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EVALUATION OF NOCTURNAL FLIGHT CALLS AS A USEFUL TOOL IN THE STUDY OF AVIAN MIGRATIONS

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Abstract. Monitoring flight calls of nocturnal migrants is a valuable tool for detecting patterns of avian migration. In conjunction with radar, morning observations, and other visual methods, acoustic monitoring of migration yields information about the numbers and types of migrants moving through an area. However, there is a general assumption that flight calls indicate an early morning peak in migration, while visual monitoring indicates a peak in the hours after sunset. In this study I use flight call data collected in Déline, NW Territories, and Lesser Slave Lake, Alberta to investigate and compare nightly and seasonal distributions of nocturnal flight calls during post-breeding migration. The results indicate that across a season the nightly distributions of flight calls at the two sites are distinct from one another. Furthermore, within each site nightly distributions appear to be very similar, though dates closer to together are usually the most similar. Thus, the results indicate that flight call distributions are related to local factors, and extrapolating information from one site may be uninformative or even misleading.

Introduction

Migration at night is typical for most passerine birds (Kerlinger 1995, Berthold 2001).

Monitoring nocturnal flight calls became a field of study in 1899 when Oren Libby counted over 3,600 flight calls as migrants streamed across the night sky. Despite a long history of research, there is much about nocturnal migration that remains uncertain (Kerlinger 1995; Evans 2002; Farnsworth 2005). Ranking high among the list of uncertain migration phenomena are functions and patterns of migratory nocturnal flight calls, as well as how the flight calls can be used in research. Farnsworth (2007) is careful to point out that (1) not only migrants give flight calls, and (2) flight calls during

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migration are not always different than those given diurnally (though very often they are). Furthermore, there are still many species whose migratory flight calls have yet to be identified. Nonetheless there is a growing body of research investigating the functions and patterns of migratory nocturnal flight calls. This research is often motivated by attempts to understand the species and numbers of migrants moving through an area at a given time.

Nocturnal migration has been studied with a variety of approaches. These techniques include radar reflectivity (Gauthreaux 1972; Larkin et al. 2002; Farnsworth et al. 2004; Barclay et al. 2007), monitoring flight call patterns (Graber and Cochran 1960; Evans 2002; Farnsworth et al. 2004;), observations of nocturnal and morning flights (Gauthreaux 1972), cage experiments (Hamilton 1962; Moore 1986), and combinations of these and other methods. Each of these methods has its own limitations, and raises interesting questions about flight calls. Radar reflectivity is inherently unable to identify the individual species in a migratory flock. Though radar will provide interesting information regarding flight speed, direction, and abundance without another source of information, we are unable to say what species are in the air. Often, radar measurements are coupled with morning counts, but counts are flawed because of the possible confusion of migratory and non-migratory birds. There is no certainty that a bird observed after dawn on the ground is a migrant. Cage experiments have been instructive in the uses and identification of flight calls, but because they are conducted in artificial environments, we cannot be sure that flight calls are used in the same way as they would be in the air. When dealing with flight call data there are a whole set of questions regarding function (Hamilton 1962; Farnsworth 2005), the effectiveness of using flight calls (Evans 2002;

Farnsworth et al. 2004; Farnsworth 2005), and the role of flock behavior during migratory flight (Lowery 1951; Gauthreaux 1972).

There is a pressing need, then, to establish the scope within which generalizations about call patterns can be made. An understanding of the function of flight calls will likely be a key to this problem. Flight calls seem to play an integral role in flock formation and maintenance (Lowery 1951; Hamilton 1962; Gauthreaux 1972). But, understanding patterns of flight calls is also going to require investigation of the diversity of flight call patterns, the amount of variation in nightly distributions within and between sites, and how factors like seasonality, migrant abundance, and species composition affect flight calls. The investigation and analysis of nocturnal flight calls is complicated by several factors including an incomplete knowledge of species-specific flight calls, uncertainty about the altitude of most migrants, mechanical limitations in the recording, and limited knowledge about individual species' patterns of migration.

A goal of nocturnal flight monitoring is to identify general trends and patterns that would allow researchers to infer densities of migrants from the call data. Stanley Ball (as cited in Farnsworth et al. 2004) reported a general pattern of calling during his extensive studies in the Gaspé Peninsula, Quebec. He observed that calls increase in the hours just before dawn. He also noted that visual observation indicated peak migration to occur before midnight. Several other studies have also indicated a peak in migration early in the night according to visual observations (Graber 1968; Newman 1956 as cited in Farnsworth et al. 2004). As a result, the morning surge of flight calls has been generalized as something of a standard flight call distribution. Furthermore, the generalization of flight call patterns has suppressed much investigation of diversity in

spatial and temporal flight call distributions. Farnsworth et al. (2004) did test the apparent discrepancies in flight call peaks and radar peaks. They found no significant difference between the peak migration of atmospheric observation and that of acoustic monitoring. However, the results of Farnsworth et al. (2004) have not since been challenged or substantiated by other researchers. Consequently, the body of literature regarding nocturnal flight call patterns is not consistent on the spatial and temporal similarities of nocturnal flight call distributions

In light of all the obstacles to applying nocturnal flight call data, this study is intended to investigate nightly and seasonal variation in hourly flight call distributions within, and between two sites in northern Canada. First, I wanted to document and analyze the amount of variation in nightly flight call distributions across a recording season at each site. Specifically, I investigate whether or not the two sites studied have flight call distributions that are similar to the observations of Stanley Ball and others. I look at the nightly distributions of flight calls to determine if either site shows an increase in the number of flight calls in the hours just before dawn. Second, I wanted to investigate the amount of variation in nightly and seasonal flight call patterns between the two sites. By comparing the sites to one another, I examine whether it is appropriate to extrapolate upon the observations at one site to infer anything about flight calls at another site. Currently, the literature seems to do just that, extrapolate on the observations of a limited number of studies. An analysis of the degree of variation in flight call distributions between two sites will either lend support to extrapolation of information, or will indicate that different sites experience significantly different patterns of flight calls.

Methods

Location and duration of study

Recordings were made August 16th to September 21, 2006 at Déline (65°11'N 123°25'W) in the Northwest Territories of Canada, and at the Lesser Slave Lake Bird Observatory (55°26'N 115°21'W) August 1 to September 12, 2007. There were no recordings at Déline September 7-9th. All recordings at Déline ran approximately 12 hours each night after civil sunset, while the recordings at Lesser Slave began at civil sunset and continued until about one hour after sunrise.

Each automated flight call detection station consisted of a pressure zone microphone mounted on the surface at the center of an 11-inch diameter rigid plastic surface and encased in light plastic waterproofing material. The microphone element was a Knowles Electronics model EK3029c that has reduced sensitivity below 2 kHz to filter low frequency sounds and make the microphone more responsive to the higher frequency sounds of migrant birds. The waterproofed pressure zone microphone was mounted on a 40-cm tubular plastic support and housed inside a large protective plastic dish with a light cotton ceiling to prevent damage from windblown vegetative material or hail. The microphone was powered with a nine-volt battery affixed with circuitry underneath the rigid plastic surface. A 10-20 meter XLR cable carries the signal from the microphone into a Rolls Mini-Mic preamp from which a mono-cable carries the amplified signal into the computer via the microphone input plug. Each microphone and housing was set 3-8 m outside the building where a computer is located where it remains for the season. Two automated detection software programs installed on each computer were set to automatically start and stop at user prescribed times. The programs save all sounds with

the proper frequency and duration with a date and time stamp while they are running. The software programs, Tseep and Thrush, were developed by Bill Evans, available at www.oldbird.org. Tseep is designed to detect and record calls emitted at frequencies between 6 and 10 kHz, capturing most warblers and sparrows; Thrush is designed for frequencies between 2.8 and 5.0 kHz, capturing most thrushes, grosbeaks, and tanagers (Evans, 2009).

Software Analysis

The calls were sorted by date and recording type – i.e. Tseep or Thrush – using the Glassofire Software, output seen in Fig. 1, available from www.oldbird.org. All of the automated recordings were displayed in Glassofire, and sorted using both visual and aural characteristics. Two major classes of sounds were discarded from the data set: (1) non-bird or non-natural sounds, and (2) non-migratory birds sounds. Both sites had recorded large amounts of mechanical sound, as well as environmental noise. Non-bird sounds could often be identified visually in Glassofire. Non-migratory birds were predominantly in the morning hours, and were often gulls and corvids. In cases where there was any uncertainty about the recording being a migrant call, I used Raven 1.2.1 (PC) spectrographic analysis software, developed by the Cornell Laboratory of Ornithology, to further examine the sound. All sounds that were not migratory flight calls were removed from the data set.

Statistics

The data were stored as the number of calls in each hour after civil sunset for each night in the recording season. Quantitative analysis was aimed at discovering patterns, and comparing distributions across nights, among dates, and between sites. All statistical

analyses were performed with Microsoft Excel or STATA 10.0 (Macintosh). To compare the distributions of flight calls between the two sites, I plotted the hourly number of flight calls averaged across the recording season. For the purposes of analysis I limit the length of recording to nine hours after sunset for both sites. Although Déline and some dates at Lesser Slave had more, every night had at least nine hours after sunset of recordings. For comparison between sites, I plotted the number of days sharing the same peak hour in flight call abundance. For both of these plots, I performed a t-test to compare the means. To compare the distributions in these two analyses, I used a Kolmogorov-Smirnov test. In the case of the peak hour analysis there were very data, so I determined the significance by using the greatest pairwise difference in values rather than actually calculating the critical value, D (Siegel 1956).

To assess differences in distributions within each site, I created correlation matrices using Spearman's rank correlation. I ordered the hourly number of flight calls within each night and then compared the distributions between nights. Using raw abundances for the correlation analyses would have almost certainly shown nights with similar abundances to be statistically similar to one another. However, the rank correlation does not measure similarities in abundance, but rather in the relative patterns of increases and decreases in flight call numbers. Finally, I applied a Euclidean distance cluster analysis to compare the temporal distribution of calls at each site. To compare distributions, I converted the raw number of flight calls into hourly proportions of the number of calls each night. By using proportions I again prevented my results from indicating similarity according to the number of calls, and instead similarity was a reflection of patterns of calling. Using Euclidean distance, I formulated dissimilarity

matrices, and then compiled them in a dendrogram . In the dendrogram, I divided the dates into ten groups based on their dissimilarity measures. More similar dates were grouped together. I used ten groups because doing so prevented all of the dates from being grouped together, and also from being divided into mostly single-date groups.

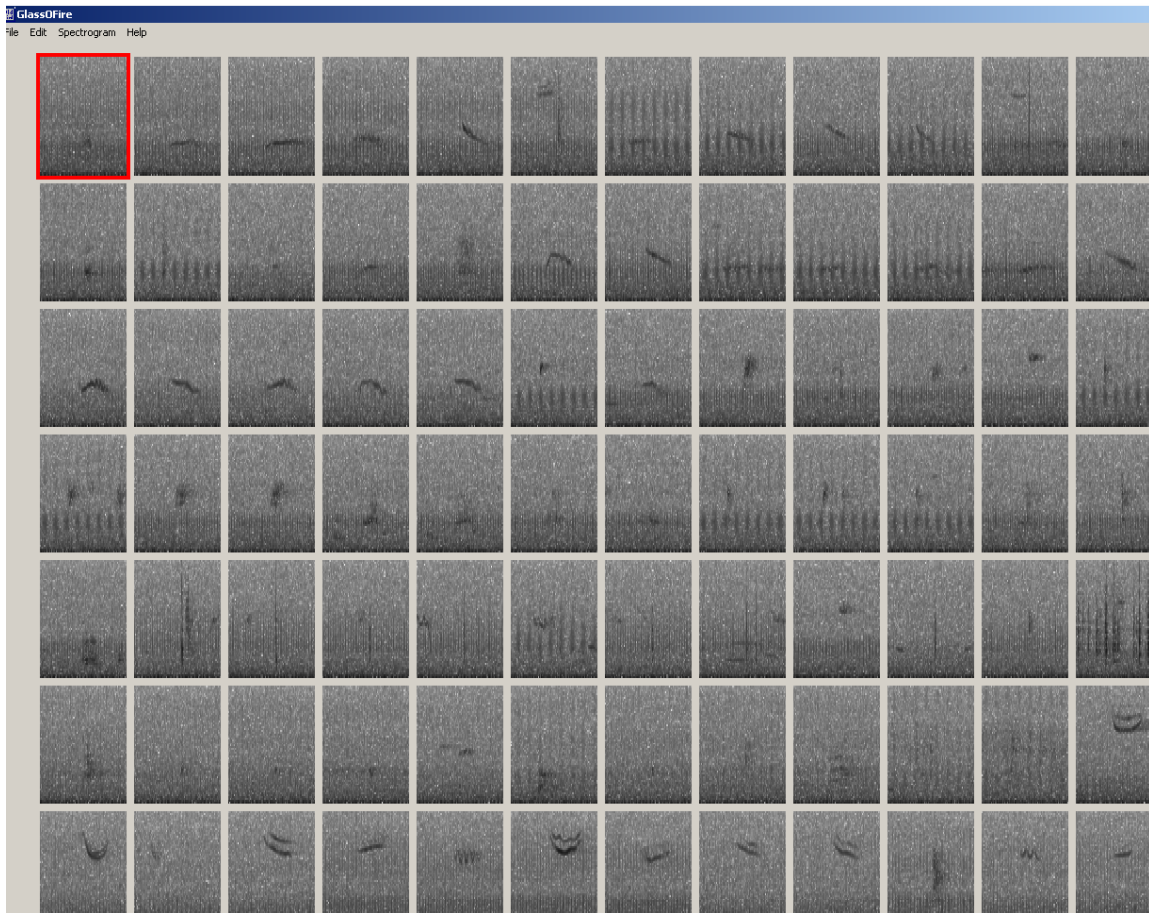


Figure 1. Glassofire software displays each recording taken by the Tseep and Thrush programs.

Results

Both sites show seasonal differences in the timing of migration (Figs. 2, 3). The recordings from Déline show a large peak in calling between the 24th and 26th of August,

followed by dramatic and continual decline in call numbers (Fig. 2). The peak calling night was August 25th during which there were nearly 1500 calls. At Lesser Slave the peak was later in the season during the night of September 6th and about 300 calls were recorded. At Lesser Slave the peaks are broader and there are two noticeable increases in calling (Fig. 3). Though we cannot compare the length of the migration season because the two recording periods are unequal, Figs. 2 and 3 indicate that migratory flight calls continue later into September at Lesser Slave compared to the more northerly Déline site. At both sites the patterns of Tseep and Thrush calls are broadly similar, showing similar increases and decreases in number of calls.

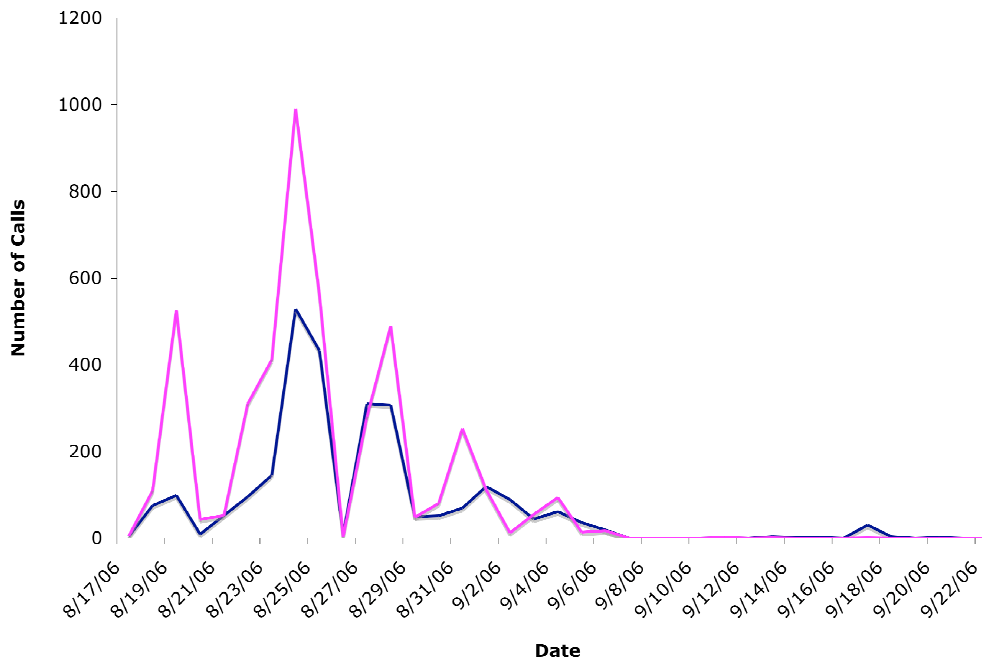


Figure 2. Seasonal distribution in nocturnal flight calls at Déline, NW Territories. The recordings made in Thrush are designated in blue and Tseep in red.

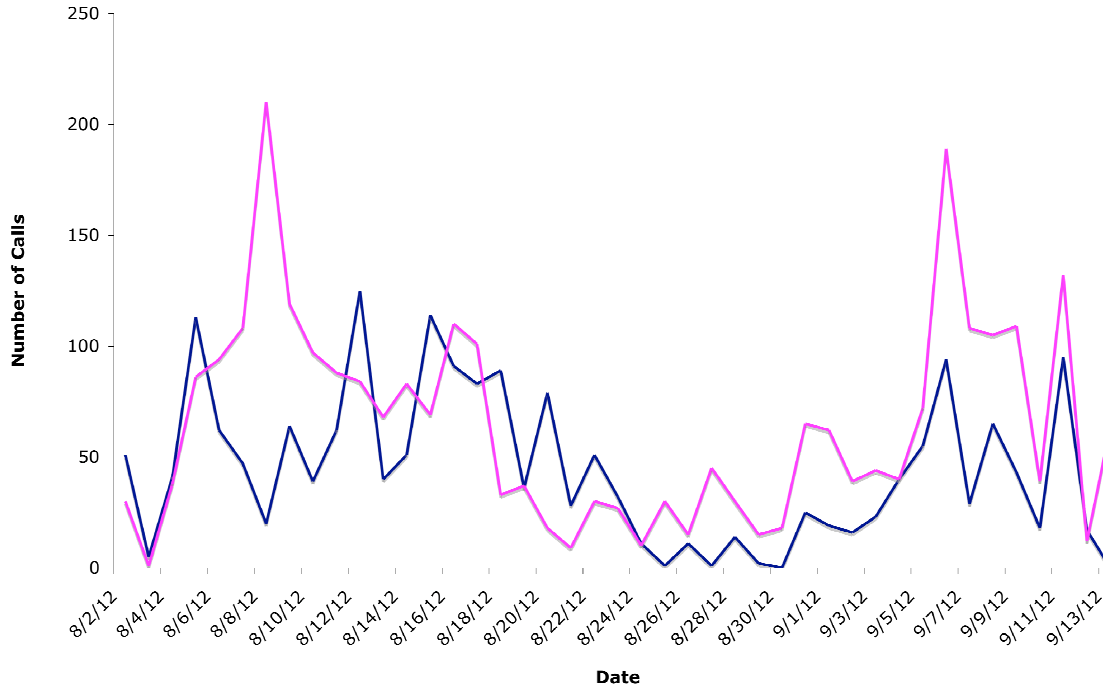
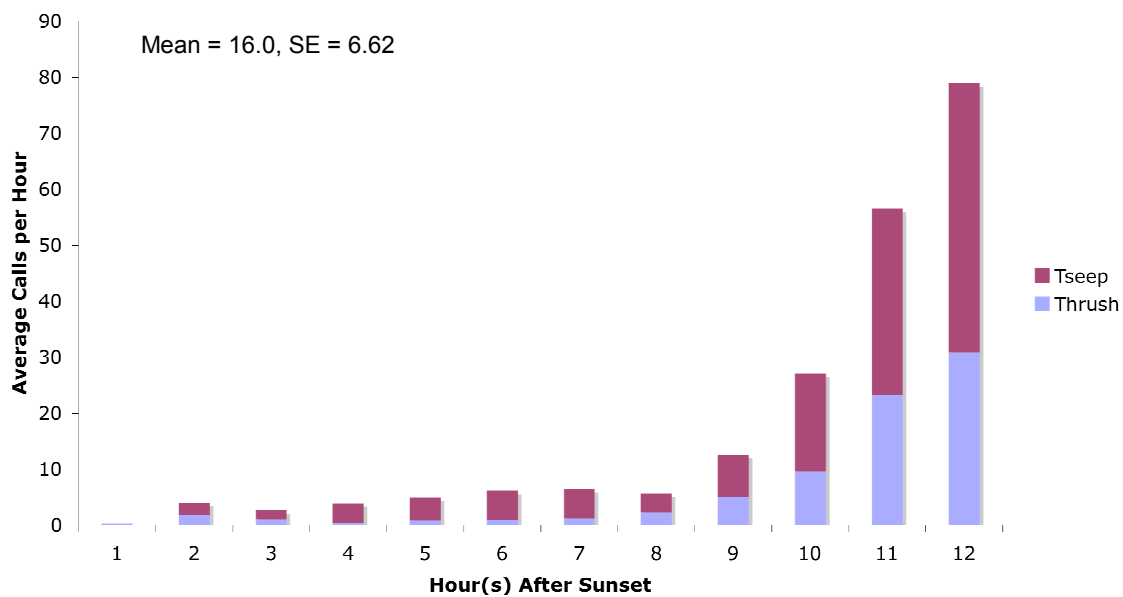


Figure 3. Seasonal distributions in nocturnal flight calls at Lesser Slave, Alberta. The recordings made by Tseep are shown in red and those by Thrush in blue.

Distinct patterns in calling also arise for the average hourly call abundances (Figs 4,5). Fig. 4a shows few flight calls at Déline throughout most of the night with a large surge in calls in the pre-dawn and dawn hours. The mean number of calls for the first nine hours after sunset at Déline (Mean = 4.78, SE = 1.03), and Lesser Slave (Mean = 10.29, SE = 1.59) are significantly different ($t(77.39) = 3.423$, $p < 0.05$). The distributions of calls are also significantly different (Kolmogorov-Smirnov, $p < 0.05$). Déline shows a steadily rising distribution, as dawn approaches (Fig. 4b), whereas Lesser Slave has a flatter distribution with peaks at four and nine hours after sunset (Fig. 5). Both sites show the highest number of calls in the ninth hour after sunset.

(a)



(b)

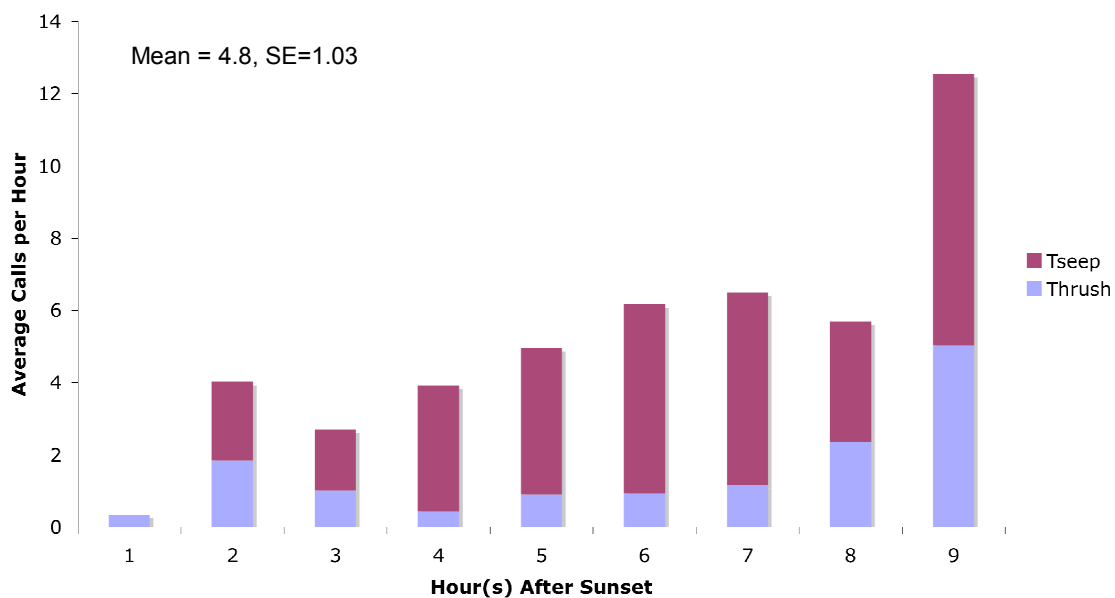


Figure 4. (a) Hourly mean number of flight calls across the entire recording period at Déline. (b) Hourly mean number of flight calls for the first nine hours (to allow comparison to Lesser Slave).

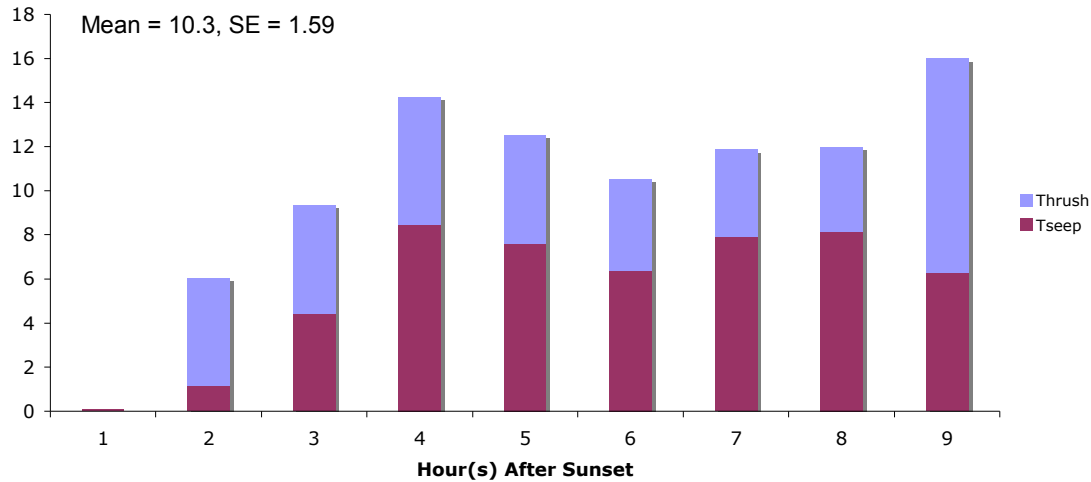
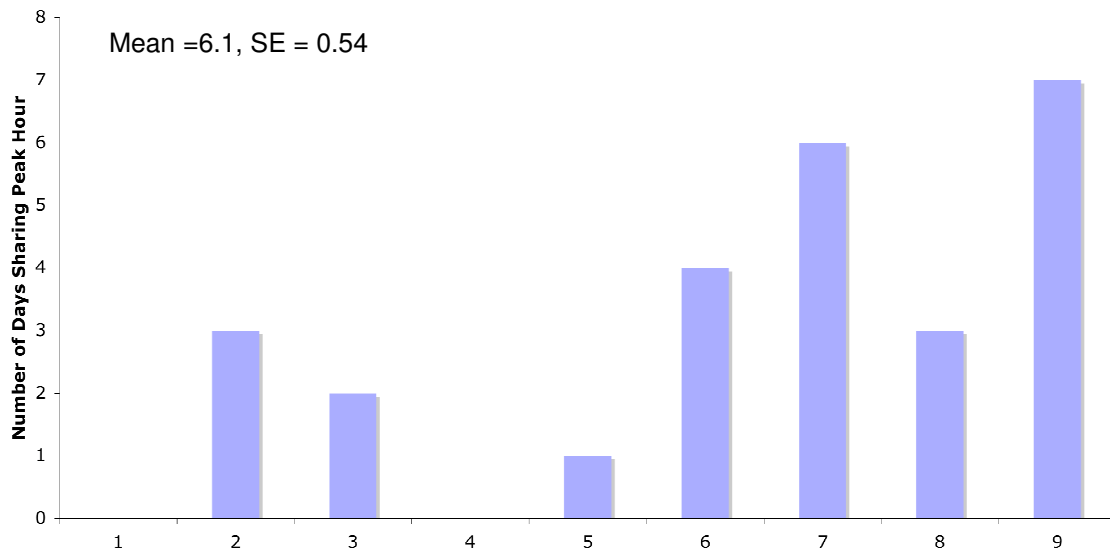


Figure 5. Hourly mean number of flights calls for the first nine hours of the night at Lesser Slave. Only nine hours were used in this case because all nights had at least nine hours of recording, though later dates had as many as eleven hours.

To visualize whether or not peak abundances in flight calls are consistent from one site to another, I plotted the number of days sharing the same peak hour of calling (Fig. 6), and distributions in Fig. 6 were significantly different (Kolmogorov-Smirnov, $p < 0.05$). The three highest hourly abundances were at six, seven, and nine hours after sunset at Déline. Conversely, the three highest peaks in flight calls at Lesser Slave were four, five, and nine hours after sunset. Not considering the ninth hour, the peaks at Lesser Slave are generally earlier in the night, as compared to Déline. Furthermore, at either site civil sunset is never before 19:00 hours over the study period, and so the high abundances at Lesser Slave are in the pre-midnight hours. At Déline, however, major peaks never fall before midnight.

The results of the Spearman's rank correlation at both sites indicate possible autocorrelation of neighboring nights within the two sites. Table 1 provides a summary of the number of significant ($p < 0.05$) and insignificant correlations, according to the number of days that separate the dates being tested.

(a.)



(b.)

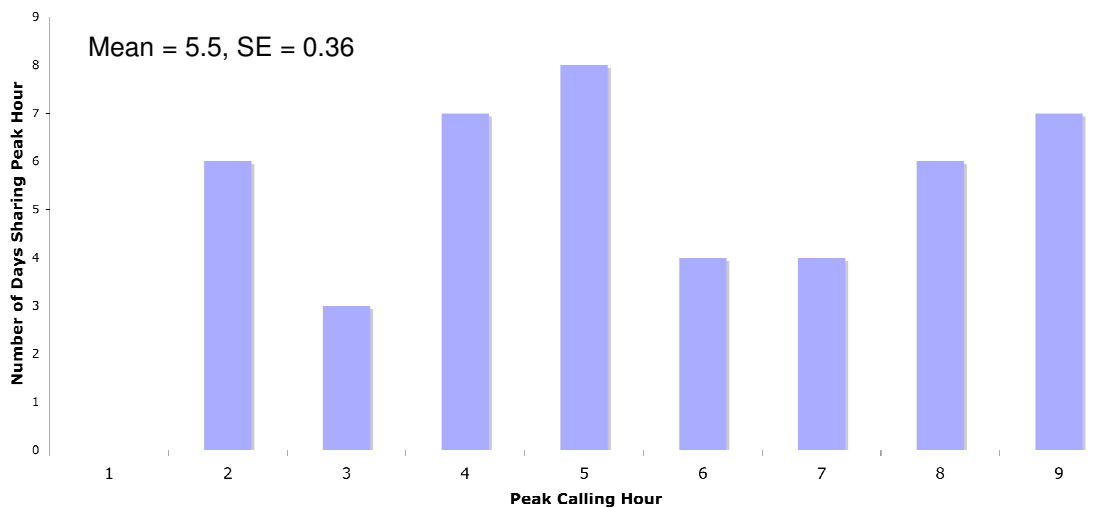


Figure 6. (a) The number of dates sharing the same peak call hour at Déline, and (b) at Lesser Slave. The peak call hours at Déline seem to be skewed towards the early evening hours, while they appear to be skewed toward dawn at Lesser Slave.

Results indicate approximately three and five times more insignificant correlations at Déline and Lesser Slave, respectively, compared to significant correlations. But, among the significant correlations there is a pattern. At both sites the significant correlations are

mostly between dates that are within ten days of each other. At Déline this pattern is true of 77.9% of the significant correlations, and at Lesser Slave 61.8%. These results indicate that there may be distributional similarities between dates close in the season, while few apparent relationships exist between dates further apart in the season.

The cluster analyses indicate a high degree of similarity between nights of calling across the season at both sites (Figs. 7,8). At Déline, four groups with more than one date, and six groups containing a single date were shown (Fig. 7). The formation of only two large groups at Lesser Slave (Fig. 8b), compared to Déline's four, as well as slightly lower dissimilarity measures at the former indicates a greater degree of seasonally consistent flight call distributions at Lesser Slave Lake. However, the differences are minimal, as Déline also shows a high degree of similarity between nightly distributions across the recording period. Fig. 8 shows a dendrogram for Lesser Slave including August 2nd in part (a), and without in part (b). August 2nd stands out with a much higher dissimilarity value probably because in three different hours there was a call count of 14 calls. This pattern was not repeated anywhere else in the recordings. After removing August 2nd the dendrograms of Déline and Lesser Slave appear quite similar.

The leaves of each dendrogram were then divided into ten groups of similar dates, based on their dissimilarity measures. At Lesser Slave two large groups each containing many dates were formed, and eight groups with only one date were formed (Fig. 8a).

Most importantly, the clustering of dates in Figs. 7 and 8 reinforce the results of the rank correlation analyses. Many of the pairings of data in the dendrograms include nights that are quite close in time. For instance, at Déline August 27th, 28th, and 29th have

Table 1. The number of significant and insignificant correlations of hourly call distributions between dates, using Spearman's rank correlation. Significance determined at a $p < 0.05$ value. The results for Déline are shown in (a), and the results for Lesser Slave are shown in (b).

a.)			b.)		
Days Apart	Non-Sig.	Significant	Days Apart	Non-Sig.	Significant
1	12	11	1	28	13
2	16	8	2	33	8
3	16	6	3	27	13
4	15	8	4	30	9
5	11	4	5	33	5
6	18	6	6	31	7
7	15	4	7	25	11
8	9	5	8	29	6
9	11	8	9	28	7
10	9	7	10	28	5
11	15	3	11	25	6
12	12	4	12	24	7
13	12	4	13	26	4
14	10	1	14	26	3
15	13	1	15	24	4
16	9	1	16	24	3
17	12	2	17	22	4
18	7	2	18	23	2
19	8	0	19	23	1
20	8	1	20	23	0
21	5	0	21	21	1
22	8	0	22	20	1
23	5	0	23	18	2
24	7	0	24	18	1
25	2	0	25	15	3
26	6	0	26	16	0
27	2	0	27	13	1
28	2	0	28	10	3
29	3	0	29	10	2
30	0	0	30	11	0
31	1	0	31	11	0
32	0	0	32	10	1
Total	279	86	33	9	1
			34	9	0
			35	7	1
			36	7	0
			37	6	0
			38	5	0
			39	5	0
			40	4	0
			41	3	0
			42	2	1
			43	1	0

the most similar distributions. At Lesser Slave the same is true for August 11th, 13th, and 14th. Nonetheless, there are also several pairings at each site of similar nightly distributions between dates that are more than ten days apart. These include dates like August 27th and September 6th (Fig. 8b), and August 22nd and September 9th at Déline (Fig. 7).

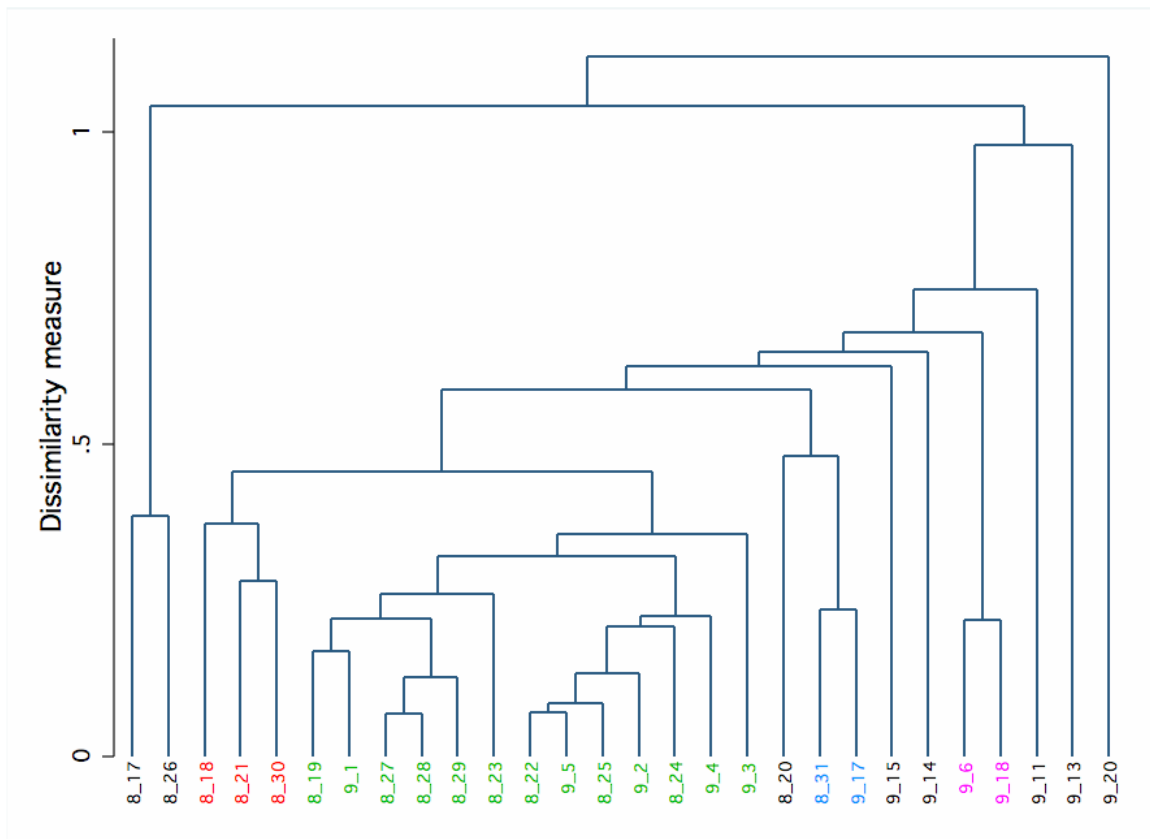
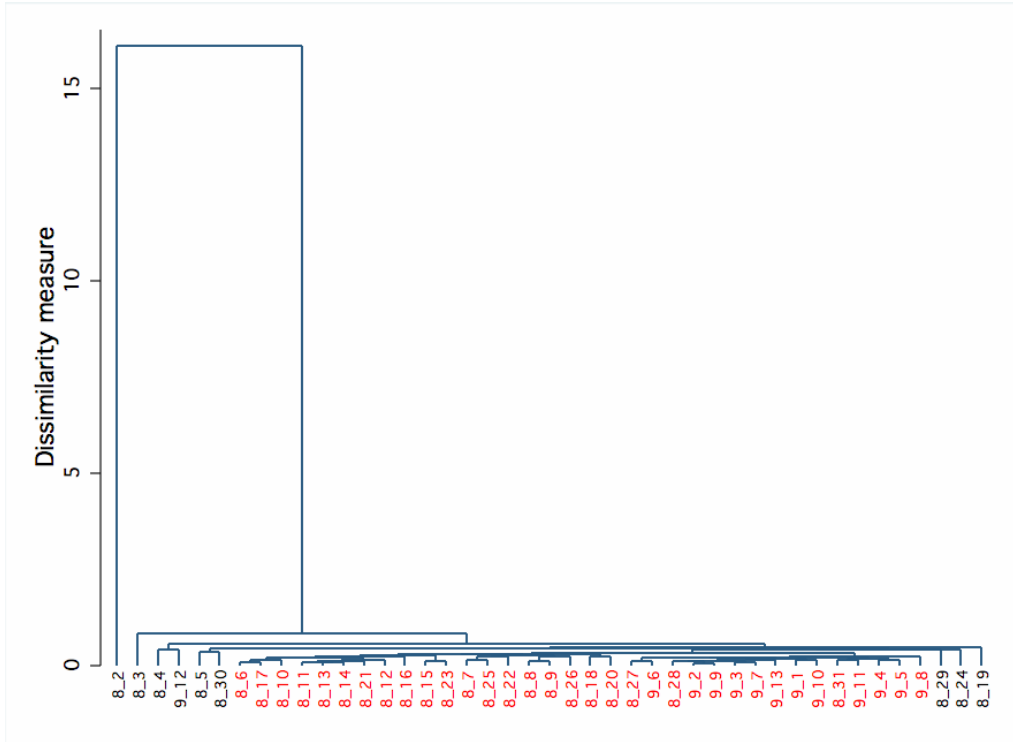


Figure 7. Cluster analysis of dissimilarities between nightly flight call distributions at the Déline site. Nights with no recorded calls are excluded from the analysis. The dates were grouped into ten groups according to dissimilarity measure. The dates shown in red, and green, blue, and purple are each one of the resulting groups. The dates shown in black, remained in their own group after the sorting.

Discussion

Since Stanley Ball published the results of his Gaspé Peninsula study in 1952, it has been generally thought that flight call monitoring indicates that the peak of nocturnal migration is in the pre-dawn hours. My results do not support the assertion that acoustic recordings indicate peak abundance in the pre-dawn hours. While the nightly distribution of calls at Déline (Fig. 4a) indicates that migration reaches its height of abundance in the hours immediately before dawn, the distribution of calls at Lesser Slave indicate a peak in abundance before midnight. The distribution of flight calls at Lesser Slave is more similar to what Ball and others observed using visual monitoring methods (Farnsworth et al. 2004). Simply because two sites differ in their nightly flight call distributions, we can not safely extrapolate upon Ball's observations at Gaspé to infer anything about flight call patterns at any another site.

(a.)



(b.)

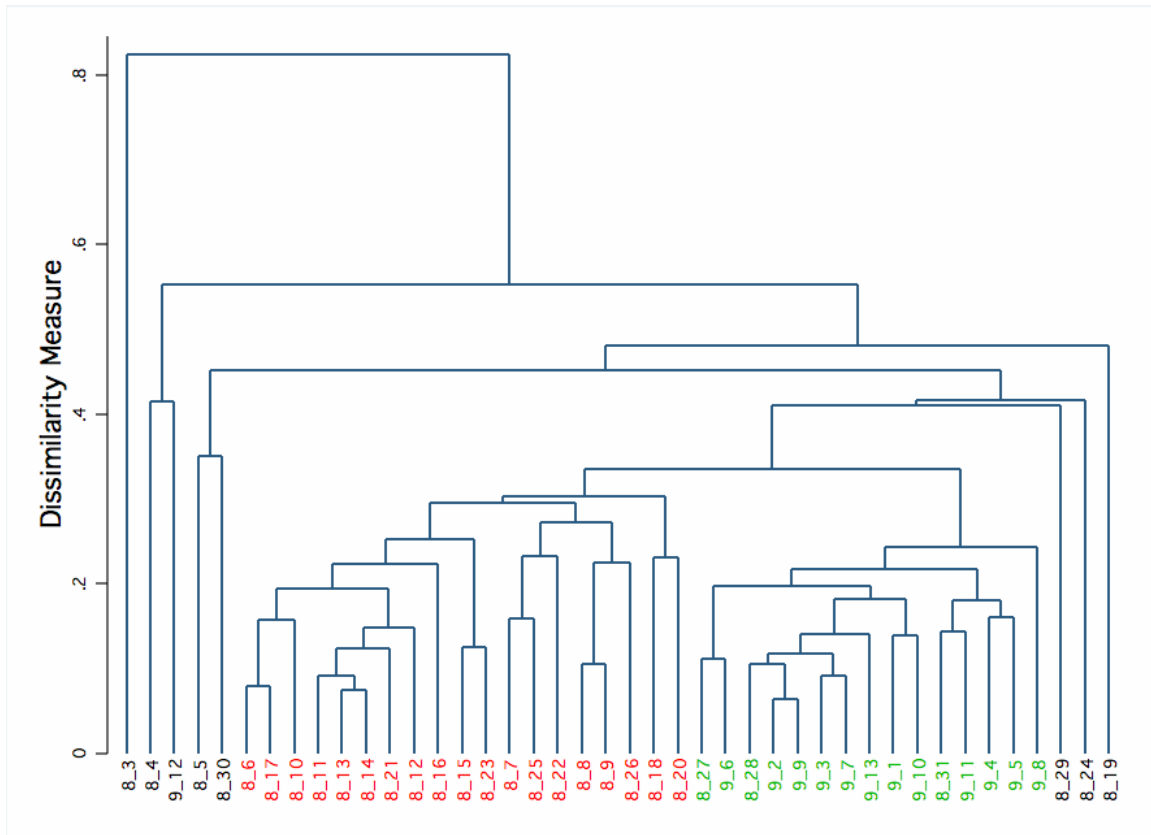


Figure 8. Cluster analysis of dissimilarities between nightly flight call distributions at the Lesser Slave site. Dendrogram (a) includes August 2nd, and (b) does not. The dates were grouped into ten groups according to their dissimilarity measures. The dates shown in red, and green compose two of the resulting groups. The remaining dates, shown in black, remained in their own group after the sorting.

Though the data provided will not allow me to conclusively determine the cause of variation in flight calls between Déline and Lesser Slave, I can speculate on likely causes. For instance, the dawn surge in flight calls at Déline (Fig.) is quite possibly a reflection of the geography of the area. Diehl et al. (2003) report that large bodies of water can act as temporary barriers to migration, causing migrants to refuse to cross late in the night, and in some cases turn around and head for the nearest shoreline as morning approaches. The recording site in Déline is situated on the northwest side of an arm of Great Bear Lake, which could possibly deter late night crossings and encourage a pile-up of migrants on the shore near the recording site. The area surrounding the Lesser Slave recording site

is on the southwest side of Lesser Slave Lake, and so the migrants have already made their crossing. There is less potential for an accumulation of migrants. Whatever the cause of these differences, Déline is more in line with earlier observations that an acoustic record of migration indicates increased migrant abundance in the hours just prior to dawn (Newman 1956 as cited in Farnsworth et al. 2004; Graber 1968). The results from Lesser Slave do not conform to such a pattern (Fig. 5).

The rank correlations indicate that only 15-24% of the correlations between nightly distributions of hourly flight call numbers were significant. This does not seem to match the high degree of season wide similarities depicted by the cluster analyses (Figs. 7, 8) However, a review of the r^2 values from the rank correlations shows that many of the significant values are only explaining little more than half of the variation. Because of the limited explanatory power of the rank correlations the cluster analysis would seem to be a more rigorous test of distribution similarities. However, both the cluster analysis and the correlations do support the findings that dates closer together have more similar nightly flight call distributions. The pattern of similar distributions occurring in neighboring nights is not universal. The pattern is more pronounced at Lesser Slave than at Déline, but both sites have aberrant observations. Again, the data used in this study will not allow for conclusive explanations, but I can speculate as to why we might observe distant nights having very similar distributions of flight calls. For instance, if the weather patterns were similar for several consecutive days the result may be a high degree of similarity in flight call distributions over those nights. However, when a front passes through, the migrant flock may shift flight patterns accordingly, which would subsequently be reflected in the patterns of calling. Were such a shift to occur, the new

flight call distribution may be more similar to a distant night than to the preceding night's distribution. We might also explain shifting flight call patterns as a result of changing species composition in the migrant flock.

Limited seasonal variation in flight call distributions within each site, combined with noticeable differences between the two sites indicates that the Déline and Lesser Slave recordings represent two distinct populations with regard to flight call distributions. The results of averaged hourly call rates (Figs. 4,5) and the results of the analysis of peak call hours (Fig. 6) indicate that flight call distributions at Déline are similar to those observed by Stanley Ball in the Gaspé Peninsula (as cited in Farnsworth et al. 2004). However, from Fig. 4a the significant morning increase in flight calls is quite late, and in many cases in the hours after sunrise. Nonetheless, flight calls seem to increase in number as the night moves towards dawn. The distributions at Lesser Slave have more flight calls earlier in the night, compared to the number of calls in the pre-dawn hours. Indication of a peak in migration in the early hours of the night has been considered more typical of visual records like radar (Newman 1956 as cited in Farnsworth et al. 2004; Graber 1968). My findings do not support the distinction between peaks of migration as measured by visual and acoustic means.

The differences between the recordings at Déline and Lesser Slave imply that flight call distributions are responsive to regional or local forces. The grouping of distributions from neighboring dates and the distinctions between the two sites could be the result of factors like weather patterns, species composition of flock, latitude, or topography. There is much less support in these findings for the idea that flight calls are a reflection of endogenous cues. Endogenous cues would likely result in more uniform

flight call distributions between these two sites than were actually observed. If, in fact, exogenous factors are more influential with regard to nocturnal flight calls, than research in the field ought not to extrapolate the observations of migration patterns from one site to indicate anything about flight calls at another site.

Despite such a limitation, we must be careful not to assume that the study of flight calls is futile. In outlining the degree of variation that researchers will encounter while studying nocturnal flight calls, I hope to draw attention to the amount of study that is needed in the area. A more thorough and organized analysis of flight call distributions across place and time will yield better information on the patterns and purposes of flight calls. Just as we rely on point counts in the North American Breeding Bird Survey conducted every year, so too could we use flight calls to learn about changes in migration. Furthermore, now, and in the foreseeable future nocturnal flight calls are the most reliable avenue to identify the exact species that are migrating in an area. Radar may be a more accurate measure of migration direction and speed, possibly even abundance, but it will not inform us about the species of birds that are actually flying.

A more complete understanding of patterns and processes is going to be necessary in the near future as we consider new energy sources to power our societies. One example of where this field can make a large impact is in the relationships between wind farms and migratory pathways. Currently many programs and evaluation protocols in place rely heavily on carcass surveys (Erickson 2003) and breeding bird analyses (Percival 2003). While these methods are manageable in terms of personnel and time, they may prove to be inaccurate and insufficient study methods. Avian migration concentrates the numbers of birds moving through an area, and thus likely increases the potential for collision.

Furthermore, migrants passing through the area are not accounted for in a breeding bird analysis, and yet migrants might very well include endangered and protected species. Radar has also played an important role in determining the risks of constructing wind turbines in an area (Barclay et al. 2007; Gauthreux 1970, 2006; Mabey and Cooper 2004). However, radar cannot answer the question of just who is at risk. At this time radar does give us a better impression of the number of migrants moving through an area (Farnsworth et al. 2004), but it does not tell us which species they are. The value of flight call monitoring, especially for nocturnal migrants is that it can instruct researchers on the species compositions that compose a pre- or post-breeding migration. Furthermore, nocturnal flight call monitoring provides the observer with information like that detailed in this paper: migration timing and location. Further consideration and study of nocturnal flight calls given by migrants will yield more detailed clues regarding the patterns and processes of avian migration.

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