

A comparison of traffic estimates of nocturnal flying animals using radar, thermal imaging, and acoustic recording

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Abstract. There are several remote-sensing tools readily available for the study of nocturnally flying animals (e.g., migrating birds), each possessing unique measurement biases. We used three tools (weather surveillance radar, thermal infrared camera, and acoustic recorder) to measure temporal and spatial patterns of nocturnal traffic estimates of flying animals during the spring and fall of 2011 and 2012 in Lewes, Delaware, USA. Our objective was to compare measures among different technologies to better understand their animal detection biases. For radar and thermal imaging, the greatest observed traffic rate tended to occur at, or shortly after, evening twilight, whereas for the acoustic recorder, peak bird flight-calling activity was observed just prior to morning twilight. Comparing traffic rates during the night for all seasons, we found that mean nightly correlations between acoustics and the other two tools were weakly correlated (thermal infrared camera and acoustics, $r = 0.004 \pm 0.04$ SE, $n = 100$ nights; radar and acoustics, $r = 0.14 \pm 0.04$ SE, $n = 101$ nights), but highly variable on an individual nightly basis (range = -0.84 to 0.92 , range = -0.73 to 0.94). The mean nightly correlations between traffic rates estimated by radar and by thermal infrared camera during the night were more strongly positively correlated ($r = 0.39 \pm 0.04$ SE, $n = 125$ nights), but also were highly variable for individual nights (range = -0.76 to 0.98). Through comparison with radar data among numerous height intervals, we determined that flying animal height above the ground influenced thermal imaging positively and flight call detections negatively. Moreover, thermal imaging detections decreased with the presence of cloud cover and increased with mean ground flight speed of animals, whereas acoustic detections showed no relationship with cloud cover presence but did decrease with increased flight speed. We found sampling methods to be positively correlated when comparing mean nightly traffic rates across nights. The strength of these correlations generally increased throughout the night, peaking 2–3 hours before morning twilight. Given the convergence of measures by different tools at this time, we suggest that researchers consider sampling flight activity in the hours before morning twilight when differences due to detection biases among sampling tools appear to be minimized.

Key words: *acoustic monitoring; birds; flight calls; Lewes, Delaware, USA; migration; NEXRAD; nocturnal monitoring; remote-sensing tools; thermal infrared; traffic rate; weather surveillance radar.*

INTRODUCTION

Nocturnal bird migration research faces several challenges, but the challenges associated with actually detecting birds flying at night are of primary concern. Radars, thermal infrared cameras, and acoustic recorders are the three principle remote-sensing tools presently used to estimate nocturnally migrating bird passage. Because these tools, usually used independently, possess their own strengths, weaknesses, and biases in detecting nocturnally flying animals, a comparative assessment is needed. Simultaneously using radars, thermal infrared cameras, and acoustic recorders will provide a better understanding of the unique perspective that each tool offers to our understanding of avian migration (Kunz et al. 2007).

The use of weather surveillance radar (WSR) in ornithological research provides a unique means of monitoring avian movements because WSR measures the electromagnetic reflectance of aerial organisms within a large sample volume of airspace across a broad spatial scale and provides estimates of animal density, speed, flight direction, and height (Diehl et al. 2003, Gauthreaux and Belser 2003, Diehl and Larkin 2005). The United States presently operates a network of 159 stationary WSR-88D units, each of which has a typical biological detection range of 120 km (Gauthreaux and Belser 1998). A strength of WSR is that it allows for the identification and monitoring of migratory bird stopover sites (Bonter et al. 2009, Buler and Diehl 2009, O'Neal et al. 2010, Laughlin et al. 2013), species-specific bird and bat roost sites (Russell and Gauthreaux 1998, Frick et al. 2012), and broad-front bird migration patterns (Gauthreaux 1971, Gauthreaux and Belser 1998). The ability of WSR to comprehensively detect aerial organisms at great distances allows for continental

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monitoring of bioscatterers (Kelly et al. 2012). The limitations of WSR include the inability to identify species or even discern among gross taxonomic types (e.g., birds vs. insects) (Schaeffer 1968, Larkin 1991, Gasteren et al. 2008, Bonter et al. 2009, Larkin and Diehl 2012).

Thermal infrared (TI) cameras are relatively new in the study of nocturnally flying animals (Burnay et al. 1988, Kunz et al. 2007). By measuring the heat radiation of individual organisms, TI cameras make it possible to count the number of animals aloft, and their flight direction and sometimes height (Liechti et al. 1995, Fortin et al. 1999, Zehnder et al. 2001, Gauthreaux and Livingston 2006). TI cameras can detect animals at a far range (1–3 km), but this detection range can become severely limited under periods of precipitation and low cloud cover (Liechti et al. 1995, Beier and Gemperlein 2004, Gauthreaux and Livingston 2006, O'Neal et al. 2010). Similar to WSR, species identification is difficult or impossible with TI cameras.

Unlike WSR and TI cameras, sampling with acoustic microphones allows for the unambiguous identification of aerial taxa (e.g., bird, bat, or insect), frequently to a narrow group of species, and often to the species level (Farnsworth 2005, Kunz et al. 2007). The simple, species-specific calls of birds given during periods of sustained flight offer one of the only methods to accurately identify bird species aloft (Evans and Mellinger 1999, Farnsworth 2005). Because microphones detect sounds produced by animals passing overhead, whereas other tools detect the physical bodies of animals, the aural detectability of animals depends on their behavior (i.e., how often they produce a sound) and the audio frequency of sound (i.e., how quickly the sound attenuates through the air). For instance, species or individuals that frequently produce calls may be detected multiple times during a single pass, while others may be missed altogether. Additionally, most bats produce ultrasonic frequency calls (>20 kHz) that are detectable only at short ranges on the order of tens of meters (Kunz et al. 2007), whereas birds give lower frequency calls (1–9 kHz) that are detected at longer ranges on the order of hundreds of meters (Evans and Mellinger 1999, Farnsworth 2005). This interplay, in addition to other factors, including poor weather conditions (e.g., precipitation, low cloud ceiling), flight elevation, time of night, and species composition, can all vary flight calling behavior and detectability, at times making it difficult to relate numbers of calls to animal density or abundance (Graber and Cochran 1960, Evans 2005, Farnsworth 2005). Also, the sound detection range of ground-based low-frequency microphones is rather short (<0.5 km) and the only flying animals that they detect are birds (Evans and Mellinger 1999, Evans and Rosenberg 2000, Farnsworth et al. 2004).

The relationships among these three techniques in detecting animals aloft remain equivocal. Comparisons of nightly mean calling rates have been shown to be

correlated with weather surveillance radar measures of relative animal density aloft (Larkin et al. 2002, Farnsworth et al. 2004, Gagnon et al. 2010), but within-night patterns of bird flight calling often contradict trends measured by WSR or TI cameras. WSR and TI camera studies of flight activity typically find that animal densities or detection rates decrease through the night, peaking near evening twilight (Graber 1968, Gauthreaux 1971, Mabee and Cooper 2004, Dokter et al. 2010). Unlike WSR or TI camera studies, however, flight calling rates tend to increase through the night (Ball 1952, Graber and Cochran 1960, Farnsworth et al. 2004, Farnsworth and Russell 2007, Hüppop and Hilgerloh 2012). Increasing detections of calling rates through the night could be driven by acoustic limitations, and/or an actual change in the calling rate, although neither has been assessed.

The simultaneous use of WSR, TI cameras, and flight call recorders to monitor flight traffic provides a more comprehensive record of activity (e.g., avian nocturnal migration), and aids in understanding the potential causes of occasionally contradictory results (Graber 1968). In this paper, we examine the correspondence of traffic estimates measured using WSR, TI cameras, and acoustics. Because within-night patterns of migratory intensity can depend on method, we predicted that within-night relationships between WSR and TI cameras would be positive, but comparisons between acoustics and both WSR and TI cameras would be negative. We predicted that between-night relationships would be positive for all pairings, with the strength of TI and WSR relationships remaining constant through the night, yet increasing later in the night for acoustic comparisons as calling frequency increases. We also predicted that variability in these relationships among measures would be related to changing detection probabilities. Changes in detection can be due to either biotic (e.g., flight behavior of birds) or abiotic factors (e.g., atmospheric conditions) that are likely to influence each tool in a unique way. We investigated the influence of biotic and abiotic factors for interpreting aero-faunal movements recorded from TI imaging and acoustics, using radar measures of migrant density, flight height, and flight speed as indices of unbiased measures of migratory movements. Because the sound detection range of ground-based low-frequency microphones is rather short, we predicted that audio-based traffic rates would be positively correlated with radar traffic rates composed only of the lowest-flying birds when birds were the dominant animals aloft. Alternatively, because TI cameras detect flying animals (primarily birds and bats) to greater heights, we predicted that TI-based traffic rates should best relate to radar traffic rates that include animals across all heights. Controlling for migrant density using WSR measures of density, we predicted that with faster flight ground speeds, the detection probability of birds through acoustics would decrease whereas TI detection probability would remain constant. Finally, we predicted that the presence of a

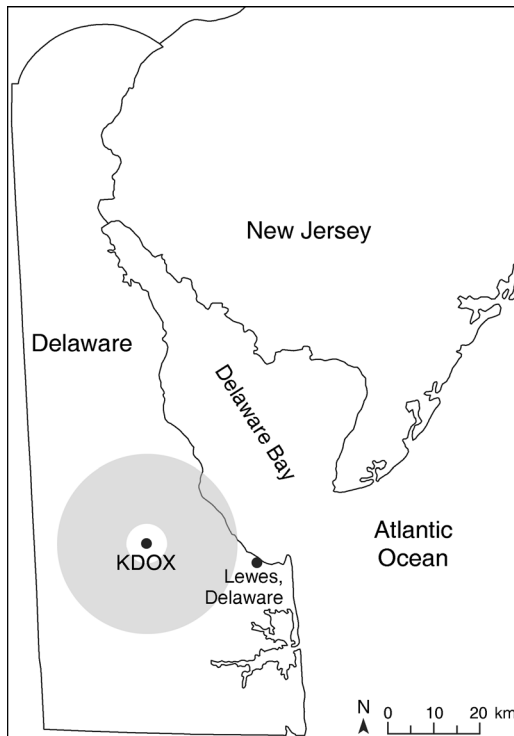


FIG. 1. Locations of the study site in Lewes, Delaware, USA, where thermal infrared camera and acoustic recordings were made of nocturnal flying animals, and of the KDOX radar station. The gray circle denotes the 5–20 km radius area where radar data were used to calculate vertical profiles of reflectivity (VPR).

low cloud ceiling would increase bird flight call detections and decrease TI camera detections.

METHODS

Study site

We measured flight activity at a single location in Lewes, Delaware (38°46'58.53" N, 75°9'53.41" W), that was ~1 km from the northwest–southeast running coastline of the Delaware Bay (Fig. 1). We sampled during the peak of land bird migration in spring from 1 April to 31 May and in fall from 1 September to 26 October of 2011 and 2012. We collected nightly data between evening civil twilight and morning civil twilight (sun 6° below the horizon). To account for daily changes in night length, we used tenths of the night (deciles) rather than absolute time relative to sunset or sunrise. Sampling effort varied daily due to weather conditions and among tools due to technical problems with equipment (Fig. 2). We included data from partial nights if more than half of the night was sampled. To limit weather-related detection biases (e.g., raindrop noise in audio files), we included data from nights with precipitation falling for less than 15% of the night. This was a subjective threshold based on a natural dichotomous break in the frequency of rainfall during nights.

Weather surveillance radar

We downloaded 1 × 1 km resolution WSR-88D National Mosaic three-dimensional composite reflectivity data (measured to the nearest 0.5 decibels of reflectivity factor Z) centered over the study site from the National Severe Storms Laboratory's National Mosaic and Multi-Sensor QPE (NMQ). We used unfiltered data that retained reflectivity from flying animals. Because the study site was nearest to the KDOX WSR-88D radar station in Dover, Delaware (24.5-km range from the radar at an azimuth of 101.5°), we assumed that all of the mosaicked NMQ data over the study site were derived from KDOX. Under standard atmospheric conditions, KDOX samples the airspace over the study site from 1 to 588 m above ground level with the lowest beam tilt angle (0.5°) sweep of a radar scan recorded every 10 minutes during clear-air mode and every 5 minutes during periods of precipitation (Crum and Alberty 1993). We excluded scans containing nonbiological targets (e.g., precipitation, chaff) and anomalous beam propagation (Greenstone 1990, Wolf et al. 1995), through visual inspection of reflectivity data using the Surveillance of the Atmosphere Using Weather Radar website (data available online).² We used the mean reflectivity across all retained radar scans as a measure of relative animal density for a given night. For brevity, we represent linear reflectivity as Z rather than the native units of mm⁶/m³. To allow reflectivity to serve as a traffic rate and make accurate comparisons between reflectivity and thermal imaging detections, and reflectivity and flight calls, we incorporated the mean animal ground speed. To convert reflectivity into a traffic rate, $Z(\text{m/s})$, we used the product of mean reflectivity and estimated mean ground speed as described by Black and Donaldson (1999).

We used Level-II KDOX radial velocity data from a single 1.5° tilt angle sweep collected approximately 3 hours after local sunset that we downloaded from the National Climatic Data Center to estimate the mean ground speed of flying animals. Velocities were dealiased when necessary, using the dealias program within the Warning Decision Support System–Integrated Information (WDSS-II) software (Lakshmanan et al. 2007). To calculate ground speed, we first fit sine wave functions to the annulus of radial velocity measures at each range distance from the radar, following Browning and Wexler (1968). From each sine function, we calculated nonzero Fourier coefficients (a_1, b_1) along the horizontal plane of animal movement and calculated mean ground speed of flying animals using the following equation:

$$\text{ground speed} = -(a_1^2 + b_1^2)^{1/2} / \cos(\text{beam tilt angle}).$$

Each range annulus samples animals flying at incrementally higher altitudes based on the height of the center of the radar beam as range increases. To

² <http://soar.ou.edu/legacy.html>

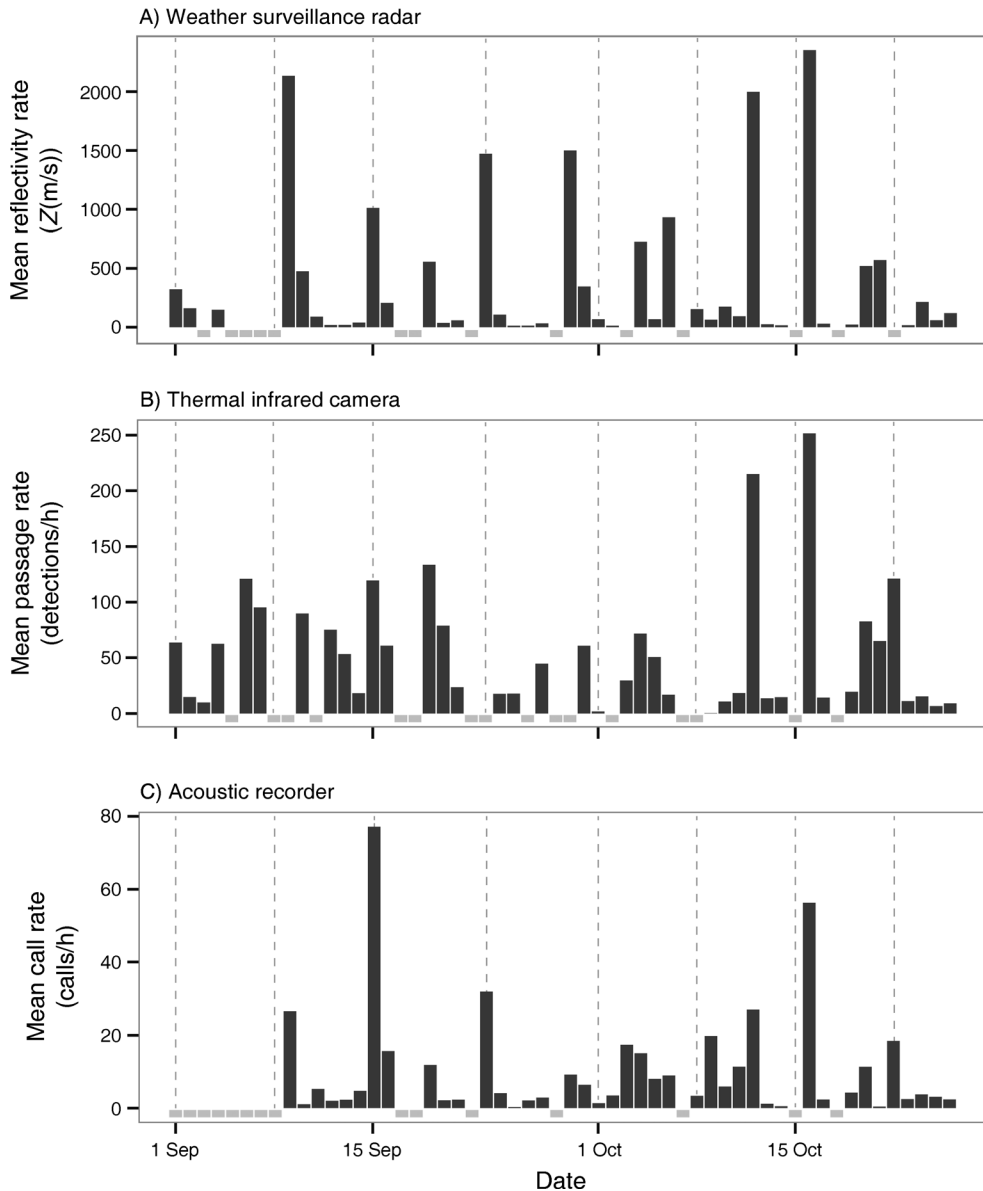


FIG. 2. Fall 2012 mean nightly traffic rate estimates derived from observations by (A) weather surveillance radar, (B) thermal infrared camera, and (C) acoustic recorder. Gray bars indicate missing data.

estimate the overall mean ground speed of animals across all heights, we weighted the mean ground speed of animals at each range (i.e., height) using a height profile of animal densities in the airspace (i.e., vertical profile of reflectivity, VPR).

We derived VPRs in 10-m height increments from 50 to 1500 m above ground level (a.g.l.) by integrating concurrently collected reflectivity data from five low tilt angle sweeps (0.5°, 1.5°, 2.5°, 3.5°, and 4.5°) at ranges of 5–20 km from the radar using the algorithms of Buler and Diehl (2009). We implemented these algorithms using the program w2birddensity within WDSS-II. During the fall of 2012, we used VPRs as measures of the relative height profiles of animal density in the

vicinity of the study site. We also used VPRs to produce estimates of the vertically integrated density of all animals in the airspace up to 1.5 km a.g.l. over the study site by adjusting the mosaic NMQ reflectivity measures, following Buler and Diehl (2009). Additionally, we processed every radar sweep during the fall of 2012 to estimate ground velocity during every decile of the night. These additional measures allowed us to construct vertical profiles of reflectivity, animal ground speed, and flight direction in 100-m height intervals for every decile of the night.

To identify bird- and insect-dominated nights, we determined animal airspeed by vector-subtracting the wind velocity from the calculated animal ground

velocity. When determining airspeeds, we calculated mean ground speed of radar animals as outlined previously, but at the 2.5° tilt angle sweep because speed and direction are less affected by refraction and beam occultation at higher tilt angles. To determine wind speed and direction aloft, we obtained Wallops Island, Virginia, radiosonde data from the University of Wyoming, Laramie archive. Radiosonde measures were collected at 00:00 UTC (Coordinated Universal Time); the single radar sweep used to assess animal airspeeds for a given night was collected within 2 hours after the radiosonde sample. We used a radar scan at the peak of nocturnal migratory flight rather than at 00:00 UTC because 00:00 UTC was too close to the onset of nocturnal migration, when animals have not yet reached their cruising altitude and speed (Gauthreaux and Belser 1998). In light of the fact that radiosonde data are only collected every 12 hours and their representativeness of wind speed and direction will decline with increasing time (Kitchen 1989), we may have compromised the accuracy of wind data when determining animal air speeds. However, we thought that sampling animals at their peak speeds would best distinguish insects from birds. We considered radar scans with mean animal airspeeds of ≥ 5 m/s to be bird dominated (Larkin 1991, Gauthreaux and Belser 1998).

Thermal infrared

We used a FLIR Guardsman (Boston, Massachusetts, USA) HG-307 Pro thermal infrared camera with a 7° field of view and 320×240 pixel image resolution. We oriented the camera vertically to detect flying animals passing overhead. We manually reviewed all video at ≤ 3 times original speed on a desktop PC and recorded the number of individual animals aloft and their identity when possible (i.e., bird, bat, or insect). We removed all positive bat and insect classifications for analysis when comparing TI camera with acoustic data because only birds are detected with acoustics. We calculated traffic rates as the number of animals passing the field of view per hour. Because we could not precisely determine heights of animals, we were unable to determine a detection probability function of the camera, which probably varied nightly due to variability in cloud cover (i.e., background temperature to contrast with flying animals).

Acoustics

We recorded bird flight calls during the spring using a Wildlife Acoustics Song Meter SM2+ recorder and SMX-NFC microphone (Wildlife Acoustics, Concord, Massachusetts, USA) located ~ 0.3 km from the TI camera and recording with a flat frequency response of 11 kHz, 3–6 dB signal gain, and 125° beam angle (Wildlife Acoustics 2011). During the fall of 2012, we also recorded bird flight calls using a pressure zone microphone with a Knowles (Itasca, Illinois, USA) Electret EK 3132 condenser microphone element

mounted on a 16.5-cm plate (design details *available online*).³ We housed the microphone element within a 5-gallon (~ 19 -L) plastic pail to reduce ground-level noise contamination and affixed the unit to a rooftop ~ 5 m a.g.l. and ~ 0.8 km from the thermal infrared camera. We amplified the acoustic signal using a Behringer (Las Vegas, Nevada, USA) Tube Ultragrain MIC100 preamplifier and digitized the audio signal using Raven Pro v1.4 (Bioacoustics Research Program 2011). We used two band-limited energy detector algorithms to automatically detect potential bird flight calls using Raven Pro v1.4. Our algorithms made detections within the frequency range of 6.5–8.0 kHz, the range of most warbler and sparrow calls, and 2.5–5.5 kHz, the range of most thrush, grosbeak, and tanager calls (Evans and O'Brien 2002). See Appendix A for detector parameters. We manually examined all automatic detections to confirm bird detections and remove false positives. To assess the efficiency of both detectors, we manually screened 2 hours of audio from six randomly selected nights (12 hours total).

Analyses

We assessed associations of traffic rate measures of flying animals between tools using Bayesian Pearson's correlations on log-transformed rates. We divided the night into 10 equal time periods (deciles) and determined the mean traffic rate during each decile. We then tested correlations of decile rates within each night between pairs of tools from nights. We only tested nights for which we had measures during at least five deciles. To assess traffic rate measures across nights, we correlated mean rates for the entire night and for each decile period across nights separately. To examine seasonal within-night differences of animal mean ground speed and median animal height, we used repeated-measures ANOVA.

We used Bayesian mixed-effects linear models to examine the influence of mean animal flight height, ground speed, and cloud cover presence on acoustic and thermal imaging detection probabilities during the fall of 2012. To avoid the confounding influence of differential detection probability of flight calls based on acoustic frequency, we limited modeling analyses to high-frequency calls (6.5–8.0 kHz). We used samples from all decile periods from all nights and controlled for variability in overall traffic rates by including decile period and vertically integrated reflectivity as covariates. Vertically integrated reflectivity does not incorporate animals below 50 m a.g.l., but it was our best comprehensive, unbiased measure of animal density aloft. Additionally, each of the two models included median animal height (m), mean animal ground speed (m/s), and cloud cover presence as fixed effects. To make population-level inferences, we assigned a random

³ http://www.oldbird.org/mike_home.htm

coefficient and intercept model to explicitly account for variability in traffic rates across nights.

To implement models, we used Markov-chain Monte Carlo simulations (MCMC) using JAGS (Plummer 2012) via the rjags package in R (Plummer 2013). We assigned uninformative uniform prior probabilities for all parameters and used the first 500 samples to tune the samplers, discarding the following 5000 MCMC samples as burn-in. We saved every fifth MCMC iteration to reduce serial autocorrelation among samples, running a total of 35 000 steps (Bolker 2008). We examined convergence of Markov chains to a stationary posterior distribution with the Gelman-Rubin (1992) diagnostic. We provide the means of the posterior distributions for all model parameters and supporting 95% credible intervals.

RESULTS

Using weather surveillance radar, seasonal reflectivity averaged 32.6 Z (i.e., 708 cm²/km³) during the spring (range = 0.4–265.3 Z, *n* = 91 nights) and 45.6 Z (i.e., 990 cm²/km³) during the fall (range = 0.9–244.5 Z, *n* = 87 nights; Fig. 2A). Using thermal imaging, we detected 16 573 animals during the spring (range = 0–1101 detections/night, *n* = 87 nights) and 27 203 animals during the fall (range = 4–2818 detections/night, *n* = 60 nights; Fig. 2B). Using acoustics, we recorded 2958 nocturnal bird flight calls during the spring (range = 0–1377 calls/night, *n* = 110 nights) and 4917 flight calls (range = 3–821 calls/night, *n* = 41 nights; Fig. 2C) during the fall of 2012. We observed that the automatic detector missed 59.1–62.5% of calls from audio sequences that were manually screened. However, we found a strong relationship between automated and manual call detection (*r* = 0.91), suggesting that automatic detections serve as an accurate index for call frequency.

Within-night comparisons

During the spring, mean within-night traffic estimates peaked early in the night for WSR (decile 2) and TI camera (decile 2), but much later for the acoustic recorder (decile 9). During the fall, mean within-night traffic estimates peaked early in the night for TI (decile 2), near midnight for WSR (decile 6), and just before morning twilight for acoustics (decile 9). Fall 2012 patterns are shown in Fig. 3.

Comparing traffic rates during the night for all seasons, we found that mean nightly call counts using acoustics and traffic estimates from the other two tools were weakly correlated (TI–MIC, *r* = 0.004 ± 0.04 SE, *n* = 100 nights; WSR–MIC, *r* = 0.14 ± 0.04 SE, *n* = 101 nights), but highly variable on an individual nightly basis (TI–MIC range, *r* = –0.84 to 0.92, WSR–MIC range, *r* = –0.73 to 0.94). The mean nightly correlation between WSR and TI camera traffic rates during the night was more strongly positively correlated (*r* = 0.39 ± 0.04 SE, *n* = 125 nights), but also highly variable for individual nights (range, *r* = –0.76 to 0.98). For the fall of 2012, we found strong evidence (Bayes factor > 10)

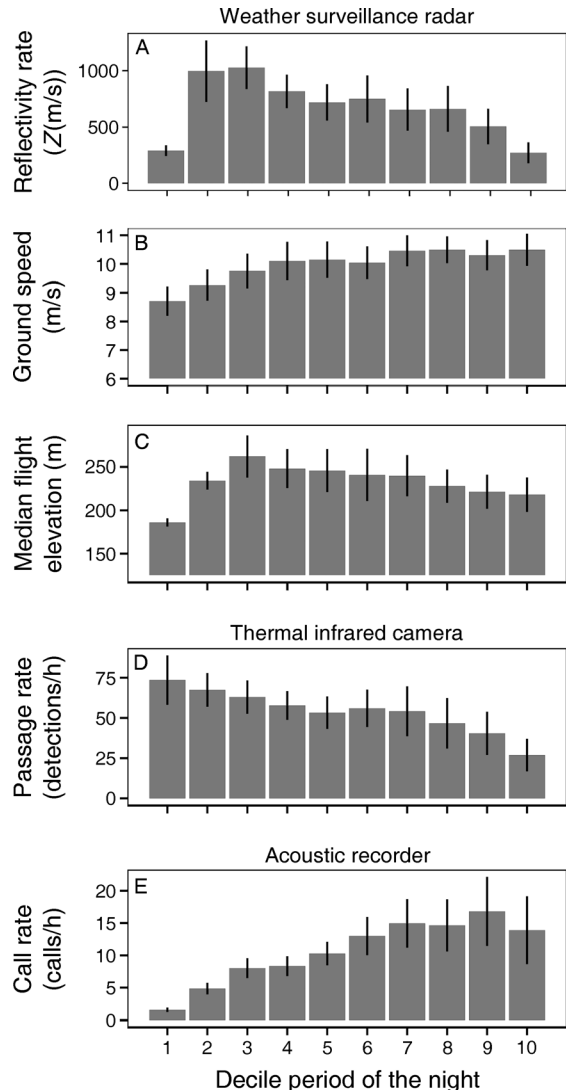


FIG. 3. Fall 2012 measures, by decile periods of the night, of (A) traffic estimates, (B) animal ground speed, and (C) median animal flight height above ground level (a.g.l.) using weather surveillance radar; and measures of traffic estimates using (D) thermal infrared camera and (E) acoustic recorder. All data are presented as mean ± SE.

for differences among decile measures of mean ground speed of animals (repeated-measures ANOVA, Bayes factor = 1096.6; Fig. 3B) but scarce evidence (1 ≤ Bayes factor < 3) for differences among decile measures of median animal heights (repeated-measures ANOVA, Bayes factor = 2.2; Fig. 3C) as determined from WSR data (Jeffreys 1961).

Between-night comparisons

All pairwise correlations among tools of nightly mean traffic rates across nights were significantly positive, both during the spring (Table 1) and fall (Table 2). Comparing bird- vs. insect-dominated nights, we found correlation coefficients of bird-dominated nights to be

TABLE 1. Bayesian Pearson's correlation coefficients (r) of pairwise correlation tests among migration monitoring tools of traffic rates across nights during the spring of 2011 and 2012 in Lewes, Delaware, USA.

| Period of night | WSR-TI | | | WSR-MIC | | | MIC-TI | | |
|-----------------|-------------|-----------------------|-----------|-------------|-----------------------|-----------|-------------|-----------------------|-----------|
| | r | CI | n | r | CI | n | r | CI | n |
| Full night | 0.46 | 0.246 to 0.638 | 68 | 0.66 | 0.506 to 0.769 | 81 | 0.34 | 0.126 to 0.526 | 82 |
| Decile 1 | 0.32 | 0.079 to 0.536 | 65 | 0.02 | -0.207 to 0.236 | 79 | -0.05 | -0.267 to 0.163 | 83 |
| Decile 2 | 0.47 | 0.259 to 0.648 | 67 | 0.19 | -0.028 to 0.396 | 80 | -0.01 | -0.237 to 0.221 | 83 |
| Decile 3 | 0.52 | 0.318 to 0.686 | 68 | 0.30 | 0.089 to 0.486 | 82 | 0.02 | -0.225 to 0.264 | 83 |
| Decile 4 | 0.43 | 0.211 to 0.620 | 68 | 0.37 | 0.152 to 0.561 | 82 | 0.21 | -0.026 to 0.420 | 83 |
| Decile 5 | 0.47 | 0.256 to 0.651 | 66 | 0.51 | 0.334 to 0.665 | 80 | 0.19 | -0.037 to 0.407 | 83 |
| Decile 6 | 0.32 | 0.077 to 0.532 | 66 | 0.56 | 0.384 to 0.707 | 80 | 0.28 | 0.046 to 0.500 | 82 |
| Decile 7 | 0.27 | 0.025 to 0.493 | 63 | 0.56 | 0.375 to 0.703 | 74 | 0.08 | -0.155 to 0.324 | 82 |
| Decile 8 | 0.37 | 0.126 to 0.576 | 63 | 0.52 | 0.340 to 0.676 | 75 | 0.17 | -0.061 to 0.397 | 82 |
| Decile 9 | 0.47 | 0.252 to 0.648 | 64 | 0.61 | 0.445 to 0.741 | 75 | 0.25 | 0.018 to 0.460 | 81 |
| Decile 10 | 0.51 | 0.290 to 0.691 | 57 | 0.47 | 0.263 to 0.648 | 74 | 0.15 | -0.150 to 0.360 | 74 |

Notes: Tests were performed using nightly means, and means for each decile period of the night of log-transformed traffic estimates. Credible intervals (CI) not overlapping zero are highlighted in bold. Abbreviations are: WSR, weather surveillance radar; TI, thermal infrared camera; MIC, acoustic recorder.

greater for five of six pairwise comparisons (Table 3). Additionally, all bird-dominated models showed positive, nonzero correlation coefficients, whereas insect-dominated comparisons showed two of six models with nonzero correlation coefficients. Examining nightly comparisons at the decile level, we observed increased correlation strength throughout the night for most comparisons. Investigating fall 2012 relationships through time and space, we observed the three strongest relationships between acoustics and weather surveillance radar during decile 8 between the ranges of 50–300 m (Fig. 4A). For comparisons between thermal imaging and weather surveillance radar, we observed the three strongest relationships during decile 7 between the ranges of 301–600 m (Fig. 4B).

Modeling results

Radar reflectivity rate was an important predictor of both bird calling rate and TI camera detections (Table 4). Relative bird calling rate increased throughout the night (99.9% of posterior distribution positive), with slower animal ground speeds (99.9% of posterior

distribution negative), and at lower median flight heights (93.4% of posterior distribution negative), but was insensitive to the presence of cloud cover (44.7% of posterior distribution positive). Thermal camera detection rates decreased later in the night (99.9% of posterior distribution negative), increased with slower animal ground speeds (99.9% of posterior distribution negative), increased with median animal height (91.8% of posterior distribution positive), and decreased with cloud cover presence (95.5% of posterior distribution negative). Date as a random intercept and reflectivity as a random slope were important in both models because a high degree of variability from night to night was observed.

DISCUSSION

Our comparisons of nightly measures of animal traffic rates among remote-sensing tools revealed positive relationships in general. Specifically, our positive correlation across nights between nocturnal flight calls and radar measures of animal traffic rates are consistent with results of others (Larkin et al. 2002, Farnsworth et al.

TABLE 2. Bayesian Pearson's correlation coefficients (r) of pairwise correlation tests among migration monitoring tools of traffic rates across nights during the fall of 2011 and 2012.

| Period of night | WSR-TI | | | WSR-MIC† | | | MIC-TI† | | |
|-----------------|-------------|-----------------------|-----------|-------------|-----------------------|-----------|-------------|------------------------|-----------|
| | r | CI | n | r | CI | n | r | CI | n |
| Full night | 0.39 | 0.128 to 0.606 | 53 | 0.72 | 0.520 to 0.854 | 40 | 0.40 | 0.074 to 0.665 | 34 |
| Decile 1 | 0.21 | -0.069 to 0.475 | 50 | 0.29 | 0.294 to 0.567 | 38 | -0.15 | -0.477 to 0.201 | 34 |
| Decile 2 | 0.22 | -0.057 to 0.478 | 51 | 0.47 | 0.174 to 0.697 | 37 | 0.24 | -0.117 to 0.555 | 34 |
| Decile 3 | 0.36 | 0.083 to 0.590 | 51 | 0.55 | 0.286 to 0.751 | 37 | 0.30 | -0.052 to 0.587 | 34 |
| Decile 4 | 0.35 | 0.080 to 0.586 | 49 | 0.41 | 0.098 to 0.666 | 34 | 0.48 | 0.168 to 0.719 | 34 |
| Decile 5 | 0.41 | 0.153 to 0.621 | 52 | 0.47 | 0.161 to 0.711 | 34 | 0.37 | 0.032 to 0.657 | 34 |
| Decile 6 | 0.43 | 0.186 to 0.643 | 53 | 0.60 | 0.334 to 0.794 | 35 | 0.39 | 0.049 to 0.661 | 34 |
| Decile 7 | 0.43 | 0.169 to 0.640 | 51 | 0.63 | 0.383 to 0.804 | 37 | 0.42 | 0.091 to 0.684 | 34 |
| Decile 8 | 0.44 | 0.171 to 0.662 | 47 | 0.75 | 0.570 to 0.872 | 37 | 0.46 | 0.135 to 0.704 | 34 |
| Decile 9 | 0.47 | 0.204 to 0.685 | 44 | 0.62 | 0.369 to 0.805 | 36 | 0.55 | 0.138 to 0.775 | 33 |
| Decile 10 | 0.41 | 0.120 to 0.656 | 39 | 0.47 | 0.160 to 0.717 | 35 | 0.14 | -0.292 to 0.532 | 25 |

Notes: Tests were performed using nightly means, and means for each decile period of the night of log-transformed traffic estimates. Credible intervals not overlapping zero are highlighted in bold. Abbreviations are: WSR, weather surveillance radar; TI, thermal infrared camera; MIC, acoustic recorder. Acoustic data were not collected during the fall of 2011.

† Only fall of 2012 was included.

TABLE 3. Bayesian Pearson’s correlation coefficients (r) of pairwise correlation tests among migration monitoring tools, with corresponding 95% credible intervals.

| Method, by season | Bird dominated | | | Insect dominated | | |
|-------------------|----------------|-----------------------|-----|------------------|------------------------|-----|
| | r | 95% CI | n | r | 95% CI | n |
| Spring | | | | | | |
| WSR–TI | 0.465 | 0.227 to 0.666 | 53 | 0.406 | –0.117 to 0.774 | 15 |
| WSR–MIC | 0.551 | 0.349 to 0.712 | 59 | 0.613 | 0.252 to 0.846 | 22 |
| MIC–TI | 0.360 | 0.118 to 0.572 | 62 | 0.202 | –0.263 to 0.601 | 20 |
| Fall | | | | | | |
| WSR–TI | 0.709 | 0.425 to 0.889 | 22 | –0.074 | –0.444 to 0.306 | 30 |
| WSR–MIC | 0.632 | 0.317 to 0.844 | 23 | 0.428 | –0.032 to 0.766 | 17 |
| MIC–TI | 0.593 | 0.207 to 0.841 | 19 | –0.136 | –0.612 to 0.408 | 15 |

Notes: Nights with mean airspeeds of <5 m/s were considered insect dominated and nights with ≥5 m/s bird dominated. Coefficients with credible intervals not overlapping zero are highlighted in bold.

2004). Additionally, we present the first comparisons of flying animal traffic rates between thermal imaging and bird acoustics, and between thermal imaging and weather surveillance radar, finding similar, although slightly weaker, correlations. However, variability in the strength of the relationships among methods highlights similarities and differences in detection ranges and taxa sampled among tools.

The density of taxa sampled can vary, both among nights and by the tools used in traffic estimation. Radar readily measures small flying insects and vertebrates to great heights (Dokter et al. 2010, Drake and Reynolds 2012, Rennie 2013), whereas TI cameras are limited in detecting small insects very close to the camera (~30 m) and perform much better in vertebrate detection at greater distances (Zehnder et al. 2001, Gauthreaux and Livingston 2006). The strength of the relationship

between WSR and TI was stronger for the subset of bird-dominated nights in comparison to insect-dominated nights. Of the three tools used, radar had the greatest detection range, able to horizontally detect small animals at great distances (~80–120 km) and well above the ground level (~4 km). Because the detection range of the radar surpasses that of the other techniques (acoustics ~0.2–0.5 km and TI ~0.8–1.2 km a.g.l.) (Evans and Mellinger 1999, Evans and Rosenberg 2000, Farnsworth et al. 2004, Gauthreaux and Livingston 2006, O’Neal et al. 2010), WSR can be used to assess detection limits of other techniques to the extent that they sample the same taxa. We found the strongest correlations between measures of acoustics and weather surveillance radar at lower flight heights than between thermal imaging and weather surveillance radar.

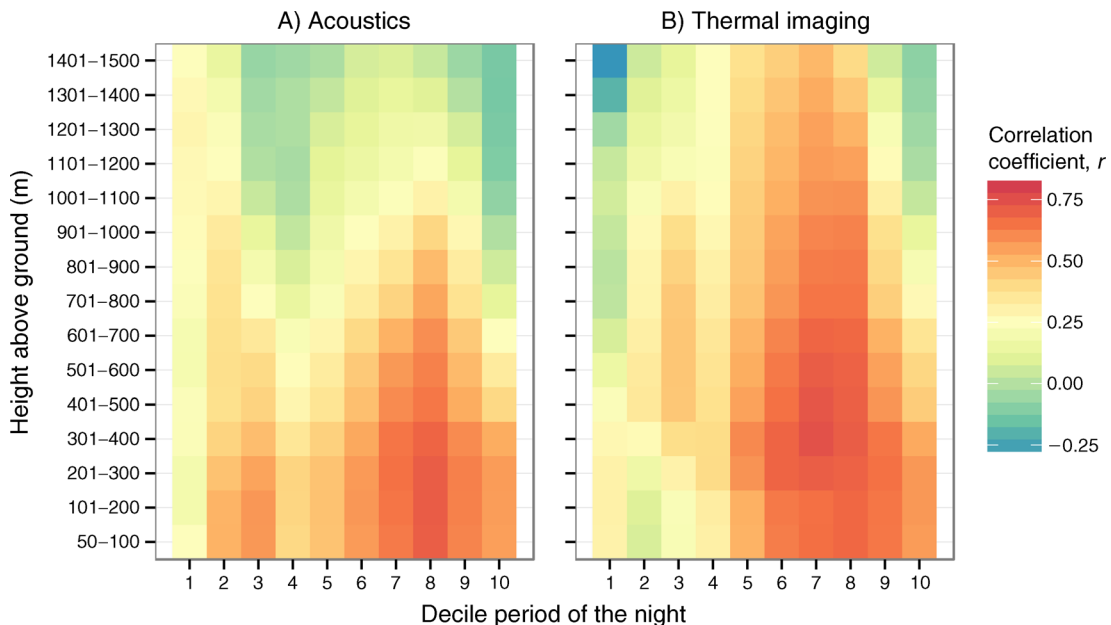


FIG. 4. Bayesian Pearson’s correlation coefficients (r) from pairwise comparisons of mean traffic rate estimates across nights by 100-m height interval and decile period of the night for (A) acoustic recorder and weather surveillance radar, and (B) thermal infrared camera and weather surveillance radar. Data are from complete sampling nights during the fall of 2012.

TABLE 4. Posterior mean values (with 95% credible intervals) for coefficients ($\hat{\beta}$) of fixed effects and variance ($\hat{\sigma}$) of random effects to explain variability in acoustic recorder and thermal camera detections measured for decile periods of the night.

| Variable | Bird flight call rate ($n = 346$) | | Thermal animal detection rate ($n = 316$) | |
|--|--|-------------------------|--|-------------------------|
| | Mean | 95% CI | Mean | 95% CI |
| Fixed effects (coefficient $\hat{\beta}$) | | | | |
| Intercept | 8.323 | 0.853 to 16.005 | 42.191 | 17.421 to 67.158 |
| Reflectivity (Z(m/s)) | 0.013 | 0.007 to 0.020 | 0.077 | 0.002 to 0.155 |
| Decile period of night (1–10) | 1.311 | 0.865 to 1.760 | -2.835 | -4.538 to -1.145 |
| Median animal height (m) | -0.020 | -0.047 to 0.006 | 0.078 | -0.031 to 0.189 |
| Mean animal ground speed (m/s) | -0.820 | -1.388 to -0.294 | -2.160 | -3.795 to -0.565 |
| Cloud cover (0, absent; 1, present) | -0.351 | -4.777 to 3.813 | -12.310 | -26.462 to 1.875 |
| Random effects (variance $\hat{\sigma}$) | | | | |
| Intercept | 5.885 | 1.951 to 9.595 | 6.688 | 0.290 to 18.027 |
| Reflectivity (Z(m/s)) | 0.011 | 0.007 to 0.017 | 0.193 | 0.127 to 0.276 |
| Residuals | 10.811 | 9.917 to 11.804 | 38.238 | 35.061 to 41.776 |

Note: Fixed and random effects with credible intervals not overlapping zero are highlighted in bold.

Understanding how measures of flying animal traffic rates throughout the night vary among remote-sensing tools illuminates the biases in the tools used to monitor nocturnal flight activity. Exploring within-night patterns, we observed peak reflectivity and detections with thermal imaging early in the night, declining toward morning twilight, but flight calling steadily increasing through the night, peaking just before morning twilight. Similarly, Lowery and Newman (1955) using moon-watching, Graber (1968) using X-band radar, and Farnsworth et al. (2004) using weather surveillance radar generally observed peak flight activity before midnight and peak calling after midnight. However, we found that activity patterns were highly variable within nights (Fig. 5; Appendix B). We found that within-night migratory activity across all methods at times peaked early in the night (e.g., 19 September 2012) and at other times late in the night (e.g., 16 October 2012). Additionally, because cloud cover can dramatically influence thermal imaging, and acoustic detections are tied to bird behavior, it is not surprising to observe such a high degree of variability. For these reasons, it may be most appropriate to assess within-night patterns for individual nights, and not generalize about overall within-night patterns of migratory activity pooled across nights.

Because most flying animals were below 500 m a.g.l., across-night variability in detection probabilities of birds by the acoustic recorder was rather subtle, although we did observe fewer with increasing flight height. However, a stark difference in traffic rates among tools, suggesting poor detection by the microphone, was exemplified during the evening of 21 October. The radar observed moderate traffic rates of animals in a bimodal vertical distribution, with most animals either below 300 m a.g.l. or higher than 1000 m a.g.l. Air speeds were slower near ground level (6.9 m/s) and faster at ~1200 m a.g.l. (14.4 m/s). Concurrently, we recorded almost no bird flight calls, yet had a

considerably large number of TI camera detections. On this night, TI camera-based animal heights were categorized as high (96.2% of animals), medium (3.2%), and low (0.6%). It is our interpretation that on the night of 21 October 2012, invertebrates dominated at the low heights (50–300 m) and birds dominated at the high heights (>1000 m) and were largely undetected by the microphone.

Examining the influence of ground speed on detection probability, we observed decreased acoustic and TI detection probabilities with increased speed. The observation of decreased acoustic detections with increased ground speed is consistent with the explanation by Black (1997), who described an interaction between the speed of birds, their calling rate, and the detection range of the microphone on the detection probability of birds. Black showed that under particular conditions (calls generated no more than once per pass), the probability of detecting an individual's call decreases with increasing ground speed. However with increasing flight speeds, greater numbers of individuals should be expected to pass overhead, thus negating the influence of decreased call detection probability. A further examination by tracking individual birds will refine these results, because we currently rely on the data measured by WSR to describe collective flight patterns of all migrant (insects, birds, and bats) at coarse resolution and not the flight behavior of individuals detected by way of acoustics and thermal imaging. Additionally, we note that many migrants do not appear to give flight calls or do so infrequently (i.e., vireos, flycatchers, mimids) (Farnsworth 2005, La 2012), and without knowing the amount of non-calling animals, estimates of flight height and speed from WSR may not be representative of detections made using acoustic techniques. Also, because the detection of calls is heavily dependent on the rate at which calls are produced by birds and their ground flight speed, further examination at the species level may yield the degree to

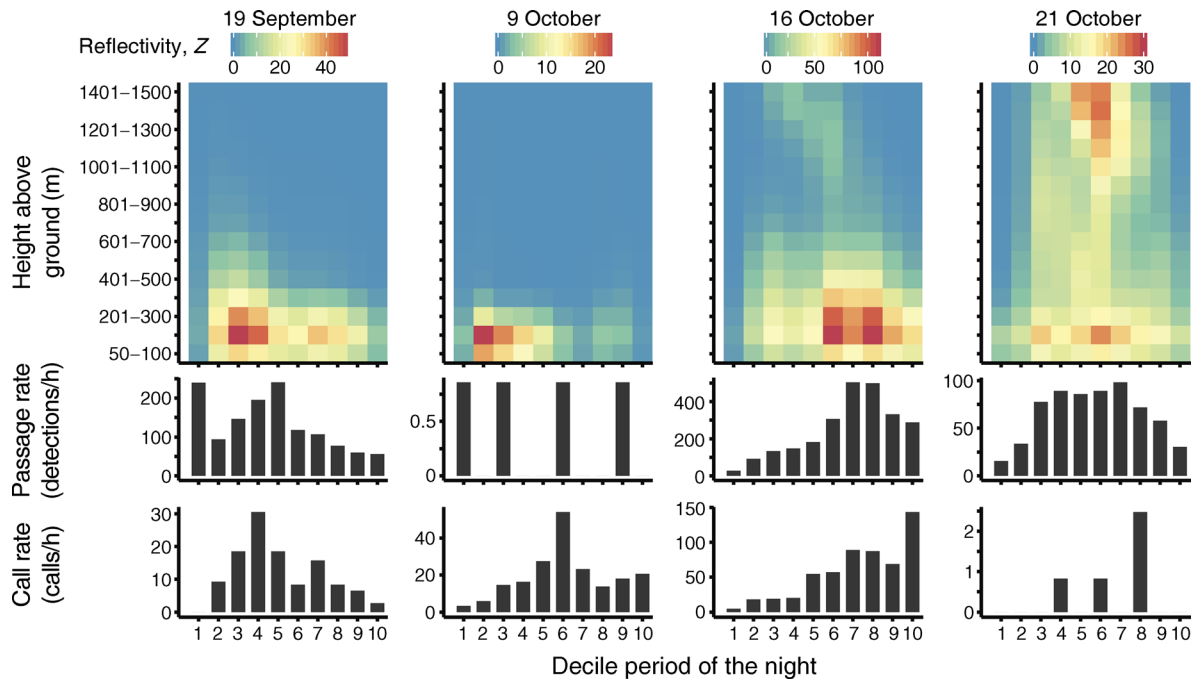


FIG. 5. Select animal flight traffic rate estimates on four dates, by decile periods of the night, derived from observations by weather surveillance radar (mean linear reflectivity Z by height above ground level in 100-m intervals), thermal infrared camera (detections per hour), and acoustic recorder (calls per hour) during the fall of 2012. Note that scales vary among nights.

which nocturnal flight call rates may be insensitive to flight speeds and act as a density measure vs. a simple measure of animal flow. Meanwhile, we were surprised to find that ground speed had any influence on TI detections, because animals should be captured by the camera regardless of their ground speed. Thus, the relatively lower detection rate at faster ground speeds probably reflected detection probability by human screeners of fast-flying animals through the field of view of the camera.

Deteriorating weather conditions (e.g., precipitation, low cloud ceiling) can increase the rate of flight calling by birds (Graber and Cochran 1960, Evans 2005, Farnsworth 2005). However, quantifying the influence of precipitation on calling behavior is made difficult because recordings are contaminated by the noise of rain. Furthermore, similar conditions that may increase calling rates tend to preclude the use of weather surveillance radar (precipitation) and thermal imaging (low cloud cover). In our effort to quantify the influence of cloud cover, we found that 95.6% of the posterior distribution values estimated a decline in thermal imaging detection probability with the presence of cloud cover, whereas only 55.9% indicated a decline in flight calling rate. Yet, although our fall 2012 data did not suggest an influence of the presence of cloud cover on calling rate, on the single night of 21 May 2012 (not included in our modeling analysis), we recorded 1377 flight calls, which represented 46.5% of all detections for the entire spring season. Furthermore, we did not detect any flying animals with thermal imaging, and WSR

recorded a relatively low mean reflectivity of 34.2 Z for the night. On this night, we recorded the second lowest mean cloud ceiling of the study (ceiling height 88.3 ± 9.96 m a.g.l., mean \pm SE) and believe this to be the primary driver of these anomalous data. Similarly, on 9 October 2012, the presence of a low cloud ceiling (mean ceiling height 97.6 ± 9.96 m a.g.l.) impaired thermal imaging detections, and was associated with high flight-calling rates. It is these types of events that make comparative assessments among tools difficult because each method can be differentially influenced by atmospheric conditions. Researchers must be mindful of these differences.

By testing correlations across nights among tools by decile period of the night, we observed increasing correlation strength between all tools from evening twilight to morning twilight. This lends evidence to suggest that as the night progressed at our site, differences in detection of birds among tools were minimized. For radar and TI, contamination from insects appeared to decline throughout the night, because WSR measures of the mean ground speeds of animals increased throughout the night, consistent with a scenario of an increasing ratio of fast-flying birds relative to slow-flying insects. WSR measures of the median heights of flying animals reached a maximum peak approximately three hours after the onset of nocturnal flights and then declined throughout the night. This decrease in flight heights of birds toward morning probably increased detection probability for the microphone such that bird flight-calling rates closer

to morning twilight were more representative of the abundance of animals aloft. Additionally, the contraction in the range of flying heights of birds near the morning would produce more consistent detection probabilities among nights for the microphone. Because TI measures vary independently of traffic rate, based on the flight height of animals (i.e., increasing sample area with height produces more animal detections with height, regardless of traffic rate), the contraction of flying heights toward morning produces more consistent flight heights. Thus, variability in TI measures would more accurately represent variability in relative traffic rates.

The relationships among measures of the activity of nocturnal flying animals by different remote-sensing tools can be incredibly complex. In our study, we have been able to demonstrate correlations among three standard methods used in assessing migrating bird passage. The correspondence of traffic rate measures at times conflicted within the night, but was more consistent and positive among all tools across nights. Our examinations of animal density and bird calling frequency relative to flight heights provide evidence that birds change their calling rates during the night, which complicates and undermines the use of flight-call detection rates as a reliable measure of within-night bird traffic rates. Yet, with existing gaps in our understanding of the flight-calling behavior of birds, interpreting and explaining temporal trends in calling rates remains difficult. The generalizability of our results to areas that differ with respect to migrant composition, stopover habitat quality, proximity to breeding and wintering grounds, prominent topographic features, and ecological barriers is uncertain. It is reasonable to expect that these factors may influence the regional and local flux of migrants and their flight behavior and modify the relationships among migration monitoring tools. We encourage additional work to compare tools at sites with different characteristics to examine the robustness of these interrelationships. Despite this, the use of bird flight calls to monitor differences in bird passage rates among nights is promising because the measures generally and positively relate to traffic estimates derived from other tools. Given the convergence of measures by different tools approximately 2–3 hours before morning twilight, we suggest that researchers consider sampling flight activity at this time when differences due to detection biases among tools appear to be minimized.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-0279.1.sm>