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SEASONAL VARIATION IN GRAY PARTRIDGE VOCAL BEHAVIOR[1]

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Abstract. Gray Partridge (*Perdix perdix*) calling data were obtained during 138 sunrise and 140 sunset surveys, winter 1982–1983 through summer 1984. Calling activity was concentrated in the 45-min periods before sunrise and after sunset. Calling was more frequent ($P < 0.05$) in mornings than evenings in summer and winter, but not late winter–spring. Gray Partridge calling frequency differed ($P < 0.05$) among seasons and peaked during February to April. Acoustical structure of calls supported predictions regarding characteristics used in grassland environments to minimize signal attenuation. Sonagraphic analysis of calls revealed that frequency of calls was low and rapidly modulated and that average call duration differed ($P < 0.05$) among seasons. We hypothesize that seasonal differences in calling behavior and acoustical structure of the calls reflect seasonal variation in the function of calls.

Key words: Gray Partridge; vocalization; calling behavior; sonograms; Washington.

INTRODUCTION

Further research on the functions of avian vocalization is needed (Catchpole 1982) especially regarding functions of avian calls. Thielcke (1976: 190) noted that "in contrast to bird song . . . bird calls have so far been given little attention by scientists," and "this is quite unjustified." The lack of detailed study of Gray Partridge (*Perdix perdix*) calls is a case in point. Gray Partridge calls have been briefly described, but no detailed analyses of calling behavior, acoustical structure of calls, or functions of calls have been reported. Furthermore, Gray Partridge call year-round. Thus, they provide an opportunity to study not only within-season variation in calling behavior, structure, and function but also, the lesser-studied subject of variation among seasons.

Objectives of this study were to investigate seasonal variation in Gray Partridge calling behavior and acoustical structure and function of Gray Partridge calls. We sought to understand more fully the meaning(s) of the primary call of the Gray Partridge and investigate how this call relates to partridge biology and behavior. In addition to the above objectives, our data provided an opportunity to examine acoustical structure of calls and test predictions regarding acoustical characteristics used in grassland environments to minimize signal attenuation. We attempted to meet our objectives by: (1) obtaining long-term records of Gray Partridge calling; (2) relating variation in calling behavior to time of day, season, and annual cycle; and (3) analyzing seasonal acoustical structure of calls via sonograms. This study was conducted in conjunction with larger long-term research efforts to estimate population density and evaluate the validity of using Gray Partridge call counts as an index to population density (Ratti et al. 1983, Rotella and Ratti 1986). Thus, while conducting this study, we were also estimating population density via line transects (Burnham et al. 1980) on the study area.

The Gray Partridge *kee-uck* call was described by Spiker (1929). This long distance call is the most commonly heard vocalization given during crepuscular periods throughout most of the year. The *kee-uck* call has also been variously described as *kee-c-cah* (Yocom 1943), *keee-uck* (McCabe and Hawkins 1946), *tur-ip* (Godfrey 1966), and *kerr-r-r-r-r-ik* (Cramp and Simmons 1980:493). We use *kee-uck* (Spiker 1929) in this paper because we feel that it appropriately describes the call. The most thorough description

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of Gray Partridge vocalization was reported by McCabe and Hawkins (1946). Rotella and Ratti (1986) discussed the relationships between calling frequency and population density and calling frequency and meteorological conditions.

We provide the following brief review of the annual cycle of the Gray Partridge to assist interpretation of vocalization data. Gray Partridge are associated with open areas that are intensively farmed (McCabe and Hawkins 1946, Murtha 1967). Gray Partridge coveys disband and pairs are formed from late January through early March, depending on weather conditions (Yocom 1943, Porter 1955, Blank and Ash 1956, Weigand 1980). Most nests are initiated during late April and May. Nests are commonly constructed in grassy fields, fencerows, roadside right-of-ways, and idle patches of farmland (McCabe and Hawkins 1946, Hupp et al. 1980, Weigand 1980). Parent birds and chicks form coveys and often remain as distinct family units into winter, but see Ratti et al. (1983:1093–1094). Dense crop fields and idle vegetation are used as brood habitat; harvested hay and grain fields and edge habitats are preferred during fall and winter (Weigand 1980, Smith et al. 1982, Mendel and Peterson 1983).

STUDY AREA AND METHODS

Our 178-km^2 study area was in southeast Whitman County, with its northern boundary 3.3 km south of Pullman, Washington, in the Palouse Prairie. The Palouse Prairie, characterized by undulating open terrain, has been described by Knott et al. (1943), Yocom (1943), and Mendel and Peterson (1977, 1980). The vast majority of the area was in small grain production (winter and spring wheat, winter and spring barley, dry peas, and lentils), with infrequent patches of pasture, hay, idle area, and coniferous forest.

Gray Partridge *kee-uck* calls were recorded along a 40-km circular route in typical partridge habitat. Twenty listening stations were positioned along the route. Because Gray Partridge *kee-uck* calls can be heard for 0.8 km (Weigand 1980), listening stations were spaced no less than 1.6 km apart. Thus, we avoided hearing the same birds at different stations. Two measures of calling frequency—the number of *kee-uck* calls and the number of calling groups—were recorded during 4 min of undisturbed listening at each station. The number of calling groups was defined as the number of identifiable locations from which calls were heard. Locations were easily distinguished because the distance between them was substantial and the number of calling groups at a listening station was usually small. Our survey methodology was similar to that used for other upland game bird species (Kimball 1949, Robel et al. 1969, Sayre et al. 1978). Relative darkness during survey periods and the secretive nature of Gray Partridge prevented observation of birds. Thus, we were unable to record behavioral contexts of vocalizations. Study of call types other than the *kee-uck* was difficult because other types, which are primarily short distance calls, were rarely heard.

Surveys were conducted morning and evening, late fall through summer. Mid-fall surveys were eliminated because of hunting activity on the study area. Exact time relative to sunrise/sunset was recorded at each listening station. Surveys were not conducted when average wind speeds exceeded 5.4 mps (12 mph) because of wind noise. Surveys were initiated 1.00 hr before sunrise and 1.25 hr before sunset, and were conducted for approximately 2.25 hr. Surveys were restricted to crepuscular periods based on previous reports (Haugen 1941, McCabe and Hawkins 1946, Blank and Ash 1956, March and Church 1980). Second-year survey times were adjusted based on first-year results (see Results). Listening point survey order (1–20 vs. 20–1) was alternated as recommended by Stirling and Bendell (1966) and March and Church (1980).

Effects of time of day and year on calling frequency were analyzed by the median test (Conover 1980:171–176) because calling data violated assumptions of parametric statistics, i.e., the data were nonnormally distributed, distribution functions were different ($P < 0.05$) among seasons, and standard deviations were proportional to calling frequency means. Data from the following 10 sampling periods were analyzed: winter 1982–1983 (am and pm), late winter–spring 1983 and 1984 (am and pm), and summer 1983 and 1984 (am and pm).

Gray Partridge *kee-uck* calls were tape-recorded during pair formation (March), nesting and brood-rearing (June to August), and fall covey (October) periods using a Uher 4200 recorder and Dan Gibson parabolic reflector microphone. Recordings were analyzed on a Kay Elemetrics 6061B Sona-Graph using 80 to 8,000 Hz, wide band, linear display modes and 40 to 4,000 Hz, wide band, linear and contour display modes.

TABLE 1. Gray Partridge call count surveys in Whitman County, Washington, 1982 to 1984.

Survey season	*n* surveys Sun-rise	Sun-set	*n* listening[a] stations
Winter 1982–1983			
18 December–20 January	18	19	740
Late winter–spring 1983			
9 February–10 April	16	15	450
Summer 1983			
7 July–15 September	33	34	1,120
Late winter–spring 1984			
6 February–14 April	31	34	390
Summer 1984			
9 July–14 September	40	38	468
Total	138	140	3,168

[a] 4 min each.

RESULTS

Between 18 December 1982 and 14 September 1984 we conducted 138 sunrise and 140 sunset surveys (Table 1). Variation in survey season dates represents adjustments based on analysis of 1982–1983 data. Winter surveys were not conducted in 1984 because calls were only recorded during 39% of winter morning surveys and 0% of winter evening surveys in the first year. Analysis of data from 99 1982–1983 surveys (48 morning and 51 evening 2.25-hr surveys) revealed that 86 and 82% of all calling groups and 82 and 73% of all calls were recorded in the 45-min periods before sunrise and after sunset, respectively (Figs. 1 and 2). Thus, during 1984, surveys were shortened and conducted in those 45-min periods (six listening stations per survey—two listening stations per 15-min survey segment). Only data from those periods were used in statistical analyses. Our useful calling data from 1983 were obtained at listening stations 1 to 7 and 14 to 20. Thus, we restricted 1984 data collection to these 14 listening stations for consistency. Additional behavioral data were not collected because of our inability to observe birds during the relative darkness of survey periods.

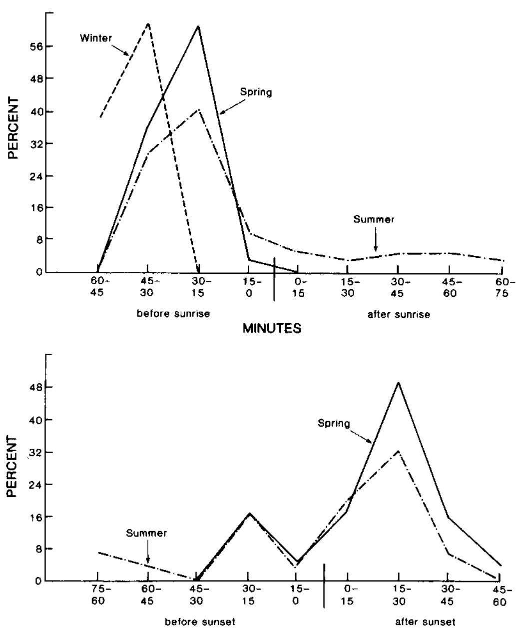

FIGURE 1. Seasonal frequency distributions of the average number of Gray Partridge calling groups recorded per survey, Whitman County, Washington, 1982 to 1983.

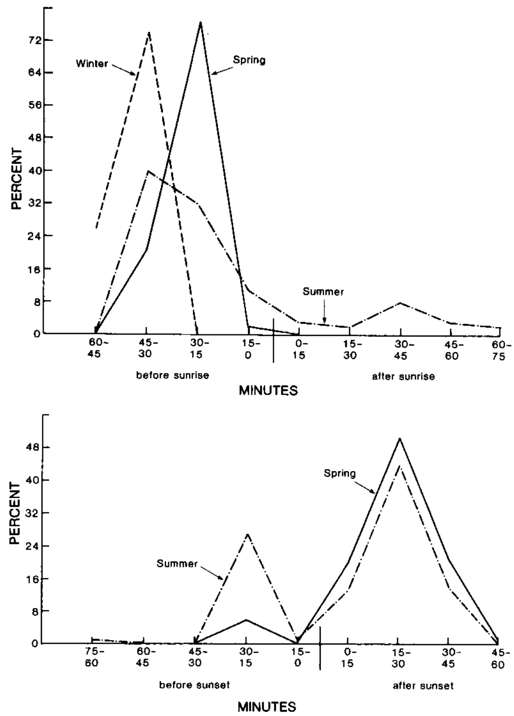

FIGURE 2. Seasonal frequency distributions of the average number of Gray Partridge calls recorded per survey, Whitman County, Washington, 1982 to 1983.

Calling frequency was different ($P < 0.05$) among the three 15-min segments of 45-min morning or evening surveys during all sampling periods except winter 1982–1983 pm, when no

TABLE 2. The number of Gray Partridge calling groups recorded in each 15-min segment of 45-min sunrise and sunset surveys, Whitman County, Washington, 1982 to 1984.

Season	n calling groups per survey segment[a] $\bar{x}$ (SD)					
	Min before sunrise			Min after sunset		
	45–30	30–15	15–0	0–15	15–30	30–45
Winter 1982–1983	0.5 (0.9)	0.0 (0.0)	0.0 (0.0)[b]	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Late winter–spring 1983	2.0 (1.8)	2.5 (2.6)	0.4 (0.7)	1.3 (1.7)	2.0 (1.8)	0.3 (0.6)
Summer 1983	1.2 (1.4)	1.6 (1.5)	0.5 (0.9)	0.2 (0.6)	0.6 (1.0)	0.1 (0.2)
Late winter–spring 1984	1.0 (1.4)	1.3 (1.9)	0.1 (0.4)	0.5 (1.0)	1.6 (1.9)	0.7 (1.0)
Summer 1984	0.4 (0.9)	1.2 (1.2)	0.3 (0.7)	0.2 (0.4)	0.5 (1.1)	0.1 (0.4)

[a] Two 4-min listening stations per 15-min survey segment.
[b] Median test; calling frequencies (number of calling groups per 8 min of listening) underscored by the same line are not different ($P > 0.05$).

calls were recorded (Tables 2 and 3). Calling was most frequent 30 to 15 min before sunrise and 15 to 30 min after sunset except in winter 1982–1983.

More calls and calling groups were recorded during morning surveys than evening surveys in winter and summer ($P < 0.05$) but not during late winter–spring ($P > 0.05$) (Table 4). Calling frequency peaked during late winter–spring and was lowest in winter (Table 4).

Average duration of *kee-uck* calls was different ($P < 0.05$) among late winter–spring, summer, and fall (Table 5). Because winter calling frequency was low, winter recordings were not obtained. Summer calls were longest ($P < 0.05$) and fall calls were shortest ($P < 0.05$). Sonograms of *kee-uck* calls appear as three-banded structures with three distinct segments to each band (Fig. 3). Frequency (measured from the lowest frequency of the lowest band to the highest frequency of the highest band with accuracy ±50 Hz) of late winter–spring, summer, and fall calls ranged from 750 to 3,500 Hz, 950 to 3,400 Hz, and 1,250 to 3,900 Hz, respectively. Calls were structurally distinct for all three seasons (Fig. 3). Late winter–spring and summer calls differed mainly in the duration of the zone of rapid frequency modulation, the *ee* segment (Table 5). Frequency range tracings of the *ee* segment of summer calls are approximate because actual sonograms of the segment were faint. Quality recordings of Gray Partridge calls were difficult to obtain in the field. The microphone could not be aimed precisely because birds could not be seen in darkness and/or vegetation, and birds were not easily approached.

DISCUSSION

Our data are not completely consistent with the results of other Gray Partridge vocalization studies. We recorded the most intense calling activity during the 45-min periods before sunrise and after sunset. This is contrary to March and Church (1980), who reported that Gray Partridge called most frequently in periods just before sunrise *and before* sunset during March and April in Wis-

TABLE 3. The number of Gray Partridge calls recorded in each 15-min segment of 45-min sunrise and sunset surveys, Whitman County, Washington, 1982 to 1984.

Season	n calls per survey segment[a] $\bar{x}$ (SD)					
	Min before sunrise			Min after sunset		
	45–30	30–15	15–0	0–15	15–30	30–45
Winter 1982–1983	7.3 (14.8)	0.0 (0.0)	0.0 (0.0)[b]	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Late winter–spring 1983	26.5 (36.7)	47.6 (53.1)	2.9 (6.1)	13.9 (20.6)	31.2 (38.2)	5.8 (17.2)
Summer 1983	14.6 (26.3)	15.0 (22.4)	4.8 (11.8)	1.8 (4.3)	5.6 (10.6)	1.2 (6.1)
Late winter–spring 1984	8.7 (15.6)	18.6 (56.9)	1.5 (4.9)	7.4 (21.8)	26.6 (51.0)	10.4 (21.7)
Summer 1984	4.8 (12.8)	13.3 (17.9)	3.8 (12.6)	2.0 (9.8)	7.1 (18.3)	0.7 (3.5)

[a] Two 4-min listening stations per 15-min survey segment.
[b] Median test; calling frequencies (number of calls per 8 min of listening) underscored by the same line are not different ($P > 0.05$).

TABLE 4. Seasonal Gray Partridge calling frequency, Whitman County, Washington, 1982 to 1984.

	n calling groups per survey[a]		*n* calls per survey[a]	
	Sunrise surveys	Sunset surveys	Sunrise surveys	Sunset surveys
Season	$\bar{x}$ (SD)	$\bar{x}$ (SD)	$\bar{x}$ (SD)	$\bar{x}$ (SD)
Winter 1982	0.5 (0.9)	0.0 (0.0)	7.3 (14.8)	0.0 (0.0)
Late winter–spring 1983	4.9 (3.4)	3.6 (3.0)	76.9 (61.1)	50.9 (48.6)
Summer 1983	3.3 (2.1)	0.9 (1.2)	34.4 (38.0)	8.6 (12.5)
Late winter–spring 1984	2.4 (2.8)	2.7 (2.3)	28.8 (59.6)	44.4 (53.4)
Summer 1984	1.8 (1.9)	0.7 (1.2)	21.9 (26.0)	9.7 (20.2)

[a] Surveys conducted during the 45-min periods before sunrise and after sunset; six 4-min listening stations per survey.

consin. Our sonograms ranged from approximately 750 to 4,000 Hz. Sonograms of *kee-uck* calls recorded in England ranged from approximately 1,200 to 6,200 Hz (D. Bower in Cramp and Simmons 1980:493). Thus, Gray Partridge call structure and behavior may vary among populations. Geographical variation in vocalization has been reported for other galliforms (Sparling 1979, Baily and Baker 1982). However, these differences may also be the result of small sample size problems in the other studies. March and Church (1980) conducted four evening surveys vs. 51 evening surveys in this study. D. Bower (in Cramp and Simmons 1980:493) prepared two sonograms vs. 106 sonograms in this study. Further research comparing the vocal behavior and acoustic structure of calls for different populations of Gray Partridge is needed.

Acoustical characteristics of *kee-uck* calls support Morton's (1975) predictions regarding grassland vocalizations. Grasslands are difficult sound propagation environments and attenuation worsens as frequency increases (Morton 1975). Thus use of low and rapidly modulated frequencies is expected. Gray Partridge *kee-uck* calls possess these characteristics (Fig. 3). In grasslands, "selection probably favors coding based on the temporal components of sound signals, for in open environments as long as the sound is audible the temporal pattern will remain little unchanged and should provide a more efficient means of communication" (Morton 1975: 29). Gray Partridge did alter the temporal pattern of calls among seasons, especially the duration of the rapid frequency modulation portion of the call (Table 5), and did not dramatically change the frequency range or overall structure of calls among seasons (Fig. 3). We hypothesize that seasonal differences in duration of the call relate to seasonal differences in functions of the call. Call functions may be affected by seasonal differences in hormone levels (Davis 1958), territoriality, aggressiveness, and family structure. Thus, seasonal differences in call structure may be manifestations of changes in the motivation-structural code and represent signal grading (see Morton 1977, 1982). However, in other examples, signals are graded via within-season changes in frequency and tonality (see summary in Morton 1982). Our data indicate possible interseasonal grading based on changes in call duration.

Gray Partridge calling peaked annually during February to April (Table 4). During late winter–spring, when partridge are establishing and defending territories and seeking mates, there may be a selective advantage to calling intensively during morning and evening. This does not appear to be the case during other times of the year.

TABLE 5. Temporal characteristics of Gray Partridge *kee-uck* calls, Whitman County, Washington, 1983 to 1985.

		Duration (sec)			
		kee-uck		*ee* segment[a]	
Season	*n* calls measured	$\bar{x}$	SD	$\bar{x}$	SD
Late winter–spring	10	0.39B[b]	0.05	0.23B	0.04
Summer	27	0.51C	0.17	0.33C	0.14
Fall	69	0.19A	0.03	0.10A	0.02

[a] Zone of rapid frequency modulation in the middle of *kee-uck* calls.
[b] Fisher's protected least significant difference test, means with the same capital letter are not significantly ($P > 0.05$) different from other means in the column.

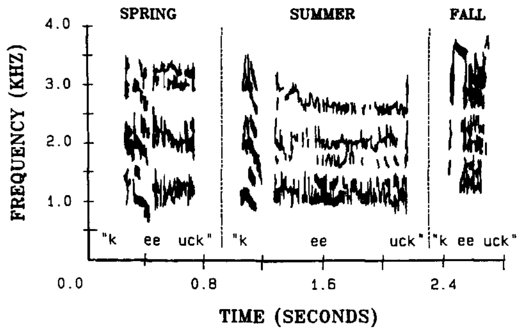

FIGURE 3. Seasonal sonograms of Gray Partridge *kee-uck* calls, Whitman County, Washington, 1983 to 1985; tracings of the *ee* segment of spring and summer calls are approximate because sonograms of these segments were very faint.

We hypothesize that during summer, Gray Partridge attending nests or accompanying broods call infrequently in the evening to avoid revealing overnight roost locations to predators. A similar hypothesis can be applied to winter. Gray Partridge *kee-uck* calls had many of the characteristics of mobbing calls: low frequency, wide frequency modulation, distinct beginning and ending, and relatively short duration (Fig. 1). Sounds with these characteristics are easily located (Marler 1955, 1957; Thorpe 1965). Evening calling during spring may enhance territory maintenance and thus provide a selective advantage outweighing an increased risk of predation.

It is difficult to determine specific functions of a call within a season because any call may transmit several types of information (see Bremond 1963, Catchpole 1979:16). Furthermore, seasonal differences in calling frequency and call duration indicate that functions of the *kee-uck* call may change throughout the annual cycle. Research regarding specific functions of the *kee-uck* call via rigorous experimentation is needed (e.g., Krebs 1977). Also, see Catchpole (1982) for a discussion of the need for, and development of, techniques to test hypotheses regarding functions of bird sounds through experimentation. However, most studies that analyze functions of vocalizations deal with species that are easily observed during vocalizations (e.g., Ficken et al. 1978, Baptista and King 1980, Sparling 1981, Howes-Jones 1985, Ritchison 1985, Rothstein and Fleisher 1987). Similar research is difficult on Gray Partridge because most calling activity takes place during periods of darkness.

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LITERATURE CITED

Baily, E. D., and J. A. Baker. 1982. Recognition characteristics in covey dialects of Bobwhite Quail. Condor 84:317–320.

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

Blank, T. H., and J. S. Ash. 1956. The concept of territory in the partridge (*Perdix perdix perdix*). Ibis 98:379–389.

Bremond, J. C. 1963. Acoustic behaviour of birds, p. 709–750. *In* R. G. Busnel [ed.], Acoustic behaviour of animals. Elsevier Publishing Co., New York.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72:1–202.

Catchpole, C. K. 1979. Vocal communication in birds. Institute of Biology's Studies in Biology No. 115. Edward Arnold Publishers, London.

Catchpole, C. K. 1982. The evolution of bird sounds in relation to mating and spacing behavior, p. 297–319. *In* D. E. Kroodsma, E. H. Miller, and H. Ouellet [eds.], Acoustic communication in birds. Vol. I. Academic Press, New York.

Conover, W. J. 1980. Practical nonparametric statistics. 2nd ed. John Wiley and Sons, New York.

Cramp, S., and K.E.L. Simmons [eds.]. 1980. Handbook of the birds of Europe, the Middle East and North Africa. Vol. 2: Hawks to bustards. Royal Society for the Protection of Birds. Oxford Univ. Press, Oxford.

Davis, J. 1958. Singing behavior and the gonad cycle of the Rufous-sided Towhee. Condor 60:308–336.

Ficken, M. S., R. W. Ficken, and S. R. Witkin. 1978. Vocal repertoire of the Black-capped Chickadee. Auk 95:34–38.

Godfrey, W. E. 1966. The birds of Canada. Natl. Mus. Can. Bull. 203.

Haugen, A. O. 1941. The roosting and rising habits of the Hungarian Partridge. Wilson Bull. 53:495–496.

Howes-Jones, D. 1985. Relationships among social activity, context, and social behavior in the Warbling Vireo. Wilson Bull. 97:4–20.

Hupp, J. W., L. M. Smith, and J. T. Ratti. 1980. Gray Partridge nesting biology in eastern South Dakota, p. 55–69. *In* S. R. Peterson and L. Nelson, Jr. [eds.], Proc. Perdix II: Gray Partridge workshop. For., Wildl. and Range Exp. Stn., Univ. Idaho, Moscow.

KIMBALL, J. W. 1949. The crowing count pheasant census. J. Wildl. Manage. 13:101–120.

KNOTT, N. P., C. C. BALL, AND C. F. YOCOM. 1943. Nesting of the Hungarian Partridge and Ring-necked Pheasant in Whitman County, Washington. J. Wildl. Manage. 7:283–291.

KREBS, J. R. 1977. Song and territory in the Great Tit *Parus major*, p. 47–62. *In* B. Stonehouse and C. Perrins [eds.], Evolutionary ecology. University Park Press, Baltimore.

MARCH, J. R., AND K. E. CHURCH. 1980. Use of roadside calling counts as an index to spring Gray Partridge abundance, p. 87–100. *In* S. R. Peterson and L. Nelson, Jr. [eds.], Proc. Perdix II: Gray Partridge workshop. For., Wildl. and Range Exp. Stn., Univ. Idaho, Moscow.

MARLER, P. 1955. Characteristics of some animal calls. Nature 176:6–8.

MARLER, P. 1957. Species distinctiveness in the communication signals of birds. Behaviour 11:13–39.

MCCABE, R. A., AND A. S. HAWKINS. 1946. The Hungarian Partridge in Wisconsin. Am. Midl. Nat. 36: 1–75.

MENDEL, G. W., AND S. R. PETERSON. 1977. The Hungarian Partridge in Idaho, p. 108–115. *In* G. D. Kobriger [ed.], Proc. Perdix I: Hungarian Partridge workshop. Cent. Mtns. and Plains Sect., The Wildlife Soc., Minot, ND.

MENDEL, G. W., AND S. R. PETERSON. 1980. Gray Partridge population structure and densities on the Palouse Prairie, p. 118–136. *In* S. R. Peterson and L. Nelson, Jr. [eds.], Proc. Perdix II: Gray Partridge workshop. For., Wildl. and Range Exp. Stn., Univ. Idaho, Moscow.

MENDEL, G. W., AND S. R. PETERSON. 1983. Management implications of Gray Partridge habitat use on the Palouse Prairie, Idaho. Wildl. Soc. Bull. 11:348–356.

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

MORTON, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am. Nat. 111:855–869.

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

MURTHA, P. A. 1967. Air photo surveillance of Hungarian Partridge habitat change. J. Wildl. Manage. 31:366–369.

PORTER, R. D. 1955. The Hungarian Partridge in Utah. J. Wildl. Manage. 19:93–109.

RATTI, J. T., L. M. SMITH, J. W. HUPP, AND J. L. LAAKE. 1983. Line transect estimates of density and the winter mortality of Gray Partridge. J. Wildl. Manage. 47:1088–1096.

RITCHISON, G. 1985. Variation in the songs of female Black-headed Grosbeaks. Wilson Bull. 97:47–56.

ROBEL, R. J., D. J. DICK, AND G. F. KRAUSE. 1969. Regression coefficients used to adjust whistle count data. J. Wildl. Manage. 33:1088–1096.

ROTELLA, J. J., AND J. T. RATTI. 1986. Test of a critical density index assumption: a case study with Gray Partridge. J. Wildl. Manage. 50:532–539.

ROTHSTEIN, S. I., AND R. S. FLEISHER. 1987. Vocal dialects and their possible relation to honest status singing in the Brown-headed Cowbird. Condor 89: 1–23.

SAYRE, M. W., R. D. ATKINSON, T. S. BASKETT, AND G. H. HAAS. 1978. Reappraising factors affecting mourning dove perch cooing. J. Wildl. Manage. 45:580–587.

SMITH, L. M., J. W. HUPP, AND J. T. RATTI. 1982. Habitat use and home range of Gray Partridge in eastern South Dakota. J. Wildl. Manage. 46:580–587.

SPARLING, D. W. 1979. Evidence for vocal learning in prairie grouse. Wilson Bull. 91:621–623.

SPARLING, D. W. 1981. Quantitative analysis of prairie grouse vocalizations. Condor 85:30–42.

SPIKER, C. J. 1929. The Hungarian Partridge in northwest Iowa. Wilson Bull. 41:24–29.

STIRLING, I., AND J. F. BENDELL. 1966. Census of Blue Grouse with recorded calls. J. Wildl. Manage. 30: 184–187.

THIELCKE, G. A. 1976. Bird sounds. Univ. Michigan Press, Ann Arbor.

THORPE, W. H. 1965. The language of birds. Sci. Am. 195:128–138.

WEIGAND, J. P. 1980. Ecology of the Hungarian Partridge in north-central Montana. Wildl. Monogr. 74:1–106.

YOCOM, C. F. 1943. The Hungarian Partridge (*Perdix perdix*) in the Palouse region, Washington. Ecol. Monogr. 13:167–202.