

EVIDENCE FOR INDIVIDUAL CONSISTENCY AND LOCATION EFFECTS ON NEST MORPHOLOGY IN A POPULATION OF YELLOW WARBLERS (*SETOPHAGA PETECHIA*)

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ABSTRACT.—The behaviors of animals can be highly variable across individuals and environments; however, recent studies have demonstrated that the behaviors of individuals in response to similar environmental stimuli are often highly consistent over time. We investigated consistency in nest building behaviors during a single breeding season in a population of Yellow Warblers (*Setophaga petechia*) in southeastern Ontario, Canada. We examined the first and second nests constructed by eight individually-marked females that were distributed among three breeding locations 1–3 km apart, to test whether individual female and location affected the similarity of nests using three methods. First, we compared morphological measures of nests among females and locations and found that nests built by the same female were more similar in their nest depth compared with nests built by different females. Second, we used human observers to rank nest similarity based on overall nest appearance (considering morphology and composition) and found that (1) nests built by the same female were more similar compared with nests built by different females, and (2) nests built by different females in the same location were more similar than nests built by different females in different locations. Third, we deconstructed all nests and compared nest composition among females and locations and found that nests built by the same female were composed of similar materials compared with nests built by different females. Our results suggest that individual females build nests consistently during a single breeding season, and that females breeding in close proximity build nests that are more similar in appearance compared with nests built by females nesting 1–3 km apart. Received 27 May 2016. Accepted 21 October 2016.

Key words: behavioral consistency, individual consistency, nest-building behavior, nest composition, *Setophaga petechia*, spatial variation, Yellow Warbler.

Animal behaviors were historically thought to show low levels of repeatability within individuals, because behaviors can change quickly in response to environmental stimuli and variability increases over time. However, a recent meta-analysis found that many animal behaviors appear to be highly consistent within individuals (Bell et al. 2009). The high repeatability of behaviors within individuals suggests that either individuals are consistently experiencing similar environments that elicit the same behaviors, or that individuals have a narrow range of variation for many behaviors that may be constrained by development (e.g., genetic basis for variation in behaviors, restricted periods for learning behavioral repertoires). These two hypotheses are not mutually exclusive.

For many behaviors, we lack estimates of individual repeatability because measuring the repeatability of behaviors in the field is often challenging. Typically, researchers estimate repeat-

ability of behaviors by comparing variation within individuals relative to variation among individuals within a population (Falconer and Mackay 1996). If within-individual variation in behavior is low relative to variation among individuals in a population, then the behavior has a high level of consistency within individuals. Thus, estimates of individual consistency are usually relative measures that are dependent upon the period of observation and the broader population that is used for comparison (Bell et al. 2009).

The nests of birds are the physical result of nest building behaviors (an extended phenotype, Dawkins 1982) and provide a unique opportunity to measure multiple components of consistency in a behavior (e.g., nest size, shape, and composition). Most studies that examined consistency of nest building behavior in birds provide evidence that nest-building behavior is consistent within individuals during a single breeding season (Nolan 1978; Schleicher et al. 1996; Powell and Rangen 2000; Møller 2006; Walsh et al. 2010, 2011; Bailey et al. 2015). However, at least three studies documented within-individual changes in nest morphology as the breeding season progressed, with nest size becoming smaller with successive nesting attempts (Nolan 1978, Powell and Rangen 2000, Walsh et al. 2010, Deeming and Mainwaring

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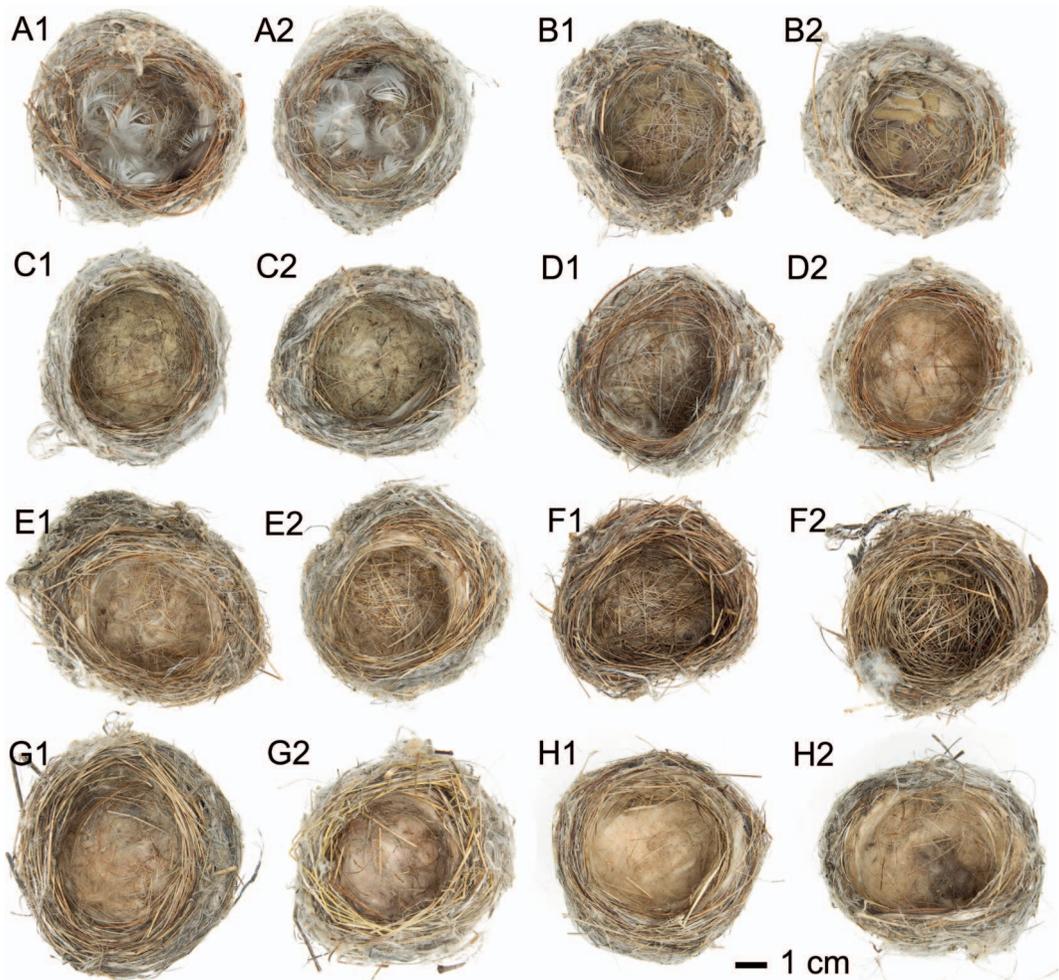


FIG. 1. Top and side view of first and second nests from the eight female Yellow Warblers; all nests were collected in 2008 from the Queen's University Biological Station in southeastern Ontario. Letters denote female identity and numbers indicate first (1) or second (2) nest.

2015). Smaller nest size may result from changes in environmental conditions, reduced time allocated to nest building, or reduced materials available for nest construction. Here, we build on previous studies of consistency in nest-building behavior by investigating three aspects of nest morphology — nest size, general appearance, and composition.

We investigated consistency of nest building behavior in a population of Yellow Warblers (*Setophaga petechia*) breeding in southeastern Ontario, Canada. In our study population, nests often vary greatly in appearance; some nests are constructed primarily with bark fibers and dry grasses while others contain fibrous plant material

and duck feathers (Fig. 1). To investigate if this population-level variation in nest composition and morphology resulted from individual consistency or individual plasticity in nest building behaviors, we examined two nests from eight different females. We estimated consistency in nest building behavior by: 1) examining nest morphology (principal components of nest width and depth), 2) using human observers to visually assess the similarity of nests, and 3) deconstructing nests to examine if individual females consistently used similar materials to build their nests. Our eight female Yellow Warblers were distributed among three breeding sites, all

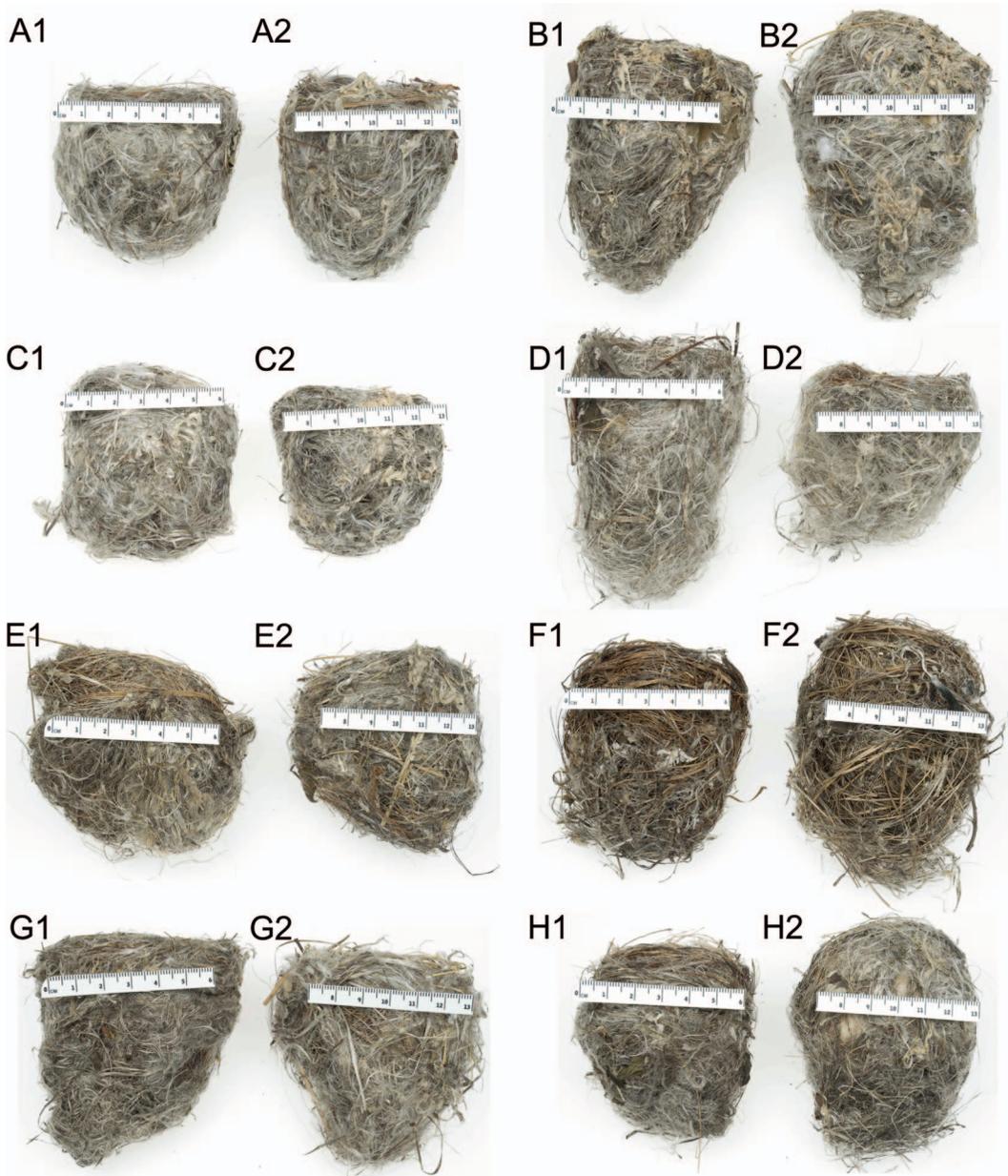


FIG. 1. Continued.

separated by >1 km, which allowed us to assess the effects of breeding location and individual female on nest similarity. If first and second nests constructed by the same female are more similar to each other compared to nests constructed by different females, both within and across locations, then this supports the hypothesis that

individual females build multiple nests with some consistency. If nests from different females in the same location appear more similar to each other than nests constructed by different females in different locations, then this supports the hypothesis that breeding location has an effect on nest appearance at fine spatial-scales (1–3 km).

METHODS

Study Species and Study Site.—Yellow Warblers are small (~10 g) migratory songbirds that construct cup-shaped nests. In general, only the female constructs the nest (Lowther et al. 1999). In parts of their breeding range, including our study site, female Yellow Warblers will build multiple nests if early nests are depredated or destroyed (Goossen and Sealy 1982, AMKP pers. obs.). Our study site is located in southeastern Ontario, Canada, at the Queen's University Biological Station (44° 34' N, 76° 20' W, elevation ~150 m a.s.l.). We studied Yellow Warblers in second-growth deciduous forest with mixed pine (*Pinus* spp.) species, scattered marshes, beaver ponds, and abandoned farmsteads with overgrown fields. Yellow Warblers breed at our site from early May until late July (Weir 1989), and often place their nests in short deciduous shrubs but also regularly place their nests several meters above ground in trees (Lowther et al. 1999, AMKP pers. obs.).

Nest Collection.—We found nests of Yellow Warblers by watching females that carried nesting material and made repeated trips to their nest site, or we searched suitable nesting habitat. Unfinished nests were checked every other day until the first egg was laid. Because we wanted to collect multiple nests from the same individual, we color banded all focal females prior to collecting their first nest and verified that we had banded the correct female by observing her return to the nest. Once the nest was completely constructed (i.e., the appearance of the first egg), we marked the nest location with a handheld GPS unit (Garmin, model 60Cx; Olathe, Kansas) and collected the nest by cutting the branches to which it was fastened, rather than removing the nest from the substrate, to minimize distorting the nest shape. We collected nests in this early stage to avoid distortion of the nest cup caused by growing nestlings (Calder 1973), with the exception of one nest (nest F2) that we collected at the end of the breeding season (unfortunately, we did not locate this nest sooner). Our collection of nests simulated a predation event and caused focal females to begin constructing a second nest. Similar to our criteria for determining when a female's first nest was complete, we waited until the first egg appeared prior to collecting a female's second nest.

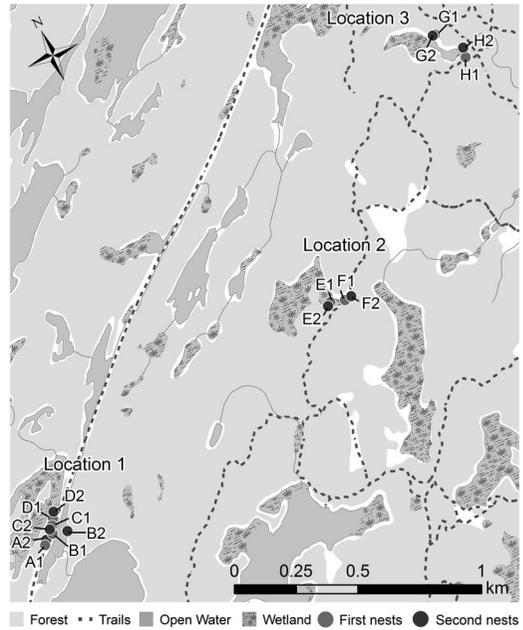


FIG. 2. Map showing the three breeding locations of Yellow Warblers and the placement of first and second nests of individual females. The average distance between a female's first and second nest was $28.8 \text{ m} \pm 16.1 \text{ SD}$; the average distance between nests of females within the same location was $92.4 \text{ m} \pm 33.0 \text{ SD}$, and the average distance between nests of females in different locations was $1857.9 \text{ m} \pm 308.5 \text{ SD}$. The distance between locations 1 and 2 was ~1.5 km; 1 and 3 was ~2.5 km; and 2 and 3 was ~1.1 km. All locations were separated by >1 km of mature deciduous forest, a habitat avoided by breeding Yellow Warblers, so it is unlikely that individuals traveled between locations to collect nesting material.

We collected first and second nests from eight female Yellow Warblers (A–H), making a total of 16 collected nests (Fig. 1). All nests were collected with appropriate permits from the Canadian Wildlife Service (CA 0199 and CA 0223), as part of a larger study of natural selection on nest morphologies (Rohwer and Law 2010, Rohwer et al. 2015). Our eight females were distributed among three locations (Fig. 2); two locations each had two females and one location had four females. Locations were separated from each other by at least 1 km of mature deciduous forest, a habitat that Yellow Warblers do not prefer; thus, it is unlikely that females traveled between locations to collect nesting material. All nests were collected between dates 17 May–23 June 2008, except for one nest (F2) that was collected on 27 July 2008.

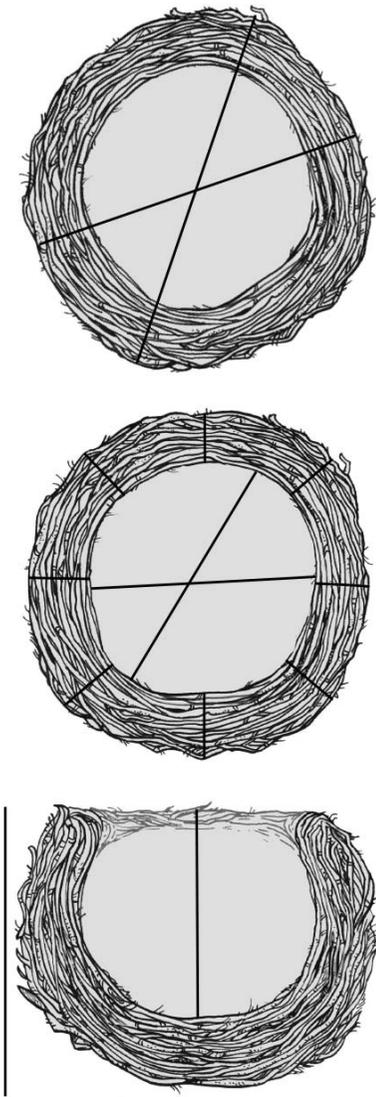


FIG. 3. Illustrations of the five measures of Yellow Warblers' nest morphology. Top two illustrations are a bird's eye view of a nest and show maximum and minimum external cup-diameter (top), maximum and minimum internal cup-diameter (middle), and eight evenly spaced measures of nest-wall thickness (middle). Bottom illustration is a cross section view of a nest and shows internal and external cup-depth.

Measuring Nest Morphology.—For all collected nests, we took five measures of nest morphology: 1) nest-wall thickness, 2) internal cup-depth, 3) external cup-depth, 4) internal cup-diameter, and 5) external cup-diameter (see Fig. 3). All measures were made in the laboratory with calipers, except

for measures of internal cup-depth, which were made using a ruler. Nest-wall thickness is the average of eight evenly spaced measures of the nest wall, which helps account for variability in nest-wall thickness (Kern and van Riper III 1984). Internal cup-depth is the distance from the deepest part of the interior nest cup (where eggs are placed) to the top of the nest rim. External cup-depth is the distance from the base of the exterior nest cup to the top of the nest rim. Internal cup-diameter is the average of the visually-assessed maximum and minimum distances across the interior of the nest cup. External cup-diameter is the average of the visually-assessed maximum and minimum distances across the exterior nest cup. All of these morphological aspects of nests were measured prior to nests being used in ranking exercises (see below) to ensure that the handling of nests did not distort their size or shape.

Ranking Similarity of Nests.—To assess if nests built by the same female Yellow Warbler appeared more similar to each other than to nests built by different females, we used human observers to rank nests based on overall similarity. While observers may not be able to identify all differences in nest appearance, humans are extremely effective at processing a large number of characters and using these characters to accurately discriminate between objects, and have been used in studies to rank color (Montgomerie 2006) and similarity in avian color patterns (Martin et al. 2010). Our methods to rank the similarity of nests using human observers were adapted from these methods (reviewed by Montgomerie 2006).

We presented 18 people with two exercises to rank similarity in nest morphologies. All observers were naïve to the hypotheses that we were testing and to our study design. For each ranking exercise, observers were asked to consider nest materials and nest morphology equally in their assessment of similarity.

Ranking Exercise 1.—Our first ranking exercise sought to examine: i) if nests made by the same female were more similar to each other than to nests made by different females, and ii) if location had any effect on the similarity of nest appearance. To examine the effects of individual female and location on the similarity of nests, we presented all human observers with 16 unique combinations of four nests. Each group of four nests contained (1) a focal nest, to which other nests were compared for

similarity (each of our 16 nests was used once as a focal nest, thus we had 16 trials), (2) the pair of the focal nest constructed by the same female within the same territory, (3) a randomly chosen nest constructed by a different female from the same location, and (4) a randomly chosen nest constructed by a different female from a different location. To control for possible effects of nest morphology changing between first or second nests, we compared the 16 focal nests with only nests of the other construction sequence. For example, if the focal nest was a first nest, then all other nests used for comparison were second nests. Nests for (3) and (4) were block-randomized such that each nest within each group (i.e., within location or among locations) was represented at equal frequencies within each trial. Observers were asked to rank the nests as 'most similar,' 'intermediate in similarity,' or 'least similar' relative to the focal nest, based on similarity of morphology and composition.

Ranking Exercise 2.—Our second ranking exercise sought to further examine similarity in nest morphology. For this exercise, the same observers were given all 16 nests at once and asked to divide nests into pairs based on similarity of morphology and composition. With this experimental design, we could not separate the effects of individual female and breeding location on the similarity of nest appearance. Nonetheless, this exercise provided an alternative method to test if nests made by the same female were more similar than nests made by different females regardless of location.

Measuring Nest Composition.—Once ranking exercises were finished, we deconstructed nests to examine similarity in nest composition as another measure of consistency in nest building behavior. For each nest, we separated the lining from the shell and separated all materials into specific categories based on physical appearance. Each type of material in the lining and shell was weighed using a scale accurate to 0.01 g (Acculab, model PP2060D; Göttingen, Germany). All plant and animal materials were identified to the best of our ability and by consulting Levine (1995).

Statistical Analyses

Nest Morphology.—We collapsed our five measures of nest morphology into two principal

components, PCwidth and PCdepth, using two separate principal components analyses. Three nest measures (internal cup-diameter, external cup-diameter, and nest-wall thickness) were correlated with each other, and thus we combined these three measures into one principal component named PCwidth. Data for external cup diameter were normalized using a log₁₀ transformation prior to running the principal components analysis. The two other nest measures (internal and external cup-depth) were also correlated with each other, and thus we combined these two measures into a different principal component named PCdepth. PCdepth fit a normal distribution, but PCwidth was transformed via log(PCwidth+3) to normalize the data prior to further analyses.

To examine individual consistency and breeding location effects on morphological measures of nests, we compared PCwidth and PCdepth (separately) between first and second nests (i) within females, (ii) among females in the same location (Fig. 2), and (iii) among females in different locations (Fig. 2). To do this, we took the absolute difference in PC scores between each female's first nest and: i) their second nest, ii) the mean PC score of the second nests of all different females in the same location, and iii) the mean PC score of the second nests of all different females in different locations. Thus, for each female, we calculated a difference (i) within female, (ii) among females in the same location, and (iii) among females in different locations, yielding $n = 8$ across the three treatments (equal to the number of females from which we collected nests).

We tested whether individual female or location had an effect on PCwidth and PCdepth (separately) using generalized linear models with quasi-Poisson distributions. For each analysis, the difference in nest principal component was our response variable and female and location (same or different) were our predictor variables. For our analysis of PCwidth, we did not alter any parameters of the model; however, for our analysis of PCdepth, we specified the link function as power(2) and error structure as mu² in our model to better fit the data (Crawley 2002).

Ranking Exercise 1.—To test the hypothesis that nests constructed by the same female were more similar in appearance than nests constructed by different females, we used a non-parametric Wilcoxon signed-rank test to compare the ob-

served proportion of correct nest rankings (where nests constructed by the same female were ranked as most similar) to the proportion expected by random chance. We used a non-parametric test because data for this analysis were not normally distributed and we could not transform them to fit a normal distribution. In this exercise, 18 observers compared a focal nest to three nests: (i) the focal nest's pair, (ii) a randomly chosen nest from the same location, and (iii) a randomly chosen nest from a different location. If individual females built similar first and second nests, then we expected observers to correctly rank nests constructed by the same female as most similar in more than 33.3% of comparisons ($n = 18$ trials).

To test for possible effects of location on nest similarity, we compared the observed proportion of nests built by different females in the same location that were ranked as more similar than nests from different locations to the proportion expected by random chance using a one-sample t -test. We normalized the data using an $(\arcsin(X))^{10}$ transformation. If location had an effect on nest similarity, then we expected observers to rank nests constructed by different females in the same location as more similar to the focal nests than to nests constructed by different females in different locations in $>50\%$ of comparisons ($n = 18$ trials).

Ranking Exercise 2.—This exercise examined the proportion of times nests constructed by the same female were correctly paired together when observers could choose from all 16 nests at once. If nests constructed by the same female were more similar to each other than nests constructed by different females, then we expected people to correctly pair first and second nests from the same female more frequently than expected by chance alone (6.78%). Data for this test were normally distributed, and thus we compared the proportion of correct pairings to the proportion expected by chance using a one-sample t -test ($n = 18$ trials).

Nest Composition.—We carefully dissected each nest and weighed the amount of each type of material used for both the nest lining and nest cup (Supplemental Material Appendix 1). We then compared nest composition within and among females and locations by taking the sum of the absolute difference in weights across each nest component in different nests, where values closer to zero represent nests constructed using similar

amounts and types of materials. To do this, we summed the absolute difference in weights for each nest component between each female's first nest and: (i) their second nest, (ii) the mean component weights of the second nests of all different females in the same location, and (iii) the mean component weights of the second nests of all different females in different locations. Thus, for each female, we calculated a difference (i) within female, (ii) among females at the same location, and (iii) among females at different locations, yielding $n = 8$ across the three treatments (equal to the number of females from which we collected nests). We tested if breeding location and individual female influenced the composition of nests using a generalized linear model with a quasi-Poisson distribution. Difference in composition between nests was our response variable, and female and location (same or different) were our predictor variables.

RESULTS

Nest Morphology.—Nest-wall thickness, and internal and external cup-diameter loaded positively with PCwidth, explaining 61.3% of the variation. Internal and external nest cup-depth loaded positively with PCdepth, explaining 79.8% of the variation. PCwidth was not significantly different between nests constructed by the same female when compared with nests constructed by different females in the same location ($F = 0.02$, $df = 1$ and 21 , $P = 0.90$; Fig. 4A), or between nests constructed by different females in the same locations compared with different locations ($F = 0.15$, $df = 1$ and 21 , $P = 0.71$, Fig. 4A), suggesting no effect of individual female or location on PCwidth. PCdepth was more similar among nests constructed by the same female compared to nests constructed by different females in the same location ($F = 5.67$, $df = 1$ and 21 , $P = 0.03$, Fig. 4B), suggesting an effect of individual female on PCdepth. PCdepth was not significantly different between nests constructed by different females in the same location compared with different locations ($F = 0.26$, $df = 1$ and 21 , $P = 0.61$, Fig. 4B), suggesting no effect of location on PCdepth.

Ranking Exercise 1.—Observers ranked the focal nest as most similar to the nest constructed by the same female in $81.3\% \pm 7.1$ SE of the comparisons ($n = 18$ trials), significantly more often than would be expected by chance (33.3%)

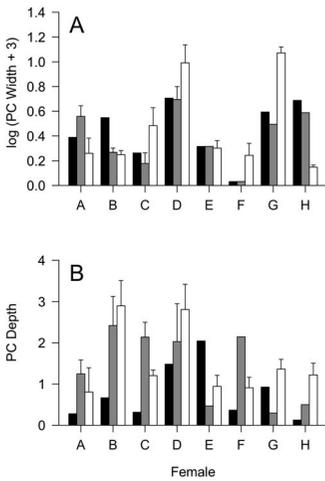


FIG. 4. Differences in nest morphology for (A) PCwidth and (B) PCdepth between first and second nests constructed by the same female and by different females in the same and different locations. Bars show the absolute values of PC scores subtracted from first and second nests within females (black bars), among females within the same location (gray bars) and among females in different locations (white bars). Nests that are more similar to each other in morphology have scores closer to zero. First and second nests constructed by the same female were more similar to each other in depth but not width compared to nests constructed by other females in the same location and by other females in different locations. Error bars are standard errors, and are shown for all comparisons where we had nests from at least three females.

(Wilcoxon signed-rank test, $Z = 3.30$, $df = 15$, $P = 0.001$; Fig. 5). This result supports the hypothesis that nests built by the same female are more similar in appearance to one another than to nests constructed by different females. Observers also ranked nests that were from the same location, but built by a different female, as more similar to each other than to nests from a different location in $63.9\% \pm 7.6$ SE of the comparisons ($n = 18$ trials), significantly more often than would be expected by chance (50.0%) (one-sample t -test, $t = 3.44$, $df = 15$, $P = 0.004$; Fig. 5). This result supports the hypothesis that nests built in close proximity (<200 m apart) are more similar in appearance than nests built in different locations (1–3 km apart).

Ranking Exercise 2.—When given all 16 nests at once, observers correctly paired nests constructed by the same female in $55.6\% \pm 11.2$ SE of the comparisons ($n = 18$ trials), significantly more often than would be expected by chance (6.8%) (one-sample t -test, $t = 9.97$, $df = 17$, $P < 0.001$;

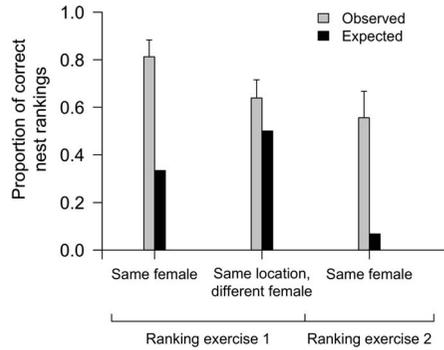


FIG. 5. Results of human nest ranking exercises, where observers ranked nests based on overall similarity of morphology and composition. Plots show the observed (gray bars) versus expected (black bars) proportion of correct nest rankings from 18 trials; error bars are standard errors. Ranking exercise 1 tested the proportion of trials where observers ranked nests constructed by the same female as more similar compared to nests constructed by different females, and the proportion of trials where observers ranked the focal nest as more similar to a nest constructed by a different female within the same location compared to a nest from a different location. Observers were given: 1) the focal nest pair constructed by the same female, 2) a nest constructed by a different female within the same location, and 3) a nest constructed by a different female from a different location. Ranking exercise 2 tested the proportion of trials where observers correctly paired first and second nests constructed by the same female when given all 16 nests at once.

Fig. 5). This result further supports the hypothesis that nests constructed by the same female are more similar in appearance to each other than to nests constructed by different females.

Nest Composition.—Nest composition was more similar among nests constructed by the same female compared with nests constructed by different females in the same location ($F = 28.4$, $df = 1$ and 21, $P < 0.001$; Fig. 6), suggesting a strong effect of individual female on nest composition. Nest composition was not significantly different between nests constructed by different females in the same location compared with different locations ($F = 2.2$, $df = 1$ and 21, $P = 0.16$; Fig. 6), suggesting little effect of location on nest composition.

DISCUSSION

Animal behaviors show high repeatability when within-individual variation is low relative to

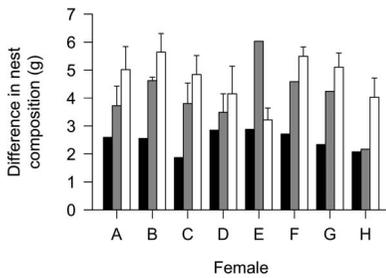


FIG. 6. Differences in nest composition between first and second nests within females (black bars), among females within the same location (gray bars) and among females in different locations (white bars). First and second nests constructed by the same female have the least differences in composition (values are closest to zero), showing that nests constructed by the same female are more similar to each other than nests constructed by different females. Error bars are standard errors, and are shown for all comparisons where we had nests from at least three females.

among-individual variation in a population (Bell et al. 2009). In our study population of Yellow Warblers, within-individual variation in nest construction was low relative to among-individual variation — first and second nests constructed by the same female appeared similar. We provide four lines of evidence to support this finding: 1) individual females constructed their first and second nests with similar morphological measures of nest depth (Fig. 4B), 2) human observers naïve to the goals of our study ranked nests constructed by the same female as most similar (Fig. 5), 3) the same observers were able to correctly pair nests constructed by the same female (Fig. 5), and 4) individual females constructed their first and second nests using similar amounts and types of materials, and these quantities and types of materials were different from those used by other females (Figs. 1 and 6). Together, these findings provide strong support that individual female Yellow Warblers construct multiple nests consistently within a breeding season.

We also provide evidence suggesting that different female Yellow Warblers build more similar nests within a location as compared to across locations 1–3 km apart (based on the similarity of nest appearance as ranked by observers, Fig. 5). This result suggests either that (i) local environments provide similar nesting components or opportunities for constructing similar nests, (ii) local environments favor similar

nest morphologies, and females respond adaptively, or (iii) local environments attract females that build similar nests. We did not find significant location effects on nest morphologies (Fig. 4) or composition (Fig. 6); however, 7 of the 8 females constructed nests of more similar composition to other females at the same location as compared with females at different locations (Fig. 6), consistent with the human ranking results.

Female Yellow Warblers may show individual consistency in nest building behaviors for several reasons:

First, different females may be different ages, thus causing differences in nest morphology and composition across females. Age is known to influence nest morphology in Village Weavers (*Ploceus cucullatus*; Collias and Collias 1964), where more experienced builders construct tidier nests. In our study, however, all marked females were scored as after second year (based on feather wear and tail; Pyle 1997, Hobson et al. 2000), and thus each female presumably had prior nest building experience from previous breeding seasons, given that females breed in their first year (Lowther et al. 1999).

Second, different females may have different nest placement preferences, causing variation in external morphology. Nests placed on top of limbs or between shallow forks in branches likely have shorter external cup-depths than nests constructed in deeply forked branches. All but one female in this study consistently placed their nest in either a shallow position (i.e., on top of a limb or between shallowly forked branches) or a deep location (i.e., between deeply forked branches), which likely resulted in similar external cup-depth dimensions within females (Fig. 1, Supplemental Material Appendix 2).

Third, nest morphology and composition could vary within females because of changing environmental constraints and opportunities over time. Previous studies have noted lighter nest masses (Nolan 1978) and thinner nest walls (Franklin 1995, Powell and Rangen 2000) with the progression of the breeding season. We found few changes, however, in Yellow Warbler nest morphology between a female's first and second nests and suspect that the time period between collecting first and second nests was short enough that environmental conditions changed too little to

warrant different nest morphologies (Bell et al. 2009).

Finally, consistency in nest building behavior could be confounded with material availability and nest placement options on individual breeding territories. Female Yellow Warblers construct nests within their mate's territory (Lowther et al. 1999), causing multiple nests constructed by the same female to be clustered in space (Fig. 2). If the availability of preferred nesting materials and nest sites varies among breeding territories (and females do not travel outside of territory boundaries to gather material), then multiple nests of a single female may appear more similar to each other, relative to nests constructed by other females. While this hypothesis awaits formal testing, our observations that females breeding in close proximity used different amounts of widely-available materials (e.g., cattail pappus, dry grasses), suggest that individual females choose some materials over others.

Most studies of bird nests focus on nest dimensions when measuring consistency in nest construction (Schleicher et al. 1996, Powell and Rangen 2000, Møller 2006, Walsh et al. 2010, but see Bailey et al. 2015). From our observations and tests, morphological measures appear to provide a conservative estimate of consistency in nest building behavior in Yellow Warblers, and may overlook consistency in nest composition. Of the three methods we used to assess consistency in nest construction, nest ranking exercises with human observers and deconstructing nests to examine composition provided the strongest evidence for consistency in nest building behavior. Nest ranking exercises, in particular, may provide one of the most useful measures of consistency because observers can consider several aspects of nest morphology and composition when assessing similarity of nests (Montgomerie 2006).

While our study examined first and second nests of eight female Yellow Warblers within a single breeding season, we lack data on the consistency of nest morphologies for subsequent nests constructed by these females later in the same and different breeding seasons. One of our banded females (female A) included waterfowl feathers in all four of her nests (located within the same territory). During the breeding season of 2009, we found the first nest of another banded female (female C), which was constructed ~20 m from her

nests in 2008 and appeared very similar in morphology and composition. These observations, and observations by Nolan (1978) of Prairie Warblers (*Setophaga discolor*) and by Møller (2006) of Barn Swallows (*Hirundo rustica*), suggest that the consistency of female nest construction may extend across years.

Comparing our measures of nest morphology and composition to measures presented in Crossman et al. (2011) for Yellow Warblers breeding at the same site but 1 year later, suggests that nest morphologies of this population are similar across years (Crossman et al. 2011; Supplemental Material Appendix 3). For example, the range of nest measures within this study (mean \pm SD) overlap the range of nest measures (mean \pm SD) in Crossman et al. (2011) for all nest measurements, and overlap the mean values in Crossman et al. (2011) for all but one nest measure (internal cup-depth).

A number of studies have assessed consistency in nest building behavior in birds (Nolan 1978; Schleicher et al. 1996; Powell and Rangen 2000; Møller 2006; Walsh et al. 2010, 2011; Bailey et al. 2015), fish (Rushbrook et al. 2008), turtles (Pfaller et al. 2009, and citations within), and rodents (Weber and Hoekstra 2009). Nearly all these studies find evidence that individuals build multiple nests consistently, and this general agreement in the literature is consistent with the hypothesis that individual variation in nest-building behavior is, to some extent, heritable. Indeed, studies using genetic crosses between oldfield (*Peromyscus polionotus*) and deer mice (*P. maniculatus*; Weber et al. 2013), artificial selection experiments in house mice (*Mus musculus*; Lynch 1980), and cross fostering experiments in Barn Swallows (Møller 2006), all suggest that variation in nest building behavior has a heritable component.

Overall, we provide evidence that individual female Yellow Warblers build first and second nests consistently within a single breeding season and that breeding location affects nest appearance. Females appear to select some materials and not others, and the apparent choice of materials may be specific to individuals, as several females breeding in close proximity used different materials in their nests. The consistency in nest building behaviors that we observed in Yellow Warblers may extend to other species, helping to explain

variation in nest morphology and composition both within and across species (Crossman et al. 2011, Deeming 2013, Deeming and Mainwaring 2015, Biddle et al. 2016). Many birds show geographic variation in nest morphologies (Crossman et al. 2011; Mainwaring et al. 2012, 2014), and this variation often co-varies with environmental variables, suggesting that geographic variation in nest building behavior is adaptive. Unfortunately, the basis of variable nest building behaviors in birds (e.g., heritable or plastic) remains poorly known (Møller 2006), limiting our ability to predict how quickly birds might respond to changing conditions on the breeding range. The consistency in nest building behavior that we observed among female Yellow Warblers, a species with one of the widest breeding distributions among North American wood warblers (Family: Parulidae), suggests that nest-building behavior may respond to divergent selection pressures operating in different breeding sites, allowing Yellow Warblers to optimize their nest morphologies to local breeding conditions (see Rohwer et al. 2015).

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LITERATURE CITED

- BAILEY, I. E., A. BACKES, P. T. WALSH, K. V. MORGAN, S. L. MEDDLE, AND S. D. HEALY. 2015. Image analysis of

- weaverbird nests reveals signature weave textures. *Royal Society Open Science* 2:150074.
- BELL, A. M., S. J. HANKISON, AND K. L. LASKOWSKI. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour* 77:771–783.
- BIDDLE, L. E., A. M. GOODMAN, AND D. C. DEEMING. 2016. Geographical effects on the mass and dimensions of finch (Fringillidae, Passeriformes) and thrush (Turdidae, Passeriformes) nests. *Avian Biology Research* 9:13–21.
- CALDER, W. A. 1973. Microhabitat selection during nesting of hummingbirds in the Rocky Mountains. *Ecology* 54:127–134.
- COLLIAS, E. C. AND N. E. COLLIAS. 1964. The development of nest-building behavior in a weaverbird. *Auk* 81:42–52.
- CRAWLEY, M. J. 2002. *Statistical computing: An introduction to data analysis using S-Plus*. John Wiley and Sons, Chichester, United Kingdom.
- CROSSMAN, C., V. G. ROHWER, AND P. R. MARTIN. 2011. Variation in the structure of bird nests between northern Manitoba and southeastern Ontario. *PLoS ONE* 6:e19086.
- DAWKINS, R. 1982. *The extended phenotype*. Oxford University Press, Oxford, United Kingdom.
- DEEMING, D. C. 2013. Effects of female body size and phylogeny on avian nest dimensions. *Avian Biology Research* 6:1–11.
- DEEMING, D. C. AND M. C. MAINWARING. 2015. Functional properties of nests. In *Nest Eggs and Incubation* (D. C. Deeming and S. J. Reynolds, Editors). Oxford University Press, Oxford, United Kingdom.
- FALCONER, D. S. AND T. F. C. MACKAY. 1996. *Introduction to quantitative genetics*. Fourth Edition. Addison Wesley Longman Limited, Harlow, United Kingdom.
- FRANKLIN, D. C. 1995. Helmeted Honeyeaters build bulkier nests in cold weather. *Auk* 112:247–248.
- GOOSSEN, J. P. AND S. G. SEALY. 1982. Production of young in a dense nesting population of Yellow Warblers, *Dendroica petechia*, in Manitoba. *Canadian Field-Naturalist* 96:189–199.
- HOBSON, K. A., S. VAN WILGENBURG, H. L. GIBBS, R. J. G. DAWSON, AND H. DER HANN. 2000. Sexing hatching-year Yellow Warblers using plumage characteristics. *North American Bird Bander* 25:8–12.
- KERN, M. D. AND C. VAN RIPER III. 1984. Altitudinal variations in nests of the Hawaiian Honeycreeper *Hemignathus virens virens*. *Condor* 86:443–454.
- LEVINE, C. 1995. *A guide to wildflowers in winter: herbaceous plants of northeastern North America*. Yale University Press, New Haven, Connecticut, USA.
- LOWTHER, P. E., C. CELADA, N. K. KLEIN, C. C. RIMMER, AND D. A. SPECTOR. 1999. *Yellow Warbler (Setophaga petechia)*. The birds of North America. Number 454.
- LYNCH, C. B. 1980. Response to divergent selection for nesting behavior in *Mus musculus*. *Genetics* 96:757–765.
- MAINWARING, M. C., I. R. HARTLEY, S. BEARHOP, K. BRULEZ, C. R. DU FEU, G. MURPHY, K. E. PLUMMER, S. L. WEBBER, S. J. REYNOLDS, AND D. C. DEEMING. 2012. Latitudinal variation in Blue and Great tit nest

- characteristics indicates environmental adjustment. *Journal of Biogeography* 39:1669–1677.
- MAINWARING, M. C., D. C. DEEMING, C. I. JONES, AND I. R. HARTLEY. 2014. Adaptive latitudinal variation in Common Blackbird *Turdus merula* nest characteristics. *Ecology and Evolution* 4:851–861.
- MARTIN, P. R., R. MONTGOMERIE, AND S. C. LOUGHEED. 2010. Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution* 64:336–347.
- MØLLER, A. P. 2006. Rapid change in nest size of a bird related to change in a secondary sexual character. *Behavioral Ecology* 17:108–116.
- MONTGOMERIE, R. 2006. Analyzing colors in *Bird Coloration* (G. E. Hill and K. J. McGraw, Editors). Volume 1. Harvard University Press, Cambridge, Massachusetts, USA.
- NOLAN, V. J. 1978. The ecology and behaviour of the Prairie Warbler *Dendroica discolor*. Ornithological Monographs 26. American Ornithologists' Union, Washington, D.C., USA.
- PFALLER, J. B., C. J. LIMPUS, AND K. A. BJORNALD. 2009. Nest-site selection in individual loggerhead turtles and consequences for doomed-egg relocation. *Conservation Biology* 23:72–80.
- POWELL, L. A. AND K. L. RANGEN. 2000. Variation in Wood Thrush nest dimensions and construction. *North American Bird Bander* 25:89–96.
- PYLE, P. 1997. Identification guide to North American birds, Part I: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.
- ROHWER, V. G. AND J. S. Y. LAW. 2010. Geographic variation in nests of Yellow Warblers breeding in Churchill, Manitoba, and Elgin, Ontario. *Condor* 112:596–604.
- ROHWER, V. G., F. BONIER, AND P. R. MARTIN. 2015. Conflict between biotic and climatic selective pressures acting on an extended phenotype in a subarctic, but not temperate, environment. *Proceedings of the Royal Society of London - B* 282:2015.1585.
- RUSHBROOK, B. J., N. J. DINGEMANSE, AND I. BARBER. 2008. Repeatability in nest construction by male three-spined sticklebacks. *Animal Behaviour* 75:547–553.
- SCHLEICHER, B., H. HOI, AND F. VALERA. 1996. Seasonal change in female mate choice criteria in Penduline Tits (*Remiz pendulinus*). *Ardeola* 43:19–29.
- WALSH, P. T., M. HANSELL, W. D. BORELLO, AND S. D. HEALY. 2010. Repeatability of nest morphology in African weaver birds. *Biology Letters* 6:149–151.
- WALSH, P. T., M. HANSELL, W. D. BORELLO, AND S. D. HEALY. 2011. Individuality in nest building: Do Southern Masked Weaver (*Ploceus velatus*) males vary in their nest-building behaviour? *Behavioural Processes* 88:1–6.
- WEBER, J. N. AND H. E. HOEKSTRA. 2009. The evolution of burrowing behaviour in deer mice (genus *Peromyscus*). *Animal Behaviour* 77:603–609.
- WEBER, J. N., B. K. PETERSON, AND H. E. HOEKSTRA. 2013. Discrete genetic modules are responsible for complex burrow evolution in *Peromyscus* mice. *Nature* 493:402–405.
- WEIR, R. D. 1989. *Birds of the Kingston Region*. Quarry Press, Kingston, Ontario, Canada.