

Going beyond a leap of faith when choosing between active and passive bat monitoring methods

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The limiting trade-off between expediency and accuracy is well exemplified by the monitoring of bats, more specifically since the onset of the White-Nose Syndrome in North America. Acoustic detection is a way of circumventing the difficulties of catching bats, and monitoring is usually done either with transects or fixed recording points, the latter generally being assumed to be superior. However, little has been done until now to assess each method's ability to maximize the quality of recordings and the number of species detected, to account for the temporal variability of bat activity, and to account for the variability in habitats and the spatial patterns of bat activity. We tested whether transects could yield similar results as fixed points for every of those aspects of accurate and reliable bat monitoring. We found it to be true for recording quality and the detection of peaks of activity, but found that either method was little affected by weather and landscape attributes. We conclude that the use of transects is a valid choice for long-term monitoring, as it performs comparably to fixed recording points and maximizes the number of detections per sampling unit. However, transects tend to record a greater proportion of migratory bats than fixed recording points, a bias which should be considered in the assessment of the state of particular species' populations.

Key words: echolocation, Chiroptera, monitoring, call identification, activity, transects, passive

INTRODUCTION

At its most simple expression, monitoring is a set of repeated assessments within a defined area over a specified time period and can be a tool to assess and achieve management objectives (Thompson *et al.*, 1998). MacDonald *et al.* (1991) define seven types of monitoring, some of which include types which aim to establish baselines or follow temporal trends in the measured variables (later defined as surveillance monitoring by Nichols and Williams, 2006) and types that aim to assess and evaluate the impact of a change, often made in a before-after basis (named target monitoring by Nichols and Williams (2006)). Pereira *et al.* (2017) give a list of essential variables in monitoring, which includes among others species abundance and distribution, species interactions, and taxonomic diversity. A rapid decline in populations like the one found

in bat species affected by White-Nose Syndrome (WNS — Frick *et al.*, 2010) is an example of a case may induce jurisdiction to rapidly implement a target type of monitoring at a large scale. Furthermore, Pereira *et al.* (2017) discuss the possible reuse of existing data, which conservation biologists may use to gather a baseline of what stimulated population variations prior to the decline and identify variables that would either influence future monitoring or impact mitigation methods.

The challenges of collecting valuable data for monitoring is well exemplified by the North American Bat Monitoring Program (NABat — Loeb *et al.*, 2015). They developed a monitoring program which combines multiple monitoring protocols, such as colony counts, hibernacula counts, and acoustic recordings to assess and inform stakeholders of the current threats to bats, but also to detect unanticipated threats in the future (Loeb *et al.*,

2015). Acoustic detection is a way to improve data collection speed when monitoring bats, which are nocturnal and notoriously hard to capture (Hayes, 2000), for example when sampling large or remote areas or when roosting locations or hibernacula are sparse or not known. It gives an estimate of activity rather than abundance but allows sampling at greater temporal scales and in habitats unsuitable for net capture (O'Farrell and Gannon, 1999). Acoustic bat monitoring methods must be amenable to: 1) maximizing the quality of recordings and the number of species detected, 2) account for the temporal variability of bat activity, and 3) account for the variability in habitats and the spatial patterns of bat activity (Duchamp *et al.*, 2006; Yates and Muzika, 2006; Fischer *et al.*, 2009). Data coming from previous baselines or trend monitoring protocols are sometimes used to answer different questions further down the line, such as climate change-related questions. In such cases, it is important to be aware of the possibilities and caveats of these protocols to maintain reasonable expectations. Moreover, although acoustic sampling may be used for population monitoring as well as for assessments of population presence and activity, this does not mean that data acquired for both purposes can be used interchangeably.

A common consideration for acoustic detection like the production of high-quality and identifiable recordings of every species detectable in the area may advantage fixed recording points which minimize background noise by eliminating movements from the detector (Limpens and McCracken, 2004). Even with the ever-improving recording technology, fixed recording points have been found to give higher species richness estimates and accumulate species more quickly than transects (Tonos *et al.*, 2014; Whitby *et al.*, 2014). In one case, Whitby *et al.* (2014) used fixed recording points as a reference point when comparing species detection on transects along waterways and roadways, meaning that they assumed recording points to yield the most reliable species counts. However, their road transects detected as many species as the fixed recording points (12 species) while the boat transects detected only nine species.

A second consideration is the unique behaviors of bats, which are known not to be uniformly active during the year (Rydell, 1991; Young *et al.*, 2012) or during the night (Britzke, 2003) for which activity follows a bimodal shape, with one peak of activity after dusk, and the second one before dawn (Baerwald and Barclay, 2011). Surveying protocols often

favor transects which are cost effective when compared to other monitoring methods (Caro, 2016). However, they are conducted during the first half of the night, only several nights in a year, which might create gaps and missed periods of high activity. Still, it has not shown to impair their ability to be an effective way of detecting declines in populations (Catto *et al.*, 2004), albeit perhaps only large ones (Greene, 2012). Bat activity may also vary according to weather conditions, for which transect protocols usually purposely constrain the range, and sometimes fixed station as well, most often posteriorly (i.e., above a certain temperature and in absence of rain or strong winds, Britzke and Herzog, 2009; Jutras *et al.*, 2012; Stahlschmidt and Brühl, 2012). The constrained range of weather conditions to initiate sampling limits the possibility to infer about the possible relationship between bat activity and barometric pressure (Baerwald and Barclay, 2011), temperature (Gruber *et al.*, 2009; Young *et al.*, 2012) and wind speeds (Fiedler, 2004; Grodsky *et al.*, 2011; Jain *et al.*, 2011; Good *et al.*, 2012).

The third consideration is one of spatial scale, and while transects may sample quickly through the landscape, they follow one type of habitat (i.e. roads) and may miss some specific habitats located away from the roads, which are within the reach of fixed recording points. Transect estimates may thus be biased towards large, open-space species (Coleman *et al.*, 2014) which are more active in recently cut stands than in forests stands (Patriquin and Barclay, 2003; Sleep and Brigham, 2003; Owen *et al.*, 2004; Morris *et al.*, 2010). On the other hand, according to their initial design, fixed recording points may over-represent small, clutter-adapted species (Tonos *et al.*, 2014) which are more active in mature forests (Patriquin and Barclay, 2003; Sleep and Brigham, 2003; Owen *et al.*, 2004; Morris *et al.*, 2010). Evidence also suggests that some species concentrate their foraging activity around water (Furlonger *et al.*, 1987; Zimmerman and Glanz, 2000; Menzel *et al.*, 2001; Owen *et al.*, 2004; Reynolds, 2006), which may be easier to target using fixed recording points than transects.

So far, studies involving both transects and fixed recording points were conducted at small spatial and temporal scales, with a limited number of recorders. In this study, we used 36 fixed recording points and 42 transects in each of two locations over three years to test whether both methods yielded similar results in term of bat activity monitoring and how they differed in terms of sensitivity to certain variables. This study is complementary to the NABat initiative as

it provides a detailed analysis of two different acoustics methods proposed for large scale bat monitoring, but it aims to go further into the exploration of the influence of timing, habitat and weather variables to elaborate on the caveats and biases of each method. Our main working hypothesis is that the monitoring of bat activity (e.g., abundance and distribution) would be more accurate using call detection at fixed stations than transects, and we expect the latter to be less sensitive to changes in species abundance or variation in space and time. We also predicted that 1) fixed recording points would provide more detections with identifiable species than motorized transect sampling, due to noise from the vehicle 2) fixed recording points would better capture temporal variation in bat activity for all species in a wider range of weather conditions, as transects are usually conducted only during the first half of the night and only several nights during the summer, and 3) that fixed recording points would be more sensitive to variations in detections linked to habitat structure than transects, which usually encounter a variability of habitats and are associated to roads, likely causing a bias toward large high-flying species.

MATERIALS AND METHODS

Sampling Area

We conducted the study in two sampling areas of southern Québec, Canada. The first sampling area was 'Forêt Montmorency' located 70 km north of Quebec City (47°19'N, 71°07'W — Fig. 1a). It is part of the eastern balsam fir-white birch bioclimatic domain (Robitaille and Saucier, 1998), and is mostly dominated by balsam fir (*Abies balsamea*). Various levels of harvesting intensities are used, ranging from clearcuts to partial cuts, with some areas of unharvested forest. Four lakes are present in this study area and are connected by a network of rivers. The climate is cold and wet, with a mean annual temperature of 0.3°C and annual precipitation of 1588 mm, one-third of which falls as snow (Environnement Canada, 2009a). The first record of WNS-affected specimens in the area was reported in 2011. The second sampling area was 'Forêt d'Enseignement et de Recherche du Lac Duparquet' (FERLD) in Abitibi (48°30'N, 79°27'W — Fig. 1b), 45 km northwest of Rouyn-Noranda. The forest is part of the western balsam fir-white birch bioclimatic domain (Robitaille and Saucier, 1998), but following the last spruce budworm outbreak, there is a greater proportion of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyfera*) than at Forêt Montmorency. Similarly to Forêt Montmorency, management intensity ranges from non-harvested forests to clearcuts. The forest contains two large lakes and the area is riddled with rivers, slow streams, and ponds. The climate is warmer and drier than Forêt Montmorency, with a mean annual temperature of 0.7°C and annual precipitation of 889.8 mm, one-quarter of it falling as snow (Environnement Canada, 2009b). The first record of WNS-affected specimens in the area was also reported in 2011.

Bat Detection using Transects and Fixed Recording Points

Sampling at Forêt Montmorency in 2011 included 36 fixed listening points and 42 motorized 2-km transects (Fig. 1a). The following year, we established a similar design at FERLD (Fig. 1b). In 2013, a reduced field season targeted periods previously found as having the highest bat activity at both field sites. Transects covered most of the roads that were safely passable, with each end separated by a minimum of 50 m. We recorded bats using Anabat II (Titley Scientific, Lawnton, Australia). During each sampling night, a set of 7 transects was assigned to each of the two teams driving a vehicle, for a total of 42 transects over three nights. We used a protocol similar to the provincial monitoring protocol, which was initially considered as more of a trend monitoring protocol but has now become both a baseline type of monitoring and an assessment type of monitoring. We drove at a speed of 20 km/h, starting 15 minutes after sunset. Every time we detected a calling bat, the driver stopped and recorded the GPS location of the recording. We drove each transect once in one direction during one visit, and in the other direction in the next visit. We visited each transect four times in 2011 (Forêt Montmorency) and 2012 (FERLD), and twice in each study area in 2013. Fixed recording points in the passive sampling method were separated by at least 500 m and covered combinations of stand types (coniferous, mixed, deciduous), disturbance intensity levels (clearcut, partial cut) and elapsed time since disturbance (0–9 years, 10–19 years, 20–39 years, 40–59 years, 60+ years). We installed three recorders at different locations every day, which recorded overnight from sunset to sunrise. We moved recorders to different locations the following day. We visited each point three times in 2011 (June–August) at Forêt Montmorency and in 2012 (June–August) at FERLD. In 2013, we visited each point once at Forêt Montmorency (July) and twice at FERLD (July–August) during the most active period of the previous sampling year.

We extracted call features using AnaloookW software (Titley Scientific, Lawnton, Australia). We used a quadratic discriminant function analysis (QDFA — Adams, 2013), which compared our unidentified data to a training dataset that included six species: *Eptesicus fuscus*, *Lasiurus borealis*, *Lasiurus cinereus*, *Lasionycteris noctivagans*, *Myotis lucifugus*, *Myotis septentrionalis*, and *Perimyotis subflavus*. All species were weighted equally. Acoustically cryptic species *L. noctivagans* and *E. fuscus* were impossible to separate using AnaloookW and we considered them as a group (*E. fuscus/L. noctivagans*). In some cases, *Myotis* calls were indistinguishable, so we created a group for all *Myotis* in addition to single species. Since *Myotis leibii* is extremely rare in the province of Québec and we lacked reference calls, we excluded it from our analysis. We converted the number of pulses into an activity index. We divided the duration of sampling into blocks of one minute and used the number of blocks which contained detections as our activity index (Miller, 2001). Since the activity index eliminates species biases related to individual flight speed, behavior, and pulse frequency, each contribution can be reliably compared to the others to assess changes in most active species over time and across methods.

Landscape Features and Weather

We have included weather variables to explore the validity of reinterpreting monitoring data with weather conditions in

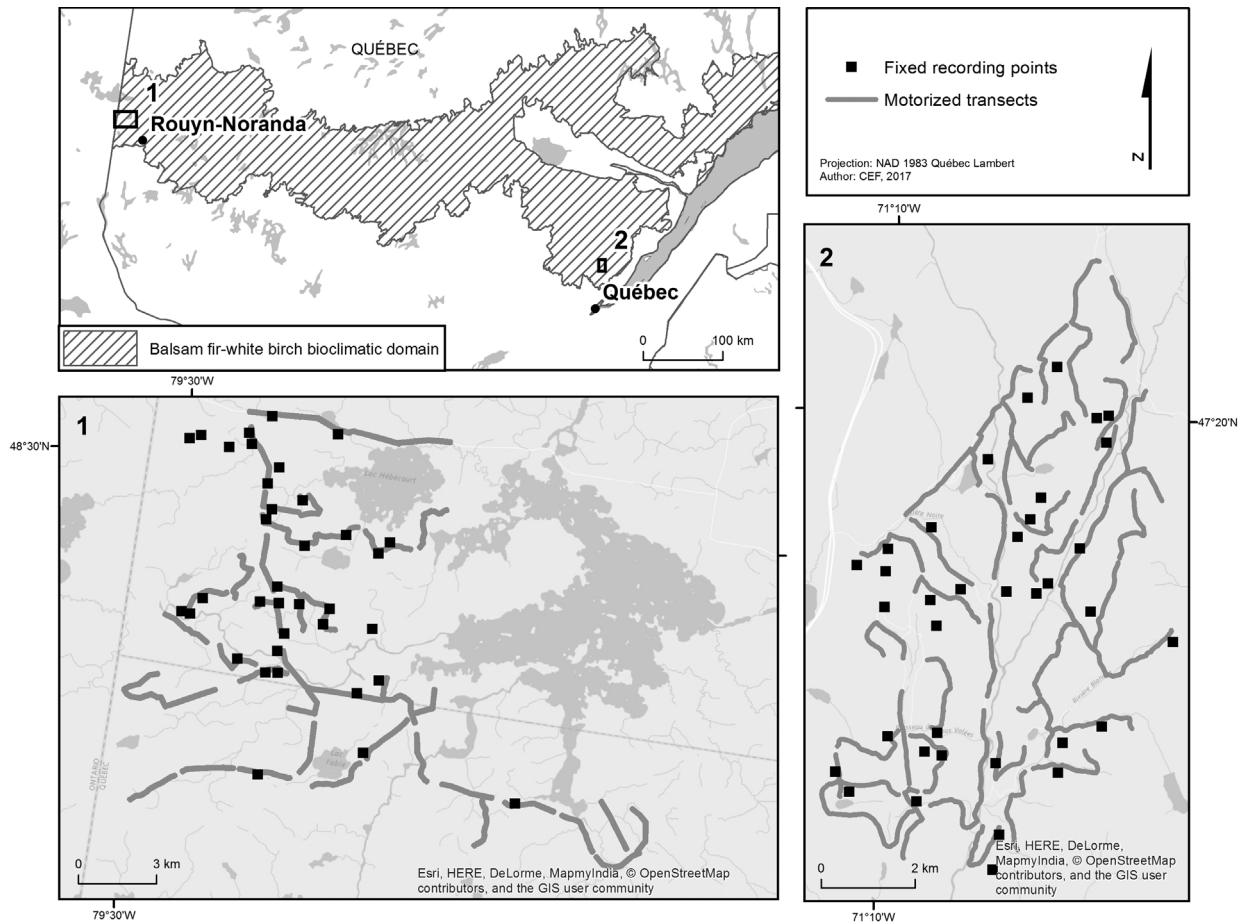


FIG. 1. Location of fixed recording points and 2-km motorized transects in both a — Forêt Montmorency and b — Lake Duparquet Research and Teaching Forest (FERLD), Québec, Canada. Both sampling methods ($n = 36$ and $n = 42$ — fixed recording points and transects per study area, respectively) covered a wide range of habitats and conditions. Bats were recorded in 2011 and 2013 at Forêt Montmorency and in 2012 and 2013 at FERLD

mind in the context of a monitoring dataset that is used years later with different research questions in mind. We collected meteorological data (barometric pressure, relative humidity, wind speed, rainfall) from local weather stations at each experimental forest. We installed iButton thermometer (Thermochron, California, USA) at every fixed recording location to measure the temperature at each hour. For fixed recording points, we calculated proportions of various habitat variables inside a 200-m buffer around the detector location using the 4th inventory maps from the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP). For transects, we split every 2 km transect into 500 m subsections and used a buffer of 100 m around these subsections to extract habitat data. Within these buffers, we characterized the weighted mean age of all stands, as well as the percentage of total area covered by various stands types (coniferous, mixed, and deciduous) and water bodies (rivers and lakes). We conducted all calculations using QGIS software (Quantum GIS Development Team, 2015).

Statistical Analyses

To test our prediction regarding nightly and seasonal activity, we identified significant peaks of activity with SaTScanTM software (v.8.0, a trademark of Martin Kulldorff). That method

has been successfully used to detect variation in peaks of bat activity (Adams, 2013). We specified a one-tailed analysis to look for clusters with unexpectedly high numbers of calls (Kulldorff *et al.*, 2005). We set temporal maximum cluster sizes at 30% and used 999 Monte Carlo replications. We used the default probability adjustment option using the sampling dates to account for the temporal gaps between each visit and year. We set the detection probability to zero when no sampling was conducted at a given location. The analysis output showed the time frame(s) when activity was significantly higher than the background expectation, with the associated log-likelihood ratio and P -value.

We performed all other analyses in R v. 3.2.0 (R Core Team, 2015). To test our prediction regarding recording quality, we used linear mixed-effect models with Gaussian errors to assess the effect of the method, mean barometric pressure, mean relative humidity and average wind speed on the proportion of poor quality activity recorded (package ‘lme4::lmer’ — Bates *et al.*, 2015). We used the overall activity during the night an offset variable and nested error terms included the recording point or transect subsection, year and sampling location.

We performed a principal component analysis (PCA; package ‘stats::prcomp’) and k -mean clustering to confirm that the ranges of landscape features covered by transects and fixed

recording locations overlapped enough at both sampling locations to allow the inclusion of both methods in further models (Khattree and Naik, 2000). We used generalized linear models with Poisson family (package ‘lme4::glmer’) to assess the effects of weather and landscape variables on the activity levels of species for which we recorded activity during more than two nights in the season. Because transect sampling targeted nights with no rain and low wind speeds, we extracted a subset of nights when weather conditions at fixed points fell within the range of transect conditions. We then conducted two analyses: one on a subset of both datasets for samples where weather conditions of transects and fixed recording point sampling overlapped, and one on complete datasets from both transects and fixed recording points. We used mean barometric pressure, mean temperature, average humidity, and average wind speed in the weather analysis. We included the Julian day and method as fixed effects and sampling location and year as nested random effects. To facilitate convergence, we scaled all fixed effects and used the BOBYQA algorithm (Bound Optimization BY Quadratic Approximation, Powell, 2009). The second analysis using complete datasets from both methods combined weather and landscape variables in one model and separated the analysis by sampling area. We used the mean weighted age, the proportion of the least common stand type (Forêt Montmorency=mixed, FERLD=coniferous), and the proportion of water within the buffer around each transect or recording point. We chose to consider the proportion of the least common stand type in each sampling area to better highlight any existing connection between stand type and bat activity.

RESULTS

Detected Species and Quality of Recordings

At Forêt Montmorency, the proportion of activity index of unknown species was generally 15% for transects, except in 2011 when it was as high as 25% (Table 1). In transect at FERLD, the proportion of the activity index from unidentified species ranged from 18% in 2012 to 16% in 2013. With fixed recording points, that percentage of activity associated with unidentified call was limited to 6–8% in 2012 and 2013. We did not find the proportion of the recorded activity index from unidentified species to change significantly with the method, or with environmental factors like barometric pressure, humidity or wind speed (all P -values > 0.10).

Fixed recording points consistently detected four to six of the six potential species or group of species. Transects obtained similar detections to fixed recording points in 2011 and 2012, but in 2013, the number of detected species dropped to three species at Forêt Montmorency and two species at FERLD (Fig. 2). Overall at Forêt Montmorency in 2011, we mostly recorded *M. lucifugus* (43%) in transects followed by *L. cinereus* (16%), while in fixed recording points, we recorded 42% *M. septentrionalis* and 40% *M. lucifugus*. Two years later, in 2013, we recorded a majority of *L. cinereus* (52%) in transects, *M. lucifugus* (28%) coming second, a drop likely due to WNS. Although the activity in fixed recording points dropped to only a few minutes in 2013, we still recorded a majority of *M. lucifugus* (40%). At FERLD in 2012, we detected a majority of *L. cinereus* in both transects (51%) and fixed recording points (54%). The next year, *L. cinereus* (81%) dominated activity in transects but we did not record any *Myotis*. *L. cinereus* also dominated activity from fixed recording points (59%), but *Myotis* species were still present (11%).

Peaks of Activity

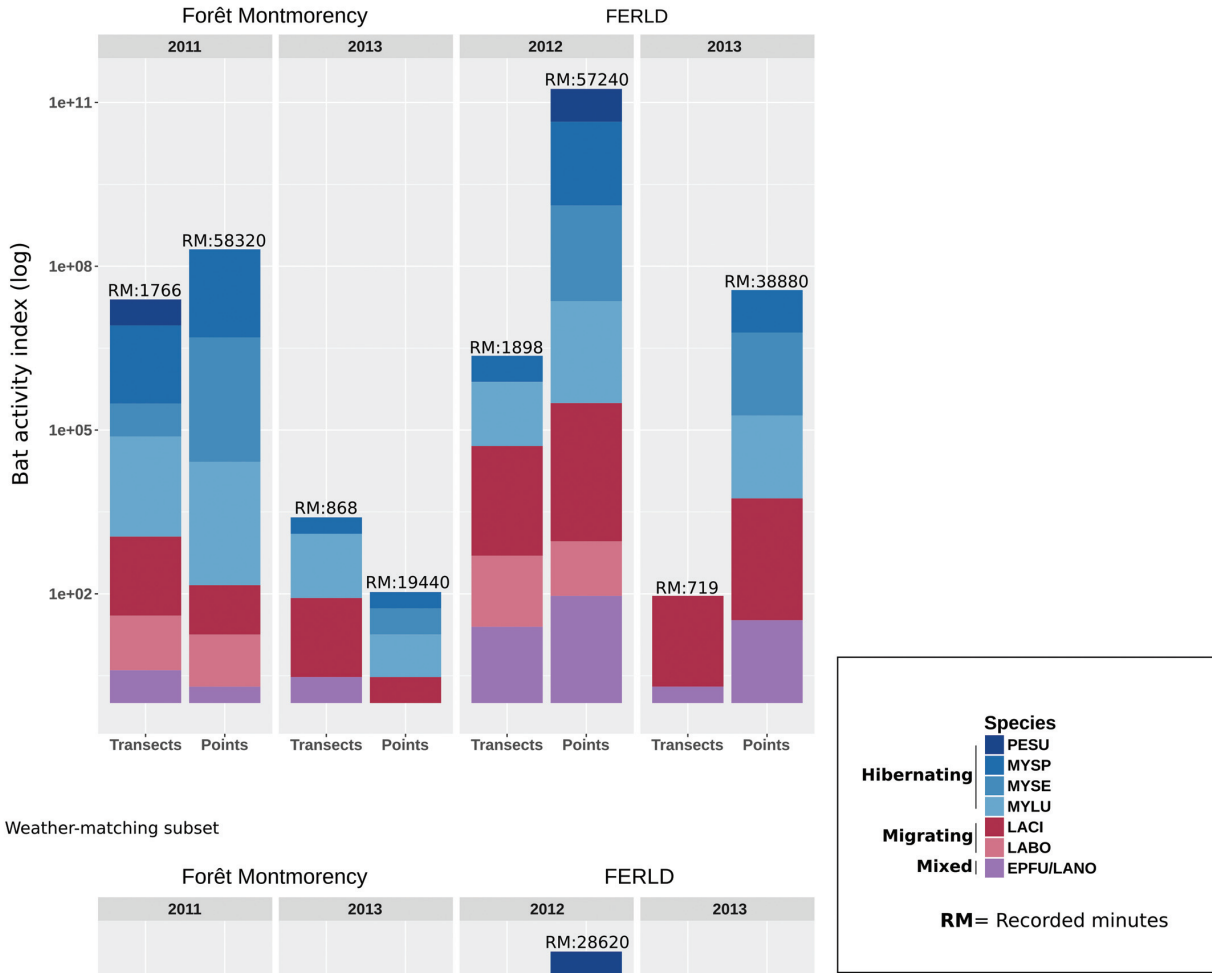
In nightly activity levels, transects identified a peak in activity between three and four hours after sunset (log-likelihood ratio, $llr = 46.87$, $P = 0.001$ — Fig. 3). Fixed recording points also identified only one peak of activity for all species, between two and four hours after sunset ($llr = 65.33$, $P = 0.001$). Even though activity increased around 7–9 hours after sunset in fixed recording points, it was not sufficient to create a significant secondary peak of activity for any species.

Both methods obtained peaks of activity occurring from mid-July to early-August. With transects, the most active period in the seasonal time frame was between Julian days 199 and 208 ($llr = 14.63$, $P = 0.001$ — Fig. 4). The large species *E. fuscus*/*L. noctivagans*, *L. borealis*, and *L. cinereus* covered

TABLE 1. Summary of sampling effort in both sampling areas, for transects and fixed recording points and for all sampling years. Bats were recorded in 2011 and 2013 at Forêt Montmorency and in 2012 and 2013 at Lake Duparquet Research and Teaching Forest (FERLD)

Location	Year	Transects			Fixed recorded points		
		Sampling effort (minutes)	Pulses recorded	Activity index (minutes)	Sampling effort (minutes)	Pulses recorded	Activity index (minutes)
Forêt Montmorency	2011	1,766	3,064	157	58,320	6,955	455
	2013	868	507	54	19,440	76	15
FERLD	2012	1,898	3,364	199	57,240	11,910	719
	2013	719	2,216	57	38,880	1,667	286

a) Complete dataset



b) Weather-matching subset

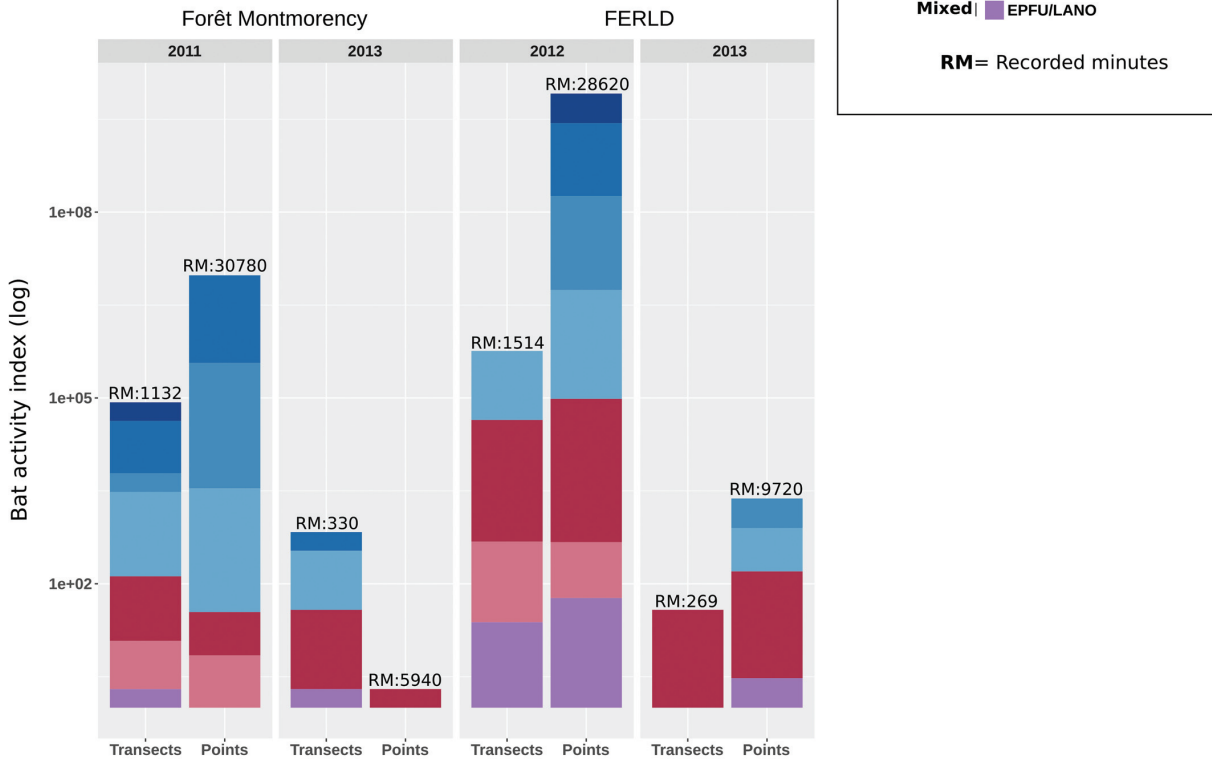


FIG. 2. Summary of species as identified by calls at fixed recording points in Forêt Montmorency and FERLD, Québec, Canada (in both cases $n = 36$) and 2-km motorized transects (in both cases $n = 42$). The y-axis is nonlinear to facilitate visualization and the number of recorded minutes (RM) are given for each site-year combination as an indication of sampling effort. Timing of call recordings as in Fig. 1

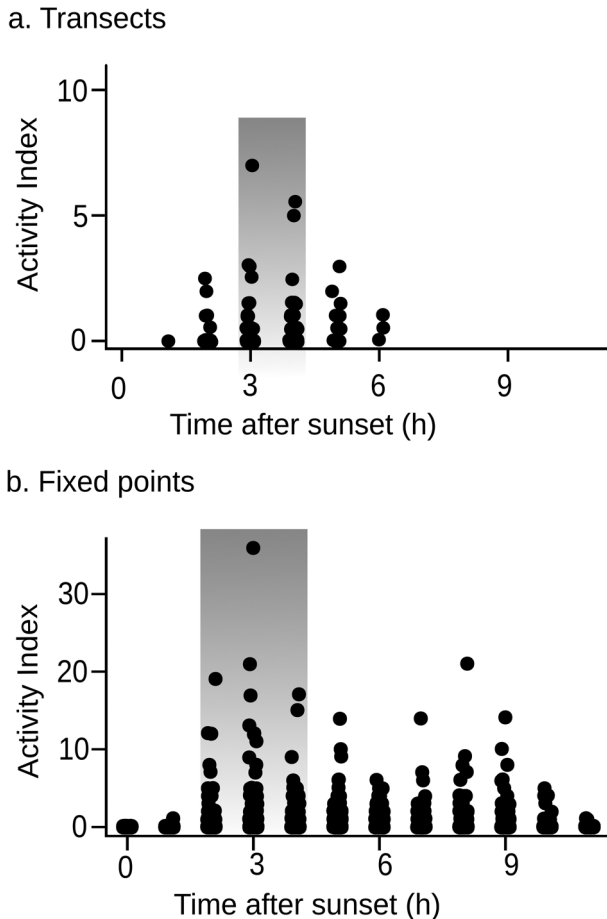


FIG. 3. Nightly peaks of activity using a — transects and b — fixed recording points in Forêt Montmorency and FERLD, Québec, Canada. The same peak of activity was detected for *E. fuscus/L. noctivagans*, *L. borealis*, *L. cinereus*, *M. lucifugus*, *M. septentrionalis*, *Myotis* sp, and the overall activity that includes unidentified data. Timing of call recordings as in Fig. 1. Bands represent the span of activity peaks as estimated by SaTScan

the majority of that peak (Julian days 199–205, $\text{llr} = 18.32$, $P = 0.001$). Small species, including *M. lucifugus* (Julian days 205–208, $\text{llr} = 53.32$, $P = 0.001$) and combined *Myotis* (204–208, $\text{llr} = 76.38$, $P = 0.001$), were most active toward the end of the global peak of activity. Similarly, fixed recording points recorded peaks of activity between Julian days 198–213 ($\text{llr} = 16.97$, $P = 0.001$), showing less segregation between large/migrating species and small/hibernating species than with transects. *Eptesicus fuscus/L. noctivagans* covered the entire global peak of activity (Julian days 198–213, $\text{llr} = 39.57$, $P = 0.001$), while *L. borealis* peaked five days after that global peak (203–212, $\text{llr} = 46.91$, $P = 0.001$) and *L. cinereus* peaked six days before (192–207, $\text{llr} = 76.66$, $P = 0.001$). Combined *Myotis* peak started at the end of *L. cinereus* peak (Julian

day 207) until Julian day 210 ($\text{llr} = 14.45$, $P = 0.001$). *Myotis lucifugus* peaks began with the global peak but ended 10 days early (199–203, $\text{llr} = 22.85$, $P = 0.001$).

Overlapping of Landscape Features

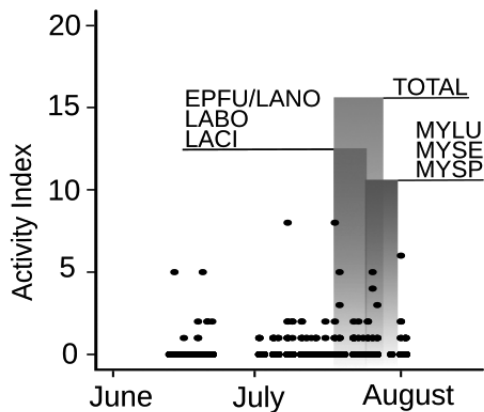
A PCA of all sampled sites from both methods in each location showed that fixed recording points and transect sampling covered similar landscape features, especially at FERLD (Fig. 5). At Forêt Montmorency, we had to venture far away from lakes and rivers to find mixed stands, and away from the roads used for transect sampling. At FERLD, we could find most landscape combinations within 150 m of roads, which led to a much closer fit between landscape covered by transect and fixed recording point sampling.

Comparative Analysis of Transects and Fixed Points

To reliably compare data from fixed recording points and transect sampling relative to weather variables, we used a subset of data that matched the range of weather conditions recorded for both methods, at each location every year. Using that subset, we did not find any significant effect of landscape variable on bat activity for any species. We recorded proportionally less *E. fuscus/L. noctivagans* and *L. cinereus* at Forêt Montmorency and more *Myotis* than at FERLD (Table 2). The effect of Julian day confirms that bats were more active later in the sampling season, with the exception of *E. fuscus/L. noctivagans* and *L. borealis*, for which the estimate was non-significant. Transects recorded more activity per unit of time than fixed recording points, except for *M. septentrionalis* (estimate, est : -0.64, SE : 0.90, $P = 0.479$).

Weather variables did not significantly influence activity for most species, with a few exceptions. We detected less *E. fuscus/L. noctivagans* during humid nights (est : -7.09, SE : 3.31, $P = 0.032$), but the negative influence of humidity was more associated to transects than fixed recording points (est : 9.23, SE : 3.91, $P = 0.018$). *Eptesicus fuscus/L. noctivagans* were also more active during windy nights (est : 1.21, SE : 0.39, $P = 0.002$). Transects recorded more *E. fuscus/L. noctivagans* activity as atmospheric pressure increased than fixed recording points (*E. fuscus/L. noctivagans* est : 7.78, SE : 3.90, $P = 0.046$). Transects recorded less *L. borealis* (est : -1.80, SE : 0.78, $P = 0.022$) and overall bat activity (est : -0.41, SE : 0.15, $P = 0.022$) at higher temperatures than transects. Because *L. borealis* was one of

a. Transects



b. Fixed points

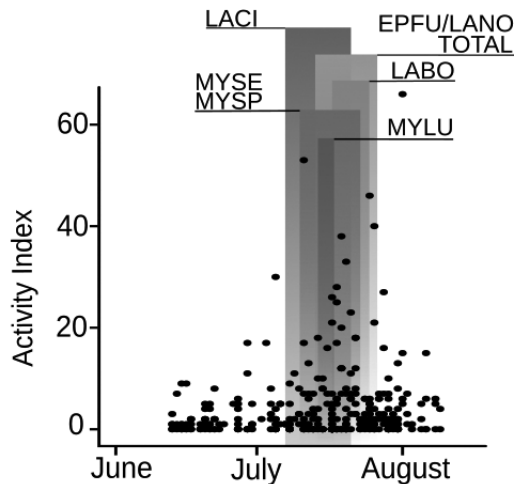


FIG. 4. Summer peaks of activity using a) transects and b) fixed recording points. Calls were recorded at Forêt Montmorency (years 2011 and 2013) and FERLD (2012 and 2013), Québec, Canada. Bands represent the span of activity peaks as estimated by SaTScan and each is a unique color to facilitate the visual distinction between groups

the species we recorded the least and because we recorded it more often in transects, this interaction might be an artifact of the method, rather than the influence of temperature itself. When we considered all species together, overall activity increased during nights with stronger winds (est: 0.23, SE: 0.10, $P = 0.028$), but less so in transects than fixed recording points (est: -0.35, SE: 0.13, $P = 0.009$). We also recorded more global activity as barometric pressure (est: 1.35, SE: 0.64, $P = 0.036$), and humidity increased (est: 1.46, SE: 0.67, $P = 0.029$) but with transects and not for fixed recording points. However, as temperature increased, we recorded less overall activity in transects than fixed recording points (est: -0.41, SE: 0.15, $P = 0.007$).

Combined Weather and Habitat Analysis using Complete Dataset

Using the complete datasets for both methods covering a wider range of weather conditions, Julian day estimates showed again that recorded activity levels were higher later in the season (Table 3). Barometric pressure and relative humidity had no effect on bat activity. Activity levels decreased during warmer nights at Forêt Montmorency for *M. septentrionalis* (est: -0.08, SE: 0.03, $P = 0.026$) and combined *Myotis* (est: -0.06, SE: 0.02, $P = 0.014$), but increased at FERLD for *E. fuscus/L. noctivagans* (est: 0.15, SE: 0.06, $P = 0.021$), *L. cinereus* (est: 0.08, SE: 0.03, $P = 0.004$), and for the overall activity index (est: 0.07, SE: 0.02, $P = 0.001$). Mean temperature during the sampling season at Forêt Montmorency was particularly cold in 2011 with 10°C, compared to 17°C in 2013. At FERLD, the mean temperature was 15°C in 2012 and 12°C in 2013. Increased wind speed had a negative effect on the activity of *M. lucifugus* (est: -0.21, SE: 0.08, $P = 0.008$), *M. septentrionalis* (est: -0.20, SE: 0.08, $P = 0.017$) and combined *Myotis* (est: -0.15, SE: 0.05, $P = 0.005$) at FERLD. Rainfall had a significant negative effect on *L. cinereus* (est: -0.06, SE: 0.03, $P = 0.004$) and the overall activity index at FERLD (est: -0.04, SE: 0.01, $P = 0.009$). Most species were generally unaffected by the mean weighted age of forest stands at recording location, except for *E. fuscus/L. noctivagans* that were more active in older forest stands at FERLD (est: 0.06, SE: 0.03, $P = 0.031$). Stand type was also nonsignificant, although *M. lucifugus* was marginally less active in areas with a higher proportion of mixed stands at Forêt Montmorency (est: -0.03, SE: 0.02, $P = 0.072$), and *L. cinereus* was marginally less active in coniferous stands at FERLD (est: -0.02, SE: 0.01, $P = 0.073$). The presence of water did not influence significantly bat activity.

DISCUSSION

When other methods of sampling are not available, data from acoustic protocols should ideally be able to provide precise and reliable information about population trends or responses to sudden events. In the case of bats, WNS has suddenly and massively affected hibernating species which were historically abundant, but shared their foraging space with migratory species, unaffected by the disease. Our general objective was to compare the outcomes of two generally used methods, transects and

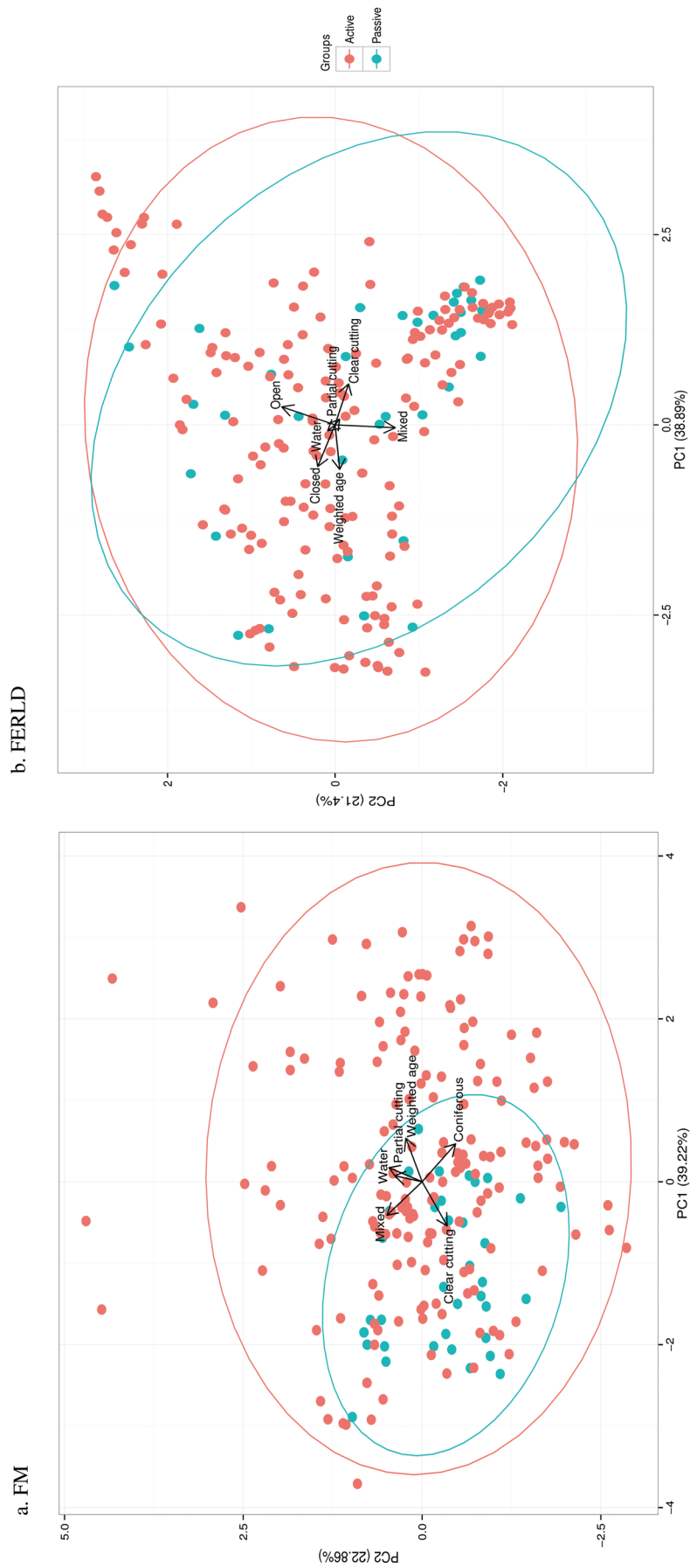


FIG. 5. Biplots comparing landscape features covered by transect and fixed recording point sampling at a — Forêt Montmorency and b — FERLD, Québec, Canada. Transects are represented in red and fixed recording points are represented in blue

fixed recording points, in bat surveys by acoustic sampling. We first predicted a better recording quality with fixed recording points than motorized transects sampling. We found that both methods yielded generally comparable recording qualities and number of species detected. Contrary to our second prediction, both methods yielded similar temporal variation in activity and the portion of activity occurring in the second half of the night and missed by transects was not significant. Moreover, the peaks of activity found throughout the sampling season were generally similar using both methods. However, contrary to our third and last prediction, habitat variables could not significantly explain variability in bat activity associated with fixed recording points and transects. Still, we found that transects recorded a greater proportion of large, high-flying species compared to fixed recording points, which recorded a greater proportion of small, clutter-adapted species.

Prediction 1: Quality of recordings and detected species

Coleman *et al.* (2014) found similarities in passive and active sampling in terms of recording quality, which is in accordance with our findings but in opposition to other previous studies (Johnson *et al.*, 2002; Britzke, 2003). As for the number of species detected, our results are in accordance with other findings that with enough sampling events, both active and passive sampling perform comparably (Coleman *et al.*, 2014; Tonos *et al.*, 2014; Whitby *et al.*, 2014). However, we discovered that some *Myotis* groups which had likely declined after the onset of WNS had disappeared from transect detections in 2013 while they were still recorded in fixed recording points.

Prediction 2: Temporal variability of bat activity

Baerwald and Barclay (2011) found a bimodal shape like the one we observed in fixed recording points but Reynolds (2006) recorded a peak of activity in the early hours of the night for *Myotis* species, followed by a steady decrease. In the United Kingdom, Swift (1980) found the patterns to be associated with parturition. Bats would shift from a one-peak pattern before parturition to a bimodal pattern of activity after parturition. Given that the recordings took place just after parturition until early August, is possible that the fixed recording points gave a middle-ground depiction of nightly bat activity, with a visible yet nonsignificant peak of activity before dawn. In any case, transects cannot be compared to those findings because the recordings do

TABLE 2. Estimates (\pm SE) for generalized linear models using a data subset that matched weather conditions for transects and sampling recordings. Calls were recorded in 2011 and 2013 at Forêt Montmorency and in 2012 and 2013 at FERLD. FERLD is the reference when comparing sampling areas and fixed recording points are the reference when comparing methods. † — $P \leq 0.10$; * — $P \leq 0.05$; ** — $P \leq 0.01$; *** — $P \leq 0.001$

Species/ Species group	Sampling area	Method	Julian day	Atmospheric pressure (kPa)	Temperature (°C)	Relative humidity (%)	Wind speed (km/h)	Interaction of Method and			
								Pressure	Temperature	Humidity	Wind speed
<i>E. fuscus/</i>	-2.61 \pm 1.04*	2.75 \pm 0.87**	0.37 \pm 0.25	-5.88 \pm 3.39†	0.46 \pm 0.79	-7.09 \pm 3.31*	1.21 \pm 0.39**	7.78 \pm 3.90*	-1.22 \pm 0.87	9.23 \pm 3.91*	-0.71 \pm 0.50
<i>/L. noctivagans</i>											
<i>L. borealis</i>	-0.31 \pm 0.96	4.39 \pm 1.44**	0.20 \pm 0.32	-0.73 \pm 2.58	0.58 \pm 0.63	-0.79 \pm 2.54	-1.52 \pm 1.15	3.85 \pm 3.17	-1.80 \pm 0.78*	4.63 \pm 3.21	1.27 \pm 1.22
<i>L. cinereus</i>	-1.76 \pm 0.36***	3.07 \pm 0.40***	0.28 \pm 0.09**	-0.48 \pm 0.69	0.12 \pm 0.22	-0.73 \pm 0.75	0.14 \pm 0.20	1.42 \pm 1.12	-0.21 \pm 0.29	1.48 \pm 1.19	-0.10 \pm 0.23
<i>M. lucifugus</i>	0.91 \pm 0.38*	2.00 \pm 0.43***	1.01 \pm 0.17***	0.50 \pm 0.54	-0.27 \pm 0.17	0.36 \pm 0.60	-0.03 \pm 0.23	-0.35 \pm 1.58	-0.44 \pm 0.36	-0.05 \pm 1.58	-0.08 \pm 0.30
<i>M. septentrionalis</i>	1.33 \pm 0.46**	-0.64 \pm 0.90	0.60 \pm 0.20**	0.63 \pm 0.51	-0.24 \pm 0.15	0.33 \pm 0.56	-0.16 \pm 0.19	1.77 \pm 5.76	-0.51 \pm 1.02	2.60 \pm 6.15	0.64 \pm 0.74
All <i>Myotis</i>	1.22 \pm 0.33***	1.09 \pm 0.37**	1.01 \pm 0.13***	0.31 \pm 0.37	-0.13 \pm 0.11	-0.09 \pm 0.40	0.06 \pm 0.16	0.03 \pm 1.36	-0.53 \pm 0.31	0.55 \pm 1.36	-0.25 \pm 0.24
Total	-0.48 \pm 0.23*	2.01 \pm 0.28***	0.57 \pm 0.06***	0.11 \pm 0.28	0.03 \pm 0.09	0.00 \pm 0.30	0.23 \pm 0.10*	1.35 \pm 0.64*	-0.41 \pm 0.15**	1.46 \pm 0.67*	-0.35 \pm 0.13**

not extend far enough into the night to pick up the presence or absence of a bimodal shape.

The seasonal timing of activity was species-specific, but for every species, the peak of activity occurred in late July to early August regardless of the method. Our transect design matched the monitoring program in the province of Quebec, Canada, and was slightly different from NABat protocol as it included timed stops at every detection. However, our findings are consistent with increasing rates of initial emergence from pregnancy to weaning found by Swift (1980), as well as several studies that focused on migrating behavior of bats (Johnson *et al.*, 2002; Fiedler, 2004; Arnett *et al.*, 2008; Jain *et al.*, 2011). The peaks of activity detected late in the sampling season were more segregated in transects compared to fixed recording points. This can be explained in part by the gaps between visits for transects which reduced the resolution needed for a precise comparison of detected peaks for each species.

Our results showed that not only the responses to weather variables are species-specific, as speculated by Baerwald and Barclay (2011), but that no strong relationship between bat activity and weather variables could be detected by either sampling method. Erickson and West (2002) concluded that although significant, weather variables explained only 37% of the variability in bat activity. Baerwald and Barclay (2009) found that although weather conditions varied spatiotemporally in their study, they did not vary in a way that could clearly explain bat activity. Temperature might play a small role in bat activity; Paige (1995) noted that when forced into a model including other environmental variables, the temperature could only explain 1% of the variability in bat activity. However, the temperatures recorded vary wildly from one study to another and, as it is the case with our study, none thoroughly sampled the full range of possible temperatures during a year, which might explain the lack of correlation observed. Our fixed sampling point results suggest a limited or nonexistent effect of weather on bat activity compared with other variables. However, should climate-related questions arise, it would be important to reassess this finding. If a relationship between weather conditions and bat activity was found, transect sampling could be conducted outside of the ideal conditions to evaluate its suitability to assess the impact of these variables.

Prediction 3: Variability in habitats and spatial patterns of bat activity

The lack of relationship between the habitat and bat activity is surprising given the number of studies

TABLE 3. Estimates (\pm SE) for generalized linear models using complete datasets. Calls were recorded in 2011 and 2013 at Forêt Montmorency and in 2012 and 2013 at FERLD. † — $P \leq 0.10$; * — $P \leq 0.05$; ** — $P \leq 0.01$; *** — $P \leq 0.001$; **** — $P \leq 0.0001$

Species/ Species group	Julian day pressure	Atmospheric (kPa)	Temperature (°C)	Relative humidity (%)	Wind speed (km/h)	Rainfall (mm)	Weighted age	Stand type (FM=Mixed, FERLD=Coniferous)	Area covered with water
FM									
<i>M. lucifugus</i>	0.76 \pm 0.15***	-2.38 \pm 4.46	-0.07 \pm 0.04†	-0.04 \pm 0.09	-0.01 \pm 0.08	0.01 \pm 0.02	0.04 \pm 0.05	-0.03 \pm 0.02†	0.01 \pm 0.13
<i>M. septentrionalis</i>	0.47 \pm 0.11***	6.95 \pm 3.55†	-0.08 \pm 0.03*	0.09 \pm 0.07	-0.06 \pm 0.06	-0.03 \pm 0.02†	0.03 \pm 0.04	0.00 \pm 0.01	0.09 \pm 0.11
All <i>Myotis</i>	0.74 \pm 0.09***	3.98 \pm 2.68	-0.06 \pm 0.02*	0.04 \pm 0.05	-0.02 \pm 0.05	-0.02 \pm 0.01	0.05 \pm 0.04	0.00 \pm 0.00	0.10 \pm 0.12
Total	0.69 \pm 0.08***	4.19 \pm 2.54	-0.04 \pm 0.02†	0.05 \pm 0.05	-0.03 \pm 0.05	-0.02 \pm 0.01	0.05 \pm 0.04	-0.01 \pm 0.01	0.10 \pm 0.11
FERLD									
<i>E. fuscus</i> / <i>L. noctivagans</i>	0.71 \pm 0.18***	-7.35 \pm 5.13	0.15 \pm 0.06*	-0.11 \pm 0.12	0.13 \pm 0.08.	-0.06 \pm 0.04	0.06 \pm 0.03*	-0.01 \pm 0.01	-0.20 \pm 0.23
<i>L. cinereus</i>	0.45 \pm 0.08***	-1.76 \pm 2.26	0.08 \pm 0.03**	-0.03 \pm 0.05	-0.03 \pm 0.03	-0.06 \pm 0.02**	0.02 \pm 0.02	-0.02 \pm 0.01	0.07 \pm 0.12
<i>M. lucifugus</i>	0.64 \pm 0.19***	1.17 \pm 3.60	0.01 \pm 0.06	0.04 \pm 0.09	-0.21 \pm 0.08**	0.01 \pm 0.04	0.00 \pm 0.02	0.00 \pm 0.01	-0.07 \pm 0.15
<i>M. septentrionalis</i>	0.44 \pm 0.18*	-1.60 \pm 4.15	-0.03 \pm 0.06	-0.05 \pm 0.10	-0.20 \pm 0.08*	0.01 \pm 0.04	0.00 \pm 0.02	0.00 \pm 0.01	-0.18 \pm 0.19
All <i>Myotis</i>	0.57 \pm 0.12***	-2.54 \pm 2.21	0.02 \pm 0.04	-0.07 \pm 0.05	-0.15 \pm 0.05**	0.00 \pm 0.03	0.00 \pm 0.02	-0.01 \pm 0.01	-0.08 \pm 0.13
Total	0.52 \pm 0.06***	-1.58 \pm 1.33	0.07 \pm 0.02	-0.02 \pm 0.03	-0.03 \pm 0.02	-0.04 \pm 0.01**	0.01 \pm 0.01	-0.01 \pm 0.01	-0.03 \pm 0.10

which have shown various associations between bat foraging preferences and landscape features (for example Grindal and Brigham, 1998; Ellis *et al.*, 2002; Erickson and West, 2002). When we only considered fixed recording point data, weighted stand age positively influenced the activity of *E. fuscus/L. noctivagans*, which is unexpected. Brigham (1991) and Morris *et al.* (2010) have found *E. fuscus* to be flexible to a wide range of landscape characteristics, while Loeb and O'Keefe (2006) recorded a negative effect of clutter on *E. fuscus* activity. *Lasionycteris noctivagans* has a rather low wing loading and appears to prefer uncluttered spaces (Norberg and Rayner, 1987), and therefore should not be associated with older stands. *Eptesicus fuscus/L. noctivagans* were most active at FERLD, for which older stands usually meant relatively more open forests than what could be found at Forêt Montmorency. It might thus be the generalist behavior of *E. fuscus*, combined with the availability of stands relatively suitable for *L. noctivagans*, that generated this increase of activity in older stands.

Distance to water did not influence bat activity. For the sake of comparison, we used GIS data both in transects and fixed recording point analyses and did not find several of the activity patterns that have previously been found in the literature. Bender *et al.* (2015), who found a negative relationship between bat occupancy and water bodies in the Southeastern Coastal Plain, which has important wetlands. They proposed that the information contained in GIS data might not cover smaller wet areas important for bat foraging. One limitation of transects compared to fixed recording points is the complexity of collecting field measurements, forcing researchers to resort to using GIS data.

During the reduced season of 2013 at both locations, transects detected proportionally fewer *Myotis* than migratory species, the former being found relatively less frequently than other species on roads (Tonos *et al.*, 2014). Several studies have found that bat activity was positively associated with roads and trails (Zimmerman and Glanz, 2000; Law and Chidel, 2001; Adams *et al.*, 2009; Hein *et al.*, 2009) but Baerwald and Barclay (2009) proposed that migrating bats may not travel randomly and might concentrate along select routes. In our study, those routes might correspond to some of our transects, but might be missed by fixed recording points. This would explain why transects usually recorded a greater proportion of migratory species than fixed recording points.

In conclusion, we hypothesized that fixed recording point would surpass transects in recording quality and description of the temporal and spatial variability of bat activity. We conclude that transects and fixed recording points are generally equivalent methods, with some caveats. Fixed recording points and transects both give good quality recordings of bats and cover the most active part of the night. However, transects proved to be more efficient at detecting most species but we also found that they also recorded proportionally more large species than fixed recording points. In North America, the small-sized species are among those most strongly affected by WNS.

Although our transect design matched the monitoring program in the province of Quebec, Canada, and was slightly different from NABat protocol, we feel it is safe to say that transects are a valuable and effective way of monitoring species decline. However, as we found in 2013 at FERLD, using a limited number of transect samples may not be enough to confirm the presence of those declining species in an area. This project is one of the first of its kind regarding the comparison between two very widely used methods of bat monitoring. Because of the increasing number of threats to bats and the number of questions asked relative to those threats, we strongly feel that more comparable studies should be conducted for other species of bats to confirm and build on the monitoring guidelines already established by NABat.

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