02 [-0.90; +0.90]	+0.57 [-0.96; +2.94]
2018	+0.03 [-0.54; +0.66]	-0.01 [-0.58; +0.55]	+0.12 [-0.36; +1.34]	+0.03 [-0.74; +0.97]	-0.23 [-2.68; +1.67]
2019	+0.31 [-0.21; +0.94]	-0.09 [-0.74; +0.35]	+0.05 [-0.55; +0.98]	-0.03 [-0.68; +0.54]	-0.34 [-2.64; +1.23]
2020	-0.16 [-0.75; +0.41]	-0.04 [-0.58; +0.44]	+0.05 [-0.53; +0.88]	+0.31 [-0.20; +1.22]	+0.58 [-0.97; +2.98]
2021	+0.00 [-0.50; +0.51]	-0.06 [-0.70; +0.45]	+0.02 [-0.62; +0.76]	-0.15 [-1.35; +0.47]	-0.13 [-2.42; +1.79]
2022	+0.41 [-0.13; +1.01]	+0.08 [-0.34; +0.62]	+0.05 [-0.54; +0.84]	-0.23 [-1.13; +0.25]	+0.55 [-0.99; +3.07]

TABLE 6	Estimates to Figures 3-7b. Estimates and 95% CI in days [1=1 January], in relation to the species and three different elevations
for an avera	age year.

Elevation	Coal tit	Alpine tit	Eurasian chaffinch	Song thrush	Mistle thrush
1650	164.9 [156.7; 173.3]	169.73 [162.8; 177.7]	177.1 [167.0; 187.2]	173.0 [159.4; 189.7]	237.8 [-343.7; 933.9]
1850	167.1 [158.3; 175.6]	170.02 [163.3; 177.1]	181.6 [169.2; 192.7]	170.1 [161.0; 179.4]	203.6 [179.0; 293.1]
2050	170.1 [157.1; 180.4]	170.45 [155.8; 180.3]	188.9 [153.3; 243.0]	169.6 [159.4; 179.1]	192.0 [167.0; 253.3]



FIGURE 5 Alpine/willow tit; for explanation, see Figure 4.



FIGURE 6 Eurasian chaffinch; for explanation, see Figure 4.

increased parental investment. Badyaev & Ghalambor (2001) investigated the life history strategies of 24 pairs of bird species along an elevational gradient and found an increased male investment additionally to the female investment for species living at higher elevations compared to species living at lower elevations. Also, they found that birds at higher elevations raised fewer but higher-quality offspring (Badyaev & Ghalambor, 2001). With increased parental investment at high elevations and fewer offspring, young birds may be able to grow faster and fledge earlier.

Another adaptation at higher elevations could be to build bigger or thicker nests: For example, Widmer (1993) found that Eurasian blackcaps (Sylvia atricapilla) built bigger and better insulated nests in the mountains compared to the lowlands. Blue tits also built bigger nests (Britt & Deeming, 2011) and changed the nest cup lining material (Mainwaring & Hartley, 2008) depending on temperatures during the nest-building period. Britt and Deeming (2011) found clearer temperature-related differences in nest size for blue tits than for great tits, and Schöll and Hille (2014) found no clear change in insulation of great tit nests along an elevational gradient (488–878 m). It therefore seems that temperature-related differences in nest insulation or nest size are species-specific.

Birds breeding at higher elevations are often not able to have a second brood due to a shortened season (Dillon & Conway, 2015: Labarbera & Lacey, 2018; Yeh & Price, 2004), which can make it difficult to compare breeding dates with lower elevations, where second broods may be possible. When birds have more than one brood, the observations of broods before and after fledging spread over a longer time, and therefore, it is more difficult to estimate the dates when 50% of the broods are certainly fledged; this is probably the main reason why for mistle thrushes and song thrushes, the estimated proportion of certainly fledged broods was lower than 100% at the end of the breeding season. Among our study species, especially song thrushes and mistle thrushes are known to often have more than one brood (Glutz von Blotzheim, 1988). For the mistle thrush, we could not obtain reasonable estimates for the mean date when broods were certainly fledged in 50% of observations, and mistle thrushes usually have more than one brood even at higher elevations. In contrast, song thrushes may have only one brood at medium and high elevations; a reason may be that the number of broods in song thrushes is more dependent on weather conditions (Glutz von Blotzheim, 1962; Mattes et al., 2005) than in mistle thrushes.



FIGURE 7 Song thrush; for explanation, see Figure 4.

Eurasian chaffinches (Glutz von Blotzheim, 1997), coal tits (Glutz von Blotzheim & Bauer, 1993) and Alpine tits (Glutz von Blotzheim & Bauer, 1993) seem to usually have only one brood both at lower and higher elevations in the Alps. For coal tits and Alpine tits, we were able to estimate the mean date when broods became certainly fledged in 50% of observations at high, medium and low elevations. For the Eurasian chaffinch, it was more difficult to examine the mean date when broods were certainly fledged in 50% of observations at high elevation, because the number of observations was low. This may have been due to lower breeding density (Knaus et al., 2018) or lower breeding success of Eurasian chaffinches at higher elevations compared to coal tits and Alpine tits. Species with a main distribution in northern latitudes or high elevations such as coal tits and Alpine tits might be better adapted to harsher conditions than species with a main distribution in southern latitudes or lower elevations such as the Eurasian chaffinch.

Still, there may be differences in detection probabilities of feeding adults or begging young in different developmental stages that may have influenced the number of observations and thus our timing estimates. In our study, we did not take such detection probabilities into account, since to the best of our knowledge there are no published estimates on detection probabilities of broods of songbirds for different developmental stages of the young, which could be addressed in future studies. Our reported elevational gradients in the timing of the broods therefore rely on the assumption that differences in detection probability among the different breeding stages are not dependent on elevation.

In summary, and similar to previous studies, we found that songbirds delay breeding with increasing elevations to a lower degree than expected if they would breed at similar environmental conditions at all elevations. Therefore, the young of the investigated songbirds were raised under harsher environmental conditions at higher elevations and probably have evolved adaptations to cope with such conditions, rather than postponing breeding dates to warmer conditions. By using a dataset from a nationwide citizen science bird monitoring scheme, we were able to obtain estimates on the date when broods became certainly fledged without the need to search for nests and thus without causing disturbances at nests. In the future, it would be interesting to expand the study to a larger geographic region allowing for comparisons of mountain regions at different latitudes and of species with differing degrees



FIGURE 8 Mistle thrush; for explanation, see Figure 4.

of adaptions to living at high elevations and thus to increase our understanding of how bird species are able to adapt to living at higher elevations.

#### AUTHOR CONTRIBUTIONS

Julia Paterno: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); methodology (equal); project administration (equal); validation (equal); visualization (equal); writing - original draft (equal); writing - review and editing (equal). Fränzi Korner-Nievergelt: Conceptualization (equal); data curation (equal); formal analysis (equal); methodology (equal); project administration (equal); supervision (equal); validation (equal); visualization (equal); writing - original draft (equal); writing - review and editing (equal). Stefanie Gubler: Data curation (equal): formal analysis (equal); validation (equal); visualization (equal); writing - original draft (equal); writing - review and editing (equal). Pia Anderwald: Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); supervision (equal); validation (equal); writing - original draft (equal); writing - review and editing (equal). Valentin Amrhein: Conceptualization (equal); data curation (equal); methodology (equal); project administration (equal); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal).

#### ACKNOWLEDGEMENTS

This project was funded by the Zigerli Hegi Foundation, the Swiss National Park, the Swiss Ornithological Institute and the Nukahiva Foundation. For analysis, we used services provided by the Swiss Ornithological Institute and the Swiss Federal Office of Meteorology and Climatology, MeteoSwiss.

#### CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data and code can be found in Data S1.

#### ORCID

Julia Paterno <sup>©</sup> https://orcid.org/0009-0009-4347-8139 Fränzi Korner-Nievergelt <sup>©</sup> https://orcid.org/0000-0001-9081-3563 Stefanie Gubler <sup>©</sup> https://orcid.org/0000-0002-3733-953X

### 18 of 20 WILEY\_Ecology and Evolution

Pia Anderwald <sup>(2)</sup> https://orcid.org/0000-0002-2594-2286 Valentin Amrhein <sup>(2)</sup> https://orcid.org/0000-0001-5173-4571

#### REFERENCES

- Altamirano, T. A., Ibarra, J. T., De La Maza, M., Navarrete, S. A., & Bonacic, C. (2015). Reproductive life-history variation in a secondary cavity-nester across an elevational gradient in Andean temperate ecosystems. Auk, 132(4), 826–835. https://doi.org/10. 1642/AUK-15-28.1
- Amrhein, V., & Greenland, S. (2022). Discuss practical importance of results based on interval estimates and *p*-value functions, not only on point estimates and null *p*-values. *Journal of Information Technology*, 37(3), 316–320. https://doi.org/10.1177/02683962221105904
- Badyaev, A. V., & Ghalambor, C. K. (2001). Evolution of life histories along elevational gradients: Trade-off between parental care and fecundity. *Ecology*, 82(10), 2948-2960. https://doi.org/10.1890/ 0012-9658(2001)082[2948:EOLHAE]2.0.CO;2
- Bairlein, F., Berthold, P., Querner, U., & Schlenker, R. (1980). Die Brutbiologie der Grasmücken Sylvia atricapilla, borin, communis und curruca in Mittel- und N-Europa. Journal für Ornithologie, 121(4), 325–369. https://doi.org/10.1007/bf01643331
- Bauer, H.-G., Bezzel, E., & Fiedler, W. (2012). Das Kompendium der Vögel Mitteleuropas (2nd ed.). AULA-Verlag Wiesbaden.
- BDM Coordination Office. (2014). Swiss biodiversity monitoring BDM. Description of methods and indicators. *Environmental Studies*, 1410, 103.
- Bears, H. (2007). Elevation and the avian phenotype: field and experimental studies of breeding dark-eyed juncos. PhD Thesis.
- Betancourt, M. (2013). Generalizing the No-U-Turn sampler to Riemannian manifolds. *arXiv* 1304, Nr. 1920.
- Blanco, G., Fargallo, J. A., Cuevas, J. A., & Tella, J. L. (1998). Effects of nest-site availability and distribution on density-dependent clutch size and laying date in the Chough Pyrrhocorax pyrrhocorax. Ibis, 140(2), 252-256. https://doi.org/10.1111/j.1474-919x.1998.tb043 86.x
- Brändli, U. B. (1998). Die haufigsten Waldbaume der Schweiz. Ergebnisse aus dem Landesforstinventar 1983–85: Verbreitung, Standort und Haufigkeit von 30 Baumarten. In Berichte – Eidgenossischen Forschungsanstalt für Wald, Schnee und Landschaft, 342. Eidgenössische Foschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf.
- Britt, J., & Deeming, D. C. (2011). First-egg date and air temperature affect nest construction in blue tits *Cyanistes caeruleus*, but not in great tits *Parus major*. *Bird Study*, *58*(1), 78–89. https://doi.org/10. 1080/00063657.2010.524916
- Brügger, R., & Vasella, A. (2003). Pflanzen im Wandel der Jahreszeiten, Anleitung für phänologische Beobachtungen/Les plantes au cours des saisons. Guide pour observation phénologiques (p. 288). Geographica Bernensia.
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical* Software, 76(1), 1–32. https://doi.org/10.18637/jss.v076.i01
- Clouet, M. (2005). Breeding biology of Coal Tit Parus ater in Central Pyrenees. Alauda, 73(2), 81–90.
- Daan, S., Dijkstra, C., Drent, R., & Meijer, T. (1989). Food supply and the annual timing of avian reproduction. Acta XIX Congressus Internationalis Ornithologici, Volume I. 19th International Ornithological Congress, I, 392–407.
- Delestrade, A. (2002). Breeding biology and distribution of the Northern Raven Corvus corax in Corsica. Alauda revue internationale d'ornithologie: Revue trimestrielle de la Société d'Etudes Ornithologiques de France, 70(2), 293–300.

- Dillon, K. G., & Conway, C. J. (2015). Elevational gradient in clutch size of red-faced warblers. *Journal of Field Ornithology*, 86(2), 163–172. https://doi.org/10.1111/jofo.12099
- Driver, J. (2005). A study of breeding carrion crows Corvus corone in Snowdonia. Welsh Birds, 4(3), 227–235.
- Dunn, P. O., Thusius, K. J., Kimber, K., & Winkler, D. W. (2000). Geographic and ecological variation in clutch size of tree swallows. Auk, 117(1), 215–221. https://doi.org/10.1642/0004-8038(2000)117[0215: GAEVIC]2.0.CO;2
- Fontanilles, P. (2022). Abundance, reproduction and habitat of the whinchat Saxicola rubetra in the Pyrenees: Compatibility with mowing and grazing practices. Alauda, 90(3), 215–232.
- Frei, C. (2013). Interpolation of temperature in a mountainous region using nonlinear profiles and non-Euclidean distances. *International Journal of Climatology*, 34(5), 1585–1605. https://doi.org/10.1002/ joc.3786
- Gibbs, H. (2007). Climatic variation and breeding in the Australian Magpie (Gymnorhina tibicen): A case study using existing data. Emu, 107(4), 284–293. https://doi.org/10.1071/MU07022
- Gil-Delgado, J. A., Lopez, G., & Barba, E. (1992). Breeding ecology of the blue tit *Parus caeruleus* in eastern Spain: A comparison with other localities with special reference to Corsica. *Ornis Scandinavica*, 23(4), 444–450. https://doi.org/10.2307/3676675
- Glutz von Blotzheim, U. (1962). Die Brutvögel der Schweiz. Verlag Aargauer Tagblatt.
- Glutz von Blotzheim, U. (1988). II Passeriformes (2. Teil) Turdidae. In Handbuch der Vögel Mitteleuropas (Vol. 11, p. 1226). Akademische Verlagsgesellschaft.
- Glutz von Blotzheim, U. (1997). II: Passeriformes (5.Teil) Fringillidae (Vol 14). In Handbuch der Vögel Mitteleuropas (Vol. 14, p. 1242). Akademische Verlagsgesellschaft.
- Glutz von Blotzheim, U., & Bauer, K. M. (1993). I: Passeriformes (4. Teil) Muscicapidae – Paridae. In *Handbuch der Vögel Mitteleuropas* (Vol. 13, p. 808). Akademische Verlagsgesellschaft.
- Hinks, A. E., Cole, E. F., Daniels, K. J., Wilkin, T. A., Nakagawa, S., & Sheldon, B. C. (2015). Scale-dependent phenological synchrony between songbirds and their Caterpillar food Aource. American Naturalist, 186(1), 84–97. https://doi.org/10.1086/681572
- Illán, J. G., Gutiérrez, D., Díez, S. B., & Wilson, R. J. (2012). Elevational trends in butterfly phenology: Implications for species responses to climate change. *Ecological Entomology*, 37(2), 134–144. https://doi. org/10.1111/j.1365-2311.2012.01345.x
- Johnson, L. S., Iser, K. M., Molnar, H. A., Nguyen, A. V., & Connor, C. L. (2018). Clutch and egg size of tree swallows along an elevational gradient. *Journal of Field Ornithology*, 89(3), 234–241. https://doi. org/10.1111/jofo.12262
- Johnson, L. S., Ostlind, E., Brubaker, J. L., Balenger, S. L., Johnson, B. G. P., & Golden, H. (2006). Changes in egg size and clutch size with elevation in a Wyoming population of Mountain Bluebirds. *Condor*, 108(3), 591-600. https://doi.org/10.1650/0010-5422(2006) 108[591:CIE5AC]2.0.CO:2
- Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P., Martí, D., Anton, M., Klvaňová, A., Kalyakin, M. V., Bauer, H.-G., & Foppen, R. P. B. (2020). European breeding bird atlas 2: Distribution, Abundance and Change. European Bird Census Council & Lynx Edicions.
- Kleindorfer, S. (2007). The ecology of clutch size variation in Darwin's Small Ground Finch Geospiza fuliginosa: Comparison between lowland and highland habitats. *Ibis*, 149(4), 730–741. https://doi.org/ 10.1111/j.1474-919X.2007.00694.x
- Knaus, P., Antoniazza, S., Wechsler, S., Guélat, J., Kery, M., Strebel, N., & Sattler, T. (2018). Schweizer Brutvogelatlas 2013-2016. Verbreitung und Bestandsentwicklung der Vögel in der Schweiz und im Fürstentum Liechtenstein. Schweizerische Vogelwarte Sempach.

#### PATERNO ET AL.

- Korner-Nievergelt, F., & Robinson, R. (2019). Birdring: Methods to analyse ring re-encounter data. R Package Version 1.4. https://CRAN.R-proje ct.org/package=birdring
- Labarbera, K., & Lacey, E. A. (2018). Breeding season length and nest mortality drive cryptic life history variation in dark-eyed juncos (*Junco hyemalis*) breeding across a montane elevational gradient. Auk, 135(2), 284–298. https://doi.org/10.1642/AUK-17-184.1
- Lack, D. (1950). The breeding seasons of European birds. *Ibis*, 92, 288-316.
- Levin, R. N., Correa, S. M., Freund, K. A., & Fuxjager, M. J. (2023). Latitudinal and elevational variation in the reproductive biology of house wrens. *Troglodytes Aedon. Ecology and Evolution*, 13(9), 1–15. https://doi.org/10.1002/ece3.10476
- Logie, J. W. (1998). Population ecology and lifetime reproductive success of dippers Cinclus cinclus. [Doctoral dissertation]. University of Stirling.
- Lu, X., Ke, D. H., Zeng, X. H., & Yu, T. L. (2009). Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: Response to more stressful environments. *Journal* of Arid Environments, 73(12), 1103–1108. https://doi.org/10.1016/j. jaridenv.2009.06.011
- Lu, X., Yu, T., Liang, W., & Yang, C. (2010). Comparative breeding ecology of two White-bellied redstart populations at different altitudes. *Journal of Field Ornithology*, 81(2), 167–175. https://doi.org/10. 1111/j.1557-9263.2010.00274.x
- Mainwaring, M. C., & Hartley, I. R. (2008). Seasonal adjustments in nest cup lining in blue tits *Cyanistes caeruleus*. Ardea, 96(2), 278–282. https://doi.org/10.5253/078.096.0213
- Martin, K., de Zwaan, D. R., Scridel, D., & Altamirano, T. A. (2023).

  Avian adaptations to High Mountain habitats. In D. E.
  Chamberlain, A. Lehikoinen, & K. Martin (Eds.), Ecology and conservation of mountain birds (pp. 35–89). Cambridge University Press.
- Mattes, H., Maurizio, R., & Bürkli, W. (2005). Die Vogelwet im Oberengadin, Bergell und Puschlav. Ein Naturführer zur Avifauna in einem inneralpinen Gebiet. Schweizerische Vogelwarte Sempach.
- Müller, M., Spaar, R., Schifferli, L., & Jenni, L. (2005). Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (*Saxicola rubetra*). Journal of Ornithology, 146(1), 14–23. https://doi. org/10.1007/s10336-004-0059-0
- Ogden, L. J. E., Martin, M., & Martin, K. (2012). Mating and breeding success decline with elevation for the pacific wren (*Troglodytes pacificus*) in coastal mountain forests. *Wilson Journal Of Ornithology*, 124(2), 270–276. https://doi.org/10.1676/11-186.1

Ormerod, S. J., & Tyler, S. J. (1987). Aspects of the breeding ecology of welsh grey wagtails Motacilla cinerea. Bird Study, 34(1), 43–51. https://doi.org/10.1080/00063658709476935

- Ornitho (2023). www.ornitho.ch
- Pereyra, M. E. (2011). Effects of snow-related environmental variation on breeding schedules and productivity of a high-altitude population of dusky flycatchers (*Empidonax oberholseri*). The Auk, 128(4), 746–758.
- Perfito, N., Tramontin, A. D., Meddle, S., Sharp, P., Afik, D., Gee, J., Ishii, S., Kikuchi, M., & Wingfield, J. C. (2004). Reproductive development according to elevation in a seasonally breeding male songbird. Oecologia, 140(2), 201–210. https://doi.org/10.1007/s0044 2-004-1576-5
- R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.r-project. org/
- Sander, M. M., & Chamberlain, D. (2020). Evidence for intraspecific phenotypic variation in songbirds along elevation gradients in central Europe. *Ibis*, 162(4), 1355–1362. https://doi.org/10.1111/ibi.12843

#### 

- Saracco, J. F., Siegel, R. B., Helton, L., Stock, S. L., & DeSante, D. F. (2018). Phenology and productivity in a montane bird assemblage: Trends and responses to elevation and climate variation. *Global Change Biology*, 25(3), 985–996. https://doi.org/10.1111/gcb.14538
- Schano, C., Niffenegger, C., Jonas, T., & Korner-Nievergelt, F. (2021). Hatching phenology is lagging behind an advancing snowmelt pattern in a high-alpine bird. *Scientific Reports*, 11, 22191. https://doi. org/10.1038/s41598-021-01497-8
- Schöll, E. M., & Hille, S. M. (2014). Do great tits Parus major nesting at high altitudes build better insulated nests? Ardeola, 61(2), 323–333. https://doi.org/10.13157/arla.61.2.2014.323
- Schweizerische Vogelwarte Sempach. (2019). Avifaunistik-Merkblatt. https://www.vogelwarte.ch/modx/assets/files/projekte/ueber wachung/id/Aussergewoehnliche\_Beobachtungen\_d.pdf
- Smith, K. G., & Andersen, D. C. (2014). Snowpack and variation in reproductive ecology of a montane ground-nesting passerine, Junco hyemalis. Ornis Scandinavica, 16(1), 8–13.
- Stan Development Team. (2023). RStan: The R interface to Stan. R package version 2.32.3. https://mc-stan.org/
- Stier, A., Delestrade, A., Zahn, S., Arrivé, M., Criscuolo, F., & Massemin-Challet, S. (2014). Elevation impacts the balance between growth and oxidative stress in coal tits. *Oecologia*, 175(3), 791–800. https:// doi.org/10.1007/s00442-014-2946-2
- Swiss Ornithological Institute. (2019). Avifaunistik-Merkblatt. Swiss Ornithological Institute.
- Tavecchia, G., Pradel, R., Lebreton, J.-D., Biddau, L., & Mingozzi, T. (2002). Sex-biased survival and breeding dispersal probability in a patchy population of the Rock Sparrow *Petronia petronia*. *Ibis*, 144(2), E79– E87. https://doi.org/10.1046/j.1474-919x.2002.00059.x
- Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., MacKay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., ... Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, 535(7611), 241–245. https://doi.org/10. 1038/nature18608
- Verhagen, I., Tomotani, B. M., Gienapp, P., & Visser, M. E. (2020). Temperature has a causal and plastic effect on timing of breeding in a small songbird. *Journal of Experimental Biology*, 223(8), 1–7. https://doi.org/10.1242/jeb.218784
- Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272(1581), 2561–2569. https://doi.org/10.1098/ rspb.2005.3356
- Visser, M. E., & Holleman, L. J. M. (2001). Warmer springs disrupt the synchrony of oak and winter moth phenology. Proceedings of the Royal Society B: Biological Sciences, 268(1464), 289–294. https://doi. org/10.1098/rspb.2000.1363
- Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., Monnerat, C., Rebetez, M., Rixen, C., Strebel, N., Schmidt, B. R., Wipf, S., Wohlgemuth, T., Yoccoz, N. G., & Lenoir, J. (2021). Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biological Reviews*, 96(5), 1816–1835. https://doi.org/10.1111/brv.12727
- Widmer, M. (1993). Brutbiologie einer Gebirgspopulation der Gartengrasmücke Sylvia borin. Ornithologische Beobachter, 90(2), 85-113.
- Williams, T. D. (2012). Physiological adaptations for breeding in birds. Princeton University Press.
- Yeh, P. J., & Price, T. D. (2004). Adaptive phenotypic plasticity and the successful colonization of a novel environment. *American Naturalist*, 164(4), 531–542. https://doi.org/10.1086/423825

## 20 of 20 WILEY\_Ecology and Evolution

 Zang, H. (1980). Der Einfluß der Höhenlage auf Siedlungsdichte und Brutbiologie höhlenbrütender Singvögel im Harz. Journal of Ornithology, 121(4), 371–386. https://doi.org/10.1007/bf01643332
 Zang, H. (1982). Der Einfluß der Höhenlage auf Alterszusammensetzung und Brutbiologie bei Kohl- und Blaumeise (Parus major, P. caeruleus) im Harz. Journal of Ornithology, 123, 145–154. https://doi.org/10.

SUPPORTING INFORMATION

1007/BF01645054

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

How to cite this article: Paterno, J., Korner-Nievergelt, F., Gubler, S., Anderwald, P., & Amrhein, V. (2024). Alpine songbirds at higher elevations are only raised with a slight delay and therefore under harsher environmental conditions. *Ecology and Evolution*, 14, e70049. <u>https://doi.org/10.1002/</u> ece3.70049

#### APPENDIX



FIGURE A1 Timeline of breeding dates (data obtained from Bauer et al., 2012), Atlas code descriptions and the developmental stage assigned for the five investigated songbird species. The dark grey shading shows the minimum time, the light grey shading the maximum time needed for a certain breeding stage. The lined area indicates the time period where the two developmental stages in our study overlap.

PATERNO ET AL.

# General discussion

he aim of this thesis was to investigate behavioural changes of songbirds

depending on physical environmental variables. On the one hand, we investigated changes in the singing behaviour of songbirds according to different environmental variables, like e.g. increased levels of anthropogenic noise or moon phase, in a near-natural area. On the other hand, we examined differences in breeding behaviour of songbirds along an elevational gradient. For this purpose, we selected common songbird species of the SNP that breed across a large elevational range in Switzerland. Three of the four conducted studies refer to the woodlands of the SNP, where the increased noise level along the Ofenpass road (running through the SNP) stands in strong contrast to the highly undisturbed areas in the rest of the SNP. Thus, the SNP represented a suitable study area to investigate effects of anthropogenic noise in a near-natural area.

### 1. Effects of anthropogenic noise

In Chapters 1, 2 and 3 we investigated changes in the singing behaviour of seven songbird species according to physical environmental variables. We found differing effects in the singing behaviour of the investigated songbird species depending on the examined variables. In the following we discuss the effects of anthropogenic noise; the discussion on the other environmental factors can be found in the section below (2. Effects of additional environmental variables).

Birds started to sing earlier at dawn in areas with increased levels of road noise, when accounting for other physical environmental variables (i.e., date, temperature, moon phase, elevation and aspect; Chapter 1). When investigating the effects of construction noise (and other environmental variables: temperature, date, cloud cover), we found consistent or contrasting effects in the start of dawn singing, depending on the number of analysis days (Chapter 2). When conducting the analysis with our own temperature data including less analysis days, we found consistent results: All six investigated songbird species started to sing earlier at the construction site during construction works than would be expected from the change (before vs. during construction works) in start of dawn singing at the control site with normal road noise. In contrast, when we added three more days, using temperature data from a nearby weather station, the effects reversed, and all six investigated bird species started to sing later or at about the same time at the construction site during construction works than could be expected from the change (before vs. during construction works) in start of dawn singing at the control site with normal road noise. Thus, we were not able to draw an interference on the main study question but used this case as a warning about drawing strong conclusions based on "statistically significant" results, especially from small-scale studies.

In Chapter 3 we investigated changes in singing activity of coal tits depending on road noise level, date, temperature and habitat type. Coal tits produced relatively more song phrases per minute during noisy times and in noisy areas compared to more silent times and areas.

Anthropogenic noise, thus, seemed to affect the singing behaviour of the investigated songbird species (start of dawn singing / singing activity) in our studies. Differences in the direction of effects or effect size may be also due to differences in data collection (i.e., sampling variation; Berner & Amrhein, 2022). The number of data points varied strongly between the two studies described in Chapter 1 and 2: For Chapter 1, we used 112 automated recording units (sound loggers), and analysed ten days of data. For Chapter 2, in contrast, we had one control and one treatment site and analysed four weeks of data. The reliability of the results of Chapter 1 therefore may be higher than the results of Chapter 2, and the inconsistency in the direction of the effects in the start of dawn singing in Chapter 2 may be due to the low number of analysis days.

All six investigated bird species started to sing earlier in areas with increased levels of road noise compared to completely silent areas (Chapter 1); this is in line with the results of previous studies on anthropogenic noise (Arroyo-Solís et al., 2013; Dominoni et al., 2016; Gil et al., 2015). A proximate explanation for an earlier start of singing at dawn near roads could be that birds may wake up earlier due to increased traffic noise in the morning. Several previous studies, however, observed that birds changed their singing behaviour also in noisy areas (i.e., Bayne et al., 2008; McClure et al., 2013; Polak et al., 2013), not only during noisy times. Thus, birds may try to avoid being masked by starting to sing earlier at dawn.

It should be noted that the biological consequences of temporal changes in singing behaviour remain unexplained, and it is unclear whether those temporal changes affect birds negatively or positively. Previous studies observed a higher extra-pair paternity in male birds that started dawn singing earlier compared to birds with a later start of dawn singing (Dolan et al., 2007; Kempenaers et al., 2010; Poesel et al., 2006). For example, Poesel et al. (2006) observed that male blue tits (*Cyanistes caeruleaus*) that started dawn singing about six minutes earlier had more mating partners and a higher probability of extra-pair paternity compared to conspecific males that started dawn singing later. Poesel et al. (2006) concluded that females may use the start of dawn singing as an honest signal (i.e., for the quality of a male). Kempenaers et al. (2010) observed a similar effect: Blue tits that woke up earlier due to increased light levels had twice as much extra pair mates compared to males living in darker territories. Thus, singing early at dawn could lead to a higher reproductive success (Kempenaers et al., 2010; Poesel et al., 2006).

This possible increase in reproductive success could be reduced by an increased mortality of adults and the resulting decrease in breeding success in territories near roads. For example, Holm & Laursen (2011) observed a reduced fledging success in great tits near a road with fast traffic compared to no disturbance or a road with slow traffic. The number of eggs was similar at all three sites, but the average number of fledglings was reduced and the number of dead broods was up to 40% higher near the fast traffic road compared to no disturbance or the slow traffic road (Holm & Laursen, 2011). The authors suggested that the higher mortality of broods and the lower number of fledglings was likely due to increased mortality rates of the parents. Kuitunen et al. (2003) also found reduced breeding success for pied flycatchers (Ficedula hypoleuca) in territories near roads compared to territories further away. The number of successful broods was nearly twice as high further away (90 – 130 m from the road) compared to near the road (10 – 20 m; Kuitunen et al., 2003). Also Kuitunen et al. (2003) postulated that reduced survival rates of parent birds might be the possible reason for differences in reproductive success. In European countries, millions of birds come to death yearly due to road kill (Erritzoe et al., 2003), and small woodland songbirds, foraging in shrubs and small trees, seem to be most vulnerable (Santos et al., 2016).

Previous studies also showed a reduced species richness / abundance near roads: For example, McClure et al. (2013) observed a 28% higher bird abundance in migratory birds in silent compared to noisy periods, and Polak et al. (2013) observed a decrease in species richness and diversity of woodland songbirds with increasing proximity to roads. Thus, territories near roads may be less suitable for birds, and species richness and diversity may be reduced at noisy locations, such as the Ofenpass road.

### 2. Effects of additional environmental variables

In Chapters 1, 2 and 3 we investigated changes in the singing behaviour of six songbird species according to physical environmental variables. Besides the effects of anthropogenic noise (that are discussed in the section above: 1. Effects of anthropogenic noise), we examined the effects of different environmental variables like temperature, habitat, cloud cover, elevation and aspect, as well as moon phase and date. In Chapter 1 we observed small but consistent effects in start of dawn singing relative to moon phase, temperature and aspect over all six investigated species, while the effects of date and elevation were more species-specific. In Chapter 2 we found

consistent effects in start of dawn singing according to temperature: All six investigated songbird species started singing earlier after warmer nights. The effect of cloud cover and date varied depending on the number of analysis days: When using our own temperature including less analysis days, five of six songbird species started singing earlier relative to sunrise as the season progressed, and two of six songbird species started singing earlier on days with 100% cloud cover. When using data from a nearby weather station including three more days, only two of six songbird species started singing earlier relative to sunrise as the season progressed, and one of six songbird species started singing earlier on days with 100% cloud cover. In Chapter 3, we investigated the effects of road noise, date, temperature and habitat on the singing activity of coal tits (i.e., number of song phrases per minute). We observed a higher number of song phrases per minute earlier in the season compared to later in the season, during times with mean temperatures compared to higher and lower temperatures, and in mountain pine compared to mixed forests.

We found consistent effects of temperature on the start of dawn singing in Chapters 1 and 2: All investigated songbird species started singing earlier at dawn after warmer nights. Furthermore, singing activity of coal tits was highest during times with mean temperatures (Chapter 3). The effects of date seemed to differ between Chapters 1 and 2. For example, in Chapter 1, we observed a later start of dawn singing for coal tits as the season progressed (day 162 vs. 132), but in Chapter 2, we observed an earlier start of dawn singing for coal tits as the season progressed (day 140 vs. 111). Coal tits show a peak of singing activity between the end of March and mid-May (Glutz von Blotzheim & Bauer, 1993) and like several other songbird species (i.e, Brown, 1963; Bruni et al., 2014; Hegelbach & Spaar, 2000b; Holmes & Dirks, 1978; Merilä & Sorjonen, 1994; Naguib et al., 2016; Slagsvold, 1977; Welling et al., 1995), male coal tits (Glutz von Blotzheim & Bauer, 1993) decrease their singing behaviour (i.e., decreased singing frequency or later start of dawn singing) after clutch initiation. This is in line with the results in Chapter 1. Since the study period in Chapter 2 was about one month earlier in the season (mid-April to mid-May) compared to the study period in Chapter 1 (mid-May to mid-June), we assume that coal tits were at different breeding stages and thus showed different singing behaviour. In Chapter 2, coal tits were probably at an early breeding stage and continued singing early to defend their territory and female; in Chapter 1, in contrast, coal tits had probably already started their brood and therefore stopped singing early. We observed a decrease in singing activity in coal tits as the season progressed in Chapter 3, where we investigated a similar time period as in Chapter 1 (beginning of May until the beginning of June). Thus, the results from Chapter 3 support the prediction that coal tits may be at a late breeding stage at the beginning of June and thus may not need to continue singing early or at high intensity.

In Chapter 4 we investigated differences in the breeding phenology of five common songbird species along an elevational gradient and compared the results with differences in climatic conditions between higher and lower elevations. Timing of breeding seemed to be similar at high and low elevations, thus birds at high elevations probably breed under harsher environmental conditions compared to their conspecifics in the lowlands.

Our observations on the singing behaviour of mountain woodland songbirds are in line with the results of previous studies. We found differences in singing behaviour according to physical environmental variables for all investigated songbird species. In contrast, the timing of breeding in birds may be less dependent on environmental variables; for birds at higher elevations, it may be beneficial to start breeding at about the same time as at lower elevations, rather than waiting for optimal environmental conditions.

### 3. Working with automated recording units

To investigate changes in the singing behaviour of songbirds in Chapters 1 and 3 we used sound loggers. Prior to data collection we tested and compared detection distances for two types of sound loggers (SM4 vs Audiomoth). Detection distances were similar in both devices, but SM4's performed somewhat better in woodland when the sound source was at a distance of more than 80 m from the sound logger. Comparisons between the results of Chapter 1 (Audiomoths) and Chapter 3 (SM4 sound loggers) have to be treated cautiously, since the detection probability in Chapter 1 might be lower than in Chapter 3.

Furthermore, detection probability varied depending on the species and type of vocalization (i.e., song or call), and thus there may be differences in the detection probability between different species in our studies. Direct comparisons between different species may therefore be difficult.

One of several advantages that sound loggers have is the possibility to collect a large amount of data in a very short time period with comparably low effort. However, the analysis of such high data volumes is not yet optimized. In the present study, we did the data analysis manually, since the precision of the results conducted with the help of artificial intelligence (AI) was not sufficient for our purpose. Due to the rapid development in the sector of AI, it may be possible in the future to analyse big datasets with low effort. Future studies may conduct the analysis done in Chapters 1, (2) and 3 with much more data and then compare those new results with the results from this thesis, as we did in Chapter 3. Such an analysis may confirm the actual results, or may lead to completely different conclusions, as we show in Chapter 3.

### 4. Conclusions

his thesis sheds light on the effects of physical environmental variables

on the behaviour of mountain woodland songbirds. The unique situation of a completely protected area (SNP) disturbed by a cantonal road running through it allowed us to investigate the effects of anthropogenic noise in an Alpine near-natural area. In the following the main conclusions are summarized as four take-home messages.



 ${igmmode M}$ oon phase, aspect, temperature and road noise had small but

consistent effects on start of dawn singing relative to sunrise for all six investigated songbird species. The effects of elevation and date were more species-specific.



When using slightly different datasets on one of the investigated

variables (temperature), we found differing results between the two analysis: The effects of temperature were consistent for all six investigated songbird species, but the effects of cloud cover, date and anthropogenic noise varied strongly between the two analysis. We thus warn against drawing strong conclusions from single studies, even if some of the results may be "statistically significant".



Coal tits showed increased singing activity at times and in areas with

increased levels of road noise and in pine forest compared to mixed forest. Temperature and date had smaller effects on the singing activity of coal tits.



In the five investigated songbird species, offspring were raised with a

relatively small delay at higher elevations, despite the harsher conditions earlier in the season.

In conclusion, we found changes in singing behaviour in the six investigated songbird species according to physical environmental variables. Bird species adapted to alpine regions may have evolved adaptations to cope with the harsh environmental conditions at higher elevations, and anthropogenic factors such as road or construction noise can affect bird behaviour even in a highly protected area.

### References

- Arroyo-Solís, A., Castillo, J. M., Figueroa, E., López-Sánchez, J. L., & Slabbekoorn, H. (2013). Experimental evidence for an impact of anthropogenic noise on dawn chorus timing in urban birds. *Journal of Avian Biology*, 44, 288–296. https://doi.org/10.1111/j.1600-048X.2012.05796.x
- Bayne, E. M., Habib, L., & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energy-sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, 22, 1186–1193. https://doi.org/10.1111/j.1523-1739.2008.00973.x
- Berner, D., & Amrhein, V. (2022). Why and how we should join the shift from significance testing to estimation. *Journal of Evolutionary Biology*, 35, 777–787. https://doi.org/10.1111/jeb.14009
- Brown, R. G. B. (1963). The behaviour of the willow warbler *Phylloscopus trochilus* in continuous daylight. *Ibis*, 105, 63–75. https://doi.org/10.1111/j.1474-919X.1963.tb02475.x
- Bruni, A., Mennill, D. J., & Foote, J. R. (2014). Dawn chorus start time variation in a temperate bird community: Relationships with seasonality, weather, and ambient light. *Journal of Ornithology*, 155, 877–890. https://doi.org/10.1007/s10336-014-1071-7
- Dolan, A. C., Murphy, M. T., Redmond, L. J., Sexton, K., & Duffield, D. (2007). Extrapair paternity and the opportunity for sexual selection in a socially monogamous passerine. *Behavioral Ecology*, 18, 985–993. https://doi.org/10.1093/beheco/arm068
- Dominoni, D. M., Greif, S., Nemeth, E., & Brumm, H. (2016). Airport noise predicts song timing of European birds. *Ecology and Evolution*, 6, 6151–6159. https://doi.org/10.1002/ece3.2357
- Erritzoe, J., Mazgajski, T. D., & Rejt, Ł. (2003). Bird casualties on European roads A Review. Acta Ornithologica, 38, 77–93. https://doi.org/10.3161/068.038.0204
- Gil, D., Honarmand, M., Pascual, J., Pérez- Mena, E., & Macías Garcia, C. (2015). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behavioral Ecology*, 26, 435–443. https://doi.org/10.1093/beheco/aru207
- Glutz von Blotzheim, U., & Bauer, K. M. (1993). I: Passeriformes (4. Teil) Muscicapidae Paridae. In *Handbuch der Vögel Mitteleuropas* (Vol 13). Akademische Verlagsgesellschaft.
- Hegelbach, J., & Spaar, R. (2000). Saisonaler Verlauf der Gesangsaktivitfit der Singdrossel (*Turdus philomelos*), mit Anmerkungen zum nachbrutzeitlichen Gesangsschub. *Journal für Ornithologie*, 434, 425–434.
- Holm, T. E., & Laursen, K. (2011). Car traffic along hedgerows affects breeding success of great tits *Parus major. Bird Study*, 58, 512–515. https://doi.org/10.1080/00063657.2011.596186
- Holmes, W. G., & Dirks, S. J. (1978). Daily song patterns in golden-crowned sparrows at 62°N latitude. *The Condor*, 80, 92–94.
- Kempenaers, B., Borgström, P., Loës, P., Schlicht, E., & Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, 20, 1735–1739. https://doi.org/10.1016/j.cub.2010.08.028
- Kuitunen, M. T., Viljanen, J., Rossi, E., & Stenroos, A. (2003). Impact of busy roads on breeding success in pied flycatchers *Ficedula hypoleuca*. *Environmental Management*, 31, 79–85. https://doi.org/10.1007/s00267-002-2694-7
- McClure, C. J. W., Ware, H. E., Carlisle, J., Kaltenecker, G., & Barber, J. R. (2013). An experimental investigation into the effects of traffic noise on distributions of birds: Avoiding the phantom road. *Proceedings of the Royal Society B: Biological Sciences*,

280. https://doi.org/10.1098/rspb.2013.2290

- Merilä, J., & Sorjonen, J. (1994). Seasonal and diurnal patterns of singing and song-flight activity in bluethroats (*Luscinia svecica*). *The Auk*, 111, 556–562.
- Naguib, M., Van Rooij, E. P., Snijders, L., & Van Oers, K. (2016). To sing or not to sing: seasonal changes in singing vary
  - with personality in wild great tits. *Behavioral Ecology*, 27, 932–938. https://doi.org/10.1093/beheco/arv235
- Poesel, A., Kunc, H. P., Foerster, K., Johnsen, A., & Kempenaers, B. (2006). Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, Cyanistes (formerly Parus) caeruleus. *Animal Behaviour*, 72, 531–538. https://doi.org/10.1016/j.anbehav.2005.10.022
- Polak, M., Wiącek, J., Kucharczyk, M., & Orzechowski, R. (2013). The effect of road traffic on a breeding community of woodland birds. European Journal of Forest Research, 132, 931–941. https://doi.org/10.1007/s10342-013-0732-z
- Santos, S. M., Mira, A., Salgueiro, P. A., Costa, P., Medinas, D., & Beja, P. (2016). Avian traitmediated vulnerability to road traffic collisions. *Biological Conservation*, 200, 122–130. https://doi.org/10.1016/j.biocon.2016.06.004
- Slagsvold, T. (1977). Bird Song Activity in Relation to Breeding Cycle, Spring Weather, and Environmental Phenology. *Ornis Scandinavica*, 8, 197. https://doi.org/10.2307/3676105
- Welling, P., Koivula, K., & Lahti, K. (1995). The dawn chorus is linked with female fertility in the willow Tit Parus montanus. Journal of Avian Biology, 26, 241. https://doi.org/10.2307/3677325

# Curriculum vitae



### Personal data

Name	Julia Paterno
Title	PhD, 2024 MSc, 2019 BSc, 2016
Address	Swiss National Park Chastè Planta-Wildenberg CH-7530 Zernez
Email	julia.paterno(at)nationalpark.ch
Date of birth	17 October 1991
Nationality	Austria
Employment	
2020 – 2024	Research assistant Swiss National Park, Switzerland
2019	Internship Research and Monitoring Swiss National Park, Switzerland
2018	Monitoring Red-backed shrike, Capercaillie, Rock ptarmigan Naturschutzverein Verwall – Klostertaler Bergwälder, Austria
2017	Monitoring Eurasian Curlew University of Vienna – Department of Botany and Biodiversity Research
2015 – 2017	Zoopedagogue Zoo Schönbrunn Tiergarten-Gesellschaft m.b.H, Austria
Education	
2020 – 2024	PhD in Zoology and Nature conservation University of Basel – Department of Environmental Sciences, Switzerland Thesis topic: Effects of physical environmental variables on the behaviour of mountain woodland songbirds Supervisor: Prof. Dr. Valentin Amrhein, Dr. phil. Pia Anderwald, Dr. Fränzi Korner-Nievergelt
2016 – 2019	Master in Nature conservation and Biodiversitymanagement University of Vienna – Department of Botany and Biodiversity Research, Austria
2012 – 2016	Bachelor in Zoology University of Vienna – Faculty of Life Sciences, Austria

### Other professional experience

2023 – 2024	Initiation and organisation of regular series of lectures to scientific topics Swiss National Park, Switzerland
2023 – 2024	Lecturer and field guide "Feldornithologischer Grundkurs Engadin" Vogelschutz Engadin, Stiftung Pro Terra Engiadina, Ornithologische Arbeitsgruppe Graubünden, Switzerland
2020 – 2024	Organisation of data processing in the camera trap study Swiss National Park, Switzerland
2020 – 2023	Collaboration in the project Monitoring common breeding birds Swiss Ornithological Institute, Switzerland
2020 – 2022	Organisation of field work in the camera trap study Swiss National Park, Switzerland
2019 – 2024	Collaboration in different monitoring programs: Black grouse, Capercaillie, Ungulates, Red fox, small mammals and fish Swiss National Park, Switzerland
2019	Educational work in the project «Expedition 2°» with schools Visitor Centre Swiss National Park, Switzerland

### Publications

- Paterno, J., Korner-Nievergelt, F., Anderwald P., Amrhein V. (2024) Start of dawn singing as related to physical environmental variables in an alpine environment. *Journal of Ornithology* 165, 533 544. https://doi.org/10.1007/s10336-023-02134-z
- Paterno J., Korner-Nievergelt, F., Gubler, S., Anderwald, P., Amrhein V. (2024) Alpine songbirds at higher elevations are only raised with a slight delay and therefore under harsher environmental conditions. *Ecology and Evolution* 14, 1 20. https://doi.org/10.1002/ece3.70049
- Paterno, J., Korner-Nievergelt, F., Anderwald P., Amrhein V. (2025) An exercise in conducting small studies: Road construction noise and start of dawn singing in mountain woodland songbirds. In revision: *peerJ.*
- Paterno, J., Korner-Nievergelt, F., Amrhein V., Anderwald P. (2025) Effects of habitat and road noise on singing activity of coal tits in subalpine woodland. In submission: *Animal Behaviour*