JOURNAL OF FIELD ORNITHOLOGY
Formerly BIRD-BANDING
A Journal of Ornithological Investigation

VOL. 56, NO. 3 SUMMER 1985 PAGES 213–320

J. Field Ornithol., 56(3):213–223

THE SHAPE OF THE AUDITORY DETECTION FUNCTION AND ITS IMPLICATIONS FOR SONGBIRD CENSUSING

BY MICHAEL J. DEJONG AND JOHN T. EMLEN

Transect counts (observer moves along a predetermined line recording all birds detected on either side of the line) and point counts (observer, while stationary at a series of points, records all birds detected) have been extensively used in estimating bird densities (Ralph and Scott 1981, Verner and Ritter 1985). These counts can be converted into estimates of absolute density (birds per unit of area) if the area and coverage lying within the range of the observer's hearing and/or sight can be determined. There are many variations of transect and point counts, but wherever absolute densities have been desired, estimates of the distance from the observer (or transect line) to each detected bird were required in order to determine the size of the sampled area (Burnham et al. 1980, Ralph and Scott 1981). During the breeding season, when songbird population data are most often desired, the great majority of detections in closed habitats are auditory rather than visual, and direct measurements of the distances to unseen singing or calling birds, however critical, are rarely feasible. Observers have resorted to subjective distance estimation based largely on the loudness of the auditory cues, a procedure that depends heavily on the development of personal skills and is at best subject to considerable error.

The error inherent in these subjective distance estimates has, we believe, led to a misconception among census takers concerning the detectability of a birdsong with distance from the sound source (the auditory detection function, Fig. 1). In this paper we examine empirical and theoretical evidence that auditory detection approximates a constant function out to a maximum detection distance where it rather abruptly decreases to zero, rather than declining gradually between the observer and the maximum detection distance.

DETECTION ATTENUATION

In the interpretation of data from census operations using subjective distance estimates, it has generally been assumed there is a *gradually decreasing* density of bird detections away from the observer from essentially full (100%) detection at the transect line or observation point to zero at the limit of detectability. The actual shape of this decreasing detection function is not known and various observers have hypothesized linear, negative exponential, and normal rates of decrease as a function of distance (Eberhardt 1968, 1978, Emlen 1971, Järvinen and Väisänen 1975, Järvinen 1978, Burnham et al. 1980:47). While it seems reasonable to assume a gradually or gently decreasing function for the visual detection of birds, since birds farther away have a directly greater probability of being hidden by some intervening object, we know of no logical basis for assuming it for auditory detections.

As sound waves radiate from a source in an ideal medium without obstacles to produce scattering or absorption, the intensity of sound attenuates at the rate of 6 decibels (dB) for each doubling of distance (Peterson and Gross 1974). Sound attenuation in deciduous forest habitats averages about 1.5–2.0 times this rate, i.e., roughly 10 dB for each doubling of distance at frequencies used by most birds (2–6 kHz), and slightly greater for birds using higher frequency ranges (Morton 1975, Marten and Marler 1977, and Marten et al. 1977).

In clinical tests on human subjects, signal intensities slightly above a personal threshold level are always heard, while signal intensities slightly below that threshold level are never heard, thus sound detection with changes in intensity (or distance from sound source) approximates an all-or-none phenomenon. Near the minimum intensity level at which a sound can be detected, a narrow belt of intensities occurs in which the test subject is uncertain and, on repetition, varies his or her decision on whether the signal was detected. This is due to moment by moment fluctuations in the subject's auditory sensitivity and attentiveness. The width of this belt can be measured in terms of standard deviations from its median (defined as the threshold point) where detections are made 50% of the time. In test subjects, individual s.d. values for belt width (where ±2 s.d. includes 95% of the observations) averaged .69 dB in single sessions, .87 dB in a series of sessions on the same day, and 1.22 dB in sessions over a 23-day period (Wertheimer 1955, in Carhart and Jerger 1971). Applying a s.d. of 1.0 dB to bird observers in forest situations where, as we have seen, sound attenuates at ca. 10 dB with each doubling of distance, the width of the belt of detection uncertainty should be about ±15% of the threshold detection distance.

Considering the above, we can distinguish 3 theoretical curves or models of sound detection with distance attenuation: (1) a strict all-or-none model, where 100% of the signals are detected up to the threshold distance and 0% are detected beyond threshold (Fig. 1A), (2) an empirical and gently-sloping model, constructed from subjective distance estimations, where signal detections gradually decrease away from the observer (Fig. 1C), and (3) a threshold and steeply-sloping model, based on the physical principles of sound attenuation and the demonstrated belt of uncertain detections, where 100% of the signals are detected far from the observer followed by a narrow belt where detections quickly drop to 0% (Fig. 1B). We propose that the steeply-sloping threshold model most closely approaches the true auditory detection function as it is reflected in census operations. In this study we tested this proposition

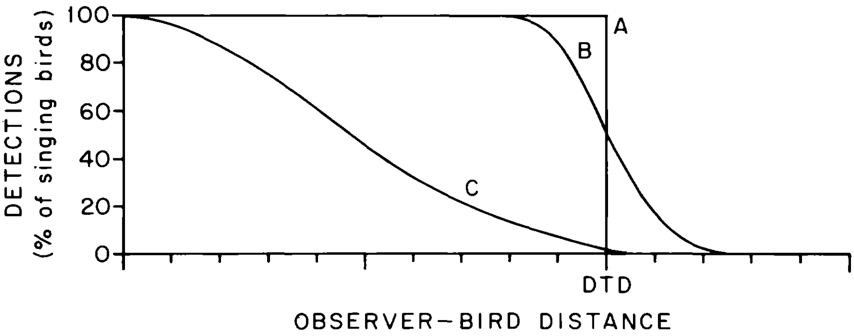

FIGURE 1. Theoretical auditory detection functions. Model "A" (a strict all-or-none curve) would be produced under conditions of complete detection of all vocalizations within the detection threshold distance (DTD) and zero detections beyond DTD. Model "B" is a steeply-sloping threshold curve based on acoustical principles of essentially all-or-none sound detection modified to account for moment by moment fluctuations in observer auditory sensitivity. Model "C" represents a characteristic empirical curve, based on data from subjective evaluations of distance to unseen vocalizing birds.

by: (a) using observer responses to taped playback of bird songs in the field, and (b) calculating the effect of realistic distance estimation errors on a simulated all-or-none curve.

METHODS

For the study using taped playback songs we used 8 observers with tested full normal hearing in a deciduous forest near Madison, Wisconsin, in late summer after most natural song had decreased to near zero. Each observer was asked to independently record the exact moment at which he/she first detected a song as they approached a pair of loudspeakers located 3 m above the ground and 40 m apart (one speaker closer than the other to the approaching observers). Each observer began 300 m from the nearest loudspeaker and advanced on command at intervals of 10 m. Recordings of 11 local species were played randomly from the 2 speakers and in random sequences at standardized and approximately natural intensities (see Emlen and DeJong 1981 for more details of the field procedure). Detection times and distances were later matched with known playback schedules to provide a record of all detected and missed playback songs at each distance for each observer. We used the mean maximum distance at which the 8 observers detected playback song of each species as the detection threshold distance (DTD) for that species.

For the study of distance estimation errors we recorded the field performance of two observers, one highly trained in distance estimation under the intensive program developed by Kepler and Scott (1981) in Hawaii; the other without such formal training. Both observers had 4 or more years of census experience in forest habitats, were familiar with the local Wisconsin forest bird fauna, were between 25 and 30 years old, and had excellent hearing as tested by audiometry.

Each observer, tested independently in early July while natural song was still plentiful, stationed himself at a series of listening points in the forest while two assistants located singing birds in the surrounding areas. All communication among the observer and assistants was through portable radios to reduce the possibility that the assistants or their voices might serve as distance cues. When a vocalizing bird was precisely located by an assistant, he radioed to determine whether the observer had detected the vocalization. If he had, the observer made a subjective estimate of the distance and the assistant marked the exact location of the bird with plastic flagging. Often a single vocalization was sufficient to be detected and recorded, much as in actual census operations. Birds that were seen as well as heard by the observer were included, as they would have been in actual census operations. After 10–15 birds had been detected from an observation point, all of the distances were measured with a tape and later compared to the observer's estimated distances.

We used these measurements of distance estimation errors in computer simulated censuses of simulated populations in order to demonstrate their effect on the shape of the detection function. For these simulations the "birds" were randomly distributed over an imaginary 500 ha grid. Census points were randomly placed, all singing birds within the detection threshold distance were considered to have been detected, and each bird was counted only once. Eight such simulated censuses of 30 points each were run. The entire census area around the observer was divided into 8 concentric zones according to the distance from the observer. The density of birds detected in each of these zones was calculated and plotted.

RESULTS

Data from the taped playback study are summarized in Fig. 2. These detection density (DD) curves approximate the steeply-sloping threshold model of auditory detection (Fig. 1B) more closely than they do the gently-sloping model (Fig. 1C). Variations between individual observers in these curves can often be attributed to observer traits, for example: the relatively gentle slope in observer D's curve is associated with lesser experience in local bird identification; the proximal misses of observer A, an older man with a slight hearing deficiency at high frequencies, are the result of his missing the Blue-gray Gnatcatcher (*Polioptila caerulea*) song at distances where the other observers heard it; and the extended detection range of observers C and E is associated with exceptionally high hearing acuity as revealed in their audiometric tests. In addition to each observer's performance with respect to the mean DTD for all observers as shown in Fig. 2, each observer detected virtually all (95–100%) playback songs at distances closer than .8 of his/her personal maximum detection distance (for each species); a substantial majority (80%) at distances between .8–.9 of his/her personal maximum distance, and a clear majority (69%) at distances greater than .9 of the maximum distance. Again this supports a steeply-sloping threshold model for sound detection with distance.

Our data on the magnitude of distance estimation errors under field conditions compared very favorably with those reported by Scott and Ramsey (1981), and revealed estimated distances ranging from .4 to 1.5 times the measured distances. The mean error approximated zero for both observers (+.7% ± 13.31 (mean ± 1 s.d.) for the trained observer (n = 90) and −.9% ± 20.66 for the untrained observer (n = 56)). This small mean error only indicates that they overestimated and underestimated distances about equally. When the signs of all distance errors are ignored, the mean error magnitude was 9.5% ± 9.33 for the trained observer and 16.6% ± 12.17 for the untrained observer. On this basis we propose that a trained observer may be expected to approach accuracies of ±10% estimation errors, while untrained observers approach

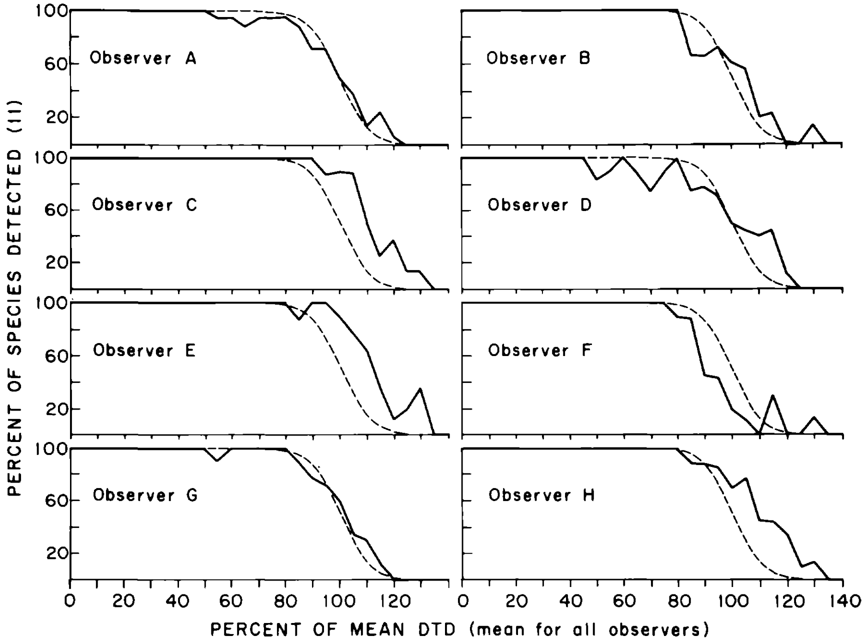

FIGURE 2. Detection density (DD) curves of 8 experienced observers (with tested full or nearly full hearing acuity) to standardized playback songs of 11 bird species broadcast on two calm days (wind speed <3 m/s) in a deciduous forest habitat. The curve for each observer represents his or her overall performance (mean of all 11 species). Since each species has its own characteristic DTD (the mean of all observer's maximum detection distance), the horizontal axis reflects a standardized distance expressed as a percent of each DTD. The dashed curve in each graph is the steeply-sloping threshold curve seen in Fig. 1B.

±15%. We used these approximate values (10% ± 9.0 and 15% ± 12.0) to demonstrate estimation error effects on detection density curves in our simulation models.

Figure 3 shows the mean (of 8 simulations) detection density curves for the census simulations with distance estimation errors. The detection density did not decrease with distance from the observer in the first histogram (3A) where all vocalizing birds within the detection range (DTD) were detected and "estimates" were without error. It did decrease, however, in histograms 3B and 3C which are based on the same data but with the incorporation of 10% and 15% mean distance esti-

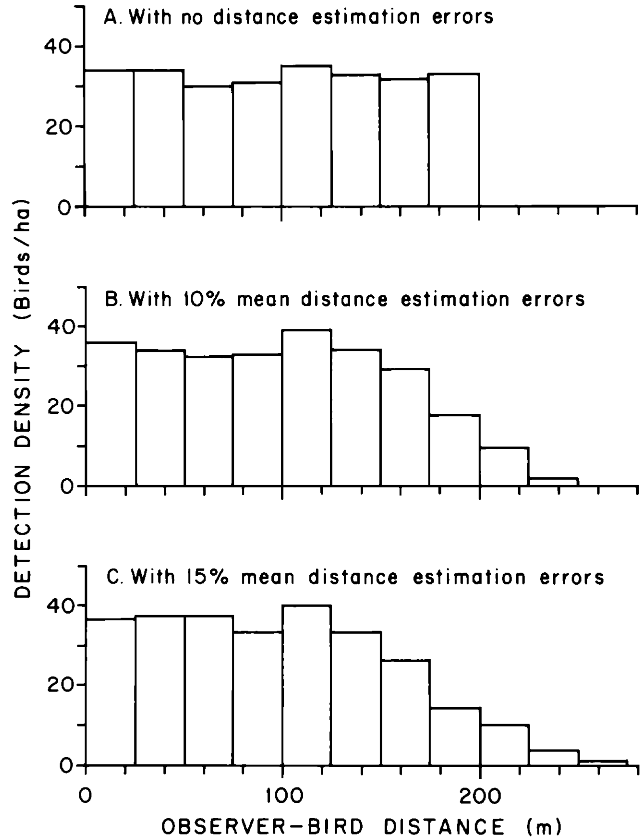

FIGURE 3. Effect of mean distance estimation errors of 10% and 15% on the shape of detection function in a computer simulation of point count censuses (mean of 8 simulations of 30 points each). Each simulation assumes a density of one bird per hectare, complete detection to a DTD of 200 m, a listening time of 4 min/point, and a random 10% singing frequency (10% of the birds sing in any given moment)—an estimate based on field data from Emlen (unpublished) and from Scott and Ramsey (1981).

mation errors respectively. These errors progressively reduce the number of apparent detections towards the detection threshold point at 200 m and also extended apparent detections beyond this actual DTD limit. This demonstrates that such errors are sufficient to transform a strict all-or-none function (Fig. 1A) into one resembling the gently-sloping estimate-based detection function (Fig. 1C).

DISCUSSION

Four direct lines of evidence appear to support the steeply-sloping threshold model of auditory detection (Fig. 1B) in deciduous forest habitats: (1) the model is based on established physical principles of sound attenuation and clinical measures of human hearing performance, (2) maximum detection distances for natural songs measured between an observer standing at his detection threshold distance and an assistant standing at the song perch were reasonably constant for each of 12 test species (Emlen and DeJong 1981), (3) maximum detection distances were similar among 8 observers listening to standardized intensity playback songs (op. cit.), and (4) records of detected and missed playback songs for each of 8 observers approaching loudspeakers playing standardized intensity songs approximated the steeply-sloping model (Fig. 2).

Indirect evidence of the threshold nature of the detection function is provided by our computer simulation of the effect of subjective distance estimation errors in census operations. These computer simulations showed that errors in distance estimation of realistic magnitude are sufficient to transform an all-or-none truncate detection function into one approximating those plotted by observers using subjective distance estimates. We can safely assume that data actually approximating the steeply-sloping threshold model could be as easily transformed as the strict all-or-none data used for illustration here.

Two field procedures commonly used in bird counting also alter the shape of the detection function and confuse their interpretation. First, visual detections are generally included with auditory detections. Visual detections tend to be much better represented in the proximal segments of a detection density curve, especially in forested habitats, producing a skew in curves based on total detections. Fortunately, visual detections constitute a minority of total detections in breeding season censuses in forested habitats (19% in Scott's Hawaiian studies (Scott et al. 1981), and as little as 6% in some of Emlen's temperate forest studies (unpublished)). We therefore suggest that visual detections should be recorded and analyzed separately or not at all in census operations where absolute density estimates are desired.

Related to this is the practice of including soft "conversational" call-notes in census operations. Most birds use soft call-notes in short distance communication. Since these soft-calls cannot be heard as far as songs and loud advertisement calls, they will skew the detection density curve similarly to the visual detections above. Any bird which is detected by such a call-note and does not also sing should be recorded separately or not used where absolute density estimates are desired. Loud call-notes used by some birds such as crows, jays, woodpeckers, etc. in long distance communication are equivalent to songs as indicators of a bird's presence and should be used in place of songs for these birds in census operations. In winter censuses where visual and call-note detections dominate and songs may be scarce or absent, different procedures reflecting those conditions are required.

Another procedural complication contributing to the gradually sloping detection density curves recorded in transect counts (but not point counts) arises from a common failure of observers to appreciate, when calculating area and time of census coverage, that the area of detection is a circle of radius DTD and not a 2DTD × 2DTD square (Affre 1976, Emlen and DeJong 1981). A geometrically decreasing relationship exists between the lateral distance of a point from the transect line and the length of time that point remains within the observer's hearing range as he moves along the line. The consequences of this lateral undersampling is a gradual lateral decrease in detection density. The amount of error and corrections for line transects have been described and discussed by Affre (1976).

There is some evidence that variability in song intensity due to song perch location may not be of major significance. Marten et al. (1977) and Marten and Marler (1977) found that the height of a song perch in a forest had little effect on excess sound attenuation (attenuation beyond the theoretical 6 dB per doubling of distance), so long as the bird was more than 1 m above the ground. Witkin (1977) showed that a small part of the Black-capped Chickadee (*Parus atricapillus*) vocalization (*chick-a-dee-dee*) had a greater intensity directly in front than directly behind the bird, but a major portion of the vocalization did not appear to have this directional limitation.

A variety of factors contributes to making the detection of bird sounds in nature more complex than the detection of a pure tone in a laboratory audiometer. Many of these factors will increase the probability of detection and thereby accentuate the threshold nature of sound detection and emphasize the truncate form of the detection function: (a) bird songs typically have complex tonal and structural features that make them more easily detected than pure tones (Gelfand 1981), (b) song durations are usually longer than the signal used in audiometric testing, again increasing the probability of detection (Small et al. 1962), and (c) many birds sing in bouts of several songs and only a single song or song fraction must be unambiguously detected during a listening period—i.e., detecting 80% of the songs of a particular bird is recorded no differently than detecting only 10%.

Broad frequency background noises can mask a low intensity signal in audiometric testing, thus requiring a higher minimum intensity signal for detection (Gelfand 1981). This type of background noise apparently does not affect the relative width of the partial detection belt (Gelfand 1981). The application of these observations to bird census operations would suggest that broad frequency background noises will decrease the detection threshold distance (DTD) but not significantly change the steeply-sloping shape of the detection function. Background noises such as highway traffic, farm machinery, or the prolonged rustling of leaves in the wind have been shown to reduce the DTD of bird vocalizations. Observers should ordinarily restrict their counting to relatively calm days. In a deciduous forest, winds below about 3 m/s (6.7 miles/h) had very little effect on DTD values (Emlen and DeJong 1981).

Interference effects of narrow-frequency background noises are largest when the interfering frequency is within 15–20% of the signal frequency (Plomp 1976). In census operations confusion due to this kind of interference is limited largely to situations in which two or more conspecific birds are singing concurrently within the DTD. In most cases staggered singing between these individuals will allow segments of time in which interference is reduced and threshold birds can be detected.

APPLICATION OF THE THRESHOLD MODEL

Assuming that errors in failing to detect vocalizing birds within threshold distances are less than errors in estimating distances to unseen vocalizing birds, we propose that the currently popular procedure for calculating detection areas from estimated detection distances be replaced by one based on species-specific detection threshold distances. No widely applicable reference tables of DTD values are yet available, but the data could be readily obtained by teams of experienced observers using the direct measurement procedure described in Emlen and DeJong (1981), or by single observers following fixed routes across areas on which individual territories have been mapped (Emlen 1984). In such areas the accumulation of clusters of many detection points over periods of weeks or months can reveal not only the areas where a particular localized bird was regularly heard, but where, within a rounded-off territory, it was *not* heard. Detection boundaries can thus be differentiated from territory boundaries, and the distances to the former inferred from major boundary segments of many territorial individuals.

Our observations and discussions in this paper have focused on forest habitats, and our suggestion for a DTD standard reference table recognizes that one table of values could not apply to all vegetation types from open grasslands and shrub-lands to closed forests. The various types of temperate deciduous forests appear to be very similar in their sound transmission properties (Morton 1975, Marten and Marler 1977, Marten et al. 1977, Wiley and Richards 1978, 1982) suggesting that a single table might suffice for them. We have doubts concerning the practicality of the steeply-sloping threshold model in open situations where visual detections comprise a significant portion of total detections. In addition, counts would have to be restricted to calm days in open situations where large air movements may produce disrupting and carrying effects on sound (Wiley and Richards 1978, 1982).

In recommending that the steeply-sloping threshold model replace the gently-sloping model we recognize that we are simply substituting one class of errors for another—the errors inherent in variable sound production, transmission, and observer acuity for those inherent in estimating distances on the basis of perceived sound intensity. Neither model is perfect, but we believe that the former, besides its logical soundness, is more reliable and more amenable to regulatory control than the latter. The advantages of counting all birds within hearing range have been summarized by Blondel et al. (1970, 1981) who have used it extensively in their IPA (index of abundance) method. We visualize two major advantages for the system: the uniformity of a standard procedure for observers, especially those with limited experience and training, and the opportunity for observers to focus full attention on detecting and counting provided by the release from distracting and frustrating problems of distance estimation.

SUMMARY

Established acoustic principles and extensive audiometric data suggest that the currently popular gently-sloping model for determining observation areas in transect and point censuses of birds is flawed and should be replaced with a steeply-sloping threshold model based on a modified all-or-none principle of song and call detection. The familiar gradual density decrease-with-distance patterns typical of empirical data sets are shown to be attributable in large part to observer errors in the subjective estimation of detection distances and to other complications inherent in current censusing procedures. Difficulties and advantages in adopting a steeply-sloping model for routine census operations are discussed.

ACKNOWLEDGMENTS

We wish to especially thank Peter Pyle for his assistance in field data collection and to Jared Verner for many helpful comments on an early draft of the manuscript. We also wish to thank the 8 experienced observers who participated in the playback song detection study.

LITERATURE CITED

AFFRE, G. 1976. Quelques reflexions sur les methodes de denombrement d'oiseaux par sondages (IKA et IPA): une approche theorique du probleme. Alauda 44:387–409.

BLONDEL, J., C. FERRY, AND B. FROCHOT. 1970. La méthode des indices ponctuels d'abondance (IPA) ou relevé d'avifaune par "stations d'éncoute." Alauda 38:55–71.

———, ———, AND ———. 1981. Point counts with unlimited distance. Stud. Avian Biol. 6:414–420.

BURNHAM, K. P., D. R. ANDERSON, AND J. L. LAAKE. 1980. Estimation of density from line transect sampling of biological populations. J. Wildl. Manage. 44:1–202.

CARHART, R., AND J. F. JERGER. 1971. Preferred method for clinical determination of pure-tone thresholds. Pp. 96–108, *in* I. R. Ventry, J. B. Chaiklin, and R. F. Dixon, eds. Hearing Measurement. Meredith Corporation, New York.

EBERHARDT, L. L. 1968. A preliminary appraisal of line transects. J. Wildl. Manage. 32: 82–88.

———. 1978. Transect methods for population studies. J. Wildl. Manage. 42:1–31.

EMLEN, J. T. 1971. Population densities of birds derived from transect counts. Auk 88: 323–342.

———. 1984. An observer-specific, full-season, strip-map method for censusing songbird communities. Auk 101:730–740.

———, AND M. J. DEJONG. 1981. The application of song detection threshold distance to census operations. Stud. Avian Biol. 6:346–352.

GELFAND, S. A. 1981. Hearing: an introduction to psychological and physiological acoustics. Marcel Dekker, Inc., New York.

JÄRVINEN, O. 1978. Estimating relative densities of land birds by point counts. Ann. Zool. Fenn. 15:290–293.

———, AND R. A. VÄISÄNEN. 1975. Estimating relative densities of breeding birds by the line transect method. Oikos 26:316–322.

KEPLER, C. B., AND J. M. SCOTT. 1981. Reducing count variability by training observers. Stud. Avian Biol. 6:366–371.

MARTEN, K., AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitat. Behav. Ecol. Sociobiol. 2:271–290.

———, D. QUINE, AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. Behav. Ecol. Sociobiol. 2:291–302.

MORTON, E. S. 1975. Ecological sources of selection on avian sounds. Am. Nat. 109: 17–34.

PETERSON, A. P. G., AND E. E. GROSS. 1974. Handbook of noise measurement. Seventh ed. General Radio, Concord, Mass.

PLOMP, R. 1976. Aspects of tone sensation: a psychophysical study. Academic Press, New York.

RALPH, C. J., AND J. M. SCOTT, EDS. 1981. Estimating the numbers of terrestrial birds. Stud. Avian Biol. 6.

SCOTT, J. M., AND F. L. RAMSEY. 1981. Length of count period as a possible source of bias in estimating bird densities. Stud. Avian Biol. 6:409–413.

———, ———, AND C. B. KEPLER. 1981. Distance estimation as a variable in estimating bird numbers. Stud. Avian Biol. 6:334–340.

SMALL, A. M., J. F. BRANDT, AND P. G. COX. 1962. Loudness as a function of signal duration. J. Acoust. Soc. Am. 34:513–514.

VERNER, J., AND L. V. RITTER. 1985. A comparison of transects and point counts in oak-pine woodlands of California. Condor 87:47–68.

WERTHEIMER, M. 1955. The variability of auditory and visual absolute thresholds in time. J. Gen. Psychol. 52:111–147.

WILEY, R. H., AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3:69–94.

———, AND ———. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pp. 131–181, *in* D. E. Kroodsma and E. H. Miller, eds. Acoustic Communication in Birds. Vol. 1. Academic Press, New York.

WITKIN, S. R. 1977. The importance of directional sound radiation in avian vocalization. Condor 79:490–493.

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706.
Received 1 Sept. 1984; accepted 17 June 1985.