



EXPERIMENTAL ANALYSIS OF THE AUDITORY DETECTION PROCESS ON AVIAN POINT COUNTS

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ABSTRACT.—We have developed a system for simulating the conditions of avian surveys in which birds are identified by sound. The system uses a laptop computer to control a set of amplified MP3 players placed at known locations around a survey point. The system can realistically simulate a known population of songbirds under a range of factors that affect detection probabilities. The goals of our research are to describe the sources and range of variability affecting point-count estimates and to find applications of sampling theory and methodologies that produce practical improvements in the quality of bird-census data. Initial experiments in an open field showed that, on average, observers tend to undercount birds on unlimited-radius counts, though the proportion of birds counted by individual observers ranged from 81% to 132% of the actual total. In contrast to the unlimited-radius counts, when data were truncated at a 50-m radius around the point, observers overestimated the total population by 17% to 122%. Results also illustrate how detection distances decline and identification errors increase with increasing levels of ambient noise. Overall, the proportion of birds heard by observers decreased by $28 \pm 4.7\%$ under breezy conditions, $41 \pm 5.2\%$ with the presence of additional background birds, and $42 \pm 3.4\%$ with the addition of 10 dB of white noise. These findings illustrate some of the inherent difficulties in interpreting avian abundance estimates based on auditory detections, and why estimates that do not account for variations in detection probability will not withstand critical scrutiny. *Received 8 February 2006, accepted 30 August 2006.*

Key words: ambient noise, detection probability, measurement error, point counts.

Análisis Experimentales del Proceso de Detección Auditiva en Puntos de Conteo de Aves

RESUMEN.—Desarrollamos un sistema para simular las condiciones de los muestreos de aves en donde los individuos son identificados por sonido. El sistema emplea una computadora portátil para controlar un juego de reproductores MP3 amplificadas ubicados en sitios conocidos alrededor de un punto de conteo. El sistema puede simular de modo realista una población conocida de aves canoras dentro de un rango de factores que afectan las probabilidades de detección. Los objetivos de nuestra investigación son describir las fuentes y el rango de variabilidad

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que afectan las estimaciones en los puntos de conteo, y encontrar aplicaciones de la teoría y las metodologías de muestreo que produzcan mejoras prácticas en la calidad de los datos de censos de aves. Los experimentos iniciales en un campo abierto mostraron que, en promedio, los observadores tienden a subestimar el número de aves en conteos de radio ilimitado, aunque la proporción de aves contadas por los observadores individuales varió entre 81% y 132% del total real. A diferencia de los conteos con radio ilimitado, cuando los datos fueron truncados a un radio de 50 m alrededor del punto, los observadores sobreestimaron la población total entre 17% y 122%. Los resultados también enseñan cómo las distancias de detección disminuyen y cómo los errores de identificación aumentan con mayores niveles de ruido ambiental. En general, la proporción de aves escuchadas por los observadores disminuyó un $28 \pm 4.7\%$ bajo condiciones de brisa, $41 \pm 5.2\%$ con la presencia adicional de aves de fondo y $42 \pm 3.4\%$ con la adición de 10 dB de ruido blanco. Estos hallazgos ilustran algunas de las dificultades inherentes para interpretar las estimaciones de abundancia de aves basadas en detecciones auditivas, y por qué las estimaciones que no tienen en cuenta las variaciones en las probabilidades de detección no soportarán un escrutinio crítico.

POINT COUNTS ARE USED extensively to monitor spatial and temporal patterns of bird abundance, to assess species-habitat relationships, to evaluate the response of populations to environmental change or management, and to estimate species diversity. Surveys of breeding birds rely heavily on auditory detections, which can make up 70% of observations in suburban landscapes (Sauer et al. 1994), 81% in tropical forests (Scott et al. 1981), and 94% in closed-canopy deciduous forests (DeJong and Emlen 1985). Hundreds of thousands of point counts are conducted annually in North America across a spectrum of scales, from short-term site-specific studies (Simons et al. 2006) to long-term continental-scale surveys such as the Breeding Bird Survey (BBS; Sauer et al. 2005). Although the BBS, which comprises ~150,000 unlimited-radius counts conducted along some 3,700 roadside routes surveyed annually in the United States and Canada, is the largest and best-known survey, many additional point-count surveys are conducted each year by state, federal, and private land-management agencies. Bart (2005) estimated that between 1,000 and 2,000 independent programs currently gather long-term data on bird abundance in the United States and Canada. Many individual state natural-resource programs now conduct hundreds to thousands of point counts annually through their participation in the Partners in Flight program (Rich et al. 2004, Bart 2005). On federal lands, point-count surveys are important components of long-term natural-resource monitoring

programs conducted by the following departments of the U.S. government: Department of Interior, National Park Service (Briggs et al. 1996); Department of Agriculture, Forest Service (Young and Hutto 2002); Department of Interior, Fish and Wildlife Service (Somershoe and Chandler 2004); and Department of Defense (Althoff et al. 2004).

Bird abundance estimates are also a common feature of applied ecological research. Our brief survey of 355 research papers published in 2004 in the *Journal of Wildlife Management*, *Ecological Applications*, and *Conservation Biology* revealed that 23% reported on bird populations and, of those, 36% reported abundance estimates based on count data. However, despite the substantial time, effort, and money expended counting birds for research and monitoring, there is still considerable disagreement over the validity of various survey methods. Most of the disparity concerns the importance of estimating detection probabilities associated with individual counts (Anderson 2002, Hutto and Young 2002, Thompson 2002, Bart et al. 2004). Nevertheless, there is a general consensus among scientists that factors producing a biased trend in detection probability over space or time are the most problematic (Pollock et al. 2002, Williams et al. 2002, Bart et al. 2004). Consider, for example, how temporal trends in two environmental factors, ambient noise and climate, might impart trends in count data unrelated to the true abundance of bird populations (Fig. 1). There is no question that our world is becoming

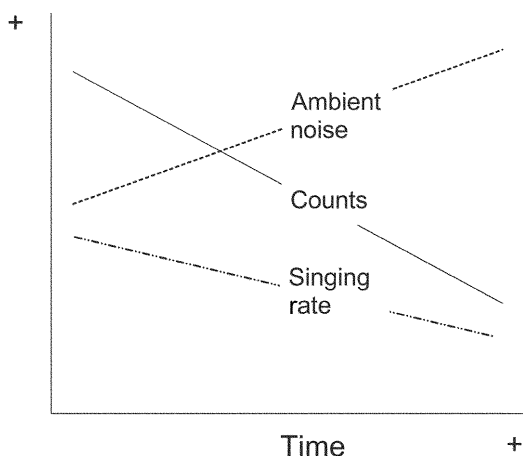


FIG. 1. Hypothetical relationship between trends in ambient noise, singing rates, and unadjusted auditory point counts.

noisier (Wolkomir and Wolkomir 2001). If ambient noise increases each year, detection probabilities and counts of birds identified by sound will presumably decline over time as well. Global climate change may affect trends in detection probability in a similar manner. There is increasing evidence that birds are breeding earlier now than in the past, presumably because of global warming (Butler 2003). Male birds sing at higher rates early in the breeding season, when competition for females is strongest (Collins 2004). Therefore, if survey dates are standardized (as they are in most monitoring programs), counts based on vocalizations are likely to decline over time, simply because observers are hearing fewer birds, even if actual population levels are stable. Trends in other factors affecting detection probabilities, such as observers or habitat conditions, can impart similar biases (Sauer et al. 1994, Norvell et al. 2003). For example, a recent analysis indicated that 76% of observers conducting Canadian BBS routes are >45 years old (Downes 2004; Fig. 2). Forty-five percent of observers cited "hearing loss" as their primary reason for retiring from the survey. As with ambient noise and singing rates, trends in age-related hearing loss can impart trends in count data that are unrelated to true abundance.

Spatial comparisons of count data can also suffer from biases attributable to differences in detection probability. Changes in vegetation density and structure over space or time

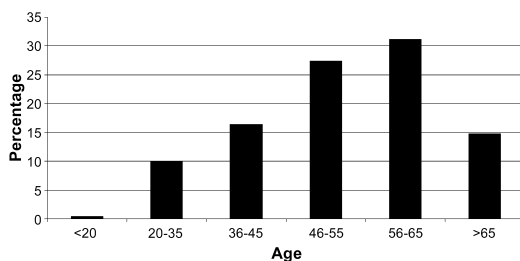


FIG. 2. Age distribution of Canadian volunteers conducting Breeding Bird Survey routes. Results are based on questionnaires returned by 263 volunteers in 2004 (Downes 2004).

can impart spatial or temporal biases in count data that are independent of true abundance (Bibby and Buckland 1987). In each of these examples, detection probability and counts are confounded. That is, there is often no way to distinguish between true differences in abundance estimates and differences in detection probability, unless detection probabilities are measured directly (Williams et al. 2002).

Standardizing protocols and modeling covariates, such as observer experience or age, can reduce biases associated with detection probability (Sauer et al. 1994, Link and Sauer 1998), but these approaches are often problematic, because multiple factors can influence detection probability simultaneously and because some factors influence both detection probability and abundance (J. D. Nichols pers. comm.). For example, two habitats with different vegetation structure may support different densities of a species because of differences in the availability of food or cover. At the same time, the detection probabilities of birds in these two habitats may vary because of differences in visibility or sound attenuation (Schieck 1997, Simons et al. 2006). Measuring detection probability directly is preferred over modeling covariates, because it is generally impossible to separate effects of covariates on detection probability and abundance and because factors affecting detection probability are often unknown or difficult to measure.

At least five methods of estimating detection probabilities on avian point counts are currently available: distance sampling (Buckland et al. 2001), multiple-observer methods (Nichols et al. 2000, Alldredge et al. 2006), time-of-detection methods (Farnsworth et al. 2002, Alldredge et

al. 2007a), double sampling (Bart and Earnst 2002), and repeated-count methods (Royle and Nichols 2003, Kéry et al. 2005). Applications of combined methods are also possible (Kissling and Garton 2006; Allredge et al. 2006, 2007a). Conceptually, the probability of detection has two components: the probability that a bird is available for detection (i.e., if detections are auditory, the probability that the bird sings during the count interval) and the probability of detecting a bird given that it is available (sings). Different methods estimate different components of the detection process. For example, distance sampling and multiple-observer approaches assume that all birds on a given sample plot are available (sing during the count interval), and they estimate the probability of detection given availability. Time-of-detection and repeated-count methods each provide unique estimates of the product of availability and detection given availability (Allredge et al. 2006, 2007a), but they cannot separate the two components.

In spite of these recent theoretical advances in our understanding of detection probability, and new methods for estimating it in the field, the use of unadjusted counts is still the norm in avian research and monitoring. Rosenstock et al. (2002) reviewed 224 papers from nine peer-reviewed journals reporting sampling techniques used to draw inference about bird abundance. They found that 95% of these studies relied on unadjusted counts. That is, count data collected in these studies were not adjusted for differences in detection probability among species, locations, observers, or sampling periods.

Quantifying detection bias and validating avian population-sampling methods is particularly difficult, because the true population size is rarely known. With some notable exceptions (Emlen and DeJong 1981, Scott et al. 1981, Bart and Schoultz 1984, DeJong and Emlen 1985, DeSante 1986, Schieck 1997, Haselmayer and Quinn 2000), many assumptions of common avian population-sampling methods remain untested.

We are in the process of conducting a series of validation experiments that simulate survey conditions when birds are identified by sound. These experiments are quantifying the biases and precision of current sampling methods by varying some of the conditions that influence

detection probability and assessing the costs and benefits of applying different methods of estimating detection probability.

The factors we are evaluating in our experiments include both "measurement error" factors associated with observer skill and ability and "signal-to-noise ratio" factors that influence how much information about bird diversity and abundance is available to observers. Measurement error factors include the ability of observers to accurately estimate distances to singing birds, to correctly identify species and the number of individual birds at a point, and the ability of observers to apply meaningful movement and countersinging rules to avoid double counting. Signal-to-noise ratio factors include the spectral qualities of the song, song volume, singing rate, orientation of singing birds (toward or away from observers), number of species and number of individuals singing during a count, vegetation structure, topography, temperature, humidity, and ambient noise. Systematic variation in any of these factors will impart a systematic bias in count data. Here, we describe the simulation system and present results from initial experiments comparing fixed-radius and unlimited-radius plots in an open field and from experiments on the effects of ambient noise on observer performance. Results from companion experiments examining other factors affecting the detection process (Allredge et al. 2007b) and evaluating distance measurement error (Allredge et al. 2007c) are presented elsewhere.

METHODS

The simulation system consisted of a laptop personal computer (PC) attached via a serial port to a radio frequency (418 MHz) transmitter capable of controlling ≤ 64 individually addressable receiver-players (Fig. 3). Play lists that controlled the timing and location of songs played during each point-count experiment were constructed using a Microsoft EXCEL-based software tool written in Microsoft VISUAL BASIC. The PC maintained the play-list database and sent brief play-stop and track-select commands to remote receivers via the transmitter. Remote receivers used a microcontroller to decode messages, operate the MP3 players, and manage power. The transmitter, receiver, amplifier, and other components were custom-fabricated

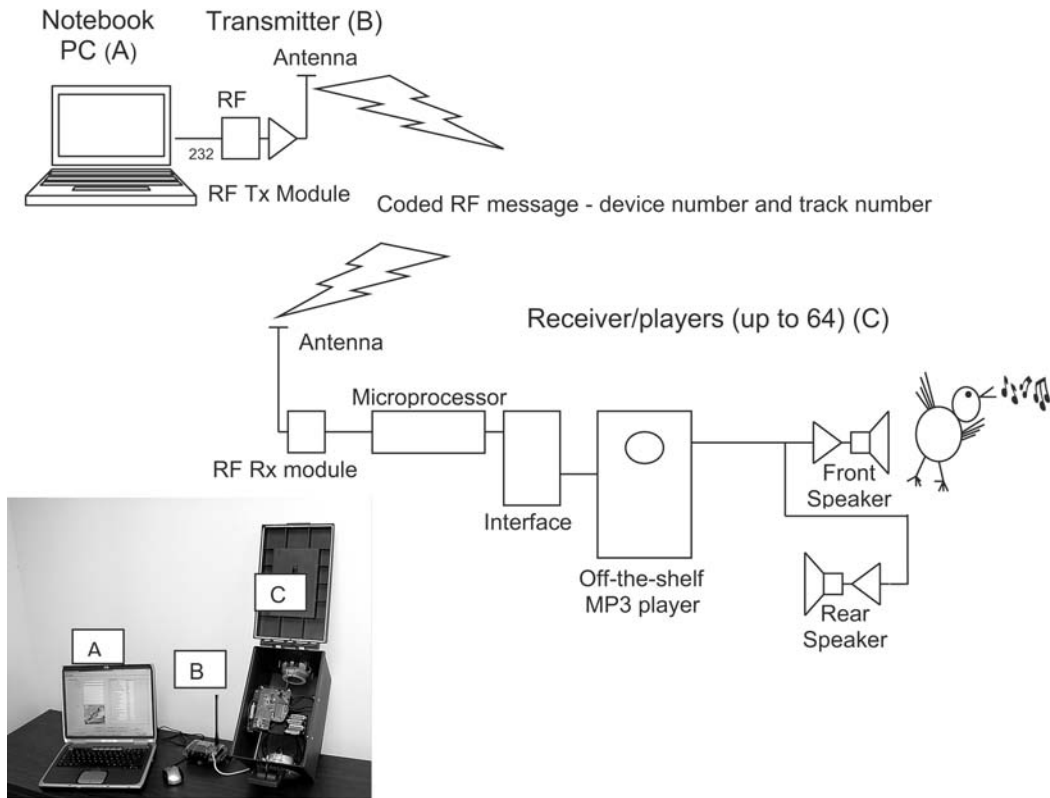


FIG. 3. System diagram of playback system: (A) laptop computer and play-list software, (B) transmitter, and (C) portable receiver–player.

to control a Rio 600 MP3 player. Headphone-level audio from the player was amplified to 3 watts (5% THD) and played through round 105-mm Poly Planar model MA 4054 waterproof marine speakers (3.8 ohms, 40 watts). Speaker frequency response was resonance-free and flat (± 3 dB) from 1 to 20 kHz. The speaker radiation pattern was a frequency-dependent teardrop cone with a minimum beam width of 30° at the highest frequencies and $\sim 180^\circ$ at 1 kHz, a pattern typical of any piston-type sound generator (Holland 2001).

Typical songs from Walton and Lawson (1999) were converted from the audio CD to 128 Kbps, 44,100 Hz, MP3 format using Adobe AUDITION software. Single examples of each species' song were used for all experiments. Singing rates based on Robbins et al. (1983) and intervals from Walton and Lawson (1999) ranged from 2–4 songs min^{-1} for the Black-and-white Warbler (*Mniotilta varia*) to 8–10 songs min^{-1} for the Wood Thrush (*Hylocichla mustelina*).

Achieving an acceptable level of system performance required several modifications of the original design during the development process. Initial calculations of the RF link budget and path loss assumed that a transmitter power level of 50 mW (150 m, -95 dBm receive MDS) was sufficient. In practice, signal attenuation caused by dense vegetation (~ 25 dB) was much higher than we expected (International Radio Consultative Committee 1990). Increasing transmit power to 1 watt resolved the problem. Initial system partitioning had most of the system logic and software burden in the PC. We subsequently determined that modern PCs running the Windows Operating System were not capable of reliably controlling our remote command system in real time. We overcame these limitations by moving all real-time logic to the remote receivers, and limiting PC–transmitter system functions to maintaining the playlist database and sending brief play–stop and track-select commands to remote receivers.

There were no practical constraints on receiver address rates, the number of receivers that could be played simultaneously, or the length and complexity of the play lists. The system had a minimum transmitter range of 500 m and a storage capacity of 50 individually selectable high-fidelity digital songs per player, and it was capable of operating on battery power for ≥ 8 h. The sound pressure of all broadcast songs was standardized to 90 dB (dBA, reference 20 μ Pa) at 1 m on the basis of sound-pressure measurements reported by Brackenbury (1979). Ambient and player sound-pressure measurements were made using a Martel Electronics model 325 sound-level meter (accuracy ± 1.5 dBA). Although all players were capable of broadcasting in both directions along a single axis, all active speakers in these initial experiments were aimed directly toward observers. Speakers were placed on 1-m-high platforms, or in trees at heights between 3 and 15 m.

Field experiments were conducted at Howell Woods, a 1,133-ha natural area in Johnston County, North Carolina. The site comprised mature bottomland and mixed pine-hardwood in an isolated rural setting. Ambient noise levels on quiet days were frequently < 40 dB. Experiments were conducted between mid-November and mid-March to minimize auditory interference from resident birds and insects. Our first experiments in March 2004 were done in an open field. Thirty players were positioned in a semicircle at distances from 10 to 120 m in front of observers. Players were placed on 1-m-high platforms distributed uniformly with respect to area. Fifteen experienced observers conducted 20 unlimited-radius 3-min counts. Eight to 12 individual birds were simulated at random locations on each 3-min count. Of these 216 individual birds, five species—Wood Thrush, Black-throated Blue Warbler (*Dendroica caerulescens*), Black-and-white Warbler, Ovenbird (*Seiurus aurocapilla*), and Hooded Warbler (*Wilsonia citrina*)—that produced 80% of the songs played were used for analysis. One or two individuals from 13 additional species were added to each count to provide variety. Observers mapped the locations of all birds heard onto data sheets, and the proportion of birds correctly identified was determined by comparing the data sheets to maps produced from the actual play list.

Experiments assessing the effects of ambient noise on observer performance were

conducted over three consecutive days in March 2005. Six skilled observers from the U.S. Geological Survey Patuxent Wildlife Research Center in Laurel, Maryland, participated. The experiment used 25 players arrayed along a linear transect in front of the observers in a mixed pine-hardwood forest. Players were spaced at 5-m intervals between distances of 40 m and 160 m. Songs of six species—Northern Parula (*Parula americana*), Yellow Warbler (*D. petechia*), Chestnut-sided Warbler (*D. pensylvanica*), Black-throated Blue Warbler, Black-throated Green Warbler (*D. virens*), and Hooded Warbler—were played randomly at each distance for ~ 20 s. Observers were given an automated auditory cue, "next," from a speaker at the survey point and asked to identify the singing species. Experiments were replicated under four ambient-noise conditions: quiet (mean ambient noise \pm SD: 40.6 ± 4.47 dB), breezy (gusty winds, $10\text{--}25$ km h^{-1} ; 55.4 ± 3.87 dB), quiet conditions with white noise added (10 dB above ambient), and quiet conditions with one to three background birds (Winter Wren [*Troglodytes troglodytes*], Yellow-throated Warbler [*D. dominica*], and Ovenbird) singing 40 m behind and to either side of the observers. White noise (uniform power; spectral frequency = 1.0) was played from a speaker facing the observers at a distance of 10 m.

We present exact 95% confidence intervals (CI) for differences between means based on the *t* distribution (Zar 1999).

RESULTS

Data from the simplified experiment conducted in an open field in March 2004 illustrate our experimental approach and initial results. Estimates were quite variable among observers. The proportion of total birds counted by individual observers ranged from 81% to 132% of the actual total (Fig. 4A). Observers tended to undercount birds on unlimited-radius counts (10 of 15 observers undercounted; mean percentage detected: $96.0 \pm 6.3\%$), and they substantially underestimated the numbers of Black-and-white Warblers (mean: $68.6 \pm 7.8\%$) and Hooded Warblers (mean: $84.1 \pm 8.9\%$) simulated in the experiment.

In contrast to the unlimited-radius counts, when data were truncated at a 50-m radius around the point, observers overestimated the

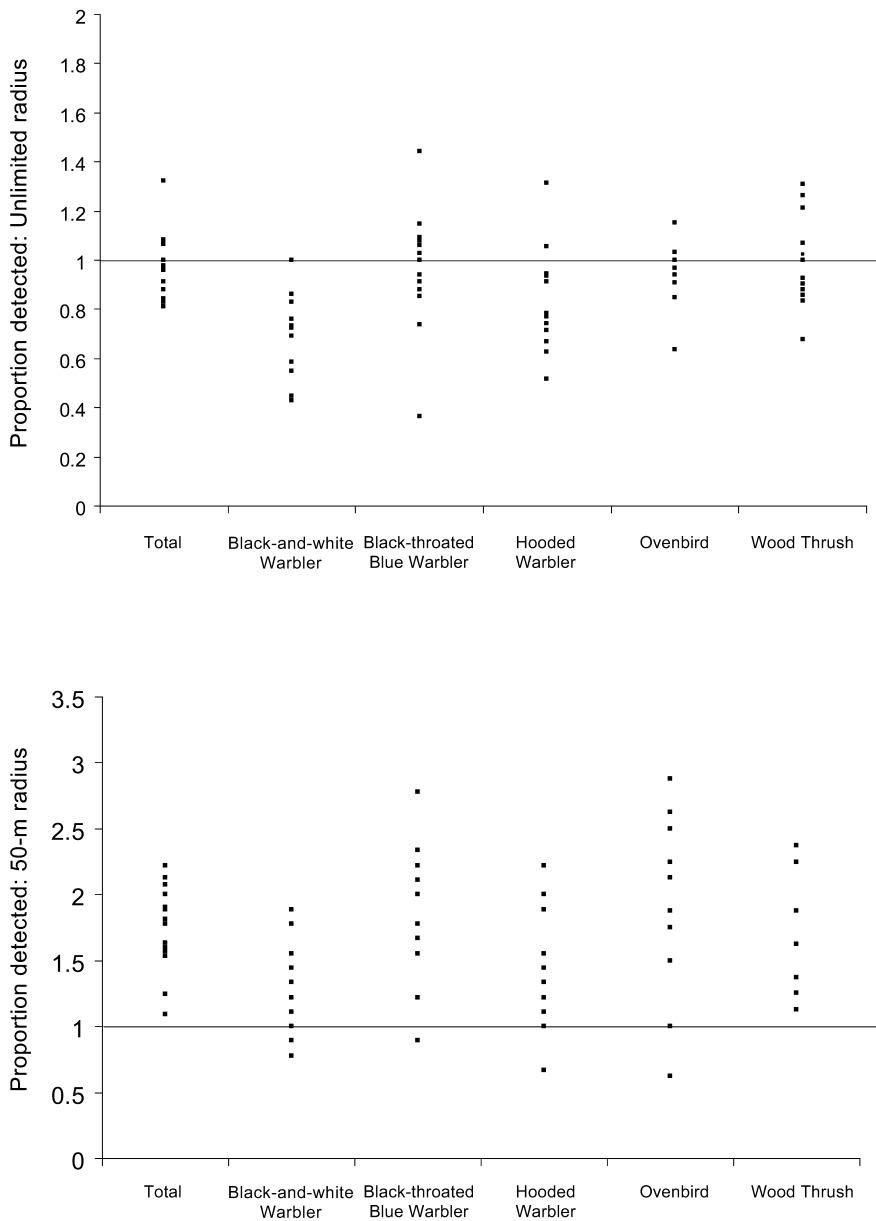


FIG. 4. (A) Proportion of 216 individual birds simulated on 20 unlimited-radius 3-min counts detected by 15 observers (symbols for some observers overlap). Observers significantly underestimated numbers of Black-and-white Warblers ($t = -7.05$, $df = 14$, $P < 0.001$) and Hooded Warblers ($t = -3.13$, $df = 14$, $P < 0.01$). (B) Ability of 15 observers to estimate birds within a 50-m radius on twenty 3-min point counts (symbols for some observers overlap). Symbols indicate each observer's total count minus the true count of 54 birds (Black-and-white Warbler = 9, Black-throated Blue Warbler = 9, Hooded Warbler = 9, Ovenbird = 8, Wood Thrush = 8). Observers significantly overestimated the numbers of each species within 50 m ($t > 3.34$, $df = 14$, $P < 0.0025$).

total population by 17–122% (mean overestimate: $77.0 \pm 15\%$; Fig. 4B). The true total number of birds within 50 m, for the 20 counts used in this experiment, was 54 birds.

Results for Black-throated Blue Warbler illustrate the performance of six observers under all four ambient-noise conditions (Fig. 5). Under quiet conditions (Fig. 5A), all six observers correctly identified Black-throated Blue Warbler out to ~ 70 m, and some observers correctly identified them all the way out to 160 m. When the wind was gusting from 10 to 25 km h^{-1} (Fig. 5B), few observers detected birds beyond 90 m, and the number of misidentifications increased. Similarly, when we added 10 dB of white noise on a quiet day (Fig. 5C), most observers did not detect birds beyond 75 m. Finally, on a quiet day, when we added additional birds calling around our observers (Fig. 5D), we saw both a reduction in detection distance and an increase in misidentifications.

Under quiet conditions, mean maximum detection distances for all six observers ranged from 114 m for Black-throated Green Warbler to 157 m for Hooded Warbler (Table 1). Overall, average maximum detection distances were reduced $24 \pm 6.8\%$ by breezy conditions, $32 \pm 5.7\%$ by the presence of background birds, and $46 \pm 5.5\%$ by the addition of 10 dB of white noise. Note that on a circular avian point-count plot, reducing the maximum detection distance on the plot by 46% results in a 70% reduction in the area sampled.

Under quiet conditions, the proportion of all songs played that were heard by observers ranged from 60% for Black-throated Green Warbler to 83% for Hooded Warbler, and the proportion of songs heard that were misidentified by observers ranged from 0% for Hooded Warbler to 10% for Northern Parula (Table 2). Overall, the proportion of birds heard decreased by $28 \pm 4.7\%$ under breezy conditions,

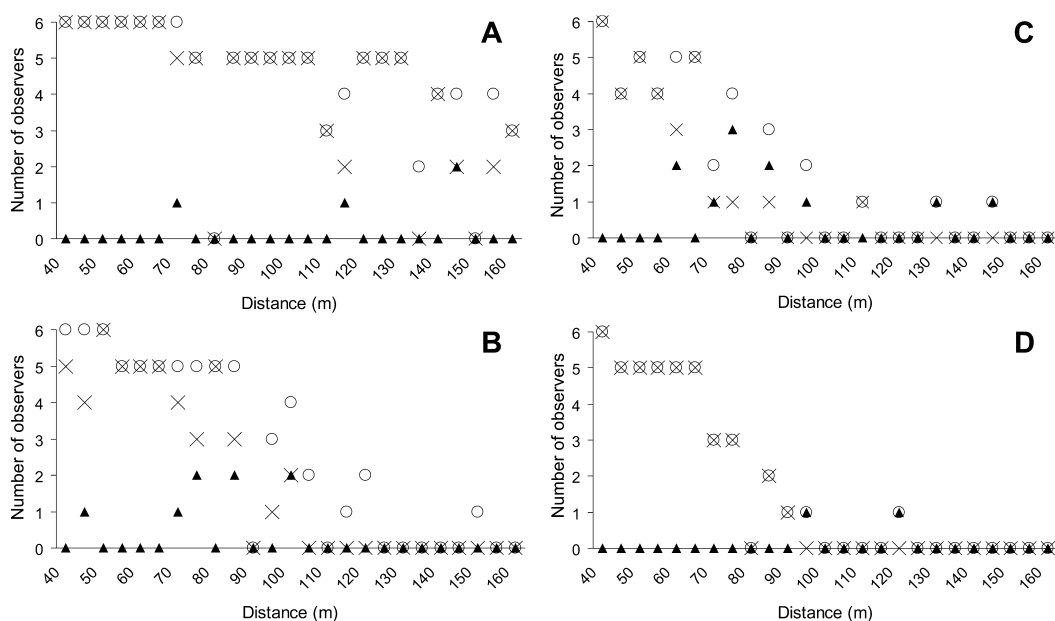


FIG. 5. Number of six observers able to hear (O) and correctly identify (x), and number of observers who misidentified (▲), calls of Black-throated Blue Warblers at 25 distances between 40 m and 160 m. Calls were played randomly at each distance for ~ 20 s. Experiments were replicated under four ambient-noise conditions: (A) quiet (mean ambient noise 40.6 ± 4.47 dB), (B) breezy (gusty winds 10–20 km h^{-1} ; 55.4 ± 3.87 dB), (C) quiet conditions with three background birds (Winter Wren, Yellow-throated Warbler, Ovenbird) singing 40 m behind or to either side of the observers, and (D) quiet conditions with white noise added (10 dB above ambient). White noise (uniform power; spectral frequency = 1.0) was played from a speaker facing the observers at a distance of 10 m.

TABLE 1. Maximum detection distances (m; means \pm SE) for songs of six species of wood warblers in four ambient-noise conditions ($n = 6$ observers; 25 distances between 40 m and 160 m; broadcast volume 90 dB at 1 m).

Conditions	Black-and-white Warbler	Black-throated Green Warbler	Chestnut-sided Warbler	Hooded Warbler	Northern Parula	Yellow Warbler	Overall
Quiet	136.7 \pm 15.6	114.2 \pm 14.9	133.3 \pm 15.9	156.7 \pm 3.7	131.7 \pm 8.8	139.2 \pm 7.1	135.3 \pm 4.7
Breezy	83.3 \pm 8.2	136.7 \pm 17.6	95.0 \pm 12.9	123.3 \pm 13.5	110.0 \pm 14.7	91.7 \pm 12.1	103.3 \pm 5.3
Quiet + background birds	63.3 \pm 10.2	71.7 \pm 19.2	103.3 \pm 10.8	110.8 \pm 6.7	80.0 \pm 9.2	115.0 \pm 11.0	91.5 \pm 5.2
Quiet + 10 dB white noise	70.0 \pm 8.0	64.2 \pm 14.4	70.8 \pm 5.4	85.0 \pm 11.2	77.5 \pm 7.2	72.5 \pm 6.0	73.3 \pm 3.4

TABLE 2. Proportions of six species of wood warblers heard and proportion heard that were misidentified (in parentheses) under four ambient noise conditions ($n = 6$ observers; 25 total songs per species at distances between 40 and 160 m; broadcast volume 90 dB at 1 m).

Conditions	Black-and-white Warbler	Black-throated Green Warbler	Chestnut-sided Warbler	Hooded Warbler	Northern Parula	Yellow Warbler	Overall
Quiet	0.74 (0.03)	0.60 (0.03)	0.74 (0.03)	0.83 (0.00)	0.77 (0.10)	0.74 (0.03)	0.74 (0.04)
Breezy	0.44 (0.05)	0.49 (0.01)	0.43 (0.01)	0.57 (0.02)	0.41 (0.02)	0.44 (0.05)	0.46 (0.03)
Quiet + background birds	0.29 (0.07)	0.29 (0.04)	0.35 (0.01)	0.43 (0.03)	0.31 (0.04)	0.28 (0.00)	0.32 (0.03)
Quiet + 10 dB white noise	0.28 (0.01)	0.31 (0.02)	0.30 (0.02)	0.39 (0.01)	0.30 (0.00)	0.33 (0.02)	0.32 (0.01)

by $41 \pm 5.2\%$ with the presence of background birds, and by $42 \pm 3.4\%$ with the addition of 10 dB of white noise. The addition of 10 dB of white noise decreased misidentification rates to $1.3 \pm 0.6\%$ compared with all other ambient-noise conditions ($>2.8 \pm 0.9\%$).

DISCUSSION

We believe that the system described here accurately simulates conditions encountered by observers on auditory avian point counts. Feedback from highly experienced observers participating in >4,000 simulated point counts has confirmed that conditions on playback experiments are essentially indistinguishable from those on actual point counts. Nevertheless, we intentionally simplified the design of most experiments to reduce the number of variables in our analyses and to isolate specific aspects of the detection process. For example, to minimize variability associated with environmental factors and species identification, we conducted most experiments in a single habitat type, under quiet leaf-off conditions, using single examples of each species' song that we provide to observers before each experiment. We do not simulate bird movement, and we maintain a minimum 45° separation between individuals of the same species to minimize matching errors when scoring observer results. Thus, in most cases, levels of accuracy and precision reported from these experiments are probably higher than those expected in actual field studies.

Avian population-sampling methods in use today have evolved from the species check-lists and tallies of abundance familiar to anyone who enjoys watching birds. Comparisons of count indices over space or time are often based on implicit assumptions that differences in detection probability among species, habitats, or locations do not impart a temporal or spatial bias to abundance estimators. Evidence from a variety of sources argues strongly against the validity of these assumptions.

Ecologists studying avian vocal communication have made tremendous progress in identifying and quantifying how factors affecting signal attenuation and degradation define the "active space" (the area within which a signal is recognizable) shared among species and individuals (Wiley and Richards 1982, Slabbekoorn 2004). Active space is synonymous in many

ways with detection probability, and the rich literature of avian communication documents how it is shaped by ambient noise, temperature, humidity, topography, vegetation, air turbulence, and the rate, volume, and spectral characteristics of avian song. If these factors influence bird-to-bird signaling in predictable ways, they surely must influence human perception of these signals when they are used to estimate bird abundance. For example, our initial experiments in an open field illustrate well-known relationships between signal frequency and attenuation (Morton 1975, Wiley and Richards 1982, Slabbekoorn 2004). Undercounting was greatest for the Black-and-white Warbler, a species with a high-frequency rapidly attenuating song, whereas overall observer performance (best precision and least bias) was highest for the Ovenbird, a species with a lower-frequency song that attenuates more slowly. When we attempted to adjust our data for species-specific differences in detection probability by truncating observations at 50 m (a practice commonly applied to point-count data to correct for unknown differences in detection probability; e.g., Lichstein et al. 2002), we introduced a positive bias for all species. Similarly, in a recent laboratory study, Lohr et al. (2003) demonstrated how variations in signal bandwidth, frequency modulation, and amplitude modulation produced signal masking that affected the ability of Budgerigars (*Melopsittacus undulatus*), Zebra Finches (*Taeniopygia guttata*), and Atlantic Canaries (*Serinus canaria*) to detect and discriminate auditory information. Results of our ambient-noise experiments suggested that similar processes affected the ability of human observers to detect and discriminate bird vocalizations. The masking effects of ambient noise reduced the proportion of songs detected on experimental counts by as much as 42%. Misidentification rates were highest among species with similar songs (Black-throated Blue Warbler, Black-throated Green Warbler, and Northern Parula) and lowest for the distinctive Hooded Warbler song. Ten percent of Northern Parula songs heard by observers under quiet ambient-noise conditions were misidentified. In all but two of these 24 misidentifications, the species heard was identified as a Black-throated Blue Warbler. Most observers indicate that they use the ascending trill at the end of the Northern Parula song to distinguish

this species from Black-throated Blue Warbler. Thus, any factor that obscured this portion of the Northern Parula song was likely to produce a misidentification.

Our results indicate that a complex interaction of factors shaping the sound environment determine the bias and precision of data collected on auditory avian point counts. Because the factors affecting detection probability can vary widely with species, habitats, and environmental conditions, it is unlikely that they are amenable to adjustments using simple calibrations. Furthermore, it is likely that our empirical estimates of bias and precision are conservative compared with those on actual point counts, because our experiments were conducted under simplified and carefully controlled conditions. The fact that a single factor, such as the addition of 10 dB of background noise, can introduce a negative bias exceeding 40% for counts of some species, suggests that detection bias can seriously compromise the quality of point-count data.

Like the literature on avian communication, the literature on the physiology and neuropsychology of human hearing is filled with knowledge of how the sound environment shapes our ability to recognize and localize sound (Blauert 2001) and the predictable patterns of age-related hearing loss (Gates and Mills 2005). Application of this knowledge to the ways we collect and interpret avian-abundance data is largely lacking. For example, consider the predictable relationships between age, hearing acuity, ambient noise, and detection probabilities on auditory avian point counts. Although prominent ornithologists have argued persuasively for >70 years that age-related hearing loss is a potentially serious source of bias in estimates of avian abundance (Saunders 1934, Mayfield 1966, Emlen and DeJong 1992), there is little evidence in the literature that avian count data are routinely adjusted to account for bias associated with hearing loss. Evidence that the average age in some observer cohorts may be increasing (Downes 2004; Fig. 2), that ambient-noise levels in most areas have increased steadily in recent decades (Wolkomir and Wolkomir 2001), and that this increase in ambient noise may be accelerating both the onset and the prevalence of hearing impairment (Wallhagen et al. 1997), suggests that multiple factors that reduce detection probabilities, but are unrelated to

true abundance, may impart declining trends in auditory avian point counts. In most cases, abundance estimates that do not account for these factors, or those based on unvalidated methods or lacking estimates of measurement error, will not withstand critical scrutiny.

As Slabbekoorn (2004:205) noted in his recent review of the ecology of birdsong, "singing in the wild is not a simple process." We hope that our attempts to experimentally evaluate the factors influencing detection probabilities on auditory avian point counts will contribute to a better understanding of this process and lead to practical improvements in the quality of bird-survey data (Fig. 6). The results presented here, and in companion papers examining the effects of detection distance, singing rate, species differences, and observer differences on detection probabilities (Alldredge et al. 2007b) and the utility of distance sampling for auditory point counts (Alldredge et al. 2007c) are the first installments of that effort. Ongoing experiments are evaluating the efficacy of multiple-observer, time-of-detection, and combined methods of estimating detection probability.

ACKNOWLEDGMENTS

We are very grateful to the many volunteers who assisted with this research: D. Allen, B. Beck, J. Begier, S. Bosworth, J. Brewster, A. Bleckinger, D. Boone, M. Brooks, G. Brown, B. Browning, S. Cameron, S. Campbell, J. Connors, D. Dawson, J. Dodson, B. Dowell, C. Dykestra, A. Ebird, P. Farrell, J. Finnegan, L. Gallitano, J. Gerwin, S. Horton, B. Hylton, M. Johns, C. Kelly, S. Kovach, E. Laurent, H. Legrand, M. Lynch, S. Mabey, J. Marcus, K. Miller, M. Miller, R. Myers, K. Pacifici, K. Pardieck, B. Peterjohn, A. Podolsky, C. Robbins, J. Sasser, S. Schulte, C. Sorenson, E. Swab, C. Szell, N. Tarr, K. Weeks, D. Williams, and D. Wray. C. M. Downes generously allowed us to cite her survey of Canadian Breeding Bird Survey volunteers. Electrical engineering students at North Carolina State University, J. Marsh, M. Williams, and M. Foster, provided valuable technical assistance. Funding for this research was provided by the U.S. Geological Survey Status and Trends Program; U.S. Department of Agriculture, Forest Service; U.S. Department of Interior, National Park Service; and the North Carolina Wildlife Resources Commission.



FIG. 6. Left panel: U.S. Geological Survey scientists associated with the Breeding Bird Survey participating in an experiment assessing the effects of ambient noise on detection probabilities (see Fig. 5) (left to right: Keith Pardieck, Bruce Peterjohn, Chandler Robbins, and Deanna Dawson; not shown: Barbara Dowell and Dan Boone). Right panel: linear array of players distributed at distances between 40 m and 160 m in front of observers.

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Associate Editor: A. M. Dufty, Jr.