FACTORS AFFECTING FEEDING AND BROODING OF GRAY CATBIRD NESTLINGS

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ABSTRACT.—Gray Catbirds (*Dumetella carolinensis*) were studied to document patterns of feeding and brooding nestlings and to relate these to nestling age, brood size, time of day, time of season, and weather. Major factors affecting feeding were nestling age and brood size. The average number of food deliveries$\cdot$brood$^{-1}\cdot$h^{-1} increased linearly with the log of nestling age for both male and female parents. Also, volume of food delivered/feeding trip increased linearly with nestling age. As brood size increased, feeding frequencies/brood increased but food deliveries/nestling decreased. Brooding and shading were affected mainly by nestling age and ambient temperature. Time spent brooding decreased substantially as nestlings grew older. Shading was important when the sun shone directly on the nest. Females spent significantly more time brooding nestlings when rain increased. As ambient temperature increased, time spent shading increased and time spent brooding declined.
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ONE of the greatest stresses on birds during the breeding season is caring for their nestlings. Frequent feeding trips are required to satisfy the food demands of the rapidly developing young, and nestling body temperature must be maintained at a relatively constant level. Rates of feeding and brooding by parent birds can be related either to requirements of the nestlings or to environmental factors affecting the adults. Knowledge of these relationships is important to understand better the nestling period of altricial birds, but few workers have addressed these topics.

Although the Gray Catbird (*Dumetella carolinensis*) is a common species throughout much of the United States and its nesting biology has been extensively documented (for a review see Johnson and Best 1980), factors affecting feeding and brooding frequencies have not been reported. Slack (1973) documented effects of temperature, time of day, and day of incubation on female attentiveness during incubation but reported very little concerning brooding of nestlings. Zimmerman (1963) collected limited information on attentive periods of female catbirds relative to nestling age.

The objectives of this study were (1) to document patterns of feeding and brooding nestling Gray Catbirds and (2) to relate these to nestling age, brood size, time of day, time of season, and weather.

STUDY AREA AND METHODS

This study was conducted in a shrubby and partly wooded pasture near Ames, Iowa during the springs and summers of 1977 and 1978. The area covered 16 ha of which approximately 50% contained shrubs, primarily gooseberry (*Ribes* spp.) and multiflora rose (*Rosa multiflora*), suitable as nesting sites for catbirds. A stream meandered through the study site. During 1976–1977, a drought occurred in central Iowa. Rainfall in Ames was 52 cm less than the normal of 116 cm during the 15-month period, May 1976–July 1977 (Natl. Ocean. Atmos. Admin. 1976, 1977, 1978). The drought ended in August 1977, and during April–July 1978, precipitation was 9 cm above the normal of 43 cm.

To locate all active nests, intensive nest searches were conducted weekly over the entire study area. The status of active nests was checked at least once daily. Nearly all adult catbirds on the study area were captured by using mist nets and marked with colored leg bands. Additionally, a spot of paint was placed on the head of one member of each pair. Nestlings were marked with a spot of paint on the top of the beak.

Catbird nests were observed from blinds during both 1977 and 1978. A mirror was positioned permanently over each nest so that its contents could be viewed. This was done prior to hatching; thus, birds became accustomed to the mirror before behavioral observations were begun. Mirrors were positioned so that they did not shade the nest. Feeding frequencies and time spent brooding and shading nestlings by each parent were recorded. Brooding was distinguished from shading because each served a different function. Brooding occurred when the female settled down on the nestlings and provided heat to them. During shading, the bird stood over the nestlings, with wings slightly spread, usually to protect them from sunlight (sometimes birds assumed this position when no direct sunlight was falling on the nest). Observations were made at each nest from the time of hatching until the nestlings fledged. Nests were observed an average of 92 h each. Ages of nestlings were divided into 24-h classes beginning from the time of hatching (0–24 h = 0 day old, 24–48 h = 1 day old, etc.). Five nests were observed in 1977, with brood sizes of 2, 2, 3, 4, and 5, and four in 1978, with sizes of 2, 3, 4, and 5. Nestling growth rates were determined by Ricklefs' (1967) method.

In 1978, food samples were collected from all catbird nestlings on the area except those for which feeding frequency was being observed. Wire ligatures were placed around the nestlings' necks, preventing them from swallowing food delivered by the parents (Johnson et al. 1980). Nestlings were watched from a blind, and, after each feeding trip made by parents, the food was collected from the nestlings' throats. Food was sampled from nestlings 0 through 8 days old; after 8 days, disturbances would cause them to fledge prematurely (young normally fledge at about 11 days old). The volume of food items was determined by water displacement.

Each day was divided into five 3-h time periods: dawn–0900, 0900–1200, 1200–1500, 1500–1800, and 1800–dusk. Observations from blinds and food sampling were conducted during alternate intervals, with the schedule reversed every other day. In this way, all intervals were represented for each part of the study during every 2-day period. Temperature (°C), relative humidity (%), barometric pressure (mm Hg), cloud cover (classes 1 through 5), wind speed (classes 1 through 7), and light intensity (foot-candles) were recorded hourly.

The relationships between each independent variable and nestling care were evaluated using either linear regression analysis or analysis of variance (ANOVA). Nestling age had a noticeable and consistent influence on both feeding and nest attendance. Thus, in ANOVA tests for the effects of brood size, time of season, and weather on the dependent variables, a two-way analysis was used in which one of the factors always was nestling age. Values used in the analysis were means of the dependent variable calculated for each age category within each class of the other independent variable (unweighted analysis of cell means; Snedecor and Cochran 1967: 475). Regression equations were determined by using means of the dependent variable for each value of the independent variable. Using means in both of the above procedures adjusted for unequal sample size. Because many of the independent variables were intercorrelated (Appendix), all variables also were considered simultaneously in a multiple regression procedure to determine the relative importance of each. The level of significance for statistical tests was set at $P \leq 0.05$ unless noted otherwise.

TABLE 1. Total volume delivered/feeding trip and estimated volume delivered·nestling^{-1}·h^{-1} for Gray Catbird young of different ages.[a]

Age (x) (days)	Number of trips sampled	Volume (cm^3) delivered/trip ($\hat{Y}$)[b] ($\bar{x} \pm$ SD)	Volume (cm^3) delivered·nestling^{-1}·h^{-1}[c]
0	11	0.10 ± 0.08	0.09
1	28	0.11 ± 0.07	0.24
2	19	0.14 ± 0.11	0.41
3	12	0.24 ± 0.15	0.60
4	31	0.26 ± 0.14	0.80
5	23	0.27 ± 0.12	1.00
6	23	0.41 ± 0.27	1.22
7	46	0.38 ± 0.25	1.44
8	11	0.35 ± 0.35	1.67

[a] For the size distributions of individual food items, see Johnson et al. 1980.
[b] Statistics are: $\hat{Y} = 0.075 + 0.047x$, $r^2 = 0.96$.
[c] See text for details on how this was computed.

RESULTS AND DISCUSSION

Nearly all factors considered had some effect on feeding or brooding frequencies, and interaction effects were common.

Nestling age.—The average number of food deliveries·brood^{-1}·h^{-1}, ($\hat{Y}$), increased linearly with the $\log_{10}$ of nestling age, (x), for both male ($\hat{Y} = 4.14 + 3.74 \log[x + 1]$, $r^2 = 0.76$) and female ($\hat{Y} = 1.55 + 3.43 \log[x + 1]$, $r^2 = 0.83$) parents. The logarithmic relationship shows that most of the increase in feeding frequency occurred early in the nestling period. A similar relationship between nestling age and feeding frequency has been reported for other species (Morton et al. 1972, Westerterp 1973).

The volume of food delivered to nestlings/unit time depends not only on frequency of feedings but also on the amount of food in each delivery. Both volume delivered/feeding trip and the variability in food volume delivered/feeding trip increased with nestling age (Table 1). These trends occurred through 8 days of age, after which food could not be sampled. Most of the increased energy requirements of older catbird nestlings were met by enlarging the amount of food delivered/feeding trip, rather than increasing the feeding frequency.

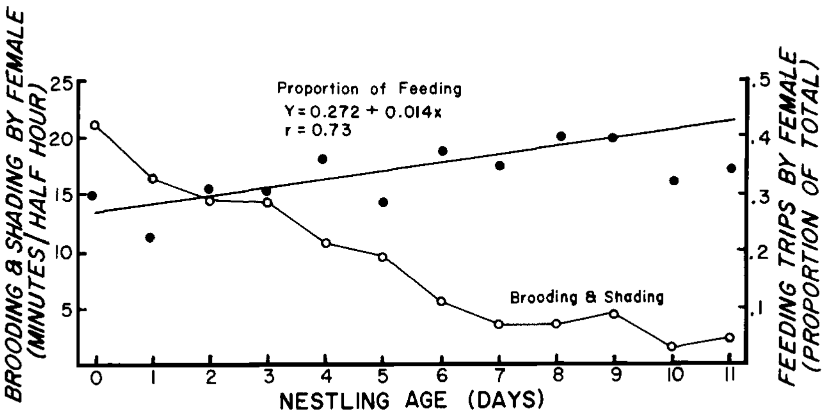

Fig. 1. Nest attendance and proportion of nestling feedings by female catbirds in relation to nestling age.

This was accomplished by feeding larger items as the nestlings increased in size and were able to consume them (Johnson et al. 1980). Volume delivered/feeding trip also increased with nestling age in Great Tits, *Parus major* (Royama 1966); Starlings, *Sturnus vulgaris* (Westerterp 1973); and Purple Martins, *Progne subis* (Walsh 1978). In our study, the number of items delivered/trip was unrelated to nestling age (Johnson and Best MS).

The volume of food delivered·nestling^{-1}·h^{-1} for each age in 1978 was estimated by multiplying values from regression equations of number of feeding trips·nestling^{-1}·h^{-1} ($\hat{Y}$ = 1.16 + 2.67 log[x + 1], r^2 = 0.90) and volume delivered/feeding trip ($\hat{Y}$ = 0.075 + 0.047x, r^2 = 0.96) versus age (Table 1). The food requirements of the young increased with age during the entire food-sampling period. Food intake of Great Tit (Van Balen 1973), Starling (Westerterp 1973), and Purple Martin (Walsh 1978) nestlings initially increased rapidly and then leveled off, but data could be collected for these species further into the nestling-development period than for catbirds. Food intake of catbird young probably begins to level off beyond 8 days of age.

The proportion of feeding trips made by females was inversely related to the amount of time spent brooding and shading the nestlings (r = −0.23, n = 2,075 half-hour intervals). As the nestlings grew, females spent less time brooding and shading and, consequently, increased their contribution to the total food delivery (Fig. 1, see also Pinkowski 1978). The feeding rates of female catbirds were always lower than those of males (averaging about one-half those of the males over the entire nestling period), but females had almost sole responsibility for brooding and shading nestlings.

The average time spent brooding and shading by females decreased linearly until nestlings were 7 days old, after which little change in nest attendance occurred (Fig. 1). Shading usually occupied only a small percentage of the females' time, but it was important when the sun shone directly on the nest (Table 2). Shading time increased as the amount of direct sunlight on the nest increased from 0 to 50% but remained relatively constant at greater exposures. Nestlings usually moved away from direct sunlight and occupied a shaded part of the nest when its exposure to sunlight was low; with exposure above 25%, however, they depended on shading by the female. Brooding decreased substantially as nestlings grew older, but shading time declined only slightly (Table 3). As young grew and began to develop plumage, they evidently could tolerate low temperatures but still required protection from excessive heat from the sun.

Brood size.—Brood size was another important factor affecting feeding frequencies. Feeding frequencies increased similarly with brood size during both years of observation; thus, 1977 and 1978 data were combined (Fig. 2). Feeding frequencies/brood (F = 71.73, df = 3, 44) and feeding frequencies/nestling (F = 6.58, df = 3, 44) varied significantly among broods of different size. Newman-Keuls multiple range tests were used to determine where the

TABLE 2. Shading time by female catbirds in relation to the percentage of the nest exposed to direct sunlight.

Percentage of nest in direct sunlight	Number of half-hour intervals observed	Time spent shading in min/half hour ($\bar{x}$ ± SD)
0	1,609	1.3 ± 4.9
1–25	55	7.6 ± 10.4
26–50	76	12.1 ± 12.6
51–75	28	11.6 ± 12.0
76–100	15	13.1 ± 12.9

differences occurred. Feeding frequencies/brood were significantly different among all brood sizes. The number of feeding trips·nestling^{-1}·h^{-1} for broods of 2 or 3 was significantly larger than that for broods of 4 or 5. The volume of food delivered/feeding trip, as determined from food samples collected from broods of 3 through 5 in 1978 (no broods of 2 were available for sampling), did not change significantly with brood size (two-way ANOVA); adults, therefore, did not adjust for different brood sizes in this way. Also, growth rates of nestlings from different-sized broods were not significantly different (Johnson and Best MS). Therefore, it appears that as brood size increases, food requirements/nestling decrease. This trend also has been reported for many other species (Moreau 1947, Lack and Silva 1949, Gibb 1950, Best 1977, Walsh 1978, Pinkowski 1978) and could be because the ratio of exposed surface area to biomass decreases with increasing brood size, resulting in lower thermoregulatory costs/nestling (Royama 1966, Mertens 1969).

Time spent brooding and shading nestlings was not significantly related to brood size according to a two-way ANOVA, contrary to results reported for Purple Martins by Walsh (1978). The lack of uniformity in weather conditions when different nests were being observed and the variation in the exposure of different nests to the sun could have masked brood-size effects in this analysis. In the multiple regression results, however, brooding decreased significantly with greater brood size. This could be because females are forced to sacrifice some brooding time in order to satisfy the greater food demands of a larger brood or because less brooding is required as the ratio of exposed surface area to biomass of nestlings decreases.

Time of day.—In general, time of day had relatively little effect on feeding frequencies (Fig. 3), although a significant difference was found (F = 5.57, df = 15, 1,712). Feeding rates for the first hour after females left the nest in the morning were significantly greater than those for all other times (Newman-Keuls multiple range test). This was probably because nestlings were very hungry after a night of fasting, and thus they begged more energetically. Feeding rates also increased slightly at 1100 and in early evening before females returned to the nest to brood for the night, but these values were statistically different only from those at 1200. No other differences were found. Peak feeding times for catbirds in Kendeigh's (1952) study were at 1000, 1200, and 1800; lowest rates occurred from 1300–1700, when temperatures were highest. Others have reported highest feeding rates in early morning and lowest rates at midday (Kluyver 1950, Best 1977, Pinkowski 1978).

TABLE 3. Time female Gray Catbirds spent brooding and shading nestlings of different ages.

Age (days)	Number of hours observed	Time spent brooding in min/h ($\bar{x}$ ± SD)[a]	Time spent shading in min/h ($\bar{x}$ ± SD)[b]
0	100	34.5 ± 17.9	7.7 ± 19.0
1	86	27.5 ± 18.1	5.3 ± 14.6
2	78	25.0 ± 17.2	4.3 ± 12.2
3	92	22.8 ± 16.0	5.8 ± 11.3
4	97	14.9 ± 16.2	6.6 ± 14.5
5	90	15.6 ± 17.8	3.8 ± 12.1
6	89	4.2 ± 11.1	7.0 ± 16.0
7	98	3.5 ± 7.3	4.0 ± 10.5
8	106	5.2 ± 10.9	2.1 ± 7.5
9	103	4.4 ± 11.3	4.6 ± 14.0
10	93	2.0 ± 5.3	1.4 ± 4.8
11	26	1.3 ± 1.2	3.3 ± 9.0

[a] Statistics are: predicted time brooding = 30.19 − 3.05 (Age), r^2 = 0.90.

[b] Statistics are: predicted time shading = 6.67 − 0.36 (Age), r^2 = 0.48.

Brooding and shading by females were related indirectly to time of day (Fig. 3). Usually brooding was highest in early morning and in evening and lowest in early afternoon, paralleling diel changes in ambient temperature (see *Weather*). Shading by females, which peaked in early afternoon, was closely correlated with changes in light intensity throughout the day. Shading by males was minimal, never averaging more than 0.8 min for any half-hour period in the day.

Time of season.—Feeding frequencies changed little with time of season. Royama (1966) re-

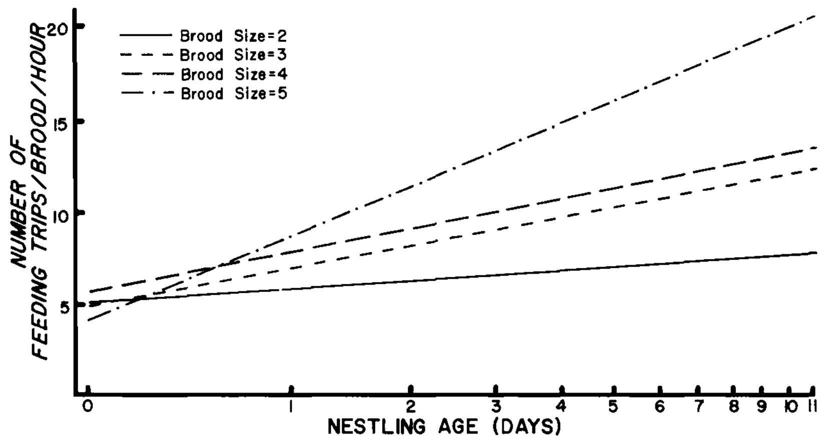

Fig. 2. Feeding frequencies·brood^{-1}·h^{-1}, ($\hat{Y}$), for different brood sizes (x = nestling age in days). Statistics for the respective brood sizes are: brood size 2, $\hat{Y} = 5.05 + 2.43 \log(x + 1)$, $r^2 = 0.52$; 3, $\hat{Y} = 4.85 + 6.87 \log(x + 1)$, $r^2 = 0.81$; 4, $\hat{Y} = 5.67 + 7.16 \log(x + 1)$, $r^2 = 0.83$; 5, $\hat{Y} = 4.10 + 15.22 \log(x + 1)$, $r^2 = 0.90$. The regression line for the brood of 5 has been extended below 1 day old, but no observations were made for that brood size at 0 day old.

ported that Great Tits made more frequent food deliveries to early broods because food size was smaller than that delivered to late broods, attributable to a seasonal change in nestling diet. In our study, time of season also affected prey species chosen (Johnson and Best MS; e.g. caterpillars were eaten more frequently early in the season, moths and grasshoppers more commonly later), but sizes of individual food items delivered were not significantly different (two-way ANOVA) throughout the season. Thus, food delivery rate/nestling was not affected by the type of food delivered.

Time of season had a slight, indirect effect on brooding but not on shading. Average daytime temperatures were significantly greater (two-way ANOVA, $F = 9.74$, df = 4, 4) during July than during June or August for both years of the study (an average of 2.9° and 2.7°C higher than the average for the rest of the season for 1977 and 1978, respectively). The average amount of time spent brooding was least (but not significantly, two-way ANOVA) in July.

Weather.—Precipitation influenced feeding frequencies of both males and females (Fig. 4). As rain increased in intensity and duration, feeding frequencies declined for both males

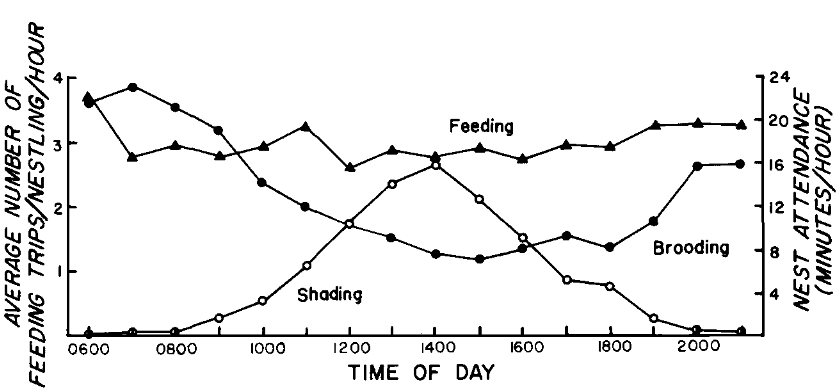

Fig. 3. Feeding frequency by both catbird parents and time spent brooding and shading by females in relation to time of day.

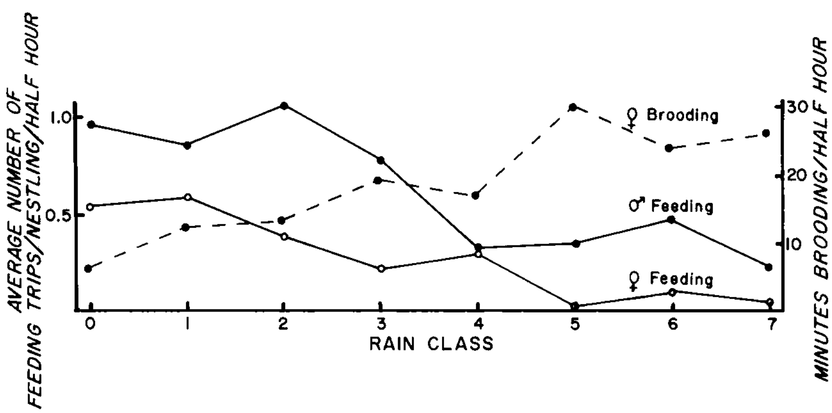

Fig. 4. Feeding frequencies and nest attendance in relation to precipitation. Rain increases in intensity and duration from 0 (no precipitation) to 7 (heavy rain >50% of the time).

and females (two-way ANOVA), although the relationship was significant only for males ($F = 5.86$, df = 4, 12). Females spent significantly more time brooding nestlings when rain increased ($F = 6.60$, df = 4, 12); males never brooded nestlings in the rain. Feeding rates of males declined during rain, probably because they spent less time foraging in the rain.

Temperature affected feeding rates mostly at temperature extremes (Fig. 5). Feeding by females dropped essentially to zero at the extremes, corresponding to maximal time spent either brooding or shading. Males' feeding rates stayed relatively constant at all temperatures (major variations probably were the result of small sample size); thus, males did not compensate for the lowered feeding rates of females at temperature extremes. Regression analyses showed that an increase in temperature up to 32°C (above this level brooding was unimportant) resulted in a linear decrease in time spent brooding by the females; conversely, temperature increases above 18°C (below this level shading ceased) caused an exponential increase in time spent shading (Fig. 6).

At higher light intensities, brooding decreased ($\hat{Y} = 8.00 - 0.49x$, $r^2 = 0.61$) while shading increased ($\hat{Y} = -1.00 + 1.04x$, $r^2 = 0.88$). The reverse was true as relative humidity became greater (brooding: $\hat{Y} = -0.28 + 1.52x$, $r^2 = 0.96$; shading: $\hat{Y} = 6.69 - 0.90x$, $r^2 = 0.72$). The relationships of these two weather parameters to nest attendance, however, may be attributed largely to their correlation with temperature (Appendix, see also *Relative importance of variables*). The multiple regression analysis (Table 4) verified three of the four significant relationships obtained when the variables were analyzed individually. The seem-

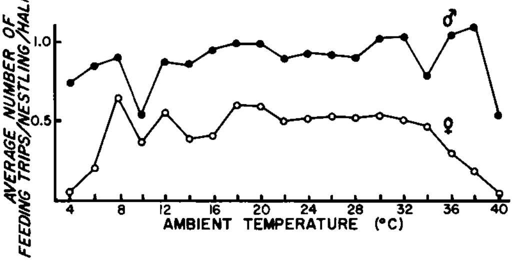

Fig. 5. Feeding frequencies in relation to ambient temperature.

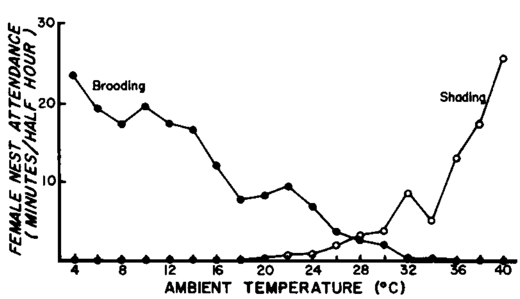

Fig. 6. Female nest attendance in relation to ambient temperature. Statistics for brooding (calculated from 4° through 32°C) are: $\hat{Y} = 25.70 - 0.81x$, $r^2 = 0.96$. Those for shading (calculated from 18° through 40°C) are: $\log(\hat{Y} + 1) = -1.14 + 0.06x$, $r^2 = 0.96$.

TABLE 4. Standardized regression coefficients for factors potentially affecting feeding, brooding, and shading of Gray Catbird nestlings.

Variable	Feeding trips · nestling^{-1} · half hour^{-1}		Brooding by female (min/half hour)	Shading by female (min/half hour)
	Male	Female		
Brood size	−0.06*[a]	−0.29**	−0.11**	−0.01
Nestling age	0.20**	0.30**	−0.64**	0.01
Ambient temperature	−0.17**	−0.15**	−0.36**	0.42**
Relative humidity	−0.04	0.02	0.19**	0.05
Wind speed	0.02	0.08**	0.06**	−0.06*
Cloud cover	−0.05	−0.03	0.01	−0.02
Barometric pressure	−0.18**	−0.03	0.00	0.14**
Light intensity	0.01	−0.00	0.14**	0.14*
Rain	−0.14**	−0.11**	0.19**	0.01
Multiple R^2	0.18	0.21	0.61	0.30

[a] * = significant at $P \leq 0.05$, ** = significant at $P \leq 0.01$.

ingly positive relationship between light intensity and brooding in the multiple regression analysis probably is spurious, resulting from high intercorrelation among variables. The relationships of feeding frequencies with relative humidity were the inverse of those with temperature. Changes in shading and brooding were complementary as light intensity increased; thus, the sum of the time spent in nest attendance remained relatively constant. Correspondingly, feeding frequencies were similar at all light intensities.

When considered individually, the other weather parameters (wind speed, cloud cover, and barometric pressure) were not significantly related to either feeding frequencies or nest attendance. In the multiple regression analysis, however, only cloud cover lacked some significant relationship (Table 4). We have no explanation for the apparent relationships of wind speed and barometric pressure to feeding rates or of barometric pressure to shading. Brooding increased at greater wind speeds, while shading decreased, probably because the dissipation of nestling body heat increases with greater convectional cooling.

Relative importance of variables.—The absolute values of the standardized regression coefficients (Table 4) were used to evaluate the relative importance of each independent variable in determining feeding frequencies and nest attendance. (Time of day and time of season were nonlinear variables in the regression analysis; consequently, they are not included in the list of standardized regression coefficients.) Nestling age was the most important variable affecting feeding frequency/nestling by both male and female catbirds. This would be expected as energy demands of the young increase with age. Although brood size was second in importance for females, it was of lesser importance for males. Females must spend a certain amount of time brooding and shading regardless of brood size. Thus, feeding frequencies/brood are more constant for females than for males, and, consequently, feeding frequencies/nestling decrease to a much greater extent for females than for males as brood size increases (see also Hails and Bryant 1979). Barometric pressure was the second most important variable predicting feeding frequencies by males. Ambient temperature and rain were third and fourth, respectively, for both males and females, with feeding decreasing as these variables increased (as discussed in *Weather*).

Brooding by females was influenced mainly by nestling age (Table 4). As nestlings grow older, they develop plumage and the ability to thermoregulate, dramatically reducing the need for brooding. The second most important variable affecting brooding was ambient temperature; rain and relative humidity were of lesser importance. Of the factors affecting shading, ambient temperature was most important, followed by light intensity and barometric pressure.

The predictive ability of the combination of variables measured (see R^2, Table 4) was quite low for both male and female feeding frequencies. The R^2 values could be low because factors not measured largely account for variation in feeding frequency. But it is also possible that feeding, particularly over short time intervals (0.5 h in our study), varies unpredictably and that feeding rhythms are adjusted over broader time periods to assure sufficient food delivery for normal nestling growth. Regulation of nestling body temperature, however, requires more immediate responses to changes in the variables measured; thus, their predictive ability for brooding and shading was greater than that for feeding frequencies (Table 4).

Acknowledgments

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APPENDIX. Correlation coefficients of independent variables measured each hour during feeding frequency observations (includes only those where $P \leqslant 0.01$).[a]

	Time of season	Time of day	Ambient tempera-ture	Relative humidity	Wind speed	Cloud cover	Baro-metric pressure	Light intensity
Time of day								
Ambient temperature		0.38						
Relative humidity		−0.43	−0.58					
Wind speed	−0.17	0.13	0.28	−0.37				
Cloud cover		−0.14	−0.26	0.52	−0.16			
Barometric pressure			−0.35		−0.13	−0.18		
Light intensity			0.32	−0.45	0.26	−0.28	0.22	
Rain			−0.12	0.25	−0.09	0.30	−0.11	−0.20

[a] Sample sizes for the calculated values range from 703 to 969.