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COMPARAISON ENTRE UN DÉNOMBREMENT DE PASSEREAUX EN MIGRATION NOCTURNE ET LA RÉFLECTIVITÉ D'UN RADAR DE SURVEILLANCE MÉTÉOROLOGIQUE CANADIEN

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RÉSUMÉ

Les radars de surveillance météorologiques sont des outils puissants pour étudier la migration des oiseaux, mais jusqu'à présent, les études qui ont fait le lien entre la réflectivité radar et des estimés auditifs du nombre d'oiseaux dans le ciel n'ont obtenus que des résultats équivoques. Cette absence de relation claire résulte de la non considération de variables pouvant brouiller la relation entre la réflectivité et le nombre d'oiseaux détectés. Ces variables incluent le bruit ambiant, l'observateur ou la technologie acoustique utilisée, mais aussi des fluctuations inconnues comme des variations intra ou inter nuits de la détectabilité des oiseaux (e.g. : l'altitude de vol, la composition en espèces). Ici, nous nous attardons à la relation entre le dénombrement auditif d'oiseaux et la mesure de réflectivité radar (*Z*) mesurés par périodes de 10 minutes, durant 16 nuits pendant la migration automnale. La mesure de réflectivité a été prise avec le radar de surveillance météorologique canadien de Val d'Irène (XAM), localisé près de Amqui, au pied de la péninsule gaspésienne (Québec, Canada). Nous avons trouvé que la réflectivité de XAM était positivement corrélée avec le nombre d'oiseaux détecté auditivement, mais cette corrélation variait entre 0,27 et 0,75 d'une nuit à l'autre (moyenne ± écart-type = 0,53 ± 0,15). En utilisant des modèles linéaires à effets mixtes où les dénombrements auditifs d'oiseaux étaient nichés par nuit, il s'est avéré que le nombre d'oiseaux détectés auditivement par les observateurs s'accroissait avec la réflectivité. La pente de cette relation ne variait

pas entre les observateurs et n'était pas non plus affectée par le nombre d'heures depuis le couché du soleil, et ce, même si le nombre d'oiseaux détectés augmentait à mesure que la nuit avançait. Le nombre d'oiseaux détectés auditivement était cependant moindre lorsque le bruit ambiant était plus important. L'intercepte ne différait pas significativement de zéro, suggérant que le radar était relativement sensible pour détecter une faible densité d'oiseaux. L'intercepte et la pente de la relation entre le nombre d'oiseaux détectés auditivement et la réflectivité variaient significativement et indépendamment l'une de l'autre entre les nuits. Une telle variation est vraisemblablement causée par la combinaison (et l'interaction) de facteurs incluant : les conditions environnementales, le comportement de migration des oiseaux, la physique radar ainsi que la détectabilité des oiseaux par les observateurs et le radar. Même si nous avons contrôlé quelques variables qui peuvent affecter la détectabilité auditive des oiseaux, il semble clair que les dénombrements auditifs (ou par microphones) ne peuvent pas être utilisés pour étalonner la relation entre la densité d'oiseaux migrant dans le ciel et la réflectivité radar. L'utilisation d'un radar de surveillance maritime ayant la capacité de détecter vraisemblablement tous les oiseaux dans le ciel serait à favoriser pour effectuer un tel étalonnage.

AVANT-PROPOS

Les principales sections de ce manuscrit sont en anglais. Elles ont été retranscrites d'un texte original intitulé *Comparison between nocturnal, aural passerine counts and radar reflectivity from a Canadian weather surveillance radar* et qui sera soumis pour publication sous forme d'article dans un périodique scientifique. Les auteurs du texte original sont : François Gagnon[1,2,3], Marc Bélisle[4], Jacques Ibarzabal[1,3], Pierre Vaillancourt[5] et Jean-Pierre Savard[3,6].

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INTRODUCTION

Since the discovery in the 1940s that radar can detect birds in flight (Lack and Varley, 1945), radar has often been used to study bird migration (Bruderer 1997, Gauthreaux and Belser 2003). Although different kinds of radars can be used to detect birds (e.g., marine, weather, tracking), weather radars present outstanding advantages over other types for monitoring bird migration: (1) they show extended detection ranges; (2) they are distributed in such a fashion as to provide a continuous coverage over large spatial scales; (3) they collect comparable information; (4) data are collected on a 24-h basis and archived for years; and (5) the information that they collect is usually freely accessible to the public. Weather radar studies of nocturnal bird migration, which began in the 1970s (Gauthreaux 1970, Gauthreaux and Belser 2003), have been refined over the past several decades with the establishment of the NEXRAD radar network radar in the United States (Diehl et al. 2003). The Internet now provides an easy and instant access to large-scale migratory movements via WSR-88D (http://www.nws.noaa.gov). In Canada, a Doppler weather radar network consisting of 30 CWSR's (Canadian Weather Surveillance Radars) of 3 types plus McGill radar of a particular type (Joe and Lapczak 2002) covers the entire East-West border with the United States, thereby providing an opportunity for studying previously untapped portions of North-South migrations on a continental scale. Although some products of these radars are available on the Internet, the information they contain cannot be used to visualise bird migration. This results partly from the focus on reflectivity scales ("reflectivity" will mean "reflectivity factor" throughout the text) that are relevant to meteorological phenomena. Reflectivity is a parameter expressing 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 visualise weaker echoes, some presumably representing birds and insects. So far, the potential of CWSR to study 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 that are characteristic of Doppler weather radar and which allow birds to be detected (Gauthreaux and Belser 1998, Koistinen 2000). Although the use of radar signals for enumerating migrants was initially met with some scepticism, this technique has proved to be more convincing when linked to traditional field estimation methods, such as moon watching (Eastwood 1967, Gauthreaux 1972, Liechti et al. 1995, Gauthreaux and Belser 1998), or to aural (by ears or microphone) 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 being 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. Nevertheless, aural studies have their own drawbacks, which stem from time-dependent calling rates, inconsistencies in the ratio between calling (e.g., thrushes, warblers, and sparrows) and non-calling species [e.g., flycatchers, kinglets, and vireos (Evans and O'Brien, 2002)], and from differential detection probabilities incurred by 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 so far led to equivocal results. For instance, both Larkin et al. (2002), who compared the relationship between aural counts of Dickcissels (*Spiza americana*) and NEXRAD reflectivity, and Farnsworth et al. (2004), who documented the relationship between flight-call counts of passerines (all species confounded) and NEXRAD reflectivity, found a positive but highly variable correlation among sites when using data pooled across nights. Such variable results 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 radar 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 characterise ambient noise levels, observer identity, and hourly variation in detectability [flight altitude decreases (Able 1970, Bellrose 1971) 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)]. We performed this evaluation with a CWSR radar that was located on the Gaspé Peninsula, Québec, Canada, and which scans a presumably major migratory route determined by the St. Lawrence Estuary (Figure 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 originating from the Québec-Labrador peninsula head south towards their wintering grounds (Ibarzabal 1999, Savard and Ibarzabal 2001). Understanding the factors that modulate the number of migrants, together with the route they use in this area, is of utmost importance, especially since nocturnal migration has not been studied in this area [except for the Gaspé Peninsula (Ball 1952)]. Furthermore, wind energy projects are expanding rapidly on both the north and south shores of the St. Lawrence Estuary and such tall structures raise conservation issues. Such understanding may be gained rapidly and at low cost only through the use of an established tool that allows the monitoring of bird migration over large spatial scales, namely weather radar technology.

METHOD

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, Québec, Canada (Figure 1). The area scanned by the radar encompasses the eastern 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° (Figure 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 to 2 km at low tide, depending on tidal amplitude.

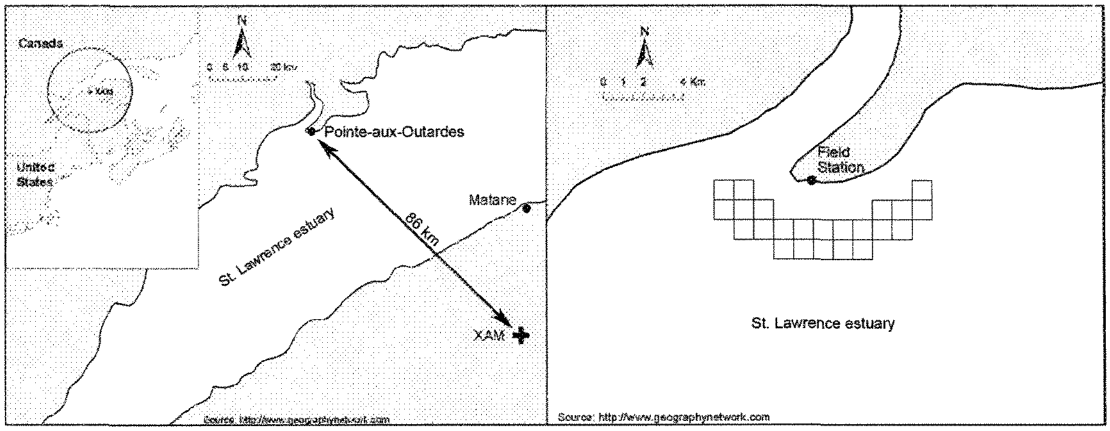

Figure 1. Maps of the study area. Left: location of the Val d'Irène CWSR radar (XAM) relative to the field station of Pointe-aux-Outardes. Right: location of the 1 km^2 pixels that were sampled for linear reflectivity (*Z*) every 10 min during aural counts. Depending on the occurrence of sea echoes, up to 16 of the 23 pixels illustrated 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 characteristics and display software

CWSR are C-band radars with a wavelength of 5.32 cm, peak power of 250 kW. XAM is a type "Andrew" CWSR (CWSR-1998A sub type), which is characterised 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 minutes in two 5-min modes, namely conventional and Doppler [details can be found in 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, Canada) to analyse raw radar data. RAPID synthesises 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 for ranges between 0-120 km. All products can be animated as a series of 5 to 36 images, with a choice of time laps that range from 10 min to 1 h.

Reflectivity data

We used reflectivity values in conventional mode of the lowest beam elevation, which is referred to as PPI (Plan Position Indicator) #1, as higher beams would detect birds flying too high to be heard by humans (see below). Conventional mode provides total reflectivity factor in dBZ (Joe and Lapczak 2002), where dBZ = $10*\log_{10}(Z)$. The scale of reflectivity was set to start at -22 dBZ, a value which allows display of very weak echoes produced by insects and birds. Such targets are usually not shown in the actual precipitation (rain) product of CWSR that is made available on the Internet, where reflectivity starts at 7 dBZ.

XAM scans lower angles than most CWSR radars, exactly because it is necessary to “look” down into the St. Lawrence estuary. PPI#1 usually set to 0.3° for typical CWSR, but because of its location on a mountaintop, XAM PPI #1 was set at -0.5°. 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, while its upper boundary reached 887 m ASL (Figure 2). Except for the sea surface, there were no obstacles intersecting the line-of-sight between the radar and the observers.

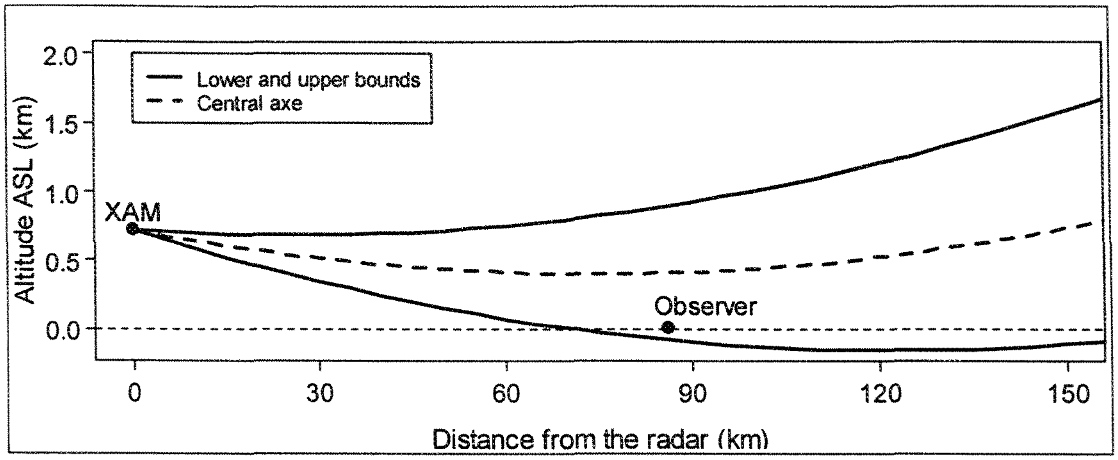

Figure 2. Air column scanned by the Plan Position Indicator (PPI) #1 of the Val d'Irène CWSR radar (XAM) as a function of distance. Altitudes are theoretical elevations for normal atmospheric conditions and calculated following Rinehart (1997). The fine dashed line represented 0 m ASL. XAM antenna sits at 722 m ASL.

Linear reflectivity ($Z = 10^{dBZ/10}$) was measured on a 10-min period basis. 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 (Figure 1). These latter echoes were recognised using Doppler velocity data and tide tables. Pixels above 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, and thus, likely passed over the pixels sampled shortly after being counted. Assuming that migrating passerine birds fly between 10 and 12 m/s (Larkin 1991), we estimate that birds counted by observers took between 3 and 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 the 13 and 29 September 2004. Counts involved two observers: observer A on days # 1 to 8; and observer B on days # 9 to 16. Observers counted birds, starting at sunset, for at least four consecutive hours when listening conditions were acceptable (i.e., wind speed below 5 on the Beaufort scale and absence of rain noise). This sampling effort led to 333 comparisons of 10-min aural counts that could be linked to reflectivity data. Observers attempted to count individual birds, differentiating them on the basis of voice similarity as well as on the time and distance flown between calls. Whenever possible, birds were identified to species or to the closest recognizable group (i.e., genus, family or order). Counts were restricted to passerines that emit night flight calls, such as thrushes, warblers, and sparrows (see Evans and O'Brien 2002). We did not include ducks, geese or shorebirds because of difficulties in estimating their numbers. Furthermore, their close flocking behaviour and the isolated flock distribution within the air space most of the time disable them as precipitation-like targets that would make them good objects for weather radar studies. These species, which contributed to radar reflectivity, inevitably contributed to the error term in our analysis. 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 10-min aural counts in order to assess potential biases due to observer efficiency at detecting birds and to differential modes of estimating the number of migrants based on 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

Correlation between aural counts and reflectivity

We explored the strength of nightly association between linear reflectivity (*Z*) and the number of birds detected within a given 10-min aural counts period based on Pearson product-moment correlations (*r*). We calculated correlations on raw data (t) as well as on moving averages that were based on three consecutive periods (t-1, t, t+1). We used moving averages partly because the pixels sampled on the radar displays corresponded to locations situated between 2 and 7 km from the observers and, therefore, could depict birds counted from either the previous or the following 10-min aural counts period: temporal averages of the aural data "simulates" the spatial averaging of the radar data.

Mixed-effects models

We formally assessed the relationship between the number of birds detected aurally within a given 10-min aural counts period and radar linear reflectivity (*Z*) using linear mixed-effects models fitted by restricted maximum likelihood (Pinheiro and Bates 2000). Although both the number of birds and reflectivity could have been used as response variables, 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. 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 counts periods nested within nights). Moreover, mixed-effects models allowed us to quantify the influence of five additional fixed explanatory variables: environmental noise (four levels), observer identity (two 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 to take into account the fact that birds tend to fly lower as the night progresses and therefore, are likely to be more 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 different random effects, whereby: (1) the intercept of the relationship between the response and the explanatory variables could vary among nights (1|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 behaviour, 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 1st-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 information criterion (AICc), following Vaida and Blanchard (2005). AICc values allowed us to compute the Akaike weight (w_i) of each model, which corresponds to the relative strength of evidence or likelihood in favour 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 based on 95% confidence intervals. We also weighed the relative importance of effects appearing as both random and fixed effects, using the equation (σ/β *100), where σ is a random effect standard deviation and β is its fixed effect coefficient value (Pinheiro and Bates 2000). Models were fitted by restricted maximum likelihood with the *lme* function of the nlme package (v. 3.1-43) within the R statistical environment (v. 1.7.1, R Development Core Team 2005). We did not consider nights #11 and 12 because the sampling effort was too low due to unfavourable weather conditions (total of 7 10-min periods [total sample size = 326]). All models met the assumptions underlying linear mixed-effects models (Pinheiro and Bates 2000).

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 (Figure 3). However, the strength of the relationship between the number of birds detected aurally and reflectivity varied among nights (Table 1, Figure 3). For example, nightly *r*-values varied between -0.27 and 0.75 (mean ± SD = 0.53 ± 0.15) or between 0.27 and 0.93 (0.70 ± 0.19), when calculated on raw data or on moving averages, respectively (n = 11; Table 1) and when excluding night #14 with negative trend. Also of interest, the radar failed to detect migrants on nights that were characterised by low migration fluxes, as determined by the few birds detected during aural counts (i.e., on nights #2, 11, 12 and 16; Figure 3). Overall, it seems that the XAM was able to properly describe the migration fluxes that were detected aurally (Figure 4).

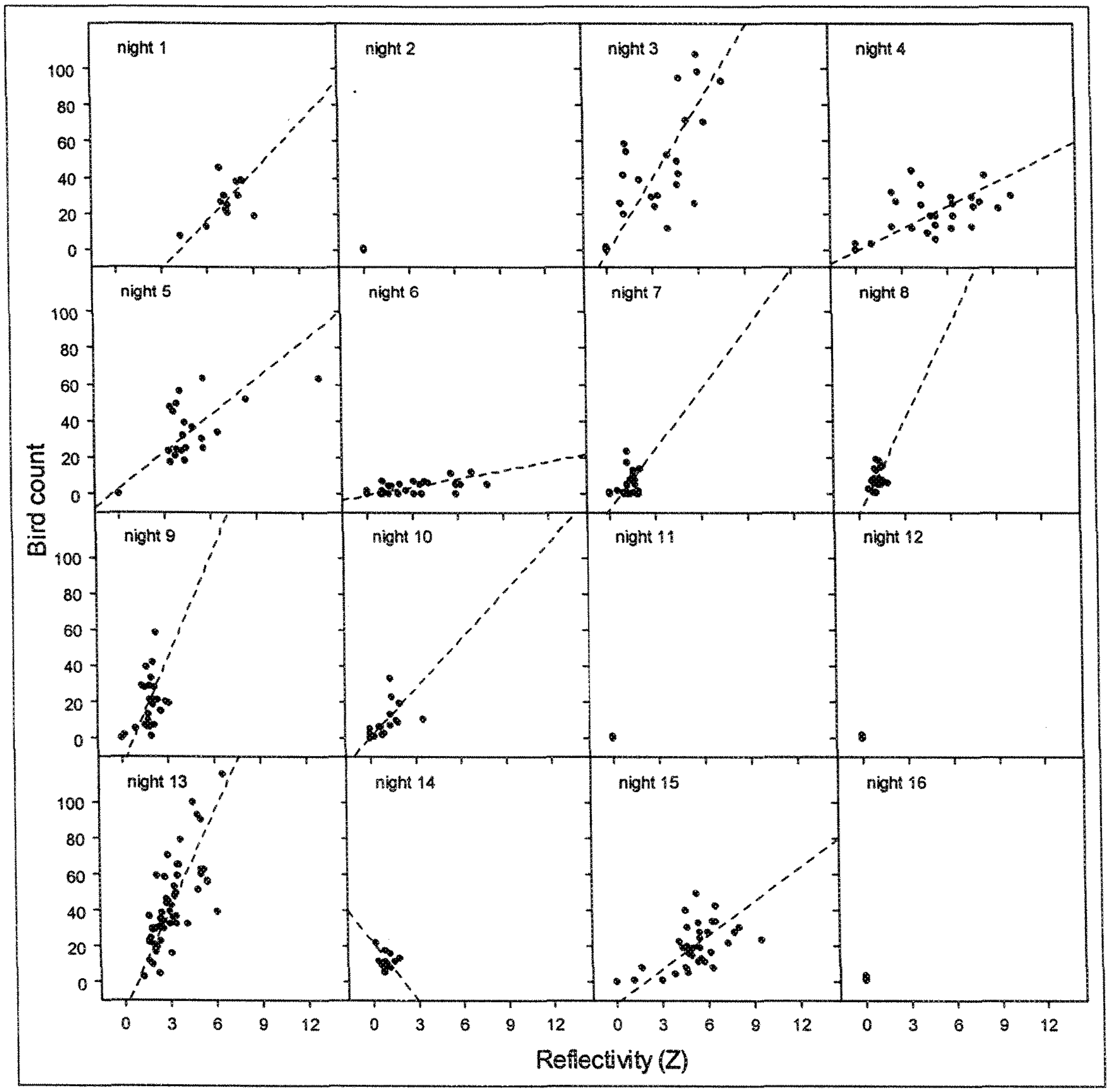

Figure 3. Relationship between the number of birds detected during 10-min aural counts near Pointe-aux-Outardes, Québec, Canada, and estimates of migrating bird density as determined by radar linear reflectivity (Z) on 16 nights between the 13 and 29 September 2004. Linear reflectivity was measured by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

Table 1. Nightly correlation (Pearson product-moment *r*) between the number of birds detected during 10-min aural counts near Pointe-aux-Outardes, Québec, Canada, and the linear reflectivity (*Z*) of the Val d'Irène CWSR radar (XAM) on 16 nights between 13-29 September 2004. Moving averages were computed on three consecutive 10-min periods

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

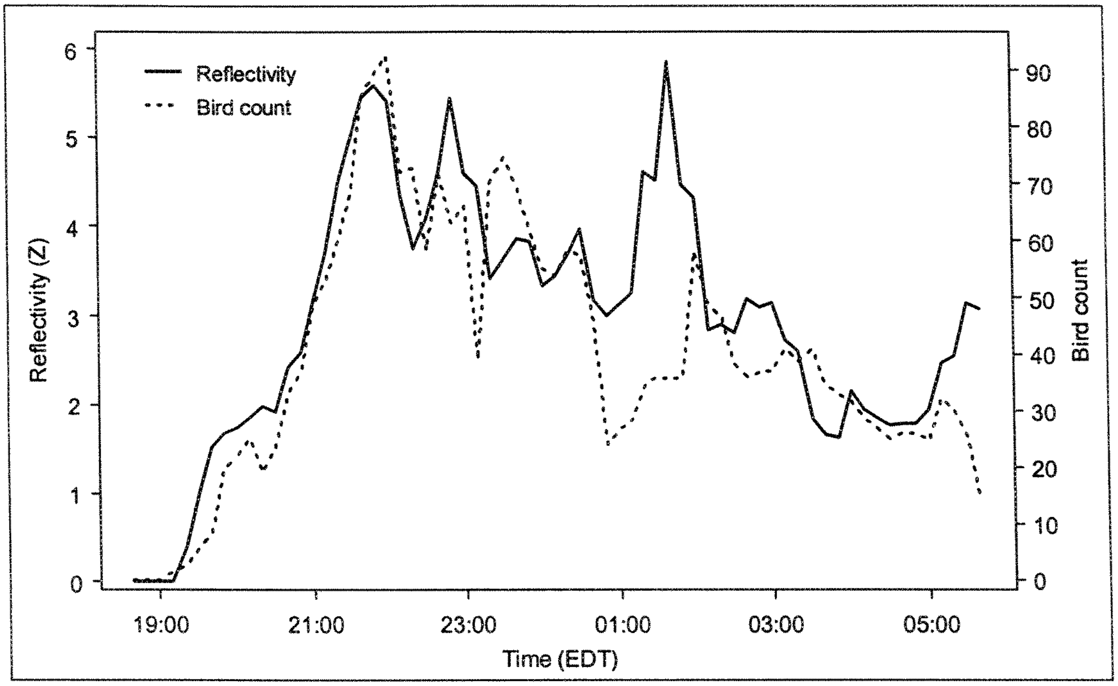

Figure 4. Relationship between the number of birds detected during 10-min aural counts near Pointe-aux-Outardes, Québec, Canada, and the radar linear reflectivity (Z) during the night of the 26-27 September 2004 (night #13) as determined by the Val d'Irène CWSR radar (XAM). Sunset and sunrise occurred at 18h20 and 6h23, respectively. Data lines depict moving averages computed on three consecutive 10-min periods.

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% (0.53 + 0.38) of the evidence, clearly indicate that the autocorrelation among consecutive 10-min aural counts had to be taken into account when modelling reflectivity measures (Table 2). Temporal autocorrelation coefficients equalled 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. 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, and this was both qualitatively and quantitatively.

Considering that passerines fly at an average of 10-12 m/s (Larkin 1991) and that the most distant pixel sampled was 7 km from the field station, birds could take between 9.7 and 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 AICc units from the best model with Z_t.

Table 2. Selection of linear mixed-effects models estimating migrating bird densities over 10-min periods above Pointe-aux-Outardes, Québec, Canada, using the linear reflectivity (Z) of the Val d'Irène CWSR radar (XAM) on 14 nights between the 13 and 29 September 2004 (n = 326). Model identification numbers appear left to random effects. Fixed effects included the radar reflectivity, the amount of environmental noise (four categories), the observer identity (2 categories), time since sunset (in hours), the interaction between reflectivity and observer identity, the interaction between reflectivity and time since sunset. Three types of correlation structures to model dependence among aural counts have been conducted on a given night: no within-group correlation, lag-1 autoregressive [AR(1)], and 1st-order moving average [MA(1)]. See Method – Statistical analysis for the meaning of symbols.

Random effects	Correlation structure	K	ΔAICc	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

Fixed effects

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. This was despite the fact that the number of birds that were detected increased as the night progressed (Table 3). The number of birds detected aurally decreased when the ambient noise level reached 3; no decrease was observed at higher noise levels (level 4: n = 30), likely as a result of low statistical power (Table 3). Lastly, the intercept was positive, but did not significantly differ from zero, suggesting that the radar was relatively sensitive to low bird densities (Table 3).

Although the linear mixed-effect model did not measure a significant difference in the number of birds detected aurally between the two observers (Table 3), double sampling revealed that observer A detected on average 1.9 additional thrushes during a 10-min aural count compared to observer B (95% CI: 1.0-2.9). On the other hand, observer B detected 5.7 additional passerines other than thrushes (mainly warblers and sparrows) compared to observer A (95% CI: 1.9-9.6).

Table 3. Coefficients (β) and standard error (SE) of fixed effects and variance (σ) of random effects and their confidence intervals bounds of the best linear mixed-effects model (#5 in Table 2) estimating the density of migrating birds within 10-min periods above Pointe-aux-Outardes, Québec, Canada, as measured by the linear reflectivity (Z) of the Val d'Irène CWSR radar (XAM) on 14 nights between the 13 and 29 September 2004 (n = 326). Bold are numbers for which model's CI did not brackets zero.

Fixed effects	β	SE	95% CI bounds	
			lower	upper
Intercept	5.085	3.306	-1.421	11.591
Z	**4.531**	**1.646**	**1.292**	**7.769**
noise2	-2.966	2.824	-8.524	2.592
noise3	**-11.526**	**3.586**	**-18.583**	**-4.469**
noise4	-5.526	7.784	-22.659	11.607
obsB	2.874	4.395	-6.801	12.548
time	**1.457**	**0.681**	**0.117**	**2.797**
Z*obsB	1.910	2.270	-2.556	6.376
Z*time	-0.319	0.244	-0.799	0.161
Random effects	**Variability**	**σ**	**95% CI**	
Intercept	**Between night**	**3.907**	**1.354**	**11.276**
Z	**Between night**	**3.009**	**1.666**	**5.434**
Residuals	**Within night**	**12.058**	**10.982**	**13.239**

Random effects

The intercept and slope of the relationship between the number of birds detected aurally and reflectivity varied significantly and independently of one another among nights (95% CI: $-0.99 \leq r \leq 0.99$; Table 3). Indeed, the relative importance of random effects with respect to their corresponding fixed effects (σ/β) was 0.77 for the intercept and 0.66 for the slope (Pinheiro and Bates 2000: 191-192). Within-night variation (random residuals) was about ± 12 birds in comparison to the predicted bird count (Table 3).

DISCUSSION

Correlation between aural count and reflectivity

We found a positive relationship between radar linear reflectivity and an aural index of bird counts, although it was highly variable among nights. We attribute this strong night-to-night variability to differences in environmental conditions, in bird migration behaviour, and in radar response in relation to bird behaviour (see below). Previous studies that have investigated the relationship between radar reflectivity or number of birds detected by radar and an aural index of bird counts pooled their data across nights (Graber 1968, Larkin et al. 2002, Farnsworth et al. 2004), and therefore, could not document such variation. Moreover, this 'data-pooling' approach may have masked or biased the correlation between radar data and the aural index of bird counts that was computed. For example, one study did not find a significant relationship (Graber 1968), while two others report (some) significantly positive but highly variable relationships among seasons and/or sites (Larkin et al., 2002; Farnsworth et al., 2004). These results and the strong night-to-night variation in the relationship linking radar reflectivity to aural bird counts that we observed in our study (Table 1, Figure 3) clearly points toward the importance of using a multilevel or mixed-effect modelling approach when relating reflectivity measures to bird migration data. Another factor that could explain the lack of consistency among studies is that we conducted individual bird counts rather than call counts. We believe that calls count removed, in part, 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) have recorded higher calling rates, and thus, a larger abundance index, in the pre-dawn hours, whereas most studies report a decrease in bird numbers aloft during this period (reviewed by Kerlinger and Moore 1989). At last, previous works with NEXRAD was at different wavelength (10 cm vs 5 cm) which might be significant since the nature of reflections varies strongly when targets (birds) sizes are near the radar wavelength.

The fact that the correlations between radar reflectivity and aural bird counts that were based on moving averages performed better than typical correlations suggests that migrating birds aloft are not homogeneously distributed in space, and this at a spatial scale constrained by 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 or fluxes. 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, migrate in loose flocks. Although the spatial distribution of migrating birds has been subjected to some empirical investigations (Balcomb 1977), it remains that no study has so far addressed the distribution of birds, within and among species, within a hierarchy of spatial scales. So far, 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 modelling

Fixed effects

The intercept in the fixed effects was positive and its 95% CI marginally included zero, indicating that observers have occasionally detected aurally a certain number of migrating birds that went undetected by the radar (Table 3, Figure 3). This likely results from the fact that the power of the radar signal which is backscattered to the radar once it has hit an object decreases with distance (Bruderer 1997, Rinehart 1997): thus, low bird densities cannot be detected at large distances from the radar (i.e., ca. 86 km in our study). As a consequence, the CWSR network may be of limited use in tracking small migration fluxes 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., < ca. 600 m; (Evans and Mellinger 1999, Evans and Rosenberg 2000); Figure 2]. The positive slope between reflectivity and aural bird counts nevertheless reinforces our confidence that linear radar reflectivity provides an index of the flux of migrating birds.

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

Although we found by double-sampling 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 be caused by the fact that both groups of birds were merged 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 for all other census types for that matter (Nichols et al. 2000, Royle et al. 2005).

We expected that bird counts would increase at an increasing rate with reflectivity as the night advanced because of an increase in detection probability on the part of the observers. Such an increase in detectability would first be caused by birds steadily decreasing their flight altitudes as the night progresses (Able 1970, Bellrose 1971), and therefore, making it easier to detect them by ear. Second, birds have been reported to increase their calling rates during predawn hours (Graber 1968, Farnsworth et al. 2004). Since calling rate is positively correlated with detection probability when performing aural counts (Farnsworth et al. 2002), this should also contribute to increasing the number of birds detected by observers for a given reflectivity level. Although observers detected an increasing number of birds as the night progressed, we did not find that the slope between counts and reflectivity changed with time (Table 3). One potential explanation lies in the fact that censuses were usually terminated well before dawn (i.e., 6h41 ± 2h41 before sunrise), thus before the calling rates start to augment and that rise an interaction starts between an increasing of detection probability and decreasing reflectivity due to birds landing gradually as night progress.

Random effects

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 scale covered by the observer, but also point out significant night-to-night variation that further justified the use of mixed-effects models when analysing bird migration data. Furthermore, the random residuals indicate that within-night variation was particularly high (i.e., ± 12 birds). Hence, not taking between-night variation into account would likely lead to high prediction uncertainty, and even to biases.

Past and prevailing meteorological conditions are, among others, known to influence the migration behaviour of birds and can thus lead to within- and between-night variation in migration activity (Richardson 1978, 1990, Kerlinger and Moore, 1989, Liechti 2006). For instance, Farnsworth et al. (2004) attributed the poor relationship they found between flight call counts and radar signal index from NEXRAD to variation in height of flight, calling rate, and flock species composition, three factors that could also explain the random effects and residuals of our model. As mentioned above, flight altitude and calling rate could affect the aural count-reflectivity relationship through their impacts on detectability by observers. Whereas flight calls of warblers and sparrows are likely detectable by ear up to 300 m above ground level (AGL), and thrushes up to 600 m AGL (Evans and Mellinger 1999, Evans and Rosenberg 2000), the radar beam could detect birds up to 800 m (Figure 2). Yet another aspect related to flight altitude is that reflectivity depends on the distribution of targets within the radar beam: an unequal vertical distribution of birds concentrated in either the lower or the upper beam boundaries will returned lowest reflectivity rather than birds concentrated than if there were concentrated in the central axe or evenly distributed in the beam (Rinehart 1997, Gosset and Zawadzki 2001).

Changes in the flock species composition may cause within- and between-night variation in the aural count-reflectivity relationship in three ways. Species may differ in their types of calls (e.g., structure, tone, loudness), calling rate, and in their body sizes. While the first two factors are expected to lead to variation in detectability on the part of the observers (Farnsworth et al. 2002, Farnsworth et al. 2004, 2005), the third will (physically) affect the reflectivity measured by the radar (Bruderer 1997, Rinehart 1997).

Because all of the above factors can operate in combination to different degrees, it is difficult to determine their respective contributions, as well as the temporal scale at which they are more likely to influence migration behaviour and estimates of migration activity. Furthermore, additional noise may originate from echoes produced by non-passerine birds (e.g., geese and shorebirds in this study) and insects (Larkin 1991). This may also explain why the model in which the intercept was allowed to vary among nights independently of the aural count-reflectivity slope (i.e., an indication of a lack of a clear pattern) performed well (see model #6; Table 2).

Effects related with physics of radars

Other aspects 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 scattering or resonance region (Eastwood 1967, Alerstam 1990, Rinehart 1997)]; (2) the fact that the power returned to the radar decreases more or less rapidly with the distance (*R*) at which targets have been hit (*Z-R* relationship), depending on the number and vertical distribution of targets [i.e., points or distributed targets and partial or total radar beam filling (Bruderer 1997, Rinehart 1997, Gosset and Zadwadski 2001)]; and (3) target orientations with respect to the radar (Edwards and Houghton 1959, Bruderer and Joss 1969, Houghton 1969). These intrinsic noise sources should incur variability in reflectivity measures at any time and under any conditions. Although, Larkin et al. (2002) expect 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; see below).

Other evidence of bird detection with XAM

Several patterns observed on XAM displays, but not reported in this paper, were characteristic of bird migration, according to Gauthreaux and Belser (1998), Koistinen (2000), and Dielh et al. (2003). For instance, we observed (1) bursts of reflectivity corresponding to takeoffs about 40 minutes after sunset (Kerlinger and Moore 1989); (2) a vertical distribution of targets with greater densities occurring under 1000 m (Able 1970, Bellrose 1971, Mabee et al. 2006) above ground level and that rarely extended above 3000 m ASL (Gauthreaux and Belser 1998); (3) main target directional movements oriented south to west-southwest (Drury and Nisbet 1964, Lowery and Newman 1966, Richardson 1972); (4) target airspeeds reaching 7-15 m/s (Larkin 1991; Gauthreaux and Belser, 1998); and (5) echoes that outlined landscape features (in our case, the shoreline of the St. Lawrence) at takeoff time (Diehl et al. 2003) and, as time passed, that either vanished or persisted (depending if birds are either crossing or following the north coast of the St. Lawrence estuary).

CONCLUSION

We found a positive relationship between linear radar reflectivity and aural field counts of nocturnal migrating passerines conducted 86 km from a Canadian weather surveillance radar (CWSR). Although our results suggest that the CWSR-98A radar can detect low bird migration fluxes, the count-reflectivity relationship nevertheless showed strong between-night variance that could originate from a combination of (interacting) causes, including environmental conditions, bird migration behaviour, radar physics, and differential bird detectability by both the observers and the radar. Such variation justified our use of mixed-effects modelling. Although we attempted to control for several variables that may affect aural bird detectability, it seems clear that aural (or microphone) counts cannot be used to calibrate the relationship between the density of migrating birds aloft and linear reflectivity given all possible variability. The use of a marine radar, which has an high capacity to detect individual birds aloft (Eastwood 1967), should be preferable to make an unbiased calibration. Moreover, the use of a marine radar would allow assessment of the respective contribution of several (interacting) variables that may contribute noise to the relationship between bird density and reflectivity (e.g., number, vertical distribution of birds and orientation relative to the radar).

The use of CWSR data, at least from CWSR-98A, has the potential to extend the NEXRAD network coverage further north by several hundreds of kilometres, thereby increasing our understanding of how birds utilise the North American landscape during migration. Weather radars are likely to become extremely valuable tools for migratory bird conservation in the short-term by providing information on migration pathways and traffic in the context of environmental assessment of wind energy projects (Gauthreaux and Belser 2003, Kunz et al. 2007) and in the long-term by providing estimates of population trends in the face of climate change (Gauthreaux 1992).

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