

The feasibility of counting songbirds using unmanned aerial vehicles

Authors: Wilson, Andrew M., Barr, Janine, and Zagorski, Megan

Source: The Auk, 134(2): 350-362

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-16-216.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



Volume 134, 2017, pp. 350–362 DOI: 10.1642/AUK-16-216.1

RESEARCH ARTICLE

The feasibility of counting songbirds using unmanned aerial vehicles

Andrew M. Wilson,* Janine Barr, and Megan Zagorski

Department of Environmental Studies, Gettysburg College, Gettysburg, Pennsylvania, USA * Corresponding author: awilson@gettysburg.edu

Submitted October 19, 2016; Accepted December 11, 2016; Published February 15, 2017

ABSTRACT

Obtaining unbiased survey data for vocal bird species is inherently challenging due to observer biases, habitat coverage biases, and logistical constraints. We propose that combining bioacoustic monitoring with unmanned aerial vehicle (UAV) technology could reduce some of these biases and allow bird surveys to be conducted in less accessible areas. We tested the feasibility of the UAV approach to songbird surveys using a low-cost quadcopter with a simple, lightweight recorder suspended 8 m below the vehicle. In a field experiment using playback of bird recordings, we found that small variations in UAV altitude (it hovered at 28, 48, and 68 m) didn't have a significant effect on detections by the recorder attached to the UAV, and we found that the detection radius of our equipment was comparable with detection radii of standard point counts. We then field tested our equipment, comparing songbird detections from our UAV-mounted recorder with standard point-count data from 51 count stations. We found that the number of birds per point on UAV counts was comparable with standard counts for most species, but there were significant underestimates for some—specifically, issues of song masking for a species with a low-frequency song, the Mourning Dove (Zenaida macroura); and underestimation of the abundance of a species that was found in very high densities, the Gray Catbird (Dumetella carolinensis). Species richness was lower on UAV counts (mean = 5.6 species point⁻¹) than on standard counts (8.3 species point⁻¹), but only slightly lower than on standard counts if nonaudible detections are omitted (6.5 species point⁻¹). Excessive UAV noise is a major hurdle to using UAVs for bioacoustic monitoring, but we are optimistic that technological innovations to reduce motor and rotor noise will significantly reduce this issue. We conclude that UAV-based bioacoustic monitoring holds great promise, and we urge other researchers to consider further experimentation to refine techniques.

Keywords: bioacoustics, drone, methodology, songbird, UAV

La factibilidad de contar aves canoras usando vehículos aéreos no tripulados

RESUMEN

La obtención de datos no sesgados de especies de aves que vocalizan es intrínsecamente difícil debido a sesgos del observador, sesgos de la cobertura del hábitat y restricciones logísticas. Proponemos que la combinación de un monitoreo bio-acústico usando la tecnología de Vehículos Aéreos No Tripulados (VANT) podría reducir algunos de estos sesgos y permitir que los muestreos de aves se realicen en áreas menos accesibles. Evaluamos la factibilidad del enfoque de VANT para muestreos de aves canoras usando un cuadricóptero de bajo costo con un grabador simple de bajo peso suspendido 8 m por debajo del vehículo. En un experimento de campo en el que reprodujimos sonidos previamente grabados de aves, encontramos que pequeñas variaciones en la altitud del VANT (28 m, 48 m, 68 m) no tuvieron un efecto significativo en las detecciones y que el radio de detección de nuestro equipamiento fue comparable con los radios de detección de los puntos de conteo estándar. Luego evaluamos nuestro equipamiento a campo, comparando las detecciones de las aves canoras con nuestro grabador colocado en el VANT con datos de puntos de conteo estándar en 51 estaciones de conteo. Encontramos que el número de aves por punto de conteo detectado con el VANT fue comparable con los conteos estándar para la mayoría de las especies, pero hubieron subestimaciones significativas para algunas—específicamente, temas de enmascaramientos del canto para una especie con un canto de baja frecuencia (Zenaida macroura) y subestimación de la abundancia de una especie que fue encontrada en densidades muy altas (Dumetella carolinensis). La riqueza de especies en los conteos con VANT (media de 5.6 especies/punto) fue más baja que en los conteos estándar (8.3 especies/punto), pero solo ligeramente más baja que en los conteos estándar si se omiten las detecciones no audibles (6.5 especies/punto). El ruido excesivo de los VANT representa un obstáculo importante para su uso en monitoreos bio-acústicos, pero somos optimistas de que las innovaciones tecnológicas para reducir el ruido del motor y del rotor disminuirán significativamente esta limitación. El monitoreo bio-acústico usando VANT es muy prometedor e instamos a otros investigadores a que consideren nuevos experimentos para refinar estas técnicas.

Palabras clave: aves canoras, bio-acústica, metodología, VANT

INTRODUCTION

Bird surveys provide crucial data for monitoring bird populations, conducting ecological studies, and determining effective environmental management strategies (Canterbury et al. 2000, Gregory and Strien 2010, Tulloch et al. 2013). A wide array of bird survey techniques is available, among which point-count and line-transect sampling are the most commonly deployed (Gregory et al. 2004). However, all bird survey techniques are known to be subject to biases, among which coverage biases (Betts et al. 2007, Leitão et al. 2011, McCarthy et al. 2012, Bird et al. 2014) and observer biases (Alldredge et al. 2007, Simons et al. 2009, Campbell and Francis 2011) are especially prevalent.

Many bird survey protocols are designed to maximize the number of bird detections, which is often achieved by minimizing travel time between survey locations. Roadbased counts, such as the U.S. Geological Survey's Breeding Bird Survey (BBS), are commonly used to assess bird abundance and trends (Sauer et al. 2013). While roadside sampling allows for highly efficient surveys, it results in underrepresentation of core habitats, areas of steep terrain, wetlands, or others areas that are dangerous, timeconsuming, or difficult to access. As a result, roadside surveys lack sufficient representation of some habitat types, and temporal changes in habitat at roadsides may not reflect changes in the wider landscape, thereby introducing bias in both abundance estimates and population trends (Keller and Scallan 1999, Betts et al. 2007).

In addition to inherent habitat biases, roadside bird surveys are subject to road noise interference, which can affect an observer's ability to detect certain species (Ralph et al. 1995). Further, several recent studies have shown that birds are sensitive to road noise pollution, with resulting behavioral changes (Brumm 2004), reductions in bird species richness, and changes in bird communities (Francis et al. 2009, 2011, McClure et al. 2013). Even in the vicinity of low traffic roads, birds are affected by visual disturbances and increases in predation, due to edge effects or increased urbanization (Keller and Scallan 1999, Forman and Alexander 2003).

There are several types of observer biases inherent in bird surveys. Field methods that are noisy or disruptive may disturb target species, making it difficult to obtain accurate population counts (Bibby et al. 2000). Variation in the observer's skills or other sources of human error can introduce temporal, spatial, and species-specific biases (Alldredge et al. 2007, Campbell and Francis 2011, Diefenbach et al. 2015). Ornithologists have developed numerous analytical techniques that allow observer biases in bird survey data to be accounted for, including distancesampling (Buckland et al. 2005), double-observer (Nichols et al. 2000), and removal or time-to-detection methods (Farnsworth et al. 2002, Alldredge et al. 2007). A potential

solution to observer biases for surveys of vocal bird species is to obtain audio recordings, which can reduce bias by allowing (1) multiple analysts to analyze recordings, (2) the archiving of recordings for future use or consultation (Celis-Murillo et al. 2009, Frommolt and Tauchert 2014), and (3) automated species identification (Aide et al. 2013).

Because audio bird recordings are generally from ground-based or close-to-ground recorders, they may still be limited by site accessibility and the logistical constraints of traversing difficult terrain. However, aerial recordings have greater range and mobility and can be used to access sites normally not surveyed by terrestrial methods (Jones et al. 2006). Aerial ecological surveys offer a solution to coverage biases and have already proved a valuable tool in wildlife monitoring (Anderson and Gaston 2013). Previous studies have used low-altitude imagery gathered from cameras mounted on unmanned aerial vehicles (UAVs) to document species occurrences (Jones et al. 2006, Watts et al. 2010, Chabot et al. 2015, Ratcliffe et al. 2015, McClelland et al. 2016) or to monitor nests (Weissensteiner et al. 2015, Hodgson et al. 2016). The use of UAVs has increased, in part, because they are safer and less expensive than aerial surveys using manned aircraft (Jones et al. 2006, Evans Ogden 2013) or result in efficiency gains when compared with traditional field techniques (McClelland et al. 2016).

We propose that bioacoustic monitoring via UAVmounted recorders could be a significant new technique for monitoring songbird populations. To our knowledge, there are no published studies of bioacoustic monitoring of birds using motorized UAVs. Fristrup and Clark (2009) demonstrated that inexpensive, lightweight, retrievable balloons equipped with a microphone and GPS locator could be used to determine songbird abundance, and they recommended the development of a powered aerial system that could offer advantages in navigational control, as opposed to a drifting balloon system (Fristrup and Clark 2009).

The aims of our study were to test the initial feasibility of collecting data on songbird abundance using a UAV and, importantly, to highlight potential problems and pitfalls associated with aerial monitoring. We hope that our initial foray into this field will spur interest in the technology among other researchers and result in a rapid advancement of techniques. Our approach was to build a low-cost and relatively low-tech aerial system, which we consider important if UAV-based bioacoustic monitoring is to become accessible to ornithologists with limited funding opportunities.

METHODS

Protocol Development: Equipment and Methods

Protocols were developed on the athletic fields of Gettysburg College in Adams County, Pennsylvania, USA

(39.8408°N, 77.2408°W). In keeping with our aim to test the feasibility of using low-cost and accessible technology, we chose to conduct our study using the DJI Phantom 2 the market leader among low-cost "consumer" drones. Autonomous UAV flight was achieved using the Ground Station app on an iPad, connected to the UAV via a 2.4G bluetooth datalink. To record bird vocalization, we used a ZOOM H1 Handy Recorder suspended below the UAV. We chose a recording device that was lightweight (89.9 g including battery) and inexpensive (less than \$100), but with an in-built cardioid microphone, ensuring an audio pickup pattern that minimized drone noise (to rear of microphone) while maximizing audio pickup from the ground below the drone. The recorder was protected by a MOVO windscreen. The recorder was attached to the UAV using fishing line (30 pound rating). Our aim was to suspend the recorder sufficiently far away from the UAV to minimize pickup of the UAV noise in our recordings. During test flights, we determined that a distance of 8 m between the recorder and UAV was optimal—we observed that a line length >8 m sometimes resulted in unwanted motion of the recorder when the UAV was hovering.

During protocol development, we conducted field experiments with 2 aims: (1) preliminary testing of feasibility and (2) determining optimal altitude of flight. We used our UAV and recorder (henceforth "aerial system") to obtain recordings of broadcasts of songs of 5 songbird species, chosen to encompass the necessary breadth of songs present in vivo, in terms of loudness, modulation, pattern, and duration (source of recordings: Cornell Lab of Ornithology, Ithaca, New York, USA). The species were Wood Thrush (n = 3 different recordings), Eastern Towhee (n = 4), Chipping Sparrow (Spizella passerina; n = 5), Song Sparrow (n = 4), and Eastern Meadowlark (Sturnella magna; n = 5), for a total of 21 different song recordings. (Scientific names of species not given in the text are listed in Appendix Table 5.)

The song recordings were amplified to ensure that the peak sound pressure level (SPL) output from speakers (SonaVERSE BXL, 12 W peak) was approximately consistent with the SPL of wild bird song. This assessment was based on measured SPL (at 1 m) for 2 of our 5 species: Song Sparrow (Anderson et al. 2008) and Eastern Towhee (Nelson 2000). Based on effective detection radii from >33,000 point counts in Pennsylvania (Wilson 2012), we assumed that the Eastern Meadowlark and Wood Thrush would be the loudest of our 5 species, and we amplified the recording by 6 dB. For Song Sparrow and Eastern Towhee, species with intermediate detection radii, we amplified by 3 dB. Assuming that the SPL of Chipping Sparrow song was the lowest of the 5 species, based on that species having smaller detection radii, we did not amplify recordings of that species. All speakers were confirmed to perform homogeneously by measuring SPL of a known

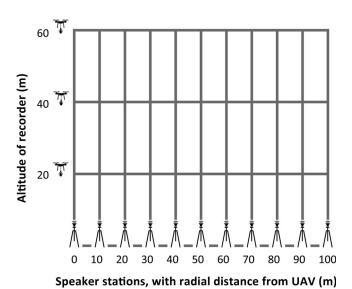


FIGURE 1. Experimental setup for protocol development. We attached an audio recorder to an unmanned aerial vehicle (UAV). which was flown at 3 altitudes while songs were played at random from 11 speaker stations located at regular intervals within 100 m radial distance from where the UAV hovered.

tone (Audacity: sine wave tone, 440 Hz, 0.6 amplitude) from a distance of 1 m. Tones were played 3 times from each speaker at full volume with no significant difference in peak SPL as determined through one-way analysis of variance using Vassar Stats (F(2) = 1.11, P = 0.346).

To determine the detection range of our aerial system at different UAV altitudes, we played each song sequence at 11 speaker stations placed along a horizontal transect radiating from the location of the hovering UAV (0 m) in 10 m increments up to 100 m. We hovered the UAV at 3 experimental altitudes (28, 48, and 68 m); hence, the recorder was positioned at the altitudes 20, 40, and 60 m (Figure 1). This resulted in between 99 and 165 experimental units (distance × altitude × song combinations) per "species."

Speaker stations consisted of a tripod supporting an mp3 player, and a skyward-facing speaker placed 1 m off the ground. While the UAV hovered at a constant height, song sequences were played at random from the 11 speaker stations. A referee's whistle was blown before each song sequence to aid interpretation of the recordings. Trials were conducted when wind speed was <10 km hr⁻¹, in an open space, and at a time of year (January-April 2015) or time of day (afternoons in June 2015) when ambient bird vocalizations were not present.

Protocol Development: Data Analysis

The audio files generated from our experiment were randomly numbered (by J.B.) so that the analyst (A.M.W.) did not know the experimental unit (species, distance, and

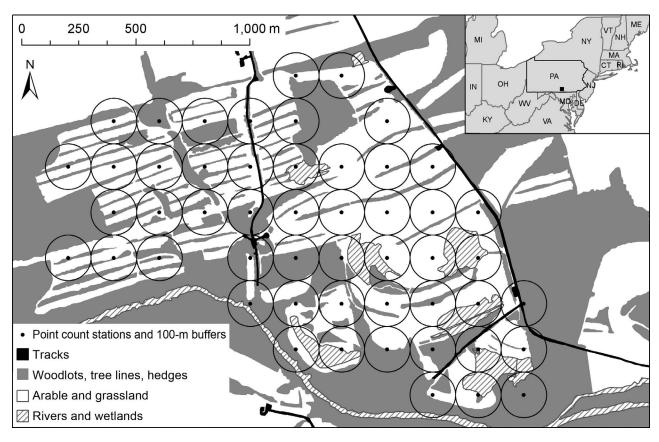


FIGURE 2. Study area at State Game Lands 249, Adams County, Pennsylvania, USA.

altitude) of each recording. Each song sequence was subjectively classified by the analyst using the following code: 3 = loud and clear, 2 = audible, 1 = barely audible, and 0 = not audible. Song sequences coded 2 and 3 were considered clear enough to be identifiable to species; code 1 was assigned to songs that the analyst considered would be difficult to identify to species, if candidate species were not known. We tested the hypothesis that detectability varied with UAV altitude (within our narrow experimental range) using chi-square tests, where audibility codes 2 and 3 were combined into "detected" and 0 and 1 were combined into "not detected." On the basis of those detections at the various radial distances, effective strip width (ESW) was calculated in the program Distance (Buckland et al. 2005), with the best of 4 candidate models of detection curves (Half-normal, Hazard Rate, Negative Exponential, and Uniform) selected using Akaike's Information Criterion (AIC). An effective strip width is the distance from a transect at which the number of detections beyond that distance is equal the number of detections missed within that distance (Buckland et al. 2005). The effective detection radius (EDR) is a circular equivalent of ESW, used to estimate detection ranges in a circular plot around point-count stations.

Field Validation: Equipment and Methods

Our field validation study was conducted on a 140 ha portion of the 793 ha Pennsylvania State Game Lands 249, Heidlersburg, Adams County, south-central Pennsylvania (39.9346°N, 77.1777°W; Figure 2). The study area is a mosaic of woodlots, hedges, wetlands, grasslands, and feedlots. The surrounding landscape is largely agricultural, with small human settlements and woodland. Although the study site is within 1 km of a major highway (U.S. Route 15), it is buffered by several hundred meters of woodland and, hence, background anthropogenic noise levels are low.

We compared UAV-based counts with standard point counts at 51 count stations, evenly spaced on a 200 m grid (Figure 2). A.M.W. conducted 5 min point counts between 0620 and 0940 hours on 5 days during June 3-17, 2015. Point counts were conducted only in optimal weather (wind <3 on Beaufort scale, no precipitation). All bird detections were assigned to five 1 min time bands, and noted as visual or audial. Where possible, the distance (m) to each individual bird was measured using a Bushnell Yardage Pro laser range finder. The remaining distances were estimated to the nearest meter, based on relative distances to landmarks or other birds. Birds >100 m from

TABLE 1. Audio recordings used in experimental trials to test rates of detection by a recorder mounted on an unmanned aerial vehicle (UAV), with overall detection rates for each species (i.e. number of audible vocalizations detected during playback of recordings, with percentage of the total played in parentheses), effective strip width (ESW, with 95% confidence interval), and chisquare test result (P) for difference in detection between three UAV altitudes (28, 48, and 68 m).

Species recording	Number of recordings	Range of peak power at 1 m (db)	Audible vocalizations detected (n)	ESW (m)	Р
Wood Thrush	3	82.7-103.6	75 (75.8%)	69.8 (57–86)	0.138
Eastern Towhee	5	83.7-86.0	88 (53.3%)	54.2 (46-64)	0.791
Chipping Sparrow	5	69.0-86.0	68 (41.2%)	40.7 (34-49)	0.088
Song Sparrow	4	79.3-86.6	80 (60.6%)	55.5 (46-66)	0.309
Eastern Meadowlark	5	87.0-101.8	116 (70.3%)	68.1 (58–90)	0.816

the count station were not included, to reduce the risk of double-counting individuals at adjacent stations.

The UAV-based counts at each station occurred on the same morning as the standard point count with a randomized starting order; hence, all paired UAV and standard counts were within 2 hr of each other, but never within 20 min. The UAV ascended to an altitude of 58 m (hence, the recorder was at 50 m), from a starting location well outside the point-count circle (i.e. >100 m), and was then flown horizontally to hover over the count station. We used this approach to minimize noise disturbance within the count circle, while maximizing survey efficiency. Other researchers have suggested that flying the UAV to a greater height and slowly descending to the required position could minimize disturbance (Pomeroy et al. 2015, Vas et al. 2015), but the extra time required to ascend and descend would likely have limited our point counts per battery pack to 2, rather than 3. We also note that behavioral responses to UAVs were negligible in waterbirds when the vehicle was flown at heights of 30-40 m (Sardà-Palomera et al. 2012, Vas et al. 2015, McEvoy et al. 2016), lower than in our study.

The UAV count duration was 3 min, which allowed 3 point counts per UAV battery. Standard point-count durations are typically between 3 and 10 min (Sutherland 2006), with 5 min considered adequate in temperate regions (Bibby et al. 2000, Bonthoux and Balent 2012). However, 3 min point-count durations are used in some of the largest bird-monitoring programs, notably the North American BBS. Following our experimental finding that there was little difference in detection between UAV altitudes of 48 and 68 m, we chose to hover our UAV at 58 m above the count station (hence, the recorder was at 50 m altitude). This altitude was also informed by the fact that trees >50 m tall are very rare in Pennsylvania (http://www. pabigtrees.com/tall_tree.aspx), where forest canopy heights are generally <30 m (Wasser et al. 2013), and confirmed by visual inspection of our study area.

Field Validation: Data Analysis

Audio files. We reduced the UAV noise on the recordings by applying 3 high-pass filters (575 Hz, 6 dB

attenuation; 550 Hz, 6 dB attenuation; 370 Hz, 12 dB attenuation) in Audacity 2.0.6 (http://www.audacityteam. org/). Filters were chosen through a process of trial and error, with the aim of reducing the possibility of causing hearing damage from listening to recordings with excessive drone noise, while maximizing the audibility of bird vocalizations. A.M.W. then listened to all recordings 3 times to document audible bird vocalizations that were identifiable to species. Aerial point-count audio file names were randomized to ensure that the analyst did not know which point-count station the recording was from.

Data analysis. We used Distance (Buckland et al. 2005) to estimate abundances and effective detection radii of the most numerous species within our study area, based on standard point-count data. We right-truncated data at 100 m to avoid potential double-counting between adjacent point-count stations. For each species with sufficient detections (>20), we tested 4 candidate detection models: Half-normal, Hazard Rate, Negative Exponential, and Uniform. The best model was selected using AIC.

We compared species richness and bird detections (per point) of the 3 min UAV recordings both with the first 3 min and with all 5 min of standard point counts, using paired t-tests. For the most common songbirds (>20detections), we compared the number of audial detections on 3 min standard and UAV counts to provide a like-withlike comparison.

RESULTS

Protocol Development

The overall rates of detection of broadcast song recordings reflected variation in their sound pressure, ranging from 41.2% for the quietest "species" (Chipping Sparrow) to 70.8% and 75.8% for the loudest (Eastern Meadowlark and Wood Thrush, respectively; Table 1 and Appendix Table 4). We found no significant difference in overall detectability between the 3 experimental UAV altitudes (chi-square tests, P > 0.05; Table 1). Because there was no significant difference in detection between UAV altitudes, we combined data for the 3 altitudes to estimate effective strip widths of our aerial system for each "species." The ESW values ranged

TABLE 2. Comparison of total numbers of species and individual birds detected on UAV (unmanned aerial vehicle) point counts and standard point counts.

			Number of spe	ecies detected	Number of individuals detected		
Count method	Duration (min)	Cues included	Mean	SE	Mean	SE	
UAV	3	Vocal	5.6	0.28	7.7	0.28	
Standard	3	Vocal	6.6	0.24	8.9	0.31	
	3	All	8.3	0.26	11.2	0.27	
	5	All	10.8	0.32	15.7	0.40	

from 40.7 m for the quietest species (Chipping Sparrow) to 69.8 m for the loudest (Wood Thrush).

Field Validation

Fifty-four bird species were detected on standard 5 min point counts (Appendix Table 5). Gray Catbird was easily the most numerous species, with detections on 50 of the 51 standard point counts, a mean of 2.43 individuals per point, and an estimated density of 146 singing males km⁻² (Appendix Table 5). Estimated densities of Willow Flycatcher and Yellow Warbler were also high within the study area (Appendix Table 5), comparable with the highest densities noted in other studies (Lowther et al. 1999, Sedgewick 2000). Of the 54 species detected on standard point counts, several were detected only as flyovers, or only as visual cues (i.e. not heard singing or calling). Effective detection radii on standard counts for the most common species ranged from 46 to 100 m, with a mean of 74.86 m for songbird vocalizations (Appendix Table 6). Taking only count data for the first 3 min of each count, and only audial cues (hence, data comparable to UAV points count), 37 species were detected on standard point counts, with a mean of 6.6 species, and 8.9 individual birds count⁻¹ (Table 2).

TABLE 3. Comparison of audial detections on standard and UAV (unmanned aerial vehicle) point counts for 9 songbird species that were detected >20 times on standard counts. Duration of each point count was 3 min. Scientific names of species are given in the text or in Appendix Table 5.

	All aud		Paired t-test for difference between means			
Species	Standard	UAV	t	Р		
Willow Flycatcher	26	11	3.64	< 0.001		
House Wren	23	14	1.77	0.08		
American Robin	24	20	0.89	0.38		
Gray Catbird	88	37	6.87	< 0.001		
Yellow Warbler	38	35	0.52	0.61		
Field Sparrow	22	27	-0.96	0.34		
Song Sparrow	66	66	0	1		
Northern Cardinal	33	27	0.88	0.38		
Red-winged Blackbird	48	52	-0.49	0.63		

Thirty-two species were audible on the 51 UAV pointcount recordings, with a mean of 7.7 individuals birds (range: 2-10) and a mean of 5.6 species count⁻¹ (range: 4-12). Both species richness ($t_{50} = 3.22$, P = 0.002) and total count ($t_{50} = 3.21$, P = 0.002) were lower on the UAV counts than on comparable standard counts (i.e. 3 min duration, only audial detections). Among the 9 most abundant songbird species, there were no significant differences in overall number of detections on 3 min standard counts (audial cues only) and UAV counts for 7 species (Table 3), exceptions being Willow Flycatcher and Gray Catbird, which were both undercounted on UAV counts.

Both species richness and total detections were considerably lower on the UAV counts than on counts that included nonvocal cues (Table 2). However, detection rates (birds point⁻¹) were similar on UAV and standard point counts for most species (Figure 3), especially if only audial detections are compared, but there were some notable exceptions, including Mourning Dove and Gray Catbird.

Almost 73% of new detections occurred within the first minute of the UAV point counts, declining to <10% during the third minute (Figure 4).

DISCUSSION

To our knowledge, the present study is the first to successfully pair bioacoustic monitoring and UAV technology. Our results demonstrate that conducting surveys of vocal bird species using recorders attached to UAVs is feasible with relatively low-cost equipment. Although we found that detection rates for some species were similar to those from standard point counts, some species were substantially underdetected by aerial monitoring. With these findings in mind, we will discuss the important methodological and analytical questions that need to be addressed through future research.

First, we must emphasize that our results may be valid only for our aerial system and study area. Different UAVs and recording devices could produce substantially different recordings, depending on the balance between UAV noise and recorder/microphone sensitivity to low-frequency sound. We suggest that future development of UAVbased bird surveying should focus initially on testing a

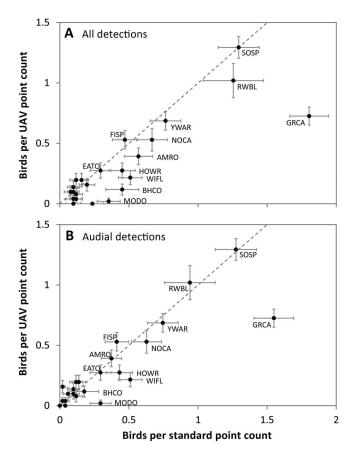


FIGURE 3. Mean detections per point for each species on standard point counts and unmanned aerial vehicle (UAV) point counts, over 3 min, plotted against an equivalency line. (**A**) Detections were lower on UAV counts for most species, but (**B**) when only audial detections were included, UAV and standard counts were very similar for most species. Species codes for the 12 most abundant species: AMRO = American Robin, BHCO = Brown-headed Cowbird, EATO = Eastern Towhee, FISP = Field Sparrow, GRCA = Gray Catbird, HOWR = House Wren, MODO = Mourning Dove, NOCA = Northern Cardinal, RWBL = Red-winged Blackbird, SOSP = Song Sparrow, WIFL = Willow Flycatcher, YWAR = Yellow Warbler. Scientific names of species are given in the text or in Appendix Table 5.

wide array of potentially suitable equipment. We also recommend that the methods be trialed in a variety of habitats and geographic areas, so that more information is gathered on potential pitfalls related to bird responses and detectability.

Our protocol development focused on a relatively narrow range of UAV altitudes, and while we rejected our hypothesis that detections varied with UAV altitude, this result is unlikely to hold for other systems. Ideal UAV altitude could vary depending on target species and habitat, and minimum altitudes would also be dictated by tree canopy height and the presence of other obstructions, such as powerlines. In single-species studies, or where a species is found in low densities, a higher UAV

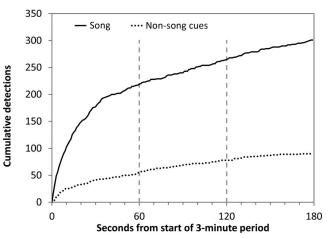


FIGURE 4. Accumulation of new bird detections during the 3 min UAV point count.

altitude (potentially providing a larger ESW) would be desirable to ensure that sufficient detections are obtained. Also, our experimental approach to ascertain ESW was based on recordings, rather than in situ wild birds, and the playback volume of our recordings was informed by rather sparse information on the volume of wild bird song. Despite this, our field trials suggest that for most species, the rate of detection, and hence the effective EDR, was broadly similar to those derived from standard point counts conducted by an experienced observer. If UAV point counts are to be used to estimate absolute rather than relative densities, establishing the EDR of the aerial system is crucial. However, even in situations where EDR is unknown, aerial sampling could still be very useful for assessing relative abundance, species richness, and approximate locations of target species.

Our field trials demonstrate that 3 min UAV point counts are sufficiently long to ensure multiple bird detections per point, while allowing for ≥ 3 point counts battery⁻¹. This compromise between short counts to maximize overall survey efficiency and long counts to maximize bird detection also affects standard point counts (Bibby et al. 2000). Analysis of data from 10 min point counts in Shenandoah National Park showed that 65% of species were detected within the first 3 min, with diminishing returns for the remaining 7 min (Keller and Fuller 1995). Increased sampling efficiency could be achieved through a lengthened battery life and, hence, longer flight times. Some commercially available quadcopters have potential flight times in excess of 1 hr (e.g., Araar et al. 2016), which would allow for longer counts, for more point counts (or longer transects) per battery, or for surveys conducted farther into inaccessible habitat (provided that legal restrictions, such as the need to keep the vehicle in line of sight, are followed).

Although bioacoustics recorders have previously been found to result in more species detections (Hobson et al. 2002, Acevedo and Villanueva-Rivera 2006) or higher detection rates of within-species detection than fieldworkers (Zwart et al. 2014), we found the reverse to be true. We attribute our lower detection rates to a combination of our use of less sensitive recording equipment (necessitated by UAV payload constraints) and masking by drone noise. This was especially apparent for the Mourning Dove-a species that has a very lowfrequency song, typically in the 300-700 Hz range (http:// www.xeno-canto.org/species/Zenaida-macroura). Masking, in combination with our application of high-pass filters to the recordings, resulted in vocalization of Mourning Doves being imperceptible on our recordings.

Gray Catbird and Willow Flycatcher were also undercounted by our aerial system, but their primary vocalizations have higher frequencies than that of the UAV (http:// www.xeno-canto.org/species/Empidonax-traillii, http:// www.xeno-canto.org/species/Dumetella-carolinensis), the sound pressure of which was predominantly <500 Hz. In the case of the Gray Catbird, song volume may play a role in UAV detection rates. In our study, the Gray Catbird had the smallest EDR from standard point-count surveys (Appendix Table 6), indicating that it is quiet compared to the other species. In their balloon-based aerial surveys, Fristrup and Clark (2009) found that species producing low-frequency but loud vocalizations such as the American Crow (Corvus brachyrhynchos) had higher detection rates. Therefore, both volume and frequency play an important role in aerial bioacoustic detections. Furthermore, the Gray Catbird has an incessant song with few breaks between phrases, which makes it more difficult to identify individuals through recordings, likely leading to underestimates of the number of birds audible. The Gray Catbird was by far the most abundant bird species at our study site, which means that vocalizations of multiple singing birds may have been captured on recordings, but differentiating multiple birds with overlapping song phrases was problematic. Hence, we caution that UAV-based bioacoustic monitoring may be challenging for species found in very high densities.

Another factor that might influence bird detection rates from our aerial system is habitat use, particularly the preferred location of song perches within vertically structured habitat (Waide and Narins 1988). Further, it is known that song attenuation varies with song frequency (Morton 1975, Cosens and Falls 1984, Koper et al. 2016) and that song frequency shows broad patterns among species found in different habitats (Boncoraglio and Saino 2007). However, we note that potential issues related to bird song attenuation among species and habitats are also inherent issues for both standard count techniques and bioacoustics recording, and hence we do not consider this a problem specific to aerial monitoring.

One potentially crucial issue that remains to be addressed is whether the presence of UAVs affects songbird behavior, and song output in particular. There is now considerable evidence that anthropogenic noise affects bird settlement patterns and song output. McClure et al. (2013) found that noise level was a key factor in road avoidance; anthropogenic noise of gas wells has also been shown to alter bird communities (Francis et al. 2009). In addition to avoidance of anthropogenic noise, some bird species have been shown to alter the frequency (Seger-Fullam et al. 2011), amplitude (Brumm 2004), or timing of song (Dominoni et al. 2016) to avoid masking by anthropogenic noise. We are not aware of any studies of the effects of UAVs on bird song output, but an experimental study found very modest behavioral responses to UAVs being flown to within 4 m of wetland birds (Vas et al. 2015), whereas others have found either no effect or very modest effects on the behavior of nesting birds (Junda et al. 2015, Weissensteiner et al. 2015, McClelland et al. 2016). We conducted an experiment to see whether bird song output detected by ground-based bioacoustics recorders (Song Meter SM3; http://www.wildlifeacoustics. com) differed in three 3 min periods: pre-, during-, and post-UAV hover, at 58 m above the recorder, at a sample of 30 of our point-count stations. Our results suggested that there may have been a very small dip in bird song output during the time when the UAV was overhead, approaching, or departing the count station, but we could not satisfactorily tease out changes in song output from the effects of masking by drone noise. Despite this, we are confident that such behavioral impacts are modest among the species in our study area. For most species, the number of detections on UAV counts was very similar to the number of audial detections on standard counts (Figure 3), which indicates that song output was not significantly affected by the presence of the UAV.

However, even a modest behavioral response could be significant; and, of course, behavioral response could vary significantly among species. Hence, we suggest that assessing the potential effects of UAVs on song output is a research priority. Reducing rotor noise would avoid the problem of masking low-frequency species and could potentially reduce or eliminate behavioral responses to a UAV's presence, allowing for more accurate population estimates. We are optimistic that there will be a broader demand for quieter UAVs, and that this will lead to the development of vehicles that are better suited for conservation and ecology applications (Hambling 2015).

Bioacoustic monitoring with UAVs would be especially efficient for bird surveys if combined with real-time automated species identification (Aide et al. 2013). The combination of these technologies would allow for realtime plotting of individual birds based on the GPS coordinates of the UAV; indeed, we foresee a time when a single UAV operator could fly ≥20 km of transects in a few hours-and have all bird vocalizations identified to species and geolocated almost instantaneously. We conclude that the combination of UAV and bioacoustic technologies could provide an important new survey tool for ornithologists and, indeed, for biologists studying other vocal species groups.

ACKNOWLEDGMENTS

We thank A. Graham, B. Lonabocker, and C. Moreno for assistance with fieldwork. W. R. Evans (director of Old Bird Inc.), M. Caldwell (Gettysburg College), and W. Piniak (Gettysburg College) were generous with their technical expertise and advice. The Pennsylvania Game Commission graciously permitted us to use State Game Land property to conduct our research.

Funding statement: This work was supported by a grant to Gettysburg College from the Howard Hughes Medical Institute, a Kolbe Research Fellowship, a grant from the Margaret A. Cargill Foundation, and a Gettysburg College Professional Development Grant.

Author contributions: A.M.W. conceived the research idea. A.M.W., J.B., and M.Z. designed the methods, performed the experiments, analyzed the data, and wrote the paper.

LITERATURE CITED

- Acevedo, M. A., and L. J. Villanueva-Rivera (2006). Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. Wildlife Society Bulletin 34:211-214.
- Aide, T. M., C. Corrada-Bravo, M. Campos-Cerqueira, C. Milan, G. Vega, and R. Alvarez (2013). Real-time bioacoustics monitoring and automated species identification. PeerJ 1:e103.
- Alldredge, M. W., T. R. Simons, and K. H. Pollock (2007). A field evaluation of distance Measurement error in auditory avian point count surveys. Journal of Wildlife Management 71: 2759-2766.
- Anderson, K., and K. J. Gaston (2013). Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Frontiers in Ecology and the Environment 11:138-146.
- Anderson, R. C., W. A. Searcy, S. Peters, and S. Nowicki (2008). Soft song in Song Sparrows: Acoustic structure and implications for signal function. Ethology 114:662-676.
- Araar, O., N. Aouf, and I. Vitanov (2016). Vision based autonomous landing of multirotor UAV on moving platform. Journal of Intelligent & Robotic Systems. In press.
- Betts, M. G., D. Mitchell, A. W. Diamond, and J. Bêty (2007). Uneven rates of landscape change as a source of bias in roadside wildlife surveys. Journal of Wildlife Management
- Bibby, C. J., N. D. Burgess, D. A. Hill, and S. Mustoe (2000). Bird Census Techniques, second edition. Academic Press, San Diego, CA, USA.
- Bird, T. J., A. E. Bates, J. S. Lefcheck, N. A. Hill, R. J. Thomson, G. J. Edgar, R. D. Stuart-Smith, S. Wotherspoon, M. Krkosek, J. F. Stuart-Smith, G. T. Pecl, et al. (2014). Statistical solutions

- for error and bias in global citizen science datasets. Biological Conservation 173:144-154.
- Boncoraglio, G., and N. Saino (2007). Habitat structure and the evolution of bird song: A meta-analysis of the evidence for the acoustic adaptation hypothesis. Functional Ecology 21: 134-142.
- Bonthoux, S., and G. Balent (2012). Point count duration: Five minutes are usually sufficient to model the distribution of bird species and to study the structure of communities for a French landscape. Journal of Ornithology 153:491–504.
- Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73: 434-440.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, S. T. Buckland, D. R. Anderson, K. P. Burnham, and J. L. Laake (2005). Distance sampling. In Encyclopedia of Biostatistics. Wiley, Chichester, UK.
- Campbell, M., and C. M. Francis (2011). Using stereomicrophones to evaluate observer variation in North American Breeding Bird Survey point counts. The Auk 128:303-312.
- Canterbury, G. E., T. E. Martin, D. R. Petit, L. J. Petit, and D. F. Bradford (2000). Bird communities and habitat as ecological indicators of forest condition in regional monitoring. Conservation Biology 14:544-558.
- Celis-Murillo, A., J. L. Deppe, and M. F. Allen (2009). Using soundscape recordings to estimate bird species abundance, richness, and composition. Journal of Field Ornithology 80: 64-78.
- Chabot, D., S. R. Craik, and D. M. Bird (2015). Population census of a large Common Tern colony with a small unmanned aircraft. PLOS One 10:e0122588. doi:10.1371/journal.pone. 0122588
- Cosens, S. E., and J. B. Falls (1984). A comparison of sound propagation and song frequency in temperate marsh and grassland habitats. Behavioral Ecology and Sociobiology 15: 161-170.
- Diefenbach, D. R., D. W. Brauning, and J. A. Mattice (2015). Variability in grassland bird counts related to observer differences and species detection rates. The Auk 120:1168-
- Dominoni, D. M., S. Greif, E. Nemeth, and H. Brumm (2016). Airport noise predicts song timing of European birds. Ecology and Evolution 6:6151–6159.
- Farnsworth, G. L., K. H. Pollock, J. D. Nichols, T. R. Simons, J. E. Hines, and J. R. Sauer (2002). A removal model for estimating detection probabilities from point-count surveys. The Auk 119:414-425.
- Forman, R. T. T., and L. E. Alexander (2003). Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.
- Francis, C. D., C. P. Ortega, and A. Cruz (2009). Noise pollution changes avian communities and species interactions. Current Biology 19:1415-1419.
- Francis, C. D., C. P. Ortega, and A. Cruz (2011). Noise pollution filters bird communities based on vocal frequency. PLOS One 6:e27052. doi:10.1371/journal.pone.0027052
- Fristrup, K. M., and C. W. Clark (2009). Acoustic Monitoring of Threatened and Endangered Species in Inaccessible Areas.

- Final report, SERDP Project SI-1185. http://www.dtic.mil/ dtic/tr/fulltext/u2/a520622.pdf
- Frommolt, K.-H., and K.-H. Tauchert (2014). Applying bioacoustic methods for long-term monitoring of a nocturnal wetland bird. Ecological Informatics 21:4-12.
- Gregory, R. D., D. W. Gibbons, and P. F. Donald (2004). Bird census and survey techniques. In Bird Ecology and Conservation: A Handbook of Techniques (W. J. Sutherland, I. Newton, and R. Green, Editors). Oxford University Press, Oxford, UK. pp. 17-56.
- Gregory, R. D., and A. van Strien (2010). Wild bird indicators: Using composite population trends of birds as measures of environmental health. Ornithological Science 9:3-22.
- Hambling, D. (2015). Silence of the drones: How to guiet that annoying aerial buzz. New Scientist. https://www. newscientist.com/article/dn27696-silence-of-the-droneshow-to-quiet-that-annoying-aerial-buzz/
- Hobson, K. A., R. S. Rempel, H. Greenwood, B. Turnbull, and S. L. Van Wilgenburg (2002). Acoustic surveys of birds using electronic recordings: New potential from an omnidirectional microphone system. Wildlife Society Bulletin 30:709-720.
- Hodgson, J. C., S. M. Baylis, R. Mott, A. Herrod, and R. H. Clarke (2016). Precision wildlife monitoring using unmanned aerial vehicles. Scientific Reports 6:22574.
- Jones, G. P., IV, L. G. Pearlstine, and H. F. Percival (2006). An assessment of small unmanned aerial vehicles for wildlife research. Wildlife Society Bulletin 34:750-758.
- Junda, J., E. Greene, and D. M. Bird (2015). Proper flight technique for using a small rotary-winged drone aircraft to safely, quickly, and accurately survey raptor nests. Journal of Unmanned Vehicle Systems 3:222-236.
- Keller, C. M. E., and M. R. Fuller (1995). Comparison of birds detected from roadside and off-road point counts in the Shenandoah National Park. USDA Forest Service General Technical Report PWS-GTR-149. pp. 111–116.
- Keller, C. M. E., and J. T. Scallan (1999). Potential roadside biases due to habitat changes along Breeding Bird Survey routes. The Condor 101:50-57.
- Koper, N., L. Leston, T. M. Baker, C. Curry, and P. Rosa (2016). Effects of ambient noise on detectability and localization of avian songs and tones by observers in grasslands. Ecology and Evolution 6:245-255.
- Leitão, P. J., F. Moreira, and P. E. Osborne (2011). Effects of geographical data sampling bias on habitat models of species distributions: A case study with steppe birds in southern Portugal. International Journal of Geographical Information Service 25:439-454.
- Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector (1999). Yellow Warbler (Setophaga petechia). In Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://birdsna. org/Species-Account/bna/species/yelwar/introduction
- McCarthy, K. P., R. J. Fletcher, Jr., C. T. Rota, and R. L. Hutto (2012). Predicting species distributions from samples collected along roadsides. Conservation Biology 26:68–77.
- McClelland, G. T. W., A. L. Bond, A. Sardana, and T. Glass (2016). Rapid population estimate of a surface-nesting seabird on a remote island using a low-cost unmanned aerial vehicle. Marine Ornithology 44:215–220.

- McClure, C. J. W., H. E. Ware, J. Carlisle, G. Kaltenecker, and J. R. Barber (2013). An experimental investigation into the effects of traffic noise on distributions of birds: Avoiding the phantom road. Proceedings of the Royal Society of London, Series B 280:20132290.
- McEvoy, J. F., G. P. Hall, and P. G. McDonald (2016). Evaluation of unmanned aerial vehicle shape, flight path and camera type for waterfowl surveys: Disturbance effects and species recognition. PeerJ 4:e1831.
- Morton, E. S. (1975). Ecological sources of selection on avian sounds. The American Naturalist 109:17-34.
- Nelson, B. S. (2000). Avian dependence on sound pressure level as an auditory distance cue. Animal Behaviour 59:57-67.
- Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund (2000). A double-observer approach for estimating detection probability and abundance from point counts. The Auk 117:393-408.
- Evans Ogden, L. (2013). Drone ecology. BioScience 63:776.
- Pomeroy, P., L. O'Connor, and P. Davies (2015). Assessing use of and reaction to unmanned aerial systems in gray and harbor seals during breeding and molt in the UK. Journal of Unmanned Vehicle Systems 3:102-113.
- Ralph, C. J., J. R. Sauer, and S. Droege (1995). Monitoring bird populations by point counts. USDA Forest Service General Technical Report PSW-GTR-149.
- Ratcliffe, N., D. Guihen, J. Robst, S. Crofts, A. Stanworth, and P. Enderlein (2015). A protocol for the aerial survey of penguin colonies using UAVs. Journal of Unmanned Vehicle Systems 3:95-101.
- Sardà-Palomera, F., G. Bota, C. Viñolo, O. Pallarés, V. Sazatornil, L. Brotons, S. Gomáriz, and F. Sardà (2012). Fine-scale bird monitoring from light unmanned aircraft systems. Ibis 154: 177-183.
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski, Jr. (2013). The North American Breeding Bird Survey 1966-2011: Summary Analysis and Species Accounts. North American Fauna 79.
- Sedgewick, J. A. (2000). Willow Flycatcher (Empidonax traillii). In Birds of North America Online (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://birdsna. org/Species-Account/bna/species/wilfly/introduction
- Seger-Fullam, K. D., A. D. Rodewald, and J. A. Soha (2011). Urban noise predicts song frequency in Northern Cardinals and American Robins. Bioacoustics 20:267–276.
- Simons, T. R., K. H. Pollock, J. M. Wettroth, M. W. Alldredge, K. Pacifici, and J. Brewster (2009). Sources of measurement error, misclassification error, and bias in auditory avian point count data. In Modeling Demographic Processes in Marked Populations (D. L. Thomson, E. G. Cooch, and M. J. Conroy, Editors). Springer, Boston, MA, USA. pp. 237–254.
- Sutherland, W. J. (2006). Ecological Census Techniques, second edition. Cambridge Univerity Press, Cambridge, UK.
- Tulloch, A. I. T., H. P. Possingham, L. N. Joseph, J. Szabo, and T. G. Martin (2013). Realising the full potential of citizen science monitoring programs. Biological Conservation 165: 128-138.
- Vas, E., A. Lescroël, O. Duriez, G. Boguszewski, and D. Grémillet (2015). Approaching birds with drones: First experiments and ethical guidelines. Biology Letters 11:20140754.

Waide, R. B., and P. M. Narins (1988). Tropical forest bird counts and the effect of sound attenuation. The Auk 105:296-302.

Watts, A. C., J. H. Perry, S. E. Smith, M. A. Burgess, B. E. Wilkinson, Z. Szantoi, P. G. Ifju, and H. F. Percival (2010). Small unmanned aircraft systems for low-altitude aerial surveys. Journal of Wildlife Management 74:1614–1619.

Wasser, L., R. Day, L. Chasmer, and A. Taylor (2013). Influence of vegetation structure on lidar-derived canopy height and fractional cover in forested riparian buffers during leaf-off and leaf-on conditions. PLOS One 8:e54776. doi:10.1371/ journal.pone.0054776

Weissensteiner, M. H., J. W. Poelstra, and J. B. W. Wolf (2015). Low-budget ready-to-fly unmanned aerial vehicles: An effective tool for evaluating the nesting status of canopybreeding bird species. Journal of Avian Biology 46:425-430.

Wilson, A. M. (2012). Analytical methods. In Second Atlas of Breeding Birds in Pennsylvania (A. M. Wilson, D. W. Brauning, and R. S. Mulvihill, Editors). Penn State University Press, University Park, PA, USA. pp. 38-47.

Zwart, M. C., A. Baker, P. J. K. McGowan, and M. J. Whittingham. (2014). The use of automated bioacoustic recorders to replace human wildlife surveys: An example using nightjars. PLOS One 9:e102770. doi:10.1371/journal.pone.0102770

APPENDIX

APPENDIX TABLE 4. Proportion of audio recordings detected by a recorder suspended from an unmanned aerial vehicle (UAV), at varying altitudes (m) and varying distances (m) from the recorder, in our feasibility experiment.

Species recording	Altitude of recorder		Horizontal distance from UAV									
		0	10	20	30	40	50	60	70	80	90	100
Wood Thrush	20	1	1	1	1	1	1	1	1	1	0	0
	40	1	1	1	1	0.67	1	1	1	1	0.33	0
	60	1	1	1	1	0.67	0.33	1	1	0	0	0
Eastern Towhee	20	1	0.8	1	0.8	0.6	0.6	0.2	0	0	0.4	0
	40	1	1	0.6	1	0.8	0.4	0.8	0	0	0.4	0
	60	1	1	0.8	1	0.4	0.8	0.6	0.6	0	0	0
Chipping Sparrow	20	1	1	0.6	1	0	0	0	0	0	0	0
	40	1	1	0.4	1	0.6	0	0	0	0	0.2	0
	60	1	1	0.8	1	0.6	1	0	0.4	0	0	0
Song Sparrow	20	1	1	1	1	0.75	1	0.5	0	0.25	0.25	0
3 1	40	1	1	1	1	0.5	0.75	0.5	0	0	0	0
	60	1	1	1	1	0.5	1	0.5	1	0.5	0	0
Eastern Meadowlark	20	1	1	1	0.8	0.4	1	0.2	1	0.8	0.4	0
	40	1	1	1	1	0.6	1	0.8	1	0.2	0	0
	60	1	1	1	1	1	1	1	0.6	0.2	0.2	0

APPENDIX TABLE 5. Total detections of all species (including fly-over) on standard and UAV (unmanned aerial vehicle) point counts in our field study.

		Standa	rd 5 min	count	Standard 3 min count			UAV count		
Common name	Scientific name	Count	Mean	SE	Count	Mean	SE	Count	Mean	SE
Canada Goose	Branta canadensis	1	0.02	0.02	1	0.02	0.02			
Wood Duck	Aix sponsa	2	0.04	0.03	1	0.02	0.02			
Mallard	Anas platyrhynchos	1	0.02	0.02	1	0.02	0.02			
Ring-necked Pheasant	Phasianus colchicus	1	0.02	0.02	1	0.02	0.02	1	0.02	0.02
Wild Turkey	Meleagris gallopavo	1	0.02	0.02	1	0.02	0.02			
Great Blue Heron	Ardea herodias	3	0.06	0.03	1	0.02	0.02			
Green Heron	Butorides virescens	5	0.10	0.07	3	0.06	0.06			
Black Vulture	Coragyps atratus	1	0.02	0.02						
Red-tailed Hawk	Buteo jamaicensis	1	0.02	0.02	1	0.02	0.02			
Mourning Dove	Zenaida macroura	22	0.43	0.09	18	0.35	0.08	1	0.02	0.02
Chimney Swift	Chaetura pelagica	1	0.02	0.02	1	0.02	0.02			
Ruby-throated Hummingbird	Archilochus colubris	2	0.04	0.04						
Red-bellied Woodpecker	Melanerpes carolinus	7	0.14	0.06	5	0.10	0.05			
Downy Woodpecker	Picoides pubescens	1	0.02	0.02	1	0.02	0.02			
Hairy Woodpecker	Picoides villosus	1	0.02	0.02	1	0.02	0.02			
Northern Flicker	Colaptes auratus	1	0.02	0.02	1	0.02	0.02	1	0.02	0.02
Eastern Wood-Pewee	Contopus virens	5	0.10	0.04	5	0.10	0.04	5	0.10	0.04
Acadian Flycatcher	Empidonax virescens	2	0.04	0.03	2	0.04	0.03	1	0.02	0.02
Willow Flycatcher	Empidonax traillii	34	0.67	0.10	26	0.51	0.09	11	0.22	0.06
Great Crested Flycatcher	Myiarchus crinitus	1	0.02	0.02						
Eastern Kingbird	Tyrannus tyrannus	7	0.14	0.05	3	0.06	0.03	1	0.02	0.02
White-eyed Vireo	Vireo griseus	3	0.06	0.03	2	0.04	0.03	1	0.02	0.02
Warbling Vireo	Vireo gilvus	1	0.02	0.02	1	0.02	0.02			
Red-eyed Vireo	Vireo olivaceus	7	0.14	0.06	5	0.10	0.04	7	0.14	0.05
Blue Jay	Cyanocitta cristata	6	0.12	0.05	3	0.06	0.03	4	0.08	0.04
Tree Swallow	Tachycineta bicolor	11	0.22	0.06	7	0.14	0.06	•	0.00	0.0 .
Barn Swallow	Hirundo rustica	5	0.10	0.05	3	0.06	0.03			
Tufted Titmouse	Baeolophus bicolor	5	0.10	0.05	4	0.08	0.05	5	0.10	0.05
White-breasted Nuthatch	Sitta carolinensis	3	0.06	0.04	2	0.04	0.03	_		
Carolina Wren	Thryothorus Iudovicianus	1	0.02	0.02	1	0.02	0.02	1	0.02	0.02
House Wren	Troglodytes aedon	26	0.51	0.10	23	0.45	0.09	14	0.27	0.06
Blue-gray Gnatcatcher	Polioptila caerulea	13	0.25	0.06	10	0.20	0.06	8	0.16	0.05
Wood Thrush	Hylocichla mustelina	10	0.20	0.06	7	0.14	0.06	8	0.16	0.06
American Robin	Turdus migratorius	46	0.90	0.14	29	0.57	0.10	20	0.10	0.07
Gray Catbird	Dumetella carolinensis	124	2.43	0.14	92	1.80	0.14	37	0.73	0.07
Northern Mockingbird	Mimus polyglottos	4	0.08	0.04	4	0.08	0.04	1	0.02	0.02
Brown Thrasher	Toxostoma rufum	7	0.14	0.05	6	0.12	0.05	'	0.02	0.02
European Starling	Sturnus vulgaris	7	0.14	0.05	4	0.12	0.05			
Cedar Waxwing	Bombycilla cedrorum	24	0.47	0.16	5	0.10	0.05	2	0.04	0.03
Ovenbird	Seiurus aurocapilla	4	0.47	0.10	3	0.16	0.04	1	0.04	0.03
Common Yellowthroat	Geothlypis trichas	12	0.24	0.07	8	0.16	0.05	10	0.20	0.02
American Redstart	Setophaga ruticilla	6	0.12	0.05	6	0.10	0.05	10	0.20	0.06
Yellow Warbler	Setophaga petechia	53	1.04	0.03	39	0.76	0.03	35	0.69	0.08
Eastern Towhee	Pipilo erythrophthalmus	20	0.39	0.08	15	0.70	0.08	14	0.09	0.06
Field Sparrow	Spizella pusilla	32	0.59	0.08	24	0.29	0.08	27	0.27	0.08
		88				1.29				0.08
Song Sparrow	Melospiza melodia	57	1.73	0.17	66 34		0.15	66 27	1.29	
Northern Cardinal	Cardinalis cardinalis	57 7	1.12	0.14		0.67	0.11	27	0.53	0.09
Indigo Bunting	Passerina cyanea		0.14	0.05	6 64	0.12	0.05	4 52	0.08	0.05 0.14
Red-winged Blackbird	Agelaius phoeniceus	77 20	1.51	0.25	64	1.25	0.22	52	1.02	0.14
Common Grackle	Quiscalus quiscula	30 27	0.59	0.13	11 22	0.22	0.08	6	0.12	0.05
Brown-headed Cowbird	Molothrus ater	37	0.73	0.15	23	0.45	0.12	6	0.12	0.05
Orchard Oriole	Icterus spurius	6	0.12	0.05	5	0.10	0.04	2	0.04	0.00
Baltimore Oriole	Icterus galbula	1	0.02	0.02	1	0.02	0.02	2	0.04	0.03
American Goldfinch	Spinus tristis	22	0.43	0.10	6	0.12	0.05	2	0.04	0.03

APPENDIX TABLE 6. Estimated effective detection radius (EDR) and density (birds km⁻²), with 95% confidence intervals (CI), for species with >25 detections on standard 5 min point counts. Scientific names of species are given in the text or in Appendix Table 5.

Species	Cues	n	Detection function	EDR	95% CI	Density	95% CI
Willow Flycatcher	Song ^a	33	Hazard	92.0	83.7–101.2	15.9	13.1–19.3
House Wren	Song	23	Uniform	69.5	52.8-91.3	21.7	12.6-37.2
	All	27	Uniform	65.7	52.6-82.1	28.0	18.0-43.8
American Robin	Song	27	Uniform	64.1	53.1-77.5	28.3	19.4-41.2
	All	35	Uniform	59.8	53.5-66.9	39.0	31.1-48.7
Gray Catbird	Song	97	Half-normal	46.0	41.4-51.5	145.9	118.2-180
	All	123	Half-normal	44.9	41.1-49.0	196.4	164.1-235
Yellow Warbler	Song	52	Half-normal	73.3	59.8-89.7	35.0	23.4-52.4
	All	53	Half-normal	72.0	59.2-87.5	37.0	25.1-54.6
Eastern Towhee	Song ^a	20	Uniform	100.0	100-100	8.8	8.5-9.0
Field Sparrow	Song	23	Half-normal	72.5	53.8-97.7	19.6	10.9-35.3
	All	31	Negative exponential	43.0	30.5-60.5	71.3	36.5-139.5
Song Sparrow	Song	85	Half-normal	79.3	67.67-93	47.8	34.7-65.7
	All	88	Uniform	76.0	65.1-88.6	53.3	39.2-72.6
Northern Cardinal	Song	46	Half-normal	69.9	56.8-86	37.0	24.5-55.9
	All	56	Negative exponential	46.6	35.5-61.2	104.2	60.8-178.6
Red-winged Blackbird	Song	55	Hazard	82.0	66.8-100.7	34.3	22.7-51.7
	All	73	Uniform	70.6	61-81.8	60.1	44.5-81.2
Brown-headed Cowbird	All ^b	19	Half-normal	48.8	37.9–62.9	56.2	32.4–97.6

^a All detections were of singing birds.

^b All detections were of non-song cues.