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Master thesis

Do Eurasian Eagle Owl chicks (Bubo bubo) set their clocks to an arctic schedule?

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Abstract

Organisms survive the earth's challenging environments by capitalising on predictable changes in biotic and abiotic conditions, thereby establishing circadian rhythms. These rhythms can be synchronised to different cues (or *zeitgebers*), the most common one being light. The interaction between light and circadian activity varies greatly between species and populations, even within the same habitat. Light is expected to be an important cue for nocturnal species; however, for nocturnal species inhabiting high-latitude areas, extended daylight during summer may pose a challenge. In the Sleneset archipelago of Northern Norway, close to the Arctic circle, there is a population of Eurasian eagle owls (*bubo bubo*), a typically nocturnal predator, which is exposed to continuous midsummer daylight. While adults have been found to maintain their nocturnality under these conditions, it is unclear whether the same can be said for nestlings and fledglings. In June-July 2018 and 2019, SM4 recorders were placed at five nest sites in Sleneset and three nest sites in Southern Norway which experience dark nights during summer. A machine learning software was used to develop, refine and assess a vocal classification algorithm, to extract Eagle owl chick begging calls from the acoustic data. Hourly calling patterns were compared between locations to assess the effect of continuous daylight. Eagle owl chicks exposed to continuous daylight were found to have a nocturnal peak in vocal activity and to call during the daytime as well. It is suggested that these activity patterns reflect entrainment to parental activity and possibly the risk of intra-guild predation by sea-eagles. Daytime calling is also in line with literature on sibling communication and vocal practice. Chicks near the Arctic circle also called more frequently than those in Southern areas with dark nights. This was related to a potential positive-feedback loop wherein prey abundance might induce more frequent begging. The vocal classification method was able to detect chick begging calls with an average of 69% accuracy, highlighting its potential as a non-invasive method for analysing activity patterns, while leaving some room for improvement.

Contents

1. Introduction

The earth's natural environments can be challenging and are constantly imposing selective pressures on organisms to increase survival and reproduction. Fortunately, some environmental conditions change in a predictable way through the days, seasons, and years. Most vertebrates have evolved an internal 'clock' mechanism known as the circadian rhythm that allows them to capitalise on these changes (Kronfeld-Schor et al., 2017). Nocturnality, for instance, is a behaviour that evolved in multiple lineages of birds and mammals, allowing them to exploit daily changes in light to access new ecological niches and benefit from reduced competition and higher quality food, amongst other features (Wcislo et al., 2004; Hall & Ross, 2007; Wu, 2022).

The circadian rhythm is synchronised by biotic and/or abiotic cues termed 'Zeitgebers' (German for *time-givers*), of which a principal one is the light-dark cycle. Most animals use light to synchronise their internal bodily cycles through a process called 'entrainment'. This allows them to make functional and behavioural changes that maximise their fitness within their environment (Aste et al., 2001; Kronfeld-Schor et al., 2017). However, an animal's clock can also be 'masked' by factors which directly influence activity but don't re-synchronise the circadian rhythm (Mrosovski, 1999). For instance, the activity patterns of nocturnal Argentinean owl monkeys (*Aotus azarai azarai*) are entrained by light. Their usual rhythm, however, can be masked by seasonal changes in temperature, precipitation, and food abundance (Erkert et al., 2012). Thus, it is the combination of entrainment and masking that determines an animal's activity patterns, and this can vary greatly even between populations of the same species (Kronfeld-Schor et al., 2017).

The complex process by which vertebrates maintain a circadian rhythm can be simplified into the production and release of the hormone melatonin in the body. Melatonin mediates the release of other hormones which regulate bodily processes like temperature control, metabolism, and sleep, and ultimately influence an animal's activity patterns (Aste et al., 2001). In mammals, the clock mechanism lies outside the pineal organ in the suprachiasmatic nuclei of the hypothalamus (Abitbol et al., 2017). Birds, on the other hand, have an oscillator within the pineal organ itself which produces melatonin rhythmically and independently of external cues (Gwinner et al., 1997). There are also photoreceptors within the avian pineal organ which allow melatonin production to be synchronised directly by light (Csernus, 2009). Melatonin is therefore produced in a daily rhythm, with lower levels during the day and higher

levels at night, using light as a cue (Aste et al., 2001). However, the importance of pineal melatonin and light in maintaining the circadian rhythm varies greatly between avian species (Aste et al., 2001; Murakami et al., 2001).

In the Arctic and Antarctic zones there is high variation in photoperiod throughout the year, from continuous darkness in winter to continuous daylight in summer. This represents a significant challenge for avian species inhabiting these zones. A recent study by Steiger et al. (2022) compared the rhythms of four free-living bird species occupying similar tundra habitat and observed a variety of adaptations to continuous daylight. Lapland longspurs (*Calcarius lapponicus*) retained a robust 24-hour rhythm, as also found by Ashley et al. (2014). It has been suggested that their rhythm is synchronised by endogenous production of an ocular clock gene (*Per2*) and melatonin secretion (Ashley et al., 2014), or perhaps by daily fluctuations in temperature and light intensity (Steiger et al., 2022). There have been similar findings for the Willow Warbler (*Phylloscopus trochilus*) and the Little Auk (*Alle alle*), wherein activity patterns during continuous daylight were linked to predation pressure and light intensity (Silverin et al., 2009; Wojczulanis-Jakubas et al., 2020).

Sandpipers (e.g., *Calidris pusilla*, *Calidris melanotos*), particularly sexually competitive and pre-incubation individuals, were found to be active arrhythmically during the arctic summer, likely in relation to sexual competition (Steiger et al., 2022). A similar adaptation has been observed in the Svalbard Ptarmigan (*Lagopus muta*), which secretes low amounts of melatonin and is consistently active under continuous daylight (Stokkan et al., 1986; Reierth et al., 1999). Steiger et al. (2022) noted that during the incubation phase, Sandpipers displayed a more 'free-running' activity rhythm (significantly different from a 24-hour pattern), wherein the lack of a stronger zeitgeber like light allows entrainment by weaker social zeitgebers linked to reproduction.

Thus, avian activity rhythms under the midnight sun can differ substantially between species, sexes, and breeding stages even within similar habitats (Steiger et al., 2022). While this plasticity has been demonstrated for diurnal species, the adaptations of a nocturnal avian lifestyle to continuous daylight has, to current knowledge, rarely been studied in nature. A study on the nocturnal migration of passerine birds such as willow warblers (*Phylloscopus trochilus*) and pied flycatchers (*Ficedula hypoleuca*) in the Arctic, found that these species did not alter their migration patterns and may even prolong their nocturnal flight period under

continuous daylight (Nilsson et al., 2015). However, as mentioned, there can be considerable diversity even within the adaptations of nocturnal species.

In the Sleneset archipelago of Northern Norway, just below the Arctic circle, there is a population of Eurasian eagle owls (*Bubo bubo*) that is exposed to continuous daylight during summer. Eriksen & Wabakken (2018) have shown that adult eagle owls in Sleneset retain their nocturnal activity patterns under continuous daylight. They proposed that this was a strategic use of slightly lower light intensity around midnight to minimise interactions with White-tailed Sea eagles, which are both competitors and intra-guild predators (Mikkola, 1976; Eriksen & Wabakken, 2018). In this case, competition may be masking the light-entrained activity patterns of the eagle owl. It remains unclear, however, whether this is mirrored by chicks which are hatched and reared during this period.

Eagle owl chicks have been known to vocalise from two weeks after hatching and call increasingly with age (Penteriani & Delgado, 2019). A study in Spain found that chicks between 70-110 days old call most around sunset and sunrise and remain relatively silent during midnight (Penteriani et al., 2005). After this age they vocalise increasingly at midnight and cyclically between sunset and sunrise (Penteriani et al., 2005). However, nestlings and fledglings have been known to call during the day when parent activity is low, particularly as they move away from the nest; this has been related to 'contact calling' between siblings as well as vocal practice (Penteriani et al., 2000; Penteriani et al., 2005; Dahl pers. comm., 2021). Chicks are also very sensitive to intruders and can stop vocalising immediately to conceal themselves from a perceived threat (Penteriani & Delgado, 2019). Furthermore, there is high variation in the behaviour of chicks in areas south of the Arctic circle.

Thus, an important question appears: how do Eagle owl nestlings and fledglings adapt their calling behaviour under continuous daylight near the Arctic circle? The focus of this study is two-fold; first, to answer the above research question; and second, to determine whether vocal classification is a viable method for this purpose. These aims will be approached by developing a classifier for Eagle owl chick vocalisations, which can be used to compare activity patterns between populations near and below the Arctic circle.

Vocal classification is a process which involves using machine learning to build an algorithm from acoustic data, which detects a target species from amongst a myriad of other sounds in an environment (Sethi et al., 2021). It is a non-invasive method of relatively low cost and

effort, which can give detailed insight into the activity of species that are cryptic or prone to disturbance (Terry et al., 2005; Eriksen & Wabakken, 2018; Sethi et al., 2021). Variations of the vocal classification method have been employed previously on other owl species [*see* Odom & Mennill, 2010; Nagy & Rockwell, 2012; Pérez-Granados et al., 2021; Segall et al., 2022], but not on eagle owls. The rate of successful classification appears to vary considerably; Odom & Mennill (2010) were able to classify different call types of the Barred owl (*Strix varia*) with 69% accuracy and classify sexes with 91% accuracy. They attributed misclassifications to an overlap in confidence intervals due to a similar number of notes in some calls (Odom & Mennill, 2010). In another study by Shonfield et al., (2018), they were able to classify different owl species with precisions varying from 16-99%. This variation was attributed to the signal-to-noise ratio, where fainter signals were sometimes misidentified. Moreover, the authors suggest a trade-off between precision and false negatives, wherein higher precision means fewer false positive classifications but more false negatives (Shonfield et al., 2018).

Since the current study aims to determine activity patterns as well as the viability of acoustic classification for detecting Eagle owl chicks; both the hours of activity as well as the level of activity in each hour of the day are relevant. It is therefore important to balance the need for precision and avoiding false negatives. Moreover, the data used in this study are considerably large (several hundreds of gigabytes) and therefore require high processing power to analyse. The more detailed the analysis, the higher the processing power demands. With these factors in mind, this study aims to develop a classifier with >60% accuracy.

Given the literature on Eagle owl chick behaviour, one might expect chicks near the Arctic to adapt their calling behaviour according to parental activity and perceived threats. Thus, one hypothesis is that (H1) chicks will be most vocal in the evenings and over midnight whilst being predominantly silent throughout the day, as observed of adult owls by Eriksen & Wabakken (2018). Alternatively, (H2) chicks may behave similarly to their southern counterparts and call most near sunset and sunrise and sporadically throughout the day, but less so close to midnight.

There is currently limited research on owl activity patterns at or above the Arctic circle; existing studies focus on detectability, survival, and behavioural aspects [*e.g., see* Bortolotti et al., 2011; Therrien et al., 2012; Reynolds et al., 2021]. There is only one known study about adult Eagle owl's activity patterns near the Arctic by Eriksen & Wabakken (2018). The current

study will elaborate on this research and enhance our understanding of the plasticity of the Eagle owl's biological clock. The method used in this study, if successful, can supplement current methods for monitoring Eagle owl populations, which are limited to manually listening for adult calls during the breeding season (Heggøy et al., 2020).

Using a classifier to identify chick vocalisations in territories where calling adults have been identified in spring, also gives the possibility of confirming reproduction without necessitating the location or disturbance of nest sites. On a local scale this study will enhance knowledge of the Eagle owl population's reproductive success, which can contribute to the greater management and conservation of the species in Norway.

2. Methods

2.1 Study areas

The data used in this study were collected from five known Eagle owl nest sites in the Sleneset archipelago in Nordland County, Northern Norway (hereafter 'North') and three in Southern Norway ('South'), in June and July of 2018 and 2019. The approximate locations of all study sites are shown in Figure 1 below, while the Sleneset archipelago is shown in Figure 2. The exact dates, as well as some key characteristics of the nest sites, are summarised in Table 1. The southern sites were located in Rendalen valley in the former Hedmark county, in the Kristiansand municipality of the former Vest-Agder County and in the Lillesand municipality in the former Aust-Agder County (Fig. 1). The study sites experienced varying hours of night-time darkness during the study periods, described below. As in Eriksen & Wabakken's (2018) study, night-time refers here to the 12-hour period centred approximately around solar midnight (i.e., from 19:00-07:00), while daytime refers to the 12-hour period centred around solar noon. All nests were observed to have chicks at the start of the recording period in June (Table 1).
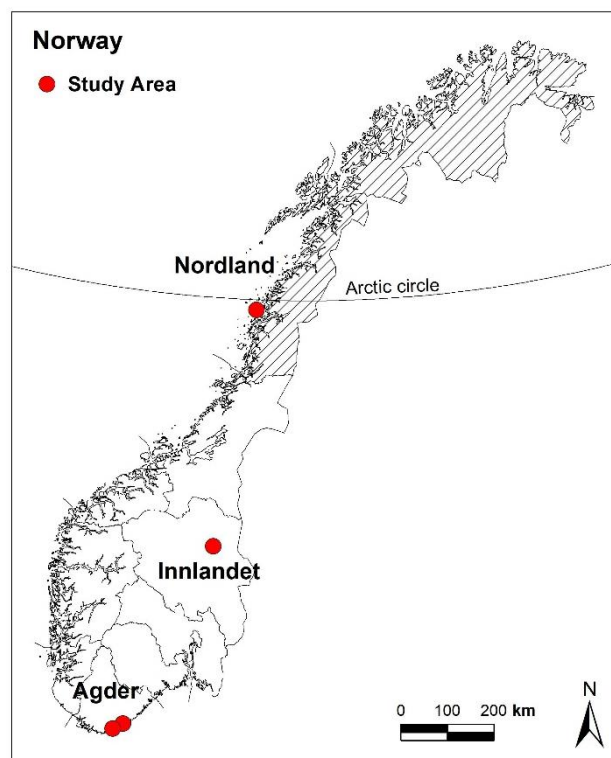

Figure 1— Approximate locations of Eagle owl nest sites for acoustic study in Norway. Diameter of all points >16km, in accordance with requirements of the Norwegian Environment Agency (Miljødirektoratet). Base map adapted from kartverket.no.
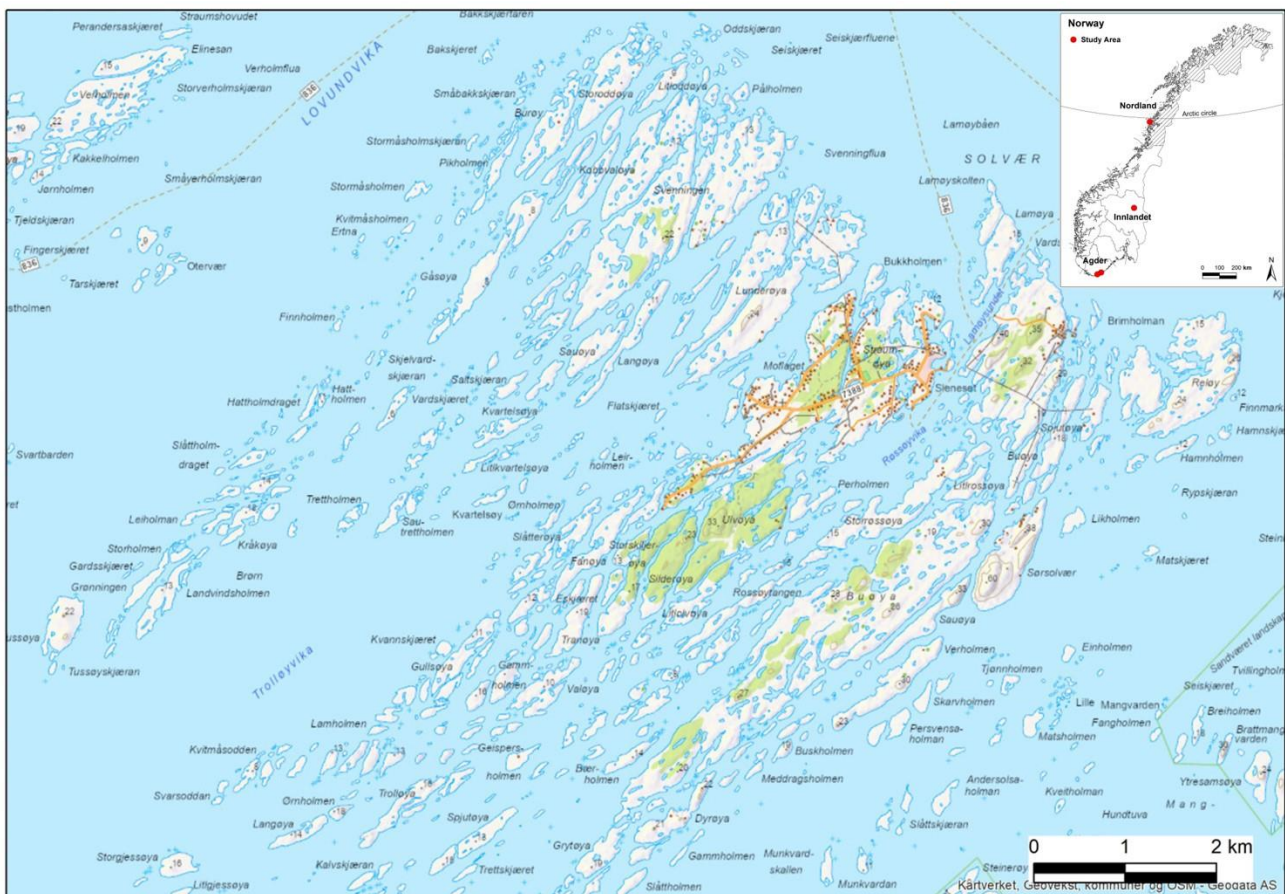
Figure 2— Map of the Sleneset archipelago in Nordland County, Northern Norway where Eagle owl nest sites are distributed.

Sleneset archipelago

In the North, the Sleneset archipelago is located 17km below the Arctic circle (Fig. 2), where the sun remains above the horizon for approximately 4 weeks during summer, centred around June 21 (Eriksen & Wabakken, 2018). Similar midnight light intensities remain for an additional 1-2 weeks before and after this period, as the sun is only partially below the horizon (Eriksen & Wabakken, 2018). Thus, during most of the study period in the North (Table 1) the sun remained above the horizon. Towards the end of the study period (i.e., early-July), the sun partially rose between 01:17-02:29 and set between 01:11-12:01, and was at its lowest (i.e., solar midnight) at 01:12, local time (Time & Date AS, 2022).

The climatic conditions in this region are generally quite mild, with temperatures remaining mostly above 0 °C in winter (Eriksen & Wabakken, 2018); however, there was some variation over the study period. In 2018, the average temperatures were 9.2°C in June and 15.0°C in

July, and the highest daily wind speed ranged from 16.2m/s in June to 14.8m/s in July. In 2019, the average temperatures were 10.8°C in June and 13.3°C in July, and the highest daily wind speed ranged from 12.7m/s in June to 15.1m/s in July (Norwegian Meteorological Institute & Norwegian Broadcasting Corporation, 2022).

The archipelago consists of 297 islands and 1544 islets and rocks and has a total land area of 30.13km^2 (Wabakken et al., 2014). The terrain is mostly flat and rocky with altitudes generally less than 10 meters above sea level (m.a.s.l.). Roughly 96% of the terrain is treeless and is covered with short-growing vegetation, bogs, rocks, and freshwater ponds, along with a thin layer of soil (Wabakken et al., 2014). There are between 350-400 residents concentrated on a single central island. Sheep graze freely on the islands which are made accessible by the tide and have been observed to interfere with Eagle owls at nesting sites, particularly when taking shelter from harsh weather (pers. comm. Dahl & Wabakken, 2021).

European water voles (*Arvicola amphibius*) are abundant on many of the islands, likely because the archipelago is one of the few areas in northern Europe that is not inhabited by the invasive American mink (*Mustela vison*). The American mink is known to greatly reduce populations of voles in Northern Europe and has already colonised many parts of coastal and mainland Norway (Bevanger & Henriksen, 1995; Bonesi & Palazon, 2007). Their absence creates a unique opportunity for nesting eagle owls to thrive from almost exclusive access to their main prey source (>75% prey biomass) (Bichsel, 2012). In fact, the Eagle owl population in Sleneset is currently one of the densest in Europe, with greater than 8 pairs/10km^2 (Jacobsen & Røv, 2007; Direktoratet for Naturforvaltning, 2009). Other prey sources in this region include seagulls (*Laridae*), geese (*Anserinae*), and ducks (*Anatinae*), all of which are shared by the Eagle owl's main competitor, the white-tailed sea eagle (*Haliaeetus albicilla*). The only other mammalian predator in the area is the Eurasian otter (*Lutra lutra*), though this species mostly feeds on fish within its European range (Jedrzejewska et al., 2001).

Rendalen valley

In the South, the Rendalen nest site was located in a post-glacial U-shaped valley at about 341 m.a.s.l. (Fig. 1). At the start of the study period (June 2018; *see* Table 1) the sun rose at approximately 03:28 and set at 23:03; towards the end of the study period (July 2018), it rose at 04:02 and set at 22:39 (Time & Date AS, 2022). There were therefore between 4.5-5.5 hours of night-time darkness during this period.

In 2018, the average temperature was approximately 14.1°C in June and 18.8°C in July (Norwegian Meteorological Institute & Norwegian Broadcasting Corporation, 2022). Wind speed data has not been recorded for the study period in this area. The terrain consists of slopes dominated by pine trees, where water streams into lake Storsjøen. The nest was located on a steep rocky hill scattered with pine trees, at an approximate elevation of 395m above sea level. Observation of the nest site revealed feathers of mallards and some smaller owl species (*Aegolius funereus*, *Strix aluco*) as likely prey sources.

Aust- and Vest-Agder

The two remaining study sites in the South were located in the former Aust- and Vest Agder counties (now combined into Agder county), 25km apart in straight-line distance (Fig. 1). During the study period (June 2019; *see* Table 1), the sun rose between 04:25-04:22 and set between 22:37-22:41, giving approximately 6 hours of darkness (Time & Date AS, 2022).

In June 2019, the average temperature in this area was 14.8°C (Norsk Klimaservicesenter, 2022), and the approximate highest wind speed was 9.9m/s (Norwegian Meteorological Institute & Norwegian Broadcasting Corporation, 2022). The Vest-Agder nest site was located at 54 m.a.s.l. and was approximately 1.4 km away from the sea. The general terrain is hilly, and the higher points are barren, dry, and dominated by pine. Lower valleys are dominated by deciduous forest with everything from old finer deciduous forest to scrub forest. There is also agricultural land and some forestry activity within the area. The nearby coastal landscape consists of small and larger islands with a great variety of vegetation.

Based on analysis of the Vest-Agder nest site by Esperås & Ulsted (2022), the prey composition of eagle owls in the area consists primarily of sea birds (particularly gull species), as well as some medium-sized owl species (*Asia otus* and *Strix aluco*) and very few rodents. There are no confirmed competitors in the area, though a sea eagle has been recorded predating on an Eagle owl chick (Torild Esperås, pers. Comm. 2022).

Table 1— Key characteristics of Eagle owl chick data collected in Norway during 2018 and 2019.

Locality	Year of data collection	Recording dates (number of days)	No. chicks in nest at start of study	Approx. age (weeks) at start of study
Sleneset locality 1	2019	11/06- 30/06/2019 (20 days) + 01/07- 11/07/2019 (11 days)	1	3
Sleneset locality 2	2018	14/06- 30/06/2018 (17 days) + 01/07- 14/07/2018 (14 days)	3	3
Sleneset locality 3	2019	11/06-25/06/2019 (14 days)	1	3
Sleneset locality 4	2018	14/06- 30/06/2018 (17 days) + 01/07- 14/07/2018 (14 days)	2	3
Sleneset locality 5	2018	14/06- 30/06/2018 (17 days) + 01/07- 14/07/2018 (14 days)	1	3
Rendalen	2018	15/06- 30/06/2018 (16 days) + 01/07- 16/07/2018 (17 days)	2	2
Aust-Agder	2019	11/06- 18/06/2019 (8 days)	2	5
Vest-Agder	2019	11/06- 16/06/2019 (6 days)	2	5*

*Approximate age based on weight, calculated using method from Penteriani et al. (2005).

2.2 Acoustic recorder calibration and deployment

Eagle owl chick vocalisations were detected at nest sites using Song Meter SM4 acoustic recorders. For most locations, the recorders were set to record continuously for two 2-week periods in mid-late June and early July (Table 1), with a short break in between to change batteries and memory cards. In Agder, recorders were only deployed for 6-8 days. The recorders produced files in either 30-minute or 1-hour segments (varied between locations) which were downloaded and used for analysis.

The study periods, described in Table 1, were selected to represent the nestling and part of the fledgling stages of chick growth. Chicks generally stay closer to the nest and are easier to detect earlier on, making this period ideal for studying vocal activity (Penteriani et al., 2005; Eriksen & Wabakken pers. comm., 2021).

At all locations, the recorders were calibrated to record at a sample rate of 24000 hZ in order to balance the temporal resolution and the size of audio files produced. The gain was set to 16dB, and the pre-amp was set to 26 dB on both right and left (stereo recording). The sensitivity was set to 0dB, allowing anything detected to be recorded.

At the start of the recording periods the recorders were placed no more than 40 meters away from each nest site. When changing batteries before the second period, the recorders were moved 200-350m away from the nest based on chick movements and placed between 5-10m away from the chicks. Eagle owl chick calls can be heard from up to 1km away, depending on the level of interference in the terrain (Penteriani et al., 2000; Penteriani et al., 2005; Penteriani & Delgado, 2019)— the placement of recorders was well within this range and was therefore considered appropriate. In the South, recorders were generally tied to trees as shown in Figure 3. In the North, on the other hand, recorders were placed in rock crevasses as in Figure 4. To minimize disturbance, the recorders were deployed while chicks were being banded for other research, and the recorders were moved/ batteries were changed without directly interfering with the nest.

Figure 3— Placement of a Song Meter SM4 audio recorder at an Eagle owl nest site in Rendalen, Norway in June 2018. Photo taken by Ane Eriksen.

Figure 4— Placement of a Song Meter SM4 audio recorder (outlined in red) at an active Eagle owl nest site in Sleneset, Norway. Photo taken by Espen R. Dahl (2019).

In the North, audio devices were only placed at nest sites with chicks of a similar age, between three to five weeks (Table 1). In Rendalen, two chicks were observed at the nest site at the beginning of each recording period. In Vest Agder, two chicks were confirmed at the nest by camera traps at the start of the study period. An acoustic recorder was placed around 40m away at this time and was then moved approximately 290m further away, as camera trap images showed that the chicks left the nest on the 1st of July. In Aust-Agder, two chicks were visually confirmed at the nest at the start of the study period.

2.3 Classifier development

The acoustic data was analysed in the software Kaleidoscope Pro version 5.4.2. Kaleidoscope Pro uses a process of cluster analysis to sort through large acoustic datasets and isolate specific sounds, which are then grouped together with similar signals. The types of sounds detected are defined by manually setting signal parameters, such as frequency range and maximum inter-syllable gap, to desired levels (Wildlife Acoustics, 2020).

The basic cluster analysis process involves the creation of spectral Hidden Markov Models for each detected signal, which are then compared to the models of other signals and used to create a 'cluster centre' (i.e., the 'average' of detected signals). This is represented as the first cluster, and all signals are placed in relation to this cluster based on their similarity to the average (Wildlife Acoustics, 2020). Signals that are most similar are placed towards the top of the cluster, and signals that pass a certain threshold of similarity are separated into subsequent clusters. Each detected signal is therefore assigned to only one cluster. For further information on the Hidden Markov Model and clustering process, see the Kaleidoscope Pro 5 User Guide (Wildlife Acoustics, 2020). The overall aim was to develop and validate a classifier which could distinguish chick begging sounds from other signals. For this purpose, it was considered sufficient to use a basic cluster analysis process on a training dataset to build a strong simple classifier for chick calls. This classifier could then be applied to new datasets from the North and South to extract and group chick vocalisations, which could be plotted over time to analyse activity patterns. The complex process of validating and building the classifier is summarised in Figure 5 and described in further detail below.
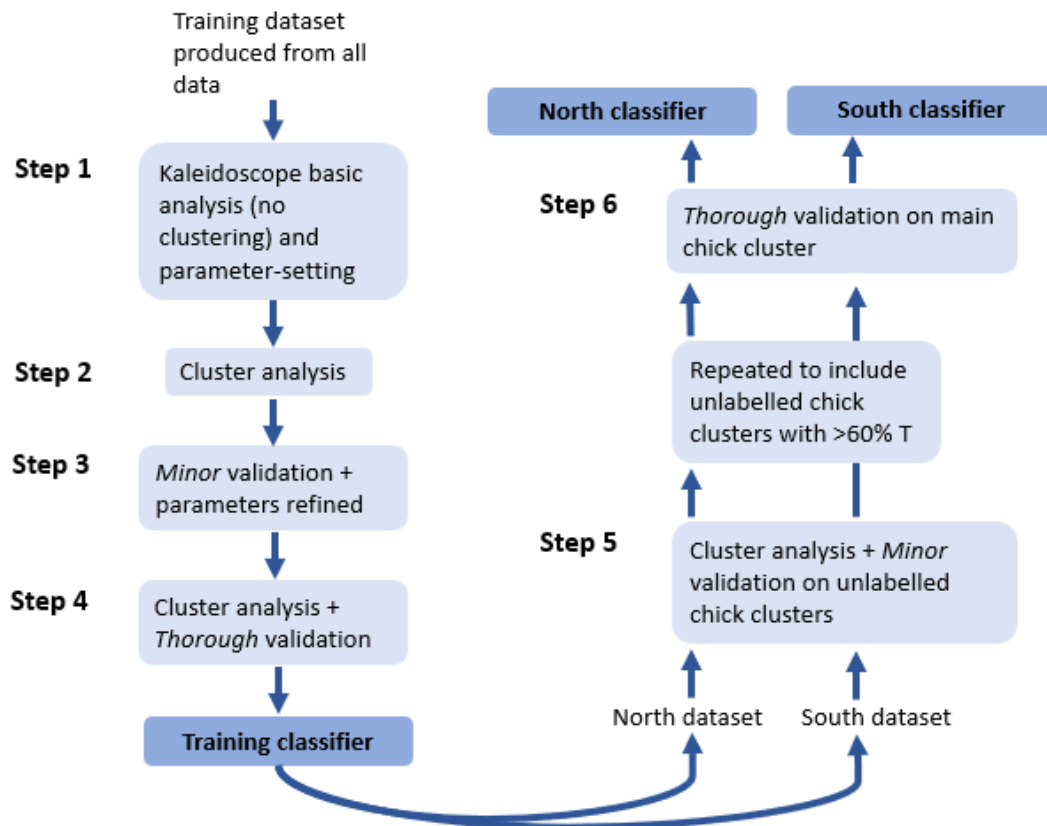
Figure 5— Workflow of the process to produce and validate classifiers for Eagle owl chick calls in Kaleidoscope Pro, version 5.4.2.

Step 1: Basic cluster analysis of training dataset and parametrization

To begin the process of making a classifier, a training dataset was created by sampling and combining a single 24-hour-period of recordings from each northern and southern study site. The dates of these samples were spread over the study period to account for differences in local conditions and chick hatching dates. An exact account of the dates of sample recordings used in the training classifier is shown in Appendix 1.

Once the training dataset was created, it was run through a basic, unsupervised cluster analysis to observe the visual outputs of different signals. The outputs were displayed as waveforms with a Fast Fourier Transform (FFT) size of 256 and a window size of 128, which is half the FFT size as recommended by Wildlife Acoustics (2020) for a 50% overlap. An example waveform is shown below in Figure 6. This display was used consistently throughout the study

for labelling clusters and validating the classifiers. It is important to note that the display characteristics did not affect the clustering process, and the display FFT size should be distinguished from the FFT window-size parameter, described later.

Eagle owl chicks can use a myriad of calls during the nestling and fledgling stages (Penteriani & Delgado, 2019). Around two weeks after hatching chicks can be heard making a characteristic *chwitsche* sound which has been identified as the most common begging call (Penteriani & Delgado, 2019). This was considered an appropriate proxy for chick activity during early growth stages and was thus used as the basis for building a classifier. Begging calls were first identified within the data manually based on expert opinion and field experience (Fig. 6), and the parameters of these signals were noted (e.g., frequency range, duration, etc.).
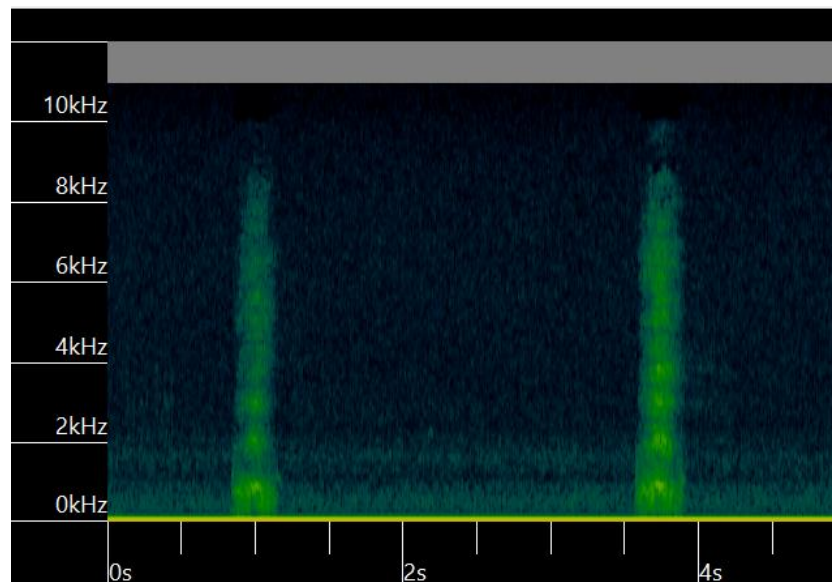

Figure 6— Example waveform of Eagle owl chick begging calls in Sleneset, Northern Norway, with an FFT size of 256 and window size of 128 samples. Recording collected by Dahl (2019).

Before beginning cluster analysis, key vocal signal and cluster analysis parameters were set to wider limits than those observed from the visual outputs, shown in Table 2. The begging call of Eagle owl nestlings and fledglings can be up to 6-8 kHz (Penteriani & Delgado 2019); however, some calls were observed to reach higher frequencies. The amplitude of chick calls appeared to vary considerably based on how far chicks were from the recorders. Calls that occurred closer to the recorders covered a larger frequency range, so higher frequencies could be captured by the recorder. Signals that were further away were only detected at the frequency where they were strongest, and therefore excluded these higher frequencies. The frequency

range was therefore set wide enough to allow some room for error (Table 2). Since chick calls are continuous, the maximum inter-syllable gap was set lower than 0.5 to avoid combining discrete calls; however, it had to be high enough to account for fainter chick signals.

Regarding cluster analysis parameters, the maximum distance from cluster centre was set to the maximum limit (2.0) in order to allow as many chick signals to be clustered as possible. Since Kaleidoscope organises signals closer to the average towards the top of the cluster, the least similar signals could simply be filtered out in the output later.

The FFT window size was also observed to have an effect on clustering. This variable determines whether the spectral analysis focuses on either the temporal or frequency resolution of the detected signals (Wildlife Acoustics, 2020). The smallest FFT window size of 2.67ms shows temporal events in higher resolution, which is appropriate for short signals with many syllables. Alternatively, the largest FFT widow size of 21.33ms provides greater resolution for frequency, which is best for distinguishing slower sounds from signals with different frequencies (Wildlife Acoustics, 2020). To select an appropriate FFT window size, four preliminary cluster analyses were run on the training data, one for each of the window sizes. Based on crude observation of output clusters, the default FFT window of 5.33ms appeared to produce the fewest clusters of chick calls with the lowest number of false positives towards the top of the clusters. As such, this FFT window size was considered to best balance resolutions for frequency and time.

Steps 2 and 3: Cluster analysis of training dataset and minor validation

The next step was to run a cluster analysis with the parameters set during the previous step and determine whether they needed to be widened further. First, output clusters of chick sounds needed to be identified. All output clusters were browsed through in Kaleidoscope, and those where the first 10 sounds were determined to be chicks were labelled as 'chick' clusters. The number of sound files within these clusters was also noted.

Next, the strength of the chick clusters needed to be identified. This was defined as the proportion of true positives (actual chick calls) versus false positives (not chick calls). This proportion was determined by manually labelling output sounds as either *T* or *F*, respectively. The chick clusters ranged in size from 26-1,464 sound files, so it was decided to manually check and label 25 recordings equally distributed throughout each chick cluster. This process is referred to here as a *minor validation*. The output clusters were saved as both a .csv file and

a .kcs file; the former could be used for analysis, while the latter could be used as a classifier on new datasets.

To check the results of the first minor validation, the.csv file was opened in R Studio Version 1.4.1103 (R Studio Team 2021). The packages tidyr (Wickham & Girlich, 2022), dplyr (Wickham et al., 2022) and rstatix (Kassambara 2021) were used to create logistic regression models for the relationships between the proportion of T's and F's and the distance to cluster centre, the minimum and maximum frequencies, and the duration (Appx. 2-4). Information from these plots were used to refine the parameters further. Table 2 below offers a summary of all the parameters manipulated in this study and the final limits they were set to. Any remaining parameters were left at Kaleidoscope's default values, listed in the Kaleidoscope Pro 5 User Guide (Wildlife Acoustics, 2020).

Table 2— Signal and cluster analysis parameters used to build clusters and develop classifiers for Eagle owl chick sounds. Descriptions adapted from Wildlife Acoustics (2020).

Vocal signal parameter	Description	Limits/ range used
Min and max frequency (Hz)	Lower and upper frequency limits for signals to be used in cluster analysis.	500 – 13,000
Min and max length of detection (s)	Duration below- and above which signals are excluded from cluster analysis.	0.1 - 3
Maximum inter-syllable gap (s)	Amount of time between syllables required to distinguish them into separate signals.	0.3
Cluster analysis parameter		
Max distance from cluster centre to include in outputs (2.0 max)	How far signals are allowed to be from the average pattern of detected signals (centre = 0).	2.0
FFT window (ms)	Resolution of frequency vs. time. Divided into 4 window sizes; a larger window size has more resolution for frequency, while a smaller window size has more resolution for time.	5.33

Max states	Target size of Hidden Markov Model, where 8-16 is default and a larger number is used to tease apart more subtle differences.	14

Step 4: Cluster analysis of training dataset and thorough validation

Once the parameters were set to values which were considered wide enough to encompass all chick sounds (Table 2), a new cluster analysis was run on the training data to look for chick calls specifically, using the classifier (.kcs file) from the previous step. This would theoretically allow chick sounds to be clustered as before, but with a higher degree of accuracy. The output included one main chick cluster and other clusters arranged in terms of their similarity to this cluster.

A *thorough validation* was then undertaken on the chick cluster to determine whether it was accurate enough to be used as the basis for building the classifier. Since this cluster was quite large (12,466 sound files), 0.5% of the sounds were validated as *T* or *F*— a total of 62 recordings, equally distributed throughout the cluster. This number was chosen given time and processing power constraints, as well as to avoid replicating what the software was designed to do itself. The relationship between T and F and the distance from cluster centre was then modelled and plotted as before. This was done so that it could be compared to similar plots for the final classifiers (*see* Step 6).

Step 5: Cluster analysis and minor validation of North and South datasets

Once the classifier was considered strong enough, it was used to identify chick sounds in the North and South datasets through new cluster analyses. This was done separately for each dataset, for two reasons. Firstly, the Northern dataset was much larger and took significant processing power to run on its own. Secondly, it was unknown whether the classifier would be equally suitable for the North and South, or if it would require further training with the respective datasets, due perhaps to differences in terrain or weather.

The cluster analyses on both datasets produced a single main chick cluster and several unlabelled clusters. The latter were browsed through, and any potential chick clusters were noted. A *minor validation* was conducted on these clusters as before, and those with >60% T's

were labelled as 'chick' to be included in the classifier. The South dataset did not produce any unlabelled chick clusters, while the North dataset did; hence the classifier was split into two versions. The process was repeated three times for the Northern dataset before the North classifier was considered complete.

Step 6: Thorough validation of North and South classifiers

Finally, a *thorough validation* was conducted on both the North and South outputs to determine their strengths as classifiers. Since these datasets were considerably larger than the training dataset (North= 609,153 recordings; South= 52,271 recordings), it was decided to validate 0.1% of the recordings (total of approx. 609 and 52 recordings for North and South, respectively). This was again due to time and processing power constraints. The resulting .csv files were opened in R Studio and the likelihood of T vs. F was modelled and plotted as a function of distance from the cluster centre, as before. The point of inflection, where the probability of T and F was equal, was calculated for each dataset and these were used as the cut-offs for behavioural analysis. The relationship between T and F and distance from cluster centre were also compared between the training-, North- and South classifiers. This indicated whether the strength of the classifier (the proportion of Ts and Fs) changed as it was developed further.

2.4 Behavioural analysis

Overlap analysis

The raw data from the North and South were filtered to exclude entries above the cut-off for maximum distance from cluster centre. The data were then compiled in a pivot table in Microsoft Excel Version 2205, so that the count of chick calls was shown per hour, for each day in each location. Hours within the recording period in which there were no calls were filled in with a 0. The data were then exported and analysed in R Studio Version 1.4.1103 (R Studio Team 2021).

First, the 'Hour' variable was converted into radians by multiplying it by 2 and pi, to represent it as a circular variable. The package *overlap* (Ridout & Linkie 2009) was then used to determine the level of overlap between call patterns in the North and South. A von Mises kernel density curve was fitted for the North and South datasets individually, corresponding

to the density distribution of the chick calls along the circular hour variable. Following Ridout & Linkie's (2009) study on species activity pattern overlap, a delta hat ($\widehat{\Delta}$) 4 estimator with an adjust of 1 was used for the coefficient of the overlap, suitable for larger sample sizes.

Modelling

The next step was to investigate the relationship between chick calling behaviour, hour of day, and whether chicks were in the North or South. Preliminary plotting of the compiled data revealed that the relationship between calling frequency and the circular hour variable was non-linear. Hence, it was decided to fit Generalised Additive Models (GAMs) using the 'gam' function from the package *mgcv* (Wood 2011). GAMs use an adjustable smoothing parameter to describe non-linear functional relationships between the response and explanatory variables, and were therefore considered appropriate (*see* Pedersen et al., 2019 *for further information on GAMs*).

The global model included the response variable 'count' of chick calls modelled against the explanatory hour variable and the North/South variable, as well as the interaction between them. The hour variable was expressed in a circular form, by including the term 'bs= "cc"' in the formula. 'bs' is the basis which represents the smooth function, and 'cc' is a smooth class which represents a cyclic cubic regression spline with matching ends (Wood 2011).

The location of each nest site within the North and South was anticipated to have some effect on the response, though the nature of this effect was not considered relevant to the study. Preliminary analysis confirmed that there was indeed variation in calling behaviour between locations. To control for pseudoreplication, the location variable was included in the global model as a random effect. Since each nest site was only sampled for one year, having the location variable as a random effect accounted for some level of spatial autocorrelation.

To determine an appropriate distribution family to fit the response variable, the quantiles of the response were analysed in R. The results revealed a highly skewed distribution. Since the response variable was in the form of a count, either Poisson or negative binomial distribution families could be appropriate. All models were fit with each of these distribution families and compared during model selection.

The smoothing parameter k, which controls the smoothness of the fitted curve, was initially left at the default value (k=10), as is generally recommended in the *mgcv* package (Wood, 2011). This was experimented with during the model diagnostics stage (*see Section 2.5*).

All models were created with a maximum likelihood (ML) method; however, the final model was expressed with a restricted maximum likelihood (REML) method, which provides a more conservative estimate of the model.

Model selection

Prior to model selection, the model was tested with a single random slope vs. with a random intercept, with location as the random effect. A model which combined a random slope and a random intercept was very unlikely to be a good fit for the data, considering there were only 11 locations, hence this model was not constructed.

Considering this study aims to compare the calling patterns of chicks under differing light exposures, rather than to establish the best model for the observed relationships, only a brief process of model selection was undertaken. The global model was selected on the random effect and on a null model (no explanatory variables). All models were compared using their Akaike Information Criterion (AIC) scores.

2.5 Model diagnostics and goodness-of-fit

Once the best model was chosen, it was tested for temporal autocorrelation using the R package *itsadug* (van Rij et al., 2022), following the process outlined in the vignette by van Rij (2016). To summarise, the 'acf' function (R Core Team, 2022) was used to produce an autocorrelation function (ACF) on the selected model, to determine the degree of correlation in the time series at different time lags (van Rij et al., 2022). An AR1 model was then included to reduce autocorrelation.

Next, the 'gam.check' function from the *mgcv* package (Wood, 2011) was used to produce diagnostic plots of the model fit, as well as information about the smoothing basis dimension (k). The package's description states that a low p-value and a k-index <1 indicates that k is too low, particularly if the estimated degrees of freedom (edf) value is close to k' (Wood, 2011). Hence, the results of the diagnostics could be used to adjust the smoothing parameter k in order to enhance the fit of the model, if needed.

Two methods were then used to check for over-dispersion: creating a dispersion parameter using the *DHARMa package* (Hartig, 2022), and by calculating the Pearson estimate ($\hat{\phi}$) of the dispersion parameter for the selected model. In the case of the former, the function 'simulateResiduals' was used to simulate scaled residuals from the fitted model, after which the function 'testDispersion' could be used to run a series of dispersion tests (Hartig, 2022). The *DHARMa* package was also used to test for zero inflation, by comparing the number of observed zeroes with the expected zeroes from simulations.

The model was then checked for concurvity between variables, using the 'concurvity' function within the *mgcv* package (Wood, 2011). Finally, the predicted results of the selected model were created using the 'ggpredict' function from the package *ggeffects* (Lüdecke, 2018) and plotted for interpretation.

3. Results

3.1 Sample sizes

Once the data were filtered to only include chick calls which were 0.74 units from the cluster centre, there were a total of 355,798 chick calls used in the behavioural analysis, of which 321,551 (90.37%) were from the North and 34,247 (9.63%) were from the South. The distribution of the response count variable (calls per chick) was strongly skewed, as revealed through analysis of its quantiles. 25% of the data had ≤1 call per hour; 50% of the data had up to 12 calls per hour; 75% of the data had up to 46 calls per hour; and the maximum calling frequency was 1,944 calls per hour.

3.2 Classifier validation

The sounds identified as Eagle owl chick calls by the Kaleidoscope cluster analysis were processed through a series of minor and thorough validations, as described in Figure 5 and Steps 2-6 of Section 2.3. The model outputs from the first minor validation on the training dataset are displayed in Appendices 2-4 and show significant relationships between all acoustic parameters and the proportion of true and false positives (p <0.001), except duration. Appendix 2 shows that the proportion of true and false positives is roughly equal at the lowest frequency (1000KHz), and Appendix 3 shows a relatively even distribution up to 10,000KHz, after which the proportion of true positives reduces. Finally, the relationship between the proportion of true and false positives and signal duration was only marginally significant (p= 0.0916), with fewer true positives after 2.5s (Appx.4). These results were used to modify parameters into their final limits, as shown in Table 2.

The results of the thorough validation of the training classifier (described in step 4 of Methods) are shown in Figure 7 below. This plot shows the proportion of true and false positives with increasing distance from the cluster centre, along with the inflection point where the proportion is equal. The proportion of true positives in the training classifier is ~0.56 (Fig. 7).
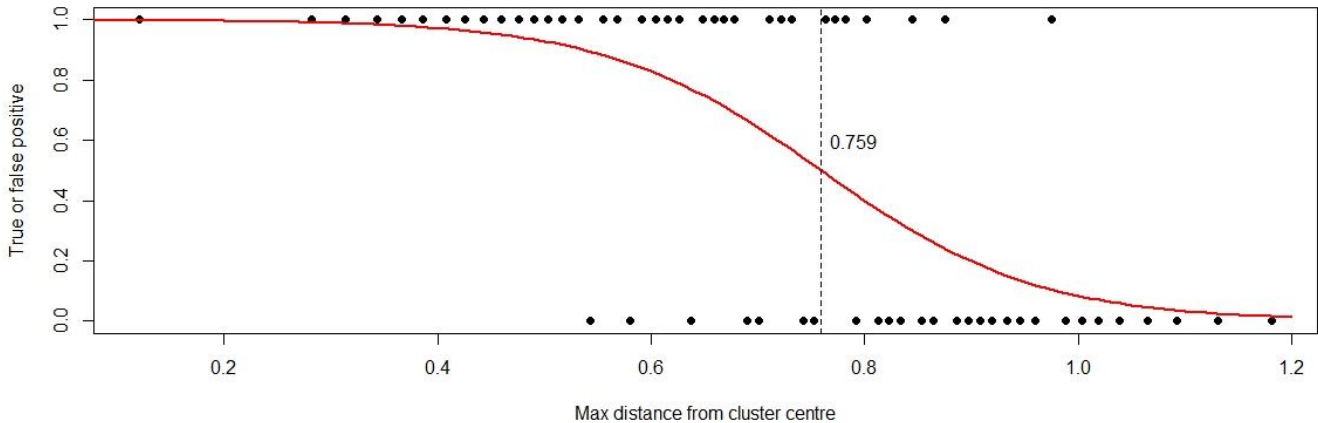

Figure 7— Distribution of true positive (1.0) and false positive (0.0) Eagle owl chick calls over distance from cluster centre, as well as point of inflection, for training vocal classifier. Plot produced in Kaleidoscope Pro version 5.4.2.

Figures 8 and 9 show similar plots for the final thorough validations of the North and South classifiers, respectively (*see* Methods step 6). For the North classifier, the proportion of true positives was 0.68 and the inflection point, where the proportion of true and false positives are equal, was 0.73 (Fig. 8). For the South classifier, the proportion of true positives was 0.70 and the inflection point was 0.75 (Fig. 9). The average of the inflection points in Figures 7 and 8 (=0.74) was used as a threshold, so all data above this distance from the cluster centre were excluded for behavioural analysis.
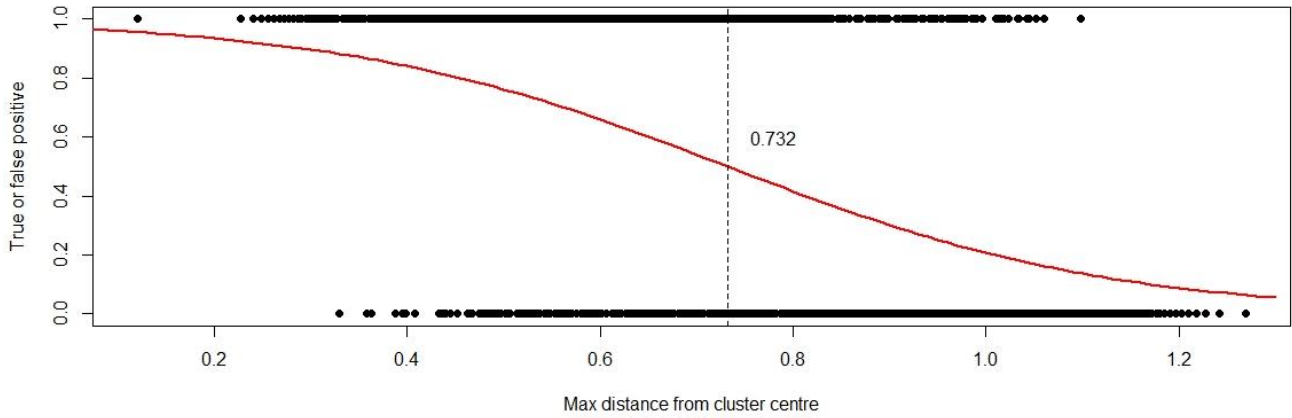
Figure 8— Distribution of true positive (1.0) and false positive (0.0) Eagle owl chick calls over distance from cluster centre, as well as point of inflection, for Northern Norway vocal classifier. Plot produced in Kaleidoscope Pro version 5.4.2.
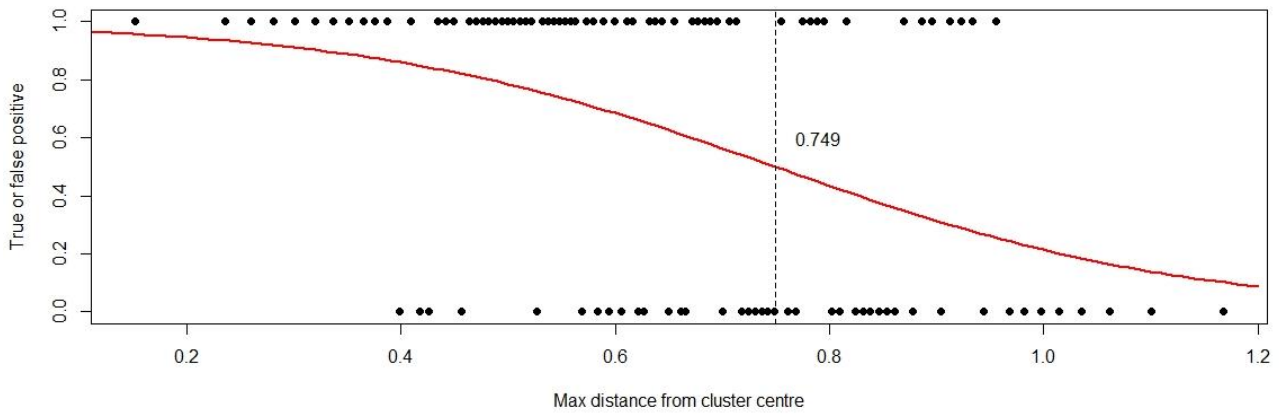

Figure 9— Distribution of true positive (1.0) and false positive (0.0) Eagle owl chick calls over distance from cluster centre, as well as point of inflection, for Southern Norway vocal classifier. Plot produced in Kaleidoscope Pro version 5.4.2.

3.3 Analysis of Eagle owl chick vocal activity patterns

From plotting the raw data, Figure 10 shows that in the North calling appeared to be relatively consistent between locations and highest around midnight, with some sporadic calling during the daytime (generally < 100 calls/hour). Figure 11 shows that in the South, calling was considerably more frequent at the Rendalen nest site than in the other two. There also appeared to be some variation in the calling patterns between locations in the South (Fig. 11). At the Aust Agder nest site, calling remained relatively low (average of <7 calls per hour) with small peaks at 10:00, 14:00, 17:00 and 22:00, all reaching an average of 5-6 calls. In Vest Agder there was a similar pattern, however there were two sharp peaks at 18:00 (average of 12 calls) and 23:00 (average of 10 calls). Different calling patterns were observed at Rendalen— three main peaks, one at 03:00 (60 calls), another at 11:00 (40 calls) and a final peak near midnight (45 calls).
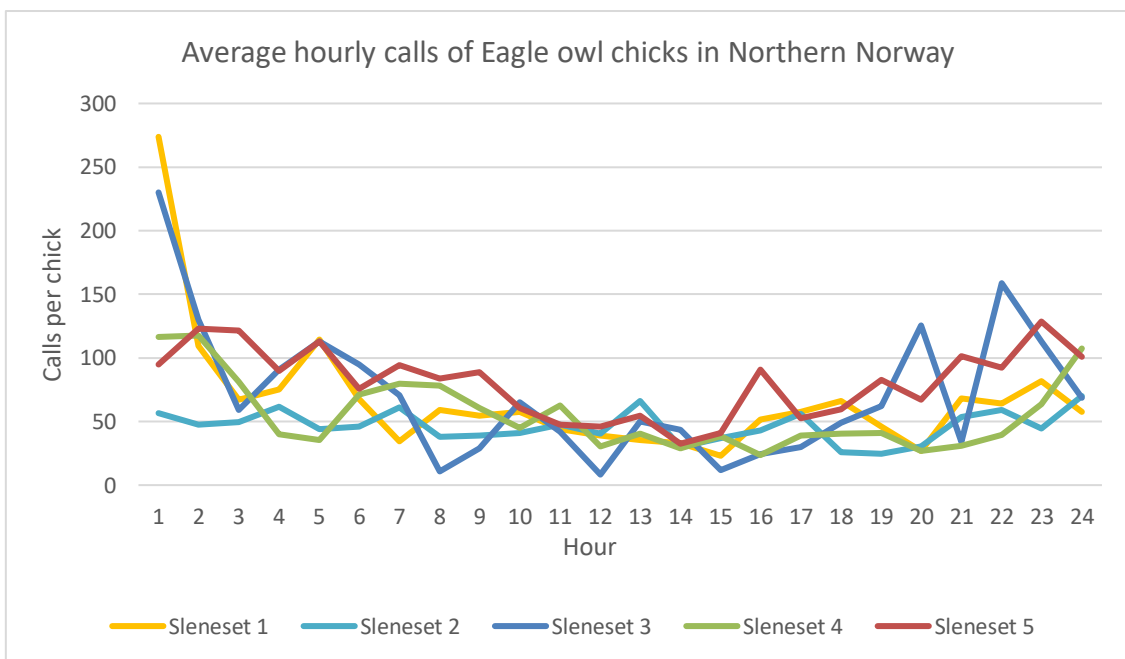

Figure 10— Average hourly calls per Eagle owl chick in five nest sites in Sleneset, Northern Norway.
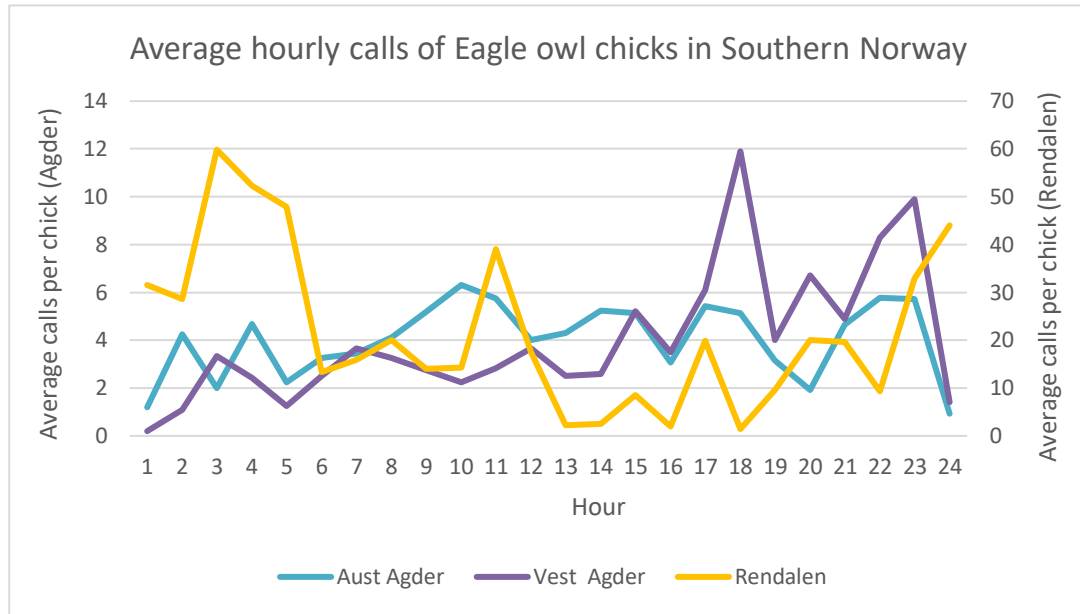
Figure 11— Average hourly calls per Eagle owl chick in three nest sites in Southern Norway.

The Kernel density overlap analysis, plotted in Figure 12 below, indicates a relatively high level of overlap between the North and South ($\widehat{\Delta}$ 4≈ 0.80). In the North vocal activity was relatively consistent throughout the day and highest around midnight. In the South there was more fluctuation in vocal activity during the day, with larger peaks at 03:00, 11:00 and 23:00.
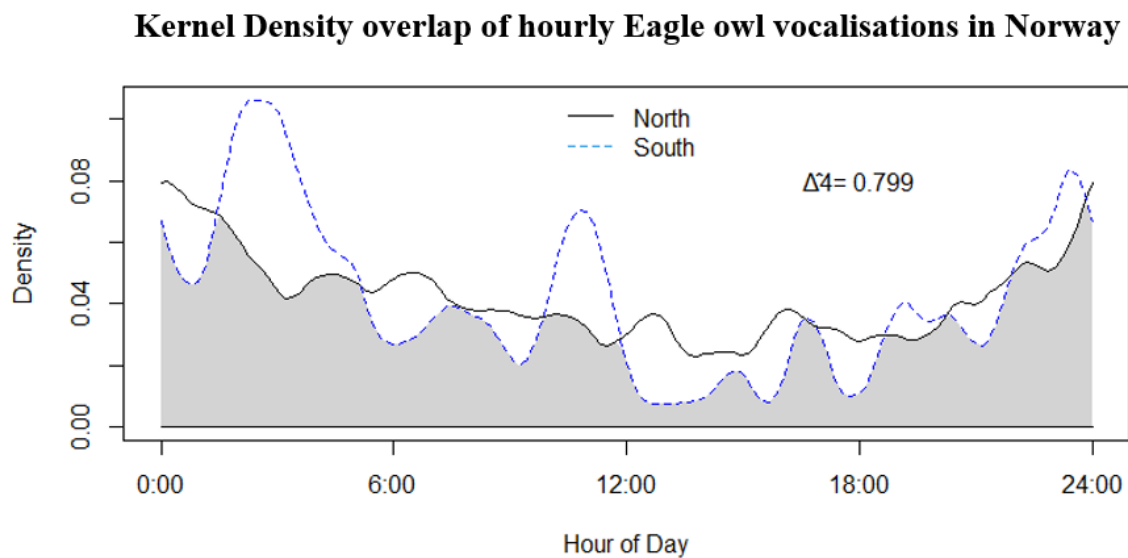

Figure 12— Kernel density overlap for Eagle owl chick vocal activity patterns in Northern and Southern Norway, with overlap coefficient (Δ̂4). Shaded area represents overlap in chick calling density.

3.4 Model diagnostics and final model

Prior to selecting the best model, the global model residuals were tested for autocorrelation. The resulting ACF plot, shown in Appendix 6, reveals an autocorrelation coefficient (rho) of 0.64 at lag 1, suggesting autocorrelation is present in the data. Autocorrelation appears to decrease after lag 1 and increase again between lags 20-24 (Appendix 5). An AR1 structure was included in the global model to reduce autocorrelation, however it did not appear to have any effect, and was subsequently removed. Furthermore, when comparing the ΔAIC scores of all models (Table 3), the global model had the lowest delta AIC (ΔAIC) and was therefore selected as the best-fitting model for the data. The summary statistics of the selected model are shown in Appendix 6.

Table 3— Delta AIC values of models for Eagle owl chick calling activity in Northern and Southern Norway, used for model selection.

Model type	ΔAIC
Global model	0.0
Global model without random effect	124.6
Null model (no predictors)	684.0

Figure 13 plots the predicted calling behaviour of Eagle owl chicks per hour, based on the selected model. There is a much higher calling frequency in the North than in the South, and activity appears to be highest between 20:00 and 05:00 and lower during the day. In the South there appears to be activity throughout the day with some small peaks around 03:00 and 10:00, though there is no discernible overall pattern.
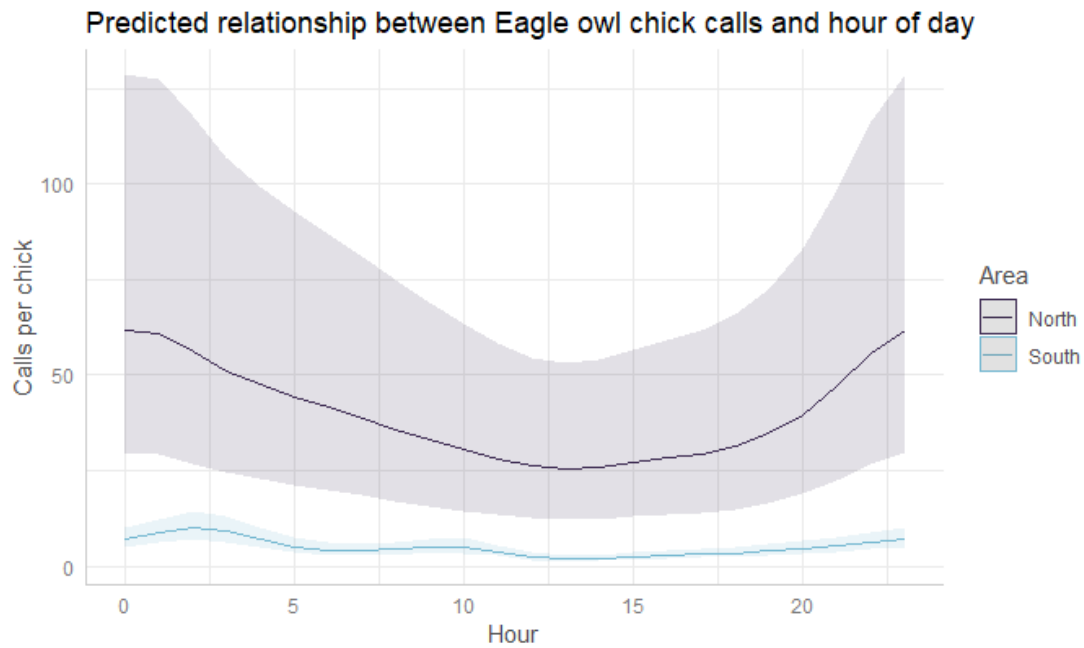
Figure 13— Predicted plot of hourly calling behaviour of Eagle owl chicks in Northern and Southern Norway, based on a model with response 'calls per chick' and predictors 'hour' and 'North/South', with negative binomial distribution.

The diagnostics of the selected model revealed low p-values (p <2e-16) and k-indices of 0.52 for the modelled interactions between hour and North/South. Reported edf values were somewhat close to k'. When the smoothing parameter k in the model was increased from its default value of k=10 to k=20 for all smoothing, the edf values in the model diagnostics increased as well.

Regarding overdispersion, the *DHARMa* approach revealed a dispersion value of 1.14 (p= 0.14) in the selected model, while the Pearson dispersion parameter $\hat{\phi}$= 1.82. In both cases this indicates slight overdispersion. The DHARMa zero inflation test yielded a ratio of 1.05 (p= 0.048), which indicates that there were slightly more zeroes in the observed data than expected. Further, three measures of concurvity were produced: the 'worst', 'observed' and 'estimate' measures (*see* Wood, 2011 for further details). All measures produced concurvity indices <0.35, indicating a low degree of concurvity between modelled variables.

4. Discussion

4.1 Behavioural analysis

The results of the behavioural analysis indicate that Eagle owl chicks exposed to continuous midsummer daylight called most around midnight and in lower amounts during the day (Figs. 11 & 12). Alternatively, in Southern Norway where there are dark nights during summer, chicks called sporadically throughout the day (average of 10 calls per chick per hour, between 07:00-19:00). There was a relatively high degree of overlap between activity patterns in Northern and Southern Norway, though in the North there was a notable nocturnal peak whereas in the South there were peaks throughout the day (Fig. 12). Furthermore, chicks exposed to continuous daylight were found to be more nocturnal than those exposed to dark nights. The findings in the North are mostly in-line with H1 of the study and are similar to the activity patterns observed in adult Eagle owls in Sleneset by Eriksen & Wabakken (2018). Following the interpretation from this study, chicks could be most active around midnight as this is when their parents are most active and can exploit slightly lower light intensity to hunt, whilst minimising the risk of interacting with Sea eagles (Eriksen & Wabakken, 2018). This would imply that in the absence of a clear light-dark cycle, the Eagle owl chick's circadian rhythm may be entrained (or masked) by parental activity and intra-guild predation (Silverin et al., 2009).

The need for Eagle owl chicks to conceal themselves, as was suggested for adults, is supported by findings of inter-specific aggression amongst other raptors. Several studies have shown that smaller/ less dominant owls (e.g., Tawny owl *Strix aluco*, Spotted owls *Strix occidentalis* spp., Little owl *Athene noctua*) restrict their calling activity to minimize interference competition and predation risk by intra-guild predators, which are usually larger owls (e.g. Crozier et al., 2006; Sergio et al., 2007; Zuberogoitia et al., 2008; Lourenço et al., 2013). There have been similar findings for other raptors; for example, Black kites (*Milvus migrans*) in the Italian alps whose young were predated by Eagle owls, responded by finding refugia in areas with lower risks of predation (Sergio et al., 2003). Similarly, Kostrzewa (1990) showed that Northern goshawks (*Accipiter gentiles*) in Europe may predate on nestlings of Common buzzards (*Buteo buteo*) and Honey buzzards (*Pernis apivorus*), subsequently displacing them from their nests. Though some of these studies do not focus on vocal responses to predation, it is reasonable to

expect that a spatial shift in nesting could translate into a shift in vocal activity for predatory birds (and their chicks) coexisting in a closed habitat, such as Sleneset.

While vocal activity peaks near midnight in Sleneset, chicks were also observed to call throughout the day at an average of ~47 calls per hour, when adults are mostly silent (Eriksen & Wabakken, 2018) (Fig. 10). This is similar to what is reported in the literature; Penteriani et al. (2000) showed that nestlings and fledglings called at an average of 65.6 times per hour, though the chicks in their study called most approximately 3 hours after sunrise and 3 hours before sunset. They suggested that such high rates of daytime calling in the absence of adult activity is perhaps related to vocal practice as well as contact calling between siblings (Penteriani et al., 2000).

Overall, Eagle owl chicks in Northern Norway called much more per hour than those in the South. During hours of peak activity (i.e., approximately between 20:00-03:00) there was an average of ~87 calls per chick, per hour (Fig. 10). Penteriani et al. (2005) describe a positive relationship between the age of Eagle owl juveniles and the number of calls per bout. They found that from 70 days old to 150 days old, calls per night can increase from 318 to 1,106, respectively. In this case, chicks in Sleneset appear to call more frequently over the peak activity period than those in the literature. This could be attributed, at least in part, to prey availability. As mentioned, Sleneset is a unique habitat for Eagle owls, wherein the lack of the invasive American mink (*Mustela vison*) has allowed for the growth of the local European water vole population (*Arvicola amphibius*), the Eagle owl's main prey source (Bichsel, 2012). It is possible that the abundance of voles has indirectly led chicks to call more frequently. Begging is used by chicks as a method of regulating parent-offspring conflict as well as competition between siblings; in general, the more begging calls a chick uses, the more food is supplied by the parents (Leonard et al., 2003; Smiseth et al., 2003; Penteriani & Delgado, 2019). It follows that a higher amount of vole prey may induce a positive feedback loop, wherein individual chicks, especially those competing with siblings, vocalise more in order to receive more food. Indeed, the interactions between parents, offspring and siblings can be quite complex. For example, a study by Dreiss et al. (2010) showed that a Barn owl (*Tyto alba*) nestling increased its calling duration and rate to negotiate with siblings and gain priority during parental feeding.

It is also possible that such a high number of hourly calls in the North is the result of misclassification, i.e., false positives within the data. Further, the distinction between the

number of calls in the North and the South could be attributed to the exclusion of Eagle owl chick calls (i.e., false negatives) in the South by the software. Both of these possibilities are discussed in section 4.2.

The daytime peaks in activity observed in the South are likely not an accurate expression of overall activity patterns in Southern Norway; rather, they reflect considerable variation in vocal activity between locations (Fig. 11). There were on average many more calls per hour in Rendalen compared to the Agder nest sites, which has likely influenced the expression of overall southern activity patterns shown in Figures 12 and 13. In Rendalen, activity was highest from around midnight to 06:00, and again around noon; in Vest Agder, activity was highest in the evenings (16:00-19:00) and just before midnight; and in Aust Agder, activity was more consistent throughout the day with no major peaks (Fig. 11). This variation may be due to individual differences, or geographical variation at various scales; this is difficult to tease apart when there is only one nest per location. Examples of geographical variation include adult activity, prey availability and/or the presence of competitors. In Vest Agder a white-tailed sea eagle, which is known to be diurnal (Krone et al., 2009), has been recorded predating on an Eagle owl chick (Esperås pers. Comm. 2022). Eagle owl chicks may respond quickly to threats by ceasing vocalisations, which may explain some of the activity patterns observed; though this is more likely to influence calling at a finer scale, i.e., within the hour (Penteriani & Delgado, 2019).

4.2 Vocal classifier

The objective for the classifier, i.e., to achieve a successful detection rate (proportion of true positives) of >60% for Eagle owl chick begging calls, was achieved for both North and South classifiers, given a threshold of 0.74 from the cluster centre. In fact, both classifiers had a success rate closer to 70% (North=68%, South=70%). This makes the results here comparable to the detection success rates of other studies (i.e., Odom & Mennill (2010) classified call types of barred owls with 69% success; Shonfield et al. (2018) classified different owls with success rate of 16-99%), while balancing the trade-off between precision (false positives) and data exclusion (false negatives). In this study, false positives were signals that the software considered to be similar to the target signal, and were usually calls of other species (i.e., *Corvus* spp.) or simply unidentifiable noise.

Between the training classifier and the North and South classifiers, there was a similar distribution and proportion of true positives and false positives along a gradient of distance from the cluster centre (Figs. 7-9). For both North and South datasets, the proportion of true positives decreased after approximately 0.75 units from the cluster centre, out of a maximum of 2.0. This means that the resulting classifiers could detect signals within the threshold with higher accuracy, however some true positive signals would be excluded from analysis. This trade-off is discussed further in section 4.3.

Signal parameters were set quite wide for cluster analysis while developing the classifier, hence there is considered to be minimal risk of missing detections outside of the parameter limits. For instance, Penteriani & Delgado (2019) state that the begging call of chicks can be up to 6-8kHz. The frequency range used in this study was much wider (0.5-13kHz), as decided based on observations of call frequencies during exploratory analysis (*see* Methods section 2.3, step 1); hence, it is unlikely that chick signals fell outside of this range.

4.3 Limitations

Behavioural analysis

This study is most limited in the strength and interpretability of the generated model for hourly calling frequency. While the selected model was the strongest representation of the relationships between variables based on available information, overall it explained a relatively low proportion of the variation in the data (R^2=0.07, Appx. 6). The model diagnostics also confirmed that the model was not an optimal fit. The diagnostics summary revealed low p-values and edf's relatively close to k', however when the smoothing parameter k was increased from 10-20, the edf values increased as well, suggesting k was not too low and some other factor(s) is likely affecting the model's fit (Wood, 2011). The dispersion tests indicated no significant overdispersion (both ratios <1.82); there was also marginal zero-inflation (1.053, p<2.2e-16), and concurvity estimates were close to 0 for all modelled relationships, suggesting this was not an issue. There are likely several explanations for why the model was not the best fit for the data.

Although the negative binomial family accounts for some of the skewness of the response variable's (calls per chick per hour) distribution, it probably does not account for all of it. This could be improved by, for instance, using an alternative distribution family. To explore this,

the 'fitDist' function from the R package g*amlss* (Rigby & Stasinopoulos, 2005) was used to fit a distribution during preliminary analysis. This function indicated that a 'Pareto Type 2' family would best fit the response variable, however it was decided to avoid this due to the complexity and uncertainty associated with this family. Regardless, the aim of the study was primarily to investigate the effect of continuous light on Eagle owl chick activity patterns, rather than to generate the best-fitting model to explain the variation in calling frequency. As such, the output of the model summary is not evaluated in particular detail here. Since light is unlikely to entirely explain the vocal activity of this species, it is reasonable to expect a model without very high explanatory power, as there are likely other environmental, biological and geographical factors at play.

One example is the role of White-tailed Sea eagles as a competitor for Eagle owls (and a predator for chicks) in Sleneset, discussed already by Eriksen & Wabakken (2018). If adult activity is linked to the activity of their competing guild-members, it is reasonable to expect that there is some effect, either direct or indirect, on chick activity. For example, regular sightings of Sea eagles throughout the day might have led chicks to avoid vocalising at certain times in all or some of the study sites. A similar effect could have occurred due to the presence of sheep. Sheep, which roam freely on some of the islands in Sleneset, are known to trample on Eagle owl nests when grazing and when taking shelter from harsh weather (pers. comm. Dahl & Wabakken, 2021). It is currently unknown how regularly this occurs, though it is possible that it may have influenced the hourly calling patterns of chicks in the northern study area.

Environmental variables such as temperature, wind and precipitation may also have influenced the observed activity patterns in this study, both by masking sound and affecting chick activity, and including such variables could therefore have enhanced the fit of the model. It would, however, be challenging to include such factors in this study as they may vary considerably between islands in Sleneset even within the same day, and data from nearby weather stations would not provide sufficient spatiotemporal resolution. While local collection of weather data could have provided more fine-scaled data, it was beyond this study's scope of highlighting the effect of continuous daylight on Eagle owl chick activity patterns. The same could be said of biological factors such as sex, size and body condition of Eagle owl chicks, all of which could have varied between nest sites and influenced activity patterns.

An issue identified with the selected model was temporal autocorrelation, or the influence of one behavioural measurement on another measurement at a different point in time (Mitchell et al., 2020). When successive data points are correlated with each other, as in Appendix 5, estimates may be biased. It was attempted to deal with this issue during analysis by including an AR1 structure in the selected model; however, this did not reduce autocorrelation or improve the model's fit (Table 3). Nonetheless, it is difficult to know in this case whether there is actually autocorrelation within the data, or if this is simply how the Eagle owl chicks behaved over time. To further understand this issue, a more comprehensive analysis including other predictors would be required, discussed below.

Vocal classification

An issue that was identified during the validation process, was that there is inevitably a trade-off between the probability of false positives and false negatives. If parameters were set wide enough and more vocal signals were allowed into the cluster analysis, this would reduce the probability of signals being missed (false negatives) but increase the likelihood of signals being confused (false positives). Alternatively, if stricter parameters were used (i.e., a cut-off closer to the cluster centre) to reduce the proportion of false positives, this would likely increase the number of false negatives, i.e., target sounds not detected by the algorithm. This raised an important question as to what was valued more in this study: creating a classifier which picks up on fewer chick signals with high certainty, or a classifier that may give a better idea of when chicks are active but with less certainty. This trade-off was addressed by plotting the proportions of true and false positives against the distance from cluster centres and creating a cut-off for analysis (*see Step 6 of the Methods section*). This method allows the same classifier to be applicable to other studies, as a threshold for distance from the cluster centre can be selected to match the aims of the study. However, this method also only allows for interpretation of the false positives and false negatives given the parameter settings used; there is no indication of how many chick sounds were not detected by the software or included in a chick cluster.

Applying a cut-off on the data obviously means that data were excluded from the analysis. In the current study, unless the missed calls (false negatives) were biased toward specific areas, locations, or times of day, this is unlikely to have affected the results. False positives are probably a bigger issue in this study as it introduces noise into the data, for instance sounds from species that call at times of day when Eagle owl chicks are not calling. Since this study

aimed to investigate Eagle owl chick activity patterns under continuous daylight, the specified trade-off between false positives and false negatives was considered to provide sufficient insight, albeit perhaps without representing the whole picture. If the vocal classification method were used instead to document breeding success at nest sites, then minimising false negatives would be of a higher priority, to avoid missing an active nest. To do so, however, one would need to create an advanced classifier, which would involve considerable manual validation (actually listening to sounds and labelling them as 'chick' or other).

4.4 Areas for improvement and future research

The data from each nest site were collected over one summer, spanning a 2-year period. Moreover, only data from the early growth stages of Eagle owl chicks were considered (i.e., June-July). This study can therefore be considered a pilot study into the activity patterns of Eagle owl chicks under continuous daylight, as well as the usefulness of the vocal classification method for this species. There is some valuable insight here which can be expanded upon in future studies, however there is certainly room for improvement in the methodology and study design.

Regarding the distribution of the response variable, there was a large gap between the 3rd and 4th quantiles; only 25% of records included from 46 to 1,944 calls per hour. The few records with very high calling frequency could reflect the presence of true outliers which skew the data distribution, or simply misidentification by the classifier inflating the apparent calling frequency. In the case of the latter, it would be prudent to check the recordings of the hours with the highest calling frequencies, to determine if there are actually that many Eagle owl chick calls or if they were simply misclassified. Further, if the misclassified calls belong to a particular period or location, this information could be used to further refine the classifier.

A more temporary solution would be to eliminate the hours with very high numbers of calls per chick. Kranz (1971) found that nestlings can make up to 600 begging calls per night in July. If this were to be used as a cut-off in the data (i.e., all hours where >600 calls were made were excluded), this would result in the loss of 29 hours of calling, approximately 0.0082% of the data included in analysis. The behavioural analysis was repeated with this cut-off applied, and there were no major differences in the model output. The global model remained the

strongest model in terms of AIC; there was still a low level of overdispersion; the zero-inflation ratio increased only by a margin of 0.022; and concurvity remained more or less the same. Further, there was still some autocorrelation in the global model which was not improved by including an AR1 structure. Thus, removing hours with highly frequent calls did not improve the model structure, suggesting once again that there are other factors which likely explain the observed variation in the model output.

For instance, creating a classifier was complicated by the fact that fainter chick calls were more difficult to identify, both manually and automatically. Fainter signals were either mistaken for other signals (i.e., excluded from the main chick cluster) or perhaps excluded entirely from analysis by the software. To minimise this issue, faint chick signals were manually labelled as *Chick* and acoustic signal parameters were set wide enough for the software to capture such signals. Nonetheless, it is difficult to determine how many fainter signals were missed (i.e., false negatives). If the distance between chicks and recorders varied consistently between locations or at different times of the day, this would have influenced the results. Thus, it would be useful to investigate the effect of distance from the recorder on signal detectability for future use of this methodology.

Despite shortcomings, the methods in this study were able to successfully produce classifiers with success rates close to 70%. The next step would be to increase the aim and further refine the classifiers, eventually combining them into one classifier for begging calls. This could be done by introducing more recordings from the given locations as well as from other geographical regions. Furthermore, the methodology presented in this study is useful not just for Eagle owl chicks but could also be used to analyse the activity patterns of adult Eagle owls.

As mentioned in the previous section, there are several factors other than light that may be affecting the calling behaviour of Eagle owl chicks in Sleneset. Thus, if the objective were to understand chick activity patterns in further detail, this could be achieved by including some of these factors and building a model that could explain more of the variation in chick calling frequency. For instance, Sea eagle and sheep vocalisations could be analysed alongside chicks to confirm whether there is a direct effect. Moreover, variation in prey density and quality between locations could be accounted for by measuring and comparing the diet composition at each nest site, as in Bichsel (2012) & Esperås & Ulsted (2022). It would also be interesting to investigate the mink-vole-eagle owl dynamic in Norway further, as the absence of the mink is believed to be one of the main reasons for the Eagle owl's success in Sleneset (Melis et al.,

2011). Comparing findings from other parts in Norway could confirm whether this is indeed an explanation for higher activity in the North.

The probability of detection for Eagle owl chicks was considered to be similar between North and South, as the same recorders and settings were used. That being said, it is possible that the terrain has some influence. Sleneset being flatter and treeless means sound carries more easily across the landscape than in the South, where sound waves can be obstructed by trees and slopes. Moreover, the presence of other species that could mask the sound of/ be confounded with Eagle owl chick calls could influence the probability of detection. There were indeed very different avian communities between the northern and southern study sites; in the North there was a higher proportion of sea birds (e.g., *Laridae*, *Ansenirae*), whereas in the south there were forest birds (e.g., *Strix aluco*) as well as some sea birds. If the difference in the detection probability of Eagle owl chicks due to terrain and the presence of other species could be quantified and included in analysis, it would provide a clearer picture of chick activity patterns under continuous daylight.

By analysing the 'changes' in calling behaviour in the North under continuous daylight, this study assumes that activity patterns are otherwise similar to the literature in other parts of the year. This may not necessarily be true, especially considering that Sleneset experiences continuous darkness during winter months. Further investigation into the activity patterns of Eagle owls and their chicks during other times of the year may give clearer insight into the patterns observed here during summer. This could be achieved using the vocal classification method developed here, though other categories of calling types would need to be included in analysis.

4.5 Conclusions

The current study provides some valuable insight into the activity patterns of Eagle owl chicks under continuous daylight during the arctic summer, which can be explored further. By developing a vocal classifier for the species, it was possible to map vocal activity in northern and southern parts of Norway with reasonable success. The methods used here achieved the aims of the study, and the classifier created is applicable to further studies on Eagle owl chicks and adults both in Sleneset and in other parts of Europe. However, it would be beneficial to strengthen the classifier by including more data and additional study periods to make it more robust. Moreover, it would be useful to quantify the proportion of false negatives (i.e., missed

calls) for the classifiers to further refine them in their abilities to detect Eagle owl chicks. To gain further insight into Eagle owl chick activity patterns, it is recommended to investigate other environmental, biological and geographical variables that may explain the variation in calling frequency between hours of the day and locations.

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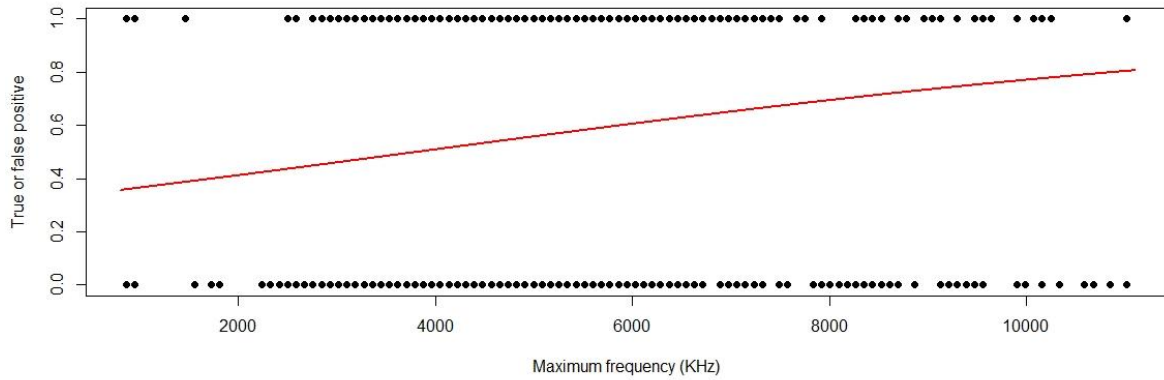
6. Appendix

Appendix 1— Dates of 24-hour recording samples used in training dataset for analysis of Eagle owl chick vocal activity

| Study site	Recording sample date
Rendalen (Southern Norway)	June 15
Vest Augder (Southern Norway)	June 12
Aust Augder (Southern Norway)	June 17
Sleneset location 1 (Northern Norway)	July 5
Sleneset location 2	July 9
Sleneset location 3	June 22
Sleneset location 4	June 26
Sleneset location 5	July 1
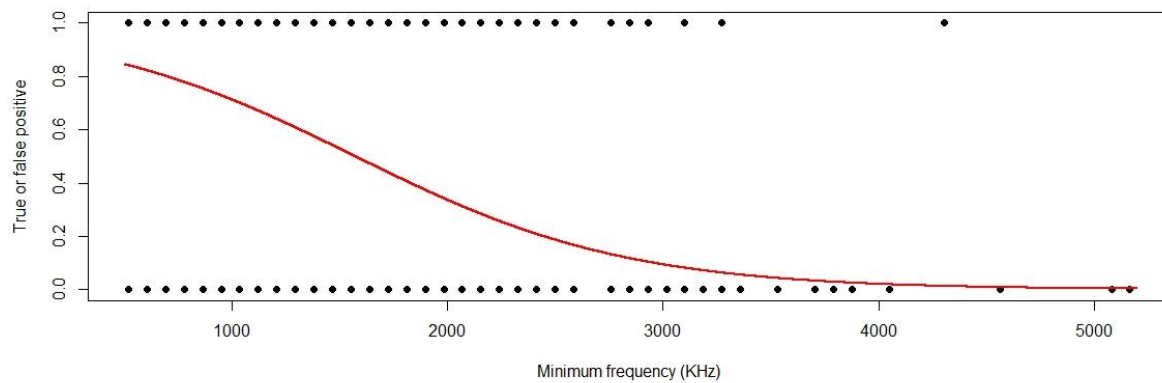
Appendix 2— Distribution of true positive (1.0) and false positive (0.0) Eagle owl chick calls at low frequencies, used to set lower limit for cluster analysis on training data. Plot produced in Kaleidoscope Pro version 5.4.2.

Appendix 3— Distribution of true positive (1.0) and false positive (0.0) Eagle owl chick calls at high frequencies, used to set upper limit for cluster analysis on training data. Plot produced in Kaleidoscope Pro version 5.4.2.
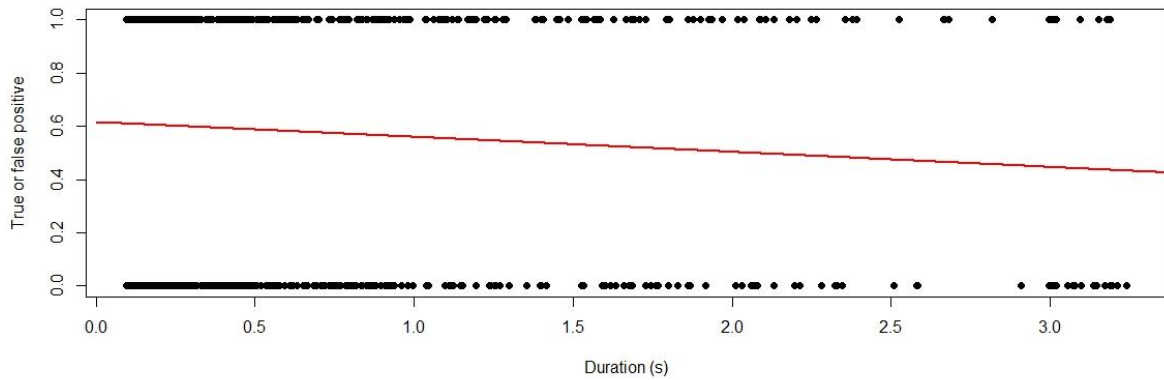
Appendix 4— Distribution of true positive (1.0) and false positive (0.0) Eagle owl chick calls over duration range, used to set duration limit for cluster analysis on training data. Plot produced in Kaleidoscope Pro version 5.4.2.
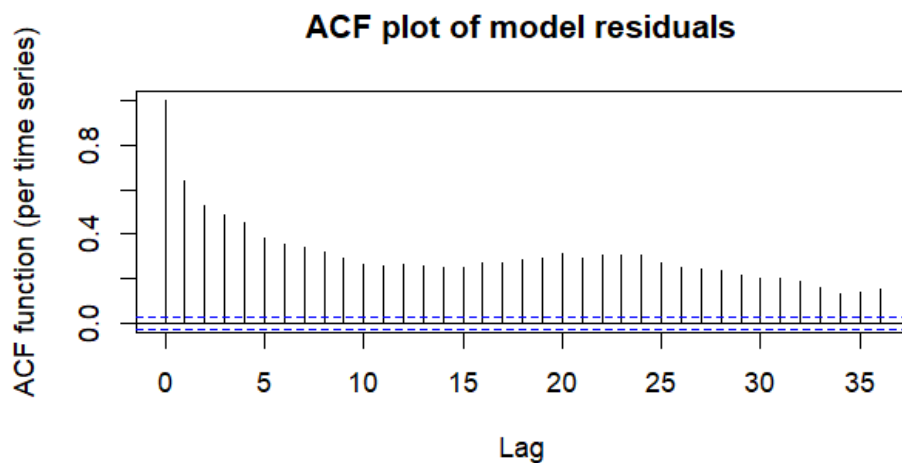
Appendix 5— Autocorrelation function plot of residuals for selected GAM of hourly Eagle owl chick vocal activity in Northern and Southern Norway.

Appendix 6— Summary statistics of selected model for Eagle owl chick calls per hour in Northern and Southern Norway.

Family: Negative Binomial(0.346)
Link function: log
Formula: countnum ~ NorthSouth + s(Hour, by = NorthSouth, bs = "cc") + s(Location, bs = "re")

Parametric coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	4.0894	0.2199	18.60	< 2e-16 ***
NorthSouthSouth	-2.1240	0.3637	-5.84	5.21e-09 ***

Signif. codes:
0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Approximate significance of smooth terms:

	edf	Ref.df	Chi.sq	p-value
s(Hour):NorthSouthNorth	4.777	8	104.61	<2e-16 ***
s(Hour):NorthSouthSouth	6.090	8	74.51	<2e-16 ***
s(Location)	5.802	6	174.68	<2e-16 ***

R-sq.(adj) = 0.0719   Deviance explained = 13.

Reference list

Ashley, N. T., Ubuka, T., Schwabl, I., Goymann, W., Salli, B. M., Bentley, G. E., & Buck, C. L. (2014). Revealing a Circadian Clock in Captive Arctic-Breeding Songbirds, Lapland Longspurs (Calcarius lapponicus), under Constant Illumination. *Journal of Biological Rhythms*, 29(6), 456–469. https://doi.org/10.1177/0748730414552323

Aste, N., Cozzi, B., Stankov, B., & Panzica, G. (2001). Sexual differences and effect of photoperiod on melatonin receptor in avian brain. *Microscopy Research and Technique*, 55(1), 37–47. https://doi.org/10.1002/jemt.1154

Bevanger, K. & Henriksen, G. (1995). The distributional history and present status of the American mink (Mustela vison Schreber, 1777) in Norway. *Annales Zoologici Fennici*, 32(1), 11–14.

Bichsel, M. (2012). *Diet of Nesting Eagle Owls (Bubo bubo) in Coastal Northern Norway*. [unpublished manuscript]. Zurich University of Applied Sciences, Zurich, Switzerland.

Bonesi, L. & Palazon, S. (2007). The American mink in Europe: Status, impacts, and control. *Biological Conservation*, 134(4), 470–483. https://doi.org/10.1016/j.biocon.2006.09.006

Bortolotti, G. R., Stoffel, M. J., & Galván, I. (2011). Wintering Snowy Owls Bubo scandiacus integrate plumage colour, behaviour and their environment to maximize efficacy of visual displays. *Ibis (London, England)*, 153(1), 134–142. https://doi.org/10.1111/j.1474-919X.2010.01067.x

Crozier, M., Seamans, M. E., GutiÉRrez, R. J., Loschl, P. J., Horn, R. B., Sovern, S. G., & Forsman, E. D. (2006). Does the Presence of Barred Owls Suppress the Calling Behavior of Spotted Owls? *The Condor (Los Angeles, Calif.)*, 108(4), 760–769. https://doi.org/10.1093/condor/108.4.760

Csernus, V. J. (2006). The Avian Pineal Gland. *Chronobiology International*, 23(1-2), 329–339. https://doi.org/10.1080/07420520500482108

Dahl, E.R. (Recordist). (17 September 2019). *XC499713* [.wav]. www.xeno-canto.org/499713

Erkert, H.G., Fernandez-Duque, E., Rotundo, M., & Scheideler, A. (2012). Seasonal Variation of Temporal Niche in Wild Owl Monkeys (Aotus azarai azarai) of the Argentinean Chaco: A Matter of Masking? *Chronobiology International*, 29(6), 702–714. https://doi.org/10.3109/07420528.2012.673190

Esperås, T. A. & Ulsted, T. H. (2022). *Proportional differences of rodents and other prey in the Eurasian Eagle Owl's diet located in alpine and boreal regions in Agder, Norway*. (182-BIO) [Bachelor Thesis, University of Agder].

Gwinner, E., Hau, M., & Heigl, S. (1997). Melatonin: Generation and Modulation of Avian Circadian Rhythms. *Brain Research Bulletin*, 44(4), 439–444. https://doi.org/10.1016/S0361-9230(97)00224-4

Guchhait, P. & Haldar, C. (1999). Circadian Rhythms of Melatoninatonin and Sex Steroids in a Nocturnal Bird, Indian Spotted Owlet Athene brama During Reproductively Active and Inactive Phases. *Biological Rhythm Research*, *30*(5), 508–516. https://doi.org/10.1076/brhm.30.5.508.1400

Hall, M.L. & Ross, C. (2007). Eye shape and activity pattern in birds. *Journal of Zoology (1987)*, 271(4), 437–444. https://doi.org/10.1111/j.1469-7998.2006.00227.x

Hartig, F. (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level /Mixed) Regression Models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa.

Heggøy, O., Gunleifsen, L., Husebø, H., Kleven, O., Steen, O.F., Steinsvåg, M.J., Undheim, O. & Øien, I.J. (2020). *Overvåking av hubro i Sør-Norge 2012–2019* (Rapport 2020-1). Norsk Ornitologisk Forening. https://www.birdlife.no/prosjekter/rapporter/2020_01_NOF.pdf

Jedrzejewska, B., Sidorovich, V. E., Pikulik, M. M., & Jȩdrzejewski, W. (2001). Feeding habits of the otter and the American mink in Białowieża Primeval Forest (Poland) compared to other Eurasian populations. *Ecography (Copenhagen)*, 24(2), 165–180. https://doi.org/10.1034/j.1600-0587.2001.240207.x

Kassamabara, A. (2021). rstatix: Pipe-Friendly Framework for Basic Statistical Tests. R package version 0.7.0. https://CRAN.R-project.org/package=rstatix

Kostrzewa, A. (1990). Interspecific interference competition in three European raptor species. *Ethology Ecology & Evolution*, 3(2), 127-143. https://doi.org/10.1080/08927014.1991.9525379

Kranz, P. (1971). Något om berguvens aktivität och föda. *Fåglar i Sörmland*, 4, 13-23.

Krone, O., Berger, A., & Schulte, R. (2009). Recording movement and activity pattern of a White-tailed Sea Eagle (Haliaeetus albicilla) by a GPS datalogger. *Journal of Ornithology*, 150(1), 273–280. https://doi.org/10.1007/s10336-008-0347-1

Kronfeld-Schor, Visser, M. E., Salis, L., & van Gils, J. A. (2017). Chronobiology of interspecific interactions in a changing world. Philosophical Transactions. *Biological Sciences*, 372(1734), 20160248. https://doi.org/10.1098/rstb.2016.0248

Leonard, M.L., Horn, A. G., & Parks, E. (2003). The Role of Posturing and Calling in the Begging Display of Nestling Birds. *Behavioral Ecology and Sociobiology*, 54(2), 188–193. https://doi.org/10.1007/s00265-003-0626-z

Lourenço, R., Goytre, F., del Mar Delgado, M., Thornton, M., Rabaça, J. E., & Penteriani, V. (2013). Tawny owl vocal activity is constrained by predation risk. *Journal of Avian Biology*, 44(5), 461–468. https://doi.org/10.1111/j.1600-048X.2013.00157.x

Lüdecke, D. (2018). "ggeffects: Tidy Data Frames of Marginal Effects from Regression Models." *Journal of Open Source Software*, 3(26), 772. https://doi.org/10.21105/joss.00772.

Melis, C., Holmern, T., Ringsby, T. H., & Sæther, B.-E. (2011). Who ends up in the eagle owl pellets? A new method to assess whether water voles experience different predation risk. *Mammalian Biology: Zeitschrift Für Säugetierkunde*, 76(6), 683–686. https://doi.org/10.1016/j.mambio.2011.06.008

Mikkola, H. (1976). Owls killing and killed by other owls and raptors in Europe. *British Birds*, 69(April), 144-154.

Mrosovsky, N. (1999). Masking: History, Definitions, and Measurement. *Chronobiology International*, 16(4), 415–429. https://doi.org/10.3109/07420529908998717

Murakami, N., Kawano, T., Nakahara, K., Nasu, T., & Shiota, K. (2001). Effect of melatonin on circadian rhythm, locomotor activity and body temperature in the intact house sparrow, Japanese quail and owl. *Brain Research*, 889(1), 220–224. https://doi.org/10.1016/S0006-8993(00)03205-4

Nagy, C. M. & Rockwell, R. F. (2012). Identification of individual Eastern Screech-Owls Megascops asio via vocalization analysis. *Bioacoustics (Berkhamsted)*, 21(2), 127–140. https://doi.org/10.1080/09524622.2011.651829

Natesan, A., Geetha, L., & Zatz, M. (2002). Rhythm and soul in the avian pineal. *Cell and Tissue Research*, 309(1), 35–45. https://doi.org/10.1007/s00441-002-0571-6

Nilsson, C., Bäckman, J., Karlsson, H., & Alerstam, T. (2015). Timing of nocturnal passerine migration in Arctic light conditions. *Polar Biology*, 38(9), 1453–1459. https://doi.org/10.1007/s00300-015-1708-x

Norsk Klimaservicesenter. (2022). *Observasjoner og værstatistikk*. Retrieved on September 16, 2022 from https://seklima.met.no/observations/

Norwegian Meteorological Institute & Norwegian Broadcasting Corporation. (2022). Yr.no. Retrieved September 15, 2022 from https://www.yr.no/en

Odom, K. J. & Mennill, D. J. (2010). A Quantitative Description of the Vocalizations and Vocal Activity of the Barred Owl. *The Condor (Los Angeles, Calif.)*, 112(3), 549–560. https://doi.org/10.1525/cond.2010.090163

Penteriani, V., Gallardo, M. & Cazassus, H. (2000). Diurnal vocal activity of young Eagle Owls and its implications in detecting occupied nests. *Journal of Raptor Research*, 34, 232-235. http://www.vincenzopenteriani.org/publications_pdfs/bubo_bubo_j_raptor_res.pdf

Penteriani, V., Delgado, M. M., Maggio, C., Aradis, A., & Sergio, F. (2005). Development of chicks and predispersal behaviour of young in the Eagle Owl Bubo bubo. *Ibis (London, England)*, 147(1), 155–168. https://doi.org/10.1111/j.1474-919x.2004.00381.x

Penteriani, V., Delgado, M. del M., Alonso-Álvarez, C., Pina, N. V., Sergio, F., Bartolommei, P., & Thompson, L. J. (2007). Importance of Visual Cues for Nocturnal Species: Eagle Owl Fledglings Signal with White Mouth Feathers. *Ethology*, 113(10), 934–943. https://doi.org/10.1111/j.1439-0310.2007.01414.x

Penteriani, V., & Delgado, M. (2019). The eagle owl. (Poyser Monographs). London: T & AD Poyser.

Pérez-Granados, C., Schuchmann, K.-L., & Marques, M. I. (2021). Vocal activity of the Ferruginous pygmy-owl (Glaucidium brasilianum) is strongly correlated with moon phase and nocturnal temperature. *Ethology, Ecology & Evolution*, 33(1), 62–72. https://doi.org/10.1080/03949370.2020.1820582

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reierth, E., Van't Hof, T. J., & Stokkan, K.-A. (1999). Seasonal and Daily Variations in Plasma Melatonin in the High-Arctic Svalbard Ptarmigan (Lagopus mutus hyperboreus). *Journal of Biological Rhythms*, 14(4), 314–319. https://doi.org/10.1177/074873099129000731

Reynolds, Shook, J., Breed, G., & Kielland, K. (2021). Detection and Density of the Great Horned Owl (Bubo virginianus) in Arctic Alaska. *The Journal of Raptor Research*, 55(1), 56–64. https://doi.org/10.3356/0892-1016-55.1.56

Ridout, M. S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3), 322–337. https://doi.org/10.1198/jabes.2009.08038

Rigby RA, Stasinopoulos DM (2005). "Generalized additive models for location, scale and shape (with discussion)." *Applied Statistics*, **54**, 507-554.

R Studio Team (2021). RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA. http://www.rstudio.com/.

Segall, M. A., Gonzaga, L. P., Kenup, C. F., & Castiglioni, G. D. A. (2022). A novel method for analysis of vocal dimorphism using recordings of unsexed pairs and its application to the neotropical owl Pulsatrix koeniswaldiana. *Journal of Ornithology*, 163(2), 589–598. https://doi.org/10.1007/s10336-022-01965-6

Sethi, S. S., Fossøy, F., Cretois, B. & Rosten, C. M. (2021). *Management relevant applications of acoustic monitoring for Norwegian nature – The Sound of Norway*. (NINA Report 2064). Norwegian Institute for Nature Research https://www.miljodirektoratet.no/publikasjoner/2022/mars/management-relevant-applications-of-acoustic-monitoring-for-norwegian-nature-the-sound-of-norway/

Sergio, F., Marchesi, L., & Pedrini, P. (2003). Spatial Refugia and the Coexistence of a Diurnal Raptor with Its Intraguild Owl Predator. *The Journal of Animal Ecology*, 72(2), 232–245. https://doi.org/10.1046/j.1365-2656.2003.00693.x

Sergio, F., Marchesi, L., Pedrini, P., & Penteriani, V. (2007). Coexistence of a generalist owl with its intraguild predator: distance-sensitive or habitat-mediated avoidance? *Animal Behaviour*, 74(6), 1607–1616. https://doi.org/10.1016/j.anbehav.2006.10.022

Shonfield, J., Heemskerk, S., & Bayne, E. M. (2018). Utility of Automated Species Recognition For Acoustic Monitoring of Owls. *The Journal of Raptor Research*, 52(1), 42–55. https://doi.org/10.3356/JRR-17-52.1

Silverin, B., Gwinner, E., Van't Hof, T. J., Schwabl, I., Fusani, L., Hau, M., & Helm, B. (2009). Persistent diel melatonin rhythmicity during the Arctic summer in free-living willow warblers. *Hormones and Behavior*, 56(1), 163–168. https://doi.org/10.1016/j.yhbeh.2009.04.002

Smiseth, P. T., Eikenaes, A. K. & Amundsen, T. 2003. Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging, and parental provisioning rules. *Behavioral Ecology*, 14, 793-801. https://doi.org/10.1093/beheco/arg083

Steiger, S. S., Valcu, M., Spoelstra, K., Helm, B., Wikelski, M., & Kempenaers, B. (2013). When the sun never sets: diverse activity rhythms under continuous daylight in free-living arctic-breeding birds. Proceedings of the Royal Society. B, *Biological Sciences*, 280(1764), 20131016–20131016. https://doi.org/10.1098/rspb.2013.1016

Stokkan, K. A., Mortensen, A., & Blix, A. S. (1986). Food intake, feeding rhythm, and body mass regulation in Svalbard rock ptarmigan. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 251(2), R264–R267. https://doi.org/10.1152/ajpregu.1986.251.2.R264

Taniguchi, M., Murakami, N., Nakamura, H., Nasu, T., Shinohara, S. and Etoh, T. (1993). Melatonin release from pineal cells of diurnal and nocturnal birds. *Brain Research*, 620(2), 297-300. https://doi.org/10.1016/0006-8993(93)90169-N

Terry, Peake, T. M., & McGregor, P. K. (2005). The role of vocal individuality in conservation. *Frontiers in Zoology*, 2(1), 10–10. https://doi.org/10.1186/1742-9994-2-10

Therrien, J., Gauthier, G., & Bêty, J. (2012). Survival and reproduction of adult snowy owls tracked by satellite. *The Journal of Wildlife Management*, 76(8), 1562–1567. https://doi.org/10.1002/jwmg.414

Time & Date AS. (2022). *Past Weather in Rendalen, Norway — June 2018*. Retrieved June 15, 2018 from https://www.timeanddate.com/weather/@9754631/historic?month=6&year=2018

Van't Hof, T. J., Gwinner, E., & Wagner, H. (1998). A Highly Rudimentary Circadian Melatoninatonin Profile in a Nocturnal Bird, the Barn Owl (Tyto alba). *Die Naturwissenschaften*, 85(8), 402–404. https://doi.org/10.1007/s001140050523

van Rij, J., Wieling, M., Baayen, R., van Rijn, H. (2022). "itsadug: Interpreting Time Series and Autocorrelated Data Using GAMMs." R package version 2.4.1.

van Rij, J. (2016). *Checking for and handling autocorrelation*. Cran R Project. https://cran.r-project.org/web/packages/itsadug/vignettes/acf.html

Wabakken, P., Dahl, E. R., Johansen, F., Bichsel, M. & Maartmann, E. (2014). *Hubro, sau og vånd på Sleneset-Solværøyene i 2014* [Rapport til Fylkesmannen i Nordland]. Høgskolen i Hedmark. https://prosjekt.statsforvalteren.no/siteassets/hubro/hubro-dokumenter/rapporter/wabakken-hubro-sau-og-vand-pa-sleneset-solvaroyene-i-2014.pdf

Wickham, H., François, R., Henry, L., Müller, K. (2022). dplyr: A Grammar of Data Manipulation. R package version 1.0.10. https://CRAN.R-project.org/package=dplyr

Wickham, H. & Girlich, M. (2022). tidyr: Tidy Messy Data. R package version 1.2.1. https://CRAN.R-project.org/package=tidyr

Wcislo, W. T., Arneson, L., Roesch, K., Gonzalez, V., Smith, A., & Fernández, H. (2004). The evolution of nocturnal behaviour in sweat bees, Megalopta genalis and M. ecuadoria (Hymenoptera: Halictidae): an escape from competitors and enemies? *Biological Journal of the Linnean Society*, 83(3), 377–387. https://doi.org/10.1111/j.1095-8312.2004.00399.x

Wildlife Acoustics (2020). *Kaleidoscope Pro 5 User Guide*. Wildlife Acoustics, Inc. https://www.wildlifeacoustics.com/uploads/user-guides/Kaleidoscope-Pro-User-Guide.pdf

Wojczulanis-Jakubas, Wąż, P., & Jakubas, D. (2020). Little auks under the midnight sun: Diel activity rhythm of a small diving seabird during the arctic summer. *Polar Research*, 39, 1–9. https://doi.org/10.33265/polar.v39.3309

Wood, S. N. (2011). "Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models." *Journal of the Royal Statistical Society (B)*, **73**(1), 3-36.

Wu, Y. (2022). Evolutionary Origin of Nocturnality in Birds. *eL*S, 1, 483-489. https://doi.org/10.1002/9780470015902.a0029073

Zuberogoitia, I., Martínez, J. E., Zabala, J., Martínez, J. A., Azkona, A., Gastillo, I., & Hidalgo, S. (2008). Social Interactions between Two Owl Species Sometimes Associated with Intraguild Predation. *Ardea*, 96(1), 109–113. https://doi.org/10.5253/078.096.0112