Circadian singing Patterns of a Subarctic Avian Community

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Abstract

I examined the hypothesis that each species in a subarctic avian community possessed a different circadian singing pattern. Based on mean circadian singing patterns and the proportions of daily singing activity attributable to each species, all species were divisible into three types of singing patterns: unimodal, bimodal and trimodal. The principal attributes which characterized these circadian patterns further differentiated each species within these groups. The interplay of several factors may have contributed to the adaptive advantage of different singing patterns: acoustic conditions of the environment, acoustic interference within the song community and foraging profitability. The importance of the dawn chorus as part of the singing patterns was discussed. The singing patterns were compared to those of species in other subarctic communities as well as species in temperate communities; both differences and similarities were found to exist.

Introduction

Bird singing activity generally follows a circadian rhythm (Kok 1971, Robbins 1981, Kowalski 1983, Barclay et al. 1985, King 1986, McNamara et al. 1987), usually a bimodal pattern typical of passerines (large morning and smaller evening peaks) (Aschoff 1966). This circadian singing pattern is dominated by the dawn chorus, the time of greatest singing activity (Robbins 1981, Gottlander 1987, McNamara et al. 1987, Mace 1989), which occurs during sunrise and continues for a short time thereafter (Davis 1965, Kok 1971, Robbins 1981, Gottlander 1987). There are several possible reasons why this is a preferred time of day for singing: highly favourable acoustical conditions for song propagation (Wiley and Richards 1978, Henwood and Fabrick 1979), a more efficient use of energy than is foraging, the major competing activity (Kacelnik 1979, Kacelnik and Krebs 1983), female stimulation (Mace 1986) or territorial advertisement to counter the high risk of intrusion by other males (Krebs 1977, Kacelnik and Krebs 1983).

The high frequency of singing during the dawn chorus results in the presence of high levels of aural interference. To counter this `masking' effect, some species have evolved the use of certain strategies to maximize the propagation of their songs. They have adjusted their singing rhythms just enough to ensure asynchronous singing with nearby competitors (Ficken et al. 1974, Wasserman 1977). Some birds also use asynchronous singing during other times of the day (Cody and Brown 1969) or they possess circadian patterns that are offset from other species (Sorjonen 1986). The majority of passerines sing only during the daylight hours, although some sing in the dark, pre-dawn period (Highsmith 1989, Mace 1989) and a very few are nocturnal singers (Harvey 1980, Hultsch and Todt 1982, Barclay et al. 1985).

Avian species in temperate regions, where the photoperiod is a well-defined light-dark cycle, possess singing patterns that parallel the daylight portion of the cycle, e.g., the White-crowned Sparrow (*Zonotrichia leucophrys*) (King 1986), Song Sparrow (*Melospiza melodia*) (Nice 1943), Kirtland's Warbler (*Dendroica kirtlandii*) (Mayfield 1960), Great-tailed Grackle (*Quiscalus mexicanus*) (Kok 1971), Great Tit (*Parus major*)

(Hinde 1952, Mace 1989), and the *Acrocephalus* warblers (Catchpole 1981). Some non-song vocalizations (i.e., calls) also follow this pattern, e.g., Budgerigars (*Melopsittacus undulatus*) (Ferrell and Baptista 1982) and Kittiwakes (*Rissa tridactyla*) (Wooler 1979).

In high latitude ecosystems the presence of continuous daylight has removed the inhibiting effect that darkness has on singing activity. The result is that some species have been reported singing at all hours of the daily cycle, e.g., White-crowned Sparrows (King 1986), Golden-crowned Sparrows (*Zonotrichia atricapilla*) (Holmes and Dirks 1978), Thrush Nightingale (*Luscinia luscinia*) (Sorjonen 1977), and some sing almost continuously throughout the `night' (Sorjonen 1986). However, birds in arctic regions continue to exhibit behavioural periodicities, in the form of peaks and lulls in activity levels, despite the absence of a well-defined light-dark cycle (Palmgren 1935, Armstrong 1954, Cullen 1954, Brown 1963) and this includes singing activity (Sorjonen 1977, King 1986, Holmes and Dirks 1978). All of these aforementioned arctic studies have described and analyzed circadian activity patterns of various passerine species but only in the context of single or dual species systems; they have not considered all members of the song community. As a result, the methods through which a northern species copes with both the unique environmental conditions as well as the rest of the song community are not known.

Northern avian communities are characterized by low species diversity and low population density. Thus, the birds do not experience the high levels of acoustic interference present in temperate and tropical communities, each of which has a much higher passerine diversity. In addition, the continuous daylight of northern regions provides a unique opportunity for singing birds: with the removal of the inhibiting effect of darkness, plus the long period of optimal acoustic conditions (i.e., cool temperatures and little wind) for singing during the night-time and morning hours, species should be able to adapt their singing times so as to reduce the levels of acoustic interference with other species in their community. The result is that each bird species in a northern environment should possess a significantly different circadian singing pattern.

The objectives of this study are to describe and analyze the circadian singing patterns of a subarctic avian community, and to compare these patters to those of species in other high latitude environments and also temperate environments.

Study Area and Methods

The study area was located in subarctic forest sixteen kilometres east of Ft. McPherson in the Northwest Territories (67° 27' N., 134° 28' W.)., approximately 100 kilometres south of the most northerly limit of trees in North America.

Song surveys were carried out between May 27 and July 12, 1989, thereby covering all of the breeding season, with the exception of the start of the territory establishment period. Each survey consisted of a five-minute period during which the number of songs heard from all species of passerines was recorded. The number of singing individuals of each species was not recorded nor was any attempt made to attribute numbers of songs to specific individuals within each species. A single song was defined as a distinct series of notes or phrases separated by a pause. This definition was sufficient to permit accurate counts of songs for all passerine species in this study. Because avian diversity and species density were both low in this study area, all songs were easily and distinctly heard, even during times of high singing activity, such as during the dawn chorus.

No formal attempt was made to ensure a random distribution of the surveys over the course of a day; they were simply done as often as possible at the same time that other, unrelated field work was being conducted. However, attempts were made to conduct surveys every half-hour, or at least once an hour, and the time of each survey was not related to any regularly occurring event. Attempts were also made to distribute the surveys evenly across all hour periods of the day. However, this was not possible because of such factors as concurrent field work and weather conditions.

Song surveys were conducted only during good weather conditions; they were not done during cold, windy or very wet weather. Because subarctic forests have small trees and a very sparse canopy, it was easy to visually detect singing birds. When wind speeds increased to the point when distant, singing birds could be seen but no longer heard, song surveys were stopped until the return of calmer conditions.

Since most of the song surveys were scattered throughout the study area, it was impossible to determine the number of individuals recorded within each species. Assuming that males sang mainly within their territories, the sample sizes presented here were determined from the number of individuals regularly heard singing at specific locations in the study area. The sample sizes should, thus, be viewed as the minimum number of individuals recorded. In addition, the number of times that each individual was recorded during the entire survey was unequal.

Most of the surveys were not done at specific locations, which would have otherwise provided guarantees that different subsets of the population were sampled. Rather, the surveys were distributed over the entire study area. The main area in which virtually all of the song surveys were done was 19.5 hectares in size (540m by 360m). Approximately 65% of the surveys were concentrated in one-ninth of this area (178m by 119m, 2.1 hectares). The general locations of the surveys within different parts of the study area were separate enough to ensure that several distinct subsets of individuals for each species were sampled.

Because the data from the song surveys were not normally distributed, and could not be normalized using transformations, they were analyzed using distribution-free methods. The circadian singing patterns of the species were compared using an approximate randomization procedure.

The index of singing activity used throughout this study is song rate, the number of songs recorded per minute.

The breeding range of all eight species extends over most or all of the subarctic ecoregion. In addition, the vegetation of the study area is characteristic of that found throughout this ecoregion. Thus, this study site and its avian population are representative of the subarctic in North America.

Results

Six hundred and ninety-nine surveys were done during the forty-seven day survey period, for a total of 58.3 hours of survey time. The number of surveys per day varied from two to fifty, with an average of seventeen. Six days were not sampled at all, because of either travel out of the study area or inclement weather conditions. The percentage of one-hour periods surveyed per day ranged from 8% to 92%, with an average of 45%.

Song Community

The song community, encompassing all species regularly heard singing in the study area, consisted of eight passerine species from three families (Fig. 1). Only two other passerine species were recorded during the song surveys (Common Redpoll *Carduelis flammea* and Pine Grosbeak *Pinicola enucleator*) but since their presence was highly inconsistent (i.e., recorded less than ten times during the survey period), they were not included in the analysis. Thus, this survey included all species that were considered an integral part of the song community in this region.

Mean Circadian Singing Patterns

To examine the daily rhythm of singing activity, diagrams illustrating the mean circadian singing patterns of the song community and each of its species were produced by determining the mean song rate during each hour period over the course of the entire survey period (Fig 1). Thus, they represent the average levels of singing activity during the breeding season at any given time of day. The song survey undoubtedly sampled many individuals more than once, and most birds would have contributed unequal numbers of observations to the data set. Because this data had to be pooled to create the mean song rates, variability measurements would be strongly underestimated and, therefore, inaccurate (Machlis et al. 1985). Thus, no indications of variance in singing activity during each hour period are provided.

Gray-cheeked Thrush

The evening quiescent period, during which songs were still commonly heard, lasted only from midnight to 0100. It was followed by a very sharp increase in singing activity to a high of 9.2 songs/min at 0300, the peak of the dawn chorus. A decrease over the next three hours led to a stable plateau of about 4 songs/min for three consecutive hours (0600-0900). The song rate then fluctuated but gradually declined over the next eleven hours before reaching 1.84 songs/min, the lowest level of the day, at 2000. The song rate then increased to the peak of the evening chorus at 2300, which was almost as high as the dawn chorus. The sudden rise in singing activity was similar for both peak periods. The lull period separating these two peak periods still had a greater song rate than that present during much of the rest of the day.

American Tree Sparrow

The evening quiescent period occurred between midnight and 0200, when the song rate was quite low, from 0.39 to 1.03 songs/min. The rapid increase in activity caused by the dawn chorus resulted in a peak song rate of 7.82 songs/min at 0500. There was an initial post-dawn chorus decrease that was quite sudden, from 0500 to 0700, after which the decrease was more gradual. The afternoon lull was reached between 1600 and 1800 when the song rate hovered between 1.71 and 2.53 songs/min. A small evening chorus occurred between 1900 and 2100 but song rates were only slightly higher than during the preceding lull.

Yellow-rumped Warbler

Between midnight and 0200, the Yellow-rumped Warbler did not sing at all. However, by 0300 it had achieved the peak of its dawn chorus at 1.58 songs/min. This decreased to a very low song rate of 0.21 songs/min by 0700. A subsequent gradual increase in singing activity created a second peak between 1100 and 1400 with song rates reaching as high as 1.17 songs/min. This was followed by the afternoon lull, lasting from 1700 to 2100, during which the song rate was similar to that of the first lull at 0700. The evening chorus occurred between 2200 and 2300, when the singing frequency was almost as great as it was during the second peak at 1200. The Yellow-rumped Warbler, thus, produced a trimodal singing pattern, as opposed to the bimodal pattern found in the Gray-cheeked Thrush and American Tree Sparrow.

White-crowned Sparrow

For the White-crowned Sparrow the dawn chorus extended from 0200 to about 0500, during which time the song rate achieved a maximum value of 3.62 songs/min. The intensity of the dawn chorus diminished rapidly until 0700, after which the song rate fluctuated from 0.47 to 1.13 songs/min until about 2000. Thereafter, singing frequency stabilized at a very low level of approximately 0.4 songs/min until the start of the dawn chorus. There was no definable peak indicating an evening chorus. Thus, the circadian singing pattern of the white-crowned sparrow was unimodal.

Dark-eyed Junco

The evening quiescent period for the Dark-eyed Junco occurred at midnight, when there was no singing activity by this species. The song rate increased rapidly to a dawn chorus which peaked at 0400 with a rate of 1.89 songs/min. It then decreased suddenly by two-thirds at 0500, but then returned to near its previous high level at 0600. It is possible that this brief interlude is an artifact of the data rather than a naturally occurring phenomenon, as indicated by the wide range of the standard error bars. The dawn chorus retained its high level of singing frequency until 0800, after which it decreased gradually to an afternoon low point of 0.1 songs/min at 1500. There was a small evening chorus which reached 0.68 songs/min at 2100, followed by a gradual decrease to the evening quiescent period.

American Robin

The evening quiescent period of the American Robin lasted from 0100 to 0400, when there was no singing activity. A peak song rate of 1.24 songs/min during the dawn chorus occurred at 0600. This was abruptly followed by a three-hour period of much lower singing activity and then a second peak at 1000, when the song rate attained 1.01 songs/min. Judging by the range of the error bars, the extent of this decrease may not be as dramatic as represented by the mean values. If this is the case, then the dawn chorus would still be present from approximately 0500 to 1000 and the song rates during this period would be more uniform. The afternoon lull lasted from 1400 to 1800, when the song rate was virtually zero. Thereafter, it fluctuated considerably before reaching the peak of the evening chorus at 2300, when it was 1.7 songs/min. This evening chorus represents the highest level of singing activity for this species, as opposed to the more traditional dawn chorus.

Fox Sparrow

From 2300 to 0300 the Fox Sparrow did not sing at all. The dawn chorus represented an abrupt change as singing reached near peak values by 0400. These song rates (0.62 to 0.71 songs/min) were maintained until 0700, after which they decreased at a steady pace, with some fluctuations occurring in mid-afternoon. A small increase in singing activity at 2100 was the only indication of anything resembling an evening chorus. After this time, the song rate was very low until it ceased at 2300.

Blackpoll Warbler

The Blackpoll Warbler maintained a quiescent period from midnight to 0400. A brief dawn chorus, with peak singing rates of 0.45 songs/min, lasted from 0500 to 0700. From 0700 to 1300 singing activity fluctuated from virtually zero to 0.26 songs/min. This was followed by a sudden, brief rise in the song rate at 1400 to a peak of the same intensity as the dawn chorus. The afternoon lull which followed immediately after lasted until 2100. At 2200 there was an evening chorus with song rates of up to 0.25 songs/min.

To assess the degree of similarity of the singing patterns among the species, the patterns were compared using the following procedure. The original survey data were transformed to observed frequencies so that comparisons could be made of the pattern shapes only, without the confounding problem of their different magnitudes. The difference between each pair of patterns was determined using:

$$D(i,I)=\Sigma(f_{ij}-f_{Ij})^2$$

where: D = distance
i = species 1
I = species 2
J = hour period

The greater the distance between each of the species the less similar their patterns were. The total distance among all species was used as the test statistic in an approximate randomization test (Noreen 1989) of the null hypothesis that the circadian singing patterns were independent of the species. This test indicated that at least one of the patterns was significantly different from the others (D=2.5405, P=0.000). Ryan's multiple comparison procedure was then used to determine which patterns could be considered distinct. Figure 2 illustrates how the species are divided according to the similarity of their singing patterns.

There were at least four distinctly different singing patterns. The singing pattern of the American Robin was significantly different from that of all other species. The Yellow-rumped and Blackpoll Warblers were similar to each other and quite different from the Gray-cheeked Thrush, White-crowned Sparrow and Fox Sparrow. The Fox Sparrow was, in turn, different from the Gray-cheeked Thrush, while the White-crowned Sparrow had attributes similar to both of these latter two species. The American Tree Sparrow and Dark-eyed Junco were the `grey' species; their patterns were so intermediate in nature that they could not be separated from any of the other groups, except for the American Robin.

It is possible that the singing patterns of all eight species were distinct. However, the randomization test was not able to separate them all, most likely because of two factors: small sample sizes for some hour periods and the large amount of variability about the mean song rates.

One method of determining what it was that made these patterns different from each other is by comparing the main attributes that characterized these patterns. These attributes include the range of singing frequency and the temporal distribution of the four main periods of singing activity (or inactivity): the dawn chorus, afternoon lull, evening chorus, and evening quiescent periods (Table 1).

The range of singing frequency differed greatly among the eight species. Three species, the Gray-cheeked Thrush, American Tree Sparrow and White-crowned Sparrow, were heard at all times of the day as they did not possess an hour period with a zero song rate. The minimum song rates for both the American Tree Sparrow and the White-crowned Sparrow were close to zero whereas the minimum for the Gray-cheeked Thrush was greater than the maximum song rate of four other species. The remaining five species all had daily periods when they were not singing at all. The difference between minimum and maximum song rates varied from a high of 7.43 songs/min for the American Tree Sparrow to a low of 0.48 songs/min for the Blackpoll Warbler, with considerable variety exhibited by the other six species.

The timing and duration of the dawn chorus were a source of some variation. For six of the species (Dark-eyed Junco and American Robin excluded) the dawn chorus was a well-defined event. The start was represented by a sharp increase in the song rate as compared to the preceding quiescent period. It began between 0200 and 0500 and terminated 2 to 4 hours later, depending on the species. The end of the dawn chorus was a more gradual process than its start. It did not signal an end to singing activity, just a decrease to much lower levels. The Dark-eyed Junco and American Robin also had noticeable dawn choruses but the start and end were not as rigidly fixed as with the other species. Rather, they were more gradual in nature and the dawn chorus was longer in duration.

The afternoon lull was a more difficult event to define. It was not readily apparent in the White-crowned Sparrow, and in the Gray-cheeked Thrush it seemed to occur at around 2000. For the American Tree Sparrow, Dark-eyed Junco and Fox Sparrow it was a three-hour period between 1500 and 2000, a slightly later four hour-period for the Yellow-rumped Warbler, and a five-hour period for the American Robin. The Blackpoll Warbler had the longest lull period, at seven hours' duration. In all species the singing frequency during this period was very low compared to the dawn chorus.

The evening chorus was similar to the afternoon lull in that it was not readily definable for all species. The White-crowned Sparrow did not exhibit an evening chorus at all, nor did the Fox Sparrow. The Gray-cheeked Thrush had a short one of 1 to 2 hours' duration at 2300. It was present for two hours at approximately 2200 for the Yellow-rumped Warbler, Dark-eyed Junco, American Robin and Blackpoll Warbler, whereas that of the American Tree Sparrow started at 1900 and lasted for three hours. For all species with a definable evening chorus, the song rate was noticeably higher than it was during the afternoon lull, though the extent of this increase varied considerably. For the American Robin, the greatest daily level of singing frequency was reached during this period, between 2200 and 2300.

All eight species exhibited a definite evening quiescent period. For the Gray-cheeked Thrush, American Tree Sparrow and Yellow-rumped Warbler this period occurred between midnight and 0200. However, while the American Tree Sparrow was singing very little (0.39 songs/min) and the Yellow-rumped Warbler not at all, the Gray-cheeked Thrush was still maintaining a high level of singing activity (5.45 songs/min). The only other species singing during its quiescent period was the White-crowned Sparrow, which sang occasionally between 2200 and 0100. Although none of the remaining species sang during this time, the start and duration of their quiescent period varied, such that no two were identical in this regard.

The information provided by the mean circadian singing patterns and the principal attributes of these patterns illustrate that there were strong differences in the temporal patterning of singing activity by each species. Although there were many differences over the course of the day, the principal ones appear to have been related to the timing and intensity of the dawn and evening choruses. As a result there were characteristics of singing behaviour that were unique to each of the species. These characteristics are listed below.

The following five species exhibited a bimodal singing pattern. That is, the pattern had two daily peaks of singing activity, the dawn and evening choruses.

Gray-cheeked Thrush

The Gray-cheeked Thrush had the highest overall song rates, the peak of which occurred in the very early morning hours when there was very little other singing activity. Its main acoustic competitor in the dawn chorus was the American Tree Sparrow, but the dawn chorus peak for the Gray-cheeked Thrush occurred an hour earlier. The Gray-cheeked Thrush also never stopped singing completely but maintained a high level of singing activity throughout the day.

American Tree Sparrow

The American Tree Sparrow also had high song rates and sang at all hours of the day, though not at the same high levels as the Gray-cheeked Thrush. Its quiescent period was much quieter than was that of the Gray-cheeked Thrush. The dawn chorus peak of the American Tree Sparrow was offset from that of Gray-cheeked Thrush by occurring one hour later. Its evening chorus was earlier than that of all other species.

Dark-eyed Junco

The dawn chorus for the Dark-eyed Junco started at about the same time as the rest of the community but lasted longer than all species, save for the American Robin.

American Robin

The dawn chorus for the American Robin started later than most other species and lasted longer into the morning. However, the highest song rate for this species occurred during the evening chorus, a characteristic not found in the other seven species. The evening quiescent period also started later and lasted quite long, approximately four hours.

Fox Sparrow

The Fox Sparrow had a very weak evening chorus and concentrated most of its singing efforts in the dawn chorus. It also had the longest evening quiescent period, along with the Blackpoll Warbler.

The following two species had a trimodal singing pattern; a midday peak of singing activity in addition to the dawn and evening choruses.

Yellow-rumped Warbler

The second peak in singing activity for the Yellow-rumped Warbler occurred after all other species had finished their dawn choruses. The evening chorus was almost as high as this second peak.

Blackpoll Warbler

The second peak for the Blackpoll Warbler also occurred after the other species had finished their dawn choruses but it was also occurring just as the second peak of the Yellow-rumped Warbler was starting its decline. This species had a late start to its dawn chorus.

The last species had a unimodal singing pattern, only one daily peak of singing activity.

White-crowned Sparrow

The White-crowned Sparrow had a dawn chorus but no evening chorus. It also had a relatively constant level of singing activity extending from the end of the dawn chorus to the start of the evening quiescent period, as opposed to a decline or any fluctuations characteristic of other species.

Mean Circadian Proportions of Singing Activity

The foregoing analysis has shown that the singing pattern of each species differs from that of all others in some specific way(s). This situation is reflected in the probability of hearing any one species at any particular time of day. As Fig. 3 illustrates, the probability of hearing a species, as well as the proportion of total singing activity attributable to that species, varied considerably during the day. What this figure also clearly illustrates is the degree to which the Gray-cheeked Thrush and American Tree Sparrow monopolized the activity of the song community through their intensive singing levels. It also shows how few of the total songs recorded belonged to the Fox Sparrow and Blackpoll Warbler. Singing activity by these latter two species did not become apparent until the level of singing by the Gray-cheeked Thrush decreased considerably from its dawn chorus peak. All other species also responded to the Gray-cheeked Thrush in approximately the same way.

Discussion

This study provided evidence for the hypothesis that the circadian singing patterns of each species within the subarctic avian community were different. To determine the possible reasons why each species would possess a unique singing pattern, and the advantages to be gained from these differences, we must first examine two factors that have had important implications in the evolution and use of bird song: acoustic conditions of the environment and acoustic interference within the song community.

The propagation of sounds, such as songs, through the atmosphere must contend with the acoustic conditions of the environment into which the sound is transmitted. These conditions are governed by a number of factors, principally temperature, wind and humidity, all of which can combine to create turbulent air eddies and thermal stratification (Morton 1975, Wiley and Richards 1978, Henwood and Fabrick 1979, Richards 1981). These factors, thus, contribute to the degradation of the intensity and quality of bird songs (Richards 1981). In addition to environmental influences affecting the transmission of bird songs, there is also a biological influence affecting the reception of a song: acoustic interference generated by the singing activity of other members of the song community.

Whereas poor acoustic conditions cause degradation of the physical qualities of a song, high levels of vocal activity tend to mask a song (Ficken et al. 1974), thereby decreasing its chances of being heard by other individuals. The end result of both the environmental and biological influences is the same: the effective communication distance and, thus, the area of broadcast coverage of a song, are diminished.

The interplay of these two factors is present at all times of the day, but the biological influence would be most prevalent during the dawn chorus, the daily period of greatest singing activity. An examination of what are currently considered to be the multiple functions of the dawn chorus, and the effects of acoustic conditions and interference during the chorus, would provide clues as to the possible reasons why each species had a different circadian singing pattern.

The dawn period is characterized by environmental conditions of low air turbulence and better microclimatic conditions for sound transmission than at any other time of the day (Waser and Waser 1977, Henwood and Fabrick 1979). These conditions are thought to have resulted in the evolution of the dawn chorus, where the cost of singing at a time of great acoustic interference from other bird songs is offset by the advantageous acoustic conditions of the environment (Henwood and Fabrick 1979). The level of acoustic interference decreases as the morning progresses because of lower levels of singing activity. However, attenuation of songs, due to air turbulence, increases at this same time (Wiley and Richards 1978, Kacelnik 1979, Richards 1981). Indeed, Henwood and Fabrick (1979) found that, in terms of broadcast area, in tropical rainforests there was a forty-fold advantage to a bird singing in the calm early morning, as opposed to the midday period when windy conditions were present.

The presence of different circadian singing patterns may also have been influenced by the two principal reasons for singing: territory establishment and maintenance, and mate attraction and stimulation.

Many studies have found that song serves to advertise the occupancy of a territory.

This may be quite important during the dawn period for two reasons. First, there is a high degree of intruder pressure just after dawn by males seeking territories (Krebs 1977, Kacelnik and Krebs 1983) and song is used to defend the territory from these intruders (Lemon 1968, Krebs et al. 1978). Second, because the energy reserves of birds are low at dawn, the energy saving benefits of using song to repel an intruder rather than using aggressive visual displays are correspondingly greater (Shy and Morton 1986). Several studies have shown that using song without visual displays is adequate for protecting territorial boundaries (Peek 1972, Goransson et al. 1974, Krebs 1976).

Females have also been shown to have an influence on the timing and duration of the dawn chorus. Since the females of many species arrive on the breeding grounds at night, it would be advantageous for males to maximize their chances of attracting a mate by concentrating their singing activity in the early morning (Gottlander 1987). Singing by males has also been found to stimulate the reproductive condition of the females (Brockway 1965, Kroodsma 1976) and reinforce the associated activities of nest-building and egg-laying (Brockway 1965, Armstrong 1973, Kroodsma 1976). In some species this has resulted in the females exerting some control over the duration of the dawn chorus. For example, in the Great Tit, the dawn chorus is thought to be a form of mate guarding and it ceases once the female has emerged from the nest hole and copulation has occurred (Mace 1986, 1987).

Foraging is the major competing activity to singing, and the level of foraging profitability is thought to have an important influence on the duration of the dawn chorus. Foraging profitability is affected by environmental variables; low temperatures reduce invertebrate abundance (Verbeek 1964, Verner 1965) and low light levels impede visibility of these prey species (Kacelnik 1979). Peiponen (1970) found that subarctic birds stopped feeding when insect food was difficult to locate during the coolest and darkest time of the night. During the first part of the dawn chorus, when it is still cool and relatively dark, foraging profitability would be low (Kacelnik 1979, Avery and Krebs 1984). Singing would, thus, be a more profitable use of time and energy, despite the high requirement for food at that time (Garson and Hunter 1979). Great tits were found to allocate more time to territorial activities (i.e., singing) just after dawn than during the rest of the day (Avery and Krebs 1984). As foraging profitability increases, the level of singing activity would decrease as individuals spend more time engaged in foraging activities. King (1986) reported that White-crowned Sparrows in Alaska first started foraging as the dawn chorus started to wane.

The hypotheses regarding the characteristics and causes of the dawn chorus as described above illustrate how there are a variety of factors affecting this important activity period. The different singing patterns present during the morning period could be the result of differential responses by each species to changing conditions, these conditions influenced either directly by the environmental and biotic factors, or indirectly by foraging profitability. The fact that these singing patterns continued to exhibit differences during the remainder of the day would signify ongoing responses to conditions which were in a constant state of flux. This adaptability would increase the probability of successful reproduction and, consequently, the level of fitness. Adjustments in singing patterns would probably be the most efficient way that natural selection could increase this fitness level (Henwood and Fabrick 1979).

Previous studies on the singing activity of birds in high latitude regions have illustrated the presence of common elements in the circadian singing patterns of different species. The Golden-crowned Sparrow (*Zonotrichia atricapilla*) in Alaska had its highest singing rates in the very early morning (0100-0400), lower rates during the rest of the day and a quiescent period in the late evening (2200-0030) (Holmes and Dirks 1978). A similar pattern was found with the White-crowned Sparrow in Alaska (King 1986), the Lapland Longspur (*Calcarius lapponicus*) in Siberia (Uspenskii 1984), and, to a lesser extent, with the Thrush Nightingale (*Luscinia luscinia*) in Finland (Sorjonen 1977) and a Bunting species (Emberizidae) in Siberia (Uspenskii 1984). The circadian singing pattern of these species is similar to that of the species in this study who exhibited a bimodal singing pattern (the reverse bimodal pattern of the American Robin excepted). This illustrates the widespread nature of this type of circadian singing pattern, both geographically and within the passerine birds.

To determine the extent to which the circadian singing patterns of species in this study are unique characteristics of high latitude regions, requires comparisons to circadian singing patterns of temperate species. Prairie Warblers (*Dendroica discolor*) in the midwestern United States do not start singing until fifteen minutes before sunrise, have peak singing rates during the first four hours after sunrise, and lower rates during the remainder of the day, with the lowest singing rates in the four hour period prior to sunset (Nolan 1978). Great-tailed Grackles (*Quiscalus mexicanus*) in Texas have peak song rates at dawn with a lesser peak in the late afternoon (Kok 1971). In Hawaii, 'Elepiao's (*Chasiempis sandwichensis*) started singing at dawn but peak song rates did not occur until about midday, with song rates lower during the afternoon than the morning (Conant 1977).

In Maryland, the circadian singing patterns of three species was studied (Robbins 1981). The Cardinal (*Cardinalis cardinalis*) and Scarlet Tanager (*Piranga olivacea*) both displayed bimodal patterns, with the dawn chorus peak for the Scarlet Tanager occurring just before sunrise and that of the Cardinal just after. The Wood Thrush (*Hylocichla mustelina*) displayed a reverse bimodal pattern, with the daily peak of singing activity during the late evening, at sunset.

The calling activity of Kittiwakes (*Rissa tridactyla*) in northern England peaked shortly after dawn, declined to a lull period by midday, had a second, lower peak in the middle of the afternoon and then quickly declined to zero by sunset (Wooler 1979). Calling by Kittiwakes was rare during darkness.

The dawn chorus of Great Tits (*Parus major*) peaked shortly after sunrise in Spain and later after sunrise in Finland, a significant difference in timing (Mace 1989). In Oregon, the number of singing birds detected from the first hour after sunrise to the fourth hour decreased significantly (Skirvin 1981).

All of these studies show that there are common elements in the circadian singing patterns of temperate and arctic species. In both groups, bimodal patterns are the most common type, and reverse bimodal patterns are found in both regions. The principal difference between the two groups is the time span over which singing occurs. Temperate species are generally restricted to singing during the period between sunrise and sunset; arctic species are not restricted in this way and sing at all hours of the day.

Conclusion

The literature and this study, together, have already shown that the bimodal singing pattern is common to both regions, although differences within this pattern type, due principally to different photoperiod regimes, do exist. However, what would be of greatest interest is to determine how the circadian singing pattern of each species within the temperate avian community would adapt to the characteristics of its region (i.e., acoustic conditions, acoustic interference), and how this adaptation compares with that of the subarctic species. For example, in temperate regions, higher species diversity and greater population densities would result in greater acoustic interference. As well, different environmental conditions would result in different periods of optimal acoustic conditions. The work of Robbins (1981) has already demonstrated the existence of some differences in the circadian singing patterns within the same avian community.

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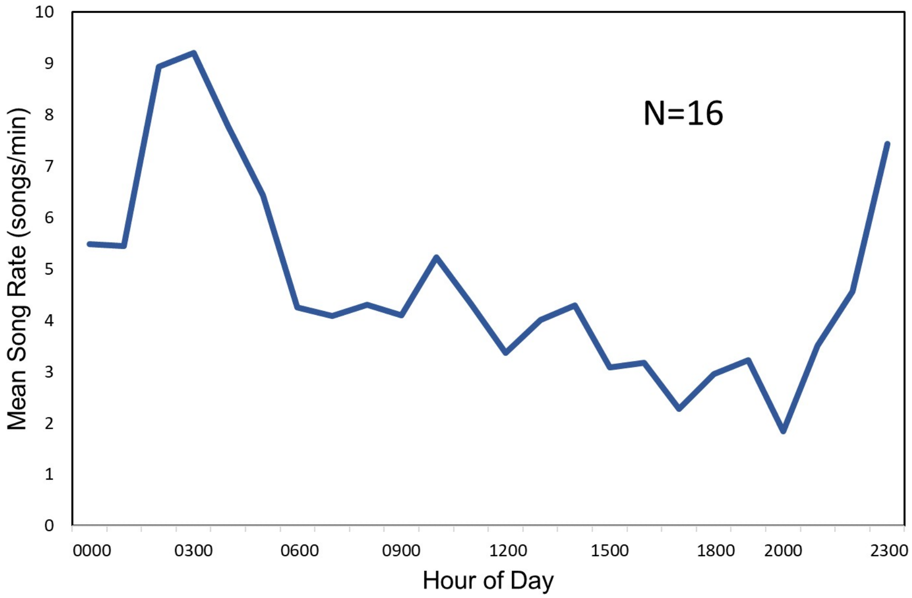
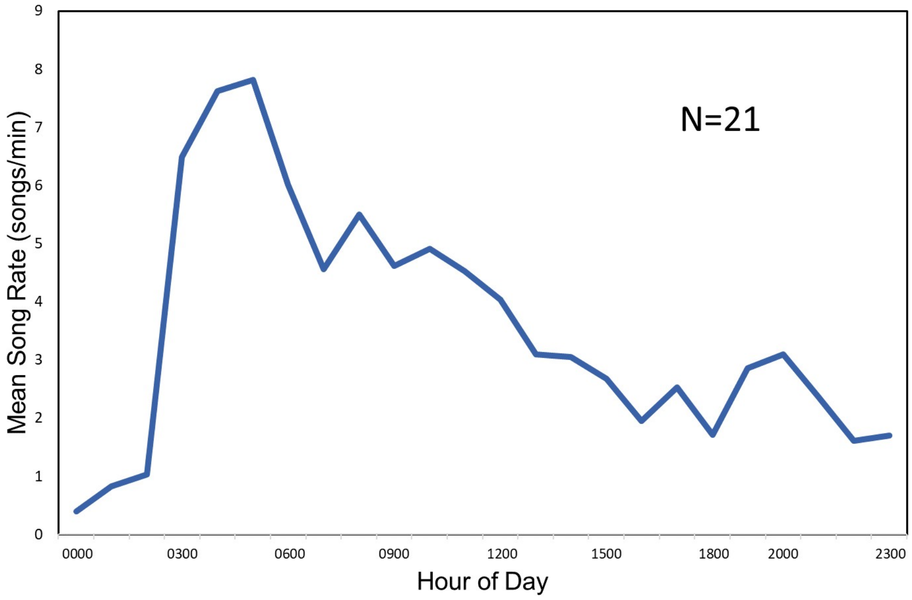
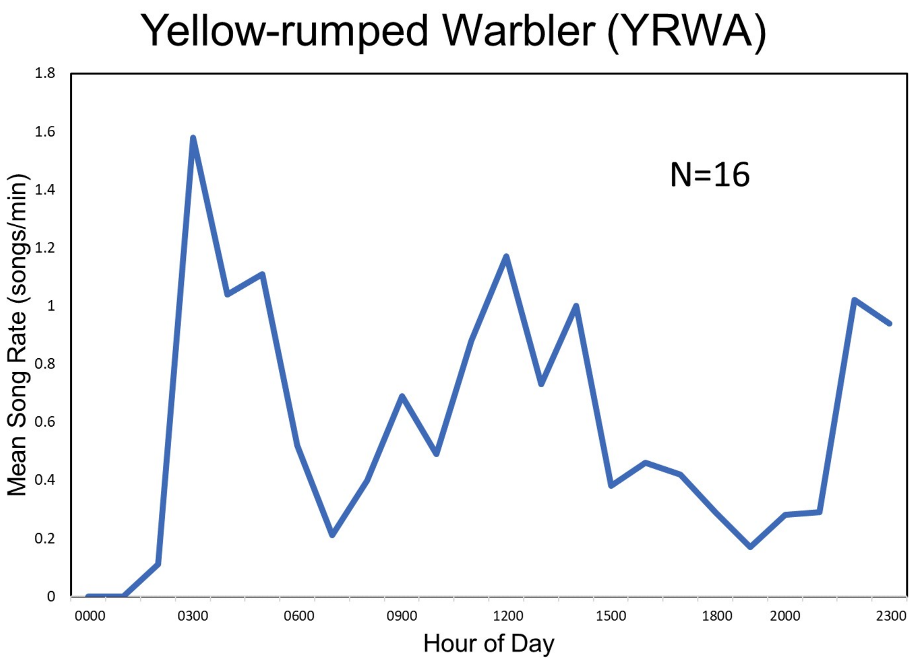
Figure 1. Mean circadian singing patterns of each species in the song community. Sample size (N) is the minimum number of individuals known to have been recorded.

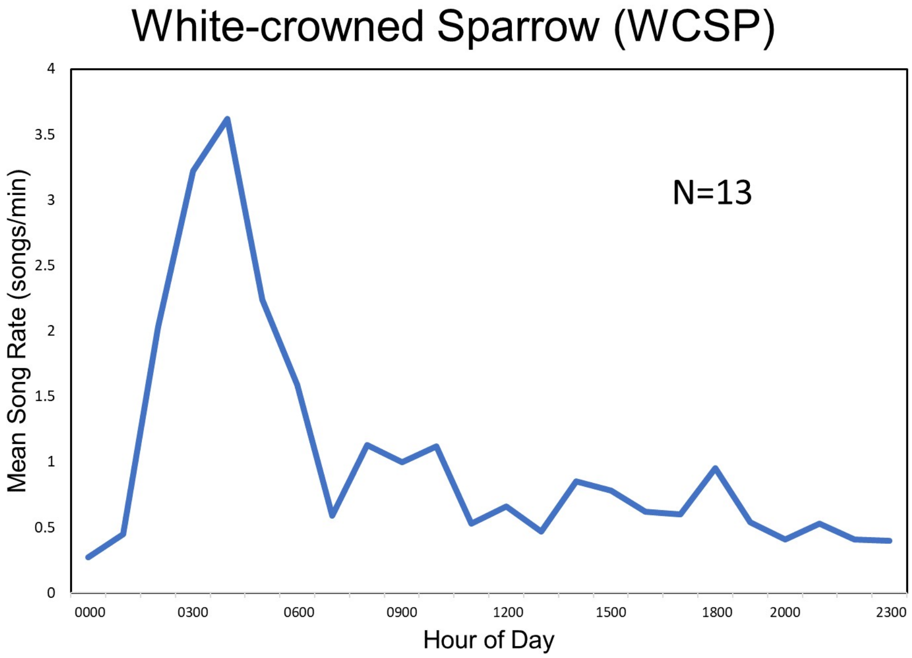
Gray-cheeked Thrush (GCTH)

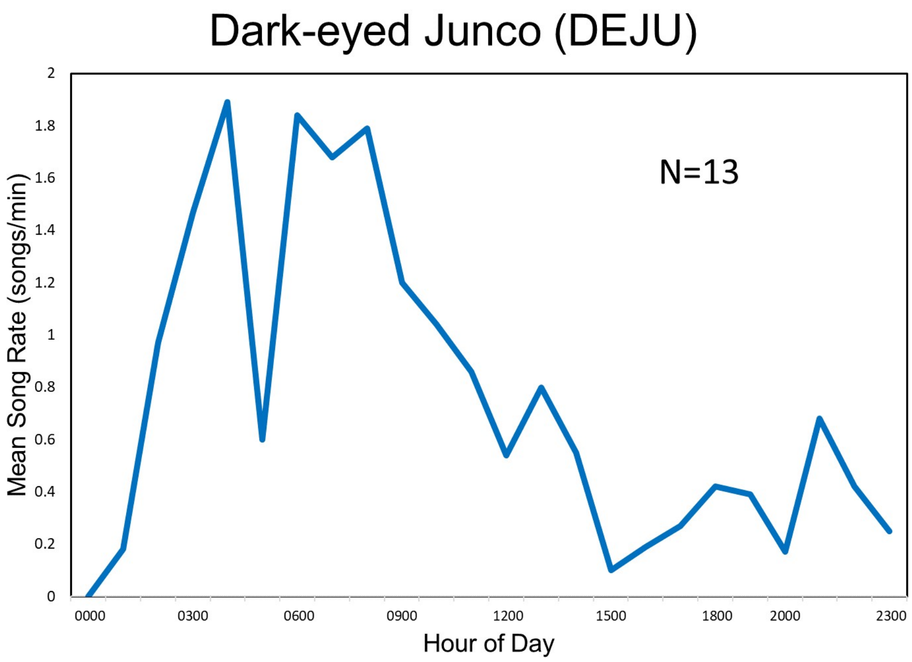


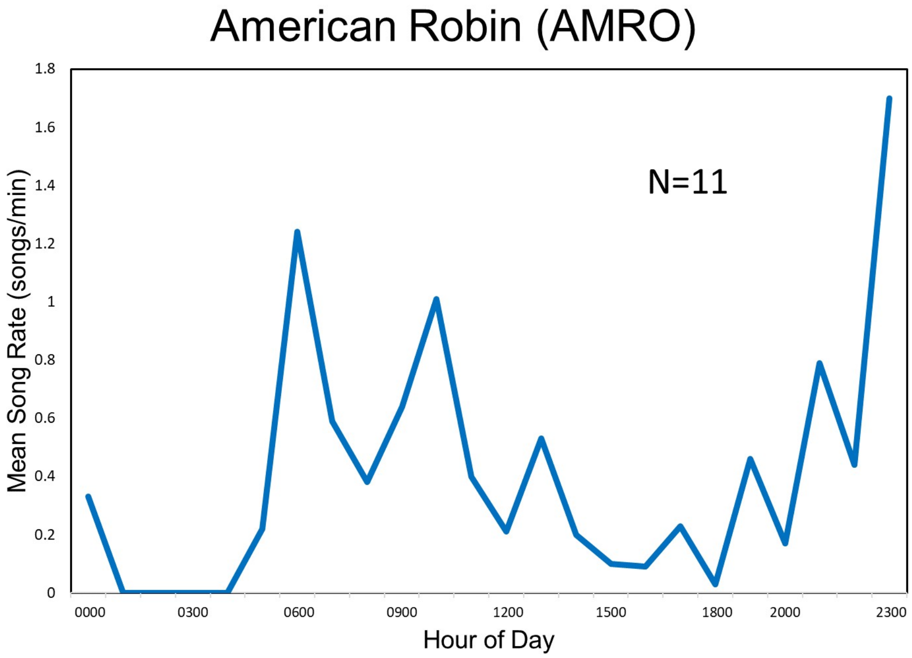
American Tree Sparrow (ATSP)

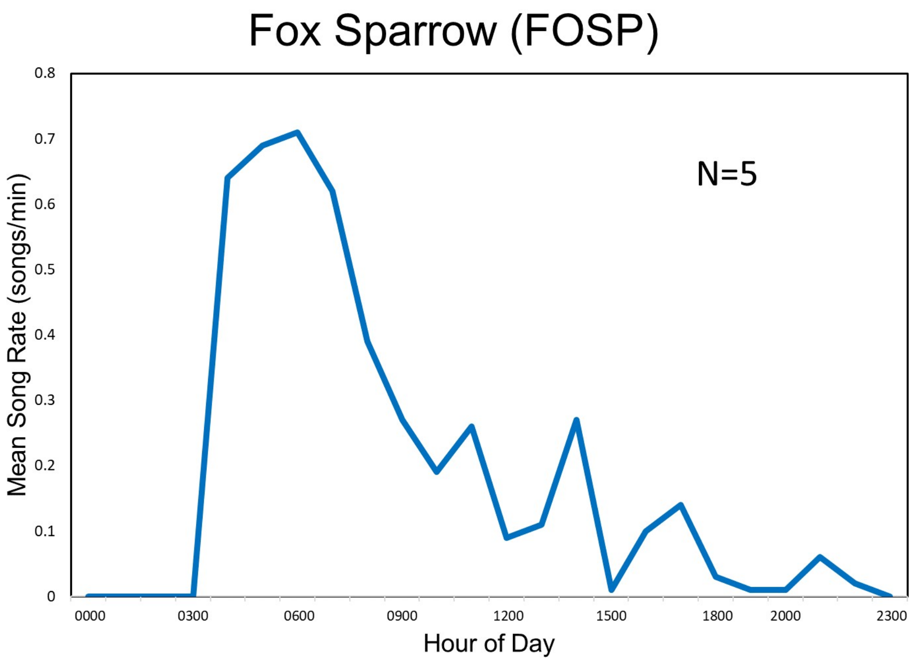



Yellow-rumped Warbler (YRWA)
N=16
Mean Song Rate (songs/min)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
0000
0300
0600
0900
1200
1500
1800
2000
2300
Hour of Day

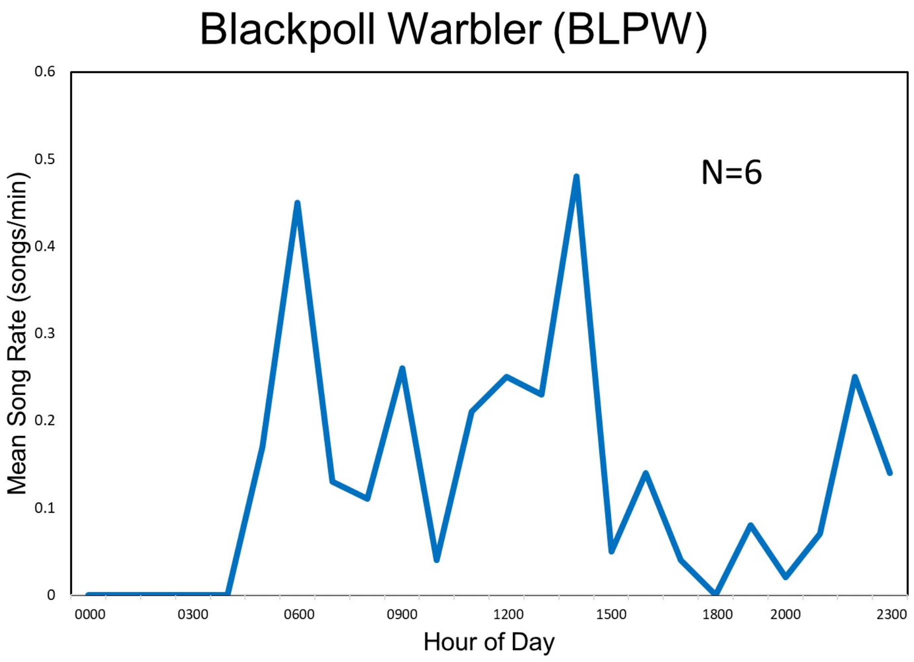

White-crowned Sparrow (WCSP)
N=13
Mean Song Rate (songs/min)
0
0.5
1
1.5
2
2.5
3
3.5
4
0000
0300
0600
0900
1200
1500
1800
2000
2300
Hour of Day


Dark-eyed Junco (DEJU)
N=13
Mean Song Rate (songs/min)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
0000
0300
0600
0900
1200
1500
1800
2000
2300
Hour of Day


American Robin (AMRO)
N=11
Mean Song Rate (songs/min)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
0000
0300
0600
0900
1200
1500
1800
2000
2300
Hour of Day



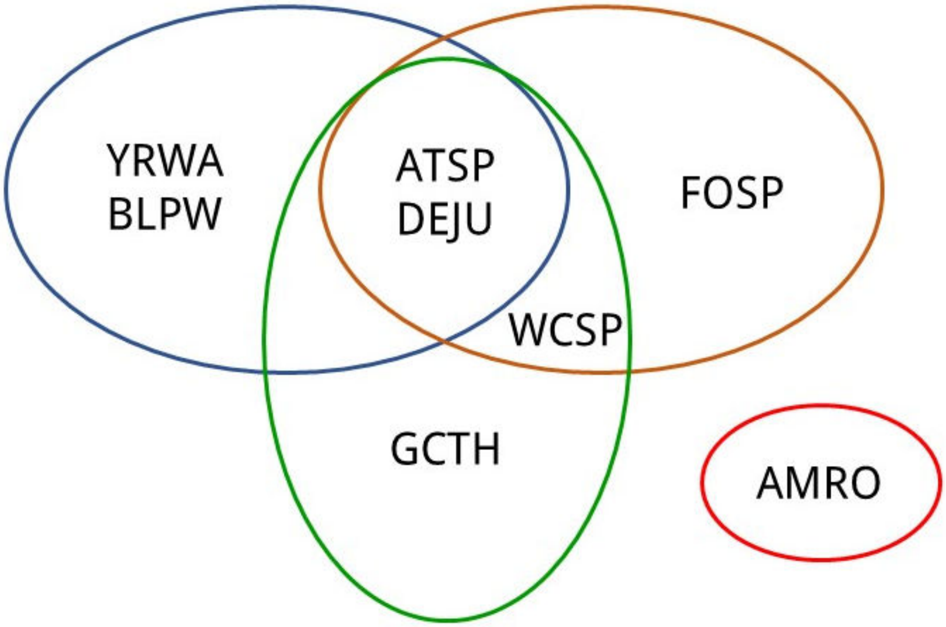
Fox Sparrow (FOSP)



Blackpoll Warbler (BLPW)

Figure 2. Diagram illustrating the division of species into groups, based upon similarities of their circadian singing patterns.

This figure is a diagrammatic representation of the results provided by the approximate randomization test and multiple comparison procedure. It simply shows the presence/absence of similarities with respect to the circadian singing patterns of each species and does not imply varying degrees of similarity.



GCTH – Gray-cheeked Thrush

ATSP – American Tree Sparrow

YRWA – Yellow-rumped Warbler

WCSP – White-crowned Sparrow

DEJU – Dark-eyed Junco

AMRO - American Robin

FOSP – Fox Sparrow

BLPW – Blackpoll Warbler

Table 1. Principal attributes of the mean circadian singing patterns

(Numbers in brackets are mean song rates during each period)

Species	**Range of Song Rates**	**Time of Main Song-related Periods**			
		Dawn Chorus	**Afternoon Lull**	**Evening Chorus**	**Evening Quiescent Period**
GCTH	1.84-9.2	0200-0500 (9.2)	2000 (1.8)	2300 (7.4)	0000-0100 (5.5)
ATSP	0.39-7.82	0300-.0600 (7.8)	1600-1800 (1.7)	1900-2100 (3.1)	0000-0200 (0.4)
YRWA	0.0-1.58	0300-0500 (1.6)	1800-2100 (0.2)	2200-2300 (1.0)	0000-0200 (0.0)
WCSP	0.27-3.62	0200-0500 (3.6)	----	----	2200-0100 (0.3)
DEJU	0.0-1.89	0300-0900 (1.9)	1500-1700 (0.1)	2100-2200 (0.7)	0000-0100 (0.0)
AMRO	0.0-1.7	0500-1100 (1.2)	1400-1800 (0.03)	2100-2300 (1.7)	0100-0400 (0.0)
FOSP	0.0-0.7	0400-0700 (0.7)	1800-2000 (0.01)	2100 (0.1)	2300-0300 (0.0)
BLPW	0.0--0.5	0500-0700 (0.5)	1500-2100 (0.0)	2200-2300 (0.3)	0000-0400 (0.0)

GCTH – Gray-cheeked Thrush

ATSP – American Tree Sparrow

YRWA – Yellow-rumped Warbler

WCSP – White-crowned Sparrow

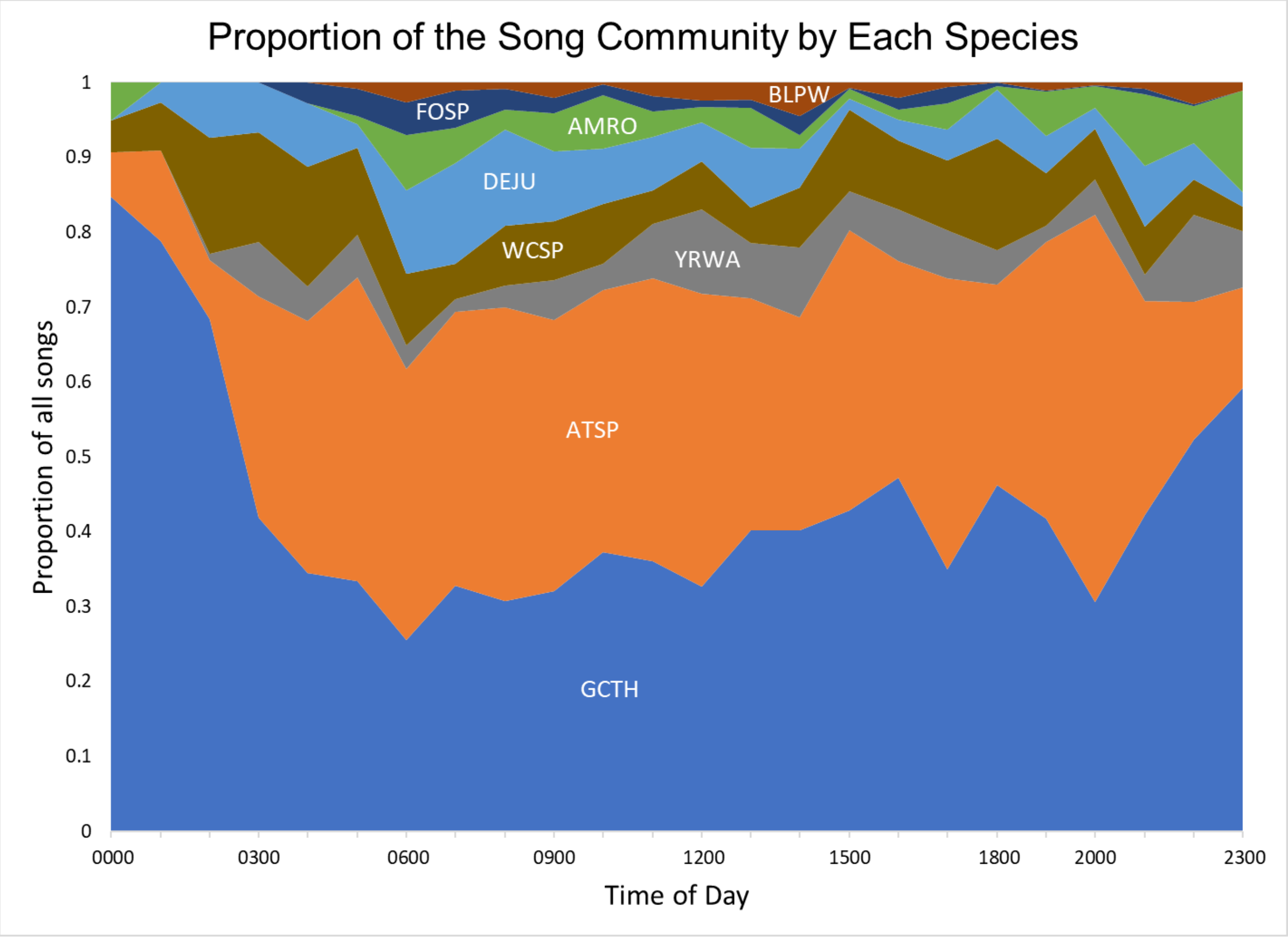
DEJU – Dark-eyed Junco

AMRO - American Robin

FOSP – Fox Sparrow

BLPW – Blackpoll Warbler

Figure 3. Proportion of singing activity by species during each hour period.



GCTH – Gray-cheeked Thrush	DEJU – Dark-eyed Junco
ATSP – American Tree Sparrow	AMRO - American Robin
YRWA – Yellow-rumped Warbler	FOSP – Fox Sparrow
WCSP – White-crowned Sparrow	BLPW – Blackpoll Warbler