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Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour

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Summary

1. Using arrays of microphones, biologists can monitor the position of free-living animals based on the sounds they produce. Microphone array technology exploits differences in sound arrival times at each microphone to calculate an animal's position. This technology provides new opportunities for studying animal ecology and behaviour and has many advantages over tracking technologies that require capturing animals and fitting them with external devices, or technologies that focus on one individual in isolation of the activities of nearby animals.

2. The efficacy of microphone arrays for triangulating the position of wild animals has been established through previous studies. Yet widespread use of microphone array technology has been limited by many factors: arrays are expensive, custom manufactured, and cumbersome. Consequently, microphone arrays are used infrequently, in spite of their transformative potential for studying animal ecology and behaviour.

3. We conducted a field test of a new wireless microphone array system that has multiple advantages over previous systems: it is relatively inexpensive, commercially available, includes an integrated global positioning system (GPS) for time-synchronizing microphones, and it is small enough to fit in a backpack. We set up an array of four stereo recorders (each with a pair of stereo microphones) at 12 sites and tested the system's accuracy for estimating the location of loudspeakers broadcasting 25 types of bird, mammal and frog sounds.

4. We found that this system produced accurate location estimates based on multi-channel recordings of many types of acoustic signals. The average location accuracy was $1{\cdot}87 \pm 0{\cdot}13$ m, on par with cable-based microphone array systems. Location accuracy was significantly higher when the recorders were closer together and when sounds were broadcast inside the area bounded by the microphones. Accuracy tended to be higher in field vs. forest habitats.

5. We discuss how this system may be used to enhance studies of animal ecology and behaviour across a wide range of contexts. As with previous arrays, this system will allow researchers to monitor animals that produce distinctive acoustic signals. In contrast to previous microphone arrays, this system is affordable, portable and commercially available. Consequently, this system stands to dramatically enhance research on wild, free-living animals.

Key-words: acoustic monitoring, bioacoustics, field research, localization, microphone array, position estimation

Introduction

Many animals are difficult to observe. Researchers have struggled to monitor the ecology and behaviour of animals that live in thick vegetation, animals that are active nocturnally, animals that travel over large distances, and animals that change their behaviour in the presence of human observers. Arrays of simultaneously recording microphones provide a tool for passively monitoring such animals, using subtle delays in sound arrival time to estimate the position of animals based on the sounds they produce (Mennill *et al.* 2006; Blumstein *et al.* 2011). Microphone array technology can be used to study

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any animal that makes distinctive sounds (Mennill 2011), and it presents an important and transformative tool for ecologists, behavioural biologists and conservation biologists.

The advantages of using microphone arrays to study animals are plentiful. (1) Array recordings allow biologists to estimate the position of animals in their natural environment, providing a spatial context for monitoring and measuring animal movement. (2) Animals can be studied with minimal invasiveness, where animals need not be captured, constrained or fitted with tracking devices. (3) Multiple animals can be studied simultaneously, and their interactions can be studied in the natural context of a communication network (McGregor 2005). (4) Animals can be monitored while human observers are absent from the area, so that animal movement patterns are not influenced by the presence of observers. (5) Monitoring can be conducted over very long time periods, exceeding the logistic possibilities of direct observation. (6) Animals can be monitored at night, or in thick vegetation, or in other situations where visual tracking would be difficult or impossible. The primary disadvantage of microphone array technology is that it focuses on acoustic behaviours; microphone arrays cannot be used to study silent animals.

Terrestrial microphone arrays pose logistical challenges because sound attenuates rapidly in air (Bradbury & Vehrencamp 2011), requiring that microphones be positioned around the study animals, and in close proximity to the study animals, to collect suitable recordings. Furthermore, spatial monitoring requires precise coordination of the recordings from each microphone, which is difficult to accomplish for microphones that are separated spatially. To ensure precise coordination of all microphones in terrestrial arrays, some researchers have relied on kilometres of microphone cable to connect microphones to a central, multi-channel recorder (e.g. Fitzsimmons *et al.* 2008a; Mennill & Vehrencamp 2008; Paticelli & Krakauer 2010; Lapierre, Mennill & MacDougall-Shackleton 2011). Others have used radio-transmission to relay sounds from distant microphones to a central, multi-channel recorder (Burt & Vehrencamp 2005). The amount of effort to set up cable-based arrays, and challenges with radio-transmission through thick vegetation, has limited the proliferation of microphone array technology. An ideal microphone array would consist of independent recorders that are not constrained by kilometres of cable or complex radio-transmission devices. But the clocks of independent recording devices drift apart over time (Schmid *et al.* 2010), producing timing errors that diminish or eliminate the ability to accurately estimate the position of the sound source (Blumstein *et al.* 2011). One solution to this problem is to integrate a global positioning system (GPS) into the recording devices to synchronize their clocks relative to an external time signal.

Autonomous recorders with integrated GPS time coordination have recently become available commercially, making microphone arrays accessible to a broad user group for the first time. We tested the accuracy of an array of GPS-synchronized digital recorders for estimating the location of animal sounds. These recording devices have numerous advantages over previously available microphone array systems. Whereas previous systems were very costly, this system is relatively inexpensive (thousands of dollars instead of tens of thousands of dollars). Whereas previous systems were custom manufactured, this system is available 'off the shelf'. Whereas most previous systems were cumbersome, either because of long stretches of cable or radio-transmission devices, this system is compact; the equipment we tested in this study fits in a small backpack. Whereas most previous systems required that microphones be placed close together, limited by cable lengths or radio-transmission capabilities, this system is unlimited; the wireless, modular recording units can record with any distance of separation, and this can be adjusted based on the active space of the signals of the animal of interest.

In this methodological study, our goal was to evaluate whether this new technology provides a useful tool for field research. Previous research demonstrated that cable-based microphone arrays provide a compelling tool for spatial monitoring of animals (reviewed in Blumstein *et al.* 2011). We sought to determine whether a new, affordable, portable, wireless microphone array could provide a similarly compelling tool with a much greater ease of operation. We evaluate the accuracy of a four-recorder array for localizing pre-recorded sounds of birds, mammals and frogs. We compare location accuracy in field vs. forest habitats, across two densities of microphones (recorders separated by 25 vs. 50 m), between sounds recorded inside vs. outside the area bounded by the microphones, and across 25 different types of animal sounds.

Materials and methods

We recorded animal sounds using an array made up of four stereo recorders arranged in a square with *c.* 25 or 50 m on each side. Each recorder housed a pair of stereo microphones, so that the four recording units collected eight channels of acoustic information. The recorders were Wildlife Acoustics Song Meters (model: SM2-GPS; Wildlife Acoustics Inc., Concord, MA, USA) with built-in omnidirectional microphones (frequency response: 20–20 000 Hz). These autonomous recorders are battery-operated stereo digital recorders capable of recording sounds at a variety of sampling frequencies and storing them to flash memory cards. With an additional GPS option, the recorders use the time signal from the GPS unit to synchronize each recorder's clock. These units are compact and portable. Each SM2 recorder is 18 × 18 × 7 cm, weighing *c.* 2 kg, including four D-cell rechargeable nickel-metal-hydride batteries. Each detachable GPS unit is 9 × 9 × 4 cm, weighing *c.* 500 g. The units can accommodate four flash memory cards permitting long recordings. The units can be programmed to record at specific times of day, extending their service-free time in the field. The units are waterproof and capable of incorporating hydrophones (for aquatic research) and ultrasound-sensitive microphones (for chiropteran research). To our knowledge, these are the first such units available commercially that can serve as a wireless microphone array.

Whenever microphone arrays are used for estimating the position of sound sources based on time-of-arrival differences, the clocks of each recording device must be synchronized on a scale of milliseconds. Recording devices suffer from clock drift, where clocks gain or lose small amounts of time per minute of recording (Schmid *et al.* 2010). Although clock drift is usually imperceptible to humans, it results in a lack of synchronization which prevents sound localization based on time-of-arrival measurements. The system we used overcomes this obstacle using time synchronization from the attached GPS units. Each recording unit resamples the sound file to ensure that it maintains synchronization with the satellite time signal.

Between 20 May and 30 June 2011, we set up the microphone array at 12 different locations within the Ojibway Prairie Conservation Preserve (42°15·848′N, 83°4·472′W) and the University of Windsor Pelee Environmental Research Centre at Leamington (42°1·221′N, 82°30·778′W) in Essex County, Ontario, Canada. Four song metres were mounted on poles at a height of 1·5 m and placed in a square arrangement at each site (Fig. 1; see supplement for maps). We chose six sites that were open fields with no vegetation above 1 m, and six locations that were mature forested sites with continuous hardwood canopy dominated by cottonwood (*Populus deltoides*), oak (*Quercus* spp.), and maple (*Acer* spp.). This allowed us to compare the accuracy of location estimates across both forest and field habitat types. At three forest and three field sites, we arranged the four recorders in a square with *c.* 25 m edges; at the other three forest and field sites, we set up the recorders in a square with *c.* 50 m edges. This allowed us to compare the accuracy of location estimates across two densities of microphone. We collected recordings only on days with little or no wind and no rain; the addition of noise, such as wind or rain, is expected to diminish recording quality for any outdoor acoustic monitoring.

At each of the 12 sites, we broadcast songs at two locations relative to the four recorders. One location was inside the area bounded by the recorders and the other location was outside the area bounded by the recorders. We determined the specific location for playback by generating random numbers (using iPod application 'Random #', E. van Zenren). For the loudspeaker location inside the array, we generated two random numbers between 0 and 50 (or 0 and 25 for the smaller arrays) to dictate the *X* and *Y* coordinates (in m) of the loudspeaker relative to the square created by the four recorders. For the loudspeaker located outside the array, we generated a random number between 1 and 4 to select one of the four edges of the array and then two random numbers between 0 and 50 (or 0 and 25 for the smaller arrays) to dictate the *X* and *Y* coordinates (in m) of the loudspeaker beyond that edge.

Fig. 1. Photographs depicting the forest and field sites where sounds were recorded with a wireless microphone array. Top: Four recorders positioned with 25 m spacing in a field habitat. Bottom: Recorders being programmed for deployment in a forest habitat.

Stimuli were broadcast from an omnidirectional loudspeaker (model: Anchor Audio Minivox PB-25, Torrance, CA, USA; output: 15 W; frequency response: 100–12 000 Hz). We mounted the speaker on a 1·5-m pole, facing upwards to minimize any influence of speaker directionality. Stimuli were stored as uncompressed WAVE files on a digital playback device (Apple iPod, Cupertino, CA, USA). We held the volume of playback constant at a sound pressure level of 95 dB at a 1-m horizontal distance from the upwards-oriented loudspeaker, measured with a digital sound level metre (model 33-2055: RadioShack, Fort Worth, TX, USA; settings: slow response, C-weighting). We broadcast sounds at a high amplitude to ensure detection by the recorders. We used recording settings on the SM-2 Song Meters of 22050 Hz sampling frequency, 16-bit accuracy, with no file compression (WAVE format).

PLAYBACK STIMULI

Stimuli for playback were chosen to represent a variety of different types of animal sounds (Table 1). We selected sounds from the group of animals we have studied during previous investigations and additional species for which we had high-quality stimuli available, as well as two synthetic sounds for comparison. Together, these 25 sounds represent a spectrum of types of sounds and thereby provide a robust test of the capabilities of this system. The stimuli are described in detail in the supplement, with spectrograms shown in Fig. S1. At each loudspeaker location, we broadcast the stimulus set three times to maximize the opportunity to record each type of sound without the influence of background noise; each stimulus set was *c.* 5 min in length, so that the total recording time for the three repeats of each internal and external playback was *c.* 15 min. We generated three independent stimulus sets, each using a different recording for each of the 25 types of sound. Each stimulus set was broadcast in four different arrays.

MICROPHONE AND SPEAKER POSITION SURVEYS

In the field, we set up the four recorders with approximate distances, using handheld GPS units (model: GPS 60CSx; Garmin, Olathe, KS, USA) to guide microphone placement. Microphone arrays require precise surveys of microphone positions because sound localization is based on the coordinates of the microphones combined with time-of-arrival differences of the recorded sounds at each microphone. We measured the exact positions of microphones and speakers using a survey-grade GPS (Ashtech ProMark 3, Santa Clara, CA, USA). We used a four-unit system to conduct a static survey of the microphone and loudspeaker locations. We sampled the position of each recorder and loudspeaker for 20–40 min. Resulting measurements had a horizontal accuracy of 1·12 ± 0·20 m (95% 2dRMS; mean ± standard error; SE) with better accuracy in the field than forest sites (see supplement). We treated these position estimates as the true coordinates of the microphone and speaker positions. The coordinates from the Ashtech GPS revealed that our recorders were set up in squares with

Table 1. The location accuracy and per cent of reliable location estimates for 25 types of sounds broadcast and re-recorded with a portable, wireless acoustic location system

Type of Sound[1]	Location accuracy (in m)[2]	Per cent reliable locations[3] (%)
1. Sine wave – modulated	1·0 ± 0·3	93
2. Sine wave – tone	1·6 ± 0·5	19
3. Black-capped chickadee (*Poecile atricapillus*) – song	3·4 ± 1·1	33
4. Black-capped chickadee – call	0·8 ± 0·2	56
5. White-throated sparrow (*Zonotrichia albicollis*) – song	2·4 ± 0·7	37
6. Eastern phoebe (*Sayornis phoebe*) – song	2·7 ± 1·0	41
7. Tree swallow (*Tachycineta bicolor*) – song	1·5 ± 0·3	58
8. Chipping sparrow (*Spizella passerina*) – song	3·1 ± 0·9	48
9. House wren (*Troglodytes aedon*) – song	2·4 ± 0·7	39
10. Song sparrow (*Melospiza melodia*) – song	2·1 ± 0·5	49
11. Carolina wren (*Thryothorus ludovicianus*) – song	1·7 ± 0·4	78
12. Rufous-and-white wren (*Thryothorus rufalbus*) – song	1·1 ± 0·2	37
13. Rufous-naped wren (*Campylorhynchus rufinucha*) – song	0·8 ± 0·2	58
14. Long-tailed manakin (*Chiroxiphia linearis*) – call	1·1 ± 0·3	83
15. Royal flycatcher (*Onychorhynchus mexicanus*) – call	1·9 ± 0·5	49
16. Barred antshrike (*Thamnophilus doliatus*) – call	1·1 ± 0·2	67
17. Pale-billed woodpecker (*Campephilus guatemalensis*) – drum	0·1 ± 0·0	1
18. Pileated woodpecker (*Dryocopus pileatus*) – drum	6·0 ± 4·5	4
19. Eastern red squirrel (*Tamiasciurus hudsonicus*) – call	2·5 ± 0·8	37
20. Richardson's ground squirrel (*Urocitellus richardsonii*) – whistle	3·3 ± 1·1	38
21. Richardson's ground squirrel – chirp	2·4 ± 1·2	46
22. Spider monkey (*Ateles geoffroyi*) – whinny	2·3 ± 0·9	45
23. Grey treefrog (*Hyla versicolor*) – call	1·4 ± 0·4	73
24. Spring peeper (*Pseudacris crucifer*) – call	1·9 ± 0·4	58
25. Yellow toad (*Bufo luetkenii*) – call	1·3 ± 0·3	68

[1]Sound spectrograms for the 25 types of sounds are shown in the supplement in Fig. S1.
[2]Location accuracy is expressed as the mean (±SE) distance between the array-estimated location of the sound source and the global positioning system coordinates of the loudspeaker (in metres).
[3]Per cent of reliable locations shows the per cent of all sounds that were analysed with the localization software that produced a high-quality estimated location (see text for details).

average edge lengths of 25·46 ± 0·61 m for our six '25 m' arrays, and average edge lengths of 48·85 ± 0·83 m for our six '50 m' arrays (means ± SE).

ANALYSIS OF RECORDINGS

To analyse recordings, we modified an existing procedure (Mennill *et al.* 2006) that we have used in prior studies involving cable-based microphone arrays (e.g. Fitzsimmons *et al.* 2008a; Mennill & Vehrencamp 2008; Lapierre, Mennill & MacDougall-Shackleton 2011). In the laboratory, we used Syrinx-PC sound analysis software (J. Burt, Seattle, WA, USA) to combine field recordings from the four recorders into synchronized eight-channel sound files. We then used Syrinx-PC to visualize all eight channels and manually annotate the recordings, highlighting sections of the time and frequency domain that we wished to locate. We then used ArrayGUI software (J. Burt), a program written in MatLab (Mathworks Inc., Natick, MA, USA), to calculate the location of the sound source. This software computes cross-correlation functions for annotated sounds and searches for the best location estimate; it uses an optimization approach involving the Euclidean distances between the sound source and the coordinates of the eight microphones. Full details are given in Mennill *et al.* (2006).

We distinguished 'reliable' from 'unreliable' location estimates based on two indicators that ArrayGUI produces for every annotated sound. (1) ArrayGUI generates a quality index for each location, a positive number that estimates the error of the location. (2) ArrayGUI generates a map of the estimated location surrounded by a probability cloud of alternative, lower-probability location estimates. We considered a location 'reliable' when the quality index was 0·7 or higher and the probability cloud had a small (< 5 m diameter) circular distribution; we considered a location 'unreliable' when the quality index was < 0·7 or the probability cloud was large (> 5 m diameter) or non-circular (see examples in supplement). Previous experience has taught us that location accuracy is better when short sections of recordings (i.e. < 1·0 s) are selected for location. Therefore, we annotated multiple, short sections of each type of sound (see below), each 0·5–1·0 s in length (average length of annotation: 0·77 ± 0·01 s). Given that our goal was to evaluate whether this system can produce reliable estimates of location, we focused only on reliable position estimates.

SAMPLE SIZE

We broadcast 25 sound types at two different locations (inside and outside the area bounded by the recorders) at each of 12 different sites, resulting in a total of 600 unique sound type/location combinations. For each sound type, we attempted to locate 12 annotations inside the array and 12 annotations of the sound outside the array (a total of 7200 attempted annotations). We rejected sounds where there was substantial overlapping background sounds (car traffic passing on nearby roads, airplanes flying overhead, and live birds vocalizing near the recording apparatus), resulting in an average of 10·2 ± 0·07 annotations per species per loudspeaker position (a total of 6085 annotated sounds, i.e. 15·5% of annotations were excluded because of overlapping background sounds). Approximately half of the remaining annotations produced unreliable location estimates and were removed from the data set (i.e. 57·2% of the remaining annotations were excluded because of ArrayGUI indicating unreliable location estimates). We were left with 5·4 ± 0·2 annotations per sound type per loudspeaker position with reliable location estimates (a total of 1964 reliable located sounds; 362 of 600 sound type/location combinations, i.e. 60·3%, had at least one reliable location estimate). We then calculated the average distance between the estimated locations and the GPS position of the loudspeaker for each type of sound. Our final data set consists of 362 averaged position estimates. This process of calculating multiple locations per sound, and then calculating an average position for that sound, would also be effective for ensuring accurate location of animals in the field.

STATISTICAL METHODS

For a given playback stimulus, we defined location accuracy as the average absolute difference between the reliable positions that were estimated by ArrayGUI and the position that was determined by the survey-grade GPS system (following McGregor *et al.* 1997). We then used a linear mixed-effects model to determine which factors affected location accuracy. Habitat type (field vs. forest), microphone density (25 vs. 50 m edges), speaker location (inside vs. outside), and all two-way and three-way interactions were included as fixed factors in the model. Array location (1–12) was included as a subject variable with random effects to account for non-independence among observations. We estimated fixed effects using the restricted maximum likelihood method and modelled the subject effect by assuming a variance components covariance structure. Residuals were not normally distributed, but were corrected by applying a log-10 transformation to localization accuracy. All other model assumptions were satisfied. We evaluate the probability of generating reliable location estimates among the playback sites using Wilcoxon sign-rank tests to compare speaker locations (internal vs. external) and Mann-Whitney U-tests to compare habitat types (forest vs. field) and microphone densities (25 vs. 50 m). We used the Hodges-Lehmann procedure to estimate the median difference between treatments and to calculate the corresponding 95% confidence intervals (Hodges & Lehmann 1963). We considered results to be statistically significant when $P \leq 0{\cdot}05$, and to be statistical trends when $0{\cdot}05 \leq P \leq 0{\cdot}1$. All statistical analyses were conducted in JMP (version 8·0; SAS Institute, Cary, NC, USA) or PASW (v. 18·0; IBM, Armonk, NY, USA). All values are reported as means ± SE. Results of our linear mixed-effects model are presented as the estimated marginal means ± SE of the model.

Results

A portable wireless microphone array, comprising four stereo digital recorders, produced accurate location estimates of loudspeakers broadcasting different types of bird, mammal and frog sounds. The system had an overall location accuracy of 1·87 ± 0·13 m for sounds broadcast inside the array (average across all reliable internal location estimates at 12 different locations). The system had an overall location accuracy of 10·22 ± 1·64 m for sounds broadcast outside the array (average across all reliable external location estimates at 12 different locations).

We found significant variation in location accuracy using a linear mixed-effects model. Location accuracy was not significantly different in open field sites compared with closed forested sites, although there was a non-significant trend for better accuracy at field sites (Fig. 2a; $F_{1,8} = 4{\cdot}4$, $P = 0{\cdot}07$). Location accuracy was significantly better when the loudspeaker broadcasting the sound was located within the area bounded by the four recorders vs. outside the area bounded by the four recorders (Fig. 2b; $F_{1,352} = 114{\cdot}8$, $P < 0{\cdot}0001$). Location accuracy was significantly better when microphones were positioned closer together rather than farther apart (i.e. arrays arranged in a 25 vs. a 50 m square; Fig. 2c; $F_{1,8} = 9{\cdot}1$, $P = 0{\cdot}02$). The model also revealed an interaction between habitat type and the loudspeaker location ($F_{1,352} = 18{\cdot}3$, $P < 0{\cdot}0001$); the location accuracy for loudspeakers outside the area bounded by the arrays was similarly poor for field and forested sites, but the location accuracy inside the area bounded by the arrays at field sites was better than the accuracy inside the area bounded by the arrays at forested sites (Fig. 3). All other two-way interactions and the single three-way interaction were non-significant (all $F < 2{\cdot}3$, all $P > 0{\cdot}17$).

The frequency with which we identified reliable location estimates varied between internal vs. external loudspeaker positions and between field vs. forest sites. On average, 48·8 ± 5·8% of estimated locations were identified as reliable when the loudspeaker was inside the area bounded by the array, significantly more than the 16·3 ± 5·3% identified as reliable when the loudspeaker was outside the area bounded by the array (Wilcoxon sign-rank: $Z = 36$, $P = 0{\cdot}002$, $n = 12$; median difference: 34·5%; confidence interval: 20·1–45·9%). A significantly greater proportion of sounds were identified as reliable at field sites (64·6 ± 4·4%) compared with forest sites (32·9 ± 5·3%; Mann–Whitney: $U = 2{\cdot}8$, $P = 0{\cdot}005$, $n = 12$; median difference: 29·1%; confidence interval: 15·7–48·4%). An equivalent proportion of sounds were identified as reliable when recorders were arranged in a square with 25 m edges (47·4 ± 9·9%) compared with 50 m edges (50·2 ± 7·1%; Mann–Whitney: $U = 0{\cdot}0$, $P = 1{\cdot}0$, $n = 12$; median difference: 0·3%; confidence interval: −30·3% to 24·1%).

The 25 types of sounds showed variation in location accuracy as well as variation in the frequency with which the analysis software generated reliable location estimates (Table 1). Our sample size precludes statistical analyses of these data, but we present them for informational purposes to help guide other researchers. The sonations of woodpeckers produced remarkably few reliable location estimates (sound types 17, 18; Table 1). Tonal sounds with little frequency modulation tended to show poorer location accuracy, fewer reliable location estimates, or both (e.g. sound types 2, 3, 5, 12, 20; Table 1). Sounds consisting of rapidly repeated notes at a high pitch (e.g. sound types 8, 19) presented similar difficulties, whereas sounds consisting of rapidly repeated notes at a low pitch showed better location accuracy with many reliable location estimates (e.g. sound types 16, 23, Table 1). Although the different types of sounds varied in location accuracy, all sounds produced sufficiently accurate and reliable data to be useful in studies of free-living animals, with the exception of

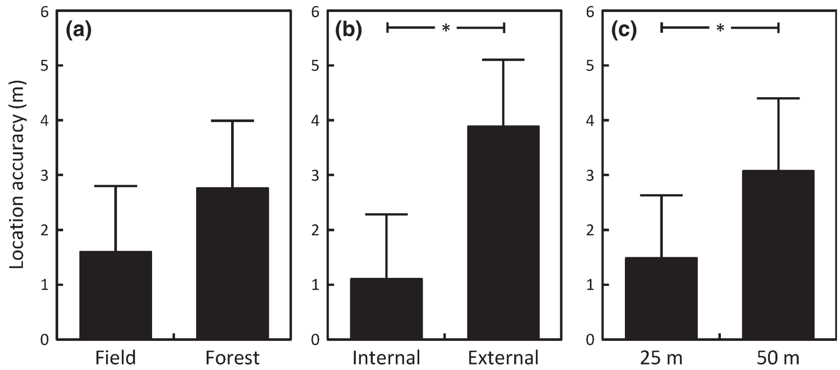

Fig. 2. Location accuracy of a portable wireless microphone array for estimating the position of a loudspeaker broadcasting sounds of birds, mammals and frogs. (a) Location accuracy tended to be better in open field habitat vs. closed forest habitat. (b) Location accuracy was significantly better when sounds were broadcast from loudspeakers inside vs. outside the area bounded by the recorders. (c) Location accuracy was significantly better when the recorders were separated by smaller distances (25 m) vs. larger distances (50 m). Means ± SE shown are reverse log(10) transformed from the estimated marginal means of our linear mixed model. Asterisks indicate statistically significant differences ($P \leq 0{\cdot}05$).

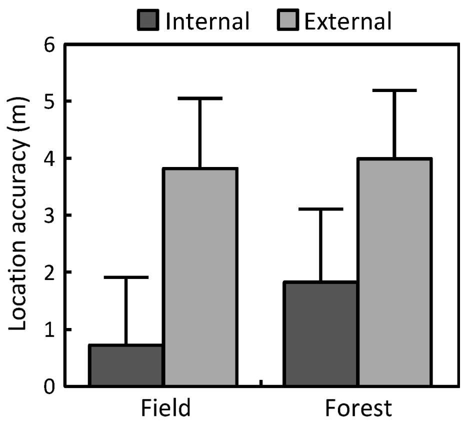

Fig. 3. Location accuracy showed a two-way interaction effect for forest vs. field habitats and internal vs. external broadcast sites. Sounds played inside a microphone array in an open field habitat had better accuracy than sounds played inside an array in a closed forest habitat; sounds played outside of arrays in both habitats were similarly poor. Means ± SE shown are reverse log(10) transformed from the estimated marginal means of our linear mixed model.

woodpecker drumming sonations and pure tone sine waves (Table 1).

Discussion

Our field test of a portable wireless microphone array demonstrates that this new technology can provide accurate estimates of the location of a sound source based on time-of-arrival differences at four autonomous recorders. In a recent review paper on microphone array technology, Blumstein *et al.* (2011) concluded that 'acoustic recording and processing technology has the potential to transform the fields of ecology, behaviour, and conservation biology', but that 'additional work is required to achieve this potential'. As with previous microphone array systems, the system we describe here produces accurate position estimates of free-living animals. The system we describe, however, represents a major advance towards microphone arrays becoming a widespread and field-ready technology; it is a commercially available, inexpensive, portable wireless microphone array that makes acoustic monitoring available to any behavioural researcher, ecologist or conservation biologist. Our findings firmly establish that this technology can provide accurate and reliable estimates of the position of a variety of different types of bird, mammal and frog sounds. Just as radiotelemetry has shed light on animal behaviour and ecology since its development in the 1960s and 1970s (Ropert-Coudert & Wilson 2005), we anticipate that this easy-to-use acoustic monitoring system will provide a wealth of new insights for field researchers.

Our findings show that the location accuracy of sounds varied with several factors. First, location accuracy varied with the density of the microphones used to record sounds. We generated a similar number of reliable location estimates for sounds broadcast within arrays set up in a square with 25 vs. 50 m edges, but the smaller arrays produced location estimates with significantly higher accuracy than the larger arrays. Recognizing that location accuracy improves as a function of microphone density, ecologists and behavioural biologists can select an ideal density of microphone arrays relative to their desired accuracy, trading off the size of the total area to be monitored against the desired accuracy, or increasing the number of microphones to increase the coverage area. For example, cable-based array studies by Paticelli & Krakauer (2010) used 24 microphones close together to distinguish fine-scale movements of multiple male greater sage grouse (*Centrocercus urophasianus*) concurrently calling on the same lek. In contrast, cable-based array studies by Fitzsimmons *et al.* (2008a) and Foote *et al.* (2008) placed 16 microphones far apart to monitor territorial dynamics in breeding neighbourhoods of male black-capped chickadees. Of course, array density is limited by the active space of animal signals, because triangulation is only possible when the sound is detected in three or more channels. Because we were testing the capabilities of this new system to act as a wireless microphone array, we broadcast sounds at high amplitude to ensure they were detected by the recorders.

Future studies should adjust array size according to the active space of the signals under study.

Second, location accuracy varied with the relative position of the sound source. When we broadcast sounds within the area bounded by the four recorders, we generated more reliable location estimates and these estimates had better accuracy compared with sounds played outside the area bounded by the four recorders. This result is expected theoretically and matches previous findings. In the most rigorous test of this idea to date, McGregor *et al.* (1997) broadcast sounds at five 15 m increments stretching outwards from the centre of a four-microphone cable-based array (microphones arranged in a square with 40 m edges). They showed that location error increased dramatically with increasing distance outside of the area bounded by the microphones. The same pattern should hold true with a cable-based or a wireless microphone array. McGregor *et al.*'s (1997) findings, together with our findings, underscore the idea that terrestrial microphone arrays work most effectively for monitoring animals within the area bounded by the microphones.

Third, location accuracy varied between forest and field habitats, although not significantly. There was a non-significant tendency for more accurate location estimates in an open field compared with a closed forest. A significant two-way interaction effect revealed that habitat differences were related to the position of sound sources in forest and field habitats; location accuracy was similarly poor for sound sources outside of the arrays in both forest and field habitats, but location accuracy was better for sound sources within the array in field habitats compared with forest habitats. There are two possible explanations for this non-significant pattern. First, our GPS survey accuracy was higher in the field sites vs. forest sites (see supplement), which likely diminished location accuracy in the forest. Secondly, the scattering, reverberation and sound attenuation in forests may have diminished location accuracy. Previous work also supports this position. McGregor *et al.* (1997) showed that location error was consistently higher in paired comparisons of sounds played back in European woodlands compared with meadows.

Finally, location accuracy varied with the type of sound. Of the 25 types of sounds that we broadcast in each microphone array, we found accuracies that ranged from 0·1 to 6·0 metres inside the area bounded by the recorders. We also found substantial variation in the proportion of annotated sounds that could be reliably localized with our software, ranging from 1% to 93% (Table 1). The sounds with the highest location accuracy represented a broad spectrum of types of sounds, including frequency-modulated sine waves, Carolina wren songs, long-tailed manakin duets, barred antshrike calls, grey treefrog calls, and yellow toad calls. Three sounds were very difficult to locate, with less than 20% of the sounds producing a reliable location estimate: the drumming sonations of two woodpecker species and the unmodulated synthetic sine wave. These sounds appear to be too acoustically simple to triangulate based on time-of-arrival differences. McGregor *et al.* (1997) compared location accuracy across four bird vocalizations and found statistically similar location accuracies across the four species, three of which were frequency-modulated vocalizations like many of the bird sounds we tested here, and one of which was a pulsating call similar to the frog sounds we tested here.

The accuracy we achieved with a wireless microphone array falls in line with the accuracy of previous cable-based microphone systems. For example, Mennill *et al.* (2006) achieved an accuracy of 2·8 ± 0·3 m, monitoring the large territories of Rufous-and-white Wrens in a Neotropical forest with an eight-microphone cable array with inter-microphone distances of 75 m. Bower & Clark (2005) achieved an accuracy of 0·8 ± 0·3 m for birds near the centre of their array, monitoring the small territories of Song Sparrows in a field using a four-microphone cable array with inter-microphone distances of 40 m. Paticelli & Krakauer (2010) achieved an accuracy of 0·4 ± 0·2 m for sounds near the centre of their array, monitoring the open habitat of a Greater Sage Grouse lek with a 24-microphone cable array with small inter-microphone distances of 15·8 ± 0·6 m (G. Patricelli & A. Krakauer, personal communication).

Several sources of error may have contributed to the accuracy measurements we report here. Most importantly, our GPS measurements of microphone positions had an error of 1·12 m, likely contributing a large fraction of the error in our overall position accuracy of 1·86 m. There are several methods that can be used to survey microphone positions, some of which may lead to lower microphone measurement error, and consequently higher localization accuracy with microphone array recordings. Direct surveys with line-of-sight surveying equipment or measuring tape may be ideal in some situations (e.g. densely concentrated arrays in open habitats, such as our six field locations where there was line-of-sight contact between the recorders; Fig. 1) but may be impossible in other situations (e.g. sparser arrays or arrays in dense forests, such as our six forest locations where there was generally not line-of-sight contact between the recorders; Fig. 1). Sampling microphone positions with a survey-grade GPS for extended periods may lead to higher microphone position estimation; we sampled microphone positions for only 20–40 min. An intriguing possibility for inexpensive surveys of microphone positions involves handheld GPS units; although any one point has low accuracy, handheld GPS units could be left collecting data at a fixed position for long periods (hours–days) to calculate a more precise average position over a long sampling period. We tested this approach (see supplement) and found that this approach still produces reasonable location estimates, but with lower accuracy than a survey-grade GPS. New techniques such as acoustic self-surveys (see Collier, Kirschel & &Taylor 2010) present new, alternative survey techniques. The remaining error in our study, beyond that because of microphone position estimates, probably arose due to attenuation and reverberation as sounds transmitted from the loudspeaker to the microphones, subtle variations in topography (the software we used assumes that sounds travel in a two-dimensional plane), or inaccuracies in the position estimation software.

When will microphone arrays provide a useful monitoring tool for studies of animal ecology, evolution and behaviour?

Microphone arrays will be most useful for studying highly acoustic animals, such as animals that produce loud territorial signals, frequent mate attraction signals, or contact calls and alarm calls. To date, microphone arrays have been used for many purposes (reviewed in Blumstein *et al.* 2011), including monitoring patterns of animal territoriality (e.g. Kirschel *et al.* 2011; Osmun & Mennill 2011), studying network-based signalling behaviours (e.g. Foote *et al.* 2008), observing the movements of countersinging animals (e.g. Fitzsimmons *et al.* 2008b), testing the directionality of animal signals (Patricelli, Dantzker & Bradbury 2007), or surveying large areas to assess the presence of rare animals (e.g. Hill *et al.* 2006; Baldo & Mennill 2011). Microphone arrays can provide insight into behaviours that could not be studied otherwise, such as behaviour evident in environments where visual information is limited, like nocturnal animals or animals inhabiting dense vegetation (Blumstein *et al.* 2011). The system we tested here is especially useful given its relative ease of operation. Previously, cable-based arrays required tremendous effort in the field. For example, the eight-microphone cable array used by Mennill *et al.* (2006) took a team of four researchers *c.* 4 h to set up and take down; the sixteen-channel cable array used by Foote *et al.* (2008) and Lapierre, Mennill & MacDougall-Shackleton (2011) took a team of eight researchers *c.* 5 h to set up and take down (see supplement). In contrast, four people were able to set up and take down the four-recorder array we used here six times in a single day. Additionally, because the digital recorders in this system are programmable, they can be set to turn on and off at specific times, minimizing the necessity for human input (and human influence on the recorded animals) after the initial setup.

In some situations, microphone arrays are unlikely to provide a useful monitoring tool. Acoustic monitoring requires that the study animals produce sound. Therefore, animals that are quiet, or animal behaviours that occur in silence, cannot be monitored with microphone arrays. For tracking individuals, sounds must have individually distinctive acoustic signatures, a feature that appears to be quite common across diverse animals (Mennill 2011). For sounds that are not individually distinctive, other research technologies can be combined with microphone array recordings, such as video recordings time-synchronized with microphone array recordings (e.g. Patricelli, Dantzker & Bradbury 2007). Excessive background noise serves as an impediment to microphone arrays whenever this noise overlaps both the time and frequency domains of the signals used to calculate the animal's location. Animals that move over very large areas will be expensive to monitor with a microphone array, because many microphones will be required to monitor their movement activities and behaviours. Nevertheless, microphone arrays have been used to monitor large breeding territories of birds (e.g. Mennill & Vehrencamp 2008) or entire neighbourhoods of breeding birds (e.g. Fitzsimmons *et al.* 2008a). In addition, our analyses reveal that certain types of sounds, including the extremely simple drumming sonations of woodpeckers and pure tone sine waves, are less effectively monitored than other types of sounds. Consequently, pilot studies with careful attention to the active space of the signals being studied, possibly using a playback approach as used here, will be valuable in future investigations.

In conclusion, our field test of a new, portable, wireless microphone array with integrated GPS time synchronization reveals that this system provides accurate measurements of the position of a sound source, supporting the idea that this is a useful new research technology for the spatial monitoring of animals. Microphone arrays have many advantages over other tracking technologies, and the advent of this user-friendly system stands to enhance ecological and behavioural studies for a broad diversity of researchers.

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Conflict of interest

The authors declare that they have no conflict of interest, financial or otherwise, and that they have no relationship with the company Wildlife Acoustics beyond having purchased their equipment for bioacoustic research.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details of the microphone arrays and additional analyses.

Fig. S1. Sound spectrograms showing examples of the sounds played back and recorded with a portable, wireless acoustic location system.

Fig. S2. Examples of the graphical output of ArrayGUI triangulation software, showing both reliable and unreliable location estimates.

Fig. S3. Photographs of GPS-enabled Song Meters used as a wireless microphone array.

Fig. S4. Maps of loudspeaker and microphone positions for the 12 deployments of the wireless microphone array.

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