Do female Yellow Warblers (*Dendroica petechia*) incubate while in the nest during the laying period?

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Introduction

Although some passerine species heat their eggs during the brief periods of nest attentiveness early in the laying period (e.g., Haftorn 1981), egg temperature data are not available for Yellow Warblers (*Dendroica petechia*). As part of a larger study on the effect of Brown-headed Cowbird (*Molothrus ater*) eggs on female Yellow Warbler nest attentiveness, I recorded Yellow Warbler nest temperatures to determine whether diurnal cycles in attentiveness exist that could confound observations made at only one time during the day. Periodogram analysis was used to ascertain whether significant periodic components existed in the nest-temperature data.

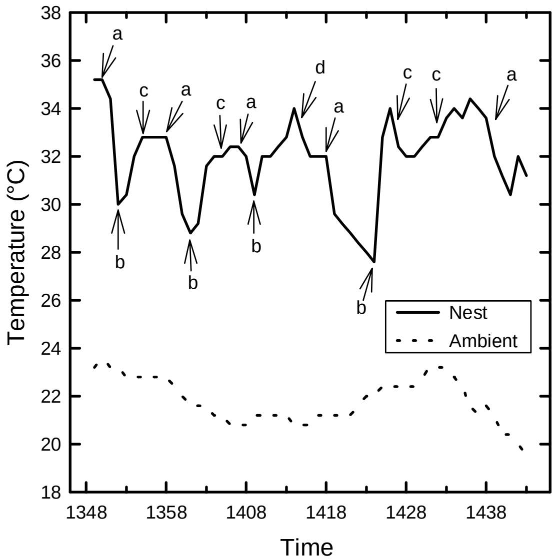
Methods

In 1994, nest and ambient temperatures were recorded at Yellow Warbler nests from the evening of the first laying day (LD1) to LD3, and throughout incubation. Recordings were made at each nest using two 6-cm thermistor probes attached to a remotely located Squirrel Data Logger. A sharp piece of wire was used to make a small hole extending from the bottom of the nest up into the nest cup. One thermistor was threaded through the bottom of the nest until the tip extended approximately 0.5 - 1 cm into the cup itself, alongside or amongst the eggs. The second thermistor was then mounted beside or under the nest, where it was shaded from sunlight. Mustad #22 Dry Fly hooks had previously been bound to each thermistor using thread. These hooks anchored the thermistor to either the nest or nearby vegetation. Squirrel Data Loggers were programmed to record the temperature of both thermistors at either 15-s, 30-s, or 60-s intervals. As the data loggers have a limited memory capacity, they were detached from the thermistors every 1 - 3 days and the data were down-loaded to a computer. Because of the remote location of the logger from the nest, it was often possible to remove the logger without flushing the incubating female. Observations were made at nests where temperatures were being recorded, to verify that declines in nest temperature were recorded when females were away from the nest.

Periodogram analysis is based on the representation of a periodic function in a time-series data set as a series of sines and cosines, derived by a process called Fourier transformation (Wei 1989). Periodogram values were calculated for each Fourier frequency in both the nest and ambient temperature data sets, each Fourier frequency corresponding to a single periodic cycle in the data set. The periodogram value, therefore, is a numerical representation of the magnitude of the periodicity present in the data at each periodic cycle. For example, a periodogram value corresponding to the Fourier frequency for 24 hours that is larger than the periodogram value for 12 hours indicates there is a stronger 24-hour periodicity in the data than 12-hour periodicity. An F-statistic was calculated for each periodogram value to test the significance of the corresponding periodic cycle. If the data contained several significant periodic components, then Fisher's exact test for the maximum periodogram (T-) was calculated for each significant periodic component to determine which explained the most variation. This process was repeated for each periodogram ordinate. Fourier transformations and periodogram calculations were made using SPSS/PC+, while calculation of the F- and T- statistics were made using Quattro Pro for Windows. I then compared the periodicity of the temperature recordings between both the nest and ambient, and the laying and incubation data sets.

Results

Nest and ambient temperatures were recorded for at least 24 hours at three nests during the laying period, and at eight nests during the incubation period. Observations at nests in concert with measurements of nest temperature showed that temperature was highly correlated with female attentiveness (see Fig. 1, for example). Nest temperature was rarely above ambient temperature early in laying, but it increased relative to ambient temperature as laying progressed (Fig. 2). Nest temperature always exceeded ambient temperature



a - female left nest
b - female onto nest
c - male fed female at nest
d - light rain

Figure 1. Ambient and nest temperatures at Yellow Warbler nest 94-G151 on the third day of incubation. Arrows and letters indicate activity at the nest noted during the one hour observation period.

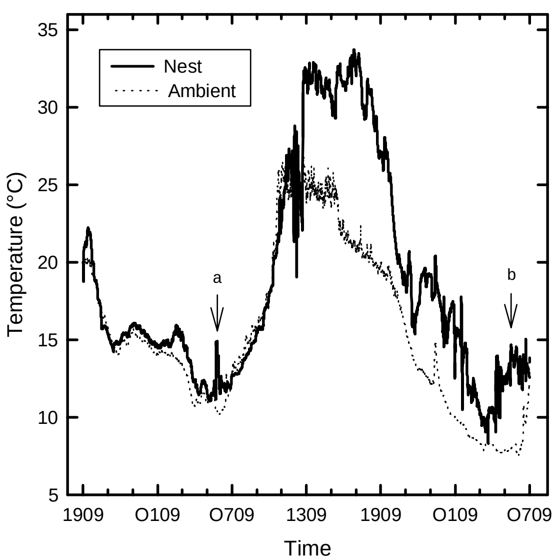


Figure 2. Ambient and nest temperatures at Yellow Warbler nest 94-S2 beginning the evening of the day on which the first egg was laid (30 May), and ending the morning the third egg was laid (1 June). Arrows indicate the approximate times the second (a) and third (b) eggs were likely to have been laid.

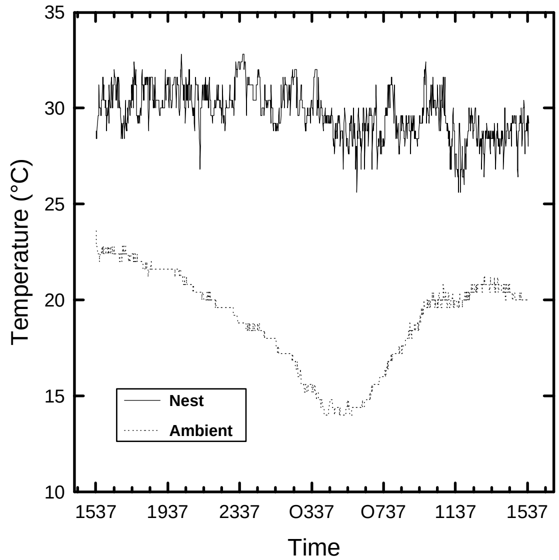


Figure 3. Ambient and nest temperatures at Yellow Warbler nest 94-G52 beginning the afternoon of the fourth day of incubation (6 June), and ending the afternoon of the fifth day of incubation (7 June).

during incubation (Fig. 3). Average nest temperatures during incubation ranged from 30 to 36°C for different nests.

Periodogram analysis identified an average of 7.33 significant cycles for nest temperatures during early laying versus an average of 9.0 significant cycles for the ambient temperature recordings taken simultaneously (see Table 1). Significant cycles in nest temperature data ranged from a minimum period of 0.83 hours to a maximum period of 21.16 hours, whereas significant cycles in ambient temperature data ranged from 1.4 to 21.1 hours (see Table 1). Most periodicity in both the nest and ambient temperature data is explained by long-period cycles, rather than short-period cycles, as indicated by the large periodogram, *F*-, and *T*-statistic values for long-period cycles (Table 1).

Relative to nest temperatures early in the laying cycle, nest temperatures during incubation showed more significant cycles (mean = 31.0 significant cycles; see Table 2), whereas the number of significant cycles in ambient temperature did not change from the laying period (mean = 10.0 significant cycles). Significant cycles in nest temperature during incubation ranged from 1.08 to 28.8 hr, whereas significant cycles in ambient temperature ranged from 6.1 to 25.8 hr. Mean periodogram values of the maximum peak of nest temperature during incubation were lower than those during laying (8407.4 vs. 48744.0, respectively; Table

Table 1. Periodogram values and duration of the corresponding periodic cycles in nest and ambient temperature recordings during the Yellow Warbler laying period.

Re-cording	No. signif. cycles	Cycle dura-tion (h)	Periodo-gram values	F[b]	T[c]
Nest 1	5	21.2	71225.8	4785.7	0.788
		10.6	14979.0	252.9	0.785
		7.1	1767.1	25.3	0.431
		5.3	952.7	13.5	0.408
		3.5	301.5	4.2	0.218
Nest 2	7	21.1	53492.3	5131.0	0.798
		10.6	8329.1	180.9	0.616
		7.1	1636.8	31.9	0.315
Ambient 1[d]	7	21.1	39862.6	3645.4	0.732
		10.6	5701.4	150.5	0.390
		7.1	4689.1	121.2	0.527
		4.2	957.0	23.0	0.227
		5.3	912.3	21.9	0.281
		3.0	507.4	12.0	0.204
		3.5	373.6	8.8	0.217
Nest 3	10	16.7	21513.9	2255.1	0.529
		8.3	11186.3	760.5	0.586
		4.2	2837.4	150.2	0.359
		5.6	2710.1	143.0	0.535
		2.8	442.2	22.0	0.188
		3.3	425.5	21.1	0.223
		1.1	152.1	7.5	0.102
		1.4	71.3	3.5	0.053
		0.8	69.9	3.4	0.055
		1.7	63.8	3.1	0.053
Ambient 2[e]	11	16.7	32001.9	3343.4	0.626
		8.3	11373.1	571.6	0.594
		5.6	2341.9	95.9	0.302
		4.2	2139.7	87.2	0.395
		2.8	769.9	30.5	0.235
		3.3	639.1	25.2	0.242
		2.1	539.8	21.3	0.270
		2.4	219.1	8.6	0.150
		1.9	201.2	7.8	0.162
		1.5	86.0	3.3	0.083
		1.4	84.2	3.2	0.088

[a] Periodogram values indicate the amount of periodicity present in the data for each cycle of specific duration. [b] *F*- value calculated to test the significance of each periodogram value. [c] *T*- value calculated to test for the maximum periodogram. [d] Ambient temperature 1 was recorded simultaneous to recordings at Nests 1 and 2. [e] Ambient temperature 2 was recorded simultaneous to recording at Nest 3.

2), although mean periodogram values for the maximum peak for ambient temperature during incubation were also lower than during laying (12571.7 vs. 35932.3, respectively).

Discussion

As noted for other passerine species (Haftorn 1981; Haftorn and Reinertsen 1985), Yellow Warbler nest temperatures gradually increased above ambient temperatures through the laying period as female attentiveness increased. Variation in nest temperature between nests was likely due to differences in the position of the thermistor relative to the incubating female within the nest. Nest temperature during early laying contained multiple significant periodic components. Significant cycles ranged in duration from just under 1 hour to 21 hours, however, maximum periodogram values were associated with long-period cycles. These results indicate most of the fluctuation in nest temperature during laying occurs over periods of slightly less than 24 hours in duration. Whereas significant temperature fluctuation occurs over several hours (about 12.5 hours), on average the magnitude of these fluctuations was quite small relative to longer-term fluctuations. The similarity in the periodic components of nest temperature in early laying, and the ambient temperature recordings taken simultaneously, suggests that much of the fluctuation in nest temperature over a 24-hour period is due to changes in ambient temperature, rather than variation in female incubation behaviour. This observation is consistent with the observations of female Yellow Warbler nest attentiveness between 1430 and 1730 h, which demonstrates that relatively little time is spent in the nest early in the laying period.

Periodogram analysis of nest temperatures during incubation indicates a much different pattern of temperature fluctuation compared to either nest temperature during laying or ambient temperature during incubation. Although maximum periodogram values still occurred at long-period cycles (28.8 hours), numerous short-period cycles explain much of the variation in nest temperature. This pattern of periodic components reflects the rapid fluctuations in nest temperature recorded during incubation, due to rapid warming of the nest when the female begins incubating, followed by rapid cooling of nest temperature toward ambient temperature after the female leaves the nest. The rate nest temperatures cool is not an accurate indicator of egg temperature, however, because eggs lose heat much less rapidly. Because egg temperatures fall in cold weather during incubation even when the female remains on the nest (Weeden 1966; Haftorn and Reinertsen 1985; Haftorn and Reinertsen 1990), ambient

Table 2. Mean (± SE) number of significant periodic cycles, mean maximum and minimum periodogram values, and mean length of maximum and minimum periodic cycles in nest and ambient temperatures during the incubation period. Values are averaged among all nests at which recordings were made.

Variable	Nest temperature (n)	Ambient temperature (n)
Mean number of significant cycles	31.0 ± 6.5 (9)	10.0 ± 2.1 (8)
Mean max. periodogram value	8407.4 ± 2184.5 (9)	12571.7 ± 3909.8 (8)
Mean max. duration of significant periodic cycle (h)	28.8 ± 6.4 (9)	25.8 ± 2.1 (8)
Mean min. periodogram value	49.8 ± 9.3 (9)	565.6 ± 457.8 (8)
Mean min. duration of significant periodic cycles (h)	1.08 ± 0.3 (9)	6.1 ± 1.9 (8)

temperatures are expected to influence the periodicity of egg temperatures to some extent, in addition to patterns of female attentiveness. The similarity between the periodic components of nest temperature and ambient temperature during laying over the 24-hour period indicate the low female nest attentiveness observed between 1430 and 1730 h is representative of female attentiveness patterns throughout the day during early laying.

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