

PATTERNS OF WOOD DUCK NEST TEMPERATURES DURING EGG-LAYING AND INCUBATION¹

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Abstract. We studied the thermal environment of Wood Duck (*Aix sponsa*) nests in southeastern British Columbia. Mean daily nest temperatures (T_N) were correlated with maximum daily air temperatures. T_N increased as the egg-laying period advanced among both successful and unsuccessful nests, although T_N was lower among unsuccessful nests. Hens began spending nights on nests when there were as few as four eggs in clutches. T_N and the precision of nest thermoregulation increased among successful nests as the incubation period advanced, although there was a great deal of variation between days and nests. Length of the incubation period was not correlated with clutch size, nor with mean overall nest temperature during incubation, but was correlated with the variance of T_N 's during incubation.

Key words: Wood Duck; *Aix sponsa*; nest temperatures; nest boxes; British Columbia.

INTRODUCTION

Providing a favorable thermal environment for developing embryos is an essential aspect of the reproductive success of any avian species. Incubation temperatures have been measured by a number of different methods for many birds (Drent 1975). Among waterfowl, actual egg temperatures during egg-laying and/or incubation have been reported for some species (see review by Afton and Paulus 1993), and the thermal tolerances of developing embryos have been reviewed (Webb 1987). However, few studies have characterized the thermal environment in which eggs are laid and incubated (Irving and Krog 1956, Caldwell and Cornwell 1975, Cooper 1978, Afton 1979), and none have involved cavity-nesting waterfowl.

Nest temperature is the result of behavior of the nesting female and of ambient temperatures. The female influences nest temperature through her behavior while on the nest and by her pattern of nest attentiveness. Nest attentiveness is in turn influenced by a hen's energetic requirements, the thermal requirements of the clutch, and perhaps by predation risk (Caldwell and Cornwell 1975, Korschgen 1977, Afton 1980, Ringleman et al. 1982, Hohman 1986, Brown and Fredrickson 1987, Thompson and Raveling 1987, Mallory

and Weatherhead 1993, Afton and Paulus 1993). We examined the temperatures of Wood Duck (*Aix sponsa*) nests to study the thermal environment breeding hens provided for their clutches throughout the nesting period, and to make inferences about the attentiveness behavior of nesting females, where possible.

METHODS

We conducted fieldwork from April to July 1989 and 1990 at the Creston Valley Wildlife Management Area (CVWMA) in southeastern British Columbia (49°05'N, 116°35'W; see Butler et al. 1986). Four hundred and fifty nest boxes have been provided for waterfowl on the CVWMA since 1972 (Wilson 1992); approximately 190 boxes were checked for Wood Duck use during this study.

We monitored nest temperatures with electronic temperature recorders that were designed and manufactured for this project (Science Electronics Shop, Simon Fraser University, Burnaby, BC, V5A 1S6). Each recorder was self-contained and consisted of an AD590 temperature transducer housed in a 5 × 3 cm dome-shaped probe, and a waterproof Plexiglas box that housed a printed circuit board and two 6 V batteries. Each recorder's central processing unit was programmed to take a reading once every 3 min from the transducer and to emit a quiet "beep" (audible only a few cm from the recorder) every time a temperature was recorded. A 3-min interval allowed continuous monitoring of nests for up to 48 days without downloading data to a

¹ Received 13 October 1994. Accepted 11 May 1995.

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TABLE 1. Pearson product moment correlation coefficients of mean daily nest temperature (T_N) and maximum daily temperature (T_{max}), minimum daily temperature (T_{min}), mean daily temperature (T), and daily precipitation by nesting period and success.

		T_{max}	T_{min}	T	Precipitation
Laying:	successful	0.44**	0.01	0.37*	-0.31
	unsuccessful	0.58**	0.16	0.36*	-0.23
Incubation:	successful	0.26**	0.22**	0.26**	-0.03
	unsuccessful	0.46**	0.18	0.41**	-0.20

* $P < 0.05$.

** $P < 0.005$.

computer. Data were stored as hexadecimal values in a zero-power random access memory chip. The output voltage of the probes changed linearly with temperature throughout their operating range (-5 – 50°C), although the slopes and intercepts of the response lines for each probe differed slightly. The manufacturer provided voltage response data ($\text{V}/^\circ\text{C}$) for each probe. We used an ice bath to calibrate each probe at a constant temperature.

When a Wood Duck nest was discovered, we usually installed a temperature recorder within 24 hr. Sawdust and eggs were removed from the nest box and a 2.5 cm hole was drilled through the center of the nest box's bottom. The temperature probe was placed into the hole and fastened to the bottom of the nest box with a plywood plate. The recorder was covered with burlap to make it less conspicuous and then fastened to the underside of the box with four wood screws. We recorded the times the recorder was started and installed. Sawdust and eggs were returned to the nest box such that the temperature transducer was at the bottom of the nest bowl. To reduce the possibility of hens burying probes under nest material, we sometimes limited the sawdust returned to the nest box. We considered temperatures recorded from this position to be "nest temperatures." We visited nests daily and marked any new eggs. Visits continued until the hen was found on the nest. We followed the fate of other nests on the study area that were not monitored electronically.

We removed recorders from nest boxes 35–40 days after the onset of incubation, or sooner during occasional nest checks if the nest had been abandoned. Data were downloaded to a computer using a terminal emulation program (ZSTEMpc-VT100 Version 2.2, KEA Systems Ltd., Vancouver, BC). Each temperature reading was assigned a date and time based on the time

the respective temperature recorder was started during installation.

We summarized nest temperatures by calculating mean daily nest temperatures (T_N) and coefficients of variation for each nest-day (CV_N), starting with the first full day of monitoring. We used CV_N as our measure of the precision of thermoregulation. This allowed us to examine variations in nest temperature relative to the T_N of each nest. Egg-laying and incubation periods were analyzed separately. We defined the first day of incubation as the first consecutive day on which an egg was not added to the nest bowl. This day was estimated for nests in which unmarked eggs or remains were found in the nest during incubation or during post-hatch checks. One day was added to the egg-laying period for each unmarked egg or egg remains that we found in the nest box. We defined the last day of incubation as the day before fledging. Fledging or abandonment was detected by a large drop in temperature that was followed by normal diurnal, ambient temperatures for the remainder of the monitoring period.

With local weather data (BC Ministry of Agriculture and Food, Creston, BC), we first examined the relationship between T_N and four available weather variables (maximum, minimum, and mean daily air temperatures, precipitation) with Pearson product moment correlation coefficients (Sokal and Rohlf 1981, Table 1). Maximum daily air temperature (T_{max}) was most closely correlated with T_N but was not closely correlated with the predictor variables "egg laid" (i.e., first, second, third, . . . ; $r = 0.17$) or with "day of incubation" ($r = 0.02$). Therefore, T_{max} was used as a covariate in subsequent analyses.

There were insufficient degrees of freedom to treat each nest as a repeated measure; therefore, we pooled observations across individuals (Mal-

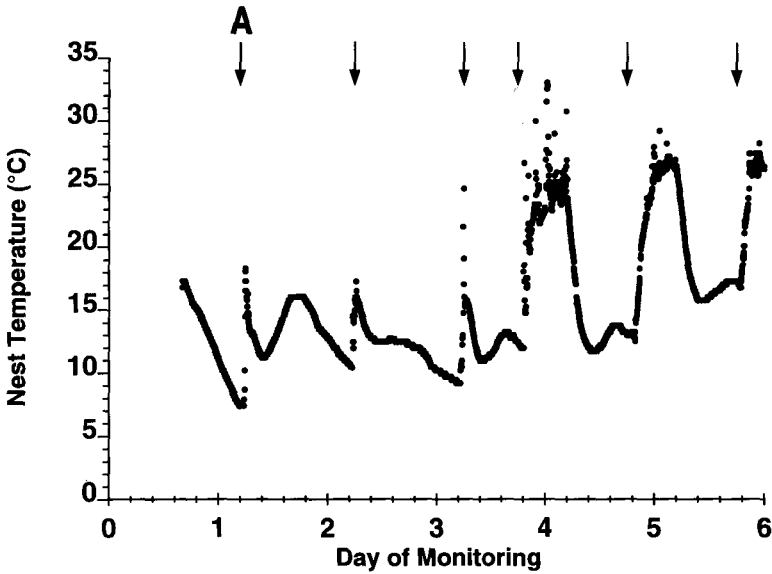


FIGURE 1. The first six days of a typical nest temperature record. Each monitoring-day began at 00:00 MST. Arrows indicate where the hen began raising the temperature of the nest. The hen returned to the nest in the morning during the first three days of monitoring, but then began returning in the evening (point "A") and spending the night on the nest.

lory and Weatherhead 1993) and used multiple linear regression to describe general changes in T_N and CV_N with T_{max} as the egg-laying and incubation periods advanced. Unadjusted temperatures and simple linear regression lines are presented in figures for descriptive purposes.

Although probes were located in the same position in all nests, the location of incubating females with respect to the probes differed due to the arrangement of eggs. We examined trends in nest temperature as the incubation period advanced while attempting to control for this source of variation. We expressed each T_N as a proportion of the maximum T_N recorded for each nest and arcsine transformed the resulting variates for regression analyses.

We report total degrees of freedom (df) in analyses that involved pooled observations to distinguish them from analyses that involved one measurement per nest, in which case sample size (n) is reported. We used SYSTAT Version 5.0 (SYSTAT, Inc. 1992) for all analyses. Means are expressed ± 1 standard error of the mean (SE).

RESULTS

Nine of 14 monitored nests hatched in 1989 and four of six hatched in 1990. Mean clutch size of successful monitored nests ($n = 13$) was 10.9 ± 0.8 , of which 9.3 ± 0.7 hatched. Nineteen eggs

were added parasitically to eight of the nests. Monitored nests were as successful as unmonitored nests when data from unmonitored nests found in 1988 were included in the analysis (Wilson 1990; $n = 49$, $\chi^2 = 1.29$, $P > 0.05$). Only one nest abandonment was attributed to the temperature recorders (the transducer was pulled from the probe into the nest bowl and the eggs scattered). Nesting females did not bury temperature probes in nest material. During nest checks, we found that probes were either visible or covered with a thin layer of sawdust in the center of the nest bowl. Temperature recorders failed at four additional nests, three in 1989 and one in 1990.

Temperature records and nest checks indicated that females began spending the night in nest boxes and raising nest temperatures when there were as few as four eggs in the nest (Fig. 1). Only one clutch was completed before the female began spending the night in the nest box. On average, this behavior began when there were 7.4 ± 0.6 eggs in the nest ($n = 22$). We were unable to detect nest visits by brood parasites (i.e., more than one morning nest visit per day) from temperature records.

T_N increased as the egg-laying period advanced for both successful and unsuccessful nests when T_{max} was included as a covariate in the model

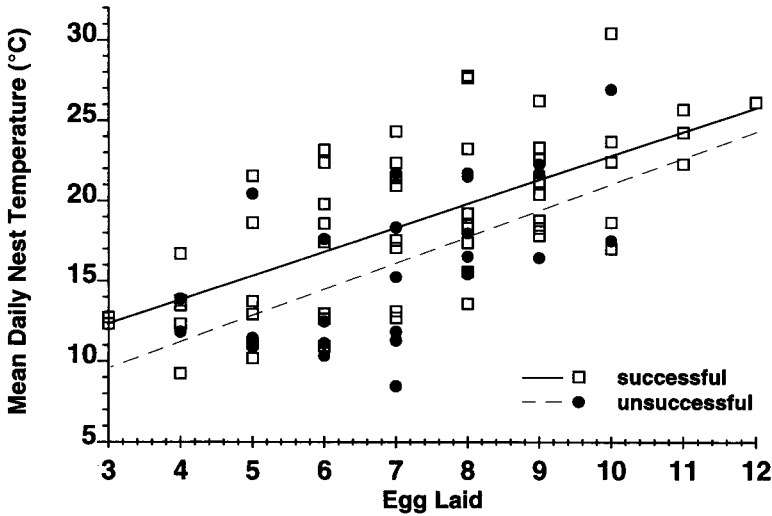


FIGURE 2. Mean daily nest temperatures (T_N ; not adjusted for covariate T_{max}) during the egg-laying period for successful ($n = 12$) and unsuccessful nests ($n = 7$). The lines of best fit for successful ($y = 7.61 + 1.52x$, $df = 55$, $r^2 = 0.43$, $F = 41.8$, $P < 0.001$) and unsuccessful nests ($y = 4.36 + 1.67x$, $df = 25$, $r^2 = 0.32$, $F = 12.9$, $P = 0.001$) were derived from the simple regression model.

(Fig. 2). T_N of unsuccessful nests were lower ($df = 81$, $r^2 = 0.55$, $F = 5.40$, $P = 0.023$). CV_N did not change predictably as the laying period advanced among successful ($df = 55$, $r^2 = 0.00$, $F = 0.92$, $P > 0.05$), or among unsuccessful nests ($df = 25$, $r^2 = 0.03$, $F = 1.44$, $P > 0.05$).

Among unsuccessful monitored nests, one hen abandoned after four eggs were laid. Abandonments during incubation occurred after 3, 8, 15, 20, 22, and 30 days. The incubation period of the 13 successful nests that we monitored was 30.9 ± 0.58 days. T_N increased as the incubation period advanced among successful nests ($df = 401$, $r^2 = 0.21$, $F = 54.0$, $P < 0.001$, Fig. 3) after adjusting for T_{max} . Since most unsuccessful nests were abandoned during the laying period or during early incubation, we were unable to examine confidently trends in T_N among unsuccessful nests during incubation.

The maximum T_N recorded for nests ($n = 13$) varied between 29.8 and 36.1°C. When T_N 's were expressed as a proportion of maximum T_N for each nest, the regression model provided a better fit than when T_N 's were used as variates ($df = 401$, $r^2 = 0.43$, $F = 150.6$, $P < 0.001$).

CV_N decreased as the incubation period advanced among successful nests ($df = 401$, $r^2 = 0.17$, $F = 85.6$, $P < 0.001$) although there was a great deal of variation between nests and days. The relationship was not linear, but was best

described by $\ln(CV_N) = 2.59 - 0.29 \ln(\text{day})$. T_{max} was not a significant covariate in this analysis ($P > 0.05$). Again, we did not analyze unsuccessful nests due to small sample size.

The length of the incubation period was not correlated with clutch size ($n = 13$, $r^2 = 0.00$, $F = 0.23$, $P > 0.05$), nor with the overall mean T_N for each nest ($n = 13$, $r^2 = 0.07$, $F = 1.87$, $P > 0.05$), but was positively correlated with the variance of the mean T_N 's ($n = 13$, $r^2 = 0.23$, $F = 4.65$, $P = 0.05$). The power of these tests was low due to small sample sizes.

DISCUSSION

Our study is consistent with others that found evidence of Wood Ducks increasing their time on the nest and raising the temperature of clutches late in the egg-laying period. Breckenridge (1956) monitored the attentiveness pattern of a female Wood Duck and found that she spent the last three nights of the egg-laying period on the nest. Stewart (1962) reported a Wood Duck laying an egg the morning after incubation began. Although the incubation period of ducks is often assumed to begin after all eggs are laid (Afton and Paulus 1993), quantitative studies have shown that incubation begins gradually during the egg-laying period (Caldwell and Cornwell 1975, Cooper 1978, Afton 1979). Kennamer et al. (1990) found that incubation late in the egg-

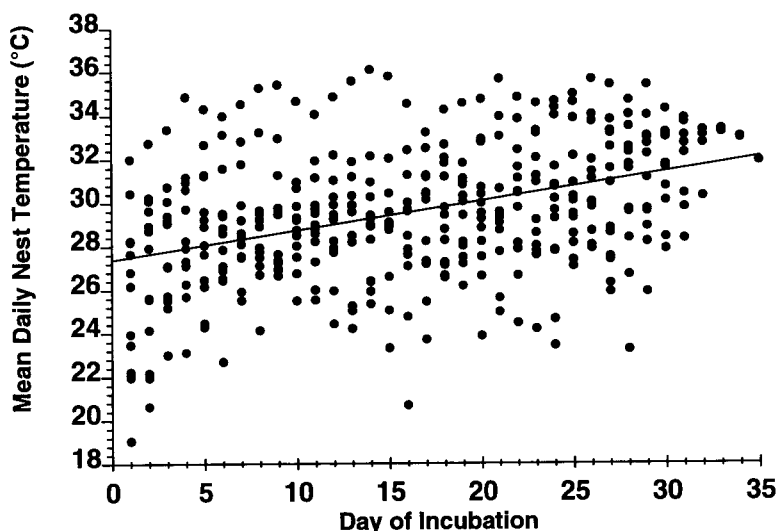


FIGURE 3. Mean daily nest temperatures (T_N ; not adjusted for covariate T_{max}) during the incubation period for successful nests ($n = 13$). The line of best fit was derived from the simple regression model ($y = 27.4 + 0.13x$, $df = 401$, $r^2 = 0.14$, $F = 68.5$, $P < 0.001$).

laying period led to developmental asynchronies within Wood Duck clutches of up to five days. Larger clutches exhibited the greatest degree of asynchrony and the lowest hatching success. Developmental asynchrony has been reported among other waterfowl species (Prince et al. 1969, Caldwell and Cornwell 1975, Afton 1979, Cargill and Cooke 1981). The function of incubation during the egg-laying period is not known. Hens that spend nights in nest boxes are probably less vulnerable to predation (Afton and Paulus 1993). Arnold et al. (1987; but see Ankney et al. 1991) hypothesized that the declining viability with time of the first few eggs laid in the clutch could be offset by early, partial incubation.

The increasing nest temperatures we measured during the egg-laying period probably reflect the increasingly attentive behavior of hens towards the end of egg-laying that has been reported for other species (Caldwell and Cornwell 1975, Afton 1980). Long absences from the nest during the early egg-laying period coincide with the peak of a hen's energetic requirements (Drobney 1980, 1982), and with the greatest tolerance of eggs to temperature fluctuations (Webb 1987).

During incubation, the thermal requirements of the developing embryos and the fasting ability of hens regulate nest attentiveness (Afton and Paulus 1993). We found that nest temperature increased as incubation advanced, after account-

ing for ambient temperature (as measured by T_{max}). Afton (1979) found a similar pattern in nest temperature at a Northern Shoveler (*Anas clypeata*) nest. This could be due to increasing attentiveness by the nesting female, although other studies have found that waterfowl are less attentive later in incubation (Afton 1980, Brown and Fredrickson 1987, Thompson and Raveling 1987, Mallory and Weatherhead 1993), or that attentiveness does not change throughout the incubation period (Caldwell and Cornwell 1975). More likely, the increase in nest temperature was due to increasing heat production by the developing embryos (White and Kinney 1974, Drent 1975, Afton 1980). The female's role during this critical period is to maintain a consistent thermal environment, given the influences of embryonic heat production and of ambient temperature fluctuations.

We found some evidence that the precision of thermoregulation, as measured by the coefficient of variation of daily nest temperatures, increased as the incubation period advanced; however, the relationship was weak. Variability in nest temperature was highest near the beginning of incubation, but generally decreased quickly and remained low for the majority of the incubation period. Precision did not vary with ambient temperature, suggesting that the attentive behavior of the nesting hen, and the heat production of

the clutch, was responsible for the increasing constancy of nest temperature.

Clutch sizes of nests in this study were not correlated with length of incubation, suggesting that clutch size did not affect the thermal efficiency of incubation; however, clutches monitored in this study were moderate in size. Larger clutches, such as those resulting from high rates of brood parasitism, may influence thermal efficiency. Higher mean nest temperatures were not correlated with shorter incubation periods, although the variance of daily mean incubation temperatures were correlated with the length of incubation. Higher variances may have been the result of low attentiveness among some females during incubation, leading to longer incubation periods. Drent (1975) suggested that variability in the length of the incubation period within species was due to the attentiveness of individual parents and possibly to external weather conditions. Results should be interpreted cautiously; statistical power was low for these tests.

The most striking result from our study was the high variability of nest temperatures between nests, between days, and within days. We attempted to minimize variation between nests by fixing the position of the temperature probes within the nest bowl; however, the exact position of the transducers with respect to the position of hens was probably responsible for a considerable proportion of the variation in temperatures recorded. From the arrangements of eggs we noted during nest checks, it was clear that some transducers were in direct contact with incubating females while others were under a single layer of eggs. This variation is difficult to control for when attempting to record nest temperatures.

The degree to which the temperature variability we measured within nests was correlated with actual egg temperatures is not known. Temperatures at the top of the clutches of many species remain constant throughout incubation, due to the constant skin temperature of the brood patch (Drent 1975). We collected temperatures at the bottom of the nest, and egg temperatures probably varied somewhat less than the recorded nest temperatures. However, developing Wood Duck embryos seem to tolerate a wide range of nest temperatures during egg-laying and incubation.

ACKNOWLEDGMENTS

R. Holland designed and built the temperature recorders. The Creston Valley Wildlife Management Area

provided logistical support. C. Pineau assisted with fieldwork. B. Charland, A. Harestad, and two anonymous reviewers provided helpful comments. Our research was supported by Natural Sciences and Engineering Research Council (NSERC) of Canada grant A0239 to NAMV, an NSERC post-graduate scholarship and a Simon Fraser University graduate fellowship to SFW, and by the Public Advisory Committee to the Creston Valley Wildlife Management Area.

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