

PROVISIONING OF NESTLINGS BY MALE AND FEMALE YELLOW-BREASTED CHATS

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ABSTRACT.—Observations of parental feeding roles were made at 19 Yellow-breasted Chat (*Icteria virens*) nests during the 1994 breeding season in central Kentucky. Male and female chats fed nestlings at similar rates, and adult feeding rates were unaffected by brood size. The absence of any change in feeding rates with increased brood size suggests that food requirements per nestling decrease as brood size increases, perhaps because of differences in thermoregulatory costs. In contrast to the results of many other studies, provisioning rates and load sizes (number of prey delivered per visit) did not increase with nestling age. However, our observations at chat nests did not begin until nestlings were 3 or 4 days old. Studies of other species have revealed that 1–3 day old nestlings may be visited less frequently and provided with smaller loads than older nestlings, and observations of nestling chats during this early period might have revealed similar behavior. Received 2 Aug. 1996, accepted 30 April 1998.

Among altricial birds, the behavior of parents providing food for nestlings may be influenced by several factors. For example, differences in brood size and nestling age may contribute to changes in feeding rates or the size and type of prey delivered to nestlings. However, previous work has revealed interspecific differences in how parents respond to changes in these and other factors. For example, adult Bachman's Sparrows (*Aimophila aestivalis*) make more feeding visits to large broods than to small broods (Haggerty 1992), but adult Field Sparrows (*Spizella pusilla*) do not (Best 1977). Previous studies have also revealed interspecific differences in the respective roles of males and females in provisioning nestlings. In some species, males and females provision nestlings at similar rates [e.g., Northern Mockingbird (*Mimus polyglottos*), Breitwisch et al. 1986] while, in other species, either males [e.g., Gray Catbird (*Dumetella carolinensis*), Johnson and Best 1982] or females [e.g., Eastern Bluebird (*Sialia sialis*), Pinkowski 1978] may deliver food at higher rates. The reasons for such interspecific variation in parental provisioning behavior remain unclear. Additional studies can help elucidate those factors contributing to such interspecific variation (Haggerty 1992).

Most Yellow-breasted Chats (*Icteria virens*) are socially monogamous (Thompson and Nolan 1973; Schadd and Ritchison, pers. observ.)

and, at least in the southern parts of their range, double-brooded. Males arrive on the breeding grounds several days before the females. Chats generally build nests 0.6–1.8 m above the ground in dense vegetation (Harrison 1975). Females typically lay three to five eggs and the incubation period is about 11 days (Bent 1953, Harrison 1975). Young fledge 8–11 days after hatching (Bent 1953; Schadd and Ritchison, pers. obs.). Currently, little is known about the parental behavior of Yellow-breasted Chats. The objectives of our study were to (1) quantify the parental behavior of adult chats, (2) compare the roles of males and females in caring for nestlings, and (3) examine the effects of brood size and nestling age on parental provisioning behavior.

STUDY AREA AND METHODS

Chats were studied at the Central Kentucky Wildlife Management Area, located 17 km southeast of Richmond, Madison Co., Kentucky. Beginning in late April 1994, male chats were captured by placing mist nets in known territories or by luring them into mist nets using playback of chat songs. Females were captured by placing mist nets in known territories or, later in the season, by placing mist nets near nests. Captured chats were banded with a numbered aluminum band plus a unique combination of colored leg bands. Beginning in early May, females were monitored for signs of nesting, such as carrying nesting material. If not located during nest building, nests were located by observing the behavior of adults or by checking likely nest sites.

From 3 June through 26 July 1994, observations of adults and nestlings were made at 19 nests using camcorders. To ensure that adults would not abandon nests, videotaping at nests did not begin until nestlings were at least 3 days old. Observation periods (i.e., taping

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sessions) were 2–6 hours in duration, with most taping conducted during the period from 06:00 to 12:00.

For each parental visit to a nest, we determined the sex of the parent using either the amount of black on the bill [males typically have completely black bills while females have varying amounts of gray in their bills (Ritchison, unpubl. data)] or the colored leg bands. We also noted the number, size, and type (adult or larval insect) of prey brought to the nest. Prey sizes were categorized as small (less than or equal to the length of the parent's beak), medium (greater than the length of the parent's beak to twice that length), or large (greater than twice the parent's beak length).

Because multiple observations were made of each nest, we used repeated measures ANOVA (Beal and Khamis 1990). To examine possible differences in the sizes of prey delivered to broods of different sizes or nestlings of different ages, analyses were conducted using weighted sums. For each observation period, we determined the number of prey in each size category (small, medium, and large) delivered by adults and then multiplied the number of small prey delivered by one, the number of medium prey by two, and the number of large prey by three. The sum of these products was divided by total observation time and the resulting rates were then subjected to analysis. Possible variation in the types of prey fed to nestlings (adult insects versus larvae) was examined using the ratio of adult to larval insects delivered during each observation period. All statistical analyses were conducted using the Statistical Analysis System (SAS Institute 1989). All values are presented as mean $\pm$ one standard error.

RESULTS

Each chat nest ($n = 19$) was videotaped over an average of 3.2 days. Overall, these nests were videotaped for 260 h ($\bar{x} = 13.7$ h/nest; range = 4–24 h/nest), and during this time adult chats made 711 feeding visits ($\bar{x} = 37.4$ visits/nest; range = 11–69). At 14 nests, both adults fed the young, while at five nests, only one adult fed the nestlings. At four of these nests ($\bar{x} = 14.3$ hours of videotaping/nest), the male made all recorded visits, while the female made all recorded visits at one nest (24 hours of videotaping).

Young fledged from 16 of 19 chat nests (84.2%). The mean number of young fledged from successful nests was 3.25 ± 0.17 . Nests at which both parents were observed feeding nestlings fledged more ($z = 2.16$, $P = 0.031$) young ($\bar{x} = 3.14 \pm 0.29$) than did nests where only one adult was observed feeding nestlings ($\bar{x} = 1.52 \pm 0.68$). Young fledged at 13 of 14 nests with both parents providing care and at 3 of 5 nests where only one parent was observed providing care, and this difference was

not significant (Fisher's exact test: $P > 0.05$). Nestlings at all three unsuccessful nests appeared to be healthy and were apparently lost to predators [a black rat snake (*Elaphe obsoleta*) was video-taped preying upon nestlings at one of these nests].

Adult chats delivered food to nestlings an average of 2.56 ± 0.16 times/h ($n = 62$ observation periods). After arrival at a nest, the mean time until adults fed a nestling was 3.69 ± 0.27 sec ($n = 701$). The mean number of prey items brought to nests by adults during each visit was 1.52 ± 0.02 ($n = 711$ visits), and adults never brought more than three items. The most common prey size was medium (56.8% or $n = 602$ of 1061). Small prey accounted for 15.8% ($n = 168$) of prey items, and large prey 27.4% ($n = 291$). Most prey brought to the nest were adult insects ($n = 601$ or 56.7%), while 43.3% ($n = 459$) were larval insects.

Only female chats brooded nestlings, and the frequency of brooding by females declined with increasing nestling age. Females brooded 3 and 4 day old nestlings during 45% of all nest visits ($n = 88$), and this frequency declined to 22% for 5 and 6 day old nestlings ($n = 129$) and 21% for 7 and 8 day old nestlings ($n = 120$).

Males vs females.—We found no differences ($F_{1,18} = 0.7$, $P > 0.05$) between the feeding rates of females ($\bar{x} = 1.24 \pm 0.14$ feedings/h; $n = 62$ observation periods) and males ($\bar{x} = 1.32 \pm 0.12$ feedings/h). Similarly, males and females did not differ in the mean number of prey brought to the nest per visit ($F_{1,14} = 0.0$, $P > 0.05$), with males averaging 1.50 ± 0.03 ($n = 373$) and females 1.54 ± 0.03 ($n = 338$) prey per visit. We also found no difference in the size of prey delivered by males and females ($F_{1,18} = 0.32$, $P > 0.05$). Both males and females brought primarily medium-sized prey to the nest (55% and 59% of prey items, respectively). In addition, males and females did not differ in the ratio of adult to larval insects brought to the nest ($F_{1,12} = 2.25$, $P > 0.05$).

Effect of brood size.—Brood size had no effect on parental feeding rates ($F_{2,19} = 0.18$, $P > 0.05$). Chats also exhibited no differences in the number of prey delivered per visit to broods of different sizes ($F_{2,20} = 1.78$, $P > 0.05$), with adults delivering an average of

1.42 ± 0.05 items/visit ($n = 113$) to broods of two, 1.47 ± 0.03 items/visit ($n = 406$) to broods of three, and 1.68 ± 0.04 items/visit ($n = 192$) to broods of four. Similarly, we found no difference in the size of prey brought to different sized broods ($F_{2,19} = 0.44$, $P > 0.05$). There was, however, a difference in the ratio of adult to larval prey brought to different-sized broods ($F_{2,19} = 4.62$, $P = 0.023$).

Effect of nestling age.—The feeding rates of adult chats did not vary with nestling age ($F_{5,26} = 1.72$, $P > 0.05$). Similarly, the number of prey items delivered per visit ($F_{5,26} = 1.44$, $P > 0.05$) and the size of prey delivered ($F_{5,26} = 0.73$, $P > 0.05$) did not differ with nestling age. For all ages, the most frequent prey size was medium. For size of prey delivered, there was a significant interaction between brood size and nestling age ($F_{9,18} = 2.31$, $P = 0.046$). However, examination of our data revealed that this interaction resulted from one unusual observation period at one nest. During one 6 h observation period at this nest (with a 7-day old brood of 4), adults (male and female combined) made only five visits and delivered primarily small prey items. The reason for this atypical behavior was unclear.

The ratio of adult to larval insects delivered to nestlings varied with nestling age ($F_{5,24} = 3.22$, $P = 0.023$), and there was a significant interaction between brood size and nestling age ($F_{9,24} = 2.55$, $P = 0.032$). Significance in these cases (as well as the significant difference in adult-to-larvae ratios among brood sizes noted previously) was due to the atypical provisioning behavior of two chats. Each of these two chats (a female with an 8-day old brood of 4 and a male with a 3-day old brood of 4) delivered an atypical number of adult insects to their nestlings during a single observation period. The female delivered 19 adult insects (and just one larva) during one observation, while, also during one observation, the male delivered 13 adult insects (and just one larva). The reason for the unusually high adult-to-larvae ratios during these two observation periods (ratios for other observations never exceeded 3.4) was unknown.

DISCUSSION

Reasons for the apparent absence of parental care by one parent at five nests are unclear. At two of the nests where the adult female

was not observed feeding young, the female was not observed during the period of videotaping and, therefore, may have deserted or been killed by a predator. However, the non-feeding adult was known to be present in three of these territories. It is possible that these non-feeding chats were simply more wary than their mates and only refrained from feeding young when camcorders were present. It is also possible that, for unknown reasons, a single adult was responsible for most or all provisioning of the young at these nests. Nestling success (young fledged/nest) was lower at chat nests where only one adult appeared to be provisioning nestlings. Bart and Tornes (1989) summarized the results of 15 studies in which adult males were temporarily removed during the nestling period and concluded that, for many species, male removal results in decreased survival of young. Our results, and those of other investigators, indicate that biparental care may improve reproductive success and, as a result, may be an important factor in the maintenance of socially monogamous mating systems (e.g., Leffelaar and Robertson 1986, Lyon et al. 1987).

Males vs females.—Male and female Yellow-breasted Chats fed nestlings at similar rates and brought similar numbers of prey items of similar size with each nest visit. Similar behavior has been reported in several other species (Best 1977, Knapton 1984, Breitwisch et al. 1986, Leffelaar and Robertson 1986, Lyon et al. 1987, Smith et al. 1988, Dittami et al. 1991, Haggerty 1992). In other passerines, females (Nolan 1978, Pinkowski 1978, Howe 1979) or males (Biermann and Sealy 1982, Johnson and Best 1982) provide more food.

The reasons for these differences among socially monogamous species are not clearly understood (Breitwisch et al. 1986). At least two factors may contribute to variation in levels of male parental care and, more specifically, to the relatively high levels of parental care exhibited by male chats. First, opportunities to engage in extra-pair copulations vary among populations and species and males may seek copulations with other females according to the costs and benefits of provisioning his own offspring (Birkhead and Møller 1992). Consequently, if male parental care is important, a male should spend more effort on parental

duties than on the acquisition of additional copulations (Birkhead and Møller 1992).

Second, the population sex ratio may dramatically influence levels of male parental care (Breitwisch et al. 1986). For example, if the sex ratio is male-biased, males probably have little opportunity to change mates or acquire additional females. As a result, females may demand a level of parental care greater than males would give if they could obtain additional mates (Breitwisch et al. 1986). In contrast, if the breeding adult sex ratio is unity or female-biased, males might be able to decrease their level of parental care with no decrease in fitness. This could occur because females might compensate for a reduced level of male parental care or the rate of weight gain by nestlings might decrease very little, and young would fledge at only slightly lighter weights. In both cases, males may not experience a reduction in fitness (Breitwisch et al. 1986).

Effect of brood size.—Feeding rates of adult chats did not vary with brood size. As a result, each nestling in broods of two was fed more frequently than those in broods of three or four. Similar results have been reported in Eastern Bluebirds (Pinkowski 1978), Nashville Warblers (*Vermivora ruficapilla*; Knapton 1984), Western Bluebirds (*Sialia mexicana*; With and Balda 1990), and Northern Mockingbirds (Breitwisch et al. 1986). Although adults could potentially compensate by bringing more prey per visit or larger prey to larger broods (Biermann and Sealy 1982, Haggerty 1992), our results indicate that adult chats did not do so. Similar observations have been reported in Gray Catbirds (Johnson and Best 1982), Nashville Warblers (Knapton 1984), and Northern Mockingbirds (Breitwisch et al. 1986). Thus, in chats as in several other species, individual nestlings in larger broods apparently receive less food than those in smaller broods. Such results suggest either that nestlings in larger broods grow more slowly and, perhaps, weigh less at fledging or, if not, that food requirements per nestling decrease as brood size increases. Although limited, our data suggest that nestling mass does not vary significantly with brood size. [We found no significant difference ($z = 0.3$, $P > 0.05$) in mass between nestlings in broods of three ($\bar{x} = 15.38 \pm 0.70$ g; $n = 5$ broods) and

broods of four ($\bar{x} = 15.18 \pm 0.76$ g; $n = 3$ broods) at five days post-hatching.] Thus, it appears that food requirements per nestling may decrease with increasing brood size. This has been suggested for other species (Best 1977, Walsh 1978, Pinkowski 1978, Johnson and Best 1982) and may be the result of differences in thermoregulatory costs. That is, the ratio of exposed surface area to biomass decreases with increasing brood size, resulting in lower thermoregulatory costs per nestling (Royama 1966, Mertens 1969, Seel 1969).

Effect of nestling age.—The feeding rates of adult chats did not vary with nestling age. In addition, the number of prey items delivered per visit and the type of prey (adult vs larval insects) delivered to nestling chats were not affected by nestling age. In contrast, several investigators have reported that parental feeding rates (Pinkowski 1978, Walsh 1978, Biermann and Sealy 1982, Breitwisch et al. 1986) and the volume of food delivered per visit (Johnson and Best 1982, Breitwisch et al. 1986, Haggerty 1992) increased with increasing nestling age. Previous workers also have noted that recently hatched nestlings may receive different prey than older nestlings, with younger nestlings receiving more larvae than older nestlings (Pinkowski 1978, Grundel and Dahlsten 1991). For example, Haggerty (1992) reported that 0–2 day old nestling Bachman's Sparrows received more lepidopteran larvae than did older nestlings.

In summary, our decision to delay observations until nestling chats were at least 3 days old (and 4 days old at some nests) may be the reason for the absence of changes in the provisioning behavior of adult chats with increasing nestling age. Several investigators have reported that young nestlings (1–3 days old) are visited less frequently and are provided with smaller loads than older nestlings (Bedard and Meunier 1983, Leffelaar and Robertson 1986, Haggerty 1992), and observations of nestling chats during this early period might have revealed similar behavior.

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