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Pinpointing the position of flying songbirds with a wireless microphone array: three-dimensional triangulation of warblers on the wing

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ABSTRACT

Flight calls, the quiet calls emitted by migratory birds on the wing, offer opportunities to understand the behaviour of birds during migration. We test the effectiveness of an eight-element microphone array for three-dimensional triangulation of the position of calling migratory birds. We constructed a microphone array out of commercially available components and used freely available software to process the recordings, so that this technology might be easily adopted for migration monitoring. In the Great Lakes region of North America, we triangulated the position of loudspeakers broadcasting synthetic tones and flight calls, as well as calls of actual passing migrants. Loudspeakers broadcasting synthetic tones showed a triangulation accuracy of 1.52 ± 0.34 m. Loudspeakers broadcasting flight calls of migratory wood-warblers showed a triangulation accuracy of 2.04 ± 0.37 m. Actual migratory warblers passing over the microphone array showed an estimated accuracy of 2.70 ± 0.48 m. We conclude that wireless microphone arrays accurately triangulate migrant birds, at least under optimal recording conditions. We present this proof-of-concept study to demonstrate the reliability of this underutilized technique which should be of interest as a tool for studying migratory bird behaviour, for quantifying migratory bird populations, and for monitoring the conservation of migratory birds.

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Introduction

Billions of migratory birds travel between temperate breeding grounds and southerly wintering grounds twice annually in migration (Dokter et al. 2018; Van Doren and Horton 2018). Their nocturnal habits (Alerstam 2009) and their fast speed and transit time (Horton et al. 2018) make it difficult to study their in-flight ecology and behaviour. Diverse techniques have been used to study songbirds during migration, although each technique has limitations. Studies that rely on bird banding at stopover sites (e.g. Holzschuh and Deutschlander 2016; Morris et al. 2016) are likely biased towards the subsample of resting individuals captured (Remsen and Good 1996) and they provide information about birds pausing during their migration rather than the composition of birds migrating together during active flight. Studies using radar provide data on the

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organization of migrants within the atmosphere (Gauthreaux and Livingston 2006; Archibald et al. 2016) but do not differentiate between species of migratory birds. The use of acoustic techniques may remedy these limitations, particularly if they can be used to provide three-dimensional monitoring of the position of migratory birds. Using three-dimensional monitoring offers the potential to allow researchers to quantify the locations of birds in flight which has previously proven challenging.

The only available method for differentiating between migrant bird species on the wing is by recording and identifying flight calls (Farnsworth 2005). Passive recording of flight calls with one or two microphones has been the traditional method for bioacoustic quantification of bird migration (Hamilton 1962; Smith et al. 2014; Sanders and Mennill 2014a). However, the total number of individuals passing overhead cannot be easily determined without knowing the position of calling birds. Prior studies looking at migrant passage have focused on assessing the overall magnitude of migration by counting total numbers of calls recorded without attempting to distinguish the number of individuals passing (e.g. Graber and Cochran 1960; Vleugel 1960). Without the ability to differentiate among individuals, traditional acoustic recording technology cannot resolve questions on the spacing or heights of migrants in flight, species-specific biases in flock composition, and individual variation in calling rates. By triangulating the locations of birds in migration using a three-dimensional microphone array, these questions can be addressed. Migrants that do not call will remain undetected when using acoustic techniques, yet this technique is still a much-improved method for studying the flight behaviour of migrants, particularly if researchers focus on migration events when calling rates are high.

In this study our goal was to test the accuracy of a wireless microphone array for triangulating the positions of migratory birds. Microphone arrays have been widely used for spatial studies of animal behaviour; these studies typically involve an array of microphones placed around breeding territories of one or more animals, enabling the triangulation of animals in the area bounded by the array (reviewed in Blumstein et al. 2011). Few studies have attempted to use microphone arrays for flying birds due to challenges associated with triangulating moving migrants. Evans and Mellinger (1999) and Stepanian et al. (2016) used custom-built microphone arrays which required expertise in electronics and signal processing. These previous studies showed arrays could be used to produce rough estimates of passing migrants (Evans and Mellinger 1999) or triangulate flight calls broadcast from an overhead speaker (Stepanian et al. 2016). If a commercially available microphone array technology could be used to triangulate the position of migrating birds, this would be a valuable development in the study of bird migration. In the first part of our study, we test the accuracy of an eight-element wireless microphone array for triangulating the position of loudspeakers broadcasting test tones and recorded flight calls of migratory songbirds. Given their high biodiversity and well-documented use of flight calls during migration, we focus our attention on migratory wood-warblers (Parulidae). In the second part of our study, we test the accuracy of the system for triangulating the position of wild wood-warbler flight calls passing above the array.

Methods

Microphone array

We set up a microphone array at a study site in the upper Great Lakes region of North America in 2018 during spring migration (from 16 May through 10 June) and fall migration (from 14 August through 30 September). We positioned the array along a known flight path of warblers on the southern coast of Lake Superior in a grassy yard with a few dispersed trees. The array consisted of four 7.1-metre poles (model: Mr. LongArm) arranged in a 25 m square (Figure 1(a)). On each pole we mounted a GPS-enabled digital recorder (model: Wildlife Acoustics Song Meter SM3) and two microphones (model: Wildlife Acoustics SMMA2 external microphone). We mounted one microphone at the top of the pole at a height of 7 m, and the other microphone near the bottom of the pole at a height of 1 m (Figure 1(b)). Microphone heights were chosen to maximize the vertical separation of

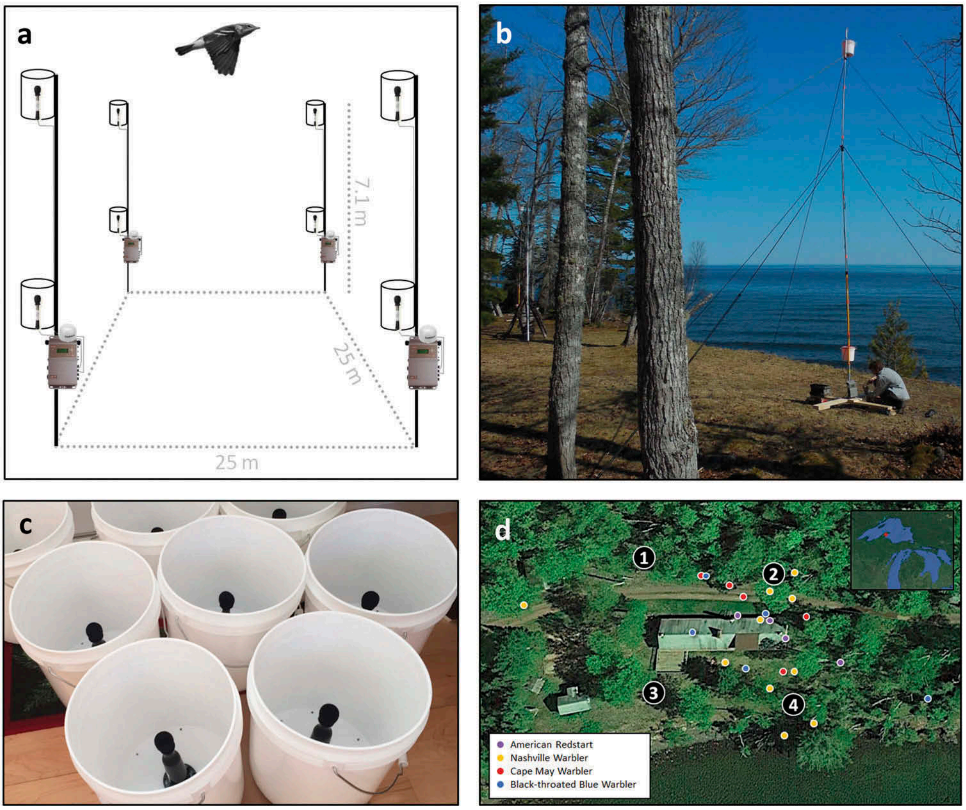

Figure 1. (a). Schematic diagram of an eight-element wireless microphone array used to triangulate the position of migrating birds in three dimensions. Bucket-mounted microphones were attached to 7.1 m poles at two heights: 7 m and 1 m. Each pair of microphones recorded sounds to a GPS-enabled automated digital recorder at the base of each pole. (b). Photograph of a portion of the microphone array on the shore of Lake Superior. (c). Close-up photograph of the bucket-mounted microphones, designed to minimize sounds recorded from below. (d). Map of microphone positions and the estimated position of 30 triangulated migratory warblers. Black circles represent positions of the four microphone poles. Inset map shows location of study site.

microphones in the y plane on the commercially available poles and increase triangulation accuracy. Inspired by the design of Evans (2005), we mounted each microphone in a bucket to minimize recording of sounds below or beside the microphone, and maximize the recording of sounds above the microphone (Figure1(c)). We used buckets that were 50 cm in height and 25 cm in diameter. To keep out rain and debris, each bucket was covered with a layer of plastic wrap (providing waterproofing) and cloth (stabilizing the plastic wrap).

Accurate triangulation depends on precise measurements of the position of each microphone in an array. We surveyed the positions of each microphone using a survey-grade global positioning system (GPS; model Ashtech ProMark II). This system allowed us to survey each of four pole positions simultaneously using four separate GPS units with tripod-mounted antennas. This allowed us to correct the position estimates based on information of multiple units simultaneously (as in Mennill et al. 2006, 2012). We sampled microphone positions by collecting repeated measurements over a period of 40 min, and we used the GPS manufacturer's software (Ashtech GNSS Solutions) to calculate the relative position of each microphone from the 40-min survey data. The Ashtech Promark II units indicated a measurement accuracy of 5 mm. We precisely measured the difference in heights between the lower and upper microphones using a tape measure (resolution: 1 mm). We controlled for offsets in the position of the top microphone relative to the bottom microphone due to uneven ground using a Bosch laser level.

Sound sources for triangulation

We recorded two different types of sounds for triangulation: sounds broadcast from loudspeakers and sounds produced by live migratory birds. In the loudspeaker test, we positioned an omni-directional loudspeaker (model: Foxpro Scorpion X1B) near the centre of the array, but shifted 2.1 m west of the true geometric centre of the four microphone poles to provide a location that would have a different time-of-arrival at each microphone. The speaker was mounted on a tree at this location for the duration of the study, at a height of 10.5 m, oriented upwards. We used the GPS system described above to survey the location of the speaker. We broadcast two types of signals from the loudspeaker for triangulation: (1) test tones consisting of frequency-modulated sine waves (hereafter 'test tones'; Figure 2), and (2) pre-recorded flight calls of warblers (hereafter 'broadcast flight calls'). We standardized the speaker used to broadcast test tones and flight calls to the same amplitude (setting: 10 on the FoxPro Scorpion speaker). We broadcast flight calls at an amplitude that matched the amplitude of wild migrants, based on our auditory assessment in the field. We created playback stimuli by choosing flight calls from the Night Flight Call database (Evans and O'Brien 2002), with an aim to include eight common warbler species at the study site: Palm Warbler (*Setophaga palmarum*), American Redstart (*Setophaga ruticilla*), Magnolia Warbler (*Setophaga magnolia*), Cape May Warbler (*Setophaga tigrina*), Ovenbird (*Seiurus aurocapilla*), Chestnut-sided Warbler (*Setophaga pensylvanica*), Yellow Warbler (*Setophaga petechia*), and Black-and-white Warbler (*Mniotilta varia*). We selected 30 recordings of test tones and 30 broadcast flight calls recordings drawn from the eight common warbler species to triangulate, for a total of 60 triangulations across both test tones and broadcast flight calls. We selected 30 broadcast flight calls for analyses by choosing four broadcast flight call recordings from each of the eight species, except Ovenbird and Magnolia Warbler for which

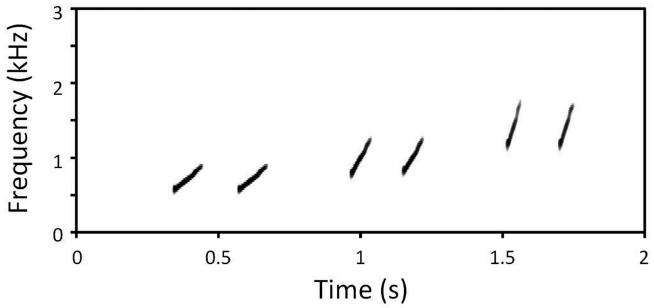

Figure 2. Spectrogram of speaker-broadcast frequency modulated sine wave test tones used to triangulate and investigate location accuracy estimates of an eight-element wireless microphone array.

we chose three calls due to fewer available recordings. This totalled 30 broadcast flight calls used in the analysis.

To triangulate live migrating birds, we selected 30 individual wild warbler flight calls (hereafter ‘wild flight calls’) representing the ten most common warbler species in order to keep sample sizes comparable to those available for loudspeaker broadcast calls (see Results). Wild flight calls were chosen from our recordings by identifying flight calls with high signal-to-noise ratios. We used existing call databases, including the Night Flight call database (Evans and O’Brien 2002) and the appendix in Sanders and Mennill (2014a) to verify species identities of wild warbler flight calls. We chose flight calls that were separated by at least one minute in recording time from conspecifics to ensure that each triangulation was of a different individual (Graber and Cochran 1959). This represents a cautious selection scheme because warblers likely fly over the array at a conservatively estimated speed of 30 km/hr or 8.3 m/s based on published data and visual flight estimates (DeLuca et al. 2015). Using these estimates that probably represent the lower end of warbler speeds, we calculated that warblers passed through a 150 m zone around our array every 18 seconds. Therefore, wild flight calls of the same species that were more than 18 sec apart likely represent separate individuals. In total we analyzed 30 broadcast test tones, 30 broadcast flight calls and 30 recorded wild flight calls for a total of 90 triangulations.

Analytical approach

We used a triangulation method that relies on time-of-arrival differences of a sound recorded at multiple microphones to cross-correlate and estimate sound position (as in Mennill et al. 2006, 2012; Stepanian et al. 2016). The 2-channel WAV recording files from each of the four digital recorders were combined into a single 8-channel AIF file in Syrinx-PC Sound Analysis Software (J. Burt, Seattle, WA), relying on the built-in GPS in the digital recorders to ensure synchronization across the four pairs of channels. We calculated the time of arrival of each target sound at each of the eight microphone channels by precisely measuring the start time of each call in Syrinx-PC. We measured start times by increasing the resolution of the time axis in Syrinx-PC until the entire flight call filled the window, and then drawing an annotation box where the call initiation was visible above background noise. The recorded time-delay values for each microphone channel were then entered into the Excel-based implementation of SoundFinder (Wilson et al. 2014), which used temporal cross-correlation (Spiesberger 2001) to produce an estimated position of the sound source, an estimate of the time the sound started, and an estimated level of spatial and temporal error in triangulation accuracy. We used a manual approach to triangulate wild flight calls because it is the most reliable method and there are currently no automated triangulation procedures.

We used different approaches to estimate triangulation accuracy for broadcast calls and calls of wild birds. For the two types of loudspeaker-broadcast sounds, we calculated triangulation accuracy by subtracting the estimated sound source position from the known speaker sound source position in three dimensions. For the wild migrant warbler flight calls for which the actual flying warbler position was unknown, we relied on the estimates of error in triangulation accuracy produced by SoundFinder (Wilson et al. 2014). SoundFinder estimates accuracy of triangulations by using a least-squares approach to produce error estimates. The reliance on SoundFinder triangulation error estimates was justified based on prior tests of the program's ability to report triangulation accuracy within 3.2 m or less for results with temporal errors between 1–2 ms in arrival time (Wilson et al. 2014). We use the term 'accuracy' to refer to exact triangulation accuracy calculated by subtracting the estimated sound source from the known sound source position for loudspeaker-broadcast calls, and the term 'estimated accuracy' to refer to SoundFinder estimates of accuracy for wild migrant warblers.

We compared differences in triangulation accuracy of loudspeaker broadcast versus wild flight calls using a two-sample *t*-test. We performed a one-factor ANOVA to examine variation in triangulation accuracy across the warbler species recorded. We used a linear mixed effect model, with distance as a fixed effect and species as a random effect, to determine if the distance birds were from the array at the time they called was a significant predictor of triangulation accuracy. We report values as means ± SE. All statistical tests were performed in RStudio (R Core Development Team 2017, Version 1. 0. 153).

Results

Loudspeaker triangulation

Eight-channel microphone recordings of a loudspeaker broadcasting test tones and flight calls provided accurate estimates of loudspeaker position (Figure 1(d)). The loudspeaker broadcasting a frequency-modulated test tone was triangulated with a mean location accuracy of 1.52 ± 0.34 m from its known position based on a sample size of 30 individual test tone triangulations (Figure 3). The loudspeaker broadcasting flight calls was triangulated across 30 individual broadcast calls with a mean location accuracy of 2.04 m ± 0.37 m from its known position across all eight warbler species (Figure 3).

Migrant flight call triangulation

Based on recordings collected over a 62-day period during both spring and fall seasons, the most commonly detected calls of wild migratory birds passing over the array were produced by 10 warbler species (Table 1). Most wild flight calls were produced by Nashville Warblers, Northern Parulas, Black-throated Blue Warblers, Cape May Warblers, and American Redstarts (Figure 4). Positions of 30 flying warblers were triangulated with an estimated mean accuracy of 2.70 ± 0.48 m across these five species (Figure 3).

In our sample of 30 individuals of each of three signal types (30 test tones, 30 broadcast calls, and 30 wild flight calls), no significant difference in triangulation accuracy was noted across test tones, broadcast flight calls, and calls of wild migrant warbler species recorded; the test tone had slightly higher triangulation accuracy than wild-bird flight calls but this was not statistically different (*t*-test: $T = 0.92$, $P = 0.18$, *95% CI*: 0.81–2.13 m, $n = 90$).

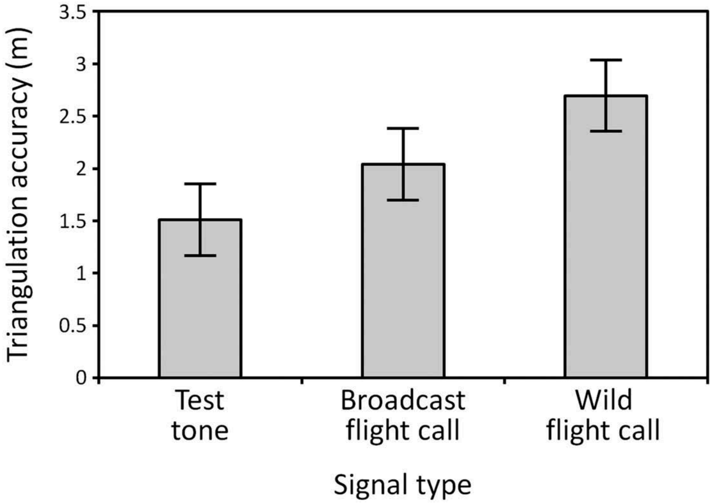

Figure 3. Triangulation accuracy of a wireless microphone array at calculating the position of three types of signals: test tones broadcast from a loudspeaker, flight calls of warblers broadcast from a loudspeaker, and flight calls recorded from wild migrant warblers. Mean triangulation accuracy is shown across the three signal types for 30 signals in each type, with Standard Error (SE) shown above each bar. Note: the first two bars show the accuracy which is the difference between the true position and estimated position; the last bar shows the triangulation accuracy from software-generated estimates.

Table 1. Average heights and triangulation accuracies of 30 warblers (Parulidae) flying over an eight-element microphone array.

Species	Average Height (m)	Average Accuracy (m)	Number
American Redstart (*Setophaga ruticilla*)	5.7	4.8	2
Black-and-white Warbler (*Mniotilta varia*)	7.0	2.0	1
Blackburnian Warbler (*Setophaga fusca*)	17.7	4.0	2
Blackpoll Warbler (*Setophaga striata*)	15.8	1.8	1
Black-throated Blue Warbler (*Setophaga caerulescens*)	15.4	0.3	1
Black-throated Green Warbler (*Setophaga virens*)	12.8	5.2	5
Cape May Warbler (*Setophaga tigrina*)	34.5	0.6	4
Nashville Warbler (*Oreothlypis ruficapilla*)	8.8	2.2	10
Northern Parula (*Setophaga americana*)	23.8	4.6	2
Northern Waterthrush (*Parkesia noveboracensis*)	2.7	0.9	2

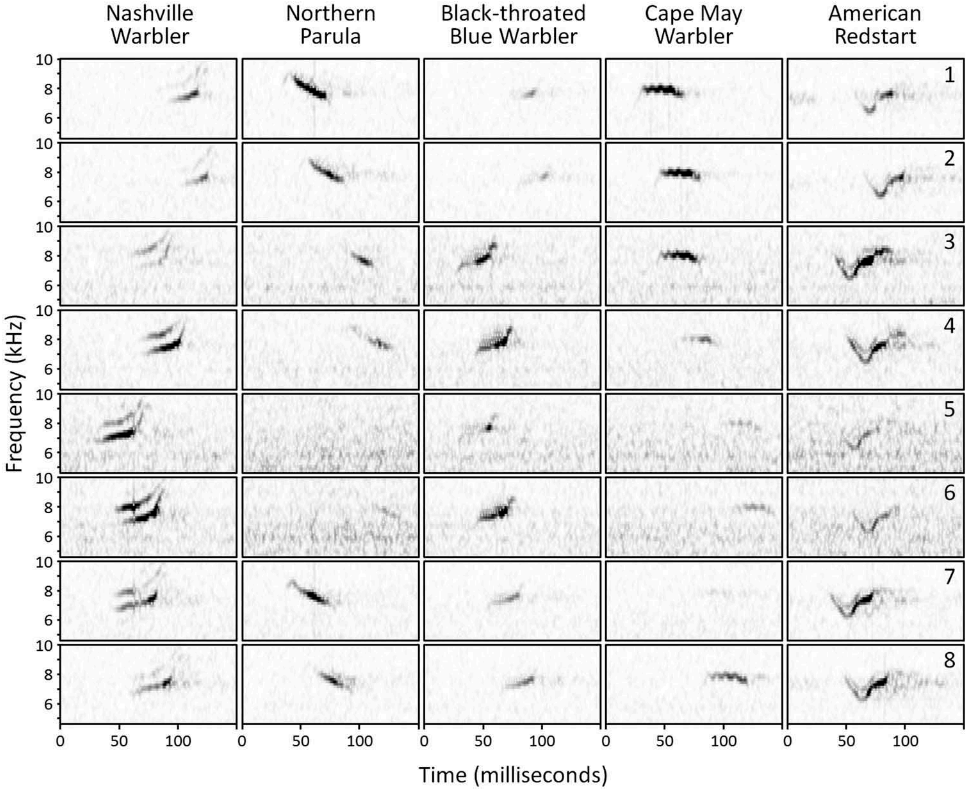

Figure 4. Composite spectrogram of five triangulated flight calls recorded with an eight-element wireless microphone array. From left to right: Nashville Warbler (Oreothlypis ruficapilla), Northern Parula (Setophaga americana), Black-throated Blue Warbler (Setophaga caerulescens), Cape May Warbler (Setophaga tigrina), and American Redstart (Setophaga ruticilla). Subtle delays in sound arrival time of the call at each of the channels were used to calculate the migrant's position.

Within triangulated calls of passing migrant warblers, there was significant variation in triangulation accuracy between species (ANOVA: $F = 3.13$, $P = 0.02$, $n = 90$). Triangulation accuracy was highest for Black-throated Blue Warblers (mean estimated accuracy of triangulation: 0.3 m), lowest for Black-throated Green Warblers (mean estimated accuracy of triangulation: 5.2 m), and intermediate in the eight other species examined (Table 1). For these triangulated warblers, Cape May Warblers flew at the highest altitudes (mean height above ground: 34.5 m) while Northern Waterthrushes flew at the lowest altitudes (mean height above ground: 2.7 m; Table 1). There was a non-significant tendency for triangulation accuracy to increase with distance birds were recorded from the array (Figure 5; LMM: $F = 4.25$, $P = 0.07$, $n = 30$, $R^2 = 0.13$).

Discussion

Microphone arrays can provide valuable information on the spatial position of animals (Patricelli et al. 2007; Blumstein et al. 2011; Mennill et al. 2012). Although two-dimensional triangulation has been used extensively, three-dimensional triangulation poses more

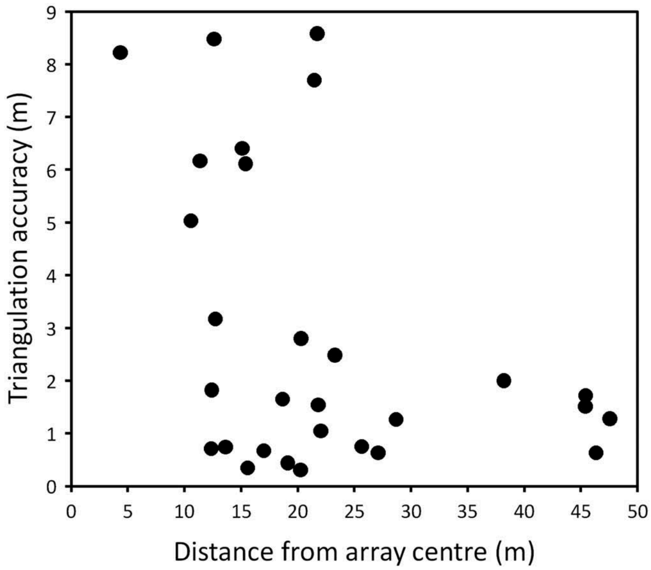

Figure 5. Triangulation accuracy showed a non-significant tendency to increase with distance from the centre of an eight-element wireless microphone array in a sample of 30 triangulated warblers.

challenges, even though three-dimensional triangulation offers special opportunities to study flying animals, such as migratory birds. In this proof-of-concept field test, we show that a microphone array produces accurate estimates of the position of loudspeakers broadcasting flight calls of migratory birds, as well as estimates of the position of actual migratory birds. This array system should be useful for localizing flying migratory birds under the same conditions as passive recording of flight calls with a single microphone takes place: conditions when ambient noise is low and when birds are calling near to the ground (Horton et al. 2015; Stepanian et al. 2016).

We triangulated sounds using a microphone array made of commercially available components that cost approximately $4000 USD: four digital recorders, eight external microphones, four GPS antennae, tall poles, and buckets for mounting the microphones. Survey equipment is an additional expense, but affordable survey solutions are available; see (Mennill et al. 2012; Stepanian et al. 2016). This microphone array requires less advanced training in electronics and signal processing than custom-built microphone arrays because all of the components are commercially available. Furthermore, the wireless design is less cumbersome than previous cable-based array systems (e.g. Mennill et al. 2006). For these reasons the wireless array system described here has widespread utility for biologists and it should provide a useful tool for studying migratory birds at a relatively low cost.

Previous investigations have shown that microphone arrays can be used to triangulate broadcast flight calls (Stepanian et al. 2016) or to assess passage rates of migrants over a microphone array (Evans and Mellinger 1999). These previous studies provide no precise estimates of accuracy of positions of wild migrants; Evans and Mellinger (1999) used an array to distinguish widely spaced individual migrants (i.e. by concluding that two similar animals were at least 1 minute apart), and Stepanian et al. (2016)

estimating accuracy of broadcast calls within 5–10 m for 60–80% of calls. The triangulation accuracy estimates in our study are comparable to those for a previous study that used similar equipment to conduct two-dimensional triangulation of 24 types of animal sounds (1.87 ± 0.13 m; Mennill et al. 2012). Our results indicate there was little difference in triangulation accuracy of broadcast calls from speakers and wild flight calls, revealing that these signals are suitable for accurate triangulation.

The flight calls of wood-warblers are challenging to measure, and therefore challenging to triangulate, because they are uniformly short (50–300 ms) with high frequency and low amplitude. We focused our analysis on recordings with little ambient noise in order to test the system under ideal conditions for recording flight calls. Under different conditions with high ambient noise, flight calls are challenging to record whether using a single recorder or a microphone array. The conditions suitable for recording flight calls with a microphone array are no different than those for a single unit often used to record flight calls; these simple and quiet calls can only be used to monitor birds under good recording conditions. Our findings provide a proof-of-concept under good recording conditions, and future investigations should explore the efficacy of flight call recordings during suboptimal ambient noise conditions.

Acoustic monitoring is becoming a widely used technique for determining migrant passage (Smith et al. 2014). Previous studies have used flight call data to study seasonal phenology of migrant passage (Sanders and Mennill 2014a) and geographic biases in migrant distribution (Smith et al. 2014; Sanders and Mennill 2014b). Microphone arrays can be used for in the same contexts as traditional acoustic studies but offer the benefit of precisely estimating migrants' spatial positions within flocks during migration. This might be a valuable technique for improving estimates of (1) migrant passage rates, (2) the role calls play in social communication within migratory flocks, and (3) understanding species-specific differences in preferred migration altitude and density. Array-based recordings may also have important implications for conservation studies of migrant passage in areas suspected of being migratory hotspots while offering more information about species composition of migrants than radar-based migration monitoring. Although this array system will require more extensive testing under a wide variety of conditions, we believe that the proof-of-concept testing that we present here shows the system has widespread promise for the study of migratory birds.

It is important to recognize an additional limitation of ground-based microphones for monitoring migrants: bird migration altitude will regularly exceed the detection range of microphones. One published study that broadcast pre-recorded flight calls had success triangulating calls originating as high as 130 m in height (Stepanian et al. 2016). Another study suggested that the calls of migratory warblers can be recorded at altitudes up to 150 metres (Horton et al. 2015). Nevertheless, microphone arrays may be very useful for at least two reasons. First, potential collision hazards to migrants such as glass buildings, windmills, and communication towers are all in the zone of detection of a microphone array. Second, the height of migrants during early morning flights, when migrants assess the suitability of stopover habitat, is lower than during nocturnal migration (Weidner et al. 1992). Evidence suggests that most collisions of migrants with obstacles may happen in the early morning as the sun is rising (Winger et al. 2019). This highlights the importance of studying the differences in species-specific migrant behaviour at altitudes near to the ground.

Wireless microphone arrays may be an important tool for monitoring migratory birds. Independent testing of the system by others in variable environments will be valuable for researchers studying migratory behaviour of passerines. Wireless microphone arrays offer a valuable technique for studying migratory birds which has been underutilized in the suite of ground based capture, radar and acoustic methods for migration monitoring.

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