JOURNAL OF AVIAN BIOLOGY 35: 365–369, 2004

A comparison of nocturnal call counts of migrating birds and reflectivity measurements on Doppler radar

Andrew Farnsworth, Sidney A. Gauthreaux, Jr. and Donald van Blaricom

Several studies have found that the peak in bird density in the atmosphere during nocturnal migration occurs before midnight, while the peak in vocalizations from migrating birds occurs after midnight, in the hours just before dawn. In a recent study, the patterns of calling from a single species of migrating birds correlated well with the patterns of density estimates of migrating birds. We test the null hypothesis that the patterns of reflectivity measurements and number of vocalizations during nocturnal migration are not related. We sampled radar data and nocturnal flight calls during spring and fall 2000 in northwestern South Carolina and southeastern New York. We analyzed changes in the hour-to-hour patterns of bird density and vocalizations for 556 hours on 58 nights. We also analyzed the night-to-night changes in the patterns of peak hour bird density and peak hour of vocalizations on 32 nights. We found that most of the hour-to-hour and night-to-night patterns of density and vocalization counts are significantly related and reject the null hypothesis. However, despite significant relationships between reflectivity measurements and vocalization counts, a great deal of variation in vocalization counts remains unexplained. These results suggest that factors other than bird density are responsible for the variation in vocalizing by migrating birds.

Andrew Farnsworth (correspondence), Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA Tel. 607-254-4240, E-mail: af27@cornell.edu. Sidney A. Gauthreaux, Jr., Department of Biological Sciences, Clemson University, Clemson, SC 296 34, USA. Donald van Blaricom, Strom Thurmond Institute, Clemson University, Clemson, SC 296 34, USA.

Many birds frequently produce flight calls while migrating at night (Ball 1952, Graber and Cochran 1959, Evans and Mellinger 1999), and these calls apparently serve to maintain flocks and to communicate information within and perhaps among flocks (Hamilton 1962). Several studies have found that the peak in bird density in the atmosphere during nocturnal migration occurs before midnight, while the peak in vocalizations from migrating birds occurs after midnight, in the hours just before dawn (Lowery and Newman 1955, Newman 1956, Graber 1968). In contrast, Larkin et al. (2002) reported that call rates for a single species and radar reflectivity from migrating birds co-vary positively. In this paper we examine whether call counts of nocturnally migrating birds are density-dependent. We test the hypothesis that there is no relationship between reflectivity measurements of the density of birds in the atmosphere and the number of flight calls. We use the same approach as Larkin et al. (2002), but unlike their study, we do not limit our recording of flight calls to a single species.

Methods

Location and duration of study

In northwestern South Carolina, we sampled flight calls in Clemson, SC and sampled radar data from the displays of the WSR-88D radar at Greer, SC. In southeastern New York, we sampled flight calls in Rye, NY and sampled radar data from the displays of the WSR-88D radar at Brookhaven, NY. Sample locations were approximately 23 km apart in both locations. We sampled during 32 entire nights (30 minutes after local sunset and ending 30 minutes before sunrise) and 26 partial nights. From northwestern South Carolina locations, we gathered data for 13 nights in the spring (6 April–25 May 2000) and 21 nights in the fall (13 August–17 October 2000). From the southeastern New York locations, we gathered data for 8 nights in the spring (9 May–1 June 2000) and 16 nights in the fall (6 September–29 October 2000).

Collection and analysis of acoustic data

To record flight calls, we used pressure zone microphones (PZMs) with Knowles Electret EK 3132 condenser microphone elements fitted on plastic dinner plates (see Evans and Mellinger 1999). The EK 3132 microphone element is sensitive to frequencies from 0.1–10 kHz, a range encompassing most vocalizations of nocturnal migrants in eastern North America (warblers and sparrows: 6–9 kHz; thrushes, grosbeaks and tanagers: 2–5 kHz; Evans and Mellinger 1999, Evans and O'Brien 2002). We evaluated the microphone's detection capabilities in different wind conditions with a dickcissel *Spiza americana* (2–5 kHz range) and a Savannah sparrow *Passerculus sandwichensis* (6–9 kHz range) vocalization. For evaluation of the microphone detection capabilities, see Farnsworth (2001). Results of the microphone trials were consistent with previous studies (warblers and sparrows within approximately 300 m above ground level (AGL), and thrushes, grosbeaks and tanagers within approximately 600 m AGL; Evans and Mellinger 1999, Evans and Rosenberg 1999).

We gathered data following the methods of Evans and Mellinger (1999) and Larkin et al. (2002); but unlike these studies we analyzed a complete spectrum of species calls using three algorithms developed and optimized by Bill Evans and Steve Mitchell to detect calls of different lengths in three frequency bands: 6–9 kHz, 50 ms (similar to "Tseepo" software available at www.oldbird.org), 2–4 kHz, 150 ms, and 1–9 kHz, 150 ms. We examined detections using visual spectrographic analysis software (GlassOFire, www.oldbird.org) which generates spectrograms from calls digitized at a 22 254 Hz sampling rate and processed using a 256 point FFT, 128 point frame length, Hamming window (hop size = 64) and spectrogram screen size of approximately 5.3 cm wide by 3.5 cm high.

Collection and analysis of Doppler radar data

For radar data, we used three WSR-88D products: base reflectivity, base velocity (radial velocity), and vertical wind profile (Gauthreaux and Belser 1998). We screened base reflectivity images and rejected those contaminated by non-biological targets (e.g., precipitation, dust) and anomalous atmospheric propagation of the radar beam (e.g., strobes), leaving a series of images with only biological targets. In an effort to discriminate birds from other biological targets, we compared the directions and speeds of targets in the radial velocity image to the directions and speeds of winds aloft (Gauthreaux et al. 2003). For wind speed data, we downloaded tabular text files (University of Wyoming, www-das.uwyo.edu) from radiosondes launched daily near 12.00 and 00.00 UTC from the National Weather Service stations at Atlanta, GA (FFC) and Brookhaven, NY (OKX), the nearest stations to our study sites. To make certain that the winds over our sample sites were the same as those measured at Atlanta and Brookhaven, we examined maps of winds aloft from surrounding stations for the 1000 mb (100 m above mean sea level) and 925 mb (800 m above mean sea level) levels. We quantified radar reflectivity in terms of birds km^{-3} within a range of 37 km using calibration curves from Gauthreaux and Belser (1999). For reference, acoustic sampling locations were approximately 23 km beyond this range at both stations (Farnsworth 2001). This range band samples altitudes from the radar antenna height to 747 m above radar antenna height (Gauthreaux et al. 2003).

We limited our analysis to nights when atmospheric conditions remained essentially unchanged throughout the night. We accomplished this by comparing radiosonde data and vertical wind profile products to check consistency of wind speed and direction over the course of the evening. Additional details can be found in Farnsworth (2001). Prior to analyses we normalized the bird density data by using a logarithmic transformation. We used PROC REG procedures to perform regression analyses to model the relationship between bird density and number of calls (SAS Institute 1999).

Results

Hourly patterns of reflectivity measurements and call counts

Although the hour-to-hour changes in the number of calls are significantly related to hour-to-hour changes in bird densities for northwestern South Carolina in the fall, the relationship is not a strong one, and changes in density account for little of the variation in the number of calls ($R^2 = 0.16$, $F_{1,214} = 41.71$, $P < 0.0001$; Fig. 1a). The relationship between number of calls and bird density during the night in the fall for southeastern New York is not significant ($R^2 = 0.01$, $F_{1,144} = 1.44$, $P = 0.23$; Fig. 1b). In the spring in northwestern South Carolina, the hour-to-hour pattern of flight calls is significantly related to the hour-to-hour pattern of migration density, but bird density explains little of the variability in number of calls ($R^2 = 0.11$, $F_{1,122} = 14.89$, $P = 0.0002$; Fig. 1c). In southeastern New York during spring nocturnal migration, there is no relationship between the density of birds in the atmosphere and the number of calls recorded ($R^2 = 0.00$, $F_{1,68} = 0.00$, $P = 0.98$; Fig. 1d). The relationship between all hourly counts of flight calls against all hourly bird migration densities is significant, although bird density accounts for little of the variation in call count ($R^2 = 0.09$, $F_{1,554} = 53.82$, $P < 0.0001$; Fig. 2a).

Nightly peak patterns of reflectivity measurements and call counts

The pattern of nightly peak call count changes as a function of nightly peak migration density for the spring and fall in northwestern South Carolina (Fig. 3a), and the relationship between the two is significant ($R^2 = 0.54$, $F_{1,17} = 20.02$, $P < 0.001$). If we remove the pair of outlying data points in the upper right of Fig. 3a, the relationship is not significant ($R^2 = 0.09$, $F_{1,16} = 1.51$, $P = 0.24$). The patterns of nightly peak density and

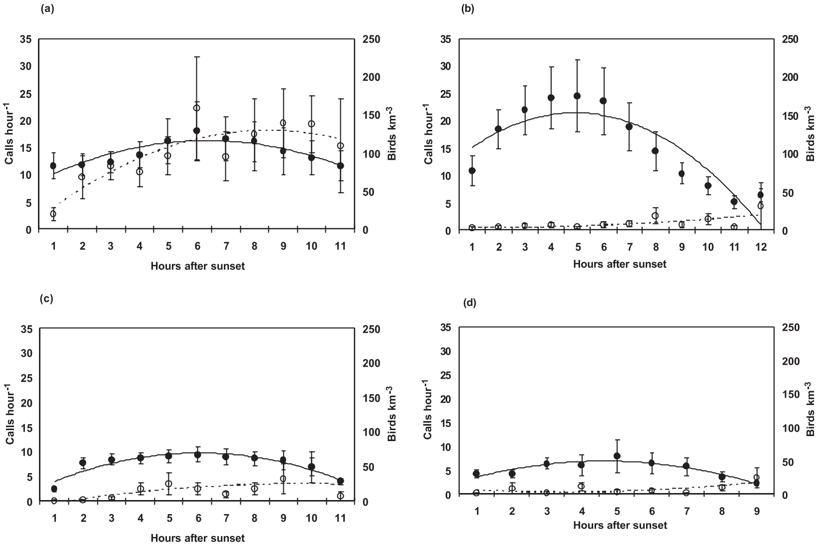

Fig. 1. Hour-to-hour means and standard errors of bird density (birds km^{-3}) (filled circles and continuous lines) and flight calls hour $^{-1}$ (open circles and broken lines). Best-fit quadratic lines are solid for bird density and broken for flight calls. (a) Northwestern South Carolina during fall 2000, N = 215. (b) Southeastern New York during fall 2000, N = 146. (c) Northwestern South Carolina during spring 2000, N = 124. (d) Southeastern New York during spring 2000, N = 70.

nightly peak call count (Fig. 3b) are not significantly related for the spring and fall in southeastern New York ($R^2 = 0.26$, $F_{1,12} = 4.27$, $P = 0.06$). The relationship between all nightly peak call counts and all nightly peak migration densities recorded during spring and fall is significant ($R^2 = 0.21$, $F_{1,31} = 8.04$, $P = 0.01$), although nightly peak migration density accounts for only 21% of the variation in nightly peak call count. If we remove the pair of outlying data points in the upper right of Fig. 3a, the overall relationship between night-to-night peak migration density and night-to-night peak call count is still significant ($R^2 = 0.08$, $F_{1,553} = 45.20$, $P < 0.0001$), but migration density explains considerably less of the variation in call count.

Discussion

Temporal patterns of bird density are generally consistent across time and space, defined by fundamental characteristics of migratory strategies (e.g., Gauthreaux 1971, 1972, Cochran and Kjos 1985, Cochran 1987, Moore 1987, Åkesson 1996, Diehl and Larkin 1998), while temporal patterns of nocturnal calling are less consistent across time and space, possibly because calling associates with communication and different species require different patterns of communication (see Hamilton 1962, Graber 1968, Griffin 1969). However, our study does not support the finding that radar and acoustic methods give different pictures of the density patterns of nocturnal migration. We found significant relationships between migration densities and call counts sufficient to reject the null hypothesis that no relationship exists between the reflectivity measurements and the number of flight calls, although the overall ability of bird density to explain the variation in call count appears weak. A study using data from WSR-88D radar and microphones in south Texas (Larkin et al. 2002) revealed similar hour-to-hour patterns in radar reflectivity measurements and the call counts of a single species.

In contrast, Lowery and Newman (1955) noted the divergence in the hour-to-hour temporal pattern of bird migration, as measured by direct visual (moon watching) and auditory means. Moon watching data showed that nocturnal migration peaks during the hours before midnight (Lowery 1951), while call counts suggested that the peak of nocturnal migration occurs after midnight in the hours just before dawn (Ball 1952). Newman (1956: 104–105) compared the patterns of hourly average flight densities computed from moon watching data and hourly average flight call counts during fall migration in southeastern Louisiana, and he found "… the visual and auditory evidences of migration to be inversely correlated."

All of the hour-to-hour patterns in our study show that call counts are greater after midnight, while bird densities are greater earlier in the evening (Fig. 1). Graber (1968) found that on clear nights near Champaign, IL, the temporal pattern of migration as seen on radar peaked shortly before midnight, whereas the temporal pattern of flight calls peaked after midnight, usually just before dawn. He concluded that "… the difference in patterns probably reflects something other than the numbers of birds flying." Graber (1968) also compared seasonal radar and audio records recorded at the same time and location, and found no statistical correlation between these measures from night-to-night ($r = 0.373$, no P-values reported).

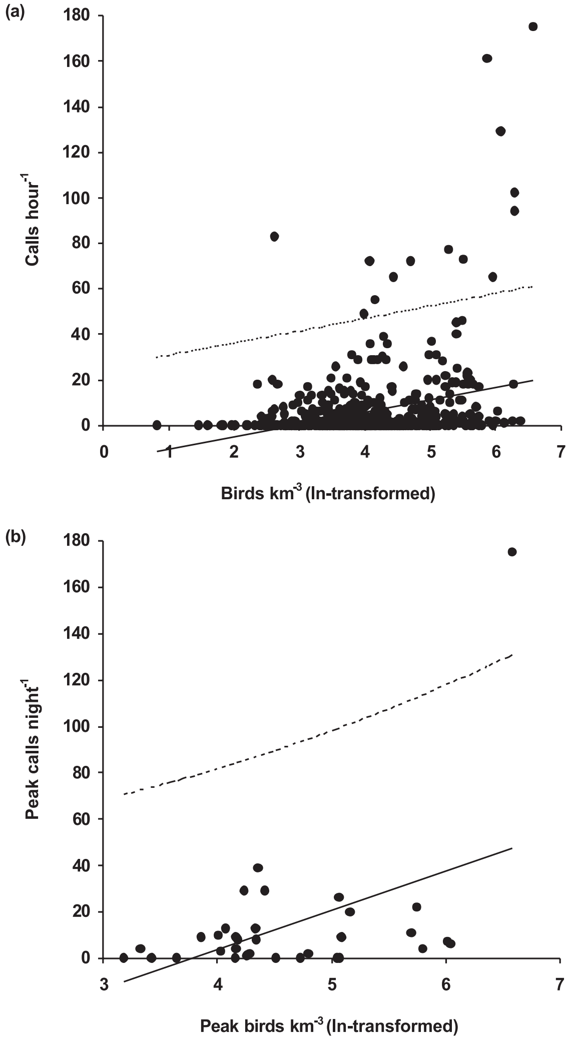

Fig. 2. Scatterplot of bird density and number of calls with 99% confidence limits. Best-fit line is solid, and 99% confidence limit is broken. (a) Hourly bird density (birds km^{-3}) and associated calls hour^{-1} pooled across 58 nights, N = 556, best-fit line: y = 5.4603x − 15.769, R^2 = 0.0885, P < 0.0001. (b) Peak bird density (birds km^{-3}) and associated nightly peak calls hour^{-1} for nights with complete sunset to sunrise radar and acoustic records, N = 33, best-fit line: y = 16.742x − 62.996, R^2 = 0.206, P < 0.001.

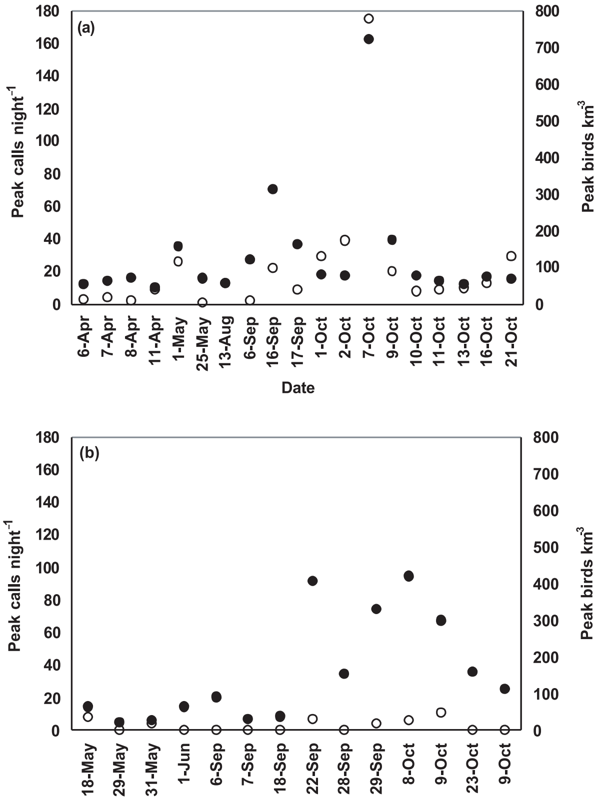

Fig. 3. Seasonal temporal patterns of bird density and number of calls. (a) Northwestern South Carolina, N = 19. During spring migration the peak bird density and number of calls occur in early May. During fall migration these peaks occur in early October. (b) Southeastern New York, N = 14. Although samples are few, during spring migration the peak bird density and number of calls occur in mid May. During fall migration these peaks occur in early October.

Our results may contain some sources of variation and error, and these sources may influence the strength of the relationships between bird density and call count. The relationship between reflectivity measurements and bird density is not perfect (R^2 = 0.89, Gauthreaux and Belser 1999), and some variation could be attributed to error associated with this surveillance radar calibration. Additionally, altitude of migration and call detection could bias temporal patterns of flight calls, although we did not relate calling activity to altitudinal distribution of birds in our study (refer to Farnsworth 2001 for pilot data on calls and altitude). Similarly, artificial night lighting, especially in conjunction with cloud cover, appears to bias calling rates of nocturnal migrants (e.g., Graber and Cochran 1960, Graber 1968), but we did not examine its effect in our study. We also know that atmospheric conditions influence the amount of migration aloft (e.g., Lack 1960, Able 1973, Richardson 1990, Erni et al. 2002), and several studies suggest that certain weather conditions (e.g., cloud cover) affect calling rates in migrating birds (Graber and Cochran 1960, Ogden 1960, Graber 1968, Evans and Mellinger 1999). Testing this hypothesis requires analyses modeling the effects of weather on call counts.

The relationship between bird density and call count is complex, and more research is necessary to clarify what is responsible for the great deal of unexplained variation in flight call counts. Although bird density accounts for little of the variation in call counts, the strongest relationship between density and call counts appears to occur when temporal patterns for calls and bird density are similar (e.g., Fig. 3a). It is possible that species that represent a large percentage of nocturnal flights at these times have calling rates that are uniform enough to represent the density of nocturnal migration. We believe that several factors could be important sources of variation, and suggest that future studies address the following: individual species calling patterns during the course of a night, individual species calling patterns during the course of a season, and the number of species that do not call during nocturnal migration. Furthermore, additional studies using Doppler radar and acoustic measures at a variety of geographical sites in conjunction with specific knowledge of the local migration system are needed.

Acknowledgements – We thank Bill Evans for providing software and comments and Marybeth Sollins and Dana Nayduch for assistance gathering acoustic data. We thank Bruno Bruderer, Ron Larkin, and Patricia Ryan for valuable comments on earlier drafts that greatly improved this manuscript. This work was supported in part by research grants from the Department of Defense Legacy Resource Management Program.

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(*Received 8 January 2003, revised 1 September 2003, accepted 7 September 2003.*)