

THE FOOD CALL AND DISPLAY OF THE BOBWHITE QUAIL (*COLINUS VIRGINIANUS*)

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COURTSHIP feeding, often with a display, occurs widely among birds. Since the review of courtship feeding by Lack (1941), the behavior has been described in many more species (Johnston, 1962). Although Lack and Johnston record courtship feeding in only two galliforms, it is known now to occur widely in this group (Table 1). Stoddard (1931: 109) briefly describes the food call and associated display of the Bobwhite (*Colinus virginianus*) as the male discovers and presents an insect to his mate. The objectives of our study were to describe the food call and display in this species, to determine the cause, function, and origin of the behavior, and to compare it with that of other galliforms.

PROCEDURES

This study is part of a larger investigation on the social behavior of North American quail. Our first study of courtship feeding was made during the breeding season when it occurs at highest intensity. We subsequently extended our observations throughout the year with emphasis on the breeding period and when adults were with chicks. We saw the behavior as it occurred among groups of birds, pairs, adults with chicks, and isolated broods. The birds were confined in outdoor pens varying in size from 250 to 2,500 square feet. Natural cover and limited natural foods were available. We provided water and wheat or commercial feed at all times. Birds paired readily and showed normal incubation, brooding, and parental behavior, except that some pairs failed to incubate their eggs to hatching.

To permit more detailed observations and to quantify the response of male and female when food was presented, we confined birds in a 4 × 4 × 6-foot indoor room. Details of these tests are given in following sections.

TABLE 1
GALLIFORM BIRDS KNOWN TO TIDBIT

<i>Species</i>	<i>Reference</i>
Chukar Partridge (<i>Alectoris chukar</i>)	Stokes, 1961
Red-legged Partridge (<i>Alectoris rufa</i>)	Goodwin, 1953
Domestic Chicken (<i>Gallus domesticus</i>)	Domm, 1927
Red Junglefowl (<i>Gallus gallus spadiceus</i>)	Kruijt, 1964
Bobwhite Quail (<i>Colinus virginianus</i>)	Stoddard, 1931
California Quail (<i>Lophortyx californicus</i>)	H. W. Williams, MS
Gambel's Quail (<i>Lophortyx gambelii</i>)	Ellis and Stokes, 1966
Painted Quail (<i>Excalfactoria chinensis</i>)	M. Vince, pers. comm.
Golden Ruffed Pheasant (<i>Chrysolophus pictus</i>)	Kruijt, pers. comm.
Reeves Pheasant (<i>Syrnaticus reevesii</i>)	H. W. Williams, personal observation
Ringnecked Pheasant (<i>Phasianus colchicus</i>)	H. W. Williams, personal observation
Vulturine Guinea-fowl (<i>Acryllium vulturinum</i>)	H. W. Williams and Stokes, personal observation

All birds were from game farm stock of undetermined race. Recordings of calls were made on Wöllensak T1500 or Model 730 Voice of Music recorders using Electro-voice 664 microphones. Spectrograms of calls were made on the Model 661A Kay Electric Soundspectrograph (FL-1 circuit; wide band filter).

BEHAVIOR OF ADULTS DURING COURTSHIP

The male normally calls while displaying but does not always display while calling, particularly during the nonbreeding season. When the call and the display occur together we term the behavior "tidbitting" after Domm (1927). The call given in the absence of the display is termed the food call. The normal sequence of behavior during the breeding season was as follows: The quail were engaged in some undisturbed maintenance behavior or loafing. Food was introduced and discovered by either sex. If the female saw the food first she generally ate without display or call. When the male was the first to see the food he moved to it and began to tidbit. Frequently he began the display at the instant he touched the food. This response was so precisely timed that touching the food seemed to serve as

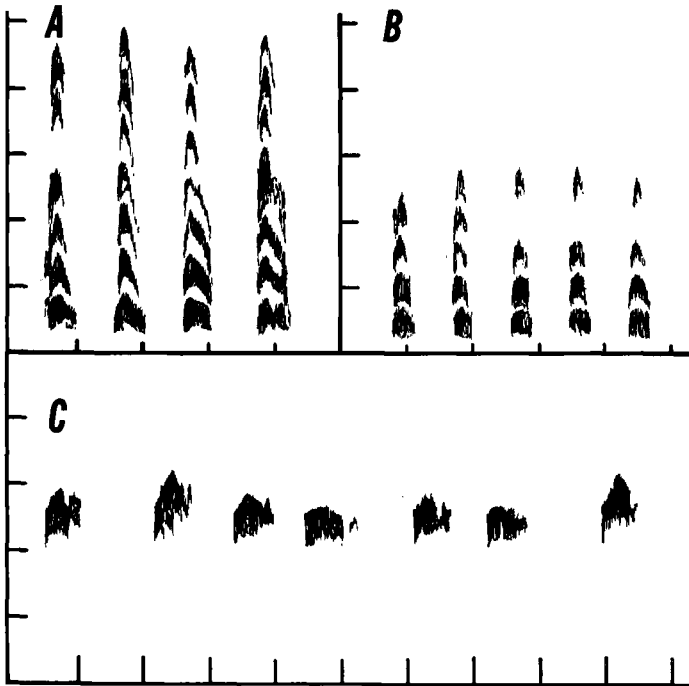


Figure 1. The "food-finding" call of Bobwhite; A, Breeding period (tidbitting call); B, Adult male with chicks; C, Juvenile "tidbitting-like" call. Intervals on horizontal axis are 0.1 second each; the vertical axis represents intervals of one Kc/sec.

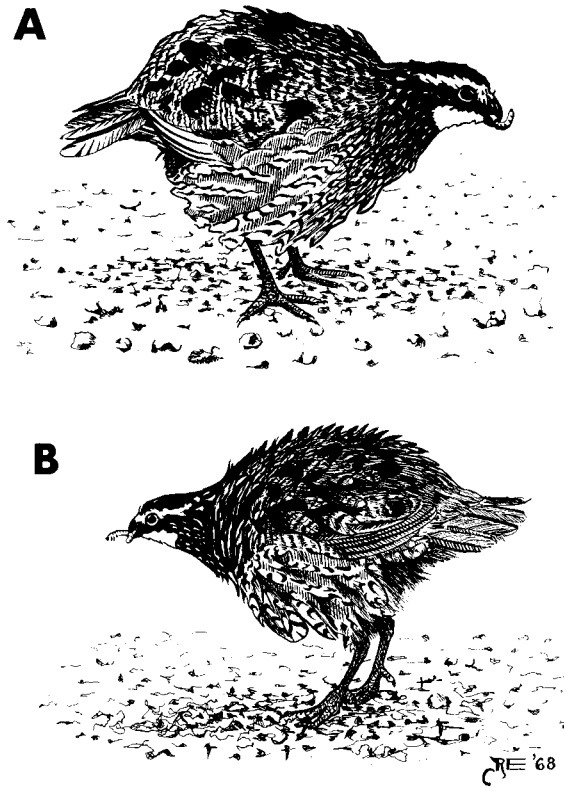


Figure 2. Male Bobwhite Quail tidbitting: A, Medium intensity display; B, High intensity display. Note extended legs, ruffled body feathers, and mealworm extending from tip of beak. (Drawing by C. R. Ellis.)

the releaser. When the food was a mealworm, the male quickly turned it so that it projected forward from the tip of his beak. Normally the female approached and took the food from the tidbitting male. She then rapidly turned away from him to eat it. The male stopped tidbitting immediately on releasing the food, and often wiped his bill vigorously against the ground several times. Copulation was seen several times to follow tidbitting within minutes.

The call.—Stoddard (1931: 109) describes the Bobwhite's food call as a soft, rapidly repeated *cu cu cu* given by the male to attract his mate. The call varies in length usually dependent on whether or not the female responds to the call (Figure 1). Males call longer when the female is slow to approach. The call of the male often starts softly and increases in loudness as the female approaches. This change in loudness normally ac-

TABLE 2
FOOD CALL AND TIDBITTING RESPONSE BY MALE BOBWHITE TO VARIOUS FOODS

Food	Breeding Season tidbitting (call + display)	Nonbreeding season (call only)
Mealworms	+	+
Crickets	+	+
Earthworms	-	-
Corn	-	+ ¹
Wheat	+ ²	+ ¹
Mixed cereal grains	+ ²	+ ¹
Purina meal	+ ²	-

¹ When presented as a new food normally not seen by the group.

² Following food deprivation for 2-3 days, normally no response.

companies a shift from low to high intensity in the display. The call is not always accompanied by display.

Food calling by birds in coveys is similar to that given during the breeding season but softer and shorter. The call is given by both sexes throughout the year, but males call much more than females.

The display.—The display varies in intensity. The lowest intensity display is merely an erection of the flank feathers as the bird manipulates or pecks at the food item. Early in the breeding season, and in several males with low motivation, this was the only component seen. At the next higher level the bird arches its body and tilts its head and anterior body below the horizontal, then extends both legs so that its body is 2-3 inches higher than in normal posture, and finally bends its neck and head forward and down as it pecks at or holds the food off the ground; erection of dorsal and flank feathers accompanies the arched body position. At maximum intensity back and flank feathers are ruffled, the wings remain folded close to the body, and the fully-fanned tail may be held in an elevated, normal, or depressed position. When the tail is in normal position or above the horizontal, the feathers around the vent are spread. Often the male rises on tiptoe and prances laterally before the female. Figure 2 shows males in varying intensities of display.

FACTORS AFFECTING BEHAVIOR DURING COURTSHIP

Type of food.—In several series of tests we added food in the form of mealworms (*Tenebrio*), crickets (*Acheta*), earthworms (*Lumbricus*), corn, and wheat to measure the response to specific foods in controlled situations (Table 2). Live mealworms and crickets elicited the most consistent tidbitting response. Dead crickets released calling only. Birds pecked at earthworms, but rarely ate them and then without calling. They appeared too large to be suitable food. Wheat stimulated calling during the nonbreeding season only after the birds had been deprived of food. Corn

TABLE 3
EFFECT OF TIME MALE IS WITH FEMALE ON RESPONSE TO
MEALWORM (1962 TESTS)

<i>Mealworms introduced (10 per trial)</i>	<i>Hours male was with female before testing</i>	<i>Male displayed or called, female ate worm (%)</i>	<i>Male ate worm (%)</i>	<i>Worm ignored (%)</i>
120	1	14	84	2
60	5	12	88	0
60	8	45	55	0
50	16	16	84	0
130	24	51	48	1
40	60	93	1	6

released low intensity tidbitting during the breeding season and mild calling at other times. Uncracked corn was probably not attractive when more easily eaten food was available. Males frequently caught insects in the pen and tidbitted with them. In contrast females catching natural food did not.

Time sexes are together.—To test more critically the conditions under which a male would tidbit, we ran a series of tests in 1962 (May, June) in which a male and female, unfamiliar with each other, were placed together in the small observation room. We then observed their response to mealworms at 1, 5, 8, 16, 24, and 60 hours following introduction. A single trial consisted of offering successively 10 worms into the room where the male could see them. The male responded in any of three ways: he tidbitted and offered the worm to the female, ate the worm without call or display, or ignored the food. Between trials the birds did not have access to mealworms and were fed mainly on commercial feed. Seven males and five females were used in these tests, the results of which appear in Table 3.

During the first 5 hours the birds were together, the male gave few food calls or displays and generally ate the worm. By the 8th hour he was displaying far more, and after the two had been together for 3 days, the male tidbitted most of the time when food was presented.

In 1963 the experiment was repeated in modified form using five

TABLE 4
EFFECT OF TIME MALE IS WITH FEMALE ON RESPONSE TO
MEALWORM (1963 TESTS)

<i>Mealworms introduced</i>	<i>Hours male was with female before testing</i>	<i>Male displayed or called, female ate worm (%)</i>	<i>Male ate worm (%)</i>	<i>Worm ignored (%)</i>
80	1	54	16	30
80	24	85	13	2

TABLE 5
ACTIVITY SCORES¹ OF MALE BOBWHITES TO 10 SUCCESSIVE MEALWORMS
OFFERED DURING 8 TRIALS

	<i>Worms 1-5</i>	<i>Worms 6-10</i>
Tidbitting by male	112	63
Food call by male	71	34

¹ Each male's response to a worm was given a score of 1, 2, or 3 as a measure of intensity of response. Total possible score was $3 \times 10 \times 8 = 240$.

males and four females in different combinations for 8 trials as shown in Table 4. Birds were placed together at 8 or 9 AM and tested at 1 and 24 hours afterwards. Again the males showed a consistent increase in the frequency of tidbitting and food calling between the 1st and 24th hour. Females likewise responded more to the males as shown by the increased number of worms they took from them.

The higher frequency of tidbitting after a lapse of 24 hours indicates that the greater response to worms resulted from the male and female being together longer rather than from mutual experience with the worms on repeated occasions.

Waning of the response.—With repeated introduction of food in a test, the response usually waned. Table 5 shows the drop in both tidbitting and food call by a male in the two halves of one trial. The activity score was designed to measure the decrease both in occurrence and intensity of display and calling. Waning of the response was greatest when the initial response was at high intensity.

The female's activity also affected the subsequent behavior of a male. If she continued to approach and take food from him, he was more likely to continue tidbitting with each worm. When she did not respond, the male stopped tidbitting and ate the worm. In three trials a female was placed in a wire cage where she was visible to the male but could not approach him. During these trials, run at 1, 8, and 24 hours after the two birds were placed together, the male tidbitted with the first three worms, but ate them when the female did not approach. He then continued to eat the last seven without any display or calling. During the display the female repeatedly went to the side of the cage on which the male was located. Hence not only approach by the female but actual female contact with the male's beak seems essential in maintaining the display.

A quick response by the female stimulated the male to continue tidbitting. On two occasions one male gave 25 and 28 consecutive tidbitting displays without waning as worms were presented to him. During both trials the female approached the male quickly. The few times she was slow to respond the male partially swallowed the food, but regurgitated it as the female approached.

TABLE 6
RANKING OF FOOD CALL IN MALE BOBWHITE¹

<i>Social rank</i>	<i>Ranking by number</i>	
	<i>Food call in observation room</i>	<i>Food call in outdoor pen</i>
1	3	2
2	5	6
3	4	3
4	2	1
5	1	5
6	6	4
7	7	7

¹ Call ranks based on number of times each male was heard to call, 1962 birds only.

Social rank of males.—Individual males varied considerably in their frequency of tidbitting. To see if this was related to social rank, we compared the tidbitting rank with the social rank (Table 6). The social ranking was obtained by observing the males in normal dominant-subordinate situations in the outdoor pen. Rank of tidbitting in both outdoor and indoor situations was obtained with the standard 10-worm test. All males were kept away from females except during indoor testing. Sexually deprived males readily tidbitted in the outdoor pen. One male gave the call in an apparent vacuum situation, interposing it with the nest-building call. All the males gave the call at least once in the absence of a female. Calling in this situation produced approach by other males, who attempted to take the worm. Calling males approached by other males seldom repeated the call on more than two to four successive worm introductions.

Tidbitting or food-calling rank and social position among males was comparable between the indoor and outdoor pens with a few exceptions. The fifth social-ranked male was the highest ranked tidbitting bird in the indoor room, but one of the lowest ranked in tidbitting in the outdoor pens. When he called or displayed in the outdoor pen he was dominated by other males, but when he was removed from the oppressing influence of dominant birds his tidbitting rate was the highest. Correlation between social position and calling rate in the outdoor pen was not great.

PERSISTENCE OF TIDBITTING BEHAVIOR

As food calling with display in adult quail was largely associated with courtship, we were interested in observing how long the behavior would persist through the breeding season. To do this we conducted a series of tests from the period of nest building through incubation on pairs placed in pens where they could nest undisturbed (Table 7). A single test series consisted of presentation of 10 mealworms, 5 to each member of the pair. The worms were offered one at a time in no particular order as to the

TABLE 7
ACTIVE RESPONSES BY BOBWHITES TO INDIVIDUAL MEALWORMS¹

	Males				Females			
	No. worms found	Food call only	Display only	Tidbitting response	No. worms found	Food call only	Display only	Tidbitting response
Courtship through egg laying	110	4	11	77	109	6	0	8
Incubation	20	0	2	17	30	2	0	2
Subtotal (per cent)	130	4(3)	13(10)	94(72)	139	8(6)	0(0)	10(7)
Chicks to age 3 weeks	68	0	20	41	62	0	11	13
Chicks to age 10 weeks	42	1	9	23	24	2	2	15
Subtotal (per cent)	110	1(1)	29(26)	64(58)	86	2(2)	13(15)	28(33)
Total	240	5	42	158	225	10	13	38

¹ Some worms were eaten without call or display.

sex receiving the food. Testing was done during the early morning and late afternoon periods of normal feeding. Males tidbitted more frequently than females during courtship and incubation. Both sexes gave the food call, but only males were seen to display without calling.

Tidbitting tests as described above were also carried out on adults with chicks. The procedures were the same except that for the first 3 days after hatching it was difficult to present 10 consecutive mealworms in the short periods in which the chicks were actively feeding. Table 7 shows the responses of male and female parents with chicks to age 10 weeks. Adults with chicks most frequently gave a soft call and low to medium intensity display. Males gave the food call with display less frequently than before the chicks hatched, but displayed without the call more often. After the chicks hatched, females showed an increase both in tidbitting and in the display alone. The food call without the display was given only three times to chicks, once by a male and twice by females. In 64 instances where the male tidbitted, chicks approached and took the worm 63 times. Of the 38 times that females tidbitted, chicks obtained the food 32 times. The youngest chick seen to approach a tidbitting adult was 3 days old. For the first 3 days past hatching the female continued to eat the worm when the male tidbitted. We noted that females began offering food to chicks on the first day of hatching, but ate it when no chicks responded. In several instances chicks apparently learned to respond to tidbitting by following the female to the male. When they saw the worm, one would grasp it and run, usually after one or two had jumped up to peck at the male's beak. After 3 days the chicks responded immediately by approaching tidbitting adults. From this age on they approached males and females 95 and 93 per cent of the times that the respective parents tidbitted.

In one case 38-day-old chicks were placed in a small cage in the pen with the adults. The male on finding a worm tidbitted at low intensity and

increased to high intensity when the chicks did not come. The female approached, took the worm, and tidbitted. The adults exchanged the worm several times, tidbitting at high intensity. The response then waned and the female finally ate the food. We obtained the same results using 3-day-old chicks except that tidbitting by both parents remained at a lower intensity. Hence when chicks fail or are unable to take the worm the tidbitting display is protracted. This is in contrast to the situation where the adult female fails to take the worm from the male.

BEHAVIOR OF CHICKS INDEPENDENT OF ADULTS

Bobwhite chicks begin pecking a few hours after hatching at almost all contrasting objects, edible or not. A chick's approach to a strange object is slow and cautious. The birds assume a characteristic tall posture with necks stretched and heads turning from side to side. Often approach is accompanied by a call sounding like the food call of adults (Figure 1). This usually elicits the attention and approach of more distant birds. If the object is edible, one bird picks it up and runs, generally pursued by others. This behavior is common among young galliforms; Kruijt (1964) calls it "food running." In several galliform species the behavior is accompanied by a food-running call similar to the distress calls of young chickens (Collias and Joos, 1953).

DISCUSSION

Function of the behavior.—Two basic functions have been ascribed to courtship feeding (Andrew, 1961; Armstrong, 1947; Lack, 1940). The first is to reduce the female's fear of the male and thus increase the likelihood of copulation. The second is to maintain the pair bond in those species where the pair remains together for more than just copulation. Tidbitting in galliforms, particularly the Bobwhite, Chukar Partridge, and Red-legged Partridge, serves both functions. When a male Chukar Partridge first meets a strange female in captivity he is aggressive toward her, and she avoids him. After a few minutes of threat he suddenly desists and tidbits. This almost at once causes the female to approach him, and copulation soon follows (Stokes, 1963). Under similar conditions the female Bobwhite avoids the male on first encounter. On several occasions during the breeding season we placed a strange sexually deprived male Bobwhite with a group of unmated hens, sexually isolated for several weeks or longer. The male acted aggressively toward the hens with characteristic frontal display. The hens avoided at first, but soon began an appeasement display of wing-quivering (Stokes, 1967). Then when the male tidbitted, the females approached immediately without wing quivering. Copulation often followed soon after. Hence tidbitting in this situation has an appeasing function permitting subsequent copulation.

TABLE 8
FEEDING AND COPULATING POSTURES OCCURRING IN TIDBITTING

<i>Feeding postures</i>	<i>Copulation postures</i>
Head down	Body and flank feathers ruffled
Neck forward	Tail fanned
Rear of body somewhat elevated	Tail elevated, normal, or depressed
Food in the mouth	Pericloacal feathers raised
Food call	Wings somewhat lowered

In both quail and partridges the male remains close to the female for several months and at least until the young become independent. Therefore the continuance of tidbitting could well function to cement this close bond, necessary for the role the male plays in incubation and rearing of the young.

Tidbitting during the chick rearing period is apparently a functional feeding of the young. Both adults tidbit and the chicks take food actively from each. Quail have an unusually high protein requirement during the first weeks of life. Although young quail are precocial, a piece of food at the end of the adult bill presents a strong contrast to which the chicks readily respond. Hence tidbitting may well function to promote better nutrition of the young.

Causation of tidbitting behavior.—Recent analyses of the causation of bird display suggest that the behavior results from the tendencies of an individual to perform two or more simultaneous but incompatible acts. Hinde (1953) goes so far as to state that “without conflict there can be no display.” Andrew (1961) suggests that display may represent one of three possible forms of compromise. It may be an alternation between one tendency to act or another, to approach or to withdraw, a compromise of body position or movement as seen in the circling of a bird about a rival, or a compromise of posture in which some parts of the body reflect one tendency while other parts indicate the tendency of another incompatible act.

There is ample evidence of conflict behavior during tidbitting. A mealworm is a palatable item of food. The sight of one leads the male to approach quickly and pick it up. The display begins at the instant of picking up the worm. Picking up palatable food must tempt the bird to swallow the food. In the absence of the female the male will often eat worm after worm without display. The presence of the female inhibits his eating it. We do not know just how this inhibition works, but the male must be in a strong state of conflict between eating and not eating the food.

As the male displays most vigorously at the height of the courtship period, we believe that his sexual motivation must be strong. Possibly

TABLE 9
OCCURRENCE OF FOOD CALLING IN BOBWHITE

<i>Time</i>	<i>Form</i>	<i>Performed by</i>	<i>Function</i>
Fall and winter	Call alone	Both sexes	Attracts others to new sources of food
Courtship period	Call + display	Males only	Attracts females
Parental period	Call + display	Male and female adults	Attracts chicks to food

the resultant tidbitting behavior also represents a compromise of postures normally present in the feeding and copulation acts as shown in Table 8.

This leaves unexplained the extreme raising up on the toes seen at the highest intensity of tidbitting. Lower intensity forms of tidbitting look much more like normal feeding. Presumably the tendency to behave sexually is less in these instances, but the tendency to feed remains strong. In these instances the male does in fact often end up by eating the worm.

Origin of the behavior.—In seeking the origin of the tidbitting behavior in Bobwhite it is important to recall that food calling occurs in three situations as shown in Table 9.

It seems most likely that the behavior originated in a generalized form and subsequently developed more specialized functions. Hence we feel the food call a quail gives while in a covey during fall and winter represents the original form. The display evolved later. In the Red Junglefowl Kruijt (1964) suggests the food call develops from the food-run call of chicks. The latter is a call chicks give on discovering a food item. They pick it up, then behave as though afraid of it by running with it while calling. In adult Bobwhite the food call closely resembles the call the bird gives on approaching a strange object (Stokes, 1967). Thus the origin of the food call in Bobwhite may be similar to that of the call in the Red Junglefowl. Outside the breeding season quail, on finding new or strange sources of food, do not necessarily share it with others, even though the call functions to attract other birds to the food. Instead the calling bird defends the food by running with it or by rotating its body to prevent others from reaching the food. Thus no conflict exists between tendencies to eat and not eat the food. Only during the breeding season does a strong conflict in tendencies to act arise.

The next most generalized form of the behavior is in the parental stage when both parents may call and display. Tidbitting display is then usually of low or medium intensity only. Finally only during the courtship phase of reproduction does the highest intensity display occur. This is also the most specialized function of the display given by males to a female. In passerines juveniles commonly beg for food both in the nest and for some time outside the nest after fledging. The same behavior reappears in the

adults when the male feeds the female during courtship and later as the female is incubating (Lack, 1940; Armstrong, 1947: 44). Thus the origin of courtship feeding in the Bobwhite seems to parallel that in passerines.

Comparison with other galliforms.—Apparently other galliform birds that give the food call or tidbit do not have the conspicuous display observed in the Bobwhite. The call has similar characteristics of low frequency and repetitiveness for most species. The display in the Chicken, Chukar Partridge, California Quail, and the Ring-necked Pheasant consists mainly of mock pecking or manipulating an object rather than picking it up and holding it for the female. Male California Quail tidbit to grass or other succulent vegetation more than to insects, although they give the food call most frequently when the food is alive. H. G. Lumsden (pers. comm.) considers the tidbitting display to be completely absent from the Tetraonidae. The females of all species observed responded to the male by approaching either to take the food offered or to feed near the male.

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SUMMARY

The food call and tidbitting display of captive Bobwhite were studied for 2 years. Particular emphasis was placed on the reproductive period. Both the call and display are given throughout the year. Food calling without the display was most frequently observed in the nonbreeding season. Factors releasing food calling were suitable, but novel, food items. Food deprivation during this period enhanced the response even to more commonly seen food.

Tidbitting, the food call accompanied by the display, occurred during the breeding season from the beginning of courtship through rearing of the young. Many factors influenced the frequency and intensity of the behavior. Again food deprivation increased the initial response. Approach by the female prolonged the male's tidbitting. Males displayed more frequently than females. Continued presentation of the same food resulted in waning of the male's behavior. Individual males varied in their tidbitting. Adults with chicks tidbitted, and chicks 3 days of age and older responded by approaching and feeding on the designated food.

The function, causation, and origin of food calling and tidbitting are discussed. The behavior in the Bobwhite is compared with that of other tidbitting galliforms.

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