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A Method for Estimating Songbird Abundance with Drones

Andrew M. Wilson
Gettysburg College

Darren Glass
Gettysburg College

Marisa A. Immordino
Gettysburg College

Precious S. Ozoh
Gettysburg College

Lauren Sherman
Gettysburg College

See next page for additional authors

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A Method for Estimating Songbird Abundance with Drones

Abstract

Using drones to conduct airborne bioacoustics surveys is a potentially useful new way to estimate the abundance of vocal bird species. Here we show that by using two audio recorders suspended from a quadcopter drone it is possible to estimate distances to birds with precision. In an experimental test, the mean error of our estimated distances to a broadcast song across 11 points between 0 and 100 m away was just 3.47 m. In field tests, we compared 1 min airborne counts with 5 min terrestrial counts at 34 count locations. We found that the airborne counts yielded similar data to the terrestrial point counts for most of the 10 songbird species included in our analysis, and that the effective detection radii were also similar. However, airborne counts significantly under-detected the Northern Cardinal (χ29 = 22.8, post-hoc test *P* = 0.007), which we attribute to a behavioral response to the drone. Airborne counts work best for species that vocalize close to the ground and have high-frequency-range songs. Under those circumstances, airborne bioacoustics could have several advantages over ground-based surveys, including increased precision, increased repeatability, and easier access to difficult terrain. Further, we show that it is possible to do rapid surveys using airborne techniques, which could lead to the development of much more efficient survey protocols than are possible using traditional survey techniques.

Keywords

distance sampling, drones, bioacoustics, time difference of arrival, songbird, marshbirds

Disciplines

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Authors

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ARTICLE

A method for estimating songbird abundance with drones

Andrew M. Wilson, Darren B. Glass, Marisa A. Immordino, Precious S. Ozoh, Lauren B. Sherman, and McKenzie D. Somers

Abstract: Using drones to conduct airborne bioacoustics surveys is a potentially useful new way to estimate the abundance of vocal bird species. Here we show that by using two audio recorders suspended from a quadcopter drone it is possible to estimate distances to birds with precision. In an experimental test, the mean error of our estimated distances to a broadcast song across 11 points between 0 and 100 m away was just 3.47 m. In field tests, we compared 1 min airborne counts with 5 min terrestrial counts at 34 count locations. We found that the airborne counts yielded similar data to the terrestrial point counts for most of the 10 songbird species included in our analysis, and that the effective detection radii were also similar. However, airborne counts significantly under-detected the Northern Cardinal ($\chi^2_9 = 22.8$, post-hoc test $P = 0.007$), which we attribute to a behavioral response to the drone. Airborne counts work best for species that vocalize close to the ground and have high-frequency-range songs. Under those circumstances, airborne bioacoustics could have several advantages over ground-based surveys, including increased precision, increased repeatability, and easier access to difficult terrain. Further, we show that it is possible to do rapid surveys using airborne techniques, which could lead to the development of much more efficient survey protocols than are possible using traditional survey techniques.

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Résumé : L'utilisation de drones pour effectuer des levés aériens bioacoustiques est une nouvelle façon potentiellement utile pour estimer l'abondance des espèces d'oiseaux vocaux. Nous montrons ici qu'en utilisant deux enregistreurs audio suspendus à un drone quadricoptère, il est possible d'estimer les distances des oiseaux avec précision. Dans un essai expérimental, l'erreur moyenne de nos distances estimées par rapport à une chanson diffusée à 11 points entre 0 et 100 m était de seulement 3,47 m. Dans le cadre d'essais sur le terrain, nous avons comparé des dénombrements aériens de 1 min à des dénombrements terrestres de 5 min à 34 emplacements de dénombrements. Nous avons constaté que les dénombrements aériens donnaient des données semblables aux dénombrements ponctuels terrestres pour la plupart des 10 espèces d'oiseaux chanteurs comprises dans notre analyse, et que les rayons de détection efficaces étaient également semblables. Cependant, dans les dénombrements aériens le cardinal rouge a été sous-détecté de façon significative ($\text{chi}^2_9 = 22{,}8$, test post-hoc $P = 0{,}007$), phénomène que nous attribuons à une réponse comportementale au drone. Les dénombrements aériens fonctionnent mieux pour les espèces qui vocalisent près du sol et qui ont des chants à haute fréquence. Dans ces circonstances, la

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A.M. Wilson, M.A. Immordino, P.S. Ozoh, L.B. Sherman, and M.D. Somers. Environmental Studies Department, Gettysburg College, PA 17325, USA.
D.B. Glass. Mathematics Department, Gettysburg College, PA, 17325, USA.
Corresponding author: Andrew M. Wilson (e-mail: awilson@gettysburg.edu).

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bioacoustique aérienne pourrait présenter plusieurs avantages par rapport aux levés au sol, notamment une précision accrue, une meilleure répétabilité et un accès plus facile en terrain difficile. De plus, nous montrons qu'il est possible de faire des levés expédiés en utilisant des techniques aériennes, ce qui pourrait mener à l'élaboration de protocoles de levé beaucoup plus efficaces que les techniques de levé traditionnelles. [Traduit par la Rédaction]

Mots-clés : échantillonnage à distance, drones, bioacoustique, différence de temps à l'arrivée, oiseau chanteur.

Introduction

Drones are now widely used in ecology to locate, count, or track organisms, and to map resources (Nowak et al. 2019). Most studies that have used drones to count birds have focused on larger species such as seabirds (Hodgson et al. 2018) and waterbirds (Afán et al. 2018; Pöysä et al. 2018) which are more likely to be detected in aerial imagery. The use of drones for bioacoustics surveys is less well-established, but initial studies have shown promising results for songbirds (Wilson et al. 2017) and bats (Fu et al. 2018; Kloepper and Kinniry 2018; August and Moore 2019). Drone-based bioacoustic studies have the potential to harness the advantages of bioacoustic techniques using autonomous recording units (ARUs) (Darras et al. 2018), together with increased mobility and ease of access in difficult terrain. Advantages of ARUs include obtaining a permanent record that can be analyzed or reanalyzed at a future date, reducing observer bias, and eliminating observer disturbance at the time of monitoring (Campbell and Francis 2013; Shonfield and Bayne 2017). Increased access could reduce habitat biases that are prevalent in bird survey data (Betts et al. 2007; Leitão et al. 2011). Further, while it is true that drones can cause disturbance to wildlife (Mulero-Pázmány et al. 2017), drones also have the potential to reduce disturbance caused by field biologists wandering through sensitive habitats (Christie et al. 2016; Borrelle and Fletcher 2017).

A previous study found that using inexpensive recording devices suspended from quadcopter drones to count songbirds produced counts that were broadly similar to those obtained by typical ground-based point count protocols (Wilson et al. 2017). However, the aim of many bird survey techniques is to estimate bird abundance, usually standardized to a given number of individuals per unit of area (Bibby et al. 2000). Such standardization allows more direct comparison across species, locations, habitats, or time (Gregory et al. 2004). For airborne bioacoustic techniques to provide a useful alternative to ground-based survey methods (e.g., point counts, transects, territory mapping), the ability to estimate abundance within a given spatial area is highly desirable.

Here, we develop methods that allow for an estimate of radial distances to vocalizing birds from a drone using two small inexpensive audio recorders, and a prosumer-grade quadcopter. We use the time difference of arrival technique (TDoA) (Mennill et al. 2006) to estimate distances to vocalizing birds on a horizontal plane either at ground level, or at given heights above the ground. Estimation of distances to birds would allow the application of distance sampling techniques (Buckland et al. 2005) to estimate population densities. We show an experimental proof of concept and a field application, where we compare density estimates from airborne counts with those of traditional terrestrial point counts and territory or spot-mapping (Bibby et al. 2000).

Methods

Equipment

We used a DJI Mavic Pro quadcopter programmed to fly missions autonomously using the Litchi app (VC Technology Ltd.) for iOS on an iPhone SE. We used aftermarket "low-noise" DJI propellers, which reduce drone noise by ~4 dB (Valle and Scarton 2019). Our recording devices were lightweight and inexpensive Zoom H1 Handy recorders, which weigh just 95 g, including battery, microSD card, and, importantly, a windshield. It should be noted that this model of audio recorder was also chosen because of its cardioid pickup pattern, which reduces sound pickup from the rear of the microphones (i.e., in the direction of the drone when the microphone is directed at the ground). We attached the recorders to the drone using a system of fishing line, zip ties, and small carabiners.

Measuring distances

To enable the use of TDoA to estimate distances, the recorders had to be sufficiently far apart that time differences were measurable, and they had to be suspended below the drone to reduce excessive drone noise on the recordings. Previous tests showed that suspending recorders up to 15 m below the drone was manageable in the field, where great care is required to avoid entangling the fishing line on the drone or vegetation. Our system placed one recorder 7.5 m below the drone, and the second recorder 15 m below the drone. To calculate TDoA, the two recorders needed to be time-synchronized. We did this manually by placing the microphones of the two recorders ~2 cm apart and playing a tree cricket (*Oecanthus* sp.) recording from an iPhone placed between them, thereby allowing the two recordings to be clipped to the same time point (to <1 ms accuracy) in Audacity (Audacity Team 2019).

We then merged the two recordings in Audacity to make a single stereo audio track, which included time-differences in sound sources. TDoAs were measured manually from spectrograms (Hanning window with 512 samples and 89% overlap) in program Raven Pro 1.5 (Bioacoustics Research Program 2014).

With TDoAs measured we were able to apply the Pythagorean Theorem to calculate the radial distance from the drone location to the sound source (x), in meters across the ground, using the following formula:

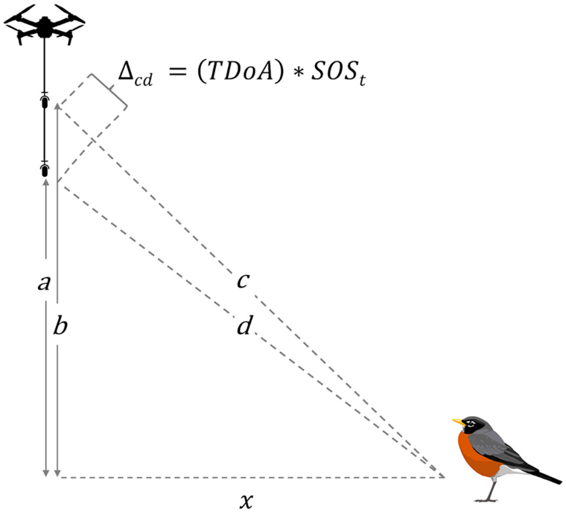
$$(1)\quad x = \frac{\sqrt{a^4 + b^4 + \Delta^4 - 2a^2b^2 - 2\,b^2\Delta^2 - 2a^2\Delta^2}}{2\Delta}$$

where a is the altitude of the bottom recorder (in meters), b is the altitude of the top recorder (meters), and Δ (Δ_{cd} in Fig. 1) is the estimated difference in the Euclidean distance from the recorders to the sound source ($c - d$). Δ is calculated by multiplying the TDoA by the speed of sound at a given air temperature ($\mathrm{SOS_t}$). Hence, for any given TDoA, we could estimate the radial distance (x) between the point under the drone and a sound source.

Because we were only able to measure time difference to whole milliseconds (the measurement limit in Raven Pro), we must assume that the actual time difference was in a range of the measured TDoA ± 0.5 ms. Hence, we calculate the distance of the bird to be in a range between a lower (x_{l}) and upper (x_{u}) limits, and assuming that birds are randomly distributed within the band between those distances, a single estimate can be derived by estimating the median distance between the two:

$$(2)\quad x_{\mathrm{m}} = \sqrt{\frac{(\pi x_{\mathrm{l}}^2) + [(\pi x_{\mathrm{u}}^2 - \pi x_{\mathrm{l}}^2)/2]}{\pi}}$$

Fig. 1. Application of the Pythagorean theorem to estimate radial distance from the location under a drone to a bird (x), from known heights of two recorders from the ground (a and b), and time difference of arrival (TDoA) of a bird vocalization at recorders, based on speed of sound at a given air temperature (SOS_t). Δ_{cd} is $c - d$, where c and d are unknown distances, to be estimated using eq. 1.



x_m is therefore the estimated radial distance to the bird, which can used in distance sampling, or fixed radius distance abundance estimation from airborne point counts.

We used MS Excel to estimate radial distances to the sound source based on the above formulae. A spreadsheet that allows the user to estimate distance from measured TDoAs based on inputted air temperature (t) and recorder heights (a, b) is provided as Supplementary Data[1]. It is important to note that eq. 1 assumes that the sound source is on a horizontal plane at ground level. However, this assumption can be changed, for example, it can be assumed that a certain species typically sings from vegetation 4 m above ground-level, hence, heights a and b would be reduced by 4 m. Height of bird from the ground is therefore included in the spreadsheet as an additional parameter, that can be varied according to species and habitat. To test how sensitive the technique would be to uncertainty in estimating the height of birds from the ground we assumed an air temperature of 20 °C and recorder heights at 40 m and 47.5 m, and varied the height of the bird from the ground parameter from 0 m to 10 m. We also used the spreadsheet to evaluate the effects of using different distances between the two recorders on TDoAs, which may be varied according to the study species, habitats, and research needs.

Experimental test

To test the method we broadcast a bird song recording (American Robin *Turdus migratorius* (Linnaeus, 1766); source: Macauley Library (2014)) at 90 dB at 1 m (measured using an Extech 407730 sound level meter) from paired Aomais Go speakers, placed on the ground. We then flew a mission where the drone hovered for 1 min at an altitude of 55 m in 10 m increments along a transect, 0 m to 100 m across the ground from the broadcast speakers. We measured TDoA for the first complete and clean (with no overlapping background noise) robin song recorded at each of the 11 distances. The experiment was conducted on

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[1] Supplementary data are available with the article at https://doi.org/10.1139/dsa-2022-0015.

sports fields at Gettysburg College, PA, where background anthropogenic and biological noise was minimal. The temperature was 21 °C and winds were light.

Field test

With proof of concept established in our experimental test, we tested the method in a field study, where we compared it to two traditional songbird survey techniques: point counts, and territory or spot mapping (Bibby et al. 2000). These survey methods are henceforth referred to as "terrestrial counts" and "mapping", and surveys using the drone are referred to as "airborne counts". The study was conducted in a section of State Game Lands 249, Adams County, Pennsylvania; 140 ha of grassland and shrubby fields, with some small woodlots and wetlands (39.9374°N, –77.1774°W). Two tracks provide vehicular access to the site, but otherwise, the area has little human disturbance. Recreational drone flying is not permitted at the site. We focused our surveys on 10 songbird species known to be present in sufficient numbers (>30 individuals at the site): the Willow Flycatcher (*Empidonax traillii* (Audubon, 1828)), House Wren (*Troglodytes aedon* Vieillot, 1809), American Robin (*Turdus migratorius*), Field Sparrow (*Spizella pusilla* (A. Wilson, 1810)), Song Sparrow (*Melospiza melodia* (A. Wilson, 1810)), Eastern Towhee (*Pipilo erythrophthalmus* (Linnaeus, 1758)), Yellow Warbler (*Setophaga petechia* (Linnaeus, 1766)), Common Yellowthroat (*Geothlypis trichas* (Linnaeus, 1766)), Northern Cardinal (*Cardinalis cardinalis* (Linnaeus, 1758)), and Indigo Bunting (*Passerina cyanea* (Linnaeus, 1766)).

For the airborne and terrestrial point counts we surveyed 34 predetermined locations evenly spaced on a 200 m grid (data from a 35th point were dropped due to excessive wind noise on drone recordings). Terrestrial and airborne counts were conducted on the same day, between 31 May and 6 June 2019, and between 0600 and 0900. The airborne counts were conducted first at 16 points, and terrestrial counts first at 18, ensuring no systematic bias due to time of the morning. Weather conditions were suitable for both count methods (i.e., no rain, and wind less than a force 4 (24 km/h) on the Beaufort scale (NOAA)). Terrestrial counts were of 5 min duration, with observations categorized by minute of first detection. Estimates of distances to birds seen or heard were aided by a laser range finder. Bird detections were categorized as singing, calling, or visual only. Terrestrial counts were all conducted by a single very experienced point count surveyor (A.M.W.).

For airborne counts, we hovered the drone at 55 m above ground-level for 1 min. As in the experimental test, the two recorders were suspended 7.5and 15 m below the drone, hence, the recorders were 40 and 47.5 m above ground-level, respectively. The drone was launched from at least 100 m away from the count locations and approached the count location at 55 m altitude. We conducted between two and five adjacent airborne counts in succession, which was readily done on a single battery. Based on personal observation and understanding of the habitat at our site, we estimated that most of the singing birds were in low vegetation. In our distance calculations we estimated that Willow Flycatcher, Field Sparrow, Song Sparrow, and Common Yellowthroat were 2 m above ground level; House Wren and Yellow Warbler 3 m; Eastern Towhee 4 m, American Robin and Northern Cardinal 5 m; and Indigo Bunting 6 m. In program Raven we labeled each bird detection on the airborne count recordings with a unique code so that we could track song output and possible movement for each individual, based on song-bout spacing, unique song patterns, apparent volume (from spectrograms) and calculated distances. We found very few instances of ambiguity when it came to identifying individual birds, even for the most abundant species.

To provide context for our point count data we conducted a territory mapping study of the entire site, visiting all areas on at least four occasions between mid-May and early July 2019. While the optimal number of visits for territory mapping is 10, a minimum of four will suffice for studies that focus on fewer species (Gregory et al. 2004). To ensure the entire study area was surveyed as quickly as possible, teams of researchers surveyed different sections of the study site simultaneously. We estimated the number of territories using standard protocols (Bibby et al. 2000), with a lower estimate where territory clusters needed observations on two visits at least 10 days apart, and a higher estimate where single visit detections were also included as territories.

Analytical methods

We estimated the density of singing birds from the terrestrial and airborne count data using the R package *Rdistance* (Miller et al. 2019). Half-normal, hazard rate, and negative exponential detection functions were fitted and the best model was selected using AIC. For the purposes of this experiment, detections were truncated at 100 m to avoid more distant detections from overly influencing detection models (Buckland et al. 2001; Miller et al. 2019), and due to concerns about the accuracy of distance estimation beyond that distance (Buckland et al. 2005). Density estimates were compared with the estimated number of territories to determine whether there was broad agreement in abundance estimates among the three bird survey techniques. Calculated effective detection radii — the distance at which as many birds beyond are detected as are missed — for terrestrial and airborne counts indicate whether the airborne counts are able to capture song detections over a similar area to a fieldworker on the ground. We tested whether there were differences in the species make-up of detections between airborne counts and 5 min terrestrial counts using chi-square tests and post hoc tests of residuals with Bonferroni adjustment, using R package *chisq.posthoc.test* (Ebbert 2019)

Results

Experimental results

Our experimental test showed that we were able to estimate the distance to the American Robin song broadcast with a high degree of accuracy; the mean absolute error was 3.47 m, which resulted in a mean overestimate of distances of 1.9 m (Fig. 2).

We found that varying the distance between the two recorders affects the precision with which TDoAs can be measured. We note that the TDoA is maximized when the sound is directly below the drone, in which case the TDoA is given by SOS $\times (b - a)$. In particular, if the recorders were 5 m apart, the maximum feasible TDoA at an air temperature of 20 °C is 15 ms, compared with 22 ms at 7.5 m, and 29 ms at 10 m. More generally, one can directly show from the formula that as the distance between recorders is increased the formula for x becomes less sensitive to errors in the measured value of TDoA (range bars in Fig. 3A).

The same computation shows that raising the height of the drone, while keeping the distance between the two recorders constant, will make the formula less sensitive to error calculations. Uncertainty with respect to the height of birds off the ground will have comparatively little effect on distance estimation for birds close to the drone, but estimates would be increasingly uncertain at greater distance (Fig. 3B). For example, if a TDoA of 10 ms is measured, the estimated distance to a bird on the ground is 85.3 m, compared with 75.6 m if it is assumed the bird is 5 m off the ground, and 65.8 m if the bird is 10 m off the ground.

Field test

We detected 603 song bouts across our 10 target species on the 34 airborne counts; of which 369 song bouts were estimated to be by birds within a 100 m radius of the point location (Table 1). We found that song output was consistent throughout the 1 min airborne counts, with no indication of a curtailment of song activity in the drone's presence

Fig. 2. Actual versus estimated radial distances from a location under a drone flown at 55 m, to a broadcast American Robin song at ground level. Error bars encompass a potential range of estimates, because time differences are only measurable to the nearest milli-second, and the actual TDoA could be ±0.5 ms.

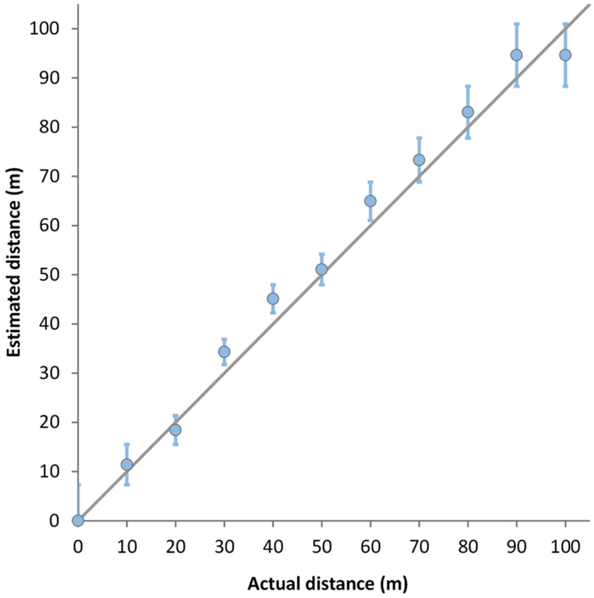
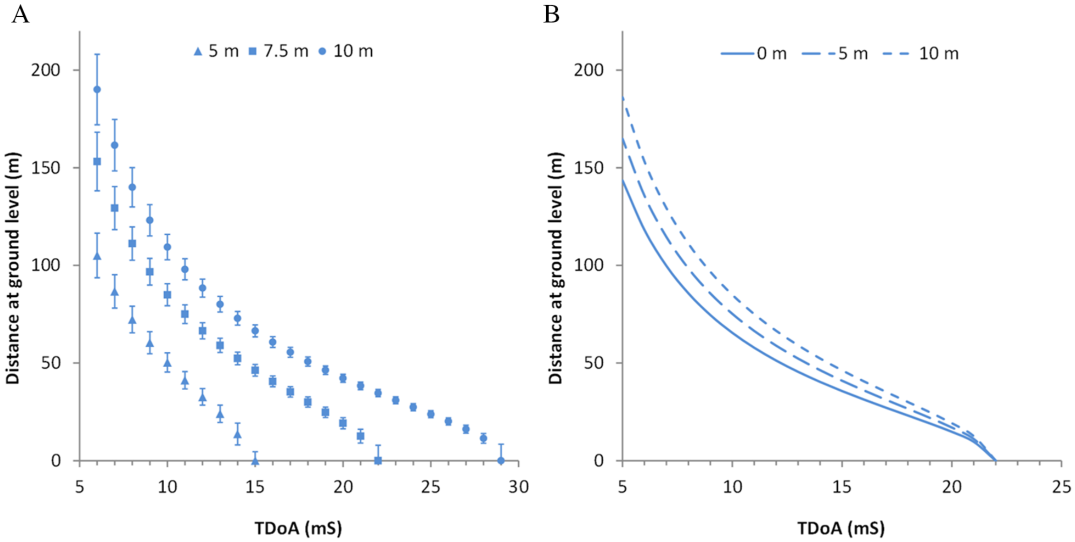


Fig. 3. (A) Hypothetical radial distance estimates for measured TDoAs for three different distances between two recorders, assuming an air temperature of 20 °C and drone altitude of 55 m. (B) Hypothetical estimated radial distances if it is assumed that a sound source is at three different heights off the ground.



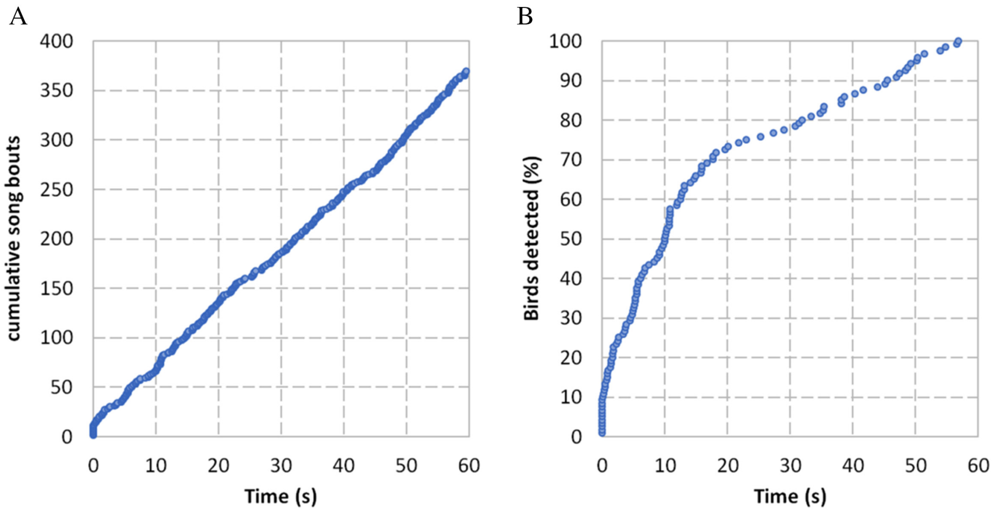
(Fig. 4A). We attributed the 369 song bouts to 120 different individuals (Table 1), of which 73% were detected within the first 20 s (Fig. 4B).

The overall patterns of detections from airborne counts were similar to those from terrestrial counts (Fig. 5); there was evidence of declining detection rates at distances of

Table 1. Estimated number of territories and point count detections (of singing birds) within 100 m of the point location, for terrestrial counts and airborne counts, 136 ha study area of State Game Lands 249, Pennsylvania, in 2019.

	Mapping (territories)		Point counts (singing birds)			
			Terrestrial			
Species	Min.	Max.	1 min	5 min	Airborne	Song bouts on airborne count
Willow Flycatcher	46	50	6	7	10	22
House Wren	23	40	6	10	11	31
American Robin	32	40	4	10	9	52
Field Sparrow	74	85	24	38	43	127
Song Sparrow	52	60	6	15	14	38
Common Yellowthroat	44	54	6	11	8	20
Yellow Warbler	49	57	11	23	8	31
Eastern Towhee	21	25	13	24	5	8
Northern Cardinal	41	46	13	25	2	13
Indigo Bunting	30	34	10	17	10	27
All ten species	412	491	99	180	120	369

Fig. 4. (A) Cumulative detections of song bouts from airborne counts, across all 34 counts. (B) Cumulative percentage of detections of individual birds from airborne counts across all 34 counts.



greater than 60 m on both point count surveys. Total song detections were higher on airborne counts than in the first minute of terrestrial counts, but lower than the number of individuals detected in 5 min (Table 1). Distance sampling derived density estimates for the two most numerous species — Field Sparrow and Song Sparrow — were higher on airborne counts than during the first minute of terrestrial counts, and very comparable with those of 5 min point counts (Fig. 6). Density estimates of singing males were lower for both point count methods than the estimated densities of territories derived from mapping (Fig. 6). The effective detection radii for Field and Song Sparrows were similar for the airborne counts and terrestrial counts (Table 2).

For six of the 10 species the 1 min airborne counts picked up more singing birds than the first minute of the terrestrial count, and, for three of the six, the 1 min airborne counts

Fig. 5. Terrestrial and airborne detections of singing birds of 10 species, across 34 point counts, by distance from point count locations.

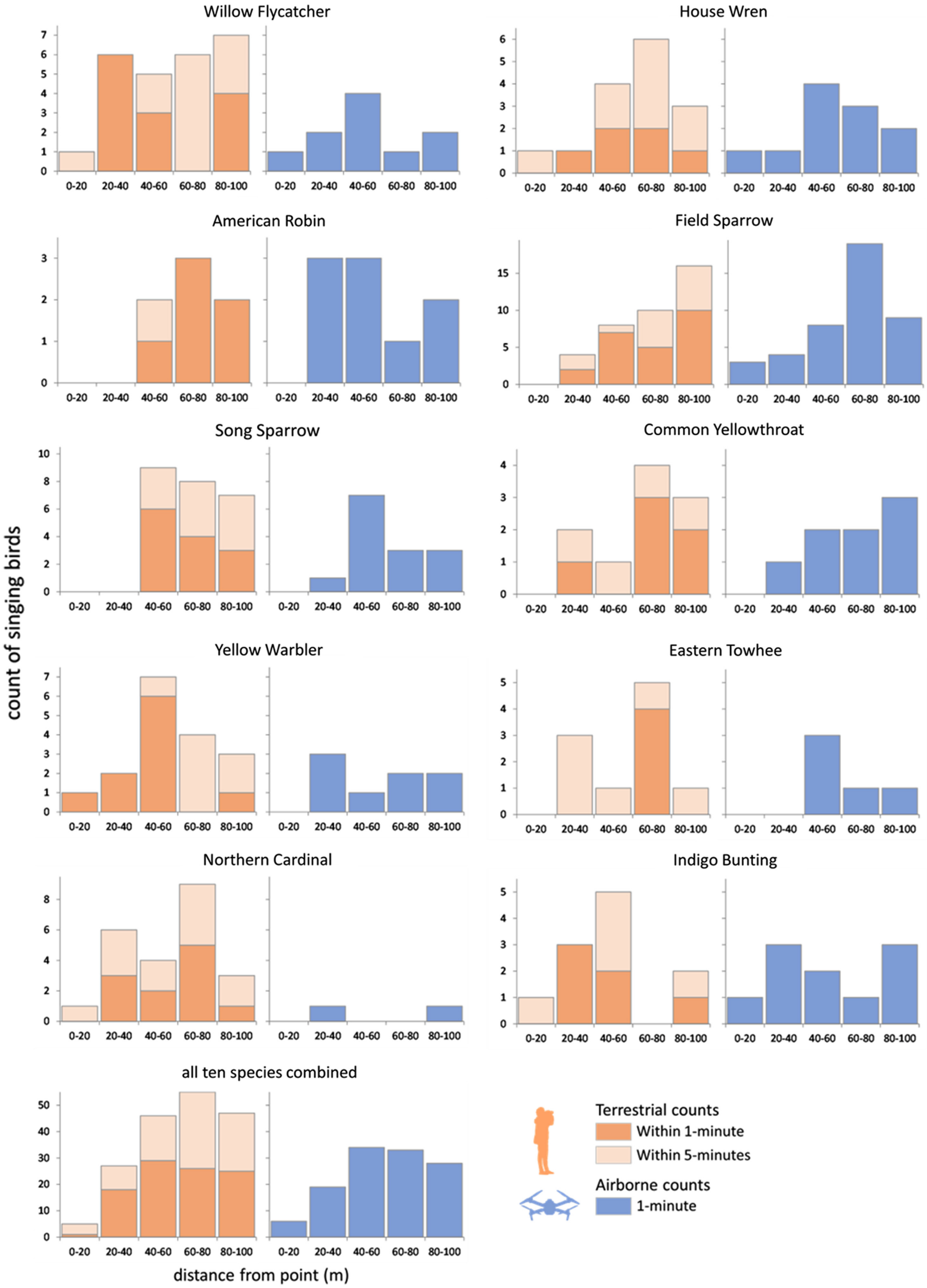
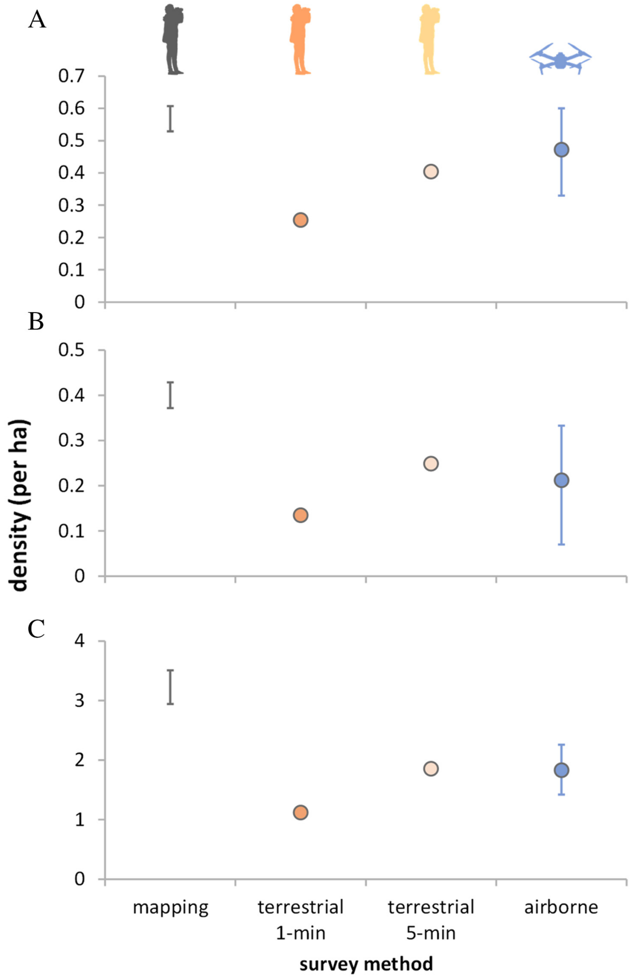


Fig. 6. Comparison of density estimates from mapping (territories) and terrestrial and airborne counts (singing birds) for (A) Field Sparrow, (B) Song Sparrow, and (C) all ten species combined. Error bars for mapping show the low and high estimates of territories. Error bars for estimates from airborne counts are 95% CI. CIs were not calculable for density estimates derived from count estimates.



were higher than after the full 5 min of terrestrial counts (Table 1; Fig. 5). There was a significant difference in the species composition of detections from airborne counts compared to 5 min terrestrial counts ($\chi^2_{[9]} = 22.8$, $P = 0.007$), with relatively more Field Sparrows (post hoc tests, $P = 0.045$), and fewer Northern Cardinals (post hoc tests, $P = 0.016$) on airborne counts.

Discussion

Our initial tests provided proof of concept that it is possible to estimate distances to vocalizing birds with a pair of synchronized recorders suspended from a drone. Our estimates of error are very modest compared to the average observer error of 19 m estimated in a field study of audio broadcast song and calls (Alldredge et al. 2007), but we acknowledge that our experimental test was under controlled conditions.

Table 2. Estimated detection radii (meters), calculated using R package *Rdistance*.

	Terrestrial	Airborne
Field Sparrow	78.3	92.4
Song Sparrow	90.1	90.0
All 10 species combined	95.0	90.0

Our field test showed that airborne counts were able to produce data suitable for density estimation that was similar, overall, to that obtained by an experienced fieldworker conducting ground-based point counts. It is important to note that some species appear to have been under-detected on airborne counts, notably the Northern Cardinal. Although our data did not show a decline in song output during the 1 min drone flights, it is possible that some individual birds stopped singing as the drone approached. Interestingly, in a previous study of seven songbird species, the Northern Cardinal was found to be the most sensitive to drone noise (Wilson et al. 2022). However, as drone technology has matured, small quadcopters have become steadily quieter, and smaller, and further technical developments (Hioka et al. 2019) could result in drones that are quiet enough to greatly reduce, if not eliminate, noise disturbance effects. Still, the effects of drone noise, however quiet, merit further study and we recommend more experiments to compare drone-based bird detection with terrestrial ARUs, and standard point count surveys.

That our density estimates from point counts were very different to those derived from territory mapping was not a surprise; differences, which appear to vary by species, habitat, and specific protocols, have been widely reported (Shankar Raman 2003; Howell et al. 2004; Newell et al. 2013). The advantages of point counts (either terrestrial or airborne) over mapping is that they do not require access to an entire study area (Gregory et al. 2004), and they are generally much more time-efficient. Even though our mapping study was scaled back to just four visits to each part of the study area, it required 66 h of fieldwork, and many hours of collating and analyzing maps.

Our point count density estimates are also lower than mapping estimates because they do not include any estimation of availability of birds for detection (Farnsworth et al. 2002), which is now standard practice in many studies that use bird point count surveys. Availability for detection techniques allow estimation of the proportion of birds missed because they were silent or not visible for the duration of a count. Point count survey protocols often include noting the time of first detection for each bird seen or heard, typically in 1 min or 2 min time bands. Estimating availability for detection could be included in analysis of airborne bioacoustic bird data, although sample sizes were too small (Sólymos et al. 2018) to allow for this in our feasibility study. The fact that audio recordings are available for meticulous inspection means that the time of first detection could be measured with high precision (Fig. 4), rather than within discrete time bands often employed by terrestrial point count protocols (Farnsworth et al. 2002; Alldredge et al. 2007). Binning time of first detection into time bands is an additional source of observer error due to assignment of detections to the wrong time band (Simons et al. 2009). Incorporating an estimate of availability for detection into our technique will be the focus of future studies.

There are several potential sources of error in our airborne count distance estimates. Error would be introduced if the actual altitude of the hovering drone from ground-level diverged from the intended altitude. Such local accuracy in the vertical plane has been measured at just 5–6 cm in the DJI Mavic Pro (Elkhrachy 2021), so we assume that error due to positional inaccuracy is low. A more important potential source of inaccuracy is that height of a vocalizing bird from ground level (i.e., distances *a* and *b* in Fig. 1) is not known, which could introduce significant imprecision and bias into distance estimates. Our method allows estimated perching heights of a particular species from the ground to be incorporated into calculations. Heights could be measured by field validation or estimated using expert opinion. Even so, we currently recommend that our technique is only valid for birds that reliably vocalize from the ground or in low vegetation, and hence is potentially useful for birds of open habitats, including grasslands, wetlands, bare ground, and shrub or scrub. We caution that overestimating the perching height of birds would lead to an underestimate of bird densities, because it would be assumed that the bird was further away than it actually was (see Fig. 3B).

Another assumption of our technique is that birds vocalize from a horizontal plane. Uneven topography and slopes would therefore introduce inaccuracy into distance estimates, the extent of which merit further investigation. We note that in the case of even and modest slopes, upslope and downslope errors should balance, hence distance estimates will be less precise, but not necessarily biased. Applying our technique in topographically complex locations, where errors could include significant biases, would be more challenging. We hope that our study will spur further innovation in airborne bioacoustics and that some of the aforementioned issues may be overcome with more sophisticated techniques, potentially including combining our methods with estimating distance to vocalizing individuals based on relative sound level (Yip et al. 2020).

A more general limitation of airborne bioacoustics is that drone noise on recordings may mask low-frequency songs and calls, such as pigeons and doves (*Columbiformes*) and cuckoos (*Cuculidae*) (Wilson et al. 2017). For such species, only those closest to the drone are likely to be detected, reducing the effective sampling distance of this survey method, which could reduce sample sizes. There are, of course, other complications inherent with using drones for survey work including ethics safety, the requirement for additional training and possibly licensing for drone pilots, and the need for relatively calm weather conditions (Linchant et al. 2015; Wallace et al. 2018); however, we have not found any of these to inhibit our ability to use these techniques in Pennsylvania, USA.

As with more general use of ARUs, airborne bioacoustics has some clear disadvantages when compared with traditional bird count techniques. The most important is that recorders do not pick up visual detections, and hence will undercount species that rarely vocalize when compared with counts by a field ornithologist. In some instances, it may be difficult to be certain how many individual birds of each species are audible in a recording, but airborne count using our method have an advantage over ARUs — the ability to estimate distances provides an additional clue when the analyst is trying to decipher how many birds are detected on a recording. Our technique could provide advantages over ground-based ARUs in allowing more points to be surveyed in a much shorter time period. Given that deployment of ARUs in off-road locations requires that a field worker walk to each location twice, for deployment and retrieval, the traveling time can be substantial; drones would be able to access the same location in a fraction of the time and would only require one visit for both deployment and retrieval. Conversely, if multiple recordings were required from a point location, for example, over several days or weeks, then a traditional ARU deployment would be much more time efficient. Hence, we recognize that the advantages of airborne counts are limited to situations where short recording durations and just one or two recordings per location are sufficient — situations where traditional point count surveys have often been used.

The airborne point count technique used in our study would be especially useful for surveying birds in open habitats where physical access is limited or disturbance should be avoided. In particular, we think this technique may be valuable for surveying vocal wetland species such as bitterns (subfamily Botaurinae), rails (family Rallidae), and wetland passerines such as wrens (genus *Cistothorus)*.

Future developments

Importantly, our airborne counts were of just 1 min duration, showing that rapid density estimation may be possible using drones. Further, as 74% of singing bird detections were within the first 20 s, we believe that it may be possible to use our method to conduct a rapid series of airborne counts in a very short period of time. For example, it would be feasible to fly two adjacent drone missions, each with up to fifteen 30 s counts spaced every 200 m, for a total of 30 point counts densely covering an area of 1.2 km^2 in point counts in just 1 h of field work. This highly efficient data gathering makes it more feasible to repeat point counts over a day or season, which potentially allows for more robust population estimates using occupancy models (Royle and Nichols 2003; Hayes and Monfils 2015) or spatially replicated *N*-mixture models (Royle 2004). An added advantage of using drones for aerial bioacoustics surveys under those circumstances is that they are highly replicable, both in terms of location and duration (due to the ability to precisely program missions), and because audio recordings provide a permanent record of bird song that can be analyzed by multiple observers after the fact (Shonfield and Bayne 2017).

Although our analysis shows that drones could be a very efficient way to collect data on songbird abundance, it is important to consider the extra analytical time that the method would entail, when compared to terrestrial counts. It took more than 1 h of data analysis per airborne count to identify each song bout and then estimate the distance to the bird using the TDoA method — but note that we localized every song bout, whereas it may be only necessary to localize the first detection.

In addition to trying very rapid assessment with short-duration point counts, our technique could easily be modified to fly airborne line transects, which would be even more time efficient. Two potential pitfalls of that approach are that the recorders may not suspend vertically from a travelling vehicle, and drone noise increases with speed — even a slow-moving quadcopter is noticeably noisier than one hovering.

Recent advances have shown that the distances of vocalizing birds from ARUs can be estimated from relative sound levels (Yip et al. 2020), which could also be measured using airborne bioacoustics. Combining TDoA-based distance estimates with those derived from measurements of sound levels offers an intriguing avenue for technique validation, and for potentially developing a robust technique that combines estimates from the two techniques to reduce uncertainty.

This initial study used off-the-shelf and inexpensive prosumer-level drones and recorders. Results might be greatly improved with custom-designed drones to reduce drone noise, and custom-built audio recorders. A recorder with the ability to simultaneously record two tracks from input lines of different lengths, would negate the need for manually synchronizing the tracks from the two recorders. We were not able to find a lightweight recording device that satisfied those requirements, but there are options that would be suitable for larger drones that are capable of carrying more payload. However, larger drones are noisier, so the trade-off between payload and the potential for noise disruption needs careful consideration.

Conclusions

We show that it is feasible to estimate distances of vocalizing birds from a drone, which therefore allows robust estimation of abundance in the same way that traditional bird surveys do. This technique could be applied to places that are difficult or dangerous for point count technicians to access. Further, our study shows that gathering bird abundance data this way could be highly efficient, so this technique may be of broader interest. While the technique outlined here is subject to various assumptions, and will likely not work for all species or habitats, we conclude that with further development of equipment and analytical methods, airborne bioacoustics could provide a useful new way to estimate the abundance of vocal bird species.

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