The Auk 127(1):119–128, 2010

A COMPARISON BETWEEN NOCTURNAL AURAL COUNTS OF PASSERINES AND RADAR REFLECTIVITY FROM A CANADIAN WEATHER SURVEILLANCE RADAR

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Abstract.—Using a Canadian weather surveillance radar (CWSR), we assessed the relationship between aural passerine counts and radar reflectivity during autumn migration on 16 nights. Reflectivity was positively correlated on all but 1 night with the number of birds detected aurally, but the correlation strength varied between −0.58 and 0.93 among nights (mean ± SD = 0.69 ± 0.42). Using linear mixed-effects models with aural counts nested within nights, we found that the number of birds detected by observers increased with reflectivity. The slope of this relationship did not vary between observers, nor was it affected by time since sunset, but the number of birds detected aurally tended to be lower when ambient noise levels were high. We know that the radar was relatively sensitive to low bird densities, because the intercept was slightly positive and its 95% confidence interval marginally included zero. However, the relationship between the number of birds detected aurally and reflectivity varied significantly among nights. Such variation was likely caused by a combination of (interacting) factors, including bird species and behavior (e.g., calling rate, flight altitude), influencing bird detectability by the observers and the radar. The weather radar network of the United States (NEXRAD) is already used for bird migration studies, and we conclude that the use of CWSR can extend NEXRAD's coverage farther north by hundreds of kilometers, thereby increasing our understanding of how birds use the North American landscapes during migration. *Received 28 August 2008, accepted 19 August 2009.*

Key words: bird detectability, Canada, flight calls, migrant songbirds, nocturnal migration, radar reflectivity, weather radar.

Comparaison entre des dénombrements auditifs de passereaux la nuit et la réflectivité d'un radar de surveillance météorologique Canadien

Résumé.—Nous avons étudié la relation entre un dénombrement auditif de passereaux et la réflectivité d'un radar de surveillance météorologique canadien (CWSR), durant la migration automnale, pendant 16 nuits. La réflectivité radar était positivement corrélée avec le nombre d'oiseaux détectés auditivement pour toutes les nuits, exception d'une, mais la puissance de cette relation variait de −0.58 à 0.93 (moyenne ± écart-type = 0.69 ± 0.42). En utilisant des modèles linéaires à effets mixtes où les dénombrements auditifs étaient nichés de manière intra-nuit, nous avons confirmé que le nombre d'oiseaux détectés par les observateurs s'accroissait avec la réflectivité. La pente de cette relation ne variait pas entre les observateurs comme elle n'était pas affectée par le temps écoulé depuis le coucher du soleil, mais le nombre d'oiseaux détectés auditivement tendait à diminuer quand le bruit ambiant était plus élevé. Le radar s'est avéré être relativement sensible à une faible densité d'oiseaux, puisque la valeur de l'intercepte était légèrement positive et ses intervalles de confiance de 95% incluaient marginalement le zéro. Cependant, la relation entre le nombre d'oiseaux détectés auditivement et la réflectivité variait significativement entre les nuits. Une telle variation est vraisemblablement attribuable à la

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The Auk, Vol. 127, Number 1, pages 119–128. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2009.09080

combinaison (ou l'interaction) de facteurs incluant les espèces d'oiseaux présentes et leurs comportements (e.g. taux de cris, altitude de vol), ce qui influence la détectabilité des oiseaux par les observateurs, mais aussi par le radar. Le réseau de radars météo (NEXRAD) des États-Unis est déjà utilisé dans des études de la migration des oiseaux et nous concluons que l'utilisation des CWSR pourrait permettent une extension vers le nord de plusieurs centaines de kilomètres de la couverture du réseau NEXRAD, permettant d'accroître la compréhension de l'utilisation des paysages nord américains par les oiseaux durant leur migration.

Following the discovery in the 1940s that radars can detect birds in flight (Lack and Varley 1945), several studies on bird migration have relied on this technology to characterize the movement of migrants (Bruderer 1997a, b; Gauthreaux and Belser 2003). Although various kinds of radars (e.g., marine, weather, tracking) can be used to detect birds aloft, weather radars present outstanding advantages over other types for monitoring bird migration: (1) they show extended detection ranges, (2) they provide continuous coverage over large spatial scales, (3) they collect comparable information, (4) they collect data on a 24-h basis that are archived for years, and (5) the data are usually freely accessible to the public. Weather radar studies of nocturnal bird migration, which began in the 1970s (Gauthreaux 1970, Gauthreaux and Belser 2003), were refined in the 1990s with the establishment of the weather surveillance radar-1988 Doppler (WSR-88D), also referred to as NEXRAD (next generation weather radar) in the United States (Diehl et al. 2003, Gauthreaux et al. 2008). The Internet now provides easy and instant access to large-scale movements of migratory birds via NEXRAD (see Acknowledgments). In Canada, a Doppler weather radar network implemented in the late 1990s and consisting of 30 Canadian weather surveillance radar (CWSR) stations of two types (in addition to another radar with parameters analogous to NEXRAD) covers the entire east–west border with the United States (Joe and Lapczak 2002), thereby providing an opportunity for studying north–south bird migration on a continental scale. Although some products of the CWSR network are available on the Internet, the information they contain cannot be used to visualize bird migration. This results partly from the focus on reflectivity factor scales that are relevant to meteorological phenomena. The reflectivity factor (hereafter "reflectivity") corresponds to the sum of the power back-scattered from individual targets to the radar antenna and depends on the material, size, and number of targets (Eastwood 1967, Rinehart 1997). When appropriate software is used to display CWSR data, the reflectivity scale can be adjusted to visualize weaker echoes, some presumably representing birds and insects. So far, the potential of CWSR for studying bird migration has not been exploited, mainly because biologists are not aware that CWSR can detect birds. This may be explained, in part, by the fact that the sole assessment of the relationship linking CWSR reflectivity to bird numbers (using a small conical marine radar) has never been published (Black and Donaldson 1998).

There are well-known echoes characteristic of Doppler weather radar that allow birds to be detected (Gauthreaux and Belser 1998, Koistinen 2000, Gauthreaux et al. 2008). Although the use of radar signals for enumerating migrants was initially met with some skepticism, this technique has proved to be more convincing when linked to traditional field estimate methods, such as moon watching (Eastwood 1967, Gauthreaux 1972, Liechti et al. 1995, Gauthreaux and Belser 1998) or aural bird counts (Graber 1968, Larkin et al. 2002, Farnsworth et al. 2004). Aural bird counts present some clear advantages over moon watching. First, aural counts are not restricted to cloud-free nights when the moon is close to full. Second, the "air column" sampled by moon watching changes with the course of the moon and varies in volume with the moon-horizon angle (Alerstam 1990). Nevertheless, aural studies have their own drawbacks, which stem from time-dependent calling rates within species, from inconsistencies in the ratio between calling (e.g., thrushes, warblers, and sparrows) and noncalling species (e.g., flycatchers, kinglets, and vireos; Evans and O'Brien 2002), and from differential detection probabilities associated with flight altitude, weather conditions, and noise pollution (Farnsworth 2005). The few studies that have compared aural counts with weather-radar estimates of migrating birds have produced equivocal results. For instance, both Larkin et al. (2002), who compared the relationship between aural counts of a single species (Dickcissels [*Spiza americana*]) and NEXRAD reflectivity, and Farnsworth et al. (2004), who documented the relationship between flight-call counts of passerines (all species combined) and NEXRAD reflectivity, found a positive but highly variable correlation among sites. Such variability may originate, at least partly, from not having considered potential confounding variables that may affect the consistency of aural counts among nights (Farnsworth et al. 2004).

Here, we provide an empirical assessment of the correspondence between the reflectivity of a CWSR unit and nocturnal, aural counts of migrating passerines. Our assessment, unlike previous ones, takes into account the potential influence of some variables that may confound the relationship between reflectivity and the number of birds detected by observers. These include variables that characterize ambient noise levels, observer identity, and hourly variation in detectability—flight altitude decreases (Able 1970, Bellrose 1971, Mabee et al. 2006) and calling rate increases (Graber 1968, Farnsworth et al. 2004, Farnsworth 2005) through the night—as well as unknown night-to-night variation in detectability: species composition aloft (number, size), calling rate, flight altitude, bird distribution within the radar beam (Farnsworth et al. 2004), and other aerofauna (Gauthreaux et al. 2008). We performed this evaluation with a CWSR unit located on the Gaspé Peninsula, Quebec, that scans a major migratory route determined by the St. Lawrence Estuary (Fig. 1). By acting as a barrier, this estuary creates a leading line for diurnal migrants such as raptors and passerines, especially in the autumn, when large numbers of birds that originate from the Quebec-Labrador peninsula head south toward their wintering grounds (Ibarzabal 1999, Savard and Ibarzabal 2001).

Methods

Study area.—The weather radar of Val d'Irène (XAM) is located at the base of the Gaspé Peninsula (49°28′29″N, 67°36′04″W), 40 km south of Matane, Quebec (Fig. 1). The area scanned by the

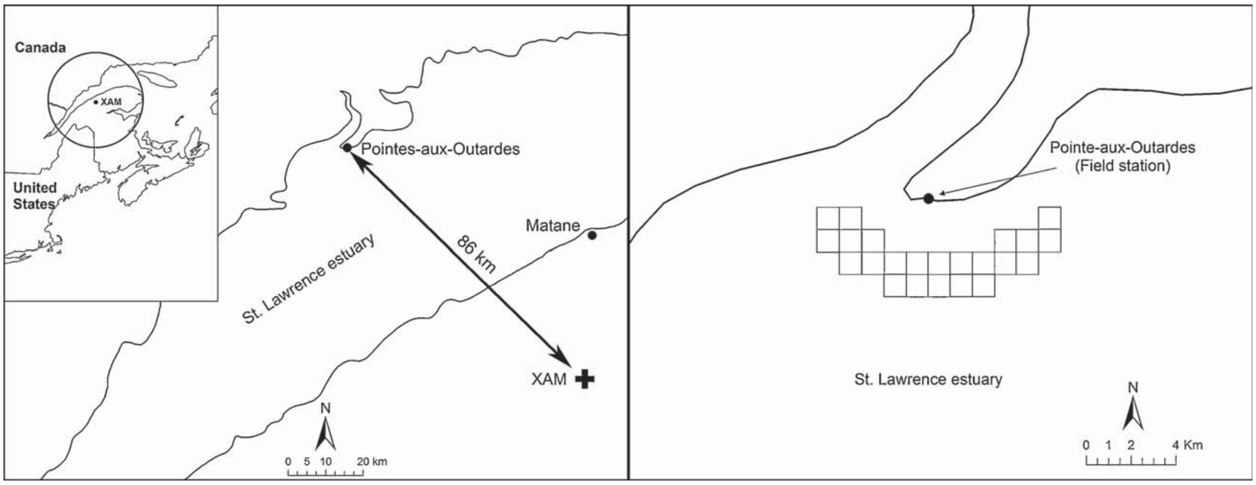

FIG. 1. Maps of the study area. Left: location of the Val d'Irène Canadian weather surveillance radar (XAM) in relation to the field station of Pointe-aux-Outardes. Right: location of the 1-km^2 pixels that were sampled for linear reflectivity (Z) every 10 min during aural counts. Depending on the occurrence of sea echoes, ≤16 of the 23 pixels were sampled. The buffer zone between the pixels and the field station was necessary to avoid ground echoes resulting from sandbanks exposed at low tide.

radar encompasses the eastern St. Lawrence Estuary and the western Gulf of St. Lawrence. The radar sits at an elevation of 722 m above sea level (ASL) and has a maximum scanning range of 256 km. Aural counts were performed near Pointe-aux-Outardes (49°05′N, 68°28′W), which is on the north shore of the St. Lawrence Estuary, 86 km from the radar and at an azimuth of 315° (Fig. 1). Observers stood in an open area with few scattered trees at an altitude of 7 m ASL, about 10 m from the St. Lawrence shoreline at high tide and 1–2 km at low tide, depending on tidal amplitude.

Radar characteristics and display software.—Canadian weather surveillance radars are C-band radars with a wavelength of 5.32 cm and peak power of 250 kW. The XAM radar is a subtype "Andrew" CWSR (CWSR-1998A) characterized by a beam width of 0.65°, a gain of 47.5 dB, and a minimum detectable signal (Z_{min}) at 50 km of –15.4 dBZ for a 2-µs pulse length in the conventional mode (Joe et al. 1998). The scanning pattern is repeated every 10 min in two 5-min modes, namely conventional and Doppler (for details, see Joe et al. 1998, Lapczak et al. 1999, and Joe and Lapczak 2002).

We used the software RAPID (Radar Data Analysis, Processing and Interactive Display; J.S. Marshall Radar Observatory, McGill University, Montreal) to analyze raw radar data. RAPID synthesizes spherical coordinate radar data into Cartesian maps and can display many products for both conventional and Doppler modes. For instance, reflectivity, azimuth, and distance from the radar can be obtained for each pixel. Pixel resolution is slightly lower than that of the raw data and corresponds to 1 km^2 and 4 km^2 for the ranges 0–120 km and 120–256 km, respectively. All products can be animated as a series of 5 to 36 images, with a choice of time lapse that ranges from 10 min to 1 h.

Reflectivity data.—We used reflectivity values in conventional mode of the lowest beam elevation (referred to as "plan position indicator [PPI] no. 1") because higher beams would detect birds flying too high to be heard by humans (see below). Conventional mode provides the total reflectivity factor in decibels of the logarithmic reflectivity (dBZ) (Joe and Lapczak 2002). The scale of reflectivity was set to start at –22 dBZ, a value that allows the display of weak echoes produced by insects and birds.

PPI no. 1 is usually set at 0.3° for typical CWSR but was set at –0.5°, an unusually low elevation for CWSR, at XAM because of its location on a mountaintop. This negative angle permitted XAM to scan at very low altitudes above the St. Lawrence coastal lowlands. According to Rinehart's (1997) beam equations under normal atmospheric conditions, the central axis of the radar beam passed over the observers at an altitude of 405 m ASL; the lower boundary of the beam reached sea level, and its upper boundary reached 887 m ASL (Fig. 2). Except for the sea surface, no obstacles intersected the line of sight between the radar and the observers.

Reflectivity was measured every 10 min and then transformed into linear reflectivity ($Z = 10^{dBZ/10}$). Linear reflectivity is an instantaneous measurement of target density in volume scanned (Black and Donaldson 1999, Gauthreaux and Belser 1999). During a given period, reflectivity was calculated as the average linear reflectivity of up to 16 1-km^2 pixels (mean ± SD = 15.5 ± 1.5 pixels), depending on the number of above-water pixels that were free of sea or tidal-flat echoes between 2 and 7 km from the observers (Fig. 1). These latter echoes were recognized using Doppler velocity data and tide tables. Pixels over water were chosen because ground echoes persistently contaminated the pixels directly above observers. The birds that were censused by the observers generally headed in a southward to westward direction (as determined by aural and moon-watch observations and later confirmed using XAM Doppler velocity data) and, thus, likely passed over the pixels sampled shortly after being counted. Assuming that migrating passerine birds fly 10–12 m s^{-1} on average (Larkin 1991), we estimate that birds counted by observers took 3–12 min to reach the closest and the farthest pixels from the sampling point, respectively.

Bird count data.—We performed aural counts on 16 nights between 13 and 29 September 2004. Counts involved two observers: observer A on days 1–8 and observer B on days 9–16. Observers counted birds, starting at sunset, for at least 4 consecutive hours when listening conditions were acceptable (i.e., wind speed <5 on

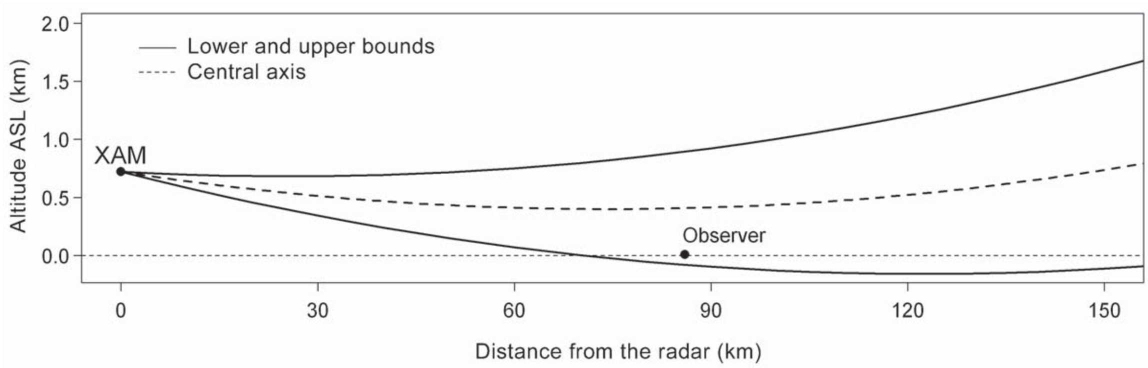

FIG. 2. Air column scanned by PPI no. 1 of the Val d'Irène Canadian weather surveillance radar (XAM) as a function of distance. Altitudes are theoretical elevations for normal atmospheric conditions and were calculated following Rinehart (1997). The fine dashed line represented 0 m above sea level (ASL). The XAM antenna sits at 722 m ASL.

the Beaufort scale and absence of rain noise). This sampling effort led to 333 ten-minute aural counts (i.e., rate estimates in terms of birds/unknown volume of sky/10 min) that could be linked to reflectivity data. Observers counted individual birds using a technique analogous to the minimum individual passing (MIP) described by Evans and Mellinger (1999). This technique considers information such as time delays in calling, amplitude differences between closely occurring calls, stereo spatial separation, species of the caller, and expected flight speeds (Evans and Mellinger 1999). Whenever possible, birds were identified to species (a minimum of 18 species were detected) or to the closest recognizable group (i.e., genus, family, or order). Analyses were restricted to passerines that emit night flight calls, such as thrushes, warblers, and sparrows (see Evans and O'Brien 2002). Flight calls of warblers and sparrows are detectable by ear up to 300 m above ground level (AGL), and those of thrushes up to 600 m AGL (Evans and Mellinger 1999, Evans and Rosenberg 2000). We did not include ducks, geese, or shorebirds in the analyses because the highly heterogeneous spatial distribution of these species among pixels precludes them from qualifying as precipitation-like targets and, thus, as appropriate for study with weather radars. Yet the reflectivity that may result from such tight-flocking, large-bodied species inevitably contributed to the error term in our analyses. However, we rarely detected >1 flock of these species per 10-min count. Hence, we expect that the bias caused by these flocks was not significant. In fact, running statistical analyses with all species detected did not affect model selection, nor did it alter the magnitude of model parameters. Noisiness in the environment, which was mainly caused by waves breaking on the shore, was rated on a scale between 1 and 4, where level 4 represented the noisiest conditions.

During 3 days, observers A and B simultaneously performed 32 ten-minute aural counts to assess potential biases attributable to observer efficiency at detecting birds and to different modes of estimating the number of migrants on the basis of calls. This comparison was applied separately to counts of thrushes (*Catharus* spp.) and to unidentified high-pitched frequencies attributed to other passerines (i.e., warblers and sparrows).

Statistical analyses.—We explored the strength of the nightly association between linear reflectivity (Z) and the number of birds detected within a given 10-min aural-count period using Pearson product-moment correlations (r). We calculated correlations on raw data as well as on moving averages that were based on 3 consecutive periods (i.e., $t-1$, t, $t+1$). We used moving averages partly because the pixels sampled on the radar displays corresponded to locations situated 2–7 km from the observers and, therefore, could depict birds counted from either the previous or the following 10-min aural-count period. We also report overall mean correlations based on nightly correlations weighted by the reciprocal of their standard error (1/SE).

We formally assessed the relationship between the number of birds detected aurally within a given 10-min aural-count period and radar linear reflectivity (Z) using linear mixed-effects models fitted by restricted maximum likelihood (Pinheiro and Bates 2000). Although either the number of birds or reflectivity could have been used as a response variable, we chose to model counts as a function of reflectivity because the former is likely to have been measured with less accuracy and precision than the latter and because users of radar images will ultimately be interested in estimating bird densities from reflectivity measures. Linear mixed-effects models, which imply a Gaussian random error, took into account the dependence of observations that may have occurred within our hierarchical design (i.e., consecutive 10-min aural-count periods nested within nights). Moreover, mixed-effects models allowed us to quantify the influence of five additional fixed explanatory variables: environmental noise (4 levels), observer identity (2 levels), time since sunset (in hours), the interaction between reflectivity and observer identity, and the interaction between reflectivity and time since sunset. The first interaction was included to allow the relationship between the number of birds detected aurally and reflectivity to vary between observers. The second was included because birds tend to fly lower as the night progresses (Able 1970, Bellerose 1971, Mabee et al. 2006) and, therefore, are more likely to be audible to observers. Assuming a constant reflectivity, this should lead to a positive interaction, whereby the slope between Z and the number of birds detected by observers becomes steeper as the night progresses.

We assessed three random-effects models, wherein (1) the intercept of the relationship between the response and the explanatory variables could vary among nights ($1 \mid$ night); (2) both the intercept and the slope relating the number of birds detected aurally and reflectivity could vary dependently among nights (Z|night); and (3) both the intercept and the slope relating the number of birds detected aurally and reflectivity could vary, but independently, among nights ([1|night] + [Z − 1|night]). These random effects were defined to control for daily variation in bird migration intensity and behavior, as well as in bird detectability, which may be linked to unaccounted variables such as meteorological conditions. We also assessed three types of correlation structures to model dependence among aural counts conducted on a given night: no within-group correlation, lag-1 autoregressive (AR[1]), and first-order moving average (MA[1]; Pinheiro and Bates 2000). We selected the best combination of random effects and correlation structure to include in the model using an information-theoretic approach based on the second-order Akaike's information criterion (AIC_c), following Vaida and Blanchard (2005). The AIC_c values allowed us to compute the Akaike weight (w_i) of each model, which corresponds to the relative strength of evidence or likelihood in favor of a given model, given the models in the set and the data (Burnham and Anderson 2002).

We quantified the effect size of fixed and random effects of the best model on the basis of 95% confidence intervals (CIs). We also weighed the relative importance of effects appearing as both random and fixed effects, using the equation ($\hat{\sigma}/\hat{\beta} \times 100$), where $\hat{\sigma}$ is the estimate of a random effect's standard deviation and $\hat{\beta}$ is its estimated fixed effect coefficient value (Pinheiro and Bates 2000). Models were fitted by restricted maximum likelihood with the lme function of the nlme package (version 3.1-43) within the R statistical environment (version 1.7.1; R Development Core Team 2005). We did not consider nights 11 and 12 because the sampling effort was too low as a result of unfavorable weather conditions (n = 3 and 4 ten-minute periods, respectively; total n = 326). The assumptions that underlie mixed-effects models were checked graphically following Pinheiro and Bates (2000). Within-group errors appeared to be independent and normally distributed, with mean zero and a given variance, and independent of random effects. We found no indication that random effects deviated from a normal distribution with mean zero and a covariance matrix that did not depend on the group or that they failed to be independent for different groups.

RESULTS

Correlation between aural count and reflectivity.—Overall, CWSR linear reflectivity was positively correlated with the number of birds detected during 10-min aural counts (Table 1 and Fig. 3). However, the strength of the relationship between the number of birds detected aurally and reflectivity varied among nights. For example, nightly r values varied between −0.18 and 0.75 (weighted mean ± SD = 0.53 ± 0.26) or between −0.58 and 0.93 (0.69 ± 0.42) when calculated on raw data or on moving averages, respectively (number of nights = 12). Also of interest, the radar failed to detect migrants on nights that were characterized by low migration rates as determined by the few birds detected during aural counts (i.e., on nights 2, 11, 12, and 16; Fig. 3). Overall, it seems that the XAM was able to properly describe the migration rates that were detected aurally (Fig. 4).

Mixed-effects models.—The above results were generally supported by the best linear mixed-effects models as identified by their weights of evidence (w_i). Models 5 and 6, which shared 91% of the evidence, clearly indicated that the autocorrelation among consecutive 10-min aural counts had to be taken into account when modeling reflectivity measures (Table 2). Temporal autocorrelation coefficients equaled 0.28 for both models. The difference in weight of evidence between the two best models was not sufficient to formally identify a single best model (0.53 vs. 0.38). We used the model with the highest w_i to report fixed and random effects (i.e., model 5). Yet both models showed very similar results, both qualitatively and quantitatively.

TABLE 1. Nightly correlation (Pearson product-moment r) between the number of birds detected during 10-min aural counts near Pointe-aux-Outardes, Quebec, and the linear reflectivity (Z) of the Val d'Irène Canadian weather surveillance radar (XAM) on 16 nights between 13 and 29 September 2004. Sample size (n) corresponds to the number of 10-min counts. Moving averages were computed on 3 consecutive 10-min counts.

Night	n	r on raw data	r on moving averages
1	12	0.51	0.76
2	9	NA	NA
3	26	0.75	0.84
4	27	0.53	0.64
5	22	0.61	0.77
6	25	0.55	0.93
7	23	0.29	0.58
8	22	0.27	0.27
9	28	0.44	0.55
10	22	0.59	0.90
11	3	NA	NA
12	4	NA	NA
13	56	0.74	0.81
14	12	−0.18	−0.58
15	36	0.59	0.63
16	6	NA	NA

Considering that passerines fly at an average airspeed of 10–12 m s^{-1} (Larkin 1991) and that the most distant pixel sampled was 7 km from the field station, birds could theoretically take 9.7–11.7 min to cover this distance. Because some birds were thus counted before they reached the area in which reflectivity was measured, we also fitted the same models as above (Table 2) but with the reflectivity measured in the following 10-min period (Z_{t+1}). Using a common database, the models with Z_t clearly showed a better overall fit than the models with Z_{t+1}. Indeed, the best model with Z_{t+1} was 18.1 AIC_c units from the best model with Z_t.

The best model indicated that the number of birds detected by observers during aural counts increased with linear reflectivity (Table 3). The slope of this relationship did not vary between the two observers, nor was it affected by the time since sunset, despite the fact that the number of detected birds increased as the night progressed. The number of birds detected aurally decreased when the ambient noise level reached 3; no decrease was observed at higher noise levels, likely because of low statistical power. Lastly, the intercept was slightly positive but did not differ significantly from zero given a moderately wide confidence interval, which suggests that the radar was relatively sensitive to low bird densities.

Although the linear mixed-effects model did not measure a significant difference in the number of birds detected aurally

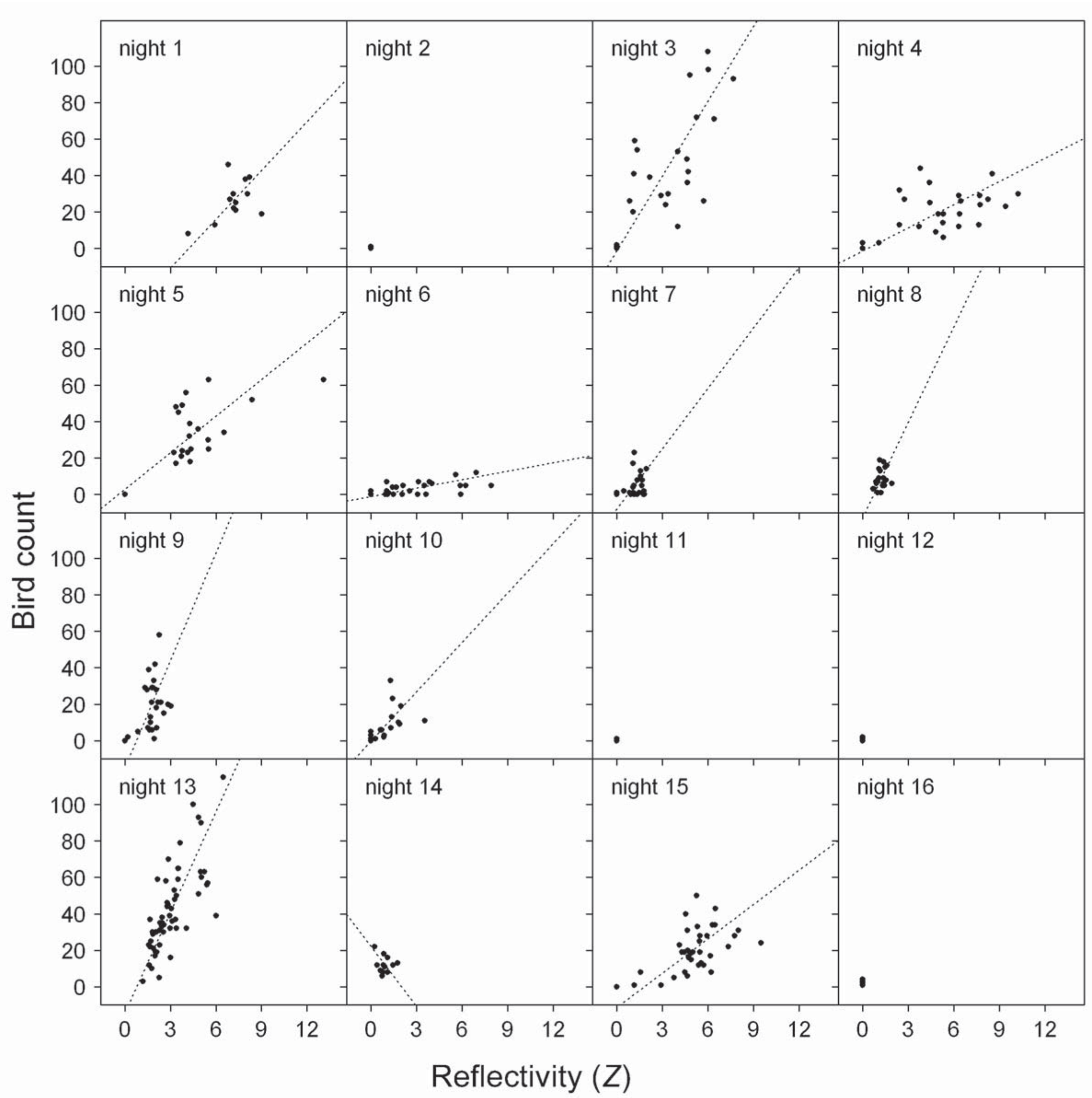

FIG. 3. Relationship between number of birds detected during 10-min aural counts near Pointe-aux-Outardes, Quebec, and estimates of migrating bird density as determined by radar linear reflectivity (Z) on 16 nights between 13 and 29 September 2004. Linear reflectivity was measured by the Val d'Irène Canadian weather surveillance radar (XAM). Dashed lines depict the standardized major axis for nights during which >10 aural counts were performed.

between the two observers (Table 3), simultaneous sampling revealed that observer A detected, on average, 1.9 more thrushes during a 10-min aural count than observer B (95% CI: 1.0–2.9). On the other hand, observer B detected 5.7 more non-thrush passerines (mainly warblers and sparrows) than observer A (95% CI: 1.9–9.6).

The intercept and slope of the relationship between the number of birds detected aurally and reflectivity varied significantly among nights (Table 3). Indeed, the relative importance of random effects with respect to their corresponding fixed effects ($\hat{\sigma}/\hat{\beta}$) was 0.77 for the intercept and 0.66 for the slope (Pinheiro and Bates 2000). Within-night variation (random residuals) was about ±12 birds in comparison with the predicted bird count (Table 3).

DISCUSSION

Correlation between aural count and reflectivity.—We found a positive but highly variable among-nights relationship between radar linear reflectivity and an aural index of bird counts. We attribute this strong night-to-night variability to the fact that we related an instantaneous measure of target density (i.e., radar reflectivity) to a measure of rate (i.e., birds/unknown volume of sky/10 min), as well as to possible differences in bird migration behavior and in radar response in relation to bird behavior.

The relationship between an instantaneous measure of target density within a given volume of air and an estimate of the number of birds that cross an undetermined portion of sky can

TABLE 2. Selection of linear mixed-effects models estimating densities of migrating birds over 10-min periods above Pointe-aux-Outardes, Quebec, using the linear reflectivity (*Z*) of the Val d'Irène Canadian weather surveillance radar (XAM) on 14 nights between 13 and 29 September 2004 ($n = 326$). Fixed effects included the radar reflectivity, the amount of environmental noise (4 categories), the observer identity (2 categories), time since sunset (in hours), the interaction between reflectivity and observer identity, and the interaction between reflectivity and time since sunset. We assessed 3 random-effects structures and 3 types of correlation structures (see text for description of statistical analysis methods; the best model according to AIC_c is highlighted in bold, *K* = number of parameters in the model, and w_i = Akaike weights).

Random effects	Correlation structure	*K*	ΔAIC_c	w_i
1. (1|night)	No within-group correlation	11	76.92	0.000
2. (Z|night)	No within-group correlation	13	12.15	0.001
3. (1|night)+(Z – 1 | night)	No within-group correlation	12	11.91	0.001
4. (1|night)	AR(1)	12	41.38	0.000
5. (Z|night)	**AR(1)**	**14**	**0.00**	**0.529**
6. (1|night)+(Z – 1 | night)	AR(1)	13	0.69	0.376
7. (1|night)	MA(1)	12	46.99	0.000
8. (Z|night)	MA(1)	14	4.78	0.048
9. (1|night) + (Z – 1 | night)	MA(1)	13	4.97	0.044

be biased when the ground speed of birds varies through time. Indeed, although the instantaneous density of birds detected by radar will not be influenced by variation in the ground speed of birds (because of variation in air speed, say), the number of birds detected per unit of time by a ground observer will. Such a bias can be avoided by transforming the detection rate into a density estimate by dividing the former by the ground speed of birds (Black and Donaldson 1999, Gauthreaux and Belser 1999). Although the ground speed of birds can be obtained from the Doppler velocity data of weather radars, it was impossible for us to standardize our detection rates because the flight direction of birds at our sampling site (i.e., roughly perpendicular to the sampling site–radar axis), combined with the remoteness of the radar, prevented unbiased ground-speed estimates (Gauthreaux and Belser 1998). Unfortunately, such a limitation is also likely to afflict weather-radar estimates of migration rates over areas where the movement of birds is determined by anisotropic, topographical features.

Studies that previously investigated the relationship between radar reflectivity or the number of birds detected by radar and an aural index of bird counts either did not find a significant relationship (Graber 1968) or reported some positive but highly variable relationships among seasons or sites (Larkin et al. 2002, Farnsworth et al. 2004). One factor that may explain these discrepancies in comparison with our more consistent results is that we conducted individual bird counts (MIP; Evans and Mellinger 1999) rather than call counts. We believe that this partly removed

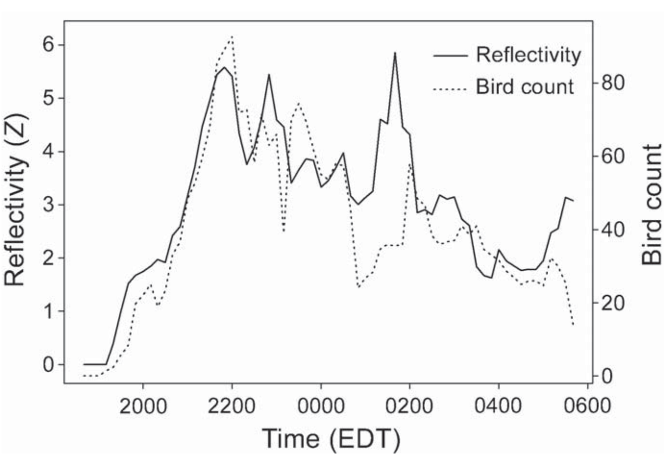

FIG. 4. Relationship between the number of birds detected during 10-min aural counts near Pointe-aux-Outardes, Quebec, and the radar linear reflectivity (*Z*) during the night of 26–27 September 2004 (night 13) as determined by the Val d'Irène Canadian weather surveillance radar (XAM). Sunset and sunrise occurred at 1820 and 0623 hours, respectively. Lines depict moving averages computed on three consecutive 10-min aural counts.

TABLE 3. Coefficients ($\hat{\beta} \pm$ SE) of fixed effects and variance ($\hat{\sigma}$) of random effects and their confidence intervals for the best linear mixed-effects model (no. 5 in Table 2) estimating the density of migrating birds within 10-min periods above Pointe-aux-Outardes, Quebec, as measured by the linear reflectivity (*Z*) of the Val d'Irène Canadian weather surveillance radar (XAM) on 14 nights between 13 and 29 September 2004 ($n = 326$). Fixed and random effects for which confidence intervals do not include zero are highlighted in bold.

Fixed effect	$\hat{\beta} \pm$ SE		95% CI
Intercept	5.085 ± 3.306		–1.421 to 11.591
Z	4.531 ± 1.646		**1.292 to 7.769**
Noise2	–2.966 ± 2.824		–8.524 to 2.592
Noise3	–11.526 ± 3.586		**–18.583 to –4.469**
Noise4	–5.526 ± 7.784		–22.659 to 11.607
ObsB	2.874 ± 4.395		–6.801 to 12.548
Time	1.457 ± 0.681		**0.117 to 2.797**
*Z**obsB	1.910 ± 2.270		–2.556 to 6.376
*Z**time	–0.319 ± 0.244		–0.799 to 0.161
Random effects	Variability	$\hat{\sigma}$	95% CI
Intercept	Between-night	3.907	**1.354 to 11.276**
Z	Between-night	3.009	**1.666 to 5.434**
Residuals	Within-night	12.058	**10.982 to 13.239**

biases associated with calling rates that may vary with time, migratory activity, species composition aloft, artificial lighting, and weather variables such as cloud cover (Farnsworth 2005). For example, both Graber (1968) and Farnsworth et al. (2004) recorded higher calling rates—and, thus, a larger abundance index—in the predawn hours, whereas most studies have reported a decrease in bird numbers aloft during this period (reviewed by Kerlinger and Moore 1989). Other factors that could explain the lower strength of the relationships found in previous studies include (1) lower data resolution, a result of pooling data across nights (Graber 1968, and some results of Farnsworth et al. 2004); (2) recording the calls of a single species (Larkin et al. 2002); and (3) the way in which reflectivity was measured and transformed into an index of birds km^{-3} (Farnsworth et al. 2004).

The fact that correlations between radar reflectivity and aural bird counts based on moving averages performed better than typical correlations suggests that migrating birds aloft are not homogeneously distributed in space within the detection range of observers. It also suggests that aural counts lasting 10 min may not be sufficient to obtain proper estimates of bird migration densities. The AR(1) correlation structures used in the mixed-effects models that were retained as best (models 5 and 6; Table 2) support such an interpretation. Furthermore, observers often noted that thrushes, and to a lesser extent other passerines, migrated in loose flocks. Although the spatial distribution of migrating birds has been subjected to some empirical investigations that suggest the existence, but not the prevalence, of loose flocks at night (Balcomb 1977, Larkin and Szafoni 2008), we have no clear information with respect to the factors that may affect this spacing and the scales at which it may be observed.

Mixed-effects modeling.—The intercept of the mixed-effects model was positive, and its 95% CI was moderately wide and marginally included zero (Table 3). These results partly reflect the fact that observers have occasionally detected aurally a certain number of migrating birds that went undetected by the radar (Fig. 3). This can happen because the power of the radar signal, which is back-scattered to the radar once it has hit an object, decreases with distance (Bruderer 1997a, Rinehart 1997): thus, low bird densities cannot be detected at large distances from the radar (i.e., ~86 km in our study). As a consequence, the CWSR network may be of limited use in detecting weak migration events at long range, inasmuch as the radar used (XAM) allowed an especially good coverage of the altitude stratum within which birds can be detected aurally (i.e., less than ~600 m; Evans and Mellinger 1999, Evans and Rosenberg 2000; Fig. 2). The positive slope between reflectivity and aural bird counts nevertheless reinforces our confidence that linear radar reflectivity provides an index of the flow of migrating birds.

Any index of bird density derived from nocturnal flight calls may imply biases attributable to extrinsic and intrinsic detection abilities of observers. In our study, bird counts tended to be lower when the noise level was high, but noisy conditions may have been confounded with windy conditions (which can, in turn, affect bird migration), given that strong noise levels were mainly caused by waves breaking on the beach. Yet there was no clear relationship between ambient noise level and wind speed ($r_s = -0.27$) or direction, likely because the effect of waves varied with their distance from the observers, which depended on tidal conditions, and because waves may have originated from wind conditions that prevailed before censuses were conducted. Hence, we conclude that the lower bird counts recorded under noisy conditions were mainly caused by a diminished observer's ability to detect birds and did not originate from lower migration activity related to a confounding effect linked to wind conditions.

Although we found, through simultaneous sampling by two observers, that observers detected thrushes and other passerines with different detection abilities, no observer effects were measured on the intercept or the count–reflectivity slope of the mixed-effects model. This discrepancy could originate from merging both groups of birds in the latter analysis. Our results nevertheless underline the importance of considering observer-dependent detection probabilities when conducting nocturnal aural counts of migrating birds, as well as for all other census types (Ramsey and Scott 1981, Nichols et al. 2000, Royle et al. 2005). For instance, observer-dependent detection probabilities related to call counts can be removed by using an automated system that records calls and automatically assigns species on the basis of sound signatures (Farnsworth 2005).

We expected that the number of birds counted would increase at an increasing rate along with reflectivity as the night advanced, because birds decrease their flight altitude as night goes on (Able 1970, Bellrose 1971, Mabee et al. 2006) and are therefore easier to detect by ear. Yet species may descend at different times, leading to variation in call counts, calling in general, and reflectivity (A. Farnsworth pers. comm.). Although observers detected an increasing number of birds as the night progressed, we did not find that the slope between counts and reflectivity increased with time (Table 3). One potential explanation is that censuses were usually terminated well before dawn (i.e., 6 h 41 min ± 2 h 41 min before sunrise) and thus before calling rates started to augment and probably before the interaction started between increasing detection probability and decreasing reflectivity caused by birds landing gradually as the night went on.

The intercept and count-reflectivity slope varied between nights by ±0.77 and ±0.66 of their values as fixed effects, respectively (i.e., 5 ± 4 birds and 4.5 ± 3 birds/Z unit). Such results indicate relatively good radar detection capabilities with respect to birds at the spatial scale sampled by the observer but also point out significant night-to-night variation. Furthermore, the residuals indicate that within-night variation was particularly high (i.e., ±12 birds). Hence, not taking sources of within- and between-night variability into account would likely lead to high prediction uncertainty, and even to biases.

The observed within- and between-night variability may have resulted from the aural method used to count birds and from modeling a rate–density relationship. Other sources of variability include variation in height of flight, calling rate, and flock species composition (Farnsworth et al. 2004). Additional noise may originate from echoes produced by nonpasserine birds (i.e., waterfowl, shorebirds, and gulls in the present study) and insects (Larkin 1991). Because all the above factors can operate in combination to different degrees, it is currently difficult to determine their respective contributions and the temporal scale at which they are more likely to influence the relationship of bird count and reflectivity.

Effects related to radar physics.—Other factors concerning the physics of radar may have affected the relationship between aural bird counts and reflectivity. These include, among others,

(1) the "sinusoidal" relationship between a bird's size (geometric area) and the cross-section area perceived by the radar (i.e., the Mie or resonance region; Eastwood 1967, Alerstam 1990, Rinehart 1997); (2) the fact that the power returned to the radar decreases with the distance (*R*) at which targets have been hit (relationship of *Z* and *R*), depending on the number and vertical distribution of targets (birds concentrated in either the lower or the upper beam boundaries will return a lower reflectivity than birds concentrated in the center or evenly distributed in the beam; Bruderer 1997a, Rinehart 1997, Gosset and Zawadzki 2001); and (3) birds' body orientations with respect to the radar (Edwards and Houghton 1959, Bruderer and Joss 1969, Houghton 1969). These intrinsic noise sources should induce variability in reflectivity measures at any time and under any conditions. Although Larkin et al. (2002) expected that the variation in reflectivity measures should be dominated by the volumetric density of the targets (i.e., the number of birds km^{-3}), this remains to be confirmed empirically using proper technology (e.g., by coupling the measures made by a marine radar to the ones made by a weather radar).

Scientific contributions of the present study.—Ours is the first published study that shows that CWSR can detect birds. The use of CWSR data thus has the potential to extend the NEXRAD network's coverage farther north by several hundreds of kilometers and to increase our understanding of how birds use the North American landscape during migration, especially in the complex coastal landscape of the St. Lawrence–Great Lakes basin. The information generated by the two networks could be coupled by adapting to CWSR the automated, radar information-extraction system developed by Gauthreaux et al. (2003) for the NEXRAD network. Although we attempted to control for some of the variables that affected aural bird detectability, aural counts were too variable and could not be used to calibrate the relationship between the flow of migrating birds aloft and linear reflectivity. Such a calibration may require the use of marine radars. Nevertheless, we are convinced that acoustic studies, particularly electronic ones to account for observer bias, should be used in conjunction with weather radar studies to provide a minimal indication of the species that compose the flow of birds crossing the radar beams.

Acknowledgments

We thank C. Cormier and O. Barden for providing the nocturnal census data we used to explore the first displays of bird migration with the Val d'Irène weather radar. B. Dumont helped collect field observations. We are indebted to the J.S Marshall Radar Laboratory of McGill University for lending us the RAPID software and to the Meteorological Service of Canada and the Canadian Wildlife Service of Environment Canada (EC) for making the radar data available. We benefited from the advice of J. E. Black (Brock University) on aural field counts and weather radar basics and that of N. Donaldson (Atmospheric Science and Technology Directorate of EC) on details of CWSR. We also thank M. A. Farnsworth and an anonymous reviewer for valuable comments on the manuscript and B. Parsons, who improved the English. This study was financially supported by the Consortium de recherche sur la forêt boréale commerciale (UQAC), the Canada Research Chair in Spatial and Landscape Ecology, and Environment Canada. NEXRAD can be accessed at www.nws.noaa.gov.

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Associate Editor: D. H. Johnson