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EFFECTS OF FOOD SUPPLEMENTATION ON FEMALE NEST ATTENTIVENESS AND INCUBATION MATE FEEDING IN TWO SYMPATRIC WREN SPECIES

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ABSTRACT.—We examined effects of incubation mate feeding on female incubation behavior and correlates of fitness by providing female Bewick's Wrens (*Thryomanes bewickii*) and House Wrens (*Troglodytes aedon*) with food supplements. Males of these species vary in their rates of feeding; Bewick's Wrens feed their incubating mates frequently, whereas House Wrens seldom engage in this behavior. Average length of incubation bout and nest attentiveness (proportion of time spent on the nest) were higher for supplemented female Bewick's Wrens and House Wrens compared to controls. Furthermore, mates of supplemented Bewick's Wrens provisioned females at lower rates than controls, and their rate of feeding was inversely correlated with ambient temperature. Incubation length and hatching success were not significantly different between treatments for either species. These results suggest that incubation mate feeding can increase female nest attentiveness and perhaps enhance fitness of both males and females. In House Wrens, potential tradeoffs between the benefits of parental care and opportunities to obtain additional mates may explain why males rarely feed incubating females. *Received 1 July 2003, accepted 15 March 2004.*

In species that exhibit parental care, there is often a division of labor between sexes, with one sex primarily attending the nest. Consequently, trade-offs between offspring development and survival versus parental condition can exist if nest attentiveness is constrained by parental food limitation (Royama 1966). Food brought to the attending adult by the nonattending mate may ameliorate food limitation, and thus, offset these trade-offs (Smith et al. 1989). Feeding of incubating females by mates occurs in more than 40% of North American passerines (Kendeigh 1952) and is most pronounced in cavity nesters. Nonetheless, considerable variation in the rate of incubation mate feeding exists (Martin and Ghalambor 1999).

Traditionally, incubation feeding was thought to maintain the pair bond between mates (Lack 1940, Kluyver 1950, Andrew 1961) or represent a premature attempt by males to feed nestlings (Skutch 1953, Nolan 1958, Ricklefs 1974, Johnson and Kermott 1992). Both of these hypotheses have been challenged, and it has been suggested that food delivered to females constitutes an essential nutritional contribution (i.e., the food limitation hypothesis; von Haartman 1958, Royama 1966, Krebs 1970, Smith 1980, Nilsson and Smith 1988).

Experimental tests of the potential adaptive benefit of incubation feeding (in terms of female attentiveness and hatching success) are relatively rare (e.g., Nilsson and Smith 1988, Moreno 1989, Smith et al. 1989). In this study, we examined effects of food supplements on female incubation behavior and correlates of fitness in two sympatric, secondary cavity-nesting species, Bewick's Wren (*Thryomanes bewickii*) and House Wren (*Troglodytes aedon*). Incubation mate feeding is common in Bewick's Wrens (Miller 1941), whereas male House Wrens rarely feed their mates during incubation (Johnson and Kermott 1992). We increased food available to incubating females by providing food supplements inside nest boxes (Nilsson and Smith 1988, Smith et al. 1989). This allowed females to have sole access to food without leaving nest cavities, simulating incubation feeding. If mate feeding constitutes an important contribution to females, we predicted that food supplements would enhance nest attentiveness. If additional food enhances female attentiveness, hatching success should increase and duration

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of incubation should be reduced at supplemented nests relative to controls. If males do monitor female attentiveness, we also predicted they would adjust their rates of mate feeding accordingly and reduce their rate of incubation feeding to highly attentive females provided with food supplements (Smith et al. 1989).

METHODS

Study area and species.—We conducted this study from early April through late August 1997 at the Konza Prairie Biological Station, 10 km south of Manhattan, Kansas (see Zimmerman 1993 for site description). We monitored 152 nest boxes along gallery forests, attenuated gallery forests, and rock-outcrop shrub communities of Konza (Kennedy and White 1996).

Bewick's Wrens are common summer residents and occasional winter residents of the attenuated gallery forest (Zimmerman 1993). In Kansas, Bewick's Wrens are double-brooded; first nests are initiated in early April and second nests are initiated in late May (Farley 1987). Bewick's Wrens are socially monogamous with only a few suspected cases of polygyny; mean clutch size for this population is 6.1 eggs (Kennedy and White 1997). Only female Bewick's Wrens incubate eggs, but males feed their incubating mates and assist in feeding nestlings (Miller 1941).

House Wrens are common summer residents of Konza, using both gallery and attenuated gallery forests (Zimmerman 1993). They are double-brooded, initiating first nests in early May and second nests in late June. House Wrens are considered socially monogamous (Johnson 1998), but the percentage of males that attract secondary females can be as high as 14% in some populations (Soukup and Thompson 1997a). Mean clutch size of first broods is 6.2 eggs, slightly larger than second broods (5.9 eggs; E. D. Kennedy pers. comm.). Only females incubate, but males generally assist in feeding nestlings. The rate of incubation feeding in a Wyoming population of House Wrens was found to be extremely low (0.2 feedings/hr; Johnson and Kermott 1992), but there are few data on this behavior for other populations.

General procedures.—We checked all nest boxes once weekly from early April until late July to determine clutch initiation dates. Active nests were then visited every 1–2 days to determine presence and number of eggs or nestlings. Initiation of incubation was determined by egg temperature (warm versus cold) and female behavior. Near the expected hatch dates, nests were visited daily to determine hatch date and hatching success.

Food supplementation experiment.—All nests discovered during egg laying were randomly allocated to either food supplemented or control treatments. Nests allocated to the food supplementation treatment were supplied with 15 g of live mealworm larvae (*Tenebrio molitor*) every day (06:00–10:00 CST) during incubation. This amount of food was chosen based on the estimate that a 10.6 g wren expends ~61 kJ/day (Dykstra and Karasov 1993). Assuming that the energy content of mealworms is 11.59 kJ/g (calculated from Bell 1990) and a wren's assimilation efficiency of mealworms is 0.65 (Kacelnik 1984), a female would need to consume 8.2 g of mealworms to satisfy daily energy requirements. Therefore, a 15-g supplement represents a substantial energy contribution to incubating females. Food supplements were placed in plastic feeding dishes (35 mm film canisters; diameter 3.33 cm, height 4.75 cm) hung inside nest boxes above the nest rim (cf. Nilsson and Smith 1988). This allowed us to simulate male provisioning at the nest entrance and enabled the female to obtain food without leaving the nest cavity.

In most cases, mealworms delivered to nests were consumed before our next visit. If food remained in the canister, dead larvae were removed and replaced with fresh larvae. Videotaped observations revealed that three female House Wrens occasionally removed mealworms from their nest box (see also Johnson and Kermott 1992). This behavior was never observed at Bewick's Wren nests. It is unclear whether these female House Wrens consumed larvae outside their nest boxes or removed them without consuming them. Thus, we performed two exploratory analyses when comparing the effects of treatment on House Wrens, one using all nests and the second excluding data from nests where females removed mealworms. Because the results were similar, we present combined data.

To identify the importance of food availability to female nest attentiveness, incubation behavior was monitored for 2–4 hr per nest from 07:00 to 12:00 by battery-operated video cameras. Each nest was recorded twice: once during early incubation (incubation day 1–6) and once during late incubation (incubation day 7–12). We observed nests twice to increase observation time and reduce effects of potential anomalous observations. Sampling early and late also allowed us to test whether nest attentiveness changed during the incubation period. Tripods were placed 5–10 m from a nest box one day before taping to acclimate adults to the disturbance. From recordings we determined average length of incubation bout (time inside the nest box), average length of recess bout (time outside the nest box), female nest attentiveness (proportion of time inside the nest box), and frequency of mate feedings at the nest. Because videotaped observations were used, we could not determine the number of mate feedings that may have occurred away from the nest site, out of camera range. It should be noted, however, that in some populations the frequency of House Wren mate feedings away from the nest is extremely low (Johnson and Kermott 1992). The extent to which Bewick's Wren males may feed females away from the nest is not known. Temperature at time of taping was obtained from hourly data recorded at a weather station located at the Konza headquarters.

Data analysis.—All statistical analyses were performed using the Statistical Analysis System (SAS Institute, Inc. 1999). Comparisons of clutch size and clutch initiation between food-supplemented and control nests for each species were performed using *t*-tests (PROC TTEST). Correlations between temperature at the time of observation and female nest attentiveness (both species) and male feeding rate (Bewick's Wrens only) were calculated using PROC CORR.

Four dependant variables describing incubation behavior were analyzed in the food supplementation experiment: lengths of incubation and recess bouts, nest attentiveness, and mate-feeding rate. Mean incubation- and recess-bout lengths were calculated for each videotape session by dividing incubation- and recess-bout lengths by the number of incubation and recess bouts taken, respectively. Female nest attentiveness was defined as the proportion of time the female spent in the nest box. Mate-feeding rate (feedings/hr; Bewick's Wrens only) was calculated by dividing the frequency of mate feedings for a videotape session by the total time. We did not calculate mate-feeding rate for House Wren males because we only observed three instances of this behavior during our videotape sessions. All behavioral response variables were analyzed using repeated measures ANOVA, with food supplementation as the independent variable of interest and species as a blocking variable. Repeated measures ANOVA was used to account for correlation between multiple nest observations of a single nest (PROC MIXED). Least-squared (LS) means and associated *P*-values were obtained using the LSMEANS statement and PDIFF option. Temperature at the time of taping was used as a covariate in the analysis of mate-feeding rate because a significant correlation was found both in our and other studies (Nilsson and Smith 1988, Smith et al. 1989, Halupka 1994). Differences between early and late incubation behavior were analyzed by species using paired *t*-tests (PROC UNIVARIATE).

Two dependant variables correlated with fitness—incubation length and hatching success—were analyzed to determine whether food supplementation potentially increased fitness. Incubation length (INCL) was calculated using hatch date (HD), clutch size (CS), and clutch initiation date (CID):

$$\mathrm{INCL} = \mathrm{HD} - [\mathrm{CID} + (\mathrm{CS} - 1)].$$

Analysis of variance was used to examine differences in incubation length with the same independent variables as described above (PROC MIXED). Hatching success was analyzed using a generalized linear mixed model approach, which is equivalent to a mixed model logistic regression (GLIMMIX Macro; Wolfinger and O'Connell 1993). The success or failure of individual eggs from successful nests (one or more eggs hatched) were response variables, and nests were considered a cluster sample because responses of individual eggs within a nest may be correlated. Standard errors of hatching success were calculated using the Delta method from standard errors computed on the logit scale (Littell et al. 1996).

TABLE 1. Least-square means of incubation behavior of Bewick's Wrens (BW) and House Wrens (HW) that were, or were not, supplied with additional food, northeast Kansas, summer 1997.

		Food supplemented			Control		
Species	Variable	n^a	$\bar{x}$	SE	n^a	$\bar{x}$	SE
BW	Incubation bout[b]		51.56	6.89		35.33	6.16
	Recess bout[c]	12	9.77	1.70	15	12.77	1.52
	Nest attentiveness[d]		0.82	0.04		0.70	0.04
HW	Incubation bout[b]		30.21	5.97		13.15	6.16
	Recess bout[c]	16	4.78	1.47	15	5.43	1.52
	Nest attentiveness[d]		0.81	0.04		0.71	0.04

[a] Number of videotape sessions.
[b] Average amount of time females spent in the nest box without leaving (min).
[c] Average of time females spent out of the nest box before returning (min).
[d] Proportion of time females spent in the nest box.

Male House Wrens without food were observed visiting nest boxes of their mates. We calculated total visits by Bewick's Wren and House Wren males (total visits = feeding trips + nonfeeding trips) and compared total visits of the two species at control nests using repeated measures ANOVA (PROC MIXED). An alpha value of 0.05 was selected to determine significant differences for all tests.

RESULTS

We observed 15 Bewick's Wren nests (7 food supplemented, 8 control) for 53.4 hr, and 17 House Wren nests (9 food supplemented, 8 control) for 64 hr. Neither clutch size nor date of clutch initiation (mean difference, 95% CI) differed between supplemented and control Bewick's Wren nests [clutch size: 0.13 eggs (−1.37, 1.63); clutch initiation date: −2.5 days (−23, 18)]. Similar results were observed for supplemented versus control House Wren nests [clutch size: 0.28 eggs (−0.63, 1.19); clutch initiation date: 2 days (−14, 18)]. No differences were detected between early and late incubation behavior for either species ($P \geq 0.25$).

Temperature was not correlated with female nest attentiveness for either species (Bewick's Wren: $r = 0.16$, $P = 0.42$; House Wren: $r = 0.03$, $P = 0.86$), but was negatively correlated with feeding rates of male Bewick's Wrens ($r = -0.66$ $P < 0.001$). Consequently, temperature was used as a covariate in the analysis of feeding rate. No significant correlation was found between Bewick's Wren mate-feeding rate and female nest attentiveness ($r = -0.23$, $P = 0.24$).

Food-supplemented females had significantly longer average incubation bouts ($F_{1,\ 28} = 6.97$, $P = 0.013$) compared to females in control nests (Bewick's Wren, $P = 0.090$; House Wren, $P = 0.057$; Table 1). Average length of recess bout was not significantly different ($F_{1,\ 28} = 1.38$, $P = 0.25$) between supplemented and control nests (Bewick's Wren, $P = 0.20$; House Wren, $P = 0.76$; Table 1). Female Bewick's and House wrens were 18 and 14% (respectively) more attentive to their nest when food-supplemented compared to control females ($F_{1,\ 28} = 8.55$, $P = 0.007$; Bewick's Wren, $P = 0.034$: House Wren, $P = 0.068$; Table 1). Male Bewick's Wrens made an average of 1.1 fewer mate feedings/hr to food-supplemented females compared to control females ($F_{1,\ 13} = 5.06$, $P = 0.042$; Fig. 1A). Furthermore, male Bewick's Wrens made 0.162 more mate feedings/hr for every 1° C drop in ambient temperature ($F_{1,\ 11} = 21.92$, $P < 0.001$). Experimental food supplementation did not explain variation in incubation length ($F_{1,\ 22} = 0.52$, $P = 0.48$; Bewick's Wren, $P = 0.28$; House Wren, $P = 0.93$; Table 2) or hatching success ($F_{1,\ 22} = 0.70$, $P = 0.41$; Bewick's Wren, $P = 0.59$; House Wren, $P = 0.52$; Table 2).

Male House Wrens from control nests made an average of 1.88 (SE = 0.48) total visits/hr to their nest box during our videotape sessions. This did not differ from the average rate of total visits for Bewick's Wren [1.56 (SE = 0.50) total visits/hr; $F_{1,\ 14} = 0.17$, $P = 0.68$; Fig. 1B].

DISCUSSION

The results of our study support the food limitation hypothesis: food provided to incu-

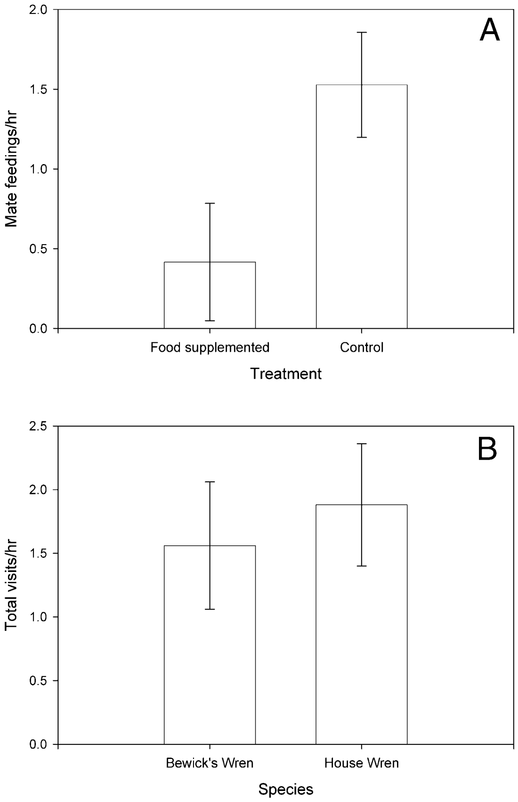

FIG. 1. (A) Feeding rate (feedings/hr ± 1 SE) of male Bewick's Wrens at food-supplemented and control (no food supplementation) nests during incubation, adjusted using ANCOVA for a mean ambient temperature of 16.78° C. (B) Total visit rate (feedings + nonfeedings/hr ± 1 SE) of male Bewick's Wrens and House Wrens at control nests.

bating females affects their parental effort. Additional food provided to females increased average length of incubation bout and nest attentiveness, suggesting that nest attentiveness is partially determined by the amount of energy available to the female. Our study supports the results of Smith et al. (1989), who found that nest attentiveness in Pied Flycatchers (*Ficedula hypoleuca*, a species that exhibits mate-feeding behavior) was greater when females were provisioned with additional food.

Bewick's Wren males adjusted rates of incubation feeding to supplemented females: females provided with additional food were fed less often than females not receiving food supplements. Smith et al. (1989) also reported lower male feeding rates to food-provisioned female Pied Flycatchers. Additionally, higher rates of mate feeding in Bewick's Wren males were observed as ambient temperature decreased. This response also has been observed in other species exhibiting incubation feeding (Nilsson and Smith 1988, Smith et al. 1989, Halupka 1994). Our results suggest that provisioning incubating females is costly to male Bewick's Wrens and that they regulate their rate of feeding depending on female nest attentiveness and nutritional state.

Providing adult females of either species with additional food did not result in significant reductions in length of incubation period or in increased hatching success relative to controls, although in Bewick's Wrens there was a trend toward a shorter incubation period for supplemented females (Table 2). Other researchers have documented that mate feeding during incubation can influence these variables (Lyon and Montgomerie 1985, Nilsson and Smith 1988). Averaging 2 years of data (17 nests), Nilsson and Smith (1988) reported significantly earlier hatching (18.9 hr) in food-provisioned Blue Tit (*Parus caeruleus*) nests than in controls. We were unable to measure time of hatching with such precision, but after

TABLE 2. Least-square means of incubation length and hatching success of Bewick's Wrens (BW) and House Wrens (HW) that were supplied with additional food, or not, in northeast Kansas in summer 1997.

		Food supplemented			Control		
Species	Variable	n^a	$\bar{x}$	SE	n^a	$\bar{x}$	SE
BW	Incubation length[b]	6	12.83	0.77	7	14.00	0.71
	Hatching success[c]		0.78	0.15		0.74	0.13
HW	Incubation length[b]	7	11.67	0.77	6	11.57	0.71
	Hatching success[c]		0.96	0.16		0.82	0.10

[a] Sample size of nests used in each analysis.
[b] Days of incubation needed to hatch a clutch.
[c] Proportion of successfully hatched eggs.

converting our data to hours, we found that hatching was 28 hr earlier in supplemented Bewick's Wren nests than in control nests. Although hatching success was not significantly different between treatment and control nests, it was greater for both species when given additional food: 0.20 and 0.95 additional eggs hatched in food-provisioned Bewick's and House wren nests, respectively. In Blue Tits, Nilsson and Smith (1988) found a significant increase (6.5%) in hatching success among food-provisioned nests. Even though we did not detect a statistical difference in hatching success, at a population level this observed difference might be of ecological importance. Furthermore, if our study had been conducted in years with poor food availability or cooler temperatures, fitness benefits of additional food might have been more apparent (the long term mean temperature for Manhattan, Kansas for May through July 1897–1994, was 18.3°, 23.7°, and 26.6° C; mean temperatures for May through July 1997 were 16.8°, 24.0°, and 27.3° C).

Enhancing nest attentiveness through incubation mate feeding could have other benefits (other than reduced incubation length or increased hatching success), such as serving to reduce intra- and interspecific nest destruction. Nest guarding has been shown to reduce nest predation in other species (Simons 1988, Cavitt 1998), and time available for guarding can be limited by food availability (Cavitt 1998). Thus, if nest destruction by House Wrens is an important source of nest loss for Bewick's Wrens, increased nest attentiveness may further enhance fitness by reducing the probability of nest destruction by House Wrens. Kennedy and White (1996) reported that the percent of failed Bewick's Wren nests caused by House Wrens on our site in other years ranged from 33 to 100%. During our study, however, House Wrens destroyed only one Bewick's Wren nest; thus, we could not test this hypothesis with our data. The nest-destruction hypothesis does not explain the lack of incubation feeding observed in House Wrens, because they are also vulnerable to nest destruction by conspecifics (Johnson 1998). Yet, House Wrens may use other strategies, such as the coordination of nest-guarding activities (Ziolkowski et al. 1997), to reduce nest destruction by conspecifics.

If providing additional food to female House Wrens can enhance nest attentiveness and, potentially, male fitness, why don't males feed their incubating mates more frequently? Several hypotheses have been proposed to explain the lack of incubation mate feeding (Moreno 1989, Johnson and Kermott 1992). The predation hypothesis (Lyon and Montgomerie 1987) proposes that species with a greater risk of nest predation should have lower rates of incubation feeding than species with lower predation risks, because increased trips to the nest may attract attention of predators and increase predation risk (Skutch 1949; Martin 1992, 1996). In fact, incubation feeding rates in a suite of coexisting species was inversely correlated with predation rate (Martin and Ghalambor 1999). Predation is not a likely explanation in the Konza population because we commonly observed male House Wrens visiting their nests during the incubation period without delivering food. Total number of visits made by House Wren males was not significantly different from the total number of trips made by male Bewick's Wrens (Fig. 1B). Thus, the occurrence of non-feeding visits by male House Wrens is not consistent with the nest predation hypothesis.

An alternative explanation for the difference between male House Wrens and Bewick's Wrens is that although food provided to the female is beneficial, other activities may provide greater gains in male fitness (Lifjeld and Slagsvold 1986, Lifjeld et al. 1987). Male House Wrens might, for example, increase fitness by seeking extra-pair copulations and attracting additional mates. Johnson and Kermott (1992) discounted this hypothesis because mate-feeding rates did not differ significantly between males that attempted to attract additional mates and those that did not. However, because House Wren incubation feeding rates are extremely low and variable, detecting any significant difference between males that vary in this behavior would be difficult. Male House Wrens frequently invest time and energy intruding onto adjacent territories (2.02 ± 0.41 intrusions/hr) to obtain extra-pair copulations (Johnson and Kermott 1989). In an Illinois population of House Wrens, Soukup and Thompson (1997b) found a high rate of extra-pair paternity (~27% of all nests sampled) and documented that approximately

14% of males were polygynous. Thus, other activities may enhance fitness of male House Wrens more than improving female attentiveness via mate feeding.

Our results demonstrate that food provided by males to incubating females can be an important factor influencing nest attentiveness and may enhance fitness. The disparity in male mate-feeding rates between these species most likely reflects differences in benefits to male fitness. The ability to maintain high levels of nest attentiveness may have a great effect on the fitness of male Bewick's Wrens because House Wrens are important nest predators. In contrast, benefits of increased nest attentiveness to the fitness of male House Wrens may be outweighed by the benefits of participation in other activities, such as extrapair copulations and polygamous mating.

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