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VARIATION IN THE SONGS OF BREEDING GAMBEL'S WHITE-CROWNED SPARROWS NEAR CHURCHILL, MANITOBA

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Abstract. Song variation was studied in Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*), breeding in tundra and boreal forest habitats near Churchill, Manitoba. No significant differences were found among habitats in song characteristics of *Z. l. gambelii*. Songs of Churchill birds had the same sequence of elements (i.e., whistle, warble, buzz, and trill) as Alaskan populations, with some variations in element form. The absence of dialects in migratory populations of White-crowned Sparrows supports predictions of the Ranging Hypothesis.

Key words: *Song; song variation; White-crowned Sparrow;* Zonotrichia leucophrys.

INTRODUCTION

Songs of the White-crowned Sparrow (*Zonotrichia leucophrys*) have been widely studied, particularly with respect to song learning and dialects (Marler and Tamura 1962; Baker 1974; Baptista 1974, 1975, 1977; Orejuela and Morton 1975; Baptista and King 1980; Trainer 1983) and geographic variation (DeWolfe et al. 1974, Baptista and King 1980). The majority of individual male White-crowned Sparrows sing one song type which is simple in structure, and this simple repertoire facilitates research on song variation (Baptista 1977).

The purpose of this study was to examine song variation in an easterly population of Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) to examine the relationship between habitat and song type, if any. DeWolfe et al. (1974) noted that variation in the temporal structure of warbles and trills of *Z. l. gambelii* seemed well suited for transmission in the open, windy habitats of their breeding grounds in Alaska. Structural variations within the repertoires of forest, edge and grassland birds are believed to facilitate sound transmission in their respective habitats (Morton 1970). Extensive literature is available concerning the relationship between the acoustic properties of environments and characteristics of vocalizations (see review by Wiley and Richards 1982).

Songs of White-crowned Sparrows breeding on territories in the tundra were compared with sparrows breeding in adjacent boreal forest areas to determine if structural variation in their songs was associated with habitat differences. These tundra and forest songs from the Eastern sub-Arctic region of Canada are also compared with songs of Alaskan populations of *Z. l. gambelii* (DeWolfe et al. 1974).

STUDY AREA AND METHODS

In this study, songs of 73 adult Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) were recorded near Churchill, Manitoba (58°45'N, 95°04'W) between 8–27 June 1988. The majority of birds recorded had the white lores typical of the subspecies *gambelii*, but a few individuals had black or grey lores more typical of *Z. l. leucophrys*, an eastern subspecies that intergrades with *Z. l. gambelii* in northern Manitoba (Godfrey 1986); their songs are not included here.

Churchill is situated in the transition zone between the northern boreal forest and the tundra. Birds were recorded in the boreal forest, the tundra, and in the transition zone between these two habitats at four main study sites near Churchill: Twin Lakes, Landing Lake, Camp Nanuk, and in the vicinity of The Churchill Northern Studies Centre (CNSC). The Twin Lakes area, 25 km southeast of Churchill, is dominated by dense stands of boreal forest species such as White Spruce (*Picea glauca*), Larch (*Larix laricina*), and willows (*Salix* spp. including *S. lanata* and *S. brachycarpa*). Labrador Tea (*Ledum groenlandicum*), Dwarf Labrador Tea (*L. decumbens*), Juniper (*Juniperus communis* var. *depressa*); lichens, and mosses were also common here. The

Churchill Northern Studies Centre, located 20 km east of Churchill, is dominated by wet tundra species such as Dwarf Birch (*Betula glandulosa*); *Salix* spp. including *S. arctophila, S. planifolia, S. lanata,* and *S. reticulata*; and scattered *Picea glauca.* Landing Lake, 10 km southeast of Churchill, lies in the transition zone of boreal forest to wet tundra and has an equal admixture of plant species typical of both of these habitats. Camp Nanuk, 13 km east of Churchill, is dominated by wet tundra species and scrub willows. Other recordings were made along Goose Creek Road, Fort Churchill and adjacent to the radio antennae located midway between Churchill and CNSC.

Songs were recorded using a UHER Model CR 260 AV tape recorder and a Sennheiser MKH 816 unidirectional microphone. Individual sparrows from the tundra and boreal forest were recorded and their general locations noted. Songs of different individuals were relatively easy to discriminate, since neighboring males often sang alternately within earshot of each other (DeWolfe et al. 1974; this study). If a bird was recorded within 200 m of an area covered the previous day, the spectrograms of those recordings were compared for similarity to determine whether or not the songs were from the same individual. The number of good recording days was limited due to the cool, windy conditions that prevailed in Churchill during the study period.

Songs were analyzed using a Uniscan II sound spectrum analyzer. Individual *Z. l. gambelii* songs were separated by an examination of the spectrograms. We used the 'cleanest' spectrograms from each bird to measure 24 commonly measured time, frequency and element-form characteristics (Table 1); these song characteristics were then used to examine the variation among *gambelii* song. The 73 songs recorded were grouped into eight categories based on warble duration, presence or absence of fast or slow trills, and the number of buzzes in the song. Song terminology used in this study follows DeWolfe et al. (1974). Their term "warble" corresponds to the now widely-accepted term "complex syllable."

Multivariate (MANOVA) and univariate (ANOVA) analyses of variance were performed using ten of the 24 song characteristics (whistle duration and frequency; frequency envelope (band width) of the warble and warble duration; frequency envelope of the buzz and buzz duration; frequency envelopes of the fast and slow trills; and the average interval between syllables of the fast and slow trills) to determine if variation in *Z. l. gambelii* song was related to habitat type. These ten characteristics were useful in distinguishing song types in other studies (DeWolfe et al. 1974; Baptista and Morton 1982; Trainer 1983). The remaining 14 characteristics (mainly maximum and minimum frequencies of the various elements) were used only for descriptive purposes (Table 1). PROC MEANS and PROC GLM SAS programs (SAS Institute Inc. 1985) were used for the data analysis.

RESULTS

Analyses of variance showed no significant differences across habitat in any of the ten song characteristics. No significant differences among habitats in song characteristics were found with multivariate analysis (MANOVA). This strongly suggests the absence of differences among habitats in *Z. l. gambelii* song characteristics because MANOVA is highly effective at eliminating chance fluctuations that can occur in univariate analyses (Harris 1985). Therefore, a description of variation in the song patterns of *Z. l. gambelii* near Churchill, regardless of habitat type follows.

A complete song of *Z. l. gambelii* included four kinds of elements sung in this order: whistle, warble, buzz and trill. Song duration varied from 1.4 to 2.5 sec ($\bar{x}$ = 1.9 sec ± 0.2 SD, n = 73). Table 1 shows the variation in time and frequency characteristics of all *Z. l. gambelii* songs recorded near Churchill. Whistles were either continuous or broken (DeWolfe et al. 1974) and 37% of individuals included a slurred portion in the whistle which had a wide frequency band (Figs. 1A, B). Three forms of warble were found: short, medium and long. The short warble was sung by 57.5% of the birds (Table 2) and corresponded to one syllable of warble form #6 in DeWolfe et al. (1974). The long and medium warbles corresponded to single syllables of warble forms 2 and 9, respectively, in DeWolfe et al. (1974). Buzzes showed little variation in form, with most birds (84.9%) incorporating a single buzz in their song. The remaining individuals (15.1%) had a double buzz in their song, with the latter buzz being lower in frequency in 90.1% of songs and often replacing the fast trill. One individual appeared to have a double buzz in its

TABLE 1. Means, standard deviations and ranges of 24 song characteristics measured from spectrograms of all *Zonotrichia leucophrys gambelii* individuals recorded near Churchill, Manitoba.

	$\bar{x} \pm$ SD	(*n*)	Range
Duration (sec)			
Whistle	0.62 ± 0.13	(72)	0.37–0.97
Warble	0.21 ± 0.17	(71)	0.04–0.46
Buzz	0.28 ± 0.03	(72)	0.20–0.35
Slow trill	0.35 ± 0.08	(70)	0.14–0.55
Fast trill	0.29 ± 0.02	(63)	0.21–0.34
Complete song	1.90 ± 0.20	(73)	1.40–2.50
Slow trill interval	0.08 ± 0.005	(70)	0.07–0.09
Fast trill interval	0.02 ± 0.003	(52)	0.02–0.03
Frequency (kHz)			
Whistle	3.7 ± 0.6	(73)	2.6–5.1
Warble			
Frequency envelope	2.1 ± 1.7	(71)	0.4–4.6
Maximum frequency	4.9 ± 0.5	(70)	4.1–6
Minimum frequency	3.2 ± 0.3	(69)	2.5–3.9
Mean frequency; long warble	4.0 ± 0.5	(30)	3.5–5.7
Buzz			
Frequency envelope	1.9 ± 0.4	(64)	0.9–3
Maximum frequency	6.1 ± 0.3	(63)	5.2–6.7
Minimum frequency	4.2 ± 0.2	(63)	3.8–5
Slow trill			
Frequency envelope	2.1 ± 0.5	(66)	1.3–4
Maximum frequency	5.6 ± 0.5	(65)	4.8–6.7
Minimum frequency	3.6 ± 0.3	(65)	2.9–4.1
Fast trill			
Frequency envelope	1.8 ± 0.6	(57)	0.9–3.4
Maximum frequency	5.5 ± 0.4	(56)	4.8–6.2
Minimum frequency	3.7 ± 0.4	(56)	3.0–4.5
Syllable number			
Slow trill	4.6 ± 1	(70)	2–7
Fast trill	11.7 ± 2	(52)	6–16

song without any trill elements. The spectrogram of this individual was indistinct, and therefore, was not included in Table 2 of Figure 1 as a separate song type. Most birds (68.5%) included a fast trill followed by a slow trill in their songs. Some birds (30.2%) omitted either the fast trill or the slow trill from their songs. Syllable form did not vary within each trill type.

Song types shown in Figure 1 and Table 2 are coded as in DeWolfe et al. (1974). WH represents whistle and a subscript "s" indicates the presence of a slur in the whistle. WA represents warble with subscripts "s," "m," and "l" standing for short, medium and long duration warbles. B, FT, and ST represent buzz, fast trill and slow trill, respectively. The predominant song type sung by birds in the Landing Lake, Twin Lakes and CNSC sites is shown in Figure 1A. Two individuals from Landing Lake sang WH WAm B FT ST (Fig. 1D), a song type that had a warble intermediate in length ($\bar{x}$ = 0.18 sec ± 0.1 SD) between the two more common warble forms. Song types shown in Figure 1 E to H all have long warbles in the song. WH WA1 B B ST (Fig. 1F) incorporated a double buzz, with the latter buzz often having a smaller frequency envelope and a lower mean frequency than the first.

DISCUSSION

Spectrograms of songs recorded from a given individual showed little variation (at least over the five to ten min interval of the recording) indicating stereotypy over a short time period. DeWolfe et al. (1974) found that the form of each song element in an individual *Z. l. gambelii* repertoire is relatively stable over a nine-day period. Stereotypy of individual song has also been re-

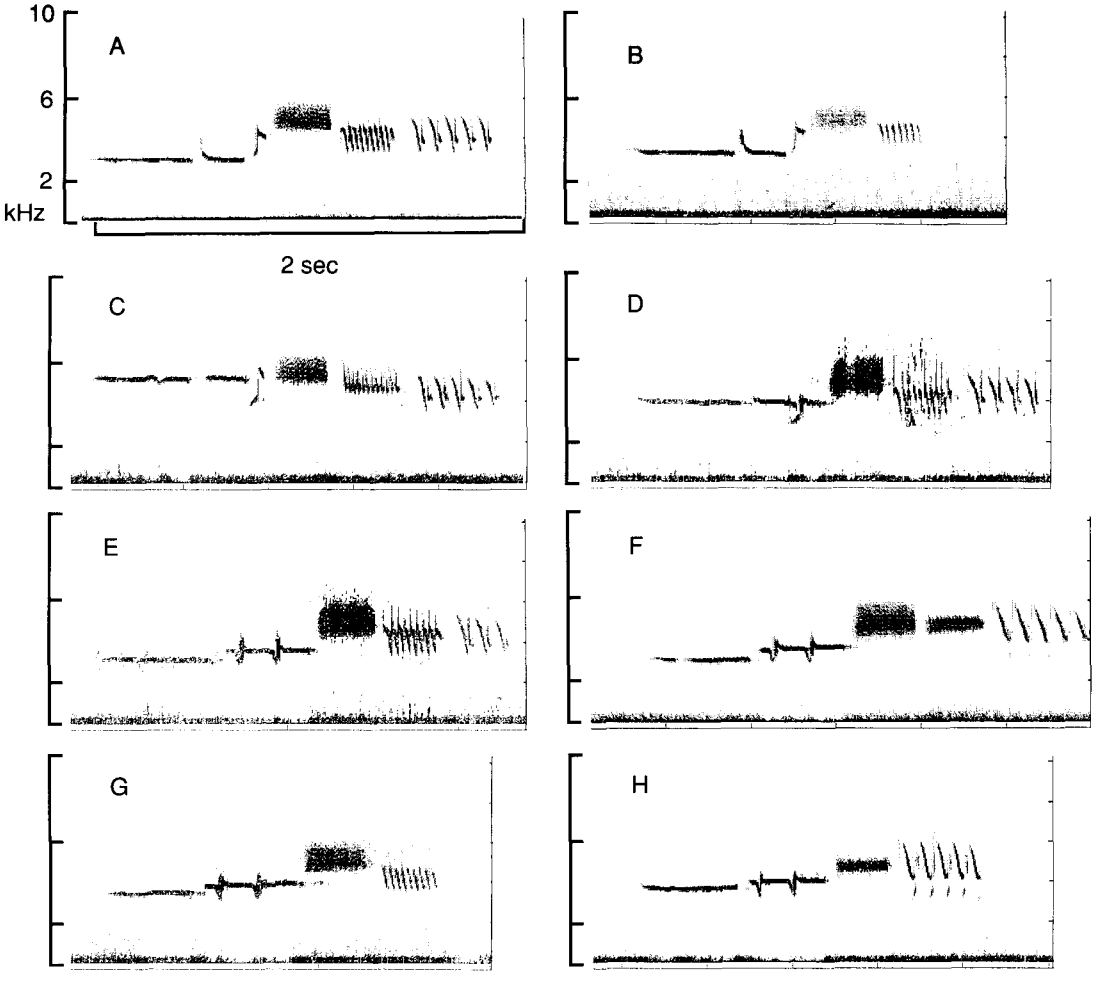

FIGURE 1. Sound spectrograms of the eight song types of Gambel's White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) identified in the Churchill area. A) WHs WAs B FT ST. B) WHs WAs B FT. C) WH WAs B FT ST. D) WH WAm B FT ST. E) WH WAl B FT ST. F) WH WAl B B ST. G) WH WAl B FT. H) WH WAl B ST. WH = whistle, WHs = slurred whistle, WAs = short warble, WAm = medium warble, WAl = long warble, B = Buzz, FT = Fast Trill, ST = Slow Trill.

ported in *Z. l. pugetensis* and *Z. l. nuttalli* (Baptista 1977, Trainer 1983).

Song type was not related to habitat type in *Z. l. gambelii*; songs of birds inhabiting boreal forest did not differ from those inhabiting the open tundra. However, the buzzes, trills, different warble forms, and slurred whistles of *Z. l. gambelii* near Churchill covered a wide range of frequencies. These song elements may increase the efficacy of sound transmission in the turbulent atmosphere of the open tundra (Morton 1970, DeWolfe et al. 1974).

Songs of *Z. l. gambelii* near Churchill had the same sequence of elements (i.e., whistle, warble, buzz, trill) as populations in Alaska (DeWolfe et al. 1974) and a *Z. l. oriantha* population in the Hart and Steens Mountains, Oregon (Baptista and King 1980). However, element form of the Churchill birds differed from that of the Alaskan birds (DeWolfe et al. 1974). Thirty-seven percent of Churchill birds incorporated a slur in the whistle element (Figs. 1A, B). This slurred whistle is previously unreported in *gambelii* and other subspecies of the White-crowned Sparrow. The slur

may be compared to some of the 'down-slurred' whistle notes of *Z. capensis* (Nottebohm 1969, Handford and Nottebohm 1976).

The warble of Churchill birds consisted of a single note, rather than the doubled or tripled warble notes found in Alaskan birds (DeWolfe et al. 1974). The warble notes of Churchill birds varied in duration. The short, medium and long warbles corresponded to three of the 10 forms (forms 6, 9 and 2, respectively) described by DeWolfe et al. (1974). A longer term study of Churchill birds may reveal a greater variety of warble forms in this population. The majority (85%) of Churchill birds only had one buzz in their song, unlike Alaska birds that usually had two buzzes in their songs (DeWolfe et al. 1974). The first buzz was lower in frequency in double buzz songs of both Churchill and Alaskan birds (DeWolfe et al. 1974; this study).

Fast and slow trills of Churchill birds showed a stereotyped syllable structure indicating an absence of local dialects, unlike trills of *Z. l. nuttalli* in the San Francisco Bay Region (Marler and Tamura 1962, Trainer 1983) and *Z. l. oriantha* in California, Oregon and Alberta (Orejuela and Morton 1975, Lein 1979, Baptista and King 1980, Baptista and Morton 1982, Baker and Thompson 1985). DeWolfe et al. (1974) recorded one syllable type in the fast trill of Alaskan birds and three syllable types in the slow trill. The variations in warble form and syllable form in the slow trill were attributed to geographic variation of *Z. l. gambelii* song (DeWolfe et al. 1974). The majority (68.5%) of Churchill birds incorporated both a fast and a slow trill in their songs similar to *Z. l. gambelii* breeding in the Upper Sheenjik Valley in northeast Alaska (Kessel and Schaller 1960). However, Alaskan populations (with the exception of two individuals) used only one form of trill during a singing bout. The replacement of the fast trill with a second buzz in Churchill birds resulted in a pattern similar to the WH WA B B ST of *Z. l. gambelii* in Alaska (DeWolfe et al. 1974) and *Z. l. oriantha* in the Cypress Hills region of Alberta (Lein 1979).

The Ranging Hypothesis of Morton (1982) proposed that birds assess their distances from one another by gauging the amount of degradation in the incoming sound signal with a stored undegraded version. Morton (1982) predicted that small repertoires and high among individual variability should be adaptive in populations where neighbor changeover is high between breeding seasons and/or there are many newcomers seeking territories. In such cases, there is a lack of selection pressure favoring newcomers that learn the song of neighbors which they interact with briefly; instead selection favors the development of individually distinctive songs so listeners can only inaccurately assess distance cues (Morton 1982). Song variability among individuals, small repertoire size (i.e., one song repertoire), and the migratory nature of *Z. l. gambelii* in Churchill support this prediction of the Ranging Hypothesis.

TABLE 2. Eight song types of *Zonotrichia leucophrys gambelii* near Churchill.

Song type		%	Number of syllables FT	Number of syllables ST
WHs WAs B FT ST	(A)	35.6	8–10	3–6
WHs WAs B FT	(B)	1.4	6	0
WH WAs B FT ST	(C)	20.5	11–15	4–6
WH WAm B FT ST	(D)	2.7	10	4
WH WAl B FT ST	(E)	9.6	9–12	2–6
WH WAl B B ST	(F)	13.7	0	4–6
WH WAl B FT	(G)	1.4	9	0
WH WAl B ST	(H)	13.7	0	3–7

WH = whistle, WHs = slurred whistle, WAs = short warble, WAm = medium warble, WAl = long warble, B = Buzz, FT = Fast Trill, ST = Slow Trill, (A . . . H) = letter designation of song type (see Fig. 1), % = percentage of sparrows recorded using each song type.

None of the eight *Z. l. gambelii* song types was restricted to certain localities in the Churchill area. Instead, they were sung at random, with neighboring males often singing different song types, as was found in Alaskan populations (DeWolfe et al. 1974). The local variability in song type indicates the general absence of local dialects in this subspecies (DeWolfe et al. 1974; this study). The absence of dialects in *Z. l. gambelii* is consistent with the absence of dialects in eastern or northern North American avian populations, and secondly, the absence of dialects in migratory avian populations hypothesized by Morton (1986). Low repertoire size and dialects are predicted by the Ranging Hypothesis to occur in situations where neighborhood stability is high and the climate is mild and stable. In this case, territorial boundaries are established between neighbors for long time periods and songs are used to threaten neighbors over established territorial borders (Morton 1986). This may explain the dialects noted in non-migratory populations of *Z. l. nuttalli* living on the mild Pacific coast of California (Baker 1974, Baptista 1975, Baker

and Thompson 1985) and *Z. l. pugetensis* in Puget Sound (Baptista 1977).

In summary, the presence of dialects in nonmigratory populations, and the absence of dialects in migratory populations of *Zonotrichia leucophrys* support the predictions of the Ranging Hypothesis.

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LITERATURE CITED

BAKER, M. C. 1974. Genetic structure of two populations of White-crowned Sparrows with different song dialects. Condor 76:351–356.

BAKER, M. C., AND D. B. THOMPSON. 1985. Song dialects of White-crowned Sparrows: historical processes inferred from patterns of geographic variation. Condor 87:127–141.

BAPTISTA, L. F. 1974. The effects of songs of wintering White-crowned Sparrows on song development in sedentary populations of the species. Z. Tierpsychol. 34:147–171.

BAPTISTA, L. F. 1975. Song dialects and demes in sedentary populations of the White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*). Univ. Calif. Publ. Zool. 105:1–52.

BAPTISTA, L. F. 1977. Geographic variation in song and dialects of the Puget Sound White-crowned Sparrow. Condor 79:356--370.

BAPTISTA, L. F., AND J. R. KING. 1980. Geographical variation in song and song dialects of montane White-crowned Sparrows. Condor 82:267–284.

BAPTISTA, L. F., AND M. L. MORTON. 1982. Song dialects and mate selection in montane White-crowned Sparrows. Auk 99:537--547.

DEWOLFE, B. B., D. D. KASKA, AND L. J. PEYTON. 1974. Prominent variations in the songs of Gambel's White-crowned Sparrows. Bird-Banding 45 (2):224–252.

GODFREY, W. E. 1986. The birds of Canada. National Museums of Canada, Ottawa, ON, Canada p. 595.

HANDFORD, P. T., AND F. NOTTEBOHM. 1976. Allozymic and morphological variation in population samples of Rufous-collared Sparrow, *Zonotrichia capensis,* in relation to vocal dialects. Evolution 30:802–817.

HARRIS, R. J. 1985. A primer of multivariate statistics, 2d ed. Academic Press, Inc., Orlando, Florida, U.S.A. p. 576.

KESSEL, B., AND G. B. SCHALLER. 1960. Birds of the upper Sheenjek Valley, northeastern Alaska. Biol. Pap. Univ. Alaska 4:1–59.

LEIN, M. R. 1979. Song pattern of the Cypress Hills population of White-crowned Sparrows. Can. Field Nat. 93:272–275.

MARLER, P., AND M. TAMURA. 1962. Song dialects in three populations of White-crowned Sparrows. Condor 64:368–377.

MORTON, E. S. 1970. Ecological sources of selection on avian sounds. Ph.D. diss. Yale Univ.

MORTON, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules, p. 183–212. *In* D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds. Vol. 1. Academic Press, New York.

MORTON, E. S. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99:65–86.

NOTTEBOHM, F. 1969. The song of the Chingolo, *Zonotrichia capensis,* in Argentina: description and evaluation of a system of dialects. Condor 71:299–315.

OREJUELA, J. E., AND M. L. MORTON. 1975. Song dialects in several populations of Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. Condor 77:145–153.

SAS INSTITUTE, INC. 1985. Sas user's guide: statistics. Version 5. Cary, NC.

TRAINER, J. M. 1983. Changes in song dialect distributions and microgeographic variation in song of White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*). Auk 100:568–582.

WILEY, R. H., AND D. G. RICHARDS. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection, p. 131–170. *In* D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds. Vol. 1. Academic Press, New York.