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A REVIEW OF COURTSHIP FEEDING IN BIRDS

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In many kinds of birds courtship feeding is a conspicuous part of overall reproductive behavior; in some birds such feeding is inconspicuous or obscure, for any of several reasons. Probably as a result of the differences in its appearance, courtship feeding has never been too precisely defined, and usually has been used to refer to any feeding by a male of a female, usually its mate, throughout the pre-parental stages of reproductive behavior. The excellent review by Lack (1940) recognized "courtship feeding" as descriptively inadequate in that it placed a certain handicap on satisfactorily classifying the several kinds of behavior included in the concept. Armstrong (1955:128) used the term "connubial feeding" to refer to that feeding by males of females in the time of incubation. Armstrong's term is perhaps better suited for use in an inclusive sense, but "courtship feeding" is well-established in the literature and there is little use in attempting to displace it at this time. In any event, courtship feeding is here considered to refer to all kinds of pre-parental feeding by an adult male of an adult female. By "adult" is meant a bird that can engage functionally in reproductive activities; this includes all reproductively active individuals that are morphologically "subadult" except those that merely assist parents in nestbuilding and rearing siblings (the helpers at the nest of Skutch, 1935).

Courtship feeding ranks as one of the best examples of adaptive convergence in birds. Because the behavior is found in such a wide variety of kinds of birds, it is likely that courtship feeding has arisen independently many times in the evolution of birds. Additionally, such feeding may involve food, or symbols of food, or no material at all; such feeding occasionally is by females of males; such feeding also may occur either in a restricted period of time (as, one link in a chain of pre-copulatory activities), or more broadly (as, throughout all stages of nestbuilding), or throughout all pre-parental activities of a pair; such feeding may be only rarely seen in a few members of the species or it may be conspicuously present in all members. There is thus no taxonomic or functional consistency, indicating that there has been a diversity of both phyletic development and functional significance. The chief feature that these diverse patterns of feeding have in common is that they occur in time prior to hatching of young, or, within that time that a mated pair exists together without young.

CLASSES OF COURTSHIP FEEDING IN BIRDS

The outline below is composed of both actual and possible classes of courtship feeding. The categories have been set up to cover the conspicuous possibilities and do not in fact cover all possibilities. All of the actual categories of courtship feeding are considered, and for such categories a few, usually well-known, examples of species characterized by the stated kind of courtship feeding are listed.

- 1.—Courtship feeding restricted to one pre-parental phase of behavior.
 - A. Feeding only prior to formation of the pair-bond: not recorded.
 - B. Feeding only in the time of formation of the pair-bond (strictly speaking, "courtship" feeding): not certainly recorded.
 - C. Feeding closely associated only with copulation: frequently recorded. Prior to copulation: *Larus argentatus*, *Columba* spp., *Streptopelia* spp., *Zenaida* spp., *Ectopistes*, *Columbina* spp., *Geopelia cuneata*, and *Camarhynchus*

- parvulus*. At copulation (symbolic): *Pygoscelis adeliae*. Subsequent to copulation: *Centropus*, *Coccyzus*, *Geococcyx*, and *Chondestes grammacus*.
- D. Feeding only at nestbuilding: not certainly recorded.
 - E. Feeding only at egg-laying: not certainly recorded (but see 2, C, below).
 - F. Feeding only in time of incubation: frequently recorded. Noted in *Rallus aquaticus*, various bucerotids, *Upupa epops*, *Ceryle alcyon*, *Stellula calliope*, *Corvus corax*, *C. corone*, *C. frugilegus*, *Troglodytes troglodytes*, *Thryomanes bewickii*, *Muscicapa hypoleuca*, *M. striata*, *Anthus pratensis*, *A. spinoletta*, *Vireo olivaceus*, *Icterus galbula*, *Fringilla coelebs*.

Note.—post-parental courtship feeding could be a valid category, but such feeding is difficult to distinguish from feeding of nestlings; such feeding possibly occurs in some hawks, as *Accipiter gentilis* (Schnell, 1958).

2.—Courtship feeding in two or more phases of pre-parental activity.

- A. Feeding from time of pair-formation to appearance of young: frequently recorded. Noted in *Cyanocitta cristata*, *Erithacus rubecula*, *Geospiza* spp., *Richmondia cardinalis*, *Spinus lawrencei*, *Loxia curvirostra*, *Coccothraustes coccothraustes*, *Chloris chloris*, *Serinus canarius*, *Pyrrhula pyrrhula*; generally present in "aggressive" species.
- B. Feeding from copulation through incubation: frequently recorded. Noted in *Milvus migrans*, *Accipiter nisus*, *Halizæetus albicilla*, *Aquila chrysaetos*, *Circus* spp., *Falco peregrinus*, *F. subbuteo*, *F. sparverius*, *Corvus monedula*, *Pyrrhocorax pyrrhocorax*, *Sitta* spp., *Lanius ludovicianus* and *L. collurio*.
- C. Feeding chiefly in time of egg-laying, but also in time of copulation: noted in western European species of *Parus*.

DISCUSSION

It is not without a certain surprise that we find no documented instance of true "courtship" feeding, which is feeding by the male of the female in that time when the pair-bond is being established. Every species that has been observed to make such presentation has been seen also to show feeding throughout almost the entirety of pre-parental activities. All such species are those characterized by Hinde (1956:13) as "aggressive." It is precisely with these aggressive species, showing courtship feeding in two or more phases of the reproductive effort, that difficulty is found in proposing suitable and convincing adaptive values for the behavior.

There is no better hypothesis available to explain this behavior than that of Lack (1940), now more than 20 years old: such feeding serves to augment the formation and maintenance of the pair-bond. Hinde's (1956:13) expression of nearly the same point of view is as follows: "It is suggested that this aggressiveness [between the mated pair], which is inhibited during the precopulatory period by the sexual factors, is reduced after the sexual phase by habituation to the mate's proximity resulting from courtship feeding." Hinde further agrees with Tinbergen (1953:120) that with females of such species the solicitation for courtship feeding must be a displacement activity ("food-begging behaviour of the young, . . . serving as an outlet for the sexual drive"); the behavior of the male in feeding the begging female may simply be derived from the "normal" response to ritual solicitation for food, a response augmented by selection for males with a low threshold for feeding behavior.

For species showing time-restricted courtship feeding, it is somewhat easier to evaluate the adaptations, because the obvious descriptive relationships have already been set forth, so to speak, by the birds themselves. The apparent relationships are two: the first associates courtship feeding and copulation, and the second associates courtship feeding and incubation.

Courtship feeding at or near the time of copulation is the simplest kind for which to assign adaptive significance, but the most difficult for which to reconstruct the evolutionary history. If the feeding occurs ritually before, during, or after copulation, it can be assumed that such feeding has function both as a synchronizer of psychosexual behavior and as a releaser of copulatory action. In some species, or entire groups of species, courtship feeding is necessary before copulation can occur; this is true for all columbids that have been studied, and it is characteristic of the Herring Gull, *Larus argentatus* (Tinbergen, 1953:120).

In non-parasitic cuculids courtship feeding occurs just after copulation. Males hold an item of food in their beaks before and during copulation. Such close relationship in time between copulation and feeding seems to argue for a causal connection between the two, although the feeding comes only after copulation. The sight of the item eventually to be fed by males to females can of course be as effective a stimulus as is the actual presentation of the item.

Courtship feeding of copulation is so completely ritualized that it is difficult to trace its possible evolutionary derivation. It does not presently occur at a time in reproductive activity when "habituation" (Hinde, 1956:12) would seem to be of real meaning, for the pair has already established an effective bond. Neither does it occur when passage of food might conceivably in the past or future have functional significance, that is, in time of incubation. It is possible that the present form of feeding is a bare remnant of a once widespread behavioral pattern used originally for purposes of habituation in the sense of Hinde. Such behavior could have arisen as a displacement solicitation for food by females, eliciting a feeding reaction in males, and later could have taken on significance as the primary synchronizer of sexual behavior.

Courtship feeding in time of incubation is characteristic of a wide variety of species. Although few species have been as well studied as *Troglodytes troglodytes* (Armstrong, 1955) or *Fringilla coelebs* (Marler, 1956), it would appear that for most species the relationship is real rather than the result of incomplete observations. The food passed is of no importance in maintaining the incubating female (save in hornbills); such feeding occurs both in species in which females only sit and in which males also sit, and in some species the behavior is extremely rare. It is probable that many, if not most, instances of such feeding represent "anticipatory" food-bringing by males for still non-existent nestlings. Our vantage point in time may actually be a poor one for assessing this adaptation. The behavior possibly is in the process of being developed as a useful pattern, or it possibly is in the process of being cast off and thus is seen presently as vestigial. Both alternatives conceivably exist today, from one group of birds to another.

In summary we may note that courtship feeding in birds is characteristic of many species 1) at time of copulation, 2) at time of incubation, or 3) throughout most of the pre-parental phases of reproductive behavior. The phyletic development and adaptive significances are diverse, indicating multiple and unrelated evolutionary origins.

SYSTEMATIC LIST

In the following list only groups for which courtship feeding has been recorded or definitely established as absent are mentioned.

Spheniscidae: penguins.—*Pygoscelis adeliae* (Sladen, 1958).

Phaethontidae: tropic-birds.—*Phaethon lepturus* (Gross, 1912); *P. aethereus* (Bent, 1922).

Accipitridae: hawks.—*Elanus leucurus* (Peyton, in Lack, 1940); *Milvus migrans* (Lack, 1940); *Accipiter nisus* (Sewart, in Lack, 1940); *Haliaeetus albicilla* (Lack, 1940); *Circus cyaneus* (many references); *C. pygargus* (Lack, 1940).

Falconidae: falcons.—*Falco peregrinus* (Bent, 1938); *F. tinnunculus* (Tinbergen, 1940), *F. subbuteo* (Lack, 1940); *F. columbarius* (Bent, 1938); *F. sparverius* (many references; Johnston, ms).

Cathartidae: vultures.—Not recorded.

Ardeidae: herons.—*Ardea herodias*, *A. cinereus* (Cottrille and Cottrille, 1958).

Scopidae: hammerheads.—Absent (Cowles, 1930).

Anatidae: ducks.—*Aix sponsa* (Heinroth, in Lack, 1940).

Phasianidae: fowl.—*Gallus gallus* (Lack, 1940); *Colinus virginianus* (Stoddard, 1936:15).

Cuculidae: cuckoos.—*Centropus* (Spennermann, in Lack, 1940); *Coccyzus* spp. (Thomas, in Lack, 1940); *Geococcyx californianus* (Rand, 1941).

Rallidae: rails.—*Rallus aquaticus* (Zimmerman, in Lack, 1940); *Gallinula chloropus* (Holstein, in Lack, 1940).

Turnicidae: button-quail.—*Turnix* spp. (Lack, 1940:177-178).

Burhinidae: thick-knees.—*Burhinus oedipnemus* (Banzhaf, in Lack, 1940).

- Laridae: gulls and terns.—*Larus* spp. (many references; see Moynihan, 1959, for a summary); *Catharacta skua* (Stonehouse, 1956:15); *Sterna* spp. (Moynihan, 1959); *Rhynchops nigra* (Pettingill, 1937).
- Pteroclididae: sand-grouse.—Seemingly unrecorded.
- Columbidae: pigeons.—*Columba* spp., *Streptopelia* spp. (many references); *Zenaidura asiatica*, *Z. macroura*, *Columbina inca* (Johnston, ms); *Ectopistes* (Craig, 1911); *Geopelia cuneata* (Goodwin, 1960); probably also most of the remaining species of the family.
- Psittacidae: parrots.—*Aratinga* spp. (J. W. Hardy, ms); *Agapornis* spp., *Loriculus*, *Neophema*, *Psephotis* (Kendeigh, 1952; Lack, 1940); probably also most of the remaining species of the family.
- Tytonidae: barn owls.—*Tyto alba* (Forbush, 1927).
- Strigidae: owls.—*Nyctea scandiaca* (Pitelka, Tomich, and Treichel, 1955); *Otus asio* (in captivity; Carpenter, 1883); *Asio otus* (Niethammer, in Lack, 1940); *Bubo bubo* (Gugg, in Lack, 1940); *Glaucidium*, *Athene*, *Aegolius* (Kendeigh, 1952).
- Alcedinidae: kingfishers.—*Alcedo atthis* (Lack, 1940); *Ceryle alcyon* (Brackbill, 1941).
- Momotidae: motmots.—*Eumomota superciliosa* (Skutch, 1947).
- Upupidae: hoopoes.—*Upupa epops* (Skead, 1950).
- Bucerotidae: hornbills.—Probably present in all species (Moreau, in Lack, 1940).
- Apodidae: swifts.—*Cypseloides niger* (Michael, 1927); *Apus apus* (Koskimies, 1950).
- Trochilidae: hummingbirds.—*Stellula calliope* (Cottam, 1941).
- Galbulidae: jacamars.—*Galbula melanogenia* (Skutch, 1937).
- Capitonidae: barbets.—*Semnormis frantzii* (Skutch, 1944).
- Indicatoridae: honeyguides.—Absent (Friedmann, 1955).
- Pittidae: pittas.—*Pitta cucullata* (in captivity; Lack, 1940).
- Tyrannidae: tyrant flycatchers.—*Pyrocephalus rubinus* (Lack, 1940); *Myiarchus crinitus* (Gillespie, 1924); *Sayornis phoebe* (de Kiriline, 1951); *S. saya* (Kendeigh, 1952); *Empidonax minimus* (MacQueen, 1950); *E. wrightii* (Kendeigh, 1952); *Contopus virens* (Bent, 1942); *C. cinereus* (Skutch, 1960).
- Alaudidae: larks.—*Eremophila alpestris* (Sutton, 1932); *Lullula arborea* (Niethammer, in Lack, 1940).
- Hirundinidae: swallows.—Usually absent; occasional in *Hirundo rustica* (Coward, 1928); *Iridoprocne bicolor* (Nice, 1941); *Delichon urbica* (Allen and Nice, 1952).
- Corvidae: crows and jays.—*Aphelocoma coerulescens* (Amadon, 1944); *Psilorrhinus mexicanus* (Skutch, 1960); *Calocitta formosa* (Skutch, 1960); *Cyanocitta cristata* (Bent, 1946); *Garrulus glandarius* (Goodwin, 1951); *Corvus corax*, *C. corone*, *C. frugilegus*, *C. monedula* (Lack, 1940); *Pyrrhonorax pyrrhonorax* (Lack, 1940); *Pica pica*, *P. nuttallii* (Linsdale, 1937); *Nucifraga* spp. (Mewaldt, 1956).
- Paridae: chickadees and tits.—*Parus major*, *P. caeruleus*, *P. ater*, *P. atricapillus*, *P. cristatus* (Lack, 1940); *P. palustris* (Morley, 1949); *P. inornatus* (Dixon, 1949); *P. hudsonicus* (Bent, 1946); *P. carolinensis*, *P. bicolor* (Brackbill, 1949); *Aegithalos caudatus* (Lack, 1958).
- Sittidae: nuthatches.—*Sitta europaea* (Steinfatt, 1938); *S. carolinensis* (Butts, 1931); *S. canadensis* (Gunderson, 1939).
- Certhiidae: creepers.—*Certhia familiaris* (Tyler, 1914).
- Timaliidae: babblers.—*Orthonyx temminckii* (McNamara, 1935); absent in *Chamaea fasciata* (Erickson, 1938).
- Troglodytidae: wrens.—*Troglodytes troglodytes* (Bent, 1948); *T. rufociliatus* (Skutch, 1960); *Thryomanes bewickii* (Miller, 1941); *Thryothorus ludovicianus* (Lasky, 1941); *Catherpes mexicanus* (Bent, 1948); *Campylorhynchus brunnei-capillus* (Nice and Thomas, 1948).
- Turdidae: thrushes.—*Cinclus cinclus* (Eggebrecht, 1937); *Turdus migratorius* (Kendeigh, 1952); *T. merula* (Tucker, 1946); *T. viscivorus* (Boyd, 1946); *Hylocichla guttata* (Bent, 1949); *Erithacus rubecula* (Lack, 1940); *Sialia sialis*

- (Lack, 1940); *S. currucoides* (Bent, 1949); *Oenanthe oenanthe* (Mildenberger, 1943).
- Muscicapidae: Old World flycatchers.—*Muscicapa striata*, *M. hypoleuca* (Lack, 1940).
- Sylviidae: Old World warblers.—*Phylloscopus collybita*, *P. sibilatrix* (Lack, 1940); *P. trochilus* (May, 1949); *Hippolais icterina* (Kendeigh, 1952); *Acrocephalus scirpaceus* (Lack, 1940); *Poliophtila caerulea* (Bent, 1949).
- Prunellidae: accentors.—*Prunella modularis* (Lack, 1940).
- Motacillidae: pipits.—*Anthus trivialis* (Lack, 1940); *A. spinoletta* (Brackbill, 1941).
- Bombycillidae: waxwings.—*Bombycilla garrulus*, *B. cedrorum* (Lack, 1940).
- Sturnidae: starlings.—*Sturnus vulgaris* (Chappell, 1949).
- Vireonidae: vireos.—*Vireo flavifrons*, *V. solitarius* (Bent, 1950); *V. olivaceus* (Lawrence, 1953).
- Parulidae: wood warblers.—*Dendroica petechia*, *D. castanea*, *D. pinus*, *D. caerulescens* (Lack, 1940); *Basileuterus fulvicauda* (Skutch, 1960); *Setophaga ruticilla* (Sturm, 1945).
- Ploceidae: weavers.—Apparently present in estrildines.
- Icteridae: blackbirds and orioles.—*Dives dives* (Skutch, 1954); *Euphagus cyanocephalus* (Williams, 1952); *Xanthocephalus* and *Icterus* (Kendeigh, 1952); *I. galbula* (Brackbill, 1941).
- Thraupidae: tanagers.—*Tangara thoracica* (Lack, 1940); *Tanagra imitans*, *Chlorophonia occipitalis*, *Tangara nigro-cincta*, *T. icterocephala*, *T. chrysophrys*, *Thraupis cana*, *Ramphoscelus passerinii*, *R. dimidiatus*, *Piranga olivacea* (Skutch, 1954).
- Fringillidae: buntings, sparrows.—*Richmondia cardinalis* (Ganier, 1937); *Salinator maximus*, *S. albicollis*, *Sporophila aurita*, *Cyanocopsa cyanooides* (Skutch, 1954); *Coccothraustes coccothraustes* (Lack, 1940); *Chloris chloris*, *Carduelis*, *Spinus*, *Pyrrhula*, *Pinicola*, *Fringilla* (Lack, 1940); *Carduelis cannabina* (Harber, 1945); *Leucosticte tephrocotis* (Twining, in Lack, 1940); *Chondestes grammacus* (Brackbill, 1941; Barlow, 1960); *Plectrophenax nivalis* (Lack, 1940); all Geospizinae (Lack, 1940).

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NOTES AND NEWS

Dates on which the Midwinter Census of birds can be taken are Wednesday, December 19, 1962 through Tuesday, January 1, 1963. Forms suitable for recording observations should reach members of K.O.S. in early December.

The *Bulletin* is presently in short supply of manuscripts intended for publication. Suitable material received soon may reasonably be expected to appear in the Number for June, 1963.

Mr. Jon C. Barlow, one of our Assistant Editors, has taken a year's leave of absence from his regular routine in order to participate in a program of field work in Uruguay. Mr. Erwin E. Klaas will take over Mr. Barlow's duties in the interim period.

One of our members, Dr. Robert M. Mengel, has been elected to serve as Editor of *The Auk* (journal of the American Ornithologists' Union).

The Annual Meeting of the K.O.S. for 1963 will be held on May 4 and 5 in Lawrence, associated with The University of Kansas and the Museum of Natural History.

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