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Grouse and Quails of North America, by Paul A. Johnsgard

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2 Physical Characteristics

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Physical Characteristics

ALL of the grouse, quails, and introduced partridges of North America share a number of anatomical traits which provide the basis for their common classification within the order Galliformes. Among these are the facts that they all have fowl-like beaks and four toes. In all the North American species the hind toe is elevated and quite short, thus is ill-adapted for perching. There are always ten primaries, thirteen to twenty-one secondaries, and twelve to twenty-two tail feathers (rectrices). Aftershafts on the contour feathers are well developed, especially in the grouse, and true down feathers are infrequent. A large crop is present, and is associated with the largely granivorous (seed-eating) behavior of most quails, and the more generally herbivorous (leaf-eating) diets of grouse. The egg colors range from pastel or earth tones (buff, cream, olive, etc.) to white, with darker spotting prevalent among those species having nonwhite eggs. The nest is built on the ground, and incubation is by the females alone or occasionally by both sexes (some quails and partridges). The young are down-covered and precocial and are usually able to fly short distances in less than two weeks. They are cared for by the female (most grouse) or by both parents (some ptarmigans, all quails). A number of external structural characteristics typical of grouse, quails and partridges are shown in figures 3 and 4.

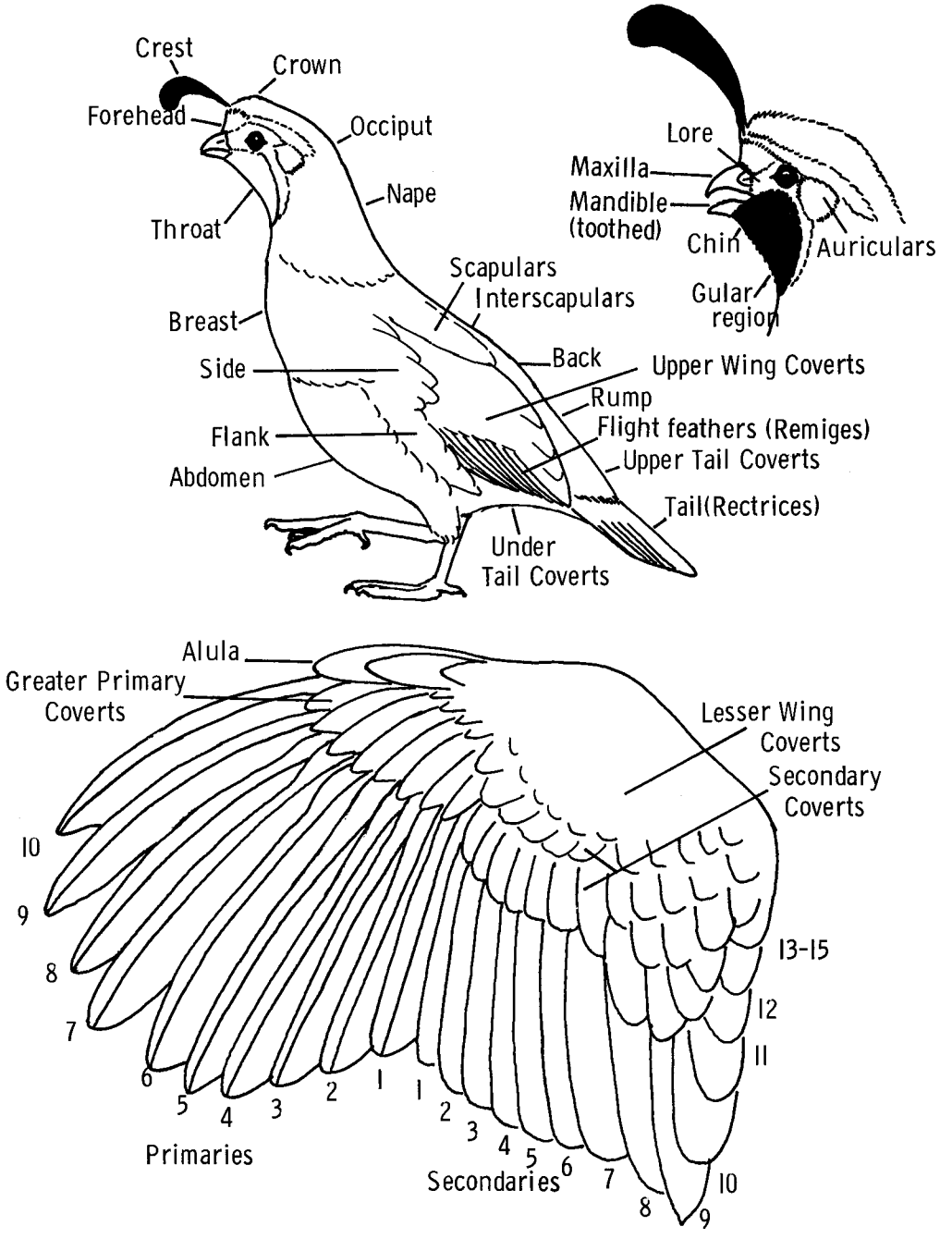


FIGURE 3. Body regions and feather areas (above) and wing regions (below) of a representative quail, with number sequence of the remiges indicated.

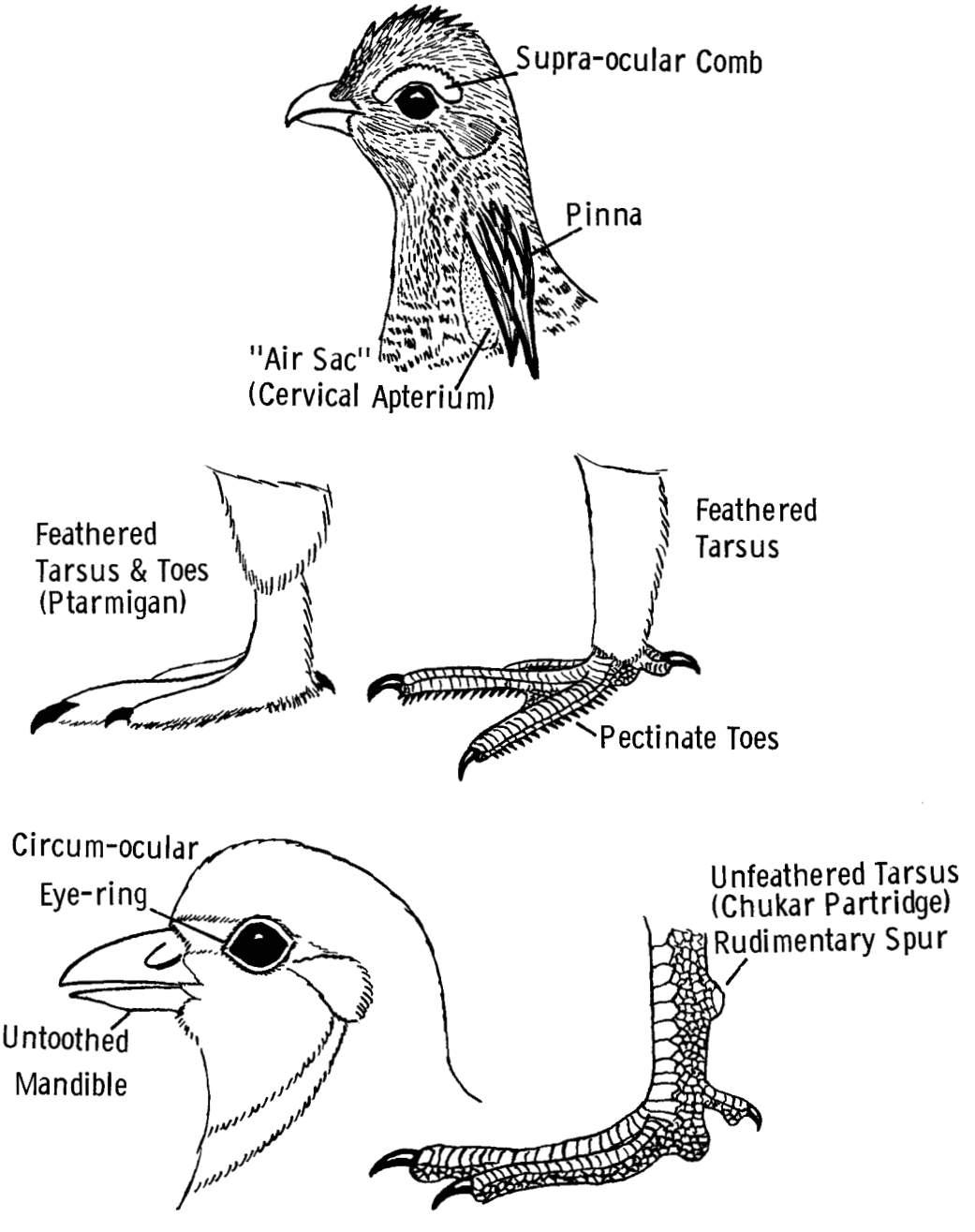


FIGURE 4. Structural characteristics typical of certain grouse species (above) and Old World partridges (below).

Additionally, the grouse may be characterized by the fact that they have feathered nostrils and feathering on the legs that usually extends to the base of the toes. Among ptarmigans this feathering extends to the tips of the toes in winter.

In the other grouse species, the toes have marginal comb-like membranes (pectinations) present in winter. Males of several species of grouse have large unfeathered areas (apteria) at the sides or front of the neck, which can be exposed and enlarged by the inflation of the esophagus. The skin associated with these "air sacs" may be variously colored, or the feathers around the area may be specialized in shape or color, but the true air sac system associated with the lungs is not directly connected to these structures. A bare area of skin (eye-comb) is usually present above the eyes in mature males also. Grouse are not normally highly gregarious, but during fall and winter some species that migrate considerable distances may form large flocks. Grouse are usually polygamous or promiscuous, but the ptarmigan are relatively monogamous. At least sixteen secondaries and twenty-two rectrices are present, but in some species (ptarmigans) the central pair closely resembles the upper tail coverts, while in others (sage grouse) some upper tail coverts may easily be confused with rectrices.

The New World quails can be distinguished from the grouse and their Old World relatives by the fact that they are relatively small (usually under twelve inches), the nostrils are unfeathered, and the edge of the lower mandible is slightly serrated or toothed (inconspicuous in some species). There are thirteen to sixteen secondaries, ten to fourteen rectrices, and the tarsus is not feathered nor is a spur present in males. The bill is very short and stout, and the toes and claws are well developed in many species for digging. They are all monogamous, and the male normally remains to help rear the young. The quails are usually highly gregarious, and occur in coveys at all times except during nesting.

The two successfully introduced Old World partridge species differ from the New World quails in that they lack serrations on the cutting edge of the lower mandible and have fourteen to eighteen rectrices, and males sometimes exhibit slight spurs on the legs. These two species are monogamous; further, males may occasionally participate in incubation and often help rear the young, although opinions differ on these points.

ADULT WEIGHTS

Weight characteristics of adults are of some interest, since they not only provide the hunter with an indication of the trophy values of his

game but are also important in the consideration of anatomical adaptations to the environment. Thus, body weights in relation to climatic conditions encountered by the species, heart weights in relationship to total body weights (Hartman, 1955), or body weights in relation to egg weights (Lack, 1968) are all significant relationships and provide useful indices of ecological and physiological adaptations. A summary of reported adult weights is therefore provided (tables 5 and 6) as they have been reported in the literature. In general, the selected references represent the largest sample sizes available and do not take into account the possibilities of geographic or seasonal variations in weights, as are known to occur often. Representative studies on the geographic or seasonal variations in adult weights include those of Gullion (1961), Stoddard (1931), Boag (1965), Zwickel, Buss, and Brigham (1966), and Bump et al. (1947).

EGG CHARACTERISTICS

The coloration, markings, and other physical characteristics of bird eggs have particular ecological interest. To some extent the physical characteristics of eggs might be expected to be the result of evolutionary relationships, but the requirements for concealment under the existing ecological conditions are probably of primary significance in the interpretation of egg coloration and patterning characteristics. In table 7 an abbreviated summary of the physical characteristics of the eggs of North American grouse and quails is presented. Known or estimated incubation periods are also indicated, and it may be seen that in all known cases these range from twenty-one to twenty-seven days. There is no apparent relationship between egg size and incubation period; the only clear example of ecological specialization in the entire group is the unusually short (twenty-one- to twenty-two-day) incubation period of the ptarmigans. The longest known incubation periods for any New World quail are those of two tropical species, the bearded tree quail, which we have recently found to have a twenty-eight- to thirty-day incubation period, and the spot-winged wood quail (*Odontophorus capueira*), with an approximate twenty-six- to twenty-eight-day period (Flieg, 1970).

It is also of interest to compare the egg size to the size of the adult female. This is perhaps most easily done by determining the ratio of the fresh egg's weight to that of the female (Lack, 1968). Average weights of fresh eggs for all the species concerned are not available, but is is possible to calculate the volume of an egg quite accurately when its linear measurements are known. Stonehouse (1966) suggests a convenient formula for calculating volume as follows:

$$\text{Volume (cc)} = .512 \times \text{length (mm)} \times \text{diameter (mm)}^2$$

TABLE 5
Adult Weights of North American Grouse

Species	*Mean or Range of Means*	*Maximum Weight*	*References*
Sage grouse			
Male	2010–2835 gm (71–100 oz.)*	3175 gm (112 oz.)	Patterson, 1952
Female	1142–1531 gm (40–54 oz.)*	1531 gm (54 oz.)	Patterson, 1952
Blue grouse			
Male	1150–1275 gm (14–45 oz.)*	1425 gm (50 oz.)	Boag, 1965§
Female	850–900 gm (30–32 oz.)*	1250 gm (44 oz.)	Boag, 1965§
Spruce grouse			
Male	501 gm (17.7 oz.) (14 birds)	630 gm (22 oz.)	Stoneberg, 1967
Female	450–548 gm (16–19 oz.)*	606 gm (21 oz.)	Stoneberg, 1967
Willow ptarmigan			
Male	535–696 gm (19–25 oz.)*	804 gm (28 oz.)	Parmelee, Stephens, and Schmidt, 1967
Female	525–652 gm (19–23 oz.)*	749 gm (26 oz.)	Irving, 1960
Rock ptarmigan			
Male	466–536 gm (16–19 oz.)*	575 gm (21 oz.)	Irving, 1960
Female	427–515 gm (15–18 oz.)*	550 gm (20 oz.)	Johnston, 1963
White-tailed ptarmigan			
Male	323 gm (11.4 oz.) (24 birds)	430 gm (15.2 oz.)	Johnson & Lockner, 1968
Female	329 gm (11.5 oz.) (14 birds)	490 gm (17.5 oz.)	G. Rogers (*in litt.*)
Ruffed grouse			
Male	604–654 gm (21.5–23.3 oz.)*	770 gm (27 oz.)	Nelson & Martin, 1953†
Female	500–586 gm (17.9–20.9 oz.)*	679 gm (24 oz.)	Bump et al. 1947
Greater prairie chicken			
Male	992 gm (35 oz.) (22 birds)	1361 gm (48 oz.)	Nelson & Martin, 1953†
Female	770 gm (29 oz.) (16 birds)	1020 gm (36 oz.)	Nelson & Martin, 1953†
Attwater prairie chicken			
Male	938 gm (33.1 oz.) (10 birds)	1135 gm (40 oz.)	Lehmann, 1941
Female	731 gm (25.7 oz.) (6 birds)	785 gm (28 oz.)	Lehmann, 1941
Lesser prairie chicken			
Male	780 gm (27.6 oz.) (20 birds)	893 gm (31.5 oz.)	Lehmann, 1941
Female	722 gm (25.5 oz.) (5 birds)	779 gm (27.5 oz.)	Lehmann, 1941‡
Sharp-tailed grouse			
Male	951 gm (33 oz.) (236 birds)	1087 gm (43 oz.)	Nelson & Martin, 1953†
Female	815 gm (29 oz.) (247 birds)	997 gm (37 oz.)	Nelson & Martin, 1953†

*Mean weights of these species vary considerably with season and/or locality.
†Reported as fractions of pounds by authors.
‡Reported as pounds and ounces by authors.
§Reported in graphic form, points interpolated.

TABLE 6

Adult Weights of Quails and Partridges

Species	*Sample Size*	*Mean Weight*	*Maximum Weight*	*References*
Long-tailed tree quail				
Male	4	433 gm (15.3 oz.)	467 gm (16.5 oz.)	Warner, 1959
Female	3	390 gm (13.8 oz.)	446 gm (15.7 oz.)	M.V.Z. data‡
Mountain quail				
Male	30	235 gm (8.2 oz.)	292 gm (10.3 oz.)	Amadon, 1943
Female	24	230 gm (8.2 oz.)	284 gm (10.0 oz.)	Miller & Stebbins, 1964
Barred quail				
Male	7	130 gm (4.6 oz.)	139 gm (4.9 oz.)	M.V.Z. data‡
Female	6	126 gm (4.4 oz.)	148 gm (5.2 oz.)	
Elegant quail				
Male	15	175 gm (6.2 oz.)	207 gm (7.3 oz.)	M.V.Z. data‡
Female	11	169 gm (6.0 oz.)	188 gm (6.6 oz.)	
Gambel quail				
Male	390	161 gm (5.7 oz.)	187 gm (6.6 oz.)	Campbell & Lee, 1953
Female	337	156 gm (5.6 oz.)	192 gm (6.7 oz.)	
California quail				
Male	418	176 gm (6.2 oz.)	206 gm (7.3 oz.)	Nelson & Martin, 1953*
Female	272	162 gm (6.0 oz.)	206 gm (7.3 oz.)	
Scaled quail				
Male	143	191 gm (6.7 oz.)	234 gm (8.2 oz.)	Campbell & Lee, 1953
Female	132	177 gm (6.2 oz.)	218 gm (7.7 oz.)	Nelson & Martin, 1953*
Bobwhite (eastern U.S.)				
Male	899	173 gm (6.1 oz.)	255 gm (9.0 oz.)	Nelson & Martin, 1953*
Female	692	170 gm (6.0 oz.)	240 gm (8.5 oz.)	
Black-throated bobwhite				
Male	3	137 gm (4.8 oz.)	146 gm (5.1 oz.)	Klaas, 1968
Female	3	139 gm (4.9 oz.)	152 gm (5.4 oz.)	Berrett, 1963
Spotted wood quail				
Male	16	300 gm (10.6 oz.)	358 gm (12.6 oz.)	Van Tyne, 1935; Hartman, 1955;
Female	5	288 gm (10.2 oz.)	316 gm (11.2 oz.)	Paynter, 1957
Singing quail				
Male	12	212 gm (7.5 oz.)	266 gm (9.4 oz.)	Warner & Harrell, 1957
Female	3	189 gm (6.7 oz.)	206 gm (7.3 oz.)	
Harlequin quail				
Male	45	195 gm (6.9 oz.)	224 gm (7.9 oz.)	Leopold & McCabe, 1957
Female	22	176 gm (6.2 oz.)	200 gm (7.1 oz.)	
Gray partridge				
Male	87	396 gm (14 oz.)	454 gm (16 oz.)	Nelson & Martin, 1953*
Female	57	379 gm (13.7 oz.)	432 gm (15.3 oz.)	
Chukar partridge (Turkish race)				
Male	44	557 gm (19.6 oz.)	631 gm (22.3 oz.)	Bohl, 1957†
Female	50	444 gm (15.7 oz.)	520 gm (18.5 oz.)	
Chukar partridge (Indian race)				
Male	20	614 gm (21.7 oz.)	722 gm (25.5 oz.)	Christenson, 1954†
Female	(both sexes combined)	501 gm (17.7 oz.)	545 gm (19.2 oz.)	

*Reported as fractions of pounds by authors.
†Reported as pounds and ounces by authors.
‡Museum of Vertebrate Zoology, University of California.

TABLE 7
Egg Characteristics and Incubation Periods

Species	*Spotting*	*Basic Color*	*Dimensions (mm)*	*Incubation (days)*	*References (for incubation)*
Sage grouse	Moderate	Buffy green or brown	55 x 38	25–27	Patterson, 1952
Blue grouse	Moderate	Buff or pale brown	48.5 x 35	24–25	Godfrey, 1966
Spruce grouse	Moderate	Buff or pale rust	43 x 31	21	Pendergast and Boag, 1971
Willow ptarmigan	Heavy	White to pale brown	43 x 31	21–22	Westerkov, 1956 Jenkins et al., 1963
Rock ptarmigan	Heavy	White to pale brown	42 x 30	21	Godfrey, 1966
White-tailed ptarmigan	Moderate	White to reddish buff	43 x 29.5	22–23	Braun, 1969
Ruffed grouse	Slight or none	Buffy white to cream	38.5 x 30	24	Bump et al., 1947
Greater prairie chicken	Slight or none	White to olive buff	43 x 32.5	24–25	McEwen et al., 1969
Lesser prairie chicken	Slight or none	White to buff	42 x 32.5	25–26	Coats, 1955
Sharp-tailed grouse	Slight	Fawn to chocolate or olive	43 x 32	24–25	McEwen et al., 1969
Bearded tree quail	None	Dirty white	46.6 x 31	28–30	this study
Barred quail	None	White	30 x 23.7	22–23	F. Strange, pers. comm.
Mountain quail	None	Pale buff to cream	34.5 x 26.5	24–25	F. Strange, pers. comm.
Scaled quail	Slight	Pale buff to cream	32.5 x 25	22–23	various studies
California quail	Moderate	Pale buff to cream	32 x 25	22–23	various studies
Gambel quail	Moderate	Pale buff to white	31.5 x 24	22	various studies
Elegant quail	None	White	34 x 24	22	this study
Bobwhite	None	White	31 x 25	22–23	Stoddard, 1931
Black-throated bobwhite	None	White to buff	30.5 x 23	24	this study
Spotted wood quail	Slight	Creamy white	40 x 29	?	Wetmore, 1965
Singing quail	None	White & yellow	31 x 25	?	Warner & Harrell, 1957
Harlequin quail	None	White	32 x 24	24–25	F. Strange, pers. comm.
Gray partridge	None	Pale olive	35 x 27	24–25	McCabe & Hawkins, 1946
Chukar partridge	Moderate	Pale brown or creamy	45 x 31	22–24	various studies

Assuming that the fresh egg has an average specific gravity of 1.08 (Barth, 1953), the preceding formula can be modified as follows:

$$\text{Weight (gm)} = .552 \times \text{length (mm)} \times \text{diameter (mm)}^2$$

Using this formula, estimated fresh weights of eggs were calculated from the linear measurements presented in table 7 and are summarized in table 8. In addition, a calculated total estimated clutch weight, based on reported average clutch sizes (see table 12), is indicated as an index to the relative physiological drain on the female in laying an entire clutch. It may be seen that a female's average clutch may represent as little as 20–25 percent of her own weight, as in spruce grouse and ptarmigan, to as much as 90 percent of her weight in certain quail species. Since some of these quail species are persistent renesters, it would seem that such a large investment of energy in a clutch is not detrimental as long as sufficient food is available. Captive bobwhites and other quail regularly lay over one hundred eggs per year (up to three hundred recorded) and may lay as many as five hundred in a lifetime (Kulenkamp and Coleman, 1968), clearly indicating their high capacity for channeling food energy into egg production.

TABLE 8

RELATIONSHIP OF ADULT FEMALE WEIGHT TO ESTIMATED EGG AND CLUTCH WEIGHTS

	Est. Egg Weight (gm)	*Percentage of Female Weight*	*Average Clutch Size*	*Percentage of Female Weight*
Sage grouse	44	3.4	7.4	25.2
Blue grouse	33	3.6	6.2	22.4
Spruce grouse	23	4.2	5.8	24.4
Willow ptarmigan	23	3.3	7.1	23.1
Rock ptarmigan	21	4.1	7.0	28.7
White-tailed ptarmigan	21	6.4	5.2	33.3
Ruffed grouse	19	3.8	11.5	43.7
Greater prairie chicken	24	3.1	12.0	37.2
Lesser prairie chicken	24	3.3	10.7	35.3
Sharp-tailed grouse	24	2.9	12.1	35.1
Mountain quail	13	4.7	10.0	47.0
Scaled quail	11	6.2	12.7	78.7
California quail	11	6.7	13.7	91.8
Gambel quail	10	6.4	12.3	78.7
Bobwhite	11	6.4	14.4	92.2
Harlequin quail	10	5.7	11.1	63.3
Gray partridge	14	3.7	16.4	60.7
Chukar partridge	24	5.4	15.5	83.7

As in nearly all birds, the contour feathers of grouse and quail are arranged in definite tracts, or pterylae, which do not differ much among the included species. The general arrangement of these tracts is shown in figure 5. At the edges of these tracts "half-down" or semiplume feathers regularly occur, and true down feathers sometimes occur on the neck and wings. There are usually numerous long and nearly hairlike filoplumes scattered among the contour feathers; these become especially conspicuous in adult male sage grouse when they are erected during display.

The general arrangement of the feather tracts is very similar in grouse and quails. The major differences to be noted are that in quails the dorsal feather tract has only a small apterium and is nearly continuous with the upper cervical tract, whereas in grouse these tracts are well separated, forming a large dorsal apterium. In quail species the lower cervical tract is also forked more anteriorly on the throat than is true of grouse (Clark, 1899). McCabe and Hawkins (1946) provide a description of the feather tracts of the gray partridge, which more closely resembles the New World quails in both these regards.

The number of primaries is the same (ten) throughout the group, but their relative lengths differ somewhat. Clark (1899) reports that in the New World quails (at least the United States genera) the longest primary is the sixth. In the North American grouse the sixth, seventh, and eighth are of about uniform length, followed by five and nine, four and ten, and finally three, two, and one. According to Clark (1899), the number of secondaries is fourteen in harlequin and scaled quail, fourteen to fifteen in bobwhites, fifteen to sixteen in the "*Lophortyx*" species, and sixteen in the mountain quail. Ohmart (1967) reports only fourteen true secondaries in both the scaled quail and the three "*Lophortyx*" species. Among the grouse they vary from fifteen to sixteen in the ruffed grouse, seventeen in the spruce grouse, eighteen in the blue, sharp-tailed, and pinnated grouse, eighteen to nineteen in ptarmigans, and twenty-one in sage grouse (Clark, 1899). In most of these species the secondaries grade gradually into the scapulars and proximal coverts and thus become very difficult to count accurately. The arrangement of the wing feathers is shown in figure 3.

Many of the New World species of quail bear elaborate crests that may be similar or different in the sexes. These insert in a distinctive arrangement on the crown. In the mountain quail this crest is made up of two feathers, while in "*Lophortyx*" six to nine are present. Although the scaled quail lacks such a distinctive crest, it too has an arrangement of ten crest feathers similar to that found in the typically crested species (Ohmart, 1967).

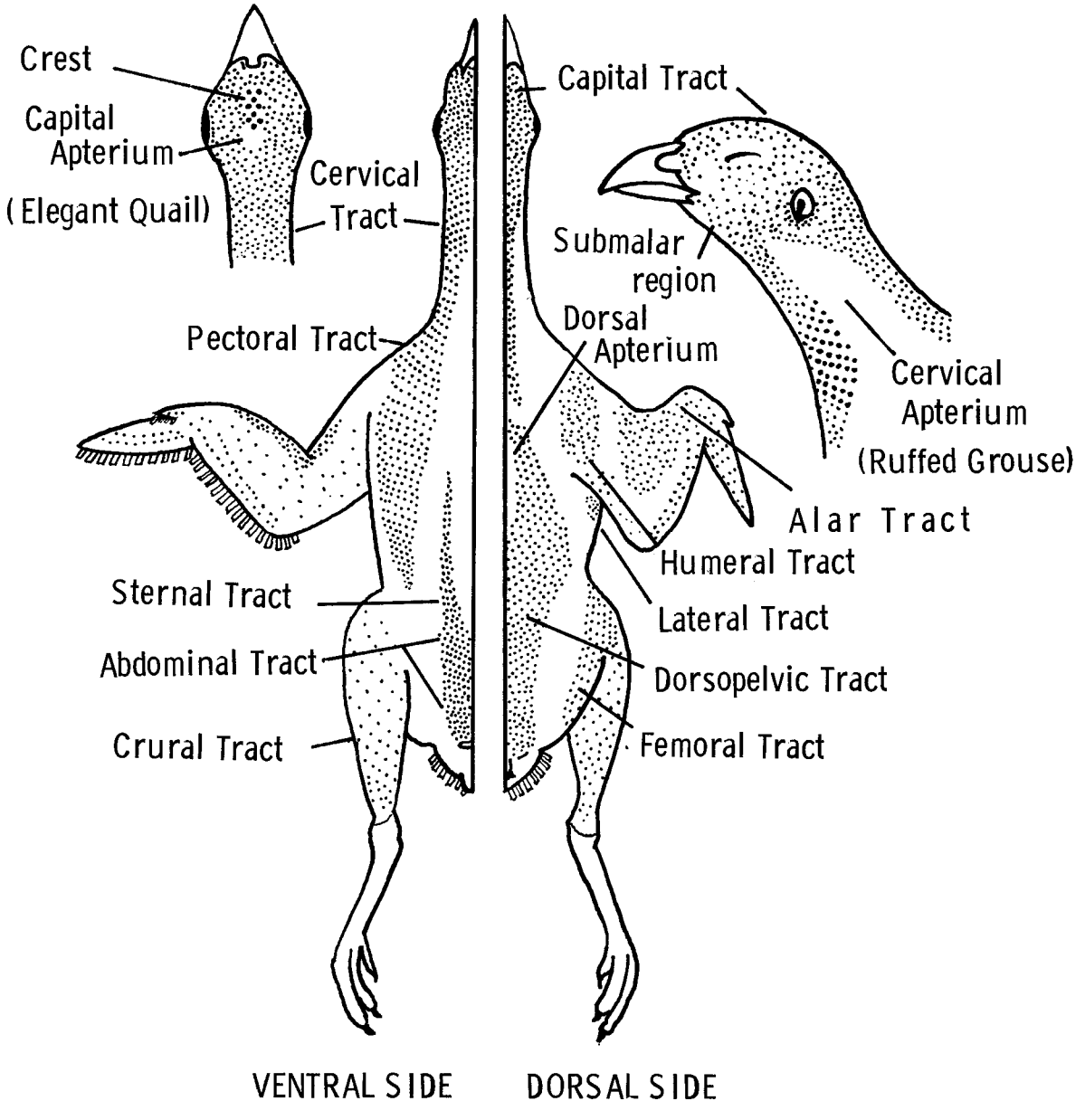


FIGURE 5. Feather-tracts of grouse and quails (primarily after Ohmart, 1967, and Clark, 1899).

None of the grouse species possess such elaborate crests, but several have special tracts of feathers on the neck or have unfeathered areas in this region. In the ruffed grouse, the special "ruff" feathers are borne on the lateral branches of the lower cervical tract, and there is no marked apterium between the lower and upper cervical tracts. However, the dozen or so feathers making up the pinnae of the pinnated grouse are similarly borne on each side of the upper cervical tract, below which is a large apterium (Clark, 1899). In the greater prairie chicken this apterium is yellowish in color, presumably because of subcutaneous fat, whereas in the lesser prairie chicken it is more reddish. The sharp-tailed grouse has a similar apterium which appears reddish to violet when expanded by esophageal inflation, but this species lacks specialization of the feathers above and below. The sage grouse lacks lateral neck spaces, but there is a large and somewhat oval apterium on each side of the neck, located quite low and somewhat frontally. These spaces are about 45 by 25 millimeters in older males, and about 25 by 13 millimeters in females (Brooks, 1930). The bare skin is olive gray, but appears yellowish when expanded during display. The lower and laterally adjacent breast feathers of male sage grouse are curiously bristly, which was once thought to be a result of wear, until Brooks (1930) discovered that newly grown feathers have the same appearance. They evidently produce the rasping or squeaking sound made when the foreparts of the wings are brushed over the lower breast during display (Lumsden, 1968).

Although the blue grouse lacks such specialized feathers on the neck, males do expose rounded areas of the neck during "hooting," which are emphasized by the whitish bases of the surrounding neck feathers. The exposed skin in these areas varies from a condition (in the interior races) of being thin, flesh-colored, and changing to purplish red when expanded to (in the coastal races) being highly thickened, gelatinous, and corrugated, and of a deep yellow color. These conditions presumably result from subcutaneous fat deposits, which are less evident during the nonbreeding periods (Brooks, 1926).

As has been mentioned, the sharp-tailed grouse lacks specialized neck feathers associated with display, but Lumsden (1965) has found that the tail feathers are unusually developed in this species and are related to the tail-rattling noises made during display. The rectrices in males are very stout basally but taper rapidly. Ventrally the shaft projects in two keels, but dorsally the shaft is rounded and projects only slightly. The outer webs of the vanes are stiff and curve sharply downward, and the inner webs are also thickened. Each clicking sound is produced by lateral feather movements, during which the inner web catches on the ventrally projecting shaft of the inwardly adjacent feather web, and after some resistance the two

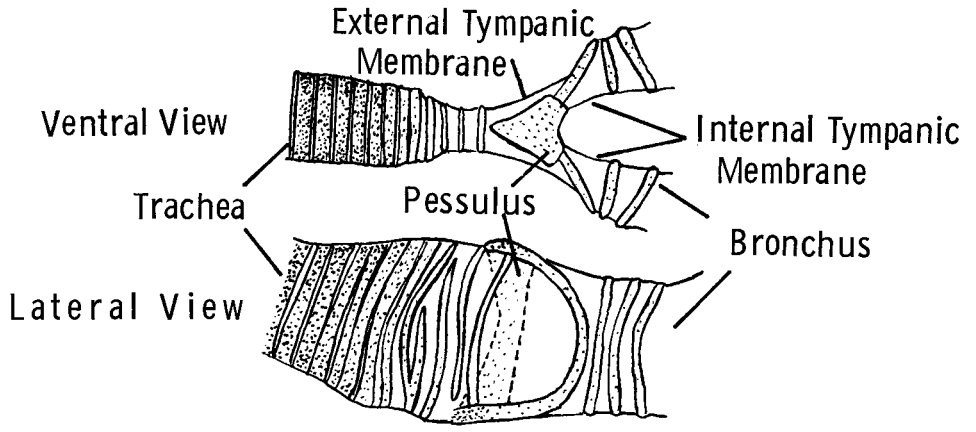
disengage, producing a click. Simultaneously the curved outer webs brush over the dorsal surface of the next outwardly adjacent feather, producing a scraping sound. Additional nonvocal noise in males of these species may be produced by foot stamping, and to a lesser degree the same can be said for the pinnated grouse. In the greater, Attwater, and lesser prairie chickens tail-spreading or tail-clicking noises that are taxon-typical occur during display (Sharpe, 1968).

VOCAL APPARATUS AND SYRINGEAL SOUND PRODUCTION

In addition to the nonvocal means of sound production such as the feather-scraping, foot-stamping, and wing-clapping sounds made either during flight as in *Dendragapus* (Wing, 1946) or while on the ground as in ruffed grouse, sound can also be produced by internal means. These include sound production by the syrinx in conjunction with the inflation and deflation of the esophageal "air sacs" of various grouse, and by the syrinx alone in all species of grouse and quails.

The anatomy of the syrinx of grouse and quail is relatively simple, and is quite similar to that of the domestic fowl, as described by Myers (1917) and Gross (1964). A diagram of the syringeal anatomy of the domestic fowl and a representative species of grouse is shown in figure 6.

The syrinx of gallinaceous birds is tracheo-bronchial in location; that is, it occurs at the junction of the trachea and the paired bronchi. The syrinx consists of a variable number of partially fused tracheal rings, collectively called the tympanum. The bony structure that is located at the junction of the trachea and the two bronchi is the pessulus, which provides important support for the two pairs of tympaniform membranes. One such pair consists of the external tympaniform membranes that are located between the fused tympanum-pessulus complex and the first pair of bronchial rings. A second pair of internal tympaniform membranes are situated medially between the pessulus and the second pair of bronchial rings. The tension on these membranes can probably be increased either by stretching the neck or by pulling the trachea forward through the action of the *tracheolateralis* muscles. The tension can also be reduced by contracting the *sternotrachealis* muscles, which insert anteriorly to the syrinx on the sides of the trachea. When these latter muscles are in a normal state of tension the internal and external tympaniform membranes are held well apart and air can pass unimpeded between them. When the muscles are contracted, however, the membranes are brought closer together and air resistance builds up pressure in



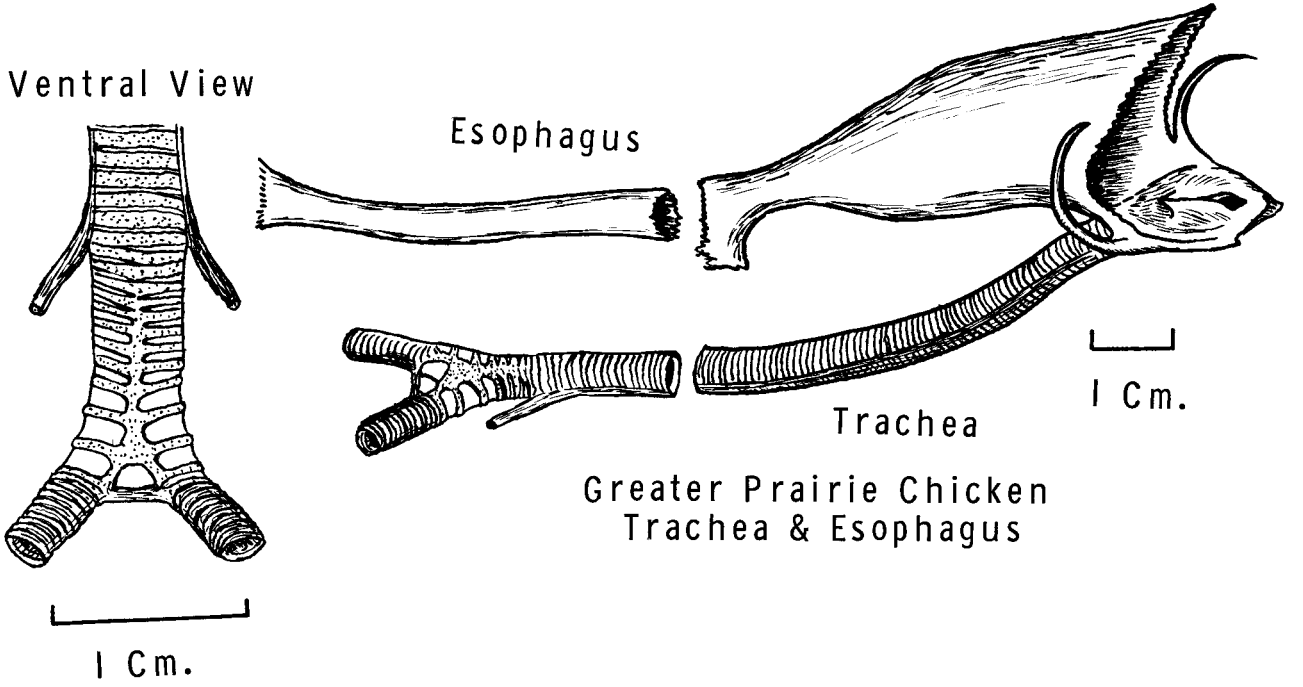


FIGURE 6. Syringeal anatomy of the domestic fowl (above, after Gross, 1964) and a male prairie chicken (below, original).

the bronchi, lungs, and air sacs. As air then passes outward between the membranes they are drawn more closely together and are set into vibration (the Bernoulli effect) thus producing sound (Gross, 1964).

In domestic fowl at least, the frequency (pitch) of the induced vibrations and associated sound production can be increased by stretching the tympaniform membranes and thus increasing membrane tension (Harris, Gross, and Robeson, 1968). Simply changing the length of the tracheal tube within the limits imposed by anatomy evidently has little effect on the fundamental frequency established by the surface dimensions and tension of the tympaniform membranes. Since smaller species have tympaniform membranes narrower in width it is not surprising that the fundamental frequencies of their calls average somewhat higher than the corresponding calls of larger relatives (Sutherland and McChesney, 1965). The fundamental frequency of vocalizations in similar-sized species having essentially identical syrinxes is thus regulated by the tension of the tympaniform membranes, which vibrate at a rate that is proportionate to the square root of their tension (Harris, Gross, and Robeson, 1968).

In species such as the turkey which have an interbronchial ligament posterior to the tympaniform membranes, posterior movement of the trachea and syrinx caused by contraction of the *sternotrachealis* muscles cannot force the bronchi back very far and instead alters the shape of the syrinx. Specifically, the internal and external tympaniform membranes are pushed closer together and the latter are stretched, thus increasing the fundamental frequency (Gross, 1968).

It is also clear that two different fundamental frequencies are sometimes simultaneously produced by one bird. This "internal duetting" is theoretically explainable by assuming that each side of the syrinx can operate independently of the other (Greenewalt, 1968), or perhaps there is a simultaneous activation of the internal and external tympaniform membranes under differential tension.

Few if any of the vocal sounds produced by grouse and quails are pure tones, rather, in addition to a basic or fundamental frequency that is generated by the vibration of the tympaniform membrane, there are usually also a considerable number of higher overtones or harmonics, which are progressive multiples of the fundamental frequency. These harmonics are of varying loudness, or amplitude, since they are differentially amplified or dampened by the resonating characteristics of the tracheal tube and pharynx. The acoustical effect of the trachea, oral cavity, and beak is thus to tune the bird's vocalizations to a resonant frequency which serves to sharpen the pitch and, perhaps, to reduce the number of harmonics (Harris, Gross, and Robeson, 1968).

There is no direct relationship between the fundamental frequency of a vocalization (which is regulated by the vibrations of the tympaniform membranes) and the resonant frequency, which is determined by physical characteristics such as the length of the tracheal tube and its associated resonating structures. The resulting sound is therefore a composite of these two independently determined acoustic characteristics. Although as an individual animal matures, the growth of its syrinx and trachea results in a concomitant lowering of both the fundamental frequency and the resonant frequency, those two variables can also have contrasting effects. For example, during "head-throw" calls the increased tension on the tympaniform membranes causes an increase in the fundamental frequency, while the stretching of the tracheal tube results in a lowering of the resonant frequency.

By means of a simple formula, the expected resonant frequency and its associated harmonics can readily be calculated for a tracheal tube of any length. Harris, Gross, and Robeson (1968), for example, compared such calculated frequencies with the observed frequencies that they generated by using differing lengths of an excised trachea and syrinx from a domestic fowl. They concluded that the trachea and bronchi combine acoustically to form a single resonant tube, and the formula they used indicates that they assumed that the combined structures represent a closed-tube acoustical system. However, Sutherland and McChesney (1965) made somewhat similar calculations for calls recorded from live individuals of two species of geese, and concluded that the vocal apparatus had resonance characteristics more closely related to those of an open tube than those of a closed tube. Thus, in an open-tube sound system only the odd-numbered harmonics above the resonant frequency should be expressed, whereas in a closed-tube system both the even-numbered and odd-numbered harmonics will be amplified. In figure 7 the calculated resonant frequencies and expected harmonics are shown for open-tube and closed-tube tracheal tubes ranging in length from five to twenty centimeters, and for frequencies up to eight thousand Hz. A comparison of these curves with the harmonic patterns produced by quail and grouse species (see Sonagrams in figures 18 to 20) will illustrate the point that an open-tube acoustic system appears to be present in grouse and quail vocalizations. We may conclude, therefore, that the fundamental frequencies of these birds' vocalizations result from the vibration rates of the tympaniform membranes but that the relative amplitudes of the fundamental frequencies as well as their associated harmonics are differentially amplified or dampened according to the resonance characteristics of the tracheal tube and pharynx.

In male grouse of those species that inflate their esophageal "air sacs" during sound production, additional complexities arise. This vocal process

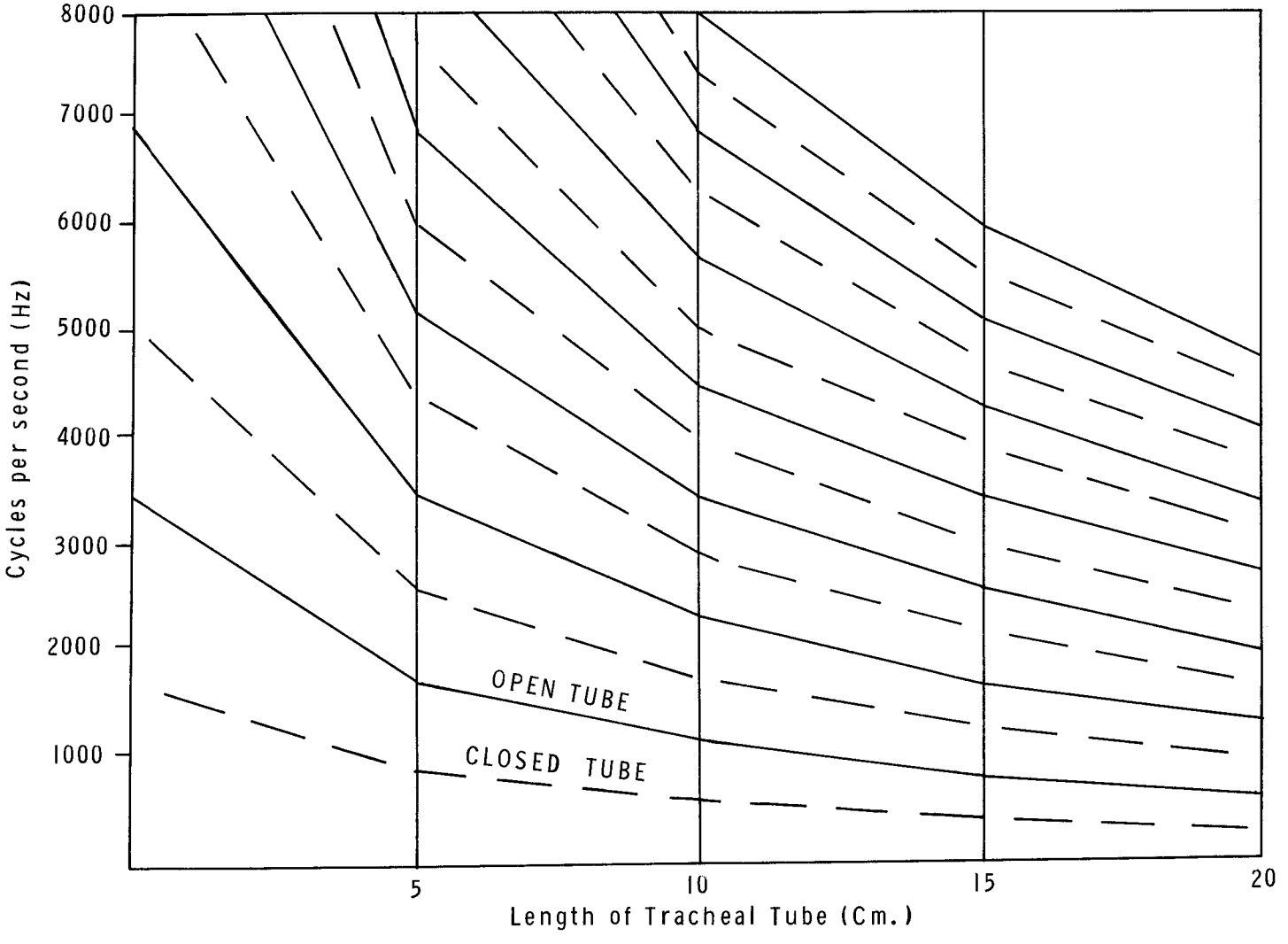


FIGURE 7. Expected harmonics of open- and closed-tube resonating tubes of varying lengths.

has been studied by Gross (1928) for the pinnated grouse, and presumably the same principle applies to the other species. When this species "booms," the beak is closed, the tongue is raised upward against the roof of the mouth, and the internal nares become blocked. The glottis thus opens directly in front of the esophagus, and the latter fills with air passing out of the trachea. The expanded anterior end of the esophagus then becomes part of the resonating structure, and the total length and volume of the sound chamber is considerably increased. This combination of the trachea and esophagus is acoustically similar to that of a cylindrical tube and an associated expansible chamber. The resonant frequency of such a combination of tube and cavity is inversely proportional to the volume of the cavity (Harris, Gross, and Robeson, 1968). This clearly accounts for the low fundamental frequency characteristics of such calls (under two hundred Hz.). Besides having the obvious visual signal value associated with the inflation of the unfeathered neck region, these low frequency sounds have considerably greater carrying power than do high frequency sounds of the same amplitude. Alfred Gross (in Bent, 1932) has mentioned that the booming sounds of the heath hen sounded softer than did the bird's more typical calls, yet carried considerably further. The ecological value of booming is thus clearly apparent.

OTHER ANATOMICAL AND PHYSIOLOGICAL ADAPTATIONS

In common with many other gallinaceous birds, the grouse and quails possess a blind sac on the dorsal wall of the cloaca, which is called the bursa of Fabricius (figure 8). In younger birds this typically opens directly into the cloaca, while in sexually mature birds it regresses in size and may completely disappear. The bursa does not always open into the cloaca and instead may be occluded by a thin membrane, so its presence cannot in all cases be detected by probing. The function of the bursa is now known to be that of antibody production (Warner and Szenberg, 1964), and its removal or inactivation interferes with immunological processes in the animal. Since the relative size and activity of the bursa decreases with age, this structure has been used as a supplementary means of estimating age in gallinaceous birds. Gower (1939) indicates its usefulness through the first November of a bird's life in determining the ages of ruffed, sharp-tailed, pinnated, and spruce grouse, as well as the gray partridge. It also has some limited value in estimating ages of California quail (Lewin, 1963), but the age-related differences in upper primary covert coloration in this group are obviously much more convenient.

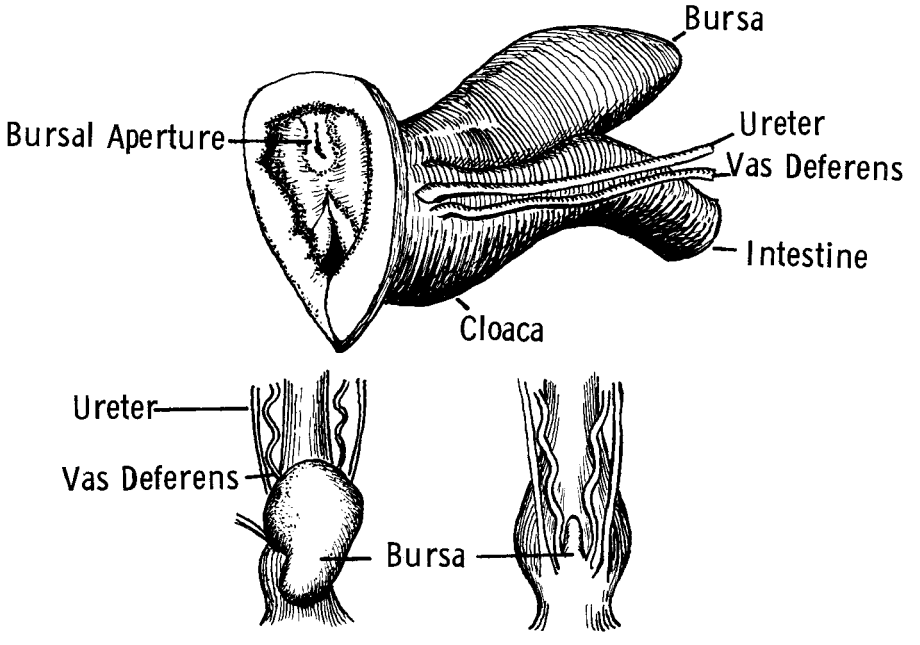


FIGURE 8. The Bursa of Fabricius in lateral view (above) and dorsal view (below) (after Godin, 1960).

IMMATURE ADULT

In most or all of the Galliformes, another outpocketing of the digestive tract occurs at the junction of the small and large intestines. Here a pair of caeca occur, which vary greatly in length among different species but are particularly long in the grouse. The function of these caeca is apparently primarily to provide a place for the bacterial breakdown on cellulose and similar fibrous materials that cannot be handled by the digestive enzymes produced by the bird. Leopold (1953) surveyed the relative development of these caeca in grouse and quail species, and found that most North American grouse with adult weights of about five hundred grams have caeca averaging about forty-four centimeters in length, with the sage grouse having the longest caeca (sixty-eight to seventy-eight centimeters) of all species studied. By comparison, although gray and chukar partridges also weigh nearly five hundred grams, their caeca lengths averaged about seventeen centimeters. Adult quail, ranging in weight from about one hundred and seventy to two hundred and fifty grams, had caeca lengths of from ten to seventeen centimeters. Additionally, grouse, which are generally herbivorous, exhibited somewhat longer total intestine lengths than did quail, which are largely granivorous. These findings support the idea that the adaptive function of the caeca in grouse species is to provide for bacterial decomposition of cellulose.

Another interesting physiological difference between grouse and quails is in their water requirements. Regrettably little is known of this situation in grouse, but probably only the sage grouse might be expected to exhibit physiological adaptations allowing minimal water requirements. Edminster (1954) states that young and old sage grouse can go many days without water, but that birds will travel considerable distances to water and that good populations occur only where a supply of water is available. With regard to the ruffed grouse, Bump et al. (1947) report that three of six adult birds died in less than four days when deprived of both food and water, but twelve birds all survived a period of nine days when given water but no food.

In the case of quail, it is known that at least the bobwhite, Gambel, and California quails can survive indefinitely without water if succulent food is available, but when fed only dried seeds they gradually lose weight. Minimum actual water needs for these birds when fed on a dry diet are about 1.6 milliliters of water for the Gambel quail, 1.9 milliliters for the California quail, and 4.5 milliliters for the bobwhite, representing from about 1.1 to 2.5 percent of the adult weight (McNabb, 1969). All these species absorb both water and salt in the intestine when forced to drink excessively salty water, but the Gambel quail is able to produce the most concentrated urine, while the bobwhite is least able to concentrate its urine. Thus, the water requirements of these species are in direct relationship to their relative ecological distributions.

Another physiological adaptation for desert living that Gambel and California quail exhibit is their ability to tolerate short-term body temperature increases of up to four degrees Centigrade above normal levels (Bartholomew and Dawson, 1958). The relatively small volume–to–surface area ratios of these quails also favor their survival in situations where body heat loss must be sufficient to avoid overheating (Miller and Stebbins, 1964). In contrast, the insulating values of ptarmigan plumage appear to be among the highest of any bird species yet studied (Sturkie, 1965). Apparently this high capacity for insulation in arctic species results from the barbules at the tips of the contour feathers being unusually soft and having extended processes that cling to adjacent feathers when erected, thus trapping air (Irving, 1960). The feathered legs and toes of ptarmigan probably serve both as snowshoes and insulation.

Quantitative data are still lacking, but it appears that grouse may have considerably larger hearts relative to their body size than do quails. In general, smaller birds have relatively larger hearts than do larger ones (Hartman, 1955). Yet, Johnson and Lockner (1968) report that the three species of ptarmigans have heart sizes ranging from 0.87 to 1.85 percent of the

body weight, whereas Hartman (1955) reports that in two genera of quails of smaller average sizes these ratios are only 0.34 to 0.39 percent. It is quite possible that the relatively large hearts of ptarmigans are related to their migratory movements (Irving, 1960); among the three ptarmigan species the relative heart size is not correlated with altitudinal distribution (Johnson and Lockner, 1968).

One of the interesting and reproductively significant ways in which the New World quails differ from grouse is in the tendency of male quail to take over the incubation and brooding of an abandoned nest or a group of young, sometimes allowing a female to produce a second brood. Broody behavior in these birds is associated with the development of a "brood patch," an extensively defeathered area which first forms in the area of the lateral apteria but which eventually includes much of the ventral body surface (Jones, 1969a). Unlike some passerines that have been studied, the brood patch does not develop in females before egg-laying, but rather forms during early stages of incubation. Incubation behavior evidently produces a strong release of prolactin through visual or tactile stimulation provided by the eggs, which in synergism with gonadal steroid hormones stimulates the defeathering that results in the formation of the incubation patch (Jones, 1969a). Most male quail do not form incubation patches in spite of their high prolactin levels during testis regression, but will do so if visually stimulated by the presence of an abandoned nest. In both sexes of the California quail it has been found that prolactin alone will not produce defeathering, but rather this defeathering results from synergism with estrogen, progesterone, or testosterone. In contrast to many passerines, in which only females form a brood patch in response to the synergistic effects of estrogen and prolactin, or to phalaropes, in which only males form a brood patch in response to the combined effects of testosterone and prolactin, the quails appear to provide an intermediate physiological situation that is clearly of adaptive value in this group.