

VOICE AND SOCIAL BEHAVIOR OF THE CHUKAR PARTRIDGE

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The Chukar Partridge (*Alectoris graeca*) is difficult to study in the rugged country in which it occurs in the United States. Life history studies of the Chukar in Nevada (Christensen, 1954), Washington (Galbreath and Moreland, 1953), and Utah (Phelps, 1954) have dealt mostly with habitat and food requirements but only slightly with calls and social behavior. Hume and Marshall (1880), in what is the best description of the bird in its native range, have little to say about calls or displays. Since so many calls of the Chukar are soft and infrequent, they are best studied under penned conditions. Goodwin's study (1953) of the closely related Red-legged Partridge (*Alectoris rufa*) has been a great help. The white chin flanked by the black V, the conspicuous dark and white vertical bars on the flanks, and the chestnut tail feathers covered with gray upper tail coverts are conspicuous plumage characters prominent in the display of both species. Many of their calls are similar in quality and the situation in which they occur. Studies of the brown leghorn chicken by Wood-Gush (1954, 1956) have been especially valuable for their descriptions and analyses of galliform behavior. Wherever possible I have used the same terminology as the aforementioned authors in describing calls and behavior patterns.

This paper presents observations on the behavior of the adult Chukar Partridge both in the wild and in captivity. This account is largely descriptive with only tentative conclusions about causation and function of behavior. For a quantitative analysis of the motivation of calls and display the reader is referred to a forthcoming paper "Agonistic and Sexual Behaviour in the Chukar Partridge" (Stokes, in press).

This study was made from 1955 through 1960. In 1955 I kept three males and five females in a pen with wire sides and top measuring 40×60 feet from January through May. The floor of this pen was bare ground during winter, but it had moderate ground cover in spring. In 1956 I used 12 males and 12 females. Three males and three females were kept in the same outdoor pen as in 1955 to observe display and pair formation. The remainder were separated as to sex and kept apart from the birds in the pen. From time to time these birds were placed singly in the pen to observe the reaction of the penned birds to newcomers. In 1957 I held 16 birds in three outdoor pens measuring 30×60 feet with emphasis on nesting behavior. In 1960 most observations were of birds kept in isolation except during paired encounters between birds of the same or opposite sex. These birds were exposed to 14 hours of artificial light daily from January 15 until the end of observation in May. Paired observations of these birds began in March at a time when sexual and aggressive behavior was increasing rapidly. In addition to the caged birds, I observed Chukar Partridges in the wild in northern Utah for about 40 hours.

I am indebted to the Utah Department of Fish and Game for the generous supply of birds from its game farm; to Dr. Carroll I. Draper, Department of Poultry Husbandry, and Dr. Arthur D. Smith, Department of Range Management, both at Utah State University, for the use of pens and other facilities; and to H. W. Williams and Dr. Keith L. Dixon for their critical reviews of the manuscript. This project was supported in part by the Division of Research and by the Utah Cooperative Wildlife Research Unit at Utah State University.

CALLS

The calls of the Chukar are numerous and variable. I have divided calls into those associated with alarm, social contact, and agonistic or sexual situations. Those occurring in the same situation as in the Red-legged Partridge I have marked with an asterisk.

ALARM CALLS

*The ground alarm call.**—A person's first experience with Chukars in the wild is likely to be in the fall as a covey of birds flushes wildly a few yards in front of the hunter. The birds separate in long, curving downhill flights. As they burst from the ground the first call is a loud piercing squeal, followed by a series of *whitoo whitoo* calls gradually subsiding as the birds disappear out of range. Birds leaving their roost on some rocky outcrop in the faint light of dawn fly downhill with these same calls, as do birds evicted from an aggressor's territory in spring. In the pens a bird when suddenly attacked or chased by another bird may give the same short squeal and *whitoo* call. Birds held in my hand gave the squeal and *whitoo* calls as I waved them up and down. Hence one cause of the call is the appearance of a sudden or unfamiliar stimulus on the ground; another is eviction by an aggressor. But I do not know what elicits the call during flights from roosts or on other occasions when there is no apparent disturbance. This call seems similar in nature to the cackling of a Ring-necked Pheasant (*Phasianus colchicus*) as it leaves its roost or is startled by the hunter.

*Hawk-alarm note.**—A large bird or airplane flying overhead generally elicits a short, guttural *kerrrr*. It is evenly pitched and given with little mouth movement, but it is audible for perhaps 100 feet. If the disturbance is not too close, the bird will crouch on the spot and turn its head sideways to get the best possible view. The call may be repeated several times by the first bird to see the disturbance and also by other birds in the pen even though they cannot see the danger. More sudden or closer sources of danger sometimes send the entire flock of Chukars flying or running hastily to cover.

When first placed in new surroundings, the birds were alarmed at many disturbances such as hawks or eagles soaring overhead, the sudden disappearance of the sun behind a cloud, or low-flying airplanes. Later the birds might give a single *errrrk* with scarcely a break in their activity. Black-billed Magpies (*Pica pica*), Crows (*Corvus brachyrhynchos*) and even Starlings (*Sturnus vulgaris*) would at times cause alarm, but this probably hinged on the suddenness of approach and the silhouette they presented to the Chukars. These same birds when perched immediately above the pens caused no alarm. This was true even for a Sparrow Hawk (*Falco sparverius*) that seconds before perching had caused the entire flock to crouch.

After the disturbance had subsided, the birds gave soft, broken rally calls. More often they would give the contentment call (see beyond).

*"On-guard" call.**—This is a low-pitched, undulating *kwerr* given when a hawk continues soaring overhead. The birds give it while frozen and looking up at the hawk either from cover or out in the open. It may be given intermittently for several minutes or until the hawk has disappeared. The call is difficult to locate and has the characteristics of a well-adapted alarm note described by Marler (1955), that is, it is easy to recognize but difficult to locate.

CONTACT CALLS

*Food call.**—Single birds feeding at the hopper or scratching in the litter frequently gave a slow *took*. This is sharp and emphatic with a clear pause between each note. I have heard this call in the wild as a pair of partridges fed slowly across a grassy opening. I believe it serves to keep the birds aware of others in the group. Among chicks the call is a turkey-like *turk*. Birds that discover a new or novel source of food will call excitedly a rapid *tu-tu-tu-tu*. I could always elicit this call by depriving my birds of food for a few hours or by introducing earthworms to the pen. The adults called their young to food using the same note.

"*All's well*" call.*—A loafing or feeding bird will at times give a soft plaintive *coo-oor*, rising in pitch on the second syllable. Birds give it when there is no apparent strife or tension from outside sources. The call frequently signifies the end of a period of alarm from the air. In the Red-legged Partridge, Goodwin (1953) believes this is the call of a paired male given while standing at ease. The same may be true of Chukars, for I have recorded it only from males in the breeding season. I have heard it, however, from two males kept isolated for over a week from the single hen with which they had been kept. They were, moreover, never paired with her and were dominated by a third male before separation. The fact that only the male gives this call, and only in the breeding season, suggests that this call may be sexual rather than purely social.

AGONISTIC AND SEXUAL CALLS

Numerous calls occur only or chiefly in the breeding season. These may be agonistic or sexual in nature.

The rally call.*—This is the most common call of Chukars and the one from which the species derives its common name. At low intensities the call is *chuck, chuck, chuck*, given slowly and with definite breaks between each call. As the intensity of the calling rises, it changes to *per-chuck, per-chuck* with accent on the second syllable, and it is given at faster tempo. This in turn gives way to *chukar-chukar-chukar* with accent on the first syllable. At highest intensity, and usually highest volume, the call becomes a three-syllable *chuckara-chuckara-chuckara*. A bird may go from one form to another quickly, and I have not been able to distinguish different functions or causation in the various forms of this call. At highest intensity a single call may last 20 seconds with as many as three calls a minute. The female gives the same call but much less often, at least during the breeding and brood season.

A bird may give the rally call while walking or running, but typically it gives the call while standing still. At low intensity the bill is scarcely opened. Otherwise, the bill is opened wide, cheek and throat feathers puffed out, and the head held high and somewhat forward. With each call the tail makes synchronized, slight, up and down movements. The neck feathers, especially those on the nape, are fluffed, creating an obvious hump. Likewise the feathers from the rump up to the middle of the back are fluffed to create a hump in this region (fig. 1a).

Chukars generally give their rally call from the ground. At times they call from low perches available to them, and the wild Chukars near my pens would even call from high fence posts. But this habit is not nearly as common as among Bobwhite Quail (*Colinus virginianus*).

I have heard the rally call in fall after the birds of a covey had been dispersed by hunting, but I have not studied it outside the breeding season. It appears that the rally call becomes more frequent and intense with the advent of the breeding season. The diurnal variation is like the variation in song birds. First calls begin about 45 minutes before sunrise and are at a peak at sunrise. Their frequency falls off rapidly within an hour after sunrise and stays low until about an hour before sunset. Calls may persist until about 45 minutes after sunset, becoming shorter, softer and less frequent as darkness falls. The evening peak is somewhat less than the morning peak.

Outside of the sunrise and sunset periods, the rally call may be given in a number of other situations. In captivity when two males are confined in a small pen together, only the dominant cock will give the rally call. Birds in pens always directed their calls to birds outside the pen. During 1957 there were several wild Chukars outside of the pen. A sudden outburst of the rally call was always a sign of a wild bird approaching.

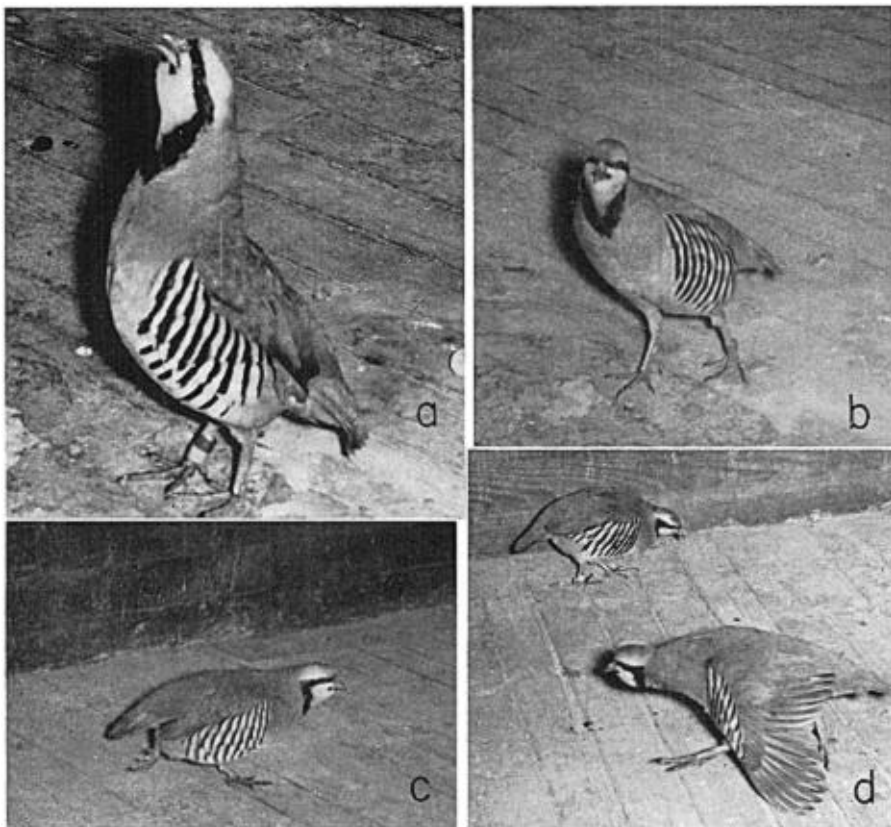


Fig. 1. Behavior of Chukar Partridge (*Alectoris graeca*). a, Rally calling by male, showing swollen throat of dominant bird. b, Head tilt; male is displaying to unseen bird at right; note barred flank feathers pulled up over wing. c, Running threat. d, Waltzing; wing of waltzing male is scraping the ground; female in rear shows no signs of fear.

Rally calls were especially loud and persistent on the several occasions when a bird had escaped from the pen and was wandering about outside. One year a group of Chukars was penned outdoors some 200 yards away and out of sight of my experimental birds. There was always a strong period of rally calling by these birds as daylight came.

Whenever a predator has scattered a covey and made it take shelter for any length of time, the first cautious movements of the birds as they leave shelter are accompanied by rally calls—somewhat quiet at first, then louder and louder. One July evening I watched a flock of 25 birds move up a steep canyon slope to roost. Halfway up, a Golden Eagle (*Aquila chrysaetos*) swooped over and forced the birds to cover. After 10 minutes of absolute quiet the birds slowly started out. First one, then several, gave the rally call. Within two minutes the cliffs were ringing with their calls. Within another few minutes the flock had reassembled and had begun working its way up the slope.

Throughout the day in spring, bursts of rally calling may occur. Typically these occurred whenever two males met aggressively. Following a chase and withdrawal of the males to their own areas one or both might call repeatedly. This in turn often started other males calling. During these bursts of calling a male seldom moved but usually

remained conspicuous in some opening or on a raised piece of ground. In these encounters it seemed to be always the males that were calling.

It appears that the rally call has three functions. First, because of its loudness, it announces the location of the calling bird. This may serve to repel intruding males, for in spring the call is certainly aggressive in nature. Second, it may be sexual in function, serving to attract females to the male as in the "advertising" song of many other birds. However, since pair formation tends to occur within the covey, this sexual function of the rally call may not exist. Unlike some quail (Stoddard, 1931; Genelly, 1955) the male Chukar continues to call long after he has paired. But persistent callers heard in mid-July were lone males and may well have been unpaired. Third, the call occurs after a covey has been scattered. In this situation it appears to serve as a means of aiding scattered birds in rejoining the covey, and it is given by females as well as males throughout the year. Rally calling in this last situation appears to come under an entirely different motivational situation than calls during the breeding season. In this respect it differs from the "advertising" songs of the Ring-necked Pheasant and quail, which appear to be entirely aggressive male behavior. However, there has been no critical study of rally calling outside the breeding season. It may be that the difference between the Chukar Partridge and other gallinaceous birds is less real than apparent.

*Steam-engine call.**—A male in breeding season may give a harsh *chak-chak-chak* call, sometimes lasting for five minutes on end; at other times, just a few isolated calls may be given. Walpole-Rond (1938) first used this name in connection with the Red-legged Partridge; but it applies equally well to the Chukar. At a distance one could easily mistake this mechanical call for some ancient-vintage steam engine of a ferry boat. The male gives it with head held high and body erect. At high intensity the body feathers are somewhat fluffed, especially those of nape and neck, as in the rally call.

The call occurs in situations that suggest a conflict between aggression and escape. Thus two males in adjacent pens may display vigorously toward each other with head tilted and circling for several minutes. The dominant male tries to peck the other through the wire. Finally it moves off several feet and starts the steam-engine call. In general whenever a dominant male is prevented from getting at another, he will give this call. A dominant wild male used to fly into one of my pens regularly and consort with a female and several males. Every time I chased it out of the pen it would fly off 50 yards to a clearing and start calling. Here the wild male's aggressive behavior was thwarted by my presence. One captive male used to dominate the wild male. Every time the wild male approached the pen, the captive male would give the steam-engine call. Here, too, the more aggressive bird was thwarted by being unable to fly out of the pen to attack the wild outsider.

In the wild, however, it appears to be the subordinate male that gives the steam-engine call while the dominant male may give the rally call. Thus I have observed a male give repeated rally calls over a 10-minute period in a small clearing on a knoll. The calls were long and loud suggesting highly aggressive motivation. Another male was skirting the clearing and keeping out of sight and somewhat lower on the knoll. It gave repeated steam-engine calls but no rally calls. Likewise birds that fly down from their roost giving the *whitoo* escape call may immediately begin the steam-engine call on landing. Although too dark to determine, it seems likely that the dominant male in a roosting covey chases the subordinate males shortly after waking. The latter "steam-engine" where they alight lower down; the dominant males give the rally call from the roosting site.

Birds in the same pen rarely give the steam-engine call. An exception is when a paired male has been forced away from his mate by a dominant male. Then the submissive

male will retreat to an uncontested area and give short bursts of this call, but usually these short bursts are quieter than normal. Perhaps when males can actually come together either aggressiveness or fear will dominate, resulting in attack or retreat rather than unresolved conflict.

Goodwin (1953) states of the Red-legged Partridge, "This is primarily the 'song' of the male in the breeding season It seems functionally parallel with the song of male passerine birds, as an advertisement of the (?territory-holding) male's whereabouts." In Chukars, at least, this call does not begin to have the important function of true song. It is given under far too limited conditions. Instead it appears definitely to be linked with strong conflict in motivation between attack and escape.

Either sex may give a quieter and much shorter form of the steam-engine call when disturbed. A bird cornered in the pen would always give this call; the more closely pressed the bird, the louder and more harsh the call; at its highest intensity the call closely resembles the steam-engine call. This is not surprising, for being cornered must also represent conflict between fear and aggression.

When I placed a young Marsh Hawk (*Circus cyaneus*) in a pen with two adult male Chukars, they gave a loud steam-engine call for several minutes while they walked back and forth some 12 feet away from the hawk. Interspersed with the steam-engine call was the "contact" note. This situation again placed the birds in a position of balance between attack and retreat with retreat dominating. Seven-week-old chicks gave a mild form of *chak-chak* on approaching the hawk, but they seemed less alarmed by it than the adults.

Another time male RY had been dominant over male R in a pen for several days. Then a third male that was somewhat dominant over RY was placed in this pen. RY no longer attempted to display toward the new male. Instead he went off some 15 feet and gave the steam-engine call. This was a situation in which RY had met his equal and no longer was able to attack, so he "vented his spleen" with the steam-engine call during his thwarted aggression.

"*Squee*" call.—When two males are placed together, the dominant male, once it has established its social position, will frequently give a characteristic, excited call. This is highly variable consisting of mouse-like squeaks (*squee*), shrill peeps, and *whitoo*-like calls. These are all given rapidly with little or no break between one call and another. This call frequently changes into the rally call and back again. It appears to share the same motivation with the rally call, but presumably at lower intensity. Dominant males appear to be the only birds giving the call. Whenever I separated a dominant male from the rest of the flock so that he could hear and perhaps see the others, he would peck vigorously at the barrier and give this *squee* call. Birds within the same pen never gave this call once the peck order was established. Hence the call occurs when a male is in conflict between attack and escape with the aggressive tendency somewhat stronger than the escape tendency.

Waltzing calls.—In between waltzing bouts while the male is standing laterally to the male or female in tense, erect position, he will often give a call of several seconds duration much like the aerial alarm call. It is either an *errrrrrr* or *errrrrk*, the latter being shorter in length.

Submissive squeal.—A bird being chased or suddenly attacked may give a rasping squeal lasting one or two seconds with bill held wide open. A hen may squeal when being chased by a particularly aggressive hen or by an aggressive cock during his attempts to copulate. Captive hens that had laid over a dozen eggs and had developed signs of broodiness resisted attempts of males to copulate and squealed frequently. Submissive

cocks also squealed when being dominated by a cock. If a bird was actually grabbed by the nape, it was likely to continue squealing until it had broken loose from the attacking bird. The merest move in the direction of the subordinate bird was often enough to elicit a squeal. This sort of squeal was most common during the breeding season, a time when aggressiveness between birds was at a peak. Although the squeal was given with extreme submission, there was no evidence that it had appeasement value. Dominant birds continued their attacks during and after squeals without letup.

The calls given during agonistic behavior are thus good indicators of the motivation of the calling birds. The rally call is an indicator of strongest dominance and aggression; the *squee* call somewhat less. The steam-engine call comes with high intensity conflict between aggression and escape where the calling bird is somewhat subordinate to the rival. The waltzing call is given by a bird that is somewhat dominant, especially over a female. Here the conflict is probably between aggression, escape, and sexual tendencies. Finally, the squeal is given by distinctly subordinate birds with strong escape tendencies.

SEXUAL CALLS

Another group of calls occurs only in the breeding season and seems to function in bringing the pair together for copulation and orientation to the nest. I have designated these as sexual calls.

Tidbitting call.*—During the tidbitting display (see courtship behavior beyond) the male utters a rapid *tu-tu-tu-tu-tu*, which becomes more rapid and higher pitched as tidbitting continues. A single round of calling may last over a minute. This call may be identical to the food call, but it is more varied in pitch and is longer and louder. This may be merely a difference of intensity.

Pitoo.—The male gives this call in the presence of the female as a single call or repeated every few seconds. At such times he is relaxed and moving about freely, never in display. But typically the call precedes a bout of tidbitting or may be injected among the tidbitting calls.

Nest-ceremony call.*—This is a soft continuous *churr*, rising and falling erratically in pitch. It is very similar to the food call. Either sex may give this while exploring for nest sites or turning in a nest scrape.

Copulation-intention call.*—When a male intends to copulate with a hen he stands erect several feet behind her, then he runs directly up to her. During this stage he invariably announces his intention to copulate with a deep-throated rattle, *uh-uh-uh-uh*. In rhythm and quality it also closely resembles the tidbitting call. But it is steady in pitch and volume and lasts for only two to three seconds, stopping the second the male mounts the female. At the height of the breeding season, when dominant males were strongly motivated sexually, I have heard them give this copulation-intention call before running up behind submissive cocks and grabbing them. Hence the call may be elicited by any crouching bird that is facing away from the male involved, so long as he is strongly motivated.

AGONISTIC BEHAVIOR

During fall and winter Chukar Partridges tolerate each other and spend much of their time in coveys. Birds roost and loaf in tight groups, and even while feeding they remain close together. However, with advent of spring, intolerance increases and males may become strongly aggressive toward others. Aggressiveness in birds is known to increase with increased testosterone output in spring (Davis and Domm, 1943). The range in behavior from attack at one extreme and escape at the other is known as agonistic

behavior. Among Chukars it becomes most frequent during the breeding season. Most intense behavior occurred when I introduced two males to each other for the first time.

AGGRESSIVE BEHAVIOR

Head tilt.—The most common display is the "head tilt." In this the male tilts his head away from the bird being intimidated. At the same time the aggressive bird turns sideways to expose his barred flank feathers to the utmost. These flank feathers may be brought well up over the tightly folded wings (fig. 1b). The feathers of neck and chin are fluffed out to such an extent that the neck appears to be half again as large as that of a female or subdued male. During a head tilt the male also stands erect and stiff. This low-intensity display is almost a necessary precursor to more intense displays. A male may make this threat toward a strange male on first encounter or toward other males as a means of forcing a subordinate male away from courting a female. Once the dominance of a male has been established, the head tilt proves an effective deterrent to subordinate males. One afternoon I observed a wild male attempt to put its head through the fence of the pen to feed. The dominant male among my captive birds, about 30 feet away at the far end of the pen, had only to cock his head to make the outsider withdraw, even though there was a tight fence between them. The head tilt is the least aggressive of threat displays and the first to appear in the spring.

Circling.—A more intense form of display occurs when the aggressive male makes a half circle about another bird, at the same time holding his head tilted toward the outside of the circle. Circling is performed by the bird destined to become the dominant one in a paired encounter. The dominant bird circles if the initial head tilts fail to make the second bird submissive. Where birds are fairly evenly matched, mutual circling may last for five minutes before the second bird escapes or crouches submissively. At lower intensity, circling may be a slow walk or a mere step or two. Circling is also frequent when a second male is courting a female. The aggressive male uses this display to force the subordinate courting male away from the hen. Should the second male persist in remaining beside the hen, the aggressive male will make a series of very rapid half circles between the two birds. Like a well-trained cow pony, the aggressor will keep cutting the second male off from the hen no matter how fast the other male may be.

When two males of equal dominance first meet in early spring, there will be mutual head tilting as the two birds stand several feet apart in stiff stance. Later they may run slowly side by side. An aggressive bird will never stand head on to another bird but always so that his flank feathers show. There may be periods in which no antagonism is demonstrated between nearly equal males. But after half an hour the dominance of one is established. Later in the season, as birds become more aggressive, an encounter seldom lasts more than two minutes before dominance is established.

Running threat.—If a male sights another male intruding on his territory, he will challenge the intruder by running straight toward him in a special manner found only in this situation. In running, the back and tail are horizontal and the head straight in front but somewhat lower than the back (fig. 1c). On stopping, the bird stands up stiffly and gives a head tilt, turning sideways as he does so. After a few seconds he will resume his run toward the intruder. He may make half a dozen such short spurts before coming close enough to the intruder to begin more intense displays. I have seen males in the wild run 100 feet or more in this manner to repel an intruder. On returning to his mate the male may run in the same way.

Waltzing.—Sometimes after several minutes of circling, a male may go into what appears to be a still more intense form of display—the waltz (figs. 1d, 2a). This appears

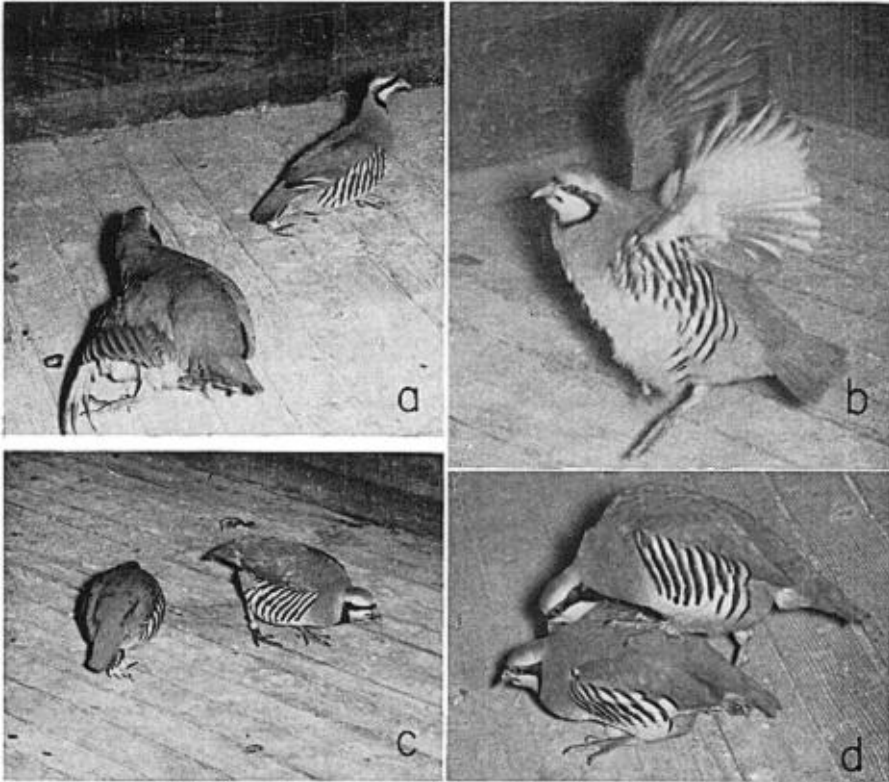


Fig. 2. Behavior of Chukar Partridge. a, Waltzing; the tremendous vigor of the waltz is shown by the tilt of the male's body and the wing extended to the floor; the female is escaping; note her raised wing tips, constricted throat, as compared with the male's, and strongly flexed legs while running. b, Wing flapping by submissive bird. c, Tidbitting by male to the right; female has joined male and the male has turned away just prior to moving away in high-stepping. d, Copulation, wings of female partly raised; male is preparing to grab the female by the nape.

comparable to that described in domestic fowl (Davis and Domm, 1943). In waltzing the body is held horizontally and head low as in threat running. Most of the body feathers, especially those of the flanks and rump, are raised during running. The head may be tilted somewhat outward as in circling. Almost always the outer wing is lowered so that the tips of the primaries scrape the ground. This wing may be lifted at an angle of about 45 degrees from the body. The inner wing is never lowered and tends to be almost entirely concealed by the fluffed flank feathers. The male may make half a dozen complete circles about the bird to which he is displaying. However, should the second bird be under a bush or in a corner, the displaying male may make figure-eight runs away from and back toward the second bird. Between waltzes the male will stand erect and laterally to the second bird. Body feathers will become normal and the extended wing withdrawn. At this time the male may give the waltzing calls. In captivity waltzing may last for five or six minutes before the aggression of the male wanes and he resorts to other behavior such as tidbitting and copulation.

When there are three or more males in the same pen with hens, one can invariably observe the following behavior: One male will dominate all other males at will but he

seldom threatens them. He does little or no courting of females. The second-ranking male will dominate all other males and will display frequently toward them with head tilt and circling. He will also court one or more hens intensively. Either of these actions will invariably elicit threats from the dominant male. He will cut between the courting male and the female, waltz vigorously, and make the second-ranking male desist.

Tidbitting.—This ritualized form of feeding accompanied by characteristic calls occurs mostly during male-female encounters and is described under "Courtship Behavior." Between males it occurs at low levels of aggressiveness and usually after the initial circling and head tilting have abated.

Attack.—A male will rarely attack another bird without some preliminary display. Attacks are usually preceded by waltzing or circling which become steadily more direct, rather than lateral, in their direction. Finally the dominant male will make a direct rush and grab the other bird by back or nape feathers, often to the point of breaking the skin of the defensive bird. Closely balanced birds may fight for several minutes before the conflict is resolved, but this is unusual. Attack, unlike copulation, is generally from the side rather than the rear.

Calls of the dominant bird.—During 15-minute paired encounters of birds in indoor pens, the dominant male always gave the *squee* call of aggression and the rally call. These were most common after the relative dominance of the two birds was settled. The submissive bird never gave either of these calls.

SUBMISSIVE BEHAVIOR

During paired encounters between males one can quickly determine by behavior which bird is destined to be submissive. Submissive birds start wing flapping almost at once after facing an aggressive male (fig. 2b). In wing flapping the bird stands straight on its feet, gives a vigorous flap of its wings and actually rises slightly off the ground. During flapping all body feathers including those of the crown are strongly fluffed, and the bird usually faces somewhat away from the aggressor. Rarely does the aggressor flap. Following flapping, and at other times as well, the submissive male may ruffle his feathers. Another sign of submissiveness is turning away from the aggressor. Under more intense aggression the submissive bird begins running away. First indicator of escape is the raising of the wings, so that the tips of the primaries meet above the bird's back. This is in contrast to the behavior of birds in non-agonistic situations, where the primary tips rest well below the back. Submissive birds run with legs well bent and body horizontal. They hold the head far back on the shoulders and squeal. Chases may persist for several minutes. Eventually the submissive bird crouches in some sheltered position. The deep motionless crouch is the very opposite of aggressive behavior and tends to conceal both barred flanks and white throat patch that stand out on an aggressive bird. This submissive behavior serves to stop further aggression for the most part.

The contrast between dominant and submissive birds is shown in table 1 which summarizes behavior of paired encounters between males. These males had been kept isolated except during encounters. They were first tested at the stage in their reproductive cycle when they were courting females actively. There was a clear-cut distinction between behavior of dominant and submissive birds. Once dominance was established, there were no reversals in social rank on subsequent encounters. I have not studied establishment of the peck order outside of the breeding season. However, in 1955 three males and three females were placed together in early January. I observed occasional gentle pecks at other birds but no overt display. I suspect that the peck order takes much longer to be established in winter than during the breeding season.

Males behave aggressively toward females as well as males. This is not surprising since the sexes are alike in appearance. In the domestic fowl Wood-Gush (1960) has found that males isolated from females during the breeding season behave very aggressively toward females when first introduced to them. This is true of Chukars also. Typically the male attempted to copulate with the hen within 30 seconds of introduction to her, and often was successful. This was followed immediately by five to ten minutes of

TABLE 1

BEHAVIOR OF DOMINANT AND SUBMISSIVE MALE CHUKAR PARTRIDGES IN 44 PAIRED ENCOUNTERS FROM MARCH TO MAY, 1960

Behavior	Dominant males		Submissive males	
	Number of occurrences	Per cent of dominant males displaying	Number of occurrences	Per cent of submissive males displaying
Attack	227	50	1	2
Waltzing	39	16	0	0
<i>Squee</i> call	372	55	7	5
Rally call	397	57	10	7
Circling	596	82	6	9
Lateral stance	188	68	12	9
Steam-engine call	8	9	3	2
Tidbitting	41	25	14	13
Bill wiping	19	16	55	25
Feather ruffling	57	68	152	93
Wing flapping	35	43	267	98
Avoidance	3	7	856	89
Squealing	0	0	939	55

intense waltzing accompanied by aggressive calls. Only after this release of aggressive behavior would the male then resort to appeasing behavior leading to further copulations. Females showed the same avoiding and appeasing behavior as submissive males, but they might be attacked just as vigorously as males.

Females rarely acted very aggressively toward other females. Usually aggressiveness consisted merely of one female running toward the other. This frequently caused the submissive hen to move a few feet to the rear of the dominant hen. Circling and waltzing were infrequent among females. Females tended to be most aggressive after pair formation while repelling females intruding into a territory.

COURTSHIP BEHAVIOR

Courtship among animals may serve four functions: orientation of male and female, persuasion, synchronization, and reproductive isolation (Tinbergen, 1953). Courtship behavior was originally thought to be solely a sexual phenomenon. We now know that this behavior stems from a conflict in the simultaneous tendencies for male and female to act sexually, aggressively, and submissively toward the partner. This conflict of tendencies has brought about the evolution and ritualization of courtship behavior (Tinbergen, 1953; Hinde, 1953). The behavior of Chukars follows these principles of causation and function of courtship.

Courtship among Chukars typically has the following pattern. The male will at first act aggressively toward the female. Circling, head tilting, and waltzing may occupy five to ten minutes. The female meanwhile continues with her activity of the moment—preening, feeding, or dusting. Only when the male is overly aggressive may she avoid,

squeal, and even take cover. The intensity and frequency of these displays gradually wane and the male tends to perform farther and farther away from the female. Eventually the male seemingly loses interest in the female and begins to feed or preen. But soon he may move off some five to 20 feet from the female and begin a display well known among domestic fowl as "tidbitting" (Davis and Domm, 1943; Wood-Gush, 1956). In this the male makes incipient pecks toward the ground, especially at conspicuous objects such as stones, feathers, earthworms, or even food particles (fig. 2c). True pecking and picking up of objects follows, associated with the tidbitting call. The male holds his legs half bent, body sloped downward from tail to head, wings held tightly to the body, crown lowered, and tail either straight back or somewhat bent under. The bill is pointed downward but seldom comes closer to the ground than a half-inch during mock pecking.

Early in the season the female makes no response to these calls. But later she may instantly break off her own activity, run to the male and begin pecking at the same or nearby objects. This lasts for a few seconds, until the male suddenly stands erect and moves off in a stiff-legged step called "high-stepping" in domestic fowl (Wood-Gush, 1956). In high-stepping the male is more erect than in any other stance, with breast almost vertical. He bends his legs only slightly in running and holds wings and feathers in normal position. The male almost always moves around to the rear of the female and again tidbits. Tidbitting, then, appears to have strong appeasement value. Hens that had just previously been strongly evasive of a waltzing cock soon approached the tidbitting male. Another indication of the appeasing value of the tidbitting display was that copulation was most likely to follow a series of tidbitting displays, but it rarely occurred during waltzing.

Precopulatory behavior is highly stereotyped. It begins with the female facing directly away from the male and crouching deeply with head forward and below the level of the back. The male stands still and erect about three to ten feet behind the female for a brief moment. He then gives the precopulation rattle and at once "high-steps" rapidly toward her with breast and flank feathers well fluffed. The female intensifies her crouch and raises her folded wings to horizontal position and holds them there throughout copulation. The male stops calling as he places his foot solidly in the middle of her back, grabs vigorously at her nape, and mounts (fig. 2d). He crouches on her back, wings outstretched and extended so that they come completely over her flanks. He presses his tail downward until it touches the ground, the female's being tilted to one side. Copulation lasts about three seconds, after which the male dismounts and "high-steps" off several feet. The female may continue her crouch for several seconds, then gets up and ruffles her feathers vigorously. Rarely does a second copulation immediately follow.

The female may crouch while feeding or dusting. This often releases copulatory behavior in the male. In this situation the female tends to rise or take a single step as she hears the male give his precopulation rattle. This suffices to stop the male from further approach. Rape, however, may occur when males have been separated from females over a long period of time. They may then be so aggressive that they grab the female from the side and then mount her vigorously despite her efforts to escape. In outdoor pens rape occurred especially late in the breeding season when the females were well along in egg laying but the males were still highly motivated sexually.

Ordinarily the necessary stimulus to release copulation behavior in the male is the sight of a female facing away from him and fully crouched. The female may initiate this orientation by turning away from the male. Or the male may move around until he is

behind her. This "rear approach" has likewise been observed in domestic fowl (Skard, 1937; Wood-Gush, 1956).

The female may disrupt the male's copulatory intentions by merely turning so that the male is no longer behind her. The male may make a series of these "rear approaches" without ever inducing crouching in the female. I agree with Wood-Gush (1956) that the sexual tendency is dominant in the "rear approach." But the escape tendency is apparently sufficiently strong so that the male breaks off his copulation attempt unless the female crouches and orients properly.

Another element of courtship is the "nest ceremony." Usually the male initiates this by entering a clump of vegetation. He then crouches, usually holds his tail almost vertical and spread so that the rusty tail feathers are conspicuous, and turns slowly in nest-scraping motions. He may also move sticks and grass with his bill in a drawing motion. At highest intensity the bird will hold its wings slightly outstretched and quiver both wings and tail rapidly. All this time he gives the nest-ceremony call. When both male and female are at the site together, the ceremony is most intense. One bird performs in the nest while the other stands close by. Birds change places every 30 seconds or so. This exchange may go on for several minutes at a time and may be repeated on and off all day.

Observations of birds on the wooden floor of the indoor pen gave some insight into the nature of the releasing stimuli for the nest ceremony. At first, birds never performed the nest ceremony, but they might make motions of scratching, turning and pulling objects into the "nest." But when I placed a clump of weeds in one corner of the room, both male and female performed the nest ceremony within a few minutes. A week later the birds performed the ceremony in any darkened corner of the room. Hence the releasing stimuli presumably became less precise as the internal motivation of the bird increased. However, at no time was the nest ceremony indoors as intense as that outdoors.

In the first three years of the study I first observed the nest ceremony on April 1, March 17, and March 16. The latest I saw it was on May 17. It preceded egg laying by a full three weeks. Highest-intensity display occurred after birds were paired. At such times the male's nest ceremony call often attracted the female to the nest. But the male rarely responded to the female's initial nest calls. I never observed nest display once egg laying began.

Wood-Gush (1954) describes a similar ceremony in domestic fowl under the name "cornering." His roosters' behavior was similar to tidbitting and dust bathing and included a call very similar to that heard in tidbitting. But since his birds were in bare pens, I suspect a corner was a substitute nest site and the behavior he observed was in fact ceremonial nest building.

Since the male Chukar shares in raising the brood, this display may serve a valuable function in keeping the male closely oriented to the female during egg laying and incubation. In addition, in various members of the genus *Alectoris*, including Chukars, the male may incubate and hatch the first clutch (Goodwin, 1953). Hence this display may be still more important in orienting the male to the future nest of eggs.

A female may also perform ritualized nest building when away from the nest. She will pick up sticks or grass and throw them over her shoulder one after another. The first time I observed this behavior the hen had been in a nest form idly tossing stalks over her shoulder for several minutes. She then moved out to the edge of the nest clump and continued this throwing, gradually working her way out until six feet from the nest.

The first occurrence in spring of the various forms of aggressive and sexual behavior followed their order of increasing intensity. Thus males in outdoor pens began tilting their heads in threat the last week of January. Circling began on February 9, and waltz-

ing on February 22. Pair formation began as early as March 9, with nest calling on March 15. Earliest copulation was witnessed on March 20 and egg laying on April 10.

PAIR FORMATION

Pair formation was a subtle act. Certainly the male's initial circling observed in late February and early March in outdoor pens was not directed toward his eventual mate. Once paired, the pair appeared to prefer a particular area of the pen, for that day at least. The pair was particularly intolerant of other females. Whether a paired male was intolerant of other males depended upon his social rank. Later in the breeding season a male might pair with a hen within 24 hours after she had been placed in the pen.

I had most success in getting birds to pair in 1955 when the three males and three females were together steadily from late December. In 1956 and 1957 I never observed a definite pair formation. Perhaps this was due to fairly frequent shuffling of birds. This was in contrast to observations by Goodwin (1953) that birds that were too familiar with each other did not pair readily.

The history of male GW in 1955 illustrates some of the behavior during pair formation. GW was lowest in peck rank of three males in the pen. He was chased frequently and pecked occasionally during early spring before and during courtship. GW started circling female R in early February, but never paired with her then. Then on March 2, GW appeared paired with female RB. They paced restlessly back and forth along one fence steadily for an entire day and kept separated from the other four birds in the pen. A week later, however, GW was definitely paired with female R, his original partner. They remained in one corner and side of the pen almost steadily. Meanwhile RB, the jilted female, kept trying to approach GW. However, female R kept chasing her away with short lunges. During the next two days the two females seemed about evenly balanced. They paced back and forth along one fence with male GW between them, so actual contact between the two hens was minimal. After that, however, RB gave up attempts to stay with GW.

In the meantime, male GW actively herded his mate R into the corner of the pen every time she strayed too far. Several days later, however, R was able to move about more. In doing so she frequently moved into an area used by G, the dominant male. When GW attempted to keep by R's side, male G almost invariably drove GW away with head tilt or actual circling or herding. Very similar behavior occurred with the second-ranking male. Hence the ability of a male to stay with his mate hinged upon his social rank. In the wild, one would ordinarily expect paired birds to withdraw from the covey and escape the intolerance or domination of higher ranking birds.

Although GW was lowest in rank of the three males, he succeeded in having four mates over a two-month span, his previous ones dying from accident or disease. On the other hand, the dominant male G did not acquire a mate until April 15, a full five weeks after GW was paired. G performed a minimum of courtship display and finally paired with the bottom-ranking female. Hence the strong aggression of dominant males may inhibit their ability to appease females, resulting in their being slower to pair.

Although paired birds tended to remain in a particular area of the pen for a day or more at a time and were intolerant of intruding birds, I do not think this was strictly a defended territory. Some pairs would remain in one area for several hours, then suddenly move to the other side of the pen, remain there for several more hours, and finally move on to still another area. So no pair held to a single area for more than a day or two. My limited observations in the wild, however, indicate that Chukars have well-defined territories that they defend vigorously.

CAUSATION OF COURTSHIP BEHAVIOR

One is immediately struck by how much of the dominant bird's display is a lateral presentation: circling, waltzing, and the stationary lateral erect posture. Indeed it is only during the running threat from a distance and in actual attack that one bird approaches another directly during agonistic encounters. These lateral displays are enhanced by the conspicuous barred flank feathers. The fact that attack rarely occurs without preliminary lateral display of some kind strongly suggests that even the most aggressive bird hesitates to attack. Circling of the opponent represents a compromise between approach and retreat, the displaying bird being in a position to move in or away at any instant, which in fact he frequently does. The first attacks by an aggressor represent a gradual transition from lateral circling or waltzing to diagonal approach and final direct attack. This is the same whether the dominant male is displaying to another male or to a female.

Tidbitting almost never occurs during waltzing sessions. Instead it tends to occur first as the aggressiveness of the male has waned and his waltzes stop. During tidbitting the male shows some fear of the female for he tends to avoid the female shortly after she runs up to him. Yet the male is sexually motivated for he often copulates with the female soon after he shifts from waltzing to tidbitting. Hence the tidbitting display appears to be the resultant of low aggressive and moderately high escape and sexual tendencies.

It is striking that the copulation, tidbitting, and nest-ceremony calls all bear a close resemblance to the aerial alarm call. It may well be that these have all evolved from the more primitive alarm call and retain an element of alarm as a causal factor in each instance. We are presently observing the ontogeny of these calls and hope to determine their relationships through sound spectrograms.

The male ordinarily attempts to copulate only when the female crouches, the least aggressive position she can take. In addition the male breaks off his approach to the female should she make a slight move. Hence it seems likely that the male is in conflict between sexual and escape tendencies.

The female shows fewer signs of conflict in her behavior. This is understandable because she shows very little aggressiveness toward other birds. Thus hens kept in isolation from cocks during the peak of the mating season were usually ready to crouch the minute a cock was placed in the same pen. Once this initial copulation had occurred, the hen was strongly evasive of the male for some time before she was again ready to solicit copulation. It appears that her sexual motivation was high when first placed with the male. But after copulation the sex tendency dropped and the escape tendency dominated her behavior. Whether a hen crouches or avoids seems to be the result of a rather sensitive balance between sexual and escape tendencies.

Courtship behavior, therefore, is the resultant of the conflicting tendencies to attack, escape, or act sexually. In early stages aggression is dominant and courtship consists chiefly of the more aggressive elements of circling, waltzing, and rally calling. As the sexual tendency increases and aggression wanes these forms give way to tidbitting, nest ceremony, and accompanying calls that serve to appease the female, eventually ending in copulation.

SUMMARY

The Chukar Partridge was studied for four years, observations in the wild augmenting those of captives. Fourteen calls of adults were classified according to their association with alarm, social contact, agonistic, or sexual situations. Most common was the

rally call. During the breeding season it was an aggressive call, serving to announce a dominant male and to repel intruders. Rally calls were at a peak at sunrise and sunset. Throughout the year the rally call also serves to reunite scattered birds.

Several calls depended upon the bird's aggressiveness. As the aggressiveness of a bird toward an opponent decreased, one heard in descending order the following calls: rally, *squee*, waltzing, steam-engine, and submissive *squeal*. Sexual calls included the tidbitting, nest-ceremony, and copulation-intention calls.

When two strange males met during the breeding season, their relative dominance was settled within a few minutes. Aggressive elements of behavior included: circling, head tilt, lateral stance, waltzing, running threat, and attack, as well as the aggressive calls listed above. Submissive birds never called except for the submissive *squeal*. They flapped their wings and ruffled their body feathers frequently, avoided the aggressor, sleeked all body feathers, and when escaping raised their wing tips over the back and held the head back on the shoulders while running. Females showed little aggressiveness toward other birds.

When a male was first placed with a female, courtship began with a period of waltzing and other aggressive display. It was followed by tidbitting and then copulation. As the breeding season advanced, the nest ceremony became important in maintaining the pair bond.

Pair formation was slow in early spring, but it became much more rapid later. The dominant male in a group did far less courting than the second-ranking male. He also paired later than less aggressive males.

Courtship displays appeared to be the resultant of the relative and absolute strengths of the attack, escape, and sexual tendencies of the male, and to a lesser extent those of the female.

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