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

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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 2200 m than at 1500 m a.s.l. The effects of date were more species-specific: Alpine Tits started to sing on average 4.9 min later 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

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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 (*Cyanistes 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 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 km², with 80 km² 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
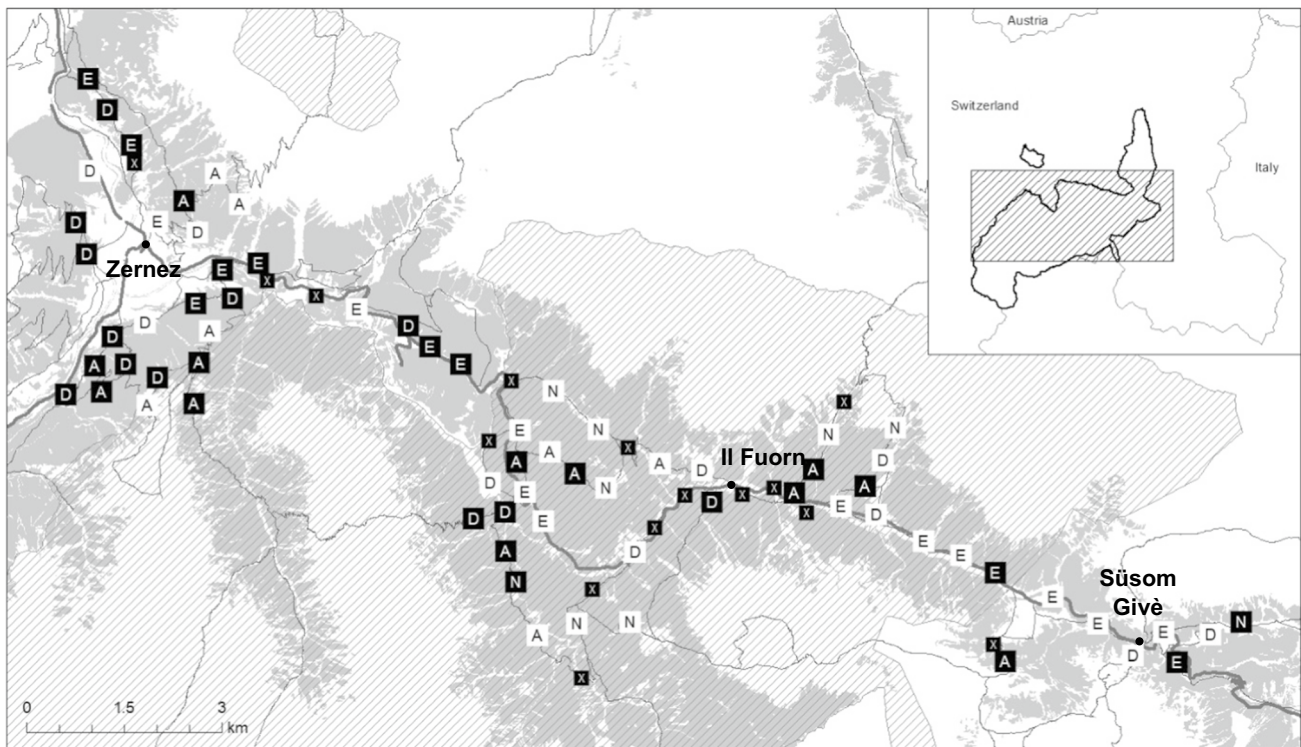
Fig. 1 Location of the study sites. The dark grey area shows the woodlands in the study area, and the grey lined area shows the Swiss National Park. Locations of sound loggers are indicated by black squares (data from 1 year) and white cubes (data from 2 years). Let- ters indicate road noise levels (*N* 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

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

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 during the two study periods

Year	Earliest deployment	Latest removal	Total number of sound loggers	Number of sound loggers used for analysis	Minimum temperature [°C]	Maximum temperature [°C]	Precipitation 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

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

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 2×2 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.

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 AudioMoths as a random effect sufficiently accounted for spatial

Table 2 Average (± SD) start of dawn singing in minutes before sunrise for the six most common songbird species in woodlands of the Swiss National Park

	Song Thrush	European Robin	Mistle Thrush	Coal Tit	Alpine Tit	Eurasian Chaffinch
Start of dawn singing						
2021	− 52.5 ± 8.6	− 52.9 ± 7.9	− 50.3 ± 7.5	− 31.3 ± 7.9	− 27.0 ± 7.3	− 22.6 ± 8.2
2022	− 50.1 ± 9.5	− 49.2 ± 8.9	− 46.0 ± 9.8	− 35.7 ± 8.5	− 30.8 ± 9.5	− 19.6 ± 8.8
Total	− 50.7 ± 9.3	− 50.2 ± 8.8	− 47.1 ± 9.4	− 34.6 ± 8.6	− 29.9 ± 9.1	− 20.4 ± 8.7
Number of observations						
2021	99	93	76	129	103	113
2022	295	252	219	371	338	292
Total	394	345	295	500	441	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 variable
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

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
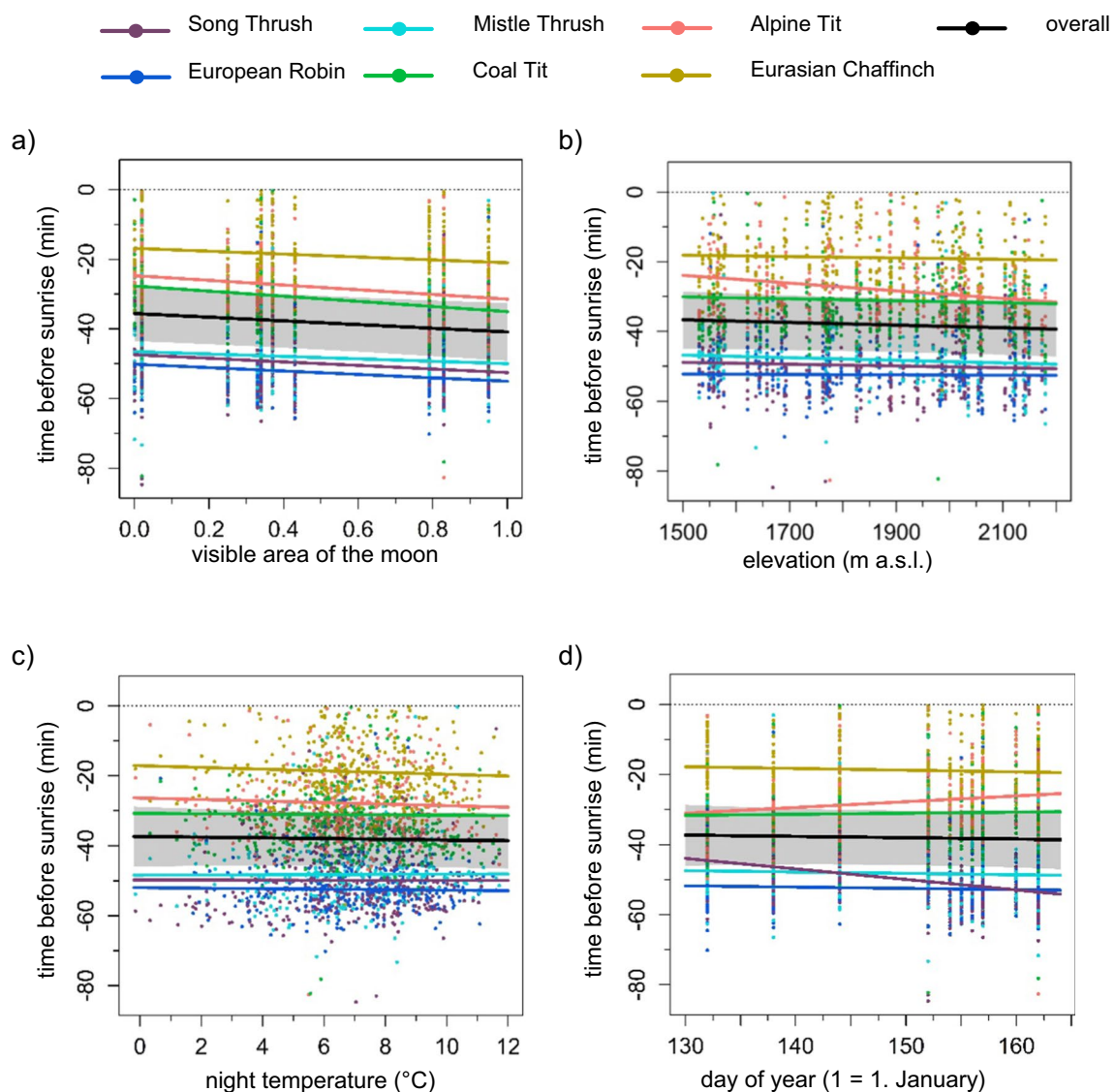
Fig. 2 Start of dawn singing relative to sunrise in relation to environmental parameters. Black lines are overall regression lines, grey areas are 95% Bayesian compatibility areas (Amrhein and Greenland 2022) based on the linear mixed model. Coloured lines show the regression lines for the different species. The dotted line represents sunrise

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).

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

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

	Visible area of the moon 100 vs. 0%	Easting E vs. W	Northing N vs. S	Road noise Extreme vs. non-audible	Elevation 2200 vs. 1500 m	Night temperature 12 vs. 0 °C	Date day 162 vs. 132
Song Thrush	−4.9 [−9.4; −0.4]	−6.6 [−10.8; −2.5]	−2.4 [−6.5; +1.6]	−2.7 [−5.6; +0.2]	−1.7 [−5.3; +1.9]	−0.2 [−5.5; +5.4]	−9.0 [−14.0; −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; +1.4]	−5.0 [−9.4; −0.4]	−0.2 [−4.7; +4.4]	−2.6 [−5.7; +0.5]	−2.4 [−6.1; +1.3]	+0.3 [−5.2; +6.2]	−1.2 [−6.2; +3.9]
Coal Tit	−7.0 [−11.5; −2.6]	−2.8 [−6.6; +1.2]	+0.6 [−3.2; +4.3]	−3.6 [−6.4; −0.8]	−1.9 [−5.2; +1.5]	−0.6 [−5.7; +4.7]	+0.9 [−3.7; +5.7]
Alpine Tit	−6.4 [−11.0; −2.0]	−1.6 [−5.9; +2.7]	−3.5 [−7.6; +0.5]	−1.9 [−4.8; +1.1]	−7.2 [−10.9; −3.5]	−2.6 [−8.1; +2.9]	+4.9 [+0.2; +9.8]
Eurasian Chaffinch	−3.9 [−8.6; +0.6]	−5.0 [−9.6; −0.5]	+8.3 [+3.8; +12.8]	−4.8 [−8.1; −1.6]	−1.3 [−5.1; +2.6]	−2.9 [−8.5; +2.7]	−1.5 [−6.4; +3.6]
Overall	−5.0 [−10.1; −0.1]	−4.7 [−9.0; −0.4]	+0.8 [−4.8; +6.3]	−2.8 [−5.6; 0.0]	−2.5 [−7.2; +2.2]	−1.2 [−6.7; +4.5]	−1.1 [−7.6; +5.3]

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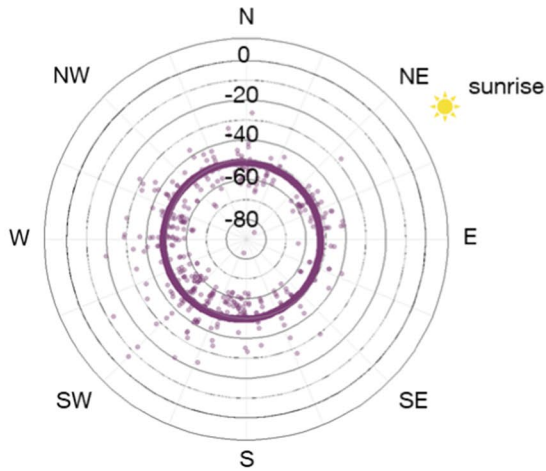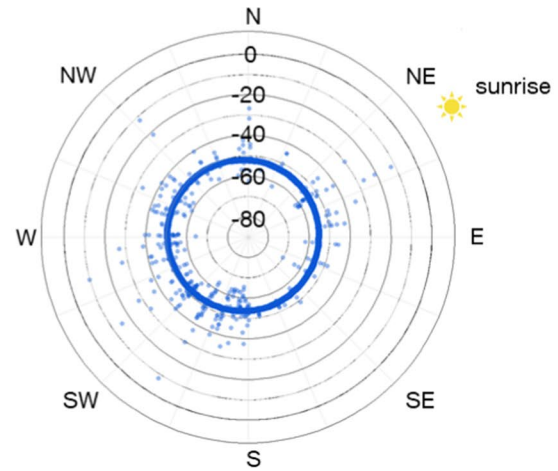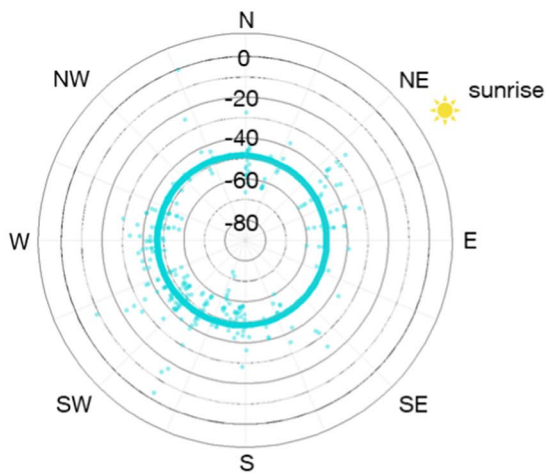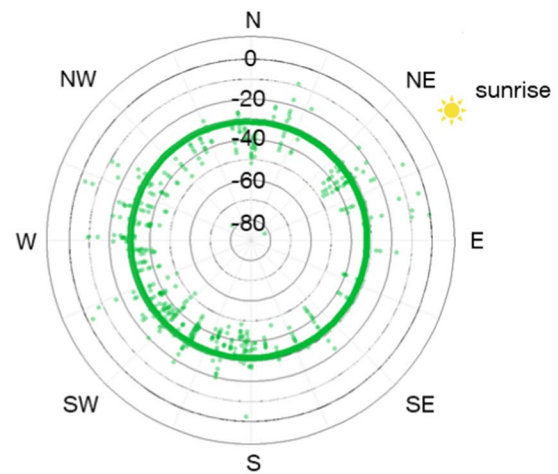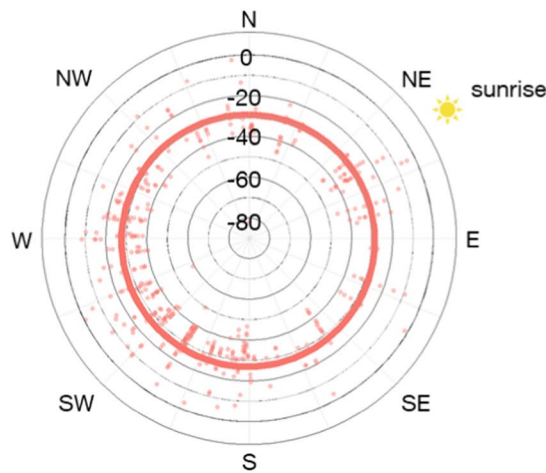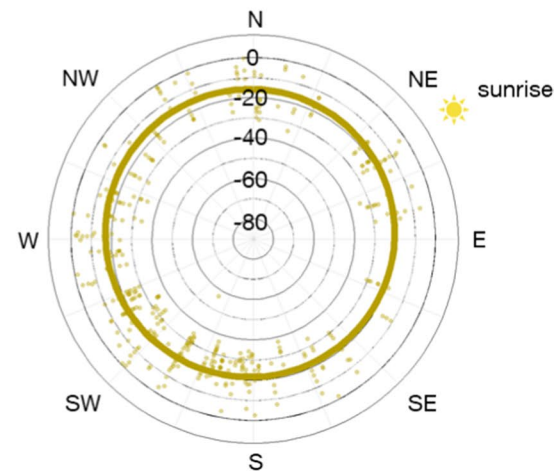
Fig. 3 Start of dawn singing in relation to aspect of a location. Black circles represent the time before sunrise in minutes (0 is sunrise and −60 is 1 h before sunrise). Coloured lines are estimates for the different species based on the GLMM. The symbol of the sun shows the angle of sunrise
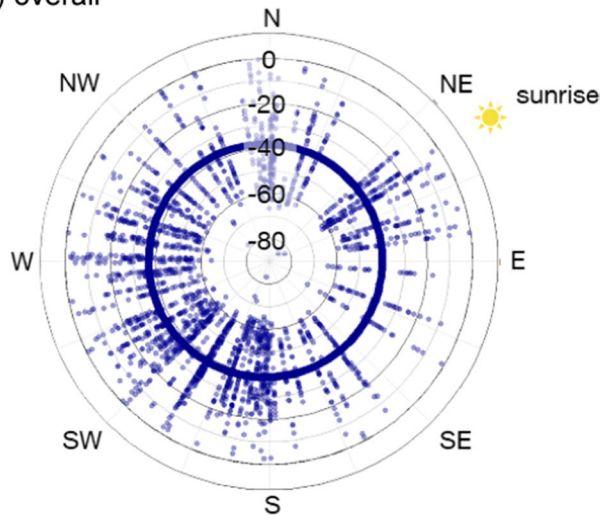
g) overall

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 breeding 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

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
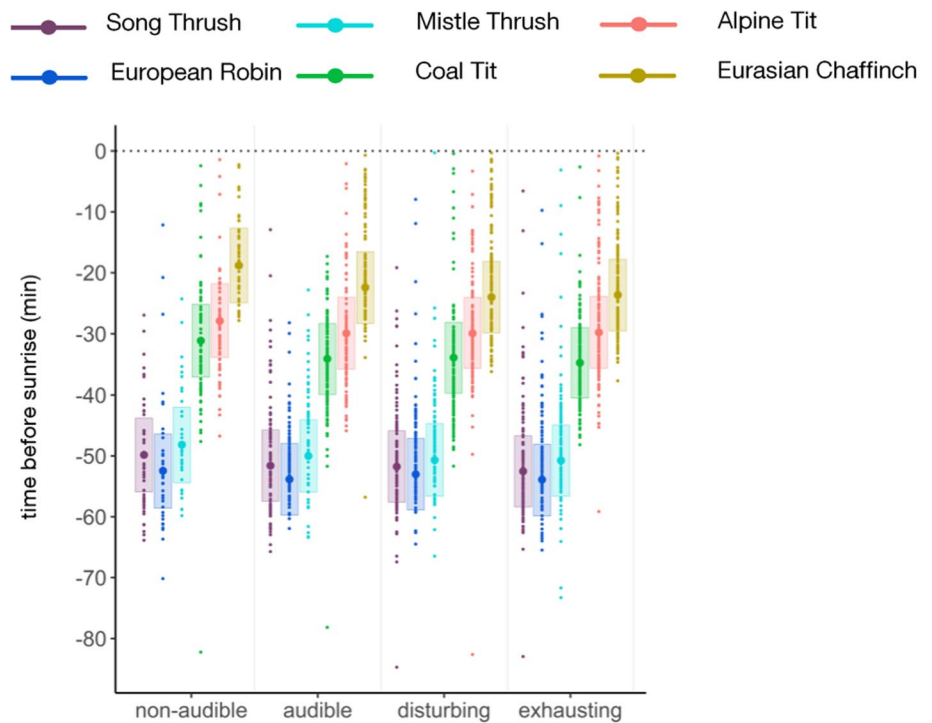
et al. 1996). For example, Thomas and Cuthill (2002) found that European Robins lost more body mass during cold than warm nights, which supports predictions from stochastic dynamic programming models of daily singing and foraging routines in birds that are based on weather variables or trade-offs between 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)

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 Ofen-pass 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.

Declarations

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