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THE UNIVERSITY OF ALBERTA

SONG, VEGETATION, AND SOUND PRODUCTION IN BLUE GROUSE

by

MARK ANTHONY DEGNER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
SPRING 1988

ISBN 0-315-42741-8

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR MARK ANTHONY DEGNER

TITLE OF THESIS SONG, VEGETATION, AND SOUND PRODUCTION IN BLUE GROUSE

DEGREE FOR WHICH THESIS WAS PRESENTED MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED SPRING 1988

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PERMANENT ADDRESS:

16109-89 Ave.
Edmonton, Alberta
Canada, T5R 4R8

DATED January 28 19 88

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SONG, VEGETATION, AND SOUND PRODUCTION IN BLUE GROUSE submitted by MARK ANTHONY DEGNER in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

Fred C. Zwickel
Supervisor

Jan O Murie

L. M. Fedigan

Date 28 Jan 1988

ABSTRACT

Variation in song and precopulatory calls was examined for three subspecies and a population where the birds appear to be hybrids of two subspecies of male blue grouse (*Dendragapus obscurus*). There were significant intra- and inter-subspecific differences in songs (hoots) among groups. Songs of coastal males were higher in frequency, longer, and structurally different than those of interior males. Songs of coastal males appear to increase in frequency with latitude, a pattern exhibited both within and among coastal subspecies. Precopulatory calls (whoots) of coastal and interior males did not differ, but both were higher in frequency than their songs.

Morphological and vegetational studies were undertaken in an attempt to examine the causes of subspecific variation in song. Syringeal morphology shows a relationship that may partially explain this variation; the smaller the syrinx, the higher the frequency of the song. Coastal males have smaller syringes that produce higher frequency songs than those of interior males. However, the same relationship does not hold for precopulatory calls. Differences in syringeal morphology of males and females also were examined. Sexual dimorphism in syringes was greater than can be explained by differences in body size. The same size relationship seen in male blue grouse is present when comparing the sexes; males have larger syringes and produce lower frequency vocalizations than those of females.

Vegetation structure at hooting sites of coastal males was denser than that of interior males, but there was considerable variation within groups. Generally, the denser the vegetation the lower the frequency of sound that should be used for best transmission. However, the opposite relationship was found in this study; song frequency increased as density of vegetation increased. To counter the attenuation of denser vegetation many coastal and hybrid zone males appear to use trees and other elevated sites (stumps and logs).

ACKNOWLEDGEMENTS

I wish to give special thanks to my supervisor, Fred Zwickel, for the encouragement, support, discussion, and comments/criticisms that he provided. I also wish to thank my supervisory committee, Linda Fedigan and Jan Murie, for their helpful discussion and comments.

Randy Mandryk prepared the histological sections and freely gave his time in helping me with histological problems. Robert Carveth and Garvin Morris did the drawings. Sonagrams were made on equipment at the Dept. of Linguistics and Terry Nearey kindly assisted me in setting-up and operating the sound spectrograph.

Numerous graduate students assisted in data collection, statistical analyses, and made helpful comments on the various papers. Of these, I would especially like to thank Jim Hines, Yves Leblanc, Rick Lewis, Don McKinnon, and Darwin Wiggett. I am grateful for the help provided by several undergraduate field assistants: Don Albright, Ginny Brown, Alexa Klimke, Cheryl Marion, Daryl Parkyn, Deanne Patsula, Heather Walker, and Ian Wishart. I would like to also thank Mark Bosworth, Colleen Cassidy, Jeff Klotz, Brenda and Dwayne Lepitzki, and Gord Youzwyshyn for their help, support, and friendship.

Research was conducted in British Columbia, California, Colorado, Oregon, and Washington state and I wish to express my appreciation to all the cooperating agencies and personal. Research on Hardwicke Island and Adam River, B.C. were conducted on lands of Crown Forest Industries Ltd. and MacMillan Bloedel Ltd., respectively. I am grateful for the hospitality and assistance from Bendickson Contractors Ltd. and the Bendickson family while on Hardwicke Island. Mrs. E. May and the May family kindly allowed me to work on their property in northern California. Funding was provided by the National Science and Engineering Research Council of Canada, the Canadian National Sportman's Fund, and the University of Alberta.

Finally, and most importantly, I wish to thank my parents for their continual support and encouragement. Without them none of this would have been possible.

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I. INTRODUCTION

Studies of geographic variation of songs of passerine birds are numerous (Nottebohm 1969; Krebs and Kroodsma 1980; Baker 1982; Mundinger 1982; Baker and Thompson 1985; and many others), but there has been little work on geographic variation of songs in non-passerines (Goldstein 1978; Mundinger 1982), especially grouse. Explanations for this variation have taken an evolutionary approach, with research concentrating on causation, ontogeny, and adaptation (Kroodsma and Miller 1982). Studies of causation deal with sound-producing structures, neural control, and auditory perception of song. These morphological and neural aspects are the least understood area in regards to variation in a species' song. The development of a species' song and its modification during the developmental stage is what concerns those who study the ontogeny of song. Song learning is the most common aspect studied to date, mainly with passerines (Kroodsma and Baylis 1982). How avian songs and calls are adapted for transmission through their natural environments has been the subject of much recent study (Wiley and Richards 1982). Vegetation structure, topography, weather conditions, and location and behavior of the singer are all interrelated aspects to consider when investigating how song structure is adapted to the local environment.

Blue grouse (*Dendragapus obscurus*) are found in the mountains and foothills of western North America and can be divided into eight subspecies (Johnsgard 1983)(Appendix 1). These subspecies can be divided equally into two groups, coastal and interior. Clear plumage, morphological, and behavioral differences distinguish the two groups. At one time coastal and interior blue grouse were considered as separate species, *D. fuliginosus* and *D. obscurus*, respectively (A.O.U. 1931). However, there is some debate as to the status of the two groups. Although the American Ornithologists' Union (1983) now considers all blue grouse as one species, Potapov (1985) maintains them as two. There are clear differences in the songs of coastal and interior blue grouse but most reports concerning these differences are anecdotal

(Brooks 1926; Bent 1932; Guiguet 1955; Blackford 1958, 1963; Rogers 1968; Johnsgard 1983).

My objectives were to describe in more detail and to quantify variations in the songs of male blue grouse and to see how variation in vocal sound-producing structures and vegetation structure might relate to those variations. Results are presented in four papers:

1. Variation in the songs and precopulatory calls of male blue grouse.
2. Sexual dimorphism in vocal sound-producing structures of blue grouse.
3. Subspecific variation in vocal sound-producing structures in adult male blue grouse.
4. Vegetative characteristics of hooting sites of coastal and interior male blue grouse.

In the first paper (Chapter II), I examine inter- and intra-subspecific variations in songs (hoots) and precopulatory calls (whoots) of male blue grouse of three subspecies and a presumed hybrid population of two of these three subspecies. In paper 2 (Chapter III), the vocal sound-producing structures of male and female blue grouse are described and compared. This is an expansion and update of a previous study (Degner 1983) and provides background and support for the relationships reported in paper 3 (Chapter IV). Possible explanations for variations in the songs of males are examined in the remaining two papers. Variation in the sound-producing structures of adult males from three subspecies and the hybrid population and its relation to sounds produced is examined in paper 3. In paper 4 (Chapter V) variation in vegetation structure at hooting sites, is described for two subspecies and the hybrid population. The relationship between these data and the differences in song, especially sound frequency, are discussed there.

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II. VARIATION IN THE SONGS AND PRECOPULATORY CALLS OF MALE BLUE GROUSE

INTRODUCTION

Blue grouse (*Dendragapus obscurus*) are birds of western mountainous regions of North America. They range in the north from southeast Alaska, the central Yukon, and western Northwest Territories south into southern California, central Arizona, and central New Mexico. They extend east from Pacific coastal islands to the eastern slopes of the Rocky Mountains (Appendix 1)(Johnsgard 1983).

Blue grouse are divided into 8 recognized subspecies which can be placed into two groups, coastal and interior, with 4 subspecies in each (Appendix 1)(Johnsgard 1983; Bendell and Zwickel 1984). Subspecies of blue grouse are separated primarily on the basis of plumage and morphology, but several behavioral differences also separate the two major groups.

Male blue grouse have a small repertoire of vocalizations. Stirling and Bendell (1970) described three; the hoot, whoot, and growl, although McNicholl (1978) believes that there are two types of growls. Others (Blackford 1958, 1963; Rogers 1968) have reported more vocalizations but most have been anecdotal and there is no detailed description of them.

Song has been defined as sounds produced by males in the breeding season that are repeated in a specific pattern and having a sexual attraction and/or territorial function (Thorpe 1961; Armstrong 1973). The song of male blue grouse, known as a hoot, meets this criteria of song, having been reported to have both a sexual and territorial function (McNicholl 1978). The hoot is one of the most striking vocal differences between coastal and interior grouse. Brooks (1926) used this difference as one characteristic for separating the two groups, and it has been commonly used by others since that time (Bent 1932; Guiguet 1955; Rogers 1968). The hoot of coastal males is usually relatively loud and composed of 6 notes and that of interior males is usually soft and composed of 5 notes (Brooks 1926; Bent 1932; Rogers 1968; Hjorth 1970a; Johnsgard 1983). Coastal males can be heard for distances greater than 500 m, whereas interior males are barely audible at 100 m (Brooks 1926, Bailey and Niedrach 1965, Hjorth 1970a, Johnsgard 1983, Bendell and Zwickel 1984). The song of male blue grouse is one of the lowest frequency avian songs (Greenewalt 1968; Hjorth 1970a) and that of interior males is supposedly lower in frequency than that of coastal males (Hjorth 1970a).

The whoot is a single or double-note call given only in the presence of females and is considered a precopulatory call (Hjorth 1970a; Stirling and Bendell 1970; McNicholl 1978). The growl is given during aggressive situations and in some interactions with humans (Stirling and Bendell 1970; McNicholl 1978). It does not appear to be directly related to reproductive behavior.

Male blue grouse also produce some mechanical sounds (Bent 1932; Blackford 1958; Bendell and Elliott 1967; Hjorth 1970a; Stirling and Bendell 1970). Flutter-flights appear to be important components of reproductive behavior of interior groups, more so than in coastal groups; interior type flutter-flights are more complex and given more frequently than those of coastal males (Hjorth 1970a; Stirling and Bendell 1970; McNicholl 1978).

In this paper, songs and whoots of male blue grouse are described and compared from sound spectrographs. Hjorth (1970a) and Stirling and Bendell (1970) are the only people to date who have analyzed the vocalizations of male blue grouse with sound spectrographs (though Greenewalt (1968) illustrates a sonagram of a hoot of a blue grouse but provides no other information about it). Their analyses included songs of three subspecies of blue grouse (coastal *D.o. fuliginosus*, and interior *D.o. pallidus* and *D.o. richardsonii*), but both studies suffered from small sample sizes and minimal quantification. As well, they provide no comparison of the whoots of coastal and interior groups. Different populations of the same subspecies and different subspecies will be compared here to examine variation in the songs and whoots that might exist within and among subspecies. A description and quantification of intra- and inter-subspecific variations in the songs of male blue grouse may provide some insight into the evolutionary relationships among the subspecies, and the relationships among habitat, song, and territorial behavior.

STUDY AREAS

Recordings and observations of male blue grouse were made in the spring of 1984 and 1985 at eight locations and include three of the eight recognized subspecies (Johnsgard 1983). The interior subspecies, *D.o. pallidus* (DOP), was examined on the Methow Game Range (48° 31′ N, 120° 4′ W) in north-central Washington state (Appendix 2). The Hart's Pass study area (48° 42′ N, 120° 39′ W) is located approximately 8 km southeast of the crest of the Cascade Mountains in Washington (Appendix 2), the recognized boundary between *D.o. fuliginosus* and *D.o. pallidus* (DOFxDOP). Birds here show morphological and behavioral traits of both subspecies.

Three study areas were within the range of *D.o fuliginosus* (DOF). Hardwicke Island, B.C. (50° 27′ N, 125° 50′ W) and the lower Adam River, B.C. (50° 27′ N, 126° 10′ W), on nearby Vancouver Island, were in the north-central part of this subspecies' range (Appendix 3). The May Ranch (40° 29′ N, 123° 28′ W), in north-west California, was near its southern limit (Appendix 2). *D.o. fuliginosus* males from Hardwicke Island and Adam River, B.C. will be referred to as DOF(BC) and those from the May Ranch, CA. as DOF(CA).

Samples from the Winema (42° 26′ N, 121° 45′ W) and Fremont (42° 23′ N, 120° 22′ W) National Forests were combined to form the Oregon study area (Appendix 2). This was done because of the close proximity of the areas to each other and the relatively small sample sizes from each. The coastal subspecies, *D.o. sierrae* (DOS), occurs here. Lassen National Forest (40° 24′ N, 121° 32′ W), in the Sierra Nevada mountains of central California was another study area within the range of *D.o. sierrae* (Appendix 2).

[illegible]RIALS AND METHODS

Singing males were located primarily by listening for them. Once a male was located, I moved in slowly trying not to disturb it. Tape recordings were made at distances that varied from 3-40+ m. A microphone was placed on the end of a 6 m aluminum pole to get it closer to males in tall trees. In a very few cases tape-recordings of female calls were used to stimulate males to hoot, or to resume hooting after they were disturbed. This was done only when necessary and no recordings were made for at least 5 minutes after the female calls were stopped.

Songs and whoots were recorded with a Nagra 4.2 reel to reel tape-recorder with either a Sennheiser MKH 105 microphone or a Sennheiser ME80 microphone head on a Sennheiser K3-U power unit. All recordings were made on Ampex 406 tape at a tape speed of 19.05 cm/s. Sound levels of songs were measured using a Nagra 4.2 tape-recorder and Sennheiser MKH 105 microphone with the record level constant at 75 dB.

The best songs and whoots (up to a maximum of 10 per individual) were analyzed with a narrow band filter (22.5 Hz) using a Kay Elemetric Digital 7800 Dual Channel Sonagraph. To examine the fundamental harmonic of the songs, all were analyzed with the scale magnifier set from 0 - 500 Hz. Sonagrams were printed with a Kay Elemetric Sonagraph Printer 7900.

The total time of the song, time of each note, and internote times were measured to the nearest 20 ms from the fundamental harmonic of each sonagram. The fundamental frequency of each note was recorded to the nearest 10 Hz. The fundamental frequency was estimated to be the point with the strongest emphasis above the inverted U part of the note (Figure II-1). Means of total time, and note length, internote time, and fundamental frequency for each note of songs (≤10) for each male were used to calculate the means for each study area.

Hooting counts were made in which number of songs and song type (number of notes per song) sung in a 5-min period were recorded. If at least one song in a

5-min period differed from the others for that male the bird was classified as a multi-type singer. Hooting counts were not made when males had just begun or resumed hooting because number of notes per song (song types) sometimes increases during "start-up" (Bendell and Elliott 1967; Stirling and Bendell 1970). The song type that was used greater than 50% of the time in the 5-min period was considered to be the predominant type for that individual.

Statistical analyses were made using the $SPSS^X$ ($SPSS^X$ Inc. 1983) statistical package. Means are reported ±1 S.E. Differences were considered significant at the five percent level.

RESULTS

Description of hoots

Coastal song. Coastal males, DOF and DOS, hooted with more than one song type (Table II-1), but predominantly used 6 notes/song (Figure II-2). At the May Ranch, one male used three song types and DOF(CA) males used two and three song types more than a single type (Table II-1). It appears that the last note(s) of songs were either added or dropped when song types changed.

Songs of DOF(BC) males at Hardwicke Island and Adam River were not significantly different in any of the variables measured (Mann-Whitney, Range of U-values=9.5-23.5, P=0.078-0.953) and were combined for further analyses. Songs were just under 3 s in length (Table II-2). The first and fifth notes were the longest, and the other notes were similar in length (Table II-2). Internote times shortened as the song progressed (Table II-2).

All notes of DOF(BC) songs had a "flattened, inverted U" shape (Figure II-3), started at low frequency and rose quickly to about 100 Hz, then dropped back to near the starting frequency. Note 5 was "double", with the two parts almost completely joined (Figure II-3). Fundamental frequency of note 1 was lower than that of note 2 and fundamental frequency of the remaining notes gradually decrease to about the same level as note 1 (Table II-3). This pattern was repeated in the songs from all coastal and interior areas examined (Table II-3).

Songs of DOF(CA) males were similar in some ways to those of DOF(BC), but different in others. Both were primarily of 6 notes, but those of DOF(CA) were longer (3.2 s) than those of DOF(BC) (Mann-Whitney, U=2, P=0.002) (Table II-2). Note lengths of DOF(CA) songs were shorter, and internote lengths longer, than DOF(BC) songs (Mann-Whitney, Range of U-values=0.0-6.5, P≤0.02) (Table II-2). This difference may be because recordings of DOF(CA) males were poorer in quality as most of these males were 25+ m up in trees. The poorer the recording, the shorter the notes will appear on the sonagrams, hence internote time will increase. This is because poorer recordings produce sonagrams that show less resonance associated with each note. Note 5 of DOF(CA) songs was "double" with the two parts slightly more separated than those of DOF(BC) (Figure II-4).

The same increasing, then decreasing pattern in frequencies of notes seen in DOF(BC) songs was present in DOF(CA) songs (Table II-3). As well, each note showed the "flattened, inverted U" shape (Figure II-4). However, each note was significantly lower in frequency than the corresponding note of DOF(BC) (Mann-Whitney, all U's=0.0, P<0.001).

Songs of *D.o. sierrae* from two areas (Oregon and Lassen National Forest) consisted of 6 notes (Figure II-5) and were similar in total length, lengths of each note, and internote times, but the fundamental frequency of each note of Lassen National Forest songs were 10-17 Hz lower than in the Oregon birds. Because songs from only one Lassen National Forest male were recorded, no statistical comparisons were made and the data from Lassen songs were combined with those from Oregon (Tables II-2 and II-3).

Each note of DOS songs had the characteristic "flattened, inverted U" shape, and first and last notes were lower than middle ones (Figures II-5 and II-6). Note 5 was "double", with the two parts only partially separated, similar to those of DOF(CA) songs.

DOS songs were similar to those of DOF(CA) males (Tables II-2 and II-3). When DOS and DOF(CA) songs were compared; total time, length of each note, and internote times were not significantly different (Mann-Whitney, Range of U-values=4.0-10.0, $P>0.10$). However, the fundamental frequency of notes 1 to 6 were significantly different between DOS and DOF(CA) songs (Mann-Whitney, Range of U-values=0.0-1.5, $P<0.05$).

Fundamental frequency of songs of DOF and DOS males appear to increase with latitude (Table II-4). This pattern becomes more evident when songs from a third coastal subspecies, *D.o. sitkensis* (DOST), is compared with the two examined in this study. F.C. Zwickel recorded the songs of one male on Mitkof Island, AK. (56° 30' N, 133° 10' W) in May 1986. The songs showed all the characteristics of a coastal type except that the fundamental frequency of the notes were between 170 and 175 Hz (Table II-4), the highest of any songs recorded. This single example is consistent with the hypothesis that song frequency increases with latitude.

Interior song. D.o. pallidus from the Methow Game Range almost all hooted with 5 notes/song (Figure II-2) and sang primarily with only one song type (Table II-1). Songs were shorter than those of coastal birds, just under 2.5 s (Table II-2). The first and last two notes were longer than the middle two (Table II-2). Internote lengths between the first three notes were longer than between the last two (Table II-2).

Notes of DOP songs showed the "flattened, inverted U" shape (Figure II-7). A major difference between DOP songs and those of coastal groups was that notes 4 and 5 were both "double" in DOP. The two parts of each note were almost completely separated, joined only at the lowest frequencies (Figure II-7). Fundamental frequencies of each note were the lowest of any songs examined, 100-110 Hz (Table II-3). Songs of DOP males followed the pattern exhibited by coastal males with frequencies of the first and last notes lower than those between (Table II-3).

Hybrid song. Songs of Hart's Pass males, an area where birds appear to be hybrids of *D.o. fuliginosus* and *D.o. pallidus* (DOFxDOP), were predominantly 5 notes (Figure II-2). Because DOFxDOP males are thought to be mostly hybrids, one might expect both song types (5 and 6 notes/song) to be used approximately equally. This was not the case; 5 notes/song were most predominant, allying DOFxDOP males with interior groups.

Songs of DOFxDOP males were 2.6 s in length (Table II-2). The first note was twice as long as the second, with the remaining notes gradually increasing till the fifth, which was the same length as the first (Table II-2). The first two internote times were longer than the last two (Table II-2).

Notes 4 and 5 were both "double", similar to those of DOP songs, with the two parts widely separated and joined only at their lowest frequencies. Songs of DOFxDOP males were similar to those of all other groups with the "flattened, inverted U" shape and rising, then declining frequencies of notes as the song progressed (Table II-3 and Figure II-8). Fundamental frequencies were between 125 and 130 Hz; higher than those of pure DOP, but lower than those of DOF(BC) songs (Table II-3).

DOF(BC), DOP and DOFxDOP songs were compared to see if they differed. DOF(BC) songs were used to represent DOF because they were the nearest coastal population to Hart's Pass and most likely represent coastal type songs near Hart's Pass. Total time, length of notes 2 and 3, and internote times between notes 1 and 2, notes 2 and 3, and notes 4 and 5 were significantly different among the three groups (Kruskal-Wallis, Range of H-values=6.340-18.187, P=0.042-0.001). Lengths of notes 1, 4, and 5 and internote lengths between notes 3 and 4 were not different (Kruskal-Wallis, Range of H-values=0.160-5.154, P=0.923-0.076). Fundamental frequency of notes 1 to 5 were significantly different among the three groups (Kruskal-Wallis, Range of H-values=18.247-18.750, P=0.001).

Pairwise comparisons of DOF(BC), DOFxDOP and DOP songs (Table II-5) showed that DOFxDOP songs were similar to both DOP and DOF(BC) songs, thus being consistent with a theory of hybridization in this area. Nine of the 15 variables (total time, and fundamental frequency, note length, and internote length of each note) examined were not significantly different between DOFxDOP and DOP songs and the remaining 6 were just different (Table II-5). Seven variables were not significantly different between DOFxDOP and DOF(BC) songs (Table II-5). However, 13 of the 15 variables were significantly different between DOF(BC) and DOP songs (Table II-5).

Volume of songs

I obtained some data on volume of songs using the tape recorder and microphone as a sound level meter because a proper sound level meter was not available. Measurements were made of DOF(BC) and DOP males. Songs of coastal males were louder than those of interior males (Table II-6). Because of the method used no statistical comparisons were made for it is really only valid to compare sounds at the same distance. The values presented do not necessarily represent true volumes, but I believe they do provide an index of loudness. Note that the decibel scale is logarithmic so that the indicated differences are greater than they appear.

In qualitative terms, songs of DOF(CA) males did not sound as loud as those of DOF(BC) males, but were considerably louder than those of DOP males. However, all hooting DOF(CA) males heard were in tall trees and many were never seen, making subjective comparisons difficult. DOS songs sounded similar to those of

DOF(CA) males, and were audible for several hundred meters.

No volume level measurements were made for DOFxDOP males. Both loud coastal and soft interior type songs were heard in this area. However, many songs in the hybrid zone were subjectively classified as intermediate in loudness between coastal and interior types. Loud and intermediate type songs appeared to be more predominate than soft types, but this difference may be because soft hooters were not identified because the louder males drew our attention. More study of DOFxDOP males is required.

Whoots

Whoots were given much less frequently than hoots and were more difficult to record because of their unpredictability. Recordings of whoots were made in only two areas, covering one coastal (DOF) and one interior (DOP) subspecies. Whoots of both groups were a single note showing the "flattened, inverted U" shape of individual notes of the hoot (Figure II-9). Frequencies rose from 90-100 Hz at the beginning to about 300 Hz in the middle to about 100 Hz at the end.

Whoots of interior males were 1.7 times longer than those of coastal males (Table II-7). Fundamental frequency of interior whoots appeared approximately 50 Hz higher than those of coastal whoots (Table II-7). However, neither length nor fundamental frequency were significantly different between the two groups (Mann-Whitney, U=6, P=0.20 for both), but both suffer from small sample sizes. The fundamental frequency of whoots of both groups was higher than the fundamental frequency of their respective hoots (Tables II-3 and II-7) and the fundamental frequency of whoots of interior hoots was higher than fundamental frequency of coastal hoots (Tables II-3 and II-7).

Volumes of whoots were not measured for the same reasons that so few recordings of them were made. Subjectively, whoots of both coastal and interior males were as loud, or louder, than coastal type hoots. Whoots of both groups can be heard clearly for several hundred meters.

DISCUSSION

The generalizations made by others (Brooks 1926; Bent 1932; Rogers 1968; Hjorth 1970a; Johnsgard 1983) that songs of coastal males are higher in frequency and louder than those of interior males, and that coastal songs have 6 notes while interior songs have 5 notes, are supported by my study. The fundamental frequency of DOF songs reported by Hjorth (1970a) and Stirling and Bendell (1970) were similar to those reported here. However, the fundamental frequency of DOP songs from my study were about 30 Hz higher than those presented by Hjorth (1970a) for this subspecies. Lengths of songs of both subspecies were similar among the three studies; coastal songs around 3.0 s and interior ones about 2.7 s.

There was some intra-subspecific variation in songs of coastal blue grouse. Three areas of the coastal subspecies, *D.o. fuliginosus*, were examined. Two of these areas were 25 km apart (Hardwicke Island and Adam River), the third area (May Ranch) was 850 km further south. Songs of DOF(BC) males from the two areas were not significantly different. However, there were significant differences between DOF(BC) and DOF(CA) songs. Songs of DOF(CA) males were longer, lower in frequency, and internote times longer than in DOF(BC).

Songs of DOF(CA) males were similar to those of the other coastal subspecies, DOS. Songs of the two DOS populations were also generally similar, although the fundamental frequency of each note of songs of one male from Lassen National Forest were 10-17 Hz lower than those of DOS in Oregon.

Songs of coastal subspecies appear to increase in frequency with latitude. The same pattern may occur in DOS. Further evidence for a latitudinal increase in frequency can be seen when songs from a third coastal subspecies, DOST, are compared with the two from this study. DOST songs of one male on Mitkof Island, AK, were higher in fundamental frequency than those of the more southern areas, but this conclusion is limited because only one bird was recorded in this area.

Only one population of interior DOP was examined, so little can be said about intra-subspecific variation in songs. However, when the results from this study are compared to those of Hjorth (1970a), possible intra-subspecific variation can be seen. Fundamental frequency of DOP songs presented by Hjorth (1970a) from a population in Montana (about 500 km southeast of the Methow Game Range) were about 30 Hz lower than those of DOP from the Methow Game Range. As with coastal males, fundamental frequency may increase with latitude. Note, however, that Hjorth presented his data in the form of melograms, produced on a "melograph Mona" (Hjorth 1970b). This machine is not commonly used in analyzing avian sounds and comparisons with sonagrams should be viewed with some caution.

I know of no study that shows a similar pattern, one in which song frequency increases with increasing latitude. Goldstein (1978) found a weak north-south trend in the "hoy" call of bobwhites (*Colinus virginianus*), but the trend was decreasing sound frequency as latitude increased.

Songs of Hart's Pass males appear to be hybrids of DOF and DOP. They show characteristics of both groups: subjective evaluations suggest that loud coastal, intermediate, and soft interior type hoots are present; the songs consist mainly, but not solely, of 5 notes/song and are about 2.5 s long, both interior traits. Note lengths and internote times are similar to both coastal and interior types; and the fundamental frequency of the notes are intermediate between coastal (DOF(BC)) and interior (DOP) songs. Hart's Pass is only 50 km northwest of the Methow Game Range so the change from coastal to interior types must occur somewhere between these areas. Birds in the Hart's Pass area are near the recognized boundary of the two subspecies.

Whoots of coastal and interior males were more similar than the songs of the two groups. Those of both groups were single notes, higher in frequency than their respective songs, and as loud or louder than coastal type hooting. Interior whoots were longer and higher in frequency than those of coastal males, although the differences were not significant. Whoots examined in this study were similar to those presented by Hjorth (1970a) and Stirling and Bendell (1970). Hjorth (1970a: 277) reported that whoots of *D.o. pallidus* and *D.o. richardsonii* were "much louder than the Multiple Hoot." Since whoots are precopulatory calls given by males when courting a female (Hjorth 1970a; Bendell and Elliott 1967; Stirling and Bendell 1970) they do not appear to be used for attraction of females or territorial advertisement. It seems peculiar that they are so loud, especially in interior populations when its principle function seems related to courtship.

Geographic variation in avian songs is common, especially in passerines (Nottebohm 1969; Hunter and Krebs 1979; Krebs and Kroodsma 1980; Mundinger 1982; Baker and Thompson 1985; and many others). However, little is known about such variation in galliformes. Hjorth (1970a) is the only one to date to provide some evidence of its occurrence among subspecies of blue grouse and the reasons for these differences are unknown. Several explanations of geographic variation have been proposed (see Hunter and Krebs 1979; Krebs and Kroodsma 1980; and Mundinger 1982 for a review). Degner (1988a, 1988b) examined two possible reasons for variation in the songs of blue grouse; morphological differences in the vocal sound-producing structures and differences in vegetation around hooting sites. There is some evidence that syringeal differences may be responsible for proximal differences in songs, but this does not account for the great similarity in whoots of coastal and interior birds (Degner 1988a). Differences in vegetation at hooting sites may be responsible for differences seen in songs; as vegetation density increases so does the frequency of song (Degner 1988b). This relationship is seen both within and among subspecies.

It is not known if male blue grouse learn their songs or if they are genetically fixed. It is important to examine the relative influence of heredity and learning on song before one can proceed to look at geographic variation in more detail. Transplant and isolation experiments are required to test the development of song in the different subspecies of blue grouse.

SUMMARY

Songs (hoots) and whoots (a precopulatory call) of male blue grouse from seven populations covering three of the eight recognized subspecies were described from sonagrams. Both intra- and inter-subspecific comparisons were made of songs and whoots.

Two coastal subspecies, *D.o. fuliginosus* and *D.o. sierrae*, were examined. Songs of both were predominantly of 6 notes, although there was some switching of song types. Songs of two northern coastal populations of *D.o. fuliginosus* differed significantly in song lengths, internote times, and fundamental frequency of each note from those of a more southern population. The songs of the more southern *D.o. fuliginosus* population showed some characteristics similar to those of *D.o. sierrae* from southern Oregon and north-central California. There appears to be a latitudinal pattern in songs of coastal male songs; frequency increases with latitude.

Songs of interior, *D.o. pallidus*, males were predominantly of 5 notes. They were shorter, lower in frequency and softer than those of coastal males.

Near Hart's Pass, WA, birds appear to be hybrids of coastal *D.o. fuliginosus* and interior *D.o. pallidus*. Songs there showed characteristics of both groups, although they were most similar to those of *D.o. pallidus*. They were predominantly 5 notes per song, with little variation of song types. The fundamental frequency of songs of Hart's Pass males was higher than that of *D.o. pallidus* males and lower than that of the population of *D.o. fuliginosus* to which it was compared.

TABLE II-1. Number of male blue grouse that used one, two, or three song types in a 5-minute period.

Location and Subspecies	Total No. of males	% of song types used 1	 2	 3
Hardwicke Island and Adam River, B.C. (*D.o fuliginosus*)	46	52%	48%	0
May Ranch, CA. (*D.o. fuliginosus*)	37	43%	54%	3%
Oregon and Lassen National Forest, CA. (*D.o. sierrae*)	14	57%	43%	0
Methow Game Range, WA. (*D.o. pallidus*)	74	70%	30%	0
Hart's Pass, WA. (Presumed *D.o. fuliginosus* x *D.o. pallidus* hybrid)	11	73%	27%	0

TABLE II-2. Lengths of time of songs, note lengths, and internote times of songs of male blue grouse.

		DOF(BC)[1]	DOF(CA)[2]	DOS[3]	DOP[4]	DOFxDOP[5]
No. males		16	4	5	8	2
		$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.
Total time (s)		2.96±.02	3.21±.04	3.19±.04	2.41±.02	2.58±.11
Note 1	note length (s)	0.37±.01	0.28±.01	0.31±.02	0.33±.02	0.37±.06
	internote time (s)	0.35±.01	0.51±.01	0.47±.01	0.39±.01	0.37±.01
Note 2	note length (s)	0.26±.01	0.21±.01	0.21±.01	0.16±.01	0.19±.04
	internote time (s)	0.31±.01	0.44±.01	0.42±.02	0.30±.01	0.37±.01
Note 3	note length (s)	0.27±.01	0.23±.01	0.23±.01	0.21±.01	0.22±.03
	internote time (s)	0.21±.01	0.31±.01	0.32±.02	0.18±.02	0.23±.08
Note 4	note length (s)	0.27±.01	0.21±.01	0.23±.01	0.32±.02	0.30±.07
	internote time (s)	0.16±.01	0.26±.01	0.25±.02	0.19±.01	0.19±.03
Note 5	note length (s)	0.34±.01	0.30±.01	0.29±.03	0.35±.01	0.36±.03
	internote time (s)	0.15±.01	0.26±.01	0.24±.02	-----	-----
Note 6	note length (s)	0.28±.01	0.21±.01	0.22±.02	-----	-----

[1] DOF(BC) = ***D.o. fuliginosus*** from Hardwicke Island (N=12) and Adam River (N=4), B.C.
[2] DOF(CA) = ***D.o. fuliginosus*** from the May Ranch, CA.
[3] DOS = ***D.o. sierrae*** from Oregon (N=4) and Lassen National Forest, CA. (N=1).
[4] DOP = ***D.o. pallidus*** from Methow Game Range, WA.
[5] DOFxDOP = Presumed ***D.o. fuliginosus*** x ***D.o. pallidus*** hybrids from Hart's Pass, WA.

TABLE II-3. Fundamental frequency (Hz) of songs of male blue grouse.

	Note 1	Note 2	Note 3	Note 4	Note 5	Note 6
	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.
DOF(BC)[1] (N=16)	148.7±2.1	154.8±1.8	154.9±1.8	153.3±1.8	149.9±1.6	147.1±2.0
DOF(CA)[2] (N=4)	109.8±0.3	120.0±0.0	119.3±0.8	118.8±1.3	114.0±2.5	112.5±2.5
DOS[3] (N=5)	124.0±3.8	136.0±2.6	134.6±2.6	132.4±3.0	129.0±2.5	126.6±2.7
DOP[4] (N=8)	103.0±2.5	108.3±3.2	106.3±2.1	104.0±2.0	101.4±2.6	-------
DOFxDOP[5] (N=2)	125.0±5.0	132.0±8.0	128.5±8.5	125.0±5.0	125.0±5.0	-------

[1] DOF(BC) = *D.o. fuliginosus* from Hardwicke Island (N=12) and Adam River (N=4), B.C.

[2] DOF(CA) = *D.o. fuliginosus* from the May Ranch, CA.

[3] DOS = *D.o. sierrae* from Oregon (N=4) and Lassen National Forest, CA. (N=1).

[4] DOP = *D.o. pallidus* from Methow Game Range, WA.

[5] DOFxDOP = Presumed *D.o. fuliginosus* x *D.o. pallidus* hybrids from Hart's Pass, WA.

TABLE II-4. Relationship between fundamental frequency of songs of coastal male blue grouse and latitude.

Subspecies	Location	No. of males	Latitude	Range of fundamental frequency (Hz)
D.o. sierrae	Lassen National Forest, CA.	1	40° 24′	110-127
D.o. fuliginosus	May Ranch, CA.	4	40° 29′	109-120
D.o. sierrae	Oregon	4	42° 24′	127-138
D.o. fuliginosus	Hardwicke Island and Adam River, B.C.	16	50° 27′	147-155
D.o. sitkensis	Mitkof Island, AK.	1	56° 30′	170-175

TABLE II-5. Statistical comparisons of songs of male blue grouse from Hardwicke Island and Adam River, B.C., Hart's Pass, WA., and Methow Game Range, WA. (Mann-Whitney U test).

		DOF[1] vs DOFxDOP[2] (N=16) (N=2)	DOP[3] vs DOFxDOP[2] (N=8) (N=2)	DOF[1] vs DOP[3] (N=16) (N=8)
Total time (s)		$P=0.013$	$P=0.178$	$P<0.001$
Note 1	note length (s)	$P=0.941$	$P=0.711$	$P=0.016$
	internote time (s)	$P=0.157$	$P=0.267$	$P=0.009$
	fundamental frequency (Hz)	$P=0.013$	$P=0.044$	$P<0.001$
Note 2	note length (s)	$P=0.026$	$P=0.533$	$P<0.001$
	internote time (s)	$P=0.013$	$P=0.044$	$P=0.320$
	fundamental frequency (Hz)	$P=0.026$	$P=0.044$	$P<0.001$
Note 3	note length (s)	$P=0.078$	$P=0.533$	$P<0.001$
	internote time (s)	$P=0.941$	$P=0.711$	$P=0.038$
	fundamental frequency (Hz)	$P=0.013$	$P=0.044$	$P<0.001$
Note 4	note length (s)	$P=0.941$	$P=0.999$	$P=0.019$
	internote time (s)	$P=0.209$	$P=0.889$	$P=0.013$
	fundamental frequency (Hz)	$P=0.013$	$P=0.044$	$P<0.001$
Note 5	note length (s)	$P=0.641$	$P=0.889$	$P=0.976$
	fundamental frequency (Hz)	$P=0.013$	$P=0.044$	$P<0.001$

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[1] DOF(BC) = *D.o. fuliginosus* from Hardwicke Island (N=12) and Adam River (N=4), B.C.
[2] DOFxDOP = Presumed *D.o. fuliginosus* x *D.o. pallidus* hybrids from Hart's Pass, WA.
[3] DOP = *D.o. pallidus* from Methow Game Range, WA.

TABLE II-6. Volume levels of songs of individual *D.o. fuliginosus* and *D.o. pallidus* male blue grouse.

	Volume[2] (dB)	
Distance (m)[1]	*D.o. fuliginosus*[3]	*D.o. pallidus*[4]
3	71	--
5	70	--
	75	--
	75	--
10	70	63
	68	--
	67	--
15	65	55
20	57	48
25	59	48

[1] Distance of microphone from singing male.

[2] A Senneheiser MKH 105 microphone and a Nagra 4.2 tape recorder were used for all sound level measurements with the record level set at 75 dB.

[3] From Hardwicke Island and Adam River, B.C.

[4] From Methow Game Range, WA.

TABLE II-3. Comparison of whoots of coastal (*D.o. fuliginosus*) and interior (*D.o. pallidus*) male blue grouse.

	D.o. fuliginosus[1]	*D.o. pallidus*[2]	U	P
	X̄±S.E. (N)	X̄±S.E. (N)		
Total time (s)	0.35±0.02 (3)	0.59±0.07 (2)	6	P=0.20
Fundamental frequency (Hz)	180.0±7.6 (3)	229.2±4.2 (2)	6	P=0.20

[1] From Adam River, B.C.
[2] From Methow Game Range, WA.

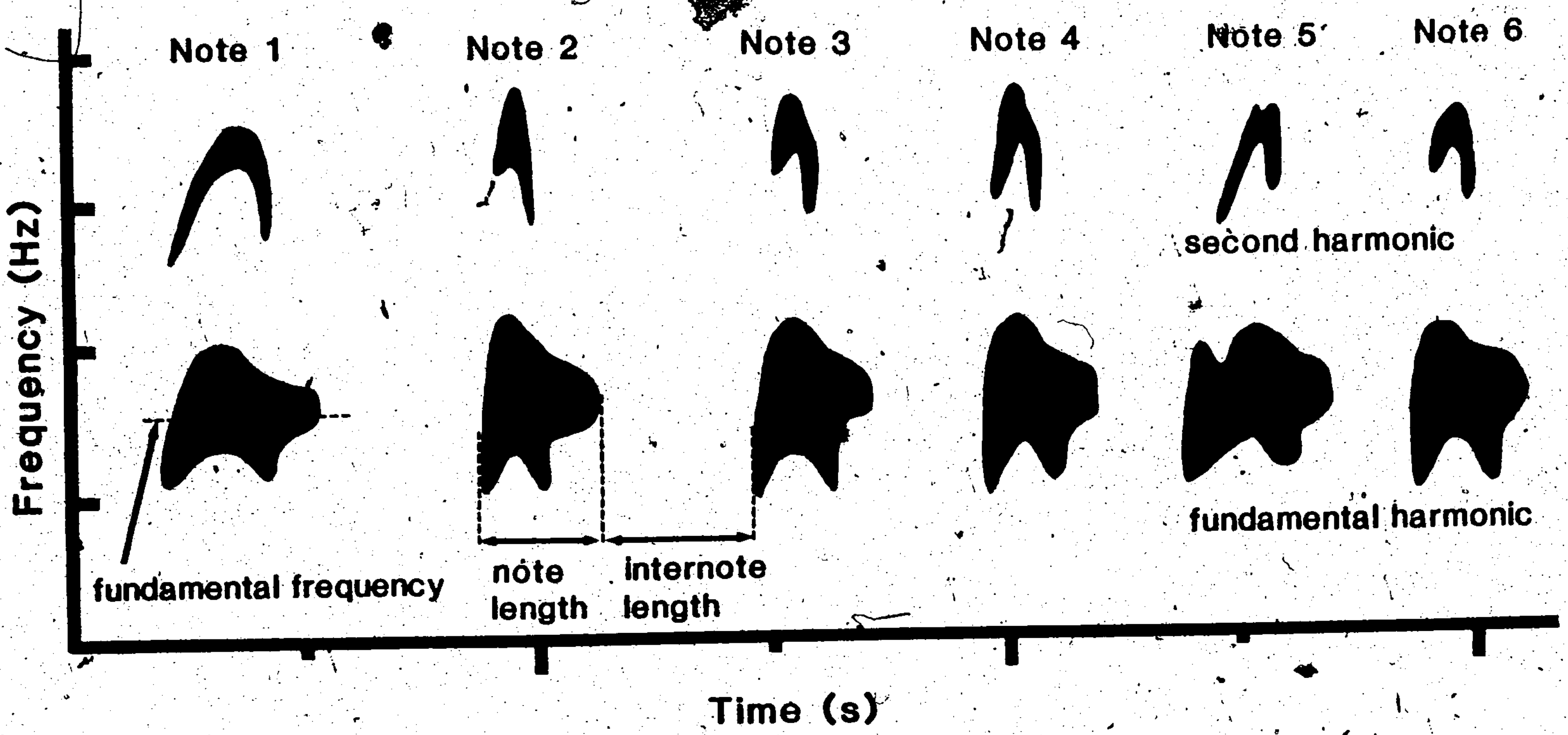

FIGURE II-1. Diagrammatic presentation of a male blue grouse song showing how measurements were made.

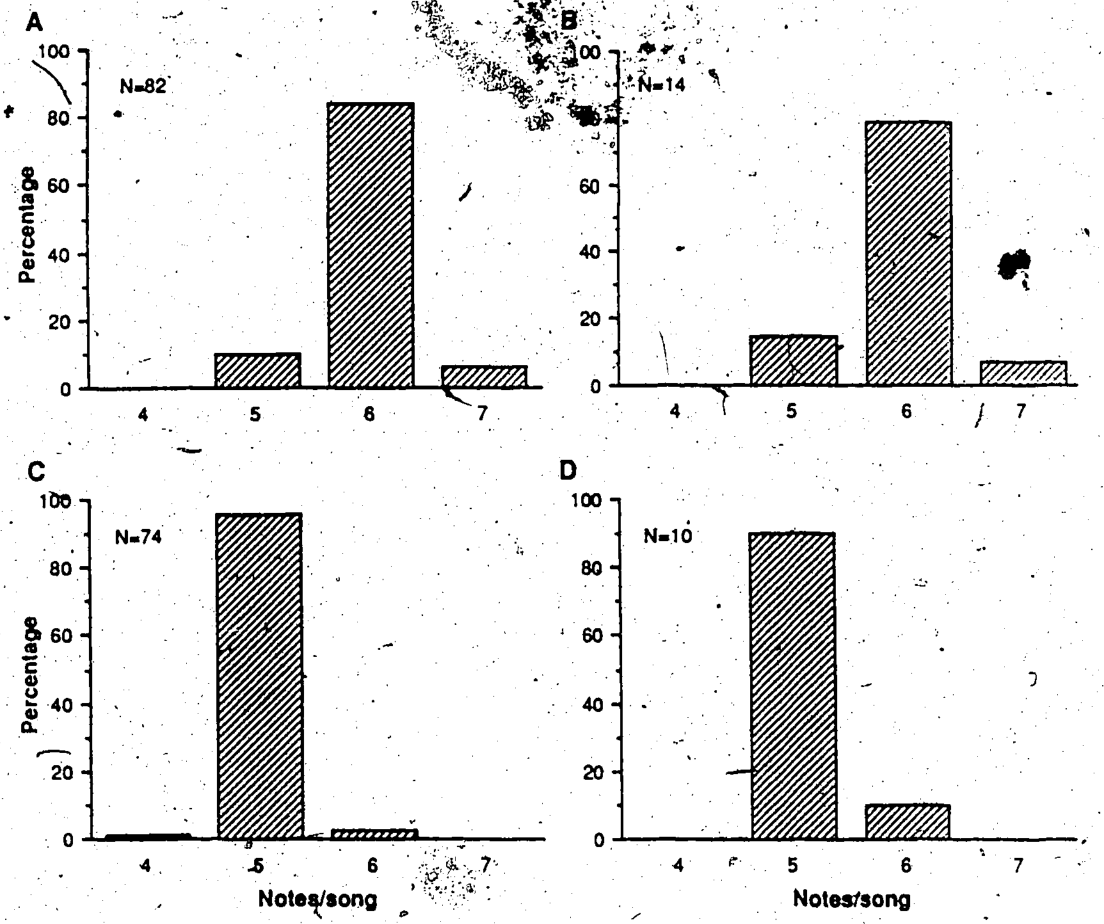

FIGURE II-2. Number of notes per song (song type) of male blue grouse. A) *D.o. fuliginosus* from Hardwicke Island and Adam River, B.C., and the May Ranch, CA.; B) *D.o. sierrae* from Oregon and Lassen National Forest, CA.; C) *D.o. pallidus* from the Methow Game Range, WA.; D) Presumed *D.o. fuliginosus* X *D.o. pallidus* hybrids from Hart's Pass, WA. N = number of songs.

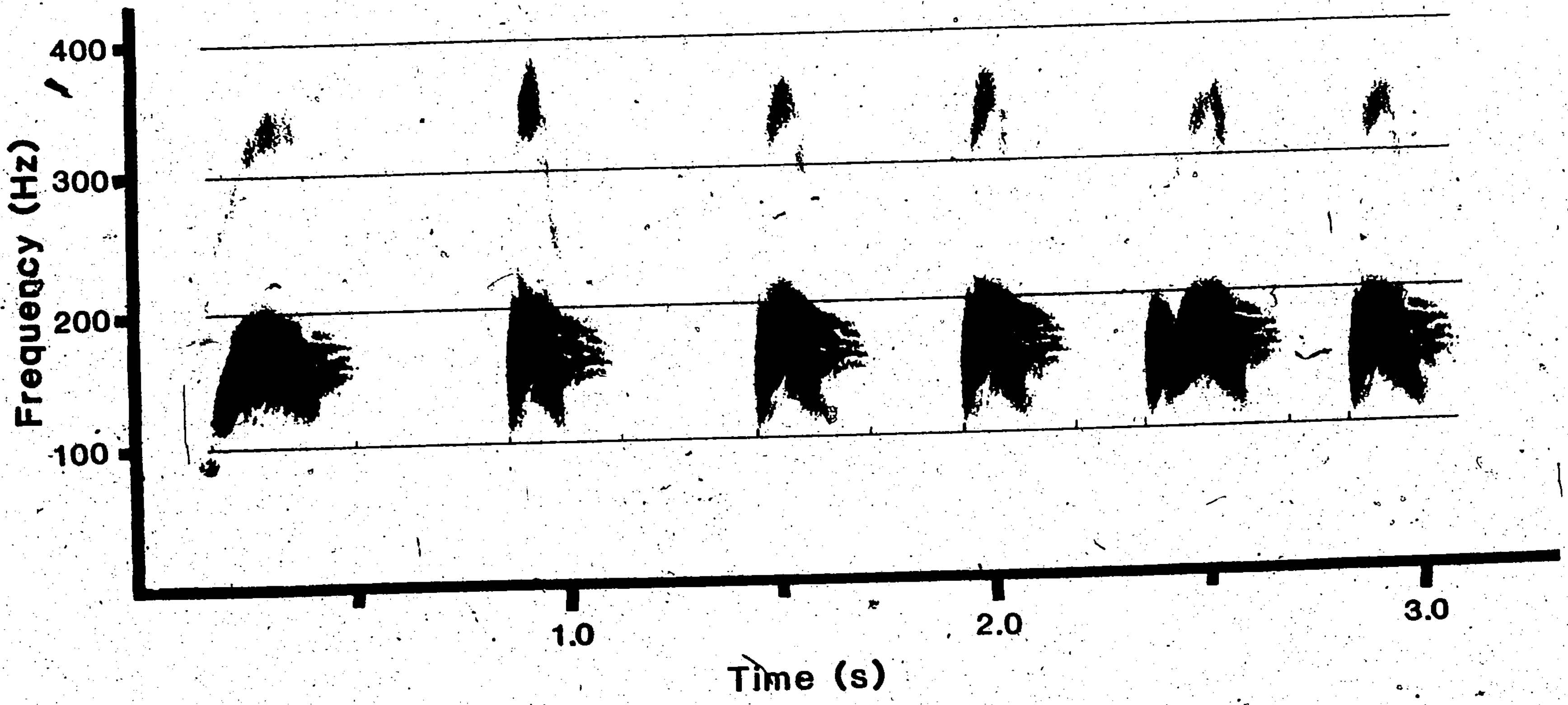

FIGURE II-3. Sonagram of a male blue grouse (*D.o. fuliginosus*) song from Hardwicke Island, B.C.

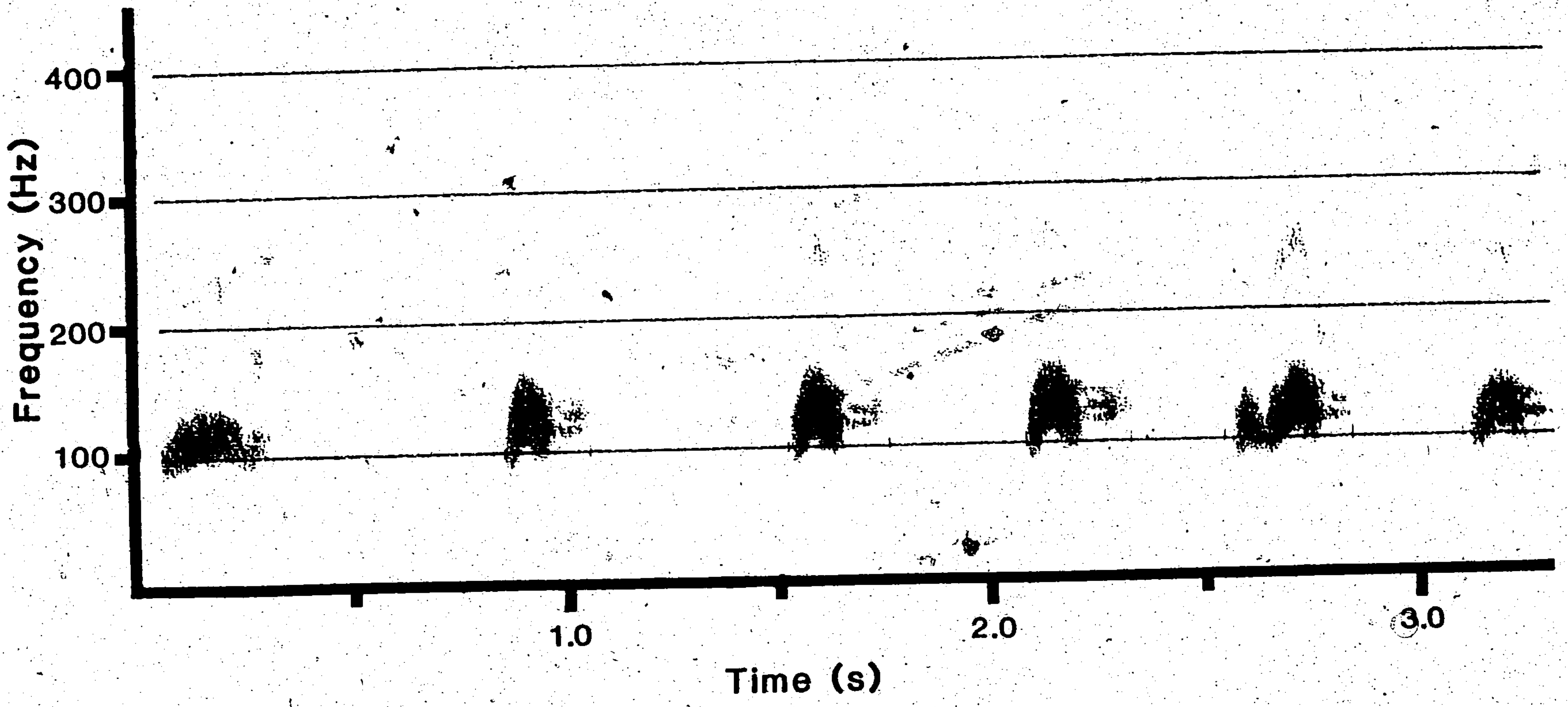

FIGURE II-4. Sonagram of a male blue grouse (*D.o. fuliginosus*) song from the May Ranch, CA.

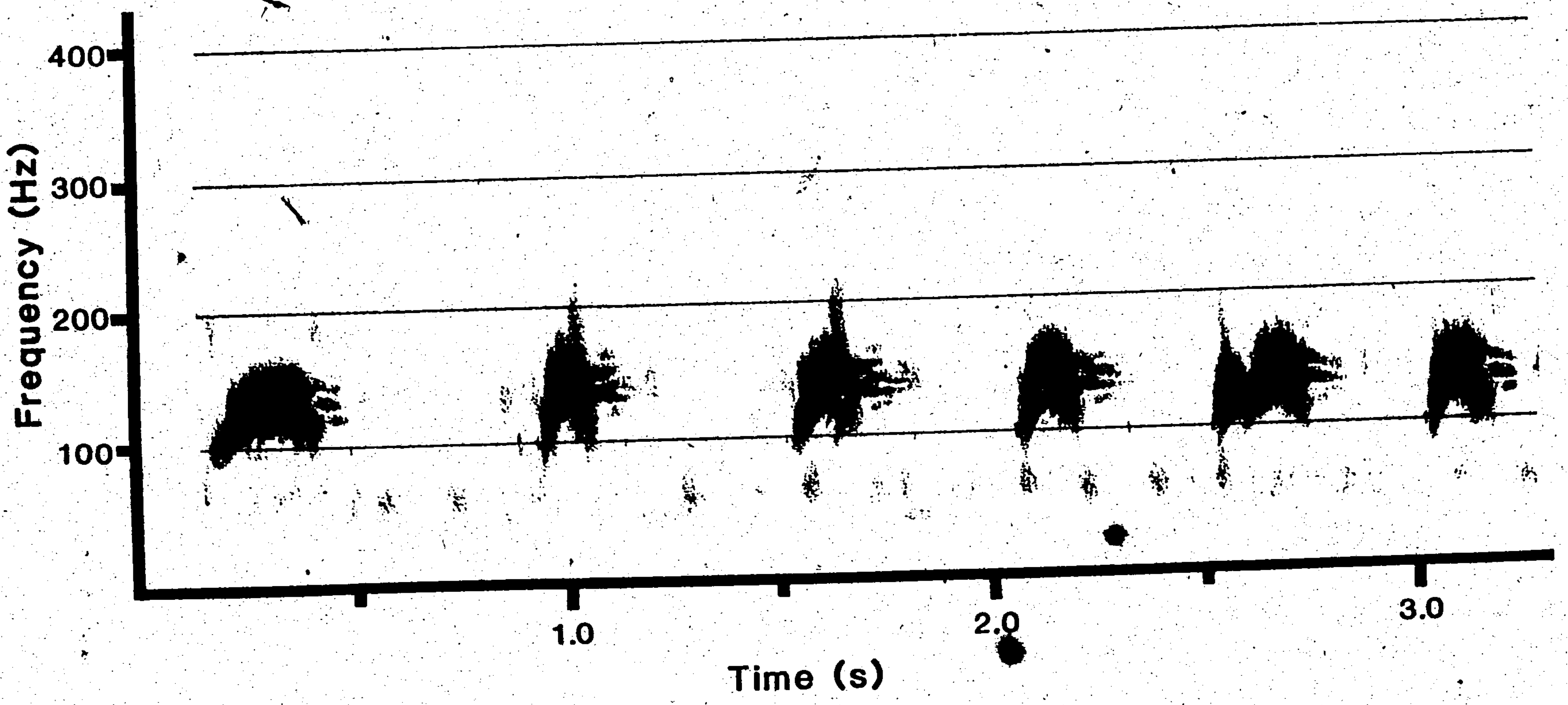

FIGURE II-5. Sonagram of a male blue grouse (*D.o. sierrae*) song from Oregon.

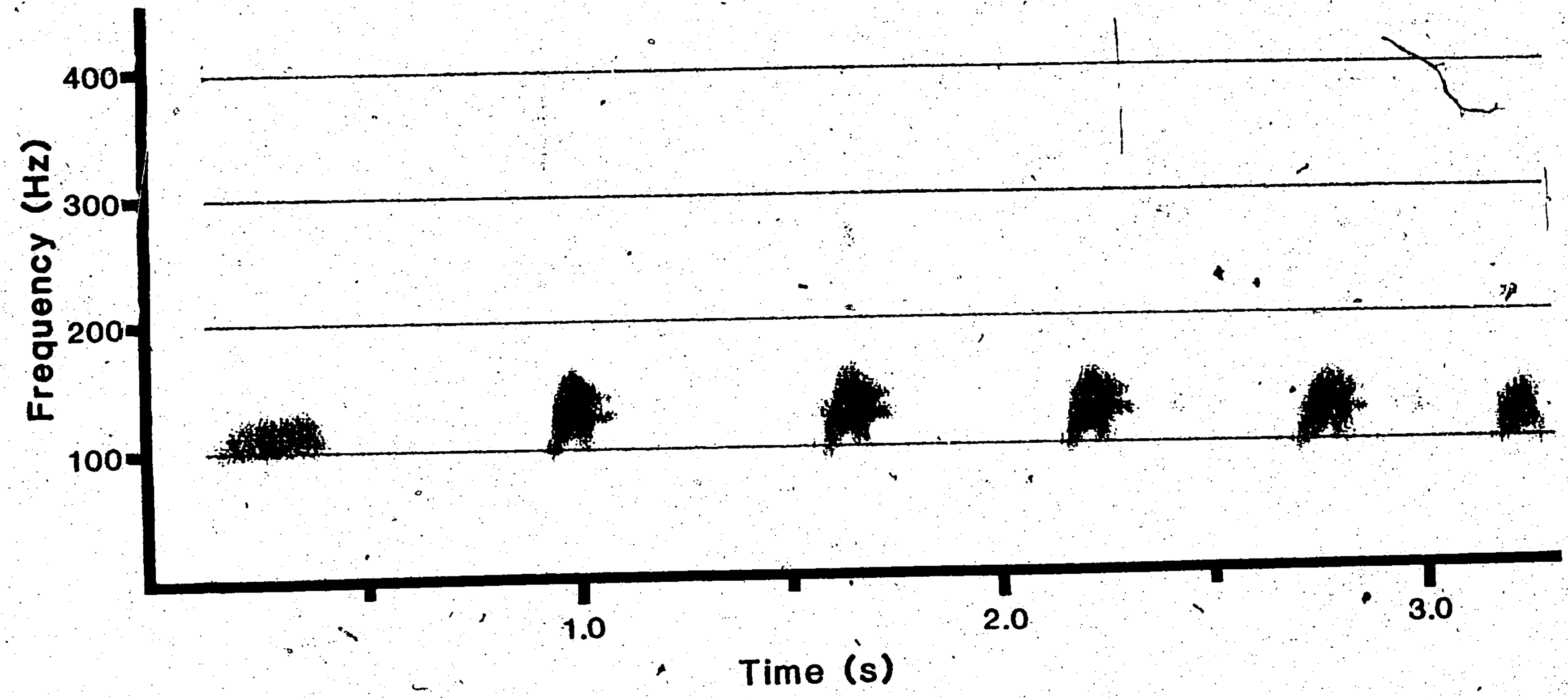

FIGURE II-6. Sonagram of a male blue grouse (*D.o. sierrae*) song from Lassen National Forest, CA.

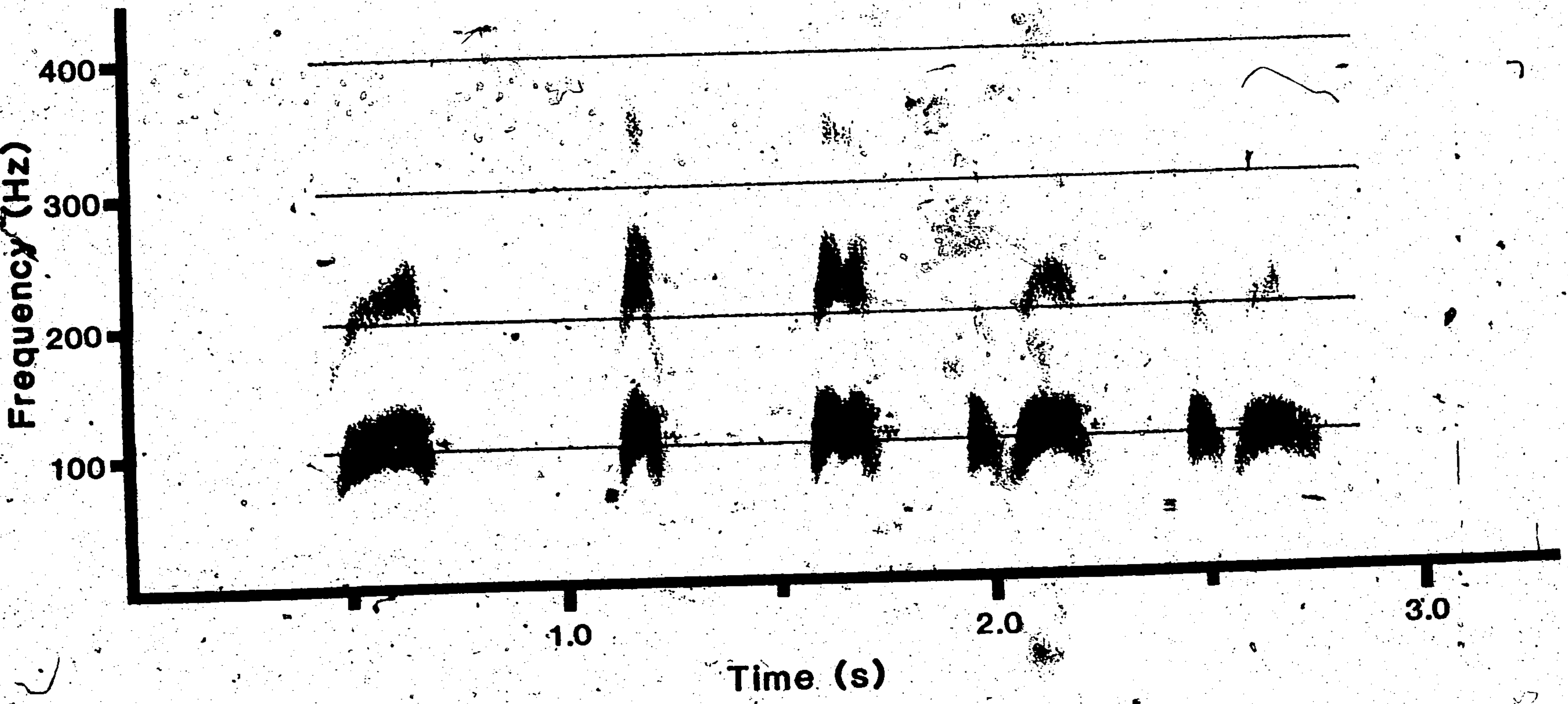

FIGURE II-7. Sonagram of a male blue grouse (*D.o. pallidus*) song from Methow Game Range, WA.

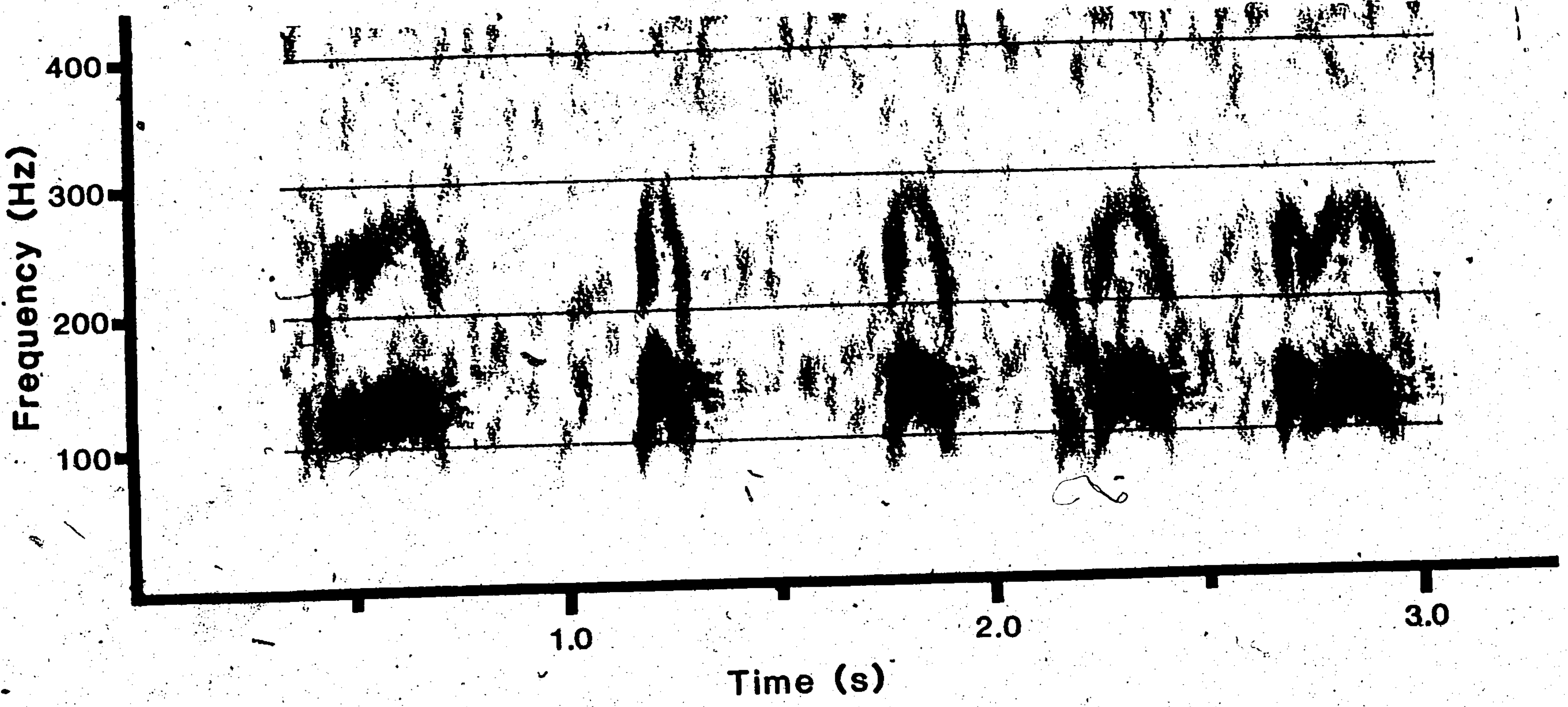

FIGURE II-8. Sonagram of a presumed hybrid male blue grouse (*D.o. fuliginosus* x *D.o. pallidus*) song from Hart's Pass, WA.

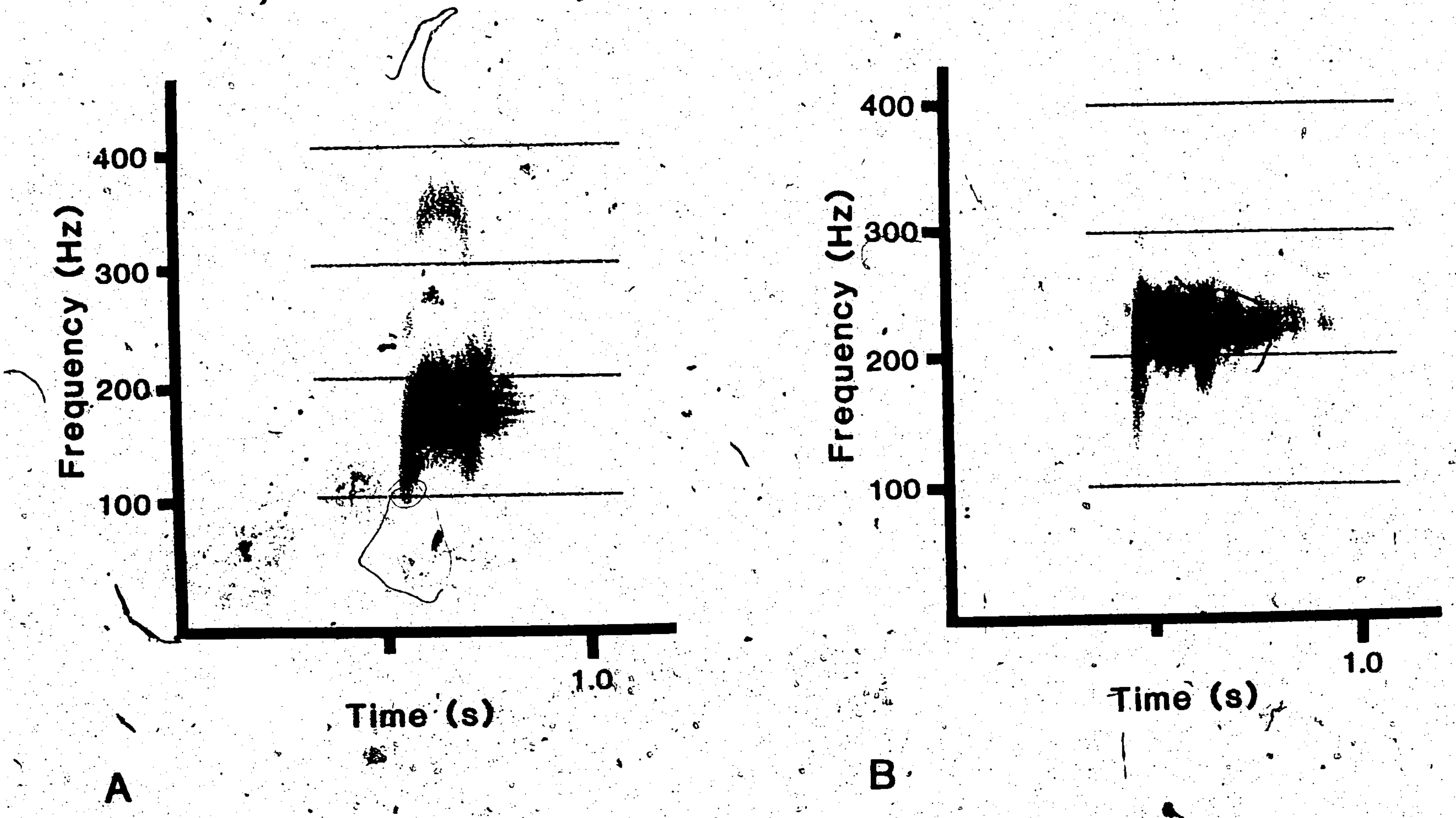

FIGURE II-9. Sonagrams of male blue grouse whoots. A) *D.o. fuliginosus* from Adam River, B.C.; B) *D.o. pallidus* from Methow Game Range, WA.

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III. SEXUAL DIMORPHISM IN VOCAL SOUND-PRODUCING STRUCTURES OF BLUE GROUSE

INTRODUCTION

The syrinx is the major vocal sound-producing structure of birds and is located at or near the junction of the trachea and bronchi. Shape of the syrinx, and its size and associated syringeal structures (i.e., muscles) vary greatly among avian species (Ames 1971) and this variation is responsible for production of a wide array of different sounds (Miller 1947; Warner 1971; Gaunt 1983).

Correlations between the physical features of bird song and body size have been proposed. In general, the larger the bird the lower the frequency of song (Gullion 1950; Bowman 1979; Ryan and Brenowitz 1985). Miller (1934) reported that the smaller male owls had a lower pitch than the larger females and that this difference was due to reverse sexual dimorphism in the syringes. However, Shy (1983) fo[illegible] relationship between song frequency and body size within North American tanagers.

Blue grouse (*Dendragapus obscurus*) occupy most of the mountainous regions of western North America from southeastern Alaska and central Yukon Territory to southern California, New Mexico, and Arizona (Appendix 1). They are sexually dimorphic in body size, plumage, and other external body features (Johnsgard 1983). Females are about 65-75% the weight of males (Zwickel et al. 1966; Redfield 1973), and have a repertoire of at least 12 calls; males, three to four (Albright 1985). Male vocalizations include the lowest frequency avian songs (50-200 Hz) (Greenewalt 1968; Hjorth 1970; Stirling and Bendell 1970). Most female calls are higher in frequency than those of males (500-1000 Hz), although some are relatively low frequency and similar to some of those of males (200-300 Hz) (Stirling and Bendell 1970; Albright 1985). Syringes of male blue grouse, sage grouse (*Centrocercus urophasianus*), sharp-tailed grouse (*Tympanuchus phasianellus*), and prairie chickens (*T. cupido* and *T.*

pallidicinctus) appear to be used in conjunction with inflated esophagi for vocal sound production (Hjorth 1970; Johnsgard 1983).

The first objective of this study is to describe the vocal sound-producing structures in yearling and adult male and female blue grouse. These structures have not been described except in an undergraduate class report (Degner 1983). This is, in part, an update and expansion of the data presented there. A second objective is to examine whether any sexual differences in the syringes and associated structures are due to differences in body sizes of males and females.

STUDY AREAS

Blue grouse were collected in the springs and summers of 1983 and 1984 from [illegible]ven locations and included birds from four of the eight recognized subspecies ([illegible]gard 1983). Hardwicke Island, B.C. (50° 27′ N, 126° 50′ W) and the lower Adam River (50° 27′ N, 126° 10′ W) on nearby Vancouver Island were the collection sites for the coastal subspecies, *D.o. fuliginosus* (Appendix 3).

Two collection sites were in north-central Washington state, the Methow Game Range (48° 31′ N, 120° 4′ W) and Hart's Pass (48° 42′ N, 120° 39′ W) (Appendix 2). The interior subspecies, *D.o. pallidus*, occurred on the Methow Game Range. Hart's Pass is approximately 50 km northwest of the Methow Game Range near the crest of the Cascade mountains. This area appears to be a zone of overlap between coastal *D.o. fuliginosus* and interior *D.o. pallidus*. Birds here show some morphological and behaviorial traits of both subspecies.

Birds from another coastal subspecies, *D.o. sierrae*, were collected about 24 km north of Klamath Falls, in the Winema National Forest (42° 26′ N, 121° 45′ W) and approximately 23 km north of Lakeview, in the Fremont National Forest (42° 23′ N, 120° 22′ W), both in Oregon (Appendix 2).

A small sample of *D.o. obscurus*, a second interior subspecies, was collected from three widely separated regions in Colorado: Cold Spring and Middle Mountains (40° 55′ N, 108° 50′ W), William's Peak and Ute Pass (39° 52′ N, 107° 30′ W), and Greyrock-Poudre Canyon (40° 50′ N, 105° 30′ W).

MATERIALS AND METHODS

A total of 93 blue grouse were collected in 1983 and 1984 for examination of the syringes and associated sound-producing structures (Table III-1). Specimens were shot specifically for this study (N=76), in connection with other studies (N=9), or found freshly killed by predators (N=8).

Collected grouse were either necropsied fresh, in the field, or embalmed. If necropsied fresh, respiratory tracts and esophagi were measured and then preserved in Bouin's fixative or 10% formalin. Some whole, or skinned and partially dissected, birds were injected with, and then immersed in, embalming fluid and stored in plastic bags.

Embalmed birds were dissected in the laboratory. Where possible measurements made on freshly necropsied birds were made *in situ* on embalmed birds. Points of origin and insertion of syringeal muscles were identified while intact in the embalmed birds. Preserved structures from previously necropsied birds were re-measured in the laboratory to determine the effects of preservatives on measurements. All measurements (Figures III-1 and III-2), except tracheal and esophageal lengths, were taken with dial calipers in the field and with dial calipers under a dissecting microscope in the laboratory. Tracheal and esophageal lengths were measured with a ruler. Some structures were damaged during collection and dissection, resulting in some variation in sample size among measurements. Only measurements from right bronchi are given.

Twenty-two freshly dissected esophagi with crops intact were tied off at the cephalic end and inflated by blowing air through a straw inserted in the caudal end. Measurements were made of the esophagi and crops before and after inflation (Figure

Frontal histological sections (7 um) were made from the middle of 25 syringes. These were stained with Masson's Trichrome stain. Descriptions of internal syringeal structures and measurements of tympaniform membranes were made from these sections (Figure III-3). Measurements were made with a micrometer equipped compound microscope. Only membrane thicknesses from the right side of the syrinx are given.

Body weights and wing lengths (unflattened wing chord) were taken from most grouse collected to give an index of body size. To increase sample sizes, birds collected in 1981 and 1982 at Hart's Pass (N=5), Methow Game Range (N=5), and Winema National Forest (N=2) were included in these analyses. Body weights of most birds were measured with a triple beam balance, or with a Pesola spring scale in some field situations. Fresh heart weights from birds necropsied in the field were also recorded. Blood was not specifically drained nor fat removed from the hearts.

Statistical analyses were made using the SPSS^X (SPSS^X Inc. 1983) and TONESTATS (Dept. of Zoology, University of Alberta) statistical packages. Differences were considered significant at the five percent level. Means are reported ±1 S.E.

RESULTS

Effects of preservatives

Of the grouse collected for this study, 59 were necropsied fresh and 34 were embalmed. However, not all birds that were necropsied fresh were measured before preservation because some were collected, dissected, and preserved by individuals other than myself.

Structures from birds necropsied fresh were re-measured after several months in preservatives. Wilcoxon matched-pairs signed-ranks tests were performed on vocal sound-producing structures of adult males and females to examine the effects of the preservatives.

There were significant differences in 16 of 26 cases between fresh and preserved tracheal, bronchial, syringeal, and esophageal measurements of adult males and females. Preservation appeared to cause shrinking in many of the structures; in 79% (220/279) of measurements of adult males and 74% (72/97) of adult females, fresh structures were larger than preserved. Therefore, fresh measurements were used for analysis as they more accurately represent the natural size of the structures, although this results in a reduction in sample sizes. Data on numbers of syringeal and bronchial rings are from preserved samples. These rings are not affected by preservation and are most accurately counted in the laboratory under a microscope.

Vocal sound-producing structures in male blue grouse

Vocal sound-producing structures of males of all subspecies examined were the same in general structure and composition, though they differed in size. This difference tends to increase the variation, making statistically significant differences between males and females conservative. Subspecific differences are discussed elsewhere (Degner 1988).

The trachea and bronchi. The trachea lies ventrally along the neck, extending from the larynx to the thoracic cavity, and ending at the syrinx, which bifurcates into the bronchi at its posterior end (Figure III-4). The trachea is comprised of a varying number (80-95) of overlapping cartilaginous rings.

The bronchi extend from the syrinx to the lungs (Figure III-4). Bronchial rings are cartilaginous and differ from tracheal rings in that they do not overlap and are only half rings with connective tissue completing them. Each bronchus consists of 7-11 half rings, the number sometimes difficult to determine because of the bronchial juncture with the lungs.

The lungs and air sacs of blue grouse were not examined. These structures, however, are important to sound production, especially loudness, as they supply the air flow required to produce sound (Brackenbury 1972, 1979; Gaunt 1983).

The syrinx. The syrinx is tracheobronchial (Figure III-4) (Myers 1917; King 1979). Externally, it is composed of 12-16 cartilaginous rings which do not overlap (Figure III-5). The syringeal rings (SR) were numbered caudad to cephalad with the first ring being SR 1. The syrinx is greatly enlarged and expanded, forming the tympanum or drum. It is approximately twice the width of the trachea. The syringeal rings are fused at the dorsal and ventral midline.

Histological examination of 13 syringes revealed that all syringeal rings are cartilaginous. The pessulus, the medial cartilage that divides the syrinx into the two bronchi, was composed of cartilage in 12 males, but appears to be partially ossified in one. A thin layer of connective tissue lies between the syringeal rings and in some cases fat is embedded within the connective tissue.

Syringeal membranes. One pair of syringeal membranes, the internal tympaniform membranes (ITM's), is located along both caudo-lateral edges of the pessulus, forming the anterior medial walls of the bronchi (Figure III-6). These membranes are composed of loose, irregular connective tissue with elastic fibers probably embedded in them. Their thickness, at the widest point, is 2.52±0.11 mm. What I call the ITM's may include the labium mediale and the membrana tympaniformis medialis as described by King (1979) but I have not been able to differentiate between the two.

It is difficult to determine positively whether there are external tympaniform membranes (ETM's) in blue grouse (labium laterale and membrana tympaniformis lateralis of King (1979)). In some syringeal sections there appears to be thicker connective tissue between SR 1 and 2 than between the other syringeal rings (Figure III-6). If these are membranes, they are thinner than the ITM's, 0.44±0.07 mm thick, and are composed of loose, irregular connective tissue. Because of tissue deformation associated with sectioning cartilaginous structures such as the syrinx, describing and measuring these structures accurately is difficult.

Syringeal muscles. Two pairs of extrinsic muscles are associated with the syrinx in male blue grouse. This is characteristic of many non-passerine birds with simple syringes (Miskimen 1963; Chamberlain et al. 1968; Gaunt 1983). No intrinsic syringeal muscles are present.

The first pair of muscles, the M. sternotrachealis, originates on the lateral cranial process of the sternum. The muscles traverse laterally across the thoracic cavity to insert on the dorso-lateral edge of the syrinx and trachea, on the last few syringeal rings (SR 8-16) and the first few tracheal rings (TR 1-8) (Figure III-4), the exact points varying among individuals and subspecies. Their width is relatively constant over their entire length (approximately 2.0 mm), with some slight widening and flattening at the origins and insertions.

The second pair, the M. tracheolateralis, originates on the laryngeal cartilage and the anterior most tracheal rings (Figure III-4). The muscles run caudad on each side of the trachea, loosely attached to it with connective tissue. Just anterior to the syrinx (at approximately TR 3-5) and anterior to the point of insertion of M. sternotrachealis, each splits into two branches. One branch goes ventrally under the M. sternotrachealis to insert on the anterio-lateral surface of the syrinx (SR 8-10). A larger, dorsal branch goes over the M. sternotrachealis and onto the dorsal surface of the syrinx where it joins that from the other side. The two then extend posteriorly along the dorsal midline of the syrinx, forming the syringeal ligament. The syringeal ligament continues posteriorly till it bifurcates and inserts on the dorso-medial surface of each bronchus. The width of these muscles is approximately 3.5 mm in their middle and is relatively constant over its entire length, except at the point of origin and where it splits at the syrinx.

The actions of these muscles were not directly examined, but actions can be inferred from their arrangement. It appears that the M. sternotrachealis draw the syrinx and trachea caudad, and perhaps steady the syrinx. The M. tracheolateralis oppose the M. sternotrachealis and likely pull the bronchi cephalad and inwards, and draw the trachea and syrinx cephalad. The actions of the muscles likely alter the configuration of the syrinx and the tension of the syringeal membranes (ITM's and possibly the ETM's) according to what has been reported for other species (Miskimen 1951; Humphrey 1958; Chamberlain et al. 1968; Lockner and Youngren 1976; Gaunt 1983).

The esophagus. The esophagus begins at the pharynx, and extends caudad along the ne[illegible] dorsal to the trachea for most of its length. The crop hangs over one side of th[illegible]chea, but the esophagus enters the thoracic cavity dorsal to the trachea and ends a[illegible] the proventriculis (Figure III-4). The esophagus is divided into two parts by the crop (the inguvies): the pars cervicalis (anterior portion), and the pars thoracica (posterior portion) (Figure III-7A) (McLelland 1979).

The saccus esophagealis or inflatable sac on the pars cervicalis, is smaller than in sage grouse (Clarke et al. 1942; Honess and Allred 1942). However, the anterior end is approximately three times the diameter of the posterior end where it enters the crop (Figure III-7A). The esophagi of 15 adult males were inflated to determine if they were capable of expansion to form potential sound-resonating chambers. The anterior three-quarters of the pars cervicalis inflated to approximately three times its original diameter (Figure III-7B). The crop also expanded, but the pars thoracica expanded only slightly. Thus the pars cervicalis of male blue grouse has the ability to inflate and serve as a sound-resonating chamber.

Yearling males. Yearling males were significantly lighter in weight and had shorter wings than adult males (Table III-2). There were no significant differences in tracheal, bronchial, or syringeal measurements between yearling and adult males (Table III-3). Sample sizes were too small to test differences in syringeal membrane thickness (Table III-4). Syringeal measurements (Table III-3) and syringeal membrane thicknesses (Table III-4) showed a trend; adult males were larger than yearlings, but the sample of yearlings was too small to provide reliable statistical tests. Esophageal measurements (Table III-5) were not significantly different between the two age classes and there were not enough inflated esophagi of yearling males to compare (Table III-6). Tracheal and bronchial (Table III-3), and esophageal (Tables III-5, III-6) measurements showed no clear size trend between yearling and adult males.

Vocal sound-producing structures in female blue grouse

The trachea, bronchi, and syrinx. Vocal sound-producing structures of female blue grouse are, in general, the same as in males, though their sizes and shapes differ (Figure III-8). The trachea is similar to that of males, except smaller and with fewer rings (70-80). The bronchi are composed of 7-11 cartilaginous, non-overlapping half rings as in males. The syrinx is located at the junction of the trachea and bronchi, hence tracheobronchial. The syrinx is smaller and the division between syrinx and trachea less clear than in males (Figure III-5). Syringeal rings do not overlap but are closer together than in males, with less connective tissue between them. The syrinx forms a small tympanum, with the rings fused at the dorsal and ventral midlines. It is not enlarged as in males (Figure III-5).

Internal composition of female syringes is the same as in males, except smaller (Figure III-9). Syringeal rings and the pessulus are composed of cartilage with no sign of ossification in the nine sections examined. As in males, ITM's are present but it is difficult to determine if there are ETM's. The ITM's are thin, 0.54±0.09 mm. If there are ETM's, they are very thin, just 0.[illegible]±0.02 mm thick.

Syringeal muscles. Two pairs of [illegible] syringeal muscles, M. sternotrachealis and M. tracheolateralis, are present in females and are generally the same as in males. The major difference is that M. sternotrachealis of females inserts more cephalad on the syrinx and trachea (Figure III-8). Widths of the female muscles are thinner than in males (1.0-2.0 mm for the M. sternotrachealis, and 1.5-3.5 mm for the M.

tracheolateralis), in about the same ratios as differences in body size.

The esophagus. The esophagi of female blue grouse contain the same sections as in males (Figure III-7A). The anterior end of the pars cervicalis is not greatly enlarged, only about one and one half times the diameter of the esophagus at the crop and there is no sign of a saccus esophagealis. The esophagi of seven females were inflated. In contrast to those of males, the mean diameter increased only slightly, from 11.8 mm to 15.5 mm (Figure III-7B).

Yearling females. Adult females were significantly heavier than yearlings. Mean wing length of adult females was larger, but not significantly different than in yearlings (Table III-7).

Tracheal, bronchial, syringeal, and esophageal measurements were not significantly different between yearling and adult females, except for syrinx lengths (Tables III-8, III-9, III-10, III-11). There was a weak trend towards adult female structures being larger than in yearlings (Tables III-8, III-9, III-10, III-11).

Sexual dimorphism ~~in vocal sound~~-producing structures

A similarity index (S.I.), the size of females relative to that of males, was calculated for all pairs of male and female measurements. Two-tailed t-tests were used to determine if there were significant differences between the sexes.

Body weight is commonly used as an index of body size (Amadon 1977; Cade 1982), but because of seasonal variation some consider it poor (McGillivray 1985). Adult females collected for this study were 78.5% the weight of adult males, a significant difference (Table III-12). Others have reported similar differences; 75-77% for interior blue grouse in autumn (Zwickel et al. 1966) and 75% for coastal blue grouse in summer (Redfield 1973). Cubic root of body weights were calculated to compare body weight to linear measurements (cubic root makes weight linear). Cubic root of body weight increased the relative size of females to 91.6% that of males, but was still significant (Table III-12).

Payne (1984) believed that wing length is a better indicator of size than body weight in similar species of birds. Wing length differences were significant and were similar to those shown by the cubic root of body weight, with females 91.2% the size of males (Table III-12).

Heart weights, representing an independent internal organ, showed a difference between the two sexes similar to that of body weight; females 80% the size of males (Table III-12). Cubic root of heart weight decreased the difference (S.I. 88.9%) and was similar to that of cubic root of body weight and wing length (Table III-12).

There were significant differences between sexes in all respiratory system measurements, except bronchial length and number of bronchial rings (Table III-13). Bronchial lengths were nearly different (P=0.060).

Syringeal measurements exhibited the greatest difference in size between adult males and females (Figure III-5). Syringeal measurements of females were from 35 to 43% those of males (Table III-13). This difference was much greater than those in body weights, heart weights, or wing lengths. Syringeal shapes also differed between sexes: male syringes were more expanded than those of females.

All other respiratory system measurements, except bronchial length and number of bronchial rings, were significantly different, but all showed smaller differences between males and females than did syringeal measurements (S.I. 55.1-88.6%)(Table III-13). There was less difference in tracheal and bronchial measurements than in those from the syrinx, yet all are in the same system and joined together. This suggests that selective pressures for sound production may be acting more on the syrinx than on other parts of the respiratory system that were examined.

In terms of internal syringeal membranes, the difference between adult male and female syringes was greater than in other syringeal measurements. Thickness of the ITM's from females was about one-fifth that of males (S.I. 21.4%) (Table III-14).

These data again suggest that selective pressures may act more on the syringes than other parts of the respiratory system.

There was no significant difference between sexes in esophageal widths at the crop; however, the rest of the esophageal measurements differed significantly between adult males and females (Table III-15). Anterior esophageal widths showed the greatest difference, adult females 49.0% the size of males (Table III-15). This is due to the presumed ability of males to inflate the pars cervicalis for use as a sound-resonating chamber (Figure III-7). All other adult female esophageal measurements were no less than 78.7% the size of those of adult males (Table III-15).

Differences in the inflatability of the pars cervicalis of males and females are striking (Table III-16). There were significant differences in the lengths and widths of the inflated pars cervicalis, but not in inflated crops (Figure III-7). That there was no difference in inflated crops is important because it shows that there was little or no bias in the amount of air used to inflate the esophagi. The inflatability of the male esophagus suggests selective pressures are acting on the anterior end of the male esophagus similar to those on the syrinx and that the esophagi likely are involved with vocalization.

DISCUSSION

The membranes in the syrinx vibrate to produce sound (Gaunt and Wells 1973; Brackenbury 1982). Gaunt and Gaunt (1985) described three models of sound generators: the compression model, the pulse generator, and the whistle. The pulse generator (membrane vibrating system) seems the most likely mechanism for sound production in blue grouse. However, no experimentation was undertaken to confirm this hypothesis and only indirect anatomical evidence is available. Briefly, the pulse generator works with the tympaniform membranes forming a valve that closes off the air passage. When sufficient pressure has built up this valve opens, causing a burst of air to pass through to produce sound. The valve closes due to elasticity of the membranes, Bernoulli forces from the air flow, and perhaps muscular contractions (Gaunt and Gaunt 1985:224).

Tracheal modulation of sound, the modification of the fundamental frequency by altering the length of the trachea, has been suggested by various authors (Harris et al. 1968; Johnsgard 1983). However, Greenewalt (1968) does not believe bird sounds are affected by the trachea and Gaunt and Gaunt (1985:228) concluded that the "role of tracheal resonance remains ambiguous". Because no experimentation was undertaken in this study, the possible role of tracheal modulation in blue grouse is unknown. There was a significant difference in tracheal lengths between adult males and females, but this difference was proportional to body size and hence likely reflects body size differences. Variation in the vocalizations of male and female blue grouse is most likely source modulated (Greenewalt 1968; Gaunt and Gaunt 1985).

There was a highly significant difference between mean tracheal diameters of adult males and females, with that of females less than 70% that of males. Posterior tracheal diameters showed the greatest difference (P.D. 55.1%). This difference was larger than one would expect on the basis of differences in body size, and may be a result of differences in syringeal sizes and shapes. The wider the air passage (tracheal diameter) the slower the air flow and this causes a lower pitch in aerodynamic vibration systems, but not in membrane vibrating systems (Gaunt and Gaunt 1985). Since blue grouse appear to have a membrane vibrating system, the effect of different tracheal diameters is unknown. The large difference in posterior tracheal diameters is probably due to differences in syrinx size.

Bronchial lengths were not significantly different between adult males and females, but bronchial diameters were. The larger male bronchi are most likely related to body and syrinx size differences, not sound production. However, I have no way of verifying this.

Since adult female blue grouse are 75-80% the weight of adult males, if body size alone is acting on the internal structures of blue grouse then these structures should be 75-80% smaller (91.6% when the cubic root of body weight is used) in females than males. Heart weight and the cubic root of heart weight show 80% and 88.9% differences, respectively. Adult female tracheal and bronchial measurements ranged from 55.1 to 88.7% the size of the corresponding structures in adult males. Syringeal measurements show even greater differences; female syringes are less than 45% the size of males. From these results there does not appear to be a pattern where female internal structures are 80% the size of males. However, when syringeal differences are compared to those of other structures, it appears that factors related to sound production may be acting on the syrinx to produce such large syringeal differences. Posterior tracheal and bronchial diameters (55.1% and 64.7%, respectively) showed larger differences than other tracheal and bronchial measurements. These differences are most likely due to syringeal differences, because of their close proximity to the syrinx.

Syringeal shapes were different between sexes; male syringes were more expanded or bulbous than those of females. Differences in syringeal shape may have some effect on sound production (Ames 1971; Gaunt 1983). This was not investigated in my study, therefore, the effects of these differences on sound production in blue grouse are unknown.

Most female vocalizations are higher in fundamental frequency than those of males (Stirling and Bendell 1970; Hjorth 1970; Albright 1985). Stirling (1965:11[illegible] reported that two captive females gave a call that "sounded like the male hooting but had a higher pitch." Therefore, since the syrinx is smaller in adult females and they produce, on average, higher frequency vocalizations than adult males, a relationship between syrinx size and frequency of sounds produced exists; the smaller syrinx of females is associated with higher sound frequency.

Miller (1934, 1935, 1947) reported that in the owls he examined females were larger in body size than males, but had smaller syrinxes. Females also had higher pitched calls than males. This evidence supports the relationship of smaller syringes producing higher pitched calls (i.e., have a higher fundamental frequency).

Sexual dimorphism is common in the syringes of many species of ducks (Johnsgard 1961, 1971; Warner 1971; Lockner and Youngren 1976). The major difference in the sexes is the development of an enlargement, the bulla syringealis, usually on the left side of the male syrinx (King 1979). Unfortunately, little work has been done on comparisons between syrinx size and sound frequencies produced. In ducks, males appear to have larger syrinxes, but higher pitched, more whistled vocalizations than females (Johnsgard 1961, 1971; Warner 1971). This may not be evidence against the relationship seen in blue grouse as male and female mallard (*Anas plathyrhynchas*) syringes may function differently (Lockner and Youngren 1976). This may be true in other ducks, while the syringes of male and female blue grouse appear to function in a similar manner.

The ITM's appear to be the vibrating, sound-producing membranes in blue grouse, though there is no direct evidence to support this statement. If ETM's are present, then they also may be involved in producing sound. The thicker the tympaniform membrane, the slower it vibrates, producing lower frequency sounds (Miller 1947; Sutherland and McChesney 1965; Johnsgard 1983; Gaunt and Gaunt 1985).

A relationship between ITM size, syrinx size, and sound frequency is apparent when the sexes are compared. Male blue grouse ITM's were four times thicker than those of females. One would expect a difference of approximately two and one half times since the syringes of adult males were about two and a half times larger than those of females. This large difference may be a result of further selection for specific sound frequencies. In blue grouse, it appears that the thicker the ITM's and the larger the syrinx, the lower the fundamental frequency of the sound produced.

Syringeal muscles act on the syrinx, trachea, and bronchi to alter their configuration, which alters tympaniform membrane tension, allowing them to vibrate and produce sound (Greenewalt 1968; Brackenbury 1982; Gaunt and Gaunt 1985). Both pairs of syringeal muscles are larger in adult males than in adult females, but this most likely is due to scaling of body size rather than specifically related to sound production. The M. sternotrachealis of females inserts more cephalad than on males. This may contribute to the greater complexity and frequency of sounds of females than of males (Phillips and Youngren 1981; Gaunt and Gaunt 1985).

When male blue grouse sing their necks appear to expand. Early observers attributed this expansion to the inflation of the "air sacs" that were associated with the bare areas (cervical apteria) on the sides of the neck. Some believed that this was where the sounds were produced, but others more accurately observed that the sound was produced in the syrinx and the "air sacs" acted to resonate the sound (Grinnell et al. 1918; Dawson 1923). They were only partially correct, as the cervical apteria are modifications of the neck skin and are not inflatable sacs.

In male blue grouse, the pars cervicalis is capable of inflating to over three times its original size. Gross (1928) was one of the first to describe the inflation of the esophagus in grouse, the heath hen (*T. cupido cupido*). He proposed that the tongue of the grouse blocks the internal nares and air from the respiratory system flows into the esophagus. Clarke et al. (1942) and Honess and Allred (1942) described a similar process in sage grouse. This is most likely the mechanism used by male blue grouse to inflate their esophagi, but this is based only on analyses of the morphology of the birds and not direct observation. The esophagi of female blue grouse appear not to be inflatable.

There is no direct evidence to support the hypothesis that male blue grouse, or for that matter any of the grouse that appear to inflate their esophagi, use it as a resonating chamber to amplify sound. That seems likely, but direct evidence is required. Gaunt et al. (1982) provide some evidence to support this suggestion from an injured ring dove (*Streptopelia risoria*). The dove was unable to inflate its esophagus and its cooing was notably softer than in normal birds.

Yearling males can occupy territories, exhibit territorial behavior, and sing if a territory is vacant, but they are normally secretive and silent (Bendell *et al.* 1972; Zwickel 1980; Jamieson 1985). Songs of yearling males appear softer and higher in pitch (higher fundamental frequency) than adults (pers. obser.; Zwickel pers. comm.). McNicholl (1978) reported that males that he believed were yearlings hooted softer when non-territorial, but that they increased the volume when they became territorial.

Yearling males were lighter and had shorter wings than adults. Redfield (1973) reported similar weight differences. Because yearlings are smaller, one would expect their vocal sound-producing structures to be smaller than those of adults. However, there were no significant differences between any of the tracheal, bronchial, syringeal, or esophageal measurements of yearlings and adults. Small samples of yearling males may be responsible for this lack of difference. However, a trend is present; adult male syringeal and syringeal membrane measurements were larger than yearlings. This difference, although not significant, could be responsible for the apparent differences in the songs of the two age classes and may be part of the reason why yearlings do not normally take territories.

Adult females are larger than yearlings females. However, all tracheal, bronchial, syringeal, and esophageal measurements, except syrinx length, were equal in the two age classes. There appear to be no basic differences in the sound-producing structures of yearlings and adult females. One would expect this since there does not appear to be any difference in adult and yearling female vocalizations (pers. obser.).

SUMMARY

The sound-producing structures of male and female blue grouse were described and compared. Morphological data suggest that the syrinx in blue grouse likely acts as a pulse generator to produce sound. The size of internal tympaniform membranes and the size of the syrinx appear to be responsible for the differences in the vocalizations of males and females. The relationship that appears to exist is the thicker the internal tympaniform membranes, and the larger the syrinx, the lower the fundamental frequency of the sound produced. Syringeal shapes also differed, but what effect, if any, this variation has on sound production is unknown.

The trachea and bronchi of male and female blue grouse are important components of the respiratory system but appear to have little direct effect on the sounds produced and probably do not have any measurable influence on the sexual differences in vocalizations. Differences that do exist appear related to differences in body size or because of their direct connection to the syrinx.

The esophagus of male blue grouse is capable of inflation and is probably used as a resonating chamber to help amplify song. The esophagus of females appears not to be inflatable.

Yearling male syringes are smaller than adults and this difference may be responsible for the softer, higher pitched hoots of yearlings. The sound-producing structures and vocalizations of yearling and adult females differ little, even though adults are larger.

The results presented here are based principally on morphological examination of the sound-producing structures of dead birds and no experimentation was undertaken. However, this is a necessary first step to gain understanding of vocalization in blue grouse.

TABLE III-1. Numbers of blue grouse collected in 1983 and 1984 by location, age, and sex.

Location	Year	Adult Males	Yearling Males	Adult Females	Yearling Females
		N	N	N	N
Hardwicke Island, B.C.[1]	1983	8	3	9	4
	1984	8	1	8	2
Adam River, B.C.[1]	1983	5	0	1	0
	1984	1	1	0	0
Methow Game Range, WA.[2]	1983	5	1	1	1
	1984	7	0	3	0
Hart's Pass, WA.[3]	1983	1	1	0	0
	1984	5	0	1	0
Oregon[4]	1984	8	1	0	0
Colorado[5]	1984	0	2	4	1
Total		48	10	27	8

[1] *D.o. fuliginosus.*
[2] *D.o. pallidus.*
[3] Presumed *D.o. fuliginosus* x *D.o. pallidus* hybrids.
[4] *D.o. sierrae.*
[5] *D.o. obscurus.*

TABLE III-2. Body weights and wing lengths of adult and yearling male blue grouse.

Characteristic	ADULT MALES $\bar{X} \pm$S.E. (N)	YEARLING MALES $\bar{X} \pm$S.E. (N)	t-value	P-value
Body weight (g)	1213.4±13.5 (41)	1064.3±26.7 (8)	4.54	<0.001
Cubic root body weight ($g^{1/3}$)	10.7±0.1 (41)	10.2±0.1 (8)	4.51	<0.001
Wing length (mm)	217.3±1.0 (42)	211.7±1.8 (9)	2.47	0.011

TABLE III-3. Tracheal, bronchial, and syringeal measurements of adult and yearling male blue grouse (mm).

Measurement[1]	ADULT MALES	YEARLING MALES	t-value	P-value
	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)		
Tracheal length	149.2±4.1 (23)	152.0±10.0 (2)		
Tracheal diameter, anterior	12.0±0.3 (26)	13.0±0.6 (3)	-1.06	0.300
Tracheal diameter, posterior	10.7±0.2 (25)	10.7±0.5 (3)	-0.05	0.963
Bronchial length	11.9±0.5 (24)	12.2±0.1 (3)	-0.60	0.556
Bronchial diameter	8.5±0.3 (25)	8.7±0.4 (3)	-0.16	0.871
Number of bronchial rings	8.8±0.1 (44)	8.5±0.2 (8)	0.94	0.350
Syrinx length	36.1±0.7 (20)	32.8±1.3 (3)	1.74	0.097
Syrinx width	23.2±0.3 (26)	22.4±0.3 (4)	1.16	0.257
Syrinx depth	18.2±0.3 (26)	17.4±0.3 (4)	1.09	0.290
Number of syringeal rings	14.5±0.3 (46)	13.9±0.6 (9)	0.96	0.340

[1] Refer to Figure III-1.

TABLE III-4. Syringeal membrane measurements of adult and yearling male blue grouse (mm).

	ADULT MALES	YEARLING MALES
Thickness of[1]	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)
Internal tympaniform membrane	2.52±0.11 (12)	2.40±0.35 (3)
External tympaniform membrane[2]	0.44±0.07 (7)	0.37±0.09 (3)

[1] Refer to Figure III-3.

[2] It is unclear whether these are true membranes, see text.

TABLE III-5. Esophageal measurements of adult and yearling male blue grouse (mm).

	ADULT MALES	YEARLING MALES		
Measurement[1]	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	t-value	P-value
Esophageal length	213.4±4.0 (23)	202.0±12.2 (4)	1.05	0.302
Length of expanded portion of the pars cervicalis	88.3±2.9 (22)	88.8±4.8 (4)	-0.07	0.947
Esophageal width, anterior	24.1±1.1 (24)	18.5±2.0 (4)	1.89	0.069
Esophageal width at crop	7.2±0.3 (22)	8.5±1.1 (4)	-1.54	0.137

[1] Refer to Figure III-2a.

TABLE III-6. Inflated esophageal measurements of adult and yearling male blue grouse (mm).

	ADULT MALES	YEARLING MALES
Measurement[1]	X̄±S.E. (N)	X̄±S.E. (N)
Pars cervicalis length	86.0±4.7 (14)	111.1±0.0 (1)
Pars cervicalis width	68.0±3.0 (14)	78.2±0.0 (1)
Crop length	71.7±5.1 (12)	96.9±0.0 (1)
Crop width	59.9±3.0 (12)	69.5±0.0 (1)

[1] Refer to Figure III-2b.

TABLE III-7. Body weights and wing lengths of adult and yearling female blue grouse.

Characteristic	ADULT FEMALES	YEARLING FEMALES	t-value	P-value
	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)		
Body weight (g)	952.3±20.3 (23)	798.7±31.0 (7)	3.77	0.001
Cubic root body weight ($g^{1/3}$)	9.8±0.1 (23)	9.3±0.1 (7)	3.73	0.001
Wing length (mm)	198.1±1.5 (25)	195.3±1.7 (9)	1.03	0.311

TABLE III-8. Tracheal, bronchial, and syringeal measurements of adult and yearling female blue grouse (mm).

Measurement[1]	ADULT FEMALES	YEARLING FEMALES	t-value	P-value
	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)		
Tracheal length	129.2±3.9 (8)	129.5±1.5 (2)	-	-
Tracheal diameter, anterior	8.4±0.3 (8)	8.6±0.0 (2)	-	-
Tracheal diameter, posterior	5.9±0.2 (8)	6.0±0.0 (3)	-0.44	0.670
Bronchial length	10.2±0.5 (9)	10.8±1.2 (3)	-0.509	0.567
Bronchial diameter	5.5±0.2 (9)	5.2±0.2 (3)	0.63	0.544
Number of bronchial rings	8.8±0.2 (18)	8.0±0.3 (7)	1.92	0.068
Syrinx length	14.4±0.5 (8)	17.2±1.4 (3)	-2.42	0.038
Syrinx width	10.0±0.4 (10)	9.1±0.3 (3)	1.06	0.312
Syrinx depth	6.4±0.2 (10)	7.0±1.2 (3)	-0.49	0.668
Number of syringeal rings	12.5±0.2 (22)	12.0±0.0 (8)	1.27	0.215

[1] Refer to Figure III-1.

TABLE III-9. Syringeal membrane measurements of adult and yearling female blue grouse (mm).

	ADULT FEMALES	YEARLING FEMALES
Thickness of:[1]	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)
Internal tympaniform membrane	0.54±0.09 (8)	0.30±0.00 (1)
External tympaniform membrane[2]	0.13±0.02 (6)	0.20±0.00 (1)

[1] Refer to Figure III-3.

[2] It is unclear whether these are true membranes, see text.

TABLE III-10. Esophageal measurements of adult and yearling female blue grouse (mm).

Measurement[1]	ADULT FEMALES $\bar{X}$±S.E. (N)	YEARLING FEMALES $\bar{X}$±S.E. (N)
Esophageal length	167.9±10.5 (11)	148.0±0.0 (1)
Esophageal width, anterior	11.7±0.9 (9)	10.9±0.0 (1)
Esophageal width at crop	6.8±0.4 (8)	7.1±0.0 (1)

[1] Refer to Figure III-2a.

TABLE III-11. Inflated esophageal measurements of adult and yearling female blue grouse (mm).

	ADULT FEMALES	YEARLING FEMALES
Measurement[1]	X̄±S.E. (N)	X̄±S.E. (N)
Pars cervicalis length	66.9±7.5 (4)	32.0±0.0 (1)
Pars cervicalis width	15.9±1.5 (6)	13.1±0.0 (1)
Crop length	68.8±4.2 (6)	96.5±0.0 (1)
Crop width	56.6±3.1 (6)	68.2±0.0 (1)

[1] Refer to Figure III-2b.

TABLE III-12. Body weights, wing lengths, and heart weights of adult male and female blue grouse.

Characteristic	ADULT MALES	ADULT FEMALES	S.I.[1]	t-value	P-value
	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	(%)		
Body weight (g)	1213.4±13.5 (41)	952.3±20.4 (23)	78.5	11.05	<0.001
Cubic root body weight ($g^{1/3}$)	10.7±0.1 (41)	9.8±0.1 (23)	91.6	10.98	<0.001
Wing length (mm)	217.3±1.0 (42)	198.1±1.5 (25)	91.2	11.17	<0.001
Heart weight (g)	5.5±0.2 (35)	4.4±0.3 (16)	80.0	3.57	0.001
Cubic root heart weight ($g^{1/3}$)	1.8±0.02 (35)	1.6±0.04 (16)	88.9	3.79	<0.001

[1] Similarity Index: Size of females relative to that of males.

TABLE III-13. Tracheal, bronchial, and syringeal measurements of adult male and female blue grouse (mm).

Measurement[1]	ADULT MALES	ADULT FEMALES	S.I.[2]		
	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	(%)	t-value	P-value
Tracheal length	149.2±4.1 (23)	129.2±3.9 (8)	86.6	2.72	0.011
Tracheal diameter, anterior	12.3±0.3 (26)	8.4±0.3 (8)	68.3	6.15	<0.001
Tracheal diameter, posterior	10.7±0.2 (25)	5.9±0.2 (8)	55.1	17.2	<0.001
Bronchial length	11.9±0.5 (24)	10.2±0.5 (9)	85.7	1.96	0.060
Bronchial diameter	8.5±0.3 (25)	5.5±0.2 (9)	64.7	8.70	<0.001
Number of bronchial rings	8.8±0.1 (44)	8.8±0.2 (18)	-	0.16	0.888
Syrinx length	36.1±0.7 (20)	14.4±0.5 (8)	39.9	24.51	<0.001
Syrinx width	23.2±0.3 (26)	10.0±0.4 (10)	43.1	25.59	<0.001
Syrinx depth	18.2±0.3 (26)	6.4±0.2 (10)	35.2	31.56	<0.001
Number of syringeal rings	14.5±0.3 (46)	12.5±0.2 (22)	-	5.73	<0.001

[1] Refer to Figure III-1.

[2] Similarity Index: Size of females relative to that of males.

TABLE III-14. Syringeal membrane measurements of adult male and female blue grouse (mm).

Thickness of:[1]	ADULT MALES	ADULT FEMALES	S.I.[2] (%)	t-value	P-value
	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)			
Internal tympaniform membrane	2.52±0.12 (12)	0.54±0.09 (8)	21.4	12.96	<0.001
External tympaniform membrane[3]	0.44±0.07 (7)	0.13±0.02 (6)	29.6	4.53	0.003

[1] Refer to Figure III-3.
[2] Similarity Index: Size of females relative to that of males.
[3] It is unclear whether these are true membranes, see text.

TABLE III-15. Esophageal measurements of adult male and female blue grouse (mm).

	ADULT MALES	ADULT FEMALES			
Measurement[1]	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	S.I.[2] (%)	t-value	P-value
Esophageal length	213.4±4.0 (23)	167.9±10.5 (11)	78.7	4.06	0.001
Esophageal width, anterior	24.1±1.1 (24)	11.8±0.9 (9)	49.0	8.58	<0.001
Esophageal width at crop	7.2±0.3 (22)	6.8±0.4 (8)	94.4	0.87	0.394

[1] Refer to Figure III-2a.
[2] Similarity Index: Size of females relative to that of males.

TABLE III-16. Inflated esophageal measurements of adult male and female blue grouse (mm).

Measurement[1]	ADULT MALES	ADULT FEMALES	S.I.[2] (%)	t-value	P-value
	$\bar{X} \pm$ S.E. (N)	$\bar{X} \pm$ S.E. (N)			
Pars cervicalis length	86.0±4.7 (14)	66.9±7.5 (4)	77.8	1.96	0.068
Pars cervicalis width	68.0±3.0 (14)	15.9±1.5 (6)	23.4	15.39	<0.001
Crop length	71.7±5.2 (12)	68.8±4.2 (6)	96.0	0.36	0.726
Crop width	59.9±3.0 (12)	56.6±3.1 (6)	94.5	0.70	0.496

[1] Refer to Figure III-2b.
[2] Similarity Index: Size of females relative to that of males.

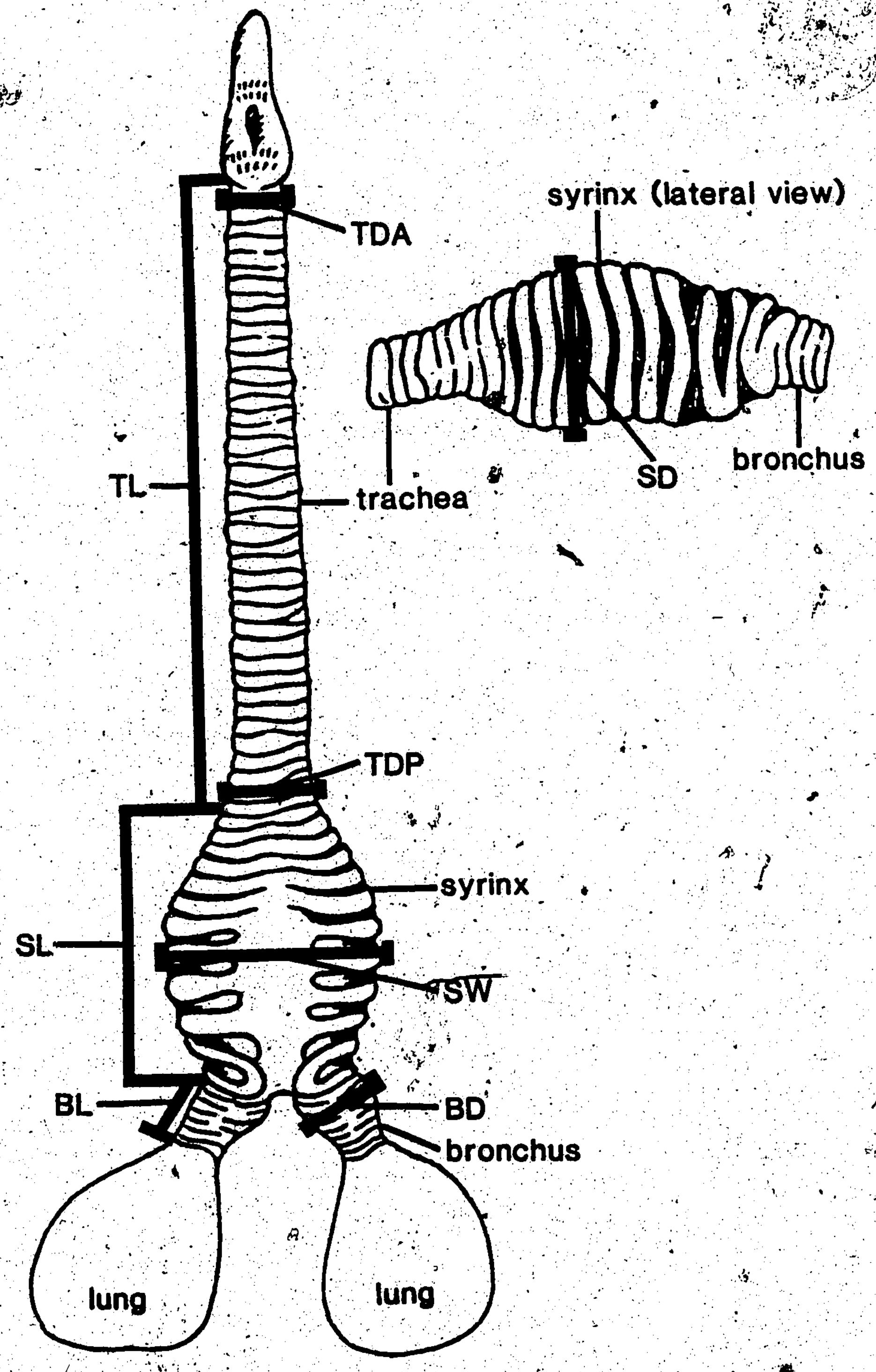

FIGURE III-1. Male blue grouse respiratory tract showing where measurements were taken. BD - bronchus diameter, BL - bronchus length, SD - syrinx depth, SL - syrinx length, SW - syrinx width, TDA - trachea diameter, anterior, TDP - trachea diameter, posterior, TL - trachea length.

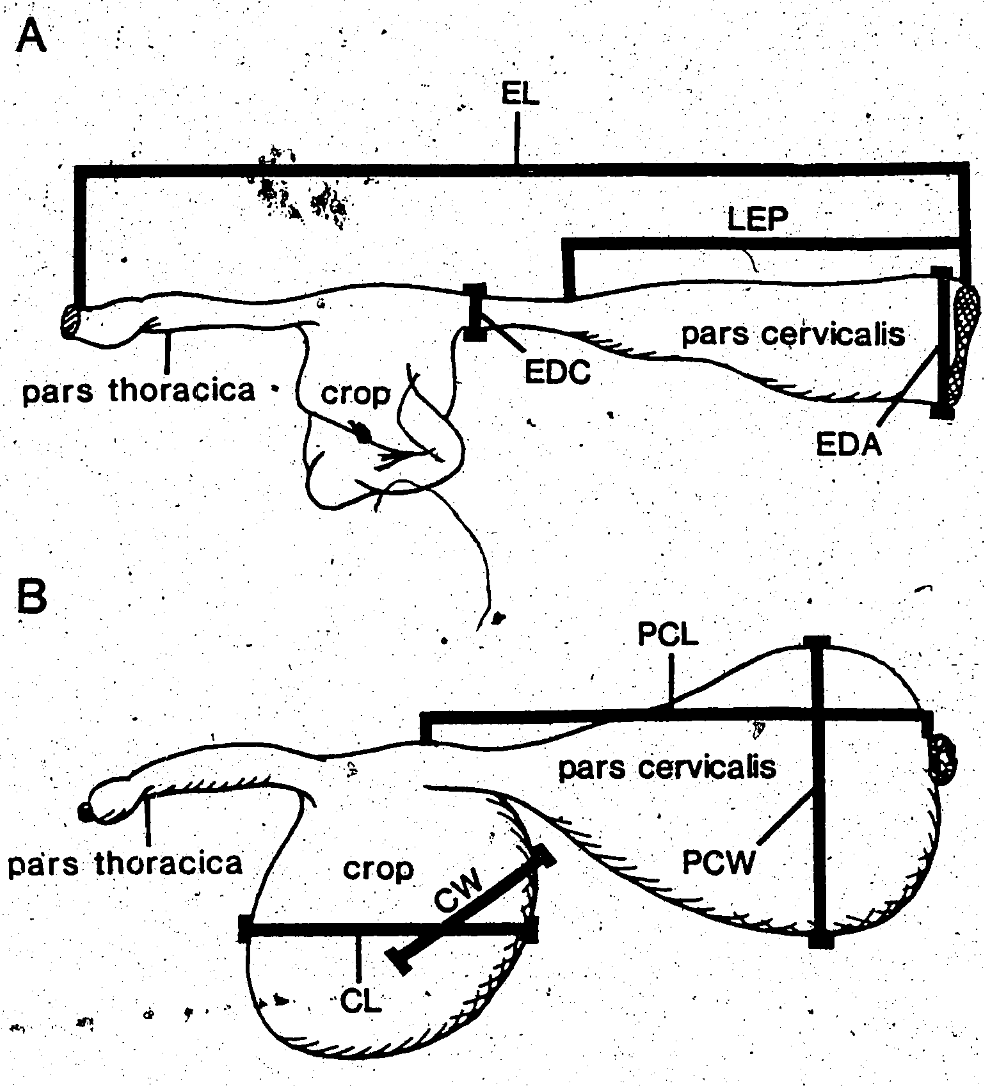

FIGURE III-2. Male blue grouse esophagus and crop showing where measurements were taken: A) natural, B) inflated. CL - crop length, CW - crop width, EDA - esophagus diameter, anterior, EDC - esophagus diameter at crop, EL - esophagus length, LEP - length of expanded portion of pars cervicalis, PCL - pars cervicalis length, PCW - pars cervicalis width.

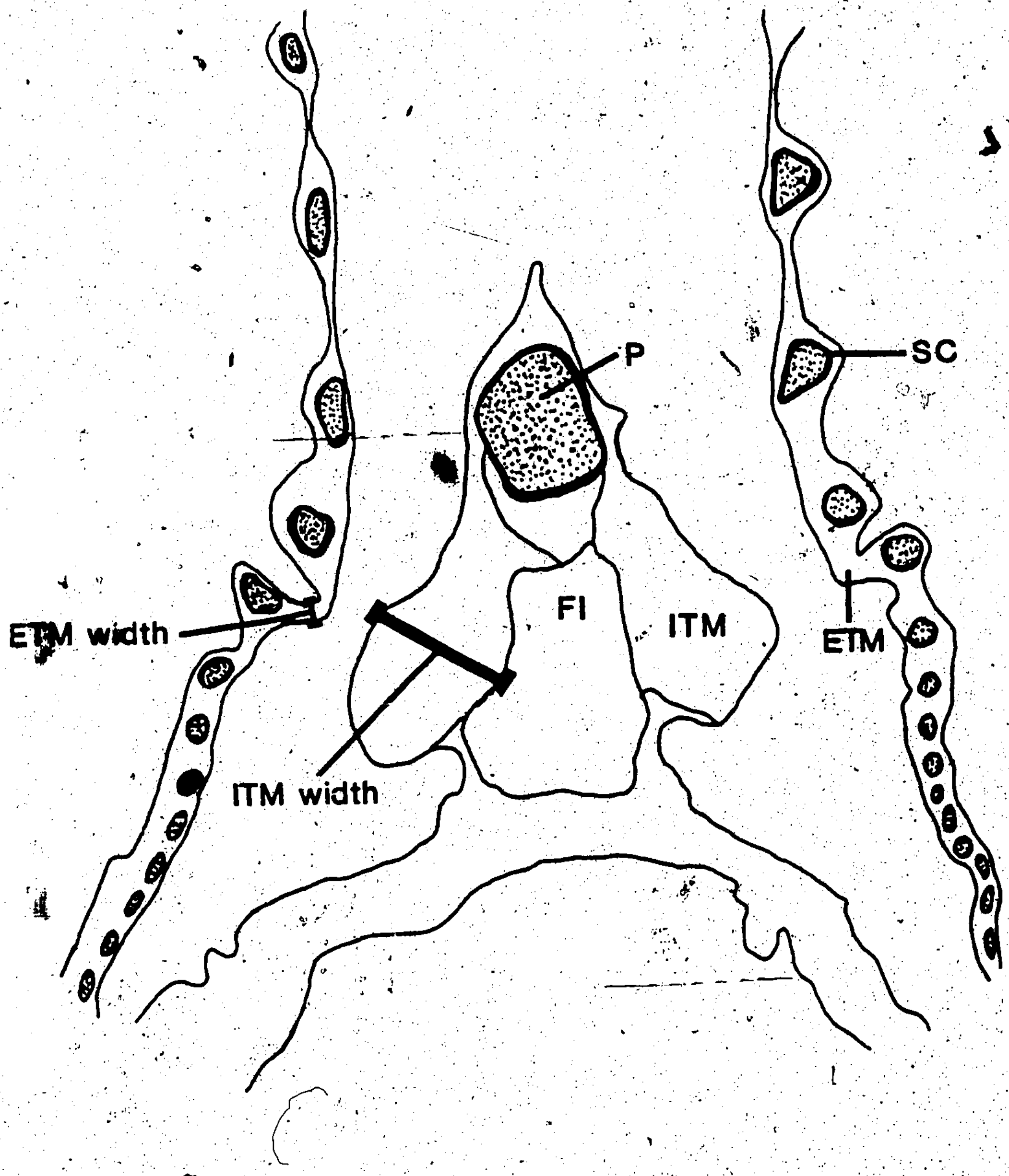

FIGURE III-3. Frontal section of an adult male blue grouse syrinx showing where measurements were taken. ETM - external tympaniform membrane, FI - foramen interbronchiale, ITM - internal tympaniform membrane, P - pessulus, SC - syringeal cartilage.

FIGURE III-4. Male blue grouse respiratory system *in situ*. Br - bronchus, C - crop, E - esophagus, MST - M. sternotrachealis, MTL - M. tracheolateralis, S - syrinx, T - trachea.

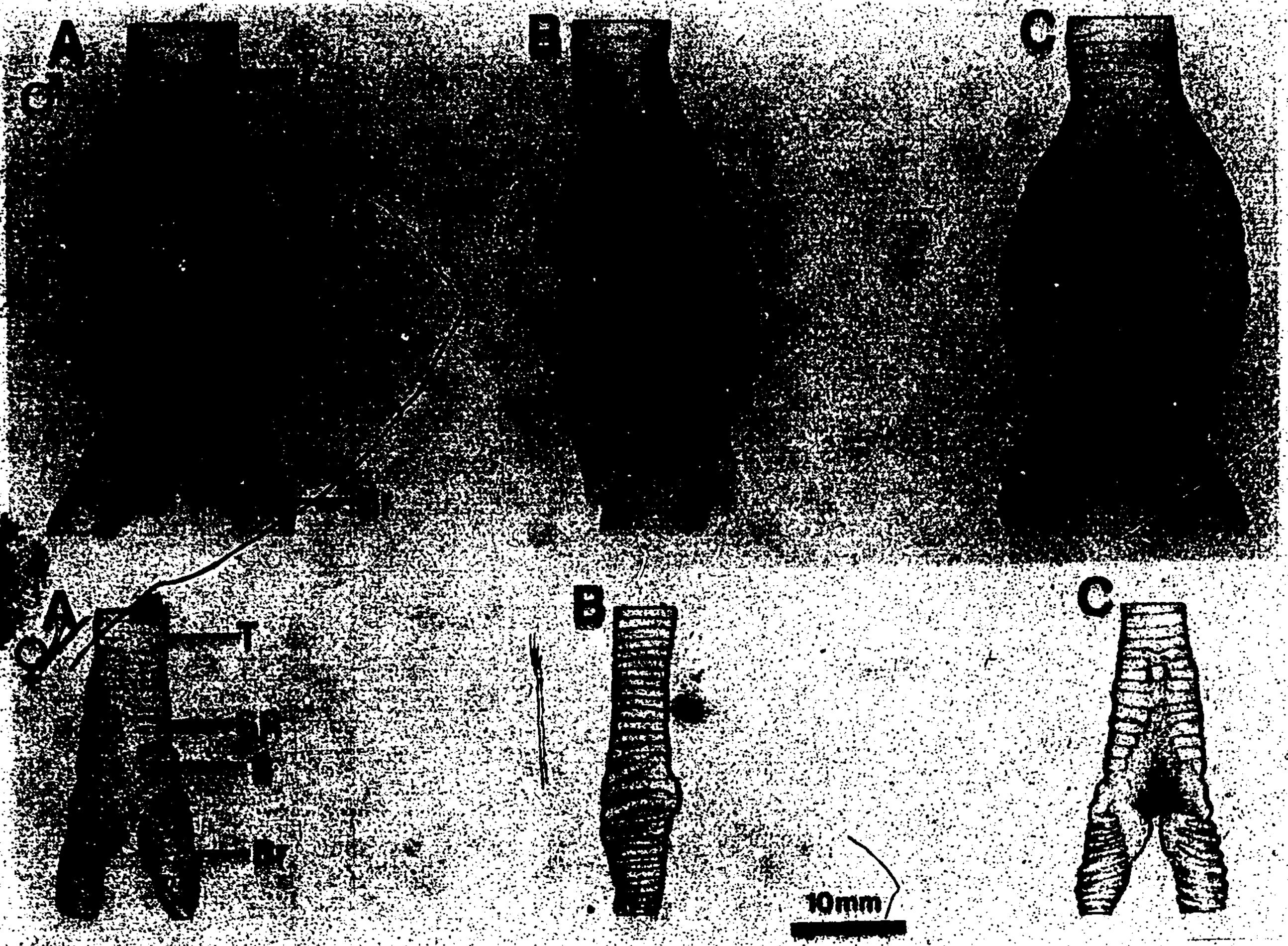

FIGURE III-5. Male and female blue grouse syringes: A) ventral view, B) lateral view, C) dorsal view. Br - bronchus, S - syrinx, SR - syringeal ring, T - trachea.

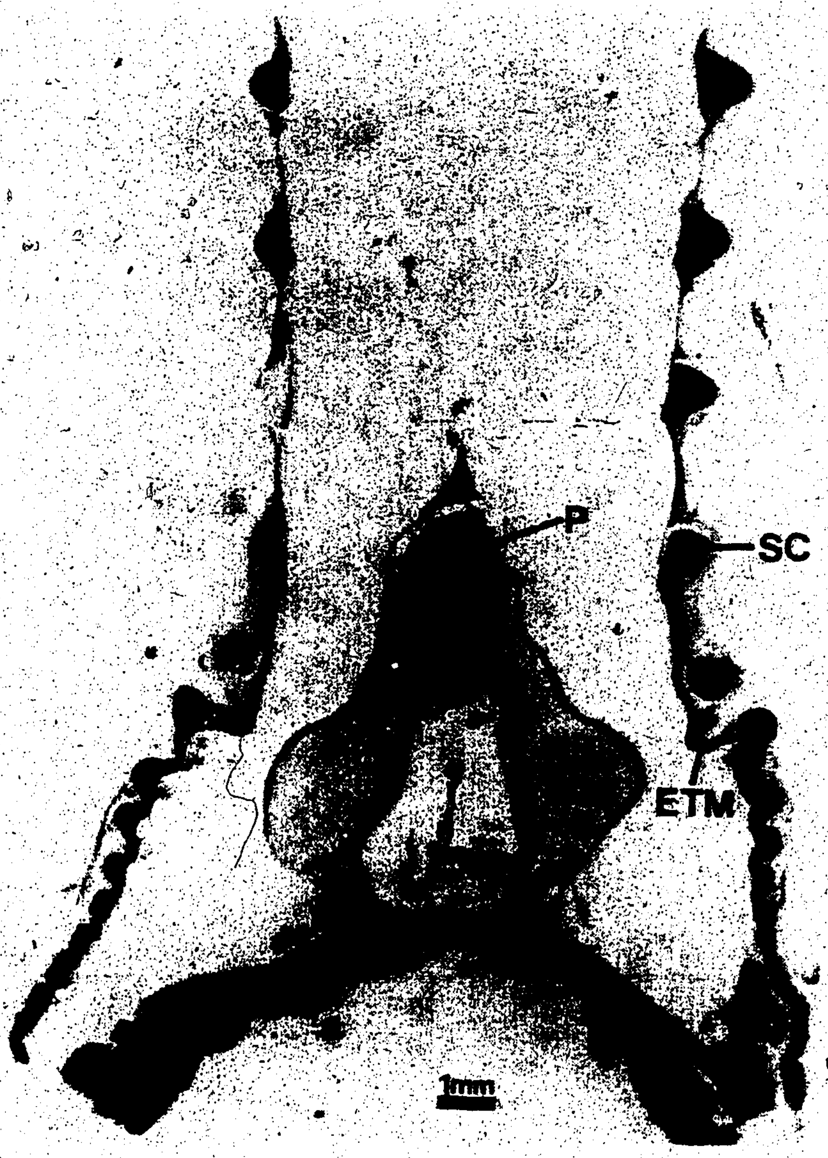

FIGURE III-6. Frontal section of male blue grouse syrinx. ETM - external tympaniform membrane, ITM - internal tympaniform membrane, P - pessulus, SC - syringeal cartilage.

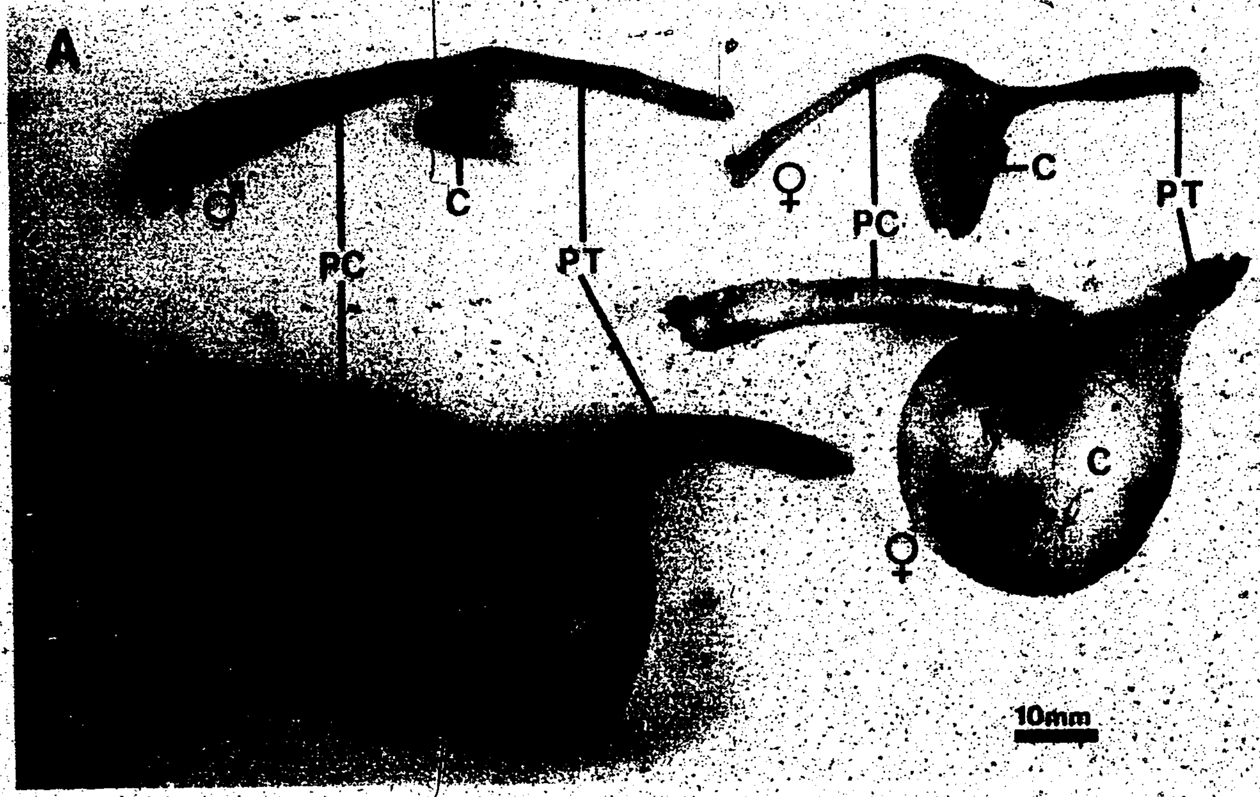

FIGURE III-7. Male and female blue grouse esophagi: A) natural, B) inflated. C - crop, PC - pars cervicalis, PT - pars thoracica.

FIGURE III-8. Female blue grouse respiratory system *in situ*. Br - bronchus, C - crop, E - esophagus, MST - M. sternotrachealis, MTL - M. tracheolateralis, S - syrinx, T - trachea.

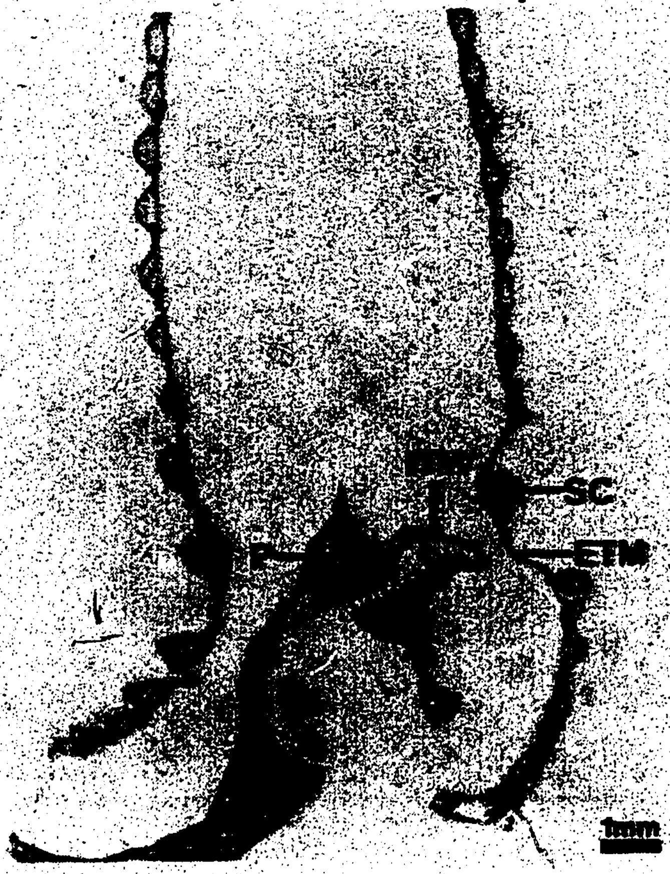

FIGURE III-9. Frontal section of female blue grouse syrinx. ETM - external tympaniform membrane, ITM - internal tympaniform membrane, P - pessulus, SC - syringeal cartilage.

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IV. SUBSPECIFIC VARIATION IN VOCAL SOUND-PRODUCING STRUCTURES IN ADULT MALE BLUE GROUSE

INTRODUCTION

Geographic variation in bird songs is common (Krebs and Kroodsma 1980; Mundinger 1982; Shy 1984; Baker and Thompson 1985). Several explanations for variation within a species' song have been proposed, such as environmental (Hunter and Krebs 1979; Krebs and Kroodsma 1980; Shy 1983), cultural (Mundinger 1982) and biological differences (Baker 1982; Mundinger 1982). Ecological factors include the influence of sound transmission/attenuation properties of different habitats and background noise (Krebs and Kroodsma 1980). Cultural differences refer to learning processes and population dialects. Genetic and morphological variations are responsible for biological differences (Mundinger 1982). Little has been reported on possible differences in the syrinx and associated structures that may be responsible for variation in song within a species.

Blue grouse (*Dendragapus obscurus*) occupy most of the mountainous regions of western North America. The eight recognized subspecies can be grouped into coastal and interior types, with 4 subspecies in each (Johnsgard 1983; Bendell and Zwickel 1984) (Appendix 1). The separation of these two groups and the eight subspecies is based on differences in plumage coloration, external morphology, song, and behavior; primarily in males.

The song of male blue grouse, called a hoot, is reported to have both a sexual and territorial function (McNicholl 1978). It is one of the most striking behavioral differences between coastal and interior males: loud and usually 6 notes/hoot in coastal birds; and soft and usually 5 notes/hoot in interior birds (Bailey and Niedrach 1965; Hjorth 1970; Bendell and Zwickel 1984; Degner 1988a). The hoots of both groups are low frequency sounds, with those of interior males (100-110 Hz) lower than those of coastal males (115-170 Hz) (Degner 1988a). The whoot (Stirling and Bendell 1970), a single or double note precopulatory call of males, is also of low frequency (approx. 200 Hz). Whoots of coastal and interior males are more similar than the hoot; both are as loud or louder than coastal-type hoots (Hjorth 1970; Stirling and Bendell 1970; Degner 1988a).

The syrinx is the major organ responsible for vocal sound production in blue grouse (Degner 1988b). The esophagus, inflated during hooting, appears to act as a resonating chamber for sounds produced by the syrinx (Hjorth 1970; Johnsgard 1983; Degner 1988b). Syringeal morphology appears to be responsible for differences in sounds produced by male and female blue grouse, and perhaps, for differences between the songs of yearling and adult males (Degner 1988b). It appears that the larger the syrinx and the thicker the syringeal membranes, the lower the sound frequency (Degner 1988b).

The objective of this paper is to determine if there are subspecific differences in the vocal sound-producing structures of male blue grouse that may explain differences in their songs. Subspecific variation in song might influence territoriality and spacing, which may determine the number of [illegible] that breed (Lewis and Zwickel 1980).

STUDY AREAS

Adult male blue grouse were collected in the springs and summers of 1983 and 1984 from six locations within the ranges of three of the eight recognized subspecies (Johnsgard 1983). Hardwicke Island, B.C. (50° 27′ N, 125° 50′ W) and the nearby lower Adam River area on Vancouver Island, B.C. (50° 27′ N, 126° 10′ W) served as collection sites for one coastal subspecies, *D.o. fuliginosus* (DOF) (Appendix 3). Males of another coastal subspecies, *D.o. sierrae* (DOS), were collected at two sites in southern Oregon; about 24 km north of Klamath Falls in the Winema National Forest (42° 26′ N, 121° 45′ W) and in an area of the Fremont National Forest, approximately

23 km north of Lakeview (42° 23′ N, 120° 22′ W) (Appendix 2).

Males of *D.o. pallidus* (DOP), an interior subspecies, were collected on the Methow Game Range, WA. (48° 31′ N, 120° 4′ W) (Appendix 2). The two subspecies *D.o. fuliginosus* and *D.o. pallidus* (DOFxDOP) appear to overlap in the Hart's Pass, WA. area (48° 42′ N, 120° 39′ W), approximately 50 km northwest of the Methow Game Range in the Cascade mountains (Appendix 2). Males there appear to show morphological and behaviorial traits of both subspecies.

MATERIALS AND METHODS

A total of 48 adult male blue grouse were collected for comparison of sound-producing structures (Table IV-1). Collected males were either necropsied fresh in the field or embalmed for later dissection. Respiratory tracts and esophagi of freshly necropsied males were measured and then preserved in Bouin's fixative or 10% formalin. Embalmed males, some whole and others skinned and partially dissected, were injected with, and then immersed in, embalming fluid. Embalmed birds were dissected in the laboratory, and where possible, measurements made on freshly necropsied males were made *in situ* on embalmed birds. All measurements (Figures IV-1 and IV-2), except tracheal and esophageal lengths were taken with dial calipers. Tracheal and esophageal lengths were measured with a ruler. Some structures were damaged during collection and dissection, resulting in some variation in sample sizes among measurements.

Preserved structures from previously necropsied males were re-measured in the laboratory to determine the effects of preservatives on measurements. Preservation appears to cause shrinking (Degner 1988b). Therefore, except where noted, fresh tracheal, bronchial, syringeal, and esophageal measurements were used for analyses. Only measurements from the right side of the bronchi are given. Data on numbers of syringeal and bronchial rings are from preserved structures. Preservation does not affect the number of these rings and they are most accurately counted in the laboratory under a microscope.

Esophagi with crops intact from 15 freshly dissected males were tied off at the cephalad end and inflated by blowing air through a straw inserted in the caudal end. Measurements were made of the esophagi and crops before and after inflation (Figure IV-2).

Frontal histological sections (7 um) were made from 13 syringes and stained with Masson's Trichrome stain for examination of internal syringeal structures. Measurements of the tympaniform membranes (Figure IV-3) were made with a micrometer equipped compound microscope. Membrane thicknesses from the right side of the syrinx are give[illegible]

Body weights and wing lengths (unflattened wing chord) were taken from most males collected to give an index of body size. Males collected in 1981 and 1982 at the Methow Game Range (N=4), Hart's Pass (N=3), and Winema National Forest (N=2) were included in these analyses to increase sample sizes. Fresh heart weights, an independent internal organ, also were recorded as an index to body size presumed not to be associated with sound production.

SPSS^X (SPSS^X Inc. 1983) and TONESTATS (Dept. of Zoology, University of Alberta) statistical packages were used for statistical analyses. Differences were considered significant at the five percent level. Means are reported ±1 S.E.

RESULTS

There were no differences among tracheal lengths of the four groups of birds (DOF, DOP, DOS, and DOFxDOP)(ANOVA, F=2.128, P=0.130)(Table IV-2). Anterior and posterior tracheal diameters were not significantly different among subspecies (ANOVA, F=0.965, P=0.427 and F=0.342, P=0.795, respectively)(Table IV-2). There were no significant differences in bronchial lengths (ANOVA, F=1.238, P=0.322), bronchial diameters (ANOVA, F=1.612, P=0.217), or numbers of bronchial rings (ANOVA, F=0.063, P=0.979) among the groups (Table IV-2). Mean number of bronchial rings were remarkably constant among groups, between eight and nine rings per bronchi. Thus the trachea and bronchi do not vary greatly and are likely not responsible for subspecific differences in the songs.

DOF males were collected from April 22 to August 8 when the 1983 and 1984 data are combined. Males from the other subspecies were collected over a much shorter time; DOS from May 12-15, DOP from April 14 to May 4, and DOFxDOP from May 8-24. Because DOF males were collected over a much longer time period than the other groups and some were collected outside the prime hooting period, I examined them to see if there is seasonal variation in syrinx size. The relationships between time of year and preserved syrinx length, syrinx width, and syrinx depth of DOF males were examined with simple linear regressions (Figure IV-4). Preserved measurements were used because of larger sample sizes covering a greater time period. The slopes of syrinx length (-0.0254)(ANOVA, F=3.183, P=0.090), syrinx width (-0.0054)(ANOVA, F=0.178, P=0.678), and syrinx depth (0.0098)(ANOVA, F=1.212, P=0.289) were not different from 0 (Figure IV-4), suggesting no seasonal changes in these measurements.

The syrinx showed small but significant variation among subspecies (Table IV-3, Figure IV-5). Syrinx length (ANOVA, F=8.957, P=0.001), syrinx width (ANOVA, F=4.192, P=0.017), and number of syringeal rings (ANOVA, F=40.983, P=0.001) were all significantly different among the four groups. Only syrinx depth did not differ (ANOVA, F=1.236, P=0.321). Pairwise comparisons (Scheffe tests) show that DOF syringes were responsible for most differences that were found (Table IV-3). Syringeal shapes also differed among subspecies, but I was unable to quantify these differences.

The syringeal data do not reveal a clear size pattern among groups, but do show some trends. Syringes of DOF males were smallest. DOS males, another coastal subspecies, had the second smallest syringeal length and width. However, size differences between DOS and DOP syringes were not significantly different and were less than between DOS and DOF. DOP and DOFxDOP males were very similar in size (Table. IV-3).

A mainly qualitative evaluation of connective tissue thickness between syringeal rings was made. Connective tissue between syringeal rings differed among the groups. DOF syringes were "fleshy", and the connective tissue between rings was up to 1 mm thick and contained a considerable amount of fat. The connective tissue was so thick in many cases that the syringeal rings could not be counted without removing it. In contrast, connective tissue between the syringeal rings of DOP males was thin, almost transparent and contained little or no fat. DOS males had syringes similar to those of DOF, but with slightly less connective tissue. The syringes of DOFxDOP males appear to be intermediate between DOF and DOP in this respect.

Table IV-4 shows the mean thicknesses of the syringeal membranes, the internal and external tympaniform membranes (although see Degner (1988b) as there is some question as to whether external tympaniform membranes exist in blue grouse). Although membranes vary considerably in thickness among groups, these differences may be because of small sample sizes and tissue deformation from sectioning. Because of small sample sizes, only internal tympaniform membranes of DOF and DOP were compared statistically. They were not different (t-test, t=-1.134, DF=7, P=0.766).

Male blue grouse appear to inflate their esophagus, using it as a sound-resonating chamber (Degner 1988b). The esophagus consists of two parts, the pars cervicalis and pars thoracica, separated by the crop. Esophageal measurements (Table IV-5) showed no differences in total length (ANOVA, F=1.096, P=0.375), length of the expanded portion of the pars cervicalis (ANOVA, F=0.716, P=0.555), anterior width (ANOVA, F=0.6319, P=0.603), and width at the crop (ANOVA, F=3.047, P=0.055) among the four subspecies. There is no clear subspecific pattern evident from these data.

Fifteen adult male esophagi were inflated and the anterior end of the esophagus of the males from all four groups were greatly enlarged (Table IV-6). There appears to be no relationship between the width of the anterior end of the esophagus before inflation and the width of the inflated area (Tables IV-5 and IV-6). Because of small sample sizes no statistical comparisons were made among subspecies and as with other esophageal measurements no pattern can be seen in the inflated esophageal measurements.

Body weight and wing length were recorded from adult males for use as indexes of body size (Table IV-7) to see if variation in size of sound-producing structures was a result of differences in body size. Body weight (ANOVA, F=6.631, P=0.001) and the cubic root of body weight (the linear equivalent of body weight) (ANOVA, F=6.443, P=0.001) varied significantly among the four groups. Wing length (ANOVA, F=2.633, P=0.06) did not differ. No clear body size pattern among groups can be seen (Table IV-7). Body size does not appear to be responsible for syringeal size differences; DOF males were heaviest, but had the smallest wings and syringes.

Heart weight was recorded as an index to size of internal structural differences among groups. Among internal organs, heart weight probably varies the least (Degner 1988b). Neither heart weight (ANOVA, F=0.819, P=0.493), nor its cubic root (ANOVA, F=0.760, P=0.525) differed among subspecies (Table IV-7). This suggests little variation in this structure of male blue grouse.

DISCUSSION

There were no differences in tracheal or bronchial lengths or diameters of males among subspecies and it is unlikely that tracheal modulation occurs in blue grouse (Degner 1988b). Thus, neither the trachea nor bronchi appear to directly influence subspecific variation in songs. They are, however, an integral part of the sound production system in birds and may have subtle effects that have not been detected.

Song is considered a secondary sex character that is influenced by hormones (Welty 1979). Hormonal changes affecting song may be acting on the vocal sound-producing structures. The syrinx of male blue grouse could possibly change in size seasonally as a result of hormonal changes similar to those described by Hannon et al. (1979) for testes. Available data from one subspecies (DOF), however, indicate no change in syrinx length, syrinx width, or syrinx depth of males collected from April 22 to August 8. However, syrinx length shows a possible decreasing trend over time. Larger samples of males collected over a longer time period are needed to fully test this hypothesis.

The size of adult male syringes differed significantly among subspecies, with those of DOF males smaller than those of DOP, DOS, and DOFxDOP males. There were significant size differences between those of the two coastal subspecies (DOF and DOS), but those of coastal DOS were not different from those of interior DOP. DOFxDOP males, which are likely hybrids of coastal and interior birds, have syringes similar in size to those of DOP.

Both coastal subspecies, DOF (140-150 Hz) and DOS (130-140 Hz), have louder hoots, with a higher fundamental frequency than interior (DOP) males (100-110 Hz). DOFxDOP males have what appears to be an intermediate, but more variable song in terms of fundamental frequency (120-135 Hz), loudness, and number of notes (Degner 1988a).

A general relationship appears to exist among subspecies; the larger the syrinx the lower the fundamental frequency. Coastal DOF males have the smallest syrinx and the highest frequency song. Interior DOP males have the largest syrinx and the lowest frequency hoot. The other coastal subspecies, DOS, has the second smallest syrinx, and it is closer in size to DOP than to DOF syringes. The frequency of DOS songs is the second highest among subspecies, intermediate to those of DOF and DOP songs. DOFxDOP syringes are intermediate in size between DOF and DOP, but most similar to those of DOP. The frequency of the hoots reflects this larger size by being lower in frequency than that of DOF, but only slightly higher than that of DOP.

It appears from the above results that syrinx size may be responsible for differences in the songs of the different subspecies of blue grouse. However, sonagraphic analyses of a small number of whoots, the precopulatory call of males, does not indicate a similar relationship to syrinx size. Whoots of two DOP males and three DOF males were both higher in fundamental frequency than the hoots of their subspecies, and the whoots of DOP males (220-240 Hz) were higher than those of DOF males (170-200 Hz) (Degner 1988a). This is opposite to the proposed relationship: the larger the syrinx, the lower the fundamental frequency. The reason for this reversal is not known, but more recordings of whoots from these two subspecies and other subspecies are needed before any conclusions should be drawn. Differences in neural control of syringeal membranes and syrinx shape are two potential elements that may be involved.

No direct evidence is available to test the syrinx size/fundamental frequency relationship, but indirect evidence is available. First, body weights were significantly different among the four groups, showing a 10% difference. Wing length did not differ. DOF males are heaviest and have the smallest syringes. Therefore, differences in syrinx size are most likely not a result of body size differences, but due to other selective pressures. Further support for this hypothesis is that tracheal, bronchial, most esophageal measurements, and heart weights did not differ among the four groups. However, syringeal measurements, with the exception of syrinx depth, did differ. These data suggest that differences in syrinx size are a result of selection for sound production.

A second set of supporting evidence for this relationship comes from the comparison of male and fema[illegible]ngeal structure. Adult female blue grouse are approximately 75-80% the s[illegible]ult males, but female syringes are less than 45% the size of males (Degner 1988b). Female vocalizations are generally higher in fundamental frequency than those of males (Stirling and Bendell 1970; Hjorth 1970; Albright 1985). The fact that the syrinx is smaller in females and they produce, on average, higher frequency vocalizations than males, is more support for the relationship proposed above between syrinx size and the frequency of the sounds produced.

The tympaniform membranes, located along the walls of the syrinx, vibrate to produce sound (Greenewalt 1968; Brackenbury 1982; Gaunt and Gaunt 1985). The thicker the tympaniform membrane, the slower it vibrates, producing lower frequency sounds (Miller 1947; Sutherland and McChesney 1965; Johnsgard 1983; Gaunt and Gaunt 1985). Morphological data suggest that the internal tympaniform membranes are the vibrating sound-producing membranes in blue grouse (Degner 1988b).

Because of the small number of sectioned syringes of male blue grouse only DOF and DOP internal tympaniform membranes were compared. There was no significant difference between these groups. No relationship can be seen between membrane thickness, syrinx size and the sound frequency produced (i.e., the thicker the internal tympaniform membranes, the larger the syrinx, the lower the frequency of sound produced). However, at this time the possibility of such a relationship should not be ruled out as it does exist between adult male and female blue grouse (Degner 1988b). With larger sample sizes the pattern may become more clear.

Coastal males have "fleshy" syringes with a thick layer of connective tissue between the syringeal rings, although those of DOS males appear to have slightly less than those of DOF males. Interior males have a thin, almost transparent layer of connective tissue between the rings. Syringeal connective tissue thickness of DOFxDOP syringes appears to be intermediate between DOF and DOP syringes. Differences in connective tissue thickness between the syringeal rings showed consistent subspecific variation and a possible relationship exists; the more connective tissue that is present between the syringeal rings the higher the frequency of sound produced. Possible reasons for this relationship are unknown at this time and more research into the possible effects that connective tissue has on sound production is needed.

Coastal male blue grouse sing louder than interior males (Brooks 1926; Bailey and Niedrach 1965; Hjorth 1970; Johnsgard 1983; Bendell and Zwickel 1984). Coastal males can be heard for several hundred meters, interior males for only about 100 m. To further complicate matters DOFxDOP males appear to have mixed song types. Here, some males have songs that approach the loudness of coastal birds, others have soft, interior type songs, and others have what could be considered intermediate type hoots (pers. obs.; Zwickel pers. comm.). Small variation in syringeal anatomy (both size and shape), as seen among the subspecies, is likely not responsible for this difference, as it is the amount of air and the force of its flow that primarily determines loudness (Gaunt and Gaunt 1985).

The esophagi of adult males from all four subspecies of blue grouse examined were expandable, but because of small sample sizes no statistical comparisons of these data were made. No clear patterns could be seen in these data. That does not mean none exists, only that larger samples are needed. If the esophagi of subspecies differ they could have some influence on the observed variations in songs.

Cervical apteria are areas of bare skin between the dorsal and ventral cervical feather tracts on each side of the neck (Hjorth 1970). They are highly developed secondary sex characters and are used in display and courtship by males (Hjorth 1970; McNicholl 1978). The cervical apteria show subspecific variation: yellowish in color, deeply corrugated, and with large amounts of fat in coastal males; and reddish in color, lightly corrugated, and almost fat-free in interior males (Degner unpubl. data). Cervical apteria may influence esophageal resonance, thus subspecific differences in the cervical apteria could contribute in some way to subspecific variation in the songs. However, until more is known about the role of cervical apteria on sound production little can be said about its effect.

SUMMARY

Variation in the vocal sound-producing structures of adult male blue grouse were examined from four geographic areas containing three of the eight recognized subspecies and from an area that appears to contain hybrids of two of the three subspecies.

The trachea and bronchi of male blue grouse appear to have little direct affect on the sounds produced, and probably do not have any measurable influence on the subspecific differences in vocalization. Male blue grouse appear to inflate their esophagus and use it as a resonating chamber, but there is no evidence of subspecific variation in the esophagi or esophageal resonance. However, the cervical apteria may influence the resonance properties of the esophagus, and more research is needed on the role of the cervical apteria.

Size of the syrinx may be responsible for subspecific differences in the songs of males. Apparently the larger the syrinx, the lower the fundamental frequency of the sound produced. Another relationship also may influence subspecific song variation; the more connective tissue between the syringeal rings, the higher the frequency of sound produced. However, this relationship is speculative.

TABLE IV-1. Location, subspecies, and numbers of adult male blue grouse collected in 1983 and 1984.

Location	Subspecies	Year	Number
Hardwicke Island, B.C.	*D.o. fuliginosus*	1983	8
		1984	8
Adam River, B.C.	*D.o. fuliginosus*	1983	5
		1984	1
Methow Game Range, WA.	*D.o. pallidus*	1983	5
		1984	7
Hart's Pass, WA.	*D.o. fuliginosus* x	1983	1
	D.o. pallidus	1984	5
Winema National Forest, OR.	*D.o. sierrae*	1984	4
Fremont National Forest, OR.	*D.o. sierrae*	1984	4
Total			48

TABLE IV-2. Tracheal and bronchial measurements of adult male blue grouse (mm).

	DOF[1]	DOP[2]	DOFxDOP[3]	DOS[4]
Measurement[5]	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)
Tracheal length	157.2±7.3 (8)	156.1±5.4 (6)	140.0±7.4 (4)	135.2±9.4 (5)
Tracheal diameter, anterior	11.9±0.6 (11)	11.3±0.7 (6)	13.1±0.5 (4)	12.2±0.3 (5)
Tracheal diameter, posterior	10.9±0.2 (10)	10.7±0.4 (6)	10.6±0.3 (4)	10.5±0.3 (5)
Bronchial length	12.5±0.6 (10)	13.0±1.9 (5)	10.9±0.6 (8)	10.6±0.7 (5)
Bronchial diameter	8.5±0.3 (10)	9.4±1.0 (6)	8.4±0.4 (4)	7.7±0.3 (5)
Number of bronchial rings	8.8±0.3 (18)	8.8±0.2 (12)	8.7±0.2 (6)	8.9±0.4 (8)

[1] *D.o. fuliginosus.*
[2] *D.o. pallidus.*
[3] Presumed *D.o. fuliginosus* x *D.o pallidus* hybrids.
[4] *D.o. sierrae.*
[5] Refer to Figure IV-1.

TABLE IV-3. Syringeal measurements of adult male blue grouse (mm). Lines join pairs that were significantly different (Scheffe tests, $P<0.05$).

Measurement[5]	DOF[1]	DOP[2]	DOFxDOP[3]	DOS[4]
	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)
Syrinx length	32.8±0.9 (7)	38.1±1.1 (5)	38.7±1.3 (3)	37.3±0.5 (5)
Syrinx width	22.6±0.4 (11)	24.7±0.6 (6)	23.0±0.4 (4)	22.8±0.5 (5)
Syrinx depth	17.6±0.3 (11)	18.3±0.5 (6)	18.3±0.3 (4)	19.1±1.3 (5)
Number of syringeal rings	12.8±0.3 (20)	16.0±0.0 (12)	15.3±0.4 (6)	16.0±0.2 (8)

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[1] *D.o. fuliginosus.*
[2] *D.o. pallidus.*
[3] Presumed *D.o. fuliginosus* x *D.o pallidus* hybrids.
[4] *D.o. sierrae.*
[5] Refer to Figure IV-1.

TABLE IV-4. Syringeal membrane measurements of adult male blue grouse (mm).

	DOF[1]	DOP[2]	DOFxDOP[3]	DOS[4]
Thickness of:[5]	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)
Internal tympaniform membrane	2.65±0.13 (4)	2.58±0.20 (4)	2.25±0.45 (2)	2.40±0.30 (2)
External tympaniform membrane[6]	0.43±0.03 (3)	0.35±0.05 (2)	0.30±0.00 (1)	0.80±0.00 (1)

[1] *D.o. fuliginosus.*

[2] *D.o. pallidus.*

[3] Presumed *D.o. fuliginosus* x *D.o pallidus* hybrids.

[4] *D.o. sierrae.*

[5] Refer to Figure IV-3.

[6] It is unclear whether these are true membranes, see Degner (1988b).

TABLE IV-5. Esophageal measurements of adult male blue grouse (mm).

Measurement[5]	DOF[1]	DOP[2]	DOFxDOP[3]	DOS[4]
	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)
Esophageal length	214.4±7.8 (8)	223.7±8.3 (6)	207.5±7.8 (4)	204.2±6.4 (5)
Length of expanded portion of the pars cervicalis	87.4±4.8 (8)	98.8±8.4 (5)	81.5±6.6 (4)	88.6±2.8 (5)
Esophageal width, anterior	22.4±1.5 (9)	24.1±3.0 (6)	27.1±1.1 (4)	24.6±3.2 (5)
Esophageal width at crop	7.9±0.4 (8)	7.3±0.6 (5)	5.8±0.3 (4)	7.3±0.6 (5)

[1] *D.o. fuliginosus.*
[2] *D.o. pallidus.*
[3] Presumed *D.o. fuliginosus* x *D.o pallidus* hybrids.
[4] *D.o. sierrae.*
[5] Refer to Figure IV-2a.

TABLE IV-6. Inflated esophageal measurements of adult male blue grouse (mm).

Measurement[5]	DOF[1]	DOP[2]	DOFxDOP[3]	DOS[4]
	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)	$\bar{X}\pm$S.E. (N)
Pars cervicalis length	86.8±5.1 (8)	72.1±16.1 (3)	102.0±0.0 (1)	95.5±3.2 (2)
Pars cervicalis width	66.7±4.6 (8)	75.1±7.3 (2)	64.1±9.9 (2)	69.8±1.0 (2)
Crop length	76.7±8.1 (7)	59.3±10.0 (2)	66.0±0.0 (1)	69.4±1.9 (2)
Crop width	62.6±4.6 (7)	52.5±4.9 (2)	64.1±0.0 (1)	55.6±1.6 (2)

[1] *D.o. fuliginosus*.
[2] *D.o. pallidus*.
[3] Presumed *D.o. fuliginosus* x *D.o pallidus* hybrids.
[4] *D.o. sierrae*.
[5] Refer to Figure IV-2b.

TABLE IV-7. Body weights, external measurements, and heart weights of adult male blue grouse.

Characteristic	DOF[1]	DOP[2]	DOFxDOP[3]	DOS[4]
	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)	$\bar{X}$±S.E. (N)
Body weight (g)	1277.5±22.3 (15)	1195.3±16.9 (12)	1160.0±30.9 (7)	1160.7±17.7 (7)
Cubic root of body weight ($g^{1/3}$)	10.8±0.1 (15)	10.6±0.1 (12)	10.5±0.1 (7)	10.5±0.1 (7)
Wing length (mm)	214.1±1.5 (16)	220.1±1.6 (12)	218.4±2.9 (7)	218.6±1.7 (7)
Heart weight (g)	5.9±0.2 (11)	5.3±0.5 (9)	5.5±0.3 (6)	5.4±0.2 (9)
Cubic root heart of weight ($g^{1/3}$)	1.8±0.03 (11)	1.7±0.05 (9)	1.8±0.05 (6)	1.7±0.02 (9)

[1] *D.o. fuliginosus.*

[2] *D.o. pallidus.*

[3] Presumed *D.o. fuliginosus* x *D.o pallidus* hybrids.

[4] *D.o. sierrae.*

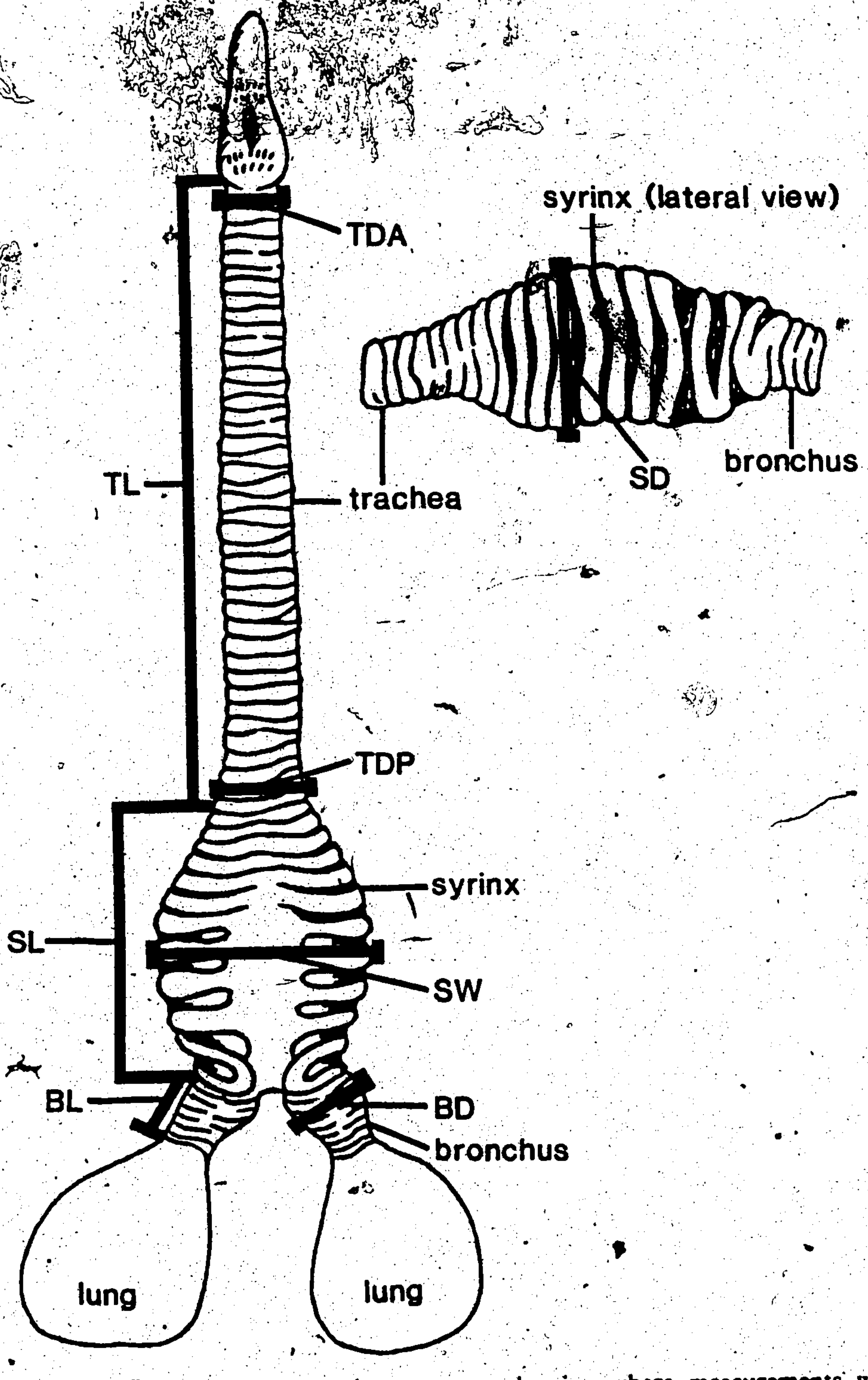

FIGURE IV-1. Male blue grouse respiratory tract showing where measurements were taken. BD - bronchus diameter, BL - bronchus length, SD - syrinx depth, SL - syrinx length, SW - syrinx width, TDA - trachea diameter, anterior, TDP - trachea diameter, posterior, TL - trachea length.

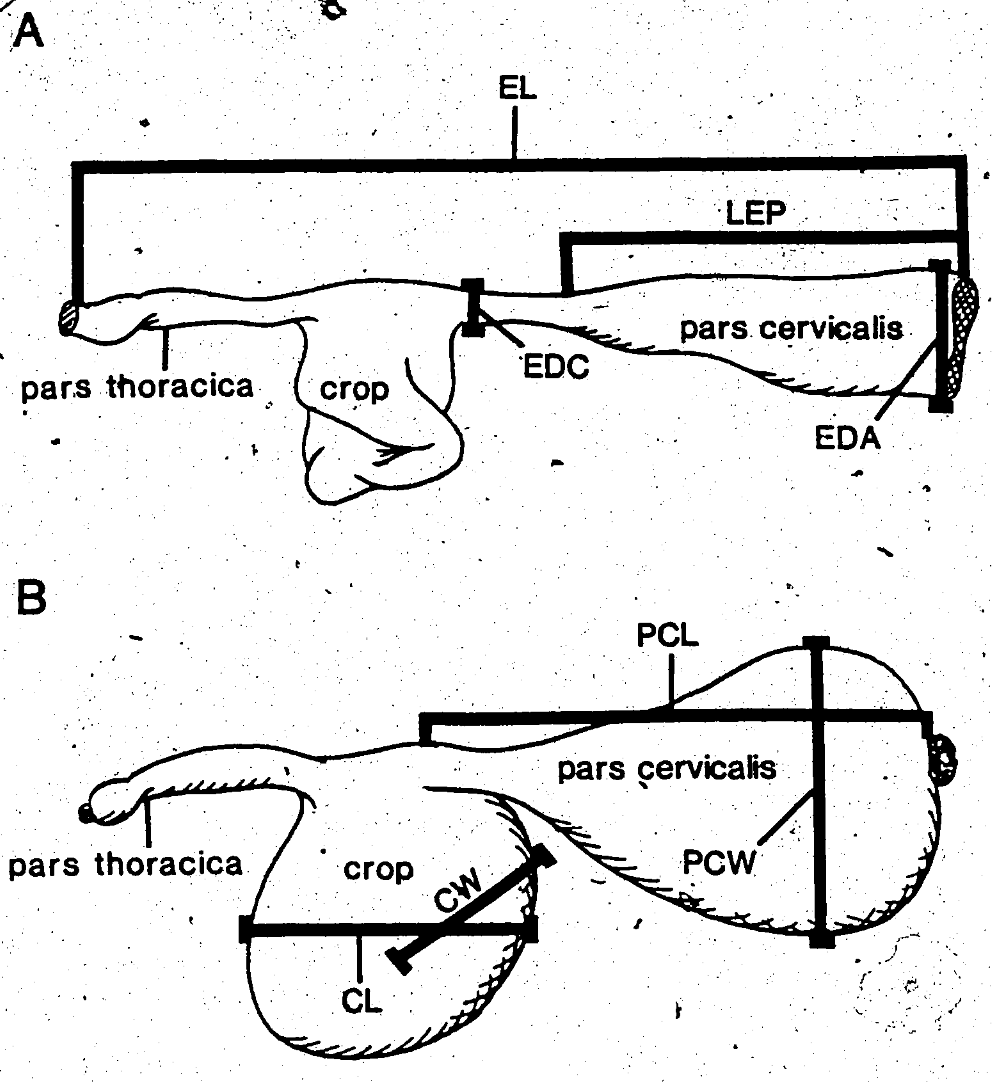

FIGURE IV-2. Male blue grouse esophagus and crop showing where measurements were taken: A) natural, B) inflated. CL - crop length, CW - crop width, EDA - esophagus diameter, anterior, EDC - esophagus diameter at crop, EL - esophagus length, LEP - length of expanded portion of pars cervicalis, PCL - pars cervicalis length, PCW - pars cervicalis width.

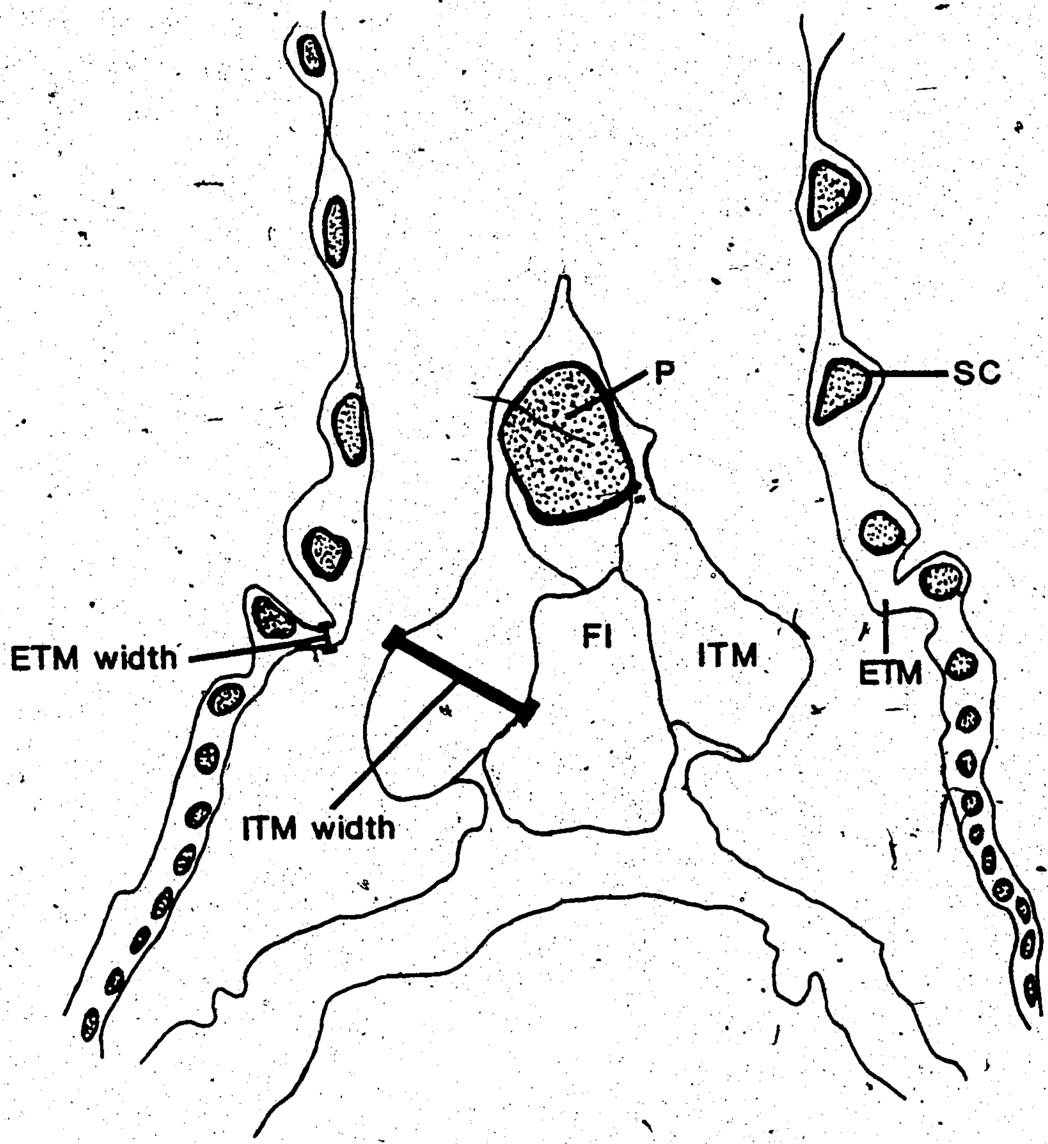

FIGURE IV-4. Relationship between the time of year collected and syrinx size of adult male blue grouse (*D.o. fuliginosus*): A) syrinx length, B) syrinx width, C) syrinx depth.

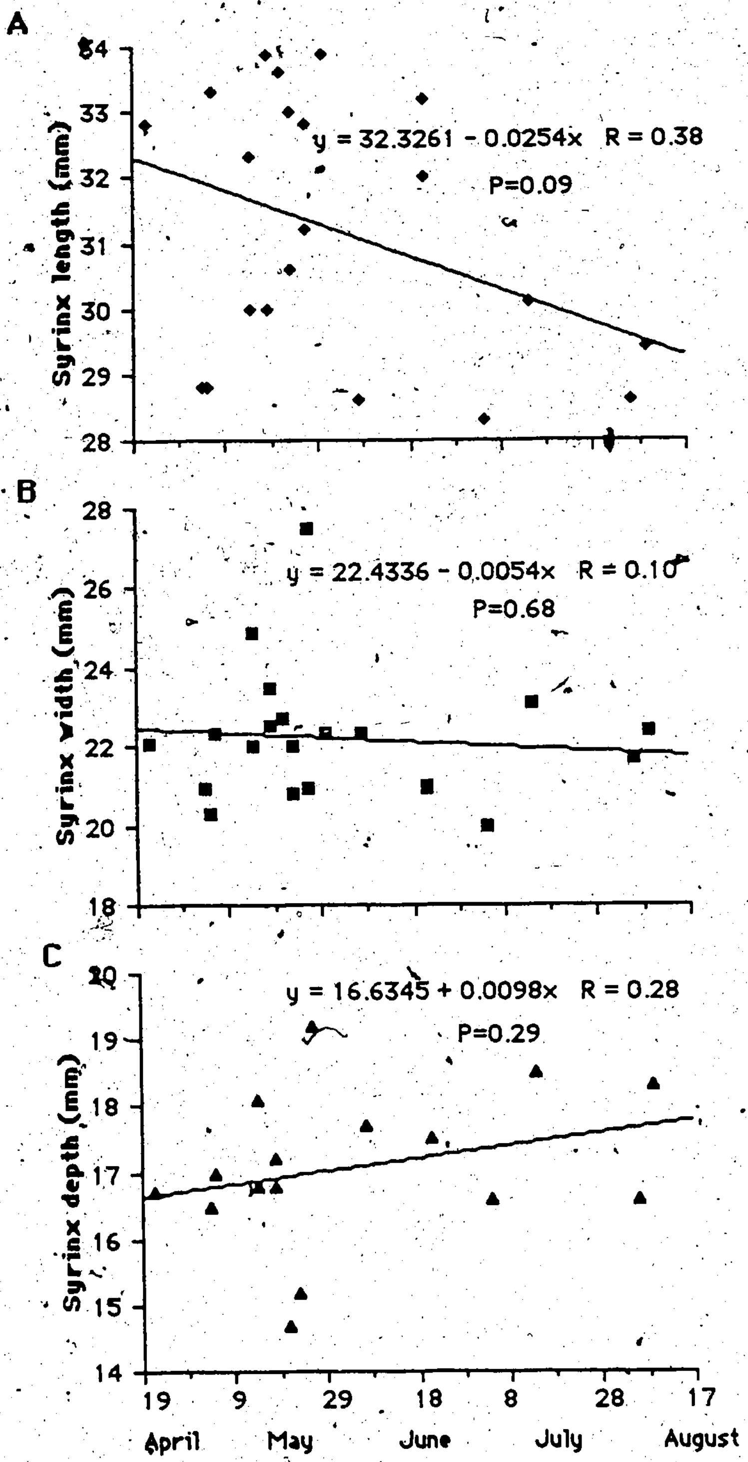

FIGURE IV-3. Frontal section of an adult male blue grouse syrinx showing where measurements were taken. ETM - external tympaniform membrane, FI - foramen interbronchiale, ITM - internal tympaniform membrane, P - pessulus, SC - syringeal cartilage.

FIGURE IV-5. Subspecific variation in syringes of adult male blue grouse (ventral view): A) *D.o. fuliginosus*, B) *D.o. fuliginosus* x *D.o. pallidus*, C) *D.o. pallidus*, D) *D.o. sierrae*.

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V. VEGETATIVE CHARACTERISTICS OF HOOTING SITES OF COASTAL AND INTERIOR MALE BLUE GROUSE

INTRODUCTION

Blue grouse (*Dendragapus obscurus*) occupy most of the Pacific coastal and mountainous regions of western North America from California and New Mexico to Alaska and the Northwest Territories (Appendix 1). Eight subspecies can be divided into 2 groups, coastal and interior, based on plumage, morphology, song, and behavior (Johnsgard 1983; Bendell and Zwickel 1984). Coastal males generally sing (hoot) from trees or other elevated sites (e.g., stumps and logs), have loud, low frequency hoots (115-170 Hz), and usually 6-7 notes per song. Interior males tend to sing from the ground, have softer, even lower frequency hoots (100-110 Hz), and usually 5 notes per song (Hjorth 1970; Stirling and Bendell 1970; Johnsgard 1983; Degner 1988).

Blue grouse occupy a wide array of habitat types, especially in spring and summer when on the breeding range. Breeding habitats vary from very open grass-shrub lands in north-central Washington (Zwickel 1973) to old-growth forests in central southeast Alaska (Doerr et al. 1984) and from sea level to subalpine forest. Most populations migrate altitudinally from relatively open spring and summer ranges to winter range in coniferous forest (Johnsgard 1983; Hines 1986).

Male blue grouse occupy territories which serve primarily as areas for the attraction and mating of females (Bendell and Elliott 1967; McNicholl 1978). Males may hoot anywhere in their territory, but usually use only one to a few sites from which they regularly sing (Bendell and Elliott 1967; McNicholl 1978).

Several authors have described general habitat characteristics of blue grouse (see Schroeder 1984 for a review). However, in only a few studies are territories and hooting sites described specifically (Martinka 1972; Lewis 1981, 1984; Doerr et al. 1984). To date no one has compared territoral or hooting sites among habitats. As well, vegetation structure of hooting sites has not been examined in terms of how it may affect sound transmission.

My objective was to compare hooting site characteristics of a coastal subspecies of blue grouse (*D.o. fuliginosus*) to those of an interior subspecies (*D.b. pallidus*) to see if subspecific song variation might be related to differences in vegetation. Vegetation structure was emphasized as it may have a major influence on sound transmission (Morton 1975; Wiley and Richards 1978, 1982), which may, in turn, affect the effectiveness of different song structures and hooting behavior.

STUDY AREAS

Hooting sites of male blue grouse were studied at four geographic locations in the springs and summers of 1984 and 1985. These include habitats of two of the eight recognized subspecies and one area in which birds appear to be subspecific hybrids. Hooting sites of *D.o. pallidus* (DOP) were examined on the Methow Game Range (48° 31′ N, 120° 4′ W), in the Methow Valley of north-central Washington State in 1984 (Appendix 2). This habitat consisted of open grass-shrubland (steppe) with scattered groves of aspen (*Populus tremuloides*) and wild cherry (*Prunus sp.*), and occasional widely scattered ponderosa pines (*Pinus ponderosa*). Bitterbrush (*Purshia tridentata*) and big sagebrush (*Artemisia tridentata*) were dominant shrubs, some reaching over 2 m in height. This was the same general area used by Zwickel (1972, 1973) and Lewis (1985) in their studies of blue grouse in this region. Grass-shrubland here intergrades into open ponderosa pine forest at higher elevations.

D.o. fuliginosus (DOF) ranges along the west slope of the coastal mountains from northern British Columbia south to California, stopping just north of San Francisco (Johnsgard 1983). Hooting sites at two areas were examined for this subspecies: Hardwicke Island, British Columbia (50° 27′ N, 125° 50′ W) and the May Ranch, California (40° 29′ N, 123° 28′ W). *D.o. fuliginosus* males from Hardwicke

Island will be referred to as DOF(BC) and those from the May Ranch as DOF(CA). Hardwicke Island is between Vancouver Island and mainland British Columbia, approximately 3 km north of the village of Sayward (Appendix 3). It is in the Coastal Western Hemlock (*Tsuga heterophylla*) Biogeoclimatic zone (Krajina 1965). Much of the island has been logged or burned, with logging dating back to the late 1800's (Hines 1986). A 465 ha area near the center of the island was used as the main study area for this and other studies (Jamieson and Zwickel 1983; Hines 1986). The area consisted mostly of successional stages less than 15 years post-logging (Hines 1986), with a few small patches of mature, unlogged timber. Grasses, ferns, forbs, shrubs, and young conifers, predominately hemlock, and in some areas, plantations of Douglas fir (*Pseudotsuga menziesii*), were abundant.

The May Ranch is approximately 50 km southeast of Eureka, California (Appendix 2). Habitat here was very different from that at Hardwicke Island. The vegetation consisted mainly of natural grassland on south-facing slopes and mature Douglas fir forest on north-facing slopes. Vegetation on a 696 ha study area was approximately 45% grassland and 30% Douglas fir forest. The remainder consisted of oak (*Quercus* spp.) forest, mixed forest, and scrub. Oak forest occurred primarily as a narrow strip at the interface of grassland and Douglas fir forest and in moist gullies on south-facing slopes. Small stands of mixed deciduous/coniferous forest were scattered throughout the area. Scrub habitat, usually along creekbeds, was dominated by a mixture of shrub species. Forests here would be considered mature and only a small amount of selective logging had taken place. Studies were undertaken here in the spring and summer of 1985.

The fourth study area was approximately 8 km southeast of Hart's Pass, Washington (48° 42' N, 120° 39' W) approximately 50 km northwest of the Methow Game Range and on the eastern slope of the Cascade mountains (Appendix 2). Here *D.o. fuliginosus* and *D.o. pallidus* (DOFxDOP) appear to overlap and many individuals show morphological and behavioral traits of both subspecies. This habitat can be classified as a ***Pseudotsuga menziesii*** (Douglas fir) zone (Franklin and Dyrness 1973). This was a dry, eastern slope type forest, different from that found at Hardwicke Island and the May Ranch. The forest was open, mature, and unlogged.

MATERIAL AND METHODS

Hooting sites were located by listening for singing males and carefully moving towards them, trying to minimize disturbance of the birds. The exact location from which males were hooting was marked with flagging tape for relocation after observations were made. Within 70 days ($\bar{X}$=14.7 days) of locating a hooting site, vegetative characteristics were measured. The exact spot from which the male had been hooting was used as the center of an 8 m diameter circle, the center plot. Four other 8 m diameter outside plots were established at each site, one in each of the four cardinal directions. Their centers were 10 m from the middle of the center plot (Figure V-1). Within each plot all trees and shrubs ≥2 m in height were identified and counted. The circumference at breast height (approximately 1.5 m) was measured for each tree and then converted to diameters. This gives an index of tree size. Heights of trees were estimated visually. Only one, usually the first, location was examined per male.

A vegetation coverboard similar to that described by Nudds (1977) was used to measure density of vegetation (forbs, shrubs, and trees) from ground level to 2.5 m in height. The coverboard consisted of a 250 cm x 30.5 cm sheet of 0.64 cm plywood. It was divided into 5, 50 cm intervals painted in alternate white and fluorescent orange colors (Figure V-2). Species composition was not recorded as only density was considered important for this analysis. I stood at the exact spot at which the male was observed hooting, the middle of the center plot, with the coverboard 15 m from this spot (Nudds 1977). The amount of vegetation covering each of the 50 cm sections was assessed and assigned a density score of 1-5 (1 = 0-20% covered and 5 = 81-100% covered). Four readings were taken at each hooting site, one in each of the four cardinal directions (Figure V-1). Data from hooting sites at which it was impossible to see the complete coverboard in one or more directions due to topography (i.e., cliffs) were excluded.

Specific location (ground, log, stump, or tree) of hooting males from Hardwicke Island and the Methow Game Range were recorded in 1984, those of males from the May Ranch in 1985. Hooting locations of males at Hart's Pass were recorded in 1981, 1983, and 1984.

Statistical analyses were made using the SPSS^{X} statistical package (SPSS Inc. 1983). Differences were considered significant at the five percent level.

RESULTS

There was little overlap in tree and shrub species present at the hooting sites among the four areas (Table V-1). The only species definitely present in more than one area was Douglas fir. Willows (*Salix* sp.) were present at three locations, but species were not identified and they may, or may not, have been the same. The two coastal sites, Hardwicke Island and the May Ranch had the highest and second highest tree and shrub diversity, respectively (Table V-1). The Methow Game Range had the second lowest diversity, Hart's Pass the lowest.

The number of trees in center plots and outside plots were significantly different among areas (Kruskal-Wallis, $H=32.82$, $P<0.001$ and $H=30.66$, $P<0.001$, respectively). Hardwicke Island had the most trees, many times the number found in other areas (Table V-2). No differences were found between the number of trees in center and outside plots when compared separately for each area (Wilcoxon, Range of P-values=0.313-0.932). Thus, the number of trees at hooting sites did not differ from those immediately surrounding them.

Tree heights were significantly different among the four areas (Kruskal-Wallis, H=32.11, P<0.001), with the Methow Game Range having the shortest trees and the May Ranch the tallest, a ten-fold difference (Table V-2). Tree diameter at breast height (DBH) provides another method of comparing tree size. The mean DBH of trees was significantly different among areas for both center plots and outside plots (Kruskal-Wallis, H=32.11, P<0.001 and H=37.27, P<0.001, respectively)(Table V-2). For each area separately, the DBH of trees in center plots did not differ significantly from those in outside plots (Wilcoxon, Range of P-values=0.1614-0.6247).

Vegetation density at hooting sites, as measured with the coverboard, increased as height above ground decreased at each of the four areas (Table V-3). At Hardwicke Island, the Methow Game Range, and the May Ranch this increase was significant among the five coverboard sections (Kruskal-Wallis, P<0.01 for all three areas), but not at Hart's Pass (Kruskal-Wallis, H=4.659, P=0.324).

Vegetation at hooting sites on Hardwicke Island were most dense and Methow Game Range sites most open (Table V-3). Hooting sites at Hart's Pass and the May Ranch had similar vegetation densities, more like those at the Methow Game Range than at Hardwicke Island (Table V-3). There were highly significant differences for each coverboard section when each of the five sections were compared separately among the four areas (Kruskal-Wallis, all P's<0.001). Pairwise comparisons indicate that the denser vegetation at Hardwicke Island hooting sites was responsible for most of the differences (Table V-3).

A relationship exists such that sound frequency of songs increases with vegetation at hooting sites (Table V-4). Using song frequencies from Degner (1988) we see that DOF(BC) songs have the highest frequency and the densest vegetation, and DOP songs were lowest frequency, and in areas with the most open vegetation (Table V-4). The vegetation at DOFxDOP and DOF(CA) hooting sites were similar, but DOFxDOP songs were of higher frequency than those of DOF(CA).

The numbers and heights of stumps and logs found at each site were not recorded. These may be important as hooting posts (places from which males sing) in some areas; e.g., 26% of DOF(BC) males hooted from logs and stumps (Table V-5). Almost all DOP males hooted from the ground (96%). Here, very few logs or stumps were available. All hooting DOF(CA) males (100%) sang from trees ≥10 m above the ground. The presence of logs and stumps were probably not important as hooting posts here.

DISCUSSION

There were highly significant differences in vegetation composition and structure at hooting sites, both within a subspecies' range and among subspecies. Tree and shrub species composition did not overlap among areas except for Douglas fir, and perhaps willows, which were present at three areas. Blue grouse and Douglas fir distributions are closely correlated, but probably because both are adapted to common conditions rather than because of a dependence by blue grouse on Douglas fir (Johnsgard 1983). Bendell and Zwickel (1984) have observed blue grouse in areas lacking Douglas fir and true firs, indicating that these species are not required. At the Methow Game Range there were no Douglas fir on the breeding areas examined, although they are found on the mountains nearby and are used in winter.

Vegetation cover at Hardwicke Island hooting sites was denser and had more trees than hooting sites at all other areas. In terms of vegetative structure the Methow Game Range, Hart's Pass, and the May Ranch hooting sites were more similar to each other than to Hardwicke Island.

In areas near the Methow Game Range study area, singing males can be found in ponderosa pine forest and subalpine Douglas fir forest at higher elevations. In these areas songs are all soft and low in frequency, and most males sing from the ground. Hardwicke Island hooting sites that were examined were in relatively early successional forest and territorial males also are found in low densities in midsuccessional and old-growth forests in this area (Niederleitner 1987). The songs of males in these different successional stages appear similar, although hooting locations vary. Differences in vegetation composition and structure between Hardwicke Island and the May Ranch, where *D.o. fuliginosus* occurs, show that there is large habitat variation within a subspecies' range. Songs of males in these areas are different in frequency, but similar in loudness (Degner 1988). Apparently habitat within a subspecies' range can vary greatly, and the frequencies of songs vary little over short distances, but greatly over long distances.

Vegetation structure was the primary characteristic that I measured at each hooting site. It is a major factor that may influence sound transmission (Wiley and Richards 1982). The denser the vegetation, the more sound is attenuated. The lower the frequency of sound the less it is attenuated. All male blue grouse songs are low frequency sounds, with those of interior males (100-120 Hz) lower than those of coastal males (115-170 Hz) (Degner 1988). Therefore, according to the above theory interior males (most open habitat) should have the highest frequency songs. However, data from the areas examined does not support this; interior Methow Game Range males and coastal May Ranch males were in relatively open habitats, while coastal Hardwicke Island males were in denser habitats. My study indicates the opposite; frequency of songs increased as vegetation density increased.

Specific location of a singing male can have a strong influence on sound transmission (Wells and Schwartz 1982). If the bird is on or close to the ground, the song experiences ground or boundary interference. That usually increases attenuation, though it has been reported that in some special cases attenuation can decrease (Michelsen 1978; Wiley and Richards 1982). If the sender moves off the ground, transmission is improved, as ground interference lessens. Also, if a male moves high enough off the ground, it may be above the often dense ground vegetation, again reducing attenuation.

Coastal males usually hoot from trees and interior males from the ground, a common generalization (Johnsgard 1983). This trend is partially seen, except at Hardwicke Island, in this study (Table V-5). Thus, coastal males may circumvent a need for extremely low frequency sounds by singing from elevated sites. The Hardwicke Island study area was primarily a clear cut, therefore, trees were not readily available for these males to use. In forested areas on the island males sang mostly in trees. The use of stumps and logs, if they get the male 1 m or more off the ground, helps substantially to reduce attenuation (Wiley and Richards 1982). However, why interior males usually sing from the ground when low frequency sounds are usually attenuated by the ground or ground level vegetation is unknown; but ground interference at very low frequencies may improve sound transmission rather than attenuate it (Michelsen 1978; Wiley and Richards 1982). This is a special situation and experimentation is required to test the hypothesis.

Coastal male songs are louder than those of interior males (Hjorth 1970; Johnsgard 1983; Degner 1988). Loudness also increases transmission distance, however, it has less influence than frequency on long-range transmission. Loudness also seemed unrelated to vegetation since *D.o. fuliginosus* males at the May Ranch and Hardwicke Island both sang loudly even though the vegetation greatly differed.

Subspecific differences in song and singing behavior may have initally evolved in relation to differences in vegetation even though some of my findings suggests that vegetation currently does not appear to be a factor influencing differences in song. Songs of coastal males do not appear to change when these males use man-made clear cut areas (open habitats) indicating that the relationship between vegetation and sound frequencies may not be too important. Sound transmission experiments are needed to see how well the songs of different subspecies are adapted to their different habitats.

SUMMARY

Vegetation characteristics of male blue grouse hooting sites were measured in the springs and summers of 1984 and 1985. Four locations were studied: two near opposite ends of the range of the coastal subspecies *D.o. fuliginosus*, one in the range of the interior subspecies *D.o. pallidus*, and the fourth in an area where these two subspecies overlap. Vegetation composition and structure were significantly different among the four areas. Douglas fir and willow were the only tree and shrub species found at two or more areas. Hooting sites on Hardwicke Island had denser vegetation cover and more trees per unit area than hooting sites at all other areas, both coastal and interior. There is considerable variation in vegetation within a subspecies' range as shown by the differences in hooting sites at Hardwicke Island and the May Ranch; *D.o. fuliginosus* occurs at both. Contrary to theory, the relationship that appears to exist is as vegetation density at hooting sites increases, the sound frequency of songs increases. However, behavioral adjustments such as increasing the elevation of song posts complicates any interpretation.

TABLE V-1. Shrub and tree species ≥2 m in height present in the center hooting site plots and their relative frequency on sites examined.

Location	Species	NO[1]
Hardwicke Island, B.C.	*Tsuga heterophylla*	16/16
	Vaccinium parvifolium	10/16
	Thuja plicata	9/16
	Abies amabilis	5/16
	Pseudotsuga menziesii	4/16
	Snag	2/16
	Salix sp.	1/16
	Pinus monticola	1/16
	V. ovatum	1/16
	Unidentified	1/16
May Ranch, CA.	*P. menziesii*	8/8
	Snag	3/8
	Quercus sp.	2/8
	Salix sp.[2]	1/8
	Toxicodendron diversiloba	1/8
	Arbutus menziesii	1/8
	Acer macrophyllum	1/8
Methow Game Range, WA.	*Populus tremuloides*	6/25
	Purshia tridentata	5/25
	Prunus sp.	3/25
	Rosa sp.	2/25
	Ceanothous velutinus	1/25
Hart's Pass, WA.	*P. menziesii*	8/9
	Salix sp.	2/9

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[1] Number of occurrences (1 or more individuals)/ N center plots examined at each location.

[2] California bay (*Umbellularia californica*) was included with the willows (*Salix* sp.).

TABLE V-2. Characteristics of blue grouse hooting sites. Lines join pairs that were significantly different (Scheffe tests, $P<0.05$).

Characteristic	DOF(BC)[1] (N=16)	DOP[2] (N=25)	DOFxDOP[3] (N=9)	DOF(CA)[4] (N=8)
	$\bar{X}$±S.E.	$\bar{X}$±S.E.	$\bar{X}$±S.E.	$\bar{X}$±S.E.
No. trees - center plots	24.3±4.6	3.2±1.1	1.9±0.5	5.3±1.5
No. trees - outside plots[5]	24.9±4.8	3.9±1.0	2.5±0.9	4.2±0.9
Tree height (m)	4.8±0.6	2.4±0.6	16.6±3.5	25.2±5.3
DBH[6] - center plots (cm)	5.0±1.1	2.8±0.9	37.4±8.8	60.6±14.2
DBH[6] - outside plots[5] (cm)	4.2±0.7	2.3±0.6	24.0±7.1	31.8±10.5

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[1] DOF(CA) = *D.o. fuliginosus* from Hardwicke Island, B.C.
[2] DOP = *D.o. pallidus* from Methow Game Range, WA.
[3] DOFxDOP = Presumed *D.o. fuliginosus* x *D.o. pallidus* hybrid from Hart's Pass, WA.
[4] DOF(CA) = *D.o. fuliginosus* from the May Ranch, CA.
[5] Mean of the four outside plots at each hooting site was used for the value at each hooting site.
[6] Diameter at breast height.

TABLE V-3. Mean vegetation density at blue grouse hooting sites as determined from coverboard readings. Lines join pairs that were significantly different (Scheffe tests, $P<0.05$).

	DOF(BC)[1] (N=12)	DOP[2] (N=20)	DOFxDOP[3] (N=8)	DOF(CA)[4] (N=8)
Height above ground (m)	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.	$\bar{X}\pm$S.E.
2.0-2.5	3.9±0.3[6]	1.2±0.1	2.1±0.4	1.8±0.3
1.5-2.0	4.2±0.2	1.3±0.1	2.1±0.4	1.8±0.3
1.0-1.5	4.6±0.2	1.5±0.1	2.4±0.5	2.0±0.4
0.5-1.0	4.8±0.1	1.8±0.2	2.5±0.5	2.3±0.4
0.0-0.5	4.9±0.8	2.3±0.2	3.3±0.5	3.8±0.4

[1] DOF(BC) = *D.o. fuliginosus* from Hardwicke Island, B.C.

[2] DOP = *D.o. pallidus* from Methow Game Range, WA.

[3] DOFxDOP = Presumed *D.o. fuliginosus* x *D.o. pallidus* hybrid from Hart's Pass, WA.

[4] DOF(CA) = *D.o. fuliginosus* from the May Ranch, CA.

[5] Density score based on a scale of 1-5, refer to text.

TABLE V-4. Relationship between vegetation density at hooting sites and fundamental frequency of songs of male blue grouse.

Subspecies	Vegetation density[1] $\bar{X}$±1 S.E. (N)	Fundamental frequency[2] Hz
DOP[3]	1.6±0.2 (10)	100-110
DOF(CA)[4]	2.3±0.4 (8)	110-120
DOFxDOP[5]	2.5±0.2 (8)	125-135
DOF(BC)[6]	4.5±0.2 (12)	145-155

[1] Mean of vegetation density scores of the five coverboard sections from Table V-3.

[2] Data from Degner (1988).

[3] DOP = *D.o. pallidus* from Methow Game Range, WA.

[4] DOF(CA) = *D.o. fuliginosus* from the May Ranch, CA.

[5] DOFxDOP = Presumed *D.o. fuliginosus* x *D.o. pallidus* hybrid from Hart's Pass, WA.

[6] DOF(BC) = *D.o. fuliginosus* from Hardwicke Island, B.C.

TABLE V-5. Hooting locations of male blue grouse.

		Hooting location			
Subspecies	Total	Ground	Log	Stump	Tree
DOF(BC)[1]	198	101 51.0%	27 13.6%	25 12.6%	45 22.6%
DOF(CA)[2]	106	0	0	0	106 100.0%
DOP[3]	71	68 95.6%	0	0	3 4.4%
DOFxDOP[4]	22	4 18.2%	2 9.1%	0	16 72.7%

[1] DOF(BC) = *D.o. fuliginosus* from Hardwicke Island, B.C.

[2] DOF(CA) = *D.o. fuliginosus* from the May Ranch, CA.

[3] DOP = *D.o. pallidus* from Methow Game Range, WA.

[4] DOFxDOP = *Presumed D.o. fuliginosus* x *D.o. pallidus* hybrid from Hart's Pass, WA.

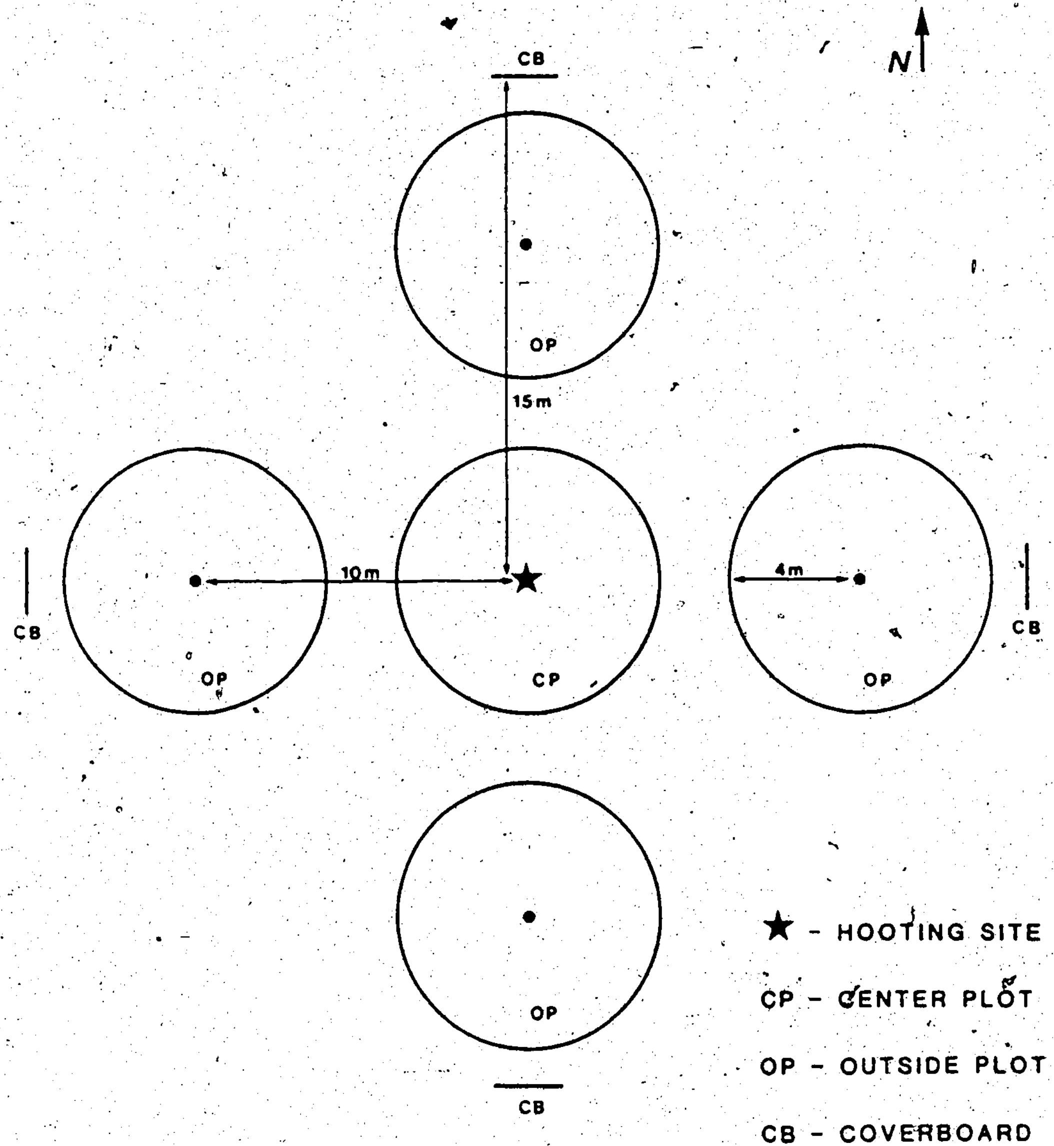

FIGURE V-1. Plot design used to measure blue grouse hooting site characteristics and vegetation density.

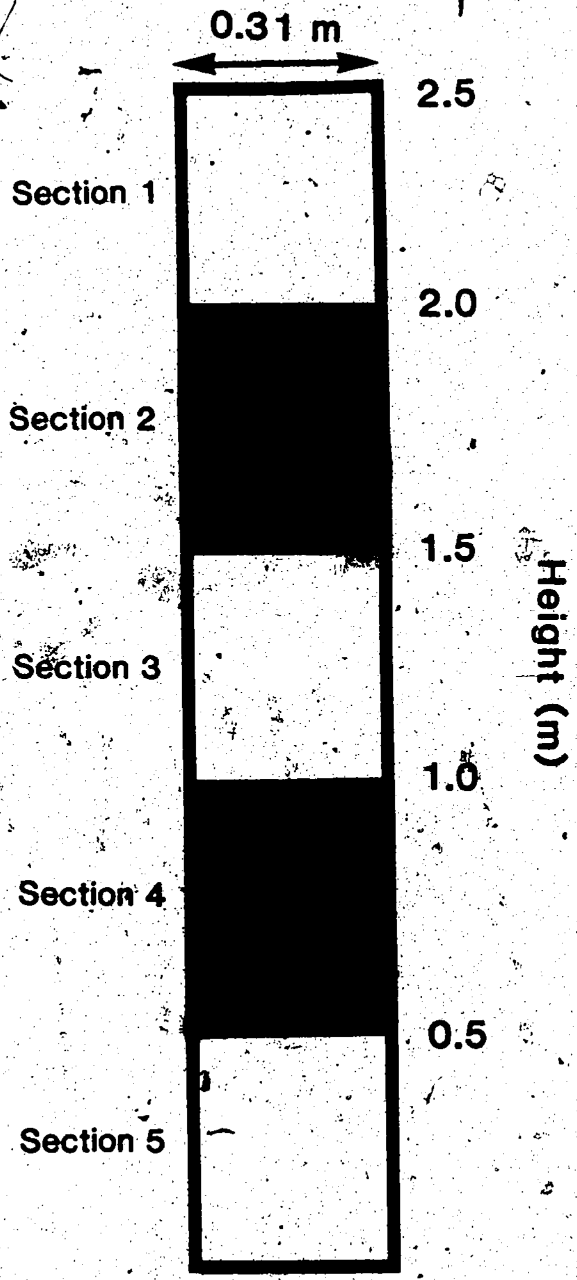

FIGURE V-2. Dimensions of vegetation cover board.

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VI. CONCLUDING DISCUSSION

Geographic variation in song has been well documented in birds, especially passerines. There are many possible explanations for such variation, which can be grouped into three main areas; ontogeny, causation, and adaptation (Kroodsma and Miller 1982). Causation and adaptation were investigated in this study; variation in the vocal sound-producing structures and differences in vegetation structure at hooting sites were the aspect of causation and adaptation examined, respectively.

Understanding the evolution of the subspecies of blue grouse (*Dendragapus obscurus*) may shed some light on the differences or patterns seen in their songs. Bendell and Zwickel (1984) and Zwickel (pers. comm.) believe that blue grouse evolved from a grassland-type grouse, and are closely related to sage grouse (*Centrocercus urophasianus*). This is different from the conventional view that they came from a forest-type grouse (Short 1967). Interior *D.o. obscurus* or some population similar to it, is believed to be the ancestral group from which blue grouse may have evolved (Bendell and Zwickel 1984; Zwickel pers. comm.). They most likely spread west to the coast in the southern part of their range (southeast California and southwest Nevada area), and gave rise to present coastal *D.o. sierrae/howardi*. Glaciation most likely separated the birds and each gave rise to the currently recognized coastal and interior groups. Both groups then spread northward along the Coastal and Rocky Mountains, respectively. Where the two groups now meet appears to be a secondary contact as a result of a coalescence of the Coastal and Rocky Mountains.

If this is, in fact, the way blue grouse evolved then the variation in songs between coastal and interior groups could have developed after geographic separation, at least during the early part of their separation. However, the mere existence of geographic separation does not necessarily account for the differentation of songs as some other factors also may have been involved.

A general relationship exists between the size of the syrinx and the sound frequencies that are produced: the larger the syrinx, the lower the frequency produced. This occurs both between males and females and among males of the different subspecies, and this does not appear to be related to body size. Unfortunately this relationship is based only on examination of the syringeal morphology, and direct experimental evidence is needed. This relationship does indicate, however, that there is a morphological basis for the differences seen in the songs of males. However, it does not tell us what the selective pressures were that caused this difference.

Different habitats may produce different selective pressures on the physical characteristics of song (Morton 1975; Wiley and Richards 1978, 1982; Gish and Morton 1981; Miller 1982). My analyses of vegetation structure at hooting sites indicate that there are differences in the vegetation at hooting sites, both between coastal and interior groups and within coastal subspecies. However, considerable variation occurs in vegetation within the range of each subspecies, nearly as much as there is between subspecies and coastal and interior groups. Although there was a general pattern in which sound frequency increased with vegetation density, it would be premature to say that vegetation at hooting sites was responsible for the differences in the songs. Vegetation does still seem a likely reason for this difference, but perhaps under conditions not present today. Males appear to be fairly adaptable in their requirements for breeding habitats as can be seen in the differences in habitats that *D.o. fuliginosus* males occupy. The variation ranges from very open clear-cuts to dense mature coastal forests.

Repulsion of rival males and female attraction are two important selective pressures that have shaped male song (Catchpole 1982). Songs of male blue grouse are said to have both territorial and mate attraction functions (McNicholl 1978). Differences in territorial behavior, spacing, and the role of female choice were not investigated in this study and these factors may be important in the evolution of the differences in the songs of coastal and interior males. When combined with differences in vegetation these behavioral factors may become even more important.

The presence of an apparent hybrid zone between coastal and interior subspecies in the north and the fact that the songs of males in these areas can be considered intermediate between coastal and interior subspecies may be important to understanding differences in songs of blue grouse. Since the songs of these males appear to be intermediate, songs are most likely not learned as in some other birds (Kroodsma and Baylis 1982). Genetically fixed songs should be more resistant to change than learned songs. This indicates that some selective factors likely acted on the songs of blue grouse to create the differences seen.

Many questions are still unanswered and more specific research is required to determine why the songs of coastal and interior male blue grouse differ and why the sound frequency of coastal songs appears to increase with latitude. These studies need to look at the genetics of song and song development, how songs are adapted to their particular habitats, and how social and behavioral differences relate to the observed differences in song.

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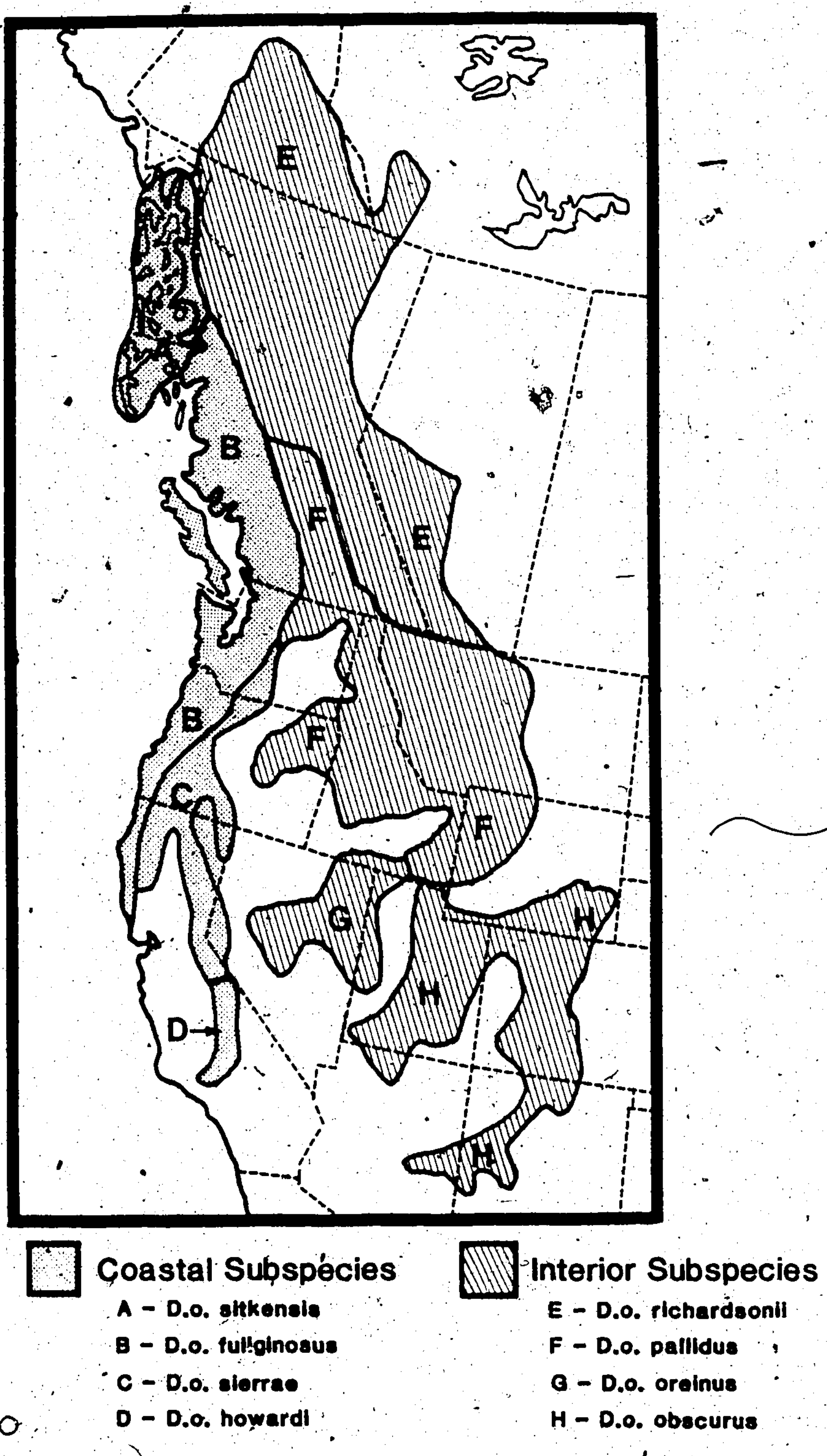
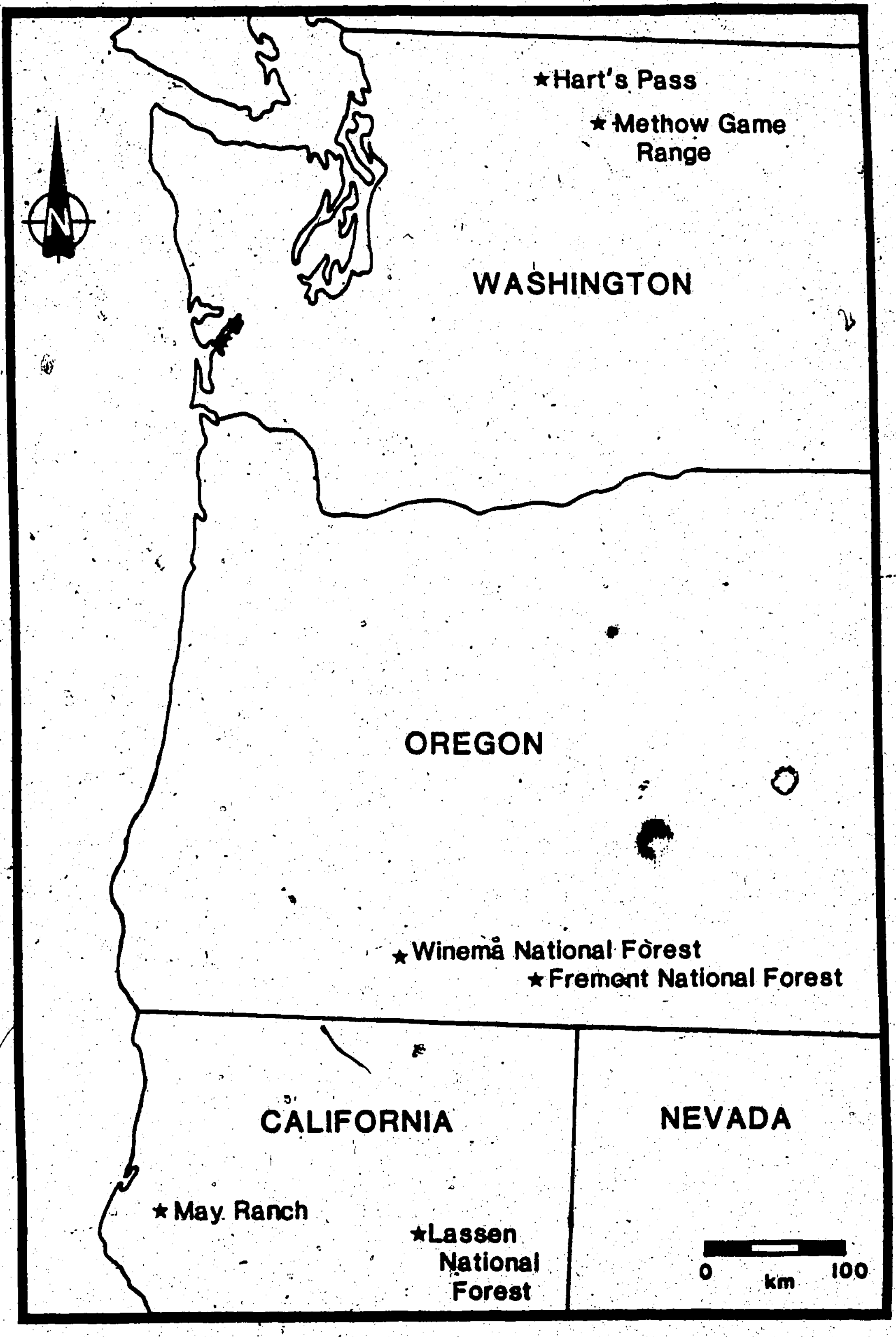
VII. APPENDIX 1: DISTRIBUTION OF THE SUBSPECIES OF BLUE GROUSE (*DENDRAGAPUS OBSCURUS*)



VIII. APPENDIX 2: LOCATIONS OF SOUTHERN STUDY SITES



IX. APPENDIX 3: LOCATIONS OF NORTHERN STUDY SITES