

ANTICIPATORY FOOD-BRINGING IN THE
PRAIRIE WARBLER

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ALTHOUGH it is a commonplace that males of many species of birds feed females engaged in incubation, there are also occasional references (Hann, 1937; Sargent, 1940; Nice, 1943) to males whose behavior has suggested that they were carrying food not to their mates but to their anticipated nestlings, in eggs as yet unhatched. It remained for Skutch (1953) to provide an explanation which removes such premature solicitude from the category of the aberrational, and to suggest that impatience to feed young leads males of some species to make anticipatory visits to the nest with food; when only the female incubates, this behavior is useful in bringing about the male's prompt awareness of hatching and his early attention to the needs of nestlings. It is the purpose of this paper to describe and discuss 34 acts of anticipatory food-bringing by male Prairie Warblers (*Dendroica discolor discolor*), to review that and similar behavior attributed to other wood warblers, and to comment on the psychological basis of this food-bringing and its place in the evolution of what is believed to be related behavior.

METHOD AND LOCALITY OF STUDY

Study of the Prairie Warbler near Bloomington, Indiana, began in 1952 (Nolan, 1955). Nest life was investigated most intensively in 1956 and 1957, when dawn-to-dark observations of single nests were made on 25 occasions distributed among 12 nests of nine pairs, six of them color-banded. (I exclude watches at nests incubated by females which had been deserted by their mates and at nests at which incubation had either not yet been begun or had been completed.) The time-advance of incubation was known exactly in every case. Five of the 25 days were those on which young began to emerge from the eggs, "hatching days," and the remaining "incubation days" were divided, as evenly as predators permitted, among the first, a middle, and the last full day of the incubation period. Because events at the nest on hatching day are of particular interest and involve special inquiries, the five hatching days are for the most part given separate treatment herein.

PREVALENCE OF ANTICIPATORY FOOD-BRINGING

During the 25 all-day watches, anticipatory food-bringing was noted 20 times on incubation days and three times before the emergence of the first nestling on hatching days; in addition, 11 other instances were witnessed during briefer and less systematic watches conducted through-

out the study. Thirteen males were seen engaging in the behavior under discussion. The one male, of those whose nests were observed in day-long watches, that was never seen to take food to eggs was a bird whose nest was studied only once; and on that day he was feeding fledglings of a first brood while his second-brood eggs were being incubated. As will appear below, this was not the only all-day incubation watch during which a male brought no food, but all the males in the other cases performed the act on some earlier or later occasion.

Age of Males. Because nestling Prairie Warblers produced on the study area very rarely returned to breed there, I have no instance of anticipatory food-bringing by a bird of known age. However, other facts support the proposition that young males without previous experience in feeding nevertheless carry food in anticipation of young. Ten of the 13 males in which the behavior was seen had been under daily study from the times of their arrivals; nine quite certainly had had no earlier nests that season and hence had not fed nestlings during the same summers in which the anticipatory food-bringing was observed; one had fed young in an earlier nest. Data on longevity and on the annual turn-over among breeding adults are still incomplete, but they indicate the very great probability that some among these nine were one-year-olds whose "anticipation" cannot have been founded on the experience of feeding young. One male, studied in both 1956 and 1957, in the former year took food to eggs which ultimately produced fledglings. He did not carry to the eggs in his mate's first nest next year, on the first day of incubation, but 18 days later he did engage in food-bringing when the female began to incubate at the third nest.

ANTICIPATORY FOOD-BRINGING AND ITS RELATION TO ACTIVITY OF FEMALE

Only the female Prairie Warbler incubates, and her departures from the nest during incubation cannot be correlated with signal songs by the male or with other behavior by him. Except as described in this paper, in extensive field work throughout the Prairie Warbler's period on the breeding area, I have never seen a male feed a female or deliver food to her except manifestly to be relayed to nestlings. Rarely, if it is persistently rejected by them, the female will eat the food.

Anticipatory food-bringing occurs largely or wholly without regard to whether the female happens to be on her nest at the time. Of the 32 occasions when food was taken to an active nest, seven were during female inattentive periods. That is, she was incubating on 78.2 percent of the male's visits, a figure so close to the proportion of time spent covering eggs as to indicate that chance determines whether the female

will be present at her mate's arrival. The existence of a nest and eggs is, of course, part of the general situation in which the male's impulse to bring food rises to the level of action, but the eggs and even the nest may exist only in memory or in prospect. One male spent 30 seconds offering a caterpillar to the spot from which I had 24 hours earlier removed the nest, three hours after a snake had caused the female to desert. A second male persisted in thrusting a larva into a nest which had succumbed to a predator four or five hours beforehand.

Behavior of the male in anticipatory food-bringing varies little and does not differ from that preceding true feeding. A single item is brought, as is usually the case when newly hatched nestlings are fed. It is possible that food chosen is slightly larger than that given to very young birds; if this is true, perhaps the male must learn from experience what sizes are acceptable. Holding the food in his bill, he ordinarily announces his arrival by singing while still some 10 to 30 yards away. Song may be repeated for two or three minutes as he gradually draws closer, finally to light a foot or so from the nest. Hopping to the rim, he proffers the food, bending forward some five or six times and persisting for an average of 30 seconds or so. Occasionally he moves a few inches away, then returns once or twice to try again from a different perch. If the female is absent, his thrusts seem oriented toward the center of the cavity, probably toward the eggs resting there. Even if she is present, he only rarely extends the food toward her head or bill; more often, standing beside or behind her he tenders it to a spot occupied by the middle of her back, and I once thought he tried to poke it down between the side of the nest and his mate's wing. These male-female encounters at the nest are silent.

Disposition of the food is often difficult or impossible to observe, both because the male leaves rather suddenly and because his position on the rim may screen his head from view. In the absence of females, males ate the food at least four times and carried it away at least two. Females were seen to receive and eat food seven times, while on seven other occasions the males ate it or left with it when their mates were present. It is clear that acceptance by the female does not stimulate the male to further efforts. Although he may bring food more than once a day, occurrence of a second visit cannot be related to any observable peculiarity of the first.

Female reaction to anticipatory food-bringing, as the foregoing statements will have suggested, ordinarily appeared to be one of complete indifference. Frequently she never looked at the male, and even when she ate the food she took it only after lapses of as long as two minutes. Twice females returned to their nests shortly after males

arrived, but these cases may have been merely coincidental since in both the females had been away for normal inattentive periods. Each of three other reactions was observed once: A female rose in the nest as though to uncover the cavity, another got to the rim beside the male, and a third left the nest the instant he lit on the rim. All these are quite common forms of behavior after the eggs have hatched, so that it would seem that anticipatory food-bringing by the male is occasionally the stimulus for a suitable but equally anticipatory response by his mate. Indeed, her acceptance of the food may belong in this category, for much that the male brings to the nestlings is taken from him and distributed by the female.

TIME OF ANTICIPATORY FOOD-BRINGING

The incidence of the activity throughout the day is shown in Table 1, in which the Prairie Warbler's waking day has been divided into five intervals of three hours each, beginning at 0415 hours, central standard time, and ending 15 hours later at 1915. In column A are the 20 instances from the 20 incubation watches, while column B shows all 34 instances. The data in B are distorted by the unequal distribution of total field hours among different times of day. Both columns reveal a high proportion of anticipatory food-bringing in the three hours following dawn, when song and feeding of young are also at a peak, and column A indicates that food-bringing, like these latter activities, wanes from mid- or late morning until mid- or late afternoon. Seven acts were performed by one male and six each by two males; no pattern or schedule can be discerned in the timing of an individual bird's visits.

TABLE 1
HOURLY DISTRIBUTION OF ANTICIPATORY FOOD-BRINGING

	<i>A. All-day watches</i>	<i>B. All instances</i>
0415-0715	9	13
0715-1015	2	9
1015-1315	1	3
1315-1615	5	5
1615-1915	3	4

Of the 20 incubation day watches there were nine when anticipatory food-bringing occurred once during the day, four when it occurred twice, one three times, and six not at all. The single day on which there were three visits was one immediately preceding hatching, but nothing else suggests an increase as hatching approaches. There was no correlation between the dates and either the time of visits or their number.

The earliest all-day incubation watch was on May 10 and the latest on July 16. These were the extreme dates of incubation in 1956 and 1957 by females whose mates were still on territory; a deserted female incubated until July 18. Table 2, in which the "incubation season" has been divided arbitrarily into five periods of two weeks each, indicates that after an initial interval when it is rare or absent anticipatory food-bringing is performed with considerable regularity as long as the pair bond lasts. It will be recalled that I earlier excluded all incubation watches at nests deserted by the males. If four such watches between June 22 and July 18 were included in Table 2, it would then show a late season decline in food-bringing by the male population as a whole, corresponding to the general regression in reproductive activity that is observable at that time.

TABLE 2
DISTRIBUTION OF ANTICIPATORY FOOD-BRINGING BY DATE

	<i>Number of watches</i>	<i>Watches without food-bringing</i>
May 10–May 23	3	3
May 24–June 6	6	1
June 7–June 20	4	0
June 21–July 4	2	1
July 5–July 18	5	1

PSYCHOLOGICAL BASIS OF ANTICIPATORY FOOD-BRINGING

Before seeking a theoretical explanation for anticipatory food-bringing, the possible influence of three factors will be considered:

1) *Time-advance of the incubation period.* The stage of incubation appears to have little bearing on the occurrence of food-bringing. One male carried food to the nest on the day before the last egg was laid, i.e., before the female had settled down to regular attentiveness. Eight nests were watched throughout the first full day of incubation, and the males brought food to five of these. The three to which they did not were the three shown in Table 2 as falling in Period 1, so that the significant point was not time-advance but some factor more closely connected with progress of the season.

2) *Weather.* Within the extremes occurring during the study, weather cannot be established as affecting the behavior in question. A number of instances of food-bringing were seen on days of steady rain, and cloud cover and temperature were without perceptible influence. All the watches in Period 1, when anticipatory food-bringing was not witnessed, took place on sunny days. The lowest mean temperature on any of these three days was 60° and the highest 71°, while anticipatory food-bringing was seen on June 3, 1956, the mean tem-

perature of which was only 54°. The unimportance of temperature at the moment of carrying is confirmed by the high percentage of the acts during the early hours of the day.

3) *Level of male attentiveness.* It seems safe to conclude that anticipatory food-bringing is what it looks like, a manifestation of male attentiveness, and this makes relevant a general inquiry into the level of his attentive behavior in May. The best measure, before the eggs hatch, of the proportion of time devoted to activity associated with reproduction rather than to self-maintenance is the frequency and incidence of song throughout the day. Song counts of mated males reveal no significant differences in early, middle, and late May. Also, male interest in the nest-building by the female seems to reach full intensity at the very beginning of construction, at about the end of April.

It is clear that a fundamental explanation of, or theoretical basis for, anticipatory food-bringing must take account of facts and probabilities which may be summarized as follows: Most male Prairie Warblers, including those without previous breeding experience, carry food to incubated nests before there are young to eat it. They do this once or twice a day, seldom more often, from the beginning of incubation onward, at an hour which for any individual male cannot be predicted from day to day; and their performance is unaffected by whether the female is present or whether she accepts the food or rejects it. Anticipatory food-bringing occurs at all hours, its frequency following about the same curve as do song and other male attentive behavior, but it is rare or absent early in the nesting season despite other indications of a high intensity of reproductive drive at that time. Among males that remain mated, food-bringing is regular from late May until females cease to incubate in mid-July.

All these facts and probabilities assume order and coherence when viewed in the light of Lorenz' (1950) theory of action specific energy and vacuum activity, to which Skutch's (1953) "impatience" is presumably akin. It is not within my competence to examine the validity of the theory, and I propose only that it provides for anticipatory food-bringing a conceptual framework consistent with the facts observed by the field investigator. A recent statement of the Lorenzian view is taken from Thorpe (1956: 18-19): Given innate or instinctive fixed action patterns, there "tends to build up a kind of specific tension in the central nervous system, and if the animal does not find itself in the appropriate situation for the action pattern to be released, this specific action potential is, as it were, dammed up. The damming-up process results in a lowering of the threshold for the stimuli effective in releasing that particular action pattern. Indeed, if continued long

enough, the tension may accumulate to the point at which the action pattern goes off without any external stimulus at all, . . . giving rise to what is called vacuum activity. . . ." The specific readiness is reduced and may disappear when the consummatory act of the charged instinct takes place.

A chief merit of this explanation is that it accounts for the curious mixture of the unpredictable and the patterned, the random and the planned, that characterizes anticipatory food-bringing. It makes understandable the carrying of food to a nest no longer in existence (a more nearly perfect vacuum activity), and it becomes a matter of course that eggs of a second brood would receive no attention while fledglings are being fed.

PROBABLE FUNCTION AND VALUE OF THE BEHAVIOR

Five nests were studied on hatching day. It will be seen from Table 3 that at least three hours elapsed after the first nestling emerged before any male fed the young. While males 2 and 4 made anticipatory

TABLE 3
MALE FOOD-BRINGING ON HATCHING DAY

<i>Nest</i>	<i>Visits before hatching</i>	<i>Time of first hatching</i>	<i>Feedings</i>	<i>Minutes from hatching to first feeding or night</i>
1	0	1333	9	183
2	1	1425	0	300
3	0	0520	30	325
4	2	1022	0	528
5	0	before 0400	15	598

visits early in the day, they failed to feed during the five and nearly nine hours, respectively, that remained between hatching and the females' retirement at night. During the nine hours at nest 4 the female made 30 trips with food, some of it quite surely gathered and carried while her mate was looking toward her. Contrast the events at nest 3: In five and one-half hours following hatching the female fed young six times. At 10:45 the male first brought food, which a nestling accepted. The male immediately darted away a few feet but returned to the rim to look into the nest for five seconds. Again he started to leave and again returned. He then flew 10 yards away, caught an insect, and promptly delivered it to a nestling. Once more he did this, so quickly that he had fed three times within one and one-half minutes of his first appearance at the nest. In the 15 minutes beginning with the first feeding, six trips with food were made, and between the first feeding and dark this male fed 29 times. The story told by the events at nests 1 and 5 is somewhat less dramatic but it differs only in degree.

Data from these five nests seem to give almost conclusive support to the statement that anticipatory food-bringing is a device by which the male Prairie Warbler learns of the hatching of the eggs. Although he occasionally goes to the nest without food and sometimes accompanies his mate more or less closely on her return at the end of an inattentive period, these activities (which occur without reference to the stage of incubation) do not together equal anticipatory food-bringing in their frequency; and it seems probable that they are, at most, relatively unimportant means of discovery. I have seen nothing to suggest an attempt by the female to communicate the fact of hatching and certainly have witnessed nothing to raise an inference that the male was responding either to a signal or to the female's food-carrying.

The advantages of early discovery and participation in the care of nestlings may be presumed to be the same as the advantages accruing to those altricial species in which the male helps feed the young, as opposed to those in which he does not help. Brood sizes can be larger, and since the female can rely at least to some extent on the male to feed the nestlings while she shelters or warms them, more rigorous weather can be endured.

That anticipatory food-bringing helps confer these benefits on the Prairie Warbler is indicated by a comparison of additional data gathered at nest 1, where the male was quick to assist his mate, and at nest 4, where he fed no sooner than about mid-day on the day after hatching day. Hatching days at these two nests were within one day of being a year apart, and weather conditions at the relevant times were indistinguishable. There was a difference of only nine inches in nest heights, but nest 1 was exposed to direct sunlight in the early afternoon, while nest 4 was in shadow all day. Table 4 shows to what extent and by which parent the nestling requirements of food and shelter were met at nests 1 and 4. The degree of protection from the weather is presented by standard attentive and inattentive data on brooding, modified only in that the first attentive period, during which the initial hatching occurred, is taken as having begun at the time of hatching and not at the time the female returned to the nest. To derive the rate of feeding per young on a day when the number of young undergoes change as the result of successive hatchings, I have used the unit "nestling minutes." This term designates the aggregate of the numbers of minutes between the time each egg hatched and the time at which the female went to the nest to brood for the night. The rate of feeding is determined by dividing the nestling minutes by the number of feedings. No differences were detected in the quantity or quality of items per feeding, and those factors are assumed to have been constant.

TABLE 4
SATISFACTION OF REQUIREMENTS OF NEWLY-HATCHED YOUNG

	<i>Nest 1, 4 young, in sun, male feeding</i>	<i>Nest 4, 3 young, in shade, male not feeding</i>
Minutes from first hatching till night	329	528
Attentive periods	14	29
average length, minutes	20.4	14
extremes, minutes	113-1	39-4
percent of total time	86.9	76.9
Inattentive periods	14	29
average length, minutes	3.1	4.2
extremes, minutes	10-1	14-1
percent of total time	13.1	23.1
Nestling minutes	558	727
Feedings by female	12	30
Feedings by male	9	0
Rate of feeding per nestling	26.5	24.2

It is apparent from Table 4 that female 1 gave shelter to her young during 10 percent more of the first hours of their lives than did female 4, and this without sacrificing their food needs, which male 1 helped satisfy. The difference in time on the nest was accounted for by an uninterrupted interval of nearly two hours during which female 1 stood over the cavity and shaded her eggs and her first nestling from the direct rays of the mid-June sun. As it happened, the location of female 4's nest was such that she did not confront the necessity of choosing between shelter and food, nor is it clear what limitations are imposed on that choice by the nestlings' constitutions. However, exposure to direct sun, to rain, and to cool temperatures would be quite common risks for young in many Prairie Warbler nests near Bloomington, if the male's attentiveness did not afford the female a certain latitude to adjust her own behavior to guard against these dangers.

Consideration of the events at nests 1 and 4 during four and one-half hours on the first morning after hatching day is equally revealing. The two females spent nearly identical percentages of time on the nests. Female 4, still unassisted, fed 15 times and female 1, 13. But because male 1 made 11 trips with food, the nestlings in nest 1 were fed at a rate of once every 45 minutes while those in nest 4 averaged once each 54 minutes. The significance of this comparative slowness in female 4's feeding rate per bird will assume its true proportion when it is emphasized that she had only three young to feed, while in spite of their greater number (four) the nestlings in nest 1 were each getting more to eat.

Lest the advantages to the Prairie Warbler of the male's assisting in feeding be overestimated, it is acknowledged that heat and shelter become decreasingly significant as the nestling period advances. Further, there is good evidence that an unassisted female is well able to supply the food requirements of her young. As an example, a male and female made a combined total of 82 trips to feed three nestlings during their ninth day of life, while three days later at a nest a few hundred yards away a female deserted by her mate fed three nine-day-old young 98 times. No appreciable differences in kind or quantity of food were noted, and both broods succeeded. Finally, in weighing the advantages of anticipatory food-bringing, its effect on the Brown-headed Cowbird (*Molothrus ater*) must be considered. The cowbird was a frequent brood parasite on the study area, and its egg or eggs invariably hatched before those of this host. I have seen male warblers feeding cowbird nestlings before their own eggs had hatched, and this doubtless contributed to the usual quick starvation of the young warblers.

FOOD-BRINGING AND RELATED BEHAVIOR IN MALES OF OTHER WARBLERS

The Appendix discloses that in addition to the Prairie Warbler male wood warblers of 20 species from 11 of the 25 genera in the family have been recorded as feeding the female, or carrying food to the nest, prior to the hatching of eggs. Nine of the 17 North American genera are represented on the list, and eight of the 17 North American species in the tabulation belong to the genus *Dendroica*. Included as a "species" is a hybrid male *Vermivora pinus* x *chrysoptera*. Also counted is the Kentucky Warbler (*Oporornis formosus*), in which feeding has been seen performed only by a second or "helper" male.

Although Lack (1940) and Armstrong (1947) state that species are rare in which the delivery of food to females occurs only during incubation, no more than four of the wood warblers have been said to engage in courtship as opposed to incubation feeding. Mousley (1928) in many hours of observation at a number of Parula Warbler (*Parula americana*) nests once saw a male feed a female as she built. The male Olive Warbler (*Peucedramus taeniatus*) feeds his mate occasionally during nest-building and incubation (Willard, 1910; Skutch, in Griscom and Sprunt, 1957). Skutch reported that the male Buff-rumped Warbler (*Basileuterus fulvicauda*) delivers food during courtship (1953), although in his subsequent life history of that species (1954) and in his most recent publication on it (in Griscom and Sprunt, 1957) he has spoken only of incubation feeding. Courtship feeding may occur occasionally in the Yellow Warbler (*Dendroica petechia*), a spe-

cies in which also feeding of the female on the nest is highly developed. Linsdale (1938: 120) saw a female Yellow Warbler "twittering and waving its wings," after which the male apparently fed her. Not far away was a nest with three eggs, to which a fourth was added next day. Since the female Yellow Warbler sometimes begins to incubate before the last egg is laid (Smith, 1943; Kendeigh, 1952), and since Mousley (1926) in one instance saw a male feed his mate as she came off the nest late in the incubation period, Linsdale's observation does not fit neatly into either the category of courtship or that of incubation feeding.

Eighteen male wood warblers have been reported to feed the females during incubation, as shown in the Appendix. In most cases the act takes place at the nest and probably not so frequently as to furnish the female with much sustenance, but there are important exceptions to both of these generalizations. The male Yellow Warbler brings food in such quantity that his mate's attentive behavior has been modified, and she has been found to cover the eggs 91.9 percent of the time (Kendeigh, 1952). The Bay-breasted (*Dendroica castanea*), occasionally the Yellow, and perhaps the Chestnut-sided (*D. pensylvanica*) females receive food from the males away from the nest (as well as on it), as does the Kirtland's Warbler (*D. kirtlandii*). In the last species the female ordinarily leaves to accept the food, fluttering her wings like a young bird as she takes it; as incubation progresses the male sometimes feeds her on the nest (Van Tyne *in* Bent, 1953).

Anticipatory food-bringing has been recognized as such (Skutch, 1953; 1954; *in* Griscom and Sprunt, 1957) only in the Buff-rumped, Pink-headed (*Ergaticus versicolor*), and Crescent-chested Warblers (*Vermivora superciliosa*) (but query the sufficiency of the reported evidence in the last species). Hann (1937) tells of several instances of premature food-bringing by a male Ovenbird (*Seiurus aurocapillus*), but the female was in the nest and the disposition of the items was not seen. In addition to these species, anticipatory visits may well have been mistaken for incubation feeding when seen only once or twice in the warblers listed in the Appendix as incubation feeders. One case is especially interesting: Sturm (1945: 197) reports a male American Redstart (*Setophaga ruticilla*) which fed the female on the nest 15 times, from one to three times a day. "More frequently, however, the female reacted to the male differently when he came to the nest with food. On twenty-six occasions she flew away at his approach. He did not remain long at the nest after she left, but ate the food and flew away." The fact that all the visits were initiated while the female was on the nest requires explanation, but it is not necessarily inconsistent with the probability that the male was anticipating his nestlings.

The difficulty of distinguishing, on the basis of a few observations, between occasional or casual feeding of the female and the premature bringing of food for young calls attention to the point, noted by Skutch (1953), that these two activities are alike in function. It seems probable that they are part of the same development, and that anticipatory food-bringing is the earlier stage in evolution. Perpetuated because it readies the male to feed young, his premature visit can, with no additional drain on his energies, acquire further value if the female eats the food he brings. This occasional incubation feeding cannot make any great contribution to the female's nourishment, and its force in maintaining the bond between the pair can only be conjectured. It is, however, a plastic bit of behavioral material which the forces of selection can mold. In the Yellow Warbler it is the physical or nutritional aspect of the feeding which appears to have become important, a fact which is objectively measurable. On the other hand, in species in which feeding during incubation has been dissociated from the nest so that the female is given food although she is free to gather it for herself, it would seem that the act has acquired a more imponderable function, presumably associated with the stability of the pair. This "symbolic" content might be expected to become more pronounced in further development; once feeding has been disengaged from the nest, its projection back to an earlier stage of the reproductive cycle in which there is no nest seems but a step.

Certainly the behavior of the wood warblers lends no support to the belief that "courtship feeding did not arise from the habit of feeding the incubating mate but vice versa" (Armstrong, 1947: 44). Lack (1940: 174) has pointed out that courtship feeding "has almost certainly originated several times independently," and he and Noble and Wurm (1943) have proposed a sequence in which parental behavior is the basis from which some courtship feeding evolved. Do not the views presented in this paper suggest the answer, for some species, to Lack's question—why, in courtship feeding, is it the male that almost invariably feeds the female?

It is unnecessary to propose, as Mrs. Nice (1941) reports G. Steinbacher (Ber. Verein Schles. Ornith., 23: 42–64, 1938) to have done, that the *function* of courtship feeding is to prepare the male to feed nestlings, but on the evidence of the wood warblers it seems probable that anticipatory food-bringing, which does so function, was one of the *origins* of courtship feeding.

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SUMMARY

The male Prairie Warbler carries food from one to three times a day throughout the incubation period, taking it to the nest without regard to whether the female is present and apparently deriving no satisfaction if she accepts it, as she sometimes does. Analysis of 34 such acts by 13 males indicates that food-bringing is probably performed by first-year as well as older birds, is not affected by normal extremes of weather, is most frequent in the early morning and late afternoon, and is rare or absent during the first two weeks of the species' nesting period.

Observations at five nests on the hatching day tend to prove that the male is unaware of hatching until he makes a food-bringing visit and that the behavior therefore functions to bring about the discovery and prompt feeding of the young by the male. Comparison of events at a nest at which the male discovered his young quickly and at a nest at which he did not suggests that his early assistance in feeding permits the female to adjust her brooding schedule to weather conditions without sacrificing the nourishment of the nestlings. In favorable weather the advantage takes the form of a more rapid feeding rate, which should be conducive to the raising of larger broods.

Anticipatory food-bringing is regarded as a vacuum activity within the theory of Lorenz. A review of the 20 other species of wood warblers in which the male is reported to carry food or to feed the female before there are nestlings leads to the view that incubation feeding in this family has evolved from anticipatory food-bringing and that courtship feeding in three or four Parulids is but a later stage in evolutionary development.

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APPENDIX

OTHER PARULIDS IN WHICH MALES FEED FEMALES OR CARRY FOOD

<i>Species</i>	<i>Kind of feeding and place</i>	<i>Authority</i>
Prothonotary Warbler	Incubation, on nest	Walkinshaw (1938; 1953; <i>in Bent</i> , 1953; in Griscom and Sprunt, 1957)
<i>Protonotaria citrea</i>		
Hybrid, "Brewster's" Warbler	Incubation, on nest	Carter (1944)
<i>Vermivora pinus x chrysoptera</i>		
Nashville Warbler	Incubation, on nest	Knight (1908); Bent (1953)
<i>Vermivora ruficapilla</i>		
Crescent-cheated (Hartlaub's) Warbler	Anticipatory, to nest	Skutch (1953; 1954)
<i>Vermivora superciliosa</i>		
Parula Warbler	Courtship, at nest during building	Mousley (1928)
<i>Parula americana</i>		
Olive Warbler	Courtship, away from nest during building; incubation, on nest	Willard (1910); Skutch (<i>in</i> Griscom and Sprunt, 1957)
<i>Peucedramus taeniatus</i>	Courtship (?), away from nest	Linsdale (1938)
Yellow Warbler	Incubation, on and off nest	Mousley (1926)
<i>Dendroica petechia</i>	Incubation, on nest	Gabrielson (1922); Schrantz (1943); Kendeigh (1952); Bent (1953)
Black-throated Blue Warbler	Incubation, on nest	Harding (1931)
<i>Dendroica caerulescens</i>		
Blackburnian Warbler	Incubation, on nest	Lawrence (1953)
<i>Dendroica fusca</i>		
Chestnut-sided Warbler	Incubation, place not clear	Sawyer (1947)
<i>Dendroica pensylvanica</i>		

<i>Species</i>	<i>Kind of feeding and place</i>	<i>Authority</i>
Bay-breasted Warbler <i>Dendroica castanea</i>	Incubation, on and off nest Incubation, on nest	Oberholser (<i>in</i> Griscom and Sprunt, 1957) Stanwood (1909); Mendall (1937); Bent (1953) Gross (<i>in</i> Bent, 1953)
Blackpoll Warbler <i>Dendroica striata</i>	Incubation, on nest	Nice (1931)
Pine Warbler <i>Dendroica pinus</i>	Incubation, on and off nest	Van Tyne (<i>in</i> Bent, 1953; <i>in</i> Griscom and Sprunt, 1957)
Kirtland's Warbler <i>Dendroica kirtlandii</i>	Anticipatory or incubation, on nest Incubation, on nest	Hann (1937) Gross (<i>in</i> Bent, 1953)
Ovenbird <i>Seiurus aurocapillus</i>	Incubation, on nest	De Garis (1936)
Kentucky Warbler <i>Oporornis formosus</i>	Incubation, on nest	Gross (<i>in</i> Bent, 1953)
Yellowthroat <i>Geothlypis trichas</i>	Anticipatory or incubation, on nest Incubation, on nest	Sturm (1945) Gabrielson (1922); Baker (1944); Gross (<i>in</i> Bent, 1953); Cruickshank (<i>in</i> Griscom and Sprunt, 1957)
American Redstart <i>Setophaga ruticilla</i>	Anticipatory and incubation, on nest	Skutch (1953; 1954; <i>in</i> Griscom and Sprunt, 1957)
Pink-headed Warbler <i>Ergaticus versicolor</i>	Courtship; anticipatory and incubation, on nest	Skutch (1953)
Buff-rumped Warbler <i>Basileuterus fulviceauda</i>	Anticipatory, to nest; incubation, on and off nest	Skutch (1954; <i>in</i> Griscom and Sprunt, 1957)