COURTSHIP FEEDING IN BIRDS

BY DAVID LACK

INTRODUCTION

IN many different groups of birds the male feeds the female during courtship or incubation. The literature on this point is large and scattered. The object of the present paper is to summarize the data so far as I have been able to collect them. So many instances have been reported in works dealing primarily with other matters that I cannot hope that the present list of birds is nearly complete. Indeed, one of the objects of this paper is to stimulate others to record instances from types of birds not recorded here. Some years ago correspondents of 'The Auk' greatly increased our knowledge of the extent of 'injury-feigning' in birds and in this, as in courtship feeding, an accurate knowledge of all those groups in which it occurs, and also of those in which it does not occur, greatly assists in interpreting the significance of the habit. Before publication, I am sending this paper to Mrs. Margaret M. Nice with the request to add all the cases that she may know from her unrivaled knowledge of the literature of bird courtship. Indeed, should the European situation make it impossible for me to see the proofs of the paper, I am asking Mrs. Nice to supervise publication. I must also thank Dr. E. Mayr and Dr. G. K. Noble for their help in discussion.

MANNER OF FEEDING

In most cases of courtship feeding, the female adopts an attitude and calls almost identical with those of a young bird begging food from its parents, and the male puts food into the female's mouth.[1] In some birds, the male simply collects the food in his beak and then presents it to the female; in others, notably in some Fringillidae (i. e. Carduelinae) and gulls, the male regurgitates the food to the female, as he also does when feeding the young. While this is the normal procedure there are a few variations. Thus in the Herring Gull and other gulls, the male regurgitates the food on to the ground in front of the female, and the female then swallows it. In terns, presentation of food is often preceded by a ceremonial flight. In some birds of prey,

[1] Monika Holzapfel in her 'Analyse des Sperrens, und pickens in der Entwicklung des Stars' (Journ. f. Ornith., 87: 525–553, 1939) suggests that 'gaping' for food is not merely a juvenal phenomenon, but that it is replaced by the tendency to peck for food, and becomes latent, reappearing later in those species where the male feeds his mate.—M. M. N.

notably *Circus,* the food is passed from the male to the female in the air, the female turning over to catch it. In the Adélie Penguin (*Pygoscelis adeliae*) the male brings not food but snow to the incubating female. Dr. Mayr draws my attention to *Gallus gallus domesticus,* which does not present the female with food, but scratches the ground up for her (as a hen does for her chicks).

THE RÔLES OF THE SEXES

In nearly all birds it is the male which feeds the female. The respective rôles of the two sexes are almost as constant as are the positions adopted in copulation. A partial exception is the waxwing (*Bombycilla*), in which male and female exchange food backward and forward, but it is again the male which first presents and the female which first receives the food. I once observed the same in *Platyspiza crassirostris,* one of the Galapagos finches, but here it is very unusual, and I have seen it once (out of hundreds of cases) in the British Robin (*Erithacus rubecula melophilus*), when the birds were disturbed by a mount near the nest.

In one bird, the Button Quail, *Turnix,* the normal procedure is reversed and the female feeds the male. This was perhaps to be expected, since in *Turnix* nearly all the sex behavior is reversed. In Common Terns (*Sterna hirundo*), Tinbergen records that, in the early stages, either sex may beg for or present food. Under artificial conditions in captivity, I have had a female British Robin feed another female, and a male beg food from a female.

Why, normally, the male should give the food and the female receive it, and not the reverse, is far from clear. The occurrence of the opposite in *Turnix,* where other sex behavior is also reversed, is confirmation that there is a fundamental distinction between male and female in this matter. Possibly it is related in some way to the phenomena classified under the term 'dominance,' but I am not too happy as regards the use of this latter term owing to its subjective implications. The captivity records of the British Robin show that the behavior normally found in one sex is latent in the opposite sex (this seems to apply to all phases of sexual behavior in birds).

SIGNIFICANCE OF THE FEEDING

In many species in which courtship feeding occurs, the male also feeds the female on or near the nest during incubation. Hence, at this stage of the breeding cycle, the food may have real significance.

Indeed, there probably exist species in which the feeding habit is restricted to the incubation period. In this case, it could not be classed as courtship feeding at all. I know of no fully established cases, but this may well occur in some of the species given in the table later in which there are records of feeding only during incubation, e. g., some titmice (Paridae), some finches (Fringillidae), some crows (Corvidae). However, there are also some species, e. g., *Aix sponsa, Gallus* and *Turnix* (? also *Centropus* and *Coccyzus*) in which the feeding of the female by the male occurs in courtship but apparently ceases before incubation. Further, in many of the species in which the male feeds the female during incubation, feeding is also regular before incubation and in some species, e. g., the British Robin, it is much commoner before than during incubation. Hence, in these latter birds the main function of courtship feeding is clearly display.

Clearly the primary object of courtship feeding is not the food which is passed. Numerous cases could be cited to show this. I may quote Goethe (1937), that a female Herring Gull (*Larus argentatus*) just returned from feeding on the shore, and, therefore, presumably well fed, may beg her mate for food although he has remained near the nest and has not fed recently. Again, in captivity a female British Robin would often beg her mate to feed her though she was standing on the food tray, surrounded by live mealworms, and he was some distance away. Again, in *Bombycilla,* the food is passed back and forth between the sexes and finally is often eaten by the male.

In some species, courtship feeding seems closely associated with copulation. Thus, in *Centropus javanicus* the male holds an insect in its beak during copulation and feeds the female immediately afterward. In the Yellow-billed Cuckoo (*Coccyzus americanus*), the male also held an insect during copulation, and, toward the end, the female slowly turned her head and took and ate it. In *Camarhynchus parvulus,* one of the Galapagos finches, Mr. W. H. Thompson saw the male feed the female during copulation. Again, in the Herring Gull, Goethe records that the initiatory stages of copulation are closely similar to those of the male feeding the female. In *Columba livia,* the male feeds the female before copulation. In the European Nuthatch (*Sitta europaea*), courtship feeding and copulation are also said to be correlated, and this may be the case in *Gallus gallus domesticus.*

The association of courtship feeding with copulation in the above species seems clear, and this applies to some other species. However,

there are other birds in which there is no connection between courtship feeding and copulation. This is clearly the case in the British Robin, in which courtship feeding and copulation occur quite independently, and whereas copulation is restricted to a very limited period during nest building and egg laying, courtship feeding occurs throughout the breeding cycle except when the birds are feeding the young. This was also true for the Galapagos finches except for the one case in *Camarhynchus parvulus,* already reported (D. Lack and W. H. Thompson); it applied to *Spinus lawrencei* (D. Lack) and evidently applies to many other species, since the observers make no records of any connection with copulation. Further data are desirable but it seems probable there are more species in which the habit is not connected with copulation, than those in which it is.

The function of courtship feeding in the latter forms is presumably to maintain the bond between the pair, which is especially important in birds in which both sexes feed the young. In this connection it seems significant that courtship feeding is found mainly in birds in which both sexes care for the young. This is especially significant in those groups of birds which include both some species which remain paired, and some which do not form a pair bond. Thus, in the gallinaceous birds, the Bob-white (*Colinus virginianus*) remains paired and courtship feeding occurs, whereas it does not occur in the many gallinaceous birds where no pair bond is formed. Again, in the cuckoos (Cuculidae), it occurs in *Centropus* and *Coccyzus,* but not (so far as known) in the parasitic forms. There are, however, exceptions to this rule. Thus in *Turnix,* the female leaves the male soon after incubation has commenced.

OTHER FEEDING HABITS

This habit of one bird feeding another seems normally part of courtship. However, two cases are reported by Murphy in which a *Fregata magnificens* and an adult Brown Booby (*Sula leucogaster*) at least four years old, were found in perfect condition at breeding colonies, although each possessed only one wing and could never have captured food for itself. Both birds apparently retained the food-begging behavior of the young and were maintained by other members of the colony.

That the begging of food by a young bird exercises a strong attraction on adults is also illustrated by the not infrequent occasions on which passing birds have fed a fledgling European Cuckoo (*Cuculus*

canorus) or Cowbird (*Molothrus ater*) reared by other foster parents. Possibly parallel are the cases reported by Skutch of individuals helping to feed a brood of young. In European Swallows (*Hirundo rustica*), the Moorhen, (*Gallinula chloropus*) and the Bluebird (*Sialia*) (see Laskey, Bird-banding, 6: 23–32, 1939), the young of the first brood may even help to feed the second brood.

The occurrences of these instances divorced from any courtship display make it easier to understand how the feeding habit could have become incorporated into display.

SYMBOLIC NATURE OF THE HABIT

Since the main function of courtship feeding is not food, it might be classified as a type of 'symbolic' display, i. e., in which an act normally playing some other part in bird behavior is introduced into display. Habit preening, and the manipulation of nest material are other examples. In many species (but certainly not all, Wood Duck (*Aix sponsa*), and *Turnix* are presumably exceptions and so probably are those species where courtship feeding occurs primarily in connection with copulation) feeding may have been introduced into the sexual cycle through an extension back into an earlier phase of the cycle of the habit of feeding the female during incubation. In this it closely parallels the 'display building' of the Galapagos finches and other birds, in which building and manipulation of nest material are a prominent feature of courtship, but the eventual functional nest is often built at a later stage. In birds, many instinctive acts are exhibited in a partially developed form before the biologically 'correct' moment arises, and this phenomenon would supply the initial element on which selection could later work.

In some cases, courtship feeding is reduced to an incipient act. Thus, billing occurs in the Mourning Dove (*Zenaidura macroura*), the European Kingfisher (*Alcedo atthis*), the Rook (*Corvus frugilegus*), the Chough (*Pyrrhocorax pyrrhocorax*), the Waxwing (*Bombycilla*), and some Fringillidae, e. g., Hawfinch (*Coccothraustes*), the Siskin (*Carduelis spinus*), *Geospiza,* and other species; also in Peregrine Falcons (*Falco peregrinus*), which touch beaks in the air. In these birds billing can be regarded as incipient courtship feeding. It should be noted that in some other birds, e. g., herons, billing has probably not developed from courtship feeding but possibly from the passing of nest material from the male to the female. In yet others, e. g.,

Fulmar (*Fulmarus glacialis*), billing has clearly originated from neither of these acts.

The 'fish flights' of terns may also occur without any exchange of food. This habit, like billing, may, therefore, be regarded as symbolic of courtship feeding, which is itself a symbolic act. In the Black Skimmer (*Rynchops nigra*), Pettingill has recorded a male presenting the female with driftwood instead of the usual food (presumably because the male had no food available at the time).

Occurrence of Courtship Feeding

So far as is known, birds are the only vertebrates which exhibit courtship feeding (omitting the sporadic occurrences in human beings). However, it rather surprisingly occurs in one other group of animals, namely, the dipterous flies of the family Empidae. In the latter, it seems associated with inducing the female to copulate and, interestingly enough, in some species the courtship feeding is symbolic in that no real food is passed but various substitute objects are used (O. W. Richards, Biol. Rev. Cambridge Phil. Soc., 2: 298–360, 1927).

Courtship feeding occurs in so many widely separated groups of birds that it has almost certainly originated several times independently. Particularly striking in this respect is its occurrence in one species of duck, in just a few gallinaceous birds, in one species of wading bird, and in Tropic-birds but no other Pelecaniformes. There are also species, e. g., Chiffchaff, Wood Warbler (*Phylloscopus* spp.), Tree Pipit (*Anthus trivialis*) and Bluebird (*Sialia sialis*) in which the habit is only rarely found and in which many individuals apparently do not show it.

Further, the survey, given below, of the species in which male feeding female occurs, shows that it plays a rather different part in the lives of different species and may have originated in different ways. Thus, in some species it occurs primarily (possibly exclusively) during incubation. In other species it is regular during incubation but commoner before it. I had thought at first that the habit might be restricted to birds in which only the female incubates, e. g., many finches, titmice, crows, and others. Further study shows that this is by no means the case. Prominent exceptions are the gulls (*Larus*), terns (*Sterna*), pigeons (Columbidae) and others. There are even species in which courtship feeding occurs although one sex leaves the other at incubation. Further, many passerine groups in which only the female incubates do not exhibit courtship feeding. Again, there are

species in which the habit seems closely linked with copulation, and others in which it has no connection with this. In Red-backed Shrike (*Lanius collurio*) it seems correlated with both copulation and incubation. All these points should be borne in mind by future observers.

In the following list it is seen that courtship feeding is sometimes typical of a whole family of birds, while in others only one or two genera in a family may show it. (I know of no cases where two species of the same genus differ.)

In the following list I follow the order and classification of bird families proposed by Wetmore (1934) and record those forms in which courtship feeding has been found, and also those forms which have been studied sufficiently for one to be fairly certain that the habit does not occur. If the word 'incubation' is written after the species, it means that the habit has as yet been recorded only during incubation. This should not be taken to mean that the habit is confined to incubation, as courtship habits have been studied much less than nesting habits. I have omitted altogether certain tropical families about which nothing is known, and have been unable to cover the Australian and New Zealand literature. I hope some reader of 'The Auk' may be able to do this.

CLASSIFIED LIST

PALAEOGNATHAE (struthious birds). Apparently absent.

SPHENISCIFORMES (penguins). Adélie Penguin (incubation) brings snow.

GAVIIFORMES (loons). Absent.

COLYMBIFORMES (grebes). Absent.

PROCELLARIIFORMES (petrels, etc.). Absent so far as known; certainly absent in *Fulmarus*.

PELECANIFORMES (tropic-birds, pelicans, frigate-birds, cormorants, boobies). Found only in tropic-birds.

CICONIIFORMES (herons, etc.). Absent.

ANSERIFORMES (geese, ducks, swans). Normally absent; occurs in *Aix sponsa*.

FALCONIFORMES (birds of prey). Regular in *Circus* (correlated with a special flight, the 'pass') and *Falco* spp., e. g. *peregrinus, subbuteo, sparverius, aesalon;* also recorded in *Accipiter nisus, Milvus migrans, Haliaeetus albicilla,* and (unusually) *Aquila chrysäetos*. In most of the above, it has been recorded only during incubation, but definitely earlier in *Falco peregrinus, F. sparverius, F. columbarius aesalon,* and *Circus pygargus*.

GALLIFORMES (gallinaceous birds). Normally absent, regular in *Colinus virginianus;* occurs in *Gallus gallus domesticus*.

GRUIFORMES (cranes, rails, etc.). Regular in Turnicidae (button-quails), where female feeds male. Recorded during incubation in *Rallus aquaticus,* and by one observer in *Gallinula chloropus;* possibly not regular in the last, since it is not mentioned by most observers.

CHARADRIIFORMES (a) Charadrii (shorebirds). Normally absent, but recorded in *Burhinus oedicnemus* (Stone Curlew). (b) Lari. In the Laridae, regular in all species of *Larus* (gulls) and *Sterna* (terns) so far studied, in the former by regurgitation, in the latter associated with a 'fish flight.' Recorded in *Rynchops nigra* (Black Skimmer), but apparently absent in the third family of the Lari, the Stercorariidae (skuas, jaegers). (c) Alcae (auks). Apparently absent.

COLUMBIFORMES (pigeons, doves, etc.). Regular, by regurgitation, in *Zenaidura, Columba, Ectopistes, Turtur,* and presumably other genera of the Columbidae.

PSITTACIFORMES (parrots). Recorded in captive *Psephotus* and *Platycercus.* Mr. Karl Plath of the Brookfield Zoo informs us that this is regular in all parrots; in homosexual pairs it may be exhibited by females.

CUCULIFORMES (cuckoos, etc.). Recorded in *Centropus* and *Coccyzus;* apparently absent in parasitic forms.

STRIGIFORMES (owls). Recorded in a captive pair of *Otus asio* (Screech Owl); other species probably not sufficiently studied.

CAPRIMULGIFORMES (nightjars). Apparently absent.

MICROPODIFORMES (swifts, hummingbirds). Apparently absent.

CORACIIFORMES (kingfishers, bee-eaters, rollers, hornbills). Recorded in *Alcedo atthis* (European Kingfisher), also *Upupa epops* (Hoopoe) (incubation) and hornbills (incubation).

PICIFORMES (woodpeckers, jacamars, toucans, barbets). Recorded in *Galbula melanogenia* (jacamar). Apparently absent in Picidae (woodpeckers), though 'billing' has been recorded in *Campephilus.*

PASSERIFORMES (treated under families, and numerous families for which there are no positive or negative data are omitted):

Tyrannidae (tyrant flycatchers). Regular in *Pyrocephalus* on the Galapagos Islands (personal observation, also W. H. Thompson). Have found no other records.

Pittidae (pittas). Recorded in *Pitta cucullata* in captivity.

Pipridae (manakins). Clearly absent in *Manacus vitellinus.*

Alaudidae (larks). Recorded only in *Lullula arborea* (Niethammer, 1: 159, 1937).

Hirundinidae (swallows). Apparently absent.

Corvidae. Regular in *Corvus* spp., e. g., *corax, corone, frugilegus* (for all of these I have found references only to incubation), *Coloeus monedula* (Jackdaw) and *Pyrrhocorax* (Chough) including before incubation; also *Pica* (magpies) and various jays, i. e., probably found throughout the family.

Paridae (titmice). Recorded in most West European species of *Parus (major, caeruleus, atricapillus, ater, cristatus)* also *Penthestes a. atricapillus* in North America during incubation.

Sittidae (nuthatches). Regular in *Sitta europaea, canadensis* and *carolinensis* in courtship and incubation.

Certhiidae (tree creepers). Regular in *Certhia familiaris.*

Chamaeidae (wren tits). Absent.

Cinclidae (dippers). Regular in *Cinclus aquaticus.*

Troglodytidae (wrens). Apparently absent.

Mimidae (thrashers, mockingbirds). Apparently absent.

Turdidae (thrushes, etc.). Apparently absent in *Turdus,* also in *Saxicola* and *Oenanthe.* Regular in *Erithacus rubecula* (European Robin), occasional in the Bluebird *(Sialia sialis)* and *Myadestes townsendi* (Townsend's Solitaire) (personal observation of R. T. Orr).

Muscicapidae (Old World flycatchers). Recorded in *Muscicapa striata* and *M. hypoleuca* (incubation).

Sylviidae (Old World warblers). Recorded in *Acrocephalus scirpaceus* and (as an abnormality) in *Phylloscopus collybita* and *P. sibilatrix;* seems normally absent.

Prunellidae (accentors). Occasional in *Prunella modularis* (Hedge Sparrow).

Motacillidae (wagtails, pipits). Seems absent in wagtails, and usually absent in pipits, but recorded (as an abnormality) in *Anthus trivialis.*

Bombycillidae (waxwings). Regular in *Bombycilla cedrorum* and *B. garrulus.*

Laniidae (shrikes). Regular in *Lanius ludovicianus,* recorded in *L. collurio* (both preceding copulation and in incubation) and *L. senator* (the last, in incubation).

Sturnidae (starlings). Absent.

Vireonidae (vireos). Not recorded.

Compsothlypidae (wood warblers). Recorded in *Dendroica aestiva, castanea, caerulescens,* and *pinus,* and *Protonotaria citrea.*

Ploceidae (weaver finches). Not recorded.

Icteridae (blackbirds, troupials, etc.). Never recorded, though several species have been studied in detail.

Thraupidae (tanagers). Recorded in captive *Calospiza thoracica.*

Fringillidae (finches). Regular in many genera, including *Richmondena* (Cardinal), *Coccothraustes* (Hawfinch), *Chloris* (Greenfinch), *Carduelis* (European Goldfinch, Lesser Redpoll, Siskin), *Spinus* (American goldfinches), *Pyrrhula* (Bullfinch), *Pinicola* (Pine Grosbeak), *Leucosticte* (Rosy Finch), *Loxia* (crossbill), *Fringilla* (Chaffinch), *Plectrophenax* (Snow Bunting) and all the Geospizinae (Galapagos finches). In some of these it has been recorded only during incubation, but in most (not, apparently, the Chaffinch) it also occurs before incubation. Typically, seems absent in buntings and American sparrows, including the well-studied *Emberiza* (Yellow and Reed Buntings), *Zonotrichia* (White-crowned Sparrow), and *Melospiza* (Song Sparrow).

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It seems better to depart from the usual custom and list the references in systematic order of the birds, not of authors' names. To save space, titles of papers are also omitted, but the name of the species referred to is retained.

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