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## 7 Social Behavior and Vocalizations

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# Social Behavior and Vocalizations

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ONE of the most complex and fascinating aspects of grouse and quail biology is their social behavior, particularly that related to reproduction. Natural selection in the quail group has seemingly favored the retention of a monogamous mating system with the associated advantages of maintaining the pair bond through the breeding season. This system allows the male to participate in the protection of the nest, possibly participate in incubation, and later care for the brood. It also provides the possibility, if not the frequent actuality, that the male might undertake the entire incubation or rearing of the first brood, while the female is freed to lay a second clutch and rear a second brood in a single breeding season.

In addition, within the quails may be seen a breakdown of typical avian territorial behavior patterns, probably resulting from the greater survival value of ecological adaptations favoring sociality in these birds. Not only do these fairly vocal species benefit from their mutual alarm signals by remaining together but also their small size and catholic feeding behavior reduce the likelihood that the optimal breeding densities will exceed the carrying capacities of the habitat.

By contrast, in the grouse there is a clear indication that selective pressures have favored the retention of strong territorial behavior, and there is a direct relationship between a male's capacities to establish and maintain a favorable territory and his ability to reproduce successfully. This territori-

ality perhaps results mainly from the wide variation among males in their aggressiveness and reproductive vigor but also from the possibility that in these species the carrying capacity of the habitat in relation to the population density may be more significant for the species' survival than are the advantages of sociality. Thus, territorial behavior among males is conspicuous in all the grouse species.

## EVOLUTIONARY TRENDS IN GROUSE SOCIAL BEHAVIOR

The size of the male's territory and the length of time during which it is defended vary considerably among grouse. From one possible extreme, that of defending a fairly large territory throughout the breeding season, within which a single female not only nests but she and her brood are also defended by the male, one may trace the progressive development of a reduced territorial size that is defended only until after fertilization of females has been completed and neither do the females nest within the territorial boundaries nor are they or their broods defended by the males. This trend toward the evolution of a polygamous or promiscuous mating system is associated with many parallel evolutionary trends. There is an increased pressure on males for enhancing their attraction value to females; thus a tendency exists for more elaborate or more conspicuous sexual signal systems among males. Since they no longer must remain near the female and the nest, pressures for protective coloration are countered by those of sexual selection, and increased behavioral and plumage dimorphism is to be expected.

Conspicuousness in male sexual displays can be enhanced not only by increase in body size and the exhibition of elaborate visual and acoustical signals in an individual male but also by multiplying such effects through the aggregation of several males. These counter pressures—those favoring the maintenance of definite and maximum territorial areas as a factor of reproductive success and those favoring the aggregation of several displaying males in a limited area to increase the likelihood of female attraction and reduce the danger of predators to individual males—have led directly to the evolution of arena behavior in several grouse species. This unlikely form of male communal display, in which individual male territories are closely adjacent, are relatively small, and serve only as mating stations, can evolve only under certain circumstances. First, the males must be totally freed from defending areas large enough for the females to nest within and also from defending the female during incubation and brooding. Next, the reproductive efficiency of a group of males must be greater than that of single males, either because of their greater attraction to females or because the assembled

males are relatively safer from predators than are solitarily displaying ones. Further, to assure assortative mating there must be enough individual variation among the males in aggressiveness that territorial size or location is directly related to breeding success; these variations are perhaps most likely among species that require two or more years to attain full reproductive development. In addition, if male display aggregations are to develop it must be advantageous for the less successful males to associate with the more successful ones. It may be argued that such early experience increases the male's chances of holding a larger or more centrally located territory that will be more reproductively efficient later in its lifetime. Peripheral males participating in arena displays may be regarded as apprentices which reproductively benefit more from such experience than they would from establishing independent and solitary territories.

Since arena displays among grouse might logically be expected to evolve more readily in open-country habitats than in heavily forested ones, open-country and polygamous species are preadapted for the evolution of arena behavior. It seems quite probable that the arena behavior of sage grouse evolved independently from that of the prairie grouse (*Tympanuchus*), and the corresponding behavior of the European black grouse (*Tetrao tetrix*) may also have evolved independently. This last species is actually a woodland edge form, but its arena displays occur in open heaths. The communal leks of the black grouse were the earliest of the arena displays of grouse studied, and the term *lek* is now generally applied to arena behavior of all grouse. Koivisto (1965) suggested that *display ground* be used to describe the general topographic location in which social display is performed, *arena* be used to indicate the specific area (the collective territories), and *lek* be more broadly applied to both the birds and their arena. Similarly, the term *lekking* can be used to indicate the general process of communal male display in grouse.

To illustrate how arena behavior may have gradually evolved from more typical territorial behavior, a series of representative grouse specimens may be mentioned that provide reference points along this behavioral spectrum.

Of all the grouse, the willow ptarmigan's actions come closest to the presumed ancestral (or most generalized) type of reproductive social behavior. In this species fairly large territories are established by the male in fall (at least in nonmigratory populations). These individual territories are largest for the most aggressive males, and many young or inexperienced males may be unable to establish territories, especially in dense populations. The female is attracted to a displaying male, and a firm pair bond is formed. Sometimes males form a pair bond with two females and may breed with both. Territorial displays and defense continue after the pair bond is established,

but such activities are diminished during the nesting season. At that time the male defends the female and nest and after hatching remains with the female and brood. After the brood is reared the territorial boundaries are again established.

In the rock ptarmigan and also in the white-tailed ptarmigan, the pair bond is established in the spring. At least in the rock ptarmigan, two or three females may sometimes be associated with a single territorial male, and Choate (1960) found some indications of polygamy or promiscuity in the white-tailed ptarmigan. The male continues to defend the territory while the female is incubating, although with reduced intensity, and the territory is abandoned about the time of hatching. The female and young may remain in the male's territory but are only infrequently accompanied by him, and he usually takes no part in defending the young. In the rock ptarmigan the male reestablishes his territory in the fall, while in the white-tailed ptarmigan this evidently does not occur until spring (Watson, 1965; Choate, 1963).

In the monogamous European hazel grouse (*Bonasa bonasia*), the male reportedly establishes his territory in the fall, with those in optimum habitats being the most successful in attracting females. A male usually remains on his territory, defending both it and the female during incubation and brooding periods, but only atypically performs distraction displays or utters warning calls to the female (Pynnönen, 1954). Some observers have, nonetheless, reported seeing males attending broods with females.

In the blue grouse exists a clearly intermediate stage between the one extreme of a monogamous or nearly monogamous pair bond associated with the establishment of a territory large enough to support the rearing of a brood and the other extreme of complete promiscuity and territorial defense limited to an area serving to attract females and provide a mating station. Other North American species that fall into this general category are the ruffed grouse and the spruce grouse, but the blue grouse will serve as an example.

Because of its winter migration, the blue grouse males probably first establish territories in spring. Although these areas may cover several acres, hooting is limited to particular places within the territorial boundaries. The home ranges occupied by females associated with territorial males may overlap the boundaries of several male territories. The typical mating system of blue grouse may thus be considered polygamous or promiscuous (Bendell, 1955c; Bendell and Elliott, 1967), but in local populations at least some birds may form strong pair bonds that persist until after the young hatch (Blackford, 1958, 1963). The location of the female's nest is not associated with the male's hooting sites, and the male does not defend the nest or brood. In general, male hooting sites are well separated and their

territories are not contiguous, but in a few cases apparently communal male displays involving four or more males have been observed (Blackford, 1958, 1963). Males remain on their territories until their late summer migration, well after active territorial defense ceases.

The forest-dwelling capercaillie (*Tetrao urogallus*) of Europe provides a slightly more advanced stage in the evolution of communal displays, judging from such reports as those of Lumsden (1961b). He studied an arena with three territories (varying from three hundred to one thousand square yards in area) that did not have contiguous boundaries but were separated by twenty to forty yards. Four nonterritorial males visited the arena, all of which were apparently yearlings; they performed partial sexual displays and sometimes threatened one another but were ignored by the territorial cocks, between whose territories they moved at will. Up to nine females visited the display ground at one time, and of thirteen copulations seen, twelve were performed by a single male. Dement'ev and Gladkov (1967) found that sixty-six display grounds contained 630 males, collectively averaging 9.5 males per display ground (individual averages ranging from 2 to 12 males). However, Hjorth (1970) does not consider the capercaillie to be a lek-forming species.

In the related black grouse, the seasonal maximum number of males occupying a display ground averages about nine and ranges from three to twenty-six, the strongest one or two of which ("first-class") occupy relatively central territories (Koivisto, 1965). The territories of this species are nearly contiguous and range in size from one hundred to four hundred square meters (Kruijt and Hogan, 1967). Koivisto (1965) estimated that territories in this species may range from two to two hundred square meters, with no significant differences in the sizes of territories of first-class and second-class males. Immature males, which make up about one-third of the population, are either nonterritorial and are not tolerated by territorial males, or they occupy small and peripheral territories ("third-class" males). Koivisto believed that the primary survival value of these immature birds for the group is their tendency to warn the actively displaying males of the presence of danger. He found that there is a direct relationship between age and hierarchical position in the arena, the first-class males being mature birds that are the most fit for reproduction and also are the most successful in attracting females. Of forty-seven copulations observed by him, 56 percent were performed by first-class males. The value to the species of such assortative mating and the relative protection first-class males gained from the presence of the other categories of males appeared to Koivisto to be the primary evolutionary advantages of communal male display.

Among the North American grouse, corresponding arena behavior occurs in the pinnated grouse, sharp-tailed grouse, and sage grouse. In both the

pinnated grouse and the sharp-tailed grouse, the average number of male birds occupying display grounds in general equals or exceeds the number reported for the black grouse. Copelin (1963) indicates that in the display grounds he studied the number of male lesser prairie chickens ranged from 1 to 43, and active grounds averaged 13.7 males over an eleven-year period. Robel's greater prairie chicken study area (1967) had from 17 to 25 resident males present in a three-year period. He found (1966) that 10 marked territorial males defended areas of from 164 to 1,069 square meters (averaging 518 square meters), and that the 2 males defending the largest territories in two years of study accounted for 72.5 percent of fifty-four observed copulations.

Numbers of male sharp-tailed grouse present on display grounds vary considerably with population density in Nebraska; leks of both this species and pinnated grouse average approximately 10 males, but sometimes exceed 20 and occasionally reach 40 or more. Hart, Lee, and Low (1952) reported that up to 100 male sharp-tailed grouse were observed on display grounds in Utah, but the average on twenty-nine grounds was 12.2 males. Evans (1961) confirmed that females select the most dominant males for matings, and Lumsden (1965) reported that on a display ground he studied one male accounted for 76 percent of the seventeen attempted or completed copulations seen. Scott (1950) concluded that the social organization of sharp-tailed grouse is more highly developed than that of the pinnated grouse but is not as complex as that of the sage grouse.

The sage grouse provides the final stage in this evolutionary sequence; it exhibits a higher degree of size dimorphism than any other species of North American grouse (adult weight ratio of females to males being 1:1.6–1.9), the display areas have a larger average number of participating males, and the central territories are among the smallest of any grouse species. Scott (1942) was the first to recognize the hierarchical nature of the territorial distribution pattern and to describe first-rank or master cocks, which were responsible for 74 percent of the 174 copulations that he observed. Dalke et al. (1960) reported that the territories held by master cocks were often forty feet or less in diameter, and Lumsden (1965) showed the territorial distribution of 19 males that exhibited an average distance from the nearest neighbor of about forty feet. In Colorado, 407 counts of strutting grounds indicated an average maximum number of 27.1 males present (Rogers, 1964). Patterson (1952) provided figures indicating that 8,479 males were counted over a three-year period on Wyoming display grounds, averaging about 70 males per display ground. Patterson reported one ground containing 400 males, and Scott's observations (1942) were made on a ground of similar size. Lumsden (1968) found that individual birds may have strutting areas that overlap those of other males, and that

although entire groups of males may move about somewhat, the relative positions of the males remain the same. Furthermore, large sage grouse leks may have several centers of social dominance, and Lumsden suggests that these should be called conjunct leks. He believes that yearling males are not tolerated by old males in the center of the lek but can move about fairly freely near the edges of the arena. They probably do not normally establish territories until their second year, when they may become "attendant" males with territorial status. The remarkably large size and complex social hierarchy of sage grouse leks, as well as their extraordinarily complicated strutting performances, would seem to qualify this species as representing the ultimate stage in evolutionary trends discernible through the entire group. Since sage grouse are ecologically isolated from all other grouse species and are known to have hybridized only once, it would seem that these complex behavioral adaptations are the result of intraspecific selective pressures rather than the need for reproductive isolation from related forms.

A possible index of the intensity of sexual selection in promoting sexual differences in behavior and morphology of the sage grouse was indicated earlier as weight differences between adult males and females which approach ratios of 1:2. Corresponding ratios can readily be calculated for the other grouse species from table 5 in chapter 2. For the essentially monogamous ptarmigan species these female-to-male weight ratios range from about 1:1 to 1:1.09. For the blue grouse, spruce grouse, and ruffed grouse they range from 1:1.1 to 1:1.33, and in the prairie grouse they range from 1:1.14 to 1:1.31. These data would suggest that the intensity of sexual selection insofar as it might affect weight differences in the sexes is about the same in the lek-forming prairie grouse as in the non-lek-forming but polygamous or promiscuous forest-dwelling species. Data presented by Dement'ev and Gladkov (1967) indicate corresponding weight ratios for the black grouse of from 1:1.27 to 1:1.38, and for capercaillie the estimated ratio is 1:2.28, even higher than in sage grouse. Berndt and Meise (1962) report the adult weight ratio of females to males in the capercaillie to be from 1:2.08 to 1:2.25. This species and a closely related one are by considerable measure the largest of the grouse, and the ecological implications of both total body size and sexual differences in body size of these two species are still obscure.

#### *Nonvocal Acoustical Signals in Grouse*

The feather specializations found in the sharp-tailed grouse that are related to tail-rattling have been mentioned in chapter 2; it might also be



mentioned that similar tail-rattling occurs in male sage grouse, that tail-clicking noises are made by pinnated grouse, and that a tail-swishing display occurs in Franklin spruce grouse, involving both alternate and simultaneous spreading of the rectrices (MacDonald, 1968). Likewise, foot-stamping sounds are made by males of many species; these are perhaps most apparent in the sharp-tailed grouse, but also occur in pinnated grouse, willow ptarmigan ("rapid stamping" of Watson and Jenkins, 1964), and probably other species.

A more interesting kind of nonvocal sexual signal used by male grouse is the drumming and clapping sounds made by various species, which apparently represent variably specialized or ritualized territorial flights. A rapid survey of the grouse with respect to such variations is instructive.

The territorial display flights of male ptarmigans may serve as a starting point from which the increasingly specialized variations of the other species may be derived. In the red grouse (willow ptarmigan), Jenkins and Watson (1964) report that the bird (either sex) "flies steeply upwards for about ten meters, sails for less than a second, and then gradually descends with rapidly beating wings, fanned tail, and extended head and neck. On landing, its primaries often touch the ground, and it then stands high with drooping wing, bobbing its body and fanning its tail in and out." Calling occurs during the ascent, descent, and after landing, with the loudness of the call and length of the flight varying with the bird's relative dominance.

Schmidt (1969) described the "scream flight" display of white-tailed ptarmigan, and Choate (1960) reported once seeing a male white-tailed ptarmigan fly upward in a nearly vertical flight, hovering, screaming, and gliding down in a single spiral, then landing with another scream about thirty-five feet from the starting point. This kind of flight was reported by Bent (1932) for the rock ptarmigan, in which the male flies upward thirty or forty feet, then floats downward on stiff wings until he is near the ground when he checks his descent and may sail up again, calling loudly. MacDonald (1970) has recently described this display of rock ptarmigan in considerable detail.

In the eastern Canadian and Alaskan forms of spruce grouse an apparently corresponding aerial display occurs as the male flies steeply downward out of a tree being used as a display perch, stops his descent about four to eight feet above the ground, and then descends rapidly with strongly beating wings (Lumsden, 1961a; Ellison, 1968b). In the Franklin spruce grouse males fly vertically and slowly up to a perch with whirring wings. They may then rush forward along the branch and spread the wings and tail, make three or four drum-like wing beats while standing upright, or

perform an aerial wing-clap display (MacDonald, 1968). In this display the bird takes flight and at some point pauses in mid-air with a deep wing-stroke, following which he sharply strikes the wings together above the back and drops downward to the ground, with a second wing-clap following landing.

Short (1967) noted that males of Franklin spruce grouse have outer primaries that are more indented and more closely approach those of the Siberian spruce grouse (*Dendragapus falcipennis*) than they do those of the eastern race *canadensis*; thus it is probable that similar whirring or wing-clapping sounds are made during aerial displays in the Siberian species.

Corresponding drumming flight behavior is found in the blue grouse (Wing, 1946). Bendell and Elliott (1967) report that a "flutter flight" occurs in both sexes of the sooty blue grouse (*fuliginosus*) but that the noise produced is a ripping sound and apparently is not so elaborate as in the interior populations such as *richardsonii* and *pallidus*. Blackford (1958, 1963) reports that individuals (both sexes) of the former race perform a wing-flutter (or flutter-jump) display some eight or ten inches off the ground. Males perform more extensive drumming flights; they may also exhibit a fairly sharp whipping of the wings on alighting in a tree, and sometimes produce a wing-clap, consisting of a single loud wing note, presumably made in the same manner as by Franklin spruce grouse. In typical drumming flights the male jumps from his display perch, flies strongly upwards with whirring wings, and returns after a horseshoe-shaped flight course to a point near where he started (Blackford, 1963). Aerial rotations during display flights may also occur (Wing, 1946; Blackford, 1958).

The well-known drumming display of ruffed grouse would appear to be an exaggerated version of the drumming movements of the Franklin spruce grouse or a ritualized drumming flight in which the male has substituted wing-beating movements for the actual flight. No actual flight displays are known to occur in this species, but the related hazel grouse (*Bonasa bonasia*) exhibits both wing-flapping displays and actual display flights with associated calling (Pynnönen, 1954; Schenkel, 1958). Male vocalizations in these two species are limited: hissing sounds are made by the ruffed grouse, while whistling notes are produced by the hazel hen. The typical flutter-jump display, in which males make short, nearly vertical flights with strongly beating wings and sometimes with associated vocalizations, would appear to be an alternate evolutionary modification of the territorial song flights of ptarmigan. Typical flutter-jump displays occur in the prairie

grouse and black grouse (Hamerstrom and Hamerstrom, 1960), as well as in the capercaillie (Lumsden, 1961b). Flutter-jumps of capercaillie, which have loud wing noises, are performed without associated vocalizations. Male sharp-tailed grouse only rarely utter calls at the start of these flights, which nonetheless are conspicuous in their open-country habitat. In the pinnated grouse calls may be uttered before, during, or after the display, and the black grouse utters hissing sounds during flutter-jumping. The sage grouse completely lacks a flutter-jump display, judging from all recent observations.

In summary, it would appear that the visually and acoustically conspicuous territorial flights of ptarmigans have, in the forest-dwelling grouse, been replaced by drumming, fluttering, or whirring flights; wing-clapping noises; and sedentary wing-drumming displays (table 23). In most of the lekking grouse they have been restricted to short and often quiet flutter-jumps, which are visually conspicuous in these open-country birds but are limited in length to the typically small territories.

As a final point, these aerial displays occur in both sexes of ptarmigan, are more common and better developed in males than in females of *Dendragapus* species, and are performed only by males in the lek-forming species of grouse. Ultimately, in the heavy-bodied sage grouse with its closely packed leks, the flutter-jump display has been lost altogether. Lumsden (1968) has suggested that the rotary wing movements made during strutting may represent the last vestigial remnants of the sage grouse's flutter-jump display.

The summary of major male social signals of grouse (table 23) may be compared with figure 16, which illustrates representative display postures of six grouse species, although it should be emphasized that these postures are not homologous in all cases. Rather, the drawings illustrate species-specific plumage characteristics that probably provide significant visual signals during display.

For additional comparison, table 24 provides a corresponding summary of male plumage features, postures and calls of representative New World quail species, which are also believed to provide species-specific signals in this group. Details on the acoustical and possible motivational variations in the calls listed and their apparent functions may be found in the individual species accounts, and the summary here is intended only as a general comparison with the grouse signals summarized in table 23. Corresponding postures assumed by male quails and partridges during the performance of some of these displays are illustrated in figure 17, which likewise are further explained in individual species accounts.

TABLE 23  
SUMMARY OF MAJOR MALE SOCIAL SIGNALS IN REPRESENTATIVE GROUSE SPECIES

	Major Male Display Features		Major Male Acoustical Signals		Major Male Display Postures and Movements		
	"Air Sacs"	Eye-comb	Vocal	Non vocal	Aerial	Strutting*	Other Displays
Sage grouse <sup>1</sup>	Yellowish	Yellow	<i>Wa-um-poo</i> Grunting	Wing-rustling Tail-rattling Air sac "plop"	None	Tail fanned equally	Shoulder spot
Blue grouse <sup>2</sup>	Yellow to reddish	Yellow to reddish orange	Hooting <i>Oop</i> call	Wing-clapping Wing-drumming	Drumming flight Flutter-jump	Tail fanned, tilted strongly	Short run with head low
Spruce grouse <sup>3</sup>	None	Red	Hooting Snoring	Wing-clapping Wing-drumming	Drumming flight	Tail fanned, "swished" laterally	Head-jerk with squatting Foot-tramping
Willow ptarmigan (red grouse) <sup>4</sup>	None	Red	Hissing <i>Kohwayo/Kohway/Korow/Ko Kok/Ka</i> etc.	Rapid stamping (audible?)	Flight song	Tail fanned, tilted strongly	Waltzing (circling) Rapid foot-stamping Bowing Walking in line Crouching with head-wagging
Ruffed grouse <sup>5</sup>	None	Orange (small)	Hissing	Wing-drumming	None	Tail fanned, tilted slightly	Short run Rotary head-shake
Pinnated grouse <sup>6</sup>	Yellow to red	Yellow	Booming or Gobbling, Cackling <i>Pwoik</i> , etc.	Tail-snapping Foot-stamping	Flutter-jump	Tail spread, snapped shut	Shoulder spot Circling Nuptial bow Running parallel
Sharp-tailed grouse <sup>7</sup>	Purplish to red	Yellow	Cooing Cackling <i>Lock-a-Lock</i>	Tail-rattling	Flutter-jump	Tail slightly spread, shaken rapidly Wings spread	Shoulder spot Circling Nuptial bow & posing Running parallel Foot-stamping (dancing)

\* "Strutting" refers to high-intensity ground display; tail-cocking and wing-drooping present in all species

1. Based on Lumsden, 1968

2. Based on Brooks, 1926, and others

3. Based on Lumsden, 1961a, and MacDonald, 1968

4. Based on Watson and Jenkins, 1964

5. Based on Bump et al., 1947, and others

6. Based on Sharpe, 1968, and Hamerstrom and Hamerstrom, 1960

7. Based on Lumsden, 1965

TABLE 24  
SUMMARY OF MAJOR MALE SOCIAL SIGNALS IN REPRESENTATIVE QUAIL SPECIES

	Major Male Display Features		Major Male Display Postures		Major Male Sexual and Agonistic Calls				
	Throat	Crest	Frontal	Lateral	High intensity threat	Low intensity threat	Tidbitting	Separation	Advertising
Mountain quail <sup>1</sup>	Chestnut	Straight, narrow	Wings partly spread	Poorly developed(?)	...	...	...	Kow (repeated)	Plu-ark
Scaled quail <sup>2</sup>	Buff	Straight, bushy	Wings drooped Head raised Crest up or down	Flanks spread Crest raised	Head-throw call	...	...	Pay-cos	Whock
Gambel quail <sup>3</sup>	Black	Recurved "Teardrop" black	Wings drooped Head raised Crest up or down	Flanks spread Body-shake Wing-flap Ground-pecking	Meah (with chin-lifting) Wit-wut-whrr	Wit-wut	cu-cu	Ka-KAA-ka-ka	Kaa
California quail <sup>4</sup>	Black	Recurved "Teardrop" Black	Wings drooped Head raised Crest up or down	Flanks spread	Squill (with head-throw)	Wip-wip	tu-tu	Ca-ca'-caw	Cow
Bobwhite <sup>5</sup>	White & black	None	Wings spread Head low	Flanks spread	Hao-po-weih (Caterwaul)	Hoy Hoy-poo Squee	tu-tu	Koilee	Bob-white

1. Based on previously unpublished studies
2. Based on previously unpublished studies
3. Based in part on Ellis & Stokes, 1966
4. Based in part on Williams, 1969
5. Based in part on Stokes, 1967

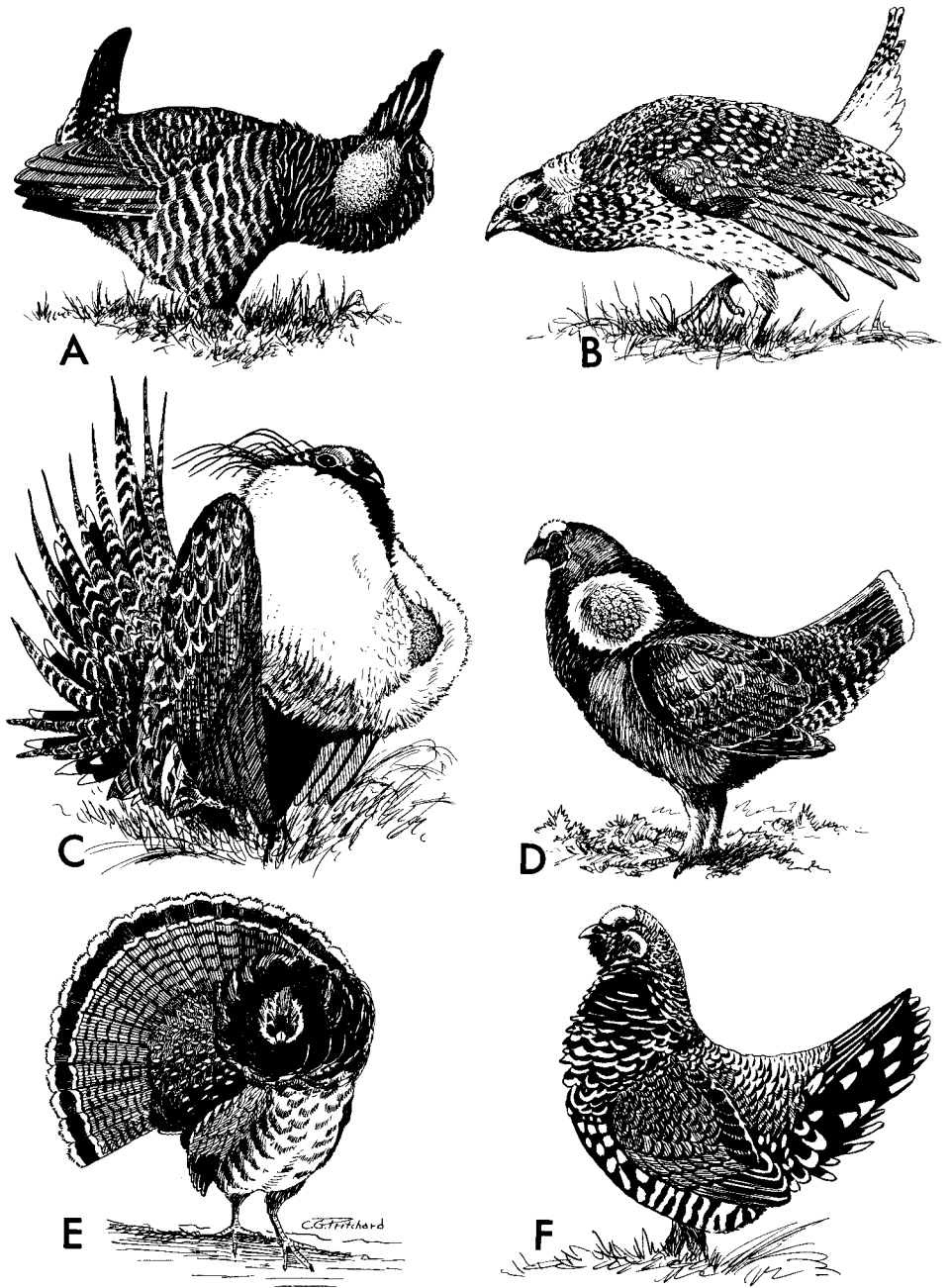


FIGURE 16. Male display postures of representative grouse, including (A) booming by greater prairie chicken, (B) dancing of sharp-tailed grouse, (C) strutting of sage grouse, (D) hooting of blue grouse, (E) strutting of ruffed grouse, and (F) strutting of spruce grouse. (From *Animal Behavior*, Wm. C. Brown Co.)

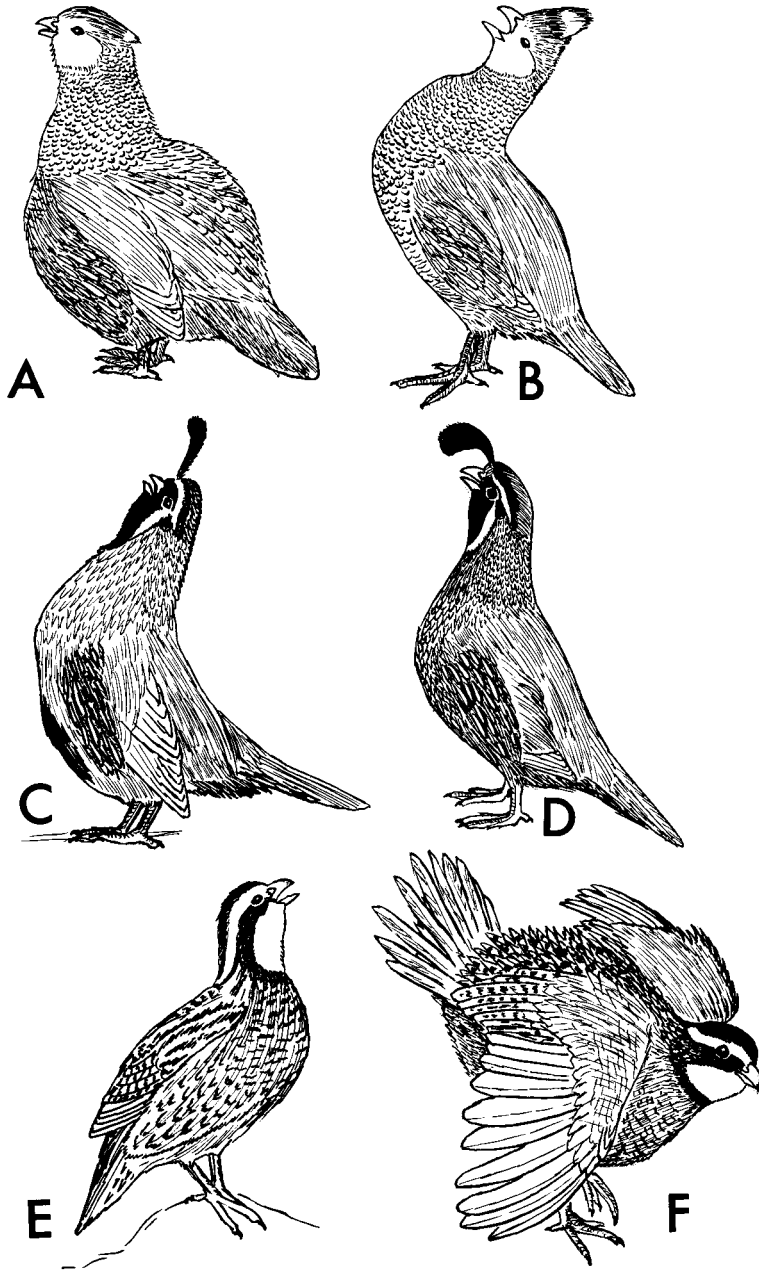


FIGURE 17. Male display postures of representative quails, including (A) scaled quail uttering *pay-cos* call, (B) scaled quail uttering head-throw call, (C) Gambel quail uttering *meah* call, (D) California quail uttering *squill* call, (E) bobwhite uttering *Bob-white*, and (F) bobwhite performing forward threat display. (Original, based on photographs.)

## EVOLUTIONARY TRENDS IN VOCALIZATIONS OF NEW WORLD QUAIL

In contrast to the grouse, in which sexual behavior patterns are closely related to and in general derived from aggressive behavior related to territorial establishment and maintenance, no such nucleus of basic social behavior patterns exists in the New World quail species. Thus, whereas in the grouse sexually active females can be selectively attracted to displaying males on the basis of male signals that perhaps originally served as male-to-male agonistic signals, the high degree of gregariousness and absence of well-defined social hierarchies in quail coveys have not promoted the evolution of elaborate male-to-male aggressive signals. Instead, a considerable number of social signals are typically present that have such functions as maintaining contact among members of a social unit, warning others of danger, and reassembling the group after forced separation.

Perhaps partly because of their vulnerability to various predators but also because of the ecological advantages of using acoustic rather than visual signals for communication, the quails in general have tended to specialize in vocalizations that serve to integrate their social requirements instead of evolving elaborate long-distance visual communication systems. There is certainly no question that species-specific body movements and postures do occur in many species (see table 24), but these are in general performed between specific individuals at close range, instead of being generally broadcast and widely visible, as is the case, for example, with the territorial display flights of ptarmigans, the flutter-jumps or drumming flights of various grouse, or the "air sac" flashing of the lekking grouse. One must therefore look for possible evolutionary origins of quail social signals among such sources as the basic sounds used by parents to coordinate brood activities and those uttered by young birds to maintain or regain contact with their parents. Stokes (1967) has shown that the "lost" call of bobwhite chicks develops with increasing age directly into the separation, or "scatter," call that serves to reassemble broken coveys and during the breeding season serves to reunite separated mates. With some modifications, this same separation call also serves in males of *Colinus* and *Callipepla* as the basis for the unmated male advertisement call. With slightly different modifications, the call is also used by paired birds during encounters with others and serves to repel them. Thus a single type of chick vocalization, through ontogeny and sexual or intensity modifications, acquires at least four fairly distinctive communication functions among bobwhite adults.

Regrettably little is known so far of the acoustical communication systems of the morphologically primitive species of New World quails that are



found primarily in tropical forests, other than the fact that well-developed vocal communication systems (often involving duetting) do occur. Indeed, future studies may prove that these species are actually quite highly specialized in this regard, judging from the apparent complexity and diversity of the calls that have so far been described among them. Instead of trying to generalize from this group, it is more practical to examine the social behavior patterns and vocalizations of the more northerly and arid-habitat genera, such as *Colinus*, *Callipepla*, and related forms. Several species from this group have been well studied behaviorally, and some evolutionary trends in behavior and vocalization may readily be detected.

Judging from observations of all four species of *Callipepla* and the bobwhite and limited information on the mountain quail, a major part of the vocabularies of these species is concerned with the coordination of pair and flock activities (table 25), with the same calls serving to keep the pair intact during the breeding season as those used by the covey for that purpose during the rest of the year. This requirement for individual recognition of the mate's separation call can readily be demonstrated under controlled laboratory conditions. The separation call, or a modification thereof, also typically serves as the advertisement call of unpaired males. In this situation the call is usually uttered from a conspicuous and often regularly used location, but in spite of these characteristics it should not be regarded as typical territorial behavior (see chapter 5). In addition, calls that are uttered by members of the flock during foraging are the same as those used by males of those species that perform the "tidbitting" display (Domm, 1927), which evidently plays an important role in establishing and maintaining the pair bond.

All the American quails and Old World partridges studied so far have several well-developed alarm signals, which usually include distinctively different notes for ground and for aerial predators, as well as more general alarm and escape notes (table 25). Although a few species may assume silent "freezing" positions (e.g., bobwhites, harlequin quail), species of the genus *Callipepla* more typically respond to threats by fleeing on foot while uttering rapidly repeated alarm notes.

The sexual and agonistic vocalizations of quail are not especially numerous, which is not surprising in view of their poorly developed social hierarchies and lack of aggressive territoriality. In *Callipepla* species, males utter two different calls in agonistic (mostly male-to-male) situations. These include a series of rather soft and frequently repeated threat notes, as well as a single louder call, sometimes repeated, that is usually associated with neck-stretching and tossing the head backward varying amounts, thus exposing the distinctive throat markings (figure 17). This latter display

TABLE 25  
SUMMARY OF ADULT VOCALIZATIONS IN THREE QUAIL AND PARTRIDGE SPECIES

	<i>Bobwhite</i> <sup>1</sup>	<i>California Quail</i> <sup>2</sup>	<i>Chukar Partridge</i> <sup>3</sup>
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I. Flock and pair activities (both sexes)

A. Covey or pair separation	2*	1	1
B. Covey or pair contact	2	1	1 (male only)
C. Feeding (and male tidbitting display)	1	1	1 or 2
Subtotals	5	3	3 or 4

II. Avoidance of enemies (both sexes)

A. Flying predator alarm	1	1	1
B. Ground predator alarm	1	1	1
C. General alarm & escape	2*	2	1
D. All's well (male only)	—	—	1
E. Hand-held distress	1*	1	(same as B)
Subtotals	5	5	4

III. Sexual and agonistic

A. Unmated male advertisement	1	1	1
B. Waltzing display (male)	—	—	1
C. Aggressive (mostly male)	3	2	2
D. Submissive (male & female)	1	1	1
E. Nesting (male & female)	1	1	1
F. Copulation	1 (female)	1 (both sexes)	1 (male)
Subtotals	7	5	7

IV. Parental (both sexes)	2†	1†	—?†
TOTALS	19*	14	14-15

1. Based in part on Stokes, 1967 (who considers four variants as separate calls)

2. Based in part on Williams, 1969

3. Based in part on Stokes, 1961

\* Plus additional variants

† Excluding calls from other categories above

is one of the few in which sounds and body movements are closely integrated into a complex display in the New World quails. In the bobwhite the corresponding call (called the caterwaul) is not associated with head movements, but is more complex acoustically. This species also has a conspicuous frontal threat posture involving wing-spreading that is less highly developed in *Callipepla*.

In the American quails and Old World partridges, unlike most grouse, vocalizations are typically associated with copulation. In the quail species studied so far, these calls are uttered by the female and sometimes also by

the male during treading. In the Old World genus *Alectoris* the male utters a copulation-intention call. Choate (1960) has reported the only copulation calls by grouse known to me, and states that calling by both sexes occurs during treading in the white-tailed ptarmigan. Watson and Jenkins (1964) state that the male red grouse does not call until copulation is completed and that the female remains silent.

As indicated in table 25, some fourteen or more calls (Stokes, 1967, reports twenty-four for the bobwhite) can be detected in the quail and partridge species so far studied, more or less equally divided among the categories of general social activities, avoidance of enemies, and sexual and agonistic signals. Sexual dimorphism in quail vocalizations is restricted, being generally limited to calls that serve to advertise the presence of unmated males or which are given only by males in agonistic situations.

It is of interest to compare these quail vocabularies with some reported for grouse species. One of the most complete surveys of grouse vocalizations is that of Watson and Jenkins (1964) for the red grouse, which is summarized in table 26. For a contrast with the monogamous grouse, in which all of the calls are common to both sexes, two lek-forming species of prairie grouse are also included in the table. Data on the sharp-tailed grouse are based on the observations of Lumsden (1965), whose study did not include possible female parental calls but is otherwise apparently comprehensive. Vocalizations of the pinnated grouse are generally so similar to those of the sharp-tailed grouse that they can be comparably organized, but no single paper adequately summarizes the call repertoire of this species. Some parental calls are mentioned by Gross (in Bent, 1932), while Lehmann (1941) and various other authors have discussed the sexual and agonistic calls of pinnated grouse. Evidently no special calls in this species serve to announce the presence of enemies; the birds typically freeze or squat silently, not giving their alarm notes until taking flight (Hamerstrom, Berger, and Hamerstrom, 1965; Berger, Hamerstrom, and Hamerstrom, 1963). Lumsden (1965) reported a possible preflight alarm note in the sharp-tailed grouse, but indicated that three silent alarm postures are usually assumed by birds when they are disturbed.

In contrast to quail, it may be seen not only that the lek-forming grouse have virtually no flock or pair integration vocalizations and very few calls that serve to provide a general alarm but also that there are a large number of male agonistic and sexually related calls. These calls are generally uttered less frequently or not at all by females. Apparent intensity differences make it difficult to judge how many male calls should be recognized, but this is to be expected considering the close relationship between male social structure and reproductive efficiency in these species.

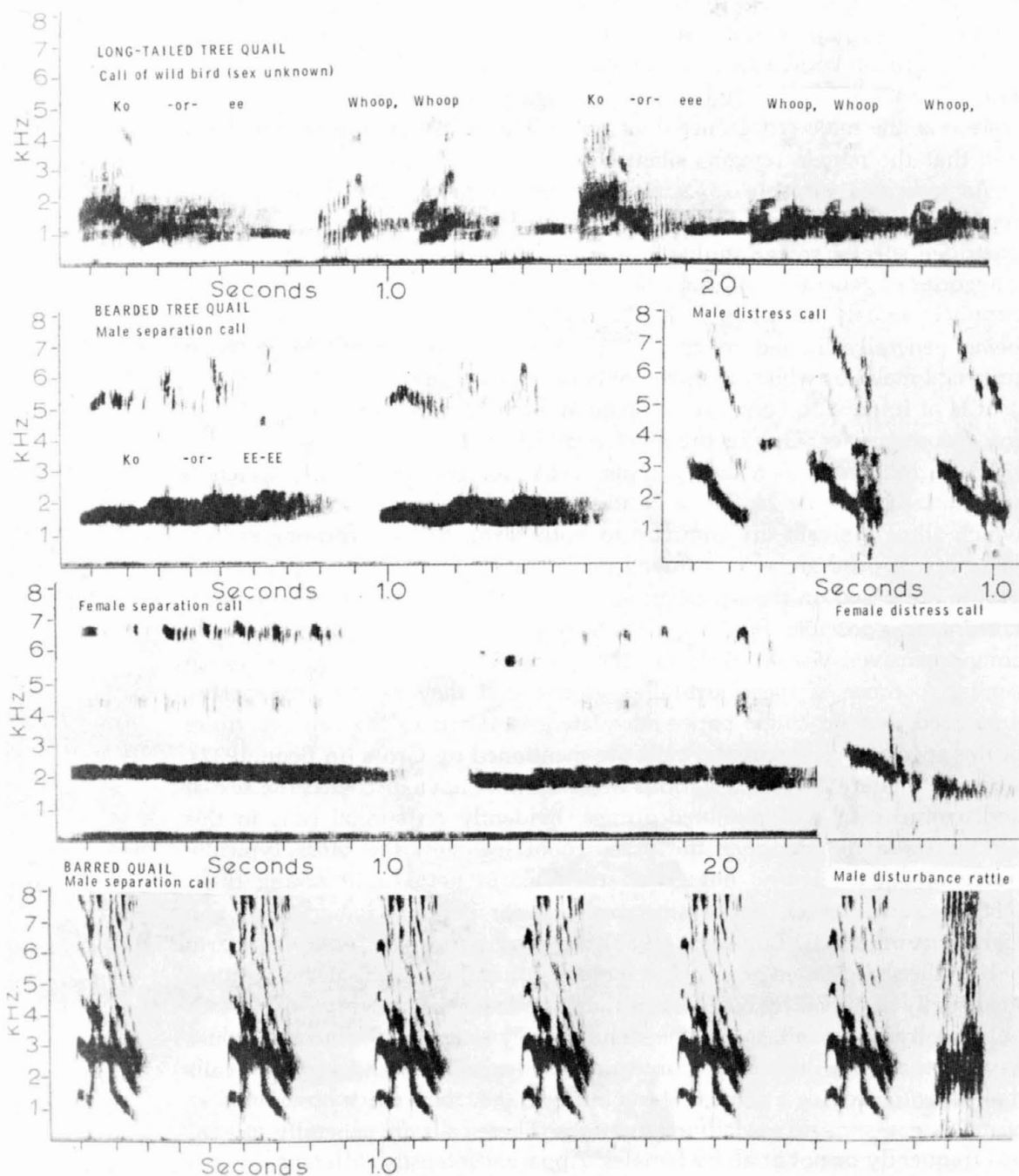


FIGURE 18. Representative sonograms of calls typical of New World quails.

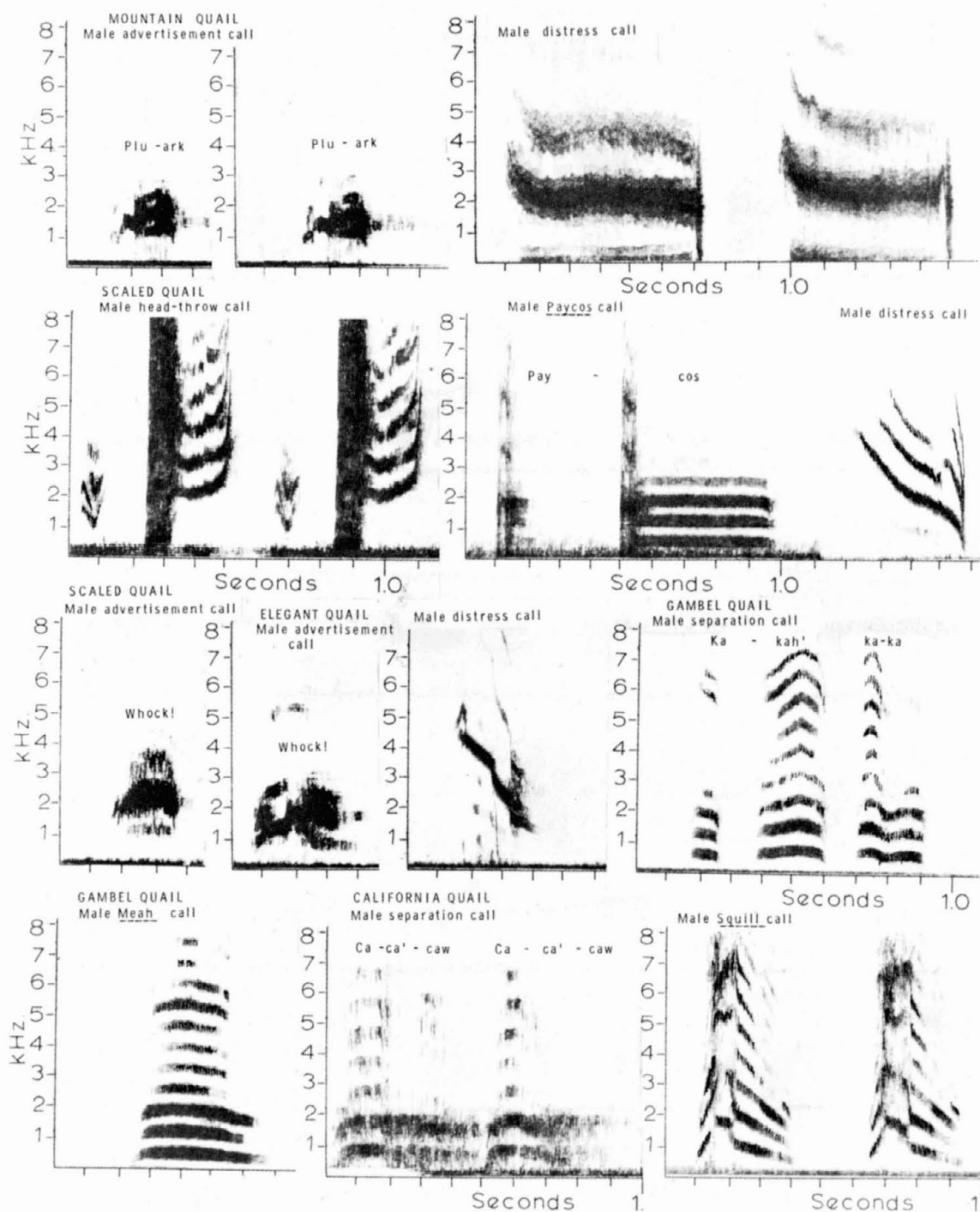


FIGURE 19. Representative sonograms of calls typical of New World quails.

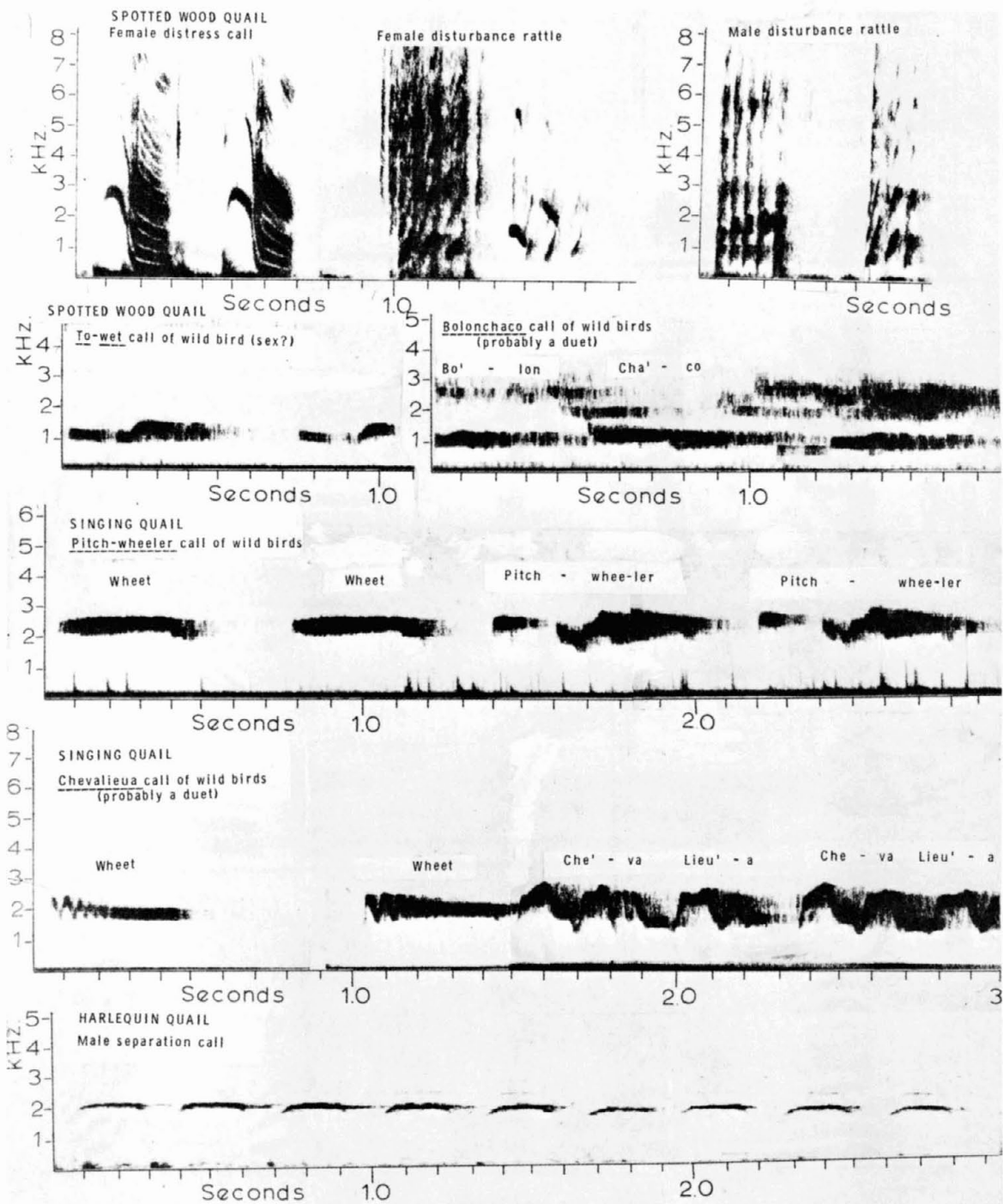


FIGURE 20. Representative sonagrams of calls typical of New World quails.

TABLE 26  
SUMMARY OF ADULT VOCALIZATIONS IN THREE GROUSE SPECIES

	<i>Willow Ptarmigan</i> ( <i>Red Grouse</i> ) <sup>1</sup>	<i>Sharp-tailed</i> <i>Grouse</i> <sup>2</sup>	<i>Pinnated</i> <i>Grouse</i> <sup>3</sup>
I. Flock or pair activities (both sexes)			
A. Flight intention	1		
B. Social contact	1		
Subtotal	2		
II. Avoidance of enemies (both sexes)			
A. Flying predator alarm	1	1?(preflight)	
B. In-flight alarm	—	1	1
C. Fleeing (& chase)	1		
D. Flying predator defense	1		
E. Hissing defense	1		
Subtotal	4	2	1
III. Sexual and agonistic			
A. Song (in flight/on ground) (both sexes)	2	A. Aggressive cackle (male & female)	1
B. Attack; attack-intention; threat (both sexes)	1- 3	B. Aggressive <i>Lock-a-</i> <i>lock</i> (both sexes)	1
C. Sexual (both sexes)	1	C. Cooing (males)	1
		D. Aggressive whine (males)	1
		E. Squeal & cork calls (males)	2
		F. <i>Chilk &amp; Cha</i> (males)	2
		G. <i>Pow</i> (male courtship call)	1
Subtotal	4- 6	9	5- 7
IV. Parental			
	2†	?	2- 3†
TOTALS	12-14	11+	8-11

1. Based on Watson & Jenkins (1964), all calls uttered by both sexes

2. Based on Lumsden (1965), female parental calls not included in study

3. Based on Gross (1928), Lehmann (1941) and personal observations

\* Probably variants of whining and *pwoik* calls

† Excluding calls from other categories above

## THE EVOLUTION OF SOCIAL SIGNALS IN PHEASANTS AND PARTRIDGES

Among the true pheasants and the Old World partridges the fundamental nucleus of galliform display patterns should be present, to which the kinds of social behavior found in the grouse, New World quails, and turkeys

must somehow be related. Within this vast phasianine array of some 150 species, about two-thirds of the species are regarded as quails, partridges, or francolins (Perdicini), while the remainder comprise the true pheasants and peafowl (Phasianini). In addition to being generally larger and having more prevalent sexual differences in plumage and morphology, male pheasants are also usually crested and iridescent and have ornamental tails of various shapes, lengths, and patterns; and their feet are usually spurred. However, no single character unequivocally separates the pheasants from the partridge-like species, and indeed the pheasant group may actually be of polyphyletic origin, simply including those phasianine species that have for the most part abandoned monogamous mating characteristics for polygamous or promiscuous ones. To mention only one example of doubtful tribal relationships, there is a remarkable similarity between the downy young of the blood pheasants (*Ithaginis*) and those of the snow partridge (*Lerwa*) that is certainly suggestive of close affinities. It is also possible that similar male plumage characteristics have evolved independently in distantly related pheasant lines and have obscured phyletic relationships. It would thus seem that downy, juvenile, and female plumages might provide the best morphological indices of relationships and bases for generic recognition, with information on hybrid viability, fertility, and chromosomal or biochemical evidence useful supporting data. Male displays are so subject to selective pressures for species isolation that they are useless for such classification purposes, although they are nonetheless of interest in their diversity and their relationships to male plumage development and signal functions.

In spite of the remarkable species diversity to be found in male plumage patterns of the pheasants and their relatives, a surprising degree of similarity in the display motor patterns can be detected (Schenkel, 1958). Functions and motivations of these motor elements have no doubt been greatly modified to fit ecological needs or other adaptations, but nonetheless the display patterns to be found among pheasants, partridges, quails, and grouse are basically so similar as to suggest that fairly close evolutionary relationships may exist among the entire group. It is, for example, most difficult to find specific display features that can be used to separate these into tribes, subfamilies, or families according to their taxonomic treatment.

Starting with the uncertain but reasonable assumption that the partridges and true quails are more generalized in behavior and morphology than are the pheasants, the behavior of such well-studied Old World genera as *Coturnix*, *Perdix*, and *Alectoris* may perhaps serve as representative of this large group. Sexual plumage dimorphism is fairly slight in these forms, and species-specific display features would appear to be centered in the



face, throat, breast, and flank regions. The tail and wings are for the most part specialized neither in pattern nor in shape, and in general do not contribute significantly to display. In at least two genera (*Alectoris* and *Excalfactoria*) a lateral display is present in which one wing is drooped, but in both these genera the wing involved is the one away from the object of the display, and thus the flank feathers are rendered more conspicuous (Harrison, 1965, Goodwin, 1953). Indeed, in such species the function of lowering the farther wing may simply be maintaining balance (Goodwin, 1953). Apparently, strong wing-lowering during lateral display is absent both in *Coturnix* and *Perdix*, which interestingly both lack specialized flank coloration. Throat patterning is well developed in *Excalfactoria*, *Alectoris*, and *Coturnix* and is probably displayed during calling or frontal displays in all these forms. The taxonomic distribution of the tidbitting display among the partridge-like forms is uncertain and seems to be unrelated to plumage morphology, but it occurs at least in *Coturnix*, (Schenkel, 1956), *Alectoris* (Goodwin, 1953; Stokes, 1961), and *Excalfactoria* (Harrison, 1965).

Judging from the observations of Stokes (1961) and Goodwin (1958), the genus *Alectoris* possesses several basic phasianid display elements, including lateral display and tidbitting. Tidbitting serves in this genus both as a low-level aggressive signal between males and as an important sexual signal of males toward females. The associated tidbitting call is also used by both sexes in directing their young to food. Other pheasant-like display postures include wing-flapping, a high-stepping posture, and a "rear approach" of the male to the female for copulation. Representative displays of *Alectoris* and *Perdix* are illustrated in figure 21.

The early studies on the behavior of the domestic form of red jungle fowl (*Gallus gallus*) have provided much of the basic terminology used to describe pheasant display patterns, and thus the domestic fowl might be considered a "type" example of phasianine display patterns. Some of the most complete studies on the behavior of the domestic fowl are those of Wood-Gush (1954, 1956). He reported that nearly all the male postures are used both in agonistic and courtship situations. As might be expected in a polygamous or promiscuous species, the female exhibits very few of these same displays and instead performs submissive or appeasement gestures. Apart from overt fighting and retreating, males perform a number of other gestures that probably reflect varying degrees of conflicting tendencies to attack, escape, or react sexually, according to ethological theory. One of these displays is "high-stepping," which is performed by the male in an erect stance as he advances on his opponent. During strutting the male droops both wings and raises his tail and ruff slightly. Stationary

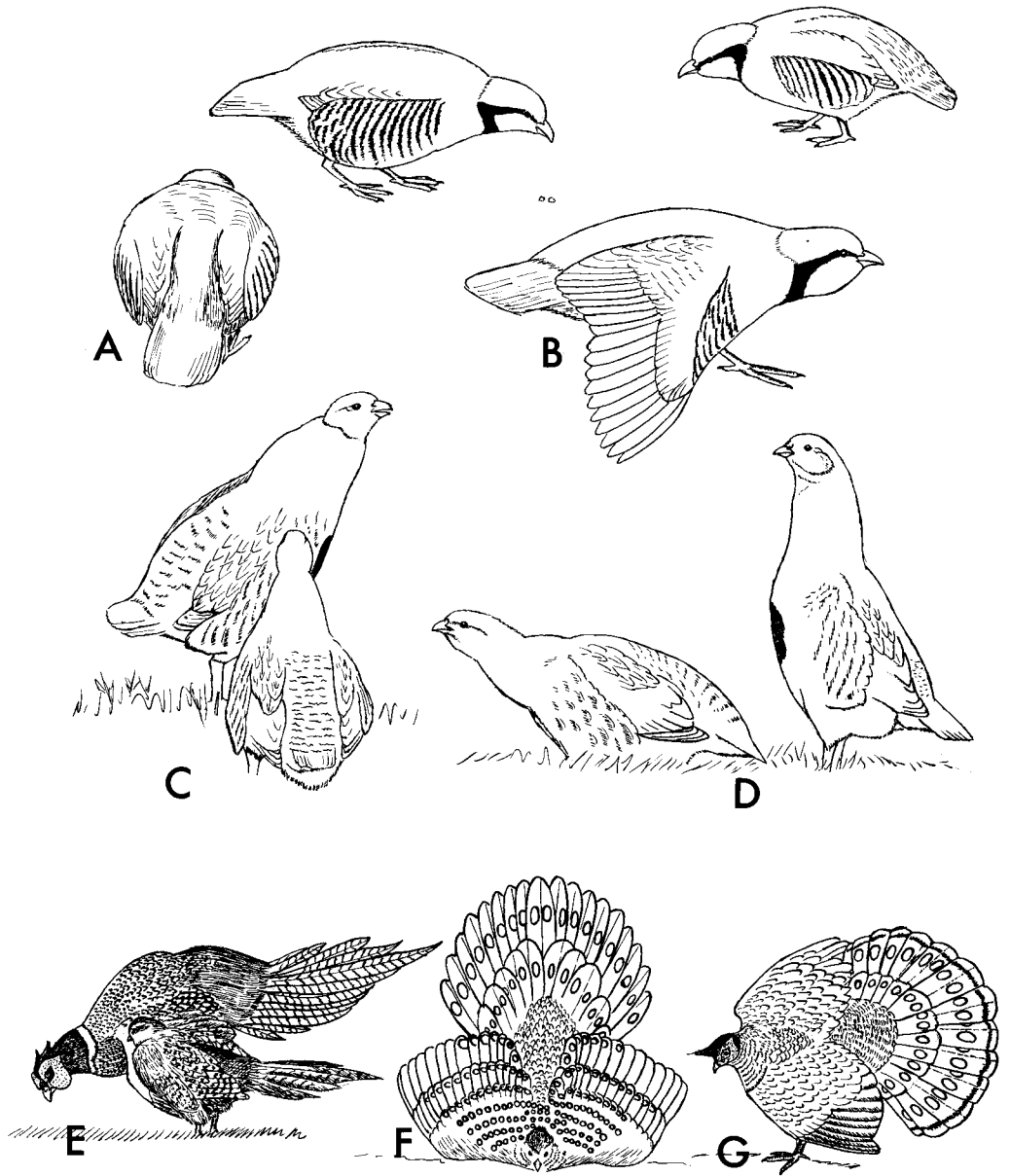


FIGURE 21. Male display postures of representative partridges and pheasants, including (A) chukar partridge tidbitting, (B) chukar partridge waltzing, (C) gray partridge in lateral courtship display, (D) gray partridge in precopulatory display, (E) ring-necked pheasant performing lateral wing display, (F) gray peacock pheasant in frontal display, and (G) Palawan peacock pheasant in lateral display. (After various sources.)

wing-flapping is performed with or without calling but with loud wing-clapping. A major display of domestic fowl is "waltzing" (Davis and Domm, 1942), which is composed of several components. These include circling the other bird, lateral display of the flanks and often the tail, and a wing display achieved by lowering the off-side wing towards the ground. Kruijt (1962) suggested that the evolutionary origin of wing display during waltzing resulted from a compromise of motor patterns reflecting tendencies to flap the wings aggressively and to fold the wings in association with escaping. Unlike the situation in partridges, wing display of pheasants seems to be limited largely to males, but it is present in females of the genus *Pucrasia* (Wayre, 1964).

Another basic phasianid display performed by domestic fowl is tidbitting (Domm, 1927), consisting of ground-pecking intention movements, which in some species are supplemented by calls. This may have had its evolutionary origin as aggressive pecking movements that are redirected toward the substrate, but in many species this activity has evolved into an important method of pointing out food sources to the young or the mate. Schenkel (1956) has described how the basic movements and calls as found in *Gallus* and *Phasianus* are increasingly modified through ritualization in *Polyplectron*, *Lophophorus*, and perhaps *Tragopan*, and are finally represented by the elaborate frontal display of *Pavo*, which typically occurs in the absence of actual food.

Other components of male agonistic and sexual display of the domestic fowl reported by Wood-Gush (1954, 1956) include ruffling the neck feathers, circular head-shaking, tail-wagging, preening, and whining. Two strictly sexual elements include "cornering," in which the male moves away from the female, partially crouches, and scratches or stamps with his feet (Kruijt, 1962). Stokes (1961) believes that cornering should be considered ceremonial nest-building, and Kruijt has made a similar suggestion. Finally, males perform the rear approach, in which the bird attempts to mount the female from behind. The domestic fowl lacks a well-developed frontal display, but during high-intensity threat the male exhibits "two-sided wing-lowering," while raising its ruff and directly facing its opponent (Kruijt, 1962).

Male displays of the pheasant species have been separated into two major classes, lateral and frontal (Beebe, 1926; Pocock, 1911). The lateral, or one-sided, display has also been called waltzing and wing display, and consists of several interrelated components. These include both a lateral orientation to the object of the display, and a variable lowering of one wing which except in the genera *Gallus* and *Pucrasia* (Wayre, 1964) is apparently always the nearer wing among the species of true pheasants. The tail is also usually raised, spread, or tilted, or combinations of these

may occur, and the body may be tilted toward the object of the display, making the upper body surface and tail a major focus of attention for specific display features. Finally, there is a circling around the other bird, which may take the form of a rapid forward running or hopping (*Polyplectron*, *Rheinardia*, and *Chrysolophus*), sideways hopping movements (*Syrmaticus reevesii*), the appearance of a somewhat drunken waltz (*Gallus*), or a slow and stately walk (*Phasianus*, *Lophura*, and *Tragopan*). Published descriptions of these movements are not always clear, and intermediate or compound situations no doubt occur; thus the great argus (*Argusianus argus*) is said to begin displaying with a circular walk and strong foot-stamping around the female, then it suddenly rushes past her while performing lateral wing display (Seth-Smith, 1925). The final stage consists of stopping, opening and erecting one wing, then opening both wings and facing the female in the climactic frontal display (Lint, 1965). Pocock (1911) astutely discerned the significance of the asymmetry of the lateral display as an evolutionary precursor to the elaborate frontal display of several pheasant species. He points out that in *Polyplectron bicalcaratum* (and, as later reported, in *Polyplectron emphanum*) not only is the tail spread and tilted but also the more distant wing is raised and tilted in a manner that exposes the ocellated dorsal patterning. This essentially dorsal-lateral display may thus readily be modified into the typical frontal display, by the bird's stopping, calling the female with the tidbitting call, lowering its head to the ground, and orienting both wings and the vertically spread tail directly toward the hen. This tremendously impressive display places the burden of signal features on the upper wing surface, especially the secondaries, and on the tail and helps to account for the fantastic development of these feather areas in the great argus. In contrast, the crested argus (*Rheinardia ocellata*) lacks a clear-cut frontal display, and its long tail feathers are simply raised and spread vertically during the lateral display while both wings are lowered (Huxley and Bond, 1942). This species lacks specialized wing and mantle patterning, such as iridescence or ocelli, and the tail, although extremely long, is not modified in shape or coloration for frontal display.

It may thus be seen that the lateral display provides the probable evolutionary basis for the frontal display, which gains equal or greater importance in *Polyplectron* and *Argus* and finally altogether replaces it in peafowl (*Pavo*). It should be noted here that at least one other genus has a very similar frontal display, namely the monals (*Lophophorus*). Literature descriptions have not permitted me to judge whether the motor origin of the frontal display of these species corresponds to that of the genera just mentioned, but it is known that a similar lateral display with associated

drooping of the near wing precedes the frontal display (Delacour, 1951). Lastly, in the peafowl and apparently also in the African peacock (*Afrapavo*), there is no lateral display at all. Kruijt (1962) suggests that wing movements during frontal display of the Indian peafowl (*P. cristatus*) may represent a derivation of wing-shaking or wing-flapping, but there is no trace of asymmetry in the display and the focus of display features has centered on the back and tail coverts instead of on the wings or tail. In addition, since the head is not hidden behind the wings during frontal display as in the argus but is visible and held upright, the entire head and neck region have also become highly iridescent and specialized. The plumage and morphology of the African peacock likewise are correlated with display, during which the male and female sit on branches facing each other and bow their heads deeply, with their spread-out tails raised to an angle of forty-five degrees (Verheyen, 1962).

In addition to lateral and frontal displays, male pheasants exhibit a variety of other male display postures and movements (figure 21). Wing-flapping, such as might occur possibly as a displacement activity in many species, is highly ritualized in *Lophura* and *Syrmaticus* (Delacour, 1951), in both of which whirring sounds are generated. An actual display flight by males is evidently present in *Lophophorus* (Ali and Ripley, 1969). Shaking of the vaulted and often distinctively patterned tail occurs in *Lophura* and *Crysolophus*, and this exists in a modified version as vibration of the peafowl's erect train. Engorgement of the brightly colored bare facial skins occurs in several genera such as *Phasianus* and *Gallus* and reaches a maximum in the display of the Bulwer pheasant (*Lophura bulweri*). Male tragopans exhibit a rather different form of facial and throat engorgement, and in contrast to the forms just mentioned the males display them in a distinctly frontal orientation. Tidbitting not only occurs in *Gallus*, in which it was first described as such, but also in *Polyplectron* (Seth-Smith, 1914) and probably other genera. Schenkel (1956, 1958) has extensively summarized other evolutionary aspects of pheasant displays, particularly male calls, which have not been considered here. It would seem that in general the pheasants exhibit a much greater degree of conservatism in motor patterns than in the morphological features exhibited by these motor patterns, thus the same display performed identically by two species may be rendered species-specific by differences in male plumage characteristics.

## INTERGROUP DISPLAY HOMOLOGIES

Although it is fairly safe to assume that lateral display with wing-lowering and the other similar postures of the Old World partridges are homologous

to those of pheasants, it is more difficult and dangerous to make such comparisons between the pheasants and the New World quails. Although in the American species lateral display is certainly a fundamental aspect of both agonistic and sexual behavior, this may or may not be associated with a circling of the other bird, and in no species has an asymmetric wing-lowering been described. Rather, as in partridges, the flank feathers seem to be the center of signal concentration for lateral displays, and these are often asymmetrically fluffed on the side toward the opponent male or the female. Wing-flapping is common during agonistic situations among New World quails, and tidbitting also plays a major role in the pair-forming processes of several species. Also in common with the Old World partridges, tidbitting calls are used by both sexes to attract the young to food.

Male display postures of the grouse also show a considerable number of similarities to those of typical pheasants, some of which are undoubtedly only superficial. The stationary wing-flapping of ruffed grouse, for example, should probably be regarded as a modification of aerial display rather than homologous with the wing-flapping associated with crowing in various pheasant species. Tail-cocking and tail-spreading displays occur in virtually all species, but it is questionable whether these postures are equivalent in a homologous sense to similar displays of male pheasants. Symmetrical wing-drooping with tail-fanning and an associated strutting is particularly well developed in ptarmigans and *Dendragapus* species (Brooks, 1926; MacDonald, 1968), and in these species the postures closely resemble those of various pheasants. This similarity is increased in ptarmigans, which perform a waltz-like circling display, during which the wing nearer the other bird is strongly drooped, the spread tail is tilted, and the displaying bird circles the other closely while performing high-stepping movements (Watson and Jenkins, 1964). Somewhat similar asymmetrical lateral display with slightly drooped wings and a widely spread, tilted tail may be seen in the ruffed grouse (see figure 16), but in this species there are no associated circling movements. A circling of the female without asymmetrical wing-lowering occurs in both sharp-tailed and pinnated grouse as well as in black grouse (Hamerstrom and Hamerstrom, 1960). Tidbitting has apparently not yet been reported for any grouse species, although C. Braun (cited by Schmidt, 1969) observed probable tidbitting as a precopulatory display in white-tailed ptarmigan.

In conclusion, it might be mentioned that a number of male displays of the common turkey (*Meleagris gallopavo*) are strikingly similar to the strutting postures of various grouse as well as to the displays of peafowl. Turkey displays include tail-cocking and tail-spreading, symmetrical wing-drooping, and short forward runs associated with breathing sounds some-

what like those of *Dendragapus*. Although it is obviously not valid to use male displays as a basis for major evolutionary conclusions, the turkey's grouse-like sexual behavior provides no contradictory evidence to the view that the New World turkeys and the grouse might have evolved from common cracid-like ancestors inasmuch as there are no known fossil remains of typical pheasants from North America.