GEOGRAPHIC VARIATION IN THE "HOY" CALL OF THE BOBWHITE

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ABSTRACT.—Intraspecific geographic variation in the "hoy" call of female Bobwhite (*Colinus virginianus*) was studied. Twelve morphometric characters of sonograms of this call for 38 individuals, recorded in the field at the 4 extreme corners of the species' contiguous range in the U.S., were examined by univariate and multivariate statistical techniques. In spite of the absence of striking qualitative differences apparent dialects have been detected for the four populations.—
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THE study of individual variation in avian vocalizations attempts to define the limits of variation for single populations (Borror 1959, 1965; Marler and Isaac 1960a, 1960b, 1961; Konishi 1964; Hutchison et al. 1969; Hekenlively 1970; Heinz and Gysel 1970; Emlen 1971a; Williams 1972; Beightol and Samuel 1973), failing to address the dimensionality of the species. Only through detailed analyses of intraspecific variation can one approach the systematics of a species.

Many studies of geographic variation in passerine vocalizations (Thielcke 1969; Lemon 1969, 1971; Nottebohm 1969; Shiovitz and Thompson 1970; Bertram 1970; Emlen 1971b; Harris and Lemon 1972; Baker 1975; Orejuela and Morton 1975) have been reported while only two such studies (Wiley 1971, Van Der Weyden 1973) have been published concerning nonpasserines. All of these studies have dealt with qualitative differences, or at best a few quantitative differences of sonograms, treated univariately, in discussing the species' variability.

This study attempts to discern geographic variation in the vocalizations of four populations of the Bobwhite (*Colinus virginianus*) within its contiguous range in the United States, through multivariate analysis of quantitative morphometric characters of sonograms of one of its calls.

The Bobwhite provides an excellent opportunity for study of geographic variation of vocalizations. With the exception of populations in northern Sonora, Mexico, Oregon, Washington, and Idaho, its range is continuous through much of the United States and Mexico. The contiguous U.S. populations have been divided into 3, 4, and 6 subspecies (Aldrich 1946, Ridgway and Friedmann 1946, A.O.U. 1957). Measurements of these subspecies (Aldrich 1946) reveal only slight morphological variation. On the basis of limited samples, Holman (1961) detected a north-south decrease in mean size of skeletal elements to be the only osteological trend for these populations. Ripley (1960) identified a similar trend in the weights of Bobwhites in the east. Aldrich (1946) and Rosene (1969) reported some color variation but suggested that this might be more ecotypic than geographic.

The fact remains that several American subspecies of Bobwhite are recognized (A.O.U. 1957), implying a degree of genetic isolation among the contiguous populations. This reduction in gene exchange might be a result of pair formation taking place within coveys, while they are still intact (Stoddard 1931), but unmated males may still pair with females separated from their mates after the coveys disperse. Coupled with the random movement of birds after the breeding season (Stoddard 1931, Agee 1957, Rosene 1969), this would allow for gene exchange between coveys. The low vagility of the Bobwhite (Stoddard 1931, Leopold 1933, Murphy and Bas-

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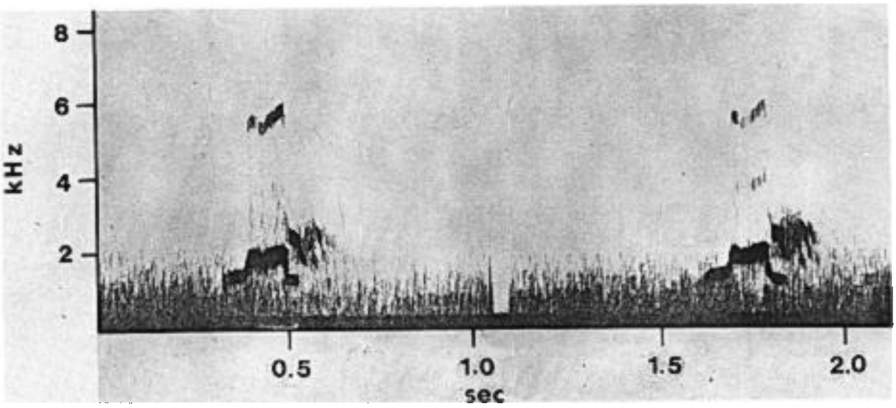

Fig. 1. Representative sonogram of two "hoy" calls of the Bobwhite.

kett 1952, Rosene 1969) would mean that gene exchange tends to occur within demes.

Vocalizations are of great importance in the biology of the Bobwhite. Stoddard (1931) described most of the calls of the species. More recently Stokes (1967) has reevaluated Stoddard's descriptions, adding sonograms of the calls and information on causation and function.

The female separation calls, "hoy," "hoy-poo," or "koilee" (Stokes 1967), are given through the year. They may be elicited when a hen is out of view of the covey or her mate. During the breeding season, males respond to these calls by performing the "hoy" or "hoy-poo" separation call of mated males or the "bob-white" reproductive call of unmated males until contact is made. Stokes and Williams (1968) demonstrated that this response is often antiphonal to the female call, emphasizing the importance of vocalization in pair formation.

Stoddard based his information on observations of wild birds in the southeastern U.S. Stokes' study was conducted under controlled conditions with birds raised in captivity for several generations. Both studies were of great importance in adding information on the behavior of this species, but neither study considered the possibility of geographic dialects nor individual variation. Williams (1972) studied this latter phenomenon in the "bob-white" call of field-recorded Maryland birds.

The present study analyzes the geographic variation in the "hoy" call of the Bobwhite from the four extreme corners of its range in the U.S. By treating the sonograms of this call as morphological units, an array of quantitative measurements are produced and may be analyzed, utilizing multivariate statistical techniques.

METHODS AND MATERIALS

The "hoy" call of the Bobwhite (Fig. 1) was recorded in the field at four locations at the periphery of its contiguous range in the U.S. between 5 December 1971 and 17 June 1973. A total of 14 quail were recorded at 2 locations in Barnstable County, Massachusetts: 2 at the Ashumet Holly Reservation and Wildlife Sanctuary, East Falmouth; and 12 at the East Sandwich State Game Farm. At the Archbold Biological Station, Highlands County, Florida, 28 individuals were recorded. A total of 28 recordings were made at two locations in Texas: 1 at Lake Corpus Christi, Jim Wells County; 27 at the King Ranch, Kingsville, Kleberg County. Nebraska quail were recorded at 4 sites: 1 at Pawnee Lake State Recreational Area, Lancaster County; 11 at Burchard Lake Special Use Area, Pawnee County; 1 at the Chet Ager Nature Center, Lincoln, Lancaster County; 1 at Homestead National Monument, Gage County. As it was

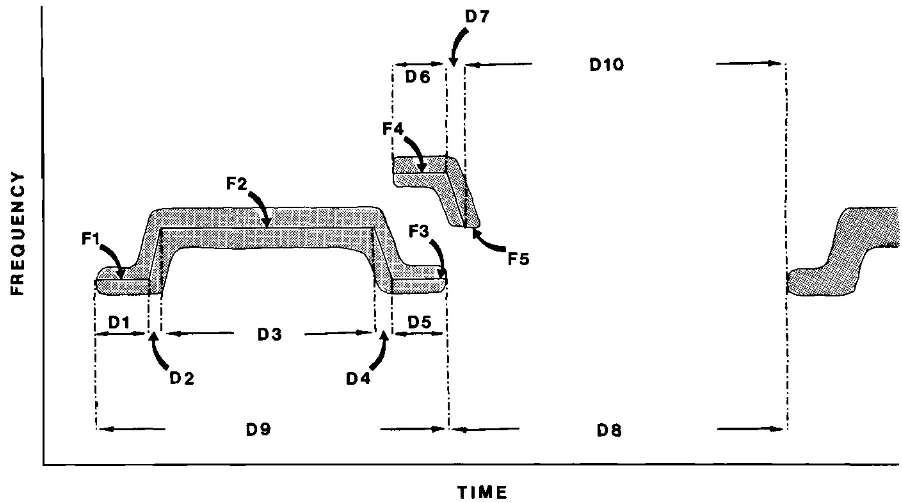

Fig. 2. Diagrammatic presentation of a "hoy" call of the Bobwhite indicating fifteen characters measured in the study. Frequency characters are labeled F, and temporal characters are labeled D.

rarely possible to see the calling birds, identification of individuals was difficult. In order to maximize the likelihood of recording individuals, particular sites were visited only once. If more than one bird was calling simultaneously at a site on a given day, only those whose position could be detected and discriminated audibly were recorded.

Massachusetts birds were recorded with a Uher 4000 Report-L tape recorder, using a Uher 514 microphone, recording at 19 cm per sec. Florida recordings were made in the same manner but with either an Electro-Voice 644 or 642 microphone. Nebraska calls were also recorded with a Uher 4000 Report-L tape recorder and an Electro-Voice 644 microphone, at the same speed as for the two preceding areas. All but one Texas recording were made with the Electro-Voice 644 microphone in conjunction with a Panasonic RQ-226S tape recorder, recording at 9.5 cm per sec. The one recording at Lake Corpus Christi was made with the same apparatus as for Nebraska. The recordings were played directly into the record circuitry of a Kay Electric Company 6061-B sound spectrograph from the tape recorder on which they had been recorded at the speed at which they had been made. Sonograms were produced with the FL-1 circuit, a "wideband" or a "narrowband" filter setting, and the reproduce circuit at 80–8,000 Hz.

Fifteen characters were measured for one call of each bird recorded (Fig. 2). Individual recordings were selected arbitrarily from a series of equal clarity. If the quality of the recordings varied, the clearest was analyzed. The 5 frequency characters were measured on "narrowband" sonograms, and the 10 temporal characters were determined from "wideband" sonograms. All measurements were made in metric units, to

TABLE 1

Comparison of Various Elements[1] of the "Hoy" Call of Bobwhite (Mean ± SE)

Character[2]	Fla. (n = 9)	Mass. (n = 11)	Texas (n = 7)	Nebr. (n = 11)
F1	20.7 ± 0.5	12.8 ± 0.3	20.7 ± 0.8	16.9 ± 0.6
F2	26.0 ± 0.7	24.0 ± 0.8	25.6 ± 0.6	22.9 ± 0.5
F3	20.4 ± 0.7	15.3 ± 0.6	22.0 ± 0.7	18.6 ± 0.6
F5	31.2 ± 1.0	24.2 ± 0.6	31.7 ± 0.9	26.5 ± 0.4
D1	6.8 ± 1.0	6.5 ± 0.7	5.5 ± 0.5	7.2 ± 0.7
D2	0.6 ± 0.1	3.7 ± 0.9	0.9 ± 0.2	1.0 ± 0.4
D3	18.9 ± 1.2	17.5 ± 1.6	13.8 ± 1.3	21.1 ± 2.3
D4	0.9 ± 0.4	5.8 ± 1.1	1.0 ± 0.2	1.1 ± 0.3
D5	8.0 ± 0.5	10.7 ± 0.8	5.6 ± 0.3	6.9 ± 0.7
D8	97.9 ± 6.3	98.7 ± 6.7	128.0 ± 9.5	137.8 ± 6.5
D9	38.1 ± 2.2	53.3 ± 2.3	32.4 ± 1.6	38.6 ± 2.5
D10	97.8 ± 5.9	87.1 ± 8.2	120.0 ± 9.5	135.3 ± 6.7

[1] Values in mm.
[2] See Fig. 2 for explanation.

TABLE 2

UNIVARIATE ANALYSIS OF VARIANCE OF MORPHOMETRIC CHARACTERS OF "HOY" CALL SONOGRAMS

Character[1]	F-ratio[2]	$P<$
F1	49.4884	0.0001
F2	4.5921	0.0084
F3	18.5464	0.0001
F5	26.7324	0.0001
D1	0.7705	0.5186
D2	7.2024	0.0008
D3	2.6417	0.0651
D4	13.6791	0.0001
D5	10.1184	0.0001
D8	8.7337	0.0002
D9	15.0713	0.0001
D10	9.0103	0.0002

[1] See Fig. 2 for explanation.
[2] Degrees of freedom = 3, 34.

the nearest 0.1 mm, with frequency being measured from the baseline and duration being measured between points (Fig. 2). Three characters (F4, D6, and D7) were excluded from consideration because of inadequate sample size. Several recordings were deleted from the analysis because not all the remaining characters could be recovered from their sonograms. The data from the remaining 38 recordings were exposed to univariate and multivariate statistical analyses, including: ANOVA (analysis of variance), MANOVA (multivariate analysis of variance), and canonical analysis. These analyses were carried out with appropriate computer programs (Fina 1972, Dixon 1973). For a detailed explanation of the computation and interpretation of the multivariate techniques employed in this study see Seal (1964), Power (1970), and Blackith and Reyment (1971).

All recordings and original sonograms are in the author's possession.

RESULTS

Means and standard errors for each morphometric sonographic character are presented in Table 1 in mm. These values may be converted to their appropriate frequency or timing equivalent from the relationships:

$$1 \text{ mm} = 77 \text{ Hz}$$
$$13.2 \text{ mm} = 100 \text{ msec}$$

All statistics were performed on the metric data to reduce rounding error.

Univariate comparisons.—The ANOVA's for each character (Table 2) reveal highly significant ($P < 0.01$) differences between populations; 95% confidence limits

TABLE 3

PRODUCT-MOMENT CORRELATION COEFFICIENTS BETWEEN CHARACTERS[1,2]

	F1	F2	F3	F5	D1	D2	D3	D4	D5	D8	D9
F2	.23										
F3	.49	.55									
F5	.45	.71	.42								
D1	.14	.10	.04	.07							
D2	−.25	.05	−.04	−.11	−.05						
D3	−.30	−.12	−.10	−.18	−.14	−.23					
D4	.10	−.18	−.12	−.01	−.07	.11	−.08				
D5	−.03	.22	−.11	.18	.05	.02	−.16	−.09			
D8	−.15	−.11	−.04	−.004	.12	−.30	.12	−.25	−.03		
D9	−.32	−.16	−.40	−.29	−.07	−.10	.46	−.01	.06	.07	
D10	−.10	−.13	−.01	−.04	.10	−.27	.14	−.11	−.14	.93	.02

[1] See Fig. 2 for explanation of characters.
[2] Underlined values are significant ($P < 0.05$).

TABLE 4

MULTIVARIATE ANALYSIS OF VARIANCE OF MORPHOMETRIC CHARACTERS OF "HOY" CALL SONOGRAMS

Character[1]	F-ratio[2,3]	$P <$
F1	49.4884	0.0001
F2	1.1322	0.3537
F3	0.2550	0.8570
F5	1.6442	0.2045
D1	0.8424	0.4831
D2	0.0660	0.9774
D3	1.4564	0.2478
D4	3.3385	0.0315
D5	2.1729	0.1127
D8	8.8036	0.0002
D9	1.4915	0.2362
D10	3.1414	0.0398

[1] See Fig. 2 for explanation.
[2] F-ratio for multivariate test of equality of mean vectors = 4.8289, degrees of freedom = 36, 68.6837, $P < 0.0001$.
[3] Degrees of freedom = 3, 34.

were computed for each significant character and every location. Florida and Texas populations are not found to be different from one another in nine of the remaining ten characters (F1, F2, F3, F5, D2, D4, D8, D9, D10). No differences are found between Massachusetts and Nebraska calls in three of the remaining characters (F2, F3, D2). In the one case where differences exist between Florida and Texas (D5), neither differs from Nebraska. For 4 characters, 2 frequency and 2 temporal, Massachusetts calls are separable from the other 2 groups (F1, F3, D4, D9). Nebraska calls are distinguishable from all other groups for F1, only. This frequency component separates the four areas into three groups: Florida and Texas; Nebraska; Massachusetts. Texas and Florida, as a couplet, are separable from Nebraska and Massachusetts in one other character, F5.

From the product-moment correlations of the characters within groups (Table 3), there appears to be very little correlation between the temporal characters. Of these, D3 is correlated with D9, and D8 with D10. Frequency characters appear to have a higher rate of correlation. F5 is correlated with F1, F2, and F3, and F3 is also correlated with F1 and F2. Only F1 and F2 are uncorrelated amongst the frequency characters. In two cases frequency and temporal characters are correlated, D9 with F1 and F3.

Multivariate comparisons.—The differences in mean vectors of the multivariate comparisons are highly significant ($P < 0.0001$). The MANOVA's for each character (Table 4) indicate statistically significant ($P < 0.05$) differences in only four charac-

TABLE 5

RESULTS OF SCHEFFE'S S-METHOD

Character[1]	Localities[2,3]			
F1	F	T	N	M
D4	M	N	T	F
D8	N	T	M	F
D10	N	T	F	M

[1] See Fig. 2 for explanation.
[2] Ranked in order of decreasing mean values (Table 1).
[3] Lines under localities connect those that are not significantly different ($P < 0.05$).

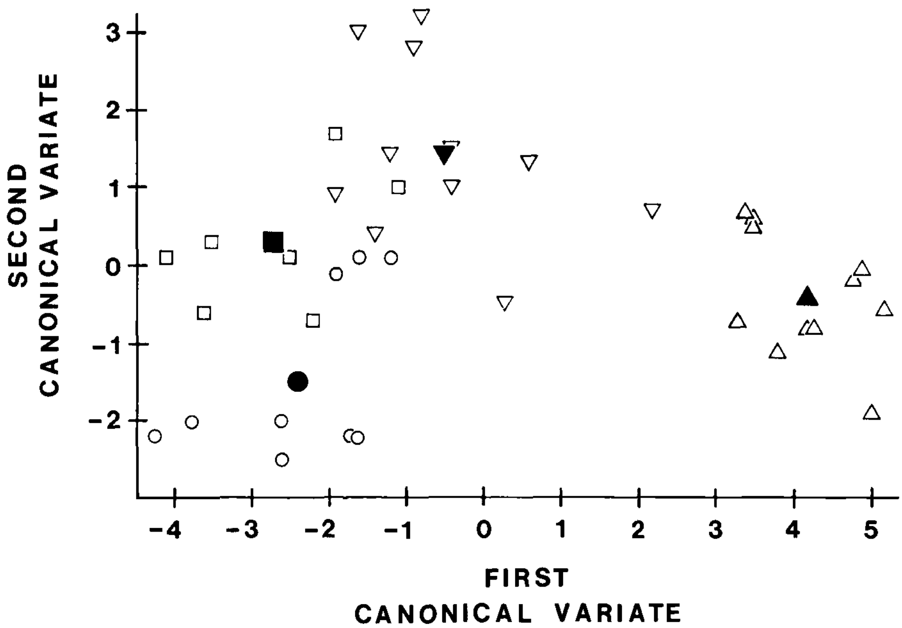

Fig. 3. Means and individuals from each location plotted by the first and second canonical variates. Circles represent Florida; squares, Texas; triangles, Massachusetts; inverted triangles, Nebraska. Closed symbols indicate means and open symbols, individuals.

ters: F1, D4, D8, and D10. Of these characters only two, F1 and D8, are highly significantly ($P < 0.001$) different in the four groups.

Scheffe's S-method (Seal 1964) was selected as the *a posteriori* test of significance between individual groups for the four significant characters. Massachusetts sonograms are separable from the other groups in two characters (Table 5). Nebraska calls are separable from all other groups for only F1 (Table 5). All four characters link Texas and Florida (Table 5), separating them, as a unit, from Nebraska and Massachusetts (F1), and Massachusetts (D4). Nebraska and Texas appear as couplets for D8 and D10, while Florida and Massachusetts couple for D10 (Table 5).

Canonical variates analysis resulted in having 100% of the variation explained along the first 3 canonical axes (Table 6), with the greatest portion of variation explained by the first axis. The eigenvectors for the canonical discriminant functions (Table 7) were then used, with the appropriate characters of individuals and group means to plot the first canonical axis against the second (Fig. 3). The first canonical variate separates the Massachusetts group from the others, while often separating the Nebraska values from Florida and Texas. Florida and Texas calls appear insepara-

TABLE 6

EIGENVALUES FOR CANONICAL VARIATES ANALYSIS

Discriminant function	Eigenvalue	Percent	Cumulative percent
I	8.7499	80.26	
II	1.2861	11.80	92.06
III	0.8653	7.94	100.00

TABLE 7

EIGENVECTORS FOR CANONICAL VARIATES ANALYSIS

Discriminant Function	I	II	III
F1	−0.3653	−0.1227	−0.0604
F2	0.2546	−0.0684	0.0106
F3	−0.0065	0.0710	0.1726
F5	−0.3011	−0.1805	0.1307
D1	0.0412	0.0080	−0.1488
D2	−0.0544	0.0142	0.0510
D3	−0.0359	0.0225	−0.1091
D4	0.2834	0.0187	0.2073
D5	0.0945	−0.1232	−0.2071
D8	0.0217	0.0564	0.0846
D9	0.0196	−0.9665	0.0391
D10	−0.0229	−0.0245	−0.0726
Constant	6.8582	6.9210	−5.3721

ble along this axis. The second canonical variate, although separating all four means from each other, would leave individuals of the groups inseparable.

DISCUSSION

Univariate comparisons.—The results of the univariate analyses indicate that variation does exist among the populations of Bobwhite for all but two temporal characters. In only two characters can a geographic trend be suggested, one (F5) north-south and one (D5) east-west. However, the temporal trend is disrupted by the lack of significant differences between Florida and Nebraska.

In view of the fact that the frequency components appear to be correlated, it is reasonable to suggest that frequency tends to vary along a north-south axis. This tendency is similar to the size trends (Ripley 1960, Holman 1961) detected for the Bobwhite. A review of the literature (Goldstein 1974) reveals a relationship between the size of the syringeal structures and frequency in birds. Thus, if it is assumed that larger birds have larger acoustical sources, frequency variation should be proportionate to size variation.

The high correlation between D8 and D10 is an example of redundancy in character selection. As can be seen in Fig. 2, both of these characters are measures of time between successive calls. The fact that D3 is correlated with D9, indicates the relative importance and magnitude of D3 as a component of D9.

Multivariate comparisons.—MANOVA, unlike ANOVA, considers all characters in the presence of all other characters, taking into account covariance as well as variance. The multivariate tests of significance for the Bobwhite's acoustical data do indicate the existence of differences between the populations. These significant characters tend to ally closely Florida and Texas populations and to separate Massachusetts birds. Although not clearly delineating a north-south tendency in frequency, comparisons made on two of the timing components do indicate an east-west displacement.

As suggested by Blackith and Reyment (1971), tests of significance are at best secondary in the value of multivariate testing. The reason for the selection of multivariate methods is to attempt to define the framework of the analyzed problem in multidimensional space. As subgroups were presupposed in this study, canonical variate analysis was the appropriate method to be used towards this end (Blackith and Reyment 1971). This method transforms the original observational data, rotating their axes in a manner that minimizes within-population variability and maximizes the variability between the means of the populations. Although the vectors for the characters are not at right angles to one another, the canonical variate axes are perpendicular to one another.

The first canonical variate in this study may at first appear to be a size-related phenomenon and thus related to a north-south axis. However, the canonical distance between Nebraska and Massachusetts samples cannot be explained by any apparent geographic trend related to a north-south gradient. It is sufficient to say that Massachusetts birds are clearly separable along the first discriminatory axis.

The second canonical variate, although not clearly separating the individuals of the populations, does tend to shift the means of the samples so as to segregate them along an east-west axis. It is difficult to perceive any basis for such a tendency for the Bobwhite.

Caution should be taken in attempting to fit any geographic trend to these data in light of the number of localities being considered (Thielcke 1969). However, if a statement may be made with the limitations of this study in mind, the differences in the vocalizations of these four populations tend to imply a mosaic pattern rather than one associated with any geographic cline. It would then be proper to refer to dialects (*sensu* Thielcke 1969) in the Bobwhite. The conclusion that dialects exist, as opposed to geographic variation along gradients, may be an artifact of the number of populations sampled. Dialectic differences have been demonstrated in passerines (Marler and Tamura 1962, Lemon 1971, Payne 1973), hummingbirds (Wiley 1971), mammals (LeBoeuf and Peterson 1969, Somers 1973) and insects (Patty et al. 1973, Miller et al. 1975).

General considerations.—Unlike morphological characters, which are genetically transmitted, acoustical characters may also be the result of learning. Marler and Tamura (1964) and Lemon (1971) suggested that dialects in sparrows and Cardinals are maintained through cultural transmittance (i.e. learning). Payne (1973) remained noncommittal as to the method of maintenance of wingflap dialects in the Flappet Lark (*Mirafra rufocinnamomea*). My approach is that of Payne, as no data are available on the role of learning in acoustical signal development in Bobwhite. In Domestic Fowl (*Gallus domesticus*), learning apparently plays no role in the ontogeny of vocalization (Konishi 1963), while the heritability of the duration of crowing in adults has been demonstrated (Siegel et al. 1965). Extrapolation of these data to Bobwhite would be dangerous. Nottebohm (1970) makes a strong case for cultural transmittance as the source of dialects, but one cannot dispute the fact that genetic transmittance may be the vector of separation. This latter control appears to be the situation in courtship wing vibrations of *Drosophila athabasca* (Dwight D. Miller pers. comm.).

At the time the sonograph was introduced to studies of avian vocalization (Borror and Reese 1953) it was lauded for its ability to give permanent visual records of a transient acoustical spectre. This visible representation allowed the potential for a degree of quantification previously unavailable. By plotting frequency against time, the sonograph produced two-dimensional "forms," which had been previously unknown, but instead of attempting to quantify these "forms," biologists measured very few characteristics, in fact in most instances these were the same as had been approximated with stopwatch and ear. The more complex "forms" were found in songbirds, and qualitative differences were easily recognizable. Somehow, in the early stages of sonographic comparisons of avian vocalizations, quantification became almost secondary to these qualitative comparisons of "form." This study has attempted to quantify the "form" of the Bobwhite's "hoy" call and has made comparisons based on their morphology.

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LITERATURE CITED

AGEE, C. P. 1957. The fall shuffle in central Missouri Bob-whites. J. Wildl. Mgmt. 21: 329–335.

ALDRICH, J. W. 1946. The United States races of the Bob-white. Auk 63: 493–508.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds, fifth ed. Baltimore, Amer. Ornithol. Union.

BAKER, M. C. 1975. Song dialects and genetic differences in White-crowned Sparrows (*Zonotrichia leucophrys*). Evolution 29:226–241.

BEIGHTOL, D. R., AND D. E. SAMUEL. 1973. Sonagraphic analysis of the American Woodcock's *Peent* call. J. Wildl. Mgmt. 37: 470–475.

BERTRAM, B. 1970. The vocal behaviour of the Indian Hill Mynah, *Gracula religiosa*. Anim. Behav. Monogr. 3: 81–192.

BLACKITH, R. E., AND R. A. REYMENT. 1971. Multivariate morphometrics. New York, Academic Press.

BORROR, D. J. 1959. Variation in the songs of the Rufous-sided Towhee. Wilson Bull. 71: 54–72.

———. 1965. Song variation in Maine Song Sparrows. Wilson Bull. 77: 5–37.

———, AND C. R. REESE. 1953. The analysis of bird songs by means of a vibralyzer. Wilson Bull. 65: 271–276.

DIXON, W. J. 1973. Biomedical computer programs. Los Angeles, Health Sciences Computing Facility, UCLA.

EMLEN, S. T. 1971a. The role of song in individual recognition in the Indigo Bunting. Z. Tierpsychol. 28: 241–246.

———. 1971b. Geographic variation in Indigo Bunting song (*Passerina cyanea*). Anim. Behav. 19: 407–408.

FINA, J. D. 1972. Univariate and multivariate analysis of variance, covariance, and regression. Ann Arbor, National Educational Resources, Inc.

GOLDSTEIN, R. B. 1974. Some physiological and zoogeographic parameters in the vocal acoustics of New World quail (Phasianidae: Aves). Unpublished Ph.D. dissertation, Lincoln, Univ. Nebraska.

HARRIS, M. A., AND R. E. LEMON. 1972. Songs of song sparrows (*Melospiza melodia*): individual variation and dialects. Canadian J. Zool. 50: 301–309.

HECKENLIVELY, D. B. 1970. Song in a population of Black-throated Sparrows. Condor 72: 24–36.

HEINZ, G. H., AND L. W. GYSEL. 1970. Vocalization behavior of the Ring-necked Pheasant. Auk 87: 279–295.

HOLMAN, J. A. 1961. Osteology of living and fossil New World quails (Aves, Galliformes). Bull. Florida State Mus. 6: 131–233.

HUTCHISON, R. E., J. G. STEVENSON, AND W. H. THORPE. 1969. The basis for individual recognition by voice in the Sandwich Tern (*Sterna sandvicensis*). Behaviour 32: 150–157.

KONISHI, M. 1963. The role of auditory feedback in the vocal behaviour of the domestic fowl. Z. Tierpsychol. 20: 349–367.

———. 1964. Song variation in a population of Oregon Juncos. Condor 66: 423–436.

LEBOEUF, B. J., AND R. S. PETERSON. 1969. Dialects in elephant seals. Science 166: 1654–1656.

LEMON, R. E. 1969. The relation between organization and function of song in Cardinals. Behaviour 32: 158–178.

———. 1971. Differentiation of song dialects in Cardinals. Ibis 113: 373–377.

LEOPOLD, A. 1933. Game management. New York, Charles Scribner's Sons.

MARLER, P., AND D. ISAAC. 1960a. Physical analysis of a simple bird song as exemplified by the Chipping Sparrow. Condor 62: 125–135.

———, AND ———. 1960b. Song variation in a population of Brown Towhees. Condor 62: 272–283.

———, AND ———. 1961. Song variation in a population of Mexican Juncos. Wilson Bull. 73: 193–206.

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

———, AND ———. 1964. Culturally transmitted patterns of vocal behavior in sparrows. Science 146: 1483–1486.

MILLER, D. D., R. B. GOLDSTEIN, AND R. A. PATTY. 1975. Semispecies of *Drosophila athabasca* distinguishable by male courtship sounds. Evolution 29: 531–544.

MURPHY, D. A., AND T. S. BASKETT. 1952. Bobwhite mobility in central Missouri. J. Wildl. Mgmt. 16: 498–510.

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

———. 1970. Ontogeny of bird song. Science 167: 950–956.

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: 146–153.

PATTY, R. A., R. B. GOLDSTEIN, AND D. D. MILLER. 1973. Sonograms prepared from D. athabasca male courtship sound. Drosophila Information Serv. 50: 67.

PAYNE, R. B. 1973. Wingflap dialects in the Flappet Lark *Mirafra rufocinnamomea*. Ibis 115: 270–274.

POWER, D. M. 1970. Geographic variation of Red-winged Blackbirds in central North America. Univ. Kansas Mus. Nat. Hist. Publ. 19: 1–83.

RIDGWAY, R., AND H. FRIEDMANN. 1946. The birds of North and Middle America. Smithsonian Inst. Bull. 50, part 10.

RIPLEY, T. H. 1960. Weights of Massachusetts quail and comparisons with other geographic samples for taxonomic significance. Auk 77: 445–447.

ROSENE, W. 1969. The Bobwhite quail, its life and management. New Brunswick, Rutgers Univ. Press.

SEAL, H. L. 1964. Multivariate statistical analysis for biologists. London, Methuen and Company Ltd.

SHIOVITS, K. A., AND W. L. THOMPSON. 1970. Geographic variation in song composition of the Indigo Bunting, *Passerina cyanea*. Anim. Behav. 18: 151–158.

SIEGEL, P. B., R. E. PHILLIPS, AND E. F. FOLSOM. 1965. Genetic variation in the crow of adult chickens. Behaviour 24: 229–235.

SOMERS, P. 1973. Dialects in southern Rocky Mountain Pikas, *Ochotona princeps* (Lagomorpha). Anim. Behav. 21: 124–137.

STODDARD, H. L. 1931. The Bobwhite quail; its habits, preservation and increase. New York, Charles Scribner's Sons.

STOKES, A. W. 1967. Behavior of the Bobwhite, *Colinus virginianus*. Auk 84: 1–33.

———, AND H. W. WILLIAMS. 1968. Antiphonal calling in quail. Auk 85: 83–89.

THIELCKE, G. 1969. Geographic variation in bird vocalizations. Pp. 311–339, *in* Bird vocalizations (R. A. Hinde, Ed.). Cambridge, Univ. Press.

VAN DER WEYDEN, W. J. 1973. Geographical variation in the territorial song of the White-faced Scops Owl *Otus leucotis*. Ibis 115: 129–131.

WILEY, R. H. 1971. Song groups in a singing assembly of Little Hermits. Condor 73: 28–35.

WILLIAMS, D. H. 1972. Individual variation in the bobwhite call of *Colinus virginianus*. Unpublished M.S. thesis, College Park, Univ. Maryland.