COURTSHIP FEEDING IN GALLINACEOUS BIRDS

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Courtship feeding is widespread among birds and has presumably evolved independently from different origins (Lack, 1940, Johnston, 1962). Lack and Johnston reported courtship feeding in only two species of Galliformes, but Williams et al. (1968) list 12 species. This paper reports on the widespread occurrence of courtship feeding in galliforms, the nature of the display movements and calls involved, and their relationship to parental feeding behavior. Information came in part from the literature but mostly from close observation of some 60 species of galliforms in captivity at the San Diego Zoo, the Los Angeles Zoo, and the large private collection of Alfred D. Hinkle, in Alpine, California. We are grateful to Mr. Hinkle and K. C. Lint, Curator of Birds at the San Diego Zoo, for their assistance.

Procedures

This study was made from January through June 1969. With few exceptions the birds were caged as pairs in dirt or sand-covered outdoor pens, their only food being provided by the keepers. At the San Diego Zoo the Red Jungle Fowl, Helmeted Guinea Fowl, and Indian Peafowl were unconfined (for scientific names see Table 1). In addition we studied the following species in enclosures with seminatural habitat: Erckel's Francolin, Mountain Quail, Common Coturnix, Rain Quail, Roulroul Partridge, Swinhoe Pheasant, and Silver Pheasant.

To test the occurrence of courtship feeding we offered mealworms, which previous experience showed us were almost certain to elicit courtship feeding if it were to occur at all. Live crickets, shelled peanuts, corn, and various berries also worked well. We ran tests throughout the 6 months to see at what stage in the breeding cycle the courtship feeding began and ended, and how it changed in form and intensity as the season progressed. Food calls were recorded on a Uher 4000-Report L at 7½ ips using Uher Model 696 semidirectional microphone. Sound spectrographs were made on a Kay Sound Spectrograph Model 6061A using Fl-1 and wide band settings. Characteristics of those calls will be presented elsewhere. Courtship feeding for 23 species of galliforms was documented on movie film.

Results

Courtship feeding, as used in this paper, is the presenting of food or pseudo-food by the male to the female during the breeding season, usually accompanied by display movement and calling. Domm (1927) called this behavior "tidbitting" in the domestic fowl, a term which has widespread usage in the literature.

In the generalized form of courtship feeding the male goes up to a piece of preferred food, or discovers something while foraging, and begins to call. He may stand over the food, dabble with it, or actually pick it up.

With few exceptions he waits in position until the hen comes to him. When the morsel is among branches or other cover, he invariably moves it to the nearest opening and there begins tidbitting. Should the hen not immediately respond, the cock then intensifies his effort to attract her with louder calling, exaggerated head or body movements, or movements toward or lateral to the hen. When the hen takes the food, the display stops abruptly and the two birds move somewhat apart and go about other nonsexual activities. At the peak of courtship the male may intermix his courtship feeding with other sexual activity: lateral display, circling, flapping or whirring of wings, and actual mounting. In no instance does the hen "beg" for food by calling and gaping as is typical for passerines.

Table 1 summarizes the occurrence of courtship feeding among galliforms. Courtship feeding may be conveniently divided into four fairly distinct forms as follows:

Type I. Holding food in beak.—This is by far the most common type and probably most species show it at times. In this type the cock approaches the food and at once picks it up, often holding it by the tip. The male usually flexes his legs and may shuffle a few steps toward or away from the hen. When she arrives she takes the food from his beak without delay. Ritualization occurs in a few species. Thus in *Mitu* the male invariably snaps his head sideways through about 45 degrees just as the hen comes up. The *Acryllium* cock would generally run 1–4 m with the food, then stop abruptly, rise fully on his legs, and give a peculiar sideways crane of the neck and head.

Galloperdix also turns the head, but more slowly and not so far. In *Perdicula, Excalfactoria,* and *Coturnix* the male crouches deeply and shuffles a few cm laterally or backwards toward the hen, especially if she delays in coming up. Additional variations occurred in the New World Quail of the genera *Oreortyx, Callipepla, Lophortyx,* and *Colinus*. In these the male, at highest intensity display, stands with legs fully extended and flank feathers fluffed, tail fanned, and the body sloping downward from tail to head with the beak close to the ground (Figure 1). In the Old World *Rollulus* the male also stands very erectly but body feathers are sleeked (Figure 2).

Type II. Dabbling and head movements.—The cock dabbles with the food, picking it up and dropping it numerous times. When the hen does not respond immediately, he exaggerates the head movements. In *Gallus* the cock alternates 2–3 times per second between having his beak close to the ground and a full erect stance. As the hen comes up, the cock stands erect and takes a few steps to the side as she takes the food. *Francolinus* and *Pternistis* usually dabble, but rarely with exaggerated head movement.

TABLE 1

OCCURRENCE OF COURTSHIP FEEDING IN GALLINACEOUS BIRDS

Species	Common name	Breeding type[1]	Courtship feeding type[2]	References
Cracidae				
Mitu salvini	Salvin's Curassow	M	1	This study
Crax fasciolata	Bare-faced Curassow	M	1	Coupe, 1966, and pers. comm.
Crax rubra	Great Curassow	M	1	Heron, 1836
Tetraonidae				
Lagopus leucurus	White-tailed Ptarmigan	M	?	Schmidt, 1969
Bonasa umbellus	Ruffed Grouse	P	?	Edminster, 1947
Phasianidae				
Oreortyx picta	Mountain Quail	M	1	This study
Callipepla squamata	Scaled Quail	M	1	This study
Lophortyx californicus	California Quail	M	1	Williams, 1969: 649
" *gambelii*	Gambel's Quail	M	1	Ellis and Stokes, 1966
Colinus virginianus	Bobwhite Quail	M	1	Stoddard, 1931: 109; Williams et al., 1968
Cyrtonyx montezumae	Mearns' Quail	M	1	This study
Alectoris graeca	Chukar Partridge	M	2	Stokes, 1961
" *rufa*	Red-legged Partridge	M	2	Goodwin, 1953
Francolinus francolinus	Black Francolin	M	2	This study
" *pondicereanus*	Gray Francolin	M	2	This study
" *clappertoni*	Sharp's Francolin	M	2	This study
" *erckelii*	Erckel's Francolin	M	2	This study
Pternistis leucoscepus	Bare-throated Francolin	M	2	This study
" *cranchii*	Humboldt Francolin	M	2	This study

[1] M, monogamous; P, polygynous. [2] ?, uncertain status (see text).

TABLE 1 (Continued)

Species	Common name	Breeding type[1]	Courtship feeding type[2]	References
Coturnix coturnix	Coturnix Quail	M	1	Heinroth and Heinroth, 1926 vol. 3: 241; this study
" *coromandelica*	Blackbreasted Quail	M	1, 2	This study
" *delegorguei*	Harlequin Quail	M	2	Trollope, 1968, and pers. comm.
Excalfactoria chinensis	Painted Quail	M	1	Meade-Waldo, 1898; Harrison, 1965; this study
Perdicula asiatica	Jungle Bush Quail	M	2	This study
Arboricola torqueola	Common Hill Partridge	M	?	Smith, 1910
Rollulus roulroul	Roulroul Partridge	M	1	Fooks, 1936; Searle, 1962; this study
Ptilopachus petrosus	Stone Partridge	M	1	This study
Galloperdix spadicea	Red Spurfowl	M	1	This study
" *bicalcarata*	Ceylon Spurfowl	M	1	Henry, 1955: 259; this study
" *lunulata*	Painted Spurfowl	M	1	Swain, 1965
Tragopan satyrus	Satyr Tragopan	M	2 ?	This study
" *temminckí*	Temminck's Tragopan	M	2 ?	Beebe, 1918–22, vol. 1: 91
Lophophorus impeyanus	Impeyan Pheasant	M	2	Beebe, 1918–22, vol. 4: 127
Crossoptilon mantchuricum	Brown Eared Pheasant	M	3	Felix, 1964; this study
" *auritum*	Blue Eared Pheasant	M	3	Felix, 1964; this study
Lophura nychthemera	Silver Pheasant	M	3	This study
" *edwardsi*	Edward's Pheasant	P	3	This study
" *swinhoei*	Swinhoe Pheasant	P	3	This study
" *diardi*	Siamese Fireback	M	3	This study
Gallus gallus	Red Jungle Fowl	P	2	Domm, 1927; this study
" *lafayettei*	Ceylon Jungle Fowl	M, P	2	This study

TABLE 1 (Continued)

Species	Common name	Breeding type[1]	Courtship feeding type[2]	References
Gallus (Continued)				
" *varius*	Green Jungle Fowl	M, P	2	This study
" *sonnerati*	Gray Jungle Fowl	M, P	2	This study
Phasianus colchicus	Ring-necked Pheasant	P	3	Kozlova, 1947; this study
" *versicolor*	Japanese Green Pheasant	P	3	This study
Syrmaticus ellioti	Elliot's Pheasant	P	?	Beebe, 1918–22, vol. 3: 193
" *humiae*	Hume's Pheasant	P	3	This study
Chrysolophus pictus	Golden Pheasant	P	3	Kruijt, pers. comm.; this study
" *amherstiae*	Lady Amherst Pheasant	P	3	Beebe 1918–22, vol. 4: 28 this study
Polyplectron bicalcaratum	Burmese Peacock Pheasant	M	1	Godry, 1888, *in* Beebe, 1918–22, vol. 3: 147–148; this study
" *germaini*	Germaine's Peacock Pheasant	M	1	Beebe, 1918–22, vol. 4: 146 (implied)
" *emphanum*	Palawan Peacock Pheasant	M	1	Lewis, 1939; this study
Pavo cristatus	Indian Peafowl	P	3 ?	Schenkel, 1956; this study
" *muticus*	Green Peafowl	P	3 ?	This study
Numididae				
Numida meleagris	Helmeted Guineafowl	M	2	This study
Guttera edouardi	Crested Guineafowl	M	2	This study
Acryllium vulturinum	Vulturine Guineafowl	M	2	This study
Meleagrididae				
Agriocharis ocellata	Ocellated Turkey	P	2	This study

[1] M, monogamous; P, polygynous. [2] ?, uncertain status (see text).

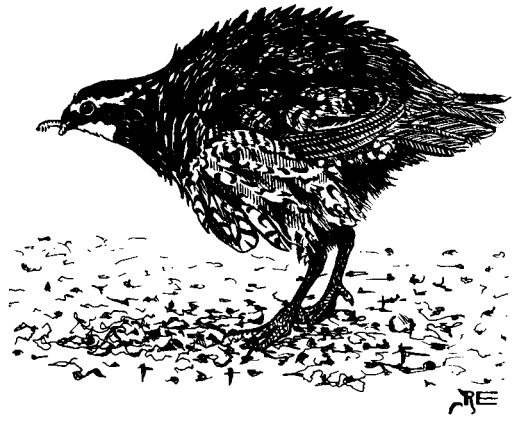

Figure 1. Type I courtship feeding, *Colinus virginianus*.

Type III. Freezing over the food.—The male approaches the food and dabbles a few times in cursory fashion, the beak held close to the ground. As he does so he begins to call. When the hen comes to within a meter of him he freezes over the food, body taut and the beak held within a few cm of the ground. The cock continues to call until the hen has taken the food from the ground in front of him. She steps off a few decimeters before eating, and the cock then relaxes. This type is characteristic of *Lophura*, *Phasianus*, *Syrmaticus*, and *Chrysolophus*. In these genera the wattles become engorged and the body is often held laterally as in lateral courtship display. In *Crossoptilon* and *Agriocharis* the wattles and other fleshy facial appendages are engorged but without special lateral display.

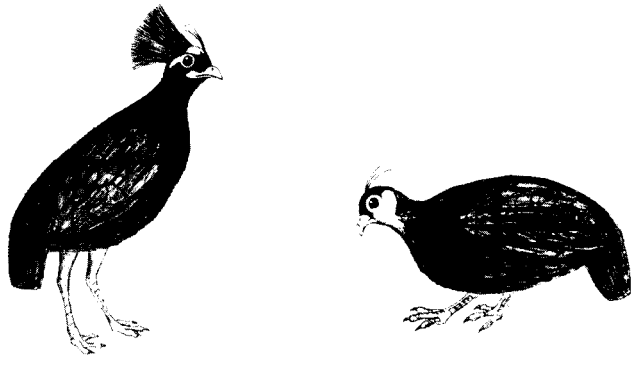

Figure 2. Type I courtship feeding in *Rollulus roulroul*. Male at left displaying while female at right approaches to take food.

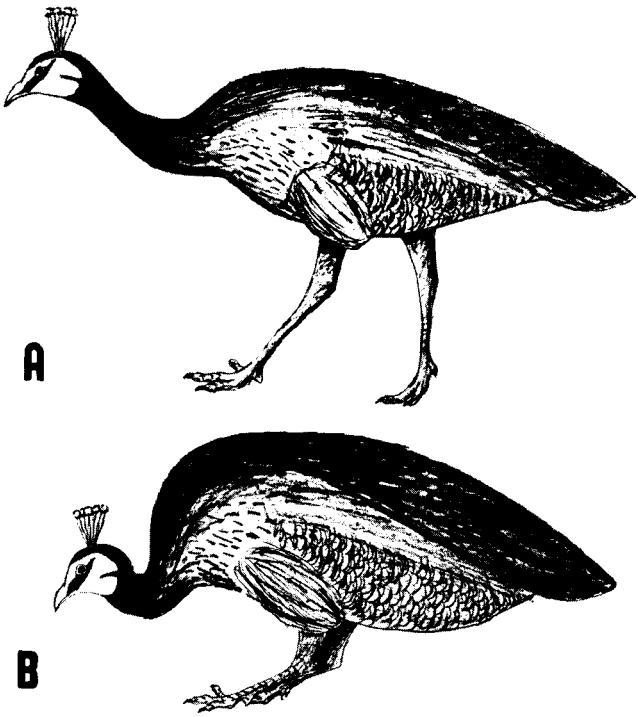

Figure 3. Type III courtship feeding as seen in *Pavo*. A, initial forward position; B, "frozen" position with head retracted.

In *Agriocharis* the male is silent during actual courtship feeding, but this always occurs at times when he has been actively gobbling and his snood is fully extended down over his beak. Invariably gobbling follows courtship feeding.

In the two species of *Pavo* we never saw the female accept food from the male, but at times the male reacted to the mealworms in a stereotyped, seemingly ritualized manner. He would approach, extend his neck so that the beak was over the mealworm, then suddenly retract his neck and freeze momentarily (Figure 3). This was the exact pattern that the hen used when indicating food to her chicks. Although the hen usually gave a very soft food call, the cock was always silent.

Mealworms were not particularly attractive to adult peafowl, even though the chicks ate them readily, so perhaps more palatable morsels might have released courtship feeding in *Pavo*.

Type IV. Fusion of courtship feeding with other sexual display.—The peacock pheasants of the genus *Polyplectron* are unusual in that courtship

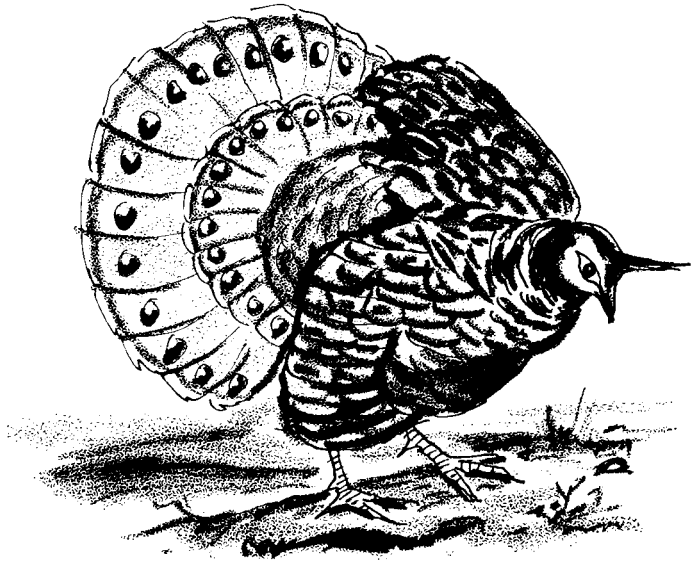

Figure 4. Type IV courtship feeding, *Polyplectron bicalcaratum*.

feeding is always an integral part of the more conspicuous lateral sexual display usually associated with gallinaceous birds (Figure 4). The behavior is nearly identical in the closely related *P. bicalcaratum* and *P. germaini*. More than 80 years ago, Godry made this precise description of the display (Bulletin de la Societé d' Acclimatation, 1888, p. 984, as quoted in Beebe, 1931, vol. 2: 147–148):

> Il marche légèrement, redressant sur sa tête une petite huppe composée de plumes fines qui retombe en avant sur le bec, il enfle son plumage avec orgueil, et deploie gracieusement, tout en marchant, l'une de ses ailes, tantôt la droite, tantôt la gauche, puis se met, de temps en temps, à gratter le sol de la volière. Après quelques recherches dès qu'il a le bonheur de trouver quelque insecte ou menu grain, il le saisit avec empressement, et tout en tenant délicatement, du bout du bec, son heureuse trouvaille, il invite sa femelle, par un gazouillement charmant et prolongé, à venir profiter de la bonne aubaine. Des que celle-ci s'avance, l'Éperonnier se redresse sur ses pattes, enfle fortement son plumage, puis lui lance la friandise si précieusement conservée, et, au moment où elle vient pour la ramasser, il la salue à sa façon en s'inclinant vivement, et en déployant, tout-à-coup, les ailes et la queue. Il se met alors à faire la roue en forme d'eventail. A ce moment, son oeil brille du plus vif éclat, et toutes les ocelles apparaissent dans leurs plus brillantes couleurs, tout en projetant de belles teintes irisées, suivant l'effet du jour. C'est alors qu'on peut juger de la grande beauté de cet oiseau dont les ocelles, en forme d'yeux brillants sont rangées avec la plus parfaite symétrie et par ordre de grandeur.

Beebe was uncertain if the projection of the morsel to the hen as Godry described it was accidental or not, but I repeatedly observed this display in three male *P. bicalcaratum* and the food was definitely launched by the sudden forward movement of the head so as to land in front of the female. In two pairs of *P. germaini* the male always held the morsel until the hen took it from him.

We saw a single *Polyplectron emphanum* male display on several occasions. He followed closely the behavior first described by Lewis (1939). He began the display by giving a single vigorous wingflap that lifted him clear of the ground as he approached the food. The cock then took the morsel in his beak and in a split second fanned and twisted his tail so that it formed a vertical fan absolutely in line with the axis of the bird's body. At the same time the outer scapulars and wing were so spread and rotated that they completed the more than half circle of these ocellated feathers. The 2-inch crest, normally vertical, was held far forward so as to almost conceal the beak and its enticing morsel. The cock then danced before the hen with all the agility of the Golden Pheasant cock, first on one side of her and then the other. With each move to the other side of the hen he made lightning-swift shifts of tail, wing, and body feathers to keep his brilliant ocellated plumage always toward her. This Palawan male held the morsel steadily in his beak and seemed to tease the hen with it, for when she tried to take it from him he shifted a few steps and displayed from another angle. Only after several attempts on her part did he finally allow her to take it from his beak, and like a flash the display ended.

Waning of the response.—The cock's first display to a series of mealworms was usually the highest in intensity. This was partly because the hen was likely to be slow to respond, and the male invariably intensified his movements and calling whenever the hen failed to come up. On successive presentations of food the hen was increasingly alert and responded so quickly that the male scarcely had time to display at all. There was also some true waning of the response as we have described in detail for *Colinus virginianus* (Williams et al., 1968). The response wanes more quickly in some species than in others. Thus in the single pair of *Acryllium vulturinum* the male would display only once, and thereafter eat any further food presented to him. In contrast, we watched a pair of *Rollulus* forage for a half hour in the seminatural conditions of a walk-in aviary. The male was finding minute soil organisms and tidbitting with them every minute or two without diminution in intensity of the display. The hen at this time was just starting to lay.

In addition to the short-term waning, seasonal changes occur in the

intensity of courtship feeding. It is most persistent and at highest intensity at the height of the courtship period. In *Rollulus* full intensity courtship feeding occurred during the entire period of this study, January through June, yet egg laying did not begin until April. *Colinus virginianus* started tidbitting at least 2 months before egg laying, but with increasing intensity as this approached. The monogamous *Polyplectron bicalcaratum* and *P. germaini* cocks were displaying at full intensity in mid-January when egg laying began. The eggs of the females were removed and they continued to lay into May, by which time the males only rarely displayed. In contrast, polygynous species of pheasants had a short period of courtship feeding, beginning with courtship and ending with egg laying. Thus it appears that tidbitting is longest in monogamous species, especially those where the male helps care for the young.

Duration of the display.—The length of a single display depended largely upon the response of the hen. If she was already near the cock he might display for a brief second only. Should she be out of sight or hearing, then the cock might call and tidbit for as long as 90 seconds. Eventually he ended by eating the morsel if the hen did not arrive. One chilly morning we saw a cock *Colinus virginianus* display at full intensity for about 40 seconds before eating the worm. The hen was brooding her 4-day-old chicks out of sight; apparently the stimulation for her to brood was stronger than the stimulus from her mate.

Factors releasing courtship feeding.—Four stimuli seem necessary to release courtship feeding: a certain level of internal motivation in the cock, presumably mediated by rising testosterone output, the sight of a hen usually within 10 m, the absence of overriding inhibiting stimuli such as alarm stimuli or the presence of a dominant rival, and the presence of suitable food. Variations in this last factor were easiest to observe. Early in the breeding season only very limited kinds of morsels released tidbitting, notably mealworms or other small moving animals. Insects naturally have the highest releasing value because they are the appropriate food that parents normally feed their young chicks. Later the variety of objects to which the male would tidbit became much broader, but only rarely did one tidbit to his regular food sources. The use of special morsels would seem a stronger reinforcement for continuing response by the hen than normal foods. At times, in *Gallus* at least, tidbitting was released by the sight or hearing of another male tidbitting to a hen. In these situations the male pecked at whatever was at hand, leaves, twigs, stones, pebbles, feathers, wood shavings, fecal pellets, and when on asphalt pavement apparently pecking without picking up anything at all.

In a previous study where we kept *Alectoris* on a wooden floor with

no food other than their normal supply, the males regularly tidbitted with feathers and pebbles, never with food.

Discussion

Function of courtship feeding.—The immediate function of courtship feeding is to induce the female to approach the male. The signals are amazingly effective, causing a hen to stop whatever she is doing and run up to the male, at least temporarily. This places the hen in a position where the cock can proceed with further courtship in the form of lateral display, circling, and even mounting. Courtship feeding serves also to keep the female close to the displaying male and thus away from competing males. In this regard a dominant Red Jungle Fowl cock may completely inhibit nearby subordinate cocks from tidbitting and calling even when presented with such an effective releaser as a mealworm (Stokes, 1971). In species where the male helps rear the young, the prolonged period of courtship feeding both before and after incubation could strengthen the pair bond.

In captive gallinaceous birds, especially polygynous species, the male will frequently not accept the female and vice versa. The cock may persistently harass the hen and forcefully mount her before she is willing to accept him. Thus in our confined *Alectoris graeca* the male intimidated the hen with prolonged waltzing and grabbing of the head and back feathers until she crouched motionless in a corner of the pen. Then suddenly he would turn aside and begin to tidbit and call. Almost like magic, the hen then relaxed and within a minute or so approached the male, thus demonstrating the efficacy of the tidbitting behavior (Stokes, 1961). The male's tidbitting served the same appeasement function in the frequently aggressive male *Coturnix coturnix* and *Excalfactoria chinensis*.

A secondary function of tidbitting occurs in the Red Jungle Fowl (Stokes, 1971). Yearling cocks in general tidbit only to hens with chicks and not to single hens. Two or three yearling cocks may court and attend the same hen. The behavior in this instance seems a means for yearling cocks to establish dominance over other yearlings, and to give them the experience in courting females they will need the following year when adults. Yearling males in other polygynous species may also do this, but the behavior is so fleeting that chances of observing it in the wild are remote.

Origin of courtship feeding.—Among altricial birds courtship feeding is believed to have evolved from the more general parental feeding behavior (Lack, 1940). We were able on many occasions to study the form of parental feeding of chicks in *Gallus gallus* and *Pavo cristatus*, and less

TABLE 2
PARALLELS BETWEEN PARENTAL AND COURTSHIP FEEDING BEHAVIOR IN GALLINACEOUS BIRDS

Jungle fowl parental feeding patterns	Similar behavior in other male galliforms during courtship feeding
Hen holds food motionless and lets chick take it from beak	Widespread, perhaps least ritualized form of courtship feeding
Hen turns head toward chick and lets chick take food from beak	Occurs sparingly in many species, regularly in *Galloperdix* and ritualized in *Crax, Mitu,* and *Acryllium*
Hen points toward food with beak, while momentarily freezing over it	Widespread, but highly ritualized in *Polyplectron*; possibly also in *Pavo*
Hen dabbles with food, often to break into smaller pieces	Widespread, but especially in *Francolinus, Coturnix, Excalfactoria*; *Lagopus* with gravel
Up and down head movements to attract chicks to food	In Odontophorinae and *Alectoris*, but most prominent in *Gallus*.

often in *Colinus virginianus* and *Numida meleagris*. Table 2 shows the various forms of feeding behavior we noted in parent jungle fowl and the appearance of similar, but often more ritualized, behavior in courtship feeding of other galliforms. We saw no movements used in courtship feeding in other birds that we did not also see in the behavior patterns of parents feeding their chicks. Even the somewhat bizarre feather fluffing of the male *Colinus* during courtship feeding is an exact copy of the hen's behavior when presenting a mealworm to her chicks.

At first glance the quick turning of the head seen in *Mitu*, the throwing forward of the food in *Polyplectron*, and the freezing over the morsel in *Lophura*, *Phasianus*, and *Crossoptilon* might appear to be ritualized male behavior. Yet we suspect that the same behavior patterns might be seen in the hen of these species toward their chicks. They could all function in either making the food more conspicuous or facilitating the taking of the food from the hen by the still poorly coordinated chicks. Unfortunately the way adult galliforms actually feed their young chicks has been described for very few species.

It is notable that the chicks of *Polyplectron* must be actually fed by the parent for their first few days. Aviculturists successful in rearing these chicks have to dangle a small mealworm back and forth over the beak of the chicks before they finally take it. Therefore the manner in which the *Polyplectron* male "teases" the hen or throws the morsel out in front of her during courtship feeding may be a direct imitation of hen behavior when feeding her chicks. The Peacock Pheasant's spectacular display might seem an exception to our belief that courtship feeding has evolved from parental feeding, but as stated earlier, this display is a

fusion of courtship feeding with other sexual display. The actual courtship feeding seems to consist of holding the food, calling, then throwing it out to the hen. Other galliforms have the two forms of behavior more completely separated, but we repeatedly saw the quick alternation between courtship feeding and other sexual display.

In *Lophura* the male often displays laterally while freezing over the food, and in *Phasianus* the wattles become engorged and breast feathers fluffed while tidbitting. In *Tragopan satyrus* we saw no true courtship feeding, but the male would alternate his lateral display to the hen by brief sessions of picking up food a few decimeters from her, a fact previously noted in *Tragopan temmincki* by Beebe (1918–22, vol. 1: 191).

This raises the question of how courtship feeding could have arisen from parental feeding in polygynous species of galliforms where the male does not feed the young. We believe that courtship feeding could have evolved before polygyny. In addition, males of polygynous species may still retain some parental instincts as evidenced by the fact that they may take over full care of a brood and even incubate, implying a latent parental motivation. This has been noted many times in *Gallus gallus* by zoo keepers at the San Diego Zoo and also reported in *Chrysolophus pictus* (Kingston, 1958), *Phasianus colchicus* (Simpson, 1906), and *Pavo cristatus* (Beebe, 1918–22, vol. 4: 176). In *Bonasa umbellus* Edminster (1947: 41) reports about 1 brood in 10 is accompanied by a male during the first 6 weeks after hatching, though he does not mention the male actually feeding the chicks.

Courtship feeding is so widespread among galliforms that one must question why it does not occur in all genera. Exceptions appear to be: 1) MEGAPODIIDAE. The most complete study has been of the Mallee Fowl, *Leipoa ocellata* (Frith, 1962). Frith says little about actual courtship, so courtship feeding should not be ruled out, but as the parents take no part in rearing the young, one would not expect to find courtship feeding, at least as a derivative of parental feeding. 2) TETRAONIDAE. Grouse differ from other galliforms in that the parents do little or no feeding of their young (Pynnonen, 1954; Zwickel, 1967; Schmidt, 1969). Hence if courtship feeding does occur, it would propably not have evolved from parental feeding, though some evidence suggests grouse do at times show this behavior.

In tundra species grit may be a critical dietary item for egg laying and digestion. In *Lagopus leucurus* in Colorado the hen often pecks in small gravel patches, at times with a high-pitched cluck that makes the chicks run over and forage in the same place (Schmidt, 1969). Also while pecking at grit during the breeding season the cock makes loud scraping sounds easily audible at 50 m. Schmidt saw one male's mate rush over

to him and begin pecking head to head with him. Schmidt (1969: 86) cites Clait Braun as having twice observed *L. leucurus* give a tidbitlike display in which "the male appeared to solicit the female by pecking at the ground and uttering low-pitched 'clucking' sounds." This evidence suggests that the hen's calling of chicks to gravel or grit is functional and that it has become somewhat ritualized in the male to serve a sexual function. This behavior in the male has no parental function because he plays no role in feeding, brooding, or defending the chicks.

In *Bonasa umbellus* Edminster (1947: 28–29) describes the behavior of the male at the height of his courtship as follows "For several feet along the old log he thus slowly strutted towards her. . . . After a moment he reached quickly down with his head and *pretended to peck at each of a couple of leaves in front of him* [italics added]. In an almost continuous gesture, he began shaking his head forward and somewhat downward and sideways, first on one side and then on the other, and with each shake emitting a most peculiar sound. With each headshake he made a double hiss—something like 'shh-ushh,' the first half with an exhale and the second with an inhale." The situation in which this feeding and calling occurred strongly suggests that it might be some form of ritualized courtship feeding.

Schenkel (1956, 1958) in his analytical paper on courtship feeding and other courtship display in Tetraonidae and Phasianidae believes that courtship feeding has become so highly ritualized in Tetraonidae that it no longer includes the "economic" aspect of actual feeding. Instead the male symbolically points his beak toward the ground during parts of his dance. Moreover in *Pedioecetes* and *Tympanuchus* the male reaches the "ecstatic" phase of courtship with a deep, frozen bow. He believes this is homologous to the "ecstatic" freezing of *Phasianus* and *Lophura* and the crouch of *Polyplectron* just as the hen takes the morsel. As the pair bond in those grouse with communal courtship grounds is brief, Schenkel believes that courtship feeding in these species is under no restraints to remain "economic," but instead could become purely symbolic. He dodges the issue of why it does not occur in the monogamous *Lagopus*.

In a more recent analysis of courtship behavior of Tetraonidae Hjorth (1967: 242) believes that the lowering of the neck is a preparation for attack, and that the bowing and nodding movements, which are often features in both courtship and aggression, are indicators of tendencies to attack. Moreover he believes that the conflict between tendencies to attack and to act sexually can result in redirected aggression in the form of pecking at objects on the ground. He does not agree with Schenkel's hypothesis that these bowing motions represent highly ritualized courtship feeding.

PHASIANIDAE. In *Pavo* the hen never took food from the male. Despite this, the fact that the male had identical reactions to food as did the hen with chicks strongly suggests that we were observing courtship feeding. The peahen does not actually hold food for her chicks. Instead she points it out with quick forward and backward movement of her beak, then freezes. *Pavo* chicks are more precocial than most galliforms, hatching with well-developed primary feathers. Thus perhaps they do not need to have the food held for them. Schenkel (1956) believes that in *Pavo* courtship feeding occurs in the form of the "ecstatic" phase of the male's tail-fanning display to the hen. As the hen comes up to the cock she may peck at the ground at real or imaginary food. This releases the climax of the cock's display—a rustling and shivering of his feathers as he crouches before her, with his beak held down perpendicular to the ground. Schenkel's evidence for courtship feeding in *Pavo* seems more convincing than that for Tetraonidae.

Nevertheless, our observations that the male will react to food or grit in the same manner as does the hen make us conclude that courtship feeding in *Pavo* and Tetraonidae is less ritualized than Schenkel postulates.

Perhaps rather than seeking to find courtship feeding in Tetraonidae and *Pavo* in highly ritualized form, one should consider the possibility that its frequency of occurrence is merely very much less than in other galliforms and that the threshold for its occurrence is correspondingly higher. Perhaps only very select morsels, such as grit or mealworms, will elicit courtship feeding, and during only a brief period in the courtship phase. Because of different selective pressures, other forms of courtship behavior may have developed greater prominence.

Derivation of courtship feeding.—At first glance the patterns of courtship feeding in gallinaceous birds appear diametrically opposite to those in passerines and other altricial species. In altricial species it is the female that calls, gapes, flutters her wings, or goes through other motions, and stays in position while the male comes up to feed her. In galliforms the male remains in position, calls, performs certain movements, and feeds the hen as she comes up silently. Yet, if courtship feeding has evolved from parental feeding patterns, this contrast seems entirely what one might expect. In altricial species the young must remain in the nest and call, gape, and flutter to attract attention of the parent, who must come to the young. By contrast, in precocial species it may be more efficient for parents to allow the young chicks to come to them. The chick that initiates movements toward the parent is likely to receive more food; also the parent's calls and movements alert the chicks to the source of food. Thus both in precocial and altricial species the female's behavior during courtship feeding mirrors the feeding behavior of the young birds. And in turn the

male mirrors the feeding behavior shown by the female to her chicks. Hence fundamentally the form of courtship feeding in both precocial and altricial species is based upon the manner of feeding the young birds.

SUMMARY

A survey of the literature and observations on over 60 captive galliform species revealed that courtship feeding is widespread through this order. The male holds or dabbles food while calling and in this way causes the female to approach. Courtship feeding may precede, alternate with, or be an integral part of other courtship behavior. Males display most readily to unusual sources of food or mock food, but rarely to items common in their diet. Courtship feeding is longest in duration in monogamous species with long pair bonds. Several functions of courtship feeding are listed. Courtship feeding probably evolved from the functional feeding of the young by the parent. In both monogamous and polygynous species the male retains some motivation to feed the young, hence his courtship feeding retains to great extent both the form and function of parental feeding.

Courtship feeding in altricial species of birds might appear to differ markedly from that of galliforms, but this is only because altricial young are confined to the nest and the parents must perforce come to them. This in turn has led to the pattern of the male's flying to the female while she is near or on the nest.

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