J. Field Ornithol., 72(3):369–379

AN INEXPENSIVE METHOD FOR QUANTIFYING INCUBATION PATTERNS OF OPEN-CUP NESTING BIRDS, WITH DATA FOR BLACK-THROATED BLUE WARBLERS

Elizabeth M. Joyce, T. Scott Sillett[1], and Richard T. Holmes
Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA

Abstract.—Quantifying incubation patterns has often involved long observation periods in the field, video cameras, or the use of other electronic devices that sometimes require the partial destruction of clutches and insertion of artificial eggs. In this study, we used an inexpensive, nondestructive method involving temperature probes combined with data loggers to examine the incubation rhythm of female Black-throated Blue Warblers (*Dendroica caerulescens*). The method provided detailed records of on–off patterns for females for selected 24-h periods during incubation. Female warblers spent an average (±SE) of 64.0% of daylight hours incubating in bouts lasting 20.5 ± 1.5 min and made 2.4 ± 0.1 departures from the nest/h on trips that lasted 10.6 ± 0.7 min. Incubation bouts were longer and females spent more time incubating per hour in the mornings and late afternoons than at mid-day. Older females had longer incubation bouts and tended to have shorter incubation periods than did yearling females, suggesting that experienced individuals were more effective incubators. Because of its ease of use and because nests with probes were not depredated at a higher rate than controls, we suggest that the temperature probe/data logger method is an efficient and effective way to quantify incubation rhythms for open-cup nesting birds.

UN MÉTODO POCO COSTOSO PARA CUANTIFICAR LOS PATRONES DE INCUBACIÓN DE AVES CON NIDOS DE COPA, INCLUYENDO DATOS DE *DENDROICA CAERULESCENS*

Sinopsis.—El cuantificar los patrones de incubación a menudo depende de largos períodos de observación en el campo, uso de videocámaras, o el uso de otros aparatos electrónicos que a veces requieren la destrucción parcial de camadas y la introducción de huevos artificiales. En este estudio usamos un método de poco costo, no destructivo, que envuelve el uso de sensores de temperatura combinados con registros de datos para examinar el ritmo de incubación de hembras de *Dendroica caerulescens*. El método provee registros detallados de patrones activos-inactivos para hembras en períodos selectos de 24 horas durante la incubación. Las hembras usaron un promedio de 64.0% de las horas diurnas incubando incubando en períodos de 20.5 ± 1.5 (SE) minutos y tuvieron 2.4 ± 0.1 salidas del nido/hora en viajes que tardaron 10.6 ± 0.7 minutos. Los períodos de incubación fueron más largos y las hembras usaron más tiempo incubando por horas en las mañanas y al final de las tardes que a mediados del día. Las hembras mas viejas tuvieron períodos mayores de incubación y la tendencia a tener menores períodos de incubación que hembras de un año, sugiriendo que los individuos más experimentados incubaban más efectivamente. Sugerimos que el método de sensores y recopiladores de datos es un método eficiente y efectivo para cuantificar los ritmos de incubación de aves que anidan en copas abiertas. Esto se debe a la facilidad de usarlos y porque los nidos experimentales no sufrieron una tasa mayor de depredación que los nidos control.

Parental care plays an important role in the reproductive success of most bird species. An individual's fitness is determined in large part by its reproductive success (Stearns 1992), and reproductive success, in turn, is influenced by the amount and quality of care given to the offspring by

[1] *Current address: U.S. Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA*

the parents (Kuitunen and Suhonen 1991; Reid et al. 2000). Parental care, however, is also costly to the parent in terms of time and energy as well as risk to their own survival (Carey 1980; Curio 1988). Incubation, in particular, must be adjusted to balance the incubating bird's energy requirements and the thermal requirements of the egg (Haftorn 1988; Moreno 1989; Reid et al. 2000). Because leaving the nest allows the eggs to cool and probably increases the risk of nest predation, the length and frequency with which the incubating parent must leave the nest may have important consequences to reproductive output.

Traditionally, the method used to document incubation rhythms of birds has involved hourly or day-long watches at nests (e.g., Nolan 1978; Halupka 1994; Norment 1995), which even when done with care, could influence parental behavior. Others have used light-sensitive photo-resistors (Weeden 1966), electronic balances under nests (Jones 1987), partial destruction of clutches and use of thermocouples attached to, or placed within, eggs (e.g., Zerba and Morton 1983; Morton and Pereyra 1985; Weathers and Sullivan 1989), and video cameras (Martin and Ghalambor 1999). In this study, we used an inexpensive system involving temperature probes and data loggers to examine the incubation rhythms of the Black-throated Blue Warbler (*Dendroica caerulescens*), a species in which only the female incubates. Our objective was to employ a system that was non-destructive and inexpensive, that could be easily managed, and that would provide day-long or even 24-h records of incubation patterns to assess how they varied with time of day, time of season, stage of the incubation period, and female age. Such data could be used subsequently to examine other related questions, such as how birds allot their incubation time and how this might influence nesting success.

STUDY AREA AND STUDY SPECIES

This study was conducted in June and July 1997 at the Hubbard Brook Experimental Forest in West Thornton, New Hampshire. This forest consists of northern hardwoods, dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). The understory is composed mostly of hobblebush (*Viburnum alnifolium*), striped maple (*Acer pensylvanicum*), and saplings of beech and sugar maple plus ferns and herbs (Bormann and Likens 1979; Holmes 1990).

Black-throated Blue Warblers are small passerine birds that breed from northern Georgia, along the Appalachian mountains to the northeastern U.S. and eastern Canada, and west to Michigan and northeastern Wisconsin (Holmes 1994). In New Hampshire, they occupy well-developed northern hardwoods or mixed coniferous/deciduous forests, and generally nest in hobblebush and other low shrubby vegetation, at an average height of 0.6 m above ground (Holmes 1994). Clutch size is normally four eggs (mean and mode; Holmes et al. 1992; Holmes 1994), and nests are incubated for 12–13 days. Using plumage characteristics (Pyle 1997), we aged female as either yearling or older individuals. Yearlings were in their first breeding season, having hatched the previous summer, while older females were in their second or later breeding year.

METHODS

Temperature changes within Black-throated Blue Warbler nests were used to quantify the arrivals and departures of females at the nest. These data were obtained by inserting the probe end of a thermistor sensor cable into the bottom of each nest after the clutch was completed. Probes were slowly worked into the nest from the underneath, following the weave of the nest, until they were just below the nest lining. Thermistor cables were attached to an Onset Computer Corp. StowAway® XTI data logger, hidden 1–2 m away in the leaf litter and enclosed in plastic waterproof containers. Loggers had a thermal time constant of 3 min when used with external probes and recorded temperature once every minute for 24 h in steps of 0.37°C. Electronic components were relatively inexpensive, the thermistors costing about U.S. $20 each and data loggers about U.S. $120 (available from Ben Meadows Co., Atlanta, GA or Forestry Supplies, Inc., Jackson, MS).

Incubation patterns were recorded at each nest for a 24-h period at approximately 2-d intervals, beginning with the day after clutch completion. Most sampling was done on clear or overcast, but not rainy, days; sampling was discontinued or not initiated when rain was heavy. Loggers were activated and removed in late morning or early afternoon to avoid flushing the female during cooler parts of the day. Probes were left in place at each nest to minimize disturbance, while data loggers, which were in more limited supply, were rotated among nests. Data were downloaded onto a laptop computer in the field. To decrease the risk of depredation due to our activities, we always wore rubber gloves and boots whenever we approached nests, as recommended by Whelan et al. (1995).

Data analysis.—We extracted incubation patterns after downloading data from the logger by first printing each 24-h incubation record (Fig. 1) and then enlarging the graph approximately six-fold for more detailed analysis. A major drop or increase in temperature was considered to indicate the arrival or departure of the female (i.e., the beginning or end of an incubation bout; see Fig. 1). These patterns were verified by videotaping the arrivals and departures of a female at one probed nest. The frequency of arrivals and departures, as measured by the distances on the chart from when a female left the nest until she returned, and her time spent incubating (see definitions below) were then obtained from the tracing. Using the known duration of each record, we converted distances back to time, and calculated the duration and timing of incubation events.

The daylight portion of each 24-h sample was divided into three 4-h observation periods, based on time of day (morning, 0600–1000 h; midday, 1100–1500 h; and late afternoon, 1600–2000 h). These 4-h observation periods were the units of replication for all statistical analyses. For each of these periods we determined the (1) duration of each incubation bout (the interval between a female's beginning to incubate and depart-

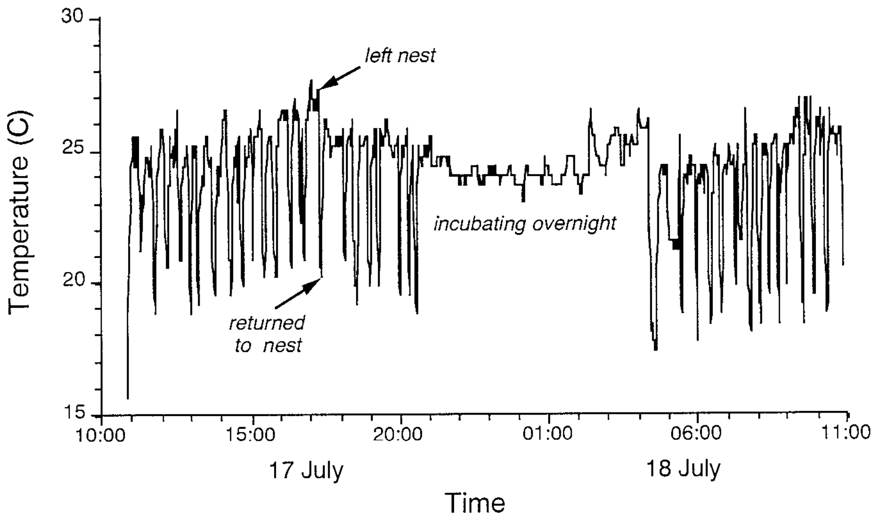

FIGURE 1. Incubation record for a female Black-throated Blue Warbler as measured by a temperature probe inserted directly under the nest lining. In this example, the temperature logger was activated at 1052 h on 17 July, and deactivated at 1050 h on 18 July. The female returned to the nest for the night at 2031 h and departed for the first time in the morning at 0423 h. Female departure from nest is indicated by sudden drop in temperature, resulting in a large downward spike. Bottom of spike indicates when female returned and resumed incubating, resulting in a rapid increase in nest temperature. Small spikes indicate minor variations in nest temperatures resulting from female movements on the nest.

ing); (2) departures per hour (number of times a female left the nest during an observation period divided by observation-period length); and (3) mean percent of time incubating per 4-h observation period. Observation periods were also grouped by stage of the 12–13 d incubation period (early, days 1–4; mid, days 5–8, and late, days 9–12 or rarely 13), by individual female, and by age of female.

Because data were missing for some females due to weather, we analyzed the incubation-pattern data with a split-plot, univariate repeated-measures design (Milliken and Johnson 1992). Fixed effects in models were time of day, stage of incubation period, and female age. Because we took multiple measurements of incubation parameters for each female, "individual female" was included in the models as a variable nested within female age. "Individual female [female age]" was a random variable because we were not interested in any particular female(s), but selected those to study that were not being used in other ongoing experiments at Hubbard Brook. Mean daily ambient temperature was included in all models as a covariate. We obtained temperature data for each day for which we had incubation data from a U.S. Forest Service weather station about 500 m from the study area and at the same elevation and same aspect. Comparisons of mean incubation bout length, departures per hour, and time spent incubating per observation period were made with three separate analyses of covariance (ANCOVA); models were fit using the Residual Maximum Likelihood or REML method (Patterson and Thompson 1971; SAS Institute 1996). All statistical analyses were performed using the JMP computer program (SAS Institute 2000). Dependent variables were transformed when necessary to meet model assumptions. Data are presented, however, as untransformed means ± 1 SE.

RESULTS

Nests of nine Black-throated Blue Warbler females were found during the early building or egg-laying stages of first clutches of the season between late May and early June. All contained four eggs. Incubation began on the day the clutches were complete, and hatching occurred either 12 (seven nests) or 13 (two nests) days later. Six of the nine females were older individuals; three were yearlings.

Analyses of data from all observation periods combined showed that females spent an average of 64.0% ± 2.0% (n = 9) of daylight hours incubating (all females incubated continuously over the nights). During the day, the average incubation bout lasted 20.48 min ± 1.48 (n = 9). Females left their nests an average of 2.37 ± 0.14 (n = 9) times per hour and were away for periods averaging 10.57 ± 0.67 min (n = 9).

The duration of incubation bouts varied significantly with incubation stage and female age, but not with time of day, mean daily temperature or among individual females (Table 1). Females incubated for shorter bouts during midday compared to morning or late afternoon (Fig. 2a). Incubation bouts were longer, on average, for older females (22.4 ± 1.56 min, n = 6) than for yearlings (16.46 ± 2.04 min, n = 3).

Females also changed their rate of departure from the nest over the incubation period. The mean number of departures per hour varied significantly with incubation stage and time of day, but not with female age, daily temperature, or among individual females (Table 1). Females made more departures from the nest during the middle of the day than in early morning or late afternoon (Fig. 2b) and made fewer trips away from the nest in the first and third stage of the incubation period than in the second (Fig. 2c).

The percent of time incubated during an observation period varied significantly with time of day and among individual females, but not with the stage of incubation, average daily temperature, or female age (Table 1). Females spent more time on the nest in the morning and late afternoon than at midday (Fig. 2d).

The mean duration of incubation bouts was significantly related to the duration of the incubation period. Females with 12-day incubation periods spent significantly more time per incubation bout than did females with 13-day incubation periods (22.1 ± 1.3 versus 14.6 ± 0.03 min; $F_{1,7}$ = 8.12, $P < 0.025$). Female age class seemed to be related to the length of the incubation period. Both females that incubated for 13 days were

TABLE 1. Results of analyses of covariance of incubation patterns of female Black-throated Blue Warblers, with mean ambient temperature as covariate. All interactions between variables were not statistically significant ($P > 0.15$).

Source of variation	MS	df	F	P
Incubation bout duration				
Time of day	61.13	2	0.95	0.39
Incubation stage	272.69	2	4.22	0.02
Female age	397.85	1	6.15	0.04
Mean daily temperature	127.87	1	1.98	0.16
Individual female [female age][a]	79.66	7	1.23	0.29
Error	64.68	88		
Departure rate from nest[b]				
Time of day	0.55	2	3.90	0.02
Incubation stage	0.63	2	4.49	0.01
Female age	0.30	1	2.13	0.19
Mean daily temperature	0.02	1	0.17	0.68
Individual female [female age][a]	0.15	7	1.05	0.40
Error	0.14	86		
% time incubating				
Time of day	0.05	2	8.01	0.0006
Incubation stage	0.001	2	0.16	0.86
Female age	0.01	1	1.95	0.21
Mean daily temperature	0.01	1	1.55	0.22
Individual female [female age][a]	0.02	7	2.14	0.05
Error	0.007	86		

[a] Random effect; test statistic refers to shrunken predictor from REML analysis (see Methods).

[b] Log transformed.

yearlings, suggesting that inexperienced individuals tend to be less effective incubators.

Lastly, because incubation rates could influence subsequent growth and survival of offspring, we also examined relationships between incubation components and mass of nestlings just prior to fledging. Fate of all nests was recorded, and nestlings were weighed on day 6 of the nestling period, the last day to handle young without risking premature fledging. For these data from one season, we found no significant relationship between nestling mass and incubation bout duration ($F_{1,5} = 2.8$, $P = 0.15$), female departures per hour ($F_{1,5} = 1.13$, $P = 0.34$), or percent of time incubating ($F_{1,5} = 2.07$, $P = 0.21$).

DISCUSSION

Implications concerning incubation rhythms.—Temperature probes implanted in the lining of Black-throated Blue Warbler nests provided detailed 24-h records on incubation rhythms of attending adults. Female warblers averaged 20.5 min per incubation bout, incubated for about 64% of daylight hours, and made 2.4 trips off the nest per hour which lasted about 10.7 min. These patterns fall within the 60–80% attentiveness that

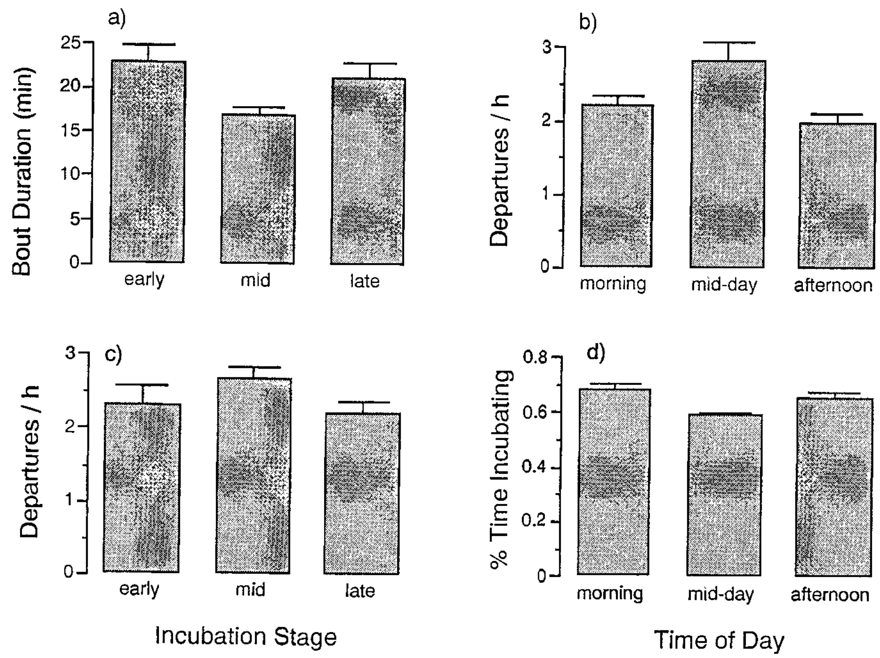

FIGURE 2. a) Mean duration of incubation bouts by female Black-throated Blue Warblers in early, mid and late stages of the incubation period; b) mean rates of female departures from nests by time of day and c) by incubation stage; d) mean percentage of time females spent incubating by time of day. Means ± 1 S.E. See text and Table 1 for statistics and sample sizes.

Williams (1990) proposed most adult passerines spend at the nest. They also coincide with the amount of time that Haftorn (1988) hypothesized was necessary for temperate zone passerines to maintain egg temperature above the "physiological zero temperature" (25–27°C). However, these values for Black-throated Blue Warblers were lower than those reported for several congeners: Kirtland's Warblers (*D. kirtlandii*) incubated for about 84% of daytime hours in bouts averaging 39 min, with inattentive periods of 9 min (Mayfield 1960); Prairie Warblers (*D. discolor*) spent 78.5% of daylight hours on nests in bouts of 37.9 min and were off the nest for periods averaging 12.7 min (Nolan 1978); and Virginia's Warblers (*Vermivora virginiae*) spent 73.7% of day incubation in bouts that averaged 31.0, with 11.1 ± 0.8 min spent away from the nest (Olson and Martin 1999).

Even with significant variation among individuals, female Black-throated Blue Warblers on average spent more time per hour on the nest, stayed on the nest for longer incubation bouts, and made fewer foraging trips in both mornings and afternoons than during midday. This pattern could be related to cooler temperatures in early mornings and late afternoons, although none of the incubation components we measured were related to mean daily temperature (Table 1). It might also be related to diurnal changes in insect availability (see Holmes et al. 1978) or to an increased exposure to direct sunlight (see Zerba and Morton 1983). Similar diurnal patterns have been noted for incubating Nashville Warblers (*V. ruficapilla*; Williams 1996), Wilson's Warblers (*Wilsonia pusilla*; Ammon and Gilbert 1999), and Prairie Warblers (Nolan 1978)

As incubation progressed, female Black-throated Blue Warblers did not alter the percentage of time they were attentive at the nest. Instead, they varied the duration of their incubation bouts and the frequency of trips to the nest. They stayed on the nest for longer time intervals in the first and third parts of the incubation period than in midday. They also made fewer trips to the nest, suggesting that they also lengthened their inattentive periods and presumably spent more time foraging. In contrast, female Yellow-eyed Juncos (*Junco phaeonotus*) made more but shorter trips off the nest as the incubation stage advanced (Weathers and Sullivan 1989), while incubation bouts of Blackpoll Warblers (*D. striata*) became longer as hatching approached (Hunt and Eliason 1999).

Incubation behavior also varied with age of female Black-throated Blue Warblers, with older females incubating for longer periods and making fewer but longer trips away from the nest than did yearlings. This age effect may be related to greater experience or better condition of older females. Additionally, older females may settle and pair with males on higher quality territories (Holmes et al. 1996), which might affect their foraging rates and hence their time and energy budgets, including incubation schedules. Our results contrast with those found by Nolan (1978) for Prairie Warblers, in which yearling females incubated more than did older ones.

One possible consequence of females spending more time incubating is that their incubation period may be shortened. For Black-throated Blue Warblers in our study, those females that incubated for greater percentages of the time tended to have a 12-d incubation period, while eggs of females that incubated less intensively hatched in 13 d, although sample sizes were small. Shorter incubation periods can have the benefit of decreasing the opportunity for predators at the nest and increasing a female's chances of initiating a second nest.

Thus, female Black-throated Blue Warblers appeared to vary their incubation bout lengths and number of departures from the nest with time of day and with stage of the incubation period. These findings suggest that the way time is allotted may be equally as important as the total amount of time spent incubating. Further studies are needed on the consequences of different incubation schedules within and among species and their impact on reproductive output and life history patterns.

Implications concerning methodology.—The temperature probe/data logger method is relatively inexpensive and does not require the presence of an observer at the nest or alteration of clutch contents that results from the insertion of thermocouples into real or dummy eggs within a nest (e.g., Morton and Pereyra 1985; Weathers and Sullivan 1989). Both probes and data loggers can be rotated among nests, although we found it most efficient, especially with a limited number of data loggers, to leave probes in place within a nest and to rotate data loggers.

One limitation of our study was that we did not have measures of ambient temperature near each nest site. However, the use of dual-channel data loggers (e.g., Hobo two channel loggers, U.S. $65) that are now available allow for simultaneous temperature measurements by a probe (U.S. $25) in the nest and a temperature sensor in the logger, ~1 m or so away. This setup would allow a better assessment of the importance of temperature variation affecting incubation patterns. Alternatively, thermocouples implanted within eggs might be necessary for such measurements (e.g., Zerba and Morton 1983; Weathers and Sullivan 1989).

Finally, one person (EMJ) was able to monitor nine nests with relative ease and without apparent risk to the nests. All nine nests survived to hatching, while during the same time seven of 28 other "control" nests that were part of an ongoing study of Black-throated Blue Warbler demography were lost to predators prior to hatching (T.S. Sillett and R.T. Holmes, unpubl. data). Four of the nine (44%) experimental nests were depredated during the nestling phase, however, as were nine of the 21 control nests that survived to hatching, a nonsignificant difference (Fisher's Exact Test: $\chi^2 = 0.006$, df = 1, $P = 0.94$).

Thus, in conclusion, the use of a temperature probe/data logger system allowed us to quantify the incubation patterns of female Black-throated Blue Warblers in an efficient and effective way. Further use of this system, perhaps as modified by the suggestions above, would provide more precise and quantified data on the incubation rhythms of open-cup nesting birds.

ACKNOWLEDGMENTS

This study formed the basis of a Senior Honors Thesis at Dartmouth College (EMJ). Funding was provided by an REU supplement to a National Science Foundation grant to Dartmouth College. Permission to conduct this study at Hubbard Brook was given by the Northeast Research Station, U.S. Forest Service, Radnor, PA. We gratefully acknowledge the assistance of J. Barg, R. Dobbs, B. Wright, and other members of the 1997 field crew at Hubbard Brook, and N. Rodenhouse, L. Nagy, and P. Roberts for their comments on the manuscript.

LITERATURE CITED

AMMON, E. M., AND W. M. GILBERT. 1999. Wilson's Warbler (*Wilsonia pusilla*). No. 478, *in* A. Poole and F. Gill, eds. The birds of North America. The Birds of North America, Inc. Philadelphia, Pennsylvania.

BORMANN, F. H., AND G. E. LIKENS. 1979. Patterns and process in a forested ecosystem. Springer-Verlag, New York.

CAREY, C. 1980. The ecology of avian incubation. BioScience 30:819–824.

CURIO, E. 1988. Realized life span and delayed cost of parental care. Am. Nat. 131:825–836.

HAFTORN, S. 1988. Incubating female passerines do not let egg temperatures fall below the "physiological zero temperature" during their absences from the nest. Ornis Scand. 19: 97–110.

HALUPKA, K. 1994. Incubation feeding in the Meadow Pipit *Anthus pratensis* affects female time budget. J. Avian Biol. 25:251–253.

HOLMES, R. T. 1990. The structure of a temperature deciduous forest bird community: Variability in time and space. Pp 121–140, *in* A. Keast, ed. Biogeography and ecology of forest bird communities. SPB Academic Publications, The Hague, Netherlands.

———. 1994. Black-throated Blue Warbler (*Dendroica caerulescens*). No. 87, *in* A. Poole and F. Gill, eds. The birds of North America. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

———, P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. J. Anim. Ecol. 65:183–195.

———, T. W. Sherry, and S. E. Bennett. 1978. Diurnal and individual variability in the foraging behavior of American Redstarts (*Setophaga ruticilla*). Oecologia 36:141–149.

———, ———, P. P. Marra, and K. E. Petit. 1992. Multiple-brooding and productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. Auk 109:321–333.

Hunt, P. D., and B. C. Eliason. 1999. Blackpoll Warbler (*Dendroica striata*). No. 431, *in* A. Poole and F. Gill, eds. The birds of North America. The Birds of North America, Inc. Philadelphia, Pennsylvania.

Jones, G. 1987. Time and energy constraints during incubation in free-living Swallows (*Hirundo rustica*): an experimental study using precision electronic balances. J. Anim. Ecol. 56:229–245.

Kuitunen, M., and J. Suhonen. 1991. Feeding time and brood-rearing capacity in the Common Tree Creeper (*Certhia familiaris*). Auk 108:180–184.

Martin, T. E., and C. K. Ghalambor. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation. Am. Nat. 153:131–139.

Mayfield, H. F. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci., Bloomfield Hills, Michigan.

Milliken, G. A., and D. E. Johnson. 1992. Analysis of messy data, vol. 1: designed experiments. Van Nostrand Reinhold, New York.

Moreno, J. 1989. Energetic constraints on uniparental incubation in the Wheatear *Oenanthe oenanthe* (L.). Ardea 77:107–115.

Morton, M. L., and M. E. Pereyra. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). Auk 102:25–37.

Nolan, V. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor.* Ornithol. Monogr. 26:1–595.

Norment, C. J. 1995. Incubation patterns in Harris' Sparrows and White-crowned Sparrows in the Northwest Territories, Canada. J. Field Ornithol. 66:553–563.

Olson, C. R., and T. E. Martin. 1999. Virginia's Warbler (*Vermivora virginiae*). No. 477, *in* A. Poole and F. Gill, eds. The birds of North America. The Birds of North America, Inc., Philadelphia, Pennsylvania.

Patterson, H. D., and R. Thompson. 1971. Recovery of inter-block information when block sizes are unequal. Biometrika 58:545–554.

Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, California.

Reid, J. M., P. Monoghan, and G. D. Ruxton. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. Proc. Royal Soc. Lond. B 267:37–41.

SAS Institute. 1996. SAS/STAT software, changes and enhancements through version 6.11, the Mixed Procedure. SAS Institute, Inc., Cary, North Carolina.

———. 2000. JMP, version 4.0.2. SAS Institute, Inc., Cary, North Carolina.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, New York.

Weathers, W. W., and K. A. Sullivan. 1989. Nest attentiveness and egg temperature in the Yellow-eyed Junco. Condor 91:628–633.

Weeden, J. S. 1966. Diurnal rhythm of attentiveness of incubating female Tree Sparrows (*Spizella arborea*) at a northern latitude. Auk 83:368–388.

Whelan, C. J., M. L. Dilger, D. Robson, N. Hallyn, and S. Dilger. 1995. Effects of olfactory cues on artificial nest experiments. Auk 111:945–952.

Williams, J. B. 1990. Energetics of avian incubation. Pp. 375–415, *in* C. Carey, ed. Avian energetics and nutritional ecology. Chapman Hall, New York.

WILLIAMS, J. M. 1996. Nashville Warbler (*Vermivora ruficapilla*). No. 205, *in* A. Poole and F. Gill, eds. The birds of North America. The Academy of Natural Sciences, Philadelphia and the American Ornithologists' Union, Washington, D.C.

ZERBA, E. AND M. L. MORTON. 1983. The rhythm of incubation from egg laying to hatching in Mountain White-crowned Sparrows. Ornis Scand. 14:188–197.

Received 25 May 2000; accepted 13 November 2000.