Variation in Wood Thrush Nest Dimensions and Construction

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ABSTRACT

We collected 48 nests from radio-marked and non-radio-marked female Wood Thrushes *(Hylocichla mustelina)* at the Piedmont National Wildlife Refuge in central Georgia and conducted statistical analyses to determine the sources of variation in nest size. Each nest measurement had a large coefficient of variation, but we found trends in six of eight nest measurements related to date, nest number, female occupant, or nest success. Regression analyses showed that cup depth, nest wall width, and exterior nest height decreased during the season, while cup width increased ($0.14 < R^2 < 0.24$). A repeated-measures linear model, comprised of study plot, nest number, and occupant effects, adequately described much of the variation in the multi-brooded, radio-marked females' (n = 24 nests) nest size ($0.55 < R^2 < 0.84$). Cup depth, cup width, exterior nest height, and nest weight showed differences among nest attempt number, while weight and exterior nest height showed differences related to individual females. We also found evidence that nestlings in successful nests apparently enlarged the nest cup. Very little is known about short-term variation in nest size and shape, but our results indicate that female Wood Thrushes may change the size of their nests for various reasons during the breeding season.

INTRODUCTION

Bird species build a large variety of nests (e.g. domed, open cup, cavity), and natural selection is presumed to favor nests that protect the nestlings while economizing the energetic effort required to build them (Collias and Collias 1984, Snow 1978). Within species, nests are known to vary in size. Kern (1984) reported that the open cup nests of three races of eastern White-crowned Sparrows *(Zonotrichia leucophys)*, each found in a distinctly different region of North America, varied in size. Another cup-nesting species, Red-winged Blackbird *(Agelaius phoeniceus)*, apparently builds slightly deeper cups when nesting higher than 3 ½ ft (1.07 m) (Holcomb and Twiest 1968). Cavity nesters, such as House Sparrows *(Passer domesticus)* and Eastern Bluebirds *(Sialia sialis)*, vary their nest size according to breeding habitat and available nest box size (Indykiewicz 1991, Pitts 1988). And, several species, such as Verdins *(Auriparus flaviceps)* and Lesser Nighthawk *(Chordeiles acutipennis)*, adapt their nest-building behavior to long-term, seasonal environmental conditions (Collias and Collias 1984).

Very little is known about short-term variation in nest size and shape. Haggerty (1986, 1995) reported that Bachman's Sparrow *(Aimophilla aestivailis)* nests varied from domed to partially domed to undomed during a single breeding season, and he surmised that domed nests become advantageous in the late summer heat. Mertins (1987) found that Great Tits *(Parus major)* change nest construction to reduce heat loss in response to cold, but similar short-term changes in passerine open cup nests have not been described in the literature.

Female Wood Thrushes *(Hylocichla mustelina)* in the Piedmont of Georgia usually build three nests during the breeding season, which begins mid-April and ends early August, in an attempt to raise two broods (Powell et al. 1999). The nest cup, often lined with rootlets, consists of mud and/or small bits of decaying logs ("sawdust"). The cup is surrounded by a fluffy layer of leaves, grasses, rootlets, and/or mosses. Nest heights range from 1m to 15 m (3 .3 ft - 49.2 ft), and nests are found in several hardwood species, with flowering dogwood *(Cornus florida)* being the most common (Lang 1998).

Objectives - During the 1996 breeding season, we noticed considerable variation in Wood Thrush nest sizes between early and late-season nests. To the eye, radio-marked females, which were followed throughout the season, had noticeably smaller nests in later nesting attempts. In this paper, we have two objectives: (1) to document variation in nest construction by Wood Thrushes, and (2) to determine if nest size does decrease throughout the breeding season.

METHODS

We conducted this study at the Piedmont National Wildlife Refuge (PNWR) near Macon, GA, during the 1996 nesting season. The PNWR consists mainly of loblolly pine *(Pinus taeda)* ridge habitat with mixed hardwood bottomlands. Our PNWR study areas were divided between forest stands that were (1) in the second year after a prescribed burn and pine thin (experimental), and (2) not burned or thinned (control). The silvicultural treatment did not affect adult or juvenile Wood Thrush survival or reproduction (Lang 1998, Powell et al. 2000).

We located nests during nest searches, call surveys, or radio telemetry searches. Eleven female Wood Thrushes were affixed with radio transmitters. Of the 11 radio-marked females, eight were marked at the location of their first nest in early May and were followed through their last nesting attempt. Three females were radio-marked in late May, and we believe that they were on their second nest. Some females moved from experimental stands to control stands or vice versa during their various nesting attempts.

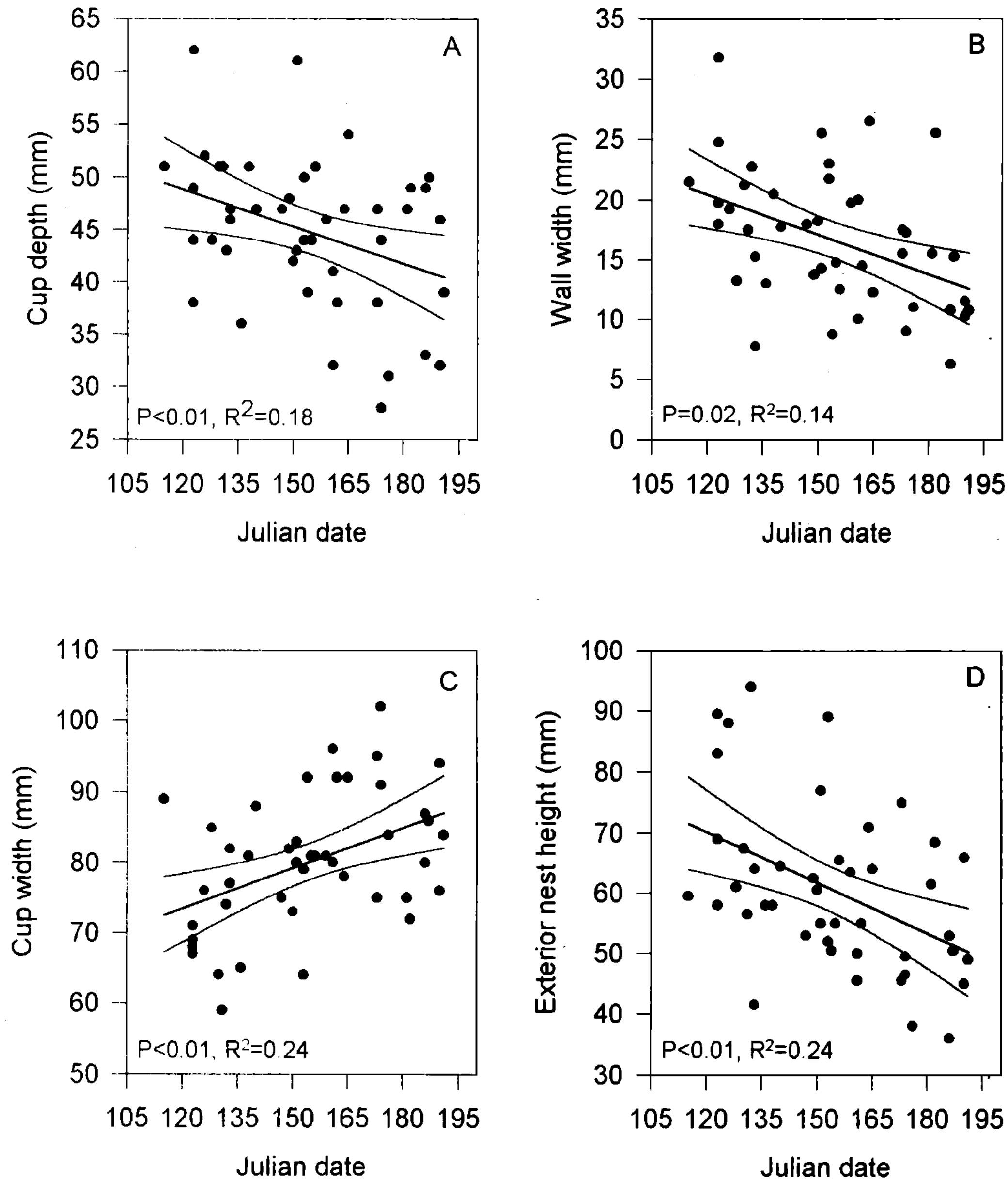
We collected the nests and all loose materials in individually labeled plastic bags. The nests were loosened from branches by gently pushing on the underside in several places with a pole. Some nests were not available for measurement due to destruction by predators.

Each nest was described quantitatively after Indykiewicz (1991). We measured three dimensions (mm) inside the cup: cup depth (from rim-level to the bottom of the cup) and cup width and length (from wall-to-wall inside the oval-shaped cup). We also measured three exterior nest dimensions (mm): nest width and length (wall-to-wall outside the oval nest) and exterior nest height (average height, from nest base to cup lip, of opposite ends of the oval nest). The average width of the nest wall was determined by averaging the wall widths at the two sides and two ends. Nests were weighed (g) on an electronic balance after air drying for two weeks, and we visually determined the construction material used for the nest cup: mud or sawdust.

Four analyses were performed. First, we obtained descriptive statistics for the nests (n = 48) in our sample (PROC MEANS, SAS Institute 1987). Second, we examined the relationship between the date of incubation initiation and the nest measurements (PROC REG, SAS Institute 1987). We included all nests (n = 41) for which we could determine a date of first incubation.

Third, we used a univariate, split-plot, repeated-measures linear model (PROC GLM, SAS Institute 1987) to describe the variability among the nests (n = 24) of radio-marked birds in our sample. This was necessary because on a given date, especially during the middle of the summer, some Wood Thrushes could be initiating their second nest, while others might be initiating their third or fourth nest. Nests constructed by the same female were not independent, but the repeated measures analysis used this characteristic to further describe the variation in size among nests. Our linear model tested three components of variation: (1) study plot (we radio-marked females on two forest management areas), (2) first, second, or third nest attempt, and (3) female occupant (or "builder"). We only had two fourth nests and one fifth nest in our sample, and we did not include them in this analysis.

Fig. 1. Regression and 95% confidence intervals of (A) cup depth, (B) nest wall width, (C) cup width, and (D) exterior nest height dimensions (mm) on Julian date of Wood Thrush nest incubation initiation. 1 May = Julian date 121, 1 June = Julian date 152, and 1 July = Julian date 182. Nests (n = 48) were collected at the Piedmont National Wildlife Refuge near Macon, GA, in 1996.



The Duncan test was used to compare means among categories. We used a separate single-factor linear model (PROC GLM, SAS Institute 1987) to test for differences in size between failed and successful nests.

And last, we analyzed the relationships between the average daily temperature on the fourth day before incubation initiation (n = 41 nests), and four nest measurements (cup depth, wall width, cup width, and exterior nest height: chosen as a result of the regression analysis). We obtained the average daily temperatures for May, June, and July from the National Weather Service station at Macon, GA. Wood Thrush nest construction is usually completed in three to six days (Roth et al. 1996), so we arbitrarily chose the fourth day as a representative day, early in the nest building process. Both temperature and nest measurement are random variables, so we used a correlation, instead of regression, analysis (PROC CORR, SAS Institute 1987, Woolf 1968).

RESULTS

We collected 48 Wood Thrush nests during July and August, 1996, after we determined that predation, abandonment, or fledging had occurred (21 nests were found during surveys or nest searching–including some nests of radio-marked females; 27 were found using radio telemetry). The earliest incubating female found was on 25 Apr 96, while the latest nest initiation was on 10 Jul 96. We marked some females during their second nest attempt, and most radio-marked females constructed at least three nests during the breeding season. However, one pair constructed four nests (all depredated), and another pair made five unsuccessful attempts (one abandoned, four depredated). All females in 1996 remained with their original mate during all nesting attempts.

Cup depth ($P < 0.01$, slope = -0.11, $R^2 = 0.18$), nest wall width ($P = 0.015$, slope = -0.10, $R^2 = 0.14$), and exterior nest height ($P < 0.01$, slope = -0.27, $R^2 = .24$) decreased with later incubation initiation date (Fig. 1). The width of the nest cup increased during the breeding season (Fig. 1, $P < 0.01$, slope = 0.19, $R^2 = 0.24$). Cup length ($P = 0.37$), nest width ($P = 0.34$), nest length ($P = 0.08$) and nest weight ($P = 0.44$) did not change during the breeding season.

The means and variance statistics of these Wood Thrush nest measurements are found in Table 1.

Table 1. Mean, standard deviation (SD), range, and coefficient of variance (CV) of variables measured on 48 Wood thrush nests at the Piedmont National Wildlife Refuge, near Macon, GA, in 1996. Units are mm unless noted otherwise.

Measurement	Mean (SD)	Min	Max	CV (%)
Cup depth	44.4 (7.8)	22.0	62.0	17.4
Cup length	89.6 (8.0)	78.0	112.0	8.9
Cup width	80.1 (9.3)	59.0	102.0	11.5
Exterior nest height	60.8 (14.0)	36.0	94.0	23.1
Nest length	126.0 (12.8)	104.0	153.0	10.2
Nest width	110.9 (9.8)	89.0	133.0	8.9
Wall width	17.2 (5.4)	7.8	31.8	32.9
Weight (g)	59.2 (22.0)	25.1	109.0	37.2

Table 2. Mean measurements (standard deviation in parentheses) of first (n=8), second (n=9), and third (n=7) Wood Thrush nest attempts during the 1996 breeding season. All females were radio marked. Units are mm unless noted otherwise.

Variable	1st Nest	2nd Nest	3rd Nest
Cup depth[a]	44.4 (5.4)	46.9 (5.0)	38.3 (7.2)
Cup length	88.9 (10.1)	87.1 (6.1)	92.1 (6.3)
Cup width[a]	74.5 (6.9)	79.8 (8.8)	83.0 (8.1)
Exterior nest height[a]	70.6 (18.3)	60.8 (11.8)	54.4 (11.9)
Nest length	125.6 (16.5)	124.3 (10.9)	132.3 (13.4)
Nest width	109.1 (10.9)	109.1 (7.6)	114.7 (10.6)
Wall width	17.8 (7.3)	16.6 (4.8)	18.0 (6.4)
Weight (g)	59.6 (26.0)	43.0 (17.7)	59.3 (25.7)

[a] Repeated-measures linear model, significant effect of nest number ($P<0.05$).

The linear model, using plot, nest number, and occupant effects, described the variation in size of Wood Thrush nests remarkably well (R^2 ranged from 0.57 to 0.89). Radio-marked birds tended to build less adorned nests (exterior nest height, $P< 0.01$) with shallower cups ($P = 0.02$) and wider cups ($P = 0.02$) later in the season (Table 2). No other nest measurements changed with nest attempt. Some females consistently built more adorned nests (exterior nest height, $P = 0.07$; $P < 0.05$, pairwise Duncan test) and heavier nests (weight, P = 0.05) than other females. These two variables were the only nest measurements to vary according to occupant. Nest weight (P = 0.01) and exterior nest height also were significantly different between the two study plots.

Nests from experimental areas (n=13) were smaller (P = 0.002) in terms of weight (44.8 g) and exterior nest height (57.9 mm) than nests from control areas (n =11; weight:= 63.3 g; exterior nest height (67.4 mm). However, these were the only two variables to vary according to study area.

Successful nests had wider (P = 0.03) and longer cups (P = 0.06; P< 0.05, pairwise Duncan test) and thinner walls (P = 0.04) than failed nests. Also, successful nests had less exterior height than failed nests (P = 0.05). No other variables showed any effects of nest success. Two nest measurements, nest length and nest width, showed no change due to any effect in the repeated-measures linear model or the single-factor linear model.

The average daily temperature in central Georgia rose from 14° C (57.2°F) on 1 May to 28° C (82.4°F) on 31 Jul 1996 (P<0.001, slope = 0.07). The average temperature on the fourth day before incubation initiation (during nest building) correlated with three of the four nest measurements that showed significant trends during the breeding season (cup depth: R= -0.38, P =0.02; exterior nest height: R= -0.29, P=0.07; cup width: R=0.51, P < 0.001).

DISCUSSION

Wood Thrush nests, in our sample, exhibited considerable variation in size, weight, and shape. Most importantly, we were able to account for much of this variability. We found significant trends in date, nest attempt, occupant, or nest result for six of the eight nest measurements we recorded. However, none of our analyses satisfactorily accounted for the variation which existed in nest length and nest width.

Because of the serendipitous nature of our field observations, this research was not designed to test causal hypotheses. The literature provides three possible explanatory hypotheses that may explain some of the changes observed in nest size during the breeding season: (1) thermal: nests built in warmer months may require less insulative materials than nests built in cooler months, (2) concealment: nests built before leaf-out may require more vegetative ornamentation to conceal the nest from predators, and (3) energetic: a female may have less energy to spend gathering nest materials as she uses energy for egg production for successive nests.

Thermal Requirements - Heat dispersal is critical to nesting birds (Paladino 1989, Rich 1980), and nest construction can be modified to adapt to a changing climate during the breeding season (Mertins 1987). Our regression analysis showed that nests built later in the summer tended to have shallower and wider cups and thinner walls, which may provide for greater heat dispersal from the nest during the hotter months. This construction trend and the correlations we found with average temperature during nest building strongly support this thermal hypothesis. Our correlation analyses cannot show causation, but they suggest the shape of the nest (i.e. cup depth, exterior nest height, and cup width) may be more important to heat dispersal than insulative qualities, such as nest wall width.

Need for Nest Concealment - Nest concealment can affect reproductive success (Best and Stauffer 1980, Martin and Roper 1988, Westmoreland and Best 1985). Many species use lavish leaf or grass nest bases as camouflage against predation (Collias and Collias 1984, Snow 1978), and many of the first-attempt Wood Thrush nests we found were very large, heavily adorned nests (Fig.1). Second- and third-attempt nests were usually smaller nests with less adornment. Because of the late spring in 1996, leaf-out occurred while the first-attempt nests were being built, making the nests, potentially, more detectable to predators (Slagsvold 1982).

Energetic Demands - Our repeated-measures analysis of the radio-marked sample showed a trend of decreasing exterior nest height, which is a measure of the amount of building material used in the nest (i.e., larger, more adorned nests require more building materials). The energy required for egg production is very significant (Ettinger and King 1980, Walsberg 1983), and ovogenesis occurs simultaneously with nest construction. A single nest can require hundreds of trips to gather materials (Collias and Collias 1984, Indykiewicz 1991), and Ettinger and King (1980) found a male Willow Flycatcher's *(Empidomax traillii)* energy expenditure to be at a seasonal maximum as he accompanied the female during nest building. A smaller, less adorned nest would require fewer trips, allowing the female to allot more energy for egg production. For the female, energy availability is critical during breeding (Martin 1986, Martin 1987, Mertins 1987, Nilsson and Svensson 1993, Paladino 1989; but see Kendeigh et al. 1977), especially for multi-brooding species like the Wood Thrush (Arcese and Smith 1988).

Nest Size Differences Not Related To Time - We did not expect to find differences in nest size between our study areas, although our study areas did differ in their silvicultural history. Experimental plots had been undergone a pine thinning and a prescribed burn in the winter of 1994-1995 (two years before this study). Control areas had not undergone such a silvicultural treatment, and nests on control areas were larger in some respects than nests from experimental areas. Silvicultural effects may have resulted in this difference in nest size due to differences in energy availability or the need for more protection from predators. However, we stress that we did not measure nest size before the silviculture took place, so differences in nest size between compartment may have existed previous to the change in habitat.

Both nest weight and exterior nest height exhibited differences between study plots and among individuals. Because many individuals remained on the same study plot during nesting, these two factors may be somewhat confounded. Age of female may have contributed to the differences in nest dimension, but we were unable to age our female Wood Thrushes. We observed that individual females were prone to use a similar blend of building materials throughout the summer, even though both types of construction material were available on both study areas. Nest cups constructed of all sawdust, probably obtained from rotting logs, were very light, smooth, and almost plaster-like in texture (e.g., 25 g), while mud cups were heavy (e.g., 109 g). The exact composition of the nest was, undoubtedly, a confounding factor in any of our analyses which involved nest weight.

Successful nests had wider, longer cups; thinner walls; and lower exterior heights than nests which failed due to predation (Table 3). We believe this was due to movements of nestlings which enlarged the cup, compressed the wall, and wore away a very small portion of the rim of the cup. We did not measure the nests during incubation due to the height of the nest trees, but Holcomb and Twiest (1968) and Kern (1984) found similar changes in nest size due to nestling activity. The effect of nestling activity may, therefore, account for much of the unexplained variation we observed in the four significant regression analyses (cup width, wall width, cup depth, and exterior nest height). However, nestling activity is not responsible for the temporal trends in nest size.

Table 3. Mean measurements and standard deviations (SD) of successful and failed Wood Thrush nests during the 1996 breeding season (n=47). Units are mm unless noted otherwise.

Variable	Successful[a]	Failed[b]
Cup depth	45.9 (7.6)	42.4 (5.0
Cup length[c]	88.0 (6.8)	92.9 (9.8)
Cup width[c]	78.2 (9.3)	84.6 (8.1)
Exterior nest height[c]	63.7 (14.1)	55.1 (12.2)
Nest length	126.3 (13.6)	135.8 (11.4)
Nest width	111.7 (10.2)	109.0 (9.4)
Wall width[d]	18.0 (5.8)	14.3 (4.1)
Weight (g)	60.1 (22.1)	57.6 (23.4)

[a] n = 14
[b] n = 33
[c] Significant at P<0.05

Implications of Research - Our research suggests that Wood Thrushes may change the size of their nests throughout the breeding season. All three time-related hypotheses have the potential to explain some variation in Wood Thrush nest size and shape, although our study was not designed to test any of the hypotheses.

Wood Thrush nests vary considerably in size and shape. We found that (1) nestlings apparently change the shape of the cup, (2) individual variation in nest-building exists among female Wood Thrushes, and (3) nests tended to have shallower, wider cups and thinner walls with less adornment later in the breeding season. While our research was not designed to test hypotheses, we do show some circumstantial evidence that the need for heat dispersal in warmer months, nest concealment before leaf-out, and energetic costs of nest building may have all contributed to the changes in nest size that we observed. The strengths of these hypothesized selective forces probably differ among individuals during certain segments of the breeding season.

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News, Notes, Comments

Breeding Site Fidelity of a Male Louisiana Waterthrush

In 1999, a MAPS station was established at the Indiana Audubon Society's Mary Gray Bird Sanctuary. This sanctuary, located southeast of Indianapolis, is about 10 km southwest of Connersville, Fayette Co., Indiana. On 12 Jun 1999, an AHY-M Louisiana Waterthrush (*Seiurus motacilla)* in breeding condition was captured in Net 1 and banded. On 12 Jun 2000, exactly one year later, this individual was again captured in Net I along with a female and juvenile Louisiana Waterthrush. The female and juvenile are presumed to be its mate and young respectively.

Net 1 is located in a well-maintained trail through a deciduous woodland bordering a small pond with a narrow wetland edge. At this point, the trail and net cross a shallow intermittent stream that runs into the pond. The edge of the pond is less than 6 m from the net. All three birds were caught together in the early morning hours (prior to 0800) while moving upstream from the pond toward the woodland. According to data posted on the BBL web page, a total of 109,499 Louisiana Waterthrushes were captured and banded between 1914 and 1998. Of these, only 67 have been recovered, representing a recovery rate of 0.061%. These figures do not include individuals that are banded on their breeding territory and recaptured in subsequent years.

The Louisiana Waterthrush winters from southern Texas through Central America to northern South America; only 13 Christmas Bird Count sites have reported this species in the U.S., mainly from Galveston, Texas, eastward along the southern border of the U.S. (Root 1988). It is unlikely that this bird was resident at or near the MAPS station over the intervening winter.

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