THE AUK

A QUARTERLY JOURNAL OF

ORNITHOLOGY

VOL. 84 JANUARY, 1967 No. 1

BEHAVIOR OF THE BOBWHITE, *COLINUS VIRGINIANUS*

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THIS paper presents the results of a three-year study of the Bobwhite. The objectives of the study were to describe the maintenance, agonistic, sexual, and parental behavior of adult quail, to determine causation, function, and derivation of the behavior, and to correlate the behavior with sex and social rank of the birds.

Little has been added to our knowledge of the behavior of Bobwhites since the classic monograph by Stoddard (1931), and this study cannot add much to the description of behavior, for Stoddard was a keen observer. It will, however, probe deeper into the causation, function, and derivation of behavior than did Stoddard's work.

METHODS

The birds used in this study were from stock reared for several generations in captivity. Most birds were kept in outdoor, wire-covered pens, the largest of which measured 20 × 40 feet. Natural vegetation covered the ground, but was clipped or thinned out to permit good observation of the birds from an enclosed and elevated observation room outside one end of this pen. From this room I recorded most of the calls described in this paper. I also played back recorded calls from this room to study the function of specific calls. Smaller pens, 10 × 40 or 10 × 15 feet housed breeding pairs or birds I wished to hold in isolation. Birds were marked with both colored plastic leg bands and plastic neck tags. Quail often completed the full breeding cycle in pens as small as 10 × 15 feet. Birds paired readily and egg laying was normal. Many hens, however, did not incubate until July, and some not at all. If the hen did incubate a clutch, she and her mate showed normal parental behavior thereafter. Some birds were kept in visual isolation by confining them in individual cages indoors. These were later introduced for brief periods into observation pens to study social relations between newcomers and established birds. Other isolated individuals were placed together in pairs or trios to study sexual and agonistic behavior in detail under controlled conditions in an indoor observation room measuring 10 × 20 feet. Observations covered the entire span of daily and annual activity of the birds with emphasis on the breeding period and in early morning and late afternoon when activity was greatest. Over 400 hours were spent in direct observation. My procedure was first, after long hours of observation, to

Male Bobwhite in typical whistling pose.

Photograph by Jack A. Stanford, Missouri Conservation Commission

categorize and describe each recognizable behavior pattern and vocalization. Second, through continued observation and through manipulation of the numbers and sexes of individuals confined in a single pen, I determined the causal factors and function of each behavior pattern and vocalization. Every item, except where noted, was observed many times. Data in various tables indicate the number of observations on which the generalizations about behavior were based.

Concurrent with this study, C. R. Ellis, Jr., was studying the behavior of Gambel's Quail (*Lophortyx gambelii*) and R. L. Rumsey and H. W. Williams that of California Quail (*L. californicus*) in the same location. References in this paper to these species relate largely to their unpublished studies.

MAINTENANCE BEHAVIOR

Stoddard (1931) has made careful descriptions of the daily activities of Bobwhites. However, since so much of the agonistic and sexual behavior of birds has been derived from maintenance behavior (Tinbergen, 1952), a brief review of this behavior is essential.

Probably the most time-consuming maintenance activity was the care of skin and feathers. This took many forms; only those significant in agonistic or sexual situations are described here.

Dusting began with a bird's pecking and then scratching at the ground several times. The crouched bird soon started to draw the dirt in toward its body with its beak, then throw dust up on its back and wings. He ruffled the body and neck feathers and slightly extended his wings to the side. Dusting was "contagious," with most of a flock soon joining in, the members thus benefitting from the dirt thrown up by each other. This contagious behavior appeared often to inhibit aggression and terminate bouts of chasing and pecking between males. The crouched position of a dusting hen, with extended flank feathers, also resembles her pre-copulation crouch. In fact, the dusting posture seemed at times to serve a sexual function in releasing approach of the male and even copulation.

After dusting, the bird freed its feathers of dust and rearranged them. The movements associated with this process also occurred at other times. The most general of these was *ruffling* of the body feathers. Here the bird slowly erected its body feathers including both breast and flank feathers and then gave one sudden *shake*, following which the feathers subsided. A bird sometimes went through initial stages of ruffling without the final sudden shake.

Preening, another form of feather and skin care, began with the breast feathers, then the scapulars and wings, and ended with the tail coverts. Preening often occurred in social situations and then was largely limited to breast and scapulars. For the care of its head feathers, a quail either rubbed its head in the dust while dusting, or made one to several quick

head scratches with its foot, or resorted to preening from another bird. In the last case, one bird gently pecked at the head feathers, especially those near the eye, of the second bird. At times, the bird being preened turned its head and neck to allow for easier preening. Both males and females preened other males and females at all times of the year.

Locomotion was highly variable. A bird stood or moved in body positions varying from a deep crouch to full leg extension. These positions have been aptly described and illustrated for the chicken (Foreman and Allee, 1959) and appear comparable in the quail. When moving in heavy cover, a bird walked with its body held horizontally but stood erectly the instant it stopped. However, a bird moving on open ground was more likely to move in semi-erect posture. An escaping bird ran in an erect position, often with head held back and wing tips meeting along the back. An attacking bird, on the other hand, ran in a low stance with head held forward. When a bird first moved out into the open, following an extended period of resting, it often suddenly stopped, rose high on its feet with extended legs, and gave a single sudden flap of its wings (*wing flapping*) which, at times, almost met overhead. The bird often actually cleared the ground. Following this, the bird might move out into the open. Flapping also occurred at times not clearly associated with the end of resting. Also occurring right after rest periods was the *leg stretch*, in which movement a bird extended one leg fully to the rear, holding it clear of the ground. At the same time, the wing on that side was usually opened so that the tips of the primaries touched the ground. Young chicks were especially prone to stretch, adults much less so. I did not observe this movement in agonistic situations, perhaps because it was a deliberate movement, taking two to three seconds, during which a bird would be vulnerable to attack without being able to escape promptly. Another conspicuous wing motion was *wing flicking*. This was a short, sudden lifting (perhaps one or two inches) in the vertical plane of the folded wing. It appeared to be a feather-settling motion. On passing another bird, usually one of uncertain social status, a bird often gave a *tail wag*, several quick, back and forth movements of the tail, which usually was fanned. Just before a bird took to the air, its tail was widely *fanned*. A standing or running bird also often fanned its tail over extended periods of time. Although a fanned tail also occurred at other times, in both sexual and agonistic situations, its occurrence seemed to signal flight preparation. A slight up and down *jerking* of the tail also occurred, often associated with the *toil ick ick* alarm call.

Food getting was a final form of maintenance behavior the movements of which also occurred in agonistic and sexual behavior. Birds frequently *pecked* at objects on the ground, either food or grit, or other inanimate

objects. Ordinarily birds fed silently, but when a male discovered a new source of food he was apt to peck at the food without eating it and to give a special "food call." This "tidbitting" at food or other objects on the ground was first described for chickens (Davis and Domm, 1943) but has been observed in other galliforms, as summarized by Williams and Stokes (MS). The call and tidbitting served to attract both males and females. Outside of the breeding season the call seemed to serve the purely social purpose of facilitating food-finding by a covey. Its sexual significance is presented later.

ALARM BEHAVIOR

When first placed in strange surroundings, a Bobwhite would take immediately to cover, from which it was reluctant to emerge. When it did, however, it was in a stereotyped manner. The bird hesitated for several minutes at the edge of cover, its crest raised fully and body feathers sleeked, and standing erectly. It then suddenly ran across the opening to further cover at full speed. The crest was lowered the instant cover was reached. With increased familiarity with new surroundings, the alarm waned much more quickly and birds then walked in a relaxed way across such openings.

Another alarm reaction occurred when a bird discovered a strange object—either a potentially dangerous one, such as a cat or snake, or any conspicuous change in the normal environment. In these situations the bird approached slowly and erectly with head and neck held forward to see the strange object clearly while staying at a distance from it. Feathers were sleeked except for the raised crest. The head was moved to right and left to improve vision. This alarm reaction was contagious and the remaining birds of the covey usually joined in the exploration of the strange object. This approach was usually silent, but if the object was sufficiently alarming, the birds called *toil ick ick.*

Quail had several responses to approaching predators. If suddenly alarmed at close range, they burst into the air; with somewhat more warning they ran off, crest raised and body sleeked, often giving a soft *tirree* call. If a human to whom they were accustomed approached, the birds did not panic. Instead they moved about in the open, tail fanned fully, breast feathers fluffed, and crest raised, giving at first the *tirree* call, which changed to *toil ick ick* if the intruder remained. If the intruder went no further and remained quiet, the birds' alarm waned rapidly, with the *toil ick ick* calls becoming softer and grading into a *teewa* call and the body feathers and posture returning to normal. This behavior was especially true of a male with mate or chicks and of a dominant male in a social group.

If the danger appeared in the sky, the bird uttered a single sharp *errk* and froze on the spot. Other birds in the group might freeze or run to cover. Chicks responded to this call and often remained frozen or under cover for an hour or more until the hen again started to move about.

Another reaction to aerial alarm was a *distraction display*. The bird gave this when a potential avian predator suddenly came into view—such as a Black-billed Magpie (*Pica pica*) flying low over the pens. In response to these alarms the quail made one or more quick short runs of one to five feet, turned quickly, and darted off in another direction in very low stance, being always silent. The run ended with a sudden deep crouch which the bird held until the danger disappeared. This response is very similar to that of the Chukar Partridge (*Alectoris chukar*) and probably other galliforms (Stokes, 1961). The suddenness with which a bird begins and ends these short runs could confuse an avian predator about to pounce on its prey.

Most strange sounds alarmed quail. With day-old chicks, the strongest alarm reaction came whenever I made high-pitched squeaks by hand, causing the chicks to dash rapidly to cover or to freeze.

AGONISTIC BEHAVIOR

Two methods were used to study agonistic behavior. In the first, seven males were placed in a 20 × 40 foot pen from October through the end of the next breeding season. The social rank of these birds was established by observing pecks, attacks, and chases. During the breeding season, individual males or females were added to this group of males to elicit agonistic behavior. Occasionally, the dominant male was removed to see the effect on the remaining males. The behavior of individual males was recorded and correlated with dominance, subordinance, and social position. The behavior of males toward other males, toward strange females, and to familiar females was then compared to form the basis for distinguishing between agonistic and sexual behavior.

I also observed the behavior of two or three birds in a 10 × 20 foot observation room. Except when being tested, these birds were kept in individual cages where they could hear but not see each other. In some tests, two birds were taken from their cages and placed in the observation room at the same time. In other tests, one bird was allowed to be in the pen for varying periods of time before the second bird was introduced. This gave the "resident" bird an advantage over a newcomer placed in the pen. Tests varied in length depending upon the activity of the birds. There were three kinds of tests: male against male, male against female, and a male placed with an established pair. Seven males and five females were used in these tests, each bird being used several times in different

combinations. Observations were made from a darkened room. Birds were generally aware of me and during early tests often crouched for periods up to 30 minutes before starting to move about. With repeated trials the birds became habituated to the test room and to me after the first few minutes.

In each test the dominant bird was recognized by such overt, aggressive actions as pecking the rival or attacking, and by the absence of avoidance behavior. In some early-season trials, males showed little interest in each other and no clear-cut dominance occurred. I eliminated these trials in the analysis of agonistic behavior that follows.

Some behavior occurred in discrete units and could be readily quantified. Thus I was able to count the total number of tail wags and wing flaps by each bird. Other body positions were maintained more or less continuously such as fanned tail or pacing. I quantified these by recording the number of minutes of the test period in which the posture or movement was maintained.

In addition to the various forms of maintenance behavior, several other types of behavior occurred during these encounters between strange birds. The most dramatic and ritualized of the displays was the *frontal display*, or wing raising. Stoddard (1931: 17) called this a courtship display. From my observations, as described below, I prefer to call it agonistic.

In this display the bird always directly faced its rival. The tail was fanned, tilted slightly back and forth, and raised somewhat above the horizontal. The breast feathers were fluffed and the flank feathers generally lowered and loose. The crest and other feather tracts were normal. The bird assumed an almost horizontal position and the wings were raised. The wings were rotated so that the upper surface faced forward, forming a vertical plane. The primaries were also extended, forming a broad fan at right angles to the body. The half-extended legs raised the back end of the body. The display usually occurred as a bird took a step or two toward the rival; the bird rarely approached the rival closer than 12 inches. If the two birds were nearly equal in social position, the displaying bird might chase the rival about the pen for up to 10 seconds. In subsequent encounters, the dominant bird usually attacked without display.

I observed 54 instances of frontal display in my all-male flock upon introduction of a stranger. Most of these displays were silent and not associated with further aggression. The exceptions were as follows: five were associated with or occurred right after *hoy* calls; eight preceded or were followed by "caterwauling"; five came immediately before or after bill fighting; and one, after a *bobwhite* call.

I saw this display only during the breeding season. It was given by

males only, virtually always by relatively dominant males either to hens or subordinate males.

The distribution of the 54 instances of display among the seven males, listed according to social rank, was: 20—4—4—13—11—2—0. The top-ranking male displayed most; the lowest ranking male never displayed.

A male might display to another male in any of the following situations:

1. A mated female moving toward a strange male, or vice versa, was likely to elicit frontal display by her mate toward the strange male.
2. After a strange and subordinate male had crouched in concealment for some time, he eventually would move and take a few steps into the open. This might elicit immediate frontal display by the dominant male.
3. If the social position of two males was so close that the subordinate male continued to move freely about the pen, the dominant male might repeatedly display to the subordinate male. This display was likely to continue until the social rank of the two birds was clearly established and the subordinate bird avoided the dominant.
4. A male might also display when separated from a rival male by a wire fence. This seemed to be particularly common in unmated males displaying to a mated male, over a period of days. These rivals were still strangers to each other, for neither bird had been able to test the other by direct contact.
5. Males in my all-male pen frequently displayed while looking under a wooden fence into an adjoining pen where there were six hens and only two males. Since their view was exceedingly restricted and no direct contact ever possible, this was essentially a display to a stranger. Despite being able to hear the birds across the fence and partially to see them, the birds continued this display for several weeks and until breeding displays waned.
6. An incubating male might display when disturbed by a human approaching to within a few feet of the nest. The male seemed to be reluctant to leave the nest and tended to display in front of the nest or actually on top of the eggs. Only with further provocation did the male move forward toward the intruder. He might also display when his mate was captured and began to scream.

A male might display to a hen under these circumstances:

1. When male and female were first placed together, the male was likely to display on his initial approach to the hen but rarely after that. She did not react. The same display occurred whenever a caged hen was introduced to an all-male group. Males approached the cage and displayed in front of the hen.
2. When a strange male was added to a pen with hens, he might discover a partially concealed hen. He then displayed to her and would even walk into the brush where she was concealed. This could happen numerous times in the course of a morning. However, the male would, in general, not display to the same hen once she had emerged.
3. A mated male might display to a strange hen when she was introduced to a pen.
4. I twice observed a male mount a hen that had been introduced only 30 minutes before, hence she was still somewhat of a stranger (pair formation did not occur). Immediately on dismounting, he displayed for a second and then moved off.

Although a male could readily recognize a hen by her plumage, nevertheless, he almost invariably would first challenge her with frontal display. Only when she failed to display in return did he accept her as a female.

In summary, males display to strangers whether male or female. Display to females is not followed by attack. Males never display to their mates once pair formation has occurred—in fact, once the initial display is over. Nor will a male display to a familiar male.

From the above observations I conclude that this elaborate display is in reality aggressive rather than sexual. If this were courtship, one would expect to see it repeated over hours or days. Instead a male may display just once to a newcomer. It seems likely that the display is a compromise between attack and escape tendencies. The attack tendency shows up in the frequency with which the display is associated with aggressive behavior such as attack, bill fighting, and "caterwauling"; in the correlation of display with social rank; and in the actual body positions. The display is frontal with body horizontal as in actual attack. In addition, the extension of the primaries so that they almost touch the ground occurs throughout the galliforms and has been shown to be associated with aggression wherever carefully studied (Kruijt, 1962: 25; Stokes, 1963: 129). The fanned tail, as will be discussed later, occurs where both attack and escape tendencies are present.

The escape tendency shows up in the failure of a displaying male to press its attack. A displaying male rarely came within 12 inches of its rival, even during rapid chases when it would have been easy for the displaying bird to catch up with and actually attack the evading bird. The frontal display, however, has a sexual function to the extent that when a female reacts indifferently to this display she identifies herself as a potential mate.

Another form of aggression was *bill-fighting*, in which a bird pecked at the other's beak. Each bird stood erectly and attempted to peck down at the rival. As pecking continued the birds might shift ground a few feet. The action sometimes led into a frontal display followed by more bill-fighting. *Squee* calls often preceded and followed the fighting. Bill-fighting often lasted 15–20 seconds but rarely ended in vicious attacks. Instead, the lower bird might move off without being pursued. Most commonly, bill-fighting occurred between males. It occurred between females only when a strange hen invaded the familiar ground of another hen, usually a mated one. Males did not fight hens. Bill-fighting among males was elicited most often when a stranger, either male or female, but especially a female, had been added to a pen of unmated males during the breeding season.

Bill-fighting was always a mutual display with both antagonists taking

the same posture. This suggests that both birds are equally motivated. Additional evidence for this conclusion was that bill-fighting was a drawn-out display and that bill-fighting was absent between the sexes, where males always ranked above females.

Actual *attacks* sometimes occurred. At low intensity, these were merely single jabs at the rival, often in the region of the eye as the rival passed close by; at other times, they consisted of direct running after an escaping bird and grabbing at the feathers of the back or nape.

A bird was unlikely to attack a stranger on first sight. Instead, there was a series of approaches and withdrawals. In this, the dominant bird stood erectly with breast feathers fully fluffed and tail fanned. Legs were extended, making the bird appear tall. When starting to attack, however, the bird crouched with its body sleeked and tail usually not fanned. This crouched position with flexed legs enabled an attacking bird to lunge with full force at its rival.

Occasionally, a male would fly up into the air toward a rival or human and attempt to rake the opponent with his toes. I have been attacked by incubating males and also by males when I held the mate in my hand. Aerial attacks also occurred when an intruding male threatened to usurp a resident male's mate. I have not seen such attacks where two males only were involved. Hence, there appears to be a much higher threshold for release of aerial attacks in Bobwhite than in the Ring-necked Pheasant (*Phasianus colchicus*) (personal observation) or Junglefowl (*Gallus gallus*) (Kruijt, 1964: 38), in which birds such attacks are frequent.

Avoidance behavior of the subordinate bird took several forms. It showed up in absence of motion or in a very slow walk; this was especially true of a hen when placed with a male. In its stance, the subordinate bird was always lower; the tips of its primaries tended to be raised and met on the bird's back, whereas those of the dominant bird were lowered to the side. A subordinate bird might avoid attack by turning away, but also by nudging in beneath the rival. This made it difficult for the aggressor to strike with his beak. If pressed hard, the subordinate would walk or run away and when fully pressed, take flight, giving an "avoidance trill." Although a bird would raise its crest when approached by a ground predator or in presence of a strange object, it seldom did so when pressed by its own kind.

It is characteristic of conflict situations that a bird may perform displacement activities or intention movements (Tinbergen, 1952). By determining the probability for a particular form of behavior to occur with dominance or subordinance, one can then use these forms of agonistic behavior as indicators of a given individual's motivation (Stokes,

TABLE 1
BEHAVIOR OF DOMINANT AND SUBORDINATE MALES PLACED TOGETHER AS STRANGERS[1]

Behavior	*Occurrence per hour of observation*	
	Dominant male	*Subordinate male*
Attack	8.6	0.1
Pecking rival	3.8	0.2
Frontal display	1.6	0.5
Erect stance	1.9	0.4
Preening	44.7	11.3
Head scratching	7.3	0.5
Head shake	3.2	1.1
Breast feathers fluffed	4.8	2.8
Caterwaul	6.2	0.8
Food call	0.9	0.4
Avoidance	0.2	12.6
Avoidance trill	0.9	2.4
Fanned tail	3.6	3.0

[1] Total observation time, 24.7 hours.

1963: 123). Tests between birds in the indoor observation room showed sharp differences between the behavior of dominant and subordinate birds. The data in Table 1 are taken from trials where a clear-cut dominance of one contestant was apparent.

Head shaking, head scratching, and preening were characteristic of dominant birds. The lower incidence of these activities in subordinate birds occurred partially because a subordinate minimized attacks by remaining motionless. Only on relaxing did he resume maintenance behavior. Also, these maintenance activities were more likely to occur as a bird was approaching or withdrawing from a rival and even more while pausing before changing direction, or continuing on in the same direction. It is in these same situations that Rowell (1961) found displacement activities most likely to occur in the Chaffinch (*Fringilla coelebs*). Hence, in the Bobwhite, these seem to occur when there is conflict in the tendencies to approach and withdraw.

When a male and female were placed together, the female showed more of these displacement activities than did the male (compare the third and fourth columns of Table 2). I often noticed that a dominant male hesitated to approach a subordinate male that was crouched in a corner, often partially concealed. The dominant male would successively approach and withdraw from the subordinate, as though uncertain about the social status of the rival. At such times, preening, head shaking, and head scratching often occurred. In contrast, when a male was placed with a female, the female was usually relaxed and conspicuous. In this situation, the male would be able to determine quickly that the female was not a threat to him and his conflict between approach and withdrawal would wane.

TABLE 2

BEHAVIOR OF DOMINANT MALE BOBWHITE IN RELATION TO PRESENCE OR ABSENCE OF RIVAL MALE OR FEMALE

Behavior	*Occurrences per hour of observation*			
	Male with rival male and female	*Male with rival male only*	*Male with female only*	*Female with single male*
Attack	13.9	4.7	0.0	0.0
Pecking rival	2.0	5.1	4.8	0.3
Frontal display	2.2	1.1	0.0	0.0
Erect stance	4.1	0.4	5.7	0.0
Preening	72.4	23.3	5.3	24.0
Head scratching	8.5	6.3	0.3	2.6
Head shake	4.1	2.5	0.8	4.1
Caterwaul	12.9	1.3	0.4	0.2
Food call	1.7	0.4	0.2	0.1
Avoidance	0.3	0.1	0.0	0.2
Avoidance trill	0.4	1.3	0.1	3.0
Fanned tail	3.8	3.6	5.6	0.5
Hours observed	10.5	14.2	11.0	11.0

Although tail-wagging was independent of social rank, it did relate to agonistic behavior, for it occurred most when two birds were at close range—just as one bird would pass by or turn away from a rival. Tail-wagging is also common in ducks at close quarters, especially immediately after one duck lands among others. It may be basically a feather-settling movement, but its common occurrence while a bird is near others suggests it is released by the close presence of a stranger or rival.

The presence of a female increased agonistic behavior between the two males (Table 2, first and second columns). Note the increase in attacks, frontal display, erect body stance, head shaking, head scratching, preening, and "caterwauling." This sudden rise in aggression was even more conspicuous when a female was added to an all-male group of birds penned outdoors. In contrast, when a single male was penned with a lone female, these same forms of behavior occurred at much lower frequencies (Table 2, third column). When a single male was with a female, his tendency to attack was probably weak, or quickly became so, for the female showed no aggressive behavior. In contrast, she walked slowly, always in a low stance, or assumed such entirely non-aggressive activities as dusting or crouching. Any conflict in the tendencies to attack, escape, or act sexually was probably minimal in this situation, hence the decrease in the male's preening and related movements. Since both dominant and subordinate males rarely stood erectly in the absence of females, this body position may reflect sexual rather than agonistic motivation.

SEXUAL BEHAVIOR

Sexual behavior was generally confined to the breeding season. The male Bobwhite had the following forms of sexual behavior: lateral display, bowing, tidbitting and associated food call, copulation, nest ceremony, and the *bobwhite* call. The hen's sexual behavior consisted of nudging, wing quivering, presentation, precopulatory crouch, copulation and associated call, and nest ceremony.

Male sexual behavior.—The *lateral display* was given by males toward females in the breeding season. At highest intensity, the male walked slowly about the hen, usually from 12 to 18 inches from her. He fanned his tail and tilted its dorsal surface toward the hen. The flank feathers were loose and extended downward almost to the ground. The male was slightly less erect than in tidbitting. He shifted the feathers of shoulder and back to the side of the hen. He held his head forward and somewhat lowered. Rarely did the male make more than half a circle about the hen, by which time the hen had often shifted position, necessitating a new approach. More often, the hen was partially concealed or protected by cover so that the male was restricted in his display. Whenever a bird displayed laterally to a hen, he was likely to be attacked by a dominant male, if one was present. Lateral display was brief, lasting from 5 to 15 seconds. The approach of another male usually interrupted the display and agonistic behavior, sometimes leading to chase, was indulged in by both males. Throughout lateral display, the hen was almost always relaxed. Her feathers were normal and she stood in a somewhat low position, silently, with her crest and tail normal. The lateral display is strongly sexual in function. It in no way intimidated a hen and she often crouched to the male during, or shortly after, his display. I observed nine situations in which copulation occurred during or after lateral display; another time a male attempted to copulate but the hen did not crouch; once the hen crouched without the male's mounting; four times the hen nudged up to and beneath the courting male, although copulation did not occur; and four times lateral display was associated with no apparent sexual behavior.

Closely associated with lateral display was *bowing*. This was similar to pouting so commonly seen in pigeons (*Columba livia*). It had also the form of an exaggerated intention pecking at food, without the bird's ever touching the ground with its beak. The body feathers were fluffed, the legs were fairly well extended, and the body was horizontal as the male moved toward and around the hen. This looked like a compromise posture between tidbitting and lateral display.

With the onset of breeding season, the food call of the male changed in function. Whereas during most of the year it served to attract both

male and female to a new source of food, it now took on sexual function. In doing so, the call was enhanced by *tidbitting* (see p. 4). The display, for Bobwhite, has been described and analyzed in detail elsewhere (Williams and Stokes, MS). In brief, the male pecked at food or inanimate objects, while at the same time giving the food call. At high intensity, the male arched his back, ruffled his body feathers, fanned his tail, and stood high on his feet. This display attracted a female quickly, especially his mate. It sometimes also attracted other males, but in the wild this display and soft call is unlikely to be heard by other males, who would have been driven off already by the male. This display was given most strongly by a mated male; the longer he had been mated, the stronger the display and less likely he was to eat the food himself. Males under sexual deprivation might tidbit and call, but not as strongly as when a female was present. During strong sexual motivation, the male might tidbit at almost any inanimate object.

The factors eliciting the behavior seem to be high sexual motivation in the male, familiarity with a female, and a suitable object at which to tidbit (insects were strong releasers). Tidbitting functions to attract a female and to strengthen the pair bond—tidbitting lasted beyond actual pair formation. J. C. Wallen ("Parental and juvenile behavior in the Bobwhite quail," Master's thesis, Vassar College, Poughkeepsie, New York, 1964) observed tidbitting up to the end of October, but it occurred with decreasing intensity once the young had hatched or the sexual activity of unsuccessful breeders had waned. In the wild, there may be a two to four week interval between pair formation and egg laying (Stoddard, 1931: 19). Hence, any display that keeps male and female together would be important in promoting parental care in the male. Outside the breeding season, the display is not seen and only the call persists, and at low intensity.

Copulation was uncomplicated, being released by the solicitation crouch of the hen. However, the sight of a hen which was crouching between dusting movements, while brooding chicks, or in fear from some disturbance often released mounting by the male. The male circled the hen to approach her from the rear. He sometimes paused before he moved quickly up onto the back of the hen and grabbed her by the head with his beak. The male first held his tail up. As she everted her cloaca, he brought his tail to one side and then down firmly upon her, and trod vigorously for up to 10 seconds before dismounting. The hen called during copulation. There was no post-copulatory display. If the male had forcefully mounted the female, he might, on dismounting, act aggressively toward her and even display frontally. But normally the birds showed little further interest in each other after dismounting. Sexually

deprived males copulated frequently when given an opportunity. One male mounted a hen five times in the first eight minutes after a hen was introduced.

I observed homosexual relations three times in my all-male pen. Twice it was the two lowest-ranking males that were involved. These two males had never had a chance to copulate with the females that were introduced to this pen. Nor did these males call. None of the males that mounted did more than grab the crouched male by the nape without treading. The crouched males did not call nor evert the cloaca as in normal copulation.

Female courtship behavior.—The most conspicuous female behavior was *wing-quivering*. This consisted of a rapid lifting and settling of the partially opened wings away from the body. At high intensity, the tips of the primaries extended one or two inches above the level of the back. Several quivers might occur within a second or two. The hen was usually approaching the male while she quivered, with legs flexed and tail normal. Tail wagging sometimes followed a quiver, usually just as the hen had passed the male. Most quivering occurred when she was within six feet of the male (Table 3) as she approached and then passed the male in a straight line without orienting to him. But quivering might occur as she came directly toward or partially circled the male.

Vigorous bouts of preening, as well as ruffling, head shaking, and head scratching, often occurred in the intervals between quivering. Quivering was strongest while the male was facing the female and especially when he was alert and moving about. It occurred regularly when I placed a male in a pen with six hens that had had no access to males. In this pen, up to four of the six hens were observed to quiver in a single morning. The dominant female did the most quivering. I have also observed quivering when I placed a single hen in a pen with one or more males. Hens have quivered even when confined in a cage, as the males approached. Quivering occurred in the first few hours that a hen was placed with a strange male, and only rarely afterwards.

I never observed quivering until May, so I think this display was given only by females that were strongly motivated sexually. Prior to this time, hens did not approach males so actively and positively. It seems likely that the sexual tendency to approach the male conflicts with the tendency to avoid him since he is a stranger.

That the display stops so quickly after the male and female have been together suggests that habituation occurs quickly and the state of conflict disappears. The low running position of this display is typical of subordinate birds, suggesting a minimum of aggression. This display

TABLE 3
THE OCCURRENCE OF WING QUIVERING BY FEMALE BOBWHITE

Situation where quivering begins	*Number of occurrences*
Hen approaching male	
0–2 feet from male	26
3–4 feet	35
5–6 feet	35
7–10 feet	27
11 feet	8
Hen leaving male	11
Hen not in motion	6

seems adapted to attract the attention of a male, yet at the same time minimizes the chances of attack because of the absence of aggression and presence of strong submissive components. The display appears to have evolved through ritualization from a flight-intention movement.

Other sexual behavior by the hens consisted of an inconspicuous *presentation* before the male. In this the hen fluffed her breast and flank feathers. She assumed a low position, making *intention pecks* at the ground as she walked slowly and deliberately past the male, breast feathers fluffed and flank feathers fluffed and somewhat extended to the side. In the California Quail, the female may at the same time roll the back and flank feathers toward the male and even tilt her entire body to his side. However, I have not seen this tilting of feathers in the Bobwhite.

Copulation was apt to occur after a series of lateral displays by the male. The female showed her sexual readiness by her presentation display. I have seen Ring-necked Pheasants and Chukar Partridges show similar behavior.

Nest-building behavior.—Both sexes shared in building the nest. Building started with birds exploring for suitable nest sites, pushing into clumps of grass, or beneath dead stalks of weeds. Shortly afterwards, the bird moved away from the future nest site and while in a crouch picked up nest materials, turned with it far over its back, and dropped the material to either side. This was repeated every three to four seconds for periods up to five minutes. The bird sometimes gradually moved away from the nest site in its search for material. In this way it moved material step by step back toward the nest, the most distant material being picked up and dropped several times before it reached the actual nest. The bird never carried material to the nest, even though quail are adept at carrying food from an early age. This may be the most efficient way for a quail to transport nest material, but it may also be less conspicuous than actually carrying material. When enough ma-

terial had been dropped into place, the bird then entered the nest site and did a considerable amount of turning and scraping as well as pulling nearby vegetation down to form a canopy. The finished nest was frequently domed with a tunnel as entrance, but when birds built underneath a wooden shelter in the pens, the dome was missing. When one bird was building, the mate usually stood close by. Two birds often exchanged duties periodically. Two to three hours of steady nest building were enough to complete most nests. Beginning with the earliest stage of nest building, either member of the pair often gave the nest call, always while within the nest.

Stoddard (1931: 23) thought that the male does most nest building. I observed that the male selected the site and began the process by calling from the potential scrape, often with the female at a distance. Later, either bird might bring material to the nest, although the male did well over half the work. I never saw an unpaired bird show nest-building behavior. However, in two instances where homosexual pairs built nests both members of the pair called as well as helped build the nest.

Nest building in many species is a display (Tinbergen, 1952). The Chukar Partridge has a nest display and nest call which both sexes give (Stokes, 1961: 117). The *cornering* that Wood-Gush (1954: 138) describes for the domestic fowl appears to be similar in nature to the nest ceremony. The nest behavior in Bobwhite appears largely functional rather than having signal value. There are no special body or feather positions suggestive of display. Nest building almost always occurs near or at the site of the future nest. Some of the motions are inefficient, a bird often dropping material in random directions, or even taking material from the nest and dropping it outside. Nevertheless, the occurrence of a special nest call while the bird is turning in the nest scrape suggests some degree of display. In some birds the sight of the male functions to speed up ovulation in the female, and Lehrman (1961: 1278) has postulated that breeding season displays may serve this function more commonly than previously suspected. However, female gallinaceous birds will ovulate in complete isolation. So it seems more likely that a quail's nest ceremony functions to orient both male and female to the nest. This may insure that both sexes share in incubation and subsequent care of the young.

PARENTAL BEHAVIOR

Both sexes shared in parental behavior but there were considerable differences between pairs. In some instances, the female did all the

incubation, in others, the male. I observed only two special parental displays: *distraction* and *tidbitting*. The latter has already been discussed.

When disturbed at the nest, the male might at first display frontally while standing on the nest, then rush still displaying and then fly up in attack. If this failed to repel the intruder, he then gave a "decoy ruse" call. I have heard only the male give this call as he decoyed the intruder from the nest. In this distraction display, he ran in a crouched position, with his body horizontal, and fluttered his wings rapidly. The wings were extended some three to four inches to the side and were lifted to a horizontal position. While running he made short turns, ending up 20 to 30 feet from the nest. The initial decoy ruse calls soon turned into *toil ick ick* as he circled the nest area, crest raised and tail fanned. By this time, quivering had stopped. If the observer remained close to the nest, the bird was likely to circle back to the nest cover and while concealed give a fast, steadily repeated *tir tir tir tip* or *tip tip tip tip*. A male sometimes gave the decoy ruse call when I captured his mate and held her, with her screaming, in my hand. The similarity in form of the distraction display with the wing quivering of a sexually aroused female suggests a common motivation of these two displays. The very low crouch of distraction display could be an expression of broody behavior. The quivering in the distraction display could be a compromise expression of escape behavior, but is possibly a modified form of the frontal display, hence aggressive. The back and forth movement during the display also denotes an alternation of approach and withdrawal tendencies. The subsequent change of the display into more typical escape behavior, when the bird returned to the nest cover, bears this out. Similarly, in wing quivering by the female, the crouch may be an expression of sexual tendency (i.e., copulation crouch) and the quivering the same as in the distraction display—a compromise between approach and withdrawal, with the escape tendency predominating.

CALLS OF THE BOBWHITE

I have used Collias' (1960) classification of calls relating to group movements, food finding, avoidance of enemies, and reproduction (subdivided into sexual and parental phases). Names of calls, for the most part, are those used by Stoddard (1931).

Group movement calls.—Next to the *bobwhite* call, the most well known call is the separation or scatter call, the name coming from the fact that scattered birds give this call when attempting to rejoin the covey. This call had three distinct forms: a soft *hoy,* a louder *hoy-poo,* and finally a still louder, clear call, *koi-lee* or *hoyee* (Figure 1, A–E). Both sexes gave these calls, although they are softer, faster, less nasal,

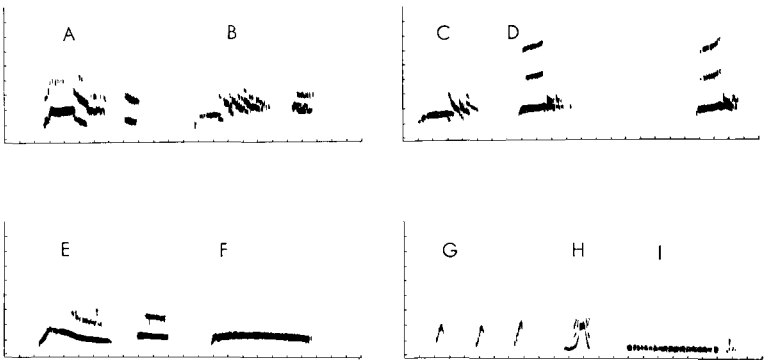

Figure 1. Group movement calls of Bobwhite. A. *hoy-poo* call, B. variant of *hoy-poo* call, C. *hoy-ee* call, D. two *hoy* calls, the musical awakening note, E. nasal, drawn-out *hoy-poo* call, F. "broody" call, G. *took* call, H. *pitoo*, I. *coo*.

Intervals on horizontal axis are 0.1 second each; the vertical axis represents the frequency, with intervals of one Kc/sec.

and more musical in the female. These calls are directed to birds farther away than is true of the contact calls which are discussed later. In my pens, birds oriented their calling to birds in neighboring pens rather than to their penmates.

I could elicit these calls by separating a bird from its group or mate for several minutes. Initially, the separated bird gave a soft *hoy* which graded into *hoy-poo*. As the breeding season progressed, the *hoy-poo* of isolated females changed into a loud, musical *koi-lee,* which was uttered 5 to 10 times in quick succession and then stopped completely for several minutes if there had been no response by the male. If the mate of the calling female was within earshot, he responded with more rapid and loud *hoy-poo* calls as he faced her. This call had a strong effect on unmated males, releasing loud bursts of *bobwhite* calls and orientation to the calling females, as shown in Table 4. For an unmated female, or one that had lost her mate, this loud call served a strong sexual function in attracting the attention of unmated males.

The clear musical form of this call, *koi-lee*, commonly occurred at roosting and awakening. As birds first stirred from their roost, the entire group might give a few brief bursts of this call. This also happened just before birds went to roost. Birds in other coveys might be calling at the same time.

Birds sometimes gave the scatter call for many days without getting a response. I kept a pair of Bobwhite in my garden one summer. Although these birds were far removed from other birds, each evening toward dusk the hen would give 10 to 20 of these clear, musical calls

TABLE 4
SUMMARY OF OCCURRENCE AND FUNCTION OF SEPARATION CALLS

Call and situations where given	*Function*
Koi-lee	
On awakening and roosting	To notify adjacent coveys or pairs of the location of the calling birds, hence, a spacing mechanism
By female separated from mate or by unmated female	Notify location of calling bird, strong attractant for separated male or unmated males
Hoy and *Hoy-poo*	
By male separated from mate	Releases *koi-lee* in mate and functions to reunite pair
By female separated from mate, then changing to *koi-lee*	As above
By female and occasionally male, with a brood	Uncertain function
During encounters with strangers	Agonistic behavior serving to repel intruders

even though her mate was standing beside her. She always faced the outside of her pen rather than toward her mate. It seems, therefore, that the call serves to keep all quail in an area in auditory contact and not just the mate or other members of a covey.

It is striking that this loud, clear call is given for only brief periods—at awakening, when scattered, or before roosting. Since it is so readily located, longer calling would only increase the risk from predation. Clearly, in the morning and evening, the *koi-lee* call cannot function to reassemble scattered birds for they are already in close contact. More likely, this call keeps a covey apprised of the location of neighboring coveys. Hence the scatter call may be epideictic in function (Wynne-Edwards, 1962: 16), spacing out coveys and regulating density. A dual function is quite possible with so variable a call. A female readily recognizes the *hoy-poo* call of her mate and when separated from him will respond only to his call. Hence, the birds of a single covey can be attracted to the recognizable calls of members of their covey when scattered, but be repelled by calls from another covey.

The same dual function of a call appears in some other galliforms. Thus, the *cu cu cow* call of the California Quail serves to attract a mate or members of a scattered covey, as well as deter approach by other birds not in that group (Williams, pers. comm.). Likewise, in the Chukar Partridge (Stokes, 1961: 113), the rally call repels other males and reunites scattered members of a covey.

The Bobwhite had two other calls besides the separation call which helped to keep birds with their covey or mate. While feeding together,

birds gave numerous soft contact calls, usually inaudible beyond 15 feet. These may be represented as *took* (Figure 1, G) and *pitoo* (Figure 1, H). They often interchanged rapidly with the food calls. I have also heard the same calls given by adults picking up nest material. These calls seem well adapted to keep birds in contact as they range throughout the grassy and herbaceous cover typical of quail habitat.

On several occasions, I kept a mated pair of birds within a small indoor observation room. These birds invariably responded to *hoy-poo* calls of an outside bird with a long, very soft *coo* note (Figure 1, I). The birds called in resting position and with such little energy that there was no motion of throat or tail. I suspect both sexes gave the call. It stopped as soon as the *hoy-poo* call stopped. Since the call was scarcely audible at six feet, it is not likely to be heard in the wild. Stoddard has described what appears to be the same call given in similar and other situations by a covey just before the birds take flight when alarmed and by the parents to their chicks. The call is very similar in appearance to the "broody" call given by adults to chicks (Figure 1, F).

Food finding.—When an adult with a brood found food it gave a soft *tu-tu-tu-tu* (Figure 2, A) while pointing its beak at the food. This elicited quick approach by the chicks. The same call occurred during tidbitting and outside the breeding season when the male found a new source of food (Williams and Stokes, MS).

Avoidance of enemies.—Bobwhite, when alarmed, gave several calls. When approached by ground predators, including humans, the first call the birds gave was a soft, musical *tirree* (Figure 2, B) given with erect crest, fanned tail, sleeked body feathers, and erect stance. As danger increased, and if the bird was unable to escape, the call changed to *toil ick ick* or *ick ick ick* or variations of these (Figure 2, C, I, and J). The change in sound of these calls as the bird became more alarmed was effected by the shortening of the horizontal *tirree* or *toil* segment of the call and the emphasis of the vertical *ick*. As the danger disappeared, or as a bird became habituated to the presence of a human, birds gave a soft *tee wa* (Figure 2, D). At this time the birds were less agitated and moved less, and the crest and tail returned to normal. A female that was not receptive to a male's courtship sometimes also gave this call while avoiding the male.

Bobwhites gave a specific alarm call when sighting an avian predator—a throaty *errrk* (Figure 2, H).

Birds held firmly in the hand gave a piercing *c-i-e-w* (Figure 2, E). The call occurred in very young chicks but underwent some changes during development of the bird (Figure 2, F). Similar calling is characteristic of many animals. Although this call spreads the alarm among

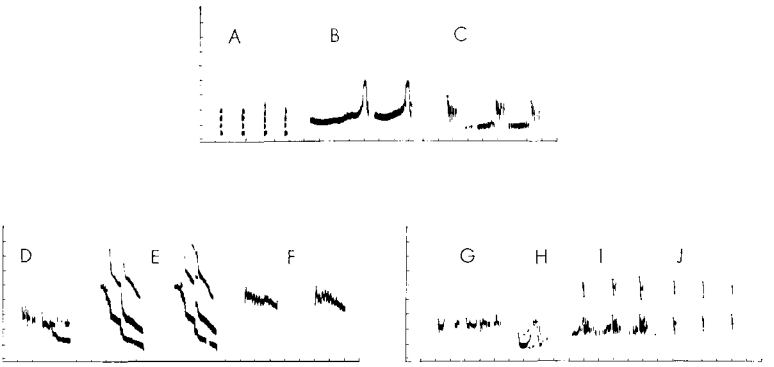

Figure 2. A. "Food-finding" call of Bobwhite; B–J. calls related to avoidance of enemies: B. *tir-ree*, C. *toil-ick, toil-ick*, D. *Tee-wa*, E. *c-i-e-w* of adult, F. *c-i-e-w* of chick, G. *tee tee tee*, H. *Errrk* alarm call, I. *toil-ick-ick* alarm, J. *tip tip tip* alarm.

See Figure 1 for scale.

other nearby birds, it may also serve to bring help. Mated males have run up quickly to me as I held the mate and threatened me within a few inches, with frontal display and incipient pecks. The onset of this sudden, loud call may so alarm the predator that it momentarily releases its grasp of the bird. L. R. Nygren (pers. comm.) once observed a Cooper's Hawk (*Accipiter cooperii*) capture an adult Chukar Partridge which at once gave the loud piercing scream. Immediately several nearby chukars ran up to the hawk which released its grip long enough for the screaming chukar to escape. Hence this scream may function to effect escape. If the bird was held in the hand for longer periods, it gave soft *tee tee tee* calls (Figure 2, G).

Birds gave other calls while avoiding rivals during agonistic encounters. A bird might give a brief, high-pitched trill when pecked suddenly by another bird; the hen called as the male first mounted her; and the male called when he ruffled his feathers or flapped his wings near a dominant rival or while actually avoiding an attacking rival. However, even dominant birds sometimes called while wing flapping without apparent interaction with other birds. Hence, the call was always associated with a tendency to move and usually with an escape tendency.

When disturbed at the nest or with a brood, the adult might give a distraction display and with this a "decoy ruse" call. Stoddard describes this as a fine cheeping *psieu psieu psieu* uttered by chicks and adults. I have heard only the male give this call as he decoyed the intruder from the nest. If the intruder remained, the male skulked under cover some 10 to 20 feet from the nest and called a staccato *tip tip tip* (Figure 2, J).

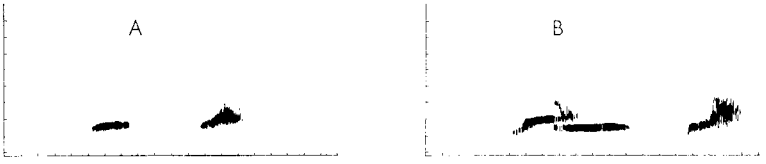

Figure 3. Some reproductive calls of Bobwhite. A. *Bobwhite* call of male, B. antiphonal calling, the *hoy-ee* of females followed by *bobwhite* of male. See Figure 1 for scale.

The same call was given by a female as she escaped from an attacking female.

Reproduction calls.—The *bobwhite* call (Figure 3, A) has been covered fully by Stoddard. This is a purely sexual call, given by an unmated male during the breeding season (see Frontispiece). Once mated he stops calling almost entirely but will resume calling if his mate is removed from him for several hours. However, Kabat and Thompson (1963: 112) think that mated males may frequently whistle, but generally only when separated from the mate, as when she is incubating.

Ordinarily, a male gave his *bobwhite* calls in any direction, changing every few minutes. The exception was when he heard the *hoy-ee* call of the female. On hearing this call, sometimes given only once, the male turned immediately and faced directly toward the calling hen. The tempo of "bobwhiting" rose from the normal 4 to 5 per minute to as high as 8 to 9, one call coming right after another without a break. The male might fly or run toward the calling hen. Bobwhiting, unlike the song of passerines, does not function to space out males. In my pen of seven males, several males would *bobwhite* at the same time with rarely a sign of intolerance between birds. I did notice, however, that subordinate birds sometimes lapsed into a "whisper" *bobwhite* as a dominant bird approached. This whisper *bobwhite* was also used by birds when alarmed while bobwhiting.

TABLE 5

THE STIMULATION OF *BOBWHITE* CALLS BY SEVEN MALES THROUGH PLAYBACK OF FEMALE *HOY-POO* CALLS

	Number of Bobwhite *calls per minute*		
	In 5 minutes before playback	*During playback lasting 2.4 minutes (total calls)*	*During 13 minutes after playback*
Test 1	2-0-0-0-0	20	13-10-7-9-10-6-3-4-4-4-3-4-7
Test 2	4-4-3-4-7	26	11-10-7-9-10-5-4-4-3-2-4-3-0

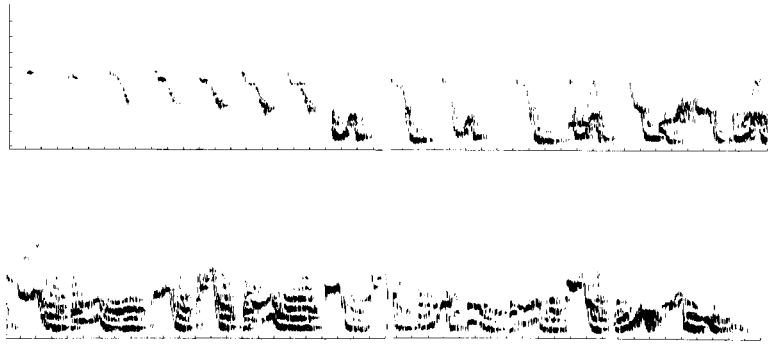

Figure 4. Copulation call of female Bobwhite. The four sonograms represent a continuous recording. See Figure 1 for scale.

I have also heard one female *bobwhite*. This occurred after I had removed her mate to a nearby pen. On removal, he soon gave the *hoy* call, to which she at first responded with a soft *hoy-poo*; 10 minutes later I saw her merely open her beak and give a series of inaudible *ab-bob-white* calls. These soon turned into soft *hoy-poo* calls becoming louder and louder. Over the next 30 minutes this hen continued to *bobwhite*, sometimes almost as loud as the normal male's call. This same female was also the only one to give a high intensity tidbit display. In other respects she was normal and frequently crouched to and was mounted by her mate. Stoddard, in his many years of observing Bobwhite, recorded one possible instance of bobwhiting by a hen. It is undoubtedly rare in occurrence. But hens might possibly give the whisper *bobwhite* so softly that humans would not hear it.

Although the playback of *bobwhite* calls could elicit bobwhiting, the response was never as strong as when the *hoy-ee* call was played. A typical sequence of calling before and after the playback of a *hoy-ee* call is shown in Table 5. *Bobwhite* calls given in response to the *hoy-ee* call tended to be antiphonal, the first syllable of the *bobwhite* call mingling with the end of the *hoy-ee* call (Figure 3, B).

A hen almost always called when mounted (Figure 4). The call began slightly before or just as the male mounted, became louder while he trod her, and ended abruptly as he dismounted. The call began with a few soft *tseeps*, then changed into 5 to 10 sharply segmented calls resembling the hand-held distress call (compare with Figure 2, E). These then changed abruptly into what appeared to be *squee* calls (compare with Figure 5, D), and ended with one or more softer *teewa* calls as the male released his grip on the female. I think the hen's copulation call is merely a form of escape or distress call released as the male hops on her

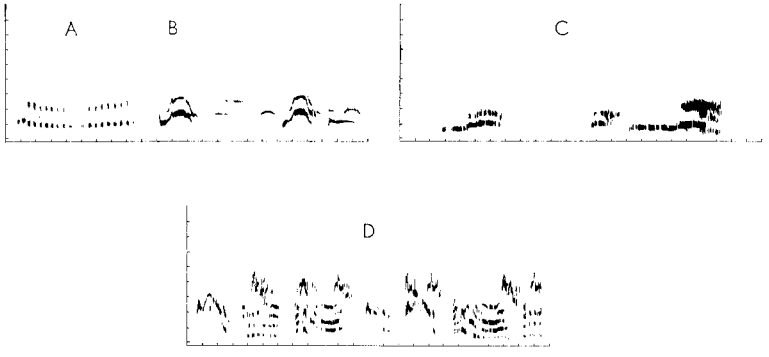

Figure 5. Some reproductive calls of Bobwhite. A. "nest" call, B and C. "caterwaul," D. *squee* call.
See Figure 1 for scale.

back and pulls at her head feathers. This in turn releases agonistic behavior in the form of *squee* and *teewa* calls. The frequency of unsuccessful copulations which the hen terminated by rising and walking off supports the conclusion that copulation occurs at a time of conflict between sexual, aggressive, and escape tendencies in the female. As far as I could tell, the male never called during copulation and certainly never before mounting.

The nest call was a series of low-pitched warbles, each lasting about one second and each warble consisting of about 25 notes undulating in pitch. It occurred only as the bird turned in the nest scrape (Figure 5, A).

Calls associated with agonistic behavior are grouped with reproduction calls because they occur during the breeding season, help space out males, and deter rivals from approaching the mate. Four calls were elicited by close-range interaction between birds: "caterwaul," *squee hoy*, and *hoy-poo* calls.

The most conspicuous was "caterwauling" (Figure 5, B and C), a loud rasping call with many variations, but with strong emphasis on the separate syllables. Stoddard's *h-a-o p-o-o w-e-i-h* may be the most common form of this call. A bird gave this call while standing still, erect, and with breast feathers fluffed and tail fanned. Caterwauling was almost entirely confined to the breeding season and mostly to the males. It occurred regularly whenever I introduced a strange male or female into a pen of male birds. The first response of the resident males was to approach the newcomer quickly and, when within about six feet, to caterwaul. Frontal display was likely to follow. Calling was most com-

mon when there were two or more males together with the female, very much less common when two strange males met, and rare when a single male was with a female (see Table 2). Dominant males called far more often than did subordinates. Caterwauling also occurred after I had entered a pen and stirred the birds up. The response was contagious and birds in adjacent pens tended to caterwaul, too, after this disturbance. My presence appeared to elicit aggression and with it caterwauling.

Caterwauling was frequently followed by frontal display, bill fighting, or pecking of nearby rival males. Caterwauling lasted for only the first few minutes of an encounter, by which time the dominance relationships of the interacting birds had been established. For these reasons, caterwauling denotes a strong attack and weak escape tendency in the calling bird. It serves to repel rival males from a potential or actual mate and in this way functions as territorial song. It differs in that the call is not "spontaneous," as is the song of the passerines, but must generally be elicited by the sight or sound of other nearby birds.

Mated hens often caterwauled when a strange male and especially a female was introduced. The hen then became almost as aggressive as a male in her reaction to the intruder.

The *squee* call was given mostly by males (Figure 5, D). The calling bird was always within 10 feet of a rival and usually within only 1 or 2 feet. The bird moved with breast fluffed but tail not fanned. The causal factor was almost always the presence of a nearby rival or strange bird. Most *squee* calls were associated with agonistic behavior—94 per cent of 172 calls in which the situations were recorded. These birds were in a state of conflict or thwarting rather than being clear-cut dominants or subordinates. The incidence of *squee* calls fell off rapidly after mid-June. This paralleled the decline in general breeding activity including bobwhiting and nest activity. Birds were more tolerant of each other from this date on.

In my well-organized, all-male flock, birds rarely gave either the *squee* or "caterwaul" calls without some outside stimulation. A sure way to elicit these calls was to introduce a strange male or female in the pen.

During an agonistic encounter, there was considerable changing back and forth from caterwauling to the *hoy-poo* calls. The *squee* calls occurred in the same general situation, but they tended to occur by themselves. A bird rarely shifted from *squee* calling to "caterwaul" or *hoy-poo* or vice versa (Table 6). This suggests a different motivation for the *squee* call than any of the other calls given in agonistic situations. This will be discussed further later.

Parental-juvenile calls.—These will be reported on more fully in a

TABLE 6
TEMPORAL RELATIONS BETWEEN DIFFERENT CALLS GIVEN IN AGONISTIC BEHAVIOR

Initial call	*Subsequent call*	*Number of occurrences*
"Caterwaul"	None	27
	Hoy	18
	Hoy-poo	30
	Squee	5
	Teewa	4
Hoy	None	23
	"Caterwaul"	26
	Hoy-poo	7
	Squee	1
Hoy-poo	None	42
	"Caterwaul"	26
	Hoy	25
	Squee	9
Squee	None	138
	"Caterwaul"	13
	Hoy	1
	Squee	4
	Teewa	> 18

later paper. Hence, I will only briefly mention some calls here; others have been mentioned already under other categories of calls.

A "broody" call is given by the male or female to chicks (Figure 1, F). The "separation" call is given by chicks when they are cold or separated from the group (Figure 6, B); this call evolves with age into the *hoy-poo* call. A "contentment" call occurs when chicks are in a group and moving slowly about (Figure 6, C). Other adult calls are the "twitter" call of mild alarm (Figure 6, D); the *tschur tschur tschur tit* note of stronger alarm (Figure 6, E); and the "take-cover" call, one to three loud, sharp calls by the hen causing strongest alarm in chicks (Figure 6, A), rarely heard.

THE EVOLUTION OF SOCIAL CALLS

The calls of species of solitary birds must serve two major social functions—both bringing male and female together and spacing out males. The first is a distance-reducer; the second, a distance-increaser. The latter may be soft or loud calls depending on whether they function to repel rivals at short or long distances.

Gregarious birds need a third basic social call—one to regroup scattered members of a group. This need will also occur in species with precocial young in which it is important for the young and parents to maintain close contact.

My study of quail suggests something of the evolution of these calls. With Bobwhite and California Quail the "lost" call of the chicks de-

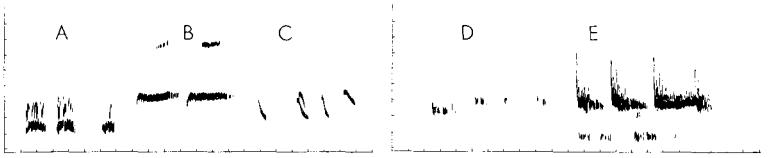

Figure 6. Parental-juvenile calls of Bobwhite. A. "take-cover" call, B. "separation" call of chick, C. "contentment" call of chick, D. *twitter* by chick (mild alarm), E. *tschur tschur tit* (stronger alarm).
See Figure 1 for scale.

velops into the loud separation call of the adults. Hence it seems likely that this call which serves to keep members of a group in contact, even when separated by several hundred yards, is a primitive call. In both the California and Gambel's quail the sexual *cow* calls are clearly related to the separation calls and derived from them (Ellis and Stokes, 1966: figure 1). Likewise in the Bobwhite the *white* syllable of the *bobwhite* call has the sound and physical structure of the musical *hoy-ee* separation call. The sexual call, i.e. "song" of these quail, thus seems to have evolved from the more generalized distance-reducing calls found in chicks and, throughout the year, in adults. This later development of "song" is perfectly possible in gregarious birds, for pair formation generally occurs while the birds are in a covey. A long-range sexual attractant is not necessary in gregarious birds in contrast to the situation in solitary species in which the sexes may migrate separately and the males take up territory well before the arrival of the females. A long-range "song" in quail would be valuable largely for the surplus, unmated males which always exist in quail (Emlen, 1940; Bennitt, 1951). In these males, calling would be a signal to females that have lost their original mate or, for some other reason, may not have found a mate while still in the covey. Quail "song" therefore, in contrast to most bird song, does not repel males. Mated male quail, in fact, rarely "sing." Unmated birds, whether male or female, probably continue to give the separation call until they locate a mate.

In the Chukar Partridge, a purely sexual call is lacking. In this species both sexes give the *chukara-chukara-chukara* call, which serves to bring individuals together throughout the year. During the breeding season males continue to give this call after becoming paired. It then serves to repel other males, so has both a repelling and attracting function. In this sense it is like typical song of passerines.

It is obvious in quail that the separation call and its derived sexual call will not function to space out mated pairs. Hence it is not surprising to find that quail, in contrast to passerines, have evolved a purely

TABLE 7
OUTCOME OF ENCOUNTERS OF MALE BOBWHITE

Dominant bird	*Subordinate bird*							*Wins*	*Losses*	*Total encounters*
	RW	*R*	*RB*	*B*	*BY*	*RY*	*RG*			
RW		5	32	2	2	0	0	41	8	49
R	2		23	100	23	8	3	159	22	181
RB	4	4		47	13	6	2	76	90	166
B	2	13	26		10	2	0	53	151	204
BY	0	0	9	2		2	0	13	49	62
RY	0	0	0	0	0		0	0	18	18
RG	0	0	0	0	1	0		1	5	6

agonistic long-distance call. This is the "caterwaul" in Bobwhite, and the *wit-wut* call in California and Gambel's quail. All of these calls in quail vary between individuals, as does typical bird song, so that male and female may readily recognize each other, as well as rival males. This functions to minimize the need for physical contact and close-range interaction.

These studies in quail point out the need to observe the calls used by both gregarious and solitary species of birds in pair formation and spacing out of breeding birds. A later paper will treat the ontogeny and origin of calls in gallinaceous birds in more detail.

SOCIAL ORGANIZATION OF AN ALL-MALE FLOCK

To see how a bird's social position affects its behavior, a group of seven males was confined to an outdoor pen from October through August. Until February there were seven females in the same pen. All these birds had previously run free in the outdoor rearing pen of the game-bird breeder from whom the birds were acquired. The birds were highly compatible in their new surroundings right from the start, and it was difficult to establish social ranking. In February, the females were removed, and with the onset of breeding the males became intolerant. Attacks, threats, bill-fighting, and pecking became more common and a precise social ranking was possible. Table 7 shows the number of attacks the individual birds made on others in the pen. The top-ranking male, RW, seldom attacked other birds. He did not need to, for the other birds kept away from him whenever he approached the food hopper or threatened them. Most interaction was between the next three males. The two lowest-ranking males were seldom attacked,

TABLE 8

THE FREQUENCY OF DISPLAYS BY MALES IN RELATION TO SOCIAL RANK

Feature	*Male*						
	RW	*R*	*RB*	*B*	*BY*	*RY*	*RG*
Social rank	1	2	3	4	5	6	7
Lateral display to hen	9	17	2	16	1	0	0
Frontal display to strange hen	9	2	1	7	8	1	0
Frontal display to strange cock	6	0	2	0	2	1	0
Frontal display to concealed bird in adjacent pen	5	2	1	6	1	0	0
Total frontal displays	20	4	4	13	11	2	0
Number of copulations	13	0	3	3	0	0	0

for they kept strictly to themselves and avoided feeding and drinking when others were present.

Starting in April, I occasionally added a single hen to the group of bachelor males. The top-ranking male seldom courted these hens. Instead, there was fierce competition between the next three males. Whichever male first succeeded in maintaining his position next to a hen was likely to dominate other competitors. For example, during June, R generally dominated B. One day B had the chance to stay near a hen for several minutes and to court her. Thereafter, B strongly dominated R for several minutes in violent chases about the pen. But finally, during a lull, R became dominant again. Hence, whenever a male was enabled, for one reason or another, to "pair" with a hen, he became more aggressive to other males and was likely to rise in social rank. On removal of the female, he returned to his previous rank.

A second influence upon social rank was the removal of a bird. Thus, after the second-ranking male had been removed from the pen for 10 days, he was attacked frequently after being replaced. Only after two days did he regain his original position but never as firmly as before.

Once a male had acquired an introduced female as mate, lower-ranking males desisted from aggression and were also compatible with other close-ranking males. Whenever a second female was added to the pen, a renewed burst of aggression and courtship began. Formerly compatible males at once became violently aggressive when they had the chance to court an unattached female.

Females kept together in the absence of males showed little aggression. When a single male was introduced to the group of females, aggression increased and social hierarchy became apparent. The highest levels of aggression in females appeared whenever I introduced a strange female to a mated female. The latter than behaved in a manner very similar to an aggressive male, even to caterwauling.

TABLE 9
FREQUENCY OF CALLS BY SEVEN MALES

Male	*Social rank*	*Call*						
		"Caterwaul"	Squee	Hoy	Hoy-poo	Bobwhite	*"Food"*	*Total*
B	4	62	77	30	82	24	14	289
R	2	33	45	21	24	38	5	166
RW	1	19	28	31	17	15	0	110
BY	5	26	38	24	6	10	1	105
RB	3	14	15	8	11	0	2	50
RY	6	9	5	3	1	0	2	20
RG	7	6	1	2	10	0	0	19
Totals		169	209	119	151	87	24	

Some correlations exist between social rank and behavior. The top-ranking male tended to keep to himself and had few aggressive encounters with other birds. The two lowest-ranking males virtually never called and were highly compatible with each other.

The top male was quick to assert by display his dominance over strangers—either male or female—that were added to the pen (Table 8). Although not as ardent a courter as R and B males (as reflected in the number of lateral displays), he was by far the most successful in the number (13) of copulations. Only the two lowest-ranking males were clearly restricted in their aggressive and sexual behavior by their social position. In fact, they became a homosexual pair.

Social rank also affected rates of calling. Table 9 shows the frequency with which each of the seven males in the all-male pen gave six different calls when a strange male or female was introduced. Table 10 ranks the frequency of these calls among the different males. Clearly, whatever released one call in a bird also influenced his other calling. Social rank could be one such factor (Table 11), although the degree of correlation is significant only at the 0.06 level. On the other hand, the frequency with which a male had agonistic encounters with other males had a

TABLE 10
RANKING OF FREQUENCIES OF CALLS

Male	*Social rank*	*Call*						*Sum of call rankings*
		"Caterwaul"	Squee	Hoy	Hoy-poo	Bobwhite	*"Food"*	
B	4	1	1	2	1	2	1	8
R	2	2	2	4	2	1	2	13
RW	1	4	4	1	3	3	6	21
BY	5	3	3	3	6	4	4	23
RB	3	5	5	5	4	6	3	28
RY	6	6	6	6	7	6	3	34
RG	7	7	7	7	5	6	6	38

TABLE 11

CORRELATIONS BETWEEN THE FREQUENCIES OF CALLING, SOCIAL RANK, AND NUMBER OF INTERACTIONS OF MALE BOBWHITE

Item	*Male*							*Correlation*	*Probability*
	B	*R*	*RW*	*BY*	*RB*	*RY*	*RG*		
Call rank	1	2	3	4	5	6	7		
Social rank	4	2	1	5	3	6	7		
Interaction rank	1	2	5	4	3	6	7		
Differences between rankings									
Calling vs. social	−3	0	+2	−1	+2	0	0	0.68	$<.06$
Calling vs. interactions	0	0	−2	0	+2	0	0	0.93	$<.01$
Social vs. interactions	+3	0	−4	+1	0	0	0	0.54	$>.10$

strong relation to calling rate ($p < .01$). Table 11 also shows the lack of correlation between social rank and the number of encounters of a male. Therefore, it seems likely that whatever caused a bird to interact with others also caused it to call. These encounters appeared to result from the combination of aggressive and sexual tendencies. A male that was successful in winning a female was likely to be approached by lower-ranking, but sexually motivated, males seeking to court the hen. These approaches led to calling and encounters between the two males. However, since the top-ranking male, RW, was strongly dominant over all other males, he was not challenged when with a hen and hence was involved in few encounters. Consequently, he had little occasion to call.

ACKNOWLEDGMENTS

This study has been supported by Grants G-12995 and GB-1358 of the National Science Foundation and Grant U-153 of Utah State University. I am grateful to H. W. Williams and Miss Cherrill Wallen for their original observations on Bobwhite behavior. I wish to thank Dr. C. I. Draper for facilities at the Poultry Farm at Utah State University.

SUMMARY

Bobwhite in captivity were studied for three years throughout their annual cycle. Maintenance behavior is described. Birds responded to strange objects on the ground with cautious group approach and an associated call. Ground and avian predators released two distinct calls and forms of escape behavior. Agonistic behavior was studied by placing together different combinations and numbers of males and females, mostly unfamiliar to each other. Behavior associated with dominance included attack, pecking rival, frontal display, erect stance, preening, head scratching, head shake, and caterwaul call. Behavior of the subordinate was characterized by absence of motion or avoidance, low stance, raising of primary wing tips above the back, nudging beneath rival, and avoidance calls. Head shaking, head scratching, and preening were typical of birds in

conflict situations. The presence of a female greatly increased agonistic behavior between two males.

Sexual behavior of the male included lateral display, tidbitting and associated food call, copulation, nest ceremony, and the *bobwhite* call. Tidbitting was a specialized display by a mated male to attract the female. The female sexual behavior included wing quivering during the time of initial contact with a male and a presentation display indicating she was ready for copulation.

Both sexes shared in nest building. Material was thrown over the back toward the nest rather than being carried. This was a display as well as being functional behavior. The male often gave a soft nest call while working in the nest.

Both sexes shared in parental behavior including incubation. While at the nest, the male had a strong distraction display and call given to ground predators. Calls of adult Bobwhite fell into five categories: group movements (4 calls), food finding (1), avoidance of enemies (11), sexual and agonistic (6), and parental (2). Some calls had several functions.

The male Bobwhite, unlike songbirds, uses one call to attract a mate (the *bobwhite*) and another call (the "caterwaul") to repel rivals. The *bobwhite* and the more generalized "separation" call have both evolved from the "lost" call of the day-old chick.

A group of seven males developed a straight-line social hierarchy established through display, calling, and attacks. Males that succeeded in gaining the side of a female rose in the social hierarchy. Presence of females always enhanced aggression among males. Females confined together showed little aggression except when a strange female was added. Rates of calling in males were closely correlated with their level of social interaction and not with their social rank.

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