

MASS LOSS IN BREEDING HOUSE WRENS: EFFECTS OF FOOD SUPPLEMENTS

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Abstract. Adult passerines commonly lose mass during the course of the breeding cycle. This loss has been ascribed to an energy deficit incurred during nesting, but recently two adaptational hypotheses have been proposed. The first, the wing-loading hypothesis, proposes that adults actively reduce mass in order to increase flight efficiency. The second, the reserve-mobilization hypothesis, proposes that females store reserves during the early stages of the breeding cycle, which they mobilize to sustain them during later stages. We tested these hypotheses by providing food supplements to House Wrens (*Troglodytes aedon*) breeding on a study area north of Bloomington, Illinois, during the 1990-1992 breeding seasons. Additional food had no effect on mass except late in one season. Females that were given additional food during the late-young stage in 1992 had significantly higher mass than controls, but their mass was not greater than that normally obtained by females not receiving food supplements in other years. We conclude that the results from this experimental study are consistent with the wing-loading hypothesis, and that House Wrens do not lose mass because of an energy deficit or because they mobilize reserves.

Key words: energy deficit; food supplementation; House Wren; mass loss; *Troglodytes aedon*; wing-loading hypothesis.

INTRODUCTION

Many adult birds lose mass during the breeding cycle (Nice 1937, Baldwin and Kendeigh 1938, Kluijver 1951, Newton 1966, Hussell 1972, Morton et al. 1973, Freed 1981, Norberg 1981, Moreno 1989a, Curlee and Beissinger 1995). This loss generally occurs during the incubation and early-nesting stages and is usually greater in females than in males (Freed 1981, Westerterp et al. 1982, Ricklefs and Hussell 1984, Finke et al. 1987, Croll et al. 1991, Curlee and Beissinger 1995).

Mass loss has traditionally been attributed to "physiological stress" induced when breeding birds incur an energy deficit during the nesting cycle (Nice 1937, Kluijver 1951, Hussell 1972, De Steven 1980, Nur 1984). The supposition that mass loss is caused by an energy deficit is reasonable when one considers the demands placed on attentive parents (Kendeigh 1952, Freed 1981, Bédard and Meunier 1983). If mass loss is caused by an energy deficit, three predictions can be made: (1) mass loss should occur during the most energetically costly period of the breeding cycle (Freed 1981, Norberg 1981), (2) adults that are manipulated so as to increase their energy demands (e.g., brood enlargement or handicapping experiments) should have greater mass loss than controls (Ricklefs and Hussell 1984, Slagsvold and Lifjeld 1986, 1988, 1990, Finke et al. 1987, Cucco and Malacarne 1995, Curlee and Beissinger 1995), and (3) differences in mass loss

should be correlated with differences in future reproductive effort and success or with differences in adult mortality, or both.

The results from studies testing these hypotheses are typically inconsistent with the energy-deficit hypothesis (Freed 1981, Croll et al. 1991, Curlee and Beissinger 1995, Sanz and Moreno 1995; but see Garcia et al. 1993 and Cucco and Malacarne 1995). Alternatively, two adaptational hypotheses have been proposed, the wing-loading hypothesis (Freed 1981, Norberg 1981) and the reserve-mobilization hypothesis (Moreno 1989a, b).

The wing-loading hypothesis explains loss in mass as an adaptation to reduce wing-loading, thereby increasing flight efficiency. Freed (1981) estimated that female House Wrens (*Troglodytes aedon*) would save 23% of the power required to remain aloft late in the nestling period if they lost mass accumulated for egg production. These energy savings would allow females to increase the number of foraging trips, thereby increasing the number or quality of nestlings raised, or to reduce their own reproductive costs (Freed 1981, Norberg 1981).

The reserve-mobilization hypothesis suggests that female passerines maintain reserves accumulated for egg production throughout the incubation period. These reserves are used as an energy buffer during incubation and are then mobilized when nestlings hatch to sustain the breeding effort (Moreno 1989a, b). This reserve is quickly depleted during the early nestling period, allowing the female to spend more time and energy brooding and foraging for newly hatched nestlings. In

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this fashion, adult energy reserves are indirectly transferred to the offspring in order to promote their faster growth and development (Norberg 1981, Moreno 1989a, b). Moreno (1989b) demonstrated that the heaviest females during the incubation period lost more mass after nestlings hatched than did lighter females. However, both groups attained the same mass levels after hatching. He suggested that incubation reserves allow females to shift resource allocation in favor of the offspring (Norberg 1981, Moreno 1989a, b). The reserve is depleted during the nestling period because it is more difficult for females to maintain reserves during a high-activity phase, such as the nestling period, than during a low-activity phase, such as incubation (Moreno 1989b).

We tested the mass-loss hypotheses in a population of breeding House Wrens by providing food supplements at different stages of the breeding cycle. According to the energy-deficit hypothesis, providing additional food to adults during the breeding season should reduce the stress of procuring food for nestlings, resulting in a reduction in mass loss and possibly increasing nestling mass and survival. For multibrooded species, such as the House Wren, food supplements may allow adults to end their first nesting attempt in better condition than those that did not receive food. Supplemented adults may, therefore, be able to start a second breeding attempt earlier, lay more eggs, and raise more nestlings than controls (Martin 1987, Arcese and Smith 1988, Eden et al. 1989, Simons and Martin 1990).

The wing-loading hypothesis predicts that an increase in the food supply will have no effect on the mass of the adult at any stage of the nesting cycle. Furthermore, supplementing adults will have no effect on subsequent breeding attempts, since additional food should not affect adult body condition. Specific predictions of the effects of food addition on nestling mass or nestling survival are not made by the wing-loading hypothesis.

The reserve-mobilization hypothesis predicts that prior to hatching, females should utilize supplemental food to increase personal reserves. Female wrens do not receive assistance in incubation and are rarely fed by their mates (Johnson and Kermott 1992). Consequently, at least 58% of their daytime activity is spent incubating eggs (Kendeigh 1952); therefore, females may be limited in the amount of time available to maintain their reserves. An inability to maintain reserves during incubation is consistent with the observation that the mass of females declines throughout incubation (Freed 1981, Finke et al 1987) and varies significantly between years and with date of nesting within a breeding season (J. F. Cavitt and C. F. Thompson, *unpublished data*). Supplemented females should be able to maintain personal reserves and thus weigh more at hatching than unsupplemented control females. After the young have hatched, females should draw on per-

sonal reserves in order to shift resource allocation in favor of nestlings. Thus, during the nestling period, both the heavier females that were supplemented during incubation and the lighter control females should lose mass and end the breeding attempt at the same mass. However, females supplemented only during incubation should fledge nestlings sooner, have a greater proportion of offspring surviving, and have higher offspring mass in their broods than unsupplemented females. The reserve-mobilization hypothesis does not predict any change in timing of reproduction for the second nesting attempt because the female is unable to accumulate reserves until after the first brood is completed, regardless of supplementation.

METHODS

Study area and species

This study was conducted during the 1990–1992 breeding seasons on a population of House Wrens breeding on a forested study area in McLean County, Illinois (Money Creek Township, 25N, R3E, 40°40' N, 88°53' W). See Drilling and Thompson (1984, 1988) for detailed descriptions of the study area. House Wrens are insectivorous, secondary-cavity-nesting passerines that are readily attracted to nest boxes. The Mackinaw study area (108 ha) contains 585 identical nest boxes distributed in north–south rows (see Drilling and Thompson 1984 for nest-box dimensions). Each box is mounted on a greased steel pole to reduce nest predation and is equipped with a sliding metal door to trap adults.

In central Illinois, House Wrens are migratory, arriving at the study area in late April, and are generally double brooded, initiating first broods in mid-May (early season) and second broods in early July (late season). The modal size of first and second clutches is seven and six eggs, respectively (Finke et al. 1987). Females alone incubate for a period of 13 d before the first eggs hatch (brood day 0). Nestlings are fed by one or both parents through nest-leaving (between brood days 14 and 17) and for an additional 1–2 wk after nest-leaving (Kendeigh 1941).

General procedures

All nest boxes were checked twice weekly from early May until mid-August to determine when clutches were begun in each nest (nest-initiation date) and to determine the status of extant nests. A clutch size was assigned for a nesting attempt when the same number of eggs was recorded on two consecutive visits and there was evidence that incubation had commenced. Near the time of hatching, nests were visited daily and any nestlings present were weighed to determine brood day 0 (Harper et al. 1992). On brood day 12, nestlings were weighed to the nearest 0.1 g on a portable Ohaus balance and banded with a numbered aluminum U.S. Fish and Wildlife Service leg band. The date of nest-leaving



PLATE 1. Adult House Wren with mealworm (dietary supplement). Photo by Brian R. Braye.

(termination date) was assigned by checking each nest daily from brood day 14 until all nestlings had left the nest.

Supplemental feeding experiment

During the 1990 early season, the experiment consisted of two treatments: (1) food added to nests during the nestling stage, and (2) unmanipulated nests. Three additional treatments were added during the 1990 late season for a total of five treatments. Nests were assigned randomly to the following treatments: (1) food supplement during the incubation period, (2) food supplement during the nestling period, (3) food supplement during both the incubation and nestling periods (multiple treatment), (4) empty food dishes on top of the nest box (1990 and 1991 only), and (5) unmanipulated nests.

Food dishes were placed on top of nest boxes, and from the 1991 late season were covered with galvanized "chicken" wire (mesh diameter = 25 mm). During the late season of 1990 we found that Blue Jays (*Cyanocitta cristata*) were also feeding on the supplement. The mesh prevented Blue Jays from feeding at the dishes, but was large enough that House Wrens had easy access to the supplement.

Each day (between 0600 and 1000 h), 20 g of live mealworm larvae (*Tenebrio molitor*) were placed in experimental containers. This amount of food was chosen based on the estimation that a 10.6-g wren expends ~61 kJ/d (Dykstra and Karasov 1993a). Assuming that the energy content of mealworms is 11.59 kJ/g (calculated from Bell 1990) and that the House Wrens' assimilation efficiency of mealworms is 0.65 (Kacelnik 1984), an adult wren would need to consume about 8.2 g of mealworms to satisfy its daily energy requirements. Dykstra and Karasov (1993b) calculated that an adult House Wren would need to collect 38.8 g/d (wet

mass) of insects to maintain itself and its nestlings during peak nestling food demands. Therefore, the 20-g supplement represents a substantial energy savings to adults, either directly through ingestion or indirectly through reduction of flight costs to collect food for nestlings.

Food was added to incubation treatment nests when nests at the laying stage had the same number of eggs recorded on two consecutive visits. Thereafter, the contents of the nest were checked daily and the supplement was delivered until at least one nestling had hatched. Food was added to nests in the nestling treatment on brood day 0 or 1. The supplement was delivered to nests until all nestlings had left the nest. Food was delivered to nests in the multiple treatment as in the incubation treatment and terminated as in the nestling treatment.

In most cases, mealworms delivered to nests were consumed before the next visit. If food remained in the dish, dead larvae were removed and 20 g of mealworms was added. During the 1992 breeding season, nest watches of ~10 min were made at each nest weekly after the food supplement was added to establish whether adults utilized the mealworms. The quantity of mealworms consumed within the 10-min observation period varied according to the stage of the nest; incubating females fed at lower rates (2–3 mealworms/observation period) than those feeding thermoregulating young (4–10 mealworms/observation period). We were able to verify the use of mealworms by parents for ~86% of all supplemented nests in 1992 ($N = 110$ nests supplemented).

To determine the extent and timing of mass loss, adults were captured at the nest using the sliding trapdoor, banded with a numbered aluminum U.S. Fish and Wildlife Service band, and weighed to the nearest 0.1 g on a portable Ohaus balance. Adult mass could not

be determined during the egg-laying stage, because female House Wrens often abandon their nest if caught before incubation begins (J. F. Cavitt, *personal observation*). Wrens were caught at the nest during three periods: (1) incubation, (2) early nestling stage (brood day 0 to brood day 5), and (3) late nestling stage (after brood day 5). The nestling period was divided into the early and late stages to correspond with changes in adult feeding rates (Morton 1984) and female brooding behavior (Kendeigh 1952). Each period reflects different time and energy demands placed on the adults, and therefore each period is considered separately. Females were captured during each period and males were captured only during the early and late nestling stages, as they rarely entered the nest box during incubation. Males were also banded with a unique combination of colored plastic bands (maximum of two bands per leg) to aid in visual identification.

To determine the effect of food supplementation on the timing and clutch size of subsequent nests, adults that attempted second broods were captured and identified. The time between the two nests (interbrood interval) and the clutch size of second nests were also determined. The interbrood interval is defined as the period between the termination date of the first brood and the date the first egg is laid in the second nest.

Data analysis

The general linear models procedure (GLM procedure) and the nonparametric procedure (NPAR1WAY) on SAS-PC software (SAS Institute 1988) were used to perform all analyses and for the calculation of least-squares means. Least-squares-means multiple comparisons were used in all follow-up tests. Early- and late-season nests were analyzed separately because of seasonal differences in clutch size (Finke et al. 1987) and adult mass (J. F. Cavitt and C. F. Thompson, *unpublished data*).

In 1992, we used nest-watch information to distinguish between females that were given additional food regardless of their utilization of the supplement and females that either ate the supplement themselves or fed it to nestlings, or both, as evidenced by direct or indirect information. Observation of adults using the food supplement constituted direct evidence; indirect evidence was the disappearance of all mealworms from the food dishes between successive visits. These analyses were performed only for females, because the number of male captures was small.

Analysis of covariance (ANCOVA) was performed on female mass for each stage of the nesting cycle (incubation, early-young, and late-young stages) for each year of the study, and on male mass during the early-young and late-young stages only. Hour of capture and brood day of capture were used as covariates because mass in House Wrens increases throughout the day and declines throughout the nesting cycle (Baldwin

and Kendeigh 1938, Freed 1981, Finke et al. 1987, this study).

We analyzed nestling mass and survival to nest-leaving in order to determine whether adults used the food supplement to increase nestling survival or mass, or both. Residuals of a linear regression of brood mass and date of hatching were used as the relative brood mass. ANCOVAs were performed on mean relative brood mass (brood day 12) by treatment for each year, with brood size as the covariate. Because age-specific nestling mass declines throughout the breeding season (C. F. Thompson, *unpublished data*), differences in brood mass associated with hatching date can be accounted for by analyzing the residuals in this fashion. An ANCOVA on the number of fledglings that survived to nest-leaving from successful nests (at least one fledgling produced) was performed by treatment for each year of the study, with both clutch size and date of hatching as covariates.

In addition, the length of the nestling period (termination date minus brood day 0) was compared between treatments to determine if adults were able to use additional food to reduce the length of the nestling period. A Kruskal-Wallis test was used to compare the number of days to nest-leaving between treatments.

The provision of additional food to adults during the first breeding attempt may also affect their subsequent nesting attempts. ANCOVA on the relative clutch size of second nests was performed by treatment for each year of the study, with the relative clutch size of the first nesting attempt as the covariate. We regressed clutch size on nest-initiation date to obtain the residuals used as the relative clutch size. The relative clutch size of first nests was used as the covariate because clutch size declines with date (Finke et al. 1987, Drilling and Thompson 1991), and the clutch size a female produced during the first nesting attempt may affect the clutch size produced during the second nesting attempt. In this way it was possible to include both the initiation date of first and second nests and the clutch size of first nests in the analysis. An ANCOVA was performed on the interbrood interval by treatment. The interbrood interval may be affected by the date of completion of the first nest, so the termination date of the first nest was used as the covariate. All assumptions of ANCOVAs were tested and met.

RESULTS

There were no significant differences between the two control treatments for any variable analyzed in 1990 and 1991 ($P > 0.05$). Therefore, both control treatments were pooled in all analyses.

Since treatments were often assigned to late-season nests before the identity of parents could be established, some adults were utilized in the experiment in both seasons. These adults fall into five possible categories: (1) supplemented during the early season and control during the late season, (2) sup-

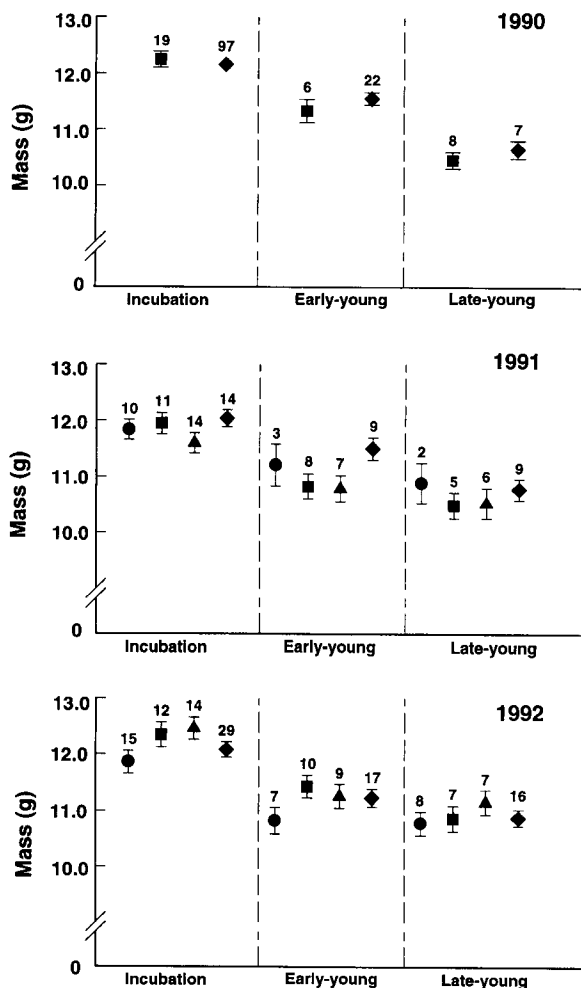


FIG. 1. Least-square mean female mass (± 1 standard error) during the 1990–1992 early seasons (\bullet = food added during incubation; \blacksquare = food added during the nestling stage; \blacktriangle = food added during both incubation and nestling stages; \blacklozenge = controls). Sample sizes are given above each mean.

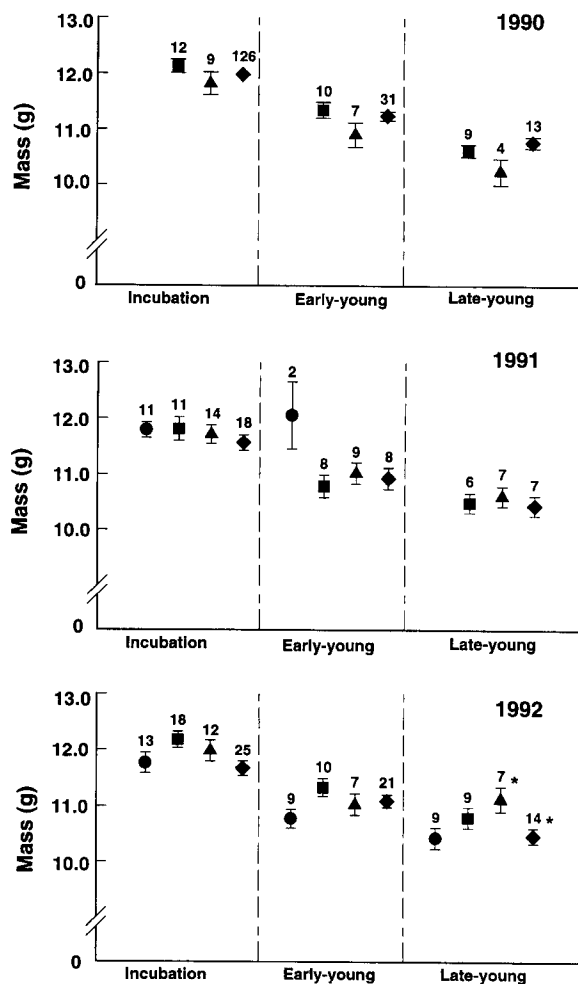


FIG. 2. Least-square mean female mass (± 1 standard error) during the 1990–1992 late seasons (symbols are as in Fig. 1). An asterisk (*) indicates a significant difference between means ($P = 0.014$). Sample sizes are given above each mean.

plemented during both seasons but in different treatments, (3) supplemented during both seasons but in the same treatment, (4) control during the early season and supplemented during the late season, and (5) control during both seasons. The first two categories have the greatest potential to bias the results of this experiment; therefore, we eliminated females that fell into either of the first two categories and compared the effects of treatment on incubation mass. There were no significant differences in any year of the study ($P > 0.05$, analyses not shown). This suggests that treatment effects did not carry over into the next breeding attempt, so these adults were included in the remainder of the analyses.

Incubation stage

The mass of females that received food supplements during the incubation stage did not differ sig-

nificantly from the mass of those that did not receive additional food (Figs. 1, 2, Table 1). There were also no significant differences among treatments when only those females known to have used the food supplement were included in the analysis (Table 1). During the 1990 late season, female mass was significantly affected by hour of capture, but not by brood day or treatment. Female mass during the 1991 early season was significantly affected by brood day, but not by hour of capture or treatment.

Early-young stage

Female mass during the early-young stage was not affected by treatment during either the early or late seasons of 1990–1992 (Figs. 1, 2, Table 2). Mass during the early season of 1992 was significantly affected by brood day, but not by hour of capture or treatment. During the 1992 late season, mass was

TABLE 1. ANCOVA *F* tests for effects of treatment on female mass during the incubation stage, with hour of capture and brood day as covariates.

Season	Year	Model				Treatment			Brood day			Hour		
		<i>F</i>	df _{model}	df _{error}	<i>P</i>	<i>F</i>	df†	<i>P</i>	<i>F</i>	df†	<i>P</i>	<i>F</i>	df†	<i>P</i>
Early	1990	1.73	3	109	0.165									
	1991	3.12	5	53	0.015	1.30	3	0.28	7.67	1	0.01	0.63	1	0.430
	1992	1.34	5	64	0.259									
		1.15‡	5	26	0.360									
Late	1990	2.44	4	255	0.047	1.01	2	0.37	0.02	1	0.89	7.71	1	0.006
	1991	1.04	5	51	0.405									
	1992	0.89	5	62	0.583									
			1.64‡	5	25	0.186								

† Error df are the same as model df_{error}.

‡ Includes only females known to have used the supplement.

significantly affected by brood day and hour of capture, but not by treatment. During the early season of 1992, there were no significant differences among treatments when only those females known to have used the food supplement were analyzed (Table 2). During the late season of 1992, however, there was a significant effect of brood day and hour of capture, but not of treatment on mass.

Male mass during the early-young stage was not significantly affected by treatment during either season in 1990, 1991, or 1992 (Fig. 3, Table 2). During the 1992 late season, mass was significantly affected by hour of capture, but not by treatment or brood day.

Late-young stage

Female mass during the late-young stage was not affected by food supplementation during either seasons in 1990–1991 or the early season of 1992 (Figs. 1, 2, Table 3). During the 1991 early season, female mass was significantly affected by brood day, but not by hour of capture or treatment. Female mass during the late season of 1992 was, however, marginally

affected by treatment and significantly by brood day, but not hour of capture. Females that were fed throughout the incubation and young stages (multiple treatment) weighed more than control females ($P = 0.014$; see Fig. 2). During both seasons of 1992, there was no significant effect on mass when only those females known to have used the food supplement were included in the analysis (Table 3). Males that received additional food did not significantly differ in mass during the late-young stage in either season of 1990–1992 (Fig. 3, Table 3).

Mean relative brood mass

Adults that received food supplements during the nestling stage (multiple and nestling treatments) did not use additional food to increase nestling mass. Mean relative brood mass did not differ among treatments during the early ($F_{2,118} = 0.07$, $P = 0.930$) or late season ($F_{3,112} = 2.10$, $P = 0.105$) of 1990, nor during the late season of 1991 ($F_{4,34} = 0.41$, $P = 0.803$) and the early ($F_{4,58} = 0.85$, $P = 0.502$) and late seasons ($F_{4,52} = 1.22$, $P = 0.314$) of 1992. There are also no significant differences among treatments

TABLE 2. ANCOVA *F* tests for effects of treatment on adult mass during the early-young stage, with hour of capture and brood day as covariates.

Season	Year	Sex	Model				Treatment			Brood day			Hour		
			<i>F</i>	df _{model}	df _{error}	<i>P</i>	<i>F</i>	df†	<i>P</i>	<i>F</i>	df†	<i>P</i>	<i>F</i>	df†	<i>P</i>
Early	1990	F	2.54	3	24	0.080									
		M	0.10	3	36	0.96									
	1991	F	2.11	5	21	0.105									
		M	0.60	5	19	0.700									
	1992	F	2.68	5	37	0.037	1.38	3	0.264	8.28	1	0.007	0.0	1	0.993
		F‡	2.15	5	30	0.087									
M		0.05	5	18	0.770										
Late	1990	F	1.90	4	71	0.119									
		M	0.44	4	84	0.781									
	1991	F	2.33	5	21	0.079									
		M	1.54	5	29	0.209									
	1992	F	4.91	5	41	0.001	1.94	3	0.138	5.12	1	0.029	13.02	1	0.001
		F‡	3.43	5	36	0.012	0.99	3	0.406	4.63	1	0.038	10.3	1	0.003
		M	3.89	5	37	0.006	2.18	3	0.106	3.24	1	0.080	4.80	1	0.035

† Error df are the same as model df_{error}.

‡ Includes only females known to have used the supplement.

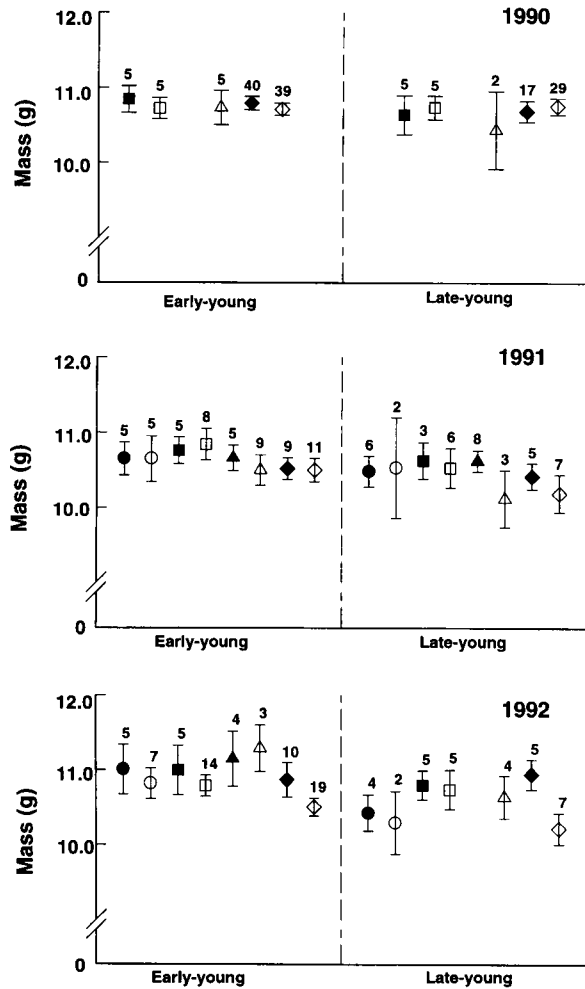


FIG. 3. Least-square mean male mass (± 1 standard error) during the 1990–1992 early (filled symbols) and late (open symbols) seasons (symbols are as in Fig. 1). Sample sizes are given above each mean.

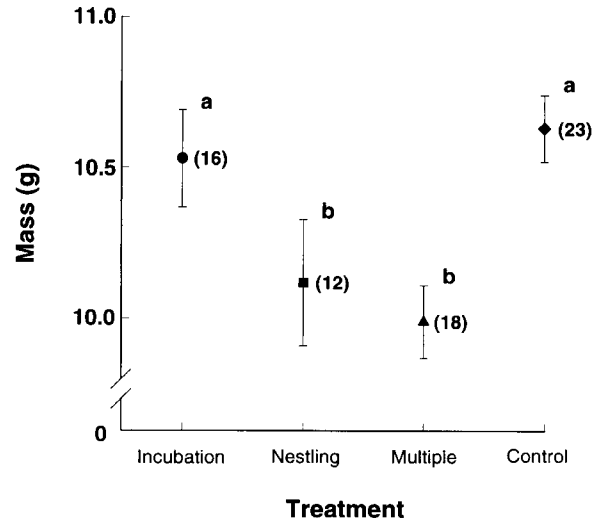


FIG. 4. Mean brood mass (± 1 standard error) during the 1991 early season (symbols are as in Fig. 1). Means with the same letter are not significantly different. Sample sizes are given to the right of each mean.

when only those adults in 1992 known to have used the food supplement were compared (early season: $F_{4,47} = 0.44$, $P = 0.782$; late season, $F_{4,41} = 1.34$, $P = 0.271$). In contrast, brood mass during the 1991 early season was significantly lowered by supplemental feeding in the nestling and multiple-feeding treatments ($F_3 = 4.48$, $P = 0.008$), but not by brood size ($F_1 = 0.20$, $P = 0.655$) (Fig. 4).

Number of fledglings produced

Additional food offered to adults did not lead to an increase in the number of fledglings produced (Table 4). There was a significant difference between treatments during the early season of 1990, with

TABLE 3. ANCOVA F tests for effects of treatment on adult mass during the late-young stage, with hour of capture and brood day as covariates.

Season	Year	Sex	Model				Treatment			Brood day			Hour		
			F	df _{model}	df _{error}	P	F	df†	P	F	df†	P	F	df†	P
Early	1990	F	1.93	3	11	0.183									
		M	0.37	3	18	0.772									
	1991	F	3.23	5	16	0.033	0.56	3	0.648	7.84	1	0.013	0.42	1	0.527
		M	0.79	5	18	0.572									
	1992	F	1.58	5	32	0.193									
		F‡	1.15	5	26	0.360									
M		1.15	4	9	0.393										
Late	1990	F	1.89	4	36	0.134									
		M	1.13	5	29	0.368									
	1991	F	0.24	5	16	0.914									
		M	0.49	5	11	0.778									
	1992	F	3.79	5	33	0.008	2.87	3	0.051	8.46	1	0.006	2.23	1	0.145
		F‡	1.64	5	25	0.186									
		M	0.97	5	12	0.476									

† Error df are the same as model df_{error}.

‡ Includes only females known to have used the supplement.

TABLE 4. ANCOVA *F* tests and least-square mean (± 1 standard error) number of nestlings per nest surviving to nest-leaving (n = number of nests/treatment).

Year	Season	Treatment	No. of nestlings	<i>n</i>	<i>F</i>	df	<i>P</i>
1990	Early	Nestling	4.08 \pm 0.16	20	7.89	1, 172	0.005
		Control	5.38 \pm 0.44	156			
	Late	Nestling	4.18 \pm 0.60	13	1.92	2, 161	
		Multiple Control	4.54 \pm 0.72 3.36 \pm 0.18	9 144			
1991	Early	Incubation	6.72 \pm 0.21	14	2.38	3, 47	0.082
		Nestling	6.89 \pm 0.28	9			
		Multiple	6.70 \pm 0.22	12			
		Control	6.14 \pm 0.19	18			
	Late	Incubation	4.00 \pm 0.41	6	2.31	3, 33	
		Nestling	5.22 \pm 0.32	9			
		Multiple	5.00 \pm 0.31	10			
		Control	5.22 \pm 0.27	14			
1992	Early	Incubation	5.05 \pm 0.32	15	1.69	3, 58	0.178
		Nestling	6.07 \pm 0.39	10			
		Multiple	5.33 \pm 0.35	13			
		Control	5.70 \pm 0.25	26			
	Late	Incubation	5.02 \pm 0.30	11	0.35	3, 51	
		Nestling	4.72 \pm 0.26	14			
		Multiple	5.09 \pm 0.34	8			
		Control	4.99 \pm 0.20	24			

adults that received food during the nestling stage producing fewer fledglings than controls (Table 4).

Time to nest-leaving

Food supplementation had no effect on the median number of days to nest-leaving in any year of the study (Table 5).

Interbrood interval

Additional food did not reduce the time between subsequent nests. There was no significant effect of treat-

TABLE 5. Effects of treatment on median number of days to nest-leaving (with upper and lower quartiles in parentheses; termination date minus brood day 0).

Year	Season	Treatment	No. days to nest-leaving	χ^2	<i>P</i>
1990	Early	Nestling	15.5 (16, 14)	0.045	0.8316
		Control	15 (18, 15)		
	Late	Nestling	15 (16, 14)	2.5019	
		Multiple Control	16.5 (18, 14) 15 (18, 13)		
1991	Early	Incubation	15 (17, 13)	4.5331	0.2094
		Nestling	15 (17, 14)		
		Multiple	15 (17, 13)		
		Control	16 (17, 15)		
	Late	Incubation	15.5 (16, 15)	5.9183	
		Nestling	15 (16, 12)		
		Multiple	15 (17, 12)		
		Control	16 (18, 15)		
1992	Early	Incubation	15 (18, 13)	2.622	0.454
		Nestling	16 (16, 14)		
		Multiple	16 (17, 13)		
		Control	16 (18, 13)		
	Late	Incubation	16 (17, 15)	0.0654	
		Nestling	16 (17, 11)		
		Multiple	16 (17, 15)		
		Control	16 (17, 14)		

ment on interbrood interval for either 1990 ($F_{2,62} = 0.97$, $P = 0.386$), 1991 ($F_{4,27} = 0.97$, $P = 0.440$) or 1992 ($F_{4,43} = 0.73$, $P = 0.576$). When only females that were known to have used the food supplement in 1992 were included in the analysis, there was no significant difference between treatments ($F_{4,34} = 1.13$, $P = 0.357$).

Clutch size of second nesting attempts

Additional food offered to females during their first breeding attempt did not lead to increased clutch sizes in their second attempt. There was no effect of treatment on the relative clutch size of second nests for 1990 ($F_{2,71} = 2.31$, $P = 0.107$), 1991 ($F_{4,28} = 1.80$, $P = 0.157$), or 1992 ($F_{4,43} = 0.71$, $P = 0.589$). There was no significant effect on clutch size of second nests when only females that used the food supplement in 1992 were included in the analysis ($F_{4,33} = 1.81$, $P = 0.151$). Success of second broods was not analyzed, because second nests were included in the late-season experiments. There were only a few females that were fed during the early season and not included in the late-season experiment; therefore, the survival and success of a female's second brood was not independent of her treatment during the late season.

DISCUSSION

The results from this experiment do not support the reserve-mobilization hypothesis. Females that received food during the incubation stage (both the incubation and multiple treatments) did not use additional food to increase body mass. Also, food supplements did not lead to a reduction in the length of the nestling period, to increased brood mass, nor to increased brood survival, as predicted by this hypothesis.

Most predictions of the energy-deficit hypothesis have also not been met in this study. House Wren food supply was experimentally increased, which potentially reduced the energy demands on adults. Only in the late season of one year and only in the late-young stage did extra food increase female mass above that of controls. In 1992 females fed during both incubation and nestling stages (multiple treatment) tended to weigh more in the late-young stage than did controls. However, adults that received food did not have higher mean brood mass, increased survival of nestlings to nest-leaving, reduced length of the nestling period, reduced interbrood interval, or increased clutch size of second nests, some or all of which are predicted by the energy-deficit hypothesis.

The results are consistent with the wing-loading hypothesis, because with the exception of females during the late-young stage of the 1992 late season, supplemented adults did not have higher mass. This suggests that adults are not balancing increased energy expenditures with increased energy intake. House Wrens apparently lose mass in order to reduce wing-loading and thereby increase flight efficiency. During the 1992 late season, the increased mass of supplemented females in the multiple treatment fell within the range normally found during the late-young stage (J. F. Cavitt and C. F. Thompson, *unpublished data*). Male mass during this period also showed the same pattern (Fig. 3); however, the difference was not significant.

During the 1991 early season, the mean brood mass of nestlings that received food supplements was significantly lower than those not receiving additional food; during the 1990 early season, controls produced more fledglings than adults supplemented during the nestling stage. The presence of Blue Jays feeding on the mealworms near the nest may have distracted parents from attending nestlings and thus reduced mean brood mass (1991 early season) and number of fledglings (1990 early season). We began using the wire-mesh screen during the 1991 late season, and its use quickly eliminated Blue Jay visits to all supplemented nests. However, the exclusion of Blue Jays from supplemented nests did not result in a corresponding increase in adult mass during any stage of the nesting cycle. In addition, when we eliminated adults that were not known to have used the supplement from analyses the results were unaffected. Thus, the results are not attributable to interference from Blue Jays, but rather suggest that this population was not food limited.

House Wrens may lose mass to some threshold level, above which sufficient gains in flight efficiency are not achieved and below which adults may experience reduced survival (Newton 1986, Jones 1987). This may be particularly important during the late season because food may be more limiting (C. F. Thompson, *personal observation*) and because it may affect the adults' ability to build reserves for the prebasic molt and fall migration. There is evidence that the food supply during

the late season of 1992 may have been lower than in other years, causing adults that did not receive additional food during the nestling stage (controls and incubation treatments) to have lower masses than those that did receive food supplements. The pattern of mass loss suggests that a lower limit of mass is typically reached during the late-young stage (between 10.75 and 10.95 g; J. F. Cavitt and C. F. Thompson, *unpublished data*). However, during the 1992 late season, the mass of females that did not receive food supplements during the nestling stage (controls and incubation treatment) declined below this level. Females that did receive food supplements maintained mass at levels normally found during this period. A similar pattern held for males; however, the difference was not statistically significant. Kendeigh (1979) found that arthropod abundance is positively correlated with precipitation in Illinois forests. During the 1992 breeding season, rainfall was 12.81 cm below the 20-yr average, a 33% decrease (NOAA 1992), whereas precipitation was 5.98 cm above the 20-yr average in 1990 and only 3.92 cm below in 1991 (NOAA 1990, 1991). Since House Wrens are strictly insectivorous, they may have experienced a period of reduced food availability in 1992.

Only a few experimental tests of the hypotheses proposed to explain mass loss have been conducted (Moreno 1989b, Garcia et al. 1993, Cucco and Malacarne 1995, Curlee and Beissinger 1995, Sanz and Moreno 1995). However, data relevant to testing these hypotheses are provided by manipulating brood size to increase reproductive effort, and, therefore, stress (Hussell 1972, Hegner and Wingfield 1987, Martins and Wright 1993) or by handicapping the adults' flying abilities (Slagsvold and Lifjeld 1986, 1988, 1990).

The energy-deficit hypothesis predicts that females given an enlarged brood should lose proportionally more mass than females having normal or reduced broods. Experiments manipulating brood size are useful in testing these hypotheses only if researchers simultaneously document feeding rates, since one or both parents may not increase their effort when their brood is enlarged (Moreno et al. 1995). The results from experiments on brood-size manipulations are equivocal. Of the five brood-size manipulation experiments in which the required data are provided, three showed a positive correlation between increased brood size and mass loss (Hussell 1972, Martins and Wright 1993, Cucco and Malacarne 1995) and two studies found no significant correlation (Hegner and Wingfield 1987, Curlee and Beissinger 1995).

Experimentally handicapping adults by removing primaries and rectrices so as to increase the energy required for flight provides data relevant to testing the mass-loss hypotheses (Slagsvold and Lifjeld 1986, 1988, 1990). If a bird's flight costs increase, a corresponding reduction in mass would be expected in order to reduce wing-loading. However, the energy-deficit hypothesis also predicts that a potential impairment in

a parent's flight abilities would increase the cost of raising nestlings, and thus also cause a reduction in adult body mass. Therefore, experiments that increase the stress of reproduction by reducing flight abilities do not discriminate between the wing-loading and stress hypotheses.

Food supplementation has been used previously to test the mass-loss hypotheses (Moreno 1989b, Garcia et al. 1993) by reducing the demands of procuring food. Moreno (1989b) provided varying amounts of mealworms throughout the breeding cycle to Northern Wheatears (*Oenanthe oenanthe*) breeding on Öland Island, Sweden. Mealworms were placed on a perch connected to an electronic balance that recorded the mass of adults that landed to consume mealworms. Food supplements significantly increased the mass of female Wheatears during the incubation and early nestling stages of the nesting cycle, but supplements had no effect on females feeding thermoregulating young. Moreno (1989b) interpreted this as evidence that adults actively reduce their intake of food and are sustained by energy stores in order that their nestlings may develop at a faster rate. Garcia et al. (1993) reported in a one-year study that food supplementation during the nestling stage reduced female mass loss in a population of Mountain Bluebirds (*Sialia currucoides*) breeding in Alberta, Canada. They concluded that since their study was conducted during a "good year for food resources," mass loss in female Mountain Bluebirds was the result of an energy deficit.

The results of this experiment on House Wrens are not consistent with results found in either of the two previous food-supplementation studies that tested the mass loss hypotheses (Moreno 1989b, Garcia et al. 1993). This may not be surprising, as species breeding in different environments may not be selected for adaptive mass loss. For example, birds breeding at high latitudes (e.g., Mountain Bluebirds) may not have the option for adaptive mass loss because of the low ambient air temperatures they experience over the course of nesting. The 20-yr average minimum temperature near Lacombe, Alberta, Canada, during the breeding season ranges from 0° to 6°C (National Climatic Data Center 1994); in contrast, average minimum temperatures reported during the breeding season on Öland island range from 4.9° to 11.4°C (Moreno 1989b), and the 20-yr average minimum temperature in central Illinois ranges from 9° to 17°C (NOAA 1992). Low temperatures may not allow females to maintain their mass at low levels in order to increase flight efficiency. Rather, it may be advantageous for these females to increase mass, thereby reducing energetic stress caused by low temperatures (Kendeigh et al. 1969, Calder 1974).

Further tests of the mass-loss hypotheses

An additional test of both the energy-deficit hypothesis and the wing-loading hypothesis is to manipulate the length of each period of the nesting cycle and to

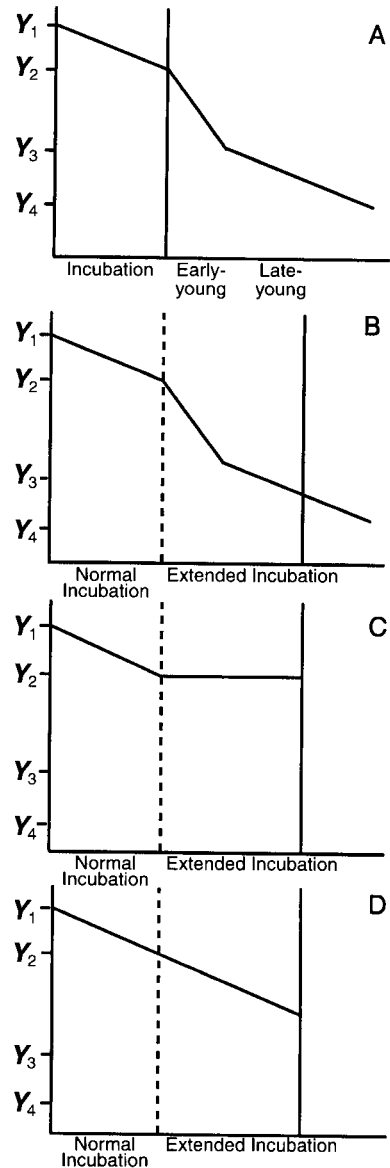


FIG. 5. Predicted effects of experimentally increasing the length of the incubation stage on female mass. (A) The pattern of mass loss normally observed in House Wrens (Y_1 = mass at the beginning of incubation, Y_2 = mass at the end of incubation and the beginning of the early-young stage, Y_3 = mass at the end of the early-young stage and the beginning of the late-young stage, Y_4 = mass at the end of the late-young stage). (B–D) Predicted effects of increasing the incubation stage on female mass. Dashed lines represent the end of the incubation period (had the stage not been prolonged), and solid lines represent the length of the incubation period for either control (A) or manipulated females (B–D).

measure the effects on adult mass (Cavitt 1993, Sanz and Moreno 1995). Predictions of experimentally increasing the incubation stage are represented in Fig. 5. If a stage of the nesting cycle (incubation, early-young, or late-young) is increased, mass may be affected in three different ways: (1) female mass may continue to

decline in the same fashion as if the stage had not been prolonged (Fig. 5B); (2) mass may not change so that the female ends the prolonged stage at the same level as females having normal stage lengths (Fig. 5C); or (3) mass may continue to decline at the same rate as for females having normal stage lengths. However, because the period is prolonged, females should end the period at a lower mass than controls (Fig. 5D). The first possibility is not consistent with any of the mass-loss hypotheses. The energy-deficit hypothesis is consistent with the third possibility. If any stage of the nesting cycle induces an energy deficit in females, then prolonging the stage would most likely cause mass to continue to decline at the same rate until a threshold level of mass is reached. Females would probably abandon their nests after mass had declined to this threshold (Newton 1986, Jones 1987), rather than allow further reductions in body mass that might affect survival. The second possibility is consistent with the wing-loading hypothesis. If an optimum mass is necessary for increased flight efficiency, females should maintain that mass so that experimental females end the prolonged stage at the same levels as controls. Results from Sanz and Moreno (1995) are consistent with this second possibility (Fig. 5C). In addition, experimentally reducing the lengths of each stage would also allow for tests of the mass-loss hypotheses.

Conclusions

The results of this study do not support the energy-deficit or the reserve-mobilization hypotheses. The pattern of mass loss in breeding House Wrens is consistent with that predicted by the wing-loading hypothesis. In times of low food, an energy deficit may play a role in mass loss by reducing mass below a threshold level, possibly leading to increased mortality. However, an energy deficit does not seem to be the underlying cause of regular mass loss in House Wrens. Adults that received additional food did not use the supplement to increase body mass during any stage of the nesting cycle beyond levels normally obtained by controls.

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