

most readily to other howling were at kills, especially fresh ones (Harrington and Mech, unpubl.). They probably often howl spontaneously at kills (Harrington 1975), and they sometimes howl after hunting in order to reassemble the pack (Murie 1944, Mech 1966, Harrington and Mech 1978). Thus by locating a howling wolf, a raven may find fresh carrion.

Although I howled throughout the year, I noted most responses by ravens to howling in fall and winter. The seasonal difference in the attractiveness of howling may be explained when the contexts of howling are considered with the wolf's prey. From mid-April through September, wolves usually hunt in small groups (Joslin 1967) and eat relatively small food items (e.g. beaver, *Castor canadensis*; Mech 1970), which can be consumed quickly or carried to young at home-sites. Most summer howling occurs at the home-sites (Harrington and Mech, unpubl.), where little or no carrion is available. Therefore, little opportunity exists for ravens to associate howling with the presence of carrion. Also, ravens rely less on carrion during the summer than they do in winter (Bent 1946).

From late September through March, however, wolf packs travel more as units, and kill larger prey such as deer and moose (*Alces alces*). Much activity is centered about kill sites. Thus the correlation between wolf howling and kill presence is probably high from October through March, but low from April through September, and the raven's association of howling with carrion probably varies accordingly.

Similar observations have been reported by Kruuk (1972:146), who noted that playback of sounds of hyenas (*Crocuta crocuta*) at kills sometimes attracted Hooded Vultures (*Necrosyrtes monachus*).

The study from which these observations were drawn was supported by funds from the Endangered Wildlife Research Program (U.S. Fish and Wildlife Service), North Central Forest Experiment Station (USDA), World Wildlife Fund, Ober Charitable Foundation, and an NSF grant to the Psychobiology Program, State University of New York, Stony Brook. I was supported by an NSF Predoctoral Traineeship

(Stony Brook) during the study and a Killam Postdoctoral Fellowship (Dalhousie University) during preparation of this manuscript. I thank L. D. Mech and C. Walcott for their help and suggestions throughout the study, D. J. Boness, E. H. Miller, D. R. Chamberlain and an anonymous reviewer for their comments on the manuscript, and individuals who provided able assistance in the field: G. Day, T. Floyd, R. Flynn, T. Fuller, N. Harrington, J. Klitzke, D. Parkinson, J. Renneberg, and T. Wallace.

LITERATURE CITED

- BENT, A. C. 1946. Life histories of North American jays, crows and titmice. U.S. Natl. Mus. Bull. 191:183-201.
- HARRINGTON, F. H. 1975. Response parameters of elicited wolf howling. Ph.D. diss., State Univ. New York, Stony Brook.
- HARRINGTON, F. H. AND L. D. MECH. 1978. Wolf vocalization. In R. L. Hall and H. S. Sharp [eds.], *Wolf and man: evolution in parallel*. Academic Press, New York.
- JOSLIN, P. W. B. 1967. Movements and homesites of timber wolves in Algonquin Park. *Am. Zool.* 7:279-288.
- KRUUK, H. 1972. The spotted hyena. Univ. Chicago Press, Chicago.
- MECH, L. D. 1966. The wolves of Isle Royale. U.S. Natl. Park Serv., Fauna Ser. 7.
- MECH, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, New York.
- MURIE, A. 1944. The wolves of Mt. McKinley. U.S. Natl. Park Serv., Fauna Ser. 5.
- SUTTON, G. M. 1932. The birds of Southampton Island. *Carnegie Mus. Memoirs* 12:1-275.
- TEMPLE, S. A. 1974. Winter food habits of ravens on the Arctic Slope of Alaska. *Arctic* 27:41-46.

Department of Psychology, Mount Saint Vincent University, Halifax, Nova Scotia, Canada B3M 2J6.
Accepted for publication 7 July 1977.

Condor, 80:237-240
© The Cooper Ornithological Society 1978

SONG VARIATION IN DARK-EYED JUNCOS IN NOVA SCOTIA

LIDLAW WILLIAMS †

AND

MICHAEL H. MACROBERTS

This paper describes the song repertoire of Dark-eyed Juncos (*Junco hyemalis*) in Baddeck, Nova Scotia. It follows a study we conducted in central coastal California (Williams and MacRoberts 1977). Our aim is to detail the song repertoire of Dark-eyed Juncos within a local population in the northeastern part of this species' range in order to determine if songs differ between geographically distant populations.

METHODS

The study was conducted between 4 July and 10 August 1976 at Bevis Point, 11 km NE of Baddeck, Victoria Co., Nova Scotia. The study area was a 120-ha peninsula on the Great Bras d'Or Lake. Habitat was mixed spruce-fir (*Picea glauca*, *P. mariana*, *Abies balsamea*) forest edge abutting hay fields and bogs. Fourteen male juncos were color-banded or were otherwise individually recognizable by peculiarities of plumage or behavior. We attempted to record all songs in each bird's repertoire. Each bird was tape-recorded on at least two different days and each was observed for at least 8 h. Playbacks were used to stimulate singing. After a bird began to sing it was allowed to complete its bout and to begin some other activity before being restimulated by more playbacks. This procedure often led to the bird changing song type. Birds usually responded well to playbacks and often continued to sing as long

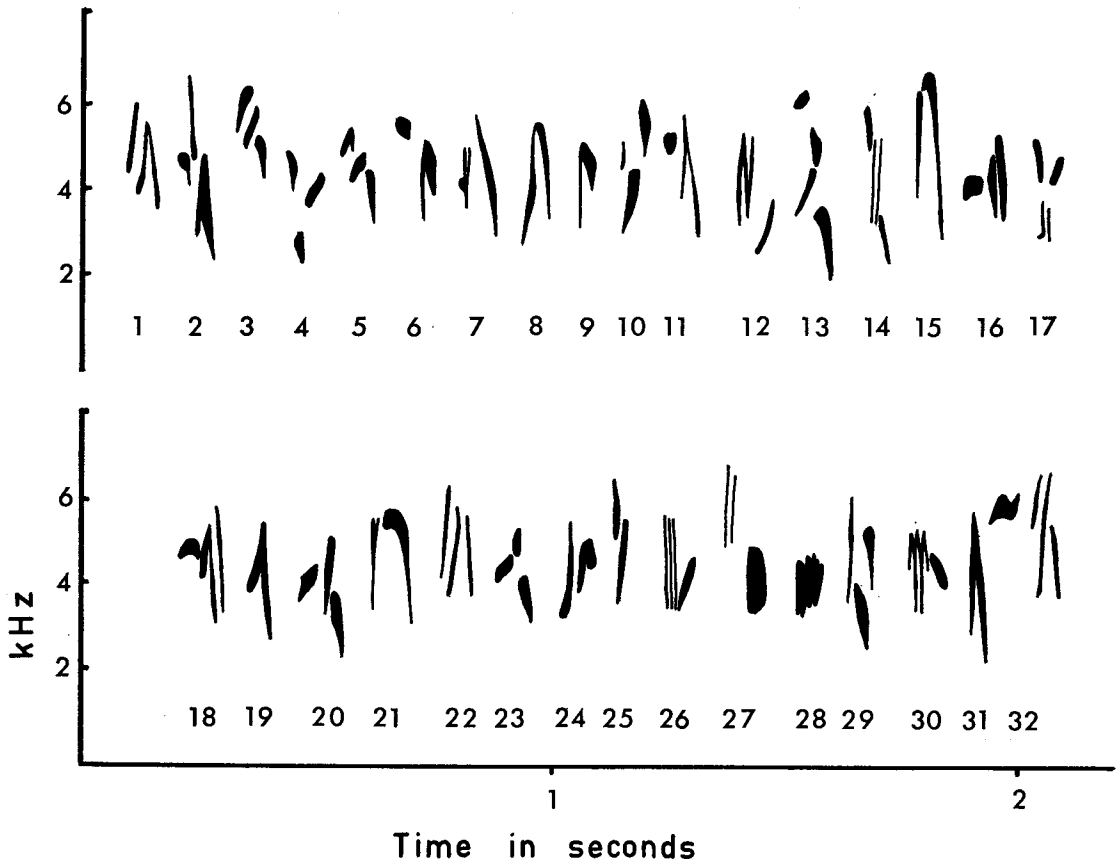


FIGURE 1. Syllables used by 14 Dark-eyed Juncos.

as they were restimulated. Previously, we found it possible to record all or most of a junco's repertoire in a relatively short period (Williams and MacRoberts 1977). In this study we were usually able to record an individual's complete repertoire in the first hour or two of recording.

Songs were recorded at 19 cm/s on a Uher 4000 Report-L using either a 45-cm parabolic reflector with an Electro-voice microphone (model 636) or a Sennheiser MKH 815 T directional microphone. Recorded songs were analyzed on a Kay Electric Company Sono-Graph (wide band filter) and by listening to playbacks. The terminology used here is defined in our 1977 paper.

RESULTS

The 14 juncos (A-N) had 38 songs (average 2.7, sd 0.96, range 1 to 5). Of these, 36 songs were monosyllabic and 2 were bisyllabic. There were 31 distinct songs. We found 27 to be unique to one individual, 2 were shared by two individuals, 1 was

shared by three individuals, and 1 was shared by four. Only one bird (N) did not have at least one unique song. Audiospectrograms of the 32 different syllables used by the juncos are shown in Fig. 1. Syllable duration varied from 0.03 to 0.10 s, intersyllable duration varied from 0.01 to 0.04 s, songs were composed of 6 to 37 syllables, and songs varied in duration from 0.7 to 2.0 s. As in our California study and in that conducted by Konishi (1964a) in Berkeley, California, we found an inverse correlation between the duration of a syllable and the number of syllables in a song or in a unit of time. Songs composed of long syllables contained fewer syllables than did songs composed of short syllables. Table 1 includes further details of mensural aspects of Baddeck junco songs and singing behavior.

Below we give vignettes of individuals in the Baddeck population which supplement and clarify data presented in Table 2.

Bird A had three monosyllabic songs (two unique) and shared one song with Bird J. Bird B had two

TABLE 1. Comparison of Dark-eyed Junco songs.^a

	Carmel Highlands	Nova Scotia
No. syllables in song	13.8 ± 4.77 (34.56)	17.7 ± 4.30 (24.29)
Song duration (s)	1.31 ± .19 (14.50)	1.57 ± .28 (17.83)
Interval between syllables (s)	0.031 ± .01 (32.25)	0.026 ± .01 (54.0)
Syllable duration (s)	0.087 ± .054 (62.07)	0.071 ± .016 (22.6)
No. songs	50	38

^a Mean plus standard deviation, with coefficient of variation in parentheses.

TABLE 2. Comparison of song and syllable repertoire of individual Dark-eyed Juncos in Nova Scotia.

Bird	No. song types	Unique song types	No. syllables	No. syllables shared	Syllables in repertoire ^a
A	3	2	3	1	1-3
B	2	1	2	1	4-5
C	5	4	5	1	5-9
D	2	1	2	1	10-11
E	3	2	4	1	5, 12-14
F	2	1	2	1	15-16
G	3	3	3	0	17-19
H	3	2	4	2	10, 20-22
I	2	1	2	1	15, 23
J	3	1	3	2	1, 10, 24
K	3	3	3	0	25-27
L	4	4	4	1	21, 28-30
M	2	2	2	0	31-32
N	1	0	1	1	5
Total	38	27			

^a As labeled in Fig. 1.

monosyllabic songs and shared one with Birds C, E and N. Bird C had five monosyllabic songs, sharing one with Birds B, E and N. Two of its songs deserve special mention. One song (syllable 6) consisted of a two-note syllable while another song (syllable 9) consisted of a one-note syllable that was the same as the second note of syllable 6. This bird either used the entire two-note syllable or sang only one of the two notes. It never combined one- and two-note syllables into a single song nor did it intersperse songs of one- and two-note syllables. Bird D had two monosyllabic songs, of which one was shared with two individuals (Birds H and J). Bird E had two monosyllabic songs and one bisyllabic song. It shared one monosyllabic song with Birds B, C and N. Its bisyllabic song was composed of syllables 13 and 14.

Bird F had two monosyllabic songs, sharing one with Bird I. Bird G had three unique monosyllabic songs. Bird H had three songs: two monosyllabic and one bisyllabic, sharing one monosyllabic song with Birds D and J. It shared the first syllable (no. 21) of its bisyllabic song with Bird L who used the syllable in one of its monosyllabic songs. The other syllable of the bisyllabic song was number 22. Thus, although Bird H had three songs composed of four syllables and shared two syllables, it only shared one song. Bird I shared one of its two monosyllabic songs with Bird F. Bird J had three monosyllabic songs, one of which was unique to it. It shared one song with Bird A and another with Birds D and H.

Bird K had three unique monosyllabic songs. Bird L had four unique monosyllabic songs. It shared one syllable (no. 21) with Bird H, but this syllable was part of H's bisyllabic song. Bird L was distinctive in that it frequently broke its songs in the middle and then resumed them. He would sing between 6 and 8 syllables, pause for 0.15 to 0.30 s, and then finish the song. He did not always do this but interspersed "paused" songs with normal songs. Bird M had two unique monosyllabic songs. Bird N had one monosyllabic song which he shared with Birds B, C and E.

DISCUSSION

In Carmel Highlands, California, we had studied 10 banded juncos, most of them for two or more

years. We found that each had an individually distinct repertoire consisting of 3 to 7 songs (average 5)—42 songs were monosyllabic, 5 were bisyllabic, 1 was trisyllabic, 1 was pentasyllabic, and 1 consisted of 32 different syllables. This last song is similar to junco songs recorded by Mirsky (1976) on Guadalupe Island and appeared to be loud subsong. The Carmel Highlands juncos shared songs and syllables; 31 of the song types were unique to one individual, 8 were shared by two individuals, and 1 was shared by three individuals. In the Carmel Highlands sample there were 40 distinct song types. No bird shared its complete repertoire with other individuals.

In our earlier paper we compared the Carmel Highlands juncos with those from Berkeley, California (Konishi 1964a, b) and Yellow-eyed Juncos (*Junco phaeonotus*) from Durango, Mexico (Marler and Isaac 1961). We concluded that although the Carmel Highlands juncos were more similar to the Berkeley juncos than they were to the Durango juncos, they showed some differences; notably, they had larger song repertoires and they used more polysyllabic songs.

Table 1 compares mensural features of the Carmel Highlands and Nova Scotia juncos. Most song features are similar in the two populations. However, the Baddeck birds have slightly longer songs composed of more, but shorter syllables with shorter intersyllable duration than the Carmel Highlands birds. The latter have larger individual song repertoires (5.0 compared to 2.7) composed of more polysyllabic songs (16% compared to 5%) than do the Baddeck juncos. There is approximately equal sharing of songs and syllables among individuals in the two populations.

Setting aside the Guadalupe Island juncos because they appear to be using subsong as normal song, the pattern that emerges is that Dark-eyed Juncos have small repertoires of monosyllabic songs, a minority of individuals having one or more polysyllabic songs. Differences between Dark-eyed Junco populations apparently consist of little more than average song repertoire size, number of syllables used, and various minor mensural features. They do not involve syllable, note or phrase differences which characterize some species (Thielcke 1969).

We wish to express gratitude to L. F. Baptista for making audiospectrograms, B. R. MacRoberts for

helping in the field, G. Kelly, W. Puente, and A. L. B. Williams for assisting in all phases of the work.

LITERATURE CITED

- KONISHI, M. 1964a. Effects of deafening on song development in two species of juncos. *Condor* 66:85-102.
- KONISHI, M. 1964b. Song variation in a population of Oregon Juncos. *Condor* 66:423-436.
- MARLER, P., AND D. ISAAC. 1961. Song variation in a population of Mexican Juncos. *Wilson Bull.* 73:193-206.
- MIRSKY, E. N. 1976. Song divergence in humming-bird and junco populations of Guadalupe Island. *Condor* 78:230-235.
- THIELCKE, G. 1969. Geographic variation in bird vocalizations, p. 311-339. In R. A. Hinde [ed.], *Bird vocalizations*. University Press, Cambridge, England.
- WILLIAMS, L., AND M. H. MACROBERTS. 1977. Individual variation in songs of Dark-eyed Juncos. *Condor* 79:106-112.

Address of second author: 740 Columbia, Shreveport, Louisiana 71104. Accepted for publication 21 September 1977.

Condor, 80:240
© The Cooper Ornithological Society 1978

RUFFED GROUSE USE OF SUPRAORBITAL COMBS IN DISPLAYS

STEPHEN J. MAXSON

Integumentary structures above the eyes, often termed "combs," are present in all grouse species and are emphasized in various displays. Both Wing (*Condor* 48:156, 1946) and Hjorth (Viltrevy (Stockh.) 7:510, 1970) erred in stating that these structures are absent or invisible in *Bonasa*. Bump et al. (The Ruffed Grouse, life history, propagation, management, Holling Press, Buffalo, p. 44-45, 1947) noted a red-orange "bare spot" over the upper eyelid in male Ruffed Grouse (*Bonasa umbellus*). This area is clearly illustrated in the frontispiece of their book but the authors did not say when these structures were exposed.

While studying and filming captive Ruffed Grouse at the Cedar Creek Natural History Area in east-central Minnesota (1971-1974), I frequently observed male birds exhibiting supraorbital combs during certain displays. The Ruffed Grouse is able to expose or conceal these structures at will. When exposed, they appear as a bright, red-orange band (about 2 × 12 mm) directly above the eye. These combs are not erectile and do not change color when exposed. Combs of yearlings and adults are similar. While the combs of Ruffed Grouse are smaller than those of other tetraonids, I was able to see them at a distance of at least seven m. Other grouse are undoubtedly able to see them as well. My observations indicate that male Ruffed Grouse expose their combs during the Upright cum Ruff Display, Bowing cum Head-twisting and Panted Hissing, and Rush cum Prolonged Hiss displays (names of displays follow Hjorth 1970). Only occasionally were they exposed during fighting postures similar to those illustrated by Bump et al. (1947:268). In one film sequence of an aggressive encounter between a resident male and an introduced male, only the dominant resident male exhibited his combs. I did not see these struc-

tures during neutral postures or Drumming. Based on these observations, I believe the illustration in Bump et al. (1947:41), showing a grouse in neutral posture with combs exposed, to be inaccurate. I never saw females exhibit combs even though they sometimes assumed display postures similar to those of males. In short, male grouse exhibited their combs whenever the ruff feathers were extended but very seldom during other circumstances.

The communicative significance, if any, of Ruffed Grouse combs remains to be determined. The contexts in which they are exposed suggest that combs may play some role in displays. The fact that only the more dominant bird exposed its combs during the fighting sequence noted above indicates that exposing these structures may reflect the motivational state of the bird. When a male is displaying with extended ruff the combs frequently are outlined against the dark ruff feathers and thereby are made more conspicuous as the head is oriented toward another grouse. The pronounced head shaking, bowing and ground pecking associated with these displays serves to emphasize both the extended ruff and the combs. While there is little doubt that the extended ruff and fanned tail constitute the major visual components of these displays the supraorbital structures may enhance the visual stimuli.

If these structures prove to be functional components of displays one would expect them to serve only in short-range communication. The displays during which I saw them occurred at distances up to several meters from other Ruffed Grouse. It is perhaps significant that during drumming, a long-range display which normally is not given in the presence of other grouse (Allen, *Auk* 51:184, 1934; pers. observ.), the combs are not exposed.

I am grateful to the personnel of the Cedar Creek Natural History Area for their cooperation during my study. I thank I. Hjorth and G. A. Maxson for critical comments on the manuscript. This investigation was supported, in part, by the U.S. Atomic Energy Commission (C00-1332-108).

Department of Biology, University of North Dakota, Grand Forks, North Dakota 58202. Accepted for publication 13 July 1977.