

DEMAND BEHAVIOR: A NEW INTERPRETATION OF COURTSHIP FEEDING

SUSAN M. SMITH

ABSTRACT.—This review examines the various interpretations of courtship feeding (away from the nest, and not necessarily associated with copulation). Courtship feeding undoubtedly functions to maintain the pair-bond in many species, and also increases a female's fitness by providing her with extra food. This behavior is also claimed to express a male's dominance over a female, the female's so-called "begging" display being termed submissive. I present evidence that courtship feeding is, in fact, strongly correlated with female dominance over the male. Since begging fledglings can commonly supplant their parents, it may be more appropriate to call begging displays "demand behavior." Various elements of demand behavior in other contexts can serve both in appeasement and in threat displays. The common factor in each is that the displaying birds' strong tendency to attack is inhibited by other drives such as hunger, sex or fear.

Besides pair-bond maintenance, energy provision, and possibly expression of female dominance, courtship feeding can also serve to increase a male's fitness by being his most direct way of contributing to the quality of his own eggs.

In many bird species, males feed their mates for at least part of the breeding season. Such behavior is reported in 11 avian orders (Lack 1940, Kendeigh 1952, Stokes and Williams 1971), and in almost three-quarters of passerine families (Kendeigh 1952, Andrew 1961, Willis 1972). While termed "courtship" feeding, it is usually not restricted to pair formation or copulation.

Except perhaps among buttonquails (Turnicidae; Lack 1940), it is the male who feeds the female. In most species males bringing food generally give little or no postural display, though they sometimes utter soft calls, especially when feeding during incubation. By contrast, females usually give well-differentiated displays, often with specific calls, which can be strikingly similar to those of a hungry fledgling.

Much diversity exists among what has generally been termed courtship feeding. In some groups, such as most nonparasitic cuckoos, males apparently feed females only at copulation (Calder 1967). Others, such as antbirds, have feeding both at copulation and during nest building and egg laying (Willis 1972). In still others, males feed their mates only on the nest during late incubation; this "anticipatory food-bringing" (Nolan 1958) may be simply an indication that the male is prepared to feed nestlings, and thus fundamentally differs from true courtship feeding. In this review, I will deal only with feeding that is not associated directly with copulation and that occurs

away from the nest. I will examine the published interpretations of courtship feeding, and will present evidence to refute one that is based on the unfounded assumption of the universality of male dominance. Finally, I will propose my own interpretation of courtship feeding.

REVIEW OF THE LITERATURE

Currently there are three published interpretations of courtship feeding. One states that the major function is pair-bond maintenance (Lack 1940, Andrew 1961, Armstrong 1965), an idea that seems highly likely, although difficult to refute. A second view is that the behavior chiefly serves to provide food for the female (Royama 1966). Krebs (1970) showed that a female Blue Tit (*Parus caeruleus*) fed by her mate received food approximately 2.5 times as often as when foraging alone; during incubation, a male Spotted Flycatcher (*Muscicapa striata*) contributed 31% of the female's total energy intake (Davies 1977). Both Krebs and Davies found that males brought prey items averaging heavier than those the female chose for herself (indicating, according to Davies, that this food-bringing is a measurable energy drain for the males, the drain being minimized by the males' selection of only large items). Perhaps the extreme of energy provision via courtship feeding occurs in raptors. Female accipiters, for example, rarely hunt from the time of pair formation until mid-nestling stage, a period of

50 to 90 days depending on the species (Reynolds 1972).

The third published interpretation of courtship feeding is that it is "an expression of dominance of a male to a female" (Hardy 1961:34; see also Goodwin 1951 and Armstrong 1965). This is a peculiar means of expressing dominance. In typical courtship feeding, the male must spend time and energy searching for food, capturing it, often preparing it, and finally carrying it to the female. His costs are measurable and his direct intake is nil. By contrast, the female spends only the energy needed for her "begging" display, and usually gains a significant amount of energy in return.

In an intensive search of the literature, I could not find a single documented case of true courtship feeding where the male was shown to be dominant over the female at the time of feeding. Spring data are critical here, since in monogamous species dominance by males in nonbreeding flocks commonly changes to dominance by females among breeding birds (Smith 1980). By contrast, I have found more than 20 examples of species that engage in courtship feeding during their period of known female dominance: Bicolored Antbird (*Gymnopithys bicolor*; Willis 1967); Eurasian Jay (*Garrulus glandarius*; Goodwin 1951); Great Tit (*Parus major*; Hinde 1952); White-breasted and Red-breasted nuthatches (*Sitta carolinensis* and *S. canadensis*; Kilham 1971, 1975); Eastern Bluebird (*Sialia sialis*; Krieg 1971); Spotted Flycatcher (Davies 1977); Red-backed Shrike (*Lanius collurio*; Curio 1959); canary (*Serinus* sp.), Greenfinch (*Carduelis chloris*), Hawfinch (*Coccothraustes coccothraustes*), and European Goldfinch (*Carduelis carduelis*; Hinde 1955-1956); American Goldfinch (*Carduelis tristis*; Coutlee 1967); Lesser (*C. psaltria*) and Lawrence's (*C. lawrencei*) goldfinches (Linsdale 1957); Common Redpoll (*Carduelis flammea*; Dilger 1960); Red Crossbill (*Loxia curvirostra*; Tordoff 1954); House Finch (*Carpodacus mexicanus*; Thompson 1960); Purple and Cassin's finches (*C. purpureus* and *C. cassinii*; Samson 1977); Bullfinch (*Pyrrhula pyrrhula*; Hinde 1955-1956); as well as the majority of hawks and owls with reversed sexual dimorphism (Earhart and Johnson 1970, Reynolds 1972). Of these, the last four plus the hawks and owls are species in which females are reported to be dominant year-round. Hawk species in which females are most markedly larger than males are those in which courtship feeding is most pro-

nounced (Reynolds 1972). Although there is much variation, female hawks often flutter when soliciting food from their mates (Bent 1937, 1938; Cade, pers. comm.). Hence, it is common for dominant females to flutter and give "begging" calls to subordinate males; this usually results in the males' feeding the females.

Courtship feeding seems restricted to monogamous species. In families with diverse mating systems this correlation is striking. Among wrens, for example, most polygynous species have no courtship feeding, but three primarily monogamous species do (Nice and Thomas 1948). Similarly in icterids, two species known to have courtship feeding are both monogamous (Orians et al. 1977, Williams 1952). Moreover, in species whose males are larger than females, courtship feeding does not occur; indeed, Orians and Christman (1968) attributed the lack of courtship feeding in three polygynous icterids to the fact that males in these species are dominant year-round. The strong correlation between courtship feeding and monogamy is important because it is monogamous females who usually dominate their mates early in the breeding season (Smith 1980).

Several instances have been reported in which a female solicited food from her mate, who did not respond promptly by bringing food. Significantly, the male was then usually supplanted by the female (e.g., Lack 1953, Marler 1956, Willis 1967, 1972).

My lines of evidence are (1) the more than 20 examples of courtship feeding in species with dominance by breeding females and lack of courtship feeding where males are dominant; (2) the strong correlation between courtship feeding and monogamy; and (3) the reports of females supplanting males who had not brought food immediately. All suggest that courtship feeding, if it reflects dominance at all, tends to express a female's dominance over a male. Since the dominant individual is generally the one who receives the food, not the one who gives it, the female's display during courtship feeding can thus better be termed "demand behavior."

Passing of food between two adult birds in somewhat different contexts is reported in three highly social species: Florida Scrub Jay (*Aphelocoma c. coerulescens*; Woolfenden and Fitzpatrick 1977), Arabian Babbler (*Turdoides squamiceps*; Zahavi, pers. comm.), and Sociable Weaver (*Philetairus socius*; Collias and Collias 1978). In the jay and babbler, it is the dominant bird who

attempts to feed the subordinate, while in the weaver, it is always the subordinate who tried to feed the dominant. This "allofeeding," as Zahavi terms it, differs from true courtship feeding in four major ways: (1) feeding attempts often occur between members of the same sex; (2) allofeeding is not restricted to the breeding season; (3) birds commonly refuse food offered by others; and (4) little or no food solicitation is given. Because of these differences, I will not discuss allofeeding further, beyond noting that it clearly involves no general correlation between relative rank and the role of feeder.

Besides courtship feeding, regular food solicitation occurs in only one other situation: when adults feed dependent fledglings. Can dominance be applied reasonably to parent-offspring interactions? Although dominance is clearly irrelevant when adults feed hatchlings, I suggest that it is relevant after the young have left the nest. Wing-fluttering and loud begging notes are usually not begun until after fledging; by this age young birds often weigh as much as or even more than their parents. In Rufous-collared Sparrows (*Zonotrichia capensis*), a species with year-round female dominance, I found (Smith 1978) that the only individuals able to supplant an adult female on her territory were the pair's fledglings. Other species in which fledglings are dominant over their parents are the Lunulated Antbird (*Gymnopithys lunulata*), White-throated Antbird (*G. salvini*), and Ocellated Antbird (*Phaenostictus mcleannani*; Willis 1968), Black-capped Chickadee (*Parus atricapillus*; Odum 1942), and canary, Chaffinch, Greenfinch, and European Goldfinch (Marler 1956). Furthermore, those who have hand-reared birds know that young birds old enough to leave the nest are highly aggressive in demanding food from their keepers (e.g., Andrew 1956, Hardy 1961, Berger 1968). Marler (1956) discussed fledgling dominance over parents and suggested that it may be a common phenomenon. Fledgling begging behavior may thus also more accurately be termed demand behavior.

In most species, this juvenile dominance is short-lived; when adults respond by supplanting attacks rather than by bringing food, the young stop their demand behavior and the family flocks break up. However, if a keeper continues to respond by giving food, hand-reared birds will continue their demand displays for months (Miller 1931). Interestingly, in the highly social Piñon Jay

(*Gymnorhinus cyanocephalus*), young birds remain with their parents long after fledging, and are deferred to and fed by most older birds throughout their first year (Balda and Balda 1978).

Various elements of demand behavior, such as wing-fluttering, may be given in other contexts not related to feeding. These displays sometimes serve to inhibit attack (e.g., Marler 1956, Brown 1963, 1964, Willis 1967, Zahavi 1971), and thus are true appeasement behavior. Wing-fluttering, however, is not necessarily submissive, or "cringing" as Willis (1967) referred to it. This behavior, particularly when performed by females, has often been assumed to be submissive, based on little or no evidence. For example, Willis (1967:73) wrote of early pair formation in Bicolored Antbirds, "She seemed to push him backward in her cringing advance . . .," and continued that the male, having been forced off his perch, then went and brought the female some food.

In fact, elements of demand behavior such as wing-fluttering can be highly aggressive threat displays. Williams (1952) found that female Brewer's Blackbirds (*Euphagus cyanocephalus*) gave the juvenile begging call (also given by females during courtship feeding) when chasing female invaders out of their territories. Wing-fluttering in male American Goldfinches is associated with high intensity aggression (Coutlee 1967), and is occasionally used by male Brewer's Blackbirds in disputes over food (Williams 1952). Andrew (1957) reported wing-fluttering by resident territorial males toward intruders in at least five species of emberizine finches. MacQueen (1950) found that when a male Least Flycatcher (*Empidonax minimus*) invaded another's territory, high intensity wing-fluttering preceded actual attack; the same is true in Loggerhead Shrikes (*Lanius ludovicianus*; Smith 1973). Not every species flutters in juvenile begging; certain estrildine finches hold the wings still and twist the head around so the bill points upward. Baptista and Atwood (1980) reported that adult Java Sparrows (*Padda oryzivora*) use head-twisting as an aggressive display in supplanting attacks. Here again, elements of demand behavior in juveniles function as threats in adults.

How is it that behavior patterns such as wing-fluttering and/or begging notes can function as appeasement in certain contexts, yet at least as often serve as threat or demand behavior in other contexts? This is not actually contradictory, since both cases

have an aspect in common: the displaying bird always experiences a strong attack tendency, which is inhibited by some other factor. Threat and other types of hostile display are commonly thought to result from conflict between two incompatible tendencies or "drives" (see Hinde 1970 for a review). Moynihan (1955) pointed out that if no conflict of tendencies exists, a bird will simply attack (or flee) without display; hence, appeasement displays always contain hostile elements, just as threat displays usually contain elements of fear. While Brown and Hunsperger (1963) criticized this concept on neurophysiological grounds, Blurton-Jones (1968) demonstrated that when Great Tits were exposed to an attack stimulus but simultaneously were prevented from attacking, the birds gave threat displays. If flutter and/or begging notes (or head-twisting in estrildines) are given when attack is inhibited, the inhibiting factor could be relatively strong fear (leading to appeasement displays), weaker fear (threat displays), hunger (fledgling demand behavior), or sex and/or hunger (female demand behavior at courtship feeding).

DISCUSSION

Major problems may arise in behavioral research from the misuse of a term associated with a particular phenomenon. It is always dangerous to apply a term with strong human social connotations to a behavior pattern observed in other animals without first carefully considering these connotations. The word "beg" is just such a term, implying in humans subservience and low rank. I suspect it is largely because of these implications that "begging" by both fledglings and females in courtship feeding has long been assumed to be submissive. Unfortunately, purely descriptive terms will not serve here because different displays may have the same function. For example, the head-twisting of estrildines is clearly equivalent to the "flutter display." The term "allofeeding" has already been applied to a different phenomenon. Since both females in the wild and hand-reared birds in captivity attack on occasion if not fed, the term "demand behavior" is perhaps the best compromise, since its connotations, while admittedly strong, more closely approximate the displays' apparent meaning.

Courtship feeding probably serves several functions at once. The frequent intra-pair contact involved in feeding probably serves to maintain and reinforce the pair-bond in many species. Courtship feeding

can also increase a female's fitness by augmenting her energy intake at a critical period of her annual cycle. However, it is clearly not an expression of a male's dominance over a female; indeed it is highly correlated with a female's dominance over a male. I strongly doubt that expression of dominance (regardless of direction) is an important function of courtship feeding. Nevertheless the very strength of the above correlation, and the absence of courtship feeding in species where the breeding male is dominant, suggest that expression of female dominance might occasionally be served by this behavior.

Courtship feeding is beneficial to the female and it can also increase the male's fitness, particularly if begun before egg-laying. While the eggs are developing within the female, courtship feeding is a male's most direct way to contribute to his own eggs' quality. In many monogamous species this contribution to egg quality could well be a major function of courtship feeding.

ACKNOWLEDGMENTS

The ideas presented here have been discussed with many people, including Jerome Jackson, Helen Lapham and Glen Woolfenden. I am especially grateful to Richard Lund for many profitable arguments, and to Millicent Ficken for her helpful suggestions on the manuscript.

LITERATURE CITED

- ANDREW, R. J. 1956. Begging responses of certain buntings. *Br. Birds* 48:107-111.
- ANDREW, R. J. 1957. The aggressive and courtship behaviour of certain emberizines. *Behaviour* 10:255-308.
- ANDREW, R. J. 1961. The displays given by passerines in courtship and reproductive fighting: a review. *Ibis* 103a:315-348, 549-579.
- ARMSTRONG, E. A. 1965. *Bird display and behaviour: an introduction to the study of bird psychology*. 2nd Ed., Dover, New York.
- BALDA, R. P., AND J. H. BALDA. 1978. The care of young Piñon Jays (*Gymnorhinus cyanocephalus*) and their integration into the flock. *J. Ornithol.* 119:146-171.
- BAPTISTA, L. F., AND A. D. ATWOOD. 1980. Agonistic behavior in the Java Finch (*Padda oryzivora*). *J. Ornithol.* 121:171-179.
- BENT, A. C. 1937, 1938. Life histories of North American birds of prey, parts 1 and 2. U.S. Natl. Mus., *Bulls.* 167, 170. (Reprinted by Dover, New York, 1961.)
- BERGER, A. J. 1968. Behavior of hand-reared Kirtland's Warblers. *Living Bird* 7:103-116.
- BLURTON-JONES, N. G. 1968. Observations and experiments on causation of threat displays of the Great Tit (*Parus major*). *Anim. Behav. Monogr.* 1:75-158.
- BROWN, J. L. 1963. Aggressiveness, dominance and social organization in the Steller Jay. *Condor* 65:460-484.
- BROWN, J. L. 1964. The integration of agonistic be-

- havior in the Steller Jay *Cyanocitta stelleri* (Gmelin). Univ. Calif. Publ. Zool. 60:223-328.
- BROWN, J. L., AND R. W. HUNSPERGER. 1963. Neuroethology and the motivation of agonistic behavior. Anim. Behav. 11:439-448.
- CALDER, W. A. 1967. Breeding behavior of the Roadrunner *Geococcyx californianus*. Auk 84:597-598.
- COLLIAS, E. C., AND N. E. COLLIAS. 1978. Nest building and nesting behaviour of the Sociable Weaver *Philetairus socius*. Ibis 120:1-15.
- COUTLEE, E. L. 1967. Agonistic behavior in the American Goldfinch. Wilson Bull. 79:89-109.
- CURIO, E. 1959. Verhaltensstudien am Trauerschnäpper. Z. Tierpsychol., Beih. 3, 118 S.
- DAVIES, N. B. 1977. Prey selection and the search strategy of the Spotted Flycatcher (*Muscicapa striata*): a field study on optimal foraging. Anim. Behav. 25:1016-1033.
- DILGER, W. C. 1960. Agonistic and social behavior of captive redpolls. Wilson Bull. 72:114-132.
- EARHART, C. M., AND N. K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. Condor 72:251-264.
- GOODWIN, D. 1951. Some aspects of the behaviour of the Jay *Garrulus glandarius*. Ibis 93:414-442, 602-625.
- HARDY, J. W. 1961. Studies in the behavior and phylogeny of certain New World jays (Garrulinae). Univ. Kansas Sci. Bull. 42:13-149.
- HINDE, R. A. 1952. The behaviour of the Great Tit (*Parus major*) and some other related species. Behaviour Suppl. 2:1-201.
- HINDE, R. A. 1955. A comparative study of the courtship of certain finches (Fringillidae). Ibis 97:706-745.
- HINDE, R. A. 1956. A comparative study of the courtship of certain finches (Fringillidae); continued. Ibis 98:1-23.
- HINDE, R. A. 1970. Animal behaviour: a synthesis of ethology and comparative psychology. 2nd Ed. McGraw-Hill, New York.
- KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Monogr. 22:1-356.
- KILHAM, L. 1971. Roosting habits of White-breasted Nuthatches. Condor 73:113-114.
- KILHAM, L. 1975. Breeding of Red-breasted Nuthatches in captivity. Avic. Mag. 81:144-147.
- KREBS, J. R. 1970. The efficiency of courtship feeding in the Blue Tit *Parus caeruleus*. Ibis 112:108-110.
- KRIEG, D. C. 1971. The behavioral patterns of the Eastern Bluebird (*Sialia sialis*). N.Y. State Mus. Bull. 415:1-139.
- LACK, D. 1940. Courtship feeding in birds. Auk 57:169-178.
- LACK, D. 1953. The life of the Robin. Penguin, London.
- LINSDALE, J. M. 1957. Goldfinches of the Hastings Natural History reservation. Am. Midl. Nat. 57:1-119.
- MACQUEEN, P. M. 1950. Territory and song in the Least Flycatcher. Wilson Bull. 62:195-205.
- MARLER, P. R. 1956. Behaviour of the Chaffinch, *Fringilla coelebs*. Behaviour Suppl. 5:1-184.
- MILLER, A. H. 1931. Systematic revision and natural history of the American shrikes (*Lanius*). Univ. Calif. Publ. Zool. 38:11-242.
- MOYNIHAN, M. 1955. Types of hostile display. Auk 72:247-259.
- NICE, M. M., AND R. H. THOMAS. 1948. A nesting of the Carolina Wren. Wilson Bull. 60:139-158.
- NOLAN, V., JR. 1958. Anticipatory food-bringing in the Prairie Warbler. Auk 75:263-278.
- ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee. 3. Auk 59:499-531.
- ORIAN, G. H., AND G. M. CHRISTMAN. 1968. A comparative study of the behavior of Red-winged, Tricolored, and Yellow-headed Blackbirds. Univ. Calif. Publ. Zool. 84:1-81.
- ORIAN, G. H., L. ERCKMANN, AND J. C. SCHULTZ. 1977. Nesting and other habits of the Bolivian Blackbird (*Oreopsar bolivianus*). Condor 79:250-256.
- REYNOLDS, R. T. 1972. Sexual dimorphism in Accipiter hawks: a new hypothesis. Condor 74:191-197.
- ROYAMA, T. 1966. A re-interpretation of courtship feeding. Bird Study 13:116-129.
- SAMSON, F. B. 1977. Social dominance in winter flocks of Cassin's Finch. Wilson Bull. 89:57-66.
- SMITH, S. M. 1973. An aggressive display and related behavior in the Loggerhead Shrike. Auk 90:287-298.
- SMITH, S. M. 1978. The "underworld" in a territorial sparrow: adaptive strategy for floaters. Am. Nat. 112:571-582.
- SMITH, S. M. 1980. Henpecked males: the general pattern in monogamy? J. Field Ornithol. 51:55-64.
- STOKES, A., AND H. WILLIAMS. 1971. Courtship feeding in gallinaceous birds. Auk 88:543-559.
- THOMPSON, W. L. 1960. Agonistic behavior in the House Finch. 2. Factors in aggressiveness and sociality. Condor 62:378-402.
- TORDOFF, H. B. 1954. Social organization and behavior in a flock of captive non-breeding Red Crossbills. Condor 56:346-358.
- WILLIAMS, L. 1952. Breeding behavior of the Brewer Blackbird. Condor 54:3-47.
- WILLIS, E. O. 1967. The behavior of Bicolored Antbirds. Univ. Calif. Publ. Zool. 79:1-127.
- WILLIS, E. O. 1968. Studies of the behavior of Lunalated and Salvin's antbirds. Condor 70:128-148.
- WILLIS, E. O. 1972. The behavior of Spotted Antbirds. Ornithol. Monogr. 10:1-162.
- WOOLFENDEN, G. E., AND J. W. FITZPATRICK. 1977. Dominance in the Florida Scrub Jay. Condor 79:1-12.
- ZAHAVI, A. 1971. The social behaviour of the White Wagtail *Motacilla alba alba* wintering in Israel. Ibis 113:203-211.

Department of Biological Sciences, Mount Holyoke College, South Hadley, Massachusetts 01075. Accepted for publication 31 August 1979.