

The effect of foraging ecology on the onset of dawn song for passerine species



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20.11.2018

**«tsip-prrup, tsip-prrup-prrup, tsip-prrup,
tsip-prrup-prrup-prrup, tsip-prrup-prrup,
tsip-prrup-prrup-prrup-prrup»**

Dawn song of the tree swallow (*Tachycineta bicolor*)

Allen (1913)

Front cover photo.

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Acknowledgements

First and foremost, I would like to thank my supervisors Sigrunn Eliassen and Christian Jørgensen for guidance, feedback and support throughout this project, and for giving me the opportunity to work with the intriguing dawn chorus. In addition, I am grateful to Julianne Netteland for collaboration, conversations and exchange of knowledge.

I am deeply grateful to Melissah Rowe for welcoming me when I moved to Oslo, and for introducing me to Jan T. Lifjeld and the Sex and Evolution Research Group (SERG) at Natural History Museum in Oslo. I would like to thank SERG for including me in their research group, and for giving me advice and suggestions.

I would like to express my gratitude to my wonderful family for love, support and motivation, and my best friend Pomba, for always being there for me. I am grateful for my beloved sister and proofreader Synne Ulltang. I want to thank all my friends during my studies, for encouraging and inspiring me. A special thanks to Randi Elisabeth Åsly for proofreading my thesis. I am very thankful for our friendship and shared enthusiasm for evolution.

Last, but not least, I want to thank my fiancé Per-Ivar Lønne. Thank you for your patience and for your unconditional love, and for waking up and listening to the dawn chorus together with me before the first cup of coffee. This work had not been possible without your continuous encouragement and support. Thank you for understanding how important this is to me.

Abstract

Passerine birds have a burst of energetic singing prior to sunrise during the breeding season, called the dawn chorus. In this thesis, I examine how interspecific differences in foraging ecology can explain the scheduling of dawn singers, by investigating how diet choice and availability and foraging adaptations are linked to the onset of dawn song.

In this thesis, data from several published studies have been combined in order to gain new insights of bird ecology related to dawn song, with a focus on foraging behaviour and diet. The arguments are gradually built through several questions, using sound methods for data analysis. Each question gathers current knowledge from available research, and combines it into new insights of the field. In order to explore how feeding ecology of birds is linked to the scheduling of dawn song, a systematic literature search was performed to collect data on dawn choruses, and morphological, ecological and dietary information available for the bird species participating in the choruses. The trends have been explored for both temperate and tropical areas.

The differences in absolute eye size, dietary trends, prey attack manoeuvres and foraging heights for early- and late-singing European and North American birds reveal that early-singing birds could take advantage of the nocturnal active prey species available during dawn, have the ability to catch them, and therefore start profitable foraging during dawn.

I suggest that foraging ecology is an important factor determining the scheduling of the dawn chorus in temperate areas. The factors affecting the timing of dawn song appear to be latitude dependent, and foraging ecology seems to be a stronger factor for temperate than for tropical choruses.

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Introduction

Bird song is a vocal signal used to influence the behaviour of other individuals (Lovette & Fitzpatrick, 2016). Communication provides information concerning individual identity, status, mood and intentions for many species, and facilitates survival, growth and reproduction (McGregor, 2005; Bradbury & Vehrencamp, 2011). The functions of bird song are generally believed to include territory defence, sustaining social relationships and mate attraction (Catchpole & Slater, 2008; Lovette & Fitzpatrick, 2016). For survival and reproduction, the right temporal timing of behaviour, both daily and seasonally, is essential (Da Silva & Kempenaers, 2017).

Many birds have a burst of energetic singing prior to sunrise during the breeding season, called the *dawn chorus* (Lovette & Fitzpatrick, 2016). It is a synchronized chorus of song that is characteristic of many passerine species, but is also performed by other bird species and a few non-avian species (Staicer *et al.*, 1996; McGregor, 2005; Poesel *et al.*, 2006). The dawn chorus typical for passerine birds begins 30 to 90 minutes before sunrise, and includes all territorial males in a neighbourhood (McGregor, 2005). The pronounced peak of singing is quite intense, and lasts for 20 to 60 minutes for each individual male (Ross Lein, 2007). As light levels increase prior to sunrise, singing usually ends, and the males begin foraging, patrolling their borders, and switch to daytime-singing (e. g. courtship-singing to potential mates or counter-singing with neighbours) (McGregor, 2005).

An intriguing aspect of the dawn chorus is that individual bird species start to sing at characteristic times each morning, forming a non-random sequence of singers (Berg *et al.*, 2006). Why the male birds sing at this very specific predawn period, and the functional significance of dawn song, are still not clearly understood. The reasons appear to be context-dependent, and differ among species, populations and studies (Ross Lein, 2007; Pérez-Granados *et al.*, 2018). Dawn song is less studied, and differs functionally, from daytime-singing (Staicer *et al.*, 1996; Ross Lein, 2007). The majority of research on the dawn chorus of birds has focused on the functions, patterns and origins of the chorusing activity (Farina *et al.*, 2015). Based on a thorough review of existing literature, Staicer *et al.* (1996) presented 12 non-exclusive hypotheses to explain the dawn chorus behaviour on individual, population and

community levels (McGregor, 2005; Farina *et al.*, 2015). They grouped the factors affecting dawn chorus behaviour into three categories: intrinsic, extrinsic and social.

The intrinsic and extrinsic hypotheses are likely proximate explanations. They do not provide an adaptive explanation for the selective advantage of dawn song, nor explain why only some species show chorusing behaviour (McGregor, 2005). The social factors represent ultimate explanations, which are not mutually exclusive. The intrinsic factors includes eye size (Thomas *et al.*, 2002; Berg *et al.*, 2006), physiological needs of individuals (e.g. nutritional state) and circadian cycles of testosterone (Cuthill & Macdonald, 1990; Thomas & Cuthill, 2002; Barnett & Briskie, 2007), self-stimulation, mate-stimulation and the reproductive stage of the female (Mace, 1987; Welling *et al.*, 1995; Foote *et al.*, 2008; Bruni & Foote, 2014; Zhang *et al.*, 2016).

The extrinsic factors include light intensity (e.g. moon brightness), time of sunrise, ambient temperature and weather conditions. The onset of dawn song is strongly linked to light levels, and the order of dawn-singing passerines could perhaps be explained by differences in species sensitivity to light (Hutchinson, 2002; Thomas *et al.*, 2002; McNeil *et al.*, 2005; Berg *et al.*, 2006; Chen *et al.*, 2015). Many species start to sing earlier on mornings with bright moonlight (Leopold & Eynon, 1961; Bruni *et al.*, 2014; York *et al.*, 2014), or when exposed to artificial light (e.g. street lights) (Kempnaers *et al.*, 2010) and later on cloudy mornings (Bruni *et al.*, 2014; Da Silva *et al.*, 2014). In addition there might be factors affecting acoustic transmission, variability of nighttime conditions (affecting the amount of energy in the morning), predation risk, or the efficiency of foraging at low light intensity (Wiley & Richards, 1978; Kacelnik, 1979; Kacelnik & Krebs, 1982; McNamara *et al.*, 1987; Dabelsteen & Mathevon, 2002; Hutchinson, 2002; Brown & Handford, 2003; McGregor, 2005; Berg *et al.*, 2006; Bruni *et al.*, 2014; Farina *et al.*, 2015). Not all species respond the same way to the proximate factors that affects the scheduling of dawn singers. For example, artificial light affects early-singing species more than late-singing species in the dawn chorus (Kempnaers *et al.*, 2010; Da Silva & Kempnaers, 2017).

The social factors, which represent ultimate explanations, which are not mutually exclusive. They include mate attraction and/or stimulation, territory defence and the resolution of social conflicts (Burt & Vehrencamp, 2005; McGregor, 2005; Tobias *et al.*, 2014; Farina *et al.*, 2015). Song characteristics and the amount of singing vary between individuals and species (McNeil *et al.*, 2005; Bruni *et al.*, 2014). Bird song is an important

cue used by females during mate selection, which suggests it has evolved as a sexually selected trait (Poesel *et al.*, 2006; Murphy *et al.*, 2008). To constitute a stable, honest indicator of male quality, song has to be a costly signal. This would be true if individual variation in song traits were dependent on male condition, so that differences in phenotypic or genetic quality between males would result in differences in song production. There are multiple song traits, which can be sexually selected, and they are not equally important in all species (Gil & Gahr, 2002). The song characteristics with greatest individual variation and repeatability in performance, such as time spent singing, song rate, amplitude or duration, are expected to be the song traits that are most important in sexual selection. The evolutionary pressure on song traits has led to an amazing variety and complexity in the songs of different species (Catchpole & Slater, 2008).

Attracting extra-pair mates (EPM) could be a possible function of dawn song, since dawn song is more pronounced during the female fertile period, but after territorial establishment and pairing. Extra-pair copulations (EPCs) is a major component of sexual selection (Garamszegi & Moller, 2004), and males that participate in the dawn chorus may increase their chance of attracting additional mates. Several studies have shown that the earliest-singing male is the one that gain most EPCs, and therefore potentially has higher reproductive success (Poesel *et al.*, 2006; Dolan *et al.*, 2007; Murphy *et al.*, 2008; Kempenaers *et al.*, 2010). Poesel *et al.* (2006) found that older blue tit (*Cyanistes caeruleus*) males sang first, had most mating partners and had more EPC than younger males. For the eastern kingbird (*Tyrannus tyrannus*), cuckolders sang earlier and faster than cuckoldees (Dolan *et al.*, 2007). Therefore, early dawn-singing could be under direct sexual selection. In addition, the intraspecific timing of the onset of dawn song can possibly be a good indicator of male EPC success (Dolan *et al.*, 2007; Murphy *et al.*, 2008; Da Silva *et al.*, 2014).

Territory establishment and pairing do not seem to be the primary functions of dawn song, since dawn song continues long after these activities have ended (Ross Lein, 2007). Territory defence is a possible function of dawn song. Dawn song is performed right after inactivity, and potential overnight mortality of territory owners caused by predation or starvation, could result in available territories for searching males. There is a higher rate of invasion early in the morning than other times of the day (Kacelnik & Krebs, 1982). Dawn song could decrease the number of intruders, and signal that the territory is occupied (Krebs, 1982).

Dawn chorusing possibly conveys different types of messages for different receivers. A study by Pérez-Granados *et al.* (2018) found that Dupont's lark (*Chersophilus duponti*) dawn vocalization included both song and calls, that likely served different functions; territorial defence and mate attraction respectively.

The visual system of birds is designed to detect food and avoid predators (Hart, 2001; Gill, 2007). Light intensity gradually increases during dawn, and the predictable order in which birds join the dawn chorus may be determined by the bird species' visual capability at low light levels. During breeding, energy requirements are high and passerines need to start foraging activity as soon as it is profitable. *The inefficient foraging hypothesis* states that birds perform dawn song when the light intensities are too low for foraging activity (Kroodsma, 1996; Thomas *et al.*, 2002).

In dawn chorus research, there has however, been little focus on bird foraging ecology. Previous studies focusing on diet have only distinguished between animal-eating, omnivore, and plant-eating birds (Chen *et al.*, 2015), or classified them as insectivores or non-insectivores (Stanley *et al.*, 2016) without giving detailed information on the differences in prey content, which prey capturing techniques were used or from where the prey was taken. One study of dawn song included foraging height (Berg *et al.*, 2006). To our knowledge, no study has linked differences in prey content, prey capturing techniques and foraging heights simultaneously and studied these factors in relation to the scheduling of dawn song in birds.

In this thesis, I examine how interspecific differences in foraging ecology can explain the onset of dawn song. With a focus on foraging profitability, which may differ at different light intensities during the twilight period, I will explore how diet choice and availability and foraging adaptations are linked to the start of dawn song for passerine species, and the scheduling of dawn singers.

Method

This thesis is conceptual, and constructs arguments using sound methods for data analysis, and comprises material from various fields. In this thesis, I have combined data from several published studies in order to gain new insights of bird ecology related to dawn song, with a focus on foraging behaviour and diet.

In order to explore how feeding ecology of birds is linked to the scheduling of dawn song, a systematic literature search was performed to collect data for a database, included in Supplementary material. In this thesis, only bird species from the order Passeriformes was included, in order to avoid any effects caused by differences among avian orders.

Empirical studies on dawn song were collected using a given set of inclusion and exclusion criteria (described in details in Appendix 1). From the collected studies, the onset of dawn song was determined for 128 passerine species participating in dawn choruses. The onset of dawn song was converted from minutes, relative to sunrise or civil twilight, to solar altitude (i.e. the range of degrees that the centre of the sun is above/below the horizon). This allows comparison of light levels at the onset of dawn song, independent of temporal differences and geographical locations. Dawn choruses from five areas: Europe, North America, Australia, Asia and South America, were represented in the database. I have analysed patterns and trends for each area separately, and compared them with the other areas.

Morphological, ecological and dietary data available for the bird species participating in the chorus were collected. From these data, absolute eye size, relative eye size and average body mass were calculated (Eq. 1-2, Appendix 2) in order to reveal trends related to energetic and visual constraints. Foraging heights and prey attack manoeuvres of birds were divided into main categories, and studied with respect to the onset of dawn song. Information concerning the breeding diet for the bird species was collected, examined and sorted into prey orders. Afterwards, the breeding diet was divided into categories based on the temporal and spatial availability of the prey orders included in the bird species' diet. The percent of each category present in a bird species' diet was calculated using a set of criteria (for complete summary, see Appendix 2) and analysed in relation to the onset of dawn song in the different areas.

Layering of forests

In this thesis, forests with the approximately same light intensities at upper and lower layers are defined as *non-layered* forests. Deciduous temperate forests are in spring bud break, and therefore non-layered during the breeding period of temperate passerines. In *layered* forests, the light intensities vary between upper and lower layers. Broad-leaf evergreen tropical forests are defined as layered forests in this thesis, as the light intensity between the canopy layer and the forest floor attenuates by up to two orders of magnitude (Engelbrecht & Herz, 2001; Berg *et al.*, 2006).

Relative eye size and absolute eye size

I have collected data for the onset of dawn song participation in choruses around the world and combined these with morphological eye data from Ritland (1982), Chen *et al.* (2015), and Berg *et al.* (2006). For calculations of RES and AES, see Eq. 1-2, Appendix 2. The dawn chorusing species of Asia and South America live in layered forests, and have therefore been divided into foraging layers when evaluating their eye size trends. European, North American and Australian passerines, which breed in non-layered forests, have not been divided into layers.

Dietary trends

In this thesis, the diets of passerine species have been grouped into five categories, based on their temporal activity patterns, and if they are flying or non-flying prey species. *Nocturnal non-flying prey* are available at low light intensities, and are difficult to find during the day, as they for example hide under stones or retreat into the soil. This group includes the orders Isopoda (woodlice), Oligochaeta (earthworms), Diplopoda (millipedes), Dermaptera (earwigs) and Chilopoda (centipedes). *Nocturnal flying prey* include species that are active flyers during low light intensities, but rest on the substrate (e.g. leaves or litter) during day. The group includes the orders Trichoptera (caddisflies), Neuroptera (lacewings), Blattodea (cockroaches), Ephemeroptera (mayflies) and Psocoptera (barkflies). *Gastropods* only includes the class Gastropoda (snails and slugs), because their temporal activity pattern seems to be more dependent of humidity levels rather than light intensities. Snails and slugs tend to emerge from their hiding places at night, and have increased activity at dusk and dawn, probably caused by the increased relative humidity as the temperature drops (Sturm *et al.*,

2006). *Variously active prey* includes orders that have very variable activity patterns, with nocturnal and diurnal, flying and non-flying prey species. For example, the order Hymenoptera consists of both nocturnal flying flies, diurnal flying bees, and nocturnal and diurnal non-flying ants. *Variously active prey* includes the orders Hymenoptera (flies, bees, sawflies, wasps and ants), Lepidoptera (butterflies and moths), Odonata (damselflies and dragonflies), Isoptera (termites), Mecoptera (scorpionflies), Orthoptera (grasshoppers, locusts, crickets), Plecoptera (stoneflies), Coleoptera (beetles), Hemiptera (true bugs), Diptera (true flies, horse flies, crane flies, hoverflies and mosquitoes), Collembola (springtails) and Arachnida (spiders, ticks, harvestmen, mites and scorpions). *Plant material* includes all sorts of plant parts taken by birds, for example seeds, berries, nectar fruit and plant buds. For further descriptions of the orders included in the categories, see Table A2.1 in Appendix 2.

Prey attack manoeuvre categories

The prey attack manoeuvres of the birds are categorized in three groups: *substrate gleaners*, *flycatchers* and *both techniques*. The first category, substrate gleaners, include bird species which only catch non-flying prey while standing on substrate, using the prey attack manoeuvres ground glean, probe, tree glean, snatch, hover glean and dive glean. The second category, flycatchers, include bird species which only catch flying prey in air by using the prey attack manoeuvres strike, sally, flush chase and hawk. The third category, both techniques, include bird species which use prey attack manoeuvres from both the substrate gleaners and flycatchers categories. For more details, see Table A2.2 in Appendix 2.

Foraging heights

In this thesis, the foraging heights of birds are categorized as *lower heights* (< 1.5 m), *mid heights* (≥ 1.5 m to < 7 m) *upper heights* (≥ 7 m), and *variable heights*. For more details, see Appendix 2.

Results

In this thesis, I explore how different aspects of the foraging ecology of passerine species affects the onset of dawn song. Based on current knowledge from available research, I gradually build an argument through a series of questions.

1. How does light change during the twilight period, in the breeding environment of birds?

Daylight is possibly the strongest environmental cue used by birds to time their daily activity (Dominoni *et al.*, 2016). The twilight period at dawn is the transition between true night and sunrise, and is controlled by the speed of sun rise (Rozenberg, 1966). Twilight is divided into three periods, defined by the solar altitude (i.e. degree of the centre of the sun in relation to the horizon): astronomical twilight ($\geq -18^\circ$ to $< -12^\circ$), nautical twilight ($\geq -12^\circ$ to $< -6^\circ$) and civil twilight ($\geq -6^\circ$ to $< 0^\circ$) (Cronin *et al.*, 2014). Duration of twilight is short at low latitudes, and increases with distance from equator (Cronin *et al.*, 2014), e.g., the twilight period lasts for 120 minutes in The Netherlands (55°N), but only 70 minutes in Ecuador (0°N) (Figure 1.1). During the twilight period, from now on referred to as *dawn*, light appears purple. This is because light-absorbing atmospheric ozone, which is particularly absorbent around 604 nm (Rozenberg, 1966; McFarland & Munz, 1975), reduces the amount of light with middle wavelengths (570-630 nm). The light environment at dawn is rich in UV light (Endler, 1993). Because of the low angle of light from the sun during dawn, light must traverse a far longer distance through the atmosphere than light coming in at higher angles, leading to more absorption of light with long wavelengths and scattering of light with short wavelengths (Endler, 1993), and due to thinner atmosphere, UV light is stronger at higher latitudes than in tropical areas (Withgott, 2000).

Duration of twilight periods at various latitudes

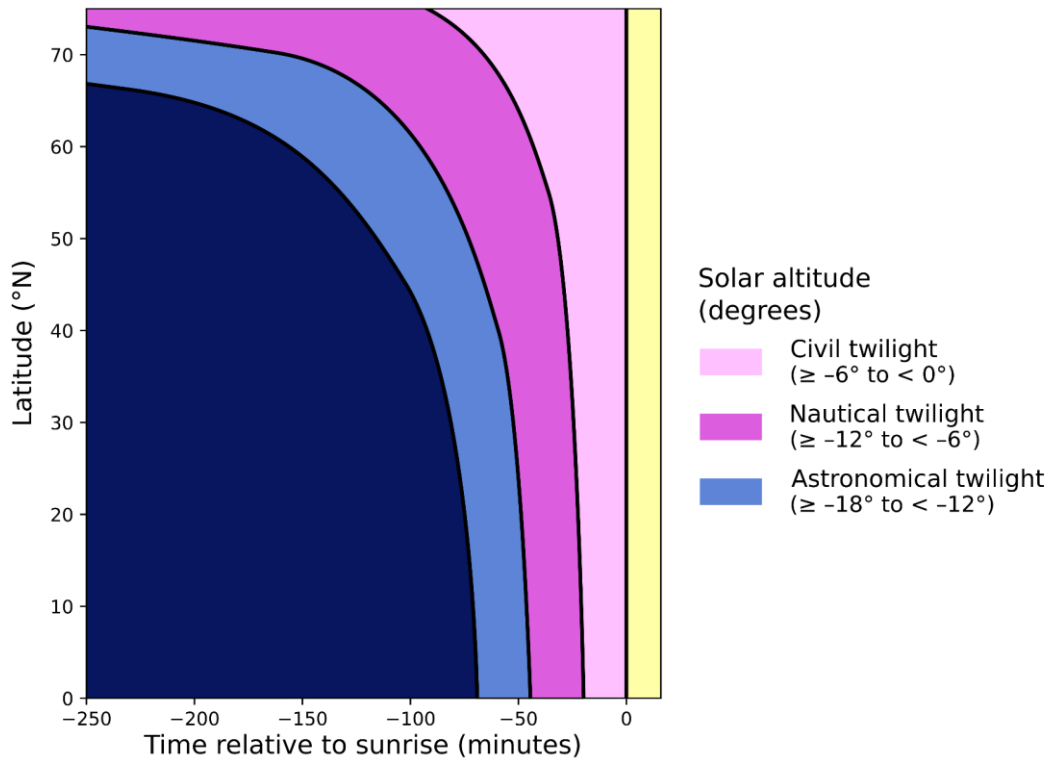


Figure 1.1: The duration of different twilight periods at various latitudes (°N) (1st April). The lines illustrate the time relative to sunrise (minutes) when the Sun is at specific solar altitudes (degrees), and the indicated twilight period begins. The duration of the twilight periods at a given latitude is represented by the width of the coloured bands, which increase towards higher latitudes. For calculations, see Appendix 1.

The vegetation structure of the breeding habitat of birds further affects light availability. In a layered forest, birds at lower levels experience lower light intensities than birds at higher levels. If the onset of dawn song and onset of profitable foraging activity is dependent on light intensities, bird species at upper and lower layers may differ in their onset of activity. For example, in a study by Berg *et al.* (2006) early singers were foraging at upper heights in a dense neo-tropical forest, whereas late singers were foraging in lower heights. Vegetation cover can also alter the light spectrum e.g. as leaves absorb UV, and therefore strongly reduced UV at lower layers (Théry, 2001). In this thesis, light level is qualified as solar altitude, which implies that experienced light intensity may vary depending on the type and layering of the forest. Therefore, song data is grouped according to whether the forest is layered or non-layered. Birds breeding in dense, layered forests therefore have reduced UV light in their environment, while birds living in non-layered forests experience rich UV light during dawn.

2. Phenology and diet during the breeding period: what are the differences between temperate and tropical areas?

Birds living at higher latitudes experience more seasonal variations in their local environment and resource availability than birds living nearer equator. Temperate passerines breed for less than two months, have one or two broods with large clutch size, and many do not renest if the breeding attempt fails. Tropical passerines breed for longer than four months, occasionally all year, and have several consecutive broods with small clutch size (Lovette & Fitzpatrick, 2016). As a result, tropical species are expected to be less energetically challenged than temperate species. Temperate species have larger clutch size than tropical species and experiences higher annual mortality (Martin, 1987). Therefore, they need to work hard to maximize clutch production during the short breeding season, hence start foraging as early as possible in the morning could be of particular importance in temperate areas.

The breeding period of most temperate passerines is during spring, which is a period with plentiful resources, where increasing temperatures result in a seasonal flush in vegetation and hatching of insects (Lovette & Fitzpatrick, 2016). Most temperate passerines are generalists, and switch from a winter diet dominated by plant material to an animal-based diet with high protein content during the breeding period (Lovette & Fitzpatrick, 2016). In many tropical regions, multiple food resources are available throughout the year, which has allowed tropical passerine birds to have a more specialised diet (Gill, 2007). The overall annual production and available prey biomass may not be higher, and the annual growth rate of plant biomass may even be lower (Thiollay, 1988). Tropical rain forests have strong seasonal fluctuation of fruit and insect production, and periods of food scarcity are often unpredictable in time and space (Thiollay, 1988). A study by Hails (1982) revealed the aerial insect biomass was ten times higher in temperate Scotland than in tropical Malaysia during the avian breeding period. Also, Thiollay (1988) reported that the abundance of understory arthropods was significantly lower in a tropical rain forest than in a temperate forest (Thiollay, 1988). Thiollay (1988) found that for small foliage gleaners, the most abundant insectivorous birds, temperate species had lower variance in foraging success than tropical species of similar size. Also, a study by Marcotullio and Gill (1985) showed that the tropical chestnut-backed antbird (*Myrmeciza excul*), spent 90% of the daily time budget on foraging activity, which indicates that tropical passerines spend much time foraging.

Although both temperate and tropical passerine species may be energetically restricted during their breeding period, the shorter breeding period of temperate species, and more seasonal variable environments might result in temperate species invest more in current reproductive events. Therefore, the effect of foraging ecology on the scheduling of dawn singers might be stronger in temperate than in tropical areas.

3. When do dawn singing passerines start their foraging activity?

The end of dawn song has received less attention in dawn chorus research compared to the onset of dawn song (Catchpole & Slater, 2008; Dominoni *et al.*, 2016). The onset, duration and end time of dawn song have been measured for five temperate passerine species included in our database (Figure 3.1). We here define early-singing species as species that starting their dawn song before the solar altitude is -6 degrees, and late-singing species when the solar altitude is -6 degrees or above.

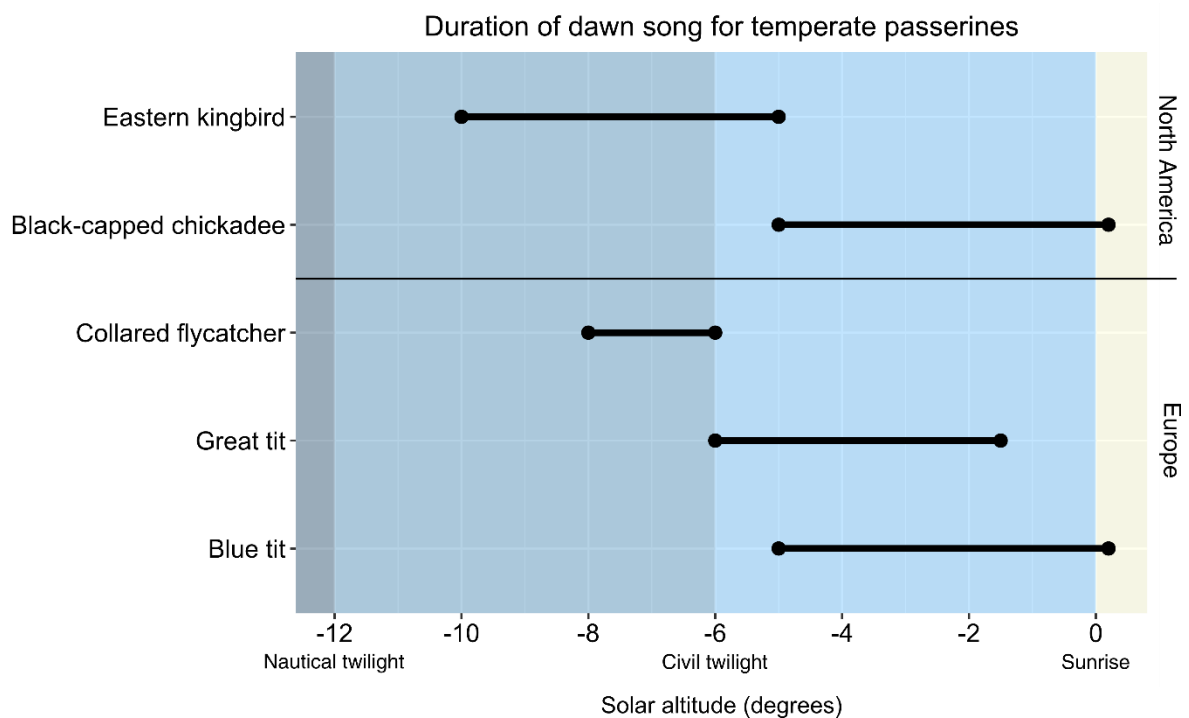


Figure 3.1: Start time, end time and duration of dawn song for 5 temperate passerines: the eastern kingbird (*Tyrannus tyrannus*), the black-capped chickadee (*Poecile atricapillus*), collared flycatcher (*Ficedula albicollis*), great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*), given in solar altitude (degrees). Results divided into two areas: North America and Europe (for more details, see Table A1.2, Appendix 1).

The average duration of dawn song for the five temperate passerines are all in the same range, from 25 minutes to over 45 minutes. According to Ross Lein (2007), individual dawn song lasts for 20-60 minutes, with early-singing species, such as the European robins (*Erithacus rubecula*) and the blackbirds (*Turdus merula*) are falling silent when late-singing species, such as the blue tits, and the chaffinches (*Fringilla coelebs*), start to sing (Thomas *et al.*, 2002). Although there is interspecific variation, early-singing species will on average end their dawn song earlier than late-singing species. We can hence assume that onset of foraging will follow approximately the same order as the onset of dawn song for passerine species.

4. Is the scheduling of dawn song affected by energetic constraints early in the morning?

According to the *unpredictable conditions hypothesis* (Kroodsma, 1996), birds build fat reserves to avoid starvation during nights with low temperatures, as they must use more energy to maintain body temperature. Since most nights are not this cold, males often have surplus fat reserves which can be used to cover the energetic costs required for dawn song production prior to foraging in the morning (Kroodsma, 1996; Thomas & Cuthill, 2002). A study on European robins supports this thesis, showing that birds lost more mass during cold nights, and sang more at dawn when they had more reserves left (Thomas & Cuthill, 2002). Several studies on temperate passerines have revealed that short-term food supplemented males sang earlier or had higher dawn song output (Cuthill & Macdonald, 1990; Barnett & Briskie, 2007; Grava *et al.*, 2009). In contrast, Saggese *et al.* (2011) found that supplemented feeding of wild great tits (*Parus major*) delayed the onset of dawn song, with a possible explanation being the presence of predators at the feeding locations.

As the weather conditions (e.g. temperature and precipitation) vary more in temperate regions than in the tropical regions, it is assumed that temperate birds need to build up more fat reserves than tropical birds (Lovette & Fitzpatrick, 2016). Small temperate passerines generally lose 5-10% of their total body mass overnight (Thomas & Cuthill, 2002), whereas small tropical passerines only maintain 5% of body mass as fat reserves (Gill, 2007). Temperate passerines build up more reserves than tropical passerines, but since the twilight period is longer at higher latitude (Kroodsma, 1996), it is possible that all surplus energy is used for dawn song in both cases.

Metabolic rates scale allometrically, and smaller birds require bigger energy reserves relative to their body mass than larger bird species. Larger bird species can generally store more fat reserves and fast longer than smaller bird species (Gill, 2007). A higher risk of overnight starvation in smaller bird species would favour an earlier start of the day, and therefore an earlier onset of the dawn song (Thomas & Cuthill, 2002). To test whether body mass is linked to the onset of dawn-singing, I collected the average body masses of passerine species with known onset of dawn song (Figure 4.1). A statistical analysis, including all geographical areas, revealed no significant relationship between body mass and onset of dawn song ($F_{1,122}=0,1911$, $n=124$, $p= 0.663$). Thus, no supporting the prediction that smaller birds start their dawn song earlier due to energetic constraints was found. Note however, that in a study of temperate passerines Thomas *et al.* (2002) found that smaller birds started to sing earlier than larger birds with equivalent eye size.

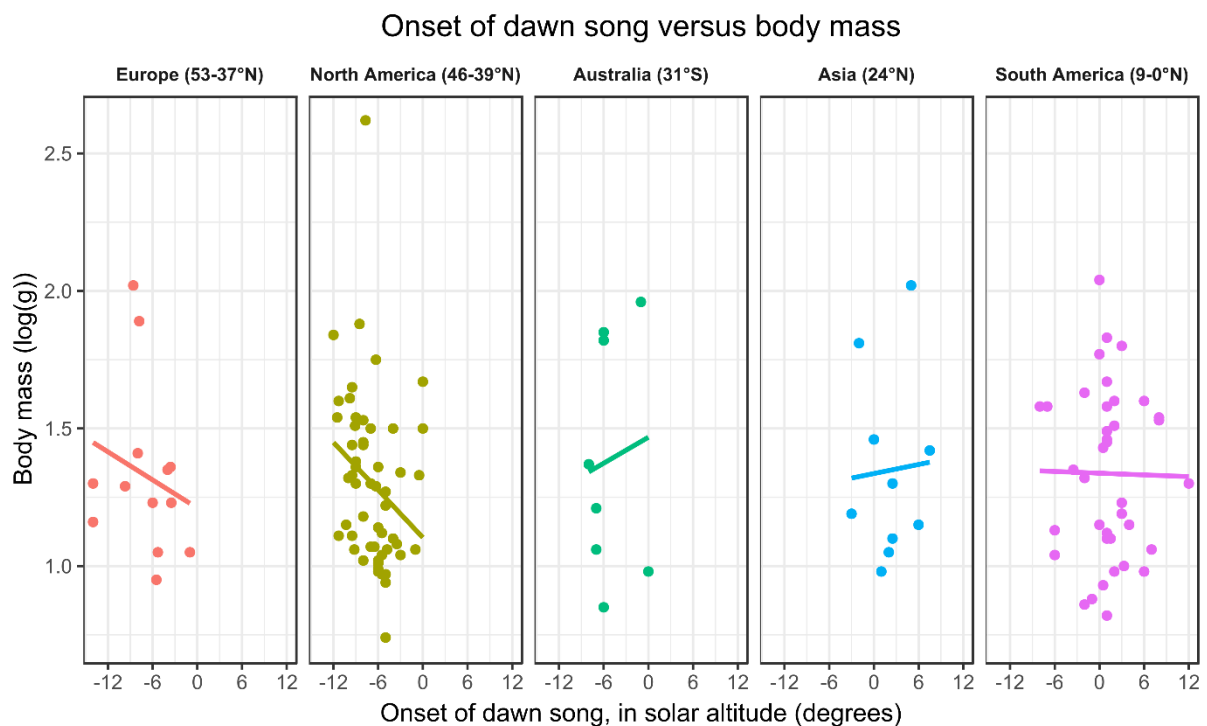


Figure 4.1: Body mass (log(g)) for passerine species with respect to the onset of dawn song (given in solar altitude). Body mass is based on species-specific average body mass from literature, average onset of dawn song is from the studies listed in Table A1.1 (Appendix 1). The studies are divided into five geographical regions, with latitudinal range of each areas as indicated.

5. Which factors determine when foraging becomes profitable in the morning?

The inefficient foraging hypothesis suggests that the timing of dawn song is related to light availability, and that insufficient light levels for foraging at dawn can be adequate for social communication (Kacelnik & Krebs, 1982; Kroodsma, 1996). The hypothesis is supported by Kacelnik (1979), which found that captive great tits usually ended their dawn song at light intensities where foraging became profitable. At what time foraging becomes profitable possibly varies for different bird species, and could depend on factors such as visual constraints, diet choice, prey availability, foraging techniques and predation risk. I will discuss each factor in the following:

Predation risk

The main cause of mortality of passerine birds is predation by small avian predators (Møller *et al.*, 2006). Predation risk depends on which predator species are present in the area, and the amount of light needed by the predator to detect prey (Møller *et al.*, 2008). Diurnal and nocturnal predators could potentially overlap at dawn, and increase the risk for passerine birds (Kroodsma, 1996). However, Netteland (2018) argued that the predation risk of passerine birds could be lower during the twilight period, as neither diurnal nor nocturnal birds of prey have optimal foraging conditions during twilight. Both diurnal and nocturnal birds of prey experience relatively short detection distances during dawn, while the dawn song post and visual acuity of passerine birds during dawn may allow them to detect predators from greater distances. Netteland (2018) claimed that these factors could create a temporal window of opportunity during nautical and civil twilight, with reduced predation risk for passerine birds. The temporal placement and duration of the temporal window of opportunity is partly determined by the visual capacity of passerine birds, which is linked to differences in foraging strategies (see Netteland (2018)).

Visual capacity of birds at low light levels

Birds are highly visual animals, with well-developed colour discrimination and movement detection capabilities (Hart, 2001; Gill, 2007). There is a great diversity of avian

visual adaptations (Pollard, 2009), and the specialisation in eye morphology affects how early birds can start their morning activity. As light intensity gradually increases during dawn, the predictable order in which species join the dawn chorus may be linked to the species' visual capability (Lovette & Fitzpatrick, 2016). According to this hypothesis, a bird will not start to sing before the light level is sufficient to, for example, detect predators and potential mates (Lovette & Fitzpatrick, 2016). Kacelnik (1979) found that the foraging efficiency of captive great tits hunting for cryptic prey was reduced at low light intensities, characteristic of the early morning.

The retina of birds contains rods and cones, which are light sensitive photoreceptor cells that transmit signals to the brain (Lovette & Fitzpatrick, 2016). Rods and cones differ in their physiological properties (Randall *et al.*, 2002), with rods facilitate monochromatic vision in low light conditions (Lovette & Fitzpatrick, 2016), and cones function best in bright light, and provide high resolution (Randall *et al.*, 2002). Diurnal passerines usually have more cones than rods, while the opposite is normal for nocturnal birds (McNeil *et al.*, 2005).

Eye size has important consequences for two main aspects of the visual capability of birds: visual resolution and visual sensitivity (Ritland, 1982). Visual sensitivity is the eye's ability to obtain visual information by capturing and processing light (Pollard, 2009), while eyes with greater visual resolution can see environment in greater detail (Land & Nilsson, 2012). Visual resolution can be improved by larger focal length, increased diameter of the retina, higher density of photoreceptor cells on the retina, increased pupil aperture, and by how the photoreceptor cells are connected to the next neurons (Garamszegi *et al.*, 2002; Randall *et al.*, 2002; Pollard, 2009; Land & Nilsson, 2012). A long focal length is especially important for birds that capture actively moving prey, as they need high resolution power, and for nocturnal species which need good vision in dim light (Garamszegi *et al.*, 2002). Since the photoreceptors of birds have a near-constant size, larger retinas generally contain more photoreceptor cells than smaller retinas (Thomas *et al.*, 2002; Hall & Ross, 2007). The resolution increases with the photoreceptor density, as the density determines how many receptors participate in the sampling of an image projected onto a given area of the retina (Thomas *et al.*, 2002; Pollard, 2009). If the retinal anatomy is the same, larger eyes provide a higher resolution (Dolan & Fernández-Juricic, 2010).

Improved visual resolution or sensitivity generally requires increased eye size (Land & Nilsson, 2012), which is particularly important during low light intensities at dawn. Increased

visual sensitivity can be achieved by increased pupil diameter, increased angular range from which each receptor accepts light, and high rod densities (Pollard, 2009; Land & Nilsson, 2012). For species being active at different light intensities, there is a trade-off between high resolution in daylight, and high sensitivity at night (Land & Nilsson, 2012). The trade-off has been solved by many vertebrates by spatial summation, which provide a flexible solution, since the size of the “receptor pool” can vary according to the light levels, and the small receptors form larger groups under low light intensities (Land & Nilsson, 2012).

According to the factors mentioned above, earlier-singing bird species are predicted to have larger eyes than late-singing bird species. The relative size of an organ could tell something about its functional significance, therefore, eye size relative to body mass (RES) may reflect the importance of vision (Ritland, 1982; Howland *et al.*, 2004). RES has been included in a few dawn song studies, which find a positive correlation between relative eyes size and early-singing species in both temperate and tropical dawn choruses (Thomas *et al.*, 2002; Berg *et al.*, 2006). In a layered forest, RES predicts the species-specific sequence of dawn singers at each layer (Berg *et al.*, 2006). The opposite trend was found in a study of a tropical dawn chorus in Taiwan, where Chen *et al.* (2015), found that earlier-singing species had smaller RES than later-singing species.

In this thesis, data collected for the onset of dawn song participation in choruses around the world has been combined with morphological eye data (Figure 5.1). RES was found to be significantly smaller for early-singing species than for late-singing species ($F_{1,109}=6.621$, $n=105$, $p= 0.011$, $slope=2.864$). This effect could be driven by differences in foraging heights among birds in the tropical Asian and South American choruses (Figure 5.1), but sample size did not allow for testing the effect of forest layering (for statistics, see Appendix 1). In temperate forests, a separate test including Europe, North America and Australia, showed no significant relationship between RES for early-singing and late-singing species ($F_{1,65}=0.016$, $n=67$, $p= 0.901$).

Relative eye size (RES) versus the onset of dawn song

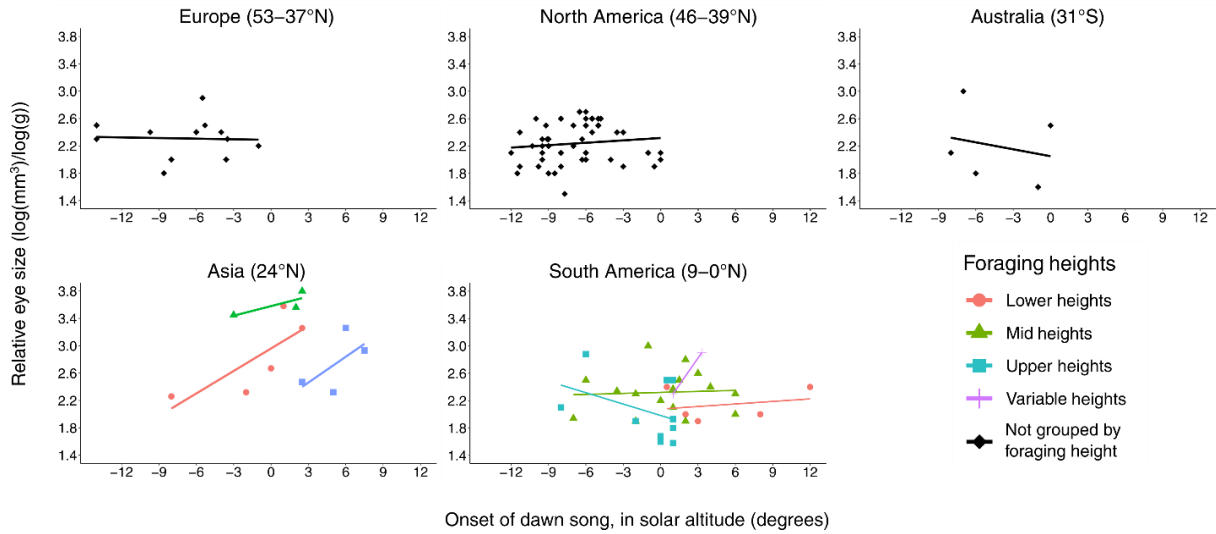


Figure 5.1: Relative eye size (RES) ($\log(\text{mm}^3)/\log(\text{g})$) of passerine species participating in the dawn chorus versus the onset of dawn song in solar altitude (degrees). The dawn choruses are divided into five different areas: Europe, North America, Australia, Asia and South America. The onset of dawn chorus is collected from several studies, included in Table A1.1 in Appendix 1. RES is calculated using Eq. 2 in Appendix 2. For the layered forests of Asia and South America, RES considered within each foraging heights, but, for Europe, North America and Australia, RES is not divided into different foraging heights. For more details, see Appendix 2.

An absolute larger eye has increased ability to resolve images, and hence higher visual resolution, regardless of body size (Hall & Heesy, 2011). Large animals which have large eyes potentially have more visual resolution and sensitivity than small animals with small eyes (Hall & Ross, 2007). I have therefore also calculated the absolute eye size (AES, see Eq. 2, Appendix 2), which is the volume of the eye in $\log(\text{mm}^3)$, and compared it with onset of dawn song (Figure 5.2). While RES values for Asian birds were reported by Chen *et al.* (2015), neither AES nor body mass data are available. Therefore, AES has been calculated only for the Asian species included in Ritland (1982). By performing a statistical analysis of AES in relation to onset of dawn song for all areas, I found no significant trend ($F_{1,103}=0.124$, $n=105$, $p=0.725$). In order to exclude confounding effects of layering in tropical forests, an analysis including only the temperate forests was performed showing a significant negative relationship between AES and song onset ($F_{1,65}=6.527$, $n=67$, $p=0.013$, $\text{slope}=-3.366$) (details in Appendix 1).

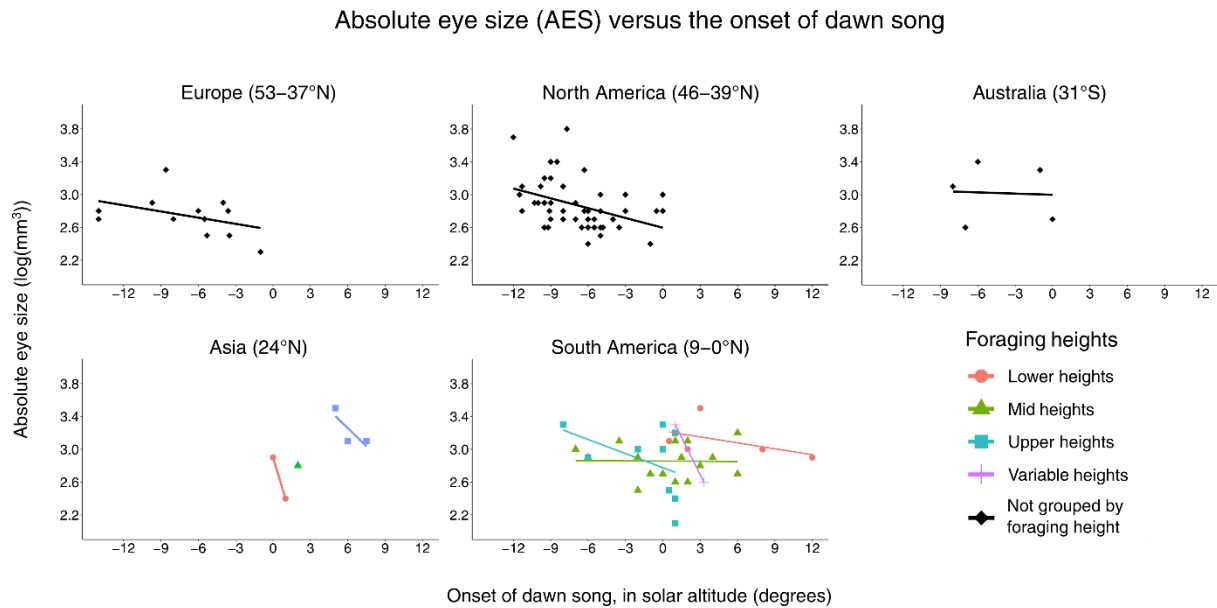


Figure 5.2: Absolute eye size (AES) ($\log(\text{mm}^3)$) of passerine birds participating in the dawn chorus versus the onset of dawn song in solar altitude (degrees). The dawn choruses are divided into five different areas: Europe, North America, Australia, Asia and South America. The onset of dawn chorus is collected from several studies, included in Table A1.1 in Appendix 1. The AES is calculated using Eq. 1 in Appendix 2, given in $\log(\text{eye volume } (\text{mm}^3))$. For the layered forests of Asia and South America, AES is divided into foraging heights. For more information, see Appendix 2.

Other features of the vision of birds not directly related to eye size can also contribute to enhanced foraging profitability and predation detection at low light intensities. Such features include spectral sensitivity, different types of oil droplets and the abundance and arrangement of retinal mosaic of different photoreceptor types (Hart, 2001; Honkavaara *et al.*, 2002; Gill, 2007).

For different bird species, the movement-sensitive double cones differ in relative abundance, retinal distribution and spectral absorption properties (Hart *et al.*, 2000). Ground foraging passerines, such as the blackbird, which is an early dawn-singing species (Table S2, Supplementary material), must be able to detect and avoid aerial predators while foraging in open areas, and at the same time detect food at short distances. Their eyes show a trade-off in retinal topography. Their ventral half of the retinae, which views the sky, has a much higher proportion of movement-sensitive double cones than the dorsal half, which views the ground (Hart *et al.*, 2000). The blackbirds therefore have both the ability to detect predators at great distances, with higher visual resolution, and detect prey on the forest floor, which needs less visual resolution. This specialisation may partly explain why blackbirds are early singers in the dawn chorus, and have good vision in dim light. The retinae of arboreal foraging passerines, such as the blue tits, show the opposite trend in double cone distribution (Hart *et*

al., 2000). The blue tits are late singers in the dawn chorus (Table S2, Supplementary material), and spends up to 44% of its time hanging upside down while inspecting the underside of leaves for prey, which leaves the blue tits less exposed while they feeds among foliage. They do not need the same distance to detect predators, and their eyes may not have the same high visual acuity as the blackbirds, which may partly explain why blue tits are late singers in the dawn chorus.

The spectral sensitivity of birds also affects their visual capability (Hart, 2001). Ultraviolet (UV) sensitivity seems to be common among birds (Church *et al.*, 1998). It is the fourth cone type in birds that allows them to distinguish light near the UV (320-400 nm) as a distinct colour. UV cues are widely used by birds in communication (e.g. sexual signalling), mate choice, egg recognition, nestling discrimination and foraging (Aidala *et al.*, 2012). Birds differ in their UV sensitivity (Honkavaara *et al.*, 2002). The colour vision of birds can be divided into two classes: violet sensitive (VS), which have maximal sensitivity less than 400 nm, and ultraviolet sensitive (UVS), which have maximal sensitivity above 400 nm (Ödeen & Håstad, 2003; Aidala *et al.*, 2012). VS vision is dominating among birds, but the orders Psittaciformes and Passeriformes have many bird species with UVS (Ödeen & Håstad, 2003). UV cues of the light environment may affect foraging behaviour of diurnal birds, since UV cues may make it easier to detect UV-reflecting prey (Honkavaara *et al.*, 2002; Lyytinen *et al.*, 2004). Differences in UV sensitivity among birds means that prey may be cryptic to some birds, but aposematic to others (Honkavaara *et al.*, 2002). Some fruits, berries and petals of flowers are covered by a waxy coating reflecting UV light, which can be detected by UVS birds (Burkhardt, 1982; Honkavaara *et al.*, 2002). A study by Church *et al.* (1998) found that blue tits detected cryptic lepidopteran caterpillars more quickly in the presence of UV light. UV-reflecting prey may be more visible to UVS bird species in the UV rich light at dawn and give these birds higher foraging profitability during dawn than less UVS bird species. Differences in UV sensitivity could therefore be a factor explaining why some bird species start dawn-singing earlier than others.

In summary, visual capability at low light levels affects the scheduling of dawn singers and foragers in the morning. From the above, I predict that flycatching birds with the visual capability to detect active flying prey in dim light, and substrate-gleaning birds with the visual capability to detect active nocturnal or inactive diurnal prey on the substrate are among the earliest foragers in the morning, and among the earliest dawn singers.

Dietary trends

For optimal foraging, a bird should adjust its foraging behaviour in response to prey availability (Lemon, 1993). The availability of prey species has a non-uniform temporal and spatial distribution (Pyke *et al.*, 1977; Hutto, 1981), and could be available at different times and places for birds with different foraging specialisations. Animal prey species taken by passerine birds during the breeding period include nocturnal, crepuscular and diurnal species (Table A2.1, Appendix 2). Based on this, I predict that bird species that have the adaptations to prey on nocturnal or crepuscular prey species during dawn are predicted to start foraging activity, and hence dawn song, early.

Many prey species use detection avoidance strategies that can make them unavailable for birds, such as hiding under rocks or burrowing into the substrate. Several of these species have nocturnal or crepuscular activity, and are therefore available when they are active during dawn. For example, the temperate earthworm (*Lubricus terrestris*, Oligochaeta) is nocturnal. During day, it retreats into soil, and becomes unavailable for birds (Laverack, 1963).

The flight of insects is periodic, and they only fly for a limited period of the day (Lewis & Taylor, 1965). Light intensity determines the time insects start their flight activity. Differences in visual efficiency for different flying insect species therefore decide how early they can start their flying activity in the morning. Insect species that seem to lack defensive traits may minimize the predation risk by concentrating their flight activity to dusk and dawn (Malmqvist 2018). Species that show this type of crepuscular activity include mosquitoes and midges (Diptera), moths (Lepidoptera) and bugs (Hemiptera) (Malmqvist *et al.*, 2018). Many of these species use detection avoidance strategies when they are inactive during day, such as cryptic colour patterns, or hide at the underside of leaves (Gill, 2007; Davies *et al.*, 2012).

Many earthworms become inactive during dry weather, and retreat deeper into the soil (Snow, 1958). During dawn, there is greater humidity (Gill, 2007), and many earthworm species could therefore be active during this period. Snails and slugs need moisture in their surroundings to be active. They to emerge from their hiding places at night, and have increased activity at dusk and dawn, probably caused by the increased relative humidity as the temperature drops (Sturm *et al.*, 2006).

Plant resources are available both day and night, at the same location. The availability of plant material in temperate areas is more seasonally variable, and many passerine species

switch to a more animal-based diet during the short breeding period, while a few species mainly eat plant material throughout the year.

According to the information given above, it could be advantageous for some prey species to become active at dawn, dusk or during night, when the temperatures are below the lethal limit, greater humidity reduces the rate of water loss through the cuticle, and predation risk is reduced (Gill, 2007). Nocturnal and crepuscular non-flying and flying prey species could possibly be active during dawn. If dawn-singing birds start their foraging activity before sunrise, they might prey on these species. Figure 5.3 presents the dietary trends of passerine birds participating at different times (solar altitudes) of the dawn chorus, in different areas.

Temperate areas

In Europe and North America, nocturnal non-flying prey, nocturnal flying prey and gastropods form a greater amount of the diet for early-singing birds than for late-singing birds. Various active prey are taken by both early- and late-singing birds. In Europe, one early- and two late-singing herbivore species take plant material. The diet of early-singing birds in North America consists of less than 10% plant material, while 4 out of 7 late-singing birds include 75-100% plant material in their diet. As a result, herbivore species (75% > plant material) sing late. The dietary trends of Europe and North America is as we predicted. However, the dietary trends of Australia contradict with our expectations. Nocturnal non-flying prey, nocturnal flying prey, variously active prey and plant material are taken by both early- and late-singing species, and gastropods are only included in the diet of one late-singing species.

Tropical areas

In Asia and South America, there is not enough information to describe the dietary trends of many species, especially for the late-singing bird species. The predicted trend is partly observed for the available information. In Asia, nocturnal non-flying prey is mostly taken by early singers, but gastropods and plant material is taken by both early- and late-singing species. In South America, nocturnal non-flying prey and nocturnal flying prey are taken by both early- and late-singing species, which contradicts with the expectation. Plant material is taken by both early and late-singing species, but all herbivores are late singers, as in North America.

The onset of dawn song linked to dietary trends of passerine birds

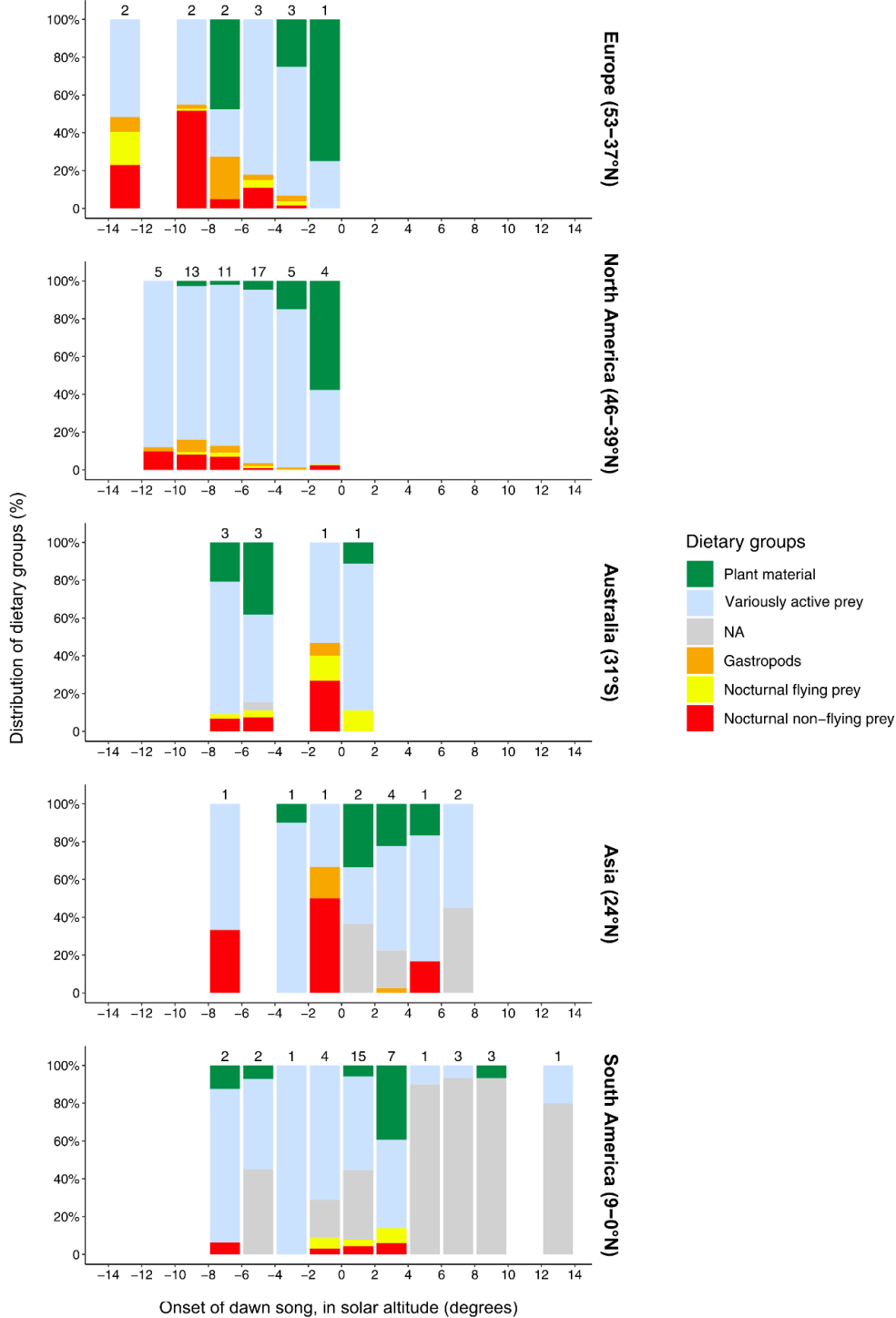


Figure 5.3: Stacked bar charts showing the dietary trends of passerine species participating in the dawn chorus, versus their onset of dawn song given in solar altitude (the degree of the sun below/over the horizon, where 0 degrees is sunrise). The dawn choruses are divided into five different areas: Europe, North America, Australia, Asia and South America. The numbers above the columns are the number of species starting to sing during the given period. The y-axis specify the fractional contribution (%) of each diet group, for birds which start to sing during a specified period. The prey orders are divided into categories; *Nocturnal non-flying prey*, *Nocturnal flying prey*, *Gastropods*, *Variesly active prey* and *Plant material*. For more details, and description of the categories, see Table A2.1, Appendix 2.

Prey attack manoeuvres

Prey attack manoeuvres of birds are adapted to the prey species they encounter (Holmes & Robinson, 1988). The increased ability to detect, capture and handle one specific type of prey often limits the ability to use other types of resources. For example, specialised substrate-gleaning birds are limited to prey species that are available on substrate, either non-flyers or inactive flyers, while specialised flycatching birds are limited to catch flying prey in air. Ground-gleaning birds that probe in decaying matter at the forest floor may prey on other species of non-flying insects than tree-gleaning birds which glean prey from tree stems and leaves higher in the canopy. Prey attack manoeuvres may affect the temporal foraging profitability of birds. In North America, foliage-gleaning birds are primarily dependent on the availability of inactive flying insects, which decreases during midday, resulting in less profitable foraging activity for foliage-gleaning birds (Hutto, 1981). Foliage-gleaning birds may have profitable foraging during dawn, when many diurnal flying insects are inactive on leaves. Foraging activity of small passerine birds with the same foraging specialisations can also differ between temperate and tropical areas, despite their similarities in size, morphology, ecology and behaviour. Tropical foliage-gleaning passerines use more energetically expensive capture modes, such as probing, striking and sallying, and have a larger foraging niche breadth than temperate gleaning passerines (Thiollay, 1988).

Temperate areas

In North America, the earliest-singing species are dominated by flycatchers and substrate gleaners (Figure 5.4). Bird species using both techniques are most plentiful in the middle of the chorus, and there is a late peak of substrate gleaners. A similar trend is shown for the few species in Europe, where the earliest singers use both techniques, and therefore have the ability to flycatch. Among the few species in Australia, there is one very early and one very late substrate gleaner, while the rest of the birds use both techniques.

Tropical areas

Interestingly, the layered tropical forests of Asia and South America show opposite trends. The early singers of the Asian dawn chorus are all substrate gleaners, while the late singers include some that use both techniques and a flycatcher. In contrast, flycatchers in South America are among the early singers, such as in North America, and most of the substrate gleaners are late-singing species.

The onset of dawn song linked to prey attack manoeuvre groups of passerine birds

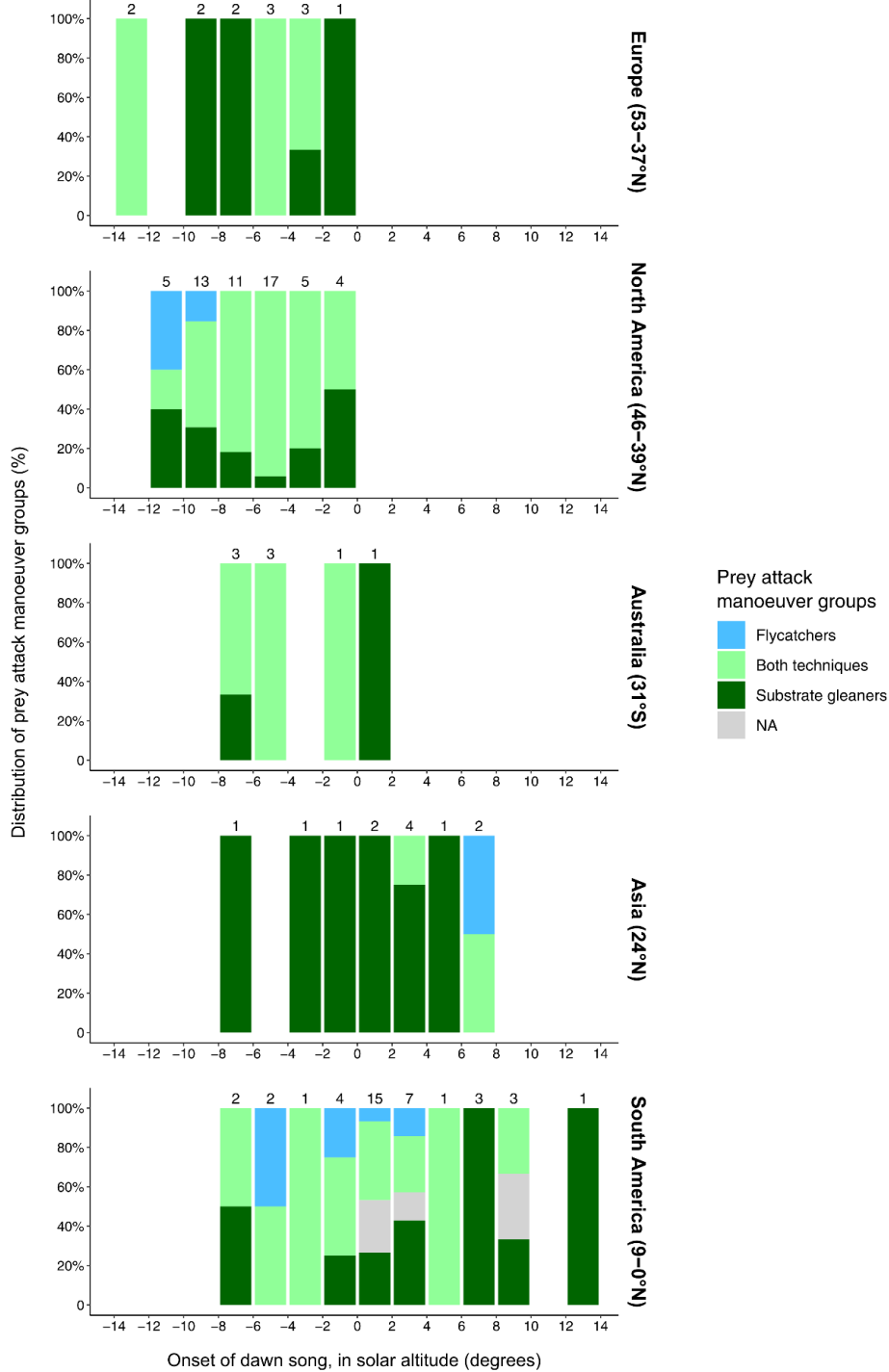


Figure 5.4: Stacked bar charts showing the prey attack manoeuvre groups of passerine species participating in the dawn chorus, versus their onset of dawn song given in solar altitude. The dawn choruses are divided into five different areas: Europe, North America, Australia, Asia and South America. The numbers above the columns are the number of species starting to sing during the given period. The y-axis specifies the fractional contribution (%) of each prey attack manoeuvre group for birds which start to sing during a specified period. The prey attack manoeuvre groups are *flycatchers*, which includes bird species that only catch flying prey in air, *substrate gleaners*, which only catch non-flying prey while standing on substrate, and *both techniques* which use both substrate-gleaning and flycatching techniques. For more details, and descriptions of the groups, see Table 2.2, Appendix 2.

Foraging heights

For birds, vegetation structure affects the distribution and availability of prey species, determines the patterns of locomotion and foraging behaviour, and provides both constraints and opportunities for successful prey search, detection and capture (Robinson & Holmes, 1982). For example, the number and arrangement of leaves along branches partly determines how many leaves can be searched per unit time, and how easily the prey species can be detected and captured. Many birds have species-specific foraging heights, while some are foraging in variable heights. In a study by Chen *et al.* (2015), species foraging at mid heights showed a greater variation in their onset of dawn song than other species foraging at lower or upper heights. The study suggests species foraging at mid heights presumably have a greater behavioural or visual flexibility, since they have a greater chance to explore both upwards and downwards.

Temperate areas

As seen in Figure 5.5, the North American and European choruses show a similar trend. There is an early and one late peak of bird species foraging at lower heights, and some of the earliest-singing species are foraging in mid and upper heights in North America, and mid heights in Europe. Bird species foraging at variable heights are in the middle of the chorus. For the few bird species of Australia, there is no trend for foraging heights.

Tropical areas

In Asia, most of the early-singing birds forage at lower and mid heights. This trend lasts until the solar altitude has reached 2 degrees above the horizon. Most late-singing bird species are foraging at upper heights. The opposite trend is found in South America, early-singing species are mostly foraging at upper and mid heights, while late-singing species are mostly foraging at mid and lower heights.

The onset of dawn song linked to foraging heights of passerine birds

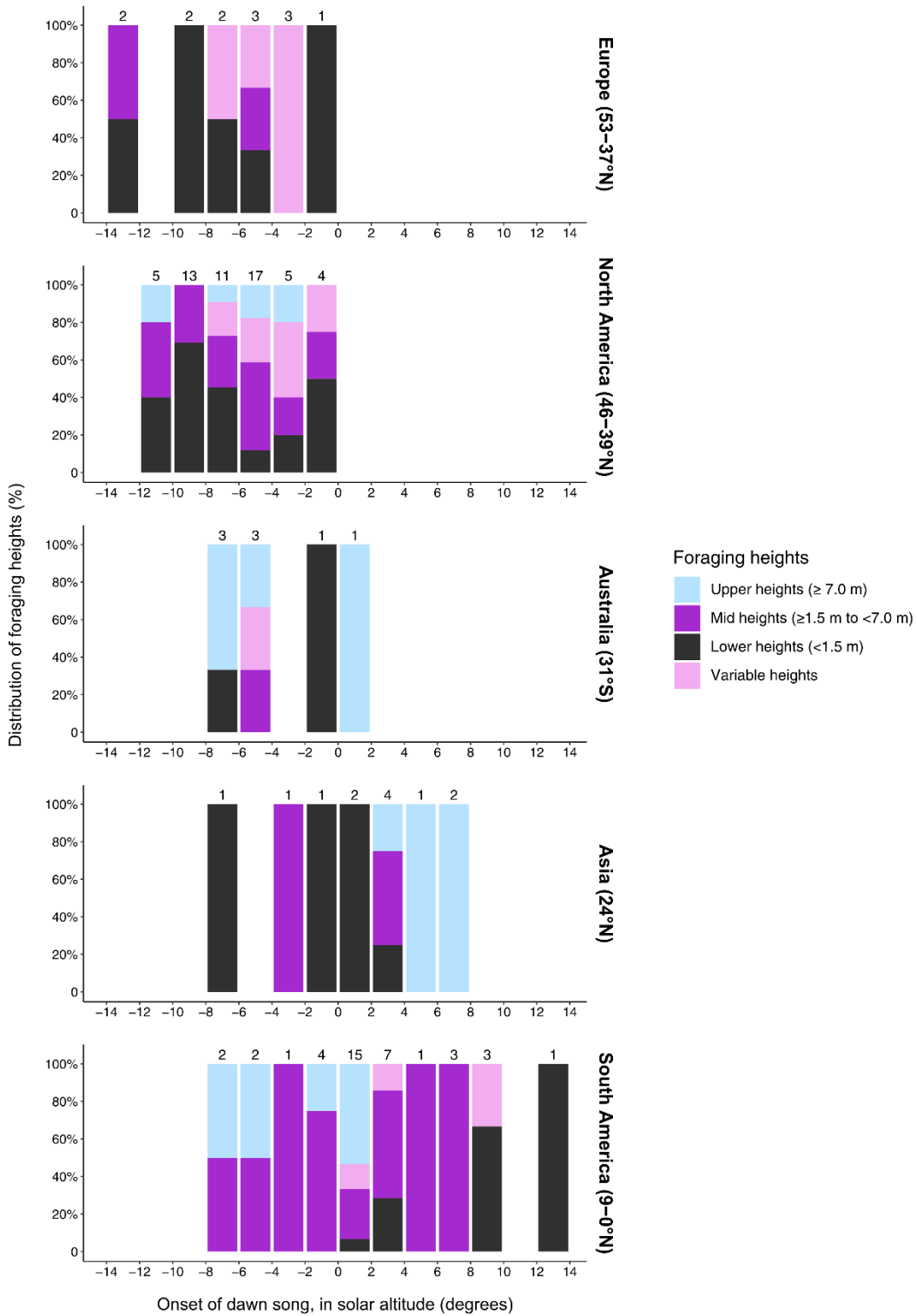


Figure 5.5: Stacked bar charts showing the foraging heights of passerine species participating in the dawn chorus, versus their onset of dawn song given in solar altitude. The dawn choruses are divided into five different areas: Europe, North America, Australia, Asia and South America. The numbers above the columns are the number of species starting to sing during the given period. The y-axis specifies the fractional contribution (%) of each foraging height, for birds which start to sing during a specified period. The foraging heights are divided into *lower heights*, *mid heights*, *upper heights* and *variable heights*. For more details, see Appendix 2.

6. How is eye size, dietary trends, prey attack manoeuvres and foraging heights linked to the scheduling of dawn song?

Temperate areas

The differences in absolute eye size, dietary trends, prey attack manoeuvres and foraging heights for early- and late-singing European and North American birds reveal that early-singing birds could take advantage of the nocturnal active prey species available during dawn, have the ability to catch them, and therefore start profitable foraging during dawn. Among the earliest-singing birds in North America, there are four flycatchers, which are foraging at mid heights. Their diet is dominated (80-100%) by variously active prey. This is logical, since various active prey is the only group that include diurnal flying prey. However, the various active prey group also includes nocturnal flying prey, and it is therefore possible that they take these nocturnal flying prey species before sunrise. Nocturnal flying prey constitutes ~20% the diet of one of the species. In Europe, the earliest-singing species take nocturnal non-flyers, nocturnal flyers and gastropods and are foraging at mid and lower layers and use both prey techniques. Therefore, they have the ability to both flycatch nocturnal flying prey and glean for nocturnal non-flying prey and gastropods during dawn. The rest of the early-singing species are substrate-gleaning birds, foraging at lower and variable layers, and include the bird species with the highest content of nocturnal non-flying prey and gastropods in their diet. The three North American and two European late-singing species which have nocturnal flyers included in their diets are all foraging in variable layers, using both foraging techniques. The nocturnal flyers they prey on are inactive on leaves or in litter during day, and are therefore available for the birds during day. Among the late-singing substrate gleaners in North America, only one bird species takes a small amount of nocturnal non-flying prey, and one bird species takes a small amount of gastropods. Plant material dominates the rest of these two bird species' diet. Therefore, it is possible that these two species eat millipedes and gastropods as a by-product. Plant material is mostly taken by late-singing birds which use substrate-gleaning or both techniques, and are foraging at variable or mid heights.

The foraging height and dietary trends of the few Australian birds contradict the trends found in North America and Europe. Not all early-singing birds with nocturnal prey included in their diet seem to have the ability to catch them during dawn. The early-singing species with nocturnal flying prey in its diet is a substrate gleaner foraging at lower heights, and

presumably do not take nocturnal flyers when they are flying at dawn, as it is not a flycatcher. However, it could catch nocturnal flyers when they are available on the substrate during day. One important difference in the dietary trends of the Australian birds, when compared to other areas, is that all, except one species, feed on nectar and manna, which is a sugary exudate from damaged eucalypt leaves or wood (Gartrell, 2000). Nectar and manna is one of the possible reasons for why both early- and late-singing Australian species take plant material.

Tropical areas

Interestingly, the tropical layered forests of Asia and South America have the opposite trend in foraging heights and prey attack manoeuvres. In South America, early-singing birds are flycatchers or use both techniques, and are foraging at upper or mid heights, while in Asia they are substrate gleaners foraging at lower heights. Late-singing birds in South America are substrate gleaners foraging at lower heights, while late-singing birds of Asia are using all techniques, and are foraging at upper heights. The flycatchers of South America are early singers, while the flycatcher in Asia is the latest participant in the dawn chorus. While the layered tropical forest of Ecuador is more than 25 meters high (Berg *et al.*, 2006), the height of the canopy of the tropical forest of Taiwan, where all the Asian species included in this study breeds, is only 12 meters (Chen *et al.*, 2015). Therefore, it is possible that the Asian forest is not as layered as expected, and that light does not attenuate as much between the canopy and the forest floor as in the South American forest. This could partly explain the contradicting trends in foraging heights and prey attack manoeuvres between the Asian and South American choruses. The trends in foraging heights and prey attack manoeuvre of Asian birds are similar to the trends of the non-layered forests of Europe, and partly North America, with exception of the early flycatching birds.

Another interesting difference between the Asian and the South American dawn choruses is that the Asian dawn chorus only includes oscine species, while the South American chorus includes 33% oscines and 67% suboscine species. There is a confirmed ultraviolet sensitivity (UVS) in most oscine lineages, while violet sensitivity (VS) is confirmed in the oscine family Corvidae, and in two suboscine families, Tyrannidae and Pipridae (Ödeen & Håstad, 2003; Aidala *et al.*, 2012). All early-singing South American passerine birds are suboscines, while in Asia, the early-singing are oscines, belonging to the same superfamilies as the early singers in Europe (Muscicapoidea and Sylviodea) where UVS has been confirmed in several families (Ödeen & Håstad, 2003; Aidala *et al.*, 2012). In

addition, the Asian chorus consist of one late-singing species from the family Corvidae, which might be VS sensitive. Therefore, early-singing birds seem to be UVS, while late-singing species could be VS. If the Asian forest is not as layered as expected, it is likely that the early-singing UVS bird species have foraging profitability caused by the advantage of using UV cues when foraging during dawn.

In Asia, early-singing birds have smaller RES than late-singing birds, both when the RES values are divided into foraging heights (Figure 5.1), and when they are not divided into foraging heights. In addition, from the limited data available, early-singing birds have larger AES when the AES values are divided into foraging heights (Figure 5.2), but smaller AES when the AES values are not divided into foraging heights. The earliest-singing bird in the Asian chorus, the Taiwan whistling thrush (*Myophonus insularis*) and the early-singing European robin are both in the family Muscicapidae, which has confirmed UVS. They have approximately the same RES (2.3 and 2.4). When comparing early-singing birds of Asia and Europe from Musciapoidea and Sylviodea, the RES and AES are within the same range, and approximately the same size. For early-singing birds from Musciapoidea, RES ranges from 1.8-2.4 in Europe, and is 2.3 in Asia. For the birds in Sylviodea, RES ranges from 2.3-2.4 in Europe, and 2.3-3.5 in Asia. AES is only available for one early-singing species of the Asian chorus, the streak-breasted scimitar-babbler (*Pomatorhinus ruficollis*) from Sylviodea. Its AES is 2.9, which is approximately the same as the AES for the two early-singing birds of Europe, which belong to the same superfamily, the Eurasian blackcap (*Sylvia atricapilla*) and the great tit, which both have an AES of 2.8. In conclusion, even though both RES and AES of the early-singing Asian birds are smaller than for late-singing birds, they are approximately the same size as early-singing birds of Europe, which they are more closely related to. For the late-singing Asian species belonging to the family Corvidae, which are assumed to only have VS vision, the RES is 2.3, which is approximately the same, and AES is 3.5, which is larger than for the oscine families. Birds with VS, and not UVS, might have compensated in other ways to achieve good vision, for example by specialisations that require larger eyes. The differences in VS and UVS vision could partly be an explanation for why late-singing birds from the family Corvidae in the Asian chorus have larger eyes than early-singing birds from Muscicapoidea and Sylviodea. The trend of early-singing species in Asia having smaller AES and RES than late-singing birds could be explained as a result of phylogenetic mixing, and inclusion of species from several families with phylogenetic differences in the chorus.

In the South American choruses, all of the early singers are suboscines. They are living in a dense tropical forest, where it is possibly not necessary to be UVS, since UV is absorbed by plants on its way down the forest column (as discussed in Question 1). Eye specialisations other than UVS vision could have been important in the evolution of suboscines, and they might have specialisations that also require increased eye size, and therefore better vision in dim light. Among the South American bird species included in this thesis, birds with larger AES sing the earliest both in upper and lower heights (Figure 5.2), and birds foraging at upper heights sing earlier than birds foraging at lower heights. These findings support the suggested hypothesis. Among the South American passerines studied by Berg *et al.* (2006), suboscine species sang earlier than oscine species, despite that they did not differ in RES, body mass or foraging height. According to Berg *et al.* (2006), suboscines and oscines could differ in their retinal sensitivity.

The differences between foraging heights and prey attack manoeuvres of Asian and South American birds could also partly be due to differences in the prey species available from the different orders, and the temporal and spatial differences in prey distribution. From the limited dietary information available, it is shown that among the bird species that prey on nocturnal non-flying prey, most of the South American birds using substrate-gleaning techniques are foraging in mid or upper heights, while most of the Asian birds are substrate-gleaners, foraging at lower heights. From the nocturnal non-flying prey group, both Asian and South American birds take centipedes (Chilopoda) and woodlice (Isopoda). Only South American birds prey on earwigs (Dermaptera) and millipedes (Diplopoda), while Asian birds are the only ones taking earthworms (Oligochaeta). In the tropical forests of Ecuador, partly decomposed organic matter, litter and humus accumulate and form a compact mat on the branches in the canopy layer (Freiberg & Freiberg 2000). Many of the prey species of birds act as decomposers in these compact mats, and are therefore available at mid and upper heights, and not only in litter on the forest floor. In the subtropical wet forests of Taiwan, soil animals of the orders Oligochaeta, Diplopoda, Isopoda and Gastropoda are important detritivores or litter fragmenters, and contribute significantly to litter decomposition at the forest floor (Hou 2005). Nocturnal non-flying prey is therefore available in the foraging heights of South American and Asian species that participate early in the chorus.

Conclusion: do foraging ecology influence scheduling of the dawn chorus?

One of the benefits of starting foraging early is more time for foraging activity during the day, and potentially more energy obtained. The surplus energy can be used to increase survival and reproduction, which ultimately results in higher fitness. Since the temperate bird species live in a more seasonal variable environment, have a shorter breeding period, and have to wait a whole year until next breeding chance (Chapter 2), they might do some extra effort in the current breeding period to gain some extra fitness (e.g. larger clutch size). Foraging start during civil twilight could therefore be more important for temperate than for tropical species. According to my results, early-singing temperate bird species end dawn song during civil twilight (Chapter 3), and possibly start their foraging activity during civil twilight, while late-singing species end dawn song after sunrise, and therefore start foraging activity after sunrise.

The thesis of Netteland (2018) claims that there could be a temporal window of opportunity during nautical and civil twilight with reduce predation risk for passerine birds. The temporal placement and duration of this window of opportunity is partly determined by the visual capacity of birds, which is linked to differences in foraging strategies. The reduced predation risk during nautical and civil twilight makes it beneficial for passerines to start their daily activity during dawn if they have the visual capacity to avoid predators and have efficient foraging activity in dim light. In temperate areas, early-singing species had significantly larger absolute eye size than late-singing bird species (Chapter 5). Therefore, early-singing species may have higher foraging profitability than late-singing species during dawn.

Birds with larger body mass sang earlier in Europe and North America (Figure 4.1), while no trend was found for tropical choruses (Chapter 4). Therefore, the scheduling of dawn singers does not seem to be decided by how energetically constrained species are after a long night. Disadvantages of feeding early in the morning are therefore more likely to be related to the availability of birds' diets rather than the physiological needs of the birds in temperate areas. Birds foraging during civil twilight can take advantage of energy rich nocturnal and crepuscular prey species that are difficult to catch for birds during day (Chapter 5). This suggest that foraging ecology is an important factor determining the scheduling of the dawn

chorus in temperate areas. However, the foraging ecology of passerines could only partly explain the scheduling of dawn singers in the tropical areas, South America and Asia. Other factors (e.g. broadcasting space and phylogenetic mixing) which possibly interfere with the results of this thesis, and affect the scheduling of dawn song in tropical areas, are discussed in **Broader implications**.

Broader implications

Previous studies have suggested several intrinsic, extrinsic and social factors (see Introduction) to explain the scheduling of passerine dawn singers. This thesis suggests that the foraging ecology of birds is an important factor determining the scheduling of dawn singers, with stronger trends in temperate than in tropical areas.

Several studies indicate that temperate passerine species start their dawn song earlier in response to artificial light and bright nights, and delay their dawn song on cloudy mornings (Miller, 2006; Kempenaers *et al.*, 2010; Bruni *et al.*, 2014; Da Silva *et al.*, 2014, but see Da Silva *et al.*, 2016). Differences in light sensitivity among birds have been suggested to be the reason why naturally early singers showed stronger plastic behavioural response to artificial light than late singers. In addition, early-singing birds sang earlier on mornings with higher temperatures, and later on mornings with precipitation (Bruni *et al.*, 2014). The results from this thesis suggest that the differences in foraging ecology of passerine birds could be a possible reason for the greater plasticity shown by early-singing species. The early singers with strong plasticity are the same species that this thesis suggests can start profitable foraging before sunrise. Therefore, it seems likely that the early singers' plastic timing of activity is linked to prey availability and foraging profitability. Artificial light and bright nights could alter the temporal and spatial distribution of crepuscular prey species, since many prey species have increased activity with increased light levels and temperature, and decreased activity during precipitation. Increased activity could make prey easier to detect, and increase the foraging profitability for early birds foraging before sunrise. Foraging could therefore be profitable earlier under these circumstances than during natural circumstances for early-singing birds. European robins, blackbirds and barn swallows, which all are early singers, have been observed hunting under artificial light during night (Outen, 2002).

The late-singing bird species with less plasticity are the same as the bird species this thesis suggests start foraging after sunrise. Their maintenance of the onset of dawn song may be an adaptive response to other factors, such as cost of sleep loss (Da Silva & Kempenaers, 2017) or predator risk, as they could be less adapted to detect predators under low light conditions. However, prey availability and foraging profitability could be an explanation for the maintenance of song onset, since their diurnal prey is not available before after sunrise,

and light intensities and temperatures during dawn do not directly affect the activity of the prey.

Vision is crucial for birds. However, other senses, such as audition and olfaction could affect the onset of dawn song and foraging activity, by affecting the detection of predators, prey and other birds. Thrushes (Turdidae) of Central America and antpittas (Grallariidae) of South America, have an acute sense of hearing, and can detect underground prey (Gill, 2007). All American thrushes included in this thesis, eastern bluebird (*Sialia sialis*), hermit thrush (*Catharus guttatus*), veery (*Catharus fuscescens*), swainson`s thrush (*Catharus swainsoni*), wood thrush (*Hylocichla mustelina*), and American robin (*Turdus migratorius*), are early singers in the dawn chorus, and are expected to start foraging activity during dawn. A study by Montgomerie and Weatherhead (1997) showed that the American robin found buried mealworms in the absence of visual, olfactory and vibrotactile cues, which suggests that it uses auditory cues when it locates prey. After the prey has been located by sound, the actual strike when catching the worm seems to be visually guided (Gill, 2007). It might be easier to detect worms by sound during dawn, when they are active higher in the soil column or on the substrate (Lee, 1985; Reece, 2011). Other prey sounds, such as moth larvae (Lepidoptera) chewing on leaves, or the dawn chorus of various insects, such as crickets and katydids (Orthoptera) and cicadas (Hemiptera) (Lang *et al.*, 2006; Stanley *et al.*, 2016), may also increase foraging profitability for birds during dawn. Species that can hunt by sound may experience increased foraging profitability during dawn, and therefore start dawn song early. In addition, the use of sound cues to detect predators could possibly decrease the predation risk during dawn.

Olfaction can possibly affect the scheduling of dawn singers, if early-singing species can use olfaction to enhance foraging profitability during dawn. Birds use olfaction for navigation, predation detection, intraspecific recognition and foraging (Lovette & Fitzpatrick, 2016). The ecological relevance and function of chemical signals in passerines is not well understood (Roth II *et al.*, 2008; Whittaker *et al.*, 2010). Research has shown that blue tits can detect lavender odour (Mennerat *et al.*, 2005), and showed anti-predator behaviour and decreased time spent feeding nestlings when their nest-boxes were exposed to scents of predators (Amo *et al.*, 2008). House finches (*Carpodacus exicanus*) delayed their first feeding and reduced time spent at the feeder when exposed to predator faecal cues (Roth II *et al.*, 2008). Dark-eyed juncos (*Junco hyemalis*) produced their own individual odor profile, which

is used in intraspecific recognition (Whittaker *et al.*, 2010). A study by Healy and Guilford (1990) showed that for 55 bird families, olfactory-bulb size did not vary with development, nest type, nest dispersion, migratory behaviour or diet. However, birds with nocturnal and crepuscular activity had larger olfactory bulbs than diurnally active birds. Therefore, olfaction could play an increased role in birds that are active during low light intensities (Pollard, 2009), and possibly affect the foraging profitability for passerines foraging under low light conditions.

Differences in broadcasting space could be an important difference between the scheduling of tropical and temperate dawn-singing birds. Changes in broadcasting time in order to minimize interspecific overlap have been observed for other non-avian species. In Sumatra, four species of forest primates had species-specific calling times, displaced from the most favoured time, the mid-morning, possibly in order to minimize overlap between interspecific calls. In Borneo, there was low density of primate species, and only one of the four species in Sumatra, the orang-utans (*Pongo pygmaeus*) were present. These orang-utans called the whole mid-morning, presumably because they experienced less interspecific competition for broadcasting space (MacKinnon, 1974). In the tropics, dawn is short and species richness high (Lovette & Fitzpatrick, 2016). The soundscape during dawn is filled with a high density of avian and non-avian species, which results in interspecific competition for broadcasting space. To avoid sound overlap with other species, some tropical passerine birds may start their dawn song later than they would have done in an environment with less sound overlap, even though they have visual capability to start earlier. The interspecific competition for broadcasting space could be an important determinant of the scheduling of tropical dawn choruses, since they would have to start dawn song later than predicted by their visual capabilities. If the onset of dawn song is delayed to a time after foraging becomes profitable, the birds may start foraging before performing dawn song, to gain as much energy as needed during the breeding period. This could possibly affect the results of this thesis, and explain why I did not find a strong link between the onset of dawn song and the foraging ecology of tropical passerine birds. In temperate areas, the dawn period is longer and the species' richness is lower. This reduces the competition for broadcasting space, and reduces the sound overlap of species. The results from this thesis suggest that dawn song for temperate passerine birds is decided primarily by visual capabilities and foraging ecology.

Supplementary feeding of birds is widespread in the winter months, and in some places, birds are fed long into their breeding period, which potentially could have affect on dawn song, the temporal profitability of foraging, and ultimately result in fitness consequences for birds. The existing research provdies contradictory results. Supplemented blackbirds (Cuthill & Macdonald, 1990), black-capped chickadees (*Poecile atricapillus*) (Grava *et al.*, 2009) and silvereyes (*Zosterops lateralis*) (Barnett & Briskie, 2007) sang earlier. However, supplemented great tits sang later, which could be due to increased predation risk at feeding tables (Saggese *et al.*, 2011). Earlier-singing males could gain more EP mates, and possibly increase reproductive success, while males that delay singing may reduce their reproductive success. Feeding tables can also attract birds to urban areas, where they are exposed to other anthropogenic factors discussed above.

Anthropogenic influence can alter the behavioural patterns and fitness of birds. Ultimately, this can cause major evolutionary consequences. Increased urbanization across the world over the last decades is a major environmental concern. It follows, then, that research on the dawn chorus is important both for conservation reasons, and for gaining information about how birds respond to human impact.

Further research

Despite the interesting findings presented in this thesis, there are some shortcomings due to lack of data concerning the foraging ecology of passerine birds. The scarce dietary information for tropical passerine species limits the result, and more research on the breeding diet of tropical passerine species is necessary to enable further studies of dietary trends in relation to the onset of dawn song.

There is a general lack of research of the onset of foraging activity in the morning. The results of this thesis are therefore based on the assumption that the scheduling of foraging activity is the same as the scheduling of dawn singers. More research is needed to better understand the relationship between foraging ecology and dawn song. For instance, we need to examine the actual length and end time of dawn song, and the exact time birds start their foraging activity in the morning.

Previous dawn song research predominantly focuses on temperate areas, and the hypotheses suggested for dawn song are therefore mostly based on research regarding temperate oscines (Kroodsma, 1996; Staicer *et al.*, 1996; Berg *et al.*, 2006). Tropical dawn choruses include a considerable number of suboscine and non-passerine species with greater diversity of morphological adaptations and foraging ecologies (Berg *et al.*, 2006). Variability among different bird species lineages can complicate the trends seen in existing dawn chorus research. To reduce the effects of phylogenetic mixing, it would be beneficial to study the interspecific differences in foraging ecology linked to the onset of dawn song for closely related species. Interestingly, the study of Berg *et al.* (2006) found that tropical suboscine species sang earlier than tropical oscine species, and suggests that they may differ in their retinal sensitivity. More research is needed on the possible differences in visual constraints among oscine and suboscine species, linked to the onset of foraging activity.

Gathering data of the mentioned factors, in addition to increasing the statistics for the data studied in this thesis, will make it possible to study trends related to dawn song and foraging ecology in greater detail, and perform more thorough statistical tests. In this way, we can increase our knowledge about different factors affecting the scheduling of the dawn singers.

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Appendix 1 – Dawn song data

Average onset of dawn song

To find the average onset of dawn song for different passerine (Passeriformes) species participating in a dawn chorus, a search for available, published empirical studies on the onset of dawn song using the database ISI Web of Science [v.5.27] (Thomas Reuters, www.webofknowledge.com) was performed. Web of Science was chosen because it covers the majority of published scientific research, and is widely recognized in the field of biology. The search included contents from 1926 to February 2018, from “all databases”, containing all subscribed products of the website. The time-frame was chosen in order to include both new and older research, and therefore extends to the earliest searchable entries of the database, published in 1926. Searches were performed for *Topic* terms, which include the following fields within a record; Title, Abstract, Author Keywords and Keywords Plus[®]. The following search string was used, where “TS=” defines a *Topic* search:

```
TS=(dawnchorus OR "dawn chorus" OR "dawn song" OR "dawnsong" OR "dawn singing" OR (((dawn AND song) OR (dawnsong)) AND (passerine OR bird))) OR TS=(light AND (birdsong OR bird song)) OR TS=(song activity) OR TS=(bird AND (awake OR awakening)) OR TS=(morning AND (vocalization OR song)) OR TS=(twilight song).
```

In addition to database searches, relevant books at the University of Bergen Library and University of Oslo Library were searched manually. Research published by key authors was also considered. The titles of all the search results were systematically evaluated in order to select articles about the dawn chorus. If a decision could not be made based on the title, the abstract and an article was evaluated. The empirical studies included are shown in Table A1.1. Any relevant references listed in the included studies were also included in this study, following the same selection criteria mentioned above, some of which predates the time-frame of the database search.

Inclusion criteria for the average onset of dawn song

The average onset of dawn song included in the database (Supplementary material) must be performed by a passerine (Passeriformes) species, in its breeding period. The study must include three or more passerine species singing at the same location, in the same time period, forming a chorus. The onset of dawn song for a control group must be included in the article or supplementary material.

Exclusion criteria for the average onset of dawn song

Studies of non-passerine species and studies of dawn song characteristics that do not provide information about onset of dawn song in their article or supplementary material have been excluded. Research only focusing on dawn song for one species, and studies of choruses only including one or two passerine species were excluded, since this thesis examines how the scheduling of the dawn chorus of passerine species is affected. Data from experimentally manipulated individuals were excluded, since manipulation of ecological factors (e.g. light availability) can alter the onset of dawn song for passerine species, and different species can be affected differently by ecological factors. Studies not providing an accurate location of samplings were excluded. Studies have been excluded if not all twilight phases (astronomical, nautical and civil twilight) were included in the sampling period. Bird species that start their dawn song before astronomical twilight ($\leq -18^\circ$ degrees) have been excluded, since the onset of dawn song in these cases is during the period defined as night. The song may therefore be nocturnal song, and not dawn song. Research not written in English or a Scandinavian language, as well as unpublished studies, were excluded.

Solar altitude and twilight period

The empirical research included in the database gave the average onset of dawn song as minutes before sunrise or civil twilight, during a given sampling period. To get a measure for average onset of dawn song for each species, independent of temporal and spatial differences of latitude, solar altitude was calculated. The onset of dawn song was converted from minutes, relative to sunrise or civil twilight, to solar altitude (i.e. the range of degrees that the centre of the sun is above/below the horizon). This allows comparison of the onset of dawn song, independent of temporal and spatial differences between different latitudes. Information about solar altitude and twilight period was acquired from the Sunrise and Sunset Calculator (<https://timeanddate.com/sun/>) for the nearest city to the study site available, see Table A1.1.

This is the same method as used in the dawn chorus research by Bruni *et al.* (2014). To find the average time of sunrise for the song-recording period, the time of sunrise for the first and the last day of the song-recording period for each dawn chorus was used. For each species participating in the chorus, the average time of sunrise and the average onset of dawn song (minutes relative to sunrise or civil twilight) were used to calculate the average solar altitude, and to find the twilight period, for each species. Average solar altitude, as an expression for the average onset of dawn song for each species participating in the dawn chorus, allows direct comparisons of the onset of dawn song between different locations at different latitudes.

The twilight period values used to create Figure 1.1 are extracted with the date set to the 1st of April 2018, using the Sunrise and Sunset Calculator (<https://timeanddate.com/sun/>).

Statistical analysis

The statistical analysis were performed using R software (version 3.3.3) and RStudio (Version 1.0.136). To test if there was a significant trend ($P < 0.05$), a linear mixed effect model, with location as random effect was used to analyse the onset of dawn song as a function of body mass, AES and RES.

The R equation was: `AES.lme <- lm(solar_altitude~AES, random=~+1|areas, data=all.df)`

Table A1.1: Details of the dawn chorus studies included in my research.

Chorus nr.	Continent	Study site	Latitude	Sample size (nr. of species)	Song recording period	Vegetation	Reference
1	Europe	Madrid, Spain	40,53°N	9	May 10 to Jun 7, 2011	Not layered	(Gil <i>et al.</i> , 2014)
2	Europe	Starnberg, Germany	48,62°N	4	Apr 1 to May 6, 2014. 15 Mar to 1 May, 2015	Not layered	(Da Silva <i>et al.</i> , 2016)
3	Europe	Apeldoorn, The Netherlands	52,22°N	6	Apr 15 to May 15, 2013	Not layered	(Da Silva <i>et al.</i> , 2017)
4	Europe	Berlin, Germany	52,59°N	8	Apr 23 to Apr 28, 2013. May 1 to May 4, 2014	Not layered	(Dominoni <i>et al.</i> , 2016)
5	Europe	Starnberg, Germany	48,00°N	5	Mar 25 to Apr 18, 2014	Not layered	(Da Silva & Kempenaers, 2017)
6	Europe	Hochbruckenber, Austria	48,22°N	5	Mar 31 to Apr 18, 2009	Not layered	(Kempenaers <i>et al.</i> , 2010)
7	Europe	Granada, Spain	37,18°N	5	Mar 25 to Apr 18, 2014	Not layered	(Da Silva & Kempenaers, 2017)

Chorus nr.	Continent	Study site	Latitude	Sample size (nr. of	Song recording period	Vegetation	Reference
8	North America	Town of Fairfield, Wisconsin, USA	43,54°N	5	May and Jun, 1944	Not layered	(Leopold & Eynon, 1961)
9	North America	Sault Ste. Marie, Ontario, Canada	46,48°N	6	Apr 3 to Jul 10, 2012	Not layered	(Bruni <i>et al.</i> , 2014)
10	North America	Lyon Park, Virginia, USA	38,88°N	5	Apr 26 to May 31, 1929	Not layered	(Allard, 1930)
11	Australia	Ebenezer Park, New South Wales, Australia	30,50°S	8	Oct 16 – 25, 1986	Not layered.	(Keast, 1994)
12	Asia	Taichung, Taiwan	23,92°N	12	Mar 1 to Oct 31, 2007 and 2008	Layered	(Chen <i>et al.</i> , 2015)
13	South America	Santo Domingo, Ecuador	0,18 °S	34	Jan 21 to Feb 27, 2003	Layered	(Berg <i>et al.</i> , 2006)
14	South America	Barro Colorado, Panamá Oeste, Panama	9,15°N	10	Aug 17 – 31, 2014	Layered	(Stanley <i>et al.</i> , 2016)
15	North America	East Lansing, Michigan, USA	42,73°N	9	Mar 7 to Jul 31, 1955 (Period 1 and 2)	Not layered	(Fisler, 1962)

Chorus nr.	Continent	Study site	Latitude	Sample size (nr. of species)	Song recording period	Vegetation	Reference
16	North America	Jefferson Highland, New Hampshire, USA	44,42°N	51	Jun 20 to Jul 15, 1912, Jun 8 to Jul 9, 1913	Not layered	(Wright, 1913)
17	North America	Weston Field, Massachusetts, USA	42,37 °N	10	May 29 to Jul 26, 1883–1913	Not layered	(Allen, 1913)
18	North America	Mount Katahdin, Maine, USA	45,90°N	5	Jun 27, 1897	Not layered	(Allen, 1913)
19	North America	Madison, Wisconsin, USA	43,07°N	3	May – Jun, 1944	Not layered	(Leopold & Eynon, 1961)

Table A1.2: Average onset, length and end time of dawn song for five temperate passerine species described in Figure 3.1. *The database is included in Supplementary material.

Location	Species	Average onset of dawn song in solar altitudes (degrees), from the database*	Onset of dawn song in minutes relative to sunrise (solar altitude (degrees))	Mean dawn song duration in minutes (solar altitude (degrees))	Average end time of dawn song in minutes relative to sunrise (solar altitude (degrees))	Reference
North America	The Eastern kingbird (<i>Tyrannus tyrannus</i>)	-10	-63.8 ± 9.2 (-10)	33.8 ± 10.6	-29.9 ± 7.5 (-5)	(Murphy <i>et al.</i> , 2008)
	The black-capped chickadee (<i>Poecile atricapillus</i>)	-5	-	40.0	-	(Foote <i>et al.</i> , 2010)
		-	-	31.8 ± 2.6	-	(Otter & Ratcliffe, 1993)
		-	-	45.0	-	(Grava <i>et al.</i> , 2012)
Europe	Collared flycatcher (<i>Ficedula albicollis</i>)	-	-88 (-8)	36.0	-	(Pärt, 1991)
	Great tit (<i>Parus major</i>)	-6	-	24.8	-	(Mace, 1986)
	Blue tit (<i>Cyanistes caeruleus</i>)	-5	-25 (-5)	27.0	2.0 (0)	(Poesel <i>et al.</i> , 2001)

Appendix 2 – Morphology and ecology data

Morphological, ecological and dietary information

Information about the ecology of each bird species was acquired from the database “Handbook of the Birds of the World Alive” (<https://www.hbw.com/>, license through the University of Bergen Library), articles and scientific book publications (see references). Descriptions of the variables included in the database are shown in Table S1.

Body mass

The average body mass (g) of bird species was acquired from the database “Handbook of the Birds of the World Alive” (<https://www.hbw.com/>, license through the University of Bergen Library). The body mass values shown in Figure 4.1 are given in log (body mass (g)), and is listed as “body_mass_log” in Supplementary material.

Eye size

Calculation of absolute eye size (AES) and eye size relative to body mass (RES) was done for a subsample of the species included. The total subsample size of AES is for Europe (n=11), North America (n=50), Australia (n=5), South America (n=32) and Asia (n=6). The total subsample size of RES is for Europe (n=11), North America (n=50), Australia (n=5), South America (n=32) and Asia (n=12). The equatorial diameter, TD1 (mm), and polar diameter, TD2 (mm), of the eye, and body mass (g) for the measured bird species were retrieved from Ritland (1982), which has measured dissected specimens conserved in ethanol. Immature specimens were excluded. The calculations of AES and RES are presented in Eq. 1 and Eq. 2, respectively, and the calculated values are available in Supplementary material. Data for some South American bird species not described by Ritland (1982) (n=8) were retrieved from Berg *et al.* (2006). Data from Berg *et al.* (2006), which are not included in (Ritland, 1982), are marked with * in Supplementary material. The RES values for Asian bird species (n=12) included in Figure 5.1 are retrieved from Chen *et al.* (2015). Data from Chen *et al.* (2015) is marked with ** in Supplementary material. However, no AES values or body mass values were available from that study. Therefore, AES for Asian bird species has been calculated for the limited sample of Asian species (n=6) available in Ritland (1982).

Absolute eye size (AES)

The eye volume (mm³) was calculated using the equation of Garamszegi *et al.* (2002), which assumes that the shape of the bird eye is spheroid;

$$\text{eye volume (mm}^3\text{)} = 2 \times 1.33 \pi a^2 \text{ (mm}^2\text{)} b \text{ (mm)}, \quad (1)$$

where a is the equatorial radius (TD1/2) and b is the polar radius (TD2/2) of the eye, measured in mm. In this thesis, absolute eye size (AES) is given as log (eye volume).

Relative eye size (RES)

To consider the allometric effect of body size, the eye size relative to body mass (RES) was calculated (Figure 5.1). For calculations of RES, body mass (g) from the studies where morphological eye data were obtained is used. Relative eye size (RES) is calculated as;

$$\log (\text{eye volume (mm}^3\text{)}) / \log (\text{body mass (g)}) \quad (2)$$

Dietary trends

The birds have been divided into three groups based on dietary content (%); animal-eating species ($\geq 75\%$ animal content), omnivores ($\geq 25\%$ to $< 75\%$ animal content) and plant-eaters ($< 25\%$ animal content). Animal content refers only to insects and non-insect invertebrates. Based on dietary information from literature, percentages of diet content has been calculated and divided among the orders included in a bird's diet. If studies have described the breeding diet of birds in percent in relevant areas, they have been included in this thesis. If more than one study describe a bird's diet content in percent, the average of the studies has been used. For some birds, for example the Blacburnian warbler (*Setophaga fusca*), research states that 91,6% Lepidoptera is included in their diet. Therefore, 91.6% is assigned to Lepidoptera, and the remaining percentages are distributed equally among the remaining mentioned orders. If «especially», «mainly», «majority», «mostly», «principally», «particularly», «[...] form the bulk of diet» or «[...] are important compound of breeding diet» is used for one prey order, 75% of the total score is given to this order, and the rest of the percentages are distributed equally among the remaining mentioned orders. The value of 75% is chosen because it is the most conservative percent limit that defines if a species is an animal eater, omnivore or plant eater in this thesis. It also makes it possible to observe trends in the other included diet orders.

For example, when the diet of the purple finch (*Haemorhous purpureus*) is described as «mostly plants, seeds [...], also some arthropods», 75% is given to plant material, while 25% is distributed among the animal orders mentioned. This defines the purple finch as a plant eater during the breeding period. If the diet distribution mentioned in one source excludes some groups mentioned in other sources, the largest groups will be decreased sufficiently to assign 1% to each excluded order. Excluded orders could be taken only occasionally, and by giving it 1% it is included, without making a large impact on the dietary distribution. For bird species where an order is mentioned, but with limited information on diet, 10% is given to the mentioned order. For example, when the diet of the grey chinned minivet (*Pericrocotus solaris*) is described as «takes small invertebrates, including termite alates (Isoptera)», 10% is given to order Isoptera. The rest of the groups are set as not available (NA). Prey species described in the included birds' diets and the codes used in Supplementary material are included in Table A2.1, Appendix 2.

Prey attack manoeuver categories

Cases where bird literature uses the description «occasionally» have been included in this thesis as a prey attack manoeuver used by the bird, as it has the capability to use it. For example, when the black-striped woodcreeper (*Xiphorhynchus lachrymosus*) is described to «occasionally sallies after flying prey», it is included as a bird that can use the prey attack manoeuver «sally» from the «flycatchers» group. The prey attack manoeuver categories: substrate gleaners, flycatchers and both techniques, and descriptions of the prey attack manoeuvres they include are listed in Table A2.2, Appendix 2.

Foraging heights

Bird literature using the description «occasionally» for the foraging heights has been included in this thesis, as the bird has the capability to use it. Foraging heights are categorized as *lower heights* (< 1.5 m), *mid heights* (≥ 1.5 m to <7 m), *upper heights* (≥ 7 m), and *variable heights*. The classification of layers is the same as used by Chen *et al.* (2015), with exception of variable heights.

Table A2.1: Categories and orders included in the dietary trend analysis.

Group	Description	Orders	Prey mentioned in literature	Information	Code
Nocturnal non-flying prey	Nocturnal non-flying species, which are active on the surface of the ground, trees and foliage during dusk, night and dawn. When they are inactive during day, they hide under e.g. crevices, stones, logs, or retreat into soil, and become mostly unavailable as prey for birds. Their activities make them easier to detect (sight, sound) by early substrate-gleaning birds, or birds using both prey attack manoeuvre techniques.	Chilopoda	centipedes	Nocturnal and crepuscular activity. Fast runners on ground. Live in leaf litter and soil. Hide under stones, bark or wood, and are difficult to detect during day. Live most of their lives cryptically (Gillott, 2005; Tuf <i>et al.</i> , 2006; Edgecombe & Giribet, 2007; Resh & Cardé, 2009).	chil
		Dermaptera	earwigs	Nocturnal and crepuscular activity. Fast runners on ground. Some species are wingless as adults. Most have short front wings. However, they only use them very rarely. Hide under for example crevices, stones, fallen logs and debris during day, which make them difficult to detect (Gillott, 2005; Resh & Cardé, 2009).	derm
		Diplopoda	millipedes	Nocturnal and crepuscular activity. Slow-moving crawlers, mainly epigeic activity. Live in litter and soil. Easier to detect when is active during night. Hide for example under stones, fallen logs when asleep during day (Bano & Krishnamoorthy, 1979; Hopkin & Read, 1992; Tuf <i>et al.</i> , 2006).	diplo
		Isopoda	woodlice	Nocturnal and crepuscular activity. Runners and creepers. During night, they come to the surface of the ground, tree stems and foliage. During day, they hide under stones, bark ect. Many temperate species live on ground, in soil and litter layers. Some temperate species found in the forest canopy, on tree bark, branches and leaves. Some tropical rain forest species are arboreal (Gorvett, 1956; Paoletti & Hassall, 1999; Warburg, 2013).	isopo

Group	Description	Order	Prey mentioned in literature	Information	Code
Nocturnal non-flying prey (continued)	-	Oligochaeta	earthworms	Nocturnal and crepuscular activity. Vertical migration. During night and periods of low light intensities, emerge from soil and move on the surface to mate and search for organic food litter. Young and medium-sized worms present within the 10-cm topsoil more often than adults, which are deeper in the soil (Lee, 1985; Reece, 2011; Zaller <i>et al.</i> , 2016).	olig
Nocturnal flying prey	Active flyers during night. Hide in vegetation, for example the underside of leaves, or in shaded areas during day.	Blattodea	cockroaches	Nocturnal activity. Most species have wings. Hide under decaying vegetation and bark, or rest on flowers, leaves, grass during day. Could be in the canopy of tall trees (Gillott, 2005; Resh & Cardé,	blat
		Ephemeroptera	mayflies	Nocturnal activity. Flyers. Dusk or dawn swarming in temperate areas, and night swarming in tropical areas, where night temperature is high enough. Most adults are short-lived, and exist for only a few hours or days (Gillott, 2005; Resh & Cardé, 2009).	ephe
		Neuroptera	lacewings	Nocturnal activity. Flyers. Sit on leaves, or dark places when inactive during day (Kral & Stelzl, 1998; Gillott, 2005; Resh & Cardé, 2009).	neur
		Psocoptera	barkflies	Nocturnal activity. Flyers. Found on vegetation, under bark, among litter, under stones or in caves during day (Thornton, 1985; Gillott, 2005).	psoc
		Trichoptera	caddisflies	Nocturnal or crepuscular activity. Flyers. Flight during night, hide among vegetation or rocks during day (Gillott, 2005; Resh & Cardé, 2009).	tric

Group	Description	Order	Prey mentioned in	Information	Code
Gastropods	Both diurnal and nocturnal. More active during moist periods, such as dawn.	Class Gastropoda	snail, slugs	Diurnal and nocturnal activity. Crawlers, no wings or legs present. Emerge from hiding place during night. More activity during moist period, such as dusk and dawn. During rainy periods with high humidity, land snails may often be found actively crawling regardless of the time of day. Found under decaying logs, in leaf litter, in the crevices of bark, on the ground and in trees. Small species spend most of their time in the top 5 cm of leaf litter. Tree-dwelling snails are found more often in tropical areas, but some also occur in temperate areas. In temperate areas, fewer than 1% of land snails are operculate, while in the American tropics, about 50% of the species are operculate (Sturm <i>et al.</i> , 2006).	gast
Variously active prey	Diverse group, all orders include both diurnal and nocturnal, flying species and non-flying species.	Coleoptera	beetles	Diurnal and nocturnal activity. Flying, walking and swimming. Can protect their wings, which enable them to occupy enclosed spaces and cryptic habitats (Chatzimanolis <i>et al.</i> , 2004; Gillott, 2005; Resh & Cardé, 2009).	cole
		Diptera	true flies, horse flies, crane flies, hoverflies, mosquitoes	Diurnal and nocturnal activity. Flying and walking on substrate. Swarming behaviour. Predominantly diurnal, but also nocturnal activity patterns of mosquito species (Gillott, 2005; Resh & Cardé, 2009).	dipt
		Hemiptera	true bugs	Diurnal and nocturnal activity. Several crepsular species with dusk and dawn flight. Flying, walking on substrate and swimming (Wheeler, 2001; Gillott, 2005).	hemi

Group	Description	Order	Prey mentioned in literature	Information	Code
Variously active prey (continued)	-	Hymenoptera	flies, bees, wasps, ants sawflies	Diverse group. Both nocturnal and diurnal activity. Wings present in most species. Active flyers and crawlers (Gillott, 2005; Kelber <i>et al.</i> , 2005; Resh & Cardé, 2009).	hyme
		Isoptera	termites	Diurnal and nocturnal activity. Swarming in dim light. Reproductive adults fly, blind workers and soldiers live deep in soil, and are crawling (Krishna & Weesner, 1970; Resh & Cardé, 2009).	isopt
		Lepidoptera	butterflies, moths	Diverse group. Nocturnal and diurnal activity. Flyers and crawlers. In deciduous forest, lepidopteran larvae is important breeding diet of temperate passerines (Gillott, 2005).	lepi
		Mecoptera	scorpionflies	Diurnal, crepuscular and nocturnal activity. Flyers and walkers. Rest on grass and under leaves in low vegetation. Fly actively when disturbed. Particularly common in the Northern Hemisphere (Gillott, 2005; Resh & Cardé, 2009).	meco
		Odonata	damselflies, dragonflies	Diurnal and nocturnal activity. In warmer areas, emerge at night (less predation risk). In colder areas, emerge during day (temperature constrained). Highly synchronized emergence in temperate areas. Generally inactive during midday and hang on vegetation in the shade (Gillott, 2005; Resh & Cardé, 2009).	odon

Group	Description	Order	Prey mentioned in literature	Information	Code
Variously active prey (continued)	-	Orthoptera	grasshoppers, locusts, crickets	Diurnal and nocturnal activity. Hind legs adapted for jumping. Wings for flying. Some burrowing species, some soil dwellers. Many have limited flight abilities, but some are good flyers (Gillott, 2005; Reece, 2011).	orth
		Plecoptera	stoneflies	Diurnal, crepuscular and nocturnal activity. Flyers. Adults emerge at night or during early morning. During spring and summer, adults often fly towards lights at night. During day, rest on vegetation or foliage (Gillott, 2005; Gibb, 2014).	plec
		Arachnida	spiders, ticks, harvestmen, mites, scorpions	Diverse group. Diurnal and nocturnal activity. Walkers. Live in all layers of the forest. Rainforest species often in canopy, temperate species often on the ground and in trees (Resh & Cardé, 2009; Suter & Benson, 2014; Chakravarthy & Sridhara, 2016).	arac
		Collembola	springtails	Nocturnal and diurnal activity. Crawlers. Live on the forest floor, in trees, moist soil, leaf litter, and rotting wood, dung, grasses or flowers (Joosse-van Damme, 1965; Hopkin, 2002; Gillott, 2005).	coll
Plant material	Nocturnal and diurnal availability. Same location.	-	seeds, berries, nectar, fruit, plant buds	Always available for birds.	plan

Table A2.2: Description of prey attack maneuvers categories, and the included prey attack maneuver groups in each category. The categorizations are based on the categories from Holmes and Robinson (1988) and Thiollay (1988), with a few changes.

Prey attack maneuver group	Description	Prey-attack maneuvers included	Information
Substrate gleaners	Do not include true flight. Catch non-flying prey while standing on substrate.	Ground glean	Standing or moving bird picking a stationary prey from the ground.
		Probe	The bird manipulates the substrate. The bird's beak moves, disturbs or enters the substrate (e.g. leaf litter, loose bark, dead wood or epiphytes) to obtain prey, as well as tearing of or uncurling leaves rolled or glued by larvae.
		Tree glean	Standing or moving bird picking a stationary prey from a surface of a tree, for example a tree trunk.
		Snatch	The bird jumps from the ground and plucks the prey, for example from the undersurface of a leaf, or hangs to reach the prey on the substrate.
		Hover glean	When a flying bird snatches or grabs prey from the surface of a substrate after hover.
		Dive glean	When a bird perched above the ground on a low branch, log or rock, is flying downwards, usually landing, and then gleans prey from the surface of the litter.
Flycatchers	Includes true flight, with prey captured in air	Strike	Short flight to pick up a prey from a substrate on which the bird does not perch.
		Sally	A bird picks up its prey without stopping to flying. Hunts for flying insects around the foliage. Similar to hawking, but at a much shorter distance than hawking birds.
		Flush chase	When a bird is diving after falling prey. Pursuing a prey flushed by the bird, usually in a long downward flight.
		Hawk	When a flying bird chases and captures airborne insects.
Both techniques	Use a combination	-	The bird has the ability to use prey attack maneuvers from both the <i>substrate gleaners</i> and the <i>flycatchers</i> category.

Supplementary material

The electronic version of this thesis contains supplementary material in a Table S2. The description of the variables included in the database is listed in Table S1.

Table S1: Information about the variables included in Table S2.

Variable	Description
chorus_nr	Each dawn chorus, at the same location, during the same dawn song recording period, has its own chorus number. For more information about the choruses, see Table A1.1, Appendix 1.
continent	The dawn choruses are divided into five areas: Europe, North America, Australia, Asia and South America.
latitude	The latitude of the dawn chorus.
location	The location of the study site.
species_name	Name of bird species participating in the dawn chorus.
species_latin	Latin name of bird species participating in the dawn chorus.
onset_minutes	The onset of dawn song in minutes relative to sunrise, obtained from the control studies from the included research (Table A1.1, Appendix 1).
onset_solar_altitude_chorus	The onset of dawn song in solar altitude (degrees) relative to sunrise, for each chorus.
onset_solar_altitude_average	The average onset of dawn song relative to sunrise from the included choruses, calculated for each bird species.
prey_attack_manoeuver_group	The bird species are categorised into the prey attack manoeuver groups. For more information, see Table A2.2, Appendix 2.
foraging_heights	The foraging height of bird species. For more information, see Appendix 2.

olig, derm, chil, diplo, isopo, coll, arac, gast, tric, neur, blat, ephe, psoc, hyme, lepi, odon, isopt, meco, orth, plec, cole, hemi, dipt, plan	Orders included in a bird species' diet (%). "NA" means that there is not enough information about the bird's diet to evaluate if the order is a part of the bird's diet. "no" means that the given order is not mentioned as a part of the bird's diet.
TD1	Average minimum transverse (equatorial) diameter of eye, retrieved from Ritland (1982).
TD2	Average maximum transverse (polar) diameter of eye, retrieved from Ritland (1982).
weight_Ritland1982	Body mass (g) of bird species, used in calculations of AES and RES (see Appendix 2). Retrieved from Ritland (1982).
AES	Absolute eye size ($\log(\text{eye volume (mm}^3\text{)})$). For more information, see Appendix 2.
RES	Relative eye size ($\log(\text{eye volume (mm}^3\text{)})/\log(\text{body mass (g)})$). For more information, see Appendix 2.
log_body_mass	Log(average body mass (g)) of the bird species. For more information, see Appendix 2.
ref_diet	References