Predation risk at dawn:
How changing light and birds' traits affect the temporal risk landscape during sunrise.

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Acknowledgements

Abstract

Passerine birds, commonly known as songbirds, have a pronounced peak of singing before sunrise during their breeding season, known as the dawn chorus. This thesis aims to explore why they sing at this time – what are the physiological and behavioral drivers, and what are the important temporal changes when determining the risks and opportunities before, during, and after sunrise?

Predation risk might be a key factor in determining the onset of the dawn chorus, and the risk birds experience during dawn song is dependent on their behavior and physiology, as well as that of both diurnal and nocturnal predators. However, few studies have looked at and compared the activity patterns of both predators and prey birds, or have addressed predation on dawn-singing birds. If predation risk varies temporally or spatially, we would expect songbirds to respond by changing their niches or habitats.

This work is conceptual, and pieces together knowledge from diverse fields, inferring the missing parts. In the following, I build my argument through a series of questions. Each question will look into a factor that could have an effect on the predation risk experienced by songbirds, and ultimately help explain the dawn chorus. Based on the answers to these questions, I present the hypothesis that songbirds make use of a temporal window of opportunity prior to sunrise, where the light environment results in a lower predation risk for the singing birds. This hypothesis is based on data collected from previous work on the visual constraints birds experience at various light environments.

The possibility of a temporal window of opportunity gives a new view on what determines and limits the onset of dawn song for passerine birds. Trade-offs in the eye, which are correlated with different foraging strategies, will in part determine the temporal placement and duration of this window. Latitude and season will also determine the extent of, and thereby the ecological importance of the window of opportunity.

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Introduction

The period around sunrise is a dynamic time of day. As the sun rises, the light intensity increases up to six orders of magnitude. In the same time frame there are significant spectral changes in the sunlight reaching the earth's surface (Johnsen et al., 2006). Compared to the light environment at midday, the spectrum at dawn is rich in ultraviolet (UV), blue, and red light, giving dawn a purplish hue (Endler, 1993). As nocturnal animals retreat after being active during the night, diurnal animals emerge. Cold and hungry, they need to start their day and go looking for their first meal. Among the diurnal species starting their day at this time are the passerine birds, which come to dominate the twilight soundscape. With a focus on changes in light environments and predation risk, this thesis aims to explore why songbirds sing at this time – what are the drivers, and what seems to be the important temporal changes when determining the risks and opportunities before, during, and after sunrise?

Passerine birds, commonly known as songbirds, have a pronounced peak of singing before sunrise during their breeding season, known as the dawn chorus (Gil & Gahr, 2002). Bird songs are some of the most intricate sounds produced by animals (Briefer et al., 2010). There is great variation in songs between species, populations and sometimes even individuals. Levels of song duration, repertoire size, and starting time are among the differing characters (Catchpole & Slater, 2008).

One function of bird song is to attract mates, linking song to sexual selection (Gil & Gahr, 2002). A study done on black-capped chickadees (*Poecile atricapillus)* showed that higher-ranking birds start their chorus earlier and sing longer than subordinate birds (Otter et al., 1997), and these earlier starting males have a higher mating success (Mennill et al., 2004). Male birds have been shown to sing more when it is warm, and when provided with extra food (Thomas, 1999). Based on this, it has been suggested that there is an energetic cost to singing, and especially to singing early. In addition to energetic costs, it has also been hypothesized that singing early could be costly to the immune system, especially in bad weather (Gil & Gahr, 2002).

If predation risk varies temporally or spatially, we would expect organisms to respond by changing their niches or habitats. Shifts in habitat used by prey in the presence of predators are well documented, with more than 70 studies cited in a review by Lima (1998).

These shifts may be short term or have far-reaching effects on prey dynamics and life histories. We already know from studies from the pelagic zone that the twilight window is rich in predator prey interactions, driven by a trade-off between predation risk and feeding opportunities (Scheuerell & Schindler, 2003; Hrabik et al., 2006). Planktivore fish have found an "anti-predation window" by taking advantage of the difference in light threshold for efficient foraging between planktivore and piscivore fishes (Clark & Levy, 1988; Giske & Salvanes, 1995). At low light at dawn and dusk, planktivore fish can still see their prey at sufficient distance to be efficient foragers, but it is much harder for their predators to spot them because they hunt at longer distances. This leads to a lower predation risk for the planktivore fish. However, due to the high activity at this time, there is still a high mortality. Therefore, the term "anti-predation window" could be misleading, as there is still a considerable amount of predation taking place in this temporal window. Here, we will rather refer to this as a temporal window of opportunity. The dynamic change of the light levels at dawn may hint to a similar light-driven effect in terrestrial systems, but this has not been a focus of studies of dawn chorus ecology.

The risk birds experience during dawn song is dependent on the behavior and physiology of both diurnal and nocturnal predators. The main cause of mortality in songbirds is predation by avian predators (Møller et al., 2005). Few birds are strictly diurnal or nocturnal, resulting in most predatory birds also being active around dawn and dusk, especially in spring (Newton, 1986; Martin, 1990). However, neither diurnal nor nocturnal predators will experience optimal light conditions at this time of day. Diurnal birds of prey need a higher visual acuity, as they hunt at high speeds. This makes them less efficient hunters at dawn, as they need a higher light intensity (González-Martín-Moro et al., 2017). Nocturnal predators, such as owls, hunt efficiently at low light intensities, by hunting in silence at low speeds (Graham, 1934). Once the light intensity becomes adequate for passerines to spot them at a safe distance, the predators will lose their advantage.

Due to both diurnal and nocturnal predators being active at dawn, there is a potential cost of early singing linked to the risk of predation, with heterospecific eavesdropping by predators making signing males more exposed (Peake, 2005). Predation risk influences the way birds sing, with the possibility of visual detection of predators regulating the onset of the dawn chorus (Berg et al., 2006). Early singing could therefore serve as a reliable signal of investment in anti-predator behaviors. In a theoretical model, Eliassen and Jørgensen (2014)

link extra-pair paternity success to male incentives for investing in cooperative anti-predator behaviors such as vigilance, alarm calls and predator mobbing. A study on blue tits (*Cyanistes caeruleus*) by Poesel et al. (2006) showed that early singers had more mating partners and gained more extra-pair paternity than those starting later. This correlation between early singing and gained extra-pair paternity has also been found in other birds, e.g. the eastern kingbird (*Tyrannus tyrannus*) (Dolan et al., 2007) and the black-capped chickadee (Mennill et al., 2004).

Nocturnal predators have a declining success rate as the sun rises, steadily losing their advantage. To make the window of opportunity even smaller, the singing males can be "smoking out" the predators, so that they lose their advantageous moment of surprise by giving away their location. Alternatively, the early singing males can be keeping a look out while singing an all-clear signal for the females (Wickler, 1985). All-clear signals and alarm calls can be important for females when leaving the nest or while foraging at dawn (Lima, 2009). By making sure the coast is clear, the singing birds could allow other birds to start foraging earlier. Whether the early singing functions by smoking out predators or as an all-clear signal, the early singing passerines are seen as high quality males that can keep the nest, and possibly also the whole neighborhood, safe (Lima, 2009).

Differences in eye sensitivity of songbirds and birds of prey could affect the risks and costs of singing earlier than other birds (Schmidt & Belinsky, 2013). The earliest singing bird species are those with larger exposed eyes relative to body size, giving them a higher visual capacity in low light (Thomas et al., 2002). This can make them better adapted to spotting predators in low-light conditions.

Few studies have looked at and compared the activity patterns of both predators and prey birds, or have addressed predation on dawn-singing birds (Lima, 2009; Schmidt & Belinsky, 2013). A study by Møller et al. (2008) showed that singing birds had a greater flight distance than non-singing birds. They suggest that this indicates that singing birds might suffer from a higher predation risk. It has been demonstrated that predation risk can affect dusk singing in birds, with a perceived increase in predation risk making passerines end their dusk chorus earlier (Schmidt & Belinsky, 2013). It is therefore suggested that there is a similar effect on dawn chorus. However, an alternative explanation for the singing males' increased flight distance than that suggested by Møller et al. (2008), is that they are more vigilant than non-singing males, and are able to spot predators from a further distance.

We expect a trade-off between potential mating success and predation risk to be more prominent during the breeding season. This is a stressful time for the passerines, where time and energy is invested in mating efforts and nest building. For females, the male's investment in anti-predation behaviors is also more important at this time, as they share responsibility for a nest. Twilight also represents a relatively large temporal window during the breeding season, as sunrise is a slow process in spring, especially at high latitudes.

The aim of this project is to use existing data on bird predators and their passerine prey to get an overview of how predation risk changes during the early morning hours and affects the cost of early singing. Previous work has focused on how energetic costs may limit song activity. Our focus however, will be on how perceived predation risk could be a key factor in determining onset of the dawn chorus. Does the difference in light thresholds for efficient foraging between passerine and predatory birds create a temporal window of opportunity for passerine birds? Could birds increase their own mating success by pushing the limit of this window and singing earlier than conspecifics?

Methods

This work is conceptual, in that it pieces together data and observations from diverse fields to give new perspectives and identifies gaps in current knowledge. In the following, I will build my argument through a series of questions. Each question will look at factors that could have an effect on the predation risk experienced by songbirds, and ultimately drive dynamics of dawn singing.

In order to explore how dawn song and other behaviors like foraging and hunting success for birds change with different light environments, we have looked at how the light changes over the course of a day. The different light environments experienced during the day depends on how the light from the sun is absorbed and scattered as it passes through the atmosphere. Along with the earth's shadow, this absorption and scattering of light changes with the sun's angle relative to the ground (Rozenberg, 1966). To generalize this in a way that is independent of latitude and seasons, solar altitude was used as a proxy for the different light environments. Solar altitude for a given place and time was calculated using Eq. 1-7 (see Appendix 1) from Brownson (2013). To calculate the ground illumination depending on solar altitude, we used a function (Eq. 8-9, Appendix 1) modified from *Explanatory Supplement to the Astronomical Almanac* (Seidelmann, 1992).

In addition to theoretical values, we used measurements of solar illuminance and spectra from Bergen, Norway, provided by S. Nedrebø and B. Hamre at the Department of Physics and Technology, UiB. The data was collected as described by Nedrebø (2017). These measurements were taken over several days in May 2016, allowing us to compare data from different times of the day, and days with various levels of cloud cover.

To assess hunting success of avian predators, and the predation risk experienced by passerine birds, we calculated detection distances at various light intensities. Detection distance was calculated as a function of the visual acuity of the subject and size of the object (Eq. 11, Appendix 1). Searches for relevant literature for visual thresholds and the light-dependent hunting success for birds were made using online publication databases. All databases available from Web of Science were searched using a combination of words in the title or abstract related to different factors associated with light availability, visual thresholds and avian hunting success. For a more detailed description of search strategy and inclusion criteria, see Appendix 1.

To compare dawn choirs from as many species as possible, we performed a thorough search for studies of dawn chorus onset for different species, as described by Ulltang (in prep). In a parallel Master's thesis, Marte Ulltang is looking into further factors that can affect the birds' motivation to start singing early, to complement the perspective on risk taken in this thesis. Ulltang has a focus on the energetic costs affecting dawn chorus onset, and this onset as a function of light and feeding habits. We have exchanged relevant findings along the way. In some places below, I therefore refer to Ulltang (in prep) to delimit the scope of this thesis from hers.

Results

Predation risk might be a key factor in determining the onset of the dawn chorus. In the following eight sections, I will build my argument step by step through a series of questions. Each question will look into a factor that could have an effect on the predation risk experienced by songbirds, and ultimately the onset of the dawn chorus. The answers to each question also highlights what we currently know and have research on, and what knowledge is missing for each of these factors.

How does light change during sunrise?

On a clear, cloudless night the light intensity, or illuminance, will be somewhere between $2x10^{-3}$ and 0.27 lux, depending on the phase and position of the moon (Seidelmann, 1992). At the beginning of astronomical dawn, when the sun is 18° below the horizon, the light from the sun only contributes an additional $6x10^{-4}$ lux. However, as the sun continues to rise, the illuminance increases up to six orders of magnitude (Johnsen et al., 2006). Radiometry data from Bergen, Norway, taken on May 25th 2016, show that from civil twilight (-6°) to sunrise the illuminance increases from 6.13 to 649 lux. At noon this day, the sun was at 47°, giving an illuminance of $8.70×10^4$ lux (Fig. 1). These are data from a cloudless day.

The light spectrum at dawn is dominated by red and blue light (Fig. 1). There is a reduction of intermediate wavelengths, caused by atmospheric ozone, which is particularly absorbent around 604 nm (Rozenberg, 1966; McFarland & Munz, 1975). This absorbance only becomes apparent at dawn and dusk, when sunlight has to pass a longer distance through the atmosphere and encounters more ozone. This gives dawn a purplish color, deficient in middle wavelengths (Endler, 1993). UV-light is also a relatively important part of the early light spectrum, as these shorter wavelengths are not absorbed while moving through the atmosphere, but scattered (Withgott, 2000). As the sun rises above the horizon, the purple hue fades, and the sunlight gets a more whitish color (Fig. 1) (Endler, 1993).
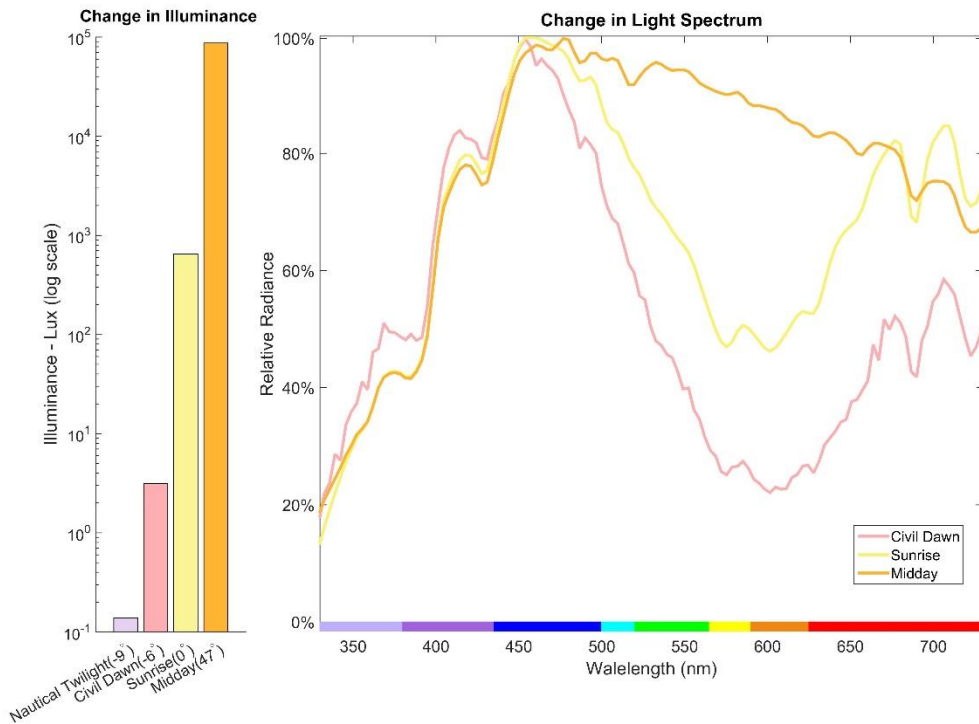
Figure 1: Change in illuminance (in lux) and spectrum composition during dawn compared to light conditions at sunrise and midday. Light measurements data were collected in Bergen on the 25th of May 2016, on a day with little to no cloud cover. The lowest solar altitude at this date and latitude was -9°, corresponding to nautical twilight (solar altitudes ranging from -12° to -6°).

In addition to time of day, these different light environments are caused by the geometry of the light paths and weather conditions (Endler, 1993). On cloudy days, the spectrum at dawn goes through a slightly different transition. Dawn still start out with a purplish color, but just before the sun rises, yellow and red light is reflected from the cloud cover to the ground. As the sun continues to rise, the spectrum evens out and turns white (Endler, 1993). The amount of cloud cover also affects illuminance, and if the sky is overcast the values of sunlight intensity are typically reduced by a factor of 10 (Seidelmann, 1992).

How is information in photons recognized by eyes?

Birds are highly visual animals, and rely primarily on eyesight to obtain information about their environment (Hart, 2001b). Bird retinas have four spectrally distinct types of single cones, as well as one type of double cone and one type of rod (Hart & Hunt, 2007). Rods mediate vision in dim light, and they all possess the same visual pigment, which means rods are not able to distinguish colors. To be able to distinguish colors, rather than just seeing shades of gray, it is necessary to possess multiple visual pigments, each of which absorbs light maximally at a different wavelength (Randall et al., 1998). This is the case for

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the four spectrally distinct types of single cones in the avian retina (Hart & Hunt, 2007). Single cones function at higher illuminance, and are responsible for color discrimination and high resolution vision. Behavioral data suggest that double cones contribute to high-resolution achromatic vision (Mitkus et al., 2017), and that they might be involved in visual tasks such as movement detection and pattern recognition (Hart & Hunt, 2007).

The photoreceptor cells in vertebrate species hyperpolarize when they are illuminated. This means that they release synaptic transmitter substances continuously in the dark, and that this release is reduced when the photoreceptors hyperpolarize due to illumination. For a signal to be carried from the photoreceptor to the central nervous system, the photoreceptor must generate an action potential when photons strike the photosensitive pigment of the cell. Rod photoreceptors can respond to the absorption of a single photon by amplification processes allowing the single photon to affect conductance through a cascade reaction eventually affecting an enormous number of ion channels (Randall et al., 1998).

A bird's visual acuity is dependent on several qualities of the eye. In terms of retinal composition, the visual acuity is dependent on both the number and ratio of rods and cones, as well as how they are spaced out on the retina (Hart, 2001b). Beginning at low light levels, visual acuity is a function of the rods. At the lowest illuminance, only a few rods are active, resulting in a very low visual acuity. With increasing illuminance, more and more rods become active, and visual acuity increases. While visual acuity is still mediated by rods, the first cones will begin to function. As illuminance increases beyond this, the rate at which cones become active is much greater than that of the rods, and at a certain point the number of active cones will surpass the number of rods. With increasing illuminance, the number of active cones, and thereby the visual acuity, will continue to increase until all the cones are active. At this point no further change in visual acuity is possible, and a saturation has been reached (Hecht, 1928). The number of activated rods and cones, and thereby visual acuity, is an approximately logarithmic function of illuminance, as shown in Figure 2.
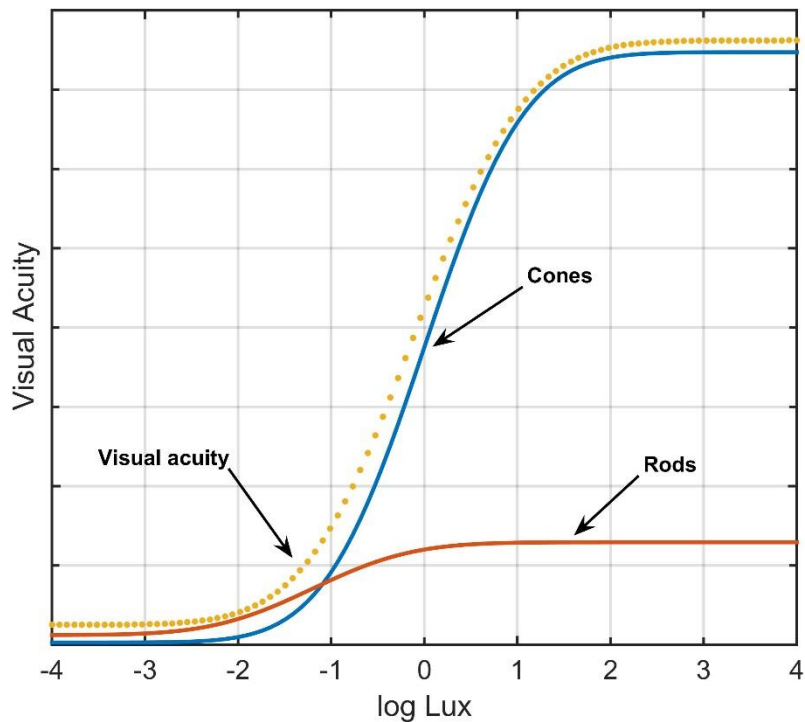
Figure 2: Relationship between visual acuity and illuminance. The shallow curve at low light is attributable to the rod response, and the large sigmoidal curve is attributable to the cone response. The size and position of the curves will depend on both the number and the ratio of rods and cones in the retina. (Figure redrawn and modified from "The relation between visual acuity and illumination", by S. Hecht, 1928, The Journal of General Physiology, 11, *p. 262. Copyright 1928 Rockefeller University Press.)*

In the retina, the photoreceptor cells are connected to bipolar cells that, in turn, connect to ganglion cells. The axons of these ganglion cells make up the optic nerve. Bipolar cells typically connect more than one photoreceptor to each ganglion cell, producing a greater summation of weak stimuli. The degree of convergence, or how many photoreceptors are connected in this way, will affect both the visual acuity and sensitivity of the eye. For greater sensitivity to dim illumination, it is beneficial for each ganglion cell to receive input from many photoreceptors, primarily rods. However, this will reduce the visual acuity. High visual acuity is best achieved by one-to-one-to-one connections between photoreceptors, bipolar cells, and ganglion cells (Randall et al., 1998).

The four single cones are classified according to their spectral sensitivity and have different wavelengths of maximum absorbance (λ_{max}). SWS1 and SWS2 are sensitive to short wavelengths between 355 and 475 nm, MWS is sensitive to medium wavelengths between 460 and 540 nm, and LWS is sensitive to long wavelengths between 505 and 630 nm (Hart & Hunt, 2007). SWS1, one of the two short-wavelength-sensitive cones, either has a violet-

sensitive or UV-sensitive cone visual pigment, with λ_{max} values between 355 and 440 nm (Hart & Hunt, 2007). This difference in the SWS1 pigment forms the basis for dividing birds into two broad groups based on their vision, the "UV group" and the "violet group" (Stevens & Cuthill, 2007). The "UV group" includes the songbirds, whose cone pigment λ_{max} lies between 355 and 380 nm (Hart, 2001b). The "violet group" includes most, but not all, non-passerine birds, with a λ_{max} of 402 to 426 nm (Hart, 2001b; Ödeen & Håstad, 2003). The primary predators of songbirds are often birds of prey that belong in the violet group (Stevens & Cuthill, 2007). While both groups are capable of detecting UV radiation to some extent, the violet group has a reduced sensitivity compared with the UV group (Vorobyev et al., 1998; Håstad et al., 2005).

Each cone type contains a particular type of pigmented oil droplet. The oil droplet is located at the distal end of the cones, and light must pass through them before reaching the visual pigment (Hart, 2001a). In single cones, these oil droplets have a positive effect on birds' vision by limiting the overlap between receptor spectral sensitivities, and thereby improving color consistency (Hart, 2001a; Vorobyev, 2003). The double cone oil droplets have a more short-wavelength-absorbing pigment than the other oil droplet types. This might be beneficial by filtering out short-wavelength light blurred by scattering, increasing the double cone's effect in high-resolution vision (Toomey et al., 2015).

What are the constraints and trade-offs in bird eyes?

The pattern of photoreceptor distribution in the retina has been shown to reflect the bird species' habitat and feeding behavior to a greater extent than their phylogeny (Hart, 2001a). The retinas of nocturnal birds are generally dominated by rods, which are more sensitive to light than cones, and are used for vision under low light conditions. Visual acuity in dim light is limited by the number of photons that receptors can obtain. In addition to convergence of signals from several photoreceptors, photon catch can be maximized in high sensitivity eyes by having wide photoreceptors (Land & Nilsson, 2012). However, wider photoreceptors will compromise acuity by limiting the number of receptors in the retina. The more densely receptors are packed, the finer the details of a pattern of light intensities that can be obtained (Bruce et al., 2003). Diurnal species have retinas dominated by and densely packed with cones, which function under brighter light levels, respond faster than

rods, and can discriminate color (Ebrey & Koutalos, 2001). This difference in retinal composition is the result of a trade-off between high visual acuity and high visual sensitivity.
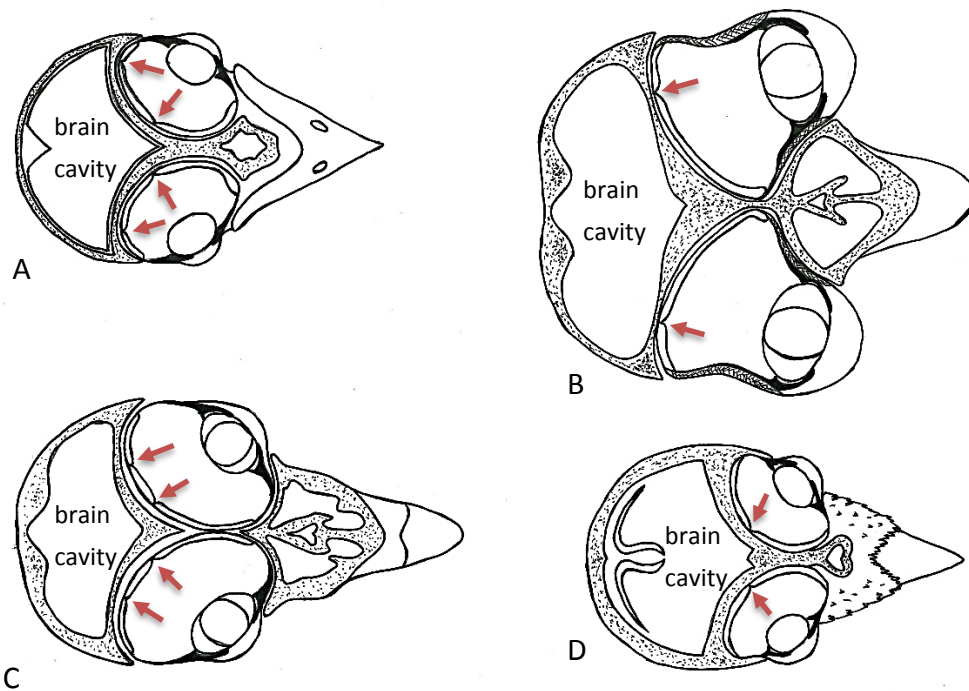
*Figure 3: Superior view showing the eye shape and size in different species of birds. The sketches also show the amount of the skull occupied by the big eyes, leaving little room for the brain and no room for eye muscle. A: Tree swallow (*Tachycineta bicolor*), B: Great horned owl (*Bubo virginianus*), C: Broad-winged hawk (*Buteo platypterus*), D: Black-capped chickadee (*Parus atricapillus*). Red arrows indicate location of foveae. (Adapted from* The fundus oculi of birds especially as viewed by the ophthalmoscope *(pp. 13-15), by C. A. Wood, 1917, Mill Valley, CA: University Science Books. In the public domain*).

In addition to retinal composition, there is also a trade-off in eye shape. A wide eye with a large corneal diameter captures more light than a narrow eye. This will help the bird produce a better picture of its surroundings in low light conditions (Hall & Ross, 2007). A long eye gives a longer focal length, which improves the bird's visual acuity (Tyrrell & Fernández-Juricic, 2017). Maximizing both of these means sacrificing space for the brain, which is already limited due to the large eye size in birds (Burton, 2008) (Fig. 3). This also leads to a trade-off between high visual acuity and high visual sensitivity. The result of these trade-offs can be seen in the visual acuity of species with different life styles at various light intensities (Fig. 4).

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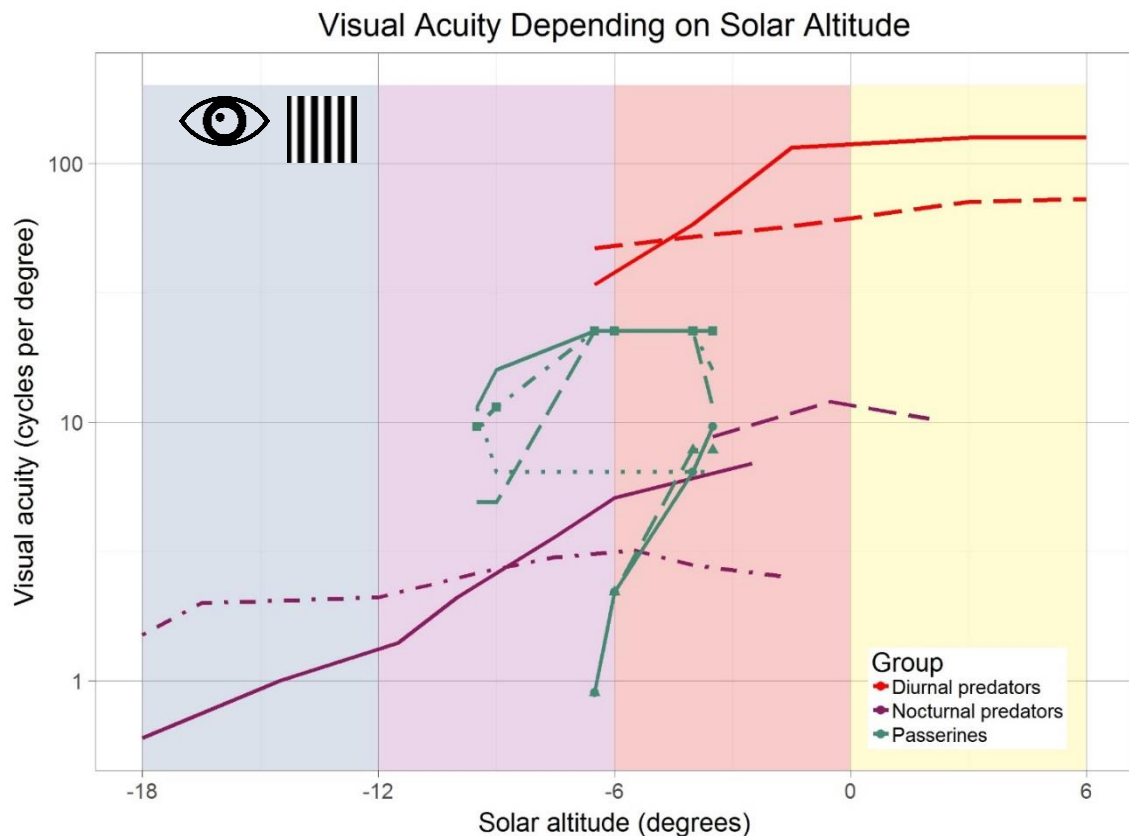
Figure 4: Visual acuity of diurnal predators (red lines), nocturnal predators (purple lines), and passerines (green lines) depending on solar altitude. Data from behavioral studies of visual acuity in wedge-tailed eagle (solid red) (Reymond, 1985), brown falcon (dashed red) (Reymond, 1987), tawny owl (dashed purple) (Martin & Gordon, 1974), great horned owl (solid purple) (Fite, 1973), barn owl (dot-dashed purple) (Orlowski et al., 2012), blackbird (solid green), fieldfare (dot-dashed green), Eurasian skylark (dashed green), yellowhammer (solid green with circles), reed bunting (dashed green with triangles), European robin (dotted green), chaffinch (dot-dashed green with squares) (Donner, 1951). See Appendix 2 for more extensive data on visual acuity.

A bird's detection distance is dependent on the visual acuity of the bird and the size of the object being detected. High visual acuity allows a bird to detect an object at great distances (Kiltie, 2000). Visual acuity therefore influences the size of a bird's detection window, or the area in which the chance of detecting prey or predators is high. In optimal light conditions, diurnal predators with their high visual acuity can see small passerine birds from very far away (Fig. 4). Nocturnal birds of prey's low visual acuity gives them a much shorter detection distance, but they can detect passerines at very low light intensities. Passerines have an intermediate visual acuity.

What are the consequences of eye characteristics for detection distance?

Using the behavioral acuity data available for different species, theoretical detection distances can be calculated (see Eq. 11 in Appendix 1). When taking the large size of a predator that passerines are trying to detect into consideration, theoretical detection distances can be up to 2600 meters under optimal light conditions (Fig. 5). The theoretical values are calculated without taking real world limitations into account, and are therefore likely to be considerably overestimated. However, they are still valid for comparing the relative visual capabilities of the different species (Spiegel et al., 2013).
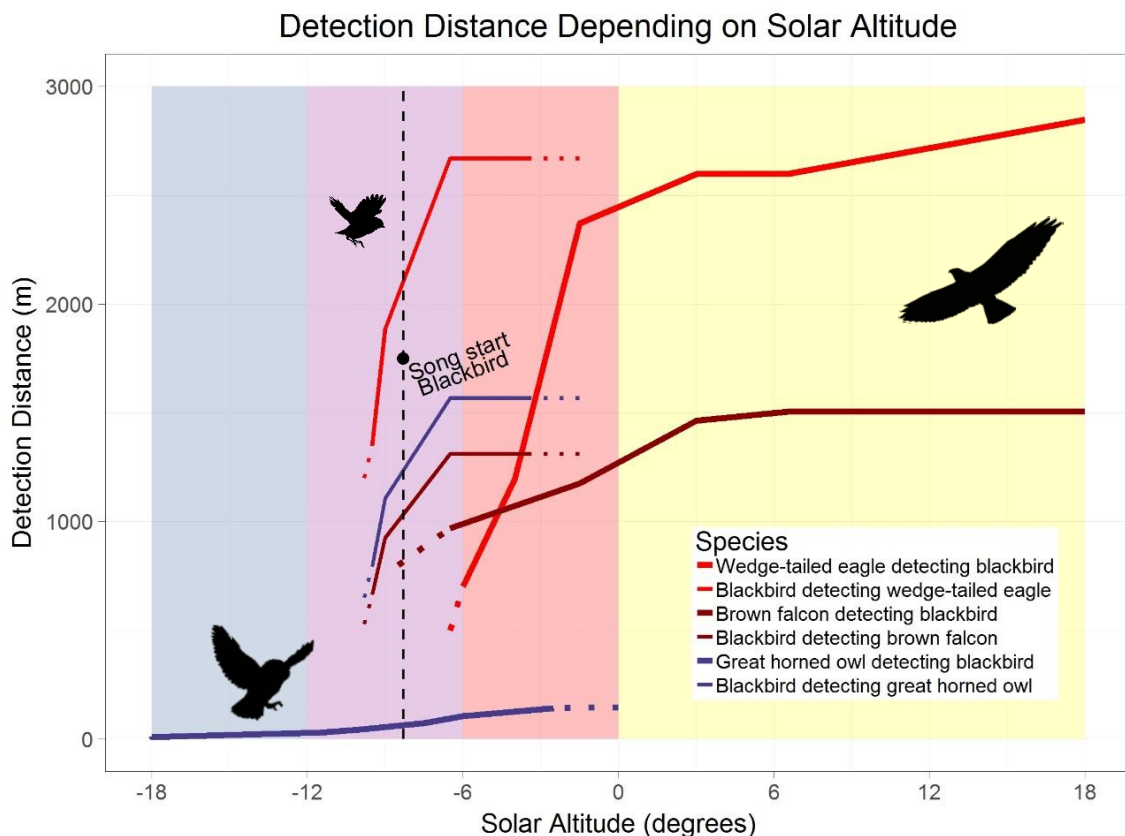
Figure 5: Detection distance depending on solar altitude. The black dashed line marks the solar altitude at the onset of dawn song for the blackbird. The detection distances are calculated using Eq. 11 (see Appendix 1) based on behavioral visual acuity values for the wedge-tailed eagle (Reymond, 1985), blackbird (Donner, 1951), brown falcon (Reymond, 1987), and great horned owl (Fite, 1973). The dotted lines indicate how detection distance might continue outside the range of illuminance with available data for visual acuity.

At the onset of dawn song, blackbirds (*Turdus merula*) have a theoretical detection distance for the wedge-tailed eagle (*Aquila audax*) close to 2100 meters, great horned owl (*Bubo virginianus*) close to 1250 meters, and for the slightly smaller brown falcon (*Falco*

berigora) just over 1000 meters (Fig. 5; calculated using Eq. 11). At the same solar altitude, the great horned owl is estimated to spot a blackbird from only approximately 70 meters away. The wedge-tailed eagle and brown falcon's visual acuity has only been tested under light intensities down to 2.5 lux. At this illuminance they would be able to detect a blackbird from just above 1000 and 700 meters, respectively. At the song start for blackbirds, this distance will likely be lower. As the calculations are based on wingspan as a measurement of the size of birds, the detection distances for a predator spotting a perching bird is likely shorter. This indicates that songbirds might have the advantage when it comes to detection distances during twilight.

What is the importance of light and vision for diurnal birds of prey?

The sharpest vision in birds is found among eagles, hawks, and falcons. These are typically considered to be diurnal, and start foraging around dawn (White et al., 2018). Species that feed on vertebrates typically begin foraging shortly after sunrise, while those foraging on insects do not become active until 1-2 hours later (Thiollay, 2018). Some diurnal predators also have crepuscular and even nocturnal activity, and are active during twilight, especially during spring (Newton, 1986). This is more common for falcon species, while very few hawks or eagles are nocturnal or even crepuscular on a regular basis (Thiollay, 2018).

Diurnal birds of prey typically hunt at high speeds. While hunting actively, they fly at speeds ranging from 15-80 km/h (Thiollay, 2018). Eagles gliding can reach speeds over 90 km/h, and some falcon species can stoop down to catch prey at speeds up to 180 km/h (Thiollay, 2018; White et al., 2018). In general, they also hunt from height. To be able to locate prey from high above the ground, and to maneuver at such high speeds, diurnal birds of prey need excellent, sharp vision (Thiollay, 2018).

The fovea is a region of the retina where photoreceptors are packed much denser than in the rest of the retina, allowing for a higher visual acuity. The retinae of most diurnal birds of prey have two fovea; one deep central fovea, and one shallower temporal fovea (Reymond, 1985) (see Fig. 3C). The raptor central fovea lacks rods, as well as double cones in some species. This allows for a higher density of cones, which is optimal for high visual acuity in bright light (Mitkus et al., 2017). Outside the fovea, their retina still has a high number of cones per rod (Jones et al., 2007). This increases their visual capabilities in bright light, at the cost of visual sensitivity.

According to Hart and Hunt (2007), birds that detect objects at a farther distance should have violet-sensitive rather than UV-sensitive SWS1 visual pigments, because scattering of light by the atmosphere is much worse at UV wavelengths compared to violet (or longer) wavelengths. Due to this, diurnal birds of prey, with their sharp vision, will benefit from being violet-sensitive rather than UV-sensitive (Ödeen & Håstad, 2003). This allows diurnal birds of prey to see better over farther distances, but also makes them less adept than their passerine prey in using UV information.

Since diurnal birds of prey have poor vision in dim light, their flight speed is significantly reduced before sunrise. Gustin et al. (2017) used GPS trackers to measure one-minute flight distance for the lesser kestrel (*Falco naumanni*). They found that the flight speed during civil twilight was over 60 % lower than that at midday. At night their flight speed decreased even further, to only 10 % of what it was during the day. This is likely due to the lower illuminance causing the kestrel's visual acuity to drop to a level where it could not maintain flight at high speeds.

Our literature search found studies on visual acuity under various illuminance for three diurnal birds of prey, the wedge-tailed eagle (Reymond, 1985), the brown falcon (Reymond, 1987) (see Fig. 4), and the American kestrel (*Falco sparverius*) (Fox et al., 1976). At optimal illuminance, the wedge-tailed eagle has a visual acuity between 132 and 143 cycles per degree. At an illuminance below 250 lux the eagle's acuity decreases rapidly (Reymond, 1985). This corresponds to the illuminance just before sunrise. The brown falcon's maximum acuity was found to be 73 cycles per degree. The visual acuity did not decrease as rapidly with lower illuminance as it did for the wedge-tailed eagle. Instead it slowly decreases to 47 cycles per degree at civil dawn. This is the result of adaptations which increase the brown falcon's visual sensitivity compared to more strongly diurnal falcon species (Reymond, 1987). There is also a study on visual acuity of the American kestrel, reporting an acuity of 160 cycles per degree at an illuminance of 4400 lux (Fox et al., 1976). However, this acuity is higher than that recorded for any other animal, and is difficult to reconcile with optical and retinal properties in the kestrel, along with the maximum anatomic resolving power being 46 cycles per degree (Dvorak et al., 1983). For further information on how visual acuity is determined at various illuminance, see Appendix 2.

What is the importance of light and vision for nocturnal birds of prey?

One of the reasons why owls, the main group of nocturnal birds of prey, are efficient hunters in the dark, is that they use both sound and vison to navigate and catch prey. Owls have outstanding sound localization skills, and are capable of capturing prey solely by auditory cues (Payne, 1971). They have a specific feather design, allowing them to be almost completely silent while flying (Orlowski et al., 2012). Silent flight helps owls sneak up on prey in low light conditions without being detected. However, owls are different from many other nocturnal animals in that vision is still an important factor in hunting. Although they can catch prey by sound alone, vision is still important for dodging obstacles and maneuvering. Vision is especially important for determining activity, distance, orientation and speed of flight of their prey (Fite, 1973). Most owls are strictly nocturnal, in that hunting and feeding takes place between dusk and dawn (Martin & Gordon, 1974), but some are crepuscular or even have occasional diurnal activity (Marks et al., 2018).

Owls have relatively large eyes, and much of the owl's visual capabilities in low light conditions is caused by their large pupils which increases visual sensitivity by allowing more light to enter the eye (Marks et al., 2018). To maximize sensitivity to small amounts of light, owls have had to sacrifice high visual acuity (Orlowski et al., 2012). For example, avian retinas generally contain relatively few rods (Manglapus et al., 1998). For nocturnal birds of prey, this is not the case. The retina of owls is dominated by rods, which make up over 90 % of the photoreceptor population. This lack of cones gives owls a lower visual acuity, and a limited ability to discriminate colors (Bowmaker & Martin, 1978). Hence, for most nocturnal predators, contrast is more important than color when spotting prey (Aragonés et al., 1999). Cones are still present, and most of them are concentrated in the foveal region (Fite, 1973). These cones contain less brightly colored oil droplets than those of diurnal birds. This might be beneficial by decreasing the filtering of light, and thereby increasing the cone sensitivity to allow some color vision during the dim light at dawn (Hart, 2001b).

Our literature search found studies on visual acuity under various illuminance for three nocturnal birds of prey, the great horned owl (Fite, 1973), the tawny owl (*Strix aluco*) (Martin & Gordon, 1974), and the barn owl (*Tyto alba*) (Orlowski et al., 2012) (see Fig. 4). The great horned owl has a maximum visual acuity of 7 cycles per degree (Fite, 1973). The barn owl has a lower maximum visual acuity of only 4.5 cycles per degree, which was

reached at an illuminance corresponding to civil dawn. This acuity did not seem to improve at higher illuminance, instead Orlowski et al. (2012) found a significant drop in acuity with increasing illuminance above 12 lux. Both the great horned owl and the barn owl are able to make spatial discriminations at illuminance as low as 2×10^{-5} lux, which is less than the illuminance on an overcast night (Seidelmann, 1992). The tawny owl has a higher recorded acuity than the other two owls. At an illuminance corresponding to sunrise, the tawny owl's maximum visual acuity was found to be 12 cycles per degree (Martin & Gordon, 1974).

Is there a trade-off between foraging and detecting predators for passerines?

In addition to time of day and weather, the light environment passerine birds experience depends on where they are located. How much light reaches a bird, and the spectrum of it, depends on whether they are in open terrain or in the forest (Endler, 1993). On a gradient from open terrain to dense forests, the illuminance decreases, while the spectrum reaching the ground goes from white, through yellow and green in more open woodlands, to blue-grey in dense forests (Endler, 1993). What light environment a bird will experience also depends on the layer of the forest they are active in (Endler, 1993; Leuchner et al., 2011).

A typical passerine bird has a flat eye, and apart from absolute size, the structure of a passerine and owl's eye is fairly similar (Martin, 1986). This gives them a shorter focal length, and thereby lower visual acuity, than diurnal birds of prey (Jones et al., 2007). However, their eye shape gives them relatively good visual sensitivity, allowing them to see fairly well even before sunrise (see Fig. 4) (Donner, 1951). Most passerines only have one central fovea in each eye that projects to either side of the head (see Fig. 3D). Outside this fovea, the retina is dominated by cones, with rods only accounting for 5-17 % of the photoreceptors (Coimbra et al., 2015).

To the best of our knowledge there is only a single study on visual acuity under various illuminance that includes seven species of passerine birds, all considered diurnal (see Fig. 4) (Donner, 1951). At an illuminance ranging from 0.07 to 42 lux, the blackbird, fieldfare (*Turdus pilaris*), skylark (*Alauda arvensis*), European robin (*Erithacus rubecula*), and chaffinch (*Fringilla coelebs*) have visual acuities between 4.9 and 22.5 cycles per degree. The

yellowhammer (*Emberiza citrinella*) and the reed bunting (*Emberiza schoeniclus*), which are granivorous species, have a lower visual acuity, ranging from 0.9 to 9.6 cycles per degree at the same illuminance (Donner, 1951).

A potential trade-off between morning vision and rest-of-day foraging will be dependent on what and where passerines forage. Birds feeding on the ground, or those feeding on seeds and berries, can find their food without detecting it from a great distance. Therefore, they probably do not need a high visual acuity, and can avoid sacrificing much visual sensitivity (Donner, 1951; Dolan & Fernández-Juricic, 2010). Passerines that hunt flying insects need to detect their prey and maneuver swiftly at relatively high speeds, and therefore need a higher visual acuity. To accomplish this, passerines that are ambush predators have an area temporalis in addition to a central fovea. Area temporalis is a region of the retina with elevated cell density, giving more acute vision. Active-pursuit predators, like swallows, have a higher degree of specialization, with a temporal fovea and a longer eye giving them a longer focal length (Tyrrell & Fernández-Juricic, 2017) (see Fig. 3A). These adaptations to high acuity vision come at the cost of eye sensitivity, and passerines adapted to active pursuit probably do not see as well in dim light as other passerines.

During the dawn chorus, it is common that passerine birds choose a song post located higher above the ground than where they typically feed and nest (Hunter Jr, 1980; Lee et al., 2010). As the sun rises, the illuminance will increase faster higher up in the canopy than it will closer to the forest floor. A higher song post is thought to improve the singer's ability to hear responses to its song (Dabelsteen et al., 1993). Møller et al. (2008) showed that singing males have a greater flight distance than non-singing males, meaning that they retreat to safety sooner at the sight of a potential predator. A possible explanation for this is that sitting high up in the tree might be beneficial as it can give a better view of surroundings and potential approaching predators.

Does plumage affect when and where birds signal?

Bird song, and especially the dawn chorus, is linked to mate choice and attraction (Catchpole & Slater, 2008). In addition to auditory signaling, male songbirds would also benefit from singing in a light environment that maximizes visual signaling to conspecifics. The different light environments within a forest are important for how conspicuous visual signals will be. The contrast between an animal and its background is dependent on the

ambient light spectrum. A cryptic pattern should have a reflectance spectrum similar to that of its background during times with high predation risk (Endler, 1978). A color pattern used for signaling however, should have a reflectance spectrum resembling the ambient light spectrum, but different from that of its background (Endler, 1993). The same color pattern will not be cryptic or conspicuous in all light environments, and within a given microhabitat the visibility of a pattern will change over the course of a day.

At night, the light coming from the moon and stars is long-wavelength shifted. This means that species signaling during the middle of the night should use red and orange colors, as these will give a higher and more stable achromatic contrast against green leaves (Johnsen et al., 2006). In their study on color perception in crepuscular and nocturnal illumination, Johnsen et al. (2006) found that blue and yellow flowers were undetectable via achromatic cues at night. It is likely that the same is true for bird plumage.

If birds singing at dawn want to maximize their visibility, blues, reds, or purple will maximize brightness in the purplish spectrum. Small patches of yellow or green will make them more visible by maximizing contrast (Endler, 1993).

Because short wavelengths like UV light scatter more readily than long wavelengths (Lythgoe, 1979), birds can use plumage that is eye-catching in UV light to display to possible mates nearby while still avoiding the cost of being simultaneously conspicuous to more-distant predators (Withgott, 2000). Songbirds are more sensitive to UV-light than birds of prey. Hence, songbirds' UV signals may be less detectable to birds of prey than to conspecifics (Stevens & Cuthill, 2007). By using a retinal model to compare reflectance from the plumages of Swedish songbirds to the reflectance of their natural backgrounds, Håstad et al. (2005) found their color badges to be significantly more conspicuous to other songbirds than to birds of prey. Thereby, they showed that there is a possibility of a shielded communication channel for songbirds, not simply because of the absence of UV-sensitivity in mammalian predators but also because their avian predators have differently tuned color receptors (Håstad et al., 2005). However, there are also contrasting studies, stating that the UV component of visual signals in birds is no more important in mate choice than other parts of the visual spectrum (Stevens & Cuthill, 2007).

Several bird species have been shown to display in light environments that increase their conspicuity to conspecifics, either by signaling at certain times of the day or choosing to display in front of a background that enhances plumage contrast (Penteriani & del Mar

Delgado, 2009; Abrahão & Alves, 2017). Moyen et al. (2006) found that the blue crown of the blue tit is the most conspicuous in the light environment before dawn. During the day, the same color pattern is least conspicuous in the blue spectrum of woodland shade, for both predators and conspecifics.

Is there a temporal window of opportunity for songbirds at dawn?

As previously stated, bird species with similar retinal compositions tend to have similar lifestyles. The distinctive retinal compositions in different groups of birds will lead to the size and position of the curves shown in Figure 2, differing. Due to the rod dominated retina in nocturnal birds of prey, their visual acuity will reach its maximum value at a low illuminance. In passerines and diurnal birds of prey, the number of cones and their density will allow for a greater visual acuity at higher illuminance. From the available data on retinal composition of these groups of birds, it is then possible to draw generalized curves for change in visual acuity with changing illuminance (Fig. 6).

The illuminance, and hence the solar altitude, where cones start to have a functional response can be determined by finding the bird's light threshold for chromatic vision. This has, to our knowledge, only been done for four species of birds; blue tit (Gomez et al., 2014), domestic chicken (*Gallus gallus domesticus*) (Olsson et al., 2015), Bourke's parrot (*Neopsephotus bourkii*), and budgerigar (*Melopsittacus undulatus*) (Lind & Kelber, 2009). With information available for more species of birds, across different orders, we could further improve the accuracy of the generalized visual acuity curves in Figure 6.
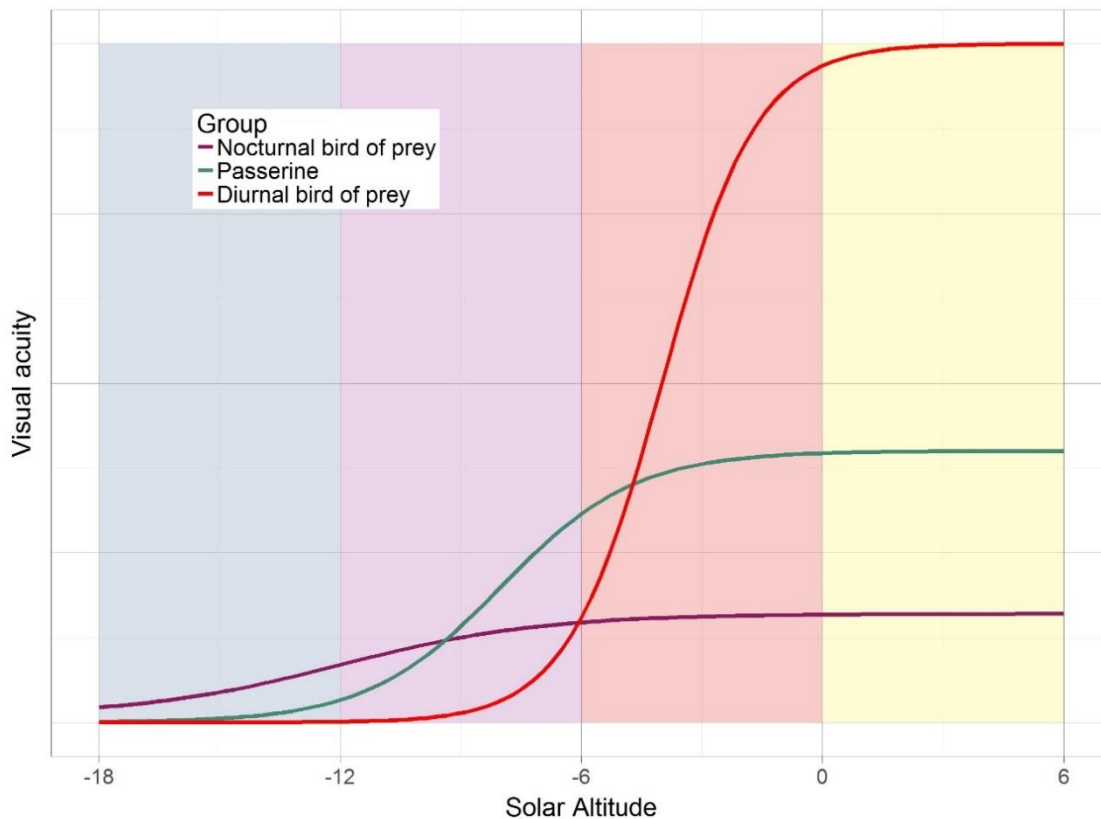
Figure 6: Conceptual figure showing potential visual acuity for diurnal predators (red lines), nocturnal predators (purple lines), and passerines (green lines) depending on solar altitude. The exact shape and size of the curves will vary depending on the number and ratio of cones and rods in the retina. Around civil dawn (-6°) there is a potential temporal window of opportunity where passerine birds are predicted to have superior in vision.

The dawn chorus for most passerine birds has its onset during nautical and civil twilight (solar altitude between -12° and 0°) (Ulltang, in prep). At civil dawn (solar altitude of -6°), calculations made using behavioral acuity data from Donner (1951) shows that e.g. the blackbird has a visual acuity which allows it to detect predators from 1.5 km away (Fig. 5), and conspecifics from almost 500 meters away. This indicates that passerine birds might see well enough in this light environment to both successfully interact visually with conspecifics and avoid predators. Because one function of dawn song is to attract potential mates, it is plausible that passerines will have adequate visual capabilities in this light to locate and maneuver to singing males.

As previously stated, it is likely that neither diurnal nor nocturnal birds of prey have optimal hunting conditions in the twilight environment. Diurnal birds of prey have poor vision in dim light, and can therefore not hunt at top speeds, which reduces their hunting success. Nocturnal birds of prey are likely to have a declining hunting success at the sun rises, due to its prey's visual capabilities improving faster with the increasing illuminance than its own. Both groups of predators also have relatively short detection distances at this

illuminance (Fig. 5). The passerine birds' song post and visual acuity allows them to detect potential predators from a great distance. The combination of these factors could create a temporal window of opportunity somewhere during nautical and civil twilight. The ecological importance of this window, and how passerines make use of it, is likely to vary with season and latitude.

Even though passerine birds seem to have the visual advantage at dawn, being active in this window is not risk free. During the day, diurnal predators have a far greater visual acuity than their passerine prey, and also a greater detection distance (see Fig.5). However, passerine birds are also able to detect their predators from a far enough distance that they are relatively safe from predation. Their detection distance is shorter in the low light intensities before sunrise, and predators might be able to get relatively close to their passerine prey before being detected, making the passerine birds vulnerable. However, this might be a risk that is manageable, making the window of opportunity worth taking advantage of in settings where the passerines are sufficiently stressed for time and energy.

How does the window of opportunity change depending on season and latitude?

The sun rises at different speeds depending on latitude and time of year. Close to the equator, the sun's path is virtually perpendicular to the horizon. Consequently, the sun's position relative to the horizon changes rapidly and twilight only lasts for about 70 minutes. Most songbirds start to become active during nautical and civil twilight, which is also where the potential window of opportunity is located (Fig. 6). This temporal window in which the sun rises from -12° to 0° only last for about 45 minutes at the equator. This stays constant throughout the year, with an annual day length variation of less than ten minutes (Quispe et al., 2017). Further away from the equator, twilight last for longer and varies more throughout the year. During the peak of the passerine's breeding season in spring, the window of opportunity lasts around 50 minutes at 30°N (Morocco, Nepal) but stretches out to 1.5 hours at 60°N (Oslo, Leningrad, southern tip of Greenland). Even further north, at 75°N, the sun does not go far below -12° (nautical dawn) during spring, and twilight makes up close to half of the 24 hours in a day (Fig. 7).
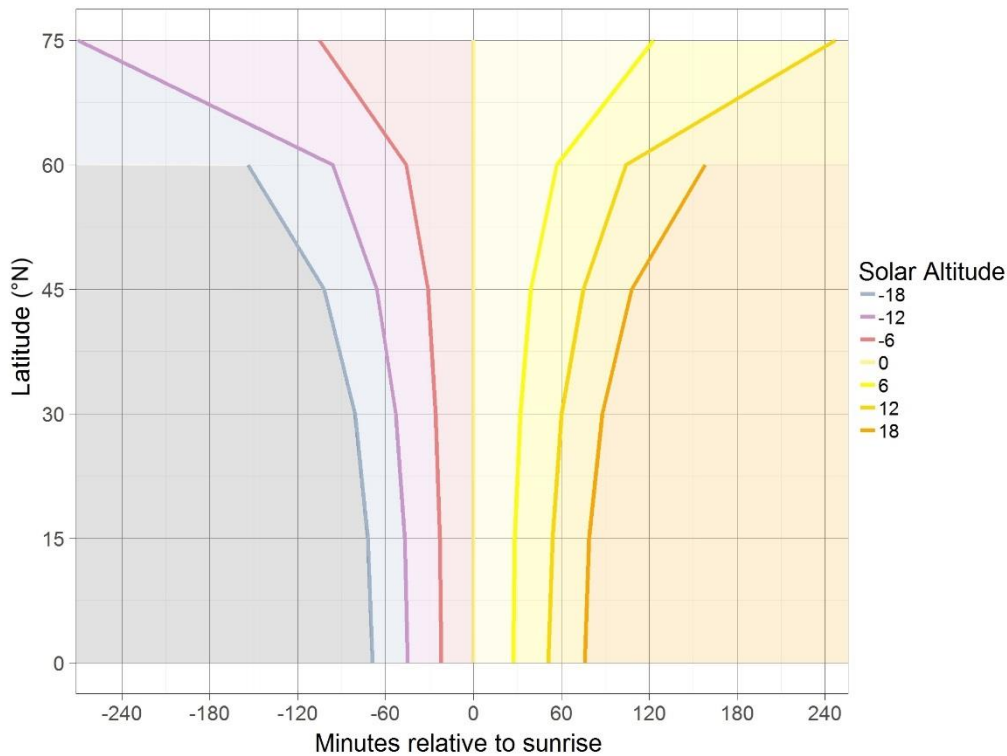
Figure 7: Duration of sunrise during spring (25ᵗʰ of March) at different latitudes. Time values calculated using Eq. 1-7 (Appendix 1).

The difference in daylight stretches out the length of the potential window of opportunity. Depending on latitude, it could more than double in duration, making it more important ecologically at higher latitudes. Twilight lasting longer at higher latitudes also allows for a greater variation in the timing of when birds start their dawn chorus (Daan & Aschoff, 1975).

When birds start their day is the result of a trade-off between costs and benefits. In early spring when twilight is a long and slow process, starting during low light conditions could be worth the risk of predation or reduced foraging success, and can even be necessary, especially for birds at higher latitudes. Nights are colder further away from the equator, making birds spend more energy to stay warm through the night. It is therefore crucial for these birds to get out and start feeding early in the morning (Beer, 1961). Closer to the equator, where the twilight period is shorter, there is less to be gained from starting before the illuminance is sufficient for the passerines to spot potential threats or forage efficiently.

During the breeding season, birds are particularly strained for time and energy, due to the rearing of young. Closer to the equator, birds have a long breeding season, allowing them to rear several broods in a season (e.g. Willis, 1974). At higher latitudes, the breeding season is shorter, and there is seldom time for rearing more than a single brood to

completion (Payne, 1976). At these higher latitudes, twilight can last for over 2 hours, and so by stretching their day out in to twilight and starting the dawn chorus earlier, birds can gain considerable time which can be used for foraging. Increased foraging time can lead to more food and energy for both the parent and offspring birds, potentially allowing the birds to rear more young. For birds at these higher latitudes, increasing the clutch size by just one egg could then result in a 10-20 % increase in fitness for that season.

A considerable cost limiting the time available for foraging comes from the predation risk due to many diurnal and nocturnal predators being active at dawn. Eavesdropping predators may be attracted to the vocalization of singing males (Peake, 2005). Using early singing as a way to smoke out predators could therefore increase the temporal window where songbirds can forage in the morning. Singing males are generally vigilant, and are likely to spot the predator at a safe distance when birds of prey are restricted to low speeds before dawn. This reduces the predator's chance of a successful attack, and may lower predation risk for the nearby songbirds. This is likely to be beneficial in terms of fitness, as it will allow songbirds to start foraging in lower light conditions than would be safe otherwise.

During the breeding season, males and females have a shared investment and interest in successfully rearing their clutch. The loss of one parent bird due to predation can have a detrimental effect on the survival of the nest, as a single parent often is not able to provide sufficient food for all the young. Due to this, dawn song's function as an all clear signal, or for smoking out predators, is likely to be especially important and valued during this time. Early singing could benefit the nest and also the whole neighborhood, which could make it an attractive quality that might be selected for. The fact that earlier singing males have a higher mating success (Mennill et al., 2004) and gain more extra-pair paternity (Poesel et al., 2006) than those starting later is a strong indicator of this being the case. The potential increase in fitness could make males push the limit of the window of opportunity by starting to sing earlier than the main chorus.

Broader implications

Previous studies on the dawn chorus in songbirds have hypothesized that the timing of when birds start to sing is determined by energetic costs or costs to the immune system (Gil & Gahr, 2002), that birds sing at dawn because sound transmission is especially advantageous at this time (Henwood & Fabrick, 1979), or that birds simply sing at times when they have low foraging efficiency (Kacelnik & Krebs, 1983). Here, we propose an alternative hypothesis that there is a temporal window of opportunity at dawn where the light environment results in a low predation risk for singing birds, allowing them to get started with the daily activities at moderate risk. This phenomenon is referred to as an "anti-predation window" in other contexts, such as the diel vertical migration in planktivore fish (Clark & Levy, 1988; Scheuerell & Schindler, 2003). We base our hypothesis on data collected from previous work on the visual constraints for birds in various light environments.

Passerines are a large and diverse group of birds, occupying many different niches (Barker et al., 2004; Barker, 2011). Just amongst insectivorous species, there are ground feeding birds that rummage for worms and crawling insects on the ground, arboreal foragers that eat insects from leaves, branches, or trunks of trees, and those who forage on flying insects, either by ambush or by active pursuit. These feeding behaviors set different requirements to the species' eyes and vision. For ground feeding birds, high visual acuity is not crucial for efficient foraging. Rather, they might benefit from high visual sensitivity to find food on the forest floor at lower light intensities. This can be achieved by having large eyes and more rods in the retina. For these birds there is probably not a big trade-off between efficiency at dawn and efficiency during the rest of the day. Active pursuit passerines need a high visual acuity, and they need to be able to respond fast to the movements of their prey and to obstacles during flight. To attain this, they must sacrifice visual sensitivity and thus have a reduced ability to see well at low light intensities. Due to this, these birds probably experience a larger trade-off between efficiency at dawn and efficiency during the rest of the day.

The trade-offs this entails for passerine birds, both in eye morphology and retinal composition, will have implications for when the different bird species can start their activities in the morning. In their study, Thomas et al. (2002) found that birds with larger exposed eyes relative to body size, and thus likely better visual capabilities in dim light, start

their dawn chorus earlier. This can make them better adapted to spotting predators in low-light conditions. Thomas et al. (2002) suggested that visual capability can affect the timing of dawn song if birds only start to sing when they see well enough to avoid predators or detect them from a safe distance. This is supported by Berg et al. (2006), who showed that predation risk influences the way birds sing, with the possibility of visual detection of predators regulating the onset of the dawn chorus. Thomas et al. (2002) also suggested that visual capability can affect dawn song timing if birds sing until they see well enough to forage efficiently. In her thesis, Ulltang (in prep) argues that the start of dawn activity may also be linked to foraging strategy and restricted e.g. by when the passerines' prey become active in the morning.

It is well documented across several taxa that the presence of predators can lead to both short and long term shifts in habitat use by prey species, both in a spatial and temporal context (Lima, 1998). A well-studied example of this is the diel vertical migration found in planktivore fish. By moving up and down the water column, planktivore fish seek out light environments where they can forage efficiently while still minimizing their predation risk. These fish have thereby found an "anti-predation window" by taking advantage of the difference in light threshold for efficient foraging between planktivore and piscivore fishes (Clark & Levy, 1988; Giske & Salvanes, 1995). For birds, we have seen that the trade-offs in eye physiology make it impossible to maximize both visual acuity and visual sensitivity under poor light conditions. Both diurnal and nocturnal birds of prey have visual characters that are optimized for their respective life strategies, but neither will experience optimal light conditions for their hunting strategy at dawn.

Both hunting success and predation risk is dependent on many factors besides vision. Auditory factors will also be important, perhaps especially in the dim light at dawn. The behavior and foraging techniques for various birds are also some of the factors likely to have an effect. However, the focus of this study has been on visual limitations and trade-offs. The effect these trade-offs have on detection distance and hunting success could, as we have seen, create a window of reduced predation risk under light conditions commonly found during nautical and civil twilight. The possibility of a temporal window of opportunity for passerine birds gives a new perspective on dawn song timing. Trade-offs in the eye, linked to differences in foraging strategies, will in part determine the temporal placement and duration of this window. As previously discussed, latitude and season will also be a big part

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of determining the scope and thereby the ecological importance of the potential window of opportunity.

Future research

The limited research on and knowledge of activity patterns and visual capabilities of birds at dawn is a limiting part of our analysis. There is little data on actual predation risk experienced by songbirds at dawn, or hunting success for both diurnal and nocturnal birds of prey at this time (Lima, 2009; Schmidt & Belinsky, 2013). As a proxy for how hunting success changes with illuminance, we therefore had to rely on theoretical estimates of detection distance. Theoretical detection distance was calculated using data from behavioral studies of visual acuity, but since these studies did not test visual acuity outside the range of light intensities where the birds are mostly active, we cannot know how diurnal birds of prey perform in relevant light environments at dawn (see Fig. 4 and Fig. 5). Behavioral acuity data is also only available from a small number of species, and there is a lot of variation in the acuity of different species within the same group. Some of the existing studies are also relatively old, and better methods and equipment for measuring acuity has been developed since. The small amount of data, in combination with the methodology used in some of the studies, makes the accuracy of the acuity data somewhat questionable.

Data on how visual acuity varies with illuminance is, to the best of our knowledge, only available for 21 species of birds. Three of these are nocturnal birds of prey (Fite, 1973; Martin & Gordon, 1974; Orlowski et al., 2012), another three are diurnal birds of prey (Fox et al., 1976; Reymond, 1985, 1987), and seven are passerine birds (Donner, 1951). In addition to these groups, which are the focus of the current study, there are also studies done on budgerigars (Lind et al., 2012), Bourke's parrots (Lind et al., 2012), domestic chickens (Gover et al., 2009), rock pigeons (*Columba livia*) (Blough, 1971), and four species of corvine birds (Dabrowska, 1975). From the data already available it is clear that there is great variation both between and within the different groups of birds. To get a clearer picture of the major trends it would therefore be necessary to study the visual acuity for more species, both passerines and birds of prey. We would expect passerine birds with different foraging strategies to show different visual capabilities, as a result of adaptation to their niche. It would be interesting to see if variation in dawn song timing could be explained by this perspective. It would also be beneficial to test visual acuity over a greater range of light intensities than what has previously been done, in order to determine where absolute thresholds and saturation for the different species is reached.

Currently, the only study to have tested the visual acuity of passerine birds at various light intensities is by Donner (1951), which is over 65 years old. The high number of birds being reported with the same maximum visual acuity in this study (see Table A2 in Appendix 2) raises questions about its accuracy. This study also only tested acuity over a short range of illuminance (0.07 to 42 lux), all corresponding to twilight conditions. Therefore, further studies should focus on how visual acuity changes at both lower and higher light intensities, and extend the analysis to birds from ecologically different niches. We would expect birds with different foraging techniques and habitats to have varying visual adaptations. For example, passerine birds adapted to active pursuit have high acuity vision, which means that they probably do not see as well in dim light as other passerines.

Behavioral studies of visual acuity in diurnal birds of prey are few. Of the three studies found, only two are considered credible. This is due to the behavioral acuity recorded for the American kestrel being higher than that recorded for any other animal (Fox et al., 1976) and also much higher than it should be based on optical and retinal properties in the kestrel (Dvorak et al., 1983). The two credible studies (Reymond, 1985, 1987) test visual acuity over a range of light intensities corresponding to levels from civil dawn to early daylight. At the highest tested light intensities, visual acuity seems to be stabilized at a maximum value. At the lower end of the intensity range, the tested species still have a relatively high visual acuity compared to other groups of birds. We know from studies of human eyes that visual acuity forms a sigmoid curve when plotted against illuminance, and drops rapidly at light intensities below 400 lux (Hecht, 1928). Further studies should be undertaken to see how rapidly visual acuity drops for diurnal birds of prey at low light intensities, and to locate the threshold illuminance where they are no longer able to tell apart spatial details.

The illuminance at which cones start to have a functional response can be determined by finding the bird's light threshold for chromatic vision. To the best of our knowledge, this has only been tested in four bird species; blue tits (Gomez et al., 2014), domestic chickens (Olsson et al., 2015), Bourke's parrots, and budgerigars (Lind & Kelber, 2009). If this information was available for more species of birds, across different orders, it could be used to further improve the accuracy of the visual acuity curves in Figure 6, to better determine the scope of the potential window of opportunity. It could be especially

interesting to find the threshold for chromatic vision in owls, which are believed to have a limited ability to discriminate colors (Bowmaker & Martin, 1978).

Similarly to auditory signaling, plumage coloration can be linked to both mating success and predation risk in songbirds. The different light environments within a forest, and the retinal composition of conspecifics and predators, are important for how conspicuous visual signals will be. A cryptic pattern should have a reflectance spectrum similar to that of its background during times with high predation risk (Endler, 1978). A color pattern used for signaling however, should have a reflectance spectrum resembling the ambient light spectrum, but different from that of its background (Endler, 1993). The same color pattern will not be cryptic or conspicuous in all light environments, and within a given microhabitat the visibility of a pattern will change over the course of a day. Whether there is a general correlation between plumage coloration and dawn song onset in bird species is beyond the scope of this paper, but should be looked into in future research as it could be an important factor affecting the predation risk experienced by passerine species.

There is a web-based archive being compiled of retinal topography maps from various vertebrate species, including birds (Collin, 2008). However, there are no complete topographic map of the total distribution of rods and cones available for any bird species (Coimbra et al., 2015). Using data on retinal composition and eye morphology from different birds, it is possible to find their anatomical resolving power (see Appendix 2 for more information on this). However, this only gives us information about the birds' visual acuity under optimal light conditions. There is no straight forward way of using data from retinal maps to see how vision changes with light intensity (Almut Kelber, personal communication, March 1, 2018). There are models for chromatic (Vorobyev & Osorio, 1998) and achromatic discrimination thresholds (Siddiqi et al., 2004) in bright light conditions, and these have recently been modified to model discrimination thresholds also in dim light (Olsson et al., 2017). Still, these models do not give any information on spatial resolution. A model for how visual acuity changes depending on illuminance has been created for the human eye (Hecht, 1928), based on and fitted to data from extensive behavioral studies. Finding a way to model visual acuity for birds depending on light intensity could provide useful information on what limits bird vision during the different stages of twilight. It would also further help confirm or rebut the presence of a window of opportunity for passerine birds in relation to avian predators at dawn.

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Few birds are strictly diurnal or nocturnal, resulting in most predatory birds also being active around dawn and dusk, especially in spring (Newton, 1986; Martin, 1990). Few studies have looked at and compared activity patterns of predators and prey birds, or have addressed predation on dawn-singing birds. In a review of behavioral flexibility under risk of predation, Lima (2009) states that he knows of no studies that have addressed the predation on dawn-singing birds. In a more recent study, Schmidt and Belinsky (2013) report that this gap in our knowledge still persists. However, their study demonstrated that predation risk can affect dusk singing in birds by making songbirds sing earlier under high perceived predation risk, and it is likely that there is a comparable effect on dawn singing. Under high perceived predation risk, songbirds might be expected to sing later at dawn, when the light intensities allows for adequate visual acuity to spot predators from a safe distance (Schmidt & Belinsky, 2013).

The lack of knowledge on how hunting success varies over the course of the day is likely due to it being challenging to observe and study hunting efforts in sufficient numbers to see any clear trends. From the existing behavioral studies on owls, it seems that visual acuity stabilizes at a maximum value already in relatively dim light. It would be interesting to see how their hunting success changes in brighter light during dawn, as their own acuity remains relatively low while songbirds see increasingly better with increasing illuminance. However, this would probably be quite time consuming, as it would require extensive observational studies. Further studies on hunting success of birds of prey at dawn would also help answer the question of whether the high mortality of passerine birds at this time is due to a high predation risk, or alternatively due to a high activity of both predator and prey birds at this time, similarly to what has been found in studies from the pelagic.

Conclusions

In this thesis, I have presented the hypothesis that songbirds make use of a temporal window of opportunity in the pre-dawn period, where the light environment results in a low predation risk for the singing birds. This hypothesis is based on data collected from previous work on the visual constraints birds experience at various light environments, and calculations I have made using these data. Other hypotheses have linked timing of dawn chorus in songbirds to e.g. energetic costs (Gil & Gahr, 2002), favorable sound transmission period (Henwood & Fabrick, 1979), or low foraging efficiency (Kacelnik & Krebs, 1983), and none of these are mutually exclusive.

The possibility of a temporal window of opportunity gives a new view on what determines and limits the onset of dawn song for passerine birds. Trade-offs in the eye, which are correlated to different foraging strategies, will in part determine the temporal placement and duration of this window. Season and latitude are also a big part of determining the scope and thereby the ecological importance of the window of opportunity, with the window being more important at the higher latitudes of the temperate regions.

Our literature review revealed a lack of research and knowledge on the activity patterns and visual capabilities of birds at dawn. There is little data on the actual predation risk experienced by songbirds, or the hunting success for both diurnal and nocturnal birds of prey at dawn. Data from behavioral studies of visual acuity is scarce, and age and methodology used in some of the studies, makes the accuracy of the acuity data somewhat questionable.

Using data on retinal composition and eye morphology from different bird species, it is possible to find their anatomical resolving power. However, this only gives us information about the birds' visual acuity under optimal light conditions and there is no straightforward way of using this data to see how vision changes with light intensity. Finding a way to model visual acuity for birds depending on light intensity could provide useful information on what limits birds' behavior during the different stages of twilight. It would also help further confirm or rebut the presence of a window of opportunity for songbirds at dawn.

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Appendix 1 – Detailed Methods

Earth-Sun angles

In order to look at how dawn song and other behaviors in birds change with different light environments, we have looked at how the light environment changes over the course of a day. To generalize this in a way that is independent on latitude and seasons, we have used solar altitude as a proxy for these different light environments. This way, even though the speed and timing on sunrise changes depending on where we are in time and space, we get the same light environment as long as the solar altitudes being looked at are the same.

Solar altitude (α) is a measure of the angle between the central ray from the sun and a horizontal plane containing the observer. The solar altitude at sunrise is 0°. Solar altitude is negative when the sun is below the horizon, and positive when the sun is above the horizon. The solar altitude can be calculated for a given place and time using the following equations (1-7) from Brownson (2013):

$$\alpha = sin^{-1}\left[sin\varphi\ sin\delta + cos\varphi\ cos\delta\ cos\omega\right] \tag{1}$$

where φ is the angle of latitude, δ is the angle of declination and ω is the hour angle. The angle of declination is a celestial coordinate to specify the relative location of the Sun with respect to the Equator, depending on the Earth's tilt through the seasons, given by:

$$\delta = 23{,}45° \sin\left(\frac{360}{365}(284 + n)\right) \tag{2}$$

where n is the day number, such that n=1 on the 1st January.
The hour angle is a celestial angular value of the sun with respect to a meridian on Earth, given by:

$$\omega = \frac{360°}{24h}(t_{sol} - 12h) = \frac{15°}{1h}(t_{sol} - 12h) \tag{3}$$

$$\omega = \begin{cases} -0\ to -180, if\ before\ noon\ (morning) \\ +0\ to +180, if\ after\ noon\ (evening) \end{cases} \tag{4}$$

where t_{sol} is the solar time. Solar time can differ from standard time, t_{std}, depending on daylight savings time, time zones and small shifts due to the wobble of Earth. The difference between solar and standard time is called the equation of time, E_t, given by:

$$
\begin{aligned}
E_t = {} & 229{,}2(0{,}000075) \\
& + 229{,}2(0{,}001868\ cosB - 0{,}032077\ sinB) \\
& - 229{,}2(0{,}014615\ cos2B + 0{,}04089\ sin2B)
\end{aligned}
\qquad [in\ minutes] (5)
$$

with

$$
B = (n-1)\frac{360}{365} \times \frac{180}{\pi} \tag{6}
$$

for the nth day of the year. Solar time is related to standard time by:

$$
t_{sol} = t_{std} + 4\left(\beta_{std} - \beta_{loc}\right) + E_t \qquad [in\ minutes] (7)
$$

where β_{std} is the standard meridian for the local time zone, and β_{loc} is the longitude of the location in question in degrees west.

Illumination depending on solar altitude

The ground illumination from natural sources varies considerably during the day as a result of changing solar altitude. Ground illumination can be calculated using a formula modified from *Explanatory Supplement to the Astronomical Almanac* (Seidelmann, 1992):

$$
\log_{10} I = l_0 + l_1 x + l_2 x^2 + l_3 x^3 \tag{8}
$$

where

$$
x = \frac{\alpha}{90} \tag{9}
$$

and α is the solar altitude in degrees. l_0, l_1, l_2, l_3 are the appropriate set of coefficients given in Table A1 for various ranges of solar altitude.

Table A1: Coefficients for calculating ground illumination (Seidelmann, 1992).

Solar altitude range (°)		l_0	l_1	l_2	l_3	Maximum error
to	from					
20	90	3.74	3.97	-4.07	1.47	0.02
5	20	3.05	13.28	-45.98	64.33	0.02
-0.8	5	2.88	22.26	-207.64	1034.30	0.02
-5	-0.8	2.88	21.81	-258.11	-858.36	0.02
-12	-5	2.70	12.17	-431.69	-1899.83	0.02
-18	-12	13.84	262.72	1447.42	2797.93	0.02

In addition to theoretical values, we received measurements of solar illuminance and spectra from Svein Nedrebø and Børge Hamre at the Institute of Physics and Technology, UiB. The data was collected as described by Nedrebø (2017). Measurements were taken during May of 2016. The radiometers were mounted on the roof of *Biologen* (Thormøhlensgate 53A, Bergen), with the sensor tip/diffuser straight up. Three radiometers produced by Trios were used. The cosine irradiance radiometers Ramses 82E6 and 80E2, as well as the scalar irradiance radiometer Ramses 84EE. The E2 device measures visible light (319.5-951.8 nm), while the E6 measures light in the UV region (279.5-501.9 nm).

Light measurements registered at dawn were compared to measurements from mid-day when the sun was at the meridian. Since measurements were taken over several days, we also compared measurements taken on cloudy days to those taken on days with clear skies. The data from these measurements were given as spectral radiance, in mW/m^2/nm. These data were converted to lux, for easier comparison to theoretical data, using an equation from Bohren and Clothiaux (2006):

$$Lux = k \int_0^\infty LV d\lambda \qquad\qquad 10$$

where k=683 lm/W, L is spectral radiance and V is the luminous efficiency.

The purpose of comparing these sunlight measurements was to see if there is a significant difference in the spectrum at dawn compared to later in the day. We then used literature to find out if the light spectrum at dawn could give either songbirds or birds of

prey an advantage. The information gathered from sunlight measurements and literature studies was used study how the likelihood of a predator spotting its prey and for the prey to spot the predator changes with illuminance at dawn.

Literature searches

Searches for relevant literature for visual thresholds and the light dependent hunting success for birds have been made using online publication databases and search engines. All databases available from Web of Science were searched using a combination of words in the title or abstract related to different factors associated with light availability, visual thresholds and avian hunting success. "Visual thresholds" was used as a rather general term to include both chromatic and achromatic visual restrictions depending on light spectrum and intensity. The studies for the review fall into three general categories. The first category includes studies that document achromatic vision, or visual acuity, depending on illuminance. The key words for this search included

"vision" AND ("contrast" OR "achromatic") and "visual acuity"

The second category includes studies that document chromatic vision depending on illuminance and spectrum. The key words for this search included

"vision" AND ("colo*r" OR "chromatic").

The third category includes studies that document the hunting success of avian predators depending on illuminance. The key words for this search included

"activity pattern", "hunting success", "flight speed" and "predation risk".

In order to limit the results to studies concerning passerine and predator birds, the following words were used to narrow down the search results in all three categories;

"bird", "avian", "passerine", "raptor" and "predator".

Selection of studies

Based on screening of the titles and abstracts eligible articles for full text reading were identified. For the first two search categories concerning chromatic and achromatic visual thresholds, these were articles where the visual thresholds of birds were determined by behavioral studies using several different light intensities. This allowed for determining how well birds see in the changing light during twilight. Where possible, the values of these behavioral studies were compared to the maximum anatomical resolving power to check the credibility of the behavioral data. For the third category articles that described a change in avian hunting success or predation risk depending on time of day or illuminance were selected. References cited in significant primary articles were screened, as were studies published by key authors. Studies not published in English or Scandinavian languages were excluded. No time or document type restrictions were applied.

Detection distance

Detection distance can be used to assess hunting success of avian predators, and also the predation risk for passerine birds. The distance at which an object occupies the same angle of retinal space as one cycle at the threshold of visual acuity can be considered the theoretical maximum distance that an animal could detect that object. This detection distance can be calculated by

$$d = r \: / \tan\frac{v}{2} \qquad\qquad 11$$

where d is the detection distance, r is the radius (half the wingspan) of the object and v is the inverse of visual acuity.

Dawn choirs

To compare different dawn choirs from as many species as possible, a thorough search was done for studies on the dawn chorus onset for differing species as described in Ulltang (in prep). Marte Ulltang is working on a master thesis parallel to mine, and we have exchanged relevant findings along the way. All databases available on Web of Science were searched for studies that had recorded the onset of dawn choirs for various passerine birds. In order to be included, a study had to have three or more passerine birds performing dawn song in the

same location (to qualify as a chorus), in the same time period, during the breeding period. In studies where choirs were recorded under manipulated conditions, only the control data for onset of dawn song was included.

Appendix 2 – Visual acuity in birds

Behavioral acuity

Visual acuity can be measured based on physical behavior. A common method for measuring this behavioral acuity is a two-choice discrimination task. This is done by training an animal to choose a displayed pattern of vertical black bars equal in width and separated by white bars of the same width, rather than a display of solid color. The task is repeated using patterns with gradually thinner lines until the animal is no longer able to choose the patterned display more than 50 % of the time. This endpoint is then used to calculate the visual acuity at the current light condition (Jones et al., 2007). Since the width of the bars at which this happens will depend on how far the observer is from the display, visual acuity is not measured in distance but as a visual angle. The number of white and black bar cycles that can fit into one degree at the eye is then reported as cycles per degree. In order to test visual acuity under various light conditions, the discrimination task is simply repeated under these light conditions.

Our literature review revealed behavioral acuity data with various light levels for 12 relevant bird species, falling into one of the three categories passerine, diurnal bird of prey, or nocturnal bird of prey (see Table A2).

Table A2: An overview of behavioral acuity thresholds across bird species.

Species name	Acuity (cycles/degree)	Luminance (lux)	Reference
Brown falcon (*Falco berigora*)	47/52/57/71/73	2.5/25.1/251/2513/6283	Reymond (1987)
Wedge-tailed eagle (*Aquila audax*)	34/58/115/126/138	2.5/25.1/251/2513/6283	Reymond (1985)
Barn owl (*Tyto alba*)	1.5/2.0/2.1/2.6/3.0/3.2/2.8/2.5	$1.5×10^{-4}$/$1.2×10^{-3}$/ $9.4×10^{-3}$/ $7.5×10^{-2}$/ 0.6/4.8/37.7/295	Orlowski et al. (2012)
Tawny owl (*Strix aluco*)	10.3/12/8.8	57.6/545/1816	Martin and Gordon (1974)
Great horned owl (*Bubo virginianus*)	0.6/1/1.4/2.1/3.6/5.1/6.9	$7.2×10^{-4}$/$2.5×10^{-3}$/ $1.3×10^{-2}$/ $5.4×10^{-2}$/ 0.8/2.9/115	Fite (1973)
Blackbird (*Turdus merula*)	11.4/15.9/22.5	$7×10^{-2}$/0.2/1.5-42.5	Donner (1951)
Fieldfare (*Turdus pilaris*)	9.6/11.4/22.5/15.9	$7×10^{-2}$/0.2/1.5-33/42.5	Donner (1951)
Skylark (*Alauda arvensis*)	4.9/22.5/11.4	$7×10^{-2}$-0.2/1.5-33/42.5	Donner (1951)
Yellowhammer (*Emberiza citrinella*)	0.9/2.2/6.4/9.6	1.5/4.5/33/42.5	Donner (1951)
Reed bunting (*Emberiza schoeniclus*)	0.9/2.2/7.8	1.5/4.5/33-42.5	Donner (1951)
European robin (*Erithacus rubecula*)	11.4/6.4	$7×10^{-2}$/0.2-42.5	Donner (1951)
Chaffinch (*Fringilla coelebs*)	9.6/11.4/22.5	$7×10^{-2}$/0.2/1.5-42.5	Donner (1951)

Maximum anatomical resolving power

A bird's maximum anatomical resolving power is a theoretical upper limit of visual acuity based on calculations that use spacing of photoreceptors or ganglion cell densities (Jones et al., 2007). In general, anatomical resolving power can be estimated from focal length, photoreceptor spacing and pupil diameter (Hirsch, 1982). Table A3 compares the maximum behavioral acuity to the maximum anatomical resolving power across species.

Table A3: Comparison of maximum recorded behavioral acuity with the maximum anatomical resolving power across bird species.

Species	Max behavioral acuity (cycles per degree)	Max anatomical resolving power (cycles per degree)	Reference (for anatomical resolving power)
Brown falcon (*Falco berigora*)	73	76	Reymond (1987)
Wedge-tailed eagle (*Aquila audax*)	138	140	Reymond (1985)
Barn owl (*Tyto alba*)	3.7	8.4	Wathey and Pettigrew (1989)
Tawny owl (*Strix aluco*)	12	-	-
Great horned owl (*Bubo virginianus*)	6.9	-	-
Blackbird (*Turdus merula*)	22.5	18.2	Donner (1951)
Fieldfare (*Turdus pilaris*)	22.5	25.7	Donner (1951)
Skylark (*Alauda arvensis*)	22.5	15.5	Donner (1951)
Yellowhammer (*Emberiza citrinella*)	9.6	10.6	Donner (1951)
Reed bunting (*Emberiza schoeniclus*)	7.8	9.4	Donner (1951)
European robin (*Erithacus rubecula*)	11.4	12.9	Donner (1951)
Chaffinch (*Fringilla coelebs*)	22.5	18.6	Donner (1951)