

2-21-2001

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ON THE RARITY OF FOOD PROVISIONING BY MALE DICKCISSELS --

Males of polygynous bird species typically provide less parental care to their offspring than males of monogamous species (Ketterson and Nolan 1994). Generally, in polygynous species, a male forfeits some potential reproductive success if he shifts his reproductive effort from mating with multiple females to parental care (Trivers 1972, Gubernick et al. 1993, Schleicher et al. 1993). In the polygynous dickcissel (*Spiza americana*), singing and foraging activities constitute much of a male's time-activity budget (Schartz and Zimmerman 1971, Finck 1984). Although male dickcissels are attentive to their nests and mates (e.g., nest protection and vigilance) females incubate the eggs and feed the young (Gross 1921). Herein, we describe an account of a male dickcissel feeding brown-headed cowbird (*Molothrus ater*) young early in the breeding season, summarize and review previous reports of food provisioning by the male dickcissel, and discuss the rarity of this behavior in the dickcissel.

Our observations were made during a study of dickcissels in alfalfa (*Medicago sativa*) fields in Adair County, Iowa. Adair County is located near the center of the species' breeding range, where nest initiation typically begins in mid-May (Frawley 1989, Igl 1991). In Iowa alfalfa fields, dickcissels abandon their territories immediately or within a few days after mowing (Frawley 1989, Igl 1991), although a few males or breeding pairs associated with field edges remain after mowing. Most males associated with Iowa alfalfa fields were monogamous or bachelors at the time of mowing, and less than 5% of the population mated polygynously (Frawley 1989; Igl, unpubl. data). The low incidence of polygyny in alfalfa fields is likely related to the timing and frequency of mowing, which abbreviated the amount of time available for males to obtain additional mates. Fields that were mowed later in the haying cycle generally had more females, fewer bachelor males, and more cases of polygyny (Igl, unpubl. data).

Of 150 male dickcissels observed during our study in 1988 and 1989 (Igl 1991), only one was seen provisioning food to young. On 9 June 1988 we observed a color-banded monogamous male dickcissel carrying an adult dragonfly to a nest and feeding two seven-day-old brown-headed cowbird nestlings. The vegetation (primarily alfalfa) in the male's territory had been mowed on 8 June except for a small, unaltered strip of roadside vegetation where the nest was located. Less than 24 hr after mowing, the male discontinued singing and began assisting his mate in feeding the brown-headed cowbird young. All other dickcissels abandoned this field after mowing, and no males were heard or seen in the immediate vicinity of this male's territory. The male continued to assist his mate in feeding the brown-headed cowbird young for the remainder of the nestling period and after they fledged on 10 June, until the female and fledglings disappeared from the area on 18 June. Incidental to other research activities, we observed the male provisioning food (primarily Lepidoptera larvae and Orthoptera) to the young brown-headed cowbirds at least 69 different times from 9 to 17 June. Although not quantified, the frequency of food deliveries seemed to be similar between

the male and female. On 19 June the male resumed singing until he abandoned his territory on 24 June.

Published observations of male dickcissels feeding young are rare and mostly anecdotal (Table 1). Recipients of male food provisioning included nestlings, fledglings, and, in one case (Wilhelm 1994), adult females. In some cases, the transfer of food was assumed to have occurred but was not observed. Most previously reported instances occurred later in the breeding season than our observation; 18 of the 20 known observations occurred at the end of June or later. The number of mates was rarely reported or known; Wilhelm (1994) observed food provisioning by a polygynous male. Six cases of food provisioning by male dickcissels occurred near the northern edge (Wisconsin) or outside (Massachusetts, Pennsylvania, and South Carolina) of the species' typical breeding range (Table 1). Finck (1984) reported that male dickcissels in Kansas spent less than 1% (three occurrences) of their total time-activity budget feeding young, and he observed this behavior only late in the breeding season and only in weedy oldfield habitats. In a similar time-activity study in Kansas, Schartz and Zimmerman (1971) did not observe this paternal behavior. In grassland fields enrolled in the Conservation Reserve Program in east-central Illinois, Maddox and Bollinger (2000) observed eight different males feeding young and found that males made 42% of the feeding trips to six male-assisted nests.

Verner and Willson (1966) suggested that the probability of male dickcissels obtaining additional mates late in the breeding season is extremely low, and it would be more advantageous to devote time to rearing young rather than advertising for additional females. At the time, Verner and Willson based their suggestion on only two known observations (Purdie 1878, Bellrose 1936). Nonetheless, their explanation is consistent with the more recent late-season observations of male dickcissels feeding young (Table 1). The explanation of Verner and Willson (1966) also parallels the observations of Beletsky et al. (1989) that only a few polygynous male red-winged blackbirds (*Agelaius phoeniceus*) fed nestlings or fledglings, and then only during the last few weeks of the breeding season.

Although involving brown-headed cowbird young and occurring earlier in the season than most other reported cases of food provisioning in the male dickcissel (Table 1), our observation is qualitatively consistent with Verner and Willson's (1966) explanation of this behavior. Factors related to a severe drought in 1988 may have influenced this early paternal care in the dickcissel. Dickcissels are well known for their erratic annual shifts in distribution and abundance on the breeding grounds, especially in years of severe drought (e.g., Taber 1947, Emlen and Wiens 1965, Sealy 1976, McNair 1990b). Poor vegetation regrowth reduced nesting opportunities and precluded dickcissels from recolonizing alfalfa fields after mowing in 1988 (Mulvihill 1989, Igl 1991). Conditions, thus, resembled those at the end of the breeding season because fewer females were present and mating opportunities likely were reduced (*sensu* Webster 1991, Whittingham 1994). Similar conditions may exist along the

Table 1. Observations of male dickcissels provisioning food to young.

Date	No. males exhibiting behavior	Recipient	Location	Habitat	Reference
9-18 June	1	Nestling/fledgling ^a	Iowa	Alfalfa/road right-of-way	Igl and Best (our study)
10 June	1	Nestling ^b	South Carolina	<i>Lespedeza</i> pasture	McNair (1990a, pers. comm.)
Late June	1	Nestling ^c	Massachusetts	Oldfield	F. E. Bean (pers. comm. in Purdie 1878)
26 June-22 July	8	Nestling	Illinois	Conservation Reserve Program field (planted grassland cover)	Maddox and Bollinger (2000)
7 July	1	Nestling ^d	Kansas	Oldfield	Zimmerman (1966, pers. comm.)
14-25 July	3	Nestling/fledgling ^e	Wisconsin	Oldfield and tame pasture	G. D. Basili (pers. comm.)
17-30 July	1	Fledgling/female ^f	Pennsylvania	Oldfield	Wilhelm (1994)

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Table 1 Cont.

Date	No. males exhibiting behavior	Recipient	Location	Habitat	Reference
Late July-early August	3	Nestling/fledgling	Kansas	Oldfield	Finck (1984, pers. comm.)
28 August-4 September	1	Unknown ^g	Illinois	Hemp (<i>Cannabis sativa</i>)	Bellrose (1936, pers. comm.)

^a Male and female observed feeding two brown-headed cowbird young; food transfer was observed.

^b One monogamous male was observed carrying food to a well-concealed nest four times when the female was present at the nest and once when the female was not present at the nest; food transfer was not observed.

^c Both adults were observed feeding nestlings.

^d One male was observed carrying food to a well-concealed nest; food transfer was not observed.

^e One male was observed carrying food to fledglings in an oldfield but food transfer was not observed; one male was observed feeding a fledgling in an oldfield; and one male in a pasture was flushed from a nest containing 9- to 10-day old nestlings, but food transfer was not observed.

^f One male was repeatedly observed carrying food to three fledglings in dense undergrowth; the same male also was observed copulating with two different females and provisioning food to two adult females late in the breeding season.

^g Two dickcissels were observed carrying food for several days into a hemp field and were assumed to be feeding young; the nest was never found, but a fledgling with weak flight capabilities was observed on 4 September.

periphery or outside of the species' breeding range, where six of the 20 known cases (including four of the nine locations) of food provisioning by male dickcissels occurred (Table 1). Fretwell and Calver (1970) showed that female dickcissels are uncommon and many males are unmated near the edge of the species' breeding range. The only other early-season observation of a male dickcissel provisioning food to young also occurred in 1988 but in South Carolina (McNair 1990a), well outside the species' typical breeding range (Table 1).

Maddox and Bollinger (2000) observed several male dickcissels provisioning food to nestlings during a year when several nests apparently failed due to starvation, but they did not observe this behavior in the following year when all nests found in the same grassland fields successfully fledged at least one nestling. Maddox and Bollinger concluded that male dickcissels fed nestlings in the former year to offset limited food resources. Reduced food availability, due to drought or mowing, also may have influenced the level of paternal care that we observed. In the nest we observed, one five-day-old brown-headed cowbird and one four-day-old dickcissel nestling died on 7 June, probably of starvation. The strategy of selective paternal care, conditional upon food availability, has been documented in other polygynous species. For example, in red-winged blackbirds, Whittingham and Robertson (1994) found that greater food availability was associated with reduced importance of paternal care to offspring survival. Similarly, Wittenberger (1982) noted that male bobolinks (*Dolichonyx oryzivorus*) allocated more time to feeding nestlings when food was scarce and prevailing weather conditions were poor.

We report the only observation of a male dickcissel feeding brown-headed cowbird young (Table 1). In the central Great Plains, dickcissel nests commonly experience high rates of brood parasitism by the brown-headed cowbird (Zimmerman 1983, Frawley 1989, Basili 1997). Brown-headed cowbird young have vigorous begging vocalizations, which have been shown to result in a higher frequency of parental food delivery to parasitized nests (Dearborn et al. 1998). Although aggressive begging by the brown-headed cowbird young might have, in part, been a factor in food provisioning by this male dickcissel, the nestlings' begging behavior and the male's parental care also might have been influenced by a shortage of food (see above) and the nestlings' hunger level. In general, nestlings change their begging behavior in relation to changes in hunger level; hungry nestlings beg more often and are fed more often (Smith and Montgomerie 1991).

Although dickcissels are considered a tallgrass prairie species, and others have studied their breeding ecology in tallgrass prairie habitat (Petersen 1978, Zimmerman 1982, Finck 1984), male provisioning of food to young has never been reported in tallgrass prairie (Table 1). Why might this occur? One explanation is that habitat type or quality may influence or interact with factors, such as food or mate availability, that influence food provisioning by the male dickcissel. For example, male food provisioning has been reported in oldfield habitats by several observers. Some authors

have found that dickcissels prefer oldfield habitats over native tallgrass prairie (Petersen 1978, Zimmerman 1982, Finck 1984). Zimmerman (1982) and Finck (1984) found that dickcissels initiated nests earlier and nesting spanned a longer season in oldfield habitats than in prairies. Thus, more active nests might be present in oldfield habitats late in the breeding season when this behavior is most commonly observed. Similarly, more active dickcissel nests might be present at the edge or outside of the species' breeding range late in the breeding season. Spring arrival (Mulvihill 1989) and nest initiation (Basili 1997) generally occur later at the northern edge or outside of the dickcissel's breeding range than in the core of the species' breeding range.

Whether it was a single factor (e.g., monogamy, reduced nesting opportunities, food abundance, brood parasitism, or habitat type) or a combination of factors that resulted in the observed cases of male dickcissels feeding young, the rarity of this behavior in the dickcissel indicates that food provisioning by males usually is not crucial for raising young. Observations of selective paternal care in the dickcissel and in other typically polygynous species (e.g., bobolink and red-winged blackbird) demonstrate the behavioral flexibility that allows some males to place proportionately more reproductive effort in parental care and less in other activities (e.g., advertising for additional mates, territory defense, or mate guarding) when environmental or ecological conditions dictate. The paucity of observations of food provisioning by male dickcissels, however, makes it difficult to assess whether this behavior is an adaptation to ensure adequate care of their offspring or whether it is a newly developing or vestigial behavior (*sensu* Lorenzana and Sealy 1998). Moreover, we cannot rule out that the apparent rarity of this behavior in the dickcissel reflects that fewer observers may be present when (i.e., late in the breeding season) or where (e.g., oldfield habitats) this behavior is most prevalent. Clearly, more detailed field observations are required to improve our understanding of the function, process, and benefit of food provisioning by the male dickcissel. Experimental approaches also are needed to elucidate the role of factors, such as mating opportunities or food availability, in determining the likelihood of food provisioning by male dickcissels.

We thank G. D. Basili (University of Wisconsin, Madison, Wisconsin), F. C. Bellrose (Illinois Natural History Survey, Havana, Illinois), E. J. Finck (Emporia State University, Emporia, Kansas), D. B. McNair (Havana, Florida), and J. L. Zimmerman (Kansas State University, Manhattan, Kansas) for providing information concerning their observations of dickcissel paternal care and for reviewing an earlier draft of our manuscript. B. M. Ballard, E. K. Bollinger, D. H. Johnson, P. J. Pietz, M. A. Sovada, and M. Winter also provided constructive reviews. Financial support for our research was provided by Sigma Xi, Wilson Ornithological Society, American Museum of Natural History, Association of Field Ornithologists, Max McGraw Wildlife Foundation, and Wisconsin Society for Ornithology. Our paper is Journal Paper J-16618 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa (Project No. 2168). -- *Lawrence D. Igl and Louis B. Best, 124 Science II, Department*

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